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Results of a survey workshop on freshwater and limno-terrestrial meiofauna of the Lake District, UK

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SUMMARY

The microscopic meiofauna dwelling freshwater and limnoterrestrial habitats remain poorly documented, despite representing an important, yet unseen, part of those ecosystems. Here, we report the results of a faunistic survey workshop intended to improve our knowledge of meiofauna diversity and distribution in a protected area: the Lake District National Park, UK. The survey workshop provided 299 occurrence records of 209 distinct morphological taxa of meiofauna belonging to 46 families, 24 orders and 11 phyla. These records are made publicly available through a shared online dataset. The highest number of taxa belonged to Arthropoda (58 taxa; i.e. 28% of records), followed by Rotifera (33; 16%), heterotrophic unicellular eukaryotes (30; 14%), Nematoda (26; 12%), Annelida (20; 10%), Tardigrada (19; 9%), Gastrotricha (12; 6%), and Platyhelminthes (11; 5%). Moss samples returned the highest number of taxa occurrences (136), followed by periphyton (54), epipsammon (34), interstitial (25), plankton (17), peat bogs (16), forest litter (7), soil (6), epizoic lifestyle on crustaceans (2), and lichen (2). By documenting a wide range of habitats and taxonomic groups, this survey workshop contributes to filling knowledge gaps on the distribution of meiofaunal taxa in nearly pristine freshwater and temperate rainforest ecosystems. The second role of the survey workshop was offering a 15-day field and laboratory training programme for a group of early career researchers, providing hands-on experience in morphotaxonomic identification, molecular barcoding techniques and finally in analysing and communicating the results in the form of the current publication.

INTRODUCTION

Meiofauna are microscopic aquatic invertebrates and heterotrophic unicellular eukaryotes that have been mostly defined based on a size-criterion (although strict size boundaries vary across the literature). Meiofauna are all those organisms that typically pass through a 500 μm (1,000 μm)-mesh, but are retained on a 44 μm (63 μm)-mesh (Giere 2009). In marine systems, meiofaunal organisms are benthic, living on various substrates, and populate interstitial habitats (and thus they are often coined meiobenthos). However in freshwater and other limno-terrestrial environments, this definition becomes blurry, and many meiofaunal groups typically include organisms that are relatively good swimmers, or which may cling onto macrophytes, algal biofilms, plant litter and logs (e.g. Palmer and Gust 1985, Ptatscheck et al. 2018, Peralta-Maraver et al. 2023, Surmacz et al.

2025a, Collins et al. 2026). Furthermore, freshwater and limno-terrestrial meiofaunal organisms have a fairly good capacity for long-distance dispersal through various types of dormant stages that can travel phoretically using insects, fishes, or birds, or are simply blown by the wind. True widespread or cosmopolitan distributions of those microscopic animals, however, are increasingly questioned (e.g., Fontaneto 2011, Morek et al. 2021, Zhu et al. 2026).

Among the meiofaunal groups well represented in lakes, streams and limno-terrestrial micro-habitats, are the nematodes, rotifers, gastrotrichs, tardigrades, ostracodes, copepods, cladocerans, microturbellarians, oligochaetes, water mites, early instars of insect larvae, as well as relatively large unicellular eukaryotes such as testate amoebae and ciliates. All these organisms occur ubiquitously in sediments, biofilms, and on submerged vegetation, as well as on a variety of limno-terrestrial habitats such as leaf litter, mosses, lichens and other tree-related microhabitats. In those habitats, the meiofauna play important ecological roles, e.g. by mediating energy and nutrient transfer between microbes and macroscopic organisms like insects and fish (Schmid-Araya et al. 2016, Majdi et al. 2025a). Despite their presumed ecological importance, meiofaunal communities remain among the least studied components of terrestrial and inland water biodiversity, presumably due to their immense taxonomic diversity and the specialized meticulous training required for their accurate identification (Majdi et al. 2020a).

Consequently, most ecological or applied studies usually focus on a couple of taxonomic groups representative of the meiofauna (e.g. nematodes, cladocerans, or copepods), or consider over-simplified meiofaunal communities usually identified at coarse taxonomic levels such as family or order, or just lumped into vaguely defined functional groups (Majdi et al. 2020b, Surmacz et al. 2026). Although DNA-based approaches now offer powerful tools for rapid and more subtle identification of genetic (and organismic) diversity, the success of molecular barcoding approaches mainly depends on the availability of robust reference libraries based on morphologically verified specimens (Schenk and Fontaneto 2020, Macher et al. 2024). With funding opportunities for morphotaxonomy shrinking, and expert taxonomists in demographic decline worldwide, the ability to generate such curated reference material is becoming increasingly challenging, especially for meiofaunal organisms (Engel et al. 2021, Martínez et al. 2025).

One possible way of addressing this gap is to train new generations of morpho-taxonomists, equipping them with a broad range of practical skills ranging from collecting environmental data and samples in the field to extracting, preparing, observing, identifying and measuring key morphological features of meiofaunal organisms prior to any molecular delineation work. Hands-on experience is irreplaceable for developing diagnostic expertise and ensuring the continuity of taxonomic knowledge in the rapidly changing technical landscape of environmental sciences. These “fresh meiobenthologists” will play a pivotal role in revitalizing meiofaunal research, using both morphological and molecular approaches to help answer important scientific and societal questions like *How meiofauna diversity responds to climate change and anthropogenic impacts?* and therefore *Shall we use meiofaunal communities as a promising integrative bio-indicator of ecosystem health?* (Martínez et al. 2025).

Since 2013, the establishment of regular “Meioschool” workshops to train early career researchers to taxonomy and ecology has been an effective way to transfer knowledge across generations of marine meiobenthologists, and to promote interdisciplinarity and the emergence of skills, projects and collaborations (e.g. Zeppilli and Sarrazin 2015). So far there has been no such equivalent training on meiofauna taxonomy in freshwater or forest environments, or if existing they generally focus on a single taxonomical group.

The present study seeks to report the results from a 15 day freshwater meiofauna survey workshop held in August and September 2025 in the English Lake District (UK), a region of exceptional ecological and biogeographical interest (Ratcliffe 2002). The Lake District includes the first National Park designated in Britain, created in 1951. Notably, this area also hosts Priest Pot pond, where one of the first comprehensive all-taxon biodiversity inventories (ATBI) was carried out for microbial eukaryotes (e.g. Fenchel and Finlay 2004, Finlay and Maberly 2000, Esteban et al. 2012). ATBIs are increasingly considered in nature conservation as a useful way to promote a local understanding of biodiversity, but their inclusiveness also brings a valuable temporal milestone for implementing efficient habitat protection and management

practices (e.g. Dangerfield and Pik 1999, Esteban and Finlay 2010, Nichols and Langdon 2007, Granjou et al. 2014)

Building upon this legacy, our initiative aims to broaden meiofaunal inventories across a diversity of aquatic and limno-terrestrial habitats in the Lake District. By combining field-based sampling, morphological identification, and data standardization, we seek to foster the acquisition of taxonomic skills, promote experience sharing between students and expert taxonomists, and produce a georeferenced dataset that establishes a foundational ATBI for freshwater and limno-terrestrial meiofauna of the Lake District, to be shared online in the Global Biodiversity Information Facility, GBIF (https://www.gbif.org/).

MATERIALS AND METHODS

Study sites

Samples were collected in the field between August 27 and September 10, 2025 and using a variety of methods (see examples in Fig. 1, and taxon-specific methodologies listed below). In total, we collected 60 different samples from 27 discrete sites, representing a wide range of ecosystems, substrates, and micro-habitat types found in the Lake District area (Fig. 2, Table 1).

After collection, samples were stored in plastic containers or ziplock bags and immediately brought to the laboratory for direct observation, or extracted within 24 to 48h whenever possible. Due to the comprehensive sampling, and time limitations, some samples of more persevering taxa (e.g., microscopic arthropods, nematodes), were kept in the dark at 5°C, for a maximum of 2 weeks, for later handling. Sample weights were between ca. 15 to 1000 g for wet substrates and between ca. 15 to 1000 mL volume for dryer material. Taxonomic identifications were performed on living individuals, to species-level whenever possible, or to the nearest reliable rank (genus or subgenus) by the expert taxonomists involved in the survey workshop. In a few cases a final determination to species level was not possible, and we had to apply the open nomenclature according to Bengtson (1988). We used the 'cf.' between genus and species name in order to hint to an insecure determination due to an inappropriate/damaged specimen (e.g., in the case of the tardigrade *Echiniscus* cf. *virginicus*), and the 'aff.' in order to hint to a specimen with characters deviating from the original species description (e.g., in the case of the gastrotrich *Chaetonotus (Zonochaeta)* aff. *voigti*), possibly indicating an undescribed new species.

Taxon-specific methods for sample extractions and microscopic identifications

For **Gastrotricha**, waterbed substrata like leaf litter, macrophytes and finer organic debris (e.g., of the littoral zone of lakes) were suspended in a 10 litre bucket with ambient water in the field and initially pre-filtered through a coarse sieve (i.e., a customary colander) in order to get rid of large particles and macrofauna. In a second step, this filtrate was sieved through a fine gauze (40 µm mesh size) and the captured meiofauna and trapped detritus particles were rinsed into the sampling jar using a squirt bottle filled with filtered ambient water. Dense patches of submerged peat mosses (*Sphagnum* spp.) and other aquatic vascular plants (e.g., *Callitriche* sp., *Elodea canadensis* Michx.) were either sampled from lake littoral and peatbog ponds with a plankton net (65 µm mesh size) mounted to a telescopic rod, or hand-picked and directly placed into zip-log plastic bags. Qualitative sampling procedures mostly follow the methods described in Balsamo et al. (2014) or Todaro et al. (2019). Back in the laboratory, subsamples of the plankton net filtrates, or remnant water from the bags of the hand-picked plant material were poured into petri dishes and screened under stereo microscopes using different illumination modes (bright field/dark field/oblique illumination) and magnifications. Single gastrotrich specimens were picked from the petri dish using either a mouth pipette (made from drawn-out glass Pasteur pipettes mounted to a silicon hose with a mouthpiece) or a 10 µL micropipette mounted on a mechanical pipette holder. For microscopic investigation and documentation, single specimens were placed on glass slides with a drop of ambient water and covered with a cover slip. Some specimens were anaesthetised prior in an embryo dish by adding a 1% solution (w/v) of MgCl2 in distilled water (see, e.g., Balsamo et al. 2014, 2019); alternatively, the non-anaesthetised specimen was gently clamped between slide and coverslip by removing excess water carefully from the edge of the coverslip using a snippet of filter paper or lab cleaning tissue. Observation and live digital recording of specimens was carried out with an Olympus BX53 microscope equipped with high-resolution objectives, differential interference contrast and a magnification changer

tube. A Euromex HD-Ultra digital microscope camera VC.3036-HDS was adapted to the camera port of the microscope using a 0.35x intermediate lens, and most specimens were recorded with a series of still and video images. Taxonomic identification was based on current monographs and taxonomic revisions (Balsamo 1983, Schwank 1990, Kisielewski 1991, Balsamo et al. 2014, 2019), original species descriptions, and with the aid of the recent taxonomy provided at the Gastrotricha World Portal (Todaro and Tongiorgi 2025). For maximum reliable morphospecies determinations, every published character variability and morphometric range reported for each species was considered.

For **Platyhelminthes**, ca. 1 L of soil, aquatic sediments, leaf litter, moss, and woody detritus samples were processed in the laboratory or stored at 5°C in the dark. For some waterlogged samples, we used an oxygen-depletion method (overnight stagnation in a wide-mouthed glass jar) to drive larger microturbellaria to the surface, where they could be handpicked and concentrated. For most samples however, microturbellarians were extracted following a modified version of the Whitehead and Hemming (1965) tray method (which also proved efficient to extract most other interstitial meiofaunal taxa). Briefly, the sample was evenly spread onto a fine gauze tissue set onto a ~2 mm polypropylene sieve stacked within a seed sprouting tray filled with water to cover the surface of the substrate, and let it sit for up to 24 h (Fig. 1L). After that, the water in the tray, containing minimal substrate, was poured on 63 µm meshes, and a squirt bottle was used to

Table 1. Name, description of samples, WGS84 GPS coordinates (in decimal degrees) and number of taxa identified from each sampling site.

Site (Full name)	Short name (Fig. 2)	Habitats sampled	Latitude (N)	Longitude (E)	Number of identified taxa
Ambleside campus 1	Ambleside	Pond, Lichen, Moss	54.432	-2.963	9
Ambleside campus 2	Ambleside	Moss	54.437	-2.964	
Borrowdale rainforest	Borrowdale	Moss, Leaf litter	54.322	-3.093	30
Derwent River	Derwent	Streambed	54.539	-3.159	4
Elterwater river kick	Elterwater	Streambed	54.422	-3.016	33
Elterwater river epilithic and hyporheic	Elterwater	Streambed, Hyporheic	54.430	-3.024	
Ennerdale water	Ennerdale	Water, Epiphyton, Epilithon, Epipsammon	54.523	-3.373	19
Marshy areas at Ennerdale water outlet	Ennerdale	Water, Epiphyton	54.523	-3.407	17
Foulshaw moss	Foulshaw	Moss, Epiphyton, Peatbog	54.245	-2.834	40
Grisedale Tarn	Grisedale	Water	54.337	-3.017	3
High peak	High peak	Peatbog	54.338	-3.035	2
Diego's hike	Hike	Moss	54.483	-2.985	6
Johnny's wood	Johnny	Soil, Leaf litter	54.519	-3.156	15
River Liza	Liza	Streambed, Hyporheic	54.514	-3.310	4
Loughrigg Tarn	Loughrigg	Periphyton, Leaf litter	54.431	-3.014	31
Low style wood	Low style	Leaf litter	54.303	-3.102	9
Meathop moss	Meathop	Moss, Peatbog	54.230	-2.854	1
Moss Dub	Moss dub	Periphyton	54.512	-3.320	12
Pool Back	Pool back	Streambed	54.280	-3.036	1
River Rothay at junction with Stock Ghyll	Rothay	Streambed	54.432	-2.971	4
River Rothay	Rothay	Moss, Leaf litter	54.443	-2.979	3
Scandale valley	Scandale	Moss	54.465	-2.958	7
Scandale Tarn	Scandale	Moss	54.480	-2.950	6
Seatoller's Wood	Seatoller	Moss, Leaf litter	54.508	-3.173	8
Troutbeck	Troutbeck	Streambed	54.408	-2.914	7
Whitbarrow reserve	Whitbarrow	Moss, Lichen, Streambed, Hyporheic	54.282	-2.872	18
Lake Windermere	Windermere	Epiphyton	54.380	-2.923	10

Figure 1. Illustration of field sites, collection and laboratory extraction methods. **A**, Brooklet and moss carpets in Seatoller wood. **B**, Peat bog pond in Foulshaw Moss nature reserve. **C**, Epiphytic and epilithic habitats near the shore of Ennerdale water. **D-E**, Moss carpets and plant litter accumulations in steep ravines in Whitbarrow forest and Seatoller wood. **F**, Marshy area filled with macrophytes near Ennerdale water. **G**, The "spate river" Rothay near King's how. **H**, Hammering a Bou-Rouch pipe into the streambed to pump-out hyporheic meiofauna. **I**, "Meiofauna trawling" with plankton nets and collecting the meiofauna inhabiting epipsammic, epiphytic and epilithic biofilms. **J**, Extracting moss-, lichen- and soil-dwelling micro-arthropods, annelids and nematodes using modified Berlese funnel traps. **K**, Kick sampling in the Rothay. **L**, Foreground: extracting moss-, soil- and litter-dwelling meiofauna in the lab using Whitehead and Hemming trays, background: fostering active migration of microflatworms, arthropods and rotifers to the surface using oxygen deprivation gradients in cylindrical jars. **M**, From counting and coarse identification under the stereomicroscope to mounting specimens on slides and High Definition (HD) filming under a Differential Interference Contrast (DIC) microscope for species-level diagnosis. **N**, Using molecular approaches to build reference DNA libraries by amplifying 18S, 28S and COI sequences from individual identified specimens.

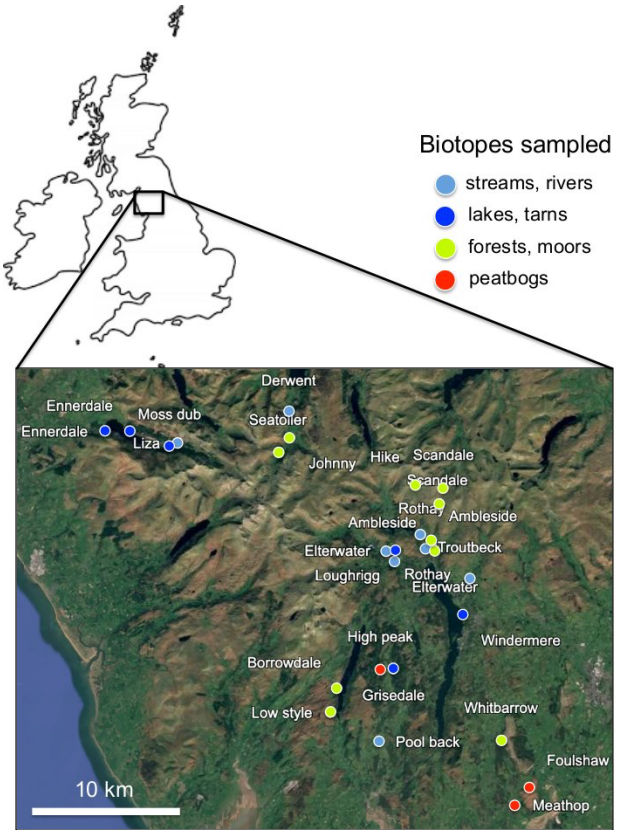

Figure 2. Localisation and type of biotopes sampled within the Lake District region.

concentrate the contents into petri dishes, which were then inspected for flatworms and other meiofauna under a binocular. Specimens were further directly identified or wet-mounted on slides, semi-squeezing animals under a cover slip using tissue paper to wick away excess water. These were then microscopically observed in a Nikon Ni-U microscope equipped with DIC. Photos and/or videos of all specimens, emphasising reproductive anatomy, were recorded as voucher data using a Nikon Digital Sight 10 microscope camera, and these were used to guide identification using primary literature and the Turbellarian Taxonomic Database (https://turbellaria.umaine.edu).

For **Rotifera**, water samples from large water bodies were collected with plankton nets of different mesh sizes and directly with plastic bottles from small water bodies. Sedimentary substrates (e.g. sediment, organic debris, leaf litter, soil, submerged mosses, terrestrial mosses, lichens, etc.) were collected in plastic bottles or envelopes and brought back to the lab for direct inspection. Qualitative sampling procedures mostly followed the methods described in Majdi et al. (2024). Back in the laboratory, subsamples were poured or rinsed into petri dishes and screened under stereo microscopes using different illumination modes and magnifications of between 6x and 80x, using bright, oblique, and dark field to avoid biases in the description of species diversity, given the differential abilities of individual species to stick to the substrate particles. For microscopic investigation and documentation, single specimens were placed on glass slides with a drop of ambient water and covered with a cover slip. Observations and live digital recordings of specimens were carried out with microscopes equipped with connections to mobile cameras. Taxonomic identifications were carried out on live specimens during the survey workshop following Donner (1965) for bdelloids and the most current taxonomic keys for monogononts.

For **Annelida**, members of some oligochaete families were found, often collaterally in samples primarily targeting other meiofaunal groups, but also more specifically by sieving suspended organic material from sandy sediments in lentic and lotic waterbodies. In rivers and streams, a 'kick-sampling' method was applied (Fig. 1K): the bottom substrate was stirred up by foot, and the organics were collected, using a fine-mesh net, immediately downstream of the kick-site. For sediments from non-flowing water, the bottom substrate was placed in a water-filled bucket and repeatedly whirled by hand, and the suspension was then (each time) decanted over into a 250 µm-sieve. Additional samples yielding annelids were material of water plants and mosses, scrapings of various surface substrates in water, and filtered water from the hyporheic zone. All worms were sorted live in petri dishes under a binocular, and individual identification was, in most cases, done in a compound microscope after compressing the individual in ambient water under a coverslip on a slide. Taxonomic identification was based on the keys by Timm (2009) and van Haaren and Soors (2013) – some of the taxa are known to be part of yet unresolved cryptic species complexes.

Testate Amoebae are a polyphyletic grouping of shelled protists spread across two kingdoms in the higher level classification used in this study; however, they are traditionally studied together. Extraction during the survey workshop was performed simply by shaking bryophyte samples in a tube with some water and then pipetting some of this liquid onto microscope slides. Slides were scanned at x200-x400 magnification to compile a species list

(such an approach is only likely to find the commonest species). A small number of spare samples from Seatoller Wood, Borrowdale, have been kept for later detailed analysis. Key texts used for identification during the survey workshop were Charman et al. (2000), Clarke (2003), Kosakyan et al. (2025) and Ogden and Hedley (1980). As with other groups, some of these taxa are thought to be cryptic species complexes (e.g. *Euglypha rotunda* Wailes & Penard, 1911).

For **Ciliates**, samples of mosses, soil, litter and lichens were extracted using standard methods as described above for testate amoebas. Additionally samples were also retrieved by subsampling through 10 µm sieves in order to retrieve smaller specimens. Petri dishes were then observed via stereomicroscope at 4-10X for cell selection. Single cells were transferred onto microscope slides with a glass micropipette. The slides were prepared with coverslips presenting vaseline in the corners following the Dragesco method (Dragesco and Dragesco-Kernèis 1986) allowing slowing down cells for features recognition under compound optical microscope at 40-100X magnification. Subsamples of the moss material were placed in sterile plastic Petri dishes (5 cm in diameter) and supplemented with 3 mL of Volvic® mineral water previously filtered through 0.2 µm Whatman® syringe filters. The subsamples were examined after 24–48 hours using a Sedgewick–Rafter counting chamber.

For **Acari**, water mite specimens were directly collected from plankton or kick net samples spread in white dissection trays, where moving mites could be spotted and further observed in Petri dishes under binoculars. Terrestrial mites were extracted from various limno-terrestrial habitats (mosses, lichens, litter, soil) using a modified version of the Berlese funnel traps (Fig. 1J). Specimens were fixed with 96% Ethanol and mounted on concavity slides, observed and identified under a compound microscope following Davids et al. (2007), Di Sabatino et al. (2010), and Gereck et al. (2016).

For **Nematoda**, living specimens were sorted out from samples extracted using Whitehead and Hemming (1965) trays and Berlese funnel traps. Moreover, we also simply rinsed aquatic macrophytes, lichens or moss patches over a 20 µm-sieve, pouring contents into a Petri dish for visual inspection of samples under a binocular. Nematode specimens were handpicked using a fine needle or an eyebrow hair glued to the tip of a wood stick, transferred onto a microscope slide and observed alive under a compound microscope, or a microscope with high-resolution objectives and differential interference contrast. For better observation of morphological structures of interest (Schenk and Traunspurger 2021), specimens were relaxed by briefly passing a lighter flame beneath the slide. Identification was performed using the keys of Andrássyi (2005, 2007, 2009).

For **Tardigrada**, samples of mosses, lichens, soil and litter were extracted using standard methods as described above for platyhelminthes, mites, rotifers and nematodes in addition to typical tardigrade-specific methods (e.g. Stec et al. 2015). Extracted samples were screened under a binocular, and single tardigrades were mounted on temporary water microscope slides. Additionally, some specimens were fixed on permanent microscope slides, in a small drop of Hoyer's medium and secured with a cover slip, following the protocol by Morek et al. (2016a). Slides were then air-dried for a month at room temperature, and sealed with a transparent nail polish. These specimens were then observed in phase contrast light microscopy, Olympus BX53 PCM associated with an Olympus DP74 digital camera for morphological identification. Taxonomic identification was carried out with the use of taxonomic keys and recent taxonomic revisions (Pilato and Binda 2010, Morek et al. 2016b, Kaczmarek and Michalczyk 2017, Gąsiorek et al. 2019a, Gąsiorek et al. 2019b, Gąsiorek et al. 2021, Gąsiorek and Vončina, 2023, Stec, 2022).

For **Cladocera**, samples were collected with plankton nets (of mesh sizes ranging between 100-120 µm) towed through the water column as well as a 100 µm handnet for macrophytes. At sampling points with dense vegetation, water collected in a 10 L bucket was filtered through a plankton net or 100 µm sieve. Samples of hyporheic water were collected using either the Bou-Rouch method (Bou and Rouch 1967) or by filtering of water flowing into a hole dug into the riverbank. Additionally, some specimens were found in moss or other macrophyte samples inspected under a stereomicroscope. Cladocerans were observed alive under a stereomicroscope and transferred to glass slides after fixation in 70% ethanol for species identification. When needed the animals were partially squeezed with a cover slip to make the postabdomen visible. For identification, we

mainly used keys by Rogers et al. (2019) and Bledzki and Rybak (2016).

GBIF dataset description

Information on taxon name, authorship, systematic hierarchy, coordinates, date of sampling, habitat, locality and taxon specialists for each record is freely available at the Global Biodiversity Information Facility, GBIF, with DOI: https://doi.org/10.15468/zxa8j3. All data were structured based on the Darwin Core standard (Wieczorek et al. 2012). The dataset covers only organisms considered as meiofauna, defined as microscopic invertebrates, belonging to groups Gastrotricha, Nematoda, Platyhelminthes, Rotifera, Annelida, Tardigrada, Arthropoda (i.e. Acari, Cladocera, Copepoda, Ostracoda) in addition to meiofauna-sized single-celled eukaryotes (i.e. testate Amoebas and Ciliates). Species identification was performed by taxonomic experts involved in the project. All reported names are provided according to the most updated nomenclature of WoRMs (Horton et al. 2017) at the time of dataset publication and checked against the taxonomic backbone of GBIF (GBIF Secretariat 2023). Note that for Rotifera, the rotifer List of Available Names, LAN (Segers et al. 2012), was used for all scientific names published before the year 2000. For Gastrotricha, the validity of generic, sub-generic and species names was checked against Balsamo et al. (2009) and Todaro and Tongiorgi (2025). For Cladocera we used the FADA checklist (Forró et al. 2008) and updated taxonomical names where necessary.

Permanent link in GBIF: www.gbif.org/dataset/f77d13e1-15c5-40ad-bb4f-210d13ab8b3a

Date of creation: 27 November 2025

Date of last revision: 24 December 2025

Date of publication: 12 January 2026

Update policy: The dataset at GBIF will not be updated as it represents the list of taxa that were identified during the survey workshop from 27th August to 11th September 2025.

Quality control for geographic data: Georeferenced data and elevation were obtained directly in the field using various GPS tools. Quality control was performed using Google maps for identification of the sites.

RESULTS

The dataset of freshwater and limno-terrestrial meiofauna from the Lake district was built from 60 different samples collected over an area of 573 Km2 in August and September 2025 from 27 different sites covering a range of 10 main habitats (Fig. 2, Table 1). Meiofaunal organisms extracted and identified from those samples covered a wide range of taxonomic groups (Fig. 3). The dataset includes 299 occurrence records of 209 distinct taxa of meiofauna belonging to 46 families, 24 orders and 11 phyla (Dataset available as Supplementary Material to this article and on GBIF, permanent link: www.gbif.org/dataset/f77d13e1-15c5-40ad-bb4f-210d13ab8b3a).

Of the taxa reported in the current dataset, 58 belonged to Arthropoda (28%), 33 were Rotifera (16%), 30 were heterotrophic unicellular eukaryotes (14%), 26 were Nematoda (12%), 20 were Annelida (10%), 19 were Tardigrada (9%), 12 were Gastrotricha (6%) and 11 were Platyhelminthes (5%). Moss samples returned the highest number of taxa occurrences (136), followed by periphyton (54), epipsammon (34), interstitial (25), plankton (17), peat bogs (16), forest litter (7), soil (6), epizoic on crustaceans (2), and lichen (2). Some taxa were relatively common in samples (such as the cladoceran *Chydorus sphaericus* (O.F.Müller, 1776) or the flatworm *Typhloplana viridata* (Abildgaard, 1789), both being found at 6 sites out of 27), or showed high abundance in one particular site, such as the gastrotrich *Lepidochaetus zelinkai* (Grünspan, 1908) at Foulshaw Moss. However, given that collection, extraction and observation were mostly unbalanced and qualitative, it was not possible to correctly assess and compare the quantitative distribution of those taxa across the different habitats and locations sampled. Moreover, a number of collection and extraction methods involved sieving using different mesh-sizes (250, 63, 40, 20 μm), hence most samples were not relevant to observe and pick out the smallest meiofaunal organisms. It might be noted, however, that despite those flaws a fairly similar number of taxa occurred in aquatic habitats (148 taxa occurrences in periphyton, epipsammon, interstitial, peat bogs, water column, epizoic) in comparison to limno-terrestrial habitats (151 taxa occurrences in mosses, soils, lichens and litter).

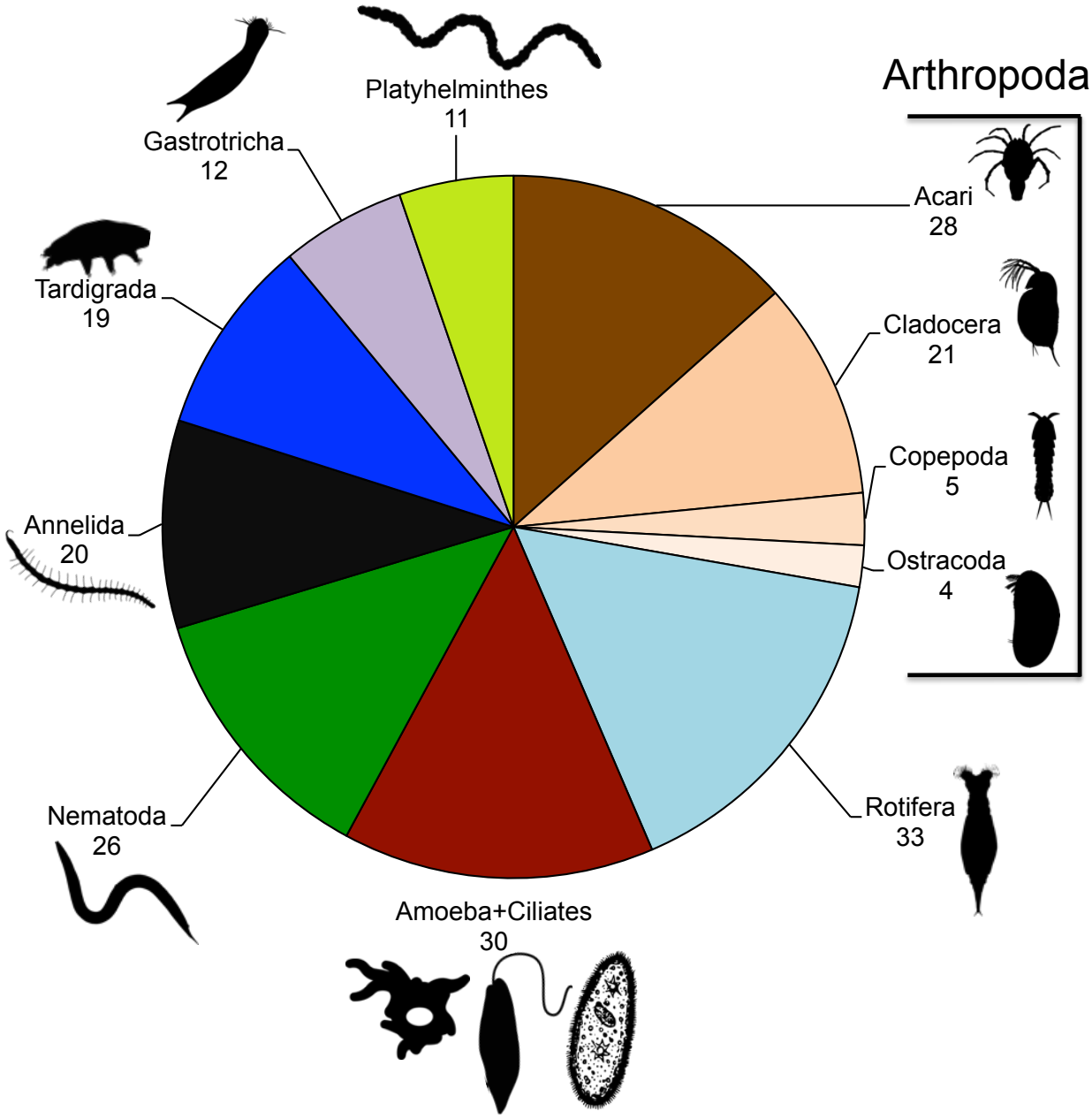

Figure 3. Number of distinct meiofaunal taxa observed across the Lake District (UK).

DISCUSSION

This first freshwater meiofauna survey workshop held during 15 days in Lake District National Park in August–September 2025 illustrated how integrative training initiatives can simultaneously advance biodiversity knowledge transfer, interdisciplinarity and scientific outreach. Despite their ecological importance and extraordinary phylogenetic diversity, meiofaunal organisms still remain largely overlooked in biodiversity inventories, particularly in freshwater and limno-terrestrial environments (Majdi et al. 2020a, 2024, Peralta-Maraver et al. 2023). However, within a relatively short period, our survey workshop documented 209 taxa across 11 phyla, revealing a remarkably diverse assemblage of tiny organisms inhabiting a wide range of habitats. The biogeographic distribution of those taxa across habitats was however difficult to evaluate

quantitatively because disparate sampling and extraction methods were used, and because this was not the primary objective of the survey workshop. Still, all expected meiofaunal groups were well represented in samples, while there was a comparable taxonomic richness observed between aquatic and limno-terrestrial habitats. This highlights that a variety of inland habitats are worth investigating in the search of meiofaunal organisms, and that meiofaunal organisms are interesting models to study ecological continuities across aquatic and terrestrial ecosystems (e.g. Kreunzinger-Janik et al. 2021).

Beyond the dataset produced, this survey workshop provided a unique occasion for installing an interdisciplinary experience, and transfer taxonomic skills across generations, since early-career researchers were mostly trained by senior taxonomic experts through a combination of lectures on the biology, systematics and ecology of each meiofaunal group, followed by practical field and laboratory sessions dedicated to experience sampling and identification techniques. An additional DNA barcoding and bioinformatics training were also proposed, enabling the validation of a low-cost protocol for processing individual meiofaunal-sized specimens and revealing important aspects of their cryptic diversity and associated microbiomes (Keene et al., 2026). This integrative approach allowed all participants to connect "traditional" morphotaxonomical determination with cutting-edge molecular approaches, while also generating verified specimen vouchers and thus genetic data of high value for establishing future DNA reference databases.

The survey workshop concluded with collaborative species documentation projects and outreach activities aimed at communicating the extraordinary diversity of meiofauna to broader audiences. Although more quantitative sampling designs and standardized processing would surely strengthen the resulting data on species distribution patterns, this first initiative still illustrates the value of integrating field-based activities with "all-taxon-all-techniques" training programmes. Such approaches can help rebuild taxonomic expertise and promote public engagement with biodiversity, offering a promising model for future capacity-building efforts focused on poorly studied groups like the meiofauna. Some specific points about some meiofaunal taxonomic groups are discussed separately below.

Nematoda

Nematodes are among the most popular and best-studied meiofaunal groups, partly because their morphology is well preserved under a wide range of fixatives, and because of their remarkable abundances in soils, freshwater and marine habitats (e.g. Van den Hoogen et al., 2019; Majdi et al. 2025b). Nevertheless, one may note that research on free-living nematodes remains a marginal field of nematology, when compared with research on parasitic nematodes for instance, which receive considerable attention (and funding) due to the major impacts nematode parasites impose on health and agriculture (Majdi and Traunspurger 2021). As a result, and even though nematodes are better studied than most other meiofaunal groups, there are still important research gaps in our comprehension of nematode species distribution patterns, and of the roles they play in freshwater and limno-terrestrial ecosystems. Across the wide range of habitats and methods considered in this survey workshop, nematodes did not dominate meiofaunal assemblages in terms of abundance or diversity, suggesting that all-taxa approaches may more accurately reflect the true structure of meiofaunal communities than nematode-focused studies.

Here, only 26 species were recorded, which is less than the 110 species reported from a previous study of a single pond in the Lake District (Fenchel and Finlay 2004). This difference likely reflects time and methodological constraints: since the present survey workshop was conducted primarily for training, short-term sampling and live observations were favored over long-term mounts and description of thousands of specimens, which inevitably reduced the probability of detecting rare taxa. Nevertheless, despite this limited sampling effort, the observed community patterns were consistent with those reported from similar habitats. No new species or unusual distribution patterns were found. As expected, nematode assemblages associated with mosses were dominated by plectids and dorylaimids (Fig. 4A,B) corroborating previous survey in similar environments (e.g. Kreuzinger-Janik et al. 2021). In contrast, periphytic communities in lake littoral zones were strongly dominated by chromadorids, and particularly by the algal-feeder species *Punctodora ratzeburgensis* (Linstow, 1876) (Fig. 4C,D). This species is known to dominate periphytic nematode assemblages in Swedish lakes (Peters et al., 2005;

Figure 4. Example of nematodes observed in the Lake District National Park. In nematodes, heads and tails are important morphological identification characters. *Dorylaimus stagnalis* Dujardin, 1845. Large, omnivorous species, commonly found in mosses: **A**, head-. **B**, tail-region. *Punctodora ratzeburgensis* (Linstow, 1876). Algivore species reaching extremely high densities in algal mats in littoral zones of lakes: **C**, head-. **D**, tail-region. Scale bars: 100 µm.

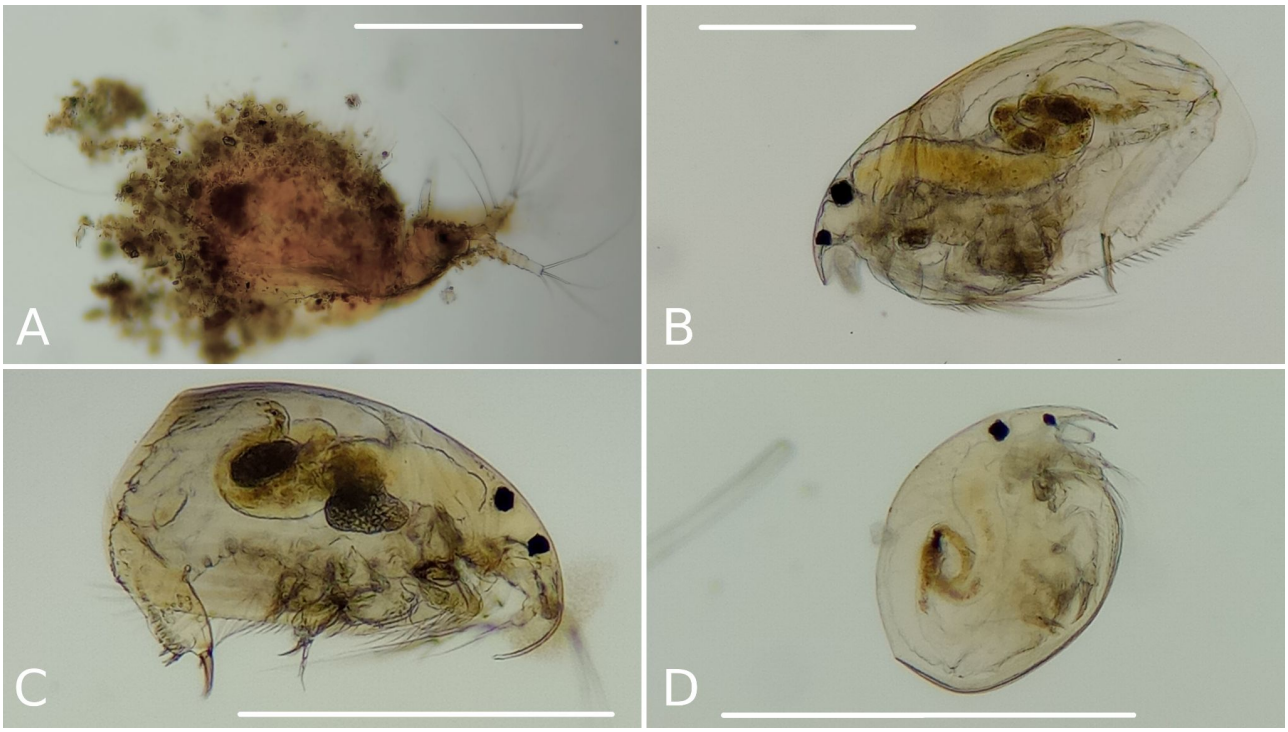

Figure 5. Example of cladocerans observed in the Lake District National Park. **A**, *Ilyocryptus cuneatus* (Johnny's wood). **B**, *Alonopsis elongata* (G.O.Sars, 1862) (Ennerdale water). **C**, *Rhynchotalona falcata* (Ennerdale water). **D**, *Chydorus sphaericus* species complex (Foulshaw moss). Scale bars: 500 µm.

Schroeder et al., 2013; Kreuzinger-Janik et al. 2021), its high prevalence in the periphyton of the lakes sampled in the present study thus probably reflects a specialisation for periphytic habitats rather than a site-specific anomaly.

Cladocera

In total, 89 freshwater Cladocera species are included in the UK national database (Gunn et al., 2018). The latter list requires an update, taking into account specialized taxonomical literature, the generally underestimated global diversity of cladocerans (Forró et al. 2008) and the ever increasing proportion of exotic freshwater cladocerans in temperate waters (Kotov et al. 2022). The number of taxa encountered during the workshop (21 species), is a fraction of the richness known in the Lake District, as nearly all waterflea species currently known from freshwater in the UK could be expected here, and we focused mainly on the most common and abundant species from littoral and benthic habitats. The majority of the species found are known to be widespread and, where present, often very abundant, in UK waters. Among the relatively rarer taxa, we identified *Ilyocryptus cuneatus* Stifter, 1988 (Fig. 5A), a benthic specialist, which is missing from the national list compiled by Gunn et al. (2018). The ilyocryptid is not a new record for the UK (Fryer 1974), yet its finding illustrates that the list of British freshwater cladocerans is an underestimation and that there is a need for a proper revision. Another species, *Rhynchotalona falcata* (Sars, 1861), which we found in Ennerdale water (Fig. 5C), is rarely recorded in the UK; this small chydorid is easily overlooked in freshwater habitats due to its ecology, as it is a predominantly psammophile species (living between sand grains).

Testate amoebae

The limited testate amoebae sampling identified 8 species from wet bryophytes from two sites (Fig. 6A, B). The approach used here was only likely to have found examples of the commonest taxa. This view is confirmed by initial analysis of samples from Seatoller Wood (post- survey workshop) - which has mainly identified the same list of taxa with the addition of *Centropyxis aerophila* Deflandre, 1929. Only three of the taxa found here were recorded earlier from Priest Pot (Finlay and Maberly 2000). However, limno-terrestrial habitats (an important habitat for testate amoebae) were not sampled at Priest Pot. In addition, testates in the Arcellidae were seen during the survey workshop in samples collected from Foulshaw Moss, but were not identified to species. Many of these morphospecies are widely distributed - for example, several of these taxa also occur in bryophyte crusts in semi-arid habitats in Australia (Wilkinson et al. 2025).

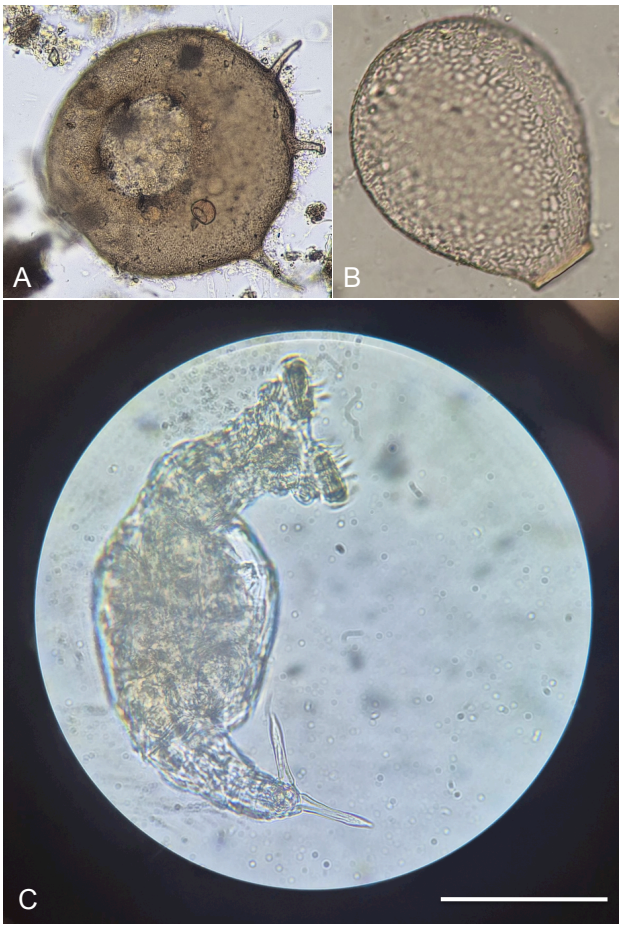

Figure 6. Example of testate amoebas and a bdelloid rotifer observed in the Lake District National Park, the two testate amoebas were **A**, *Centropyxis aculeata* (Ehrenberg, 1832) found in Elterwater River, the very small hemispherical testates within the test of *C. aculeata* are *Pyxidicula operculata* J.W.Bailey, 1841. Since the larger *C. aculeata* seems to be dead, it is unclear if the *P. operculata* are the remains of its last meal or if they have entered the larger test as scavengers, feeding either on the remains of the dead larger amoeba and/or on bacteria associated with its decay. **B**, *Nebela collaris* (Ehrenberg, 1848) found on moss (*Sphagnum fallax* (H.Klinggr.) H.Klinggr.) from the wet edge of Moss Dub in Ennerdale. **C**, The bdelloid rotifer *Rotaria magnacalcarata* (Parsons, 1892) from Elterwater River. Scale bar: 50 μm.

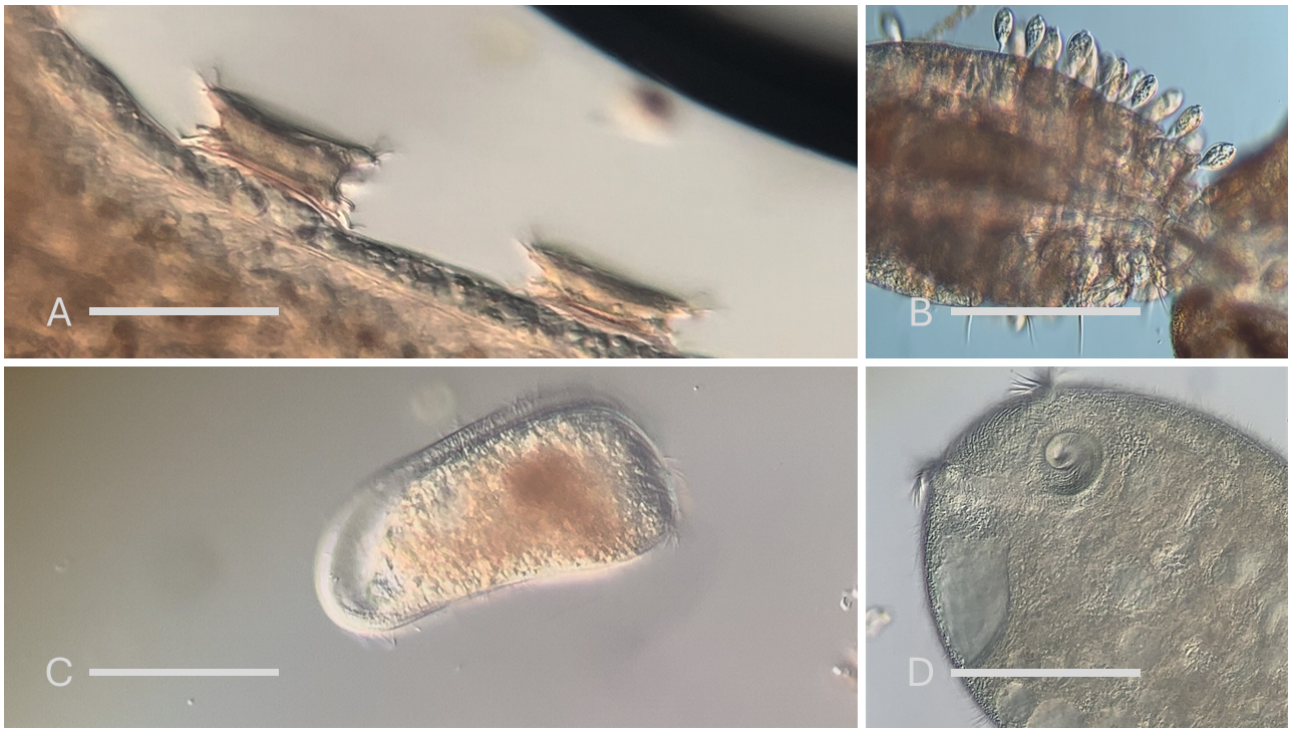

Figure 7. Example of ciliates observed in the Lake District National Park. **A**, *Trichodina pediculus* Ehrenberg, 1831 ectocommensals of *Hydra vulgaris* Pallas, 1766. **B**, *Epystilis* sp. on the surface of a cyclopoid copepod. **C**, *Penardiella* sp. **D**, *Stentor coeruleus* Ehrenberg, 1830. Scale bars: 100 µm.

Rotifera

The sampling of rotifers was mostly focused on bdelloid rotifers, for which the species list could also be considered rather reliable, whereas for monogononts only occasional species were collected and identified. According to the checklist of Fauna Europaea, 118 species and subspecies of bdelloid rotifers were known from the UK in 2004 (de Jong 2014). Two of the species found here, namely *Didymodactylos carnosus* Milne, 1916 and *Otostephanos donneri* Bartoš, 1959, were not listed in Fauna Europaea but have already been mentioned in following studies from the UK (e.g. Fontaneto et al. 2007, Nowell et al. 2021). An additional species, *Pleuretra hystrix* Bartoš, 1950, is an actual novelty for the country: until now it was known only from Italy, Switzerland, Canada and Korea (Song 2017). Overall, the bdelloid species (Fig. 6C) found in the survey were typical of European aquatic habitats.

Ciliates

The number of ciliate species retrieved was relatively low, most likely due to the nature of the habitats investigated, namely limno-terrestrial environments. In such habitats, most ciliates remain inactive because of limited water availability. To mitigate this limitation, several moss subsamples were incubated after adding filtered mineral water (see Methods), resulting in the detection of a few additional species, including *Colpoda steinii* Maupas, 1883, *Podophrya* sp., and *Halteria grandinella* (Müller, 1773) Dujardin, 1840. All ciliate species identified have previously been reported from the Lake District (Finlay and Maberly 2000, Esteban et al. 2010), except for *Penardiella* sp. Unfortunately, only a single individual of *Penardiella* sp. was observed (Fig. 7C), preventing the confirmation of species-level identification. The ciliate species recorded in this study are globally distributed and commonly occur in moss, soil, and freshwater habitats (Weiss and Esteban 2024).

Platyhelminthes

The sampling resulted in records of 11 species, principally of species with widespread Palearctic and Nearctic, and sometimes cosmopolitan distributions. As expected, the major represented higher taxa were Catenulida (*Stenostomum* and *Catenula* spp.), Macrostomida (*Macrostomum rostratum* Papi, 1959), Prorhynchida (two cosmopolitan

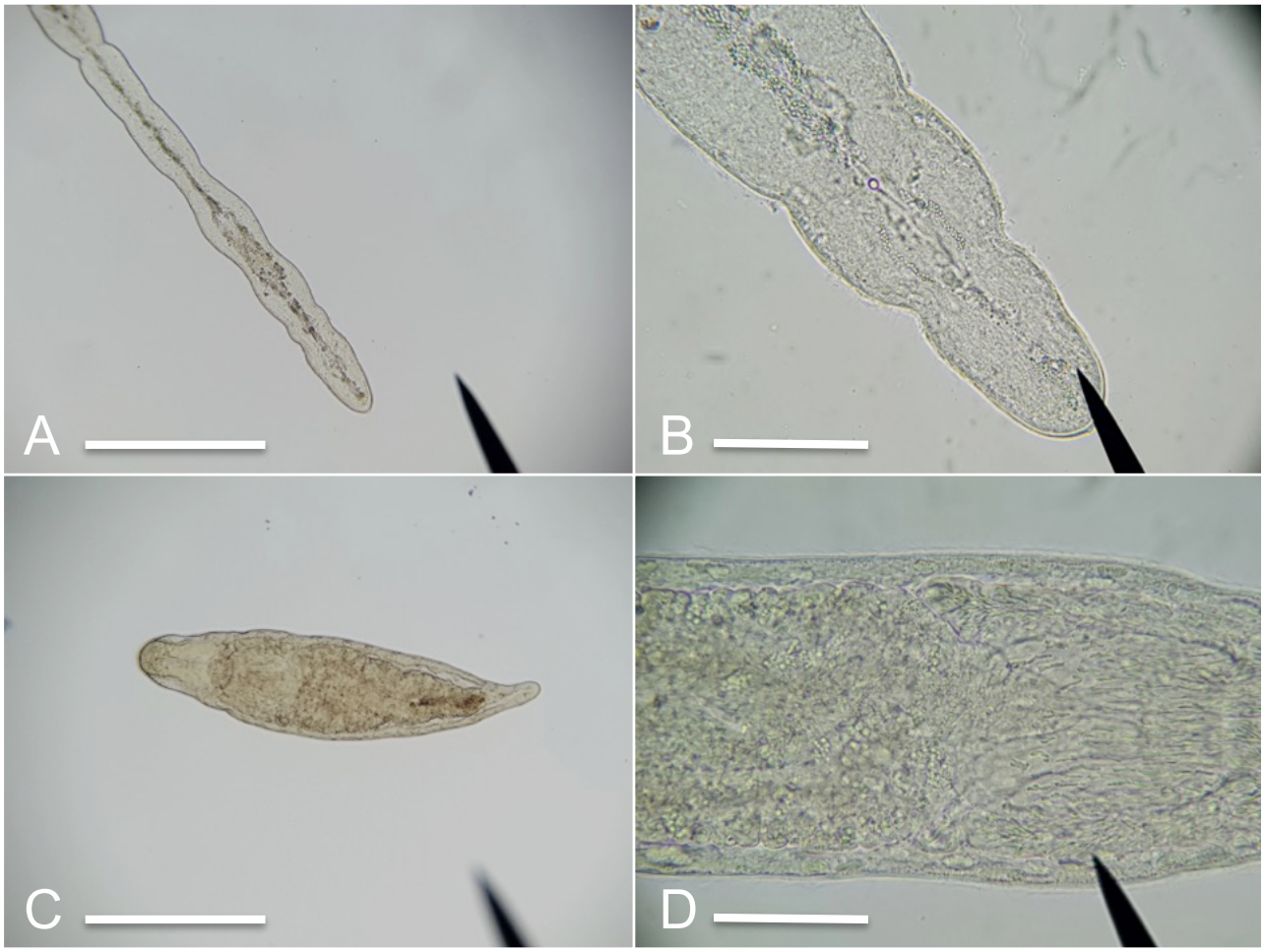

Figure 8. Example of micro-flatworms observed in the Lake District National Park. **A**, **B**, Anterior part and head region of *Catenula lemnae* Duges, 1832 found dwelling in a *Sphagnum* moss patch in the Foulshaw Moss Nature Reserve. **C**, **D**, Body and pharynx region of *Stenostomum ventronephrium* found from leaf litter packs in Loughrigg Tarn. Scale bars **A**, **C**: 500 µm. Scale bars **B**, **D**: 100 µm.

Geocentrophora spp.), Rhabdocoela (widespread species such as *Typhloplana viridata* (Abildgaard, 1789), *Opisthocystis goettei* (Bresslau, 1906), and *Rhynchomesostoma rostratum* (Müller, 1774)), and Tricladida (*Rhynchodemus* sp. - albeit this species is arguably non-meiofaunal). As time and attention for detailed species identification was limited during this survey workshop, these surely represent only a few of the most abundant and easily observed microturbellarian species to be found in the Lake District. Nonetheless, these 11 species represent 20% of the 56 microturbellarian species recorded from Britain by Young's (2001) key. *Stenostomum ventronephrium* Nuttycombe, 1932 (Fig. 8C, D), a species described originally from the southeastern USA, is recorded in the UK for the first time.

Gastrotricha

The majority of the 33 collected specimens of Gastrotricha could reliably be assigned to morphological species. In two cases a final determination to species level was not possible, i.e., in *Stylochaeta* cf. *scirtetica* and in *Chaetonotus (Zonochaeta)* aff. *voigti*, the latter possibly representing an undescribed new species. This record was a putative new species of the subgenus *Zonochaeta* Remane, 1927 (genus *Chaetonotus* Ehrenberg, 1830) which was observed and recorded. However, we only found a single specimen and we were not able to extract genomic DNA from it. As in the case of the two putative new tardigrade species (see below), resampling is necessary to permit high-quality integrative descriptions.

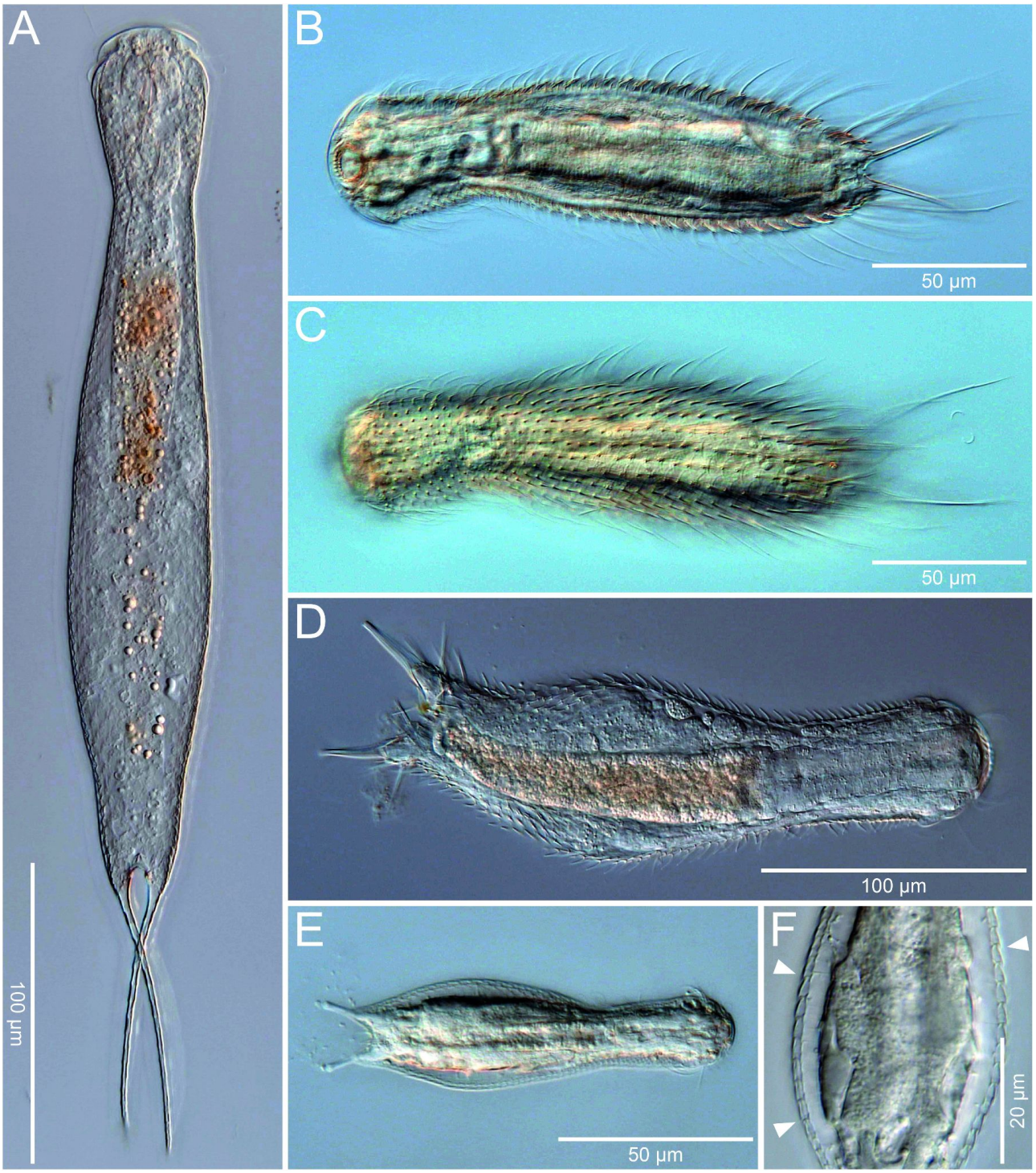

Figure 9. Example of gastrotrichs observed in the Lake District National Park. **A**, *Polymerurus rhomboides* from leaf litter of the littoral zone of Loughrigg Tarn, stacked image from 24 single images. **B**, **C**, Median and dorsal views of *Lepidochaetus zelinkai* from a pond of the Foulshaw Moss Nature Reserve. **D**, Median view of *Chaetonotus (Chaetonotus) polyspinosus* dwelling in the periphyton of Moss Dub. **E**, **F**, Habitus and detail of the mid trunk of *Aspidiophorus oculifer* dwelling on *Elodea* sp. leaves from Loughrigg Tarn. Note the stalked scales in **F** (arrowheads). Scale bars defined in the figure.

Four specimens could only be determined to subgenus level, i.e., to *Chaetonotus (Primochaetus)* sp. and one specimen only to genus level, i.e., *Haltidytes* sp. With all our determinations we have to keep in mind that in gastrotrichs, like in most other meiobenthic taxa, there is increasing evidence for the occurrence of complexes of (genetically distinct, but phenotypically) cryptic species. One such example concerns the morphospecies *Lepidodermella squamata* (Dujardin, 1841), a species recorded nearly from all over the world which was also found here. However, a previous survey of Swedish freshwater gastrotrichs revealed a certain genetic inhomogeneity among the specimens of *L. squamata* that were analysed (covering specimens from different Swedish sites and from Belém, Brazil), possibly attributed to the existence of a species complex (Kånneby et al. 2012). Another 'candidate case' concerns the species *Lepidochaetus zelinkai* (Fig. 9B, C): currently, the nominate species *L. zelinkai* plus four described morphological variants are known (Grünspan 1908, Steiner 1913, d'Hondt 1967, Sudzuki 1971, Kisielewski 1991), which could be subspecies according to Križanová & Vd'ačný (2021). In their description of the most recent species of *Lepidochaetus*, *L. tirjakovae* Križanová & Vd'ačný, 2021, the authors already mention the likelihood of *L. zelinkai* and its varieties/subspecies representing a species complex (Križanová and Vd'ačný 2021). All such cases need to be explored in more detail using DNA-based analyses and a broad geographic and taxon sampling, also covering further congeneric species.The current knowledge about freshwater and limno-terrestrial gastrotrichs from the UK is rather limited. There were only a handful of singular records and descriptions of freshwater gastrotrichs from Great Britain from the mid and late 19th century and from the early 20th century (Gosse 1851, 1864, Slack 1861, Spencer 1890, Thompson 1891, Parsons 1896, Murray 1913), until the most comprehensive and most recent surveys on British freshwater gastrotrichs have been made in Surrey by Martin (1981, 1990). According to Martin's (1990) provisional list, there were so far 52 species known from Great Britain plus the records of *Ichthydium (Forficulichthys) forcipatum* Voigt, 1902 by himself (Martin 1981) and of *Polymerurus rhomboides* (Stokes, 1887) by Thompson (1891), which were both not considered by the former author in his list of 1990. Eight species found here were already reported from the UK, i.e., *Polymerurus rhomboides* (Fig. 9A), *Aspidiophorus ophiodermus* Balsamo, 1983, *Chaetonotus (Chaetonotus) oculifer* Kisielewski, 1981, *C. (Hystricochaetonotus) persetosus* Zelinka, 1889, *C. (Chaetonotus) polyspinosus* Greuter, 1917 (Fig. 9D), *C. (Zonochaeta) voigti* Greuter, 1917 (but putative new species in Lake District, see above), *Lepidochaetus zelinkai*, and *Lepidodermella squamata*. Two species represent new records of freshwater gastrotrichs from the UK, i.e., *Aspidiophorus oculifer* Kisielewski, 1981 (Fig. 9E, F) and *Stylochaeta* cf. *scirtetica*. Furthermore, we could add the genus *Haltidytes* Remane, 1936 as the first record of this taxon from the UK to the list. Accordingly, there are now 56 species of freshwater Gastrotricha from 14 genera known from British inland waters.

Tardigrada

During our sampling we identified 19 species, representing all three limno-terrestrial orders, Echiniscoidea Richters, 1926, Apochela Schuster, Nelson, Grigarick & Christenberry, 1980 and Parachela Schuster, Nelson, Grigarick & Christenberry, 1980. The fauna of England currently includes 63 species (Kayastha et al. 2025), thus our sampling recovered ~30% of the known diversity. It should be noted that the most sampled environments were freshwater habitats, but we did not recover several species known from Scotland, for example *Cucumibius annulatus* (Murray, 1905) or *Dactylobiotus* spp. (Murray 1905). Given the modest number of samples analysed, the inventory of Lake District tardigrade diversity is certainly far from complete, given this area encompasses diverse habitats suitable for meiofauna and tardigrades in particular, thanks to the elevational gradient (Dastych 1980, Surmacz et al. 2025b).

Here we identified two tardigrade species that are potentially new to science. One of them represents the genus *Pseudechiniscus* Thulin, 1911 and was already suggested as candidate species *Pseudechiniscus* sp nov. 9 in Gąsiorek et al. (2021) (Fig. 10B). The second species belongs to the genus *Grevenius* Gąsiorek, Stec, Morek & Michalczyk, 2019 and is characterised by a unique claw curvature and bump, together with macroplacoid traits (Fig 10A). The identifications to the species level were possible only on fixed slides. Unfortunately, the number of preserved specimens does not allow the description of both new species here, hence resampling is necessary to permit high-quality descriptions. This inventory should be treated as a

starting point towards more comprehensive sampling.

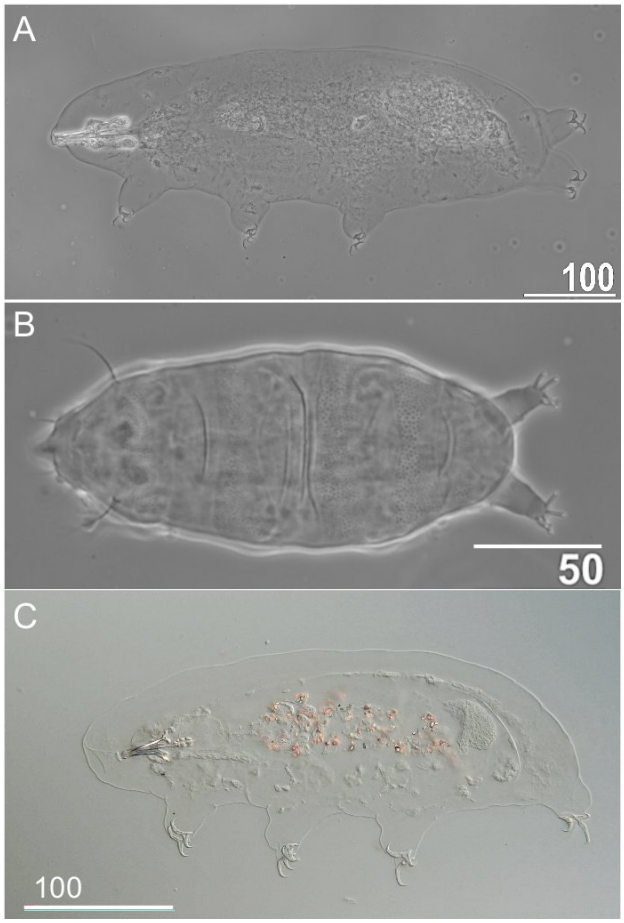

Figure 10. Example of tardigrades observed in the Lake District National Park. **A**, *Grevenius* sp.1 (candidate new species). **B**, *Pseudechiniscus* sp.1 (candidate new species). **C**, *Doryphoribius* sp. Scale bars defined in the figure.

AUTHOR CONTRIBUTIONS

NM: sampling, identification, data curation, manuscript writing, figure preparation; WD: sampling, identification, figure preparation; IE: sampling, identification; LT: sampling, identification, figure preparation; MG: sampling, identification, figure preparation; AL: sampling, identification, figure preparation; HS: sampling, identification; DF: sampling, identification, manuscript writing; LK: data curation, manuscript writing; WD: sampling, identification, figure preparation; WT: sampling, identification; MC: sampling, identification; CE: sampling, identification; MS: sampling, identification; AK: sampling, identification, figure preparation, manuscript writing; ARSG: sampling, identification, figure preparation, manuscript writing; WM: sampling, identification, figure preparation, manuscript writing; EMS: sampling, identification; ET: sampling, identification; VB: sampling, identification, figure preparation; JB: sampling, identification; GMRAV: sampling, identification; CGB: sampling, identification; KT: sampling, identification, figure preparation; HG: sampling, identification, figure preparation; DK: sampling, nanopore sequencing; DMW: sampling, identification, manuscript writing; RH: sampling, identification; DH: sampling, identification; HB: sampling, identification; GN: sampling, identification; GFE: identification, figure preparation, manuscript writing; KVD: sampling, identification, manuscript writing; SA: sampling, identification, bioinformatics; CL: Survey workshop organisation, sampling, identification, manuscript writing.

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