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New data on *Thecamoeba striata* (Penard, 1890) (Amoebozoa, Discosea, Thecamoebida), and the geographical distribution of "*T. striata* species group"

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Summary

Until recently, it was believed that amoebae of the genus *Thecamoeba* Fromentel, 1874 could be relatively easily distinguished from each other at the light-microscopic level. The main characteristics were the shape and size of the locomotive form and the morphology of the nucleus. However, recent studies with molecular methods have shown that several sibling species may be hidden behind every "classical" morphological species of *Thecamoeba*. Therefore, re-description and obtaining molecular data on "classic" *Thecamoeba* species became necessary tasks. However, during recent decades, almost all type cultures have been lost from international culture collections. During our study of the fauna of Moscow ponds, we isolated a strain identical to the type culture of *T. striata* established by F.C. Page both at the morphological level and by the sequence of the 18S rRNA gene. We obtained new images that clearly illustrated the diversity of locomotive forms and the morphology of the nucleus of the species *T. striata*. An analysis of faunistic studies showed that amoebae of "*T. striata* species group" are distributed almost worldwide and are a common component of freshwater and terrestrial ecosystems.

Key words: Amoebozoa, phylogeny, systematics, *Thecamoeba*

Introduction

Lobose amoebae of the genus *Thecamoeba* Fromentel, 1874 are widely distributed in a variety of habitats: bottom sediments of freshwater and saltwater bodies, soil, leaf litter, plant surfaces and other terrestrial habitats (Greeff, 1866; Penard, 1905, 1913; Page, 1971, 1977; Kudryavtsev and Hausmann, 2009; Mesentsev and Smirnov, 2019, 2021; Mesentsev et al., 2020, 2022, 2023). The members of this group have remarkable morphological features, such as smooth rounded or oval contours of the locomotive form. They do not produce discrete pseudopodia or subpseudopodia, but form surface wrinkles and folds. These features make it easy to distinguish members of the genus *Thecamoeba* from other amoebae. Most species have a complex nuclear structure. For some time, it was thought that species of the genus *Thecamoeba* could be easily identified by light microscopy (Page, 1977).

However, recent studies suggest that each "classical" *Thecamoeba* morphospecies is likely to

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contain several sibling species that have tiny morphological differences and can only be distinguished by molecular methods. Nowadays, three such groups of species are known (Mesentsev and Smirnov, 2019; Mesentsev et al., 2020, 2022). Each of them forms a monophyletic branch on the phylogenetic tree. The discovery of sibling species made it necessary to obtain molecular data on "classical" species. Light microscopic data for many "classical" species were obtained in the second half of the 20th century (Page, 1971, 1977; Smirnov, 1999). Type cultures of these species have never been established or have been lost, and there are no molecular data for them. There are only two 18S rRNA gene sequences from *Thecamoeba* type cultures: those of *T. similis* (Fahrni et al., 2003) and *T. striata* (Mesentsev et al., 2022).

The species *Amoeba* (=*Thecamoeba*) *striata* was described by Penard (1890). These flattened amoebae have a smooth, elongated to oval outline, and usually form 3–4 longitudinal dorsal ridges. The nucleus of *Amoeba striata* contains flattened peripheral nucleoli. Schaeffer placed the species *Amoeba striata* in the genus *Thecamoeba* (Schaeffer, 1926). Bovee and Jahn (1966) proposed to separate small amoebae with distinct dorsal ridges from those with irregular dorsal ridges and multiple folds. Two suborders, Rugina and Striatina, were established within the order Thecida Bovee et Jahn, 1966. The suborder Striatina contained the single family Striamoebidae with the type species *Striamoeba* (=*Thecamoeba*) *striata*. Bovee (1985) listed this family as a member of the suborder Thecina and included the species *Striamoeba munda* (Schaeffer, 1926) in the genus *Striamoeba*. However, Page (1971, 1977) and other authors (e.g. Rogerson and Patterson, 2000; Smirnov and Brown, 2004) did not support the division of the genus. Some species, including *T. striata*, have been re-described and neotypified on the basis of Penard's original description (Page, 1977; Smirnov, 1999). Recently, a sibling species of *T. striata, T. vumurta*, was described by Mesentsev et al. (2022).

The amoebae identified as *T. striata* have been mentioned in studies from various fields of biology: from cell biology to faunistic studies. Its laconic, almost "bilateral" locomotive form attracted the attention of researchers of amoeboid locomotion (Rhumbler, 1898; Abé, 1961, 1962). Experiments on aspects of cultivation and nutrition of *Thecamoeba* spp. were carried out by Page (1977). In particular, he obtained data on selective feeding and the need for *T. striata* to hunt smaller amoebae. In faunistic and ecological studies, amoebae identified as *T. striata* have been found in a wide range of freshwater and terrestrial habitats. Furthermore, amoebae morphologically identified as *T. striata* are hosts of unique intranuclear parasites of the species *Nucleophaga striatae* (Rozellomycota) (Michel et al., 2021), as well as fungi of the genus *Acaulopage* (Zoopagales; Fungi; Opistokonta) (Michel et al., 2014; Corsaro et al., 2017).

Despite the interest of researchers and frequent records, there is a noticeable lack of modern data on *T. striata*. GenBank contains three 18S rRNA gene sequences attributed to *T. striata*. One of these sequences was obtained from type culture CCAP 1583/4, which was established by Page as the neotype of *T. striata* (Page, 1977; Mesentsev et al., 2022). It is a partial sequence of 1083 bp. The other two show significant divergence from the type sequence as well as from the sequence of *T. vumurta*, the second species belonging to the "*T. striata* species group" (Patsyuk, 2023).

During our studies of the fauna of amoeboid organisms in urban freshwater reservoirs, we isolated an amoeba belonging to the "*T. striata* species group". The sequence of the 18S rRNA gene of this isolate was found to be identical to that of the type culture of *T. striata* CCAP 1583/4. From this, we concluded that we had re-isolated the species *T. striata*. We re-described *T. striata* using modern light microscopy and obtained a more complete sequence of the 18S rRNA gene.

Material and methods

Isolation and cultivation

Thecamoeba striata strain T1O1 was isolated from the upper layer of pond sediment of Oleniy Pond, in the park Sokolniki, Moskow, Russia (Surkova et al., 2022). To isolate cells, a small volume of the sediment was placed in sterile 60 mm Petri dish filled with wMY agar (Spiegel et al., 1995). In order to get a clonal culture, tiny fragments of agar containing a single amoeba cell were cut off and transferred each to a fresh dish filled with the same medium. Clones were cultured with accompanying bacteria, fungi, and small non-identified amoebae.

Light microscopy

Live cells were studied, measured, and photographed on the glass object slides using a Leica DM2500 upright microscope equipped with diffe-

rential interference contrast (DIC) and phase contrast optics and a DS-Fi3 camera (Nikon, USA). To increase the focal depth, we applied z-stacking as described by Mesentsev et al. (2020).

DNA extraction and sequencing

To extract DNA, cells were washed off from the agar surface with an aliquot of sterile Prescott and James (PJ) medium (Prescott and James, 1955) and left to starve for three days (Mesentsev et al., 2023). After that, the cells were transferred in 0.2 ml PCR tubes in small volume of sterile PJ medium. The genomic DNA from a few cells was extracted using the Arcturus PicoPure DNA Extraction Kit (Thermo Fisher Scientific, USA). For PCR amplification of the 18S rRNA gene, we used the forward RibA (5'>ACCTGGTTGATCCTGCCAGT<3') primer, which is the second half of the original "Primer A" (Medlin et al., 1988) and the reverse RibB (5'>TGATCCTTCTGCAGGTTCACCTAC<3') primer (Pawlowski, 2000); also Thermo Scientific Taq DNA Polymerase (Thermo Fisher Scientific, USA) were used. Thermal cycle parameters were: initial denaturation (10 min at 95 °C) followed by 39 cycles of 30 s at 94 °C, 60 s at 58 °C, and 120 s at 72 °C, followed by 10 min at 72 °C for the final extension. Amplicons were purified in 1.5% agarose gel using the Cleanup mini Purification Kit (Eurogene, Moscow, Russia). All amplicons were sequenced directly using the ABI-PRISM Big Dye Terminator Cycle Sequencing Kit with s6F, s12.2, s12.2R, s14 and s20R primers for the 18S rRNA gene (Medlin et al., 1988; Pawlowski, 2000; Adl et al., 2014). A search in the GenBank database (Benson et al., 2013) was performed using BLASTN (Zhang et al., 2000) on the NCBI site (https://www.ncbi.nlm.nih.gov/). The system by Petrov et al. (2014) was used as a reference to identify regions and helices in the sequence of the 18S rRNA gene.

Phylogenetic analysis

Obtained sequences were added in the alignment of Thecamoebida sequences, containing all named sequences of these organisms and a set of outgroups. Sequences were automatically aligned using the Muscle algorithm (Edgar, 2004) implemented in SeaView 4.0 (Gouy et al., 2010); the alignment was further refined manually. Initial selection of nucleotide sites for tree inference was done using GBlocks (Castresana, 2000). The phylogenetic analysis was performed using the maximum likelihood method as implemented in the RaxML program (Stamatakis, 2014) with the GTR + γ model; 1655 sites were selected for the analysis, and 1000 bootstrap pseudoreplicates were used. Bayesian analysis of the same dataset was performed using MrBayes 3.2.6, GTR model with gamma correction for intersite rate variation (8 categories), and the covarion model (Ronquist and Huelsenbeck, 2003). Trees were run as two separate chains (default heating parameters) for 10 million generations, by which time they had ceased converging (the final average standard deviation of the split frequencies was less than 0.01). The quality of chains was estimated using built-in MrBayes tools and additionally using the software Tracer 1.6 (Rambaut et al., 2014); based on the estimates by Tracer, the first 25 % of generations were discarded as burn-in. RaxML and MrBayes programs were run at the Cipres V.3.3 website (Miller et al., 2010).

The obtained sequence was deposited with Gen Bank under the number OR994897 (*Thecamoeba striata* T1O1, length 1962 bp).

Results and discussion

Light microscopy

On slides, the cells adhered relatively quickly to the glass surface and began to move. The locomotive form of strain T1O1 amoebae was similar to that described by Page (1971, 1977) for *T. striata*. The amoebae moved as a whole and did not form pseudopodia or subpseudopodia. Locomotive amoebae had the shape of an elongated oval with a slightly narrowed posterior end (Fig. 1, A-I). The anterior edge was usually rounded and could have small smooth irregularities. The lateral sides of the cell were either slightly convex or almost parallel. The posterior end was noticeably tapered, smoothly rounded and had no differentiated uroidal structures. The widest part of the cell was the central area or anterior half of the amoeba. The size range of T1O1 cells overlapped with that of the type strain and three other cultures of *T. striata* isolated by Page (Table 1). During locomotion, the cells were unevenly flattened. The anterior end was often flatter and continued smoothly into the thicker main body of the cell. The posterior end was usually raised above the substrate. The central part of the cell, filled with granuloplasm, was convex. Clearly thinner lateral

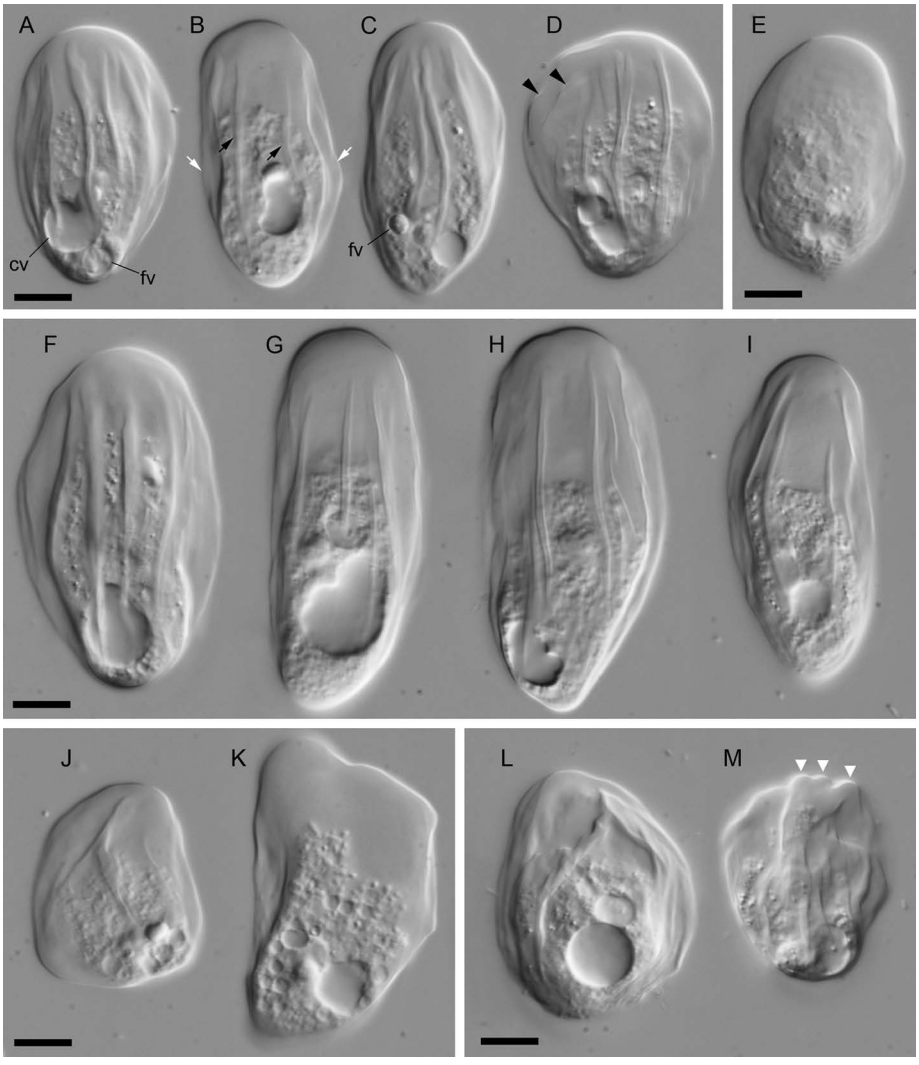

Fig. 1. Light microscopy of *T. striata* strain T1O1, DIC. A–D and F–I – Locomotive forms, z–stacking; E – ventral surface of the amoeba; J and K – slowly moving locomotive forms, z–staking; L and M – stationary forms, z–staking. *Abbriviation*: cv – contractile vacuole; fv– food vacuole; white *arrow* – lateral lobe; black *arrow* – dorsal fold; black *arrowhead* – ridge; white *triangle* – hyaloplasm outgrows. Scale bar: 10 μm.

lobes were located along the sides of the cell. The lateral lobes started smoothly in the frontal area and extended almost to the posterior end of the cell. The anterior part of the cell consisted of the hyaloplasm, which could occupy up to half the length of the cell. The hyaloplasm continued to the lateral sides of the cell, forming the antero-lateral hyaline crescent. The dorsal side of the cell usually had several well-defined longitudinal ridges. The ridges began in the frontal hyaline area with a small, gently sloping extension and typically continued to the posterior end of the cell. In the frontal area, we occasionally observed small wrinkles running parallel to the frontal edge of the cell. The ventral side had small smooth irregularities that were clearly visible only in the frontal area of the hyaloplasm (Fig. 1, E).

When the cell changed the direction of movement during continuous locomotion, it moved the frontal hyaline area slightly sideways and bent in a new direction. Sometimes cells reversed the direction of movement. When this happened, the cell stopped and formed a new hyaline region in the uroidal area. A similar radical change in direction of movement was observed by Rhumbler (1898). Rarely, at the beginning of the observation, individual cells could stop, detach from the substrate and begin to float as irregular bodies. Slowly moving cells were wider in outline and more wrinkled (Fig

Table 1. Morphometric data of the strains of "*T. striata* species group".

Species (source)	75, CCAP 1583/4 (Page, 1971)	76 (Page, 1971)	77 (Page, 1971)	112 (Page, 1971)	T1O1	*T. vumurta* Ta130 (Mesentsev et al., 2022)
Length	28–78	30–62	32–78	31–60	32–66	46–73
Mean length	48	49	52	49	46.2	60.7
Breadth	–	–	–	–	18–35	32–59
Mean breadth	–	–	–	–	24.7	46.1
L/B ratio	1.1–2.2	1.2–2.3	1.4–3.4	1.1–2.1	1.4–2.5	1.0–1.8
Mean L/B ratio	1.5	1.7	2.0	1.4	1.9	1.3
Nucleus diameter	7–10	6–9	6.5–9	–	6–9	9–15
Mean nucleus diameter	7.7 (Page, 1988)	–	–	–	7.5	13

1, J and K). Slow moving cells frequently changed direction. Such cells produced several hyaline areas so that the outline of the cell resembled an irregular polygon with rounded corners. The dorsal ridges of such cells were arranged in different directions, corresponding to the new and previous directions of movement. Stationary cells had irregular, rounded outlines (Fig. 1, L and M). The surface of stationary cells was covered with multidirectional folds and ridges. The peripheral hyaline layer in such cells was more uniform in width. A single or a few small rounded protrusions could appear at the edges of the cell.

The size and structure of the nucleus was consistent with the description of *T. striata* by Page (1971, 1977). The single nucleus had a clearly visible flexible envelope (Fig. 2). The outline of the nucleus was round or slightly elongated. The nuclear envelope could be deformed in contact with organelles or denser areas of cytoplasm (Fig. 2, C and D). The nucleus contained peripheral nucleoli that were almost adjacent to the nuclear envelope (Fig. 2). Nucleoli had lens-like or broad plate shape, and occupied more than half of the inner nuclear surface. Small nucleoli were homogeneous in texture and smooth in outline (Fig. 2, A, E and G). Plate-shaped nucleoli showed lacunae and invaginations. Depending on the projection of the nucleus, one to four nucleoli could be visible. However, the visible nucleolar material often represented an optical section of several lobes belonging to the single broad nucleolus (Fig. 2, H). Page (1971) described the same number of nucleoli, but Penard (1890) indicated in the original description that there were only two nucleoli, located on opposite sides of the nucleus. A similar nuclear morphology with oppositely located nucleoli has been described for *T. munda* (Schaeffer, 1926; Smirnov, 1999), but it is almost impossible to confuse it with *T. striata*, both because of other morphological differences and because *T. munda* has only been isolated from marine habitats. The central part of the karyoplasm never contained nucleolar material. Rarely, small spherical or slightly flattened structures could be seen adjacent to the inner side of the nucleoli or close to the nuclear envelope (Fig. 2, K–M). Similar differences in the shape and texture of nucleoli within a nucleus have been noted in the sibling species *T. vumurta* and may be a feature of the "*T. striata* species group" (Mesentsev et al., 2022).

Numerous food vacuoles containing amoeba cysts, bacteria or fungal conidia (Fig. 1, C; Fig. 2, M) were present in the cytoplasm. The contractile vacuole was usually several times larger than the nucleus and was highly deformable, in agreement with older observations (Penard, 1890, 1902, 1905; Page, 1971, 1977). As it moved in the cytoplasm, multiple invaginations could reach almost to the centre of the vacuole (Fig. 1). The cell produced empty vacuoles of various sizes which, after a short time, fused with the contractile vacuole. The cytoplasm of the cell also contained small round or oval bodies (Fig. 2, M) and spherical dense granules, clearly visible by DIC.

Molecular phylogenetic analysis (Fig. 3)

The length of the 18S rRNA gene sequence obtained is 1962 bp, corresponding to helices 20–44. The degree of identity between the sequences obtained from type strain CCAP 1583/4 and T1O1 was 99.82% (corresponding to two single substitutions in

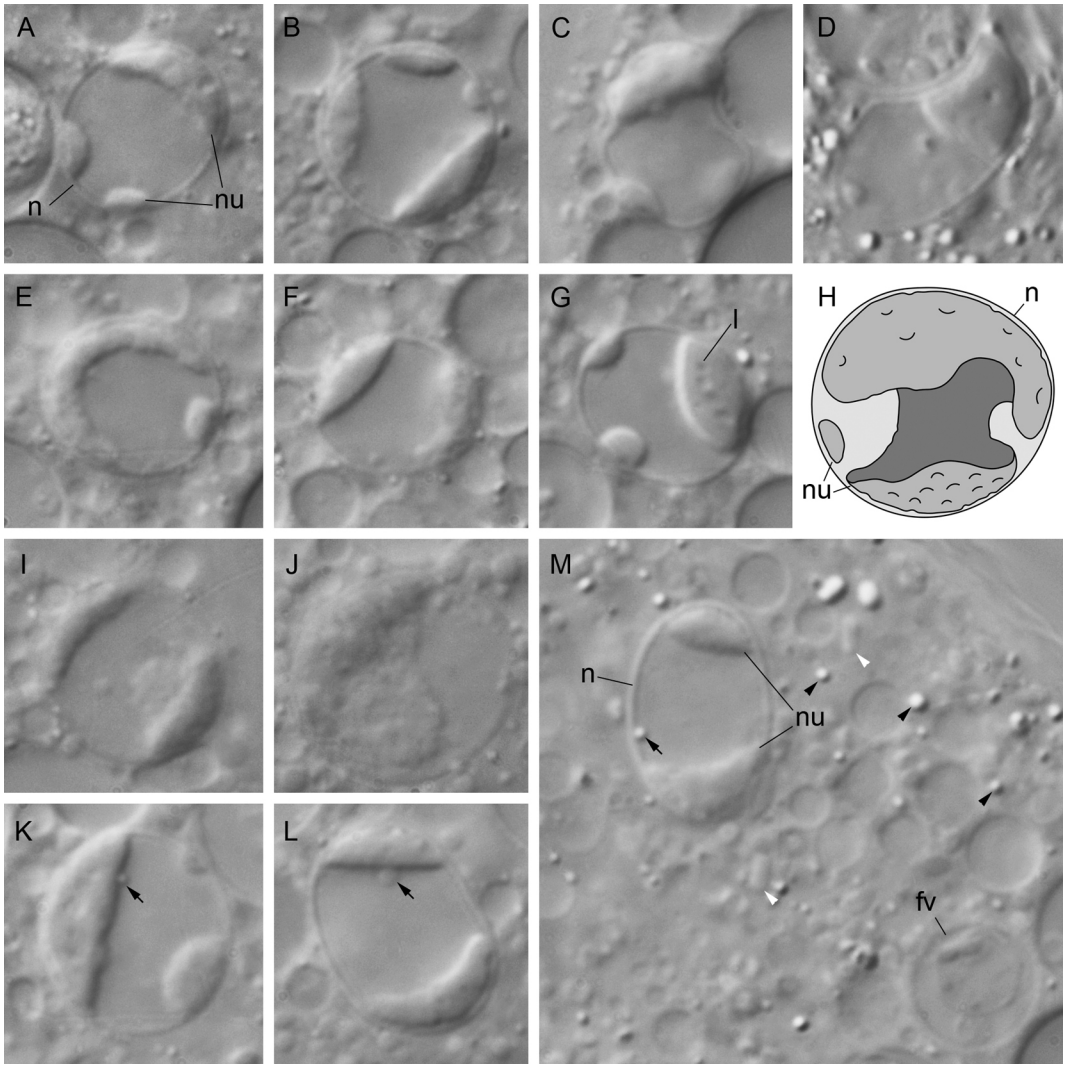

Fig. 2. Light microscopy of the cytoplasm of *T. striata* strain T1O1, DIC. A–G, I –L – Nuclei of *T. striata*; H – schematic drawing of the nucleus of *T. striata*; M – higher magnification of the cell showing granuloplasm, nucleus, and cytoplasmic inclusions. *Abbriviation*: fv – food vacuole; l – lacuna; n – nucleus; nu – nucleolus; black *arrow* – intranuclear spherical body; black *arrowhead* – cytoplasmic spherical body, white *arrowhead* – citoplasmic small granule.

the 1083 bp fragment). Comparison of the sequences of *T. striata* and *T. vumurta* confirmed the presence of motifs unique to this clade in conserved and semi-conserved regions of the 18S rRNA gene (e.g. the 22nd and the end of the 21st helices) (Mesentsev et al., 2022).

Comparison of the obtained sequence with other sequences named *T. striata* (OQ134482 and OQ134483) showed significant differences in conserved regions (Patsyuk, 2023). The two sequences are almost identical. BLAST analysis of these sequences showed a high degree of similarity (more than 99%, at 1613 bp) to the sequence of *Thecamoeba* sp. ATCC PRA-35. The strain ATCC PRA-35 was initially identified as a Thecamoeba-like organism (Yoon et al., 2008), but was later described as *Parvamoeba monura* (Himatismenida) (Cole et al., 2010). Despite the re-description of strain ATCC PRA-35 and the change in its systematic position, the sequence is still listed in NCBI as *Thecamoeba* sp. This appears to be partly responsible for the misidentification of sequences OQ134482 and OQ134483. This highlights the need for critical evaluation of GenBank sequence annotations. At the same time, the data obtained by Patsyuk (2023) raise some questions. The material used to obtain the

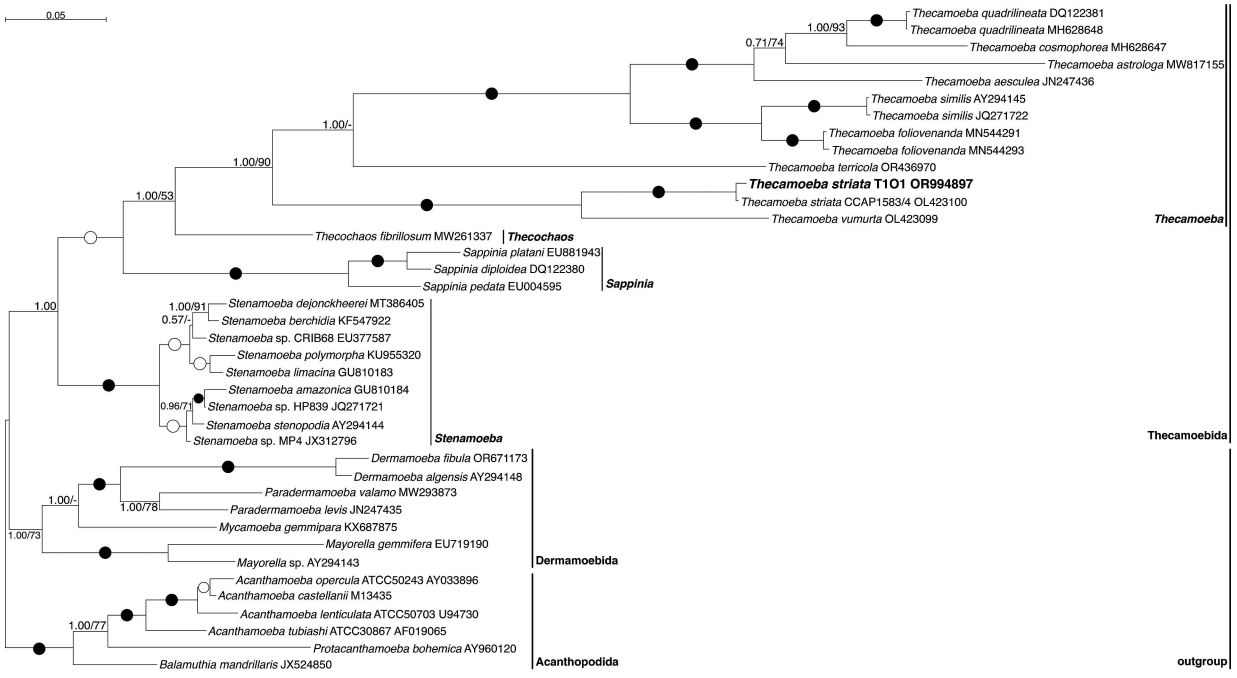

Fig. 3. Molecular phylogenetic tree based on 18S rRNA gene sequences of all named species belonging to Thecamoebida and some species of Dermamoebida and Acathopodida used as outgroup. 1655 sites used in the analysis. Node supports indicated as PP/BS values; black circles mark fully supported nodes (1.0/100 support), white circles mark highly supported nodes (PP>0.95 and BS>95).

sequences were amoebae isolated from freshwater habitats. However, both known representatives of the genus *Parvamoeba* are marine amoebae (Rogerson, 1993; Cole et al., 2010).

Identification and geographical distribution of "*T. striata* species group"

Despite the presence of clearly visible characters in cell morphology and nuclear morphology, there are many identifications of amoebae of the genus *Thecamoeba* in the literature that apparently do not correspond to the original descriptions and modern species boundaries. There are cases where striate amoebae with a vesicular nucleus have been identified as *T. striata* (e.g. Bovee, 1953; Pappas, 1954), although in modern understanding this set of characters corresponds to the species T. *quadrilineata* (Page, 1977). Part of the reason for this misidentification may be the uncertainty about the morphology of the nucleus that remains from Penard's work. In the original description, Penard (1890) characterised *T. striata* as an amoeba with peripheral opposite nucleoli. In later studies, Penard pointed out that the nuclei of *T. striata* had a compact nucleolus, often containing lacunae that could be large enough to give the nucleolus the appearance of a peripheral ring, which could be fragmented (Penard, 1902, 1905). The restructuring of nucleoli proposed by Penard erased the clear morphological boundaries between the striate amoebae of the species *T. striata* and *T. quadrilineata* in the modern sense (Page, 1988). This confusion persisted until the neotypification of both species by Page (1971, 1977). However, names such as "*Amoeba striata*" or "*Striamoeba striata*" can also be found in some relatively recent papers (e.g. Jiang and Shen, 2003, 2005; Liu et al., 2008). The use of such names, especially "*Striamoeba striata*", may indicate the use of outdated identification keys, e.g. those by Bovee, who also did not distinguish between *T. quadrilineata* and *T. striata* (Bovee, 1953). In most of these studies, it is not possible to verify the correctness of the species identification, because no detailed illustrative material was provided.

However, even correct morphological identification without the use of molecular methods cannot be considered reliable. A sibling species, *T. vumurta*, has been described for *T. striata* (Mesentsev et al., 2022). This species cannot be distinguished on the basis of the morphology of individual cells because their size ranges overlap, while minute differences

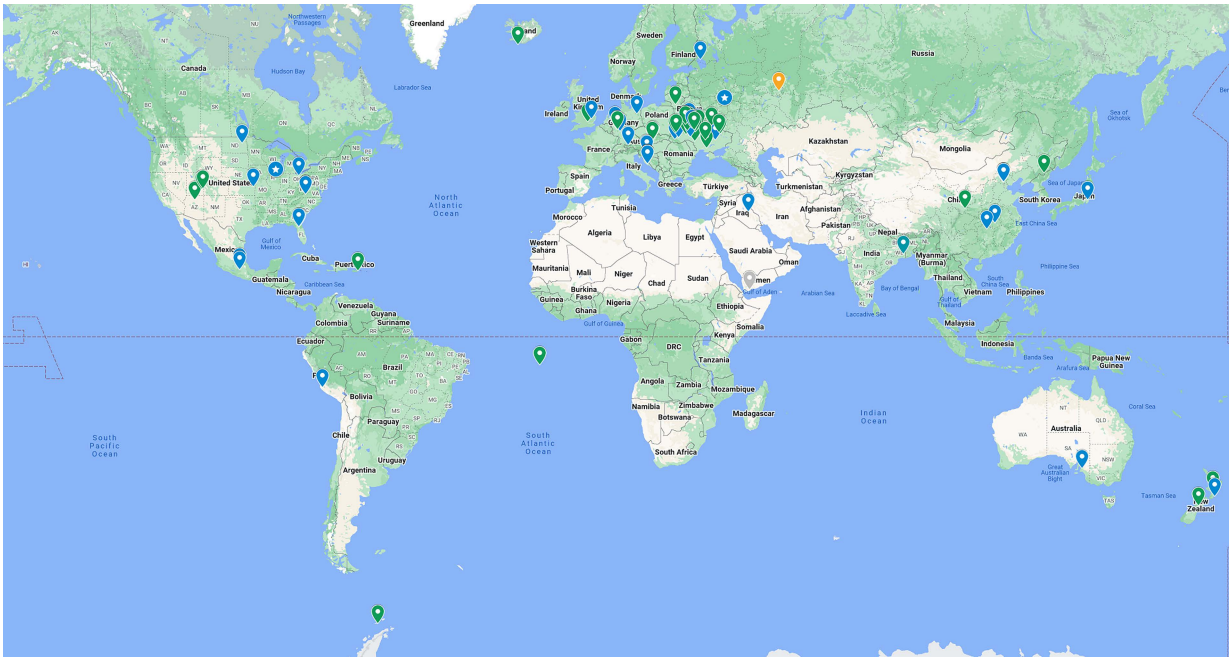

Fig. 4. Map showing the finding sites of "*T. striata* species group". Circle marker with a star – a molecular confirmed finding of *T. striata*; green marker – terrestrial habitat; blue marker – freshwater habitat; gray marker – unidentified habitat, orange marker – finding of *T. vumurta*.

in the morphology of the nucleus are not constant features. The lack of molecular identification in most faunistic studies suggests that the isolated amoebae may belong to the "*T. striata* species group" rather than the species *T. striata*.

Amoebae of the "*T. striata* species group" have been recorded almost all over the world (Fig. 4; Table 2): repeatedly in Eurasia and North America, and once in South America and Australia. The closest records to the poles have been made near the polar circles: on Surtsey Island near Iceland in the north and on Livingston Island near Antarctica in the south. There is evidence of their presence on islands quite far from the mainland; in addition to the islands near the Arctic Circle, there are references to their discovery in Puerto Rico, Ascension Island and New Zealand. An interactive map of isolation sites for amoebae identified as *T. striata* is also available at the following link: https://www.google.com/maps/d/u/0/edit?mid=18XSybJUxUEqmWHeOVZMPdukgbMNTXqE&usp= sharing.

Generally, these works indicate that these amoebae are isolated from the bottom sediments of lakes and rivers, from the water column and groundwater, and there is also evidence of their presence on the surface of freshwater soft-shelled turtles. In terrestrial habitats, they have been isolated from samples of various soils, cyanobacterial mats, lichens, mosses, tree bark and leaf litter. In addition to isolation from natural habitats, amoebae identified as *T. striata* have been found in water samples from urban swimming pools (Rivera et al., 1983) and municipal wastewater treatment systems of various designs (Liu et al., 2008).

Almost all faunal studies lack photographs or other images of the amoebae to verify the correct identification of the organisms found. The need for such verification arises in the context of the difficulties in distinguishing *T. quadrilineata* from *T. striata*, and the unclear origin of the two *T. striata* sequences in GenBank (both cases are described above). We can only speak with confidence of a few cases of reliable isolation of amoebae belonging to the "*T. striata* species group": Wisconsin, USA and Cambridge, UK (Page, 1971, 1977), Moscow, Russia (Surkova et al., 2022) and Izhevsk, Russia (Mesentsev et al., 2022). Even these few data indicate a wide distribution of amoebae of this morphological species, but only in the Northern Hemisphere.

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Table 2. Findings of amoebae of the "*T. striata* species group".

No	Reference	Geographic location	Sample type	Habitat
1	Penard, 1890	Germany, Wiesbaden	pond, bottom sediment (?)	aquatic
2	Edmondson, 1920	USA, North Dakota, Stump lake	plant infusion from the lake	aquatic
3	Stout, 1958	New Zealand, in central North Island near Waiouru (Thornton, 1958)	Taupo hill soil, the topsoil (2- 4 in.) between tussock plants and the topsoil near to the tussock plants	terrestrial
4	Stout, 1958	New Zealand, Canterbury, Black Range near Bealey (Thornton, 1958)	Tekoa steepland soil, the topsoil (2- 4 in.) between tussock plants and the topsoil near to the tussock plants	terrestrial
5	Stout, 1960	New Zealand, near Waiouru (Stout, 1958)	brown and in-rolled tussock leaves	terrestrial
6	Bovee, 1960	USA, Virginia, Giles County, Mountain Lake region	water, some surface and bottom detritus from the small muddy, turbid pool at piped spring	aquatic
7	Bovee, 1960	USA, Virginia, Giles County, Mountain Lake region	water, some surface and bottom detritus from shallow, rain-filled rock pool Bald Knob of Salt Pond Mt., with lechens and dead leaves	aquatic
8	Bovee, 1960	USA, Virginia, Giles County, Mountain Lake region	water, some surface and bottom detritus from small brook in gully parallelling main pond creek draining pond seepage	aquatic
9	Stout, 1963	UK, Chiltern Hills, The acid mull site: Oaken Grove	loose overlying litter consisted predominantly of beech leaves with some twigs and some ash leaves	terrestrial
10	Stout, 1963	UK, Chiltern Hills, The calcareous mull site: Hobbs Hill	granular, chalky soil also with many fine roots	terrestrial
11	Bovee, 1965	USA, Florida, Gainesville, culvert under NW 16th Avenue at the north end of NW 19th Street.	slightly polluted water from the flowing stream	aquatic
12	Bovee, 1965	USA, Florida, Gainesville, rural creek (Lazonby's Branch)	water from creek accepted runoff from several small suburban areas and a cattle pasture, and has meandered slowly through dense woodland ; seldom any evidence remaining of pollution, human or industrial	aquatic
13	Page, 1971	USA, Wisconsin, Janesville, edge of Rock River	Bottom sediment (?)	aquatic
14	Holmberg and Pejler, 1972	Iceland, Surtsey island	moss patches 1 m S of the fenced area	terrestrial
15	Page, 1977	UK, River Great Ouse (Old West River)	Bottom sediment (?)	aquatic
16	Robinson, 1980	Australia, Adelaida	water samples	aquatic
17	Bovee, 1981	USA, Kansas, Kansas river near Lawrence	the surface of the smooth softshell turtl from Kansas river	aquatic
18	Rivera et al., 1983	Mexica, Mexico	water from indoor and outdoor swimming pools	aquatic
19	Stout, 1984	New Zealand, south-east of North Island, Ngakawau, 4.5 km south-west of Castlepoint	the surface 2.5 cm of topsoil seasonally flooded grassland. From the negative control area or experimental area with treatment of insecticide/ nematicide	aquatic
20	Flößner et al., 1985	Germany, Lake Stechlin	–	aquatic
21	Inamori Y. et al., 1987	Japan, Lake Kasumigaura	–	aquatic
22	Guhl, 1987	Germany, Düsseldorf, Baggersee Eller lake	the surface water	aquatic
23	Das et al., 1993	India, Kamarkundu, Calcutta and Hughly districts	Soil and freshwater	aquatic and terrestrial
24	Smirnov and Goodkov, 1996	Russia, Republic of Karelia, Ladoga lake, Valaamo Island, Leshchevo lake	upper 10 cm of sediments	aquatic

Table 2. Continuation.

No	Reference	Geographic location	Sample type	Habitat
25	Herdendorf et al., 2000	USA, Ohio, Old Woman Creek Estuary	–	aquatic
26	Mrva, 2003	Slovakia, Dechtice, Naháč, Katarínka	dendrotelmae (sediment with decaying leaves, water)	terrestrial
27	Jiang et al., 2003	China, River Hanjiang	The PFU (Polyurethane foam Unit) method	aquatic
28	Bamforth, 2004	USA, Arizona, Grand Canyon	Crusts compounded by Cyanobacteria, or Bryophytes, or together	terrestrial
29	Golemansky and Todorov, 2004	Antarctica, Livingston Island, Hurd Peninsula	moss	terrestrial
30	Mrva, 2005	Slovakia, Malé Karpaty Mts., Fúgelka (Zlinská et al., 2005)	3 km NW from the village of Dubová, oak-hornbeam forests, mosses growing on soil	terrestrial
31	Mrva, 2005	Slovakia, Malé Karpaty Mts., Naháč, Katarínka (Zlinská et al., 2005)	old oak-hornbeam forest stand under the monastery ruins, mosses growing on soil	terrestrial
32	Mrva, 2005	Slovakia, Trnavská pahorkatina hills, Lindava (Zlinská et al., 2005)	1 km on E from the village of Píla, oak-hornbeam forests, mosses growing on soil	terrestrial
33	Mrva, 2005	Slovakia, Malé Karpaty Mts., Lošonec-lom quarry (Zlinská et al., 2005)	oak-hornbeam forests, mosses growing on soil	terrestrial
34	Jiang and Shen, 2005	China, Hunan, Changde	The PFU blocks placed at the depth of 1 m below the surface water for 15–20 days	aquatic
35	Khaled and Saeed, 2006	Yemen, Lahej Governorate, Al-Anad bridge, Tuban valley	–	-
36	Wilkinson and Smith, 2006	Ascension Island, Sisters Peak	Moss and lichen "crust" just below the summit. Soil; arid, limited plant cover e.g. Ipomoea pescaprae	terrestrial
37	Bamforth, 2007	USA, Puerto Rico, The Luquillo National Forest	In tabonuco forest: - soil under the litter on 30° slope. - litter on riparian soil, a young soil due to periodic floodin - litter on riparian soil and soil; many palm fronds on ground	terrestrial
38	Bamforth, 2007	USA, Puerto Rico, The Luquillo National Forest	Liana adventitious roots in palo verde and tabonuco zones: - moss covered soil between liana roots and rock. - between liana adventitious roots attaching to tree trunk.	terrestrial
39	Bamforth, 2008	USA, Utah, the ''Island in the Sky'' area of Canyonlands National Park	Three crusts, a cyanobacteria (Microcoleus), a Scytonema/Nostoc lichen, and a black moss, Syntrichia caninervis, were collected from a shallow sandy soil	terrestrial
40	Bamforth, 2008	USA, Utah, Kane Creek Road, near Moab	crust was composed of two lichens, Fulgensis bracteata and Squarmarina lentigera, on an exposed evaporate containing gypsum	terrestrial
41	Liu et al., 2008	China, Beijing, Gaobeidian	wastewater treatment systems	aquatic
42	Liu et al., 2008	China, Beijing, Qinghe	wastewater treatment systems	aquatic
43	Liu et al., 2008	China, Beijing, Beixiaohe	wastewater treatment systems	aquatic
44	Liu et al., 2008	China, Beijing, Jiuxianqiao	wastewater treatment systems	aquatic
45	Zou et al., 2009	China, Xiaolong Mountains, National Nature Reserve, Mayan Forest Region	soil	terrestrial
46	Ramirez et al., 2009	Mexico, Mexico	wells of the Zacatepec aquifer	aquatic
47	Paziuk, 2010	Ukraine, Zhytomyr Oblast, near Radomyshl'	water samples from the lake with sandy bottom	aquatic

Table 2. Continuation.

No	Reference	Geographic location	Sample type	Habitat
48	Šatkauskiene, 2012	Lithuania, near highway Vilnius-Prienai-Marijampolë	lichen on the soil (turf and sandy loam) along the road	terrestrial
49	Patsyuk, 2012	Ukraine, Zhytomyr Oblast, Kam'yanka river	–	aquatic
50	Patsyuk, 2013	Ukraine, Zhytomyr and Volyn' parts of Ukrainian Polesia	fresh water	aquatic
51	Michel et al., 2014	Austria,Tyrol, Tannheim, Grotto Tannheim	–	-
52	Patsyuk, 2014a	Ukraine, Zhytomyr and Volyn' parts of Ukrainian Polesia	water of river, bog, canal and floodplain	Aquatic
53	Patsyuk, 2014b	Ukraine, Kyev Polesia	bottom sediment	aquatic
54	Fang et al., 2014	China, Changbai Mountains	soil	terrestrial
55	Dominska et al., 2015	Ukraine, Zhytomyr, Huiva river	–	aquatic
56	Patsyuk, 2016	Ukraine, Zhytomyr, Teterev river	the upper layer of bottom sediments and the near-bottom layer of water	aquatic
57	Corsaro et al., 2017	Germany, Andernach	bark of a sycamore tree	terrestrial
58	Špoljar et al., 2017	Croatia, North West Croatia, Sutla river	the complex and submerged C. demersum in the littoral zone of shallow water body	aquatic
59	Špoljar et al., 2017	Croatia, North West Croatia, Zajarki gravel pit	floating-leaved yellow waterlily, N. lutea in the littoral zone of shallow water body	aquatic
60	Patsyuk, 2017	Ukraine, small standing water body near the Dnieper	the upper layer of bottom sediments and the near-bottom layer of water	aquatic
61	Patsyuk, 2018	Ukraine, Zhytomyr Oblast, Hnylop'yat' river	upper layer of bottom sediment representsed by sands occupied by higher aquatic plants (0-15 cm)	aquatic
62	Mattos Conislla et al., 2018	Peru, Huacachina, Regional Conservation Area (ACR) "Laguna de Huacachina"	water samples	aquatic
63	Lordan, 2018	Croatia, Krka, Roski Slap	glass substrate in fast and slow flows in the water	aquatic
64	Patsyuk and Uvayeva, 2019	Ukraine, Zhytomyr Oblast , Sinevir lake	the upper layer of bottom sediments and the near-bottom layer of water	aquatic
65	Patsyuk and Uvayeva, 2019	Ukraine, a floodplain pond near Ivano-Frankivsk	the upper layer of bottom sediments and the near-bottom layer from floodplain pond	aquatic
66	Olehnovich et al., 2020	Ukraine, Rivne Oblast, Sarny Raion	soil sample; pine forest with lichen; soil - weak sub-leaved, clay-sandy	terrestrial
67	Olehnovich et al., 2020	Ukraine, Zhytomyr Oblast, Turchynets'ke Lisnytstvo	soil sample; oak forest, gray forest soils	terrestrial
68	Olehnovich et al., 2020	Ukraine, Zhytomyr Oblast, Bohuns'ke Lisnytstvo	soil sample; hornbeam-oak forest; gray forest soils	terrestrial
69	Olehnovich et al., 2020	Ukraine, Zhytomyr Oblast, Zytomirs'ke Lisove gospodarstvo	soil sample; hornbeam-oak-pine forest, gray forest soils	terrestrial
70	Olehnovich et al., 2020	Ukraine, Vinnytsia Oblast, Chechel'nyts'k Raion	soil sample; oak forest, gray forest soils	terrestrial
71	Olehnovich et al., 2020	Ukraine, Lviv Oblast	soil sample; oak-beech forest; gray forest soils	terrestrial
72	Olehnovich et al., 2020	Ukraine, Kiyv Oblast	soil sample; hornbeam-oak forest; gray forest soils	terrestrial
73	Olehnovich et al., 2020	Ukraine, Sumy Oblast	soil sample; maple-linden-oak forest, dark-gray silty soils	terrestrial
74	Olehnovich et al., 2020	Ukraine, Khmelnytskyi Oblast	soil sample; hornbeam-oak forest, degraded chernozems	terrestrial

Table 2. Continuation.

No	Reference	Geographic location	Sample type	Habitat
75	Olehnovich et al., 2020	Ukraine, Kharkiv Oblast	soil sample; maple-linden-oak forest; gray forest soils	terrestrial
76	Patsyuk, 2020a	Ukraine, Zhytomyr Oblast, Berdychiv Raion	soil from oak forest	terrestrial
77	Patsyuk, 2020a	Ukraine, Zhytomyr Oblast, Popilnya Raion	soil from oak forest	terrestrial
78	Patsyuk, 2020a	Ukraine, Zhytomyr Oblast, Novograd-Volhynsky Raion	soil from oak forest	terrestrial
79	Patsyuk, 2020a	Ukraine, Zhytomyr Oblast, Baraniv Raion	soil from mixed foreststst	terrestrial
80	Patsyuk, 2020a	Ukraine, Zhytomyr Oblast, Lyubar Raion	soil from mixed foreststst	terrestrial
81	Patsyuk, 2020b	Ukraine, Zhytomyr Oblast , Novohrad-Volynsky Raion	mosses, lichens	terrestrial
82	Patsyuk, 2020b	Ukraine, Zhytomyr Oblast , Olevsk Raion	mosses	terrestrial
83	Patsyuk, 2020c	Ukraine, Rivne oblast, Sarny raion	moss and soil	terrestrial
84	Patsyuk, 2020c	Ukraine, Zhytomyr Oblast	soil	terrestrial
85	Patsyuk, 2020c	Ukraine, Zhytomyr Oblast	moss and soil	terrestrial
86	Patsyuk, 2020d	Ukraine, Kharkiv Oblast	soil sample from the forest	terrestrial
87	Patsyuk, 2020e	Ukraine, Vinnytsia Oblast, Floodwater reservoir near the Lemeshivka village	the upper layer of bottom sediments and the near-bottom layer of water	aquatic
88	Patsyuk, 2020e	Ukraine, Vinnytsia Oblast, the river near the Zhmerynka city	the upper layer of bottom sediments and the near-bottom layer of water	aquatic
89	Michel et al., 2021	Germany, Mayen-Koblenz District, Rhineland-Palatinate, Bendorf	sycamore tree	terrestrial
90	Gulin et al., 2021	Croatia, Krka River	permanent streams in the site where water had been present before and after A. altissima removal and displaying well-developed moss cover	aquatic
91	Gulin et al., 2021	Croatia, Krka River	newly reactivated streams	aquatic
92	Gulin et al., 2021	Croatia, Krka River	newly reactivated streams	aquatic
93	Patsyuk, 2022	Ukraine, Mykolaiv region	soil samples; the dark chestnut chernozems	terrestrial
94	Patsyuk, 2022	Ukraine, Khmelnytsky region	soil samples; the podzolized chernozems	terrestrial
95	Patsyuk, 2022	Ukraine, Kirovohrad region	soil samples; the weakly podzolic clayey sandgrounds	terrestrial
96	Patsyuk, 2022	Ukraine, Rivne region	soil samples; grey podzolic soils	terrestrial
97	Patsyuk, 2022	Ukraine; Lviv and Zhytomyr regions	soil samples; forest grey soils	terrestrial
98	Surkova et al., 2022	Russia, Moscow, Sobachiy Pond	bottom sediment	aquatic
99	Kadhim, 2022	Iraq, Baghdad City	Tigris riverbank, the samples of water were obtained using plankton net	aquatic
100	Patsyuk and Konstantynenko, 2022	Ukraine, Zhytomyr Oblast	bottom sediment	aquatic
101	Mesentsev et al., 2022	Russia, Izhevsk, Shkolnii pond	bottom sediment	aquatic
102	Patsyuk et al., 2023	Ukraine, Zhytomyr Oblast, Korostishivski region	forest soil	terrestrial

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