Diversity and Distribution of Naked Amoebae in Different Types of Water Bodies in Ukraine

Ann. Zool. Fennici 63: 1–20
Helsinki 13 February 2026
eISSN 1797-2450

Diversity and distribution of naked amoebae in different types of water bodies in Ukraine

Marina Patsyuk

Zhytomyr Ivan Franko State University, 40, Velyka Berdychivska Str., Zhytomyr, 10008, Ukraine (e-mail address: kostivna@ukr.net)

Received 27 Aug. 2025, final version received 22 Dec. 2025, accepted 23 Dec. 2025

Patsyuk M. 2026: Diversity and distribution of naked amoebae in different types of water bodies in Ukraine. — *Ann. Zool. Fennici* 63: 1–20.

Forty-four species of naked amoebae were identified across different types of water bodies in Ukraine. The highest number of species was recorded in rivers (44 species), while the lowest was found in swamps (15 species); 27 species were found in floodplains and 23 species in lakes. Based on cluster analysis, two distinct species complexes were identified: one for swamps and another encompassing lakes, floodplains and rivers. The specificity of the species complexes of naked amoebae was determined by abiotic factors of the aquatic environment, such as water temperature, dissolved oxygen concentrations and organic substances in water, analysed using the permanganate oxidation method. According to the Chekanovsky–Sørensen index of similarity, a high degree of similarity was observed between the studied water bodies. In freshwater bodies, species of naked amoebae are unevenly distributed and form species complexes differentiated by key environmental factors.

Introduction

Naked amoebae are a group of protists that, according to the modern classification system of Eukaryotes, belong to three molecular clades: Tubulinea, Discosea and Evosea (Adl *et al.* 2019). Despite numerous molecular phylogenetic studies (Cavalier-Smith *et al.* 2004, Kang *et al.* 2017), their exact placement within the Eukaryotic tree remains under discussion. Characteristic morphological features include the lobopodia—cytoplasmic projections involved in movement—and the use of an actomyosin-based cytoskeleton devoid of microtubules for locomotion.

Naked amoebae remain a poorly studied component of aquatic biocoenoses, although the role of these protists in their functioning has long been known. These organisms are an essential link in the microbial food chains, which play an important role in the transformation of matter and energy in water bodies. Naked amoebae are good indicators of the state of the aquatic environment, since they are characterised by a rapid response to even slight environmental influences (Arnd 1993). By forming cysts, naked amoebae can withstand sharp changes that occur in water bodies; however, only about 40% of the described species of naked amoebae are capable of forming resting cysts. From natural samples, usually only the active forms (trophozoites) are selected and identified and subsequently studied under laboratory conditions. Most species of naked amoebae lose their ability to form cysts in culture (Page & Siemensma 1991).

In favourable conditions, naked amoebae enter an active state, reflecting the degree and nature of pollution of the aquatic environment. Observations of amoebae thus provide meaningful information about processes occurring in a water body. Many issues related to biodiversity, autecology and organisation of species complexes of naked amoebae remain unresolved. It is unclear which factors determine the formation of species complexes or how changes in habitat affect their structural organisation. In ecological and faunal studies of protists, naked amoebae are rarely considered (Finlay & Clarke 1999; Finlay *et al.* 2006; Payne 2013). This is due to difficulties associated with sampling and species identification. Species determination requires the isolation of amoebae in culture, followed by propagation and study (Page & Siemensma 1991). Consequently, only limited knowledge exists about the distribution patterns of naked amoebae.

According to Foissner (2008), small cell size and the ability to form resting stages (cysts) allow naked amoebae to disperse over long distances via air and sea currents and to persist in different locations until favourable conditions occur. However, this view cannot be confirmed or refuted due to the lack of data on the autecology of naked amoebae. Therefore, the aim of this study is to establish the species composition of naked amoebae in different types of Ukrainian water bodies and to examine how key environmental factors affect their distribution in freshwater habitats.

Material and methods

Sampling took place in Ukraine during 2014–2021. It was designed to identify naked amoebae and to examine the relationship between their species composition and environmental factors. This study used data from Patsyuk (2024), supplemented with 58 additional samples; in total, more than 1700 freshwater samples were collected and analysed. New samples were collected from the Tereblya River in the Khust and Tyachiv Rayon of Zakarpattia Oblast, the Pripyat River in Rivne Oblast, and the Prut River near the slopes of Mount Hoverla. The selection of sampling sites aimed to ensure representativeness and to account for the diversity of environmental conditions in Ukrainian water bodies. Compared to other regions, water bodies in Western Ukraine are characterised by a low content of organic substances, minimal anthropogenic load and high water transparency, the latter being an important indicator of their purity.

Samples were taken from the bottom soil of water bodies with a small amount of bottom water (Appendices 1 and 2). Subsamples of 1 mL were taken with a sterile instrument and inoculated onto non-nutrient agar in Petri dishes. For the propagation of naked amoebae, culture media based on Prescott-James solution with the addition of rice grains were used (Page & Siemensma 1991). The Prescott-James solution was prepared as follows: Solution 1: 0.433 g of $CaCl_2 \cdot 2H_2O$ and 0.162 g KCl was dissolved in 100 mL of distilled water. Solution 2: 0.512 g of K_2HPO_4 was dissolved in 100 mL of distilled water. Solution 3: 0.280 g of $MgSO_4 \cdot 7H_2O$ was dissolved in 100 mL of distilled water. 1 mL of each solution was mixed and 997 mL of distilled water added.

Naked amoebae were propagated under laboratory conditions at room temperature. Each Petri dish was examined every eight days for one month. Amoebae were propagated by removing one cell at a time with a long Pasteur pipette from the original medium and transferring it to a dish with fresh medium. Only one morphological species was seeded into a Petri dish. Amoebae were studied using a light microscope (Axio Imager M1) with differential interference contrast. Species were determined based on a set of morphological characters, including the morphology of the locomotor form; nature of the cytoplasm flow (uniform or eruptive); presence or absence of uroid structures; presence of pseudopodia, subpseudopodia or dactylopodia; and formation of a floating form. The taxonomic key of Page (Page & Siemensma 1991) was used. Identification of 20 species was confirmed using 18S rRNA gene sequences, including *Amoeba proteus* (NCBI GenBank accession ON907618), *Saccamoeba limax* (OP894078), *Saccamoeba* sp. (MZ079370), *Thecamoeba striata* (OQ134482), *Thecamoeba similis* (OL604177), *Thecamoeba quadrilineata* (ON398269), *Thecamoeba* sp. (MZ079371), *Stenamoeba stenopodia* (OP375108), *Korotnevella stella* (ON398267), *Vexillifera bacillipedes*

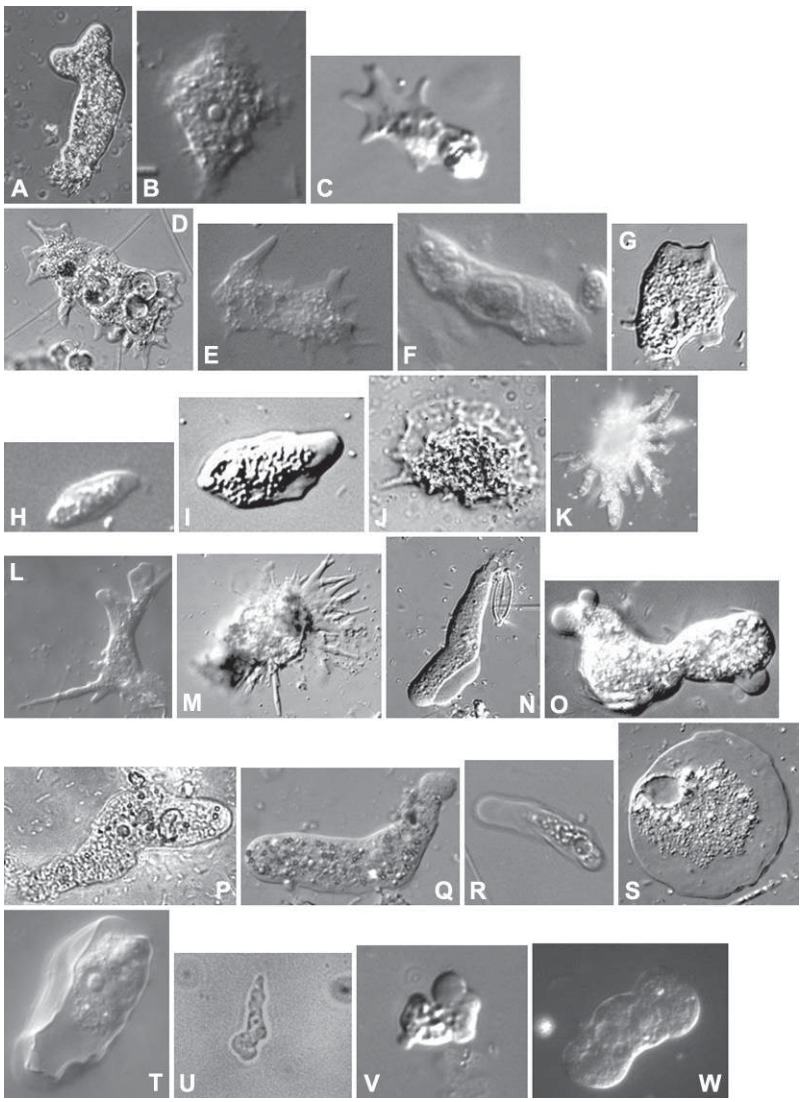

Fig. 1. Types of naked amoebae, identified by morphological characters. — **A**: *Deuteramoeba mycophaga*. — **B**: *Flamella* sp. — **C**: *Korotnevella diskophora*. — **D**: *Mayorella cantabrigiensis*. — **E**: *Mayorella penardi*. — **F**: *Mayorella viridis*. — **G**: *Mayorella* sp. (2). — **H**: *Paradermamoeba levis*. — **I**: *Paradermamoeba valamo*. — **J**: *Pellita digitata*. — **K**: *Polychaos dubium*. — **L**: *Rhizamoeba* sp. (1). — **M**: *Rhizamoeba* sp. (2). — **N**: *Saccamoeba stagnicola*. — **O**: *Saccamoeba wakulla*. — **P**: *Saccamoeba* sp. (1). — **Q**: *Saccamoeba* sp. (2). — **R**: *Stenamoeba stenopodia*. — **S**: *Thecamoeba sphaeronucleolus*. — **T**: *Thecamoeba verrucosa*. — **U**: *Vahlkampfia* sp. (1). — **V**: *Vahlkampfia* sp. (2). — **W**: *Vahlkampfia* sp. (3).

(OK649262), *Vannella lata* (OL305063), *Vannella* sp. (MZ079372), *Ripella* sp. (MZ079369), *Mayorella vespertilioides* (OP739500), *Mayorella* sp. (OP729930), *Acanthamoeba* sp. (MZ079366), *Cochliopodium actinophorum* (MZ079367), *Cochliopodium minus* (OK649264), *Vahlkampfia avara* (OP179657) and *Willaertia magna* (OK649263) (Patsyuk 2023). The remaining 22 species were identified based on morphological characteristics (Fig. 1).

Additionally, water samples were taken to determine physical and hydrochemical parameters. Water temperature was measured using a calibrated mercury thermometer with a graduation of 0.1–0.5 °C. The concentration of dissolved oxygen in water was determined using the Winkler method following Nabyvanets *et al.* (2007). This method is based on the reaction of dissolved oxygen with manganese hydroxide in an alkaline medium, under which conditions dissolved oxygen is quantitatively fixed. During subsequent dissolution of the $MnO(OH)_2$ precipitate in acid with an excess of potassium iodide, iodine is released in an amount equivalent to the dissolved oxygen content. The released iodine is titrated with a sodium thiosulfate solution using

starch as an indicator. The concentration of dissolved oxygen is calculated from the volume of sodium thiosulfate solution consumed for titration, according to the formula given by Nabyvanets *et al.* (2007):

$$X_k = \frac{V \times K \times 8 \times 1000}{V_1 - V_2} \quad (1)$$

where X_k is the concentration (mg/dm^3) of dissolved oxygen in water, V the volume (mL) of titrated sodium thiosulfate solution used for titration, K the titre of sodium thiosulfate solution, V_1 the volume (mL) of the oxygen flask, V_2 the total volume (mL) of reagents added to the flask during oxygen fixation, and 8 the oxygen equivalent.

For the analysis of organic matter in freshwater bodies, the Kubel method was used, based on the oxidation of organic substances by potassium permanganate in a sulphuric acid solution during boiling. Calculations were carried out using the formula given by Nabyvanets *et al.* (2007):

$$C_x = \frac{8N(n_1 - n_2) \times 1000}{V} \quad (2)$$

where C_x is the concentration of organic matter (mg O_2/L), N the normality of the thiosulfate solution, n_1 the volume (mL) of thiosulfate solution used to titrate the control sample, n_2 the volume (mL) of thiosulfate solution used to titrate the water sample, and V the volume (mL) of the water sample.

Since the available methods could not provide data on the abundance of naked amoebae, we determined the frequency of occurrence of species (R), defined as the proportion of samples in which a species occurred relative to the total number of samples studied (Barnes 1989).

To analyse the distribution of naked amoebae in different types of water bodies, the sampling sites were classified into swamps, rivers, lakes and floodplains based on the classification of continental water bodies by Romanenko (2001). Calculations were performed using Microsoft Excel (2002) and PAST version 3.11 (Hammer *et al.* 2001) software packages. Cluster analysis with bootstrap analysis for 1000 permutations and non-metric multidimensional scaling (nMDS) were applied (Legendre & Legendre 1998). nMDS was performed using the algorithm implemented in the program PAST version 3.11 (Hammer *et al.* 2001). In this study, direct ordination illustrates the relationship between the species composition of naked amoebae in different habitats and environmental factors.

The Chekanovsky–Sørensen (*Ichs*) and Shimkevich–Simpson (*Ishs*) indices were used to compare faunal lists (Ramette 2007):

$$Ichs = \frac{2c}{a + b} \quad (3)$$

$$Ishs = \frac{c}{\min(a,b)} \quad (4)$$

where c is the number of shared species between two data sets (samples or sampling plots), and a and b the numbers of elements in the first and second data sets.

Results

In total, we found 44 species of naked amoebae in the water bodies of Ukraine during the study period in 2014–2021. Species richness was greatest in rivers, where all 44 species were recorded. The lowest species richness was recorded from swamps (15 species), while 27 species were recorded in floodplain water bodies and 23 species in lakes.

Of the 44 identified species of naked amoebae, 11 (25%) were found in all four types of water bodies. These include the following species: *Rhizamoeba* sp. (1), *T. striata*, *S. stenopodia*, *Mayorella* sp. (1), *V. bacillipedes*, *Ripella* sp., *V. lata*, *Acanthamoeba* sp., *C. actinophorum*, *V. avara* and *Vahlkampfia* sp. (2). These species may be considered eurytopic. Ten species (23%) were recorded exclusively in rivers, including *A. proteus*, *P. dubium*, *Saccamoeba* sp. (2), *T. sphaeronucleolus*, *T. similis*, *M. penardi*, *M. viridis*, *P. digitata*, *C. minus* and *W. magna*. The remaining species (52%) occurred in two or

three types of water bodies and were characterised by a broad ecological valence. These include *Rhizamoeba* sp. (2), *D. mycophaga*, *S. stagnicola*, *S. limax*, *S. wakulla*, *Saccamoeba* sp. (1), *Saccamoeba* sp. (3), *T. quadrilineata*, *T. verrucosa*, *T. terricola, Thecamoeba* sp., *P. valamo*, *P. levis*, *M. cantabrigiensis*, *M. vespertilioides*, *Mayorella* sp. (2), *K. stella*, *K. diskophora*, *R. platypodia*, *Vannella* sp., *Flamella* sp., *Vahlkampfia* sp. (1) and *Vahlkampfia* sp. (3).

Most of the detected species were characterised by a low frequency of occurrence (Table 1).

Table 1. The frequency of occurrence (%) of species of naked amoebae in different types of water bodies in Ukraine, including rivers, floodplains, lakes and swamps.

		River	Floodplain	Lake	Swamp
1.	*Rhizamoeba* sp. (1)	10.5	2.8	3.1	3.2
2.	*Rhizamoeba* sp. (2)	1.5	2.0	9.4	0.0
3.	*Amoeba proteus*	0.6	0.0	0.0	0.0
4.	*Polychaos dubium*	0.9	0.0	0.0	0.0
5.	*Deuteramoeba mycophaga*	15.4	7.9	0.0	0.0
6.	*Saccamoeba stagnicola*	27.0	11.2	7.8	0.0
7.	*Saccamoeba limax*	3.2	0.5	0.0	0.0
8.	*Saccamoeba wakulla*	0.7	2.0	0.0	0.0
9.	*Saccamoeba* sp. (1)	1.2	4.0	0.0	0.0
10.	*Saccamoeba* sp. (2)	2.0	0.0	0.0	0.0
11.	*Saccamoeba* sp. (3)	10.5	5.6	7.8	0.0
12.	*Thecamoeba striata*	30.6	15.7	43.8	4.2
13.	*Thecamoeba quadrilineata*	1.4	2.0	0.0	0.0
14.	*Thecamoeba sphaeronucleolus*	1.3	0.0	0.0	0.0
15.	*Thecamoeba verrucosa*	2.3	2.3	0.0	0.0
16.	*Thecamoeba terricola*	1.9	0.0	2.3	0.0
17.	*Thecamoeba similis*	4.1	0.0	0.0	0.0
18.	*Thecamoeba* sp.	10.0	0.0	0.0	11.7
19.	*Stenamoeba stenopodia*	23.9	26.6	6.3	5.3
20.	*Paradermamoeba valamo*	9.9	0.0	2.3	0.0
21.	*Paradermamoeba levis*	9.3	0.0	3.1	0.0
22.	*Mayorella cantabrigiensis*	38.5	13.4	7.8	0.0
23.	*Mayorella vespertilioides*	26.6	7.4	7.8	0.0
24.	*Mayorella penardi*	0.9	0.0	0.0	0.0
25.	*Mayorella viridis*	0.7	0.0	0.0	0.0
26.	*Mayorella* sp. (1)	1.0	4.1	6.3	5.3
27.	*Mayorella* sp. (2)	1.9	6.9	0.0	5.3
28.	*Korotnevella stella*	37.1	11.4	7.8	0.0
29.	*Korotnevella diskophora*	3.9	0.0	6.3	0.0
30.	*Vexillifera bacillipedes*	28.7	15.5	14.1	38.3
31.	*Ripella platypodia*	3.9	10.9	0.0	0.0
32.	*Ripella* sp.	2.5	23.1	6.3	3.2
33.	*Vannella lata*	38.6	9.6	15.6	4.3
34.	*Vannella* sp.	22.1	11.9	0.0	1.1
35.	*Acanthamoeba* sp.	26.2	15.5	13.3	2.7
36.	*Pellita digitata*	3.2	0.0	0.0	0.0
37.	*Cochliopodium actinophorum*	42.7	9.6	7.8	19.7
38.	*Cochliopodium minus*	0.6	0.0	0.0	0.0
39.	*Flamella* sp.	3.3	0.0	4.7	0.0
40.	*Vahlkampfia* sp. (1)	2.7	6.6	0.0	10.6
41.	*Vahlkampfia* sp. (2)	6.0	10.9	5.5	14.9
42.	*Vahlkampfia* sp. (3)	2.5	0.0	6.3	0.0
43.	*Vahlkampfia avara*	24.9	11.4	6.3	29.8
44.	*Willaertia magna*	9.3	0.0	0.0	0.0
Total number of species		44	27	23	15

This is likely due to their rarity and small numbers, rather than stenotopicity.

The distribution of naked amoebae was analysed by comparing species lists from different types of water bodies using the Chekanovsky–Sørensen similarity index (*Ichs*) (Table 2). The analysis showed a relatively high degree of similarity between the studied habitats. Rivers showed high faunal similarity with floodplain water bodies (*Ichs* = 0.76) and lakes (*Ichs* = 0.66), whereas similarity with swamps was lower (*Ichs* = 0.51). Floodplain water bodies exhibited the highest similarity with lakes (0.67) and swamps (0.67), and a high degree of similarity was also observed between lakes and swamps (0.59).

Cluster analysis of species composition separated swamps from the other studied water body types with strong bootstrap support (100%; Fig. 2). The swamp complex included the following species: *Rhizamoeba* sp. (1), *T. striata*, *Thecamoeba* sp., *S. stenopodia*, *Mayorella* sp. (1), *Mayorella* sp. (2), *V. bacillipedes*, *Ripella* sp., *V. lata*, *Vannella* sp., *Acanthamoeba* sp., *C. actinophorum*, *V. avara, Vahlkampfia* sp. (1) and *Vahlkampfia* sp. (2). The water conditions in swamps were distinctive: in their natural state, the water was generally slightly acidic (pH 5.8–6.74), with a relatively high content of organic substances (12.03–46.18 mg O_2/L), a low concentration of dissolved oxygen (4.83–9.64 mg/L) and temperatures of 9–20 °C.

The cluster comprising lakes, floodplains and rivers received moderate bootstrap support (58%; Fig. 2). The following species of naked amoebae were found in these habitats: *Rhizamoeba* sp. (1), *Rhizamoeba* sp. (2), *A. proteus*, *P. dubium, D. mycophaga*, *S. stagnicola*, *S. limax, S. wakulla*, *Saccamoeba* sp. (1), *Saccamoeba* sp. (2), *Saccamoeba* sp. (3), *T. striata*, *T. quadrilineata*, *T. sphaeronucleolus*, *T. verrucosa*, *T. terricola, T. similis, Thecamoeba* sp., *S. stenopodia*, *P. valamo*, *P. levis*, *M. cantabrigiensis*, *M. vespertilioides*, *M. penardi*, *M. viridis*, *Mayorella* sp. (1), *Mayorella* sp. (2), *K. stella*, *K. diskophora*, *V. bacillipedes*, *R. platypodia*, *Ripella* sp., *V. lata*, *Vannella* sp., *Acanthamoeba* sp., *P. digitata*, *C. actinophorum*, *C. minus*, *Flamella* sp., *V. avara*, *Vahlkampfia* sp. (1), *Vahlkampfia* sp. (2), *Vahlkampfia* sp. (3) and *W. magna*. These species were associated with higher water temperatures (2–24 °C), higher levels of oxidisable organic substances (5.01–50.4 mg O_2/L) and higher dissolved oxygen concentrations (5.42–20.04 mg/L). The following species were not found from swamps: *Rhizamoeba* sp. (2), *A. proteus*, *P. dubium, D. mycophaga*, *S. stagnicola*, *S. wakulla*, *Saccamoeba* sp. (1), *Saccamoeba* sp. (2), *Saccamoeba* sp. (3), *T. quadrilineata*, *T. sphaeronucleolus*, *T. verrucosa*, *T. terricola, T. similis, P. valamo*, *P. levis*, *M. cantabrigiensis*, *M. vespertilioides*, *M. penardi*, *M. viridis*, *K. stella*, *K. diskophora*, *R. platypodia*, *P. digitata*, *C. minus*, *Flamella* sp., *V. avara, Vahlkamp-*

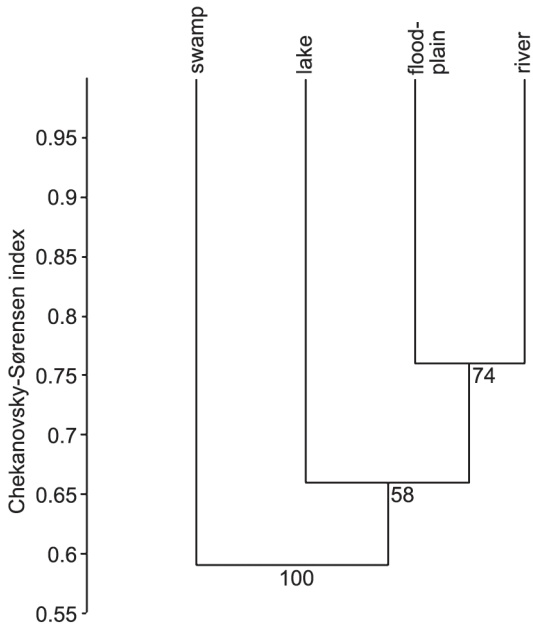

Fig. 2. Distribution of naked amoebae in water bodies of different types in Ukraine based on the Chekanovsky–Sørensen similarity index. Bootstrap support values are shown at the nodes of the dendrogram.

Table 2. Chekanovsky–Sørensen (upper triangle) and Shimkevich–Simpson (lower triangle) similarity indices based on the species composition of naked amoebae in different types of water bodies in Ukraine.

	River	Floodplain	Lake	Swamp
River	1	0.76	0.66	0.51
Floodplain	0.99	1	0.67	0.67
Lake	0.98	0.94	1	0.59
Swamp	0.99	0.93	0.75	1

fia sp. (3) and *W. magna*. The species present seemed to depend on the proximity of the lake or floodplain to a river, where the largest number of species were detected.

The Shimkevich–Simpson overlap coefficient showed a similar pattern in species composition among habitat types (Fig. 3): swamps were separated from the other habitat types with strong bootstrap support (100%). Floodplains and rivers formed a cluster with moderate support (72%) and lakes joined this group at a lower similarity level (67%).

The nMDS analysis (Fig. 4), based on species composition and associated environmental variables, indicated that species composition in swamps was associated with the content of organic substances, in floodplain water bodies with water temperature, and in rivers and lakes with dissolved oxygen concentration.

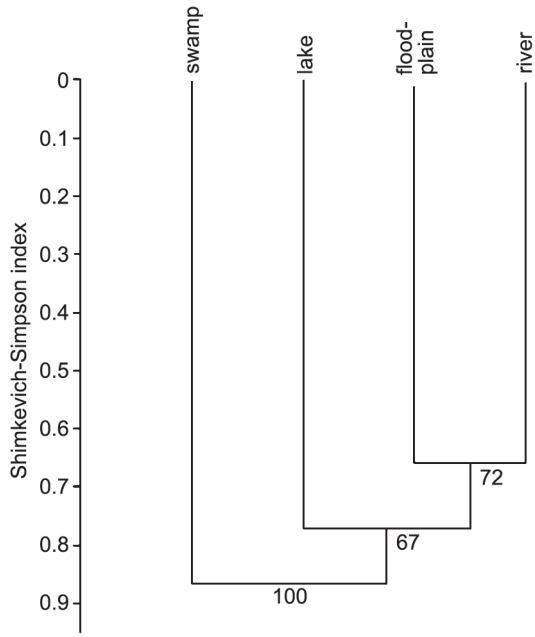

Fig. 3. Distribution of naked amoebae in water bodies of different types in Ukraine based on the Shimkevich–Simpson similarity index. Bootstrap support values are shown at the nodes of the dendrogram.

Discussion

This study provides one of the most comprehensive surveys of naked amoebae in freshwater habitats. The observed distribution patterns support the existence of distinct species complexes associated with environmental variables.

The diversity of amoebae observed within a single habitat is usually explained by adaptation to different microniches (Bischoff & Anderson 1998, Bischoff 2002). Local habitats are characterised by high heterogeneity, mosaic structure and vertical stratification (Anderson 2002). Variability in microconditions (food resources and physicochemical properties of microreservoirs) influences the composition of amoebae communities. Under favourable environmental conditions, species may exhibit outbursts of abundance (Baldock & Sleigh 1998, Taylor & Berger 1980). Nevertheless, most species are rare and occur at low abundance, and their distribution within habitats is mosaic. Information on the autecology of naked amoebae is largely limited to descriptions of habitats in which they have been recorded.

The ecological features of different groups of protists are described in several studies (Alpatova 2012, Gaponova 2009, Shevchuk 2008). For example, testate amoebae are classified into stenotopic and eurytopic based on their biotopic distribution, and the distinctiveness of these complexes has been linked to the combined influence of hydrochemical factors (Alpatova 2012). In Ukrainian water bodies, heterotrophic flagellates form two species complexes: one occurring in rivers and ponds, another in lakes, swamps and melioration canals (Shevchuk 2008). The species composition of flagellates is largely determined by proximity to rivers, where the highest diversity has been recorded. This may explain the higher similarity between pond and river fauna, as ponds are often formed in river beds (Shevchuk 2008). Centrohelea are not restricted to specific types of water bodies, except for acidophilic species that mainly occur in swamps (Gaponova 2009).

In previous studies on the distribution patterns of naked amoebae, I showed that distinct faunal complexes were characteristic of different types of water bodies in the Zhytomyr and Volyn regions in Ukrainian Polissya (Patsyuk 2013, 2014). The distribution of naked amoebae was primarily associated with microhabitat type and the hydrophysical and hydrochemical properties of the aquatic environment (Patsyuk

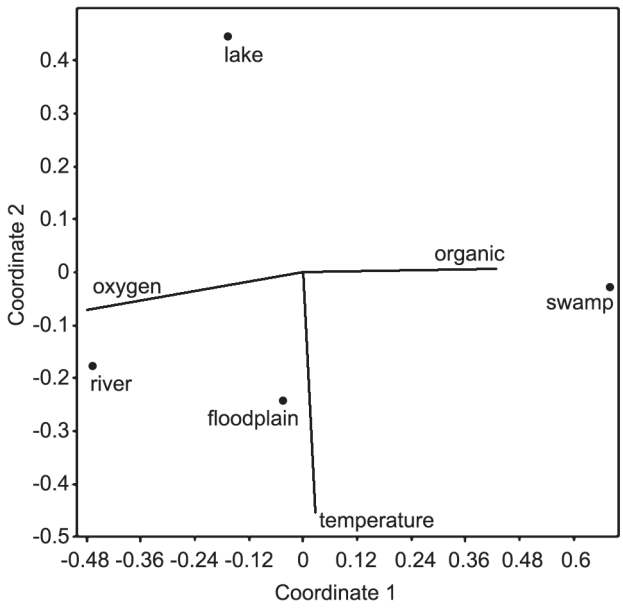

Fig. 4. Non-metric multidimensional scaling (nMDS) ordination of naked amoebae species composition in floodplains, lakes, rivers and swamps in Ukraine, with fitted environmental vectors (dissolved oxygen, temperature and organic content).

2013–2015). The study included rivers, floodplain water bodies, swamps and canals; lakes characteristic of the Shatsk National Nature Park were studied separately. The largest number of species was recorded in floodplain water bodies (24 species) and the smallest in canals (8 species); 14 species were recorded in swamps, 20 in rivers and 19 in lakes. Cluster analysis indicated that in Ukrainian Polissya, lake and floodplain species complexes were clearly separate. Their distinctiveness was associated with species confined to oligotrophic lakes of fluvioglacial origin (sandy-muddy bottom, calcium carbonate water with a low level of mineralisation) and to water bodies in river valleys (Patsyuk 2012).

Additionally, during a long-term study of species composition of naked amoebae in water bodies of certain regions of Ukraine, we identified ecological groups of naked amoebae in relation to environmental factors: water temperature (eurythermal, stenothermal thermophilic, stenothermal cold-loving); dissolved oxygen concentration (euryoxyd, stenooxyd); and concentration of organic substances (broadly tolerant and narrowly tolerant and stenobiont) (Patsyuk 2013–2015, 2018, Patsyuk & Konstantynenko 2022). Targeted studies further demonstrated that species composition in natural habitats is associated with abiotic environmental factors (Patsyuk 2024).

Having analysed the habitat distribution of naked amoebae and the factors that determine it across Ukraine, we found that the largest number of species was recorded in rivers (44 species) and the smallest in swamps (15 species). In floodplain water bodies and lakes, 27 and 23 species, respectively, were recorded. Additional lakes examined in Ukraine were small and unevenly distributed. In freshwater bodies, naked amoebae are grouped into two complexes: the swamp complex and the lake, floodplain and river complex. The specificity of each complex was determined by species adapted to a particular combination of abiotic factors, including water temperature, pH, dissolved oxygen concentration and organic content.

The distinctiveness of the species composition of naked amoebae in various types of water bodies in Ukraine can be used to assess changes in the ecological status of water bodies and to develop bioindication approaches for aquatic ecosystems.

Conclusions

The results of the study showed that the species composition of naked amoebae in different types of water bodies is associated with water

temperature, dissolved oxygen concentration and organic content. Naked amoebae play an important role in the functioning of aquatic ecosystems and are informative indicators for assessing ecological status. Changes in species composition of naked amoebae reflect both natural changes and anthropogenic pressure on aquatic ecosystems.

Naked amoebae represent a key component of microbial food chains, regulating bacterial and algal populations and influencing the self-purification of water bodies, while also serving as indicators of saprobity. Despite their potential, the use of naked amoebae in water quality monitoring systems has several limitations, including the complexity of taxonomic identification, seasonal variability of species composition and the lack of standardised sampling and analysis methods.

Future research should focus on combining classical methods of light microscopy with molecular genetics to improve species identification and detect cryptic biodiversity. Particular attention should be given to the responses of naked amoebae to modern forms of water pollution, their potential role in biomonitoring urbanised and transformed water bodies, as well as developing measures for their protection and restoration.

References

Adl S.M., Simpson A.G.B., Lane C.E., Lukes J., Schoch C.L., Smirnov A., Agatha S., Berney C., Brown M.W., Burki F., Cardenas P., Cepicka I., Chistyakova L., Dunthorn M., Edvardsen B., Eglit Y., Guillou L., Hampl V., Heiss A.A., Hoppenrath M., James T.Y., Karnkowska A., Karpov S., Kim E., Kolisko M., Kudryavtsev A., Lahr D.J.G., Lara E., Gall L.L., Lynn D.H., Mann D.G., Massana R., Mitchell E.A.D., Morrow C., Park J.S., Pawlowski J.W., Powell M.J., Richter D.J., Rueckert S., Shadwick L., Shimano S., Spiegel F.W., Torruella G., Youssef N., Zlatogursky V. & Zhang Q. 2019: Revision to the classification, nomenclature and diversity of eukaryotes. — *Journal of Eukaryotic Microbiology* 66: 4–119, https://doi.org/10.1111/jeu.12691.

Alpatova O.N. 2012: [*Shell amoebae (Testacealobosea; Silicofilosea) of Zhytomyr and Kyiv Polissya (fauna, taxonomy, ecology): thesis for the degree of Candidate of Biological Sciences*]. — National Academy of Sciences of Ukraine, Schmalhausen Institute of Zoology, Kyiv. [in Ukrainian]

Anderson O. 2002. Laboratory and field-based studies of abundances, small-scale patchiness, and diversity of gymnamoebae in soils of varying porosity and organic content: evidence of microbiocoenoses. — *Journal of Eukaryotic Microbiology* 49: 17–23, https://doi.org/10.1111/j.1550-7408.2002.tb00334.x.

Arndt H. 1993: A Critical Review of Importance of Rhizopods and Actinopods in Lake Plankton. — *Marine Microbial Food Webs* 7: 3–29.

Barnes R.S.K. 1989: What if any thing, is a brackish-water fauna? — *Transactions of the Royal Society of Edinburgh* 80: 235–240.

Baldock B. & Sleigh M. 1988. The ecology of benthic protozoa in rivers — seasonal variation in numerical abundance in fine sediments. — *Archiv für Hydrobiologie* 111: 409–422.

Bischoff P. & Anderson R. 1998. Abundance and diversity of Gymnamoebae at varying soil sites in north-eastern U.S.A. — *Acta Protozoologica* 37: 17–21.

Bischoff P. 2002: An analysis of the abundance, diversity and patchiness of terrestrial Gymnamoebae in relation to soil depth and precipitation events following a drought in Southeastern USA. — *Acta Protozoologica* 41: 183–189.

Cavalier-Smith T., Chao E.E. & Oates B. 2004: Molecular phylogeny of Amoebozoa and the evolutionary significance of the unikont *Phalansterium*. — *European Journal of Protistology* 40: 21–48, https://doi.org/10.1016/j.ejop.2003.10.001.

Finlay B.J. & Clarke K.J. 1999: Ubiquitous dispersal of microbial species. — *Nature* 400: 828.

Finlay B.J., Esteban G.F., Brown S., Fenchel T. & Hoef-Emden K. 2006: Multiple cosmopolitan ecotypes within a microbial eukaryote morphospecies. — *Protist* 157: 377–390.

Foissner W. 2008: Protist diversity and distribution: some basic considerations. — *Biodiversity and Conservation* 17: 235–242, https://doi.org/10.1007/s10531-007-9248-5.

Gaponova L.P. 2009: [*Centroheleid ladybirds (Centrohelea Cavalier- Smith, 1993) of Kyiv and Chernihiv Polissya: PhD thesis*]. — Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, Kyiv 16. [in Ukrainian]

Hammer O., Harper D.A.T. & Ryan P.D. 2001: PAST: Palaeontological statistics software package for education and data analysis. — *Palaeontologia Electronica* 4: 1–9.

Kang S., Tice A.K. & Spiegel F.W. 2017: Between a pod and a hard test: the deep evolution of amoebae. — *Molecular Biology and Evolution* 34: 2258–2270, https://doi.org/10.1093/molbev/msx162.

Legendre P. & Legendre L. 1998: *Numerical Ecology*. Amsterdam, Elsevier Science BV 853.

Nabyvanets B.Y., Osadchyj V.I., Osadcha N.M. & Nabyvanets Yu. B. 2007: [*Analytical chemistry of surface water*]. — Naukova Dumka, Kyiv. [in Ukrainian]

Page F.C. & Siemensma F.J. 1991: *Nackte Rhizopoda und Heliozoea (Protozoenfauna Band 2)*. — Gustav Fischer Verlag, Stuttgart, New York 3–170.

Patsyuk M.K. 2012: [*Naked amoebae of Zhytomyr and Volyn Polissya (fauna, taxonomy, ecology)*]. — PhD thesis, Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, Kyiv. [in Ukrainian]

Patsyuk M.K. 2013: Tolerance of naked amoebas (Protista) to the abiotic factors. — *Nature Montenegrina, Podgorica* 12: 319–323.

Patsyuk M.K. 2014: Morphotypes in naked amoebas (Protista): Distribution in water bodies of Zhytomyr and Volyn Polissia (Ukraine) and possible ecological significance. — *Vestnik zoologii* 48: 547–552.

Patsyuk M.K. 2015: Species of naked amoeba (Protista) new for the fauna of Ukraine. — *Vestnik zoologii* 49: 387–392.

Patsyuk M.K. 2018: Peculiarities of the Spatial Distribution of Naked Amoebas in Sandy Bottom Sediments of a Small River. — *Hydrobiological Journal* 54: 102–111.

Patsyuk M. & Konstantynenko L. 2022: Influence of aquatic environmental factors on the distribution of naked amoebae in waters of Zhytomyr region (Ukraine). — *Visnyk of the Lviv University. Series Biology* 86: 103–113. [in Ukrainian with English summary]

Patsyuk M. 2023. Phylogenetic relationships among naked amoebae found in natural biotopes. — *Cytology and Genetics* 57: 567–578, https://doi.org/10.3103/S0095452723060063.

Patsyuk M.K. 2024. [*Formation of the taxonomic structure and diversity of naked amoebae*]. — PhD thesis, Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, Kyiv. [in Ukrainian]

Payne R.J. 2013: Seven reasons why protists make useful bioindicators. — *Acta Protozoologica* 52: 105–113.

Ramette A. 2007: Multivariate analyses in microbial ecology. — *FEMS Microbiology Ecology* 62: 142–160.

Romanenko V.D. 2001: [*Fundamentals of hydroecology*]. — Oberegi, Kyiv. [in Ukrainian]

Shevchuk S. 2008: [*Heterotrophic flagellates of the central part of Ukrainian Polissya: thesis for the degree of Candidate of Biological Sciences*]. — National Academy of Sciences of Ukraine, Schmalhausen Institute of Zoology, Kyiv. [in Ukrainian]

Taylor W. & Berger J. 1980: Microspatial heterogeneity in the distribution of the ciliates in a small pond. — *Microbial Ecology* 6: 27–34.

Appendix 1. The sample collection locations in Ukraine. Each sample included the surface layer of bottom soil and a small amount of bottom water. Also the year of collection, the number of sampling sites in each location and the total number of samples from each location are reported.

		Year	Sites/samples
Vinnytsia Oblast			
1.	river near Zhmerynka city	2018	15/20
2.	swamp near Illintsi city	2017	10/10
3.	river near Korivka village, Kalynivka Raion	2015	10/10
4.	floodplain near Lemeshivka village, Kalynivka Raion	2017	10/16
5.	Shpykivka river near Shpykiv village, Tulchyn Raion	2017	15/20
6.	floodplain near Ulaniv city, Khmilnyk Raion	2016	12/17
7.	Spivoda river, Khmilnyk Raion	2016	15/20
Volyn Oblast			
8.	Rudka river near Moshchena village, Kovel Raion	2014	10/10
9.	Turia river near Bakhiv village, Kovel Raion	2014	10/10
10.	swamp near Sytnytsia village, Manevychi Raion	2014	8/10
11.	Rudka river near Sytnytsia village, Manevychi Raion	2014	8/10
12.	Cherevakha river near Cherevakha village, Manevychi Raion	2015	10/10
13.	Stokhid river, Kovel Raion	2014	10/10
14.	Pripyat river	2014	10/10
15.	floodplain near Dnipro city	2015–2016	15/40
16.	Dnipro river from different collection points	2014, 2015, 2020	15/38
17.	swamp near Stepanivka village, Krynychanskyi Raion	2014	10/10
18.	Chaplynka river near Yevdokiivka village, Magdalynskyi Raion	2014	10/10
19.	lake near Novomoskovsk city	2014	10/10
Zhytomyr Oblast			
20.	Guyva river near Andrushivka city	2015	10/10
21.	river near Zarubintsi village, Andrushevsky Raion	2016	10/10
22.	Khomora river near Pershotravensk village, Baranivskyi Raion	2014	10/10
23.	floodplain near Berdychiv city	2020	10/10
24.	Zdvyzh river near Brusyliv city	2014	10/10
25.	Hnylopyat river near Zhytomyr city	2014–2017	60/108
26.	Kamianka river near Zhytomyr city	2014–2020	50/100
27.	Teteriv river near Zhytomyr city	2014	10/20
28.	Guiva river near Zhytomyr city	2017–2021	60/110
29.	Uzh river near Korosten city	2015	10/10
30.	Bilka river near Sushky village, Korosten Raion	2014	10/10
31.	Tenka river near Yasna Poliana village, Luhyn Raion	2017	10/10
32.	Sluch River near Lubar city	2016	10/10
33.	swamp near Morozivka village, Malyn Raion	2016	10/10
34.	Sluch river near Zvyagel city	2018	10/10
35.	Smilka River near Zvyagel city	2018	10/10
36.	Noryn river, Ovruch Raion	2016	8/8
37.	lake near Pishchanytsia village, Ovruch Raion	2020	8/8
38.	river Ubort near Olevsk city	2017	8/8
39.	Ubort river near Khochyno village, Olevsk Raion	2017	10/10
40.	floodplain near Romaniv city	2016	8/8
41.	Lesna river near Romaniv city	2016	10/10
42.	Chobotivka river near Myropil village, Romaniv Raion	2016	8/8
43.	river near Chornoudka village, Ruzhinsky Raion	2020	8/8
44.	floodplain near Vysoke village, Cherniakhiv Raion	2018	8/8
Zaporizhzhia Oblast			
45.	Dnipro river from different collection points	2014	10/10
46.	swamp near Novopokrovka village, Orikhiv Raion	2018	10/10
47.	lake near Polohy city	2018	10/10
Zakarpattia Oblast			
48.	lake Synevyr	2018	15/20
49.	Tereblya river near Synevyrska Polyana village, Mizhhiria Raion	2018	10/10

50.	Tereblya river, Khust Raion	2021	10/14
51.	Tereblya river, Tiachiv Raion	2021	10/14
52.	swamp near Uzhhorod city	2018	10/10
53.	floodplain near Uzhhorod city	2018	10/10
54.	Rika river near Berezovo village, Khust Raion	2018	10/10
Ivano-Frankivsk Oblast			
55.	Dniester river near Dubivtsi village, Halych Raion	2018	10/12
56.	floodplain near Ivano-Frankivsk city	2018	10/10
57.	Duba river near Duba village, Rozhniativ Raion	2018	10/10
58.	Prut river	2021	15/20
Kropyvnytskyi Oblast			
59.	swamp near Ivanivka village, Dolyna Raion	2017	8/8
60.	swamp near Kropyvnytskyi city	2017	8/8
61.	river near Mala Vyska city	2017	10/10
Kyiv Oblast			
62.	floodplain near Maryanivka village, Vasylkiv Raion	2015	10/10
63.	floodplain near Kyiv city	2014	10/10
64.	swamp near Khotiv village, Kyiv-Svyatoshyn Raion	2014	10/10
65.	floodplain near Obukhov city	2014	10/10
66.	Stugna river near Ukrainka city	2014	10/10
Lviv Oblast			
67.	swamp near Brody city	2017–2018	10/10
68.	lake near Velikie Mosty city	2017–2018	10/10
69.	swamp near Davydiv village, Vynnyky Raion	2017–2018	10/10
70.	floodplain near Drohobych city	2017-2019	10/10
71.	Bystrytsia river near Hrushytsia village, Drohobych Raion	2017–2018	10/10
72.	floodplain near Pochaly village, Zolochiv Raion	2017–2018	10/10
73.	Western Bug river near Kamianka-Buzka city	2017–2018	15/20
74.	floodplain near Lviv city	2017–2018	10/10
75.	Dniester river near Novyi Kalyniv city	2017-2019	10/10
76.	floodplain near Starychi village, Novoyavoriv Raion	2017–2018	10/10
77.	swamp near Ivanivka village, Peremyshlyany Raion	2017–2018	8/8
78.	floodplain near Synkiv village, Radekhiv Raion	2017–2018	10/10
79.	floodplain near Skole city	2017-2019	8/8
80.	Karbivka river near Smykiv village, Sokal Raion	2017–2018	10/10
81.	floodplain near Tershiv village, Starosambir Raion	2017–2018	10/10
82.	floodplain near Stryi city	2017–2018	10/10
83.	swamp near Turk city	2017–2018	8/8
Mykolaiv Oblast			
84.	Ingul river near Mykolaiv city	2016	15/20
85.	Southern Bug River near Mykolaiv city	2016	15/20
Odesa Oblast			
86.	floodplain near Mykolaivka city	2019	10/25
87.	floodplain near Odesa city	2019	10/25
Poltava Oblast			
88.	floodplain near Hlobyne city	2014	10/10
89.	Dnipro river from different collection points near Kremenchuk city	2014	15/20
90.	Khorol River near Cherevky village, Myrhorod Raion	2018	10/10
91.	swamp near Poltava city	2014	10/10
Rivne Oblast			
92.	Lake Bile, Volodymyrets Raion	2017	10/10
93.	Ikva river near Ivanne village, Dubno Raion	2017	10/10
94.	swamp near Velyki Omeliany village, Rivne Raion	2014	8/8
95.	Goryn river near Oleksandriia village, Rivne Raion	2015	10/10
96.	Lake Zaliv, Sarnia Raion	2017	10/10
97.	Pripyat river	2021	10/10
Sumy Oblast			
98.	floodplain near Budivelne village, Hlukhiv Raion	2016–2017	10/10
99.	floodplain near Pryvillia village, Hlukhiv Raion	2016–2017	10/10
100.	Esman river near Hlukhiv city	2016–2017	10/15

101.	Ulitsa river near Znob-Trubchevska city	2016–2017	10/10
102.	swamp near Vyrivka village, Konotop Raion	2015	10/12
103.	floodplain near Krasnopillya city	2016–2017	10/10
104.	floodplain near Shepetivka village, Lebedyn Raion	2016–2017	10/10
105.	Khorol river near Berestivka village, Lipova Valley area	2016–2017	10/15
106.	floodplain near Nedryhailiv city	2016–2017	10/10
107.	river near Khukhra village, Okhtyrka Raion	2016–2017	10/11
108.	floodplain near Brusky village, Putivl Raion	2016–2017	8/8
109.	Romny river near Romny city	2016–2017	10/12
110.	Psyol river near Sumy city	2016–2018	10/15
111.	floodplain near Oleksiivka village, Sumy Raion	2016–2017	8/8
112.	floodplain near Trostianets city	2016–2017	10/10
113.	Shostka river near Shostka city	2016–2017	10/12
Ternopil Oblast			
114.	Goryn River near Vyshnivets village, Zbarazhiv Raion	2015	10/10
115.	swamp near Ternopil city	2016	10/10
116.	Ruda river, Ternopil Raion	2016	10/10
Kharkiv Oblast			
117.	Siverskyi Donets River, Zmiiv Raion	2019	8/8
118.	swamp near Kharkiv city	2017	10/10
Kherson Oblast			
119.	Dnipro river from different collection points	2015	15/20
120.	Ingulets river near Kherson city	2015	10/12
Khmelnytskyi Oblast			
121.	lake near Khmelnytsky city	2018	10/10
122.	lake near Starokonstantinov city	2014	10/10
123.	Ikva river, Starokostiantyniv Raion	2014	10/15
Cherkasy Oblast			
124.	Khorobra river near Zarichchia village, Korsun-Shevchenkivskyi Raion	2014	15/20
125.	lake near Cherkasy city	2014	10/12
Chernivtsi Oblast			
126.	lake near Chernivtsi city	2014	8/8
127.	swamp near Chernivtsi city	2014	8/8
128.	Prut river near Chernivtsi city	2016	20/20
Chernihiv Oblast			
129.	lake near Chernihiv city	2018	10/10
130.	swamp near Chernihiv city	2018	10/10
131.	Desna river near Oster city	2018	10/10

Appendix 2. Detection locations of the naked amoebae species

1. *Rhizamoeba* sp. (1)
   Hnylopyat river near Zhytomyr city
   floodplain near Kyiv city
   Southern Bug River near Mykolaiv city
   floodplain near Mykolaivka city
   swamp near Uzhhorod city
   lake near Khmelnytsky city
   Khorobra river near Zarichchia village, Korsun-Shevchenkivskyi Raion (Cherkasy Oblast)
2. *Rhizamoeba* sp. (2)
   lake Synevyr (Zakarpattia Oblast)
   Bystrytsia river near Hrushytsia village, Drohobych Raion (Lviv Oblast)
   floodplain near Skole city (Lviv Oblast)
   Ikva river near Ivanne village, Dubno Raion (Lviv Oblast)
   Prut river near Chernivtsi city (Chernivtsi Oblast)
3. *Amoeba proteus* Stokhid river, Kovel Raion (Volyn Oblast)
   Prut River near slopes of Mount Hoverla
4. *Polychaos dubium*
   Goryn river near Oleksandriia village, Rivne Raion (Rivne Oblast)
   Prut river near Chernivtsi city
   Prut River near the slopes of Mount Hoverla
5. *Deuteramoeba mycophaga*
   Spivoda river, Khmilnyk Raion (Vinnytsia Oblast)
   Rudka river near Moshchena village, Kovel Raion (Volyn Oblast)
   Tereblya River, Tyachiv Raion (Zakarpattia Oblast)
   Kamianka river near Zhytomyr city
   Teteriv river near Zhytomyr city
   Zdvyzh river near Brusyliv city (Zhytomyr Oblast)
   Noryn river, Ovruch Raion (Zhytomyr Oblast)
   Dnipro river (Zaporizhzhia Oblast)
   Duba river near Duba village, Rozhniativ Raion (Ivano-Frankivsk Oblast)
   river near Mala Vyska city (Kropyvnytskyi Oblast)
   floodplain near Kyiv city
   floodplain near Drohobych city (Lviv Oblast)
   floodplain near Hlobyne city (Poltava Oblast)
   Siverskyi Donets River, Zmiiv Raion (Kharkiv oblast)
   Khorobra river near Zarichchia village, Korsun-Shevchenkivskyi Raion (Cherkasy Oblast)
   Prut River near the slopes of Mount Hoverla
6. *Saccamoeba stagnicola*
   river near Zhmerynka city (Vinnytsia Oblast)
   Spivoda river, Khmilnyk Raion (Vinnytsia Oblast)
   Rudka river near Moshchena village, Kovel Raion (Volyn Oblast)
   Rudka river near Sytnytsia village, Manevychi Raion (Volyn Oblast)
   Hnylopyat river near Zhytomyr city
   Kamianka river near Zhytomyr city
   river near Zarubintsi village, Andrushevsky Raion (Zhytomyr Oblast)
   Khomora river near Pershotravensk village, Baranivskyi Raion (Zhytomyr Oblast)
   floodplain near Romaniv city (Zhytomyr Oblast)
   floodplain near Maryanivka village, Vasylkiv Raion (Kyiv Oblast)
   floodplain near Drohobych city (Lviv Oblast)
   floodplain near Pochaly village, Zolochiv Raion (Lviv Oblast)
   Khorol River near Cherevky village, Myrhorod Raion (Poltava Oblast)
   floodplain near Uzhhorod city
   Rika river near Berezovo village, Khust Raion (Zakarpattia Oblast)
   Tereblya River, Khust Raion (Zakarpattia Oblast)
   Siverskyi Donets River, Zmiiv Raion (Kharkiv Oblast)
   lake near Starokonstantinov city (Khmelnytskyi Oblast)
   Ikva river, Starokostiantyniv Raion (Khmelnytskyi Oblast)
   Khorobra river near Zarichchia village, Korsun-Shevchenkivskyi Raion (Cherkasy Oblast)

Desna river near Oster city (Chernihiv Oblast)

7. *Saccamoeba limax*
   Stokhid river, Kovel Raion (Volyn Oblast)
   Tereblya River, Khust Raion (Zakarpattia Oblast)
   floodplain near Obukhov city (Kyiv Oblast)
   Western Bug river near Kamianka-Buzka city (Lviv Oblast)
   Khorol River near Cherevky village, Myrhorod Raion (Poltava Oblast)
   Siverskyi Donets River, Zmiiv Raion (Kharkiv oblast)
8. *Saccamoeba wakulla*
   floodplain near Starychi village, Novoyavoriv Raion (Lviv Oblast)
   Goryn River near Vyshnivets village, Zbarazhiv Raion (Ternopil Oblast)
9. *Saccamoeba* sp. (1)
   floodplain near Lemeshivka village, Kalynivka Raion (Vinnytsia Oblast)
   Tenka river near Yasna Poliana village, Luhyn Raion (Zhytomyr Oblast)
   river near Mala Vyska city (Kropyvnytskyi Oblast)
10. *Saccamoeba* sp. (2)
    Turia river near Bakhiv village, Kovel Raion (Volyn Oblast)
    Cherevakha river near Cherevakha village, Manevychi Raion (Volyn Oblast)
11. *Saccamoeba* sp. (3)
    Teteriv river near Zhytomyr city
    Uzh river near Korosten city (Zhytomyr Oblast)
12. *Thecamoeba striata*
    river near Zhmerynka city (Vinnytsia Oblast)
    floodplain near Lemeshivka village, Kalynivka Raion (Vinnytsia Oblast)
    Rudka river near Moshchena village, Kovel Raion (Volyn Oblast)
    Turia river near Bakhiv village, Kovel Raion (Volyn Oblast)
    Kamianka river near Zhytomyr city
    Teteriv river near Zhytomyr city
    Uzh river near Korosten city (Zhytomyr Oblast)
    Sluch River near Lubar city (Zhytomyr Oblast)
    floodplain near Romaniv city (Zhytomyr Oblast)
    lake Synevyr (Zakarpattia Oblast)
    Dnipro river (Zaporizhzhia Oblast)
    lake near Polohy city (Zaporizhzhia Oblast)
    floodplain near Ivano-Frankivsk city
    floodplain near Maryanivka village, Vasylkiv Raion (Kyiv Oblast)
    swamp near Ivanivka village, Dolyna Raion (Kropyvnytskyi Oblast)
    Bystrytsia river near Hrushytsia village, Drohobych Raion (Lviv Oblast)
    Western Bug river near Kamianka-Buzka city (Lviv Oblast)
    Karbivka river near Smykiv village, Sokal Raion (Lviv Oblast)
    Southern Bug River near Mykolaiv city
    swamp near Velyki Omeliany village, Rivne Raion (Rivne Oblast)
    Esman river near Hlukhiv city (Rivne Oblast)
    Ruda river, Ternopil Raion (Ternopil Oblast)
    Dnipro river (Kherson Oblast)
    lake near Khmelnytsky city
    lake near Cherkasy city
    lake near Chernihiv city
13. *Thecamoeba quadrilineata*
    Teteriv river near Zhytomyr city
    Chobotivka river near Myropil village, Romaniv Raion (Zhytomyr Oblast)
    Dnipro river (Zaporizhzhia Oblast)
    floodplain near Skole city (Lviv Oblast)
    Ingulets river near Kherson city
14. *Thecamoeba sphaeronucleolus*
    Cherevakha river near Cherevakha village, Manevychi Raion (Volyn Oblast)
    Psyol river near Sumy city
    Prut river near Chernivtsi city
15. *Thecamoeba verrucosa*
    Uzh river near Korosten city (Zhytomyr Oblast)

floodplain near Obukhov city (Kyiv Oblast)
river near Mala Vyska city (Kropyvnytskyi Oblast)
Khorol River near Cherevky village, Myrhorod Raion (Poltava Oblast)
Dnipro river (Kherson Oblast)

16. *Thecamoeba terricola*
river Ubort near Olevsk (Zhytomyr Oblast)
lake Synevyr (Zakarpattia Oblast)
Tereblya river near Synevyrska Polyana village, Mizhhiria Raion (Zakarpattia Oblast)
Dnipro river near Kremenchuk city (Poltava Oblast)
17. *Thecamoeba similis*
Duba river near Duba village, Rozhniativ Raion (Ivano-Frankivsk Oblast)
Dniester river near Dubivtsi village, Halych Raion (Ivano-Frankivsk Oblast)
Western Bug river near Kamianka-Buzka city (Lviv Oblast)
Prut river near Chernivtsi city
18. *Thecamoeba* sp.
Teteriv river near Zhytomyr city
swamp near Kropyvnytskyi city
swamp near Velyki Omeliany village, Rivne Raion (Rivne Oblast)
swamp near Vyrivka village, Konotop Raion (Sumy Oblast)
Khorobra river near Zarichchia village, Korsun-Shevchenkivskyi Raion (Cherkasy Oblast)
19. *Stenamoeba stenopodia*
Shpykivka river near Shpykiv village, Tulchyn Raion (Vinnytsia Oblast)
floodplain near Ulaniv city, Khmilnyk Raion (Vinnytsia Oblast)
Rudka river near Sytnytsia village, Manevychi Raion (Volyn Oblast)
Hnylopyat river near Zhytomyr city
Guiva river near Zhytomyr city
Zdvyzh river near Brusyliv city (Zhytomyr Oblast)
floodplain near Vysoke village, Cherniakhiv Raion (Zhytomyr Oblast)
floodplain near Budivelne village, Hlukhiv Raion (Sumy Oblast)
swamp near Vyrivka village, Konotop Raion (Sumy Oblast)
floodplain near Shepetivka village, Lebedyn Raion (Sumy Oblast)
floodplain near Nedryhailiv city (Sumy Oblast)
floodplain near Brusky village, Putivl Raion (Sumy Oblast)
Tereblya river near Synevyrska Polyana village, Mizhhiria Raion (Zakarpattia Oblast)
lake near Khmelnytsky city
20. *Paradermamoeba valamo*
Cherevakha river near Cherevakha village, Manevychi Raion (Volyn Oblast)
Kamianka river near Zhytomyr city
river near Mala Vyska city (Kropyvnytskyi Oblast)
Siverskyi Donets River, Zmiiv Raion (Kharkiv Oblast)
lake near Khmelnytsky city
21. *Paradermamoeba levis*
Kamianka river near Zhytomyr city
Duba river near Duba village, Rozhniativ Raion (Ivano-Frankivsk Oblast)
lake near Khmelnytsky city
22. *Mayorella cantabrigiensis*
floodplain near Dnipro city
Kamianka river near Zhytomyr city
Dnipro river (Zaporizhzhia Oblast)
Stugna river near Ukrainka city (Kyiv Oblast)
Dniester river near Novyi Kalyniv city (Lviv Oblast)
floodplain near Stryi city (Lviv Oblast)
floodplain near Odesa city
swamp near Poltava city
lake near Khmelnytsky city
Siverskyi Donets River, Zmiiv Raion (Kharkiv Oblast)
Desna river near Oster city (Chernihiv Oblast)
23. *Mayorella vespertilioides*
Tereblya River, Tyachiv Raion (Zakarpattia Oblast)
Kamianka river near Zhytomyr city

Hnylopyat river near Zhytomyr city
Sluch river near Zvyagel city (Zhytomyr Oblast)
river Ubort near Olevsk city (Zhytomyr Oblast)
lake near Polohy city (Zaporizhzhia Oblast)
Ingul river near Mykolaiv city (Mykolaiv Oblast)
Southern Bug River near Mykolaiv city
floodplain near Odesa city
Khorol River near Cherevky village, Myrhorod Raion (Poltava Oblast)
floodplain near Budivelne village, Hlukhiv Raion (Sumy Oblast)

24. *Mayorella penardi*
Stokhid river, Kovel Raion (Volyn Oblast)
Pripyat river (Volyn Oblast, Rivne Oblast)
Karbivka river near Smykiv village, Sokal Raion (Lviv Oblast)

25. *Mayorella viridis*
Cherevakha river near Cherevakha village, Manevychi Raion (Volyn Oblast)
Goryn river near Oleksandriia village, Rivne Raion (Rivne Oblast)

26. *Mayorella* sp. (1)
floodplain near Lemeshivka village, Kalynivka Raion (Vinnytsia Oblast)
Rudka river near Moshchena village, Kovel Raion (Volyn Oblast)
swamp near Poltava city
Lake Zaliv, Sarnia Raion (Rivne Oblast)
Pripyat river (Rivne Oblast)
Rika river near Berezovo village, Khust Raion (Zakarpattia Oblast)

27. *Mayorella* sp. (2)
swamp near Novopokrovka village, Orikhiv Raion (Zaporizhzhia Oblast)
floodplain near Obukhov city (Kyiv Oblast)
Ingul river near Mykolaiv city
floodplain near Odesa city
Dnipro river from different collection points near Kremenchuk city (Poltava Oblast)
floodplain near Krasnopillya city (Sumy Oblast)
floodplain near Trostianets city (Sumy Oblast)

28. *Korotnevella stella*
Rudka river near Moshchena village, Kovel Raion (Volyn Oblast)
Kamianka river near Zhytomyr city
Hnylopyat river near Zhytomyr city
river near Zarubintsi village, Andrushevsky Raion (Zhytomyr Oblast)
Smilka River near Zvyagel city (Zhytomyr Oblast)
lake near Polohy city (Zaporizhzhia Oblast)
floodplain near Synkiv village, Radekhiv Raion (Lviv Oblast)
Ikva river near Ivanne village, Dubno Raion (Rivne Oblast)
floodplain near Uzhhorod city
Khorobra river near Zarichchia village, Korsun-Shevchenkivskyi (Cherkasy Oblast)

29. *Korotnevella diskophora*
Spivoda river, Khmilnyk Raion (Vinnytsia Oblast)
river near Zarubintsi village, Andrushevsky Raion (Zhytomyr Oblast)
river near Mala Vyska city (Kropyvnytskyi Oblast)
Ikva river near Ivanne village, Dubno Raion (Rivne Oblast)
lake near Khmelnytsky city
Dnipro river (Kherson Oblast)

30. *Vexillifera bacillipedes*
floodplain near Lemeshivka village, Kalynivka Raion (Vinnytsia Oblast)
Turia river near Bakhiv village, Kovel Raion (Volyn Oblast)
swamp near Sytnytsia village, Manevychi Raion (Volyn Oblast)
Hnylopyat river near Zhytomyr city
Teteriv river near Zhytomyr city
Khomora river near Pershotravensk village, Baranivskyi Raion (Zhytomyr Oblast)
Sluch River near Lubar city (Zhytomyr Oblast)
swamp near Morozivka village, Malyn Raion (Zhytomyr Oblast)
river Ubort near Olevsk city (Zhytomyr Oblast)
floodplain near Ivano-Frankivsk city

floodplain near Maryanivka village, Vasylkiv Raion (Kyiv Oblast)
swamp near Ivanivka village, Dolyna Raion (Kropyvnytskyi Oblast)
swamp near Davydiv village, Vynnyky Raion (Lviv Oblast)
swamp near Turk city (Lviv Oblast)
floodplain near Pryvillia village, Hlukhiv Raion (Sumy Oblast)
Ulitsa river near Znob-Trubchevska city (Sumy Oblast)
swamp near Vyrivka village, Konotop Raion (Sumy Oblast)
floodplain near Krasnopillya city (Sumy Oblast)
lake near Cherkasy city
swamp near Chernivtsi city
Desna river near Oster city (Chernihiv Oblast)

31. *Ripella platypodia*
floodplain near Dnipro city
Dnipro river (Dnipropetrovsk Oblast)
Prut river near Chernivtsi city

32. *Ripella* sp.
floodplain near Dnipro city
Teteriv river near Zhytomyr city
Guyva river near Andrushivka city (Zhytomyr Oblast)
lake near Pishchanytsia village, Ovruch Raion (Zhytomyr Oblast)
river near Chornoudka village, Ruzhinsky Raion (Zhytomyr Oblast)
floodplain near Maryanivka village, Vasylkiv Raion (Kyiv Oblast)
swamp near Kharkiv city

33. *Vannella lata*
Teteriv river near Zhytomyr city
Hnylopyat river near Zhytomyr city
Kamianka river near Zhytomyr city
swamp near Morozivka village, Malyn Raion (Zhytomyr Oblast)
Noryn river, Ovruch Raion (Zhytomyr Oblast)
floodplain near Ivano-Frankivsk city
floodplain near Obukhov city (Kyiv Oblast)
Western Bug river near Kamianka-Buzka city (Lviv Oblast)
Karbivka river near Smykiv village, Sokal Raion (Lviv Oblast)
floodplain near Stryi city (Lviv Oblast)
Dnipro river (Poltava Oblast)
Ikva river near Ivanne village, Dubno Raion (Rivne Oblast)
Esman river near Hlukhiv city (Sumy Oblast)
floodplain near Oleksiivka village, Sumy Raion (Sumy Oblast)
river near Khukhra village, Okhtyrka Raion (Sumy Oblast)
Shostka river near Shostka city (Sumy Oblast)
floodplain near Uzhhorod city

34. *Vannella* sp.
swamp near Sytnytsia village, Manevychi Raion (Volyn Oblast)
Teteriv river near Zhytomyr city
Hnylopyat river near Zhytomyr city
floodplain near Berdychiv city (Zhytomyr Oblast)
floodplain near Vysoke village, Cherniakhiv Raion (Zhytomyr Oblast)
floodplain near Ivano-Frankivsk city
Tereblya river near Synevyrska Polyana village, Mizhhiria Raion (Zakarpattia Oblast)
floodplain near Odesa city

35. *Acanthamoeba* sp.
river near Zhmerynka city (Vinnytsia Oblast)
Turia river near Bakhiv village, Kovel Raion (Volyn Oblast)
Chaplynka river near Yevdokiivka village, Magdalynskyi Raion (Volyn Oblast)
Guyva river near Andrushivka city (Zhytomyr Oblast)
floodplain near Berdychiv city (Zhytomyr Oblast)
Teteriv river near Zhytomyr city
Lesna river near Romaniv city (Zhytomyr Oblast)
Uzh river near Korosten city (Zhytomyr Oblast)
Dniester river near Dubivtsi village, Halych Raion (Ivano-Frankivsk Oblast)

Duba river near Duba village, Rozhniativ Raion (Ivano-Frankivsk Oblast)
river near Mala Vyska city (Kropyvnytskyi Oblast)
lake near Velikie Mosty city (Lviv Oblast)
swamp near Davydiv village, Vynnyky Raion (Lviv Oblast)
floodplain near Starychi village, Novoyavoriv Raion (Lviv Oblast)
Ingul river near Mykolaiv city
floodplain near Odesa city
floodplain near Mykolaivka city (Odesa Oblast)
Esman river near Hlukhiv city (Sumy Oblast)
floodplain near Brusky village, Putivl Raion (Sumy Oblast)
Ruda river, Ternopil Raion (Ternopil Oblast)
Dnipro river (Kherson Oblast)
Ikva river, Starokostiantyniv Raion (Khmelnytskyi Oblast)
lake near Cherkasy city
Khorobra river near Zarichchia village, Korsun-Shevchenkivskyi Raion (Cherkasy Oblast)
Desna river near Oster city (Chernihiv Oblast)

36. *Pellita digitata*
Khorol river near Berestivka village, Lipova Valley area (Sumy Oblast)
Khorobra river near Zarichchia village, Korsun-Shevchenkivskyi Raion (Cherkasy Oblast)

37. *Cochliopodium actinophorum*
Shpykivka river near Shpykiv village, Tulchyn Raion (Vinnytsia Oblast)
Teteriv river near Zhytomyr city
Hnylopyat river near Zhytomyr city
Kamianka river near Zhytomyr city
floodplain near Berdychiv city (Zhytomyr Oblast)
Smilka River near Zvyagel city (Zhytomyr Oblast)
Bilka river near Sushky village, Korosten Raion (Zhytomyr Oblast)
river near Chornoudka village, Ruzhinsky Raion (Zhytomyr Oblast)
swamp near Kropyvnytskyi city
swamp near Ivanivka village, Peremyshlyany Raion (Lviv Oblast)
Ingul river near Mykolaiv city
floodplain near Oleksiivka village, Sumy Raion (Sumy Oblast)
floodplain near Trostianets city (Sumy Oblast)
swamp near Uzhhorod city
floodplain near Uzhhorod city
Tereblya river near Synevyrska Polyana village, Mizhhiria Raion (Zakarpattia Oblast)
Siverskyi Donets River, Zmiiv Raion (Kharkiv Oblast)
Dnipro river (Kherson Oblast)
Ikva river, Starokostiantyniv Raion (Khmelnytskyi Oblast)

38. *Cochliopodium minus*
Stokhid river, Kovel Raion (Volyn Oblast)

39. *Flamella* sp.
Stokhid river, Kovel Raion (Volyn Oblast)
Tenka river near Yasna Poliana village, Luhyn Raion (Zhytomyr Oblast)
Sluch River near Lubar city (Zhytomyr Oblast)
Lake Zaliv, Sarnia Raion (Rivne Oblast)
Goryn River near Vyshnivets village, Zbarazhiv Raion (Ternopil Oblast)
lake near Khmelnytsky city

40. *Vahlkampfia* sp. (1)
floodplain near Lemeshivka village, Kalynivka Raion (Vinnytsia Oblast)
swamp near Sytnytsia village, Manevychi Raion (Volyn Oblast)
swamp near Uzhhorod city
floodplain near Uzhhorod city
Tereblya river near Synevyrska Polyana village, Mizhhiria Raion (Zakarpattia Oblast)
Rika river near Berezovo village, Khust Raion (Zakarpattia Oblast)
swamp near Kharkiv city
Desna river near Oster city (Chernihiv Oblast)

41. *Vahlkampfia* sp. (2)
river near Korivka village, Kalynivka Raion (Vinnytsia Oblast)
floodplain near Lemeshivka village, Kalynivka Raion (Vinnytsia Oblast)

Spivoda river, Khmilnyk Raion(Vinnytsia Oblast)
swamp near Sytnytsia village, Manevychi Raion (Volyn Oblast)
Duba river near Duba village, Rozhniativ Raion (Ivano-Frankivsk Oblast)
swamp near Khotiv village, Kyiv-Svyatoshyn Raion (Kyiv Oblast)
Ingul river near Mykolaiv city
lake near Starokonstantinov city (Khmelnytskyi Oblast)
Khorobra river near Zarichchia village, Korsun-Shevchenkivskyi Raion (Cherkasy Oblast)

42. *Vahlkampfia* sp. (3)
Esman river near Hlukhiv city (Sumy Oblast)
Romny river near Romny city (Sumy Oblast)
Goryn River near Vyshnivets village, Zbarazhiv Raion (Ternopil Oblast)
lake near Starokonstantinov city (Khmelnytskyi Oblast)
Desna river near Oster city (Chernihiv Oblast)

43. *Vahlkampfia avara*
river near Zhmerynka city (Vinnytsia Oblast)
swamp near Illintsi city (Vinnytsia Oblast)
Shpykivka river near Shpykiv village, Tulchyn Raion (Vinnytsia Oblast)
Teteriv river near Zhytomyr city
Kamianka river near Zhytomyr city
floodplain near Ivano-Frankivsk city
swamp near Khotiv village, Kyiv-Svyatoshyn Raion (Kyiv Oblast)
swamp near Brody city (Lviv Oblast)
Ingul river near Mykolaiv city
swamp near Uzhhorod city
floodplain near Uzhhorod city
swamp near Ternopil city
Dnipro river (Kherson Oblast)
lake near Chernivtsi city

44. *Willaertia magna*
Teteriv river near Zhytomyr city