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Terrestrial algae, bryophytes, and lichens of biological soil crusts and corticolous biofilms on the bed of the former Kakhovka Reservoir

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ABSTRACT

Question: What is the diversity and role of terrestrial algae, bryophytes and lichens in the initial stages of overgrowth of the former Kakhovka Reservoir bed, in particular, in the formation of soil biocrusts and corticolous biofilms?

Location: Kakhovka Reservoir, Dnipropetrovsk, Kherson and Zaporizhzhia regions, Ukraine.

Materials and methods: field and laboratory methods of collection and investigation of algae, bryophytes and lichens, direct microscopy and culture methods (Kostikov *et al.* 2001, Bischoff & Bold 1963, Stanier *et al.* 1971)

Nomenclature: algae and cyanobacteria (Guiry & Guiry 2026), bryophytes (Virchenko & Nyporko 2022), lichens (https://www.indexfungorum.org/)

Results: During a three-year study of the exposed bed of the former Kakhovka Reservoir (2023-2025), 55 species of terrestrial algae (Cyanobacteria – 17 species, Chlorophyta – 27, Charophyta – 4, Heterokontophyta – 7), 2 species of bryophytes (*Marchantia polymorpha* and *Funaria hygrometrica*) and 1 species of lichen (*Physcia adscendens*) were identified. 50 algal species were found in soil biocrusts. Cyanobacteria and Chlorophyta were the most numerous there, dominating species were *Phormidium takyricum*, *Chlorosarcinopsis* cf. *aggregata*, *Stenomitos* sp., *Microcoleus vaginatus*, *Klebsormidium* cf. *flaccidum*, etc. On takyr-like (silt) substrates, 30 species of algae were found. Here, in a young willow-poplar forest, the liverwort *Marchantia polymorpha* was occasionally observed. A greater diversity of algae was found on sands: 36 species. Biocrusts dominated by the moss *Funaria hygrometrica* were often recorded on sands. 10 species of algae were recorded within the biofilms on willow bark, with green algae prevailing and *Chloroidium* cf. *ellipsoideum* as the dominant species. Additionally, the first epiphytic lichen (*Physcia adscendens*) was recorded at the same substrate.

Conclusions: High cyanobacterial diversity of and their dominance in communities are characteristic for soils in the steppe zone of Ukraine. A distinctive feature of biocrusts on silt is the predominance of fine-filamentous cyanobacteria. Biocrusts on sand were characterized by a higher diversity of algae and the occurrence of aquatic species due to the periodic flooding of these areas. During the three years following the dam destruction, algal diversity in the biocrusts increased considerably. The low species richness in willow bark biofilms and the dominance of green algae are characteristic of aerophytic bark communities in the temperate zone. In the early successional stages of biodiversity recovery, bryophytes and lichens contribute minimally to the development of soil biocrusts and corticolous assemblages of willow trees.

KEYWORDS

biodiversity, biological soil crusts, takyr, silt, sand, bark of trees, willow forest, war, Ukraine

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INTRODUCTION

Biological soil crusts (biocrusts) are pioneers in the colonization of exposed substrates and represent the initial stage of vegetation recovery in disturbed terrestrial ecosystems. They are complex microecosystems, the main components of which are cyanobacteria, algae, microfungi, lichens, liverworts, mosses and bacteria that live in the surface layers of the soil, forming a structured crust of various morphology (Belnap *et al.* 2001). Filamentous cyanobacteria and algae penetrate between soil particles, binding and stabilizing the substrate, while unicellular and packet-like forms fill the crust. Soil biocrusts serve critical ecological functions: they stabilize the soil surface (Van den Acker & Jungerius 1985), enhance organic matter content through photosynthesis and nitrogen fixation (Belnap 2002, Grote *et al.* 2010), regulate nutrient cycling (Wu *et al.* 2013), improve moisture retention (Belnap 2006), and facilitate the establishment and productivity of vascular plants (Harper & Belnap 2001).

Following the breach of the Kakhovka Hydroelectric Power Station dam, vast areas of the reservoir bed were exposed, revealing diverse substrates primarily composed of mussel shell deposits, silt (takyr-like) and sandy sediments (Didukh *et al.* 2024, Kuzemko *et al.* 2025). After the water recession to the primary Dnipro riverbed and its tributaries, the active formation of pioneer biological soil crusts began on exposed substrates, which mainly included terrestrial algae and cyanobacteria. They played a key role in stabilization the surface layers of silt, preventing their deflation during the summer period of 2023 (Kuzemko *et al.* 2025).

Thus, biological soil crusts are an integral component of terrestrial ecosystems, representing the initial stage of successional processes that facilitate vegetation recovery. Consequently, investigating the species composition of cyanobacteria and algae as the basic structural elements of these crusts, and analyzing their dynamics and temporal transformation on the exposed bed of the former Kakhovka Reservoir, will elucidate the patterns of formation and restoration of biodiversity after catastrophic impacts.

The aim of this work was to investigate the formation of biological soil crusts during the initial stages of colonization of the former Kakhovka Reservoir bed from 2023 to 2025. In 2025, a more detailed study of the established soil biocrusts was conducted across different substrates, specifically silt (takyr-like) and sandy soils. Furthermore, the study examined aerophytic communities of the bark of young willow trees (corticolous biofilms), which currently form a willow forest at the exposed reservoir bed, was conducted.

MATERIAL AND METHODS

The material for the study was based on samples of soil biocrusts and aerophytic communities of the bark of young willow trees (*Salix* x *rubens*). In total, 10 samples of biocrusts and 2 samples of bark communities were selected and examined during the period of investigation of the exposed bed of the former Kakhovka Reservoir. Among them, 3 samples of soil biocrusts were selected and examined in the first (KSA02, 2023, 1 sample) and second (KR0524_10, 2024, 2 samples) years of ecosystem recovery. The remaining samples (7 biocrust samples and 2 samples of bark communities) were selected in 2025, in the third year of ecosystem recovery. The list of samples and their brief characteristics are given in TABLE 1, the general view of the sampling sites is shown in FIGURES 1 and 2.

Algae were studied by direct microscopy and culture methods. Cultures were grown on the agar-solidified Bold's Basal Medium (1N BBM) (Bischoff & Bold 1963), under standard laboratory conditions, with a 12-hour alternation of light and dark phases and illumination of 25 μmol photons m^{-2} s^{-1} at a temperature of +20 ± 5 ºC. Cultures were studied starting from the third week of cultivation. Algae were identified in enrichment and uni-algal cultures isolated according to the method described in Kostikov *et al.* (2001). Pure eukaryotic uni-algal cultures were grown on Bold Basal medium (1N BBM), cyanobacterial cultures – on BG-11 medium (Stanier *et al.* 1971) under the conditions described above. Isolation and purification of uni-algal cultures were carried out using a stereoscopic microscope MBS-9. Identification and morphological studies were performed using an

Olympus BX53 light microscope (Tokyo, Japan) with Nomarski differential interference optics (DIC). Microphotographs were taken using an Olympus LC30 digital camera integrated into the microscope and processed with cellSens Entry software (Tokyo, Japan).

The nomenclature and taxonomic position of the identified algae and cyanobacteria species follow AlgaeBase (Guiry & Guiry 2026). Ecological characteristics and distribution data were obtained primarily from “Algae of Ukraine” (2006, 2009, 2011) and “Prodromus of Spore Plants of Ukraine: Algae” (Tsarenko *et al.* 2024a, b), supplemented by online resources such as AlgaeBase (Guiry & Guiry 2026) and partially NCBI (http://ncbi.nlm.nih.gov). Bryophyte nomenclature follows “Prodromus of Spore Plants of Ukraine: Bryophytes” (Virchenko & Nyporko 2022), while lichen names are provided according to Index fungorum (https://www.indexfungorum.org/).

Table 1. List and characteristics of the algal samples collected from the exposed bed of the former Kakhovka Reservoir

Sample number	Administrative Location	Site description / Substrate	Date	Coordinates
KSA02 (soil biocrust)	Kherson region, Beryslav district, environs of the village Mylove	Kamianska Sich National Nature Park, Mylivska Balka, willow shoots, takyr-like substrates (silt) with shells	19.10.2023	47.08536° N 33.65193° E
KR0524_10-1 (soil biocrust, horizontal takyr surface)	Zaporizhzhia region, village Malokaterynivka	Dnipro floodplain, willow community, takyr-like substrates (silt)	22.05.2024	47.65271° N 35.24790° E
KR0524_10-2 (soil biocrust, crack in takyr)				
1 (soil biocrust, horizontal takyr surface)	Kherson region, Beryslav district, environs of the village Mylove	Kamianska Sich National Nature Park, Mylivska Balka, willow forest, takyr-like substrates (silt)	6.05.2025	47.08595° N, 33.64611° E
2 (soil biocrust, crack in takyr)				
1a (bark of willow, 10 cm from the ground)				
3 (soil biocrust, horizontal takyr surface)	Dnipropetrovsk region, Kryvyi Rih district, environs of the village Maryanske	Willow forest, takyr-like substrates (silt)	6.05.2025	47.55262° N, 33.93278° E
4 (soil biocrust, crack in takyr)				
3a (bark of willow, 10 cm from the ground)				
5 (soil biocrust)	Zaporizhzhia region, Zaporizhzhia district, environs of the village Lysohirka	Dnipro floodplain, sand	7.05.2025	47.66034° N 35.10919° E
6 (soil biocrust)	Zaporizhzhia region, Zaporizhzhia district, Khortytsia island	Dnipro floodplain, sand	7.05. 2025	47.81244° N 35.14314° E
7 (soil biocrust)				

Results

Over the study period (2023–2025), a total 55 species of terrestrial algae, two species of bryophytes, and one species of lichen were identified on the exposed bed of the former Kakhovka Reservoir. Algae, especially representatives of Cyanobacteria and Chlorophyta, were dominant (Table 2, Figure 3, 4, Appendix 1). Microphotographs of the dominant and taxonomically interesting algal species are shown in Figures 5, 6, 7.

TABLE 2. Species diversity of terrestrial algae, bryophytes, and lichens found at the exposed bed of the former Kakhovka Reservoir

Divisions	Soil biocrusts			Bark of the willow trees	Total
	Total in biocrusts	Silt (takyr-like substrate)	Sand		
Algae					
Cyanobacteria	17	12	12	2	17
Chlorophyta	22	11	18	8	27
Charophyta	4	2	3	–	4
Heterokontophyta	7	5	3	–	7
Totally (algae)	*50*	*30*	*36*	*10*	*55*
Bryophytes					
Bryophyta	1	–	1	–	1
Marchantiophyta	1	1	–	–	1
Totally (bryophytes)	*2*	*1*	*1*	–	*2*
Lichens					
Ascomycota	–	–	–	1	1
Totally (lichens)	–	–	–	*1*	*1*
Total	**52**	**31**	**37**	**11**	**58**

The highest algal species richness was recorded in soil biocrusts with 50 species identified (Cyanobacteria – 17 species, Chlorophyta – 22, Charophyta – 4, Heterokontophyta – 7). These crusts were sampled on two distinct substrate types: a takyr-like substrate (silt) and sand both characteristic of the former reservoir's exposed bed.

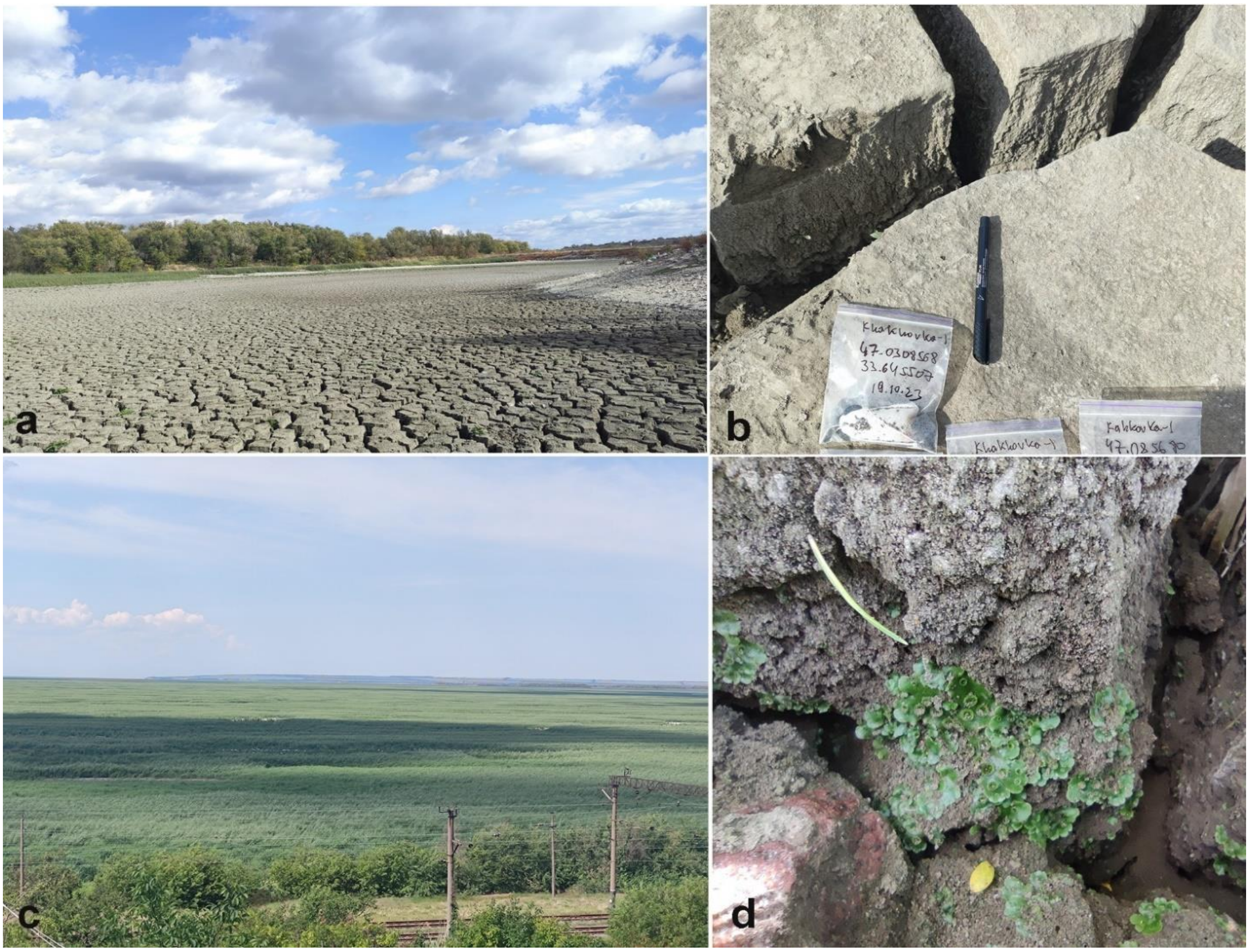

FIGURE 1. Algal sampling locations on the exposed bed of the former Kakhovka Reservoir in 2023 and 2024: a–b – takyr-like substrate (silt) with soil biocrusts in Mylivska Balka (sample KSA02); c–d – takyr-like substrate (silt) with soil biocrusts near the village of Malokaterynivka (KR0524_10). Photo by O. Khodosovtsev.

FIGURE 2. Algae sampling sites from the exposed bed of the former Kakhovka Reservoir in 2025: a–c – takyr-like substrate (silt) with soil biocrusts (samples 1, 2 (a, b) and 3, 4 (c)); e–i – sandy substrate with soil biocrusts (samples 5 (e, h), 6 (i), and 7 (f, g)); d, j – green biofilms on the bark of young willows (samples 1a (d) and 3a (j)). Photo by O. Khodosovtsev.

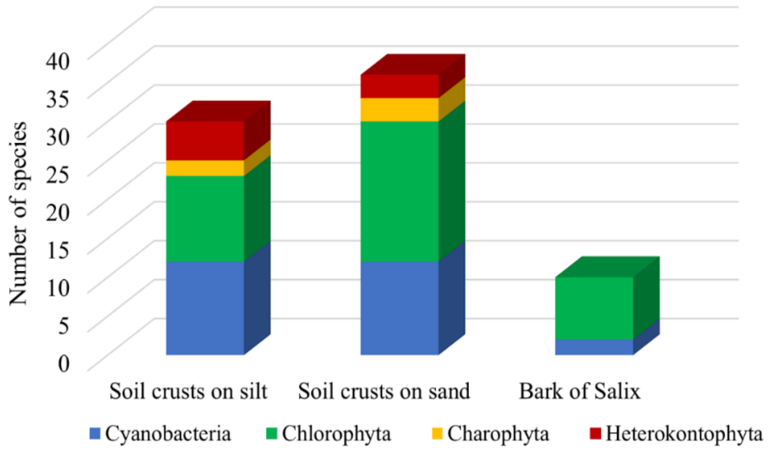

FIGURE 3. Algal species richness in soil biocrusts and on willow bark throughout the study period on the exposed bed of the former Kakhovka Reservoir.

Following the water recession, takyr-like substrates developed on the exposed silt sediments. The development of soil biocrusts on the substrate surface and within the crack system marks the initial stage of colonization and the subsequent establishment of vegetation cover. The studied areas are currently covered with dense young willow forest. A total we identified 30 species of algae in the soil biocrusts on the silt substrates throughout the study period including Cyanobacteria (12 species), Chlorophyta (11), Charophyta (2), Heterokontophyta (5). Thus, in the initial stages of colonization of the exposed bed of the former Kakhovka Reservoir (2023), only 4 species of algae were found, cyanobacteria prevailed and *Phormidium takyricum* (FIGURE 5d, g) dominated. After a year of ecosystem recovery in 2024, 7 species were found in the biocrusts, and the green alga *Chlorosarcinopsis* cf. *aggregata* (FIGURE 5h) joined the dominant complex (Didukh *et al.* 2024). In crusts collected two years after the dam breach (2025), the diversity of algae increased considerably, 30 species were identified, the number of species varies from 9 to 15 in different samples. The dominant complex also became more diverse, consisting primarily of cyanobacteria such as *Stenomitos* sp. (FIGURE 5a), *Oculatella* cf. *kazantipica* (FIGURE 5b), *Microcoleus vaginatus* (FIGURE 5c), and *Nostoc commune* (FIGURE 5f). In certain samples, this complex was supplemented by green algae including *Valeriella* cf. *incrassata* (FIGURE 5k, l) and *Klebsormidium* cf. *flaccidum* (FIGURE 5i). The gradual increase in algal species richness within the silt-based biocrusts on over three-year study period is presented in FIGURE 4. Other biocrust component, in particular bryophytes (mosses and liverworts), were very rarely recorded on silts.

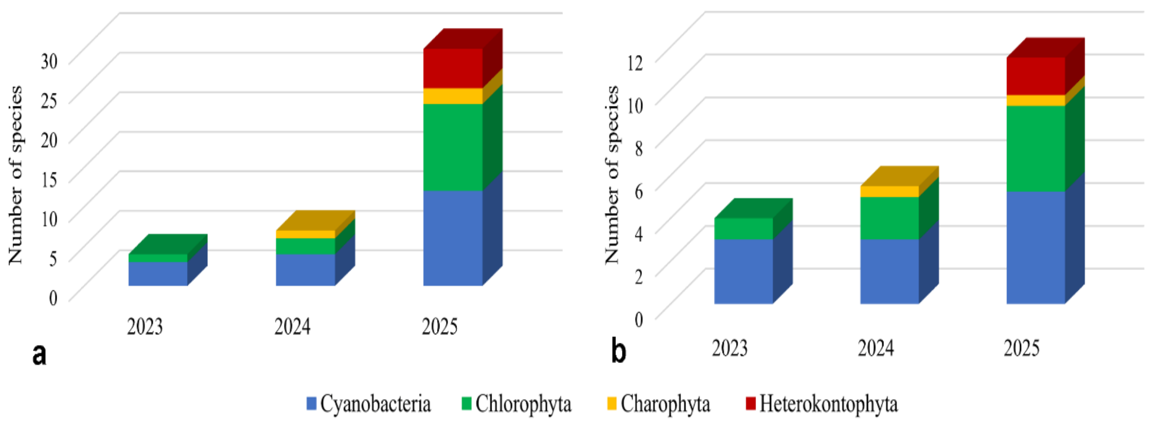

FIGURE 4. Dynamics of algal species richness across different taxonomic groups in silt (takyr-like) biocrusts over the entire study period on the former Kakhovka Reservoir bed: a – total number of species, b – mean number of species per sample.

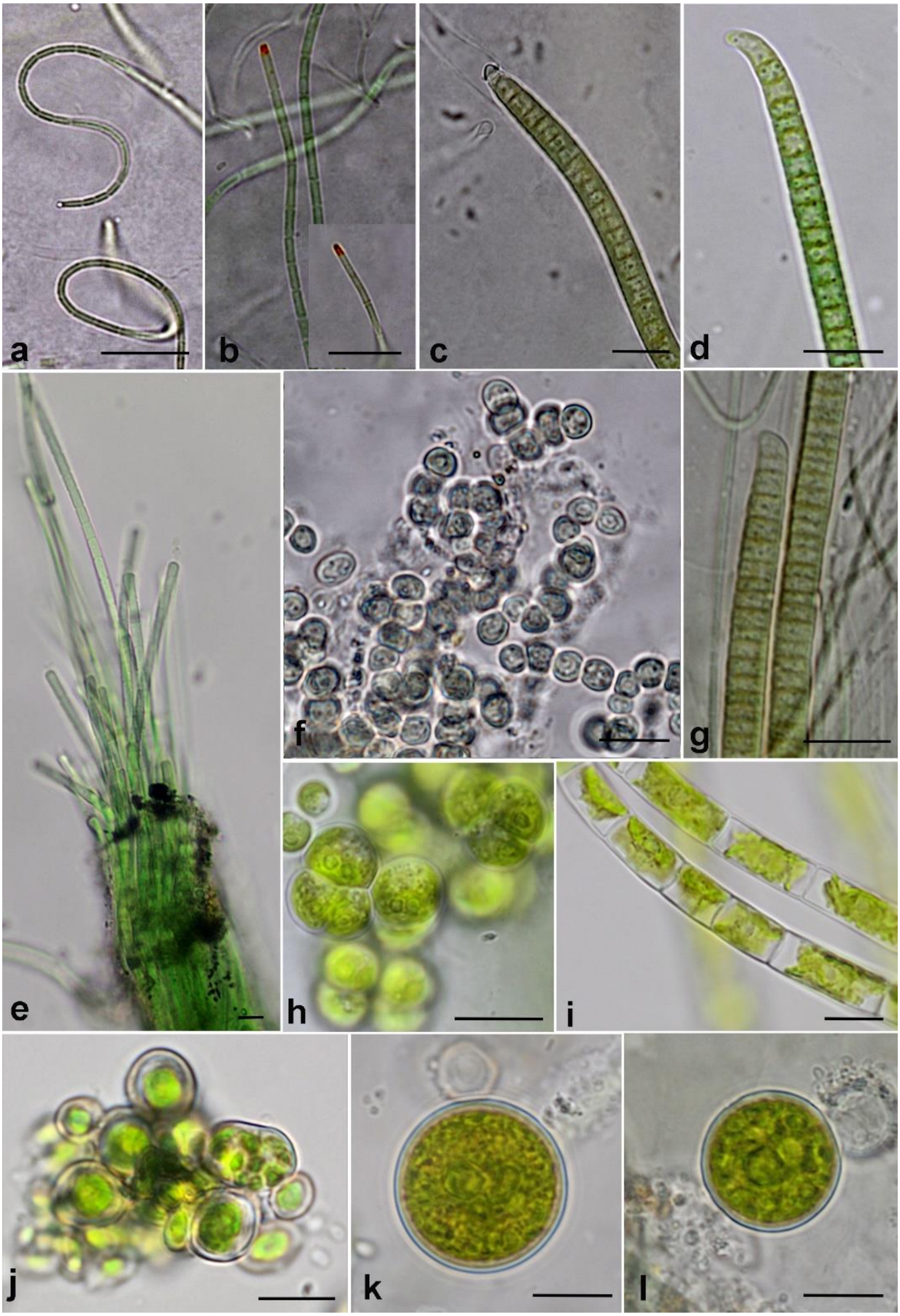

FIGURE 5. Dominant algal species in soil biocrusts and aerophytic biofilms of willow bark: a – *Stenomitos* sp., b – *Oculatella* cf. *kazantipica*, c – *Microcoleus vaginatus*, d, g – *Phormidium takyricum*, e – *Konicacronema sociatus*, f – *Nostoc commune*, h – *Chlorosarcinopsis* cf. *aggregata*, i – *Klebsormidium* cf. *flaccidum*, j – *Chloroidium* cf. *ellipsoideum*, k, l – *Valeriella* cf. *incrassata*. Scale bars: 10 µm. Photo by T. Mikhailyuk and A. Leonov.

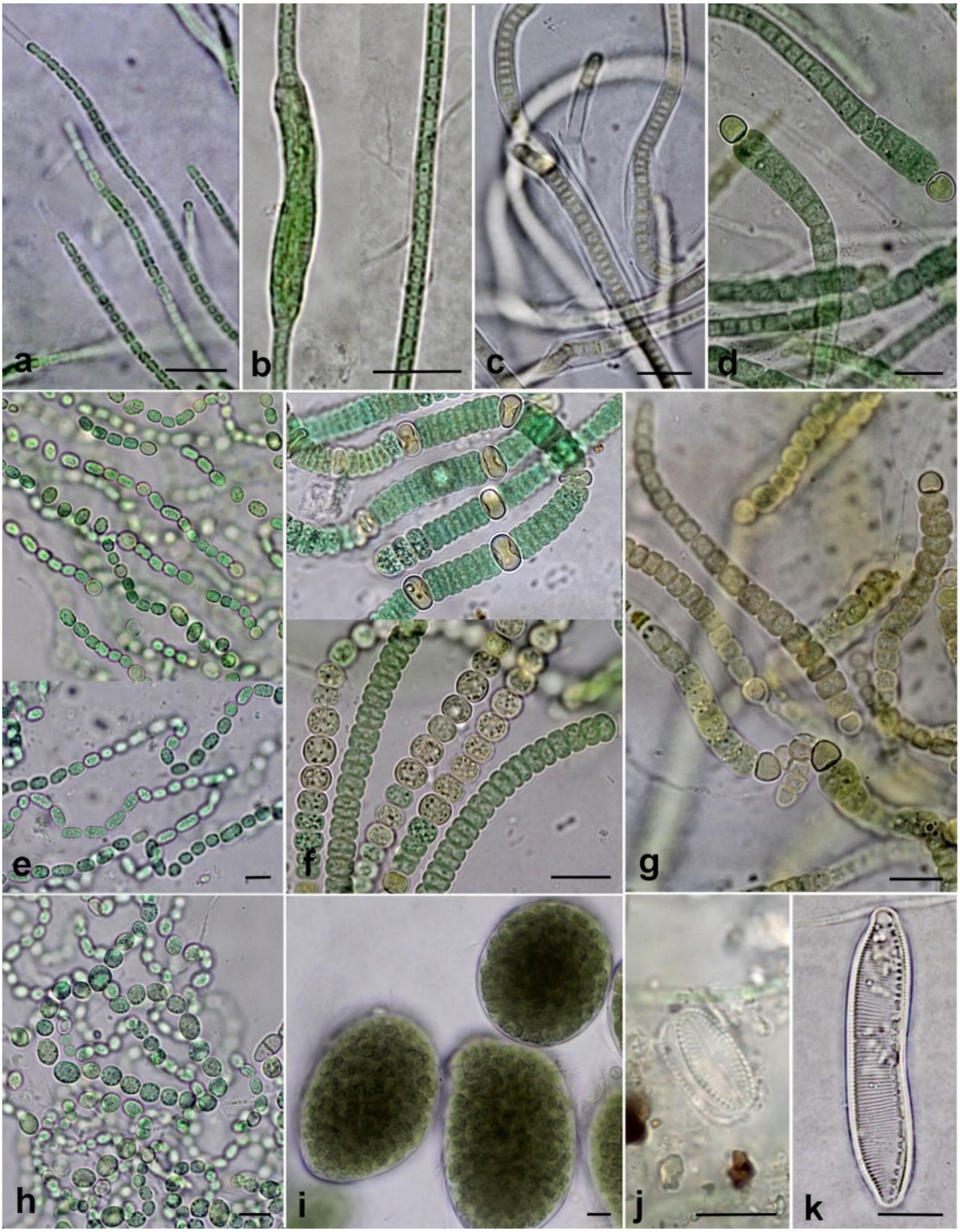

FIGURE 6. Algal species (Cyanobacteria and Heterokontophyta (Bacillariophyceae)) occurring occasionally in soil biocrusts and aerophytic biofilms of willow bark: a – *Phormidesmis* sp., b – *Nodosilinea bijugata*, c – *Timaviella edaphica*, d – *Calothrix* cf. *elenkinii*, e – *Desmonostoc* cf. *muscorum*, f – *Nodularia harveyana*, g – *Roholtiella* cf. *edaphica*, h – *Nostoc* cf. *calcicola*, i – *Nostoc punctiforme*, j – *Luticola cohnii*, k – *Hantzschia amphioxys*. Scale bars: 10 µm. Photo by T. Mikhailyuk and A. Leonov.

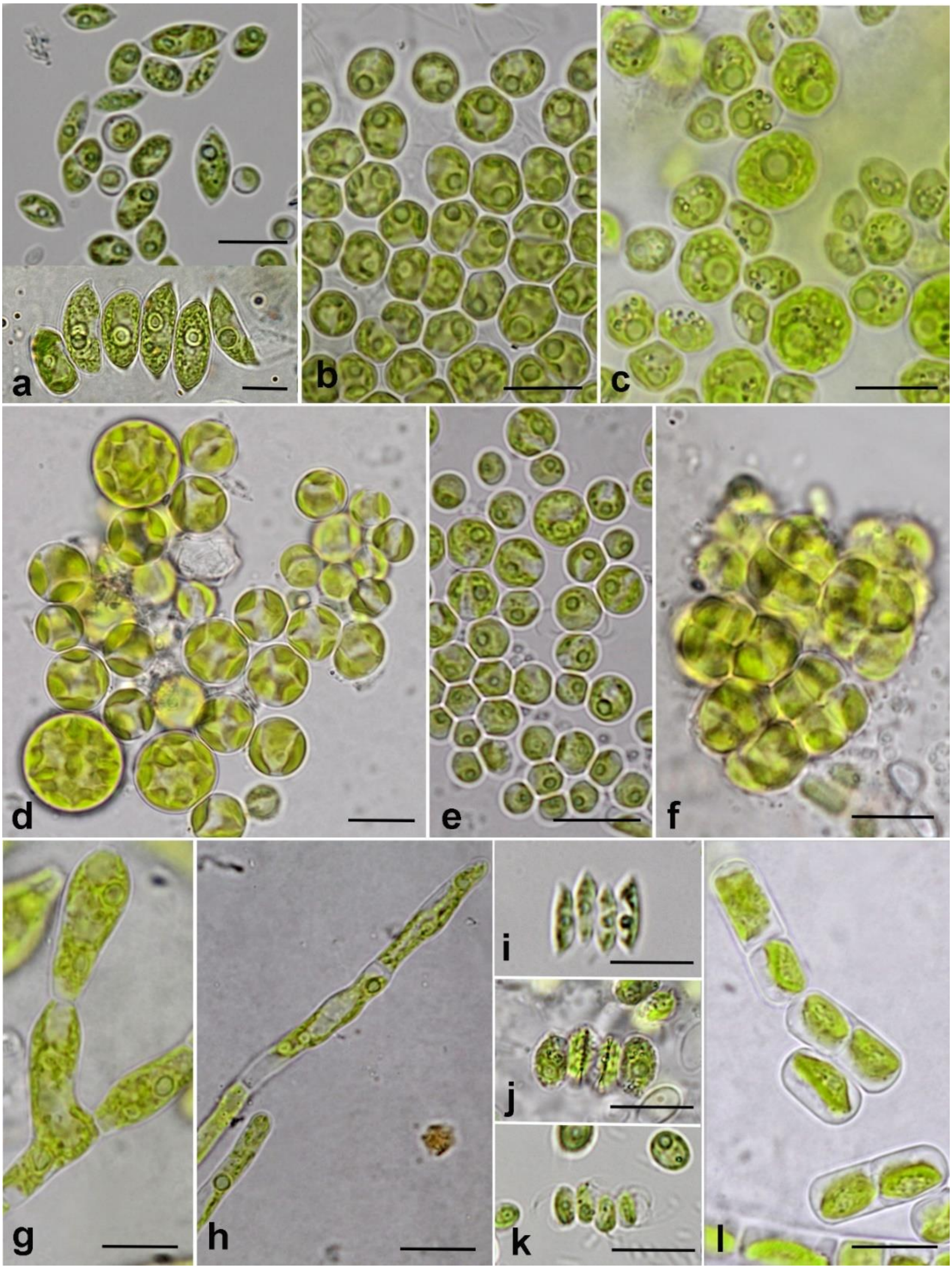

FIGURE 7. Algal species (Chlorophyta and Charophyta) that occurring occasionally in soil crusts and aerophytic biofilms on willow bark. a – *Tetradesmus* cf. *arenicola*, b – *Coelastrella* sp., c – *Pleurastrum minutum*, d – *Bracteacoccus minor*, e – *Chlorella vulgaris*, f – *Diplosphaera chodatii*, g, h – *Pseudopleurococcus* cf. *printzii*, i – *Tetradesmus obliquus*, j – *Desmodesmus brasiliensis*, k – *Desmodesmus intermedius* var. *balatonicus*, l – *Klebsormidium dissectum.* Scale bars: 10 µm. Photo by T. Mikhailyuk and A. Leonov.

No mosses or liverworts were found on takyr-like substrates (silt) in the Kamianska Sich National Nature Park during the entire observation period, while the liverwort *Marchantia polymorpha* was registered on the crack walls of takyr-like substrates in a dense young willow forest in May 2024 near the village Malokaterynivka (Zaporizhzhia region) (FIGURE 1d).

Soil biocrust samples on sandy substrates were collected within the Dnipro floodplain, mainly from open riparian areas adjacent to emerging willow forests. Sandy substrates are mainly localized in the northern part of the former Kakhovka Reservoir (Zaporizhzhia region). 36 species of algae were identified in the biocrusts on sandy substrates (Cyanobacteria – 12 species, Chlorophyta – 18, Charophyta – 3, Heterokontophyta – 3). Algal communities in these sandy biocrusts were more species rich than those that developed on silt (takyr-like) substrates, with 15–23 species recorded per sample. The dominant complex comprised Cyanobacteria (including *Konicacronema sociatus* (FIGURE 5e) and *Nostoc edaphicum*) and green algae such as *Klebsormidium* cf. *flaccidum* (FIGURE 5i). In contrast to the takyr-like areas, sandy substrates frequently hosted biological crusts dominated by the moss *Funaria hygrometrica* (FIGURE 2i).

In the aerophytic biofilms on bark of young willow trees, which currently forms forest on the former Kakhovka Reservoir bed, 10 algal species were identified (Cyanobacteria – 2 species, Chlorophyta – 8). Species richness was 8-10 species recorded per sample. The dominant species of algae in a green biofilm on tree bark was *Chloroidium* cf. *ellipsoideum* (FIGURE 5j). The first epiphytic lichen (*Physcia adscendens*) was recorded on the bark of *Salix* × *rubens* on May 6, 2025 (sample 1a, vicinity of Mylove village), i.e. 1 year and 10 months after the initial germination of willows at this location. The lichen was represented by a juvenile thallus, consisting of a single blade approximately 80 μm in diameter. The thallus had a single rhizine and was at a developmental stage preceding sorales formation.

DISCUSSION

Biocrusts on both silt (takyr-like) and sandy substrates are mainly formed by cyanobacteria belonging to the genera *Microcoleus*, *Phormidium*, *Oculatella*, *Stenomitos*, *Konicacronema*, and *Nostoc*. These include thin-filamentous and filamentous homocytic forms as well as colonial filamentous heterocytic structure of the thallus. The significant participation of cyanobacteria in the formation of biocrusts, and especially their predominance in the dominant complex, is typical for the algal flora of the steppe zone of Ukraine (Prikhodkova 1992, Kostikov *et al.* 2001). Less frequently, biocrusts were formed by green algae of the genus *Klebsormidium.* These filamentous algae are typical components of soil biocrusts across various biogeographic zones worldwide (Büdel *et al.* 2016). Certain green algae, specifically *Chlorosarcinopsis* and *Valeriella* with coccoid packet-like and unicellular thalli, joined the dominant cyanobacterial complex to form crusts of mixed nature. Most of the identified green and yellow-green algae as well as terrestrial diatoms occurred only occasionally within the biocrusts.

In terms of species richness within the biocrusts, coccoid unicellular green algae and occasionally diatoms prevailed (totaling 16 species), while fine-filamentous homocytic cyanobacteria were slightly less frequent (6 species). Among the 43 species identified to the species level within the soil biocrusts, aquatic-terrestrial and terrestrial species prevailed (23 and 16 species). Most of them (37 species) are recognized as soil algae, 20 species were previously documented in soil biocrusts. Nearly all identified species had been previously recorded within the steppe zone of Ukraine with the exception of *Chlorosarcinopsis gelatinosa*. Among these, 14 species are widely distributed across all natural zones of Ukraine.

A distinguishing feature of the biocrusts on silt (takyr-like) substrates is the dominance and high diversity of fine-filamentous and small-celled cyanobacteria (e.g. *Stenomitos*, *Oculatella*, *Phormidesmis*, and *Nostoc*) probably due to the fine-textured nature of the silt substrate. This trend is consistent with our previous observations during investigations of soil biocrusts on fine-grained Baltic coastal sand dunes (Schulz *et al.* 2016, Mikhailyuk *et al.* 2019). A noteworthy find with the silt-based biocrusts was *Oculatella* cf. *kazantipica* (FIGURE 5b) This species was recently described from biocrusts in coastal Crimea (Vinogradova *et al.* 2017) and later reported from semi-arid habitat in Spain (Munoz-Martin *et al.* 2019) and cave walls on Corfu Island (Greece) (Panou & Gkelis 2022). This species is probably characteristic of southern regions with continental and Mediterranean climates.

On sandy substrates with coarser texture, cyanobacteria with thick trichomes (e.g., species of *Microcoleus*, *Konicacronema*, *Calothrix*, *Roholtiella*) predominated and reached high abundance. This trend was observed during study of soil biocrusts of coastal dunes composed of coarse-grained sand (Schulz *et al*. 2016, Mikhailyuk *et al*. 2019). A notable feature of the studied biocrusts on sandy substrates was the significant presence of aquatic algae, identified through both direct microscopy and in culture. In particular, these are the species *Monoraphidium contortum*, *M. minutum*, *Tetradesmus obliquus* (FIGURE 7i), *Desmodesmus communis*, *D. brasiliensis* (FIGURE 7j) and *D. intermedius* var. *balatonicus* (FIGURE 7k). Additionally, a significant number of empty frustules of aquatic diatoms were observed in several samples; however, these were not included in the current study. These findings confirm the previous inundation of the study sites. A noteworthy find was *Tetradesmus* cf. *arenicola* (FIGURE 7a), a species recently described from coastal sand dunes of Ukraine and Germany (Mikhailyuk *et al.* 2019). Notably, this taxon was subsequently identified from another locality within southern Ukraine – the sands of Kinburn Spit (Mykolaiv region, unpublished data, NCBI, https://www.ncbi.nlm.nih.gov/nuccore/MZ546612.1). This species has been recorded exclusively on coastal sands across two localities in Ukraine and three in Germany. Such distribution pattern suggests that it is typical for sandy substrates exposed in terrestrial conditions. Another noteworthy cyanobacterium was the recently described *Roholtiella* cf. *edaphica* (FIGURE 6g). This species was originally documented in soil biocrusts along the Crimean coast (Mikhailyuk *et al*. 2016) and chalk outcrops of the Kharkiv region (Vinogradova *et al*. 2019). Globally, this taxon has been previously recorded in soils across the USA (Bohunicka *et al*. 2015) and Russia (Gaysina *et al*. 2018).

A significant increase of species diversity of soil biocrust algae on silt (takyr-like) substrates was recorded during the third year of ecosystem recovery on the exposed bed of the former Kakhovka Reservoir (FIGURE 4a). The observed increase in the species richness may partly reflect both successional processes and differences in sampling effort, as the number of samples varied between study periods (see TABLE 1). To account for this sampling bias, we compared the species richness of biocrust algae based on the mean number of species per sample. This approach revealed a more gradual yet but considerable increase in both algal species richness and taxonomic diversity during the third year of ecosystem recovery (FIGURE 4b).

The low total species richness (10 species) and the predominance of green algae on the bark of young willow trees are typical for aerophytic algal communities on tree bark in temperate regions (Barkmann 1958, Mikhailyuk *et al*. 2025). However, the dominant species was the unicellular green alga *Chloroidium* cf. *ellipsoideum* (FIGURE 5j), which is not typical for such habitats. In the temperate zone, epiphytic biofilms on tree bark are mainly formed by representatives of the genera *Desmococcus* and *Apatococcus* with a packet-like morphotype, with only occasional occurrence of other green algae (Barkmann 1958, Mikhailyuk *et al*. 2025). *Chloroidium* cf. *ellipsoideum* is a typical terrestrial green alga, though it rarely dominates in the epiphytic communities on tree bark, where it usually occurs only occasionally (Darienko *et al*. 2010). The observed dominance of *Chloroidium* in this study may be attributed to the initial successional stages of algal community formation of on the bark of young willow trees.

Coccoid unicellular and packet-like algae (4 and 3 species respectively) predominated within the aerophytic communities on willow bark. Among 7 algal representatives identified to the species level, 5 are aquatic-terrestrial and 2 are terrestrial algae. Notably, all 7 species were previously found in soil, 6 of them are also components of biocrusts, while 5 had been previously recorded on tree bark. All identified species were previously recorded within the steppe zone; most of them (4 species) are widely distributed across all natural zones of Ukraine. A noteworthy representative was the cyanobacterium *Nodularia harveyana* (FIGURE 6f), which has been previously documented as an epiphyte on tree bark (Kondratyeva 1968). Most records of this species in Ukraine originate from the steppe zone (Tsarenko *et al.* 2024a).

Bryophytes and lichens play only a minor role in the formation of biological soil crusts and epiphytic communities on the bark during the initial stages of primary succession on the exposed bed of the former Kakhovka Reservoir. At the same time, sandy substrates proved to be more favorable for the development of pioneer monospecific communities of the moss *Funaria hygrometrica*.

CONCLUSIONS

High cyanobacterial diversity of and their dominance in communities are characteristic for soils in the steppe zone of Ukraine. A distinctive feature of biocrusts on silt is the predominance of fine-filamentous and small-celled cyanobacteria whereas on sandy substrates, which represent a coarser texture, cyanobacteria with thick trichomes are abundant. Biocrusts on sand were characterized by a higher diversity of algae and the occurrence of aquatic species due to the periodic flooding of these areas. During the three years following the dam destruction, algal diversity in the biocrusts increased considerably. The low species richness in willow bark biofilms and the dominance of green algae are characteristic of aerophytic bark communities in the temperate zone. However, the prevalence of the green alga *Chloroidium* cf. *ellipsoideum* as a dominant species, is an atypical phenomenon may be attributed to the initial successional stages of epiphytic community formation. In the early successional stages of biodiversity recovery, bryophytes and lichens contribute minimally to the development of soil biocrusts and corticolous assemblages of willow trees. At the same time, sandy substrates proved to be more favorable for the development of pioneer monospecific communities of the moss *Funaria hygrometrica*. Our findings regarding the diversity of algae, bryophytes, and lichens reflect the initial stages of soil biocrust and corticolous biofilm formation on the exposed bed of the former Kakhovka Reservoir, providing a critical baseline for long-term monitoring of successional processes in this region.

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ADDITIONAL INFORMATION

Conflict of Interest

The authors declare that they have no conflicts of interest.

Ethical Statement

The authors declare that no ethical standards were violated during the research.

Use of AI

AI was not used during preparation of the article.

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Author Contributions

T.M.: Conceptualization, Resources, Identification of algae, Formal Analysis, Visualization, Writing – original draft; **A.L.:** Identification of algae, Writing – review & editing; **O.K.:** Idea, Field Investigation, Identification of lichen and mosses, Resources, Writing – review & editing. All authors have read and agreed to the published version of the manuscript.

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Data Availability

All data supporting the findings of this study are available in this paper.

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Резюме

Михайлюк, Т.І., Леонов, А.О., Ходосовцев, О.Є. (2026). Наземні водорості, мохоподібні і лишайники біологічних ґрунтових кірок та епіфітних біоплівок на дні колишнього Каховського водосховища. *Чорноморський ботанічний журнал* **22** (1): 46–65. https://doi.org/10.32999/ksu1990-553X/2026-22-1-3

За результатами досліджень дна колишнього Каховського водосховища, ідентифіковано 55 видів наземних водоростей, 2 види мохоподібних та 1 вид лишайника. Найбільша кількість видів водоростей виявлена у ґрунтових біокірках: 50 видів. У структурі ґрунтових біокірок переважають представники Cyanobacteria та Chlorophyta, з домінуванням *Phormidium takyricum*, *Chlorosarcinopsis* cf. *aggregata*, *Stenomitos* sp., *Microcoleus vaginatus*, *Klebsormidium* cf. *flaccidum* та ін. Значна частка ціанобактерій у формуванні кірок та їхня домінантна роль в угрупованнях є характерною рисою альгофлори ґрунтів степової зони України. Специфікою біокірок на мулистих (такироподібних) субстратах є переважання та високе різноманіття тонконитчастих і дрібноклітинних ціанобактерій (роди *Stenomitos*, *Oculatella*, *Phormidesmis*, *Nostoc* та ін.), що, ймовірно, зумовлено тонкодисперсністю мулу. Натомість на піску, як більш грубому субстраті, домінували та рясно траплялися представники ціанобактерій з товстими трихомами (види *Konicacronema*, *Calothrix*, *Roholtiella* та ін.). Особливістю кірок на піщаних субстратах також стало більше різноманіття водоростей та значна присутність водних видів (родів *Monoraphidium*, *Tetradesmus* та *Desmodesmus*), ймовірно, через періодичне затоплення досліджених територій. Вивчення динаміки розвитку біокірок на такироподібних субстратах протягом трьох років, відразу після підриву дамби до сьогодні, показало значне зростання біорізноманіття водоростей, від 4 та 7 видів у 2023 та 2024 роках до 30 видів у 2025 році. Таксономічне різноманіття та склад домінуючих видів також стали різноманітнішими. У ґрунтових біокірках виявлено флористично цікаві та рідкісні види: *Oculatella* cf. *kazantipica*, *Roholtiella* cf. *edaphica*, *Nodularia harveyana*, *Tetradesmus* cf. *arenicola*. Невисоке видове багатство альгофлори на корі молодих дерев верби (10 видів) та домінування зелених водоростей є типовими ознаками аерофітних обростань кори у помірній зоні. Проте превалювання зеленої водорості *Chloroidium* cf. *ellipsoideum* як домінантного виду є нетиповим явищем і, ймовірно, пояснюється початковими стадіями формування епіфітних угруповань. Мохоподібні та лишайники відіграють другорядну роль у формуванні ґрунтових біокірок та епіфітних обростань кори верб на початкових етапах відновлення біорізноманіття на дні колишнього Каховського водосховища. Водночас піщані субстрати виявилися більш сприятливими для розвитку піонерних моновидових угруповань за участю моху *Funaria hygrometrica*.

Ключові слова: біологічне різноманіття, біологічні ґрунтові кірки, такир, мул, пісок, кора дерев, вербовий ліс, війна, Україна.

APPENDIX 1. Characteristics of algal species recorded in biological soil crusts and on willow bark on the exposed bed of the former Kakhovka Reservoir

Algal species	Soil biocrusts: Silt (takyr-like substrate) 2023	Silt 2024	Silt 2025	Sand 2025	Bark of willow trees 2025	Morphological structure	Ecological characteristics: Ecology	Habitats	Distribution: In Ukraine	In the world
Stenomitos sp.	+	+	D	+		fine-filamentous homocytic	–	–	–	–
Stenomitos sp.2			+			fine-filamentous homocytic	–	–	–	–
Phormidesmis sp.			+			fine-filamentous homocytic	–	–	–	–
Nodosilinea cf. *bijugata*	+	+	+	+		fine-filamentous homocytic	aquatic-terrestrial	rivers, floodland water bodies, lakes, reservoirs, pools, takyrs, salty soils, soils	Polissya, Forest-steppe, Steppe, Mountain Crimea, Carpathians	Europe, Asia (Israel), New Zealand
Timaviella edaphica				+		fine-filamentous homocytic	terrestrial, aerophytic, subaerophytic, soil	rivers, floodland water bodies, salty soils, soils, soil biocrusts	Forest-steppe, Steppe, Mountain Crimea	Europe (Germany, Russia, Czech Republic) Asia (Tajikistan, Israel), North America
Oculatella cf. *kazantipica*			D	+		fine-filamentous homocytic	terrestrial, soil	soils, soil biocrusts	Steppe	Southern Europe (Spain, Greece)
Phormidium takyricum	D	D	+			filamentous homocytic	terrestrial, soil	soils, soil biocrusts subaerophytic biotopes	Forest-steppe, Steppe (widely distributed), Mountain Crimea, Azov Sea (supralittoral?)	Central Europe and Central Asia
Microcoleus vaginatus			D	+		filamentous homocytic	terrestrial, soil	soils, soil biocrusts	widely distributed in all climatic zones	cosmopolitan
Konicacronema sociatus				D		filamentous homocytic	aquatic-terrestrial	cooling ponds, ponds, streams, dripping rocks, soils, soil biocrusts	Polissya, Forest-steppe, Steppe, Mountain Crimea, Carpathians	Europe, Asia, North and South America, Australia

Desmonostoc cf. *muscorum*		+	+	+	+	colonial filamentous heterocytic	aquatic-terrestrial	rivers, streams, dripping rocks, soils, soil biocrusts	Forest-steppe, Steppe, Mountain Crimea, Carpathians	cosmopolitan
Nostoc edaphicum				D		colonial filamentous heterocytic	terrestrial, soil	aerophytic biotopes, ponds, bogs, soils, salty soils, soils, soil biocrusts, bark of trees	Forest-steppe, Steppe, Mountain Crimea, Carpathians	Europe, Asia, North and South America
Nostoc cf. *calcicola*			+			colonial filamentous heterocytic	terrestrial, subaerophytic, soil	rocks, soils, salty soils	Forest-steppe, Steppe, Carpathians	cosmopolitan
Nostoc commune			D			colonial filamentous heterocytic	terrestrial, soil	soil surface, soils, soil biocrusts, subaerophytic biotopes	Polissya, Forest-steppe, Steppe (widely distributed), Mountain Crimea, Carpathians, Black Sea (supralittoral)	cosmopolitan
Nostoc punctiforme			+	+		colonial filamentous heterocytic	aquatic-terrestrial	terrestrial and aquatic biotopes	widely distributed in all climatic zones	cosmopolitan, one of the most common species
Calothrix cf. *elenkinii*				+		filamentous heterocytic	aquatic-terrestrial, freshwater, soil	rivers, lakes, ponds, reservoirs, bogs etc., soils, chasmolithic biotopes, salty soils	Polissya, Forest-steppe, Steppe	Europe, South and North America, Asia, Australia
Roholtiella cf. *edaphica*				+		filamentous heterocytic	terrestrial, soil	soils, soil biocrusts	Forest-steppe, Steppe	Europe (Russia), North America (USA)
Nodularia harveyana			+	+	+	filamentous heterocytic	aquatic-terrestrial, freshwater, brackish water, soil	rivers, lakes, bogs, pools, brackish water bodies, soils, salty soils, bark of trees	Polissya, Forest-steppe, Steppe	cosmopolitan
Lobochlamys sp.			+	+		flagellated unicellular	–	–	–	–
Heterochlamydomonas callunae				+		flagellated unicellular	terrestrial, soil	soils, soil biocrusts	Polissya, Forest-steppe, Steppe, Carpathians	Europe (Czech Republic, Germany, Russia, Ukraine)

Ankistrodesmus arcuatus			+			coccoid unicellular	aquatic-terrestrial, freshwater, planktonic-benthic, soil	rivers, ponds, lakes, bogs, estuaries etc., soils	widely distributed in all climatic zones	probably cosmopolitan
Monoraphidium contortum				+		coccoid unicellular	aquatic, freshwater, planktonic-benthic	rivers, ponds, lakes, bogs, reservoirs etc.	widely distributed in all climatic zones	cosmopolitan
Monoraphidium minutum				+		coccoid unicellular	aquatic, freshwater, planktonic-benthic	rivers, ponds, lakes, bogs, reservoirs etc.	widely distributed in all climatic zones	all continents, probably cosmopolitan
Coelastrella sp.			+	+	+	coccoid unicellular	–	–	–	–
Coelastrella rubescens				+		coccoid unicellular	terrestrial, soil	soils	Polissya, Forest-steppe, Steppe, Mountain Crimea, Carpathians	Europe (Italy, Russia, Ukraine), Asia (China, Russia), North America
Tetradesmus obliquus				+		coccoid cenobial	aquatic-terrestrial, freshwater, planktonic-benthic, soil	rivers, ponds, lakes, bogs, reservoirs etc., soils	widely distributed in all climatic zones	cosmopolitan
Tetradesmus cf. *arenicola*				+		coccoid cenobial	terrestrial, soil	soils, soil biocrusts	Steppe	Europe (Germany, Ukraine)
Desmodesmus communis				+		coccoid cenobial	aquatic, freshwater, planktonic-benthic	rivers, ponds, lakes, bogs, reservoirs etc.	widely distributed in all climatic zones	cosmopolitan
Desmodesmus brasiliensis			+	+		coccoid cenobial	aquatic-terrestrial, freshwater, planktonic-benthic, epilithic, aerophytic	rivers, ponds, lakes, bogs, reservoirs etc., aerophytic biotopes	widely distributed in all climatic zones	cosmopolitan
Desmodesmus intermedius var. balatonicus				+		coccoid cenobial	aquatic, freshwater, planktonic	rivers, ponds, lakes, floodland water bodies	Polissya, Steppe	Europe, South America, Asia, Africa
Valeriella cf. *incrassata*			D			coccoid unicellular	terrestrial, aerophytic, soil	soils, soil biocrusts, dry rocks, chasmolithic biotopes	Polissya, Steppe	Europe (Russia), Asia (Russia, Saudi Arabia)
Chlorococcum cf. *lobatum*				+		coccoid unicellular	aquatic-terrestrial, freshwater, benthic, soil	pools, soils, dry rocks, chasmolithic biotopes	Polissya, Forest-steppe, Steppe, Carpathians	Europe (Czech Republic, Great Britain, Russia, etc.), Asia

										(Russia), Antarctica
Neospongiococcum sp.				+		coccoid unicellular	–	–	–	–
Pleurastrum minutum			+			coccoid unicellular	terrestrial, soil	soils	Polissya, Forest-steppe, Steppe, Mountain Crimea, Carpathians	Europe, Asia, North and South America
Tetracystis sp.					+	coccoid packet-like	–	–	–	–
Chlorosarcinopsis cf. *aggregata*		D	+	+		coccoid packet-like	terrestrial, soil	soils	Forest-steppe, Steppe, Carpathians	Europe (Belgium, Russia), Asia (Mongolia), Central America (Cuba), Antarctica
Chlorosarcinopsis gelatinosa				+		coccoid packet-like	terrestrial, soil	soils	Polissya, Forest-steppe	Europe (Italy, Russia, Ukraine), Asia
Bracteacoccus minor					+	coccoid unicellular multinucleate	terrestrial, soil, freshwater, subaerophytic, aerophytic	soils, soil biocrusts, dry rocks, chasmolithic biotopes	widely distributed in all climatic zones	Europe (Italy, Russia, Ukraine), Asia
Chlorella vulgaris	+	+	+	+	+	coccoid unicellular	aquatic-terrestrial, freshwater, brackish water, planktonic-benthic, aerophytic, subaerophytic, soil	rivers, ponds, lakes, bogs, reservoirs, seas etc., aerophytic biotopes, soils, soil biocrusts, salty soils, bark of trees, dry rocks, caves, chasmolithic biotopes	widely distributed in all climatic zones	cosmopolitan, one of the most common algae
Stichococcus bacillaris			+	+	+	filamentous easily disintegrating	aquatic-terrestrial, freshwater, planktonic-benthic, aerophytic, subaerophytic, epilithic, soil, photobiont	rivers, ponds, lakes, bogs, reservoirs etc., aerophytic biotopes, soils, soil biocrusts, salty soils, bark of trees, dry rocks, caves, chasmolithic biotopes	widely distributed in all climatic zones	cosmopolitan
Nannochloris sp.			+			coccoid unicellular	–	–	–	–
Chloroidium cf. *ellipsoideum*					D	coccoid unicellular	aquatic-terrestrial, freshwater,	ponds, lakes, pools, etc., aerophytic	Polissya, Forest-steppe, Steppe,	Europe, Asia, North and South

							planktonic-benthic, aerophytic, epilithic, soil, photobiont	biotopes, soils, soil biocrusts, salty soils, bark of trees, dry rocks, caves, chasmolithic biotopes	Mountain Crimea, Carpathians	America, Africa, Australia
Diplosphaera chodatii					+	coccoid packet-like	terrestrial, aerophytic, subaerophytic, epilithic, soil, photobiont	aerophytic biotopes, soils, soil biocrusts, salty soils, bark of trees, dry rocks, caves, chasmolithic biotopes	widely distributed in all climatic zones	one of the most common terrestrial algae, probably cosmopolitan
Trebouxia sp.					+	coccoid packet-like	terrestrial, aerophytic, soil, photobiont	aerophytic biotopes, soils, bark of trees, dry rocks	–	–
Pseudopleurococcus cf. *printzii*			+			filamentous branched	terrestrial, aerophytic, soil, photobiont	aerophytic biotopes, soils, salty soils, dry rocks	Forest-steppe, Steppe, Mountain Crimea, Carpathians	Europe (Great Britain, Czech Republic, Romania, Ukraine), Asia (Japan)
Klebsormidium cf. *flaccidum*		+	D	D		filamentous	aquatic-terrestrial, freshwater, benthic, aerophytic, epilithic, soil	ponds, rivers, streams, bogs etc., aerophytic biotopes, soils, soil biocrusts, salty soils, bark of trees, dry rocks, caves, chasmolithic biotopes	widely distributed in all climatic zones	one of the most common terrestrial algae, cosmopolitan
Klebsormidium dissectum			+			filamentous easily disintegrating	aquatic-terrestrial, freshwater, benthic, aerophytic, subaerophytic, epilithic, soil	ponds, aerophytic biotopes, soils, soil biocrusts, salty soils, bark of trees, dry rocks, chasmolithic biotopes	Polissya, Forest-steppe, Steppe, Mountain Crimea, Carpathians	Europe (Great Britain, Slovakia, Austria, etc.), Asia (Israel, Turkey, etc.), North America, Australia
Klebsormidium subtile				+		filamentous	aquatic-terrestrial, freshwater, planktonic-benthic, soil	rivers, ponds, lakes, bogs, reservoirs etc., aerophytic biotopes, soils, soil biocrusts	Polissya, Forest-steppe, Steppe, Mountain Crimea, Carpathians	cosmopolitan
Cylindrocystis brebissonii				+		coccoid unicellular	aquatic-terrestrial, freshwater, benthic, subaerophytic, soil	rivers, ponds, lakes, bogs etc., dripping	Polissya, Forest-steppe, Steppe, Carpathians	cosmopolitan

								rocks, soils, soil biocrusts		
Xanthonema exile			+			filamentous easily disintegrating	aquatic-terrestrial, freshwater, benthic, soil	reservoirs, ponds, flood-land water bodies, soils	Polissya, Forest-steppe, Steppe, Mountain Crimea, Carpathians	perhaps cosmopolitan
Xanthonema stichococcoides			+			filamentous easily disintegrating	aquatic-terrestrial, freshwater, soil	ponds, soils	Polissya, Forest-steppe, Steppe, Mountain Crimea, Carpathians	Europe (Slovakia, Czech Republic, Russia), Asia, South America
Fistulifera pelliculosa			+			coccoid unicellular	aquatic-terrestrial, freshwater, benthic, soil	rivers, ponds, lakes, etc, soils	Polissya, Forest-steppe, Steppe, Mountain Crimea, Carpathians	perhaps cosmopolitan
Luticola cohnii			+			coccoid unicellular	aquatic-terrestrial, freshwater, marine, benthic, subaerophytic, soil	ponds, pools, seas, aerophytic biotopes, soils, soil biocrusts,	Polissya, Forest-steppe, Steppe, Azov Sea	cosmopolitan
Luticola binodis				+		coccoid unicellular	aquatic-terrestrial, freshwater, benthic, soil	rivers, soils, salty soils	Forest-steppe, Steppe	Europe (Iceland, Great Britain, etc.), Asia (Iraq, Mongolia, China, etc.), North and South America, Africa
Luticola mutica				+		coccoid unicellular	aquatic-terrestrial, brackish water, freshwater, benthic, aerophytic, subaerophytic, soil	ponds, lakes, pools, seas etc., dripping and dry rocks, chasmolithic biotopes, soils, salty soils	Polissya, Forest-steppe, Steppe, Mountain Crimea, Carpathians Azov and Black seas	cosmopolitan
Hantzschia amphioxys			+	+		coccoid unicellular	aquatic-terrestrial, freshwater, benthic, soil	ponds, lakes, rivers, pools, seas etc., soils, soil biocrusts, salty soils, dry rocks, chasmolithic biotopes	widely distributed in all climatic zones	cosmopolitan
D – dominating species.										