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RESEARCH ARTICLE

Terrestrial algae and cyanobacteria of the Holosiiv National Nature Park (Kyiv, Ukraine), with the description of *Leptochlorella arboricola* sp. nov. (*Trebouxiophyceae*, *Chlorophyta*)

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Abstract. The article provides the results of a study on terrestrial algae inhabiting various substrates in the Holosiiv National Nature Park, which was established to protect the remnants of natural ecosystems in the Kyiv metropolitan area, Ukraine. Totally, 75 species were identified: *Cyanobacteria* (10 species), *Chlorophyta* (52), *Charophyta* (7), and *Heterokontophyta* (6). The largest number of species was recorded on concrete (44 species) and dead wood (41); both substrates exhibited the most diverse composition of dominant species of algae. Less species were found on tree trunks (34), soil crusts (25), and fruiting bodies of the polypore fungus (18). The genera *Klebsormidium* (5 species) and *Stichococcus* (4 species) were the most diversely represented on different substrates. Representatives of green algae, *Stichococcus bacillaris*, *Coccomyxa subellipsoidea*, *Interfilum terricola*, *Desmococcus olivaceus*, *Elliptochloris subsphaerica*, and *Trentepohlia* cf. *umbrina*, were most frequent in the studied habitats. Some new and noteworthy taxa have been revealed using molecular phylogenetic methods. Among them, three genera (*Wilmottia*, *Chromochloris*, and *Leptochlorella*) and five species (*Wilmottia murrayi*, *Drouetiella epilithica*, *Chromochloris zofingiensis*, *Neocystis mucosa*, and *Coccomyxa arvernensis*) were for the first time recorded for the algal flora of Ukraine. In addition, five rare species of the genera *Coelastrella*, *Pseudochlorella*, *Coenochloris*, *Dictyochloropsis*, and *Coccomyxa* are also reported. Finally, a new species of the genus *Leptochlorella*, *L. arboricola* Mikhailyuk, is described.

Keywords: algae, biological soil crusts, cyanobacteria, dead wood, forest phytocenoses, fruiting bodies of polypore fungi, ITS, *Leptochlorella arboricola*, *rbc*L, stony substrates, tree trunks, Ukraine, 16S/18S rRNA

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Introduction

Cyanobacteria and microalgae are important components of terrestrial ecosystems. Inhabiting soil, rocks, tree trunks, and other substrates of natural and artificial origin, they not only enrich the environment with carbon and nitrogen, but also exert a direct and/or indirect impact on its substrate due to their biological activity or presence (Evans, Johansen, 1999; Büdel et al., 2014; Hauer et al., 2015; Baumann et al., 2017, 2021). The diversity of this terrestrial group has been studied much less than that of aquatic forms, although in recent decades the interest in studying terrestrial algae has noticeably increased (Hallmann et al., 2017). A special focus was placed on taxonomic studies using an integrative (polyphasic) approach, which has resulted in the description of numerous taxa of various ranks (Neustupa et al., 2013a, 2013b; Škaloud et al., 2016; Rybalka et al., 2020; Kaštovský, 2023, etc.). It is obvious that terrestrial habitats, with their almost infinite variety of microecological conditions, are an inexhaustible source of new knowledge about the diversity of microalgae and cyanobacteria. In this context, algological studies of protected areas are especially important.

The Holosiiv National Nature Park (HNNP) was established in Kyiv in 2007 (Decree of the President of Ukraine, 2007) to protect and preserve the especially valuable natural complexes of the Forest-Steppe (the western reaches of the East European Forest Steppe ecoregion) and Kyiv Polissya (the eastern edge of the Central European Mixed Forests ecoregion). The uniqueness of this territory is evident from the fact that the national park is located within the metropolitan area, in the southern (and western) parts of Kyiv City, west of the Dnipro River. It includes several territorially separated forest areas: the Holosiiv Forest (together with the Maxim Rylskyi Holosiiv Park), the Bychok and Teremky forest tracts, the Lisnyky protected area (Southern section), and the Svyatoshyn-Bilychi Forest. The soils in the park are relatively rich, formed on loess deposits. The territory of the HNNP belongs to a region with a temperate continental climate along with the background microclimatic influence of a large industrial city. The average annual temperature is +7.2 °C, with an average annual rainfall of 600 mm, which provides sufficient moisture to the study site.

Due to its location within and near the territory of Kyiv City, this area has long attracted the attention of naturalists. Scientific research has been conducted here for a century and a half; in particular, its flora and vegetation have been reported in a number of publications (Onishchenko et al., 2012, 2016, and references therein). Considerable attention has been paid to algae occurring in water bodies of the park (Radzimovskyi, 1928; Frolova, 1955; Dubyna et al., 2002, 2005; Tsarenko et al., 2004; Klochenko et al., 2006, 2010, 2018, 2022; Klochenko, Tsarenko, 2007; Zub et al., 2007; Berezovska, 2018). There exists also some information on terrestrial algae, in particular, soil algae of the Lisnyky tract (Demchenko, 2000, 1996; Kostikov et al., 2001, 2009).

The aim of our research was to study the diversity of cyanobacteria and microalgae in various terrestrial habitats of the HNNP, using an integrative (polyphasic) approach, with special attention to their taxonomy and ecological peculiarities. Under terrestrial habitats we understand, as proposed in Hoffmann (1989), all habitats situated outside water bodies, such as soil and aerophytic habitats on stony substrates, bark of trees, decomposing wood, etc.

Materials and Methods

The material for the study was based on 43 samples taken in different parts of the Holosiiv National Nature Park: Lisnyky (22 samples), Holosiiv Forest (10), Teremky (8), and Bychok (3), collected during 2012–2015, usually in spring and autumn. Samples were taken from the soil surface (biological soil crusts), hard substrates (mainly pillboxes, concrete fortifications of World War II), dead wood, fruiting bodies of polypore fungi, and trunks of living trees. Fragments of algal biofilms were collected as intact as possible with a scalpel and placed in a paper box or a Petri dish. In the laboratory, samples were dried and stored in the dark.

Strains isolation, cultivation, and morphological studies. To obtain enrichment cultures, samples were placed in Petri dishes with Bold (1N BBM) agarized medium (Bischoff, Bold, 1963). The cultures were grown under standard laboratory conditions: with a 12-hour alternation of light and dark phases and irradiation of 25 μmol photons • m^{-2} • s^{-1} at a temperature of +20 ± 5 °C. Microscopic observation of enrichment cultures began in the third week of cultivation. Unialgal cultures were established using an Olympus ZS40 stereomicroscope

(Tokyo, Japan), isolated and purified from other organisms through multiple passages. Purified strains of cyanobacteria were cultivated on BG-11 medium (SigmaAldrich, Stanier et al., 1971), eukaryotic algae — on 3N BBM (Bischoff, Bold, 1963), under the conditions specified above. Identification and morphological treatment of isolated cultures were performed using Olympus IX70 and BX51 light microscopes with Nomarski differential interference (DIC) optics. Photomicrographs were taken using ColorView II and Olympus UC30 digital cameras attached to the microscopes, and then processed with analySIS and cellSens Entry software.

The algae that did not grow on nutrient media (including those dominating on tree trunks) were studied using a humid chamber. Particles of the bark with algal biofilms were placed on the surface of agar medium in Petri dishes for the period of several days to 1–2 weeks, and examined.

Molecular studies. Phylogenetic analysis was performed for 19 strains of cyanobacteria and eukaryotic microalgae based on the sequences of the 16S/18S rRNA, ITS, and sometimes *rbc*L genes. Genomic DNA was extracted using a special DNeasy Plant Mini Kit (Qiagen GmbH, Hilden, Germany) using the manufacturer's instructions. Nucleotide sequences of the 16S/18S rRNA gene together with the 16S-23S ITS/ITS-1,2 region was amplified using the Taq PCR Mastermix Kit (Qiagen GmbH) in a T gradient Thermoblock thermocycler (Biometra, Germany) under the conditions described in Mikhailyuk et al. (2016). Information on the primers used and sequencing conditions was also provided in earlier publications (Rybalka et al., 2020; Mikhailyuk et al., 2021). For the *Leptochlorella* strain, primers Pras1F and ellaR2 were used for PCR and sequencing of the *rbc*L gene (Nozaki et al., 1995; Neustupa et al., 2013a).

The resulting sequences were assembled and edited using Geneious software (version 8.1.8; Biomatters) and deposited with GenBank under the accession numbers PV102503-PV102512, PV102579, PV107113, and PV156796-PV156800.

For comparison with the original strains, nucleotide sequences of cyanobacteria and eukaryotic microalgae from the GenBank database were used, as well as the BLASTn software (http://blast.ncbi.nlm.nih.gov) to search for similar sequences. Multiple alignment of nucleotide sequences was performed using the MAFFT web server (version 7: see Katoh, Standley, 2013) with subsequent manual editing in the BioEdit program (version 7.2). Alignment for phylogeny along the 16S-23S ITS/ITS-1,2 region was performed manually in BioEdit, taking into account the secondary RNA structure of this region (see below). The evolutionary model that best fits the available data sets was selected based on the smallest AIC index (Akaike, 1974) calculated in MEGA (version 6, Tamura et al., 2013).

Phylogenetic trees were constructed in MrBayes 3.2.2 (Ronquist, Huelsenbeck, 2003), using the GTR+G+I evolutionary model, with 5,000,000 generations. Two of the four runs of the Markov chains Monte Carlo method were performed simultaneously, with the trees selected every 500 generations. Split frequencies between runs at the end of the calculation were below 0.01. The trees selected before the likelihood rate reached saturation were rejected. The reliability of tree topology verified by the maximum likelihood analysis (ML) was performed using iqtree (version 2.3.6) with the model GTR+G4+I and 1000 bootstraps (Minh et al., 2020; Hoang et al., 2018). Bayesian probability below 0.9 and bootstrap support below 75 are not shown in the phylogenetic tress for better visibility.

To model and visualize the secondary structure of the 16S-23S ITS region of cyanobacteria or some helices of 18S rRNA and ITS-2 of green algae, the online service mfold (Zuker, 2003) and Pseudoviewer (Byun, Han, 2009) were used.

Species identification and the adopted classification. For identification of cyanobacteria and algae, we used appropriate identification manuals and monographs (Lokhorst, 1996; Komárek, Anagnostidis, 2005; Komárek, 2013; Ettl, Gärtner, 2014), as well as publications on phylogeny of some taxonomically problematic groups (Pröschold et al., 2001; Darienko et al., 2010, 2015, 2016; Fučíková, Lewis, 2012; Eliáš et al., 2013; Neustupa et al., 2013a; Škaloud et al., 2016; Kim et al., 2023, etc.).

Taxonomic position of the revealed cyanobacterial species is given according to Strunecký et al. (2023). Eukaryotic algae are presented according to the system adopted in the compendiums *Algae of the Soils of Ukraine* (Kostikov et al., 2001) and *Algae of Ukraine* (2006, 2009, 2011, 2014), with changes according to the modern interpretation of *Chlorophyta* s. l. (Guiry, Guiry, 2025).

The frequency of occurrence (F) was defined as the ratio of the number of samples in which the species was detected to the total number of studied samples.

Results

As a result of the cultural study of the samples from terrestrial habitats of the HNNP, 75 species from 4 divisions and 8 classes of cyanobacteria/algae were identified (Table 1). The leading role in the taxonomic diversity (Table 2) is played by green algae sharing 68.0% of all revealed species, while cyanobacteria (13.3%) ranked second. The divisions *Charophyta* (9.3%) and *Heterokontophyta* (8.0%) were less diverse. Among classes, *Trebouxiophyceae* (48.0%) and *Chlorophyceae* (17.3%) prevailed.

Hard substrate was represented by concrete fortifications of World War II. The largest number of microalgae (44 species) was found there. The samples were also the most species-rich, containing 8 to 17 species, on average 11.8 species per sample. Green algae (63.6%) were the most diverse group, followed by cyanobacteria and charophytes (13.6 and 11.4%, respectively). Representatives of *Heterokontophyta* (xanthophytes, eustigmatophytes, and diatoms, 2.3, 2.3, and 6.8%) were scarce. Among the green algae, representatives of the class *Trebouxiophyceae* prevailed (40.9%). The taxonomic spectrum of dominant species was also most diverse among all studied types of substrates. It was formed by representatives of *Chlorophyceae* (*Tetracystis vinatzeri*, Fig. 1I, M), *Trebuxiophyceae* (*Coccomyxa subellipsoidea*, Fig. 3H; *Elliptochloris bilobata*), *Ulvophyceae* (*Pseudoendoclonium* sp.), and *Klebsormidiophyceae* (*Interfilum terricola*, Fig. 3I; *Klebsormidium flaccidum*, Fig. 3E; *K.* cf. *dissectum*, Fig. 3N; *K. nitens*). The species composition of microalgae on concrete was most specific: 34.9% of the species were revealed only on this substrate. From this microhabitat, we isolated strains of two genera (*Wilmottia* O. Strunecký, J. Elster & J. Komárek and *Chromochloris* Kol & Chodat), which are new for the flora of Ukraine (see below).

Biological soil crusts mainly occurred on paths, fallen trees, and near-trunk areas. They were characterized by a small number of species, 25, among which green and charophyte algae prevailed (64 and 20%, respectively, see Table 2). *Cyanobacteria* (12%) and xanthophytes (4%) were less diverse. The crust framework was mainly formed by representatives of the genus *Klebsormidium* P.C. Silva, Mattox & W.H. Blackwell (*K. flaccidum*; Fig. 3E; *K.* cf. *dissectum*, Fig. 3N; and *K. crenulatum*), sometimes by moss protonema. Other species were found sporadically, only *Nannochloris* sp. (Fig. 2J) was abundant. The number of species in biocrust samples ranged from 7 to 11 and averaged 8.8 species per sample. A strain of the taxonomically interesting alga *Coccomyxa subellipsoidea* was isolated from the biocrust (Fig. 3H).

On tree bark, 34 algal species were identified; among them chlorophytes (82.4%) from the class *Trebouxiophyceae* (64.7%) prevailed (see Table 2). *Charophyta* (11.7%) and cyanobacteria (5.9%) were sporadically found. The number of species per sample ranged from 3 to 12, with an average of 6.4 species. On the tree trunks, algae formed macroscopic spots mainly colored green and, sometimes, orange-brown. The dominant species of green biofilms were *Desmococcus olivaceus* (Fig. 2N) or *Apatococcus lobatus* (Fig. 2O, P), of orange-brown ones — *Trentepohlia* cf. *umbrina* (Fig. 3L, M). Algal growths on tree trunks were studied at different distances above the ground. On the pine trunk at a height of 1–2 m from the ground *A. lobatus* dominated, while at a 10–20 cm from the ground *Klebsormidium* cf. *subtile* prevailed. At the same time, the samples were similar in the number and composition of accompanying species. This difference in dominant taxa probably was caused by higher humidity and soil particles that fall at the base of the tree trunk.

Some differences in abundant species on the tree bark were noted at different sites of the park. In particular, in the Holosiiv Forest and Teremky, *D. olivaceus* dominated in green biofilms, while in the Lisnyky and Bychok tracts the dominant species was *A. lobatus*. Although both species have a similar sarcinoid morphotype, they differ in certain details of morphology, in particular, in cell dimensions, structure of chloroplasts, etc. (see Fig. 2N and Fig. 2O, P). This allows to confidently confirm their occurrence in a particular site of the park.

In the present study we investigated samples of the bark from various tree species: *Quercus robur* L. (20 species of algae were revealed), *Pinus sylvestris* L. (18), *Robinia pseudoacacia* L. (12), *Carpinus betulus* L. (16), *Acer platanoides* L. (8), *Betula pendula* Roth (7), and *Populus nigra* L. (7). In general, we did not observe notable effect of the tree species on the algae composition, except for one case. The green powdery coating on the bark of *R. pseudoacacia* (black locust) was characterized by the consistent occurrence of the dominant species (*D. olivaceus*) regardless of the tract in which it grew. Probably, the bark chemistry or some physical properties contribute to the development of this particular species. Earlier we conducted a similar comparative study in Rostock, Germany. It has been found that *A. lobatus* dominated on the bark of birch and maple. However, on the black locust trunks neighboring these trees in the same locality, *D. olivaceus* dominated. We additionally examined the bark of other taxa of *Fabaceae* (*Caesalpinia* L., *Gleditsia* L.) cultivated in the city of Rostock, but their trunks were covered by *A. lobatus* as well.

The most interesting records were made on the Scots pine bark. There we isolated the strains of *Leptochlorella* Neustupa, Veselá, Nemcová & Škaloud, a genus new for Ukraine (Fig. 3A–D, F), and the rather rare taxa *Drouetiella epilithica* (Fig. 1A) and *Coccomyxa arvernensis* (Fig. 3G). These species are first observed and hence reported for the algal flora of Ukraine.

Dead wood, unlike the bark of living trees, was characterized by a rather diverse composition of algae, as 41 species were found. Green algae (75.5%), mainly *Trebouxiophyceae* (56.1%), were significantly predominant, followed and accompanied by cyanobacteria, charophytes, xanthophytes, and diatoms (see Table 2). The number of species per sample ranged from 10 to 12 and averaged by 11.7 species. The dominant biofilm complex was rich in species, including the trebuxiophycean algae, *S. bacillaris*, *D. olivaceus* (Fig. 2N), *C. subellipsoidea* (Fig. 3H), *Elliptochloris subsphaerica*, *Chloroidium ellipsoideum* (Fig. 3J), *Dictyochloropsis splendida* (Fig. 2K, L), *Gloeocystis* cf. *polydermatica* (Fig. 2H), and the ulvophytes *Trentepohlia* cf. *umbrina* (Fig. 3L, M) and *Printzina lagenifera*. Quite often the dominant species on dead wood were identical to those that sporadically occur on the bark of living trees (see Tab. 1). The most interesting and rare species of the genera *Coelastrella* Chodat, *Coccomyxa* Schmidle, *Neocystis* Hindak, and *Dictyochloropsis* Geitler (see below) were found on dead wood.

Fruiting bodies of polypore fungi. Green biofilms on the fruiting bodies of *Trametes versicolor* were also studied. This fungus is usually characterized by significant greening of its fruiting bodies due to the associated microalgae. On this living substrate, 18 species of algae were found; 77.7% of them belonged to green algae and 16.7% to charophytes. Cyanobacteria were represented by only one species, *Nostoc* cf. *edaphicum*. The number of species per sample ranged from 5 to 8 (mean 7 species). The dominant taxa were *S. bacillaris*, *D. olivaceus* (Fig. 2N), *C. subellipsoidea* (Fig. 3H), and *Interfilum terricola* (Fig. 3I). Similar to the pattern observed on dead wood, some of the dominant species are those that occur sporadically on the bark of living trees. A strain of a rare alga belonging to the genus *Pseudochlorella* J.W.G. Lund was isolated from the fruiting bodies (see below).

Comparison of the species composition of algae on different substrates. The genera *Klebsormidium* P.C. Silva, Mattox & W.H. Blackwell (5 species) and *Stichococcus* Nägeli (4 species) were most diversely represented on the different substrates investigated. *Nostoc* Vaucher ex Bornet et Flahault, *Chloromonas* Gobi, *Coccomyxa*, and *Elliptochloris* Tschermak-Woess had three species each. Representatives of the green algae, *S. bacillaris* (F = 69.0%), *C. subellipsoidea* (66.7%), *I. terricola* (47.6%), *D. olivaceus* (40.5%), *E. subsphaerica* (40.5%), and *Trentepohlia* cf. *umbrina* (38.1%), were most common in the studied habitats.

Comparison of the species composition of algae according to the Sørensen-Czekanowsky coefficient (Fig. 4) showed that the closest (most similar) communities are those on woody substrates, i.e. bark of living trees and dead wood, followed by concrete, soil crusts, and fruiting bodies of polypore fungus.

Study of isolated strains using an integrative approach. Nineteen strains isolated from the terrestrial habitats of HNNP were studied by molecular phylogenetic methods. This helped to clarify their taxonomic position and species affiliation. On phylogenetic trees based on the 18S rRNA gene strains of cyanobacteria joined molecular clades formed by representatives of the genera *Wilmottia*, *Drouetiella* Mai, J.R. Johanson & Pietrasiak, and *Timaviella* Sciuto & Moro, associating with the already known species: *W. murrayi*, *D. epilithica*, and *T. edaphica* (Fig. 5). For the original strain of *Drouetiella*, its relation to *D. epilithica* was also confirmed by the analysis based on the 16S-23S ITS region (Fig. 8A) showing a high level of support.

The strains of green algae of the class *Chlorophyceae* on the phylogenetic tree based on the 18S rRNA gene were included in the clades of the genera *Chloromonas*, *Lobochlamys* Pröschold, B. Marin, U.G. Schlösser & Melkonian, *Chromochloris*, and *Coelastrella* (Fig. 6). Analysis of this phylogeny and the phylogeny based on the ITS region (Fig. 8B, Supplementary Fig. S1A) showed the clustering of our strains with the species *Chloromonas reticulata*, *L.*

Table 1. **Species composition of algae found in terrestrial habitats of the Holosiiv National Nature Park**
(* — species whose strains were studied by molecular phylogenetic methods; D — dominant species)

Taxon	Concrete	Biocrusts	Tree bark	Dead wood	Polypore fungus fruiting bodies
CYANOBACTERIA					
Cyanophyceae	**6**	**3**	**2**	**2**	**1**
Drouetiella lurida (Gomont) Mai, R.J. Johansen & Pietrasiak	+	–	–	–	–
**Drouetiella epilithica* D.-H. Kim, N.-J. Lee, H.-R. Wang, A.-S. Lim & O.-M. Lee	–	+	+	–	–
**Timaviella edaphica* (Elenkin) O.N. Vinogradova & Mikhailyuk	+	+	–	+	–
Phormidium corium Gomont	–	+	–	–	–
Microcoleus autumnalis (Gomont) Strunecký, Komárek & R.J. Johansen	–	–	+	–	–
Microcoleus vaginatus Gomont	+	–	–	–	–
**Wilmottia murrayi* (West & G.S. West) Strunecký, Elster & Komárek	+	–	–	–	–
Nostoc cf. *punctiforme* Hariot	+	–	–	–	–
Nostoc cf. *edaphicum* N.V. Kondrateva	+	–	–	–	+
Nostoc sp.	–	–	–	+	–
CHLOROPHYTA					
Chlorophyceae	**8**	**6**	**4**	**6**	**1**
Chlamydomonas sp.	–	–	+	–	–
**Chloromonas* sp.	+	+	–	+	–
**Chloromonas reticulata* (Goroschankin) Gobi	–	–	–	+	–
Chloromonas chlorococcoides (H. Ettl & K. Schwarz) Matsukaki, Y. Hara & Nozaki	–	+	–	–	–
Lobochlamys culleus (Ettl) Pröschold, B. Marin, U.W.Schlösser & Melkonian	–	+	+	+	+
Chlorococcum sp.	–	–	+	–	–
Tetracystis vinatzeri Ettl & Gärtner	D	–	–	–	–
Chlorosarcinopsis sp.	+	–	–	–	–
Bracteacoccus cf. *minor* (Schmidle ex Schodat) Petrová	+	+	–	+	–
Bracteacoccus giganteus H.W. Bischoff & Bold	+	+	–	+	–
**Chromochloris zofingiensis* (Döns) Fucíková & L.A. Lewis	+	–	–	–	–
Coelastrella sp.	+	+	+	+	–
Coelastrella cf. *multistriata* (Trenkwalder) Kalina & Punkochárová	+	–	–	–	–
Trebouxiophyceae	**18**	**10**	**22**	**23**	**13**
Neocystis sp.	–	+	+	+	–
**Neocystis mucosa* Krienitz, C. Bock, Nozaki & M. Wolf	–	–	+	+	–
Gloeocystis cf. *polydermatica* (Kützing) Hindák	+	–	–	D	+
**Coenochloris* cf. *signiensis* (Broady) Hindák	+	+	+	+	+
Keratococcus bicaudatus (A. Braun ex Rabenhorst) J.B. Petersen	+	–	–	–	–
Nannochloris sp.	+	D	+	–	–
Apatococcus lobatus (Chodat) J.B. Petersen	–	–	D	+	–
**Leptochlorella arboricola* Mikhailyuk sp. nov.	–	–	+	+	–
Chlorella vulgaris Beijerinck	–	+	–	–	–
Chlorella sp.	–	–	–	+	–
Stichococcus bacillaris Nägeli	+	+	+	D	D
Stichococcus minutus Grintzesco & Petefi	+	–	–	–	–
Stichococcus sp.	–	–	+	+	+
Pseudostichococcus undulatus (Vinatzer) Van & Glaser	–	–	+	–	–

Taxon	Concrete	Biocrusts	Tree bark	Dead wood	Polypore fungus fruiting bodies
Desmococcus olivaceus (Persoon ex Archarius) J.R. Laundon	–	–	D	D	D
Diplosphaera chodatii Bialosuknia	+	–	+	+	+
**Pseudochlorella signiensis* (Friedl & O'Kelly) Darienko & Pröschold	–	–	–	–	+
Elliptochloris subsphaerica (Reisigl) Ettl & Gärtner	+	+	+	D	+
Elliptochloris bilobata Tschermak-Woess	D	–	–	–	–
Elliptochloris cf. *reniformis* Ettl & Gärtner	–	–	+	–	–
Chloroidium ellipsoideum (Gerneck) Darienko & al.	+	+	+	D	–
**Chloroidium saccharophilum* (W. Krüger) Darienko & al.	+	–	+	+	–
Myrmecia biatorellae J.B. Petersen	–	+	–	+	–
Lobosphaera incisa (Reisigl) Karsten & al.	+	–	–	–	–
Parietochloris cf. *alveolaris* (Bold) Shin Watanabe & G.L. Floid	+	+	–	+	–
**Dictyochloropsis splendida* Geitler	+	–	+	D	+
Symbiochloris cf. *symbiontica* (Tschermak-Woess) Skaloud, Friedl, A. Beck & Dal Grande	–	–	+	–	–
Symbiochloris cf. *reticulata* (Tschermak-Woess) Skaloud, Friedl, A. Beck & Dal Grande	+	–	–	+	–
Trebouxia cf. *arboricola* Puymaly	+	–	+	+	+
Trebouxia cf. *crenulata* Archibald	–	–	+	–	–
Asterochloris sp.	–	–	–	+	–
**Coccomyxa subellipsoidea* E. Acton	D	+	+	D	D
Coccomyxa cf. *simplex* Mainx	–	–	+	+	+
**Coccomyxa arvernensis* Jaag	–	–	+	+	+
Leptosira sp.	+	–	–	–	–
Xerochlorella minuta (J.B. Petersen) Mikhailyuk & P.M. Tsarenko	–	–	–	+	–
Ulvophyceae	**2**	–	**2**	**2**	–
Pseudoendoclonium sp.	D	–	–	–	–
Trentepohlia umbrina (Kützing) Bornet	+	–	D	D	–
Printzina cf. *lagenifera* (Hildebrand) R.H. Thompson & Wujek	–	–	+	D	–
CHAROPHYTA					
Klebsormidiophyceae	**5**	**5**	**4**	**4**	**3**
Interfilum terricola (J.B. Petersen) Mikhailyuk & al.	D	–	+	+	D
Interfilum cf. *massjukiae* Mikhailyuk & al.	–	–	+	–	–
**Klebsormidium flaccidum* (Kützing) P.C. Silva, Mattox & W.H. Blackwell	D	D	+	+	–
Klebsormidium cf. *subtile* (Kützing) Mikhailyuk, Glaser, Holzinger & Karsten	+	+	D	+	+
Klebsormidium dissectum (F. Gay) Ettl & Gärtner	D	D	–	–	+
Klebsormidium nitens (Kützing) Lokhorst	+	+	–	+	–
Klebsormidium crenulatum (Kützing) Lokhorst	–	D	–	–	–
HETEROKONTOPHYTA					
Xanthophyceae	**1**	**1**	–	**2**	–
Pleurochloris cf. *meiringensis* Vischer	+	+	–	+	–
**Xanthonema bristolianum* (Pascher) P.C. Silva	–	–	–	+	–
Eustigmatophyceae	**1**	–	–	–	–
Vischeria magna (J.B. Petersen) Kryvenda, Rybalka, Wolf & Friedl	+	–	–	–	–
Bacillariophyceae	**3**	–	–	**2**	–
Luticola cohnii (Hilse) D.G. Mann	+	–	–	–	–
Luticola mutica (Kützing) D.G. Mann	+	–	–	+	–
Hantzschia amphioxys (Ehrenberg) Grunow	+	–	–	+	–
Number of species, units	**44**	**25**	**34**	**41**	**18**

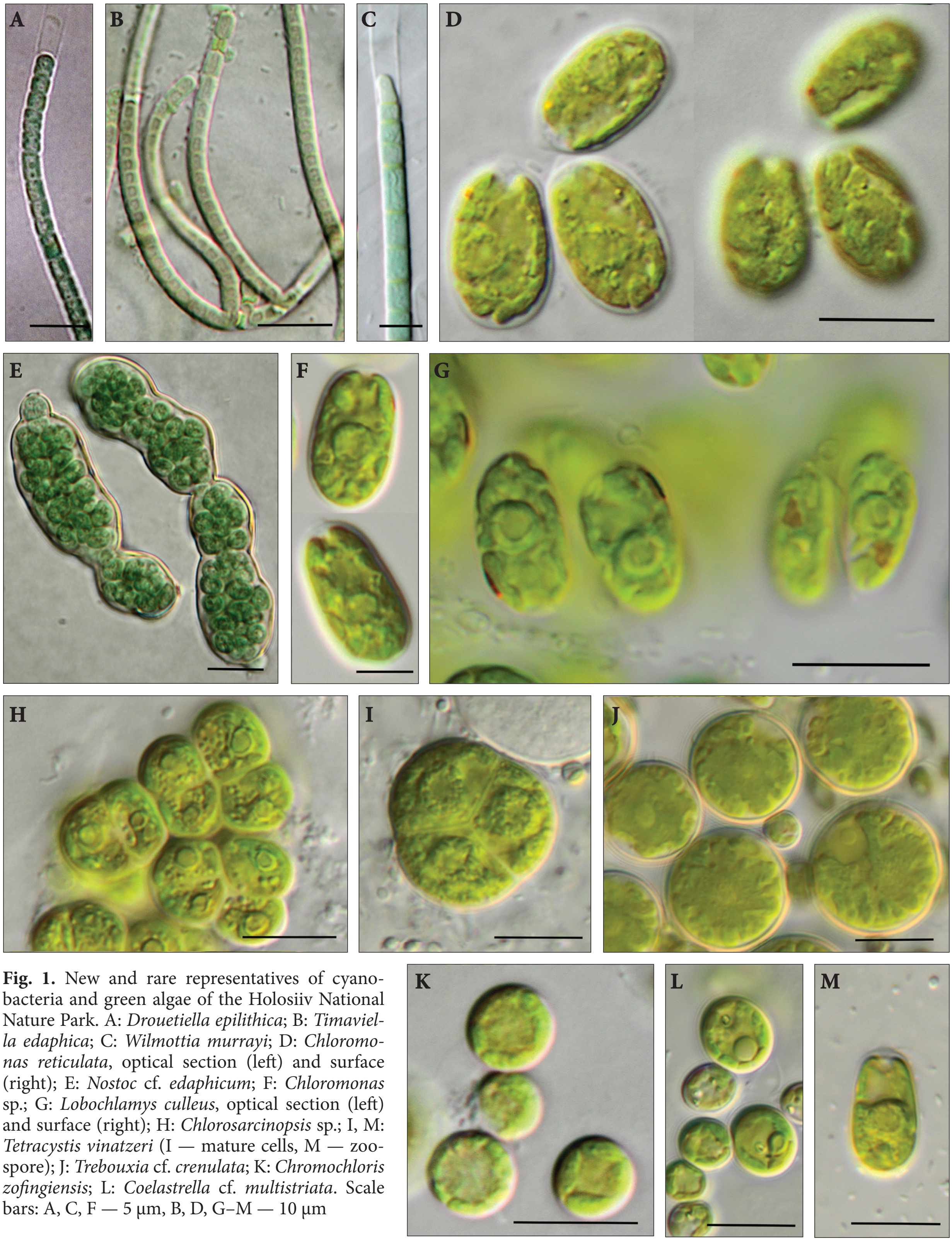

Fig. 1. New and rare representatives of cyanobacteria and green algae of the Holosiiv National Nature Park. A: *Drouetiella epilithica*; B: *Timaviella edaphica*; C: *Wilmottia murrayi*; D: *Chloromonas reticulata*, optical section (left) and surface (right); E: *Nostoc* cf. *edaphicum*; F: *Chloromonas* sp.; G: *Lobochlamys culleus*, optical section (left) and surface (right); H: *Chlorosarcinopsis* sp.; I, M: *Tetracystis vinatzeri* (I — mature cells, M — zoospore); J: *Trebouxia* cf. *crenulata*; K: *Chromochloris zofingiensis*; L: *Coelastrella* cf. *multistriata*. Scale bars: A, C, F — 5 µm, B, D, G–M — 10 µm

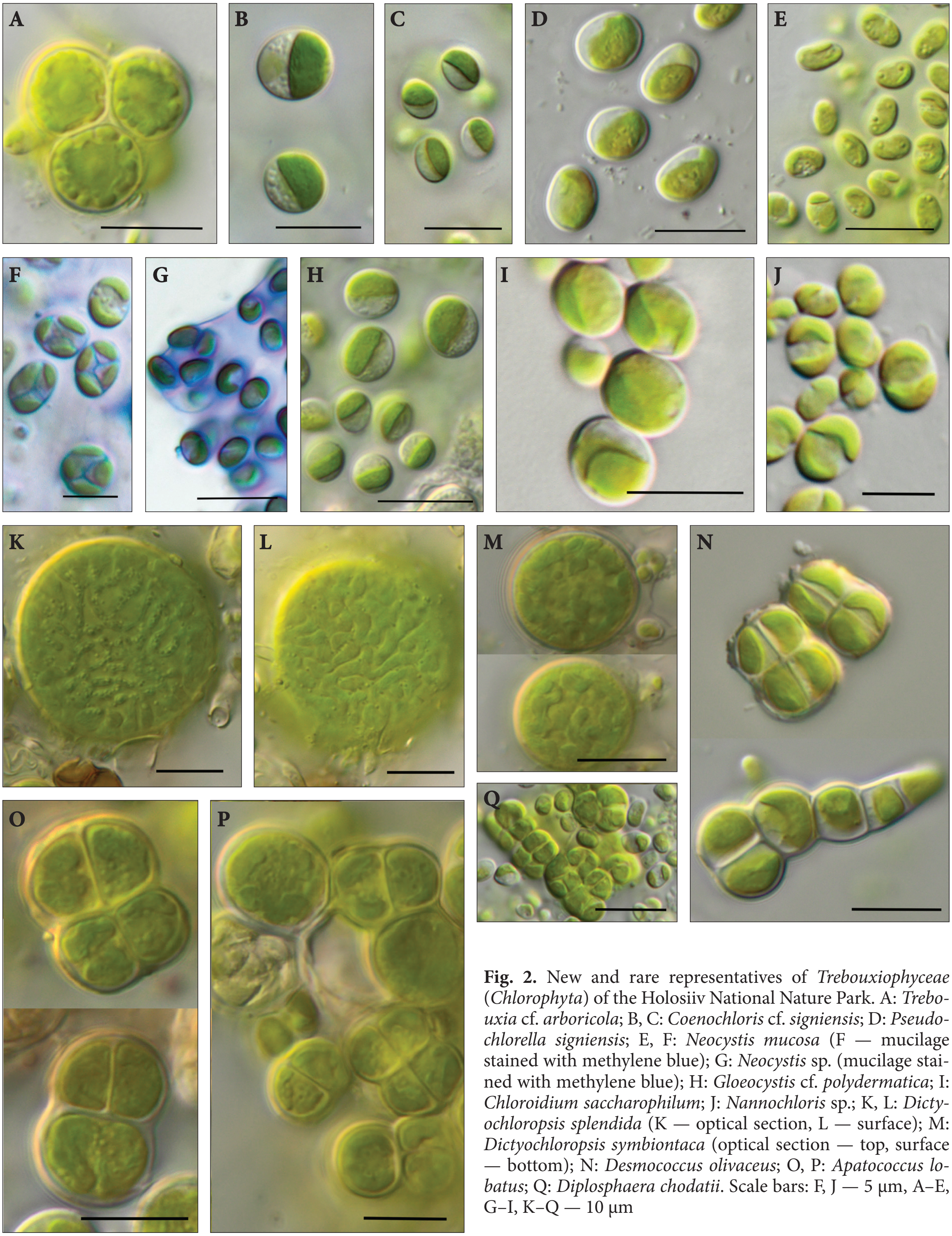

Fig. 2. New and rare representatives of *Trebouxiophyceae* (*Chlorophyta*) of the Holosiiv National Nature Park. A: *Trebouxia* cf. *arboricola*; B, C: *Coenochloris* cf. *signiensis*; D: *Pseudochlorella signiensis*; E, F: *Neocystis mucosa* (F — mucilage stained with methylene blue); G: *Neocystis* sp. (mucilage stained with methylene blue); H: *Gloeocystis* cf. *polydermatica*; I: *Chloroidium saccharophilum*; J: *Nannochloris* sp.; K, L: *Dictyochloropsis splendida* (K — optical section, L — surface); M: *Dictyochloropsis symbiontaca* (optical section — top, surface — bottom); N: *Desmococcus olivaceus*; O, P: *Apatococcus lobatus*; Q: *Diplosphaera chodatii*. Scale bars: F, J — 5 µm, A–E, G–I, K–Q — 10 µm

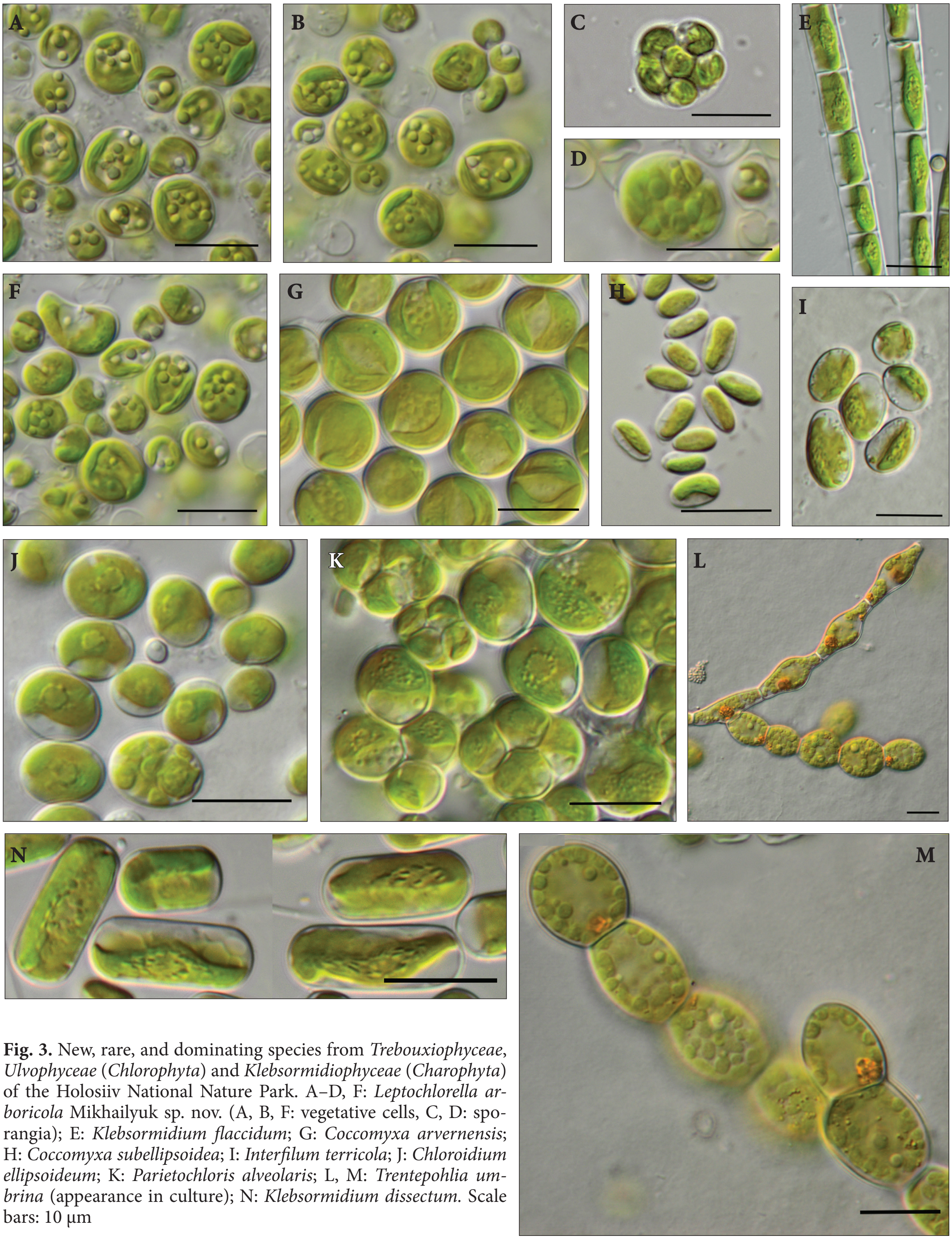

Fig. 3. New, rare, and dominating species from *Trebouxiophyceae*, *Ulvophyceae* (*Chlorophyta*) and *Klebsormidiophyceae* (*Charophyta*) of the Holosiiv National Nature Park. A–D, F: *Leptochlorella arboricola* Mikhailyuk sp. nov. (A, B, F: vegetative cells, C, D: sporangia); E: *Klebsormidium flaccidum*; G: *Coccomyxa arvernensis*; H: *Coccomyxa subellipsoidea*; I: *Interfilum terricola*; J: *Chloroidium ellipsoideum*; K: *Parietochloris alveolaris*; L, M: *Trentepohlia umbrina* (appearance in culture); N: *Klebsormidium dissectum*. Scale bars: 10 µm

Table 2. **Taxonomic structure of the terrestrial algal flora of the Holosiiv National Nature Park**

Taxon	Number of species, units (%)					
	Concrete	Biocrusts	Tree bark	Dead wood	Polypore fungus fruiting bodies	In total
CYANOBACTERIA	**6 (13.6)**	**3 (12.0)**	**2 (5.9)**	**2 (4.9)**	**1 (5.6)**	**10 (13.3)**
Cyanophyceae	6 (13.6)	3 (12.0)	2 (5.9)	2 (4.9)	1 (5.6)	10 (13.3)
CHLOROPHYTA	**28 (63.6)**	**16 (64.0)**	**28 (82.4)**	**31 (75.5)**	**14 (77.7)**	**51 (68.0)**
Chlorophyceae	8 (18.2)	6 (24.0)	4 (11.8)	6 (14.5)	1 (5.6)	13 (17.3)
Trebouxiophyceae	18 (40.9)	10 (40.0)	22 (64.7)	23 (56.1)	13 (72.1)	36 (48.0)
Ulvophyceae	2 (4.5)	-	2 (5.9)	2 (4.9)	-	3 (4.0)
CHAROPHYTA	**5 (11.4)**	**5 (20.0)**	**4 (11.7)**	**4 (9.8)**	**3 (16.7)**	**7 (9.3)**
Klebsormidiophyceae	5 (11.4)	5 (20.0)	4 (11.7)	4 (9.8)	3 (16.7)	7 (9.3)
HETEROKONTOPHYTA	**5 (11.4)**	**1 (4.0)**	-	**4 (9.8)**	-	**6 (8.0)**
Xanthophyceae	1 (2.3)	1 (4.0)	-	2 (4.9)	-	2 (2.7)
Eustigmatophyceae	1 (2.3)	-	-	-	-	1 (1.3)
Bacillariophyceae	3 (6.8)	-	-	2 (4.9)	-	3 (4.0)
Total, units (%)	**44 (100)**	**25 (100)**	**34 (100)**	**41 (100)**	**18 (100)**	**75 (100)**
Mean number of species per sample	11.8	8.8	6.4	11.7	7.0	8.4

culleus, *Chromochloris zofingiensis*, and *C. multistriata*. However, one of the original *Chloromonas* strains formed an independent branch on the tree based on the ITS-2 region. The strains of the class *Trebouxiophyceae* joined the clades of the genera *Coenochloris*/*Gloeocystis*, *Chloroidium* Nadson, *Dictyochloropsis*, *Pseudochlorella*, *Neocystis*, *Leptochlorella*, and *Coccomyxa*, while only one strain joined the combined clade of *Nannochloris*- or *Chlorella*-like algae (Fig. 7). This phylogeny and analysis of the ITS region showed the association of our strains with the clades of known species: *Coenochloris signiensis*, *Chloroidium saccharophilum*, *Dictyochloropsis splendida*, *Pseudochlorella signiensis*, *Neocystis mucosa*, *Coccomyxa subellipsoidea*, and *C. arvernensis* (Figs. 9, 10A, Supplementary Fig. S1B). The *Leptochlorella* strain formed a separate branch in the phylogeny of this genus according to the 18S rRNA gene. It was also confirmed by the tree based on the *rbc*L gene (Fig. 10B). The strain of the streptophyte algae of the genus *Klebsormidium* on the phylogenetic tree based on the ITS-1,2 region joined the clade formed by *K. flaccidum* strains (Supplementary Fig. S2).

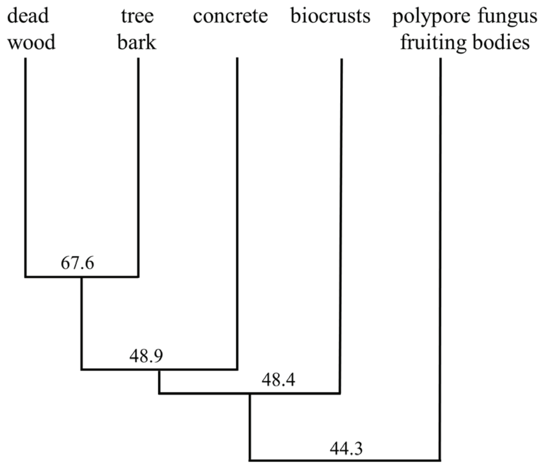

Fig. 4. Dendrite of the floristic resemblance of the species composition of terrestrial algae of different habitats of the Holosiiv National Nature Park according to the Sørensen-Czekanowsky coefficient (%)

Discussion

Concrete is a mixture of cement, water, and sand. Cement, in turn, consists mainly of calcium oxide and silicon dioxide. Therefore, it is most similar in chemical properties to natural sandstone, although some types of concrete have a low pH (John, 1988). Concrete is a light and porous material often inhabited by algae of various taxonomic groups (Ferrari et al., 2015; Nowicka-Krawczyk et al., 2022). High overall algal diversity and significant diversity of dominant species for similar substrates, such as concrete fences and building walls, in the Kaniv Nature Reserve were also previously noted (Mikhailyuk, 1999).

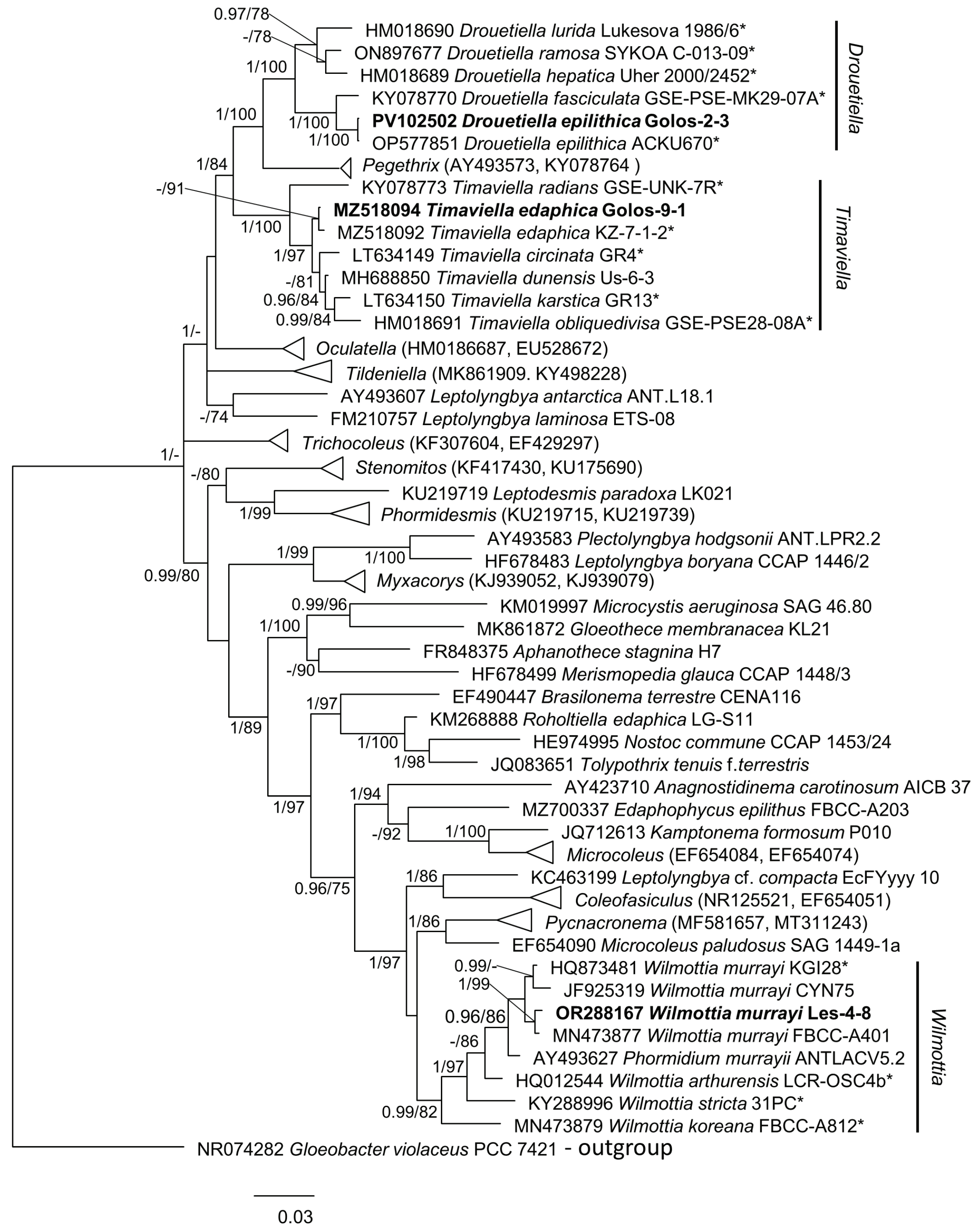

Fig. 5. Molecular phylogeny of *Cyanobacteria* based on comparison of the nucleotide sequences of the 16S rRNA gene. Phylogenetic trees in Figs. 5–10 were inferred by the Bayesian Posterior Probabilities (PP) values (left) and Maximum Likelihood bootstrap support (BP, right). Only values of PP above 0.8 and BP above 50% are specified. Sequences in bold represent newly sequenced strains. Authentic strains are marked with an asterisk

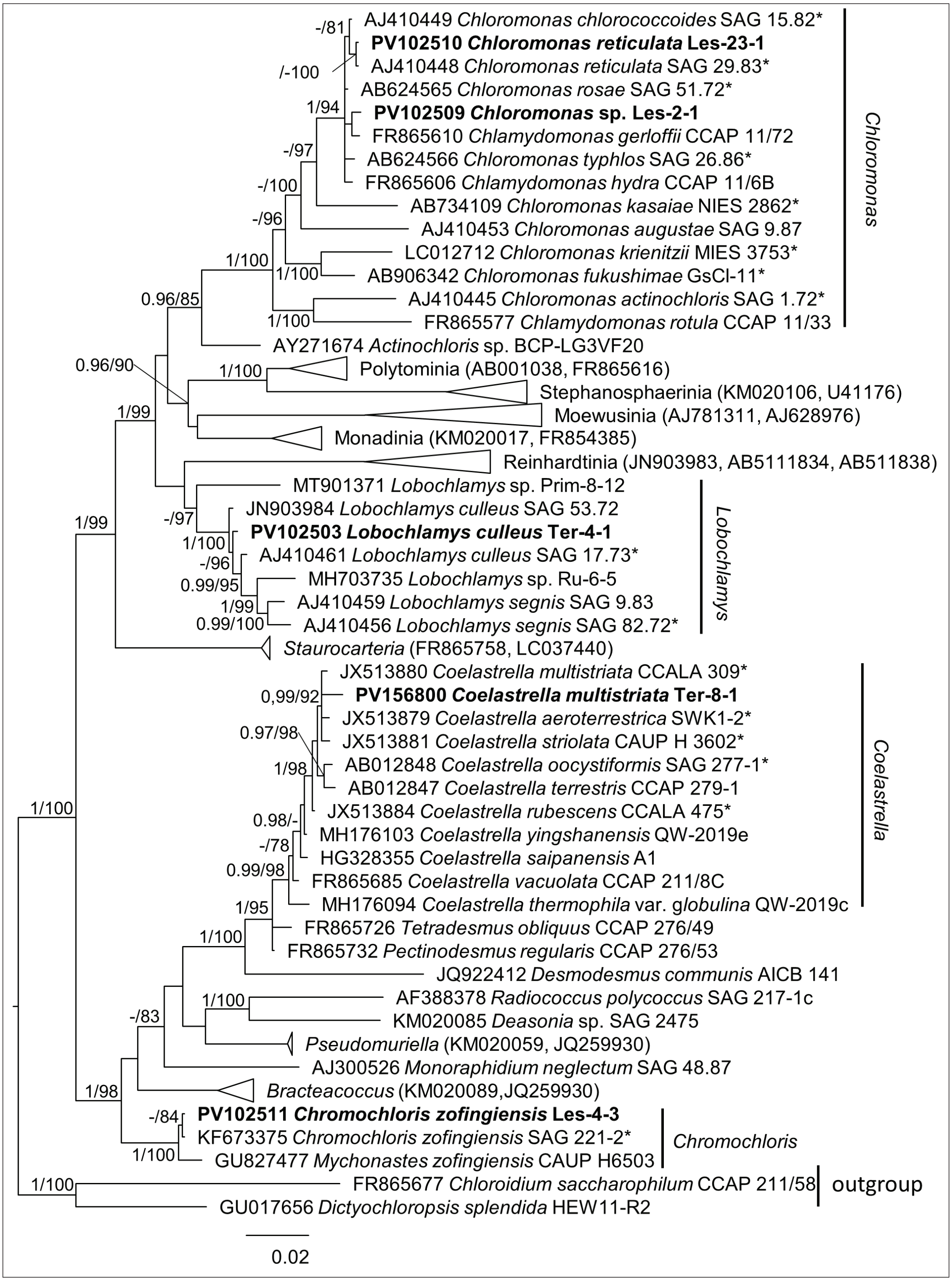

Fig. 6. Molecular phylogeny of *Chlorophyceae* (*Chlorophyta*) based on comparison of the nucleotide sequences of the 18S rRNA

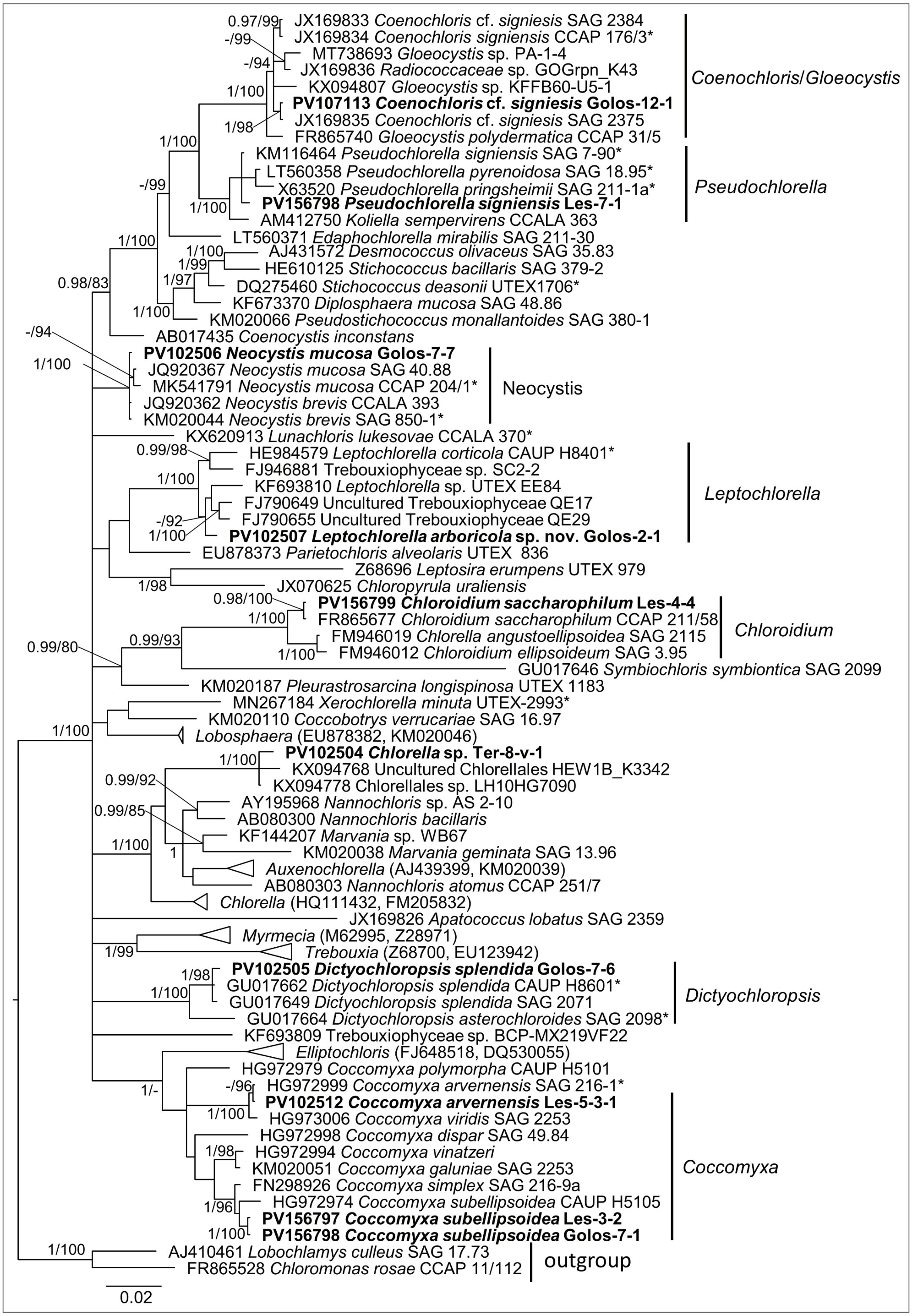

Fig. 7. Molecular phylogeny of *Trebouxiophyceae* (*Chlorophyta*) based on comparison of the nucleotide sequences of the 18S rRNA

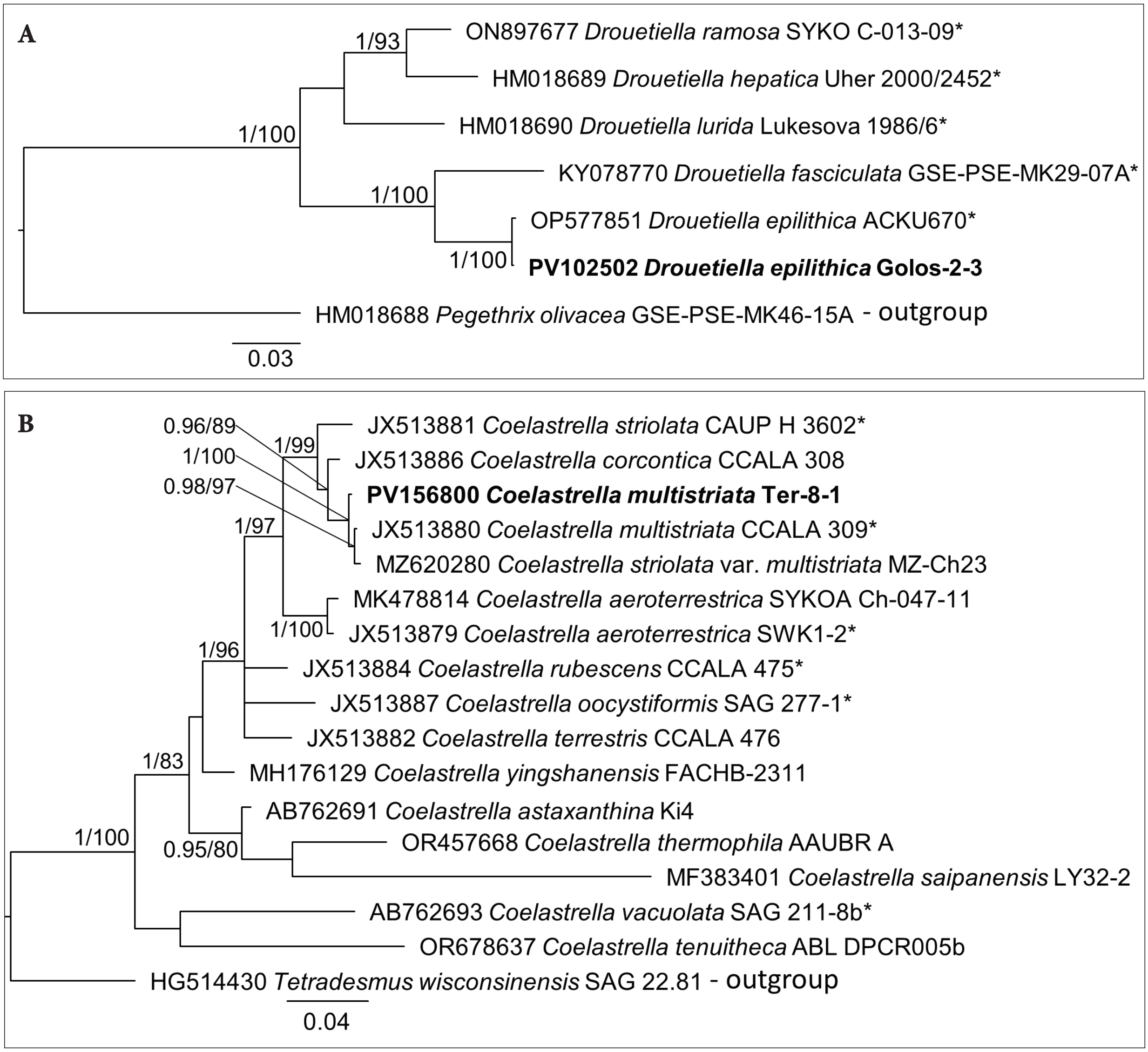

Fig. 8. Molecular phylogeny based on comparison of the nucleotide sequences of sites containing the ITS region. A: *Drouetiella*, 16S-23S ITS; B: *Coelastrella*, ITS-1,2

The dominating species complex included representatives of the genera *Coccomyxa*, *Pseudoendoclonium*, and *Klebsormidium*. Green filamentous algae, such as *Klebsormidium* and *Prasiola*, have been found to be typically abundant in biofilms on buildings in Western European cities, along with a high diversity of cyanobacteria under conditions of high humidity (Rindi, Guiry, 2003; 2004). Green algae and cyanobacteria are considered pioneers of rocky substrate colonisation, with representatives of *Chlorophyta* dominating sandstones (Macedo et al., 2009). Representatives of *Trebouxiophyceae* and *Klebsormidiophyceae* are the most common taxa in terrestrial habitats, especially on hard anthropogenic substrates (Leliaert et al., 2012; Nowicka-Krawczyk et al., 2022). Diatoms occur sporadically on rocky substrates with sufficient moisture (Nienow, 1996; Johansen, 1999). *Luticola* and *Hantzschia* have been found on concrete structures, as they are typical terrestrial representatives of diatoms (Johansen, 1999). It has been reported that the development of algae on substrates of anthropogenic origin mainly depends on the physical properties (porosity, roughness, hygroscopicity) and to a lesser

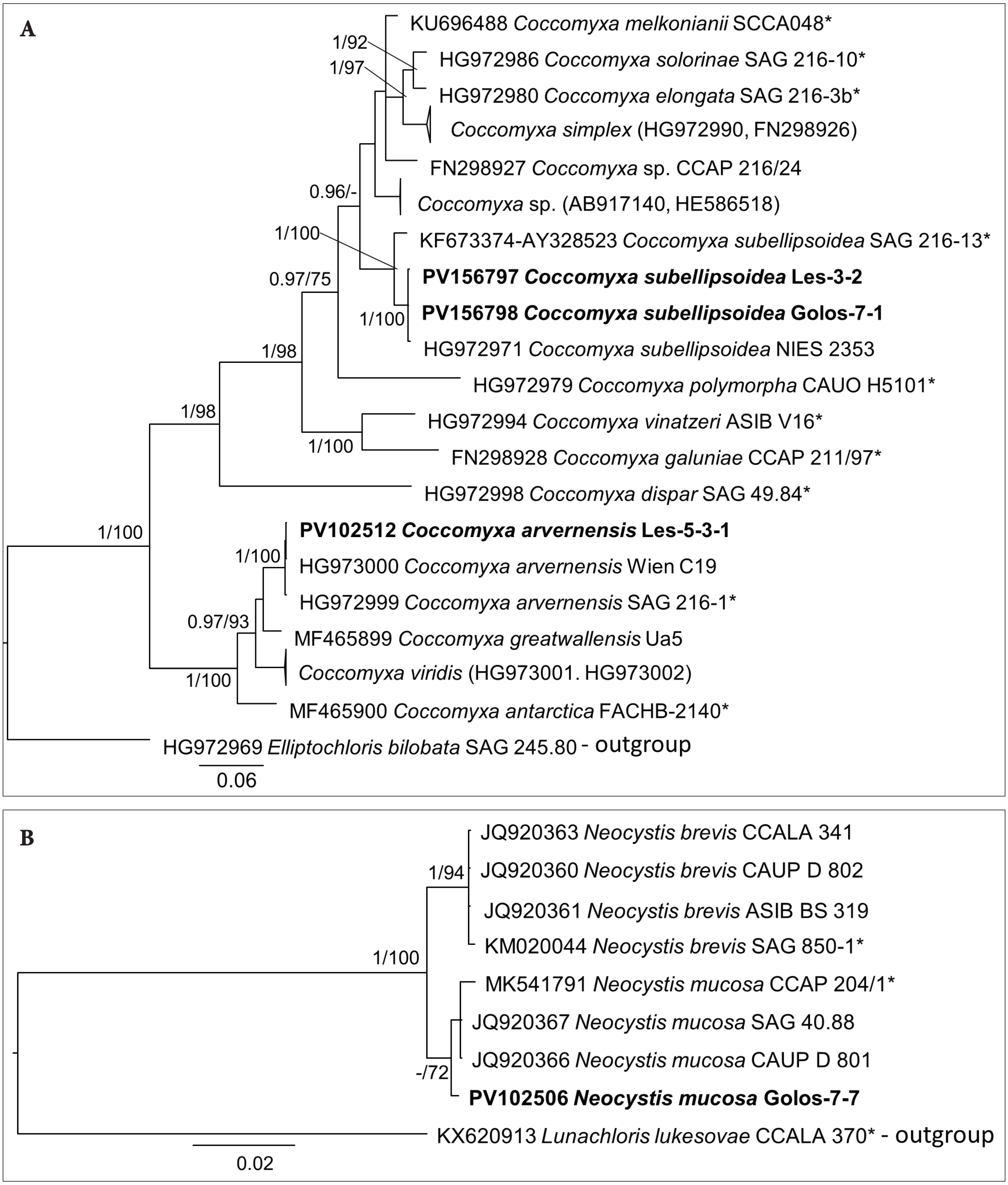

Fig. 9. Molecular phylogeny based on comparison of the nucleotide sequences of 18S rRNA and ITS-1,2. A: *Coccomyxa*; B: *Neocystis*

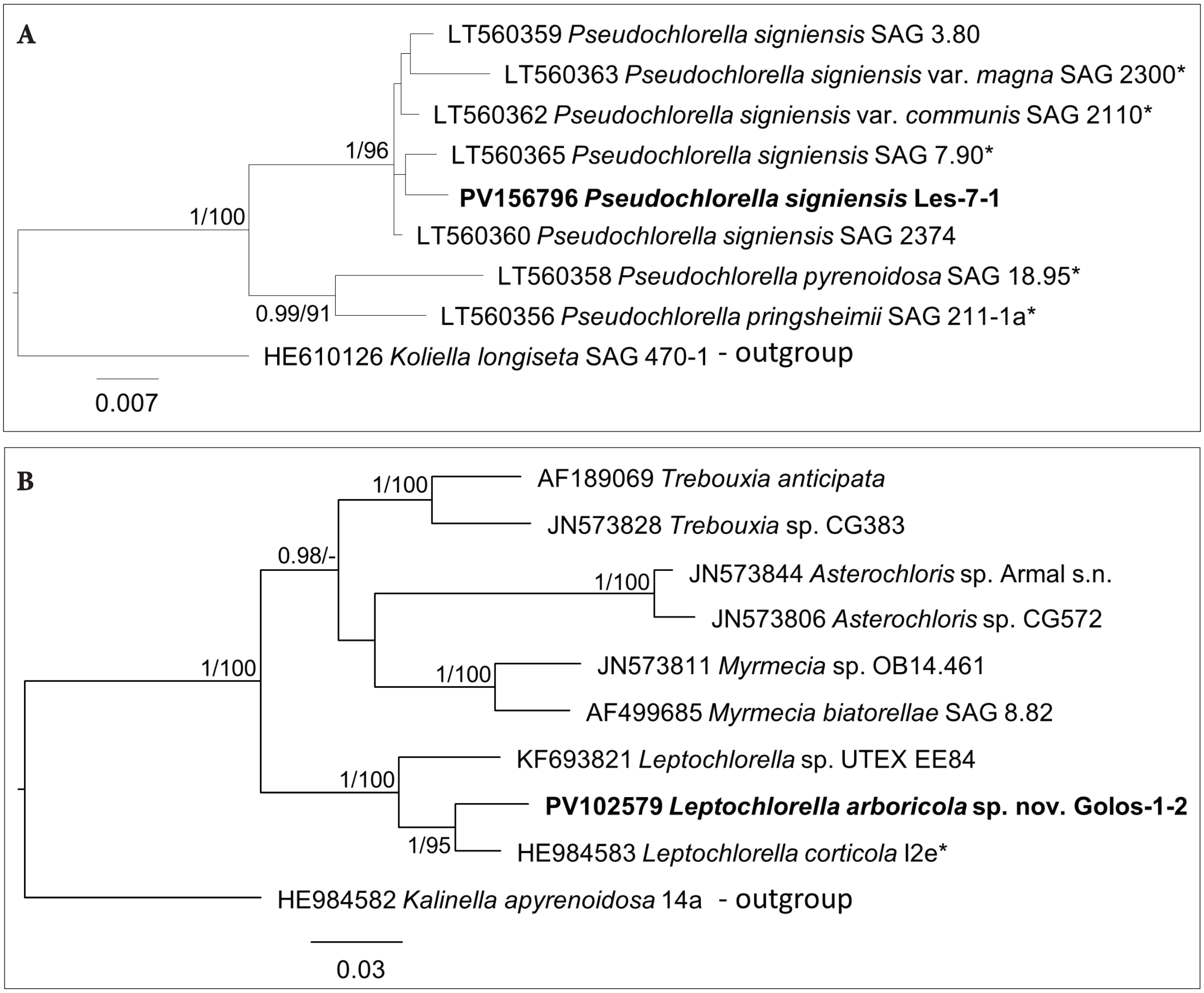

Fig. 10. Molecular phylogeny based on comparison of the nucleotide sequences of 18S rRNA and ITS-1,2 (A: *Pseudochlorella*) and *rbc*L gene (B: *Leptochlorella* species and relatives)

extent on chemical composition of these substrates (John, 1988; Nienow, 1996; Macedo et al., 2009). However, the influence of the local climate on algae is usually more significant than the properties of the substrate (Rindi, Guiry, 2004; Macedo et al., 2009; Nowicka-Krawczyk et al., 2022). In tropical humid climates, buildings are predominantly covered with cyanobacteria and *Trentepohliales*, while in temperate latitudes green trebuxiophycean algae mainly develop (John, 1988). The seasonal changes are minor on stony substrates of anthropogenic origin (Mikhailyuk, 1999; Rindi, Guiry, 2004).

Biological soil crusts are complex microecosystems consisting of many organism groups that play a significant role in numerous phytocenoses, mainly in drylands (Belnap, Lange, 2001; Weber et al., 2016). However, in temperate forests, the biocrusts, as a rule, do not play such a significant role as abundant vegetation, as they occur only sporadically in places where the plant cover had been damaged, for example, after wind breakage. Here, the dominance of mainly *Klebsormidium* and moss protonema along with the low occurrence of cyanobacteria are typical for biocrusts of forest plant communities (phytocenoses), which has been shown for forests of central Germany (Glaser et al., 2017; 2018). *Klebsormidium* is one of the main algal components of biocrusts, especially in temperate zones (Mikhailyuk et al., 2015; Donner et al., 2017; Rindi et al., 2011). Forest biocrusts are characterized by an impoverished and homogeneous species composition compared to sand dune biocrusts, where green algae and cyanobacteria are diverse and the number of taxa per sample can vary within wider limits (from 16 to 31 species; Schulz et al., 2016). The biocrusts of deserts and other arid regions are more diverse, with a predominance of cyanobacteria, and an important and often dominant ecological role in phytocenoses (Tomas, Dougill, 2006; Büdel et al., 2009).

Bark of living trees. The dominant algal species *D. olivaceus*, *A. lobatus*, and *Trentepohlia* cf. *umbrina* are typical edificators of tree biofilms in temperate zones (Hoffmann, 1989; Nienow, 1996). Such algal communities have been described in Europe (Barkmann, 1958), including Pleurococcocetum (green biofilms on bark dominated by *Apatococcus* or *Desmococcus*), Trentepohlietum (dominance of trentepohlian algae, with the formation of orange or brown biofilms) and Prasioletum (woolly green biofilms dominated by *Prasiola*). It is known that with the advancement from Western to Eastern Europe, *Klebsormidium* replaces *Prasiola* as the dominant in communities (Rindi, Guiry, 2003). Therefore, it can be stated that in the Holosiiv NNP we revealed all three communities of corticolous algae: Pleurococcocetum or Trentepohlietum along the tree trunks, and Prasioletum near the bases of trees.

The change of the main dominant taxa on tree bark from *D. olivaceus* to *A. lobatus* probably occurs due to the influence of microclimatic factors, in particular due to the higher atmospheric humidity of the Lisnyky and Bychok tracts, which are located near the Dnipro floodplain. We observed a similar replacement of *D. olivaceus* dominating on the bark of trees in the forest tract of the Kaniv Nature Reserve, by *A. lobatus* on the trees of Zmiyini Islands (not to be confused with Zmiinyi/Snake Island in the Black Sea), which are surrounded by the waters of the Dnipro River (Mikhailyuk, 1999). *Apatococcus lobatus* is common in the aerophytic communities of Western Europe (Hallmann, et al., 2011; Neustupa, Štifterová, 2013; Karsten et al., 2022). It was also noted that *Desmococcus* and *Apatococcus* can replace each other in aerophytic communities (Hallmann et al., 2013).

Epiphytic algal habitats are generally among the most arid sites compared to other terrestrial habitats (Hoffmann, 1989). The bark of living trees does not accumulate or retain moisture, unlike porous or fissured rocky substrates and soil. Atmospheric moisture is the main water source in epiphytic communities (Barkmann, 1958; Hoffmann, 1989; Nienow, 1996), therefore their development and diversity directly depend on the amount and frequency of precipitation and/or on the present air humidity. The rapid runoff and evaporation of water is also facilitated by vertically oriented tree trunks. The low number of algae species found on the bark is typical for this type of habitat in the temperate zone (Mikhailyuk, 1999). The number of species on tree bark is significantly higher in tropical regions (Neustupa, Škaloud, 2010; Neustupa, Štifterová, 2013), evidently because of the generally more humid air.

The species composition of corticolous algae is significantly dependent on climate, so their distribution clearly demonstrates geographical trends. In particular, the distribution of typical inhabitants of Pleurococcocetum decreases in tropical regions, while the frequency of Trentepohlietum increases, where they compete in distribution and diversity with cyanobacteria (Nienow, 1996; Lemes-da-Silva et al., 2010; Kharkongor, Ramanujam, 2014; Arguelles, 2019; Saraphol et al., 2024). *Trentepohliales* on tree bark can grow in the temperate zone locally, where there is the sufficient moisture, but they are common in humid tropical and subtropical regions, where cyanobacteria (*Scytonema*, *Brasilonema*, etc.) also form the main part of the epiphytic algal flora (Hoffmann, 1989; Neustupa, Škaloud, 2008; 2010; Neustupa, Štifterová, 2013). Terrestrial cyanobacteria require periodic moistening for their active development; therefore, they are common on tree bark only in regions with frequent rains, which provide water flowing down the trunks (Nienow, 1996). They are probably not able to exist only due to water evaporation (unlike representatives of *Trebouxiophyceae*), and therefore they typically lack occurrence in bark biofilms in the temperate zone.

The composition of tree bark algae depends mainly on external conditions and much less on the host tree species (Hoffmann, 1989; Mikhailyuk, 1999; Neustupa, Škaloud, 2008; 2010; Neustupa, Štifterová, 2013). However, it is likely that such parameters as the pH value of the bark and the degree of its fracturing can affect the composition and diversity of algae. A certain influence of these parameters on algae has been noted (in particular, the higher the pH and fracturing, the more diverse the communities), but it is rather indirect (Neustupa, Štifterová, 2013; Kulichová et al., 2014).

Dead wood, unlike the bark of living trees, is a completely different, much more favorable substrate for both algae and other cryptogams (Mikhailyuk, 1999; Neustupa, Škaloud, 2010). It is a porous material capable of retaining water, which is available in the form of vapor and liquid moisture (Nienow, 1996). In addition, water retention is often facilitated by the horizontal arrangement of fallen trunks or fallen branches. Dead wood is also characterized by its increased trophicity; decomposing wood promotes active development of algae and occurrence of representatives of various taxonomic groups with different environmental requirements. The fact that some dominant species on dead wood and fruiting bodies of polypore fungi sporadically occur on the bark of living trees has been reported earlier (Mikhailyuk, 1999).

Fruiting bodies of polypore fungi. The literature concerning the development of algae on the surface of fruiting bodies of fungi is scarce (Stoyneva et al., 2015). The question of what underlies this phenomenon remains debatable, whether algae use the fruiting bodies as a suitable substrate, or whether there is some kind of consortial relationship between them and the fungus, similar to recently described *alcobiosis* (Vondrák et al., 2023), i.e. symbiotic relationships between algae and corticioid fungi living on trees. It has been proven that carbon is transferred as part of the synthesized organic matter from the algae to the fungus. Interestingly, one of the components of alcobiosis, *Desmococcus olivaceus* and a representative of *Stichococcus* s.l., were dominants of algal biofilms on polypore fungi in the HNNP. The data on algal participation in symbiotic relationships was obtained concerning algae growing on wood-destroying fungi (Mukhin et al., 2016, 2017). Such algae were called *mycetobionts*, although it was shown that they are not fungi-specific taxa, but rather common aerophytic species growing on tree bark. The number of species in the fungal sample was low and ranged from 4 to 6, which is consistent with our data. Another study (Voytsekhovich et al., 2015) showed that wood-destroying fungi of the genus *Hyphodontia* can exist both without algae and with them (species of *Coccomyxa* and *Elliptochloris*), forming symbiotic associations.

Molecular studies and novel floristic discoveries. Our molecular phylogenetic study of the strains isolated from terrestrial habitats of the HNNP allowed not only to clarify their taxonomic affiliation, but also to find a number of new floristic novelties and the habitats of rare and noteworthy species. In particular, the strains of cyanobacteria studied using the polyphasic approach turned out to be representatives of the genera *Wilmottia*, *Drouetiella*, and *Timaviella* (Fig. 5). For *Wilmottia*, it is the first morphologically and molecularly confirmed record in Europe (for details, see Mikhailyuk et al., 2023). The strain of fine-filamentous cyanobacteria isolated from the pine bark, on a phylogenetic tree based on the both the 16S rRNA gene and the 16S-23S ITS sequences joined the subclade of *Drouetiella epilithica* with a similarity level of 100% (Fig. 8A). This is the second discovery of this species in the world. It was so far described only from a stone monument in South Korea (Kim et al., 2023), and hence our Kyiv record expands the ecological and biogeographical spectrum of *D. epilithica* (Fig. 1A). Another *Leptolyngbya*-like strain isolated from a biocrust sample joined the subclade of *Timaviella edaphica* (Fig. 1B, Mikhailyuk et al., 2022).

Among the studied *Chlorophyceae* strains, two were found to be representatives of *Chloromonas*, one each of *Lobochlamys*, *Chromochloris*, and *Coelastrella* (Fig. 6). Phylogeny based on the ITS region showed that one of the strains is *Chloromonas reticulata* (Fig. 1D), while the other can only be assigned as *Chloromonas* sp. (Fig. 1F, Supplementary Fig. S1A). Both strains were isolated from dead wood. The *Lobochlamys* strain (black locust bark) on the 18S rRNA tree joined the clade with *L. culleus* (Fig. 1G; Fig. 6), together with its authentic strain. The ITS-1,2 sequence for the *Chromochloris* strain was identical to the authentic strain of *Ch. zofingiensis* (Fučíková, Lewis, 2012). It also joined the clade of *Ch. zofingiensis* on the tree based on 18S rRNA (Fig. 6). This record is a new genus and species for the flora of Ukraine. *Chromochloris zofingiensis* (Fig. 1K) is a cryptic taxon widely distributed worldwide (Fučíková, Lewis, 2012). Probably, based on morphological features, it was previously identified as a species of *Bracteacoccus* Tereg. or *Muriella* J.B. Petersen. The *Coelastrella* strain on the ITS based phylogenetic tree joined the clade of *C. multistriata* (Fig. 8B). It is the second record of this species (Fig. 1L) in Ukraine; previously, it was reported from granite outcrops of the Teteriv River (Mikhailyuk et al., 2011).

Nine strains, according to our phylogenetic analysis, belong to class *Trebouxiophyceae* (Fig. 7). Two of them joined the clades of still unrevised groups. Therefore, at present their molecular identification is impossible. One of these strains (Fig. 2J), isolated from the dead wood, joined the clade of *Nannochloris*- or *Chlorella*-like algae. Most often, such microalgae from terrestrial habitats are identified as *Chlorella minutissima* or *Mychonastes homosphaera* (*Chlorophyceae*), but phylogenetically they belong to another class of green algae. The second strain is a representative of the *Coenochloris signiensis* / *Gloeocystis polydermatica* group (Fig. 7), which has also not yet been phylogenetically studied in depth. We identified this representative as *Coenochloris* cf. *signiensis* (Fig. 2B, C). In Ukraine, it was reported from the granite outcrops of the Southern Bug, Teteriv, and Ros rivers valleys (Mikhailyuk et al., 2011), sandstone outcrops of the Hutsulshchyna National Nature Park (Mikhailyuk, Darienko, 2013), and tuff breccias and lichen thalli (as an epiphyte) of the Karadag Nature Reserve in Crimea (Voytsekhovich, 2008; Voytsekhovich et al., 2009). Molecular phylogenetic data confirmed the morphological identification of other trebouxiophycean strains; among them, the common species, *Chloroidium saccharophilum* (Supplementary Fig. S1B), and the rare one, *Dictyochloropsis splendida* (Fig. 2K, L, Fig. 7; *Prodromus*, 2024). One of the strains was identified as *Pseudochlorella signiensis* (Fig. 2D, Fig. 10A; on *Trametes* fruiting bodies) by the results of 18S rRNA and ITS phylogeny. It is its second record in Ukraine. Previously this species was found on sandstone outcrops of the Hutsulshchyna National Nature Park (Mikhailyuk, Darienko, 2013). Based on the same molecular markers, two strains were assigned to *Coccomyxa subellipsoidea* (Fig. 3H, Fig. 9A; dead wood and biocrust). This species has been repeatedly found in Ukraine (*Prodromus*, 2024), but its record has been molecularly confirmed for the first time.

Several strains represent new taxa for the flora of Ukraine. Among them are *Neocystis mucosa* (Fig. 2E, F, Fig. 9B) isolated from dead wood and *Coccomyxa arvernensis* (Fig. 3G, Fig. 9A) inhabiting *Pinus* bark. These species are difficult to identify by morphological characters which are implicit, but they are clearly separated by molecular phylogeny (Fig. 7, Fig. 9A, B). Previously we identified *C. arvernensis* as *Elliptochloris bilobata* due to their high morphological similarity. *Coccomyxa arvernensis* in mature culture has large broadly ellipsoidal cells with a bilobate chloroplast without a pyrenoid, which is similar to *E. bilobata* (Fig. 3G, Darienko et al., 2015). Also, from the pine bark we isolated unicellular alga with *Chlorella*-like morphology. According to 18S rRNA phylogenetic analysis, our strain joined the clade of the rare monospecific genus *Leptochlorella* (Fig. 7; Neustupa et al., 2013a). It was described from the bark of *Cupressus sempervirens* L. in Slovenia, and up till now is known only from this location. On the 18S rRNA based phylogenetic tree, the Ukrainian strain of *Leptochlorella* distances itself from the type species of this genus (Fig. 7); therefore, we propose the description of a new species (see below).

Among streptophyte algae, molecular phylogenetic methods revealed *Klebsormidium flaccidum* (*Robinia* bark, Fig. 3E, Supplementary Fig. S2). To identify the strain of the yellow-green alga isolated from the dead wood, the sequence of the chloroplast gene *rbc*L was analyzed. As a result, it turned out to be a noteworthy species *Xanthonema bristolianum*, which has already been reported previously (Rybalka et al., 2020).

Description of a new species of the rare genus *Leptochlorella*. Besides the authentic strain *Leptochlorella corticola* (CAUPH8401) (Neustupa et al., 2013a), other strains of this clade include *Leptochlorella* sp. (UTEX EE84) isolated from the Negev Desert, Israel (Fucíková et al., 2014) and two unidentified representatives, from hypolithic communities growing on quartz in the high-altitude tundra of Central Tibet (Uncultured *Trebouxiophyceae* clone QE17 and clone QE29; Wong et al., 2010) and from a lake in Antarctica (SC2-2, Schirmacher Oasis; De Wever et al., 2009). Thus, this clade contains ecologically diverse algae inhabiting various extreme habitats (tree bark in subtropical and temperate climates, desert, high-mountain tundra or an Antarctic lake). The strain we isolated forms a separate lineage on the 18S rRNA tree (Fig. 7). Comparison of the 18S rRNA sequence of our strain with others showed that their similarity ranges from 90 to 93%, which corresponds to different species of the same genus (Supplementary Tables S1, S2). Compared to the authentic strain of *L. corticola*, the Ukrainian strain has 16 different nucleotides of the 18S rRNA gene. A comparison of the most informative helices of the secondary structure of 18S rRNA (E23_1/E23_2, 43 and 49, see Darienko et al., 2016) showed their significant similarity (Supplementary Fig. S3). The Ukrainian strain differs from *L. corticola* (CAUPH8401) by 1 hCBC, 2 mismatches and 3 changes in the loops of helix E23_1/E23_2. With other helices (43 and 49), the differences were only in a few nucleotides in the loops. A model of the

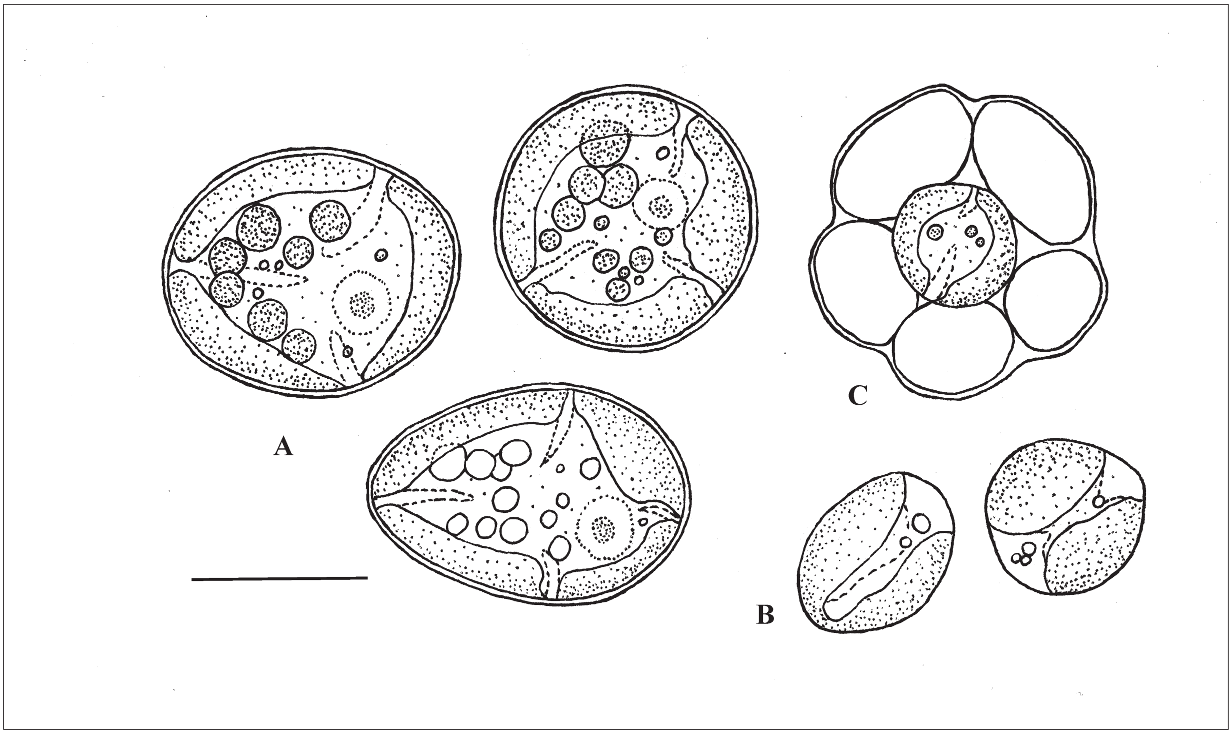

Fig. 11. *Leptochlorella arboricola* Mikhailyuk sp. nov. A: mature vegetative cells; B: young cells; C: sporangium. Scale bar: 10 µm

secondary structure of ITS-2 of our strain (Supplementary Fig. S4) is characterized by a unique structure, since it consists of 3 helices, the last of which is branched. Unfortunately, the ITS was not obtained for the authentic strain of *L. corticola*; however, the sequence of the *rbc*L gene was obtained (Neustupa et al., 2013a). Comparison of the *rbc*L gene sequences of the original strain and *L. corticola* (CAUPH8401) (Fig. 10B) showed a significant difference in 45 nucleotides (59% similarity, see Supplementary Tables S3, S4). *Leptochlorella corticola* strain CAUPH8401, *Leptochlorella* sp. UTEX EE84, and Ukrainian strain Golos-2-1 have *Chlorella*-like morphology, a parietal chloroplast without a pyrenoid, and differ only in details. All of the above data provide justification for the description of a new species of *Leptochlorella*.

***Leptochlorella arboricola* Mikhailyuk sp. nov.** (Fig. 3A–D, F, Fig. 11).

Diagnosis: Vegetative cells solitary, uninucleate. Cells widely ellipsoid, ovoid to almost spherical and pyriform, (11.1–)13.9–17.8(–21.1) µm in length, (8.3–)10.6–15.6(–20.6) µm in width. Chloroplast single, parietal, without a pyrenoid, divided into two or three-four lobes. Vegetative cells richly filled with transparent spherical droplets. Secondary carotenoids not produced. Asexual reproduction via 2–8(16) widely ellipsoid to spherical autospores, 5.6–8.3 × 5.0–6.7 µm.

Morphologically differs from *L. corticola* by the cell shape and transparent spherical droplets richly filling vegetative cells. Phylogenetically differs by its composition and secondary structure of 18S rRNA region (PV102507) and *rbc*L sequences (PV102579).

Type locality: algal biofilm growing on the bark of *Pinus sylvestris*, Holosiiv Forest, Holosiiv National Nature Park, Kyiv, Ukraine.

Holotype (designated here): KW-A32656, preserved culture material of authentic strain Golos-2-1 (IBASU-A-812), Algotheca, Herbarium of the M.G. Kholodny Institute of Botany of the National Academy of Sciences of Ukraine (KW).

Iconotype (in support of the holotype indicated here): Figures 3A–D, F, 11.

Authentic strain: Golos-2-1 was deposited in IBASU-A collection, M.G. Kholodny Institute of Botany of NASU of Ukraine, Kyiv, Ukraine, under number IBASU-A-812.

Etymology: *arboricola* = from the Latin word *arbor*, meaning tree (referring to the type habitat).

Conclusion

As a result of the study of terrestrial algae and cyanobacteria of the Holosiiv National Nature Park, 75 species were discovered. Among them, *Chlorophyta*, especially representatives of class *Trebouxiophyceae*, dominated. The most diverse species composition of algae was found on rocky substrates (44 species) and dead wood (41), the same substrates had the most diverse composition of dominant species. Fewer species were found on tree trunks (34), biocrusts (25) and fruiting bodies of polypore fungus (18). The genera *Klebsormidium* (5 species) and *Stichococcus* (4 species) were most diversely represented on different substrates. Representatives of green algae, *Stichococcus bacillaris*, *Coccomyxa subellipsoidea*, *Interfilum terricola*, *Desmococcus olivaceus*, *Elliptochloris subsphaerica*, and *Trentepohlia* cf. *umbrina*, were most frequent in the studied habitats. A study on the relationship between the species composition of algae and the tree species revealed a positive interaction only for *Robinia*, while other tree trunks were dominated by the same algal species regardless of the location. The algal species composition differed at the base of the tree and at a height along the trunk. The dominant algal species of dead wood and fruiting bodies of polypore fungi are the same that sporadically occur on the bark of trees. Woody substrates (tree bark and dead wood) have the closest composition of algae. A number of new and noteworthy taxa was revealed using molecular phylogenetic methods. Among them, three genera (*Wilmottia*, *Chromochloris*, and *Leptochlorella*) and five species (*Wilmottia murrayi*, *Drouetiella epilithica*, *Chromochloris zofingiensis*, *Neocystis mucosa*, *Coccomyxa arvernensis*) are for the first time reported for Ukraine. Five rare species of *Coelastrella*, *Pseudochlorella*, *Coenochloris*, *Dictyochloropsis*, and *Coccomyxa* were found, and a new species of *Leptochlorella*, *L. arboricola* Mikhailyuk, was described.

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SUPPLEMENTARY MATERIAL

This article includes Supplementary Material (Tables S1–S4, Figs. S1–S4) available as: ukrbotj82-01-003-S1.pdf (1,498 KB).

ETHICS DECLARATION

The authors declare no conflict of interest.

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Водорості наземних місцезростань Національного природного парку "Голосіївський" (Київ, Україна) з описом *Leptochlorella arboricola* sp. nov. (*Trebouxiophyceae*, *Chlorophyta*)

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Реферат. Національний природний парк "Голосіївський" створено з метою охорони природних екосистем Лісостепу та Київського Полісся, що збереглися на території мегаполісу Києва. У природному парку активно вивчали мікроводорості водойм, тоді як дані про наземні водорості дуже обмежені. Досліджено різноманіття водоростей наземних місцезростань в урочищах Голосіївський ліс, Теремки, Лісники та Бичок. Всього виявлено 75 видів: *Cyanobacteria* (10 видів), *Chlorophyta* (52), *Charophyta* (7), *Heterokontophyta* (6). Найрізноманітніший видовий склад виявлено на кам'янистих субстратах — бетонних довготривалих оборонних точках Другої світової війни (ДОТах, 44 види, з домінуванням *Tetracystis vinatzeri*, *Coccomyxa subellipsoidea*, *Elliptochloris bilobata*, *Pseudoendoclonium* sp. та ін.) та мертвій деревині (41, *Stichococcus bacillaris*, *Desmococcus olivaceus*, *Coccomyxa subellipsoidea*, *Elliptochloris subsphaerica* та ін.). Менше видів виявлено на корі дерев (34, *Desmococcus olivaceus*, *Apatococcus lobatus*, *Trentepohlia* cf. *umbrina*, *Klebsormidium* cf. *subtile*), ґрунтових кірочках (25, *K. flaccidum*, *K.* cf. *dissectum* та *K. crenulatum*, *Nannochloris* sp.) та плодових тілах трутовикового гриба (18, *Stichococcus bacillaris*, *Desmococcus olivaceus*, *Coccomyxa subellipsoidea*, *Interfilum terricola*). Найспецифічнішими за видовим складом водоростей виявилися кам'янисті субстрати, а найбільш подібними — деревні субстрати, кора живих дерев і мертва деревина. За допомогою молекулярно-філогенетичних методів виявлено низку нових і рідкісних таксонів. Серед них три роди (*Wilmottia*, *Chromochloris* і *Leptochlorella*) та п'ять видів уперше наведено для флори України (*Wilmottia murrayi*, *Drouetiella epilithica*, *Chromochloris zofingiensis*, *Neocystis mucosa* та *Coccomyxa arvernensis*). Виявлено п'ять рідкісних видів з родів *Coelastrella*, *Pseudochlorella*, *Coenochloris*, *Dictyochloropsis* і *Coccomyxa* та описано новий вид з роду *Leptochlorella*.

Ключові слова: біологічні ґрунтові кірочки, водорості, кам'янисті субстрати, кора живих дерев, лісові фітоценози, мертва деревина, плодові тіла трутовиків, Україна, ціанобактерії, 16S/18S рРНК, ITS, *rbc*L, *Leptochlorella arboricola*