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RESEARCH ARTICLE

# Species richness of scaled Chrysophytes in arctic waters in the Tiksi Region (Yakutia, Russia)

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## Abstract

Searching for regularities in the species composition and diversity of scaled chrysophytes is crucial for monitoring Arctic waters within the concept of global climate change since these organisms are good indicators of environmental changes. Transmission electron microscopy allowed us to investigate the species diversity of scaled chrysophytes in 14 Arctic water bodies near the town of Tiksi (Yakutia) relative to hydrochemical gradients. We described a high species richness of scaled chrysophytes, 65 species from 6 genera: *Chrysosphaerella* (2), *Paraphysomonas* (8), *Lepidochromonas* (3), *Spiniferomonas* (10), *Mallomonas* (23), *Synura* (19). The water bodies we studied had a significantly different species composition. The composition of the species in the study area was confirmed to be affected by concentrations of water dissolved oxygen ($O_2$), ion nitrate ($NO_3^-$) and copper ion ($Cu_2^+$) as well as by indicators of biological and chemical oxygen demand (BOD and COD). The species richness (α richness) is proved to be higher within creasing concentrations of COD and $O_2$, while increasing concentrations of copper ions ($Cu_2^+$) in water led to its reduction. According to ecological and biogeographic data, ubiquitous and cosmopolitan species prevailed in the longitudinal group of the study area (60 %), while polyzonal species (55 %) predominated in the latitudinal group. A high share of Arctic boreal species (19 %) and the presence of typically boreal species (11 %) were identified in the latitudinal group. A biogeographical distribution of scaled chrysophytes typical of Arctic water bodies in contemporary conditions that reflect global warming trends was described.

**Keywords**
Chrysophyceae, Arctic, scaled chrysophytes

## Introduction

The representatives of the class Chrysophyceae Pascher are a widespread group of colonial or single-celled flagellate shaving an exogenous siliceous sheath formed of scales and/or bristles found mostly in fresh waters. Despite the ubiquity of these organisms, from the Tropics (Dürrschmidt and Croome 1985; Cronberg 1989; Gusev et al. 2012; Gusev and Martynenko 2022) to the Arctic (Kristiansen et al. 1997; Bessudova et al. 2018) up to 80° N (Ikävalko et al. 1996), the highest species richness of scaled chrysophytes is typical of northern areas having a temperate climate and rich in small water bodies (Hällfors and Hällfors 1988; Němcová et al. 2012; Siver and Lott 2017; Bessudova et al. 2018). At the same time, the highest species diversity (82 species) and an increased share of boreal species of scaled chrysophytes were recently described at the mouths of rivers in Arctic Yakutia, Russia (Bessudova et al. 2021). This fact has not yet been reported for the Arctic.

It had already been demonstrated that the species diversity and richness of scaled chrysophytes in Arctic waters are affected by regional peculiarities such as water temperature, conductivity, transparency and color, concentration of carbon dioxide, magnesium ions, total iron, surfactant materials and mineral oils (Bessudova et al. 2021; Bessudova et al. 2021).

The water bodies investigated in our paper are situated near the town of Tiksi, the northernmost port of Russia on the Laptev Sea. The area refers to tundra and mountain-tundra zones. The climate is marine polar with average annual temperature -9 to -11 °C (Konstantinov et al. 2022). The average multiyear amount of atmospheric precipitation reaches 241 mm, it mostly falls from June to August (Konstantinov et al. 2022). The depth of seasonal thawing of permafrost is 0.2–1.2 m (Permafrost... 1989). Limited soild rain age due to a small thickness of the defrosted permafrost layer typical for this area and for the rest of Yakutia leads to the formation of numerous small tundra water bodies (Kirillov and Chernyshev 2006).

The research area is situated at the northern slope of the Primorsky Ridge, which is an eastern offshoot of the Kharaulakh Range of the Verkhoyansk Mountainous System, and represents a part of the coast of the Laptev Sea, the Arctic Ocean. The upper rocks in the research area are formed with deposits of shale, sandstone, limestone, and effusive rock (Gvozdetsky and Mikhailov 1978) that were accumulated, according to some data, as a result of catastrophic break of an ice-dammed lake in the late Pleistocene – Early Holocene (Grosswald and Spektor 1993; Spektor et al. 2021).

The article aims to study species composition and richness of scaled chrysophytes in 14 small freshwater lakes and pools, perform biogeographical analysis, to evaluate the degree of richness of the species, composition of boreal species and detect habitat parameters affecting the diversity of these aquatic organisms in the study area.

## Materials and methods

### Field and laboratory methods

Samples were collected 3–7 July 2021 from 14 different-type water bodies near the town of Tiksi (Table 1, Fig. 1). Planktonic samples were collected with an Apstein net (SEFAR NITEX, mesh 15 µm). The collected was fixed with 25 % glutaraldehyde. The samples were processed according to methods previously described (Bessudova et al. 2021). A Quanta 200 (FEI Company) scanning electron microscope and LEO 906E (Carl Zeiss) transmission electron microscope were used for microscopic studies. The hydrochemical analysis of the samples was performed according to methods previously described (Bessudova et al. 2021).

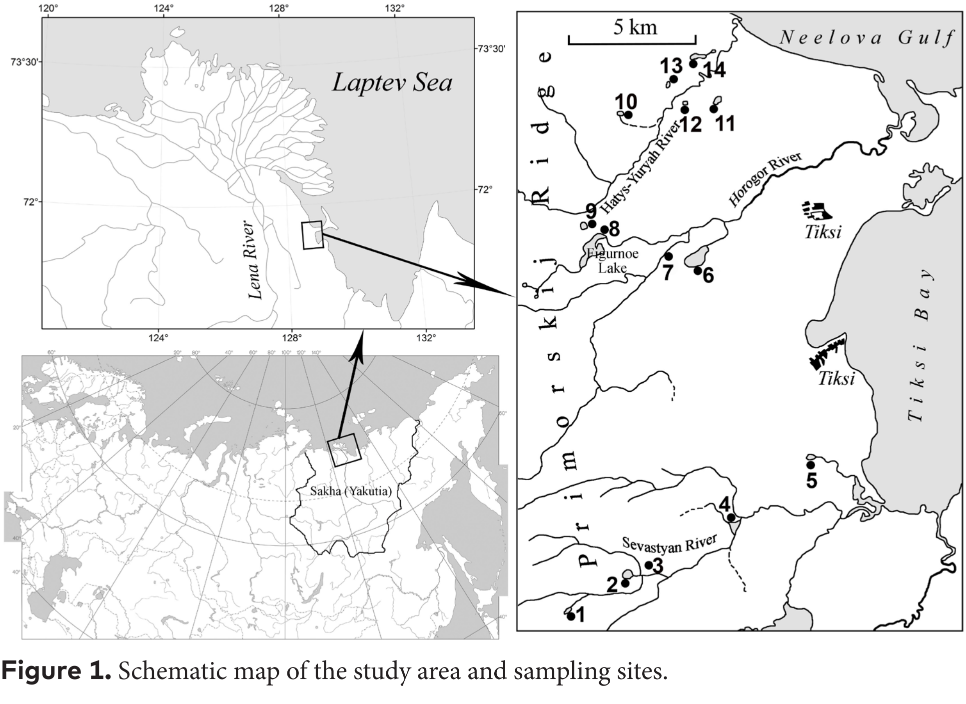

**Figure 1.** Schematic map of the study area and sampling sites.

**Table 1.** Content of chemical agents in waters near the town of Tiksi (site numbers in Figure 1). Note: values in bold point at exceeded maximum allowable concentrations for waters of commercial fishing importance.

| Parameters | Reservoir number | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Lake_1** | **Lake_2** | **Swampy tundra pool_3** | **Lake_4** | **Lake_5** | **Lake_6** | **Pool_7** | **Figurnoe Lake_8** | **Lake_9** | **Lake_10** | **Lake_11** | **Lake_12** | **Lake_13** | **Lake_14** |
| Coordinates | 71.543<br>128.582 | 71.555<br>128.648 | 71.560<br>128.674 | 71.576<br>128.764 | 71.599<br>128.852 | 71.670<br>128.724 | 71.674<br>128.689 | 71.681<br>128.620 | 71.684<br>128.601 | 71.725<br>128.642 | 71.729<br>128.743 | 71.730<br>128.710 | 71.737<br>128.694 | 71.746<br>128.720 |
| Sampling date | 06.07.21 | 06.07.21 | 06.07.21 | 06.07.21 | 07.07.21 | 04.07.21 | 04.07.21 | 04.07.21 | 04.07.21 | 03.07.21 | 03.07.21 | 03.07.21 | 03.07.21 | 03.07.21 |
| T, °C | 14.70 | 14.60 | | 14.00 | 13.30 | 15.10 | | 14.50 | 16.10 | 15.00 | | 20.40 | 15.10 | 16.70 |
| pH, Epi | 7.34 | 7.22 | | 6.65 | 6.89 | 7.30 | | 7.30 | 6.73 | 6.70 | | 6.74 | 7.42 | 7.51 |
| Suspended matter, mg/L | < 3.00 | < 3.00 | | < 3.00 | < 3.00 | < 3.00 | | < 3.00 | < 3.00 | < 3.00 | | < 3.00 | < 3.00 | < 3.00 |
| $O_2$, mg/L | 9.77 | 9.86 | | 9.60 | 10.10 | 9.98 | | 10.47 | 10.10 | 9.40 | | 8.70 | 10.28 | 9.87 |
| Mineralization, mg/L | 259.83 | 260.95 | | 234.05 | 243.21 | 181.60 | | 160.74 | 177.49 | 225.63 | | 178.92 | 168.73 | 267.53 |
| Water hardiness, μmol $m^{-2}s^{-1}$ | 3.34 | 3.61 | | 3.16 | 3.34 | 2.44 | | 2.13 | 2.37 | 3.09 | | 2.29 | 2.28 | 3.48 |
| $Ca^{2+}$, mg/L | 38.20 | 32.40 | | 36.80 | 35.20 | 28.40 | | 28.60 | 27.20 | 38.60 | | 32.00 | 22.44 | 45.00 |
| $Mg^{2+}$, mg/L | 17.40 | 24.20 | | 16.10 | 19.20 | 12.40 | | 8.60 | 12.30 | 14.20 | | 8.40 | 14.09 | 15.00 |
| $Na^{+}$, mg/L | 6.03 | 1.39 | | 1.28 | 0.93 | 1.43 | | 0.66 | 1.12 | 1.14 | | 3.91 | 2.60 | 5.87 |
| $K^{+}$, mg/L | 1.60 | 0.86 | | 0.37 | 0.48 | 0.57 | | 0.58 | 0.57 | 0.49 | | 0.46 | 0.81 | 1.46 |
| $HCO^{3-}$, mg/L | 110.20 | 130.40 | | 120.50 | 120.40 | 90.60 | | 89.40 | 98.60 | 98.60 | | 79.50 | 67.12 | 100.00 |
| $Cl^{-}$, mg/L | 4.80 | 8.20 | | 4.00 | 3.50 | 3.20 | | 3.40 | 3.50 | 4.80 | | 4.25 | 3.55 | 6.20 |
| $SO_4^{2-}$, mg/L | 81.60 | 63.50 | | 55.00 | 63.50 | 45.00 | | 29.50 | 34.20 | 67.80 | | 50.40 | 58.12 | 94.00 |
| $NH_4$, mg/L | 0.20 | 0.12 | | 0.31 | 0.25 | 0.15 | | 0.19 | 0.18 | 0.10 | | 0.24 | 0.26 | 0.34 |
| $NO_2$, mg/L | < 0.02 | < 0.02 | | < 0.02 | < 0.02 | < 0.02 | | < 0.02 | < 0.02 | < 0.02 | | < 0.02 | < 0.02 | < 0.02 |

| **Parameters** | **Reservoir number** | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Lake_1** | **Lake_2** | **Swampy tundra pool_3** | **Lake_4** | **Lake_5** | **Lake_6** | **Pool_7** | **Figurnoe Lake_8** | **Lake_9** | **Lake_10** | **Lake_11** | **Lake_12** | **Lake_13** | **Lake_14** |
| $NO_3$, mg/L | 0.56 | 0.60 | | 0.58 | 0.54 | 0.48 | | 0.42 | 0.62 | 0.54 | | 0.82 | 0.54 | 0.74 |
| Si, mg/L | < 1.00 | < 1.00 | | < 1.00 | < 1.00 | < 1.00 | | < 1.00 | < 1.00 | < 1.00 | | < 1.00 | < 1.00 | < 1.00 |
| $PO_4$, mg/L | < 50 | < 50 | | < 50 | < 50 | < 50 | | < 50 | < 50 | < 50 | | < 50 | < 50 | < 50 |
| $P_{total}$, μg/L | 100 | 100 | | 110 | 90 | 70 | | 130 | 140 | 50 | | 80 | 80 | 200 |
| $Fe_{total}$, μg/L | **0.50** | **0.62** | | **0.68** | **0.65** | **0.29** | | **0.67** | **0.55** | **0.40** | | **0.70** | **0.29** | **0.41** |
| Color, Pt-Co | 19 | 18 | | 10 | 11 | 15 | | 19 | 12 | 13 | | **25** | 13 | 16 |
| BOD, μg/L | 0.83 | 1.43 | | **2.39** | **2.48** | 1.61 | | **2.00** | 1.01 | 1.46 | | **2.45** | 1.75 | **2.48** |
| COD, μg/L | **16.40** | **16.80** | | **16.20** | **18.00** | **17.80** | | **18.40** | **18.20** | **17.60** | | 14.00 | 14.40 | 14.20 |
| Phenols, mg/L | < 5 | < 5 | | < 5 | < 5 | < 5 | | < 5 | < 5 | < 5 | | < 5 | < 5 | < 5 |
| Petrochemicals, mg/L | < 0.005 | < 0.005 | | < 0.005 | < 0.005 | < 0.005 | | < 0.005 | < 0.005 | < 0.005 | | < 0.005 | < 0.005 | < 0.005 |
| $Cu^{2+}$, mg/L | **0.004** | **0.003** | | **0.004** | 0.001 | **0.003** | | **0.002** | **0.003** | **0.003** | | **0.005** | **0.003** | **0.005** |
| $Zn^{2+}$, mg/L | < 0.001 | < 0.001 | | < 0.001 | < 0.001 | < 0.001 | | < 0.001 | < 0.001 | < 0.001 | | < 0.001 | < 0.001 | < 0.001 |
| $Ni^{2+}$, mg/L | < 0.005 | < 0.005 | | < 0.005 | < 0.005 | < 0.005 | | < 0.005 | < 0.005 | < 0.005 | | < 0.005 | < 0.005 | < 0.005 |
| $Pb^{4+}$, mg/L | < 0.005 | < 0.005 | | < 0.005 | < 0.005 | < 0.005 | | < 0.005 | < 0.005 | < 0.005 | | < 0.005 | < 0.005 | < 0.005 |
| $Mn^{2+}$, mg/L | 0.007 | 0.006 | | 0.007 | 0.007 | 0.004 | | 0.002 | 0.003 | 0.002 | | 0.006 | 0.004 | 0.007 |

## Geographical distribution

To determine eventual changes in the context of global climate change, we analyzed the geographical distribution of scaled chrysophytes. We ascribed the taxa of scaled chrysophytes to the formerly proposed latitudinal and longitudinal groups of geographical distribution (Kristiansen 2000; Kristiansen 2008; Voloshko 2017) according to their preferred distribution in a given geographic zone and their geographic range over the continents. The following types of geographic distribution were included within the latitudinal group: P: polyzonal (species found in all climatic zones); A-Bor: Arctic boreal (species found in the Northern Hemisphere in the temperate and/or Arctic zones); Bor: boreal (species only found in the boreal zone); and Arc: Arctic (species only found in the Arctic zone). The following types of geographic distribution were included within the longitudinal group: K: cosmopolitan (species found on all six continents); W: widespread (species absent from one or two continents); R: species with scattered distribution (species rarely found across different latitudes); and BP: bipolar species (species occurring at the middle latitudes of the northern and Southern Hemispheres). We used the tag 'unknown', that is, with an unknown geographical characteristic), for new species, bipolar species, or species identified only at the genus level.

## Statistical Analysis

For the statistical analysis, we combined the information on the community structure of chrysophycean algae into a single table, with columns and rows characterizing water bodies and species of algae, respectively. The value 1 was assigned to the presence of a species in a water body. The absence of a species was marked with 0. The same table was also composed to compare the quantitative characteristics of the physical and chemical parameters of the water bodies.

The influence of physical and chemical environmental parameters on the taxonomic composition of chrysophycean algae in the water bodies was assessed using the PERMANOVA test (Anderson 2001) (10000 permutations for calculation of p-value) realized in the package 'vegan' (Oksanen et al. 2013) for the R programming language. The Euclidean distance was used for the test to calculate a distance matrix showing differences in the taxonomic composition of communities. The influence of a factor was assumed to be reliable if the p-value was $< 0.05$; intensity of the influence of the factor was evaluated using the PERMANOVA $R^2$ covariance coefficient (a higher $R^2$ value corresponds to a higher intensity of influence of a factor).

The influence of physical and chemical environmental parameters on the species richness (α richness) was assessed using the Spearman rank correlation coefficient. The influence of a factor was assumed to be reliable if the p-value of the Spearman statistics was $< 0.05$.

The PERMANOVA p-values and the reliability of Spearman rank correlation coefficient values were corrected for multiple hypothesis testing problem according to the Benjamini-Hochberg Procedure (Benjamini and Hochberg 1995).

Similarities and differences in water bodies in species composition of communities were visualized using non-metric multidimensional scaling (NMDS) based on the Euclidean distance in the package 'vegan' (Oksanen et al. 2013) for the R programming language. Gradient vectors showing changes in direction of environmental factors reliably affecting the species composition of communities according to the PERMANOVA results were calculated and added to the NMDS scatter plot under a guide for the package 'vegan' (Oksanen 2015).

The water bodies were clustered by the degree of the similarity of the species composition of communities (the Euclidean distance) using the 'average' method with the clustering being evaluated for reliability by bootstrapping (10000 boot strap replicates) in the package (Suzuki and Shimodaira 2006) for the R programming language.

## Results

### Environmental conditions of study sites

According to their pH, the lakes studied can be classified as acid to neutral (Table 1). The content of suspended matter in these lakes is quite low. The concentration of dissolved oxygen shows a favorable oxygen regimen. The water of the lakes is fresh, soft to medium hard, with low and medium mineral content, calcium bicarbonate carbonate, except Lakes 12 and 14 where water contains calcium sulfate. Among nutrients, a high content of total iron was detected (3–7 times exceeding maximum allowable concentrations for waters of commercial fishing importance (MACwcfi). The content of nitrate and total phosphorus is not high; concentrations of phosphate, nitrate, and silicon are insignificant too. The water color index inmost lakes is low, except Lake 12 where it is 25 Pt-Co (1.3 times exceeding the MACwcfi). The content of readily oxidizable matter ($BOD_5$) in Lakes 4, 5, 8, 12 and 14 is high (Table 1). The remaining lakes have a low concentration of readily oxidizable matter. The content of resistant to oxidation matter (COD) in Lakes 3, 4 and 5 is not high. The remaining lakes have COD 1.0-1.2 times greater than the MACwcfi (16.20–18.40 $mg{\cdot}L^{-1}$) typical of Arctic waters. The content of industrial pollutants is low. The concentration of oil derivatives and phenol is below the detection limit. Among the microelements, a high content of copper and a low content of manganese, zinc, nickel, and lead were detected (Table 1).

## Diversity and geographic distribution of chrysophytes

A high richness of scaled chrysophytes was found in these Arctic lakes: 65 species of 6 genera: *Chrysosphaerella* (2), *Paraphysomonas* (8), *Lepidochromonas* (3), *Spiniferomonas* (10), *Mallomonas* (23) and *Synura* (19) (Table 2, Figs 2–7). 3 species, *Paraphysomonas* cf. *ovalis*, *P. segmenta*, and *Synura obesa*, were found in waters of Russia for the first time. Analysis of species composition showed a prevalence of ubiquitous and cosmopolitan species (60 %) in the longitudinal group (Table 2; Fig. 8A). The contribution of rare species with scattered distribution is 30 % (20 species). 9 % of the species have an unknown geographical characteristic, hence we included potentially new species as well as the species *Paraphysomonas* cf. *ovalis* and *P. segmenta* found for the first time after their description (Scoble and Cavalier-Smith 2014). 2 % were bipolar species, among them *Mallomonas alata* f. *hualvensis* and *M. pillula* f. *valdiviana*. The latitudinal group demonstrated a predominance of polyzonal species (55 %) (Table 2; Fig. 8B). 19 % (12 species) are Arctic boreal. The contribution of boreal species and those with unknown geographic distribution is 11 % and 12 %, respectively (7 and 8 species). Arctic species have 3 %, among them *Synura obesa* and *S. petersenii* f. *taymyrensis*.

The most wide spread species in the study area, which occur in 55 % of the lakes, are *Spiniferomonas bourrellyi*, *S. trioralis*, *Mallomonas akrokomos*, *M. heterospina*, *M. papillosa*, *Synura* cf. *americana*, *S. borealis* and *S. petersenii*. Three of these species, *S. trioralis*, *Synura borealis*, and *S. petersenii*, occur in 77 % of the lakes. All these species are cosmopolitan and polyzonal, i.e. they are distributed over all 6 continents. We found 3 species, *Paraphysomonas* cf. *ovalis*, *P. segmenta*, and *S. abrupta*, previously described only in temperate latitudes; in Arctic waters, they were detected for the first time. The species *Lepidochromonas butcheri*, *L. eiffelii* and *Mallomonas kuzminii* typical of temperate latitudes had been already reported from mouths of Arctic rivers of Yakutia in our previous paper (Bessudova et al. 2021).

## Peculiarities of the species composition of scaled chrysophytes

Rare species, species having an unusual scale morphology, and potentially new species were found in the study area.

*Paraphysomonas* cf. *ovalis* (Fig. 3A). The species *Paraphysomonas ovalis* was detected and described in soil samples from Great Britain (Scoble and Cavalier-Smith 2014). Spine scales have an oval or irregular base plate, 0.7–0.9 µm in diameter, with a discernible thick rim. Spines are 1.4–1.7 µm long, slightly expanded at the base, smoothly tapering toward a rounded tip. We found the species in Lake 11 (Tables 1, 2).

*P. segmenta* (Fig. 3F) was detected and described in a pond in Great Britain (Scoble and Cavalier-Smith 2014). We found the species in Pool 7 (Tables 1, 2).

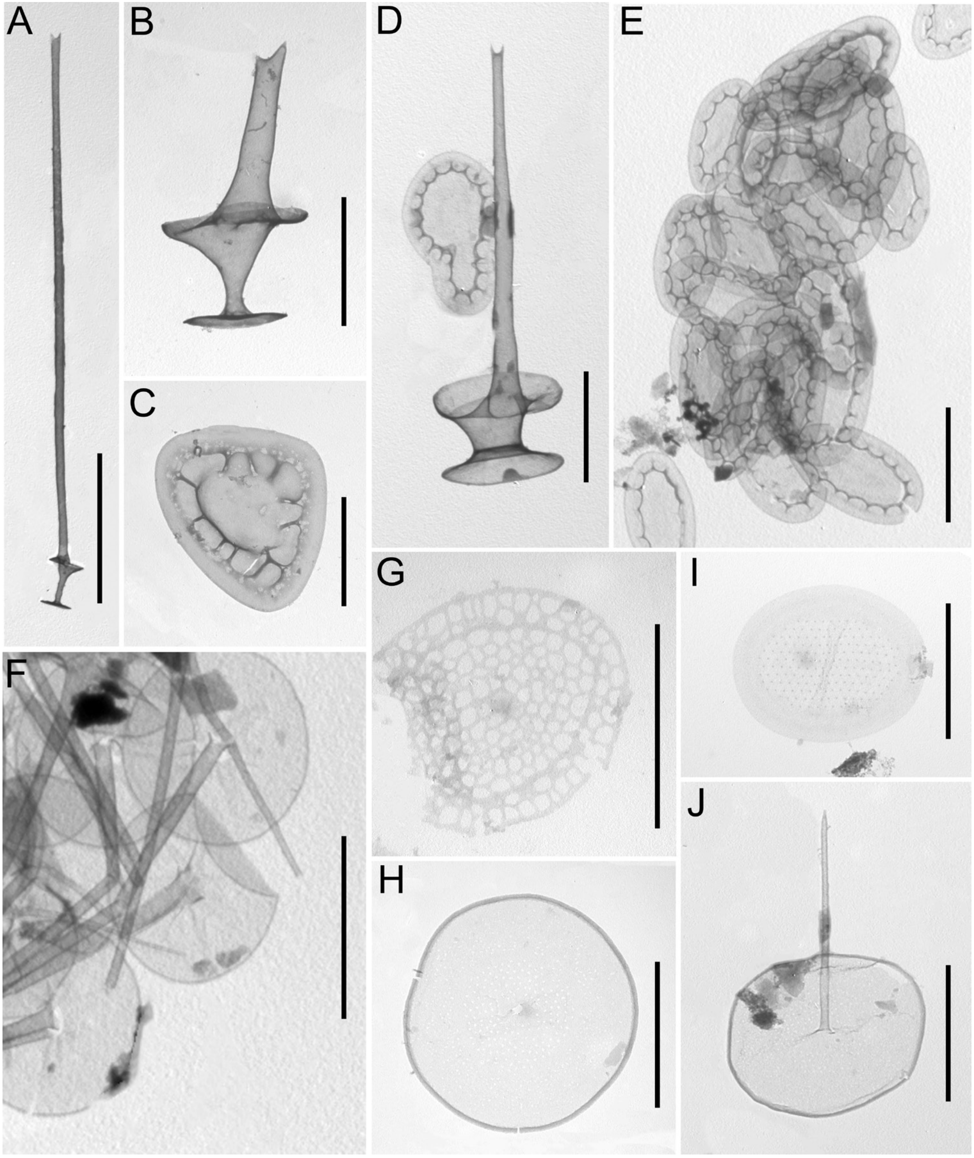

**Figure 2.** TEM of scaled chrysophytes: **A–C**, *Chrysosphaerella longispina* (reservoir 11); **D**, **E**, *Ch. brevispina* (reservoir 1); **F**, *Paraphysomonas uniformis hemiradia* (reservoir 1); **G**, *Lepidochromonas* sf. *butcheri* (reservoir 7); **I**, *P. punctata* (reservoir 5); **H**, **J**, *Paraphysomonas* sp. (reservoir 7). Scale bars: **G**, **I**, 500 nµ; **H**, **J**, 1 µm; **B–F**, 2 µm; **A**, 10 µm.

*Mallomonas kalinae* (Fig. 6G) has a scattered distribution worldwide. The species was detected and described in waters of the Czech Republic (Řezáčová 2006; Janatková and Němcová 2009), later the species was identified in a lake of the Bolshezemelskaya tundra, Russia (Siver et al. 2005), in waters of Australia (Croome and Tyler 1988) and Malaysia (Dürrschmidt and Croome 1985). Therefore, the species is reported from waters with pH in the range of 5.5 (Řezáčová 2006) to 6.74 (this article, Lake 12), temperature 0 (Janatková and Němcová 2009) to 20.4 °C (this article, Lake 12), conductivity 46 (Janatková and Němcová 2009) to 56 µS·cm$^{-1}$ (Řezáčová 2006). We found the species in Swampy tundra pool 3 and Lake 12 (Table 1, 2).

**Table 2.** List of scaled chrysophytes and their distribution in the from the in freshwater Arctic pools and lakes from area Tiksi. Site numbers correspond to those in Figure 1 and Table 1. Species found in Russia for the first time are in bold.

| № | Geographical distribution | | | Site number | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Latitudinal group | Longitudinal group | Spices | 1 | 2 | 3 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
| 1 | K | P | *Chrysosphaerella brevispina* Korshikov | + | | | | | | + | + | | | | + | |
| 2 | K | P | *Ch. longispina* Lauterborn | | + | + | | | + | | | | + | | | |
| 3 | W | P | *Paraphysomonas acuminata acuminata* Scoble & Cavalier-Smith | | | + | | | | | | + | + | | | |
| 4 | W | P | *P. corynephora* Preisig & Hibberd | | | | | | | | | | + | | | |
| 5 | - | - | ***P.*** cf. ***ovalis*** Scoble & Cavalier-Smith | | | | | | | | | | + | | | |
| 6 | - | - | ***P. segmenta*** Scoble & Cavalier-Smith | | | | | | + | | | | | | | |
| 7 | W | P | *P. punctata* Preisig & Hibberd | | | | + | | | | | | | | | |
| 8 | R | Bor | *P. vulgaris vulgaris* Scoble & Cavalier-Smith | | | | | | + | | + | + | + | | | |
| 9 | W | P | *P. uniformis hemiradia* Scoble & Cavalier-Smith | + | | | | | + | | + | | | + | | |
| 10 | - | - | *Paraphysomonas* sp. | | | | | | + | | | | | | | |

| **№** | **Geographical distribution** | | | **Site number** | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Latitudinal group** | **Longitudinal group** | **Spices** | **1** | **2** | **3** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** | **14** |
| 11 | K | P | *Lepidochromonas* sf. *butcheri* (Pennick & Clarke) Kapustin & Guiry | | | | | | + | | | | | | | |
| 12 | R | Bor | *L. eiffelii* (Thomsen) Kapustin & Guiry | | | + | | | + | | | | | | | |
| 13 | K | P | *L. takahashii* (Cronberg & Kristiansen) Kapustin & Guiry | | | | + | | | | | + | | | | |
| 14 | W | P | *Spiniferomonas abei* Takahashi | | | + | + | | + | | | | | | | |
| 15 | R | Bor | *S. abrupta* Nielsen | | | | | | | | | | | | + | |
| 16 | K | P | *S. bourrellyi* Takahashi | + | + | + | + | | + | | + | | | + | + | |
| 17 | R | A-Bor | *S. cornuta* Balonov | | | | + | | | | | | | | + | |
| 18 | W | A-Bor | *S. minuta* Nicholls | | | | + | | | | | | | | | |
| 19 | K | P | *S. serrata* Nicholls | | + | | | | | | | | | | + | |
| 20 | R | A-Bor | *S. triangularis* Siver | | | | + | | | | | | | | | |
| 21 | K | P | *S. trioralis* Takahashi | + | + | + | + | + | + | + | + | + | | | + | |
| 22 | R | A-Bor | *S. trioralis* f. *cuspidata* Balonov | | | | + | | | | + | | | | | |
| 23 | R | A-Bor | *S.* cf. *involuta* Jacobsen | | | | + | | | | | | | | | |
| 24 | K | P | *Mallomonas acaroides* Perty | | + | | | | | | | | | | | |
| 25 | R | Bor | *M. annulata* Harris | | | | | | | | | | | | | + |
| 26 | K | P | *M. akrokomos* Ruttner | | + | | + | + | | + | + | + | + | | | |
| 27 | K | P | *M. alpina* Pascher & Ruttner | + | + | | | | | + | + | | | | + | |
| 28 | BP | - | *M. alata* f. *hualvensis* Asmund, Cronberg & Dürrschmidt | | | + | + | | + | | | | + | + | | |
| 29 | K | P | *M. crassisquama* (Asmund) Fott | | + | | + | | | + | | | + | | + | |
| 30 | R | A-Bor | *M. crassisquama* var. *papillosa* Siver & Skogstad | | + | | | | | | | | | | | |
| 31 | W | P | *M. eoa* Takahashi in Asmund & Takahashi | | | | | | + | | | | | | | + |
| 32 | W | P | *M. flora* Harris & Bradley | | | | | | | | | | | | + | |

| **№** | **Geographical distribution** | | | **Site number** | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Latitudinal group** | **Longitudinal group** | **Spices** | **1** | **2** | **3** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** | **14** |
| 33 | W | P | *M. heterospina* Lund | | | | + | + | + | + | + | + | + | | | |
| 34 | R | P | *M. kalinae* Řezáčová | | | + | | | | | | | | + | | |
| 35 | R | Bor | *M. kuzminii* Gusev & Kulikovskiy | | + | | | | | | | | | + | | |
| 36 | R | A-Bor | *M. lelymene* Harris & Bradley | | | + | | | | | | | | | | |
| 37 | R | A-Bor | *M. maculata* Bradley | | + | + | | | | | | | | | | |
| 38 | K | P | *M. matvienkoae* (Matvienko) Asmund & Kristiansen | | | | | | | | + | | | + | | |
| 39 | K | P | *M. papillosa* Harris & Bradley | | | + | + | | + | + | | | + | + | | + |
| 40 | W | P | *M. parvula* Dürrschmidt | | | | | | | + | | | | | | |
| 41 | R | A-Bor | *M. pillula* f. *latimarginalis* Dürrschmidt | | | + | | | | | | | | | | |
| 42 | BP | - | *M. pillula* f. *valdiviana* Dürrschmidt | | | + | | | | | | | | | | |
| 43 | R | A-Bor | *M. scrobiculata* Nicholls | | | + | | | | | | | + | | | |
| 44 | K | P | *M. striata* Asmund | | | | | | | + | | | | | | |
| 45 | R | A-Bor | *M. tolerans* Asmund & Kristiansen | | | | | | | | | | | | + | |
| 46 | K | P | *M. tonsurata* Teiling | | | | | | | + | | | | | | |
| 47 | - | - | *Mallomonas* sp. | | | + | | | + | | | | | | | |
| 48 | K | P | *Synura* cf. *americana* Kynclová & Škaloud | + | | | + | | + | + | + | | + | | + | + |
| 49 | W | P | *S. borealis* Škaloud & Škaloudová | + | + | + | | + | + | + | + | + | | | + | + |
| 50 | K | P | *S. conopea* Kynclová & Škaloud | | | + | | | | | | | | | | |
| 51 | K | P | *S. curtispina* (Petersen & Hansen) Asmund | | | + | | | + | + | | | + | | | |
| 52 | K | P | *S. echinulata* Korshikov | | | + | + | | | + | + | + | | + | + | |
| 53 | W | Bor | *S. glabra* (Korshikov) Škaloud & Kynclová | + | | | + | | | + | + | | | | | |
| 54 | R | Arc | ***S. obesa*** Němcová, S. Nováková & Řezáčová-Škaloudová | | | + | | | | | | | | | | |

| **№** | **Geographical distribution** | | | **Site number** | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Latitudinal group** | **Longitudinal group** | **Spices** | **1** | **2** | **3** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** | **14** |
| 55 | K | P | *S. macropora* Škaloud & Kynclová | | | + | | | | | | | | | | |
| 56 | W | Bor | *S. mammillosa* Takahashi | | | | | | | | | | | | + | |
| 57 | K | P | *S. petersenii* (Korshikov) Škaloud & Kynclová | + | | | | + | + | + | + | + | + | + | + | + |
| 58 | R | Arc | *S. petersenii* f. *taymyrensis* Kristiansen | + | | + | + | | | | | | | | | |
| 59 | R | A-Bor | *S. praefracta* (Asmund) Škaloud & Škaloudová | | | | | + | | + | + | | | | + | + |
| 60 | W | P | *S. sphagnicola* Korshikov | | | | | | | + | | | | | | |
| 61 | K | P | *S. synuroidea* (Prowse) Pusztai, Čertnerová, Škaloudová & Škaloud | | | + | | | | | | | + | | | |
| 62 | K | P | *S. uvella* Ehrenberg | | | + | | | + | | | | | | + | |
| 63 | R | - | *S.* cf. *vinlandica* Škaloud, Škaloudová & Siver | | | + | | | | | + | | | | + | |
| 64 | - | - | *Synura* sp. 1 | | | + | | | | | | | | | | |
| 65 | - | - | *Synura* sp. 2 | + | + | + | | | + | | | | + | | | + |
| | | | Total | 11 | 13 | 27 | 19 | 6 | 21 | 18 | 17 | 9 | 16 | 9 | 18 | 8 |

*Spiniferomonas abrupta* (Fig. 4B) has a scattered distribution worldwide. The species was detected and described in a lake in Denmark(Nielsen 1994). The species was later identified in the waters of Russia, in lakes Labynkyr and Vorota (Yakutia) (Bessudova et al. 2019), in Lake Baikal, the Barguzin River, and in the delta of the Selenga River (Bessudova et al. 2018).Thus, species in nowadays found at pH within 6.92 (Bessudova et al. 2019) to 8.3 (Nielsen 1994), temperature 2 to 18 °C (Nielsen 1994), conductivity 13 (Nielsen 1994) to 151 µS·cm$^{-1}$ (Bessudova et al. 2018). We found the species in Lake 13 (Tables 1, 2).

Two rare species, *Synura obesa* (Fig. 7D) and *S. petersenii* f. *taymyrensis* (Fig. 7A) were identified in the Swampy Tundra Pool 3. The *Synura obesa* was previously detected and described in a small lake near Abisko, Swedish Lapland at pH = 5.5, T = 17 °C, conductivity 25 µS·cm$^{-1}$ (Němcováet al. 2008). This is the second site where the species is detected (Tables 1, 2).

*Synura petersenii* f. *taymyrensis* was found in a small water body on the Taymyr Peninsula (Kristiansen et al. 1997) and recently found at the mouth of the Olenyok River, Russia (Bessudova et al. 2021) at pH = 6.78, T = 17.4 °C (Tables 1, 2).

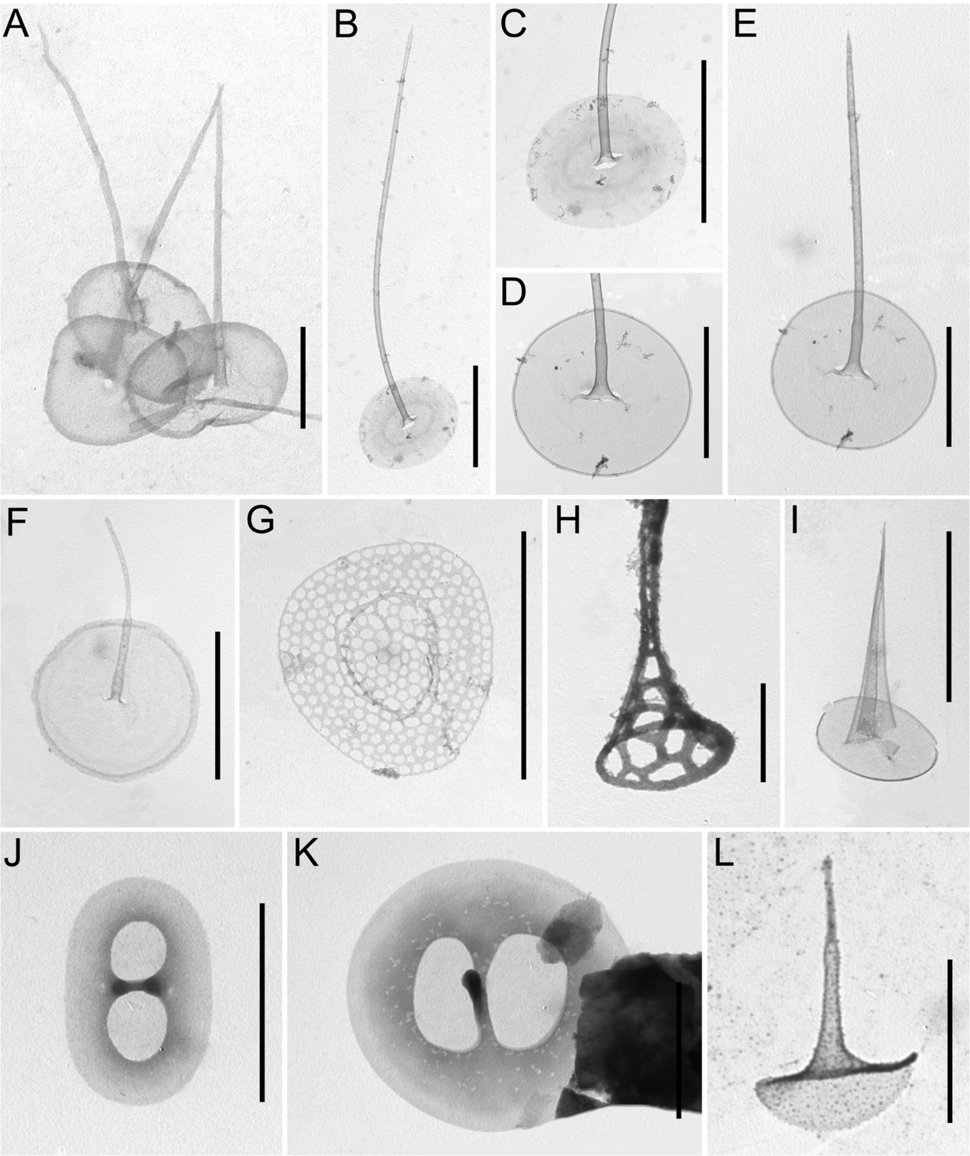

**Figure 3.** TEM of scaled chrysophytes. **A**, *Paraphysomonas* cf. *ovalis* (reservoir 11); **B**, **C**, *P. a. acuminata* (reservoir 3); **D**, **E**, *Paraphysomonas vulgaris vulgaris* (reservoir 9); **F**, *P. segmenta* (reservoir 7); **G**, *Lepidochromonas takahashii* (reservoir 10); **H**, *L. eiffelii* (reservoir 3); **I**, *S.* cf. *involuta* (reservoir 5); **J**, *S. cornuta* (reservoir 13); **K**, *S. triangularis* (reservoir 5); **L**, *P. corynephora* (reservoir 11). Scale bars: **A**, **F**, **H**, 500 nμ; **J**, **L**, **K**, 1 μm; **B-E**, **G**, I, 2 μm.

We also found spine scales presumably belonging to *Spiniferomonas* cf. *involuta* (Fig. 3I). The *S.* cf. *involuta* was previously detected and described in small lakes in West Greenland at pH = 6.3–7.5, T = 7–15 °C, conductivity 13–20 μS·cm$^{-1}$ (Jacobsen 1985; as *Chromophysomonas involuta*).Spine scales consist of a circular basal plate (0.7 μm in diameter) with a distinct upturned rim, and a short (2.6 μm) three-winged spine, which taper into a pointed apex (Fig. 3I). We found the species in Lake 5 at pH = 6.89, T = 13.3 °C (Tables 1, 2).

*S.* cf. *vinlandica* (Fig. 7I). The body scales are 5.3 μm long, 2.4 μm wide, and the basal plate has a rounded keel elevated in the center (Fig. 7I). The keel is cylindrically widened anteriorly, ornamented with large pores. There are 38 interchangeable struts divided with lateral ribs that evenly go from the keel to the perimeter of the scale. The only scale we found was larger than those described before (Škaloud et al. 2020), plus it had more struts. We identified the species in Lakes 9, 12, and Swampy tundra pool 3.

We found scales of *M. eoa* having an atypical morphology (Fig. 6D). Sometimes, when there is a low content of silicon in water, the scale structures are weakly silicified. However, the pores of the weakly silicified *M. eoa* scales remain "rounded" (Kristiansen and Presing; Fig. 27n). The scales we found had hexagonal pores on the shield with distinct ribs (Fig. 6C). Scales with normal structure and those with an atypical morphology were detected in Lake 7. Scales with unusual structure were also found in Lake 14 (Tables 1, 2).

We found scales of *S. echinulata* whose morphotype resembled that previously described in waters of Ontario, Canada (Nicholls and Gerrath 1985). This morphotype differs in a curved spine and a large area of distinctive labyrinthic pattern, spreading almost to the proximal part of the scale. This morphotype is presumed to belong to a separate species other than *S. echinulata* (Škaloud et al. 2020; Fig. 4m). The labyrinthic pattern on the scale from Station 5 reaches the proximal part of the scale (Fig. 7N) and stands in glaring contrast to the scale morphology typical of *S. echinulata* (Fig. 7N). Scales of this morphotype occur in Lakes 5, 9 and 11 (Tables 1, 2).

We discovered 4 species whose morphology differed from all known species. It is likely that they are potentially new species.

*Paraphysomonas* sp. (Figs 1H, J). Base plate of round to oval 1.57 μm (1.1–1.60). The base plate is covered with small pores. The spine is 1.62 μm (1.3–1.7) long, gently tapering to a pointed tip. The species occurs in Pool 7 (Tables 1, 2).

*Mallomonas* sp. (Figs 6J, K). The collar scales, 3.6 × 2.5 μm in size, are trapezoidal in shape with a well-developed suboval dome. The submarginal rib is well developed along the dorsal and the ventral edges. The flange is smooth, forming a prominent rounded protrusion at the dorsal and the ventral edges. The proximal border encompasses the posterior and dorsal parts of the collar scale. The reticulum are weak, not developed on the shield. A rhombic scale, apparently belonging to this species, was also found. Body scales, 3 ×1.74 μm in size, are rhombic. The posterior flange is smooth, and the proximal border is considerably attenuated at the posterior end of the scale. The rhombic scale was found in Pool 7, and the collar scales was discovered in Swampy tundra pool 3 (Table 1, 2).

*Synura* sp. 1 (Figs 7F–H). Body scales are 4.7–5.6 μm long and 1.2–2.0 μm wide, consisting of a basal plate with a centrally raised keel protruding from an acute tip. The keel is anteriorly widened, giving it a triangular shape, ornamented with medium-sized pores (diameter, 49–89 nm). The ratio between the scale and the keel width varies from 2.7 to 3.9. The basal plate is ornamented with numerous small pores and anteriorly perforated with a rounded base hole (diameter, 0.5–0.6 μm). A large number of struts (36-43) extend regularly from the keel to the scale perimeter. The scale was found in Swampy tundra pool 3 (Tables 1, 2).

*Synura* sp. 2 (Figs 7B, C). Scales are oval, 2.9–4.0 μm × 1.4–2.2 μm in size. The keel is cylindrical, 0.5–0.66 μm wide, ornamented with medium-sized pores (diameter 66 to 100 nm) and large pores (diameter 120 to 170 nm). Keel ends with an acute tip, with medium-sized pores. The foramen pore on the base plate is circular and large, 0.36–0.6 μm in diameter. The basal plate is adorned with numerous small pores. Struts reach the proximal rim of the scale and, in some places, are connected to each other with a parallel rib. The posterior rim is narrow, 0.16–0.19 μm wide, encircling about a half of the perimeter of the scale. The scales were found in Lakes 1, 2, 11, 14, Swampy tundra pool 3, Pool 7, at pH = 7.22 to 7.51, T = 14.6 to 16.7 °C (Tables 1, 2).

## Physical and chemical parameters and species composition and richness

The PERMANOVA results (Table 3) show that the species composition of the communities in the study area plausibly (positive value of the correlation coefficient) depends on the concentrations of dissolved water oxygen ($O_2$), dissolved nitrate ion ($NO_3^-$) and copper ion ($Cu^{2+}$) as well as biological and chemical oxygen demand (BOD and COD). All these factors have an almost equal intensity of impact on the species composition of communities determined by scattering $R^2$ values from 0.121 to 0.165.

The richness of the species richness (α richness) in the study area is confirmed to be higher (Table 3) (positive value of the correlation coefficient r from 0.457 to 0.664) with increasing COD (indicator of organic matter concentration in water) and increasing $O_2$ concentration. The species richness became lower at increasing concentrations of copper ions ($Cu^{2+}$) in water (negative value of the correlation coefficientr = –0.7).

Cluster analysis detected neither group nor couple of lakes that would have a plausible support of 95 % and more similarity of species composition of scaled chrysophytes (Fig. 9A). However, both clustering (support 92 %) and NMDS results (Fig. 9B) allow identifying a group of 7 lakes (Lake 1, Lake 6, Figurnoe Lake 8, Lake 9, Lake 10, Lake 12, and Lake 14) that have the closest species composition with predominance of ubiquitous and cosmopolitan species compared to other six lakes. Three lakes of those with the closest species composition of scaled chrysophytes

(Lakes 1, 12 and 14) have the highest concentration of copper ion ($Cu^{2+}$) –0.005 mg/L. In two lakes (Lakes 14 and 8), we found species that do not occur in the other lakes. These are *M. annulata* identified only in Lake 14 and *M. parvula*, *M. striata*, *M. tonsurata* and *Synura sphagnicola* found only in Lake 8. The remaining lakes with the closest species composition differed among themselves in combination of species.

Six water bodies (Lake 2, Swampy tundra pool 3, Lake 5, Pool 7, Lake 11 and Lake 13) considerably differed in the species composition both among themselves and from the other water bodies. Thus, *Spiniferomonas abrupta*, *M. flora*, *M. tolerans* and *Synura mammillosa* occur only in Lake 13, *Paraphysomonas* sp. and *P. segmenta*in Pool 7, *P. corynephora*, and *P.* cf. *ovalis* in Lake 11, *Spiniferomonas minuta*, *S. triangularis*, *S.* cf. *involuta*, and *P. punctata* Lake 5, *M. lelymene*, *M. pillula* f. *latimarginalis*, *M. pillula* f. *valdiviana*, *Synura* sp. 1, *S. conopea*, *S. obesa*, and *S. macropora* in the Swampy tundra pool 3 (Table 2). Rare species with scattered distribution characterize the above-mentioned water bodies (Table 2).

Gradient vectors of environmental factor on the NMDS scatter plot (Fig. 9B) formed two groups of coherent markers. Group 1 includes positively correlated biotic factors such as biological oxygen demand (BOD) and chemical oxygen demand (COD) and negatively correlated markers such as copper ion concentration. Group 2 includes positively correlated abiotic factors such as magnesium ion concentrations and nitrate ion and negatively correlated markers such as oxygen concentration.

**Table 3.** Results of statistic assessment of correlation between habitat parameters, species richness and species composition of communities. Note: significant relationships (p-value < 0.05) are in bold, factors for the absence of variation in the content in samples (impossibility of statistical analysis) are marked with a dash.

| **Factor** | **PERMANOVA test, dependence of species composition from environmental factors** | | **Spearman's correlation coefficient, dependence of species richness from environmental factors** | |
|---|---|---|---|---|
| | **$R^2$** | **p-value** | **r** | **p-value** |
| T, °C | 0.103 | 0.441 | -0.291 | 0.386 |
| pH, Epi | 0.107 | 0.328 | 0.195 | 0.567 |
| Suspended matter, mg/L | - | - | - | - |
| $O_2$, mg/L | **0.148** | **0.035** | **0.664** | **0.026** |
| Mineralization, mg/L | 0.112 | 0.257 | -0.333 | 0.316 |
| Water hardiness, µmol $m^{-2}s^{-1}$ | 0.114 | 0.238 | -0.243 | 0.472 |
| $Ca^{2+}$, mg/L | 0.117 | 0.22 | -0.401 | 0.209 |
| $Mg^{2+}$, mg/L | 0.12 | 0.211 | 0.037 | 0.915 |
| $Na^{+}$, mg/L | 0.106 | 0.372 | -0.427 | 0.168 |

| **Factor** | **PERMANOVA test, dependence of species composition from environmental factors** | | **Spearman's correlation coefficient, dependence of species richness from environmental factors** | |
|---|---|---|---|---|
| | **$R^2$** | **p-value** | **r** | **p-value** |
| $K^+$, mg/L | 0.097 | 0.537 | 0.197 | 0.562 |
| $HCO^{3-}$, mg/L | 0.113 | 0.278 | -0.158 | 0.643 |
| $Cl^-$, mg/L | 0.121 | 0.219 | -0.250 | 0.458 |
| $SO4^{2-}$, mg/L | 0.093 | 0.626 | -0.146 | 0.667 |
| $NH_4$, mg/L | 0.097 | 0.533 | -0.073 | 0.831 |
| $NO_2$, mg/L | 0.105 | 0.448 | -0.151 | 0.658 |
| $NO_3$, mg/L | **0.122** | **0.038** | -0.295 | 0.379 |
| Si, mg/L | - | - | - | - |
| $PO_4$, mg/L | - | - | - | - |
| $P_{total}$, µg/L | 0.074 | 0.831 | 0.069 | 0.841 |
| $Fe_{total}$, µg/L | 0.094 | 0.569 | 0.062 | 0.857 |
| Color, Pt-Co | 0.078 | 0.804 | -0.002 | 0.995 |
| BOD, µg/L | **0.121** | **0.042** | -0.055 | 0.873 |
| COD, µg/L | **0.134** | **0.039** | **0.457** | **0.029** |
| Phenols, mg/L | - | - | - | - |
| Petrochemicals, mg/L | - | - | - | - |
| $Cu^{2+}$, mg/L | **0.165** | **0.002** | **-0.700** | **0.016** |
| $Zn^{2+}$, mg/L | - | - | - | - |
| $Ni^{2+}$, mg/L | - | - | - | - |
| $Pb^{4+}$, mg/L | - | - | - | - |
| $Mn^{2+}$, mg/L | 0.137 | 0.044 | -0.235 | 0.486 |

## Discussion

Scaled chrysophytes being prospective diagnostic bioindicators are very sensitive to any environmental change (Siver 1995; Siver and Lott 2017) dependent on latitude (Eloranta 1995). E.g., the high contribution of Arctic boreal species in our study (19 %) and the presence of Arctic species reflect regional features of the study area such as temperature preferences. The presence of typical boreal species of scaled chrysophytes in Arctic waters is becoming regular. We found 11 % (7 species) of the boreal species in the study area: *Paraphysomonas vulgaris vulgaris*, *Lepidochromonas eiffelii*, *Spiniferomonas abrupta*, *Mallomonas annulata*, *M. kuzminii*, *Synura glabra* and *S. mammillosa*. According to our previous investigations, the share of boreal species in the mouths of the Arctic rivers of Yakutia was 12 % (10 species) (Bessudova et al. 2021). Only 4 from 7 boreal species we identified had been previously found in mouths of rivers of Yakutia, these are *Paraphysomonas vulgaris vulgaris*, *Lepidochromonas eiffelii*, *Synura glabra* and *S. mammillosa*. These data agree with previously reported trends of scaled chrysophytes populations growth in some boreal and Arctic lakes that could reflect the global climate warming (Wolfe and Siver 2013; Mushet et al. 2017; Bessudova et al. 2021).

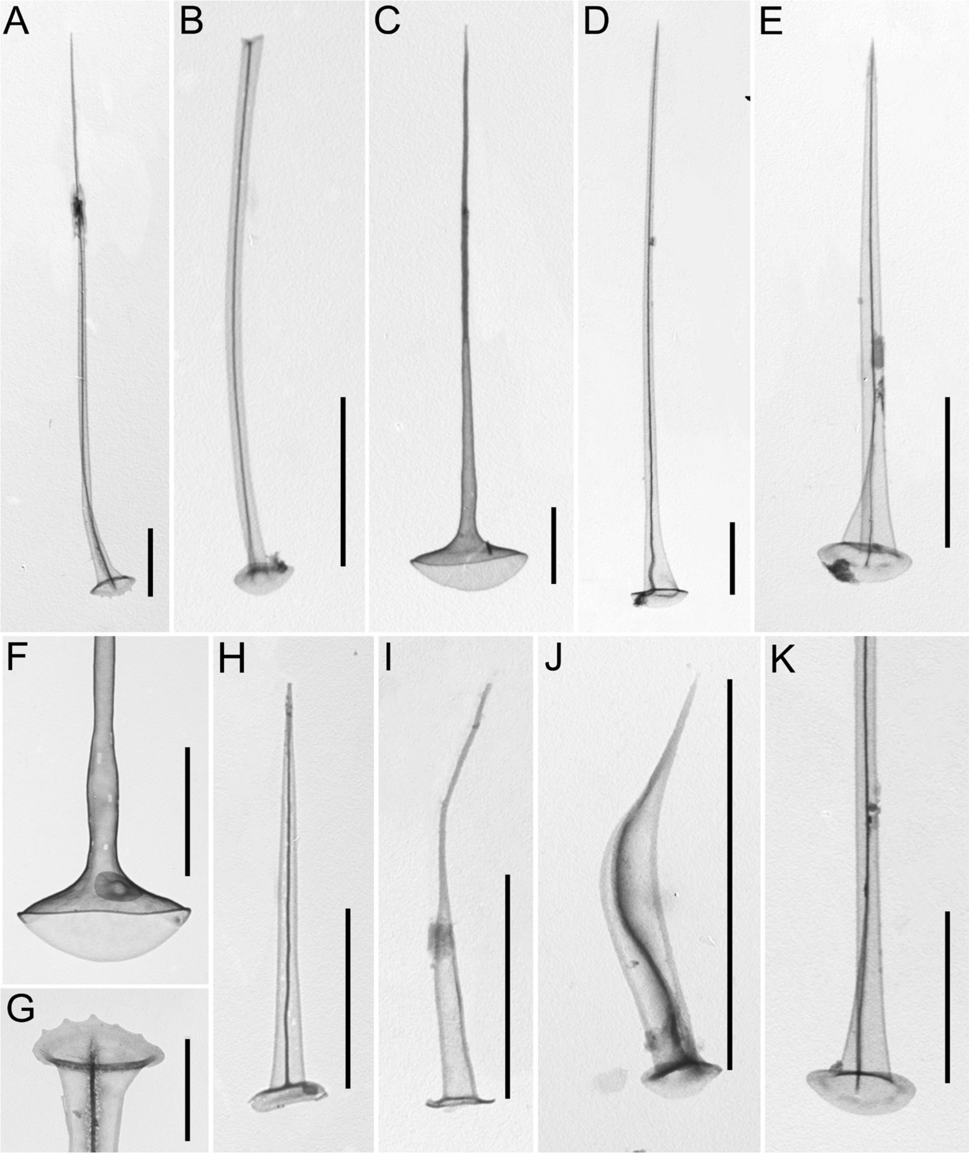

**Figure 4.** TEM of scaled chrysophytes. **A**, **G**, *Spiniferomonas serrata* (reservoir 2); **B**, *S. abrupta* (reservoir 13); **C**, **F**, *S. bourrellyi* (reservoir 9);**D**, *S. triorali* sf. *cuspidata* (reservoir 9); **E**, **K**, *S. triangularis* (reservoir 5); **H**, *S. trioralis* (reservoir 1); **I**, *S. abei* (reservoir 7); **J**, *S. minuta* (reservoir 5). Scale bars: **G**, 1 µm; **A–F**, **H–J**, 2 µm.

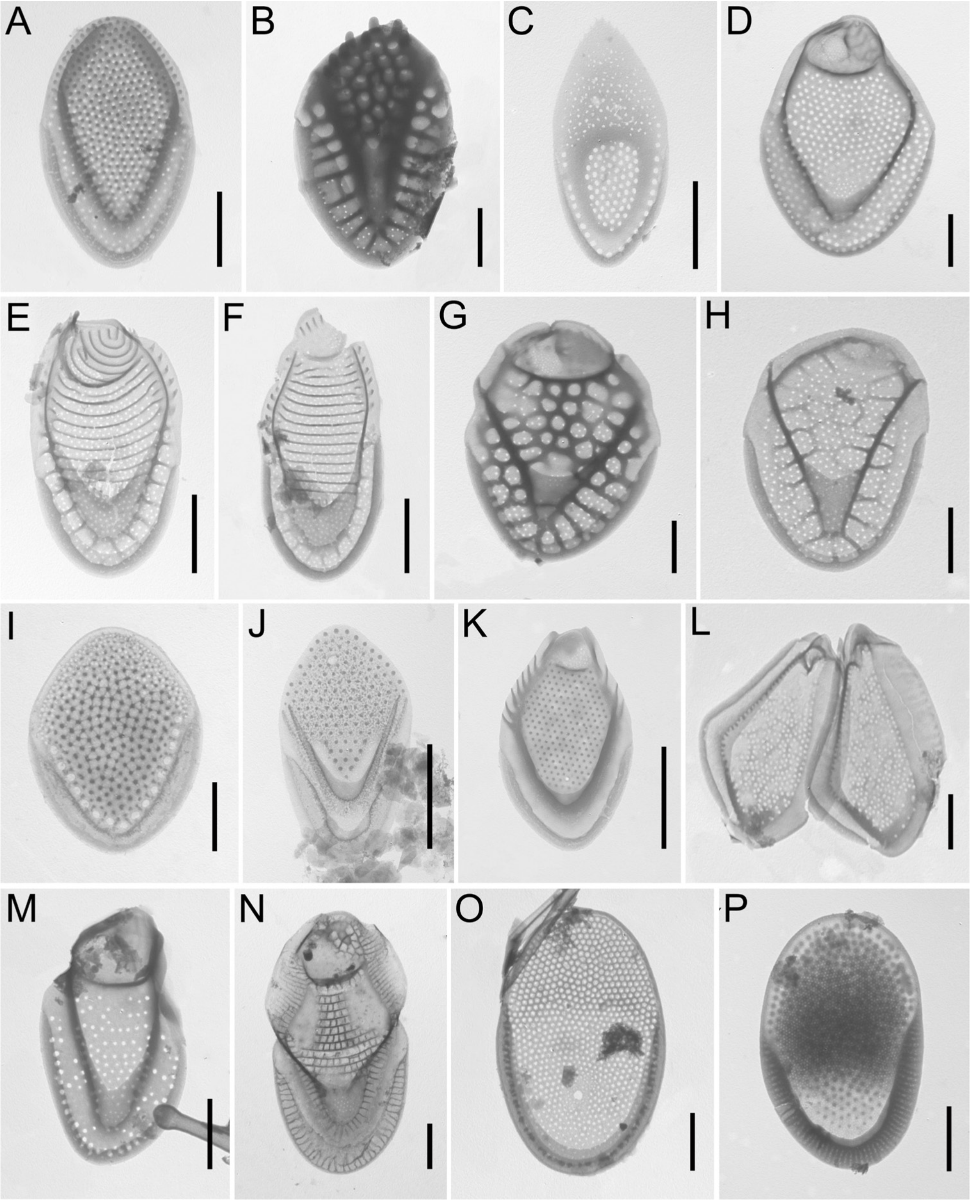

**Figure 5.** TEM of scaled chrysophytes. **A**, *Mallomonas annulata* (reservoir 14); **B**, *M. crassisquama* var. *papillosa* (reservoir 2); **C**, *M. akrokomos* (reservoir 6); **D**, *M. alpina* (reservoir 9); **E**, **F**, *M. flora* (reservoir 13); **G**, *M. crassisquama* (reservoir 2); **H**, *M. acaroides* (reservoir 7); **I**, *M. maculate* (reservoir 3); **J**, *M. parvula* (reservoir 8); **K**, *M. papillosa* (reservoir 5); **L**, *M. alata* f. *hualvensis* (reservoir 7); **M**, *M. kuzminii* (reservoir 2); **N**, *M. lelymene* (reservoir 3); **O**, *M. matvienkoae* (reservoir 9); **P**, *M. tolerans* (reservoir 13). Scale bars 1 µm.

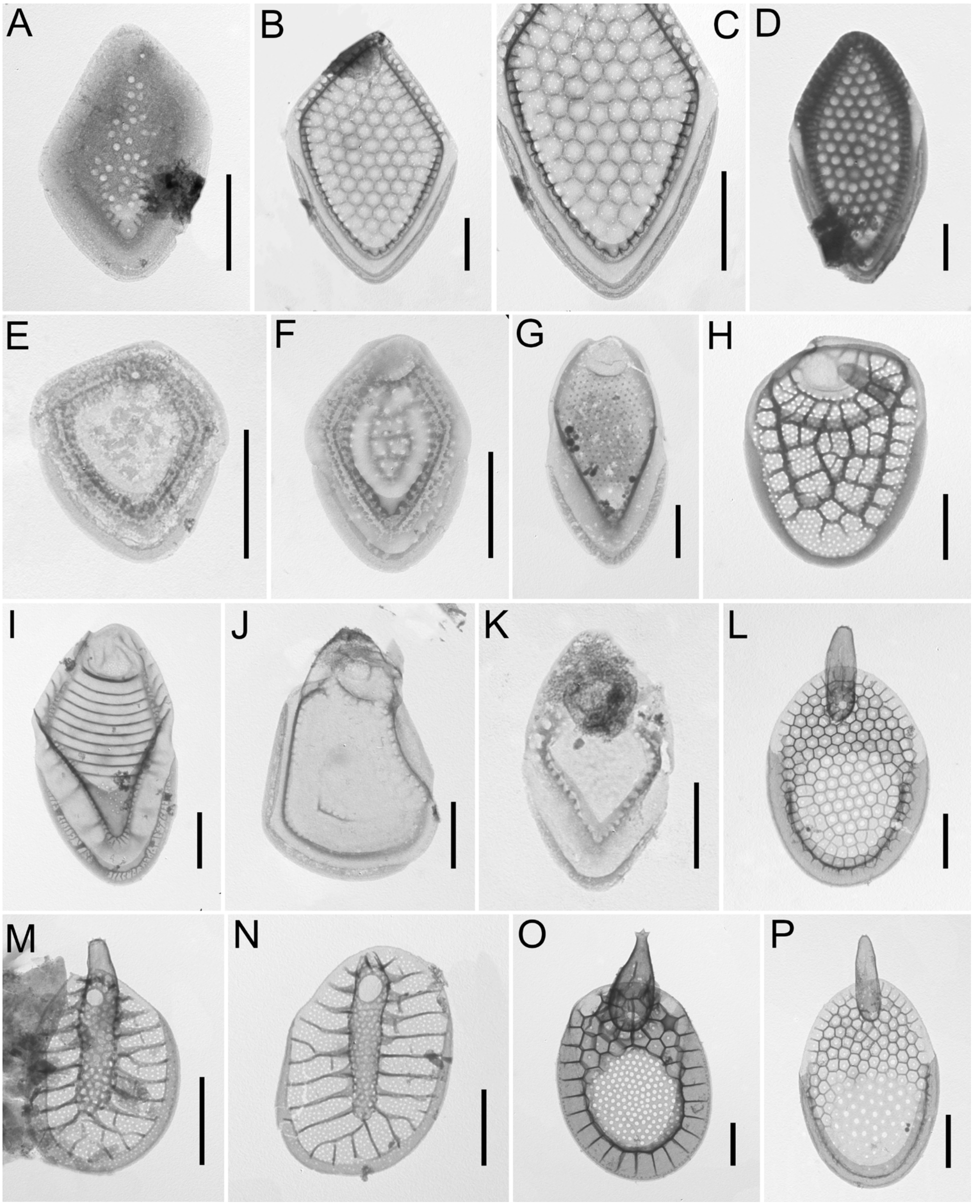

**Figure 6.** TEM of scaled chrysophytes. **A**, *Mallomonas scrobiculata* (reservoir 3); **B**, **C**, *M.* sf. *Eoa* (reservoir 7); **D**, *M. eoa* (reservoir 7); **E**, *M. pillula* f. *latimarginalis* (reservoir 7); **F**, *M. pillula* f. *valdiviana* (reservoir 7); **G**, *M. kalinae* (reservoir 12); **H**, *M. heterospina* (reservoir 9); **I**, *M. striata* (reservoir 8); **J**, **K**, *Mallomonas* sp. l (reservoirs 3, 7), **P**, *Synura curtispina* (reservoirs 8, 3); **M**, *S. praefracta* (reservoir 8); **N**, *S. glabra* (reservoir 5); **O**, *S. uvella* (reservoir 5). Scale bars 1 µm.

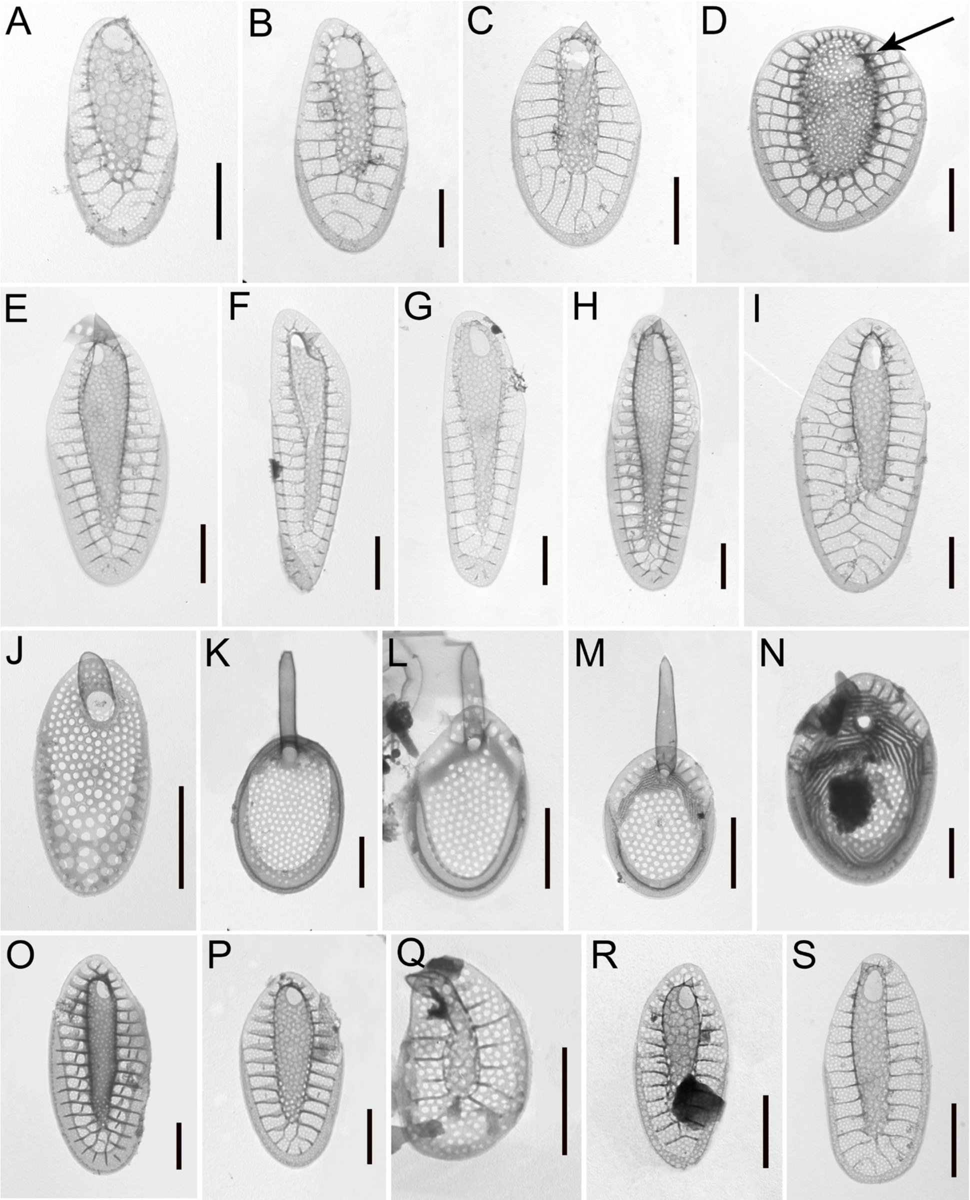

**Figure 7.** TEM of scaled chrysophytes. **A**, *Synura petersenii* f. *taymyrensis* (reservoir 3); **B**, **C**, *Synura* sp. 2 (reservoirs 2, 3); **D**, *S. obesa* (reservoir 3) the arrow shows that the ridge terminates with a short and narrow keel tip. There are no pores at the keel tip; **E**, *S. borealis* (reservoir 9); **F–H**, *Synura* sp. 1 (reservoir 3); **I**, *S.* cf. *vinlandica* (reservoir 3); **J**, *S. synuroidea* (reservoir 3); **K**, *S. sphagnicola* (reservoir 8); **L**, *S. mammillosa* (reservoir 13); **M**, **N**, *S. echinulata* (reservoirs 3, 5); **O**, *S. petersenii* (reservoir 1); **P**, *S.*cf. *americana* (reservoir 5); **Q**, *S. macropora* (reservoir 3); **R**, **S**, *S. conopea* (reservoir 3). Scale bars 1 μm.

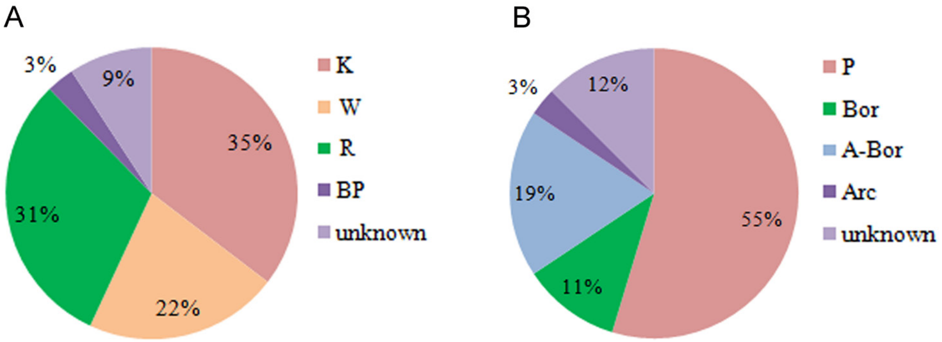

**Figure 8.** Geographical distribution of the species composition of scaled chrysophytes in Arctic basins and lakes from the Tiksi area relative to the longitudinal (**A**) and latitudinal (**B**) distribution groups (according to Kristiansen 2000; Kristiansen 2008; Voloshko 2017).

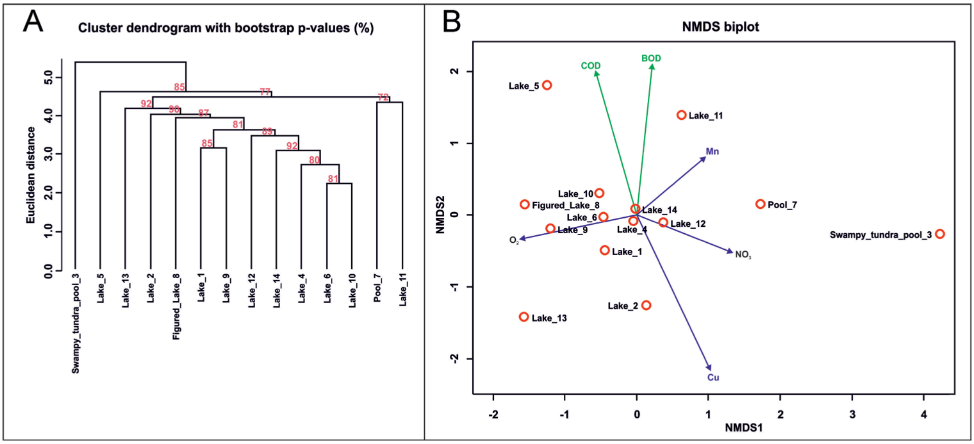

**Figure 9. A.** Results of clustering with assessment of topology reliability by bootstrap method, supports in % are in red. **B.** NDMS scatter plot of the sites. Arrows show gradient vectors, physical and chemical parameters that are confirmed to affect taxonomic composition of a community according to the PERMANOVA testing (blue vectors are abiotic factors, green vectors are biotic factors).

Hydrochemical measurements show different production-destruction processes that take place in the lakes studied at the time of sampling. Statistic analysis results show a positive correlation with factors such as BOD, COD and increasing $O_2$ concentration. Concentrations of dissolved oxygen are tightly related with production-destruction processes during development of phytoplankton (photosynthesis, respiration, destruction of organic matter). Impact of COD on the species composition reflects regional features determining formation of the species composition in the study area. BOD and COD are proxy indicators of dissolved organic matter concentrations. Their higher concentration in the studied waters depends on carbon-enriched soils of the catchment areas in the Arctic region where paludification and prevalence of anaerobic conditions lead to accumulation of huge reserves of organic matter (Smith et al. 2004; Shepelev et al. 2016). It should be noted that the distribution of waters with low and high BOD and COD values in the study area is chaotic, i.e. they are affected by local factors such as surface topography, which regulates the runoff from adjacent ares, and vegetation, which is a source of organic matter enriching soils of the catchment area in organic substances.

Being mixotrophs, chrysophytes have two types of metabolism, auto- and heterotrophic. This apparently determines the dependence of their species richness on concentrations of organic matter (BOD, COD) and nutrients ($NO_3^-$) in water. The ability of mixotrophs to change one type of metabolism to the other is thought to be related to deficiency of an inorganic or organic nutrient (Olrik 1998). It is also known that increasing concentrations oforganic substancesmay cause an abundance of mixotrophs and enhance their role in a community (Sládečeková and Sládeček 1993; Korneva 2015).

The impact of increasing concentrations of ($Mn^{2+}$) and ($Cu^{2+}$) ion on growth of chrysophyceans manifested in decreasing species richness observed in the study area is driven by high inhibiting and algicidal activity of heavy metals reported in previous papers (Jindal and Verma 1989; Knauer 1996; Dong et al. 2020). Copper is known to be the most toxic element for algae among all heavy metals (Proshkina 1997). E.g., golden algae strains manifest sensitivity to 0.00025–0.005 mg/L of copper ion after 2 min of exposure (Voloshko and Chaplygina 2016). However, it is also known that natural waters modify toxicity of heavy metals. The toxic activity of copper ion ($Cu^{2+}$) may reduce in natural waters due to interaction of the toxic agent with components of these waters such as various complexing agents able to form complexes with heavy metals and thus neutralize them (Stravinskene and Grigoriev 2012). This paper shows a negative impact of high copper ion ($Cu^{2+}$) concentrations (up to 0.005 mg/L) on scaled chrysophytes in natural waters that, however, do not completely inhibit their growth. Waters having the highest concentrations of copper ion ($Cu^{2+}$) demonstrate the presence of mainly ubiquitous and cosmopolitan species that seem to be more resistant. Two rare species, *Synura praefracta* and *Mallomonas annulata*, showed an ability to survive under high concentrations of copper ion($Cu^{2+}$).

Thus, investigating the species richness of scaled chrysophytes in shallow waters near the town of Tiksi, we may confirm once more previously obtained data (Siver et al. 2005; Bessudova et al. 2021) on their high diversity in Arctic waters. It is surprising that even closely situated lakes with similar habitat parameters may have different species composition as it had been shown before (Siver and Lott 2012; Bessudova et al. 2021). It seems that regional Arctic features of lake formation such as permafrost, absence of soil drainage and micro-relief create different conditions for formation of an individual ecosystem with different species composition of scaled chrysophytes in each shallow water body. Each single lake, being a multifactor separate ecosystem due to individual hydrochemical and biological factors such as duration of vegetation period, concurrence with other organisms) form its own species composition.

In addition, our study shows an abundance of ubiquitous and cosmopolitan species of scaled chrysophytes in the species composition of the longitudinal group, and polyzonal species in that of the latitudinal group of the small Arctic lakes. There is a high share of Arctic boreal species as well as the presence of typical boreal species. These results agree with previously obtained data about the trend of progression of boreal species northwards (Bessudova et al. 2021), and they are important for evaluating potential changes in Arctic ecosystems related to the global climate warming.

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