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Dispersal of Silica-Scaled Chrysophytes in Northern Water Bodies

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Abstract: Silica-scaled chrysophytes have an ancient origin; nowadays they inhabit many northern water bodies. As the territories above the 60th parallel north were under the influence of glaciers during the Late Pleistocene, the local water bodies and their microalgal populations formed mainly during the Early Holocene. Now, the arctic, sub-arctic and temperate zones are located here and the water bodies in these regions have varying environmental characteristics. We analyzed the dispersal of silica-scaled chrysophytes in 193 water bodies in 21 northern regions, and for 135 of them determined the role of diverse environmental factors in their species composition and richness using statistical methods. Although the species composition and richness certainly depend on water body location, water temperature and conductivity, regions and individual water bodies with similar species composition can be significantly distant in latitudinal direction. Eighteen species and one variety from 165 taxa occurring here have clear affinities to fossil congeners; they have been encountered in all regions studied and amount to 6–54% of the total number of silica-scaled chrysophytes. We also compared the distribution of the species with a reconstruction of glacier-dammed lakes in the Northern Hemisphere in the Late Pleistocene–Early Holocene. The dispersal of silica-scaled chrysophytes in the northern water bodies could take place in the Late Pleistocene–Early Holocene over the circumpolar freshwater network of glacier-dammed lakes, the final Protista composition being subject to the environmental parameters of each individual water body and the region where the water body is located. This species dispersal scenario can also be valid for other microscopic aquatic organisms as well as for southerly water bodies of the Northern Hemisphere.

Keywords: northern water bodies; silica-scaled chrysophytes; environmental parameters; Holocene; Pleistocene; glacier-dammed lakes

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1. Introduction

The golden algae of the class Chrysophyceae Pascher, families Paraphysomonadaceae Preisig and Hibberd, Mallomonadaceae Diesing and Synuraceae Lemmermann are able to form a scaled frustule of biogenic silica, and 250 such species are known in total [1]. Silica-scaled chrysophytes are a ubiquitous group of algae and an important component of water bodies. They occur in all climatic zones, including the tropical [2–5] and arctic areas [6–8]. The highest species richness is, however, a feature of the temperate latitudes [9–11]. Inaccessibility and extreme climate are a limiting factor for such investigations in northern regions. At the same time, these organisms can dominate in the plankton of oligo- and mesotrophic waters in the North, contributing 60–80% of the total number and 50–70% of the total biomass of phytoplankton [12–16].

The taxonomic attribution of these organisms is based on the details of the fine structure of their silica scales visualized by means of transmission and scanning electron microscopy (TEM, SEM) [17–19] (Figure 1).

The siliceous elements of the frustule preserve their structure even when the cells are destroyed. They can be buried in sediments and act as evidence of the presence of a species

in the ecosystem of a water body in the past. The genus *Synura* Ehrenberg was very likely formed before the Cambrian period of the Paleozoic era (330 mya) [20]. Ancient scales and bristles of *Mallomonas* Perty and *Synura* having various and complex structures were identified in the Eocene Giraffe Pipe sediments and in the Paleocene Wombat sediments in the area of the Lac de Gras kimberlite field in the Northwest Territories of Canada (64°44' N, 109°45' W; paleolatitude 62°–64° N) [21–26]. It turned out that some of the modern species identified by the structure of their scales were similar to, and some closely related to, the fossil taxa. Some fossil species are lacking a modern analogue and presumed extinct [25,26]. Data on the distribution of silica-scaled chrysophycean taxa in sediments, their abundance and stratigraphy are important for paleolimnology and paleoclimatology [27,28]. Such studies have become especially urgent due to the actual growth of silica-scaled chrysophycean populations in some boreal and arctic lakes over the last ten years, as the authors believe this could be evidence of global climate change [29,30] and CO₂ concentration increase [31–33].

Figure 1. Micrographs of silica-scaled chrysophytes of the genus *Mallomonas* (ASEM; B—TEM). (A) Cell of *Mallomonas crasssquama* var. *papillosa*; (B) scale of *M. vannigera*. Scale: (A) 10 µm; (B) 2 µm.

In recent years, investigations of factors and regularities of distribution of biodiversity of organisms at different levels of organization became especially relevant [34–38]. Such investigations are not only of ecological but also evolutionary importance [36]. Geographical, physicochemical, climatic and historical factors may be the most important for the distribution of protists [34,36–38]. The majority of these investigations deals with the analysis of biotopes either within one continent [36,37] or within one water body [34,38]. Although there are few studies on intercontinental factors and regularities influencing the distribution of protists [35,39,40]. Studies are of great interest due to the last Pleistocene glaciation 18,000–22,000 years ago when the Arctic region was covered with ice sheets [41–48] (Figure 2), with the exception of the Vashutkiny lakes [49,50].

Table 1. Regions above the 60th parallel north, in which silica-scaled chrysophytes have been found.

No.	Region	Climatic Zones	Locality	Coordinates	References	Number of Water Bodies in the Region	Variation of the Number of Taxa in Water Bodies of a Region	Total Number of Taxa in the Region
1.	Alaska	Temperate	Alaska	60°20′–68°6′ N, 154°5′–165°45′ W	[51–54]	15	0 to 13	32
2.	Northern Canada	Subarctic	Northern Canada	68°20′–69°30′ N, 132°30′–133°50′ W	[12]	9	0 to 9	17
3.	West Greenland	Arctic	Disko Island Oqaq Island district S. Nipisat Island Strømfjord	67°–69° N	[55,56]	52	0 to 9	53
				63°40′–64°25′ N, 50°10′–52° W	[57]	21	0 to 24	
4.	Southern Greenland	Arctic	Southern Greenland	60°91′24″ N, 46°04′76″ W	[58]	2	3 to 10	12
5.	Iceland	Subarctic	Northern Iceland	65°41′42″ N, 18°7′15″ W	[59]	10	4 to 8	30
			South-West	64°11′49″ N, 21°8′13″ W	[13]	1	1	
6.	Sweden–Norway border	Temperate	Sweden–Norway border	69°05′ N, 20°87′ E	[14]	1	2	4
	Central Norway		62°15′ N, 0°15′ E	[60]	1	2		
	Central Norway		Barduelva Norway	69°0′50″ N, 18°29′5″ E	[56]		1	
			a pond in Nygårdsparken, Bergen	60°23′10″ N, 5°19′28″ E	[56]			

Table 1. Cont.

No.	Region	Climatic Zones	Locality	Coordinates	References	Number of Water Bodies in the Region	Variation of the Number of Taxa in Water Bodies of a Region	Total Number of Taxa in the Region
7.	Sweden	Temperate	Sweden	63°35'36" N, 19°50'11" E	[61]	2	7 to 35	55
			Sweden	67°75'66"–68°43'30" N, 18°23'96"–20°09'29" E	[56]	10	1 to 2	
			Swedish Lapland	68°20'–68°26' N, 18°15'–19°6' E	[62]	5	2 to 23	
				68°21'N, 18°49'E	[63]	8	1 to 4	
8.	Baltic Sea	Temperate	Baltic Sea	59°58'–64°15' N, 20°25'–25°27' E	[64]	1	14	14
9.	Finland	Temperate	Finland	64°31'12" N, 26°16'59" E	[9]	141	1 to 37	92
			Finland	62°36'3.0456" N, 26°32'51.27" E	[65]	1	20	
			Finland	61°75'65"–62°88'11" N, 25°49'72"–26°48'58" E	[64]	8	1 to 2	
			Finnish Lapland	69°45'–69°46' N, 27°0'–27°1' E	[66]	1	6	
			Western Finland	62°7'–63°29' N, 24°36'–26°48' E	[67]	10	3 to 9	
			Southern and central Finland	61°42'–63°17' N, 22°9'–25°28' E	[68,69]	42	6 to 22	
			Southern and central Finland	61°37'–61°43' N, 26°54'–26°44' E	[70]	8	21 to 34	
			Southwestern coast of Finland	60°2'30.75" N, 23°29'36.46" E	[71]	1	49	

Table 1. Cont.

No.	Region	Climatic Zones	Locality	Coordinates	References	Number of Water Bodies in the Region	Variation of the Number of Taxa in Water Bodies of a Region	Total Number of Taxa in the Region
10.	Russia, Leningrad oblast–Karelia border	Temperate	Russia, Leningrad oblast–Karelia border	60°48′7.4304″ N, 31°30′48.1212″ E	[18,72,73]	1	26	31
				61°46′23.24″ N, 35°19′12.46″ E	[73]	1	10	
11.	Russia, Karelia	Temperate	Russia, Karelia	61°7′–64°27′ N, 33°0′–35° 25′ E	[74]	26	31	31
12.	Russia, Bolshezemelskaya tundra	Subarctic	Vashutkini lake Kharbey Vash.-Kharbey	67°57′49.64″ N, 61°31′08.58″ E	[50]	18	5 to 29	55
13.	Russia, Vorkutinskaya tundra	Subarctic	Vorkuta tundra	67°23′35″ N, 63°15′80″ E	[50,75]	4	12 to 28	51
14.	Russia, Polar Urals	Subarctic	Russia, Polar Urals	67°17′–68°07′ N, 65°30′–66°04′ E	[76,77]	9	6 to 19	44
15.	Russia, Lower Yenisei basin	Subarctic	Russia, Lower Yenisei basin	66°35′–73°23′ N, 75°17′–86°34′ E	[78,79]	6	0 to 25	36
16.	Russia, Kara Sea gulfs and bays	Subarctic	Russia, Kara Sea gulfs and bays	69°58′ N–73°23′ N, 80°28′ E–83°32′ E	[78,80]	4	10 to 18	22
17.	Russia, Khantay Reservoir	Temperate	Russia, Khantay Reservoir	67°40′4″ N, 87°45′32″ E	[81]	4	0 to 25	27
18.	Russia, Taymyr Peninsula	Arctic	Russia, Taymyr Peninsula	74°37′ N, 101°45′ E	[6,7]	13	0 to 15	28
19.	Russia, North-Western part of Yakutia	Arctic	Russia, Yakutia	73°05′ N, 113°59′ E	[8]	1	7	7
20.	Russia, Eastern part of Yakutia	Temperate	Russia, Yakutia	62°26′–62°33′ N, 143°33′–143°39′ E	[82]	2	13 to 20	22
21.	Russia, Magadan oblast	Temperate	Russia, Magadan oblast	62°34′33″ N, 154°2′13″ E	[8,83]	12	0 to 10	22

Figure 2. Map of the studied regions (numbers correspond to Table 1). Climatic zones are set up according to B.P. Alisov (1936) [48]: rose—arctic; blue—subarctic; green—temperate; solid line—Northern Polar Circle. Boundaries of the Pleistocene glaciation (dotted line) are given according to M.G. Grosswald (2009) [47]; the star shows the location of the Giraffe and Wombat kimberlite deposits [21,26]. The map was generated using the free software QGIS v. 3.14.16 and edited in free image editor GIMP 2.10.0.

Nowadays, three climatic zones (arctic, sub-arctic and temperate) are located above the 60th parallel north and near the Northern Polar Circle [48].

Since most of the modern lakes located here emerged after the deglaciation in the Early Holocene, we set up the following aims: (1) to compare the current taxonomic structure of silica-scaled chrysophytes in these water bodies; (2) to explore the degree to which these water bodies have inherited the ancient Eocene and Paleocene Protista of silica-scaled chrysophytes as a marker of the magnitude of dispersal of silica-scaled chrysophytes; (3) to identify the main factors that could determine species richness, species composition and dispersal of silica-scaled chrysophytes in northern water bodies.

2. Materials and Methods

2.1. Site Locations

The studied area is located between 18° and 165° W and between 0° and 154° E, above the 60th parallel north (Figure 2). The boundaries of distribution of ice sheets are given according to M.G. Grosswald (2009) [47]. The localization of glacier-dammed lakes throughout the period of their existence as well as the direction of rivers were reconstructed by the authors according to published data [45,84–90].

We analyzed our published data as well as the data of other authors (references in Table 1); the total number of analyzed water bodies where silica-scaled chrysophytes were found amounted to 193 (Supplementary Material S1).

2.2. Statistical Analysis

Data preparation and missing value corrections. A summary table of species and habitat parameters metadata (water temperature [T], pH, conductivity, sampling region and month) is given in Supplementary Material S1. All data were assembled into a table (Supplementary Material S1) whose rows correspond to the sampling sites and columns correspond to the measured parameters. The presence or absence of a species in the table is coded by 1 and 0. All characteristics are given as dependent variables (presence or absence of species in samples, and species richness) and explanatory variables (T, pH, conductivity, sampling region and month).

The statistical analysis of the impact of habitat parameters on the species richness and species composition of silica-scaled chrysophytes only included the water bodies where three or more species of algae were found (135 water bodies).

When combining data from different sources into one body of metadata, some features of the studied objects were found to be absent (e.g., T, pH, conductivity, or sampling month). We decided not to exclude samples with missing data from the multidimensional statistical analysis because this approach reduces statistical power and increases the systematic bias of the estimate [91–93]. We took the mean value for waters with unknown quantitative temperature, conductivity and/or pH values, and used random values from the list of known values for missing qualitative data (sampling month) according to the authors' guidelines [94,95].

Analysis of the relationship between species composition and explanatory variables. The explanatory variables in the analysis of variables (T, pH, conductivity, sampling month and sampling region) form 31 potential linear combinations (Supplementary Material S2). We applied the PERMANOVA analysis [96] based on the Jaccard dissimilarity metric matrix, carried out in the “vegan” package for the R programming language with user's scripts [97] to detect the linear combination of explanatory variables that could reliably determine the species composition in the samples. Based on the algorithm proposed by [98], we calculated the R^2 coefficient and Akaike information criterion for small sample sizes (AICc) for each linear combination of explanatory variables. The linear combination with the minimal AICc value contained a set of explanatory variables that reliably affected the species composition of algae in the samples. The other variables had no reliable influence on species richness.

In order to test the influence of the different number of localities within regions, a separate PERMANOVA analysis was carried out. A quantitative characteristic was used to define this factor, i.e., the number of samples entering the region, which was matched to each sample within the region. Such a check was necessary in order to exclude the possibility of revealing the reliability of the influence of the region on the species composition because of the different number of samples in the studied regions.

Data visualization and cluster analysis. The table indicating the presence or absence of species in individual waters (135 water bodies where three or more species occur) was visualized as a heat map in the “gplot” package of the R programming language.

We grouped samples into 21 regions (see Section 2.1) and made lists of species that occurred at least once in one water body within a region. The lists were summarized into a table in which 0 means the absence and 1 means the presence of a species in a region. The table was visualized as a heat map in the “gplot” package of the R programming language.

The average (UPGMA) method based on the Jaccard dissimilarity metric was used for clustering and ordering of rows and columns in the heat map.

Analysis of the impact of abiotic environmental factors on species richness. The impact of abiotic environmental factors (T, pH and conductivity) on species richness was determined by means of linear regression analysis with the following regression models:

linear regression ($y = ax + b$); second degree polynomial ($y = ax^2 + bx + c$); third degree polynomial ($y = ax^3 + bx^2 + cx + d$); exponential dependence ($y = \exp(ax + b)$); logarithmic dependence ($y = \log(ax + b)$). The best regression model was chosen by the AICc value (minimal AICc value for the best model) [99]. For the best regression model chosen, we calculated the R^2 covariance coefficient and estimated its reliability by means of the F -test (F). We assumed that the regression model indicated interdependence at $p < 0.05$. The regression analysis and visualization were done using the standard function set of the R programming language according to the guidelines [99]. When analyzing the impact of conductivity, we used only the data of the water bodies where the conductivity corresponded to freshwater values.

To estimate the relationship of species richness with qualitative abiotic factors (sampling month and sampling region), we applied an analysis of variance (ANOVA) based on F . The impact of a factor was considered reliable at $p < 0.05$. Standard R programming language functions were used for the analysis. Additionally, ANOVA was carried out to analyze the relationship between species richness and number of samples entering the region. Such a check was necessary in order to exclude the possibility of revealing the reliability of the influence of the region on species richness due to an unequal number of samples in the regions.

3. Results and Discussion

3.1. Species List and Geographical Distribution

The studied regions were inhabited in total by 165 species and intraspecific taxa of silica-scaled chrysophytes (Supplementary Material S3). Some previously identified species were brought to synonymy, and the species composition is given in Supplementary Material S3 with due revision. More than one half of taxa (86 [52%]) are represented by *Mallomonas*. *Paraphysomonas* De Saedeleer, *Synura*, *Spiniferomonas* Takahashi, and *Chrysosphaerella* Lauterborn accounted for 29 species (18%), 27 species (16%), 17 species (11%) and 4 species (2%), respectively. The genus *Neotessella* Jo, Kim, Shin, Škaloud and Siver was represented by a single species *N. lapponica*, and the monospecific genus *Polylepidomonas* Preisig and Hibberd was represented by the species *P. vacuolata*.

The analysis of geographical types of species distribution according to J. Kristiansen (2000, 2008) [100,101] showed that 75 taxa (45%) were widespread and cosmopolitan, 50 (30%) were arctoboreal, and the rest were either bipolar, rare, or had a scattered distribution (Supplementary Material S3).

Representatives of 18 species occurred most frequently in the 21 regions, namely *Mallomonas crassisquama* (in 19 regions), *Synura petersenii* (in 19), *M. akrokomos* (in 18), *Spiniferomonas trioralis* (in 16), *M. striata* (in 15), *Chrysosphaerella brevispina* (in 15), *C. coronacircumspina* (in 15), *M. acaroides* (in 15), *M. heterospina* (in 15), *Paraphysomonas vestita* (in 14), *M. alpina* (in 14), *Synura spinosa* (in 14), *M. tonsurata* (in 13), *M. caudata* (in 13), *M. punctifera* (in 13), *Spiniferomonas bourrellyi* (in 13), *M. elongata* (in 12) and *C. longispina* (in 12). These taxa, according to the published data, occur in a wide range of geographical locations (Supplementary Material S3) and water temperatures, pH and conductivities (Supplementary Material S1).

The analysis of species distribution based on climatic zones demonstrated that 43 of 165 taxa were present in water bodies of all three climatic zones—arctic, subarctic and temperate. Thirty-five taxa occurred in the subarctic and temperate zones; 48 taxa were encountered only in the temperate zone; 11 taxa were present in the arctic and temperate zones; 5 taxa were present in the arctic and subarctic zones; 17 taxa were present only in the subarctic zone; and 6 taxa were present only in the arctic zone (Figure 3). Additionally, T in the water bodies of the temperate, subarctic and arctic zones varied between 0 and 23 °C, 7.5 and 19.7 °C, and 7 and 15 °C, respectively, showing a pronounced zonality (Supplementary Material S1).

Figure 3. Distribution of 165 species and intraspecific taxa of silica-scaled chrysophytes among the climatic zones (see Figure 2).

Thus, the geographical distribution analysis showed that silica-scaled chrysophytes have no strict distribution over the climatic zones in the northern regions, and 57% of species occur in the water bodies of 2–3 zones.

3.2. Fossil Species in Current Water Bodies

Eighteen species and one variety of silica-scaled chrysophytes having clear affinities to fossil congeners from Eocene [21,22,26] and Paleocene deposits [25] of Canada inhabited the studied regions. Seven species had a scale structure similar to a fossil taxon, these being *Chrysosphaerella brevispina*, *C. coronacircumspina* [21], *Mallomonas insignis*, *M. asmundiae*, *Synura nygaardi*, *S. macracantha* [26] and *S. petersenii* [25]. It is noteworthy that five of the seven species similar to a fossil taxon were also widespread or cosmopolitan species: *Mallomonas insignis*, *M. asmundiae*, *Chrysosphaerella brevispina*, *C. coronacircumspina* and *S. petersenii*, while two species, *Synura macracantha* and *S. nygaardi*, are arctoboreal. The Protista of silica-scaled chrysophytes from the analyzed regions (Figure 4 and Supplementary Material S3) were characterized by the presence of 11 species and one variety that had their scale structure closely related to the fossil taxa, namely: *Mallomonas matvienkoae* (= *M. pleuriforamen* P.A. Siver, Lott, B.Y. Jo, W. Shin, H.S. Kim and R.A. Andersen, in: Siver et al., 2015, Figure 5E), *M. mangofera* f. *foveata* (= *Mallomonas* GP1, in: Siver et al., 2015, Figure 7D), *M. caudata* (= *M. pseudocaudata* Siver and Wolfe, in: Siver et al., 2015, Figure 5H), *M. oviformis* (= *Mallomonas* GP19, in: Siver et al., 2015, Figure 5F), *M. eoa* (= *Mallomonas* GP2, in: Siver et al., 2015, Figure 7C), *M. multisetigera* (= *M. ampla* Siver and Lott, in: Siver et al., 2015, Figure 8D), *M. paludosa* (= *Mallomonas aperturae*, in: Siver, 2018, Figures 3–8), *M. lelymene* (?) (= *M. giraffensis* Siver and Wolfe, in: Siver et al., 2015, Figure 7H), *M. alpina* (= *Mallomonas* GP11, in: Siver et al., 2015, Figure 9D), *Synura uvella* (= *S. recurvata* Siver and Wolfe, in: Siver et al., 2015, Figure 5C) [26,102].

The fossil species *M. lancea* Siver, Lott and Wolfe had a scale structure that was simultaneously similar to two modern species, *M. intermedia* and *M. corcontica* [26]. The most frequently occurring of the fossil species in the current water bodies were *M. alpina* (in 14 of 21 regions studied), *M. caudata* (in 13) and *S. uvella* (in 9). Three species were arctoboreal: *M. eoa*, *M. intermedia* and *M. lelymene*. The remaining 8 species and one variety were either cosmopolitan or widespread (Supplementary Material S3).

As can be seen from Figure 4A, most of the fossil species are included in the species lists of Regions 7 (Sweden), 9 (Finland) and 20 (Russia, Eastern Yakutia)—13, 14 and 12, respectively. The contribution of the fossil species to the Protista of silica-scaled chrysophytes varied between 6% and 54% by region, (Figure 4B), the biggest being in Region 20 (Russia, Eastern Yakutia), which is significantly distant from the Giraffe and Wombat kimberlite deposits (Figure 2). It reached 50% in Region 6, but only 4 species occurred there.

Figure 4. Number of species to a fossil taxon, species closely related to the fossil taxa (to Siver et al., 2013; 2015) [25,26], and other species of silica-scaled chrysophytes in the analyzed regions. The numbers of the regions correspond to those given in Figure 2 and Table 1; data on species occurrence are given in the references in Table 1. (A) Number of species; (B) Percentage of species.

To sum up, all the regions are characterized not only by the presence of modern silica-scaled chrysophytes, but also by the presence of species having affinities to the Paleocene and Eocene Protista identified earlier in the western part of the Northern Hemisphere [25,26,102].

3.3. Regional Peculiarities of the Protista

A preliminary PERMANOVA analysis showed that the number of samples entering the region within the analyzed data set does not significantly affect the species composition at the sampling points ($R^2 = 0.0108$, $p = 0.0735 > 0.05$). Therefore, in further analysis, we could neglect errors in the interpretation of the analysis result associated with a different number of localities within regions.

Table 2 shows a reliable influence of water body location (sampling region) on the species composition of silica-scaled chrysophytes ($p < 0.05$ from PERMANOVA analysis). This was also confirmed by the UPGMA dendrogram (Supplementary Material S4), which shows that water bodies of the same region usually cluster together, while the regions have different species compositions (Figure 5). Overall, each region had regional peculiarities in the flora.

We hereby discuss some examples from the species list (Supplementary Material S3) and the UPGMA dendrogram (Figure 5).

Waters of Region 9 (Finland) are the most studied; they have the highest species richness of silica-scaled chrysophytes (92 species; Table 1). The species *Mallomonas mangofera*, *M. mangofera* var. *gracilis*, *M. scrobiculata*, *M. torquata* var. *simplex*, *M. trummensis*, *M. zellensis*, *Clathromonas subrotacea*, *Paraphysomonas circumvallata* and *P. caelificra* were found only in waters of this region. There were many arctoboreal species (30%).

Region 3 (West Greenland) is the closest to Finland in terms of the species composition of silica-scaled chrysophytes (Figure 5); there is also a variety of rare arctoboreal species like *M. hamata*, *M. pillula* f. *exannulata*, *Mallomonas pillula* var. *latimarginali*, *M. schwemmlei*, *M. teilingii*, *M. cristata*, *M. duerrschmidtiae*. Additionally, waters of the region abound in species of the genus *Spiniferomonas*, particularly in arctoboreal *S. cornuta*, *S. conica*, *S. serrata*,

S. silverensis and rare *S. involuta*. The species *Paraphysomonas stephanolepis* and *Synura mammosa* are also found only there.

Table 2. Results PERMANOVA analysis with estimates based on AICc for selection of the most optimal linear combination of abiotic factor affecting the species richness of chrysophytes in samples.

Influence Model	AICc Information Criterion	Total R ²	Residual R ²
Best influence model: community ~ regions + T	526.46	0.315	0.685
Total influence model: community ~ T + pH + conductivity + month + regions	536.61	0.376	0.624

Best influence model of the factors on the species composition of communities in water bodies—the combined influence of the facts of the sampling region and the temperature factor at the time of sampling. The individual value of R² is indicated for the corresponding factor in the formula

Factor + Formula	Factor R ²	Residual R ²	p
Regions community ~ regions + T	0.30079	0.69921	0.000999
Regions community ~ T + regions	0.295	0.705	0.000999
T community ~ regions + T	0.01421	0.98579	0.000999
T community ~ T + regions	0.02	0.98	0.000999

Figure 5. Heat map of species representation status in the regions. Painted boxes at the intersection of rows and columns indicate that the species occurs in at least one water body in the region. Rows and columns of the heat map are ordered according to clustering results. Left and upper parts show dendrograms of clustering of regions and species by similarity of representation status.

Region 7 (Sweden) unites into the same cluster with those two regions (Figure 5). It is notable for a high total number of arctoboreal species (15 species, 27%); some of them, namely *Clathromonas diademifera*, *C. elegantissima*, *Synura senarioidea*, *S. obesa*, *Mallomonas rasilis*, *M. pumilio* var. *dispersa* and *M. mangofera* f. *foveata*, occur only in waters of Sweden. The species of the genera *Mallomonas*, *Spiniferomonas* and *Synura* are various. The rare arctoboreal species of genus *Synura*, namely *S. bjoerkii* and *S. macracantha*, that were previously found in waters of Alaska, also occur there.

The peculiarity of Region 1 (Alaska) is the absence of species of the genera *Paraphysomonas*, *Lepidochromonas* and *Spiniferomonas*. Waters of the region abound in species of the genus *Synura*, including rare arctoboreal species like *S. mollispina*, *S. macracantha*, *S. bjoerkii* and the rare bipolar species *S. petersenii* f. *prae fracta*. Two of the abovementioned rare species, *S. macracantha* and *S. bjoerkii*, occur in the same water body located near the town of Napaskiak.

Region 12 (Russia, Bolshezemelskaya tundra), Region 14 (Russia, Polar Urals) and Region 13 (Russia, Vorkutinskaya tundra) have a high variety of species from the genera *Synura* and *Spiniferomonas*. There are no species of the genus *Lepidochromonas* in Region 13 and Region 14. Region 13 is rich in species of silica-scaled chrysophytes. The species *Mallomonas vorkutiensis* occurs only in that region.

The cladogram (Figure 5) shows two regions that differ considerably in the species composition of silica-scaled chrysophytes—Region 8 (Baltic Sea) and Region 4 (Southern Greenland). A feature of the first region is a variety of species of the genera *Paraphysomonas* and *Lepidochromonas* (11 species in total, comprising 69% of all species found there), with *Lepidochromonas diademifera* and *L. elegantissima* being found only in that region. Region 4 (Southern Greenland) differs in the absence of species of the genera *Lepidochromonas* and *Spiniferomonas*, and the genus *Paraphysomonas* is represented only by one ubiquitous species, *P. uniformis hemiradia*. On the other hand, the species *M. doignonii* has been described only in this region.

The rare arctoboreal species *Paraphysomonas limbata* and *Spiniferomonas conica* are found in Region 20, while *Synura mollispina*, *S. papillosa*, *S. punctulosa*, *S. truttae*, *Spiniferomonas minuta* and *Mallomonas pseudomatvienkoae* are found in Region 15.

The presence of the rare arctoboreal species *Synura senuroidea* is a regional feature of Region 5 (Iceland).

Thus, despite the presence of ubiquitous taxa as well as closely related and similar-to-fossil taxa in almost all regions, regional peculiarities can be traced in the flora of silica-scaled chrysophytes.

3.4. Differences in the Species Composition of Geographically Adjacent Water Bodies

According to the UPGMA dendrogram, individual water bodies/samples in any given region can differ in species composition and cluster apart regardless of the regional peculiarities of the flora (Supplementary Material S4).

We hereby examine the most-studied water bodies, e.g., those of Sweden (Region 7) in the area of Swedish Lapland. Small water bodies grouped by the author into five groups according to their geographic proximity were studied in this area [62]. Only four species were found in the group “Water bodies closest to Abisko” (Supplementary Material S4), while 23 species were identified in small reservoirs near the road towards Kiruna. The bedrock of these two groups belongs to the same type of phyllitic and quartzitic rocks [103]. The environment parameters differed between these two groups. T, pH and conductivity in the water bodies closest to Abisko were 12.1 °C, 7.8, and 125 $\mu\text{S cm}^{-1}$, respectively, while these parameters were lower in the reservoirs near the road towards Kiruna, with T, pH and conductivity being 9–11 °C, 6.3–6.7 and 38–77 $\mu\text{S cm}^{-1}$, respectively. Multiyear investigations by some authors [62,69,104–107] of the dependence of vegetation of some species of silica-scaled chrysophytes on specified pH values evidenced that even a moderate change in this parameter can influence both abundance and species diversity [62]. As the authors [62] noted, some species found in these groups of water bodies agreed with the traditional autecology [106] concerning the pH values. For example, species typical of slightly acidic and neutral pH values, i.e., acidophilic, acidobiontic and indifferent species *Chrysosphaerella longispina*, *Mallomonas heterospina*, *M. caudata*, *M. crasssquama*, *Synura sphagnicola* and *S. echinulata* occurred in the group “Reservoirs near the road towards Kiruna”. The alkaliphilic *M. tonsurata* and indifferent *M. caudata* were recorded in the group “Water bodies closest to Abisko”. As 40 $\mu\text{S cm}^{-1}$ [106] is considered to be the optimal conductivity value at which maximum diversity of silica-scaled chrysophytes occurs, it is

no surprise that the threefold increase in conductivity (up to $125 \mu\text{S cm}^{-1}$) significantly reduced species richness in the group “Water bodies closest to Abisko”. Differences in temperature seemed not to affect the species composition of silica-scaled chrysophytes in these water bodies as they were within the optimal values for vegetation, i.e., below 12°C [106]. Only two of 25 species recorded were shared between these two groups of water bodies, the cosmopolitan *Mallomonas caudata* (closely related to the fossil taxa) and the widespread *M. striata*.

Although differences in species composition can be observed in waters with differing physical and chemical parameters, close water bodies with similar parameters can also differ in species richness and composition. We take the example of the waters of Region 14 (Russia, Polar Urals). The environmental parameters in the Bolshoye Schjuchie Lake and Usvaty Lake had similar values. T and pH were 13°C and 7.0 in Bolshoye Schjuchie Lake, and 12.0°C and 7.0 in Usvaty Lake, respectively. Ten species were recorded in Bolshoye Schjuchie Lake and seven in Usvaty Lake [76]. Nevertheless, only two species, *Synura petersenii* (species similar to a fossil taxon) and *Mallomonas striata* (widespread species), of 15 found there, were shared between these two lakes (Supplementary Material S3 and S4).

Thus, the water bodies located in the same latitude and in the same region having different or similar environment parameters can differ in species richness and composition.

3.5. Estimation of Environment Parameters Influencing Species Composition and Richness

The results of the PERMANOVA analysis with selection of the most reliable linear combination of abiotic factors affecting the species composition of algae (see Table 2, Supplementary Material S4) demonstrated that the minimal AICc value was observed at the sampling region and sampling water temperature combination (community $\sim$ regions + T). The AICc value for this model (AICc = 526.46) was less than for the model including all qualitative and quantitative abiotic factors considered for this paper (AICc = 536.61; see Table 2). We may conclude that only two factors, T and sampling region, of all those considered (T, pH, conductivity, sampling month and sampling region), reliably affected the species composition. The factors T and sampling region can be permuted: regions + T and T + regions. The analysis of these two permutations (Table 2) showed that the sampling region was the factor with the highest R^2 value, while the temperature played a much less considerable, although statistically significant, role.

According to the regression and variance analyses (Figure 6), the species richness was reliably ($p < 0.05$) influenced by T, conductivity and sampling region, while pH and sampling month did not affect the species richness. We did not find an influence of the number of samples entering the region on species richness (ANOVA $p = 0.487 > 0.05$). Therefore, we can exclude the possibility of revealing the reliability of the influence of the region on species richness through an unequal number of samples in the regions.

The dependence between the species richness and T was described by a third-degree polynomial (species richness = $-19.65 \times T^3 - 14.9 \times T^2 + 6.83 \times T + 10.07$; minimal AICc value; Figure 6A). We can see in Figure 6A that the highest values of species richness in waters located above 60°N were observed in the range $13\text{--}16^\circ\text{C}$. Any change in these values towards increase or decrease led to an impoverishment of the species composition. The boundaries of T values recorded in analyzed water bodies of temperate ($0\text{--}23^\circ\text{C}$), subarctic ($7.5\text{--}19.7^\circ\text{C}$) and arctic ($7\text{--}15^\circ\text{C}$) zones evidenced an overlap of optimal temperatures. It is likely that this regularity could explain the presence of 57% species in the waters of 2–3 zones. The dependence between species richness and conductivity (Figure 6B) is described by a linear function (species richness = $-0.04 \times \text{conductivity} + 12.04$; minimal AICc value). The maximal values of the species richness were observed at conductivity $20\text{--}35 \mu\text{S cm}^{-1}$; further increase in conductivity led to decrease in species richness.

Figure 6. Impact of qualitative abiotic factors on species richness. (A) Dependence of the species richness on water temperature (T) described by third degree polynomial (species richness = $-19.65 \times T^3 - 14.9 \times T^2 + 6.83 \times T + 10.07$); circles show data of real observations, central dashed line shows the main dependence, upper and lower dashed line and gray sector show the 96% confidence interval. (B). Dependence of the species richness on conductivity described by a linear function (species richness = $-0.04 \times \text{conductivity} + 12.04$); circles show data of real observations, central dashed line shows the main dependence, upper and lower dashed line and gray sector show the 96% confidence interval. (C) Dependence of the species richness on sampling region factor visualized as boxplots.

According to the authors [30,31], the increase in abundance of silica-scaled chrysophytes in boreal and arctic lakes is related to global warming. Comparing the diversity of silica-scaled chrysophytes in the Baikal Region, we noted that the species richness of these organisms was considerably higher in warmer tributaries and streams than in the colder Lake Baikal, reducing from 66 taxa at 13 °C to 19 taxa at 5 °C [11,108]. These results contradict the traditional view that chrysophytes are psychrophilic [109–112]. As for the lakes located above the 60th parallel north, the maximum species richness was observed at 13 to 14 °C. Given the fact that the temperature in the majority of the studied water bodies was below these values, we may suppose that the warming climate and gradual rise in temperature to the optimum values will first increase the species richness, but further rise

in temperature will reduce it (see Figure 6A,D). The climate can thus be the factor that regulates both the abundance and the species richness of silica-scaled chrysophytes.

We did not detect any reliable impact of pH on species richness, although Siver and Lott (2012) [113] previously indicated a key role of pH and conductivity in the biogeographical distribution of silica-scaled chrysophytes in fresh waters of the east coast of North America in longitudinal gradient (29° to 48° N). This can be related with the non-linear effect of pH on the species richness described in other papers [114]. It is likely that in our case, the unreliability of the effect of pH on species richness was related to an insufficient number of samples with known pH. It is to be noted that pH monitoring is important in areas under strong anthropogenic stress because air pollutants can cause acid depositions that in turn will shift pH towards increasing acidity [115,116]. In this case, pH values can change beyond the optimum for silica-scaled chrysophytes, leading to a drastic reduction of their species richness.

The statistical analysis thus allows the conclusion that the sampling region has a statistically significant effect both on species composition and on species richness and reinforces the assumption about regional peculiarities of floras. The other factor that significantly affected species composition and species richness was sampling T, the most favorable for the species richness of chrysophytes being 13–16 °C. The conductivity, whose maximal values were 20–35 $\mu\text{S cm}^{-1}$, was important only for species richness.

3.6. Similarity of the Species Composition of Geographically Distant Regions

As we can see from Figure 5, considerably distant regions cluster together from the perspective of similarity of the flora of silica-scaled chrysophytes.

The floras of Region 1 (Alaska) and Region 5 (Iceland) are similar due to the presence of *nine* identical widespread and ubiquitous species (see Supplementary Material S3).

The floras of Region 19 (Russia, North-Western part of Yakutia) and Region 21 (Russia, Magadan oblast) are similar due to the presence of five identical widespread species (see Supplementary Material S3).

The floras of Region 16 (Russia, Kara Sea gulfs and bays), Region 10 (Russia, Leningrad oblast–Karelia border) and Region 2 (Northern Canada) are similar due to an even representation of species within the genera *Chrysosphaerella*, *Mallomonas*, *Spiniferomonas* and *Synura*, *Mallomonas* species being the most abundant. Species of the genera *Neotessella* and *Polylepidomonas* do not occur in these regions. The presence of 12 identical widespread species is a common trait of Regions 16, 10 and 2 (see Supplementary Material S3).

There is a variety of species of the genus *Spiniferomonas* (six shared species) in Region 15 (Russia, Lower Yenisei basin) and Region 20 (Russia, Eastern part of Yakutia), but there are no species of the genera *Polylepidomonas* and *Neotessella* (see Supplementary Material S3).

Five geographically distant regions (22, 15, 16, 10 and 2) form the same clade (Figure 5). We examine in detail the examples of Region 16 (Russia, Kara Sea gulfs and bays) and Region 20 (Lakes Labyntyr and Vorota, Russia, Eastern Yakutia). These water bodies are separated by a distance of more than 2700 km and their environmental parameters are absolutely different.

The Lakes Labyntyr and Vorota (Region 20) are located at the Pole of Cold of the Northern Hemisphere and are under ice for about 260 days a year. The water of these lakes is ultrafresh, and T, pH and conductivity at the time of sampling were 9.7 °C, 7.6 and 54 $\mu\text{S cm}^{-1}$ in Lake Vorota, and 15.6 °C, 6.8 and 35 $\mu\text{S cm}^{-1}$ in Lake Labyntyr, respectively [82]. A mixing of marine and fresh water coming from the south takes place in the gulfs and bays of the Kara Sea. The maximum species richness of silica-scaled chrysophytes was recorded in the Lower Yenisei River and Yenisei Gulf (Table 1), where water temperature, pH and conductivity varied at the time of sampling between 8.1 °C and 11.6 °C, 7.9 and 8.2, 15.8 $\mu\text{S cm}^{-1}$ and 1273 $\mu\text{S cm}^{-1}$, respectively [80]. What then unites these areas? Why do they have a similar species composition of silica-scaled chrysophytes? The large Yenisei River, running into the Kara Sea, has as a tributary the Angara River,

which nowadays flows from Lake Baikal. On the other hand, Lake Baikal was connected to the other large river, Lena, up to the Middle Pleistocene (800,000–700,000 years BP) [117]. This river has a vast watershed on the lowlands of Yakutia and runs into the Laptev Sea. Lake Baikal was free of ice during the last Pleistocene glaciation (Figure 7), but streams from glacier-dammed lakes could disseminate the Baikal microalgal flora, as evidenced by the identification of the Baikal-endemic diatom species *Lindavia minuta* (Skvortzow) by Nakov et al. in the phytoplankton of some lakes in the Transbaikalian region [118] and in Lake Khövsgöl [119–122].

Figure 7. Circumpolar freshwater network. Distribution of ice sheets during maximum glaciation according to M.G. Grosswald (2009) [47] and of ice-dammed lakes throughout their existence and migration according to Thorleifson (1996) [84], Grosswald (1999) [45], Teller et al. (2005) [85], Rudoy (2008) [86], Rudoy and Zemtsov (2010) [87], Rudoy, (2011) [88], Michalek (2013) [89] and Lepper et al. (2013) [90]. The blue and red lines correspond to clustering of regions similar in representation status of the species shown in Figure 5. The map was generated using the free software QGIS v. 3.14.16 and edited in free image editor GIMP 2.10.0.

Recently, this species was found not only in the phytoplankton, but also in the Holocene sediments of Lakes Vorota and Labyntyr [123]. It would be natural to assume that both diatoms and silica-scaled chrysophytes, as other microalgae, could share the same dispersal scenario. Hence, the species composition similarity of these two distant areas, the lakes of Yakutia and the gulfs of the Kara Sea, is no longer extraordinary.

3.7. Global Dispersal in Latitudinal Direction

The dispersal of silica-scaled chrysophytes is traditionally associated with two pathways, i.e., abiotic (transfer with water and wind) [100] and biotic [100,101,113,124]. Biotic factors include dispersal on the hair of mammals and the feathers and legs of aquatic birds [100,113,124]. The stomatocysts of silica-scaled chrysophytes can endure hostile environments including low temperature and drying, which can facilitate dispersal success [101]. However, we propose to more widely examine the abiotic dispersal scenario, or water transfer, as being the most extensive pathway.

The areas located above the 60th parallel north were covered with ice sheets during the last Pleistocene glaciation (18,000–22,000 years BP; see Figure 2). At the time, a system of glacier-dammed lakes went from east to west in the Northern Hemisphere [47,84–90] (see Figure 7).

The dispersal of species from one water body to another could be favored by catastrophic outbreaks of glacier-dammed lakes releasing a huge quantity of energy and matter [46,94]. The largest of the known glacier-dammed lakes were lakes Agassiz, Missoula and Bonneville, formed during the retreat of the Cordilleran ice complex and the Laurentide Ice Sheet in the territory of present-day United States, Canada and Alaska, approximately 13,500 years ago [86,89]. The melting of the Eurasian, Kara and East-Siberian ice sheets also formed large glacier-dammed lakes in the territory of Eurasia. These were Lake Darkhat (currently non-existent) and Lake Khövsgöl (still existent) in the territory of present-day Mongolia, the Khvalyn Basin of the Caspian Sea, the Chuya-Kuray Lake System and Lake Uymon in the Altai mountains, and the large Kaz-Ket system of ice-dammed lakes formed at the point of the present-day low water divide between the catchment areas of the rivers Yenissei and Ob at the upper reaches of the rivers Kaz and Ket [47,84–90]. The intercontinental dispersal of silica-scaled chrysophytes could take place along the north Beringia that emerged due to recession of the ocean level and retreat of the Cordilleran Ice Sheet. During the glaciation, it connected Northeast Asia and Northwest North America. Its territory is known to be covered by systems of small, interconnected lakes and rivers that could serve as routes for the dispersal of chrysophytes [125]. The retreat and melting of the ice sheets in the Early Holocene favored water temperature, salinity and circulation changes in the respective parts of the Atlantic and Arctic Oceans [87,89]. This gave rise to the modern climatic zones, three of which are being examined in the paper (arctic, subarctic and temperate).

This probable dispersal scenario is, in our view, the main force facilitating the dispersal of microalgae after the last Pleistocene glaciation, although later biotic factors also could play a role. In addition, Finlay and Clarke (1999) [126] and Finlay (2002) [127], advanced the concept that, despite the “ubiquitous” dissemination of microalgae, they would be found only in the water bodies meeting the ecological requirements of a species, i.e., “the environment selects”. This concept correlates with our investigation and is quite convincing. First, many species of silica-scaled chrysophytes in the analyzed water bodies were cosmopolitan or widespread species (45%). Second, the majority of these species inhabited two–three zones (78 species of 165). The same characteristics were typical of the majority of the species, having clear affinities to fossil congeners. Thirteen species and one variety, and 18 species and one variety, were either cosmopolitan or widespread, respectively.

Only five of 18 species occurring in more than one half of the regions located above the 60th parallel north (see Supplementary Material S3) had clear affinities to fossil congeners. Table 3 shows that these species as well as the remaining 18 inhabit water bodies with high variability in environmental parameters. Such ecological plasticity could facilitate their survival during the glaciations and the subsequent successful dispersal.

On the other hand, the catastrophic change of habitats at the boundary between the Pleistocene and Holocene, as well as the subsequent geographical isolation, could favor the development of cryptic species or intraspecific taxa among both widespread and cosmopolitan species.

Table 3. Species of silica-scaled chrysophytes found in the majority of the water bodies located above the 60th parallel north (see Table 1 for references).

No.	Taxon	T, °C	pH	Conductivity, $\mu\text{S cm}^{-1}$
1.	<i>Chrysosphaerella brevispina</i>	3.9–19.7	5.5–8.3	10–708
2.	<i>C. coronacircumspina</i>	4.5–17.7	5–8.4	10–708
3.	<i>C. longispina</i>	4.5–21	5–7.6	13–146
4.	<i>Paraphysomonas vestita</i>	3.9–19.7	5–8.1	13–708
5.	<i>Spiniferomonas bourrellyi</i>	4.5–19.1	5–8.3	11–246
6.	<i>S. trioralis</i>	3.9–19.7	5–8.4	10–708
7.	<i>Mallomonas acaroides</i>	0.3–18	5.5–8.3	19–708
8.	<i>M. akrokomos</i>	0.3–19.4	5–8.4	10–708
9.	<i>M. alpina</i>	5–19.7	5.5–8	19–708
10.	<i>M. caudata</i>	3.7–17	5–8.1	19–708
11.	<i>M. crassisquama</i>	0.3–20	5–8.4	17–709
12.	<i>M. elongata</i>	8.5–16.8	5.5–8.3	21–664
13.	<i>M. heterospina</i>	6.8–19.7	5.5–8	14–708
14.	<i>M. punctifera</i>	8.4–17.7	5–8.3	19–708
15.	<i>M. striata</i>	3.9–18	5.5–8.1	20–708
16.	<i>M. tonsurata</i>	6.8–16.8	5–8.4	16–708
17.	<i>Synura spinosa</i>	0.3–18.7	5.5–8.1	16–664
18.	<i>S. petersenii</i>	0.3–19.7	5–8.5	13–708

4. Conclusions

In this study, we applied statistical methods to analyze data on the chrysophyte flora of water bodies in 21 regions located above the 60th parallel north, defined the role of main environmental factors in determining species composition and richness and reconstructed the circumpolar freshwater network of ice-dammed lakes throughout the period of their existence and migration based on scattered data.

The taxa typical of two–three climatic zones, mostly widespread and cosmopolitan species, prevail in the analyzed regions. Despite certain differences in the species composition of individual regions, the core of the flora of silica-scaled chrysophytes consists of only 18 environmentally flexible species shared by most of the regions.

The main factor determining the species composition is the sampling region, i.e., each region located above the 60th parallel north has regional features in terms of the flora of silica-scaled chrysophytes. The present-day species composition of chrysophytes in these regions credibly depends on water temperature and conductivity. There are the most optimal values of environmental parameters favorable for the maximum species richness of silica-scaled chrysophytes. Any deviation from these values in either direction impoverishes the species composition. The results obtained show that the species composition of silica-scaled chrysophytes can be similar in areas that are quite distant from each other in longitude direction.

The flora in the eastern part of the Northern Hemisphere, where large rivers flow northwards opposed to the western part of the Northern Hemisphere, was first pushed southwards by the glacier, then mixed in glacier-dammed lakes with southern species brought by rivers. When the glacier regressed, this flora invaded the new Holocene lakes. We assume that this scenario prevails in the dispersal of silica-scaled chrysophytes (and likely in that of other planktonic microorganisms) in northern water bodies.

Finally, this study supports the ubiquity hypothesis, “everything is everywhere: but the environment selects” [126–129], which is still being discussed both in the general microbial biogeography [130] and in phytoplankton studies [129]. We demonstrate through the example of silica-scaled chrysophytes in water bodies located above the 60th parallel north how the dispersal of “everything everywhere” can happen and exactly what kind of environmental factors select or limit the maximum species richness or change the species composition of these organisms.

Supplementary Materials: <https://doi.org/10.6084/m9.figshare.12400739>—Supplementary Material S1. Integrated Data Table including the species composition and hydrochemical parameters (pH, T, conductivity) of all 193 analyzed water bodies located above the 60th parallel north. <https://doi.org/10.6084/m9.figshare.12400739>—Supplementary Material S2. Results PERMANOVA analysis with estimates based on AICc for selection of the most optimal linear combination of abiotic factor affecting the species richness of chrysophytes. <https://doi.org/10.6084/m9.figshare.12400739>—Supplementary Material S3. Species list of silica-scaled chrysophytes and their distribution in study regions (numbered as in Table 1). Geographic distribution types according to Kristiansen (2000, 2008) [100,101]: (cp) cosmopolitan, (wd) widely distributed, (sc) scattered, (bp) bipolar, (r) rare, (ab) arctoboreal. Species occurring in fossil floras (from Siver et al., 2013, 2015) [25,26]: (*) species similar to a fossil taxon (relict species); (**) species closely related to the fossil taxa; (***) relict species *M. lancea* that is similar in scale structure to two modern species, *M. intermedia* and *M. corcontica*. <https://doi.org/10.6084/m9.figshare.12400739>—Supplementary Material S4. Heat map of species representation status in the regions. Painted boxes at the intersection of rows and columns say the species occur at least in one water body of the region. Rows and columns of the heat map are ordered according to clustering results. Left and upper parts show dendrograms of clustering of regions and species by similarity of representation status.

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