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RESEARCH ARTICLE

Influence of tributaries on the species richness of silica-scaled chrysophytes in the Angara River (Russia, Eastern Siberia)

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Abstract

The escalating impact of climate change requires comprehensive monitoring of aquatic microeukaryotic communities. Specifically, it is essential to study their successional dynamics under natural thermal fluctuations and identify organisms particularly sensitive to these changes. During the hydrological spring (early June), the watercourses of the Angara region differ in the intensity of water warming and can serve as promising model systems for studying such variations. Chrysophytes, which form siliceous scaled shells, serve as indicators of water temperature changes. In this study, we analyzed the influence of the main tributaries in the upper reaches of the Angara River–Irkut, Kuda, Kitoy, Belaya, and Ida–on the species richness of silica-scaled chrysophytes in the river channel, which is mainly affected by the cold, oligotrophic waters of Lake Baikal. During research performed in June 2024, a total of 57 silica-scaled chrysophytes species were identified in the study area using scanning and transmission electron microscopy. Among these, 11 species are potentially new to science, while one rare species *Paraphysomonas capreolata* and the form *Synura petersenii* f. *columnata* were recorded for the first time in Russian water bodies. The analysis demonstrated a positive correlation between the species diversity of silica-scaled chrysophytes and both water temperature and silicon concentration, alongside a negative correlation with pH levels. Statistical analysis of silica-scaled chrysophytes occurrence revealed two main profile groups: those from the main channel of the Angara River and those from its tributaries. Thus, it was determined that tributaries considerably increase the species richness of silica-scaled chrysophytes communities in the large river system, thereby increasing the overall stability of the aquatic ecosystem. This research is important for understanding the underlying mechanisms of the formation of biodiversity in freshwater ecosystems.

Keywords
Chrysophyceae, tributaries, Baikal Region, environmental factors

Introduction

The Angara River is the only outlet from Lake Baikal. Its water regime is controlled by Lake Baikal and a series of reservoirs, beginning with the Irkutsk Reservoir, followed by Bratsk, Ust-Ilim, and Boguchany reservoirs downstream. To understand the formation of microeukaryotic communities under climate change, natural systems with different degrees of thermal influence are of particular interest. One such system is the Southern Baikal–Angara River source–Irkutsk Reservoir–Angara riverbed system, which is hydrologically connected. Previous studies have shown that the impact of the cold, oligotrophic waters of Southern Baikal on the species composition and structure of phytoplankton in the Angara River source and the Irkutsk Reservoir is evident only during the hydrological spring (early June). During this season, "Baikal" diatoms typical of the spring community were detected in the central sections of the reservoir. Meanwhile, in the warmer waters of the reservoir's bays, species characteristic of both spring and summer communities of Lake Baikal were identified. According to Firsova et al. (2024), water temperature is the main driver of changes in phytoplankton structure during the spring season along the gradient from Southern Baikal to the Irkutsk Reservoir. This factor is known to considerably influence the bioavailability of nutrients (Suikkanen et al. 2013; Xu et al. 2024). During the summer season, the phytoplankton structure in both the lake and the reservoir exhibits considerable differences, even when water temperatures are comparable. By autumn season, when water temperatures become similar, discrepancies in the species composition of phytoplankton tend to diminish (Firsova et al. 2024). Therefore, in the framework of potential changes driven by climate change, the spring period is the most informative period. This underscores the need for comprehensive characterization of the spring microeukaryotic community.

It has been demonstrated that, in addition to diatoms, the group of silica-scaled chrysophytes (class Chrysophyceae) is particularly sensitive to variations in water temperature (Firsova et al. 2024; Bessudova et al. 2024). These organisms, which rely on silicon, transform dissolved silicic acid in water into species-specific silica elements that form a distinctive siliceous shell composed of scales and bristles on the cell surface. When faced with sudden unfavorable environmental conditions or following the vegetative period, the siliceous shell disintegrates, and the cell enters a silicon-based dormant stage called a stomatocyst (Cronberg 1980; 1986). The group of silica-scaled chrysophytes comprises approximately 400 species (Kristiansen and Preisig 2007; Scoble and Cavalier-Smith 2014; Kapustin and Kulikovsky 2022;

Bessudova 2024), representing various evolutionary lineages classified into three orders: Paraphysomonadales Cavalier-Smith (heterotrophs), Chromulinales Pascher (mixotrophs), and Synurales Andersen (autotrophs) (Kristiansen and Škaloud 2016). Owing to their diverse nutritional strategies in the group, these organisms can achieve substantial population densities, often dominating other phytoplankton groups under conditions of low light availability or low nutrient concentrations (Forsström 2006; Bessudova et al. 2023a).

The species composition of silica-scaled chrysophytes in Lake Baikal was previously studied by Bessudova et al. (2017). During the hydrological spring season (June), when water temperatures were in the range of 1.8 °C–3.7 °C, 12 species were identified in the lake's waters. The dominant species during this period included *Chrysosphaerella baikalensis*, *C. brevispina*, *Lepidochromonas takahashii*, *Spiniferomonas cuspidata*, *S. trioralis*, *Mallomonas alpina*, and *M. tonsurata*. At two monitoring stations where water temperatures reached 6 °C, the species diversity increased to 17 species. Among these, individual cells of species typical for the lake's summer community were detected: *Spiniferomonas abrupta*, *S. cornuta*, *Mallomonas crassisquama*, *Synura glabra*, *S. heteropora*, and *S. petersenii* (Bessudova et al. 2017). Earlier studies in Southern Baikal, the source of the Angara River, and the Irkutsk Reservoir – areas differing in water warming intensity – demonstrated changes in the structure and species richness of silica-scaled chrysophytes in June (Bessudova et al. 2023d; 2024). In Southern Baikal during this period, where water temperatures were in the range of 3.6 °C–4.5 °C, cells and scales of only 7 species were predominant: *Chrysosphaerella baikalensis*, *C. brevispina*, *Spiniferomonas bourrellyi*, *S. trioralis*, *S. cuspidata*, *Mallomonas alpina*, and *M. vannigera*. At the source of the Angara River, where the water temperature was 5.3 °C, eight species were identified. Of these species, six were also present in Southern Baikal, while two additional species – *Synura glabra* and *Synura* sp. 2 – expanded the overall species composition. In the bays of the Irkutsk Reservoir, where water temperatures were in the range of 8.6 °C–11.5 °C, a considerable community change was observed. Cold-water species typical of Southern Baikal either occurred singly or were completely absent from the species composition. The species diversity of the bays increased with the addition of 19 species characteristic of the summer community (Bessudova et al. 2023d; 2024). Thus, as reservoir waters warmed, changes in species composition were observed, including increased species richness and the appearance of summer community species. This indicates a shift in the phenology of silica-scaled chrysophytes communities, with hydrological summer beginning earlier than in Lake Baikal (Bessudova et al. 2024).

Numerous tributaries – small and medium-sized rivers originating from basins with different hydrochemical characteristics – are essential in shaping the hydrological and hydrochemical regime of the Angara River. During the spring season, the shallow waters of these tributaries can warm up to higher temperatures more rapidly than the main channel of the Angara. Consequently, these warmer tributaries support a more diverse community of silica-scaled chrysophytes, highlighting their potential as indicators of water temperature changes driven by ongoing climate change.

The purpose of this study was to clarify the extent to which small tributaries (Irkut, Kuda, Kitoy, Belaya, and Ida) influenced the species richness of silica-scaled chrysophytes in the Angara River.

Materials and methods

Site description

This study was performed in the Irkutsk Region, focusing on two right-bank tributaries (Ida and Kuda) and three left-bank tributaries (Belaya, Kitoy, and Irkut) of the Angara River (Fig. 1).

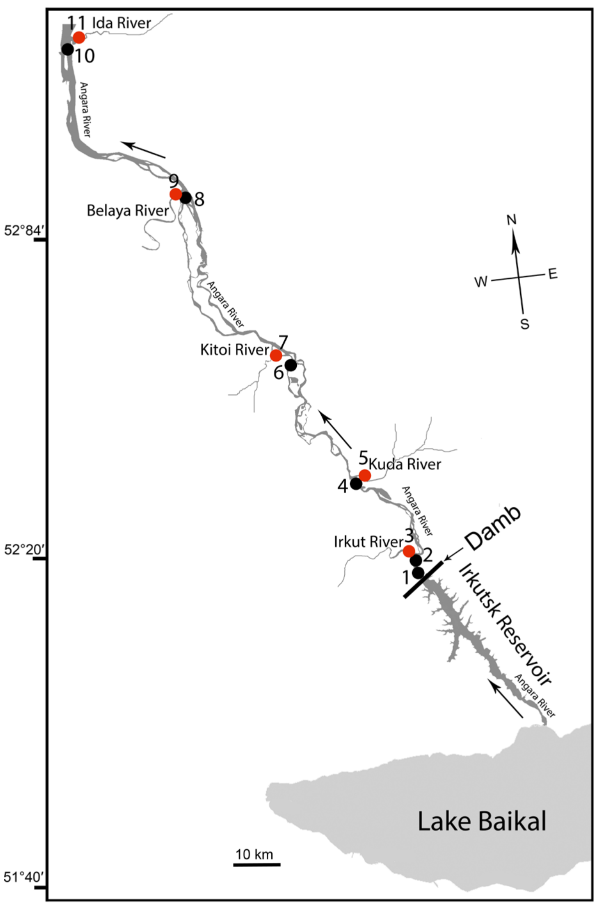

Figure 1. Map of sampling sites. Sampling stations located at the mouths of the Angara River tributaries are highlighted in red.

The left-bank tributaries near the source exhibit a distinctly mountainous character. In contrast, the right-bank tributaries are more vulnerable to anthropogenic impacts owing to their proximity to urban areas and industrial facilities.

The climate along the right-bank tributaries, specifically the Ida and Kuda Rivers, is characterized by a sharply continental regime, featuring prolonged cold winters and relatively brief but warm summers. Annual precipitation averages 320–406 mm, with the majority occurring during the summer months. Precipitation patterns show a clear seasonal variation, peaking in July and reaching their lowest levels in February and March (Berkin et al. 1993; Yanchuk 2018). Hydrologically, these rivers are primarily rain-fed (Bochkarev 1959).

The climate along the left-bank tributaries – the Belaya, Kitoy, and Irkut Rivers–exhibits a continental character, featuring optimal moisture levels, moderately warm summers, and moderately severe winters with low snowfall. Annual precipitation averages 300–400 mm, peaking in July and reaching its lowest levels in March (Atlas. Irkutsk region … 2004). During the summer months, the Belaya and Irkut Rivers receive water from multiple sources, including rainfall, snowmelt, and ice melt from mountainous areas (Nokhrin et al. 2008; Golubtsov et al. 2024). In contrast, the Kitoy River mainly relies on snowmelt, with the majority of its runoff occurring during the spring flood period.

The Ida River stretches for 153 km and is classified as a waterway in the forest–steppe zone. Characterized by a gentle current, its floodplain exhibits swampy features. The river's channel displays pronounced meandering, with a bottom composition of sand and pebbles, while the banks are formed from sandy and silty deposits. Hydrochemically, the river's waters fall into the sulfate class and calcium group (Bochkarev 1959; Yanchuk 2018). The ionic composition of the water is dominated by sulfates, constituting over 52% of the total mineral content – a characteristic atypical for Eastern Siberia, where most rivers are predominantly bicarbonate-calcium in composition. The distinctive ionic composition of the Ida River's waters can be attributed to the extensive drainage of Upper Cambrian sediments with high gypsum content (Yanchuk 2018). The Ida basin experiences active karst processes (Bochkarev 1959). By October, the river's waters exhibit a slightly alkaline reaction and increased oxygen concentration levels, measuring 17.6 mg/L. Based on ion content, the river's waters are classified as moderately mineralized (Yanchuk 2018).

The Kuda River spans 226 km, with its mouth located at an elevation of 417 m above sea level (a.s.l.). The river originates near the village of Timoshinsk and is characterized as a shallow waterway. Along its course, the Kuda supports 22 settlements. The river basin exhibits a complex geological structure and numerous small tributaries, resulting in a heterogeneous chemical composition of the waters throughout its length. The riverbed has undergone changes owing to both natural processes and human activities (Opekunova and Tukhta 2017). During winter, the channels of the tributaries and the Kuda River itself experience localized freezing to the riverbed. The ice cover persists from November to April. The upper reaches of the river and its tributaries exhibit a bicarbonate-calcium ion composition, attributable to the dissolution of limestones and clay dolomites. In the waters of the middle section, there is an increase in mineralization and a change in the anionic composition toward a higher proportion of sulfate ions, indicative of active leaching of gypsum and anhydrites. Long-term observations indicate a decrease in pH levels and an increase in concentrations of major ions, particularly sulfate ions (Tarasyuk et al. 2023).

The Belaya River stretches for 359 km and is classified as a mountain–plain river (Leksakova 1987). Its source lies in the Belsky Goltsy mountains of the Eastern Sayan range at an elevation of 1729.4 m a.s.l., while the mouth is located at 368 m a.s.l. In the foothill region, the river originates from the confluence of the Bolshaya and Malaya Belaya rivers. This area has wide valleys with swampy floodplains and old trees (Golubtsov and Opekunova 2022). The terrain in the river basin varies from low-mountain to plateau-like and flat landscapes (Atlas. Irkutsk region ... 2004). The riverbed exhibits a combination of different types: adapted, wide-rimmed, and embedded (Golubtsov et al. 2024). The river experiences a pronounced summer flood period (Atlas. Irkutsk region ... 2004).

The Irkut River spans 500 km and exhibits a distinctly mountainous character. Its source originates in Lake Ilchir in the Eastern Sayan Mountains at an elevation of 1963 m a.s.l., while the mouth is located at 368 m a.s.l. The Irkut River is formed by the confluence of two tributaries – the Bely Irkut and the Cherny Irkut. The waters of the White Irkut appear whitish owing to the rocky cliffs lining its shores, particularly those originating from the Munku Sardyk range. The Black Irkut appears darker owing to silty deposits originating from its source, Lake Ilchi. Approximately half of the river's length (247 km) traverses the territory of Tunka National Park, located within the Tunka basin. The river then flows through the Zyrkazun gorge and, in its northern course, empties into the Angara River in the central part of Irkutsk, located 76 km from Lake Baikal (Nokhrin et al. 2008). The riverbed exhibits a straight course in the upper reaches, changing to a winding channel with rapids in the middle and lower reaches. Ice formation typically occurs from late October to mid-November, with the ice cover breaking up in late April to early May (Nokhrin et al. 2008). The highest monthly average turbidity levels are recorded during summer (July), ranging from 310 to 2200 g/m^3 (Opekunova and Silaev 2018). The annual average water discharge at the river mouth is 140 m^3/s. The water in the upper and middle sections of the Irkut River is characterized as ultra-fresh and soft. In terms of pH, it exhibits a slightly acidic reaction, similar to atmospheric precipitation ($pH < 6.5$), with higher pH values observed in the lower reaches of the river (Nokhrin et al. 2008).

The Kitoy River extends for 316 km. It originates from the confluence of the Samarta and Ulzita rivers, which themselves originate on the Nuhu-Daban hill near the headwaters of the Irkut River. The mouth elevation is 316 m a.s.l. A substantial portion of the river's course passes through inaccessible terrain. In the lower reaches, after the Chinese expansion, the river takes on a flat character. The river basin is part of the Angara lowland forest–steppe and low-water forest region (Opekunova et al. 2018). Despite its flat nature, the presence of a pebble bed retains certain characteristics of a mountain river in this area. The lower reaches are characterized by swamp–forest, meadow–swamp, and anthropogenic landscapes (Irkutsk region … 1993).

Sampling and microscopy

Sampling from the Angara riverbed, upstream of the tributary confluences, and from the estuaries of the Angara River's tributaries (Fig. 1, Table 1) was performed by boat on May 18–19, 2024.

Table 1. Sampling stations in June 2024 (station numbers correspond to Fig. 1).

Station numbers	Code stations	Name stations	Date of sampling dd.mm.yy	Coordinates N/E
1	A_IHP	The Angara River downstream of the Irkutsk Hydroelectric Power station	18.05.2024	52.247608/104.306479
2	A_Irk	The Angara River before the Irkut River	18.05.2024	52.292466/104.269285
3	Irk	Irkut River	18.05.2024	52.298802/104.272390
4	A_Kud	The Angara River before the River Kuda	18.05.2024	52.426560/104.114075
5	Kud	Kuda River	18.05.2024	52.430585/104.114504
6	A_Kit	The Angara River before the Kitoy River River	18.05.2024	52.631560/103.940277
7	Kit	Kitoy River	18.05.2024	52.636140/103.924283
8	A_Bel	The Angara River before the Belaya River	18.05.2024	52.912325/103.679350
9	Bel	Belaya River	19.05.2024	52.919695/103.653045
10	A_Ida	The Angara River before the Ida River	19.05.2024	53.170620/103.357143
11	Ida	Ida River	19.05.2024	53.178949/103.376633

Plankton samples were collected in a 1.5-L bottle. The collected samples were transported to the laboratory, where 1155 mL were filtered through analytical track membrane (Reatrek, Russia) with a pore size of 3 μm using a filtration unit (Vladisart, Russia) to analyze the species composition. After that, the filter was transferred to a 50-mL Falcon tube with 45 mL unfiltered sample, and fixed with a formaldehyde solution, achieving a final concentration of 3.7%–4%.

To assess the species richness of silica-scaled chrysophytes, the filtered sample was rinsed to remove the fixative. The procedure involved transferring 1 mL of the sample into a 1.5-mL Eppendorf tube, followed by centrifugation in a MiniSpin centrifuge (Eppendorf, Germany) at a maximum speed of 13400 revolutions per min (rpm) for 10 min. The supernatant was then removed by pipetting, and the precipitate was resuspended in distilled water and centrifuged three times. Then, 30% hydrogen peroxide (H_2O_2) was added to the washed precipitate and heated in a thermostat at 80 °C for 2–4 h. Finally, the sediment was washed free of H_2O_2 using distilled water, followed by three additional centrifugation steps. Next, the washed sample was prepared for observation using scanning electron microscopy (SEM) or transmission electron microscopy (TEM).

For SEM analysis, the washed sediment (50 µL) was thoroughly mixed by shaking. A droplet was then applied to an SEM specimen holder, which had been previously cleaned with alcohol. The specimen holder number was recorded in the laboratory logbook. The samples were subsequently air-dried and coated with gold using a vacuum sputtering unit SCD 004 (Balzers, Liechtenstein). The prepared specimens were examined using either a Quanta 200 SEM instrument (FEI Company, USA).

For TEM examination, the sample was deposited onto a pre-prepared 3 mm diameter mesh coated with a formvar film substrate. The sample was then allowed to dry at room temperature. Analysis was performed using a LEO 906E TEM instrument (Carl Zeiss, Germany).

To determine the abundance of silica-scaled chrysophytes 20 mL of each unfixed sample was precipitated into analytical track membrane (Reatrec, Russia) with a pore size of 3 µm using a syringe equipped with a special nozzle. 20 mL of 70% ethanol was then pumped through the filters, which were then attached to SEM stubs with double-sided tape and dried. They were then coated with gold in the laboratory using an SCD vacuum evaporator (Blazers Union Ltd., Balzers, Liechtenstein) and analyzed using a Quanta 200 SEM.

Environmental parameters

The pH and temperature of the water were measured in the field using an Aquilon pH-410 device (Russia). Some of the samples were transported in thermo containers and frozen for further measurement of nutrients in vitro. Electrical conductivity (EC) was determined in the laboratory using an Expert-002 conductometer (Econix-Expert, Russia). The concentration of biogenic elements was determined using a PE-5400VI spectrophotometer (Ecohim, Moscow, Russia). Hydrochemical analyses were carried out in the laboratory for the content of Si, PO_4^{3-}, NO_2^-, NO_3^-, and NH_4^+. Information about methods hydrochemical analyses can be found in our previous article (Bessudova et al. 2023d).

Correlation analysis

Environmental factors and community richness were assessed for collinearity. Pearson correlation coefficients and their corresponding *p*-values were calculated for every pair of explanatory variables using the R packages corrplot (Taiyun and

Simko 2021) and Hmisc (Harrell 2022). The correlation matrix was visualized using the corrplot function, incorporating hierarchical clustering to organize variables into groups. Correspondence analysis of silica-scaled chrysophytes profiles was performed using the R package vegan version 2.5-6 (Oksanen et al. 2022). For cluster analysis of β-diversity, the apcluster R package (Bodenhofer et al. 2011) was used. The pairwise distance matrix was generated using the Bray–Curtis similarity index via the vegan: vegdist function with the parameter "binary = TRUE". Clusters were then formed using affinity propagation, followed by exemplar-based agglomerative clustering.

Results

Water parameters of the Angara riverbed and its tributaries

In June 2024, the measured electrical conductivity of the studied water bodies varied between 94.7 and 278 mS/m. The closest values to those typical of Lake Baikal waters (108–110 mS/m, as reported by Grachev et al. 2004) were recorded at stations along the Angara riverbed (94.7–109.9 mS/m) and at the mouth of the Kitoy River (Station 7, 96.8 mS/m). The highest electrical conductivity readings were detected at the mouths of the right-bank tributaries: the Kuda River (Station 5, 206 mS/m) and the Ida River (Station 11, 278 mS/m). The conductivity values at the mouths of the Irkut River (Station 3, 146 mS/m) and the Belaya River (Station 9, 137 mS/m) were also recorded.

The measured pH values of the water ranged from 7.8 to 8.9. At Stations 1–3, the pH levels (8.1–8.2) were most similar to the slightly alkaline waters of Lake Baikal (approximately 8, as reported by Grachev et al. 2004). Further downstream, at Stations 4–7, the pH values increased to 8.5–8.9, indicating alkaline waters. The high pH values observed at the mouth of the Kuda River (Station 5) may be attributed to natural factors. The riverbed is characterized by the presence of limestones and dolomites, whose leaching can contribute to higher pH levels (Tarasyuk et al. 2023). Additionally, the development of alkaline water reactions is influenced by anthropogenic factors, as noted by Yanchuk (2018). At the mouth of the Kitoy River (Station 7), the high pH value is naturally occurring and can be attributed to the leaching of forest–steppe and steppe landscapes prevalent in the region (Opekunova et al. 2018). At Station 8, located upstream before the confluence with the Belaya River, the pH level decreased to 8.3. Upon reaching the mouth of the Belaya River (Station 9), the water exhibited a slightly alkaline reaction with a pH of 7.8. Further downstream at Station 10, located along the Angara River bed, the pH value decreased to 7.9 owing to the influence of the incoming waters from the tributary.

Water temperature varied widely, ranging from 4.8 °C to 15.9 °C. In the Angara riverbed, temperatures ranged between 5.0 °C and 8.2 °C, while at the mouths of the tributaries, temperatures were higher, ranging from 8.8 °C to 15.9 °C.

The concentrations of biogenic elements were predominantly low across the study area. Silicon levels were relatively uniform at most sampling stations, with typical values ranging from 0.33 to 0.68 mg/L. Notable exceptions were observed at the mouths of the Irkut, Belaya, and Kuda Rivers, where silicon concentrations increased considerably to 3.05, 2.29, and 1.28 mg/L, respectively. Phosphate concentrations (PO_4^{3-}) varied between 0.007 and 0.023 mg/L. The levels of ammonium ions (NH_4^+) remained below 0.013 mg/L, while nitrite concentrations (NO_2^-) did not exceed 0.006 mg/L. Nitrate levels (NO_3^-) exhibited a range of 0.12 to 0.4 mg/L across the sampled locations.

Influence of hydrochemical parameters on the distribution of silica-scaled chrysophytes

A total of 57 species of silica-scaled chrysophytes were identified in the Angara riverbed and its tributaries (Table 2; Figs 2–8).

Table 2. List of silica-scaled chrysophytes and their distribution in the Angara River. Station numbers correspond to those in Figure 1 and Table 1. Bold type indicates species found in Lake Baikal (Bessudova et al. 2017), Southern Baikal, the source of the Angara River, Irkutsk Reservoir (Bessudova et al. 2023d) and the present study

№	Species	Station numbers										
		1	2	3	4	5	6	7	8	9	10	11
1	***Chrysosphaerella baikalensis*** Popovskaya	+	+		+	+	+	+	+	+	+	
2	***C. brevispina*** Korshikov	-	-	-	-	+	-	-	-	+	-	-
3	***C. coronacircumspina*** Wujek et Kristiansen	-	-	-	-	-	-	-	-	+	-	+
4	*C. rotundata* Škaloudová et Škaloud	-	-	-	-	-	-	-	-	+	-	-
5	*Spiniferomonas abei* Takahashi	-	-	-	-	+	-	-	-	+	-	-
6	***S. abrupta*** Nielsen	-	-	-	-	-	-	-	-	-	+	+
7	***S. bourrellyi*** Takahashi	-	-	-	-	-	-	-	-	+	+	+
8	***S. cornuta*** Balonov	-	-	-	-	-	-	-	+	+	-	+
9	*S. silverensis* Nicholls	-	-	-	-	-	-	-	-	+	-	-
10	***S. trioralis*** Takahashi	-	-	+	+	+	-	-	+	+	+	+
11	***S. cuspidata*** Balonov	+	+	-	-	+	+	+	+	+	+	+
12	*Spiniferomonas* sp.	-	-	-	-	-	-	-	-	+	-	-
13	*Paraphysomonas* cf. *acuminata* Scoble et Cavalier-Smith	-	-	-	-	-	-	-	-	+	-	-
14	*P. capreolata* Preisig et Hibberd	-	-	-	-	-	-	-	-	+	-	-
15	*P. gladiata* Preisig et Hibberd	-	-	-	-	-	-	-	-	+	-	-
16	*P. circumvallata* Thomsen	-	-	-	-	-	-	-	-	+	-	-

№	Species	Station numbers										
		1	2	3	4	5	6	7	8	9	10	11
17	*P. punctata* Zimmermann	-	-	-	-	-	-	-	-	+	-	-
18	*P. uniformis* subsp. *hemiradia* Scoble et Cavalier-Smith	-	-	-	-	-	-	-	-	+	-	-
19	*Paraphysomonas* sp. 1	-	-	-	-	-	-	-	-	+	-	-
20	*Paraphysomonas* sp. 2	-	-	+	-	-	-	-	-	-	-	-
21	*Paraphysomonas* sp. 3	-	-	+	-	-	-	-	-	+	-	-
22	*Paraphysomonas* sp. 4	-	-	+	-	-	-	+	-	+	-	-
23	*Paraphysomonas* sp. 5	+	-	-	+	-	-	+	-	-	-	-
24	*Lepidochromonas subquadrangularis* (Preisig et Hibberd) Kapustin et Guiry	-	-	-	-	-	-	-	-	+	-	-
25	***Mallomonas acaroides*** Perty	-	-	+	-	+	-	+	-	+	+	+
26	*M. akrokomos* Ruttner	-	-	-	-	-	-	-	-	+	+	-
27	*M. alata* Asmund, Cronberg et Dürrschmidt	-	-	+	-	-	-	-	-	+	+	-
28	***M. alpina*** Pascher et Ruttner	-	-	+	+	+	-	+	+	+	+	+
29	*M. costata* Dürrschmidt	-	-	+	-	-	-	-	-	-	-	-
30	***M. crassisquama*** (Asmund) Fott	-	-	-	-	-	-	-	+	+	+	+
31	*M. cratis* Harris et Bradley	-	-	+	-	+	-	-	-	-	-	+
32	*M. annaulata* Harris	-	-	+	-	+	+	-	-	+	+	-
33	*M. multiunca* Asmund	-	-	-	-	-	-	-	-	+	+	+
34	*M. papillosa* Harris et Bradley	-	-	+	-	-	-	-	-	+	-	-
35	*M. kuzminii* Gusev et Kulikovskiy	-	-	+	-	-	-	-	-	-	-	-
36	*M. pechlaneri* Némcová et Rott	-	-	-	-	-	-	-	+	+	+	-
37	***M. striata*** Asmund	-	-	+	-	-	-	-	-	+	+	-
38	*M. tolerans* Asmund et Kristiansen	-	-	-	-	-	-	-	-	+	-	-
39	***M. tonsurata*** Teiling	-	-	+	-	-	-	-	-	+	-	-
40	*M. torquata* Asmund et Cronberg	-	-	-	-	+	-	-	-	-	-	-
41	*M. trummensis* Cronberg	-	-	-	-	+	-	-	-	-	-	-
42	***M. vannigera*** Asmund	+	-	+	+	+	+	+	+	-	+	+
43	*Mallomonas* sp. 1	-	-	+	-	-	-	-	-	+	-	+
44	*Mallomonas* sp. 2	-	-	-	-	-	-	-	-	+	-	-
45	*Mallomonas* sp. 3	-	-	-	-	-	-	-	-	+	-	+
46	*Mallomonas* sp. 4	-	-	-	-	-	-	-	-	+	-	-
47	*Synura asmundiae* (Cronberg et Kristiansen) Škaloud, Kristiansen et Škaloudová	-	-	-	-	-	-	-	-	+	+	+
48	***S. glabra*** (Korshikov) Škaloud et Kynclová	-	-	+	+	+	-	+	-	+	+	-

№	Species	Station numbers										
		1	2	3	4	5	6	7	8	9	10	11
49	*S. heteropora* Škaloud, Škaloudová et Procházková	-	-	-	-	-	-	-	-	+	-	-
50	*S. macropora* Škaloud et Kynclová	-	-	+	-	-	-	-	-	-	-	-
51	*S.* cf. *nyagaardii* (Petersen et Hansen) Kristiansen	-	-	+	-	-	-	-	-	-	-	-
52	*S. spinosa* Korshikov	-	-	+	-	-	-	-	-	+	+	-
53	*S. petersenii* f. *petersenii* (Korshikov) Škaloud et Kynclová	-	-	+	-	-	-	-	-	-	+	+
54	*S. petersenii* f. *columnata* Siver	-	-	-	-	+	-	-	-	-	-	-
55	*S. uvella* Ehrenberg	-	-	+	-	-	-	-	-	+	+	-
56	*S. punctulosa* Balonov	-	-	-	-	-	-	-	-	+	-	-
57	*Synura* sp.	-	-	-	-	-	-	-	-	+	-	-
	Total	4	2	22	6	14	4	8	8	44	20	16

Correlation analysis between environmental variables and community richness (Fig. 9A) demonstrated strong positive correlations between temperature, silicon concentration, nitrite, and nitrate anion levels. A significant negative correlation was observed between richness and pH, indicating that pH could potentially limit chrysophyte diversity. Furthermore, moderate positive correlations were also found for phosphate anions, ammonium cations, and pH levels.

Cluster analysis of silica-scaled chrysophytes community profiles (Fig. 9B) identified two major clusters, with site groupings closely corresponding to water sources: the Angara mainstem and its tributaries, reflecting a clear separation in community composition between these hydrological inputs.

Correspondence analysis of the chrysophyte community data (Fig. 9C) confirms the clustering observed in Fig. 9B, with tributary samples separated from Angara mainstem samples along the first CA axis, which explains 25% of the variance. Sample 3 stands out as an outlier, exhibiting a distinct community composition compared to other sites.

Changes in the species structure of silica-scaled chrysophytes in response to water temperature

The distribution of species richness and the structure of silica-scaled chrysophytes (Fig. 10) are closely related to variations in water temperature.

Low species richness was observed at Stations 2, 4, 6, and 8 in the Angara riverbed (Fig. 10), where the influence of Lake Baikal's waters is strongest. Moving away from the lake, water temperature increased, accompanied by higher species richness and changes in the structure of silica-scaled chrysophytes (Table 2; Fig. 11).

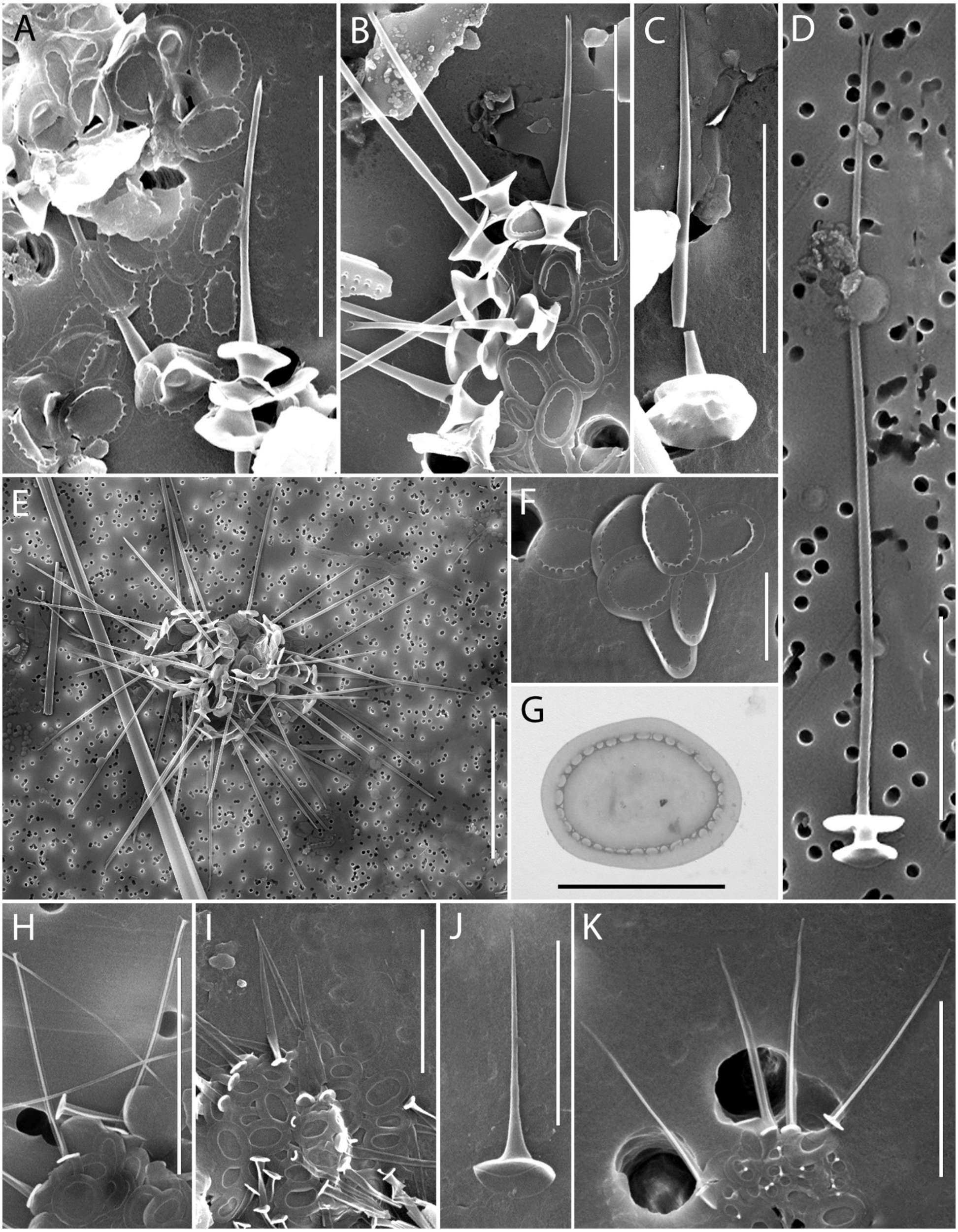

Figure 2. Individual plate and spine scales of genera *Chrysosphaerella* and *Spiniferomonas*. **A** – *Chrysosphaerella rotundata* (Belaya River); **B** – *C. brevispina* (Belaya River); **C** – *C. coronacircumspina* (Ida River); **D–G** – *C. baikalensis* (**D**, **G** – Belaya River; **E**, **F** – Kitoy River); **H** – *Spiniferomonas abrupta* (Ida River); **I** – *S. abei* (Belaya River); **J** – *S. bourrellyi* (Belaya River); **K** – *S. cornuta* (Ida River). SEM (**E–F**, **H–K**), TEM (**G**). Scale bars: **F**, **G** – 3 μm; **H–K** – 5 μm; **A–D** – 10 μm; **E** – 30 μm.

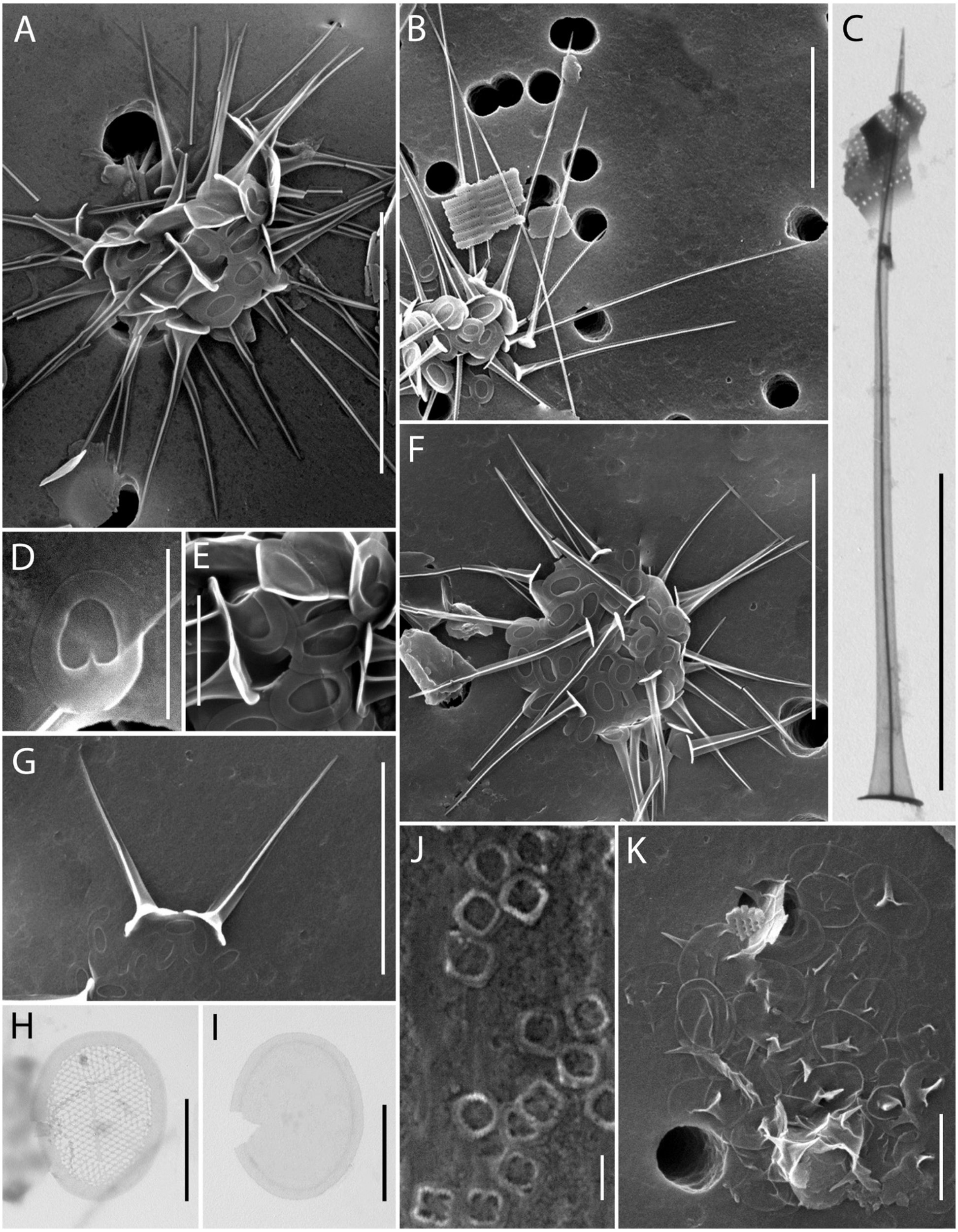

Figure 3. Individual plate and spine scales of genera *Paraphysomonas* and *Lepidochromonas*, as well as individual plate and spine scales, and cells of the genus *Spiniferomonas*. **A**, **D**, **E** – *Spiniferomonas* sp. (**A** – disintegrated cell, the arrow shows a plate scale with incomplete bridges; **D** – individual plate scales with incomplete bridges; **E** – plate scales two types, the arrow shows a plate scale with incomplete bridges (Belaya River)); **B**, **C** – *S. cuspidata* (Ida River); **F** – *S. trioralis* (Belaya River); **G** – *S. silverensis* (Belaya River); **H** – *Paraphysomonas punctata* (Belaya River); **I** – *P. circumvallata* (Belaya River); **J** – *Lepidochromonas subquadrangularis* (Belaya River); **K** – *P. gladiata* (Belaya River). SEM (**A**, **B**, **D–G**, **J**, **K**), TEM (**C**, **H**, *I*). Scale bars: **J** – 0.3 μm; **H**, **I** – 1 μm; **D**, **E**, **K** – 3 μm; **A**, **B**, **C**, **F**, **G** – 10 μm.

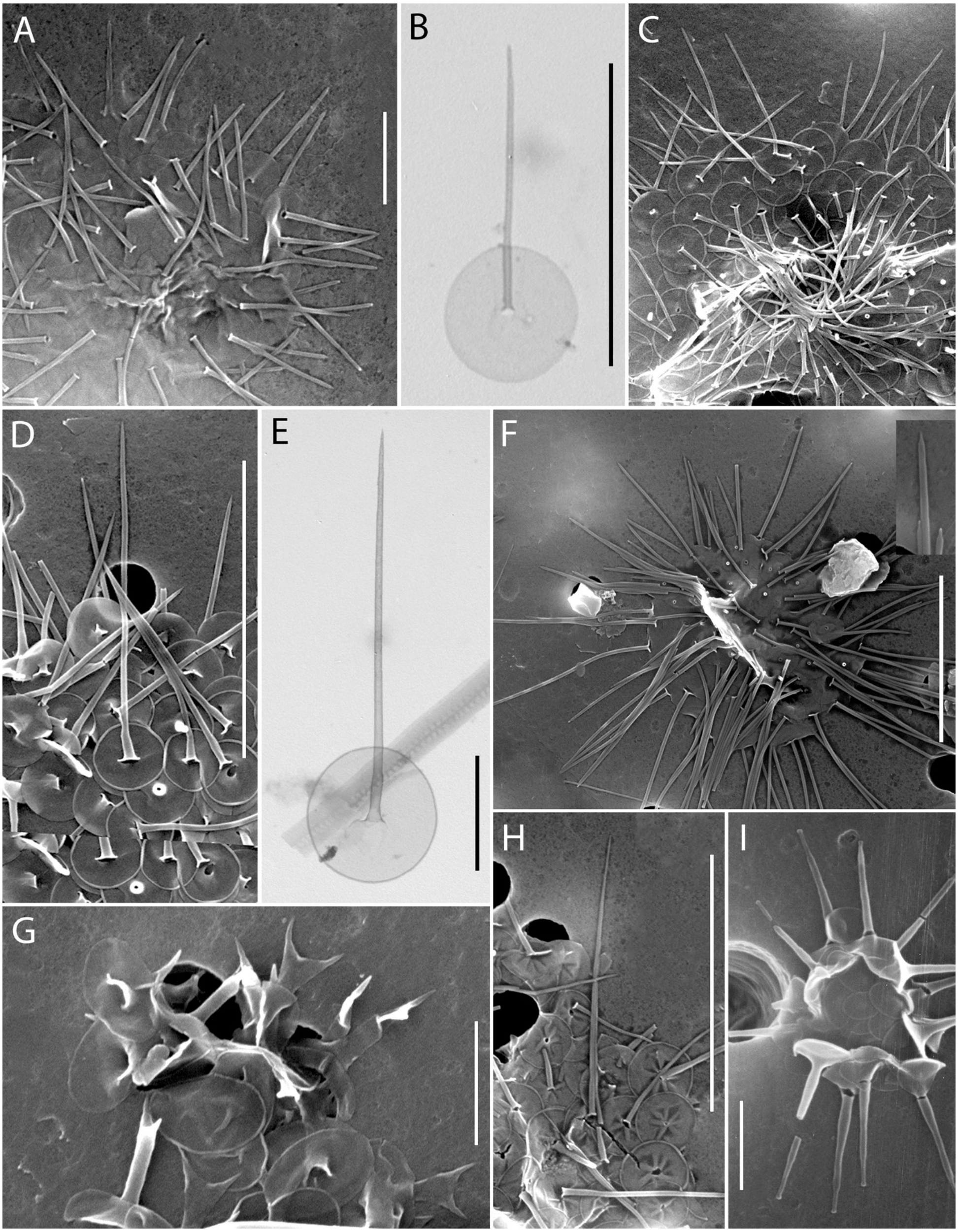

Figure 4. Individual spine scales and disintegrated cells of genus *Paraphysomonas*. **A** – *Paraphysomonas* sp. 1 (Belaya River); **B** – *Paraphysomonas* sp. 2 (Irkut River); **C** – *Paraphysomonas* sp. 3 (Belaya River); **D**, **E** – *Paraphysomonas* sp. 4 (**D** – Belaya River; **E** – Irkut River); **F** – *P.* cf. *acuminata* (Belaya River); **G** – *P. capreolata* (Belaya River); **H** – *P. uniformis* subsp. *hemiradia* (Belaya River); **I** – *Paraphysomonas* sp. 5 (the Angara River downstream of the Irkutsk Hydroelectric Power station). SEM (**A**, **C**, **D**, **F–I**), TEM (**B**, **E**). Scale bars: **A–C**, **E**, **G**, **I** – 2 μm; **D**, **F**, **H** – 10 μm.

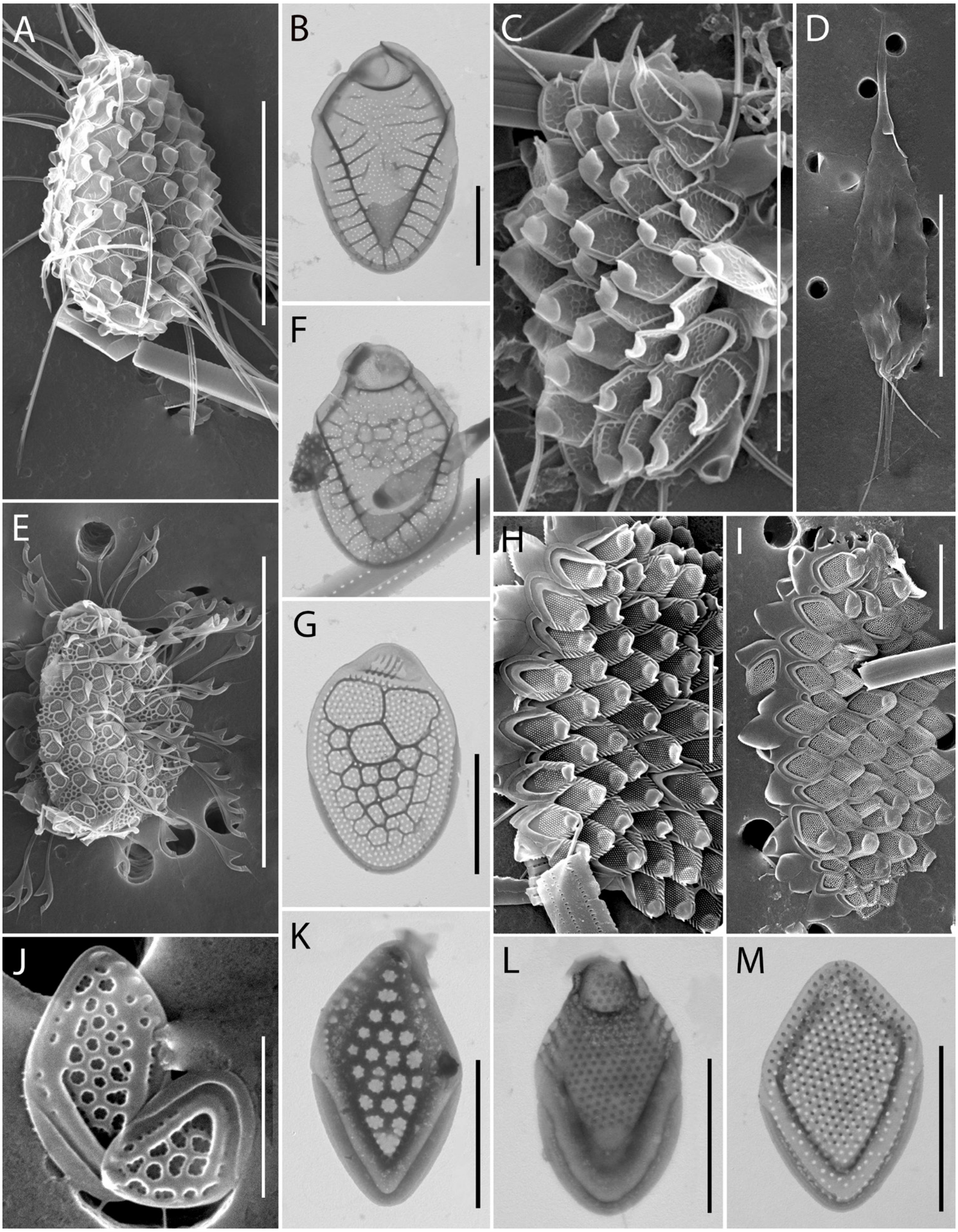

Figure 5. Individual scales and cells of genus *Mallomonas*. **A**, **B** – *Mallomonas acaroides* (**A** – Belaya River; **B** – Ida River); **C**, **F** – *M. crassisquama* (**C** – Belaya River; **F** – Ida River); **D** – *M. akrokomos* (Belaya River); **E**, **G** – *M. multiunca* (**E** – Belaya River; **G** – Ida River); **H**, **L** – *M. papillosa* (**H** – Belaya River; **L** – Irkut River); **I**, **M** – *M. annaulata* (Irkut River); **J**, **K** – *M. alata* (**J** – Belaya River; **K** – Irkut River). SEM (**A**, **C–E**, **H–J**), TEM (**B**, **F**, **G**, **K–M**). Scale bars: **B**, **F**, **G**, **J–M** – 2 µm; **H**, **I** – 5 µm; **A**, **C**, **D**, **E** – 10 µm.

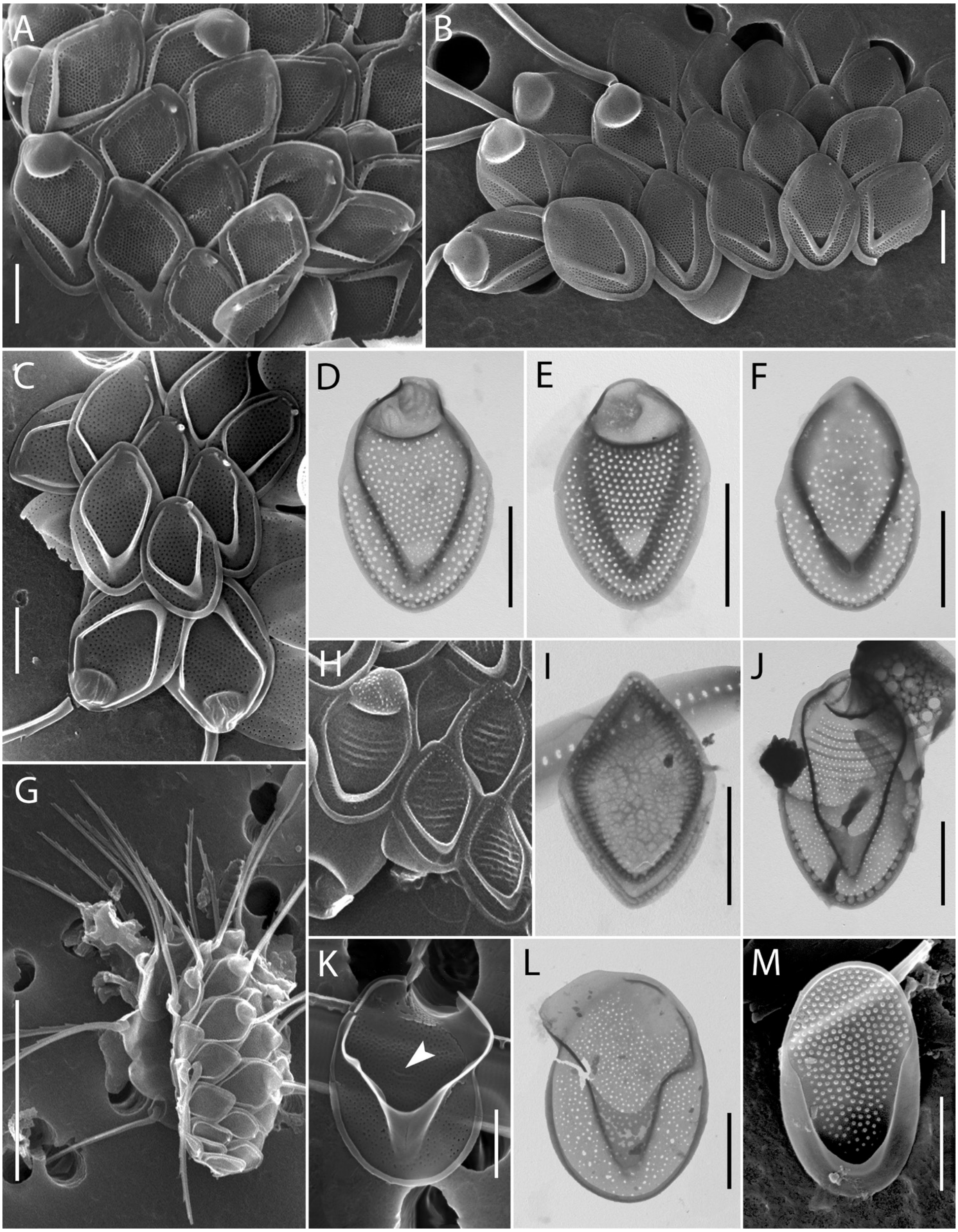

Figure 6. Individual scales and cell of genus *Mallomonas*. **A** – *Mallomonas* sp. 4 (Belaya River); **B**, **E** – *M. tonsurata* (**B** – Belaya River; **E** – Irkut River); **C**, **D**, **G** – *M. alpina* (Belaya River); **F** – *M. kuzminii* (Irkut River); **H** – *M. trummensis* (Kuda River); **I** – *M. torquata* (Kuda River); **J** – *M. costata* (Irkut River); **K**, **L** – *M. vannigera* (**K** – Irkut River, the arrow shows the so-called "parallel rib" on the shield; **L** – Ida River); **M** – *M. tolerans* (Belaya River). SEM (**A–C**, **G**, **H**, **K**, **M**), TEM (**D–F**, **I**, **J**, **L**). Scale bars: **A–F**, **H–M** – 2 μm; **G** – 10 μm.

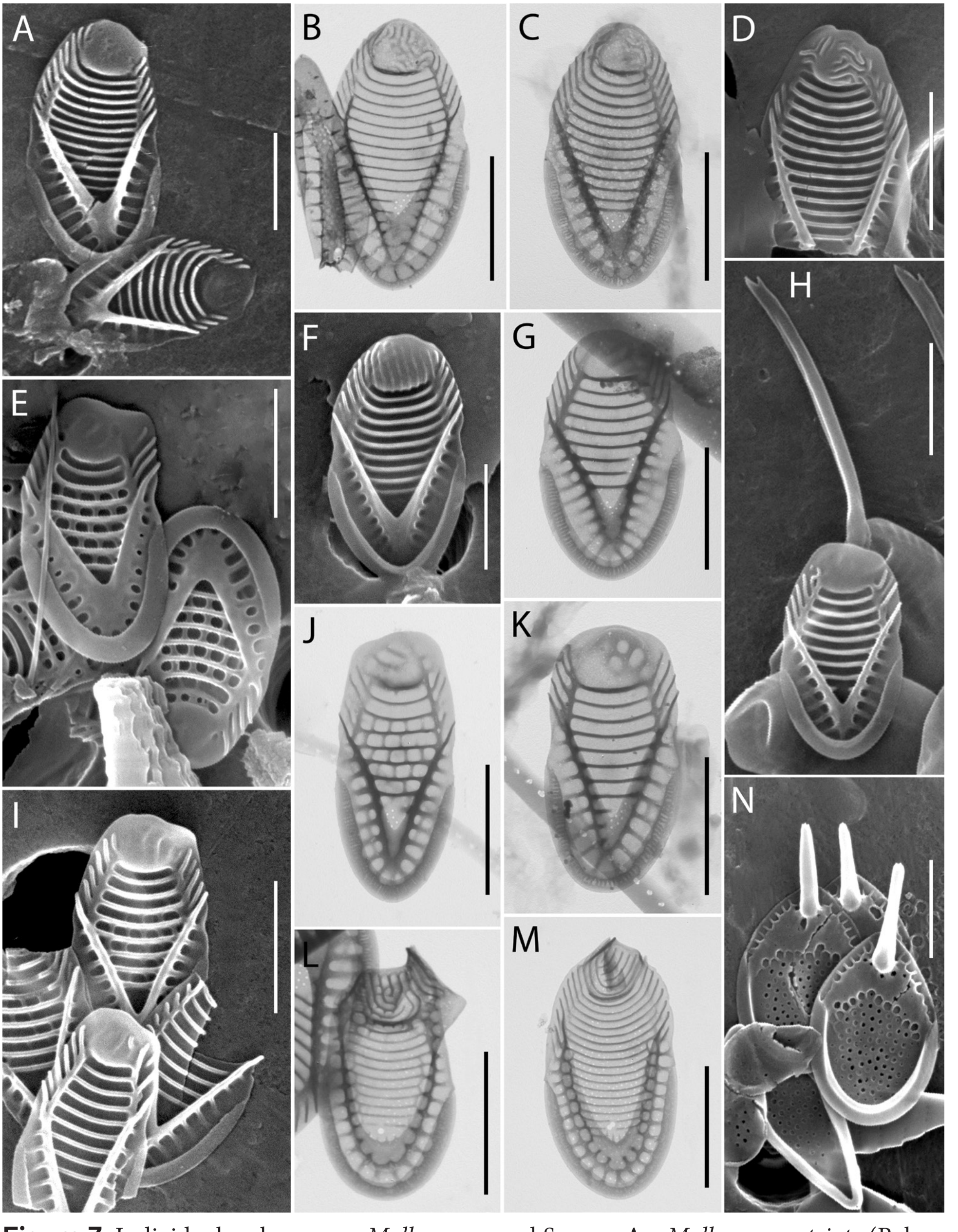

Figure 7. Individual scales genera *Mallomonas* and *Synura*. **A** – *Mallomonas striata* (Belaya River); **B–D** – *Mallomonas* sp. 1 (**B** – Irkut River; **C**, **D** – Belaya River); **E** – *Mallomonas* sp. 2 (Belaya River); **F–H** – *M. pechlaneri* (Belaya River); **I–K** – *Mallomonas* sp. 3 (**I** – Belaya River; **J**, **K** – Ida River); **L**, **M** – *M. cratis* (Irkut River); **N** – *Synura spinosa* (Belaya River). SEM (**A**, **D–F**, **H**, **I**, **N**), TEM (**B**, **C**, **G**, **J–M**). Scale bars 2 μm.

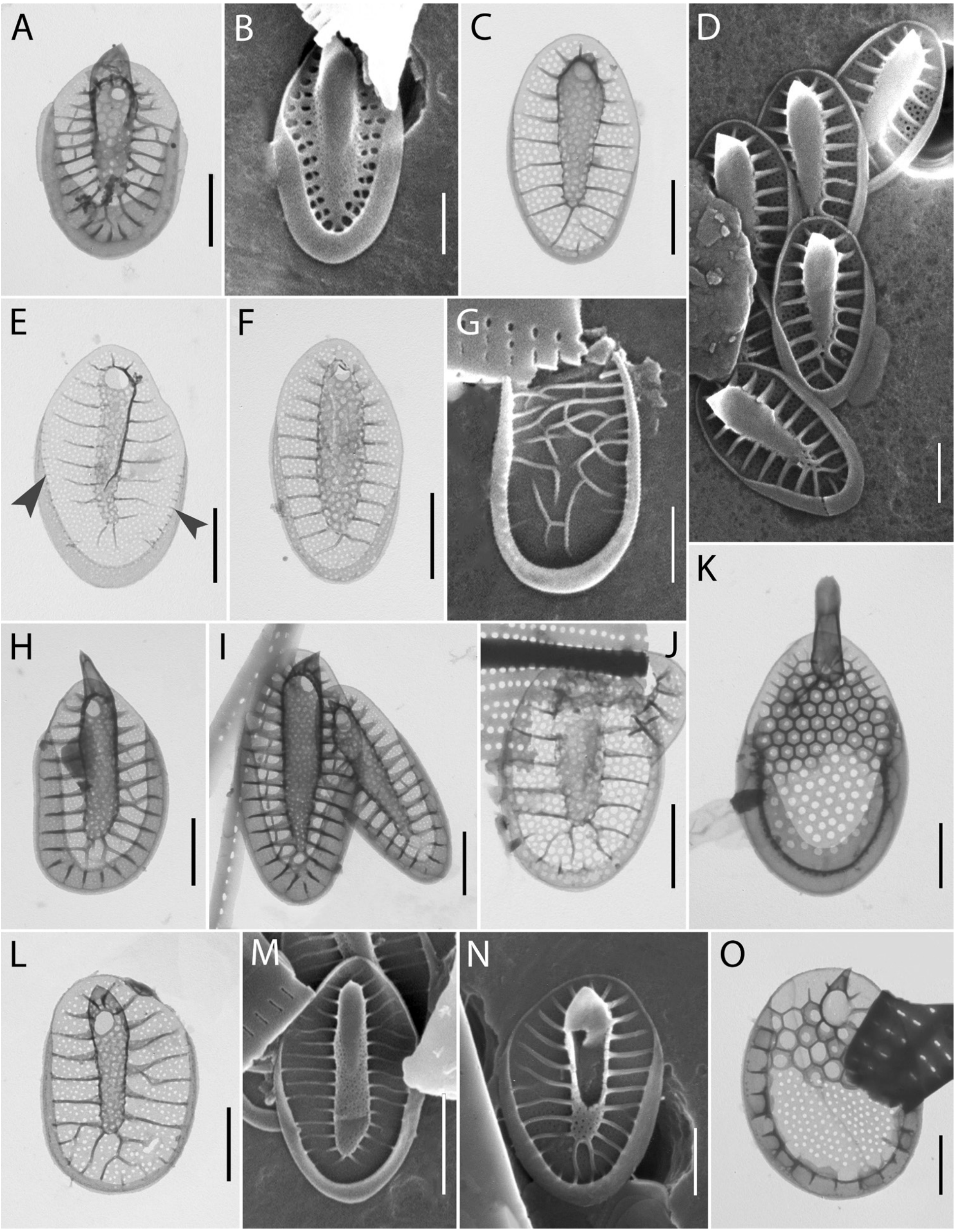

Figure 8. Individual scales of genus *Synura*. **A** – *S. asmundiae* (Ida River); **B** – *Synura* sp. (Belaya River); **C**, **D** – *Synura* cf. *macropora* (**C** – Irkut River; **D** – Belaya River); **E** – *S. petersenii* f. *columnata*, The arrows show well-developed posts located under the proximal rim (Kuda River); **F** – *S. heteropora* (Belaya River); **G** – *S. punctulosa* (Belaya River); **H**, **I** – *S. petersenii* (Ida River); **J** – *S. macropora* (Irkut River); **K** – *S.* cf. *nyagaardii* (Irkut River); **L–N** – *S. glabra* (**M** – Belaya River; **L**, **N** – Irkut River); **O** – *S. uvella* (Irkut River). SEM (**B**, **D**, **G**, **M**, **N**), TEM (**A**, **C**, **E**, **F**, **H–L**, **O**). Scale bars 1 μm.

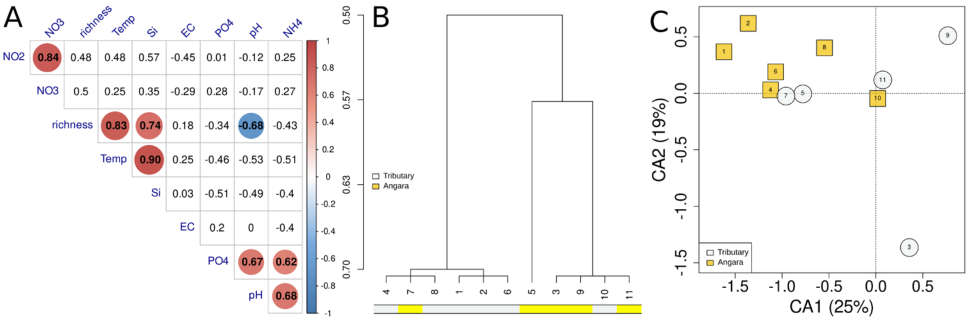

Figure 9. Statistical analysis examining the relationship between environmental factors and the distribution of silica-scaled chrysophytes. **A** – Correlation analysis of environmental variables, with values representing Pearson correlation coefficients and a color-coded legend on the right. Circles indicate statistically significant correlations (p ≤ 0.05). **B** – Cluster analysis of silica-scaled chrysophytes profiles using affinity propagation. **C** – Correspondence analysis of silica-scaled chrysophytes profiles. Station numbers correspond to those shown in Fig. 1.

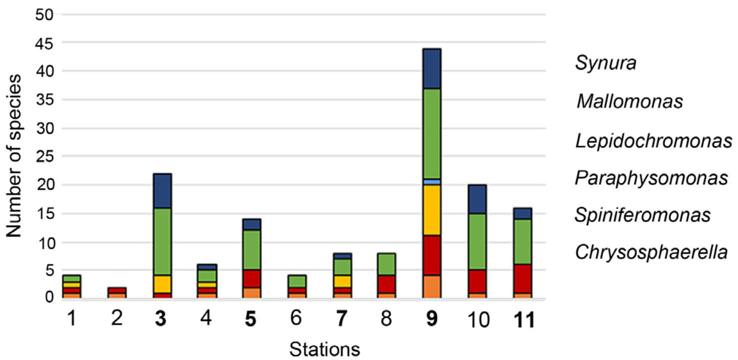

Figure 10. Distribution of silica-scaled chrysophytes species richness by genus in the Angara riverbed and at the mouths of tributaries (station numbers shown in bold). Station numbers correspond to those in Fig. 1.

At Stations 1 and 2, the water exhibited minimum temperatures of 4.8 °C and 5 °C, respectively. The species composition was represented by four species typical of the lake's spring community: *Chrysosphaerella baikalensis*, *Spiniferomonas cuspidata*, *Paraphysomonas* sp., and *Mallomonas vannigera* (Table 2). At Stations 4 and 6, after the confluence of the Irkut and Kuda rivers into the Angara riverbed, the water temperature increased to 5.3–6.5 °C. The species composition expanded to include three additional species characteristic of the spring community (*M. alpina*), as well as those typical of the warmer waters of Lake Baikal and the bays of the Irkutsk Reservoir – *Synura glabra* and *M. annaulata*. At Stations 8 and 10, the water temperature increased to 8.2–8.3 °C. At Station 8, the species composition expanded by two additional representatives of the summer community from the Irkutsk Reservoir's bays – *M. crassisquama* and *Spiniferomonas cornuta*. The *M. pechlaneri* species, absent from upstream stations, was detected here. At Station 10 in the Angara riverbed, after the confluence of the Belaya River tributary, the silica-scaled chrysophytes species composition increased dramatically from 8 to 20 species, with 17 of them originating from the Belaya River mouth. Consequently, the Angara riverbed's species composition at Station 10 included new species not observed upstream: *Spiniferomonas bourrellyi*, *Mallomonas akrokomos*, *M. multiunca*, and *Synura asmundiae* (Table 2).

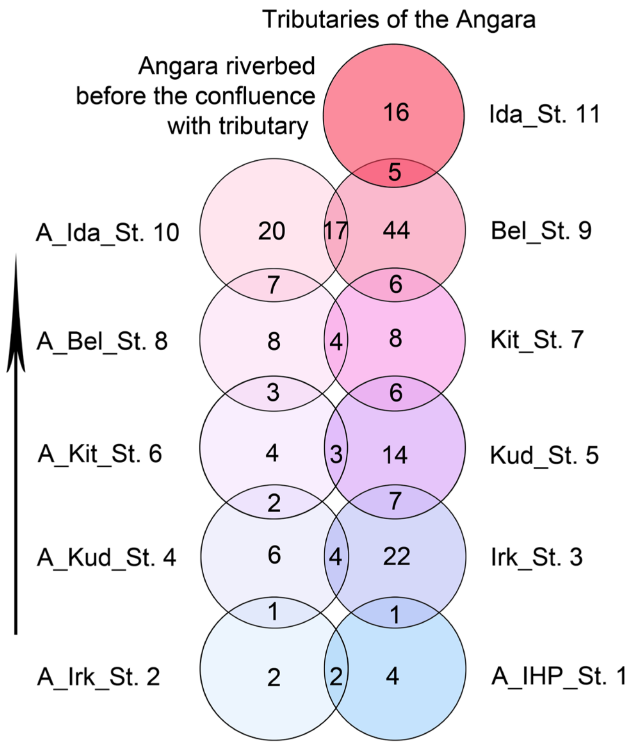

Figure 11. Venn diagram showing changes and relationships in the species richness of silica-scaled chrysophytes at tributary stations (Stations 3, 5, 7, 9, and 11) and at Angara riverbed stations downstream of their confluence (Stations 4, 6, 8, and 10). The arrow indicates the flow direction of the Angara River relative to the sampling stations, starting from the upper reaches of the Irkutsk Reservoir (Station 1). Station numbers correspond to those in Fig. 1.

In the warmer waters of the tributaries, the species richness of silica-scaled chrysophytes was higher than at the Angara riverbed stations (Figs 10, 11). However, species composition varied among the tributaries. Additionally, certain spring community species of Lake Baikal – *Chrysosphaerella baikalensis*, *Spiniferomonas cuspidata*, *Mallomonas vannigera*, and *M. alpina* – were found in the tributaries (Table 2). The lowest species diversity was recorded at the Kitoy River mouth (Station 7), where the water temperature was the lowest among the studied estuaries, measuring 7 °C. A total of eight species were found there, most of which were typical of the lake's spring community. Notably, only one species, *Paraphysomonas* sp. 4, had not been previously detected in the area. At the Kuda River mouth (Station 5), the most affected by anthropogenic factors, 14 species were recorded at a water temperature of 8.8 °C. Only three species – *Mallomonas torquata*, *M. trummensis*, and *Synura petersenii* f. *columnata* – were found exclusively at this site and not at other stations. At the mouth of the Ida River (Station 11), where the water temperature was 11.3 °C, 16 species were recorded. The highest species richness was observed at the mouth of the Irkut River (Station 3), with 22 species found at a water temperature of 15.9 °C. Five species were unique to this station and not observed elsewhere: *Paraphysomonas* sp. 2, *Mallomonas costata*, *M. kuzminii*, *Synura macropora*, and *S.* cf. *nygaardii*. The highest species richness – 44 species – was recorded at the mouth of the Belaya River (Station 9), where the water temperature was 14.6 °C. Seventeen species were found only at this station and not at other upstream sites. These include *Chrysosphaerella rotundata*, *Spiniferomonas* sp., *S. silverensis*, *Paraphysomonas* cf. *acuminata*, *P. capreolata*, *P. gladiata*, *P. circumvallata*, *P. punctata*, *P. uniformis* subsp. *hemiradia*, *Paraphysomonas* sp. 1, *Lepidochromonas subquadrangularis*, *Mallomonas* sp. 2, *Mallomonas* sp. 4, *M. tolerans*, *Synura heteropora*, *S. punctulosa*, and *Synura* sp. (Table 2).

Rare and undetermined species

Among the 57 species identified in the study area, 11 exhibited silica structure morphologies distinct from those of known species, suggesting they may represent potentially new taxa. Additionally, one rare species and one unique form were also discovered during the investigation.

The form *Synura petersenii* f. *columnata* (Fig. 8E) was originally described from reservoirs in North America and has not been reported from any other locations since its initial discovery. This form is characterized by the presence of additional ribs located beneath the proximal rim. It was initially documented in a small, shallow lake with humic pollution, low electrical conductivity, slightly acidic pH, and mesotrophic-eutrophic conditions (Siver 1988). In this study, this variety was detected in a river mouth, where a single specimen was found at a temperature of 8.8 °C and a pH of 8.5.

After the initial description of *Paraphysomonas capreolata* (Fig. 4G) from reservoirs in England (Preisig and Hibberd 1982), this species has been documented in only three additional locations worldwide: Denmark (at a temperature of 12 °C and pH of 7.9, Nielsen 1994), Greece (Kristiansen 1983), and Japan (Ito 1988). In this study, this species was detected in the mouth of the Belaya River, where it was found at a temperature of 14.6 °C and a pH of 7.8.

Spiniferomonas sp. (Figs 3A, D, E). The cells are spherical measuring 5–7 µm in diameter, with numerous 27–40 straight, tapering spines, 5.7–7.7 µm in length. Each spine consists of a flat, circular base plate with a diameter of 1.3–1.7 µm, from the center of which extends a triangular shaft that terminates in a tapering apex. The plate scales of two types: elliptical or circular scales measuring 1.1–1.3 µm × 1.5–1.8 µm, featuring a single lacuna and a thickened margin 0.25–0.3 µm wide; rounded scales with measuring 1.4–1.6 µm × 1.5–1.8 µm, with a single lacuna, an incomplete bridge, and a thickened margin 0.25–0.3 µm wide.

Paraphysomonas sp. 1 (Fig. 4A). This species has one form of spine scales. The spines are straight, 1.5–2.3 µm long, tapering to an obliquely cut, pointed tip. The basal plate is rounded, 1.2–1.4 µm in diameter, without a rim. Scales of similar morphology were previously observed in October in the Irkutsk Reservoir (Bessudova et al. 2024; Figs 4c, d, identified as *Paraphysomonas* sp. 3).

Paraphysomonas sp. 2 (Fig. 4B). This species has one form of spine scales. The spines are straight, 1.5–1.7 µm long, tapering to a pointed, slightly pinched tip. The basal plate is rounded, 0.8–1 µm in diameter, without a rim.

Paraphysomonas sp. 3 (Fig. 4C). This species has one form of spine scales. The spines are straight 5.8–6.5 µm in long, tapering gradually to a pointed tip. The basal plate is rounded, 1.8–2.4 µm in diameter, and has a thin rim. Scales with similar morphology were previously detected in June in the Irkutsk Reservoir (Bessudova et al. 2023d; Fig. 3a, identified as *Paraphysomonas* sp. 1).

Paraphysomonas sp. 4 (Figs 4D, E). This species has one form of spine scales. The spines are either straight or slightly curved, 5–8 µm long, widened at the base before tapering to a sharp tip. The basal plate is rounded, 2–2.7 µm in diameter, and possesses an edge rim.

Paraphysomonas sp. 5 (Fig. 4I). This species has one two types of scales: plates and spines. Plate scales are oval, flattened, or slightly convex, measuring 0.75–0.9 µm × 0.6–0.7 µm, with a raised edge rim. Spine scales feature a rounded base, 1–1.2 µm in diameter, with a thickened rim and a continuing spine, 2–3.2 µm long. The spine is hollow for 1/5 of its length before tapering to form a pronounced cephalic tip. These scales resemble those of *P. corynephora* Preisig et Hibberd but differ in having smaller plate scales and larger spine scales. Additionally, the spine scales possess a rounded base rather than the expanded, funnel-shaped base found in *P. corynephora*. According to unpublished data, cells of this species occur in spring season in Lake Baikal at a water temperature of 1.8 °C.

Mallomonas sp. 1 (Figs 7B–D) belongs to the *Striatae* section. The body scales are oval, measuring 4.1–4.9 µm × 2–2.3 µm, weak lateral incurvings. The dome is almost rounded shape, with a labyrinthine reticulum. The shield is marked with 13–15 regularly spaced transverse ribs. The V-rib on the scales is acutely angled, slightly hooded. A “window” is located in the posterior part of the shield, in the angle of the V-rib. The V-rib is continuing on wing-like extensions. The anterior flange with 6–8 closely spaced struts on each side. The anterior submarginal ribs are well developed. The posterior flange bears approximately 18–20 struts. The posterior rim is smooth. Bristles have not been observed. Previously, scales with similar morphology were detected in June in the Irkutsk Reservoir (Bessudova et al. 2023d; Fig. 5I, identified as *Mallomonas* sp. 1).

Mallomonas sp. 2 (Fig. 7E) belongs to the *Striatae* section. The body scales are oval, measuring 2.9–4.7 μm × 1.3–2.6 μm, weak lateral incurvings and slight asymmetry. The dome is rounded shape, smooth, with a more or less pronounced lateral protrusion on the right side. The shield is marked with 4–6 regularly spaced transverse ribs, between which a thick secondary siliceous layer of coarse-meshed reticulation (oval or rounded) is present, containing 1 pore in each mesh. A group of numerous pores, usually about 10, is located at the angle of the V-rib in the posterior part of the shield. Both this area and the area of the first 2 transverse ribs lack a secondary siliceous layer. The V-rib is continuing on wing-like extensions. The anterior submarginal ribs are well developed. The anterior flange with 2–5 closely spaced struts on each side. The posterior flanges are covered with a secondary layer, exhibiting reduced struts that partially merge to form reticulation mesh. The posterior rim is wide, smooth, with numerous thin parallel strokes internally. Bristles are 3.7–6.2 μm in length, slightly curved, and terminate in an expanded, forked tip with asymmetrically diverging branches. One branch is short and pointed, while the other is broad, ending in a sharp tip with a flat dorsal surface. Previously, scales with similar morphology were described in Lake Baikal (Bessudova et al. 2023c; Fig. 5, identified as *Mallomonas sibirica*).

Mallomonas sp. 3 (Figs 7I–K) belongs to the *Striatae* section. The body scales are oval, measuring 3–4.5 μm × 1.3–2.2 μm, weak lateral incurvings and slight asymmetry. The dome is rounded either smooth or featuring rounded depressions. The shield is marked with 7–9 regularly spaced transverse ribs. The transverse ribs, except for the area between the first and second (closest to the dome), are connected in random order by short ribs-jumpers. A group of numerous pores, usually about 10, is located at the angle of the V-rib in the posterior part of the shield. The V-rib is continuing on wing-like extensions. The anterior flange with 4–6 closely spaced struts on each side. The anterior submarginal ribs are well developed. The posterior flange bears approximately 16–20 struts. The posterior rim is wide, smooth, with numerous thin parallel strokes internally. Bristles have not been observed.

Mallomonas 4 (Fig. 6A) belongs to the *Mallomonas* section. The scales are rhomboid, measuring 5–5.7 μm × 3.2–3.4 μm. The apical scales with a large smooth dome, in the proximal area of which there are small struts – fused meshes of the reticulum oriented toward the shield. The base plate is perforated by small pores and overlain by a well-developed secondary layer of dense, somewhat irregular reticulum in the central area. Each reticulum mesh contains one or several pores. In the proximal area of the scale, at the base of the V-rib, a "window" is located – an area without a secondary siliceous layer. The V-rib is acute and slightly hooded, and it is continuous with the arms of the anterior submarginal ribs. The anterior flange is narrow. On both the outer and inner sides of the V-rib and the anterior submarginal rib, the secondary layer with cellular structures approaches the ribs, forming struts at the points of contact. The posterior rim is narrow, smooth, and the posterior flange is wide, perforated with pores, and covered by a secondary layer. The caudal scales are small, measuring 4–4.3 µm × 2.2–2.5 µm, without a dome, with 1 or 2 short spines.

Synura sp. (Fig. 8B) belongs to the *Peterseniana*e section. The scale is oval, measuring 3.6 µm × 2 µm. The cylindrical keel terminates into an acute tip. Numerous struts (31–34), interconnected by transverse folds, regularly extend from the keel to the edge of the scale. The proximal rim is wide, measuring 0.4–0.5 µm width

Discussion

In contrast to large rivers, small and medium-sized rivers demonstrate greater sensitivity to various local and global effects, requiring their continuous monitoring. The observed patterns in the distribution of silica-scaled chrysophytes in the Angara riverbed and the mouths of its main tributaries, which differ in warming intensity, highlight the strong potential of these organisms as indicators of climatic changes in the study area. The findings of this research are consistent with data obtained in June 2023 from Lake Baikal (Bessudova et al. 2017) and from the Southern Baikal–Angara River source–Irkutsk Reservoir system (Bessudova et al. 2023d; 2024). In this unique system, influenced by the cold, oligotrophic waters of Lake Baikal, two distinct communities emerge during the hydrological spring–spring and summer. The spring species community originates from the pelagic zone of Lake Baikal following ice melt, where these species occur as intact cells within a narrow temperature range of 1.8–4.5 °C (Bessudova et al. 2017). This group comprises *Chrysosphaerella baikalensis*, *Lepidochromonas takahashii*, *Paraphysomonas* sp. 5, and *Mallomonas vannigera*. These species complete their developmental cycle (with only individual scales, bristles, and spines detectable) upon entering the warmer waters of the Irkutsk Reservoir's bays (Bessudova et al. 2023d) or the waters of tributaries. Previously regarded as endemic only to Lake Baikal (Vorobyova et al. 1992), this species was also detected in tributaries, albeit represented only by individual scales and spines. The species comprising the spring community begin their development even under the lake's ice cover by the end of March, alongside the subglacial species *M. baicalensis* Bessudova, *M. grachevii* Bessudova, and *M. getseniae* (Voloshko) Bessudova, at water temperatures in the range of 0.1–0.6 °C (Bessudova et al. 2023b; Bessudova and Likhoshway 2023; Bashenkhaeva et al. 2025).

The second community of species is characteristic of early summer, emerging when water temperatures rise above 5.3 °C. Plankton samples during this period reveal colonies of *Synura petersenii* forma species, including representatives such as *S. glabra*. At temperatures exceeding 6 °C, the community includes cells of *Spinif-*

eromonas abrupta, *S. cornuta*, *S. bourrellyi*, *S. silverensis*, *S. triangularis*, *Mallomonas acaroides*, *M. crassisquama*, *M. striata*, *M. tonsurata*, and *M. annaulata* (Bessudova et al. 2017). When temperatures reach 8.2 °C and above, the community expands to include *Spiniferomonas abei*, *Mallomonas pechlaneri*, *M. alata*, *M. akrokomos*, *M. cratis*, *M. punctifera*, *M. multiunca*, *M. torquata*, *M. trummensis*, *Synura asmundiae*, *S. punctulosa*, and *S. uvella* (Bessudova et al. 2023d). At temperatures above 11.5 °C, the following species were detected: *Chrysosphaerella coronacircumspina*, *Paraphysomonas bandaiensis*, *Mallomonas elongata*, *Synura echinulata*, and *S. spinosa* f. *longispina* (Bessudova et al. 2023d). When the temperature increases to 14.6 °C, the community expands to include *Paraphysomonas capreolata*, *P. gladiata*, *P. circumvallata*, *P. punctata*, *P. uniformis* subsp. *hemiradia*, *Lepidochromonas subquadrangularis*, *Mallomonas costata*, *M. papillosa*, *M. kuzminii*, *M. tolerans*, and *Synura macropora*. Analysis of the study area revealed a clear pattern: as water temperature increased, species diversity also increased, and the composition of silica-scaled chrysophytes communities changed from a spring to a summer type. Furthermore, in addition to temperature-sensitive species, the study identified taxa capable of withstanding considerable thermal fluctuations (4.8–15.9 °C). Three such species – *Spiniferomonas trioralis*, *S. cuspidata*, and *Mallomonas alpina* – were identified. These taxa have previously been recorded during the entire growing season within a broad temperature range of 1.8–18.3 °C, from Southern Baikal to the Angara River downstream of the Irkutsk Hydroelectric Power station (Bessudova et al. 2017; 2024).

A similar trend of increasing species richness with increasing water temperature can also be observed along the gradient from Lake Baikal and the Irkutsk Reservoir to the upper basin of the Angara River (Fig. 12).

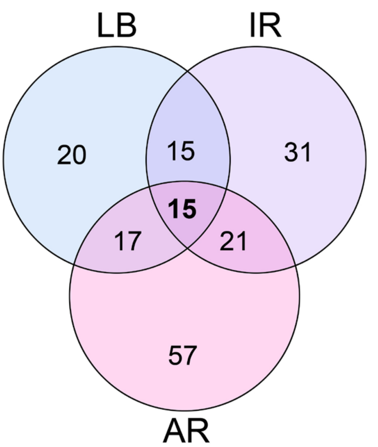

Figure 12. Venn diagram illustrating the relationship in species composition of silica-scaled chrysophytes in Lake Baikal (LB) (Bessudova et al. 2017; 2023d), the Irkutsk Reservoir (IR) (Bessudova et al. 2023d), and the studied Angara River basin (AR) during the hydrological spring.

The increased species richness in the upper Angara basin is mainly attributed to the hydrological and hydrochemical diversity of its tributaries. Among all the studied tributaries, the Belaya River stands out because it exhibits not only a high overall species diversity but also contains rare and potentially new species. This suggests that the environmental conditions in the Belaya River are most favorable for the development of silica-scaled chrysophytes. During spring surveys, 70 species were recorded across several locations: Lake Baikal (Bessudova et al. 2017), Southern Baikal, the source of the Angara River, the Irkutsk Reservoir (Bessudova et al. 2023d), and the upper Angara River basin, including its riverbed and tributary estuaries. Of these, 15 species (Table 2, Fig. 12) are common to all studied areas, reflecting the regional characteristics of the spring community of silica-scaled chrysophytes.

Conclusions

The study revealed that the station most influenced by the waters of Lake Baikal, with a water temperature of 4.8 °C, had the lowest species richness – only 4 species. In contrast, the highest species richness was recorded at the mouths of the warmest tributaries – the Belaya (14.6 °C, 44 species) and Irkut (15.9 °C, 22 species) rivers. In these tributaries, both individual scales characteristic of the spring community and whole cells of species typical of the summer community of silica-scaled chrysophytes were observed. In the Angara riverbed, following the confluence with tributaries, water temperature increased from 5 °C to 8.3 °C, accompanied by an increase in silica-scaled chrysophytes species richness – from 2 species (upstream of the Irkut River) to 20 species (downstream of the Belaya River). Along this section of the Angara, species typical of the spring community of Lake Baikal were recorded, and as the water warmed downstream, the species composition was supplemented by representatives of the summer community. The silica-scaled chrysophytes assemblage included both temperature-sensitive species and those tolerant to thermal fluctuations. In the future, rising water temperatures in the reservoirs of the Angara region may lead to an increase in species richness and the displacement of cold-water species that develop within a narrow temperature range of 0.1–4.5 °C. Thus, observations of silica-scaled chrysophytes species richness and community structure during spring season – when watercourses exhibit pronounced differences in warming intensity – offer valuable insights into the mechanisms driving biodiversity formation and serve as a predictive tool for assessing future changes under climate warming conditions.

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