Limnology and Freshwater Biology 2022 (5): 1663-1670 DOI:10.31951/2658-3518-2022-A-5-1663

Review Article

ISSN 2658-3518

LIMNOLOGY FRESHWATER BIOLOGY

www.limnolfwbiol.com

Silica scaled Protista and Stomatocysts in East Siberia

Bessudova A.Yu., Firsova A.D.*

Limnological institute of the Siberian Branch of the Russian Academy of Sciences, 3 Ulan-Batorskaya Str., Irkutsk, 664033, Russia

ABSTRACT. The review examines the work on biodiversity in the reservoirs of Eastern Siberia of a wide, but poorly studied group of organisms forming siliceous scales and bristles – these are scaled chrysophytes, chrysophycean stomatocysts and heterotrophic protists: rotosphaerids, colorless free-living thaumatomonad flagellates, centrohelid heliozoans. The difficulty in studying these objects is the need to use electron microscopy for their species identification. High biodiversity of silica scaled Protozoa has been revealed in the reservoirs of Eastern Siberia and the relationship of their species composition with the parameters of the aquatic environment, including in areas of local anthropogenic impact, has been shown. The recorded enrichment of the mouths of Arctic rivers with boreal species is important for predicting changes in aquatic ecosystems in the context of GCC. The proposed scenario of the settlement of siliceous chrysophytes at the beginning of the Holocene may be valid for other small planktonic organisms. The high degree of preservation of siliceous stomatocysts in sediments allows them to be used as an additional signal of changes in lake ecosystems in the past, this is based in particular on the reconstruction of the ecosystem and changes in the level of Lake Vorota (Yakutia) in the Holocene-Upper Pleistocene.

Keywords: silicon utilizing protists, scaled chrysophytes, heterotrophic protists, stomatocysts, Eastern Siberia

In addition to diatoms, whose role in the global Si cycle is well known (Nelson et al., 1995; Ragueneau et al., 2000; Tréguer and De La Rocha, 2013), other silicon utilizing microeucaryotes live in aquatic ecosystems – these are scaled chrysophytes, heterotrophic protists rotosphaerids, colorless free-living thaumatomonad flagellates, centrohelid heliozoans. These organisms transform silicic acid dissolved in water into elements of shells of a species-specific structure – siliceous scales and bristles (Fig. 1) or resting stomatocysts (Fig. 2).

The scaled chrysophytes include representatives of the Chrysophyceae class Pascher, from the families of Paraphysomonadaceae Preisig, Hibberd, Mallomonadaceae Diesing, Synuraceae Lemmermann. In total, about 350 taxa of silica-scaled chrysophytes are described (Guiry and Guiry, 2022). Scaled chrysophytes are a widespread group, they form a significant part of the plankton biomass of many freshwater reservoirs, there fore they play an important role in the structural and functional organization of freshwater ecosystems. Thaumatomonads are silica-scaled colorless free-living flagellates. Rotosphaerids are silica scaled organisms with filopodia that facilitate phagotrophic nutrition and a slowly rolling or creeping form of motility (Nicholls, 2012) Centrohelid heliozoans are predatory amoeboid flagellate protists, uniting more than 100 species (Zlatogursky, 2012; Shishkin et al., 2018). Representatives of these groups of heterotrophic protists play an important role in the food webs of aquatic microbenthos ecosystems, acting as passive predators. During periods of their maximum abundance, heterotrophic protists rise into the plankton for the purpose of settling (Ostroumov, 1917; Mikrjukov, 2002). Silicon utilizing protists and stomatocysts of

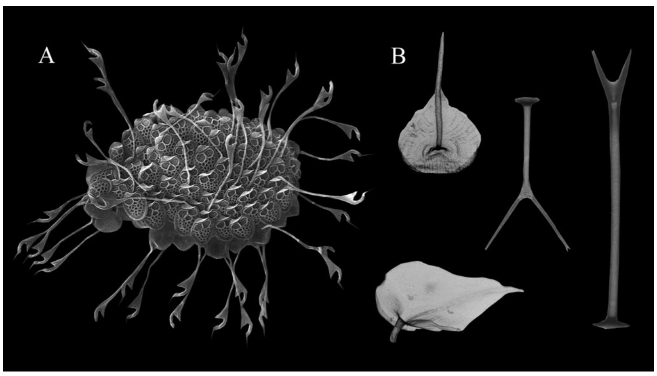

Fig.1. Scales of different silicon utilizing protists. A – a decayed cell of scaled chrysophytes; B – siliceous scales of centrochelid heliozoans.

*Corresponding author.
E-mail address: adfir71@yandex.ru (A.D. Firsova)

Received: November 03, 2022; ***Accepted:*** November 30, 2022; ***Available online:*** December 07, 2022

chrysophytes have micron sizes and species-specific ornamentation, which is detected using transmission and scanning electron microscopy methods.

In aquatic ecosystems, certain types of silicon utilizing protists are indicators of environmental factors such as pH, temperature, electrical conductivity, total phosphorus concentration, salinity, etc. (Hahn et al., 1996; Mikrjukov, 2002; Gavrilova et al., 2005; Leonov and Mylnikov, 2012; Siver, 2015; Prokina and Mylnikov, 2019; Prokina and Philippov, 2019; Lengyel et al., 2022). In addition, with an increase in the concentration of CO^2 in the atmosphere (Schindler, 2001; Rühland et al., 2008) in some boreal and Arctic lakes, an increase in populations of scaled chrysophytes is increasingly observed (Wolfe and Siver, 2013; Mushet et al., 2017). One of the characteristic features of scaled chrysophytes is the ability to form siliceous stomatocysts when changing chemical or physical parameters, In some temperate zones a low percentage of chrysophycean cysts often shows a more eutrophied stage, since these algae are most often less competitive in water with a high nutrient content (Smol, 1985). In the polar regions, this ratio has been proposed to be used to assess the ice cover (Smol, 1983; 1988). Later, the ratio of cysts to diatoms was used (Cumming et al., 1993), Later, the ratio of cysts to diatoms was used to illustrate the potential of cysts as indicators of lake water salinity in the past, and this ratio was also used to study the climatic trends of the Holocene history of Lake Losiny (Minnesota State) (Zeeb and Smol, 1993). The seasonality of their formation was determined by the layers of cysts in layered sediments (Battarbee, 1981; Peglar et al., 1984; Grönlund et al., 1986). Heterotrophic protists and centrohelid heliozoans live in a wide range of environmental factors and are considered eurybionts (Stoupin et al., 2012). However, in most publications there is no data on the parameters of the habitat during the sampling period, identifying the boundaries of such parameters at which a particular species was detected in natural samples would allow determining the autecology of species (Finlay et al., 1998) and to clarify the degree of their eurybiont. Thus, the study of silicon utilizing protists may have an application value for use in environmental monitoring.

The presence of relevant species and morphotypes of stomatocysts in samples can be detected not only from modern reservoirs, but also in sediments of different ages, therefore, silicon utilizing protists, like stomatocysts, are relevant objects not only in monitoring modern plankton, but also in paliolimnology, paleogeography, in terms of evolution and paleoreconstructions. For example, scaled chrysophytes belonging to the genus *Synura* Ehrenberg was very likely formed before the Cambrian period of the Paleozoic era (330 mya) (Boo et al., 2010). And already formed scales, having a different and complex structure, of heterotrophic protists of the genus *Rabdiophrys* Raine and scaled chrysophytes genera *Mallomonas* Perty and *Synura*, were found in deposits of 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) (Siver and Wolfe, 2005a; 2005b; 2009; Siver and Lott, 2012; Siver et al., 2013; 2015; Siver and Skogstad, 2022). Chrysophycean stomatocysts in paleolimnological studies were assigned to one group and considered relative to the total number of diatoms calculated on the same microscopic preparations (for example, Smol, 1983; Stoermer et al., 1985; Grönlund et al., 1986; Harwood, 1986). D. Smol suggested (Smol, 1985) using the ratio of diatoms to cysts (D/C) as a coefficient of eutrophication of reservoirs. The proposed methods, with their relative simplicity, provide useful information about the environmental conditions in paleovodoems (Zeeb and Smol, 2001). Due to the complexity of determining the species of stomatocysts, the international group for the study of statospores International Statospore Working Group (ISWG) (Cronberg and Sandgren, 1986), digital designations of morphotypes of stomatocysts have been adopted. To date, more than 800 morphotypes of stomatocysts have been described in the world, of which more than 200 are known for Russia. On the territory of Russia, studies of modern and fossil stomatocysts were carried out in the lake. Baikal in the sediments of the Lena River and Lake "TS-9" on the Taimyr Peninsula, the Chukotka Peninsula, in Lake Khubsugul, Lake Teletskoye and in the North of Russia (Vorobyova et al., 1996; Wilkinson et al., 2001; Firsova and Likhoshway, 2006; Firsova et al., 2008; 2012; Bazhenova et al., 2012; Voloshko, 2016).

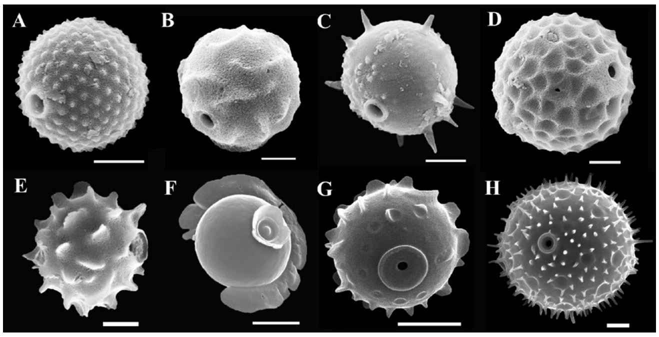

Fig.2. The variety of morphotypes of chrysophycean stomatocysts from Vorota Lake (Yakutia) (1-5) and Boguchany reservoir (6-8). A – Stomatocyst 031, Duff & Smol; B – Stomatocyst 498, Firsova & Bessudova; C – Stomatocyst 314, Firsova; D – Stomatocyst 506, Firsova & Bessudova; E – Stomatocyst 501, Firsova & Bessudova; F – Stomatocyst 489, Firsova & Bessudova; G – Stomatocyst 487; Firsova & Bessudova; H – Stomatocyst 076 Duff & Smol. Scale – 2 μm.

The first studies of scaled chrysophytes of Eastern Siberia using electron microscopy were carried out in the Khanty reservoir, the Khanty River, in small rivers flowing into the reservoir, and in the Big Khanty Lake (Balonov and Kuzmina, 1986); as a result, 29 species were identified. The use of new methods has made it possible to reliably identify 14 species of scaled chrysophytes in Lake Baikal (Vorobyova et al., 1992), and 5 species in the Irkutsk reservoir (Vorobyova et al., 1996). Later, foreign scientists investigated the species composition of scaled chrysophytes on the Taimyr Peninsula (Duff, 1996; Kristiansen et al., 1997). The study area included small unnamed lakes (Duff, 1996), Lake Taimyr, Lake Engelhardt, a lake in the north of the village of Khatanga, a lake in the Talnakh district (the city of Norilsk) and small temporary reservoirs (Kristiansen et al., 1997). A total of 23 species have been found on the Taimyr Peninsula. Recent studies on the scaled chrysophytes of Eastern Siberia have been conducted in the lake. Frolikha (Transbaikalia) (Gusev and Kulikovsky, 2013; Gusev, 2016). As a result, 10 species were identified.

The first study of chrysophycean stomatocysts carried out using electron microscopy on the basis of the cell ultrastructure department was published in 1996 by S.S. Vorobyova and co-authors. The article contained descriptions and illustrations of 7 morphotypes, 5 of which were described for the first time. As a result of studies of the continuous Baikal chronicle of sedimentary deposits of siliceous microfossils, mainly diatoms, the presence of siliceous cysts in sediments of Lake Baikal of different ages was noted (Bradbury et al., 1994; Likhoshway, 1999) and in modern bottom sediments (Stoermer et al., 1995; Likhoshway et al., 2005), but their structure has not been described.

The method of electron microscopy has significantly expanded the possibilities for studying these organisms. The species composition of scaled chrysophytes was studied in the zone of mixing of the waters of the Yenisei River and the Kara Sea, as well as in thermokarst lakes of the Lower Yenisei basin (Bessudova et al., 2015; Bessudova et al., 2016; Firsova et al., 2017; Bessudova et al., 2018a). In total, 40 species of scaled chrysophytes were found in the studied areas. Based on the original data obtained on the species diversity, the distribution of scaled chrysophytes relatively changing hydrochemical parameters of the environment in the river-sea water mixing zone, summary data taking into account the literature on the occurrence of these organisms and their autecology, a monograph has been compiled (Bessudova et al., 2016).

The study of scaled chrysophytes inevitably led to a more detailed consideration of heterotrophic protists due to the similarity in size, timing of development and structure of siliceous elements. Since earlier studies of the ecology of diversity and seasonal dynamics of silicon utilizing protists from reservoirs in Eastern Siberia have not been conducted, electron microscopy methods have opened up new prospects.

For the first time in Eastern Siberia, the species composition of heterotrophic protists in a system connected by watercourses, from Lake Baikal to the Kara Sea, has been studied. A total of 29 species of heterotrophic protists were found: 21 species of centrohelid heliozoans, 6 species belonging to rotospherids and one flagellate protist (Bessudova et al., 2021a). It is shown that the most diverse silicon utilizing heterotrophic protists are represented in the river-sea and river-lake ecotonic zones. It was revealed that even a small increase in salinity sharply limits the diversity of these organisms. However, two species with a wide ecological valence have been identified, occurring from the mouth of the Yenisei River to the northernmost section of the northeastern part of the Kara Sea (Bessudova et al., 2021a). The distribution of chrysophycean stomatocysts during mixing of fresh and salty waters was also studied (Firsova and Tomberg, 2012). 12 morphotypes of stomatocysts were found in plankton and sediments of mineralized meromictic Lake Shira (Khakassia, Russia) (Firsova, 2014).

The species composition and ecology of scaled chrysophytes and stomatocysts in the Baikal region have been studied in the most detail. In 2006, an atlas of chrysophycean stomatocysts was created, which included a detailed description of 93 morphotypes of fossil cysts from Holocene and Upper Pleistocene bottom sediments and 33 morphotypes from Baikal plankton (Firsova and Likhoshway, 2006). In the future, the seasonal dynamics of stomatocysts from phytoplankton of Southern Baikal was studied. It was revealed that siliceous stomatocysts of golden algae make a significant contribution to phytoplankton, reaching the highest values (46.8×10^3 cysts per l) in August-October with a minimum concentration of biogens. The D/C coefficient (the ratio of diatom and cyst cells) varies throughout the year, reflecting the seasonal succession of phytoplankton and changes in the concentration of biogenic elements in the photic layer. 50 morphotypes of cysts have been identified, which are divided into 25 groups according to morphological features. The selected groups of cyst morphotypes have different seasonal dynamics. Group 5 cysts (with spikes of various lengths on the equatorial and posterior parts of the cysts) dominate over the other morphotypes and reach the highest concentration (13.6×10^3 cysts per l) in August (Firsova et al., 2008). The geography of research gradually expanded. Siliceous microfossils were studied in the Upper Miocene deposits of Transbaikalia (in the Jilindin formation of the eastern part of the Amalat paleodoline of the Amalat plateau of the Vitim Plateau). It was noted that stomatocysts of chrysophycean algae were found almost throughout the section. A total of 26 morphotypes of cysts were found, among which 6 new ones were identified. The dominant (up to 57%) were smooth, without collar and ornamentation (*Mallomonas*, *Paraphysomonas* (Stokes) DeSaedeleer, *Chrysosphaerella* Lauterborn). The total number of cysts varied from 7 thousand to 82 million copies/g. The largest number of cysts (65-82 $\times 10^6$ cysts per g) was observed in the depth range from 176-172 m. The values of the D/C coefficient (2.7-6.1) proposed earlier to characterize the trophic capacity of the reservoir (Smol, 1985) at this horizon were minimal, which indicates a possible decrease in the trophic content of the water reservoir during this period (Usoltseva et al., 2008). In the Pleistocene-Holocene deposits of Lake Elgygytgyn (Chukotka), 8 morphotypes of cysts were found, of which 3 were new to science. It was shown that smooth unornamented cysts without collars and complex ornamentation (more than 40%) most often prevailed among the morphotypes. The distribution pattern of various morphotypes of golden algae cysts has been studied (Firsova, 2013). In the Miocene deposits of the Vitim plateau in the core of sle. 7236 in the depth range of 126-249 m, 60 morphotypes of cysts were found, of which 9 are new to science. To study the nature of the distribution of various morphotypes, they were divided into 28 groups (GV) according to the shape, ornamentation and structure of the collar. It was revealed that the distribution of morphotype groups in the core had a different character. In the middle part of the core (depth interval 199-168 m), the greatest variety of stomatocysts was noted. During this period, the conditions in the reservoir were most favorable for both the development of cysts and planktonic diatoms (Firsova et al., 2010).

In 2012, the analysis of microfossils from the core of Upper Pleistocene and Holocene sediments of the southern part of Lake Khubsugul revealed 36 different morphotypes of stomatocysts. Some of them were assigned to the genera *Mallomonas*, *Chrysosphaerella*, *Paraphysomonas* and *Dinobryon* Ehrenberg 20 morphotypes were described as new to science. The abundance and diversity of morphotypes of stomatocysts in the core sample varied depending on the age of the deposits. It is noted that the highest diversity of morphotypes is observed in the layers corresponding to the periods of development of the cold-water diatom *Cyclotella bodanica* Eulenstein ex Grunow. Smooth (unornamented) morphotypes are the most common in sediments. It has been established that the morphotypes H12, H19 and H22 are typical for Lake Khubsugul, which occur throughout the core depth and, at certain intervals, account for up to 40% of the total number of stomatocysts. The intervals when the dried-up southern part of the lake was again filled with water were characterized by the highest values of D/C, which means that the trophic level of the lake temporarily increased during these periods (Firsova et al., 2012).

The revision of the scaly chrysophytes of Lake Baikal made it possible to supplement the species list with 13 species, and amounted to 25 species (Bessudova et al., 2017). The seasonal dynamics of these organisms is revealed, it is shown that the greatest variety of scaly chrysophytes is characteristic of the Southern and Middle regions of Lake Baikal. The maximum abundance and species diversity was noted in the autumn period. Also, the composition of chrysophytic stomatocysts was replenished with 8 morphotypes new to Baikal, of which 5 are described as new to science. For 3x, the presence of scales and their structure made it possible to establish the species (Firsova et al., 2017; 2018)

A study of the mouths of rivers flowing into Baikal, small bays and straits revealed a high diversity of scaled chrysophytes, which amounted to 66 species (Bessudova et al., 2018b, 2018c) and morphotypes of stomatocysts – 58, of which 25 were described as new (Firsova et al., 2018). It is shown that large rivers – Upper Angara, Barguzin and Selenga affect the lake. Baikal, increasing the diversity of scaled chrysophytes in its Southern, Middle and Northern basins, however, due to the difference in habitat conditions, their distribution is limited. The greatest diversity recorded in shallow, well-warmed waters rich in nutrients is significantly reduced (from 66 to 17) when entering a cold oligotrophic lake. It was found that out of 25 species registered in the lake, 8 species were not found in the tributaries. Rare species have been found in the mouths of these large rivers, modified scales of the species *Mallomonas striata* Asmund have been observed. The change in the morphology of the scales could be triggered by a high phosphorus content (Bessudova et al., 2018b). In July 2018 in the floodplains of the Selenga and Barguzin rivers, a continuous period of low water was interrupted by high water. A study of the waters during this period showed that the species composition of the scaled chrysophytes on the one hand significantly decreased (to 23 species), on the other hand, it was enriched with new species for the Baikal region, amounting to 79 species (Bessudova et al., 2020). After analyzing two years of different water content, we came to the conclusion that the high diversity of scaled chrysophytes in the mouths of the main tributaries of Lake Baikal, Selenga, Upper Angara and Barguzin in low water conditions may be caused by previous floods. Flooding of floodplains led to the unification of small streams and lakes, which enriched their flora due to the spread of a wide range of species. The retreat of water stimulated the flowering of phytoplankton, in particular scaled chrysophytes, in warm and shallow reservoirs with a high level of biological productivity, which contributed to the diversity of scaled chrysophytes in the Baikal region. The alternation of floods and low water levels created different environmental conditions and stimulated the dynamics of the ecosystem, which allowed the formation of a “hotspot” for the diversity of scaled chrysophytes (Bessudova et al., 2020).

The waters of the largest hydroelectric power plant in Russia during the first years of operation at full capacity – the Boguchany reservoir have been studied. The influence of the source of the Angara River – Lake Baikal can be traced in the species composition of the scaled chrysophytes of the Boguchany reservoir. The species composition is not high and consists of only 23 species (Bessudova and Likhoshway, 2017). At the same time, 35 morphotypes of stomatocysts were found, 10 of them were registered for the first time in Russia and nine morphotypes new to science were described (Fig. 2) (Firsova et al., 2019). As a result of these studies, the list of chrysophycean stomatocysts of the Baikal region was expanded to 203. The data obtained not only expand the information about the diversity of stomatocysts, but also will allow further assessment of changes in the state of the reservoir.

After analyzing the scattered literature data on the distribution of scaled chrysophytes in northern reservoirs, above the 60th parallel north after the last glaciation of the Pleistocene, we identified hydrochemical parameters that significantly affect the distribution of these organisms (Bessudova et al., 2021b). Territories above the 60th parallel north were affected by glaciation at the end of the Pleistocene, and the lakes located here and their microflora were formed mainly at the beginning of the Holocene. We analyzed the distribution of scaled chrysophytes in 193 northern reservoirs. The formation of flora and species richness of scaled chrysophytes is most influenced by the location of the reservoir, temperature and water conductivity. Reservoirs similar in species composition can be significantly removed in the latitudinal direction. Eighteen species and one variety out of 165 discovered taxa found here have a clear similarity with ancient related groups; they are found in all studied regions and account for 6 to 54% of the total number of scaled chrysophytes. The settlement of scaled chrysophytes in northern reservoirs could occur at the end of the Pleistocene – the beginning of the Holocene along the circumpolar freshwater network of glacial-underground lakes, and the final composition of the flora was determined by the parameters of the habitat of each individual reservoir and the region in which the reservoir is located.

We continued our research on the biodiversity and ecology of scaled chrysophytes in collaboration with colleagues from the Institute of Cryolithozone Problems SB RAS in the remote and unexplored northern and Arctic regions of the Asian part of Russia, the Republic of Sakha (Yakutia). The biodiversity of silicon utilizing protists of reservoirs of Kotelny Island, Arctic, latitude 75°53 N was studied (Bessudova et al., 2022a (in press)). The research area is part of the Novosibirsk Islands archipelago. 17 species of silica scaled and 8 heterotrophic protists were found in the studied small reservoirs. On an Arctic island remote from the mainland, widespread species and cosmopolitans predominate, however, there are also some species specific to the area.

In large lakes located at the Cold Pole of the Northern Hemisphere – Labynkyr and Vorota, 23 species of scaled chrysophytes were identified (Bessudova et al., 2019). Rare species have been discovered, seasonal dynamics of chrysophytes has been investigated. 76 morphotypes of stomatocysts were also found in the waters of lakes, 51 of which are widespread, 24 of them were noted in Russia earlier and 25 were described as new (Firsova et al., 2020).

A high species diversity of scaled chrysophytes was revealed in the mouths of the Arctic rivers of Yakutia, numbering 82 species (Bessudova et al., 2021c), as well as in the Arctic waters of the Tiksi region, numbering 65 species (Bessudova et al., 2022b). New and rare Arctic species of scaled chrysophytes have been discovered (Bessudova et al., 2022b; 2022c). The hydrochemical parameters of the waters are analyzed and the main factors affecting their high diversity are identified (Bessudova et al., 2022b). The high diversity of these organisms is formed mainly from polyzonal and widespread species, but since 2008-2010 there has been an increase in the relative content of boreal species compared to the data obtained over the previous 30 years of studying northern reservoirs. The observed trends of climate warming may contribute to the Northward movement of representatives of the boreal flora. For a number of species, the research area is the northernmost habitat to date. Physico-chemical factors affecting the species composition and species richness of scaled chrysophytes in the study area have been identified.

The studied reservoirs of the Baikal region, the mouth of the Olenek River, as well as the Tiksi area can be considered “hot spots” of the scaled chrysophytes biodiversity, along with 3 previously marked points of the world. Also, in the mouths of the Arctic rivers of Yakutia and in small reservoirs of the Tiksi region, a high species diversity of silicon utilizing heterotrophic protists numbering 50 species was revealed (Bessudova et al., 2022d (in press)).

The study of the biodiversity of silicon utilizing protists using electron microscopy methods in combination with hydrochemical parameters has made a significant contribution to our knowledge of these organisms as indicators of changes in environmental conditions, which can serve as a criterion in assessing the state of modern reservoirs and an additional basis in the construction of paleoreconstructions in Eastern Siberia.

Acknowledgements

This study was performed using the facilities of the Instrumentation Center for Electron Microscopy at the Integrated Center of Ultra micro analysis (Limnological Institute, Siberian Branch, Russian Academy of Sciences. The study was supported by the project No. 0279-2021-0008.

Conflict of interest

The authors declare no conflict of interest.

References

Balonov I.M., Kuzmina A.E. 1986. Golden algae. In: Votintsev K.K. (Ed.), Izvestiya Limnologicheskogo instituta SO AN SSSR. Gidrokhimicheskiye i gidrobiologicheskiye issledovaniya Khantayskogo vodokhranilishcha. [Proceeding of Limnological Institute of the Siberian Branch of the Academy of Sciences of USSR. Hydrochemical and hydrobiological studies of the Khantay Reservoir]. Novosibirsk: Nauka, pp. 59-70. (in Russian)

Battarbee R.W. 1981. Diatom and Chrysophyceae microstratigraphy of the annually laminated sediments of a small meromictic lake. Striae 14: 105-109.

Bazhenova O.P., Mitrofanova E.Yu., Shakhoval E.V. 2012. Stomatocysts of chrysophyte algae from bodies of water in territory near Irtysh River in Omsk Region and Lake Teletskoe in Gorny Altai, Russia. Contemporary Problems of Ecology 5(4): 423-429. DOI: 10.1134/S1995425512040026

Bessudova A., Sorokovikova L.M., Tomberg I.V. et al. 2015. The diversity of chrysophycean algae in an arctic zone of river and sea water mixing, Russia. American Journal of Plant Sciences 6: 2439-2452. DOI: 10.4236/ajps.2015.615246

Bessudova A.Yu., Firsova A.D., Sorokovikova L.M. et al. 2016. Cheshuychatyye khrizofity basseyna Nizhnego Yeniseya i zalivov Karskogo morya s elementami autekologii [Scaled chrysophytes of the Lower Yenisei basin and bays of the Kara Sea with autecology elements]. Irkutsk: Institute of Geography. (in Russian)

Bessudova A.Yu., Likhoshway Ye.V. 2017. Silica chrysophytes (Chrysophyceae) of the Boguchany reservoir. Sovremennaya Nauka: Aktual’nyye Problemy Teorii i Praktiki. Seriya: Yestestvennyye i Tekhnicheskiye Nauki [Modern Science: Actual Problems of Theory and Practice. Series: Natural and Technical Sciences] 11: 4-11. (in Russian) URL: http://www.nauteh-journal.ru/index.php/----etn17-11/3936-a

Bessudova A., Domysheva V.M., Firsova A.D. et al. 2017.

Scaled chrysophytes of Lake Baikal. Acta Biologica Sibirica 3(3): 47-56. DOI: 10.14258/abs.v3i3.3615

Bessudova A., Bukin Y.S., Sorokovikova L.M. et al. 2018a. Scaled chrysophytes in Small Lakes of the Lower Yenisei Basin, the Arctic. Nova Hedwigia 107(3-4): 315-336. DOI: 10.1127/nova hedwigia/2018/0473

Bessudova A., Sorokovikova L.M., Tomberg I.V. et al. 2018b. Scaled chrysophytes in large tributaries of Lake Baikal. Cryptogamie Algologie 39(2): 1-21. DOI: 10.7872/crya/v39.iss2.2018.145

Bessudova A., Firsova A.D., Tomberg I.V. et al. 2018c. Biodiversity of scaled chrysophytes in tributaries of northern limit of Lake Baikal. Acta Biologica Sibirica 4(3): 75-84. DOI: 10.14258/abs.v4i3.4411

Bessudova A., Tomberg I.V., Firsova A.D. et al. 2019. Scaled chrysophytes in lakes Labynkyr and Vorota of the Sakha (Yakutia) Republic, Russia. Nova Hedwigia, Beiheft 148: 35-48. DOI: 10.1127/nova-suppl/2019/049

Bessudova A.Yu., Sorokovikova L.M., Sinyukovich V.N. et al. 2020. Effects of water levels on species diversity of scaled chrysophytes in large tributaries of Lake Baikal. Acta Biologica Sibirica 55: 7-22. DOI: 10.3897/abs.6.e52840

Bessudova A., Firsova A.D., Likhoshway Y.V. 2021a. Silica scaled heterotrophic protists Rotosphaerida, Thaumatomonadida, and Centroplasthelida in the large continuous ecosystem connecting Lake Baikal to the Kara Sea. Journal of Eukaryotic Microbiology 69(1). DOI: 10.1111/jeu.12871

Bessudova A., Bukin Y., Likhoshway Y.V. 2021b. Dispersal of scaled chrysophytes in Northern Water Bodies. Diversity 13: 1-23. DOI: 10.3390/d13070284

Bessudova A.Yu., Gabyshev V.A., Firsova A.D. 2021c. Diversity of scaled chrysophytes and physicochemical parameters of their environment in the estuaries of rivers in the arctic watershed of Yakutia, Russia. Sustainability 13: 13768. DOI: 10.3390/su132413768

Bessudova A., Gabyshev V., Firsova A.D. 2022a. Siliceous scales protists (Chrysophyceae, Centroplasthelida, Thaumatomonadida and Rotosphaerida) in the some reservoirs of the Arctic Island of Kotelny, Russia. Polar Biology. (in press)

Bessudova A., Gabyshev V., Bukin Yu. 2022b. Species richness of scaled Chrysophytes in arctic waters in the Tiksi Region (Yakutia, Russia). Acta Biologica Sibirica 8: 431-459. DOI: 10.14258/abs.v8.e26

Bessudova A., Gabyshev V., Likhoshway Y.V. 2022c. Record of two rare taxa from *Synura* genus (Chrysophyceae) with a description of a new species (*Synura tiksiensis* sp. nov.) near the arctic settlement of Tiksi, Yakutia, Russia. Phytotaxa 560(1): 1-7. DOI: 10.11646/phytotaxa.560.2.8

Bessudova A., Gabyshev V., Likhoshway Ye.V. 2022d. Silica scaled heterotrophic Protists Rotosphaerida, Thaumatomonadida, and Centroplasthelida in the Arctic Reservoirs of Russia. Diversity. (in press)

Bradbury P., Bezrukova E.V., Chernyaeva G.P. et al. 1994. A synthesis of post-glacial diatom records from Lake Baikal. Journal of Paleolimnology 10: 213-252. DOI: 10.1007/BF00684034

Boo S.M., Kim H.S., Shin W. et al. 2010. Complex phylogeographic patterns in the freshwater alga Synura provide new insights into ubiquity vs. endemism in microbial eukaryotes. Molecular Ecology 19: 4328-4338. DOI: 10.1111/j.1365-294X.2010.04813.x

Cronberg G., Sandgren C.D. 1986. A proposal for the development of standardized nomenclature and terminology for Chrysophycean statospores. In: Kristiansen J., Andersen R.A. (Eds.), Chrysophytes: aspects and problems. Cambridge: Cambridge University Press, pp. 317-328.

Cumming B.F., Wilson S.E., Smol J.P. 1993. Paleolimnological potential of chrysophyte cysts and scales and of sponge spicules as indicators of lake salinity. International Journal of Salt Lake Research 2: 87-92. DOI: 10.1007/BF02905055

Duff K.E. 1996. Chrysophyte microfossils in arctic Siberian lakes. Chrysophytes: progress and new horizons. Nova Hedwigia, Beiheft 114: 253-263.

Izmestyeva L.P., Kozhova O.M. 1988. Dolgosrochnoye prognozirovaniye sostoyaniya ekosistemy [Long-term forecasting of the state of ecosystems]. Novosibirsk: Nauka, pp. 97-129. (in Russian)

Finlay B.J., Esteban G.F., Fenchel T. 1998. Protozoan diversity: converging estimates of the global number of free-living ciliate species. Protist 149: 29-37. DOI: 10.1038/383132a0

Firsova A.D., Likhoshway Y.V. 2006. Atlas tsist khrizofitovykh vodorosley ozera Baikal [Atlas of chrysophycean algae cysts of Lake Baikal]. Novosibirsk: Nauka. (in Russian)

Firsova A.D., Kuzmina A.E., Tomberg I.V. et al. 2008. Seasonal dynamics of the formation of stomatocysts of chrysophycean algae in the plankton of Southern Baikal. Biology Bulletin 35: 507-514. DOI: 10.1134/S1062359008050129

Firsova A.D., Usoltseva M.V., Vorobyeva S.S. et al. 2010. Stomatocysts of golden algae in Miocene deposits of the Vitim plateau. In: The fifth Vereshchagin Baikal Conference, pp. 95-97. (in Russian)

Firsova A.D., Tomberg I.V. 2012. Stomatocysts of chrysophycean algae when mixing fresh and salt water. In: XV All-Russian Micropaleontological Meeting “Modern Micropaleontology”, p. 373. (in Russian)

Firsova A.D., Vorobyova S.S., Likhoshway Y.V. 2012. Chrysophycean stomatocysts in the upper pleistocene and holocene sediments from Lake Hovsgol, Northern Mongolia. International Journal of Geosciences 3: 664-674. DOI: 10.4236/ijg.2012.34067

Firsova A.D. 2013. Stomatocysts of golden algae from sediments of Lake Elgygytgyn (Chukotka). In: LIX session of the Paleontological Society “Systematics of organisms. Its significance for biostratigraphy and Paleogeography”, pp. 131-132. (in Russian)

Firsova A.D. 2014. Stomatocysts of Chrysophytes in Lake Shira. Acta Geologica Sinica 88(1): 68-69. DOI: 10.1111/1755-6724.12266 12

Firsova A.D., Bessudova A.Yu., Likhoshway Y.V. 2017. New data of chrysophycean stomatocysts from Lake Baikal. Acta Biologica Sibirica 3(4): 113-122. DOI: 10.14258/abs.v3i4.3637

Firsova A.D., Bessudova A., Likhoshway Y.V. 2018. Chrysophycean stomatosysts in tributaries of northern limit of Lake Baikal. Acta Biologica Sibirica 4(4): 25-44. DOI: 10.14258/abs.444872

Firsova A.D., Bessudova A.Yu., Sorokovikova L.M. et al. 2019. Stomatocyst diversity in the first years of the plankton species structure formation in reservoir of hydropower plants (Boguchany reservoir, Russia). Phytotaxa 424(1): 18-32. DOI: 10.11646/phytotaxa.424.1.2

Firsova A.D., Bessudova A., Kopyrina L.I. et al. 2020. Chrysophycean stomatocysts from two unique lakes of Yakutia (Russia). Phytotaxa 474(3): 197-217. DOI: 10.11646/phytotaxa.474.3.1

Gavrilova O.V., Nogina N.V., Voloshko L.N. 2005. Scale structures and growth characteristics of *Synura petersenii* (Synurophyceae) under different pH conditions. Nova Hedwigia. Beiheft 128: 249-256.

Grönlund E., Simola H., Huttunen P. 1986. Paleolimnological reflections of fiber-plant retting in the sediments of a small clearwater lake. Hydrobiologia 143:

425-531. DOI: 10.1007/BF00026693

Guiry M., Guiry G. 2022. AlgaeBase. Worldwide electronic publication, National University of Ireland, Galway. URL: https://www.algaebase.org; searched on 2022. március 13

Gusev E.S., Kulikovskiy M.S. 2013. A new species of the genus *Mallomonas* (Chrysophyceae: Synurales), *Mallomonas kuzminii* sp. nov., from lake Frolikha (Russia, Baikal region). Phytotaxa 155(1): 66-70. DOI: 10.11646/phytotaxa.155.1.6

Gusev E.S. 2016. Contribution to the flora of scaled chrysophytes of Frolikha Lake (North transbaikal area). Trudy Instituta Biologii Vnutrennikh Vod im. I.D. Papanina RAN [Transactions of Papanin Institute for Biology of Inland Waters RAS] 76(79): 25-30. (in Russian)

Hahn A., Gutowski A., Geissler U. 1996. Scale and bristle morphology of *Mallomonas tonsurata* (Synurophyceae) in cultures with varied nutrient supply. Botanica Acta 109: 239-247.

Harwood D.M. 1986. Do diatoms beneath the Greenland Ice Sheet indicate interglacials warmer than present? Arctic 39: 304-308. DOI: 10.14430/arctic2092

Kozhova O.M., Zagorenko G.F. 1982. About the state of phytoplankton of Baikal. Vodnyye resursy [Water Resources] 4: 149-157. (in Russian)

Kristiansen J., Düwel L., Wegeber S. 1997. Scaled chrysophytes from the Taymyr Peninsula, Northern Siberia. Nova Hedwigia 65: 337-351. DOI: 10.1127/nova.hedwigia/65/1997/337

Lengyel E., Barreto S., Padisák J. et al. 2022. Contribution of silica-scaled chrysophytes to ecosystems services: a review. Hydrobiologia. DOI: 10.1007/s10750-022-05075-5

Leonov M.M., Mylnikov A.P. 2012. Centroheliozoa from Southern Karelia. Zoologicheskii Zhurnal 91(5): 515-523.

Likhoshway Ye.V. 1999. Fossil endemic centric diatoms from Lake Baikal, upper Pleistocene complexes. In: XIV-th International Diatom Symposium, pp. 613-628. (in Russian)

Likhoshway Ye.V., Popovskaya G.I., Genkal S.I. et al. 2005. Biodiversity and evolution of siliceous algae in Lake Baikal and their role in sedimentation. In: IV-th Vereshchagin Baikal Conference, pp. 113-114. (in Russian)

Mikrjukov K.A. 2002. Tsentrokhelidnyye solnechniki (Centroheliozoa) [Centrohelid heliozoans (Centroheliozoa)]. Moscow: KMK Scientific Press. (in Russian)

Mushet G.R., Laird K.R., Das B. et al. 2017. Regional climate changes drive increased scaled-chrysophyte abundance in lakes downwind of Athabasca Oil Sands nitrogen emissions. Journal of Paleolimnology 58: 419-435. DOI: 10.1007/s10933-017-9987-6

Nelson D.M., Trrguer P., Brzezinski M.A. et al. 1995. Production and dissolution of biogenic silica in the ocean: revised global estimates, comparison with regional data and relationship to biogenic sedimentation. Global Biogeochemical Cycles 9(3): 359-732.

Nicholls K.H. 2012. New and little-known marine species of *Pinaciophora*, *Rabdiaster* and *Turriplaca* gen. nov. (Rotosphaerida: Pompholyxophryidae. Journal of the Marine Biological Association of the UK 93: 1211-1229. DOI: 10.1017/S002531541200135X

Ostroumov A.A. 1917. On a new species of heliozoans from marine plankton (*Acanthocystis wiasemskii*). Trudy Karadagskoy nauchnoy stantsii im. T.I. Vyazemskogo [Proceedings of the T.I. Vyazemsky Karadag Scientific Station] 1: 62-65. (in Russian)

Peglar S.M., Fritz S.C., Alapieti T. et al. 1984. Compostition and formation of laminated sediments in Diss Mere, Norfolk, England. Boreas 13: 13-28.

Prokina K.I., Mylnikov A.P. 2019. Centrohelid heliozoans from freshwater habitats of different types of South Patagonia and Tierra del Fuego, Chile. Inland Water Biology 12(1): 10-20. DOI: 10.1134/S1995082919010164

Prokina K.I., Philippov D.A. 2019. Centrohelid heliozoans (Haptista: Centroplasthelida) from mires in the North Caucasus, Russia. Mires and Peat 36: 1-20. DOI: 10.19189/MaP.2019.OMB.StA.1806

Ragueneau O., Treguer P., Leynaert A. et al. 2000. A review of the Si cycle in the modern ocean: recent progress and missing gaps in the application of biogenic opal as a paleoproductivity proxy. Global and Planetary Change 26: 317-365.

Rühland K.M., Paterson A.M., Smol J.P. 2008. Hemispheric-scale patterns of climate-related shifts in planktonic diatoms from North American and European lakes. Global Change Biology 14: 2740-2754. DOI: 10.1111/j.1365-2486.2008.01670.x

Schindler D.W. 2001. The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. Canadian Journal of Fisheries and Aquatic Sciences 58: 18-29. DOI: 10.1139/cjfas-58-1-18

Shishkin Y., Drachko D., Klimov V.I. et al. 2018. *Yogsothoth knorrus* gen. n., sp. n. and *Y. carteri* sp. n. (Yogsothothidae fam. n., Haptista, Centroplasthelida), with notes on evolution and systematics of Centrohelids. Protist 169: 682-696. DOI: 10.1016/j.protis.2018.06.003

Siver P.A., Wolfe A.P. 2005a. Scaled chrysophytes in middle Eocene lake sediments from northwestern Canada, including descriptions of six new species. Nova Hedwigia. Beiheft 128: 295-308.

Siver P.A., Wolfe A.P. 2005b. Eocene scaled chrysophytes with pronounced modern affinities. International Journal of Plant Sciences 166: 533-536. DOI: 10.1086/428702

Siver P.A., Wolfe A.P. 2009. Tropical ochrophyte algae from the Eocene of Northern Canada: a biogeographical response to past global warming. Palaios 24: 192-198. DOI: 10.2110/palo.2007-p07-077r

Siver P.A., Lott A.M. 2012. Fossil species of *Mallomonas* from an Eocene maar lake with recessed dome structures: early attempts at securing bristles to the cell covering? Nova Hedwigia 95: 517-529. DOI: 10.1127/0029-5035/2012/0057

Siver P.A., Lott A.M., Wolfe A.P. 2013. A summary of *Synura* taxa in early Cenozoic deposits from northern Canada. Nova Hedwigia. Beiheft 142: 181-190.

Siver P.A. 2015. Synurophyte algae. In: Wehr J.D., Sheath R.G., Kociolek J.P. (Eds.), Freshwater algae of North America: ecology and classification. 2nd ed. Boston, MA: Academic Press, pp. 607-651.

Siver P.A., Jo B.Y., Kim J.I. et al. 2015. Assessing the evolutionary history of the class Synurophyceae (Heterokonta) using molecular, morphometric, and paleobiological approaches. American Journal of Botany 102: 921-941. DOI: 10.3732/ajb.1500004

Siver P.A., Skogstad A. 2022. A first account of the heterotrophic eukaryote *Rabdiophrys* Rainer from the fossil record and description of a new species from an ancient Eocene Arctic freshwater lake. European Journal of Protistology 82: 125857. DOI: 10.1016/j.ejop.2021.125857

Stoupin D., Kiss A.K., Arndt H. et al. 2012. Cryptic diversity within the choanoflagellate morphospecies complex *Codosiga botrytis* – phylogeny and morphology of ancient and modern isolates. European Journal of Protistology 48: 263-273. DOI: 10.1016/j.ejop.2012.01.004

Smol J.P. 1983. Paleophycology of a high arctic lake near Cape Herschel, Ellesmere Island. Canadian Journal of Botany 61: 2195-2204.

Smol J.P. 1985. The ratio of diatom frustules to chrysophyceanstatospores: a useful paleolimnological index. Hydrobiologia 123: 199-204.

Smol J.P. 1988. Chrysophycean microfossils in paleolimnological studies. Palaeogeography, Palaeoclimatology, Palaeoecology 62: 287-297.

Stoermer E.F., Wolin J.A., Schelske C.L. et al. 1985. An assessment of ecological changes during the recent history of Lake Ontario based on siliceous algal microfossils preserved in the sediments. Journal of Phycology 21: 257-276.

Stoermer E.F., Edlund M.B., Pilskaln C.H. et al. 1995. Siliceous microfossil distribution in the surficial sediments of Baikal. Journal of Paleolimnology 14: 69-82. DOI: 10.1007/BF00682594

Tréguer P., De La Rocha C. 2013. The world ocean Silica cycle. Annual Review of Marine Science 5: 477-501. DOI: 10.1146/annurev-marine-121211-172346

Usoltseva M.V., Vorobyeva S.S., Firsova A.D. et al. 2008. Siliceous microfossils in the Upper Miocene deposits of Transbaikalia. Novosti Paleontologii i Stratigrafii. Prilozheniye k zhurnalu Geologiya i Geofizika [News of Paleontology and Stratigraphy. Supplement to the journal Geology and Geophysics] 10-11(49): 360-362. (in Russian)

Vorobyova S.S., Bondarenko N.A., Karpov S.A. et al. 1992. By the autumn of the species composition of Baikal Chrysophyta. Al’gologiya [Algology] 2(3): 68-72. (in Russian)

Vorobyova S.S., Pomazkina G.V., Baranova E.Yu. et al. 1996. Chrysophycean cysts (stomatocysts) from lake Baikal and Irkutsk Reservoir, Siberia. Journal of Paleolimnology 15: 271-277. DOI: 10.1007/BF00213046

Voloshko L.N. 2016. Golden algae (Chrysophyta) North-west of Russia. A variety of stomatocysts. Botanicheskiy Zhurnal [Botanical Journal] 101(11): 1257-1281. (in Russian)

Wilkinson A.N., Zeeb B.A., Smol J.P. 2001. Atlas of Chrysophycean cysts. Dordrecht: Kluwer Academic Publishers.

Wolfe A.P., Siver P.A. 2013. A hypothesis linking chrysophyte microfossils to lake carbon dynamics on ecological and evolutionary time scales. Global and Planetary Change 111: 189-198. DOI: 10.1016/j.gloplacha.2013.09.014

Zeeb B.A., Smol J.P. 1993. Chrysophycean stomatpcyst flora from Elk Like, Clearwater Couty, Minesota. Canadian Journal of Botany 71: 737-756.

Zeeb B.A., Smol J.P. 2001. Chrysophyte scales and cysts. In: Smol J.P., Birks H.J.B., Last W.M. (Eds.), Tracking environmentaI change using lake sediments. Volume 3: Terrestrial, algal, and siliceous indicators. Dordrecht: Kluwer Acad. Publ., pp. 203-223.

Zlatogursky V.V. 2012. *Raphidiophrys heterophryoidea* sp. nov. (Centrohelida: Raphidiophryidae), the first heliozoan species with a combination of siliceous and organic skeletal elements. European Journal of Protistology 48: 9-16. DOI: 10.1016/j.ejop.2011.09.004