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Articles

The contribution of the "Darwin Initiative" collection in the Lake Baikal benthic diatom survey

Tatyana A. Sherbakova	Limnological Institute of the Siberian Branch of the Russian Academy of Sciences, 3 Ulan-Batorskaya, Irkutsk, 664033, Russia
Galina V. Pomazkina	Limnological Institute of the Siberian Branch of the Russian Academy of Sciences, 3 Ulan-Batorskaya, Irkutsk, 664033, Russia
Dmitri Yu. Sherbakov	Limnological Institute of the Siberian Branch of the Russian Academy of Sciences, 3 Ulan-Batorskaya, Irkutsk, 664033, Russia
Yelena V. Rodionova	Limnological Institute of the Siberian Branch of the Russian Academy of Sciences, 3 Ulan-Batorskaya, Irkutsk, 664033, Russia

The joint Russian-British collection "Darwin Initiative. Benthic samples of Lake Baikal", was established at the end of the 1990s. Here we briefly overview the data on the survey of the Lake Baikal coastal diatom diversity obtained exclusively using the materials from the collection and methods of light and scanning electron microscopy. The collection contains over 500 initial samples taken at 53 stations of the lake littoral zone from depths 1–20 m. Studying the samples Russian and foreign algologists have identified many new for science diatom taxa, including over 20 genera and 750 species. Data on the collection survey are published in six monographs and atlases, and more than 20 scientific papers. The observed patterns of diversity, distribution, and levels of endemicity in different taxa of Lake Baikal benthic diatoms are discussed.

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Corresponding author: Tatyana A. Sherbakova (tsherb@lin.irk.ru)

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Keywords

Diatom diversity, new taxa, species flocks

The benthic flora of Lake Baikal and, in particular, diatoms, have been studied for more than 100 years. Up to the thirties of the last century, the works of the first researchers of Lake Baikal laid the basic knowledge about the benthic flora of the lake, the heterogeneity of its spatial distribution, the existence of vegetation belts, species composition of diatom assemblages in shallow waters and

deeper areas of the littoral zone (Gutwinski 1890, 1891; Dorogostaysky 1906; Meyer 1930). The following essential studies revealed the diversity of benthic diatoms composed of elements of the Siberian flora, relict organisms, cosmopolitan taxa, and a significant portion (up to 40%) of endemic Baikal species (Skvortzov and Meyer 1928; Skvortzov 1937; Jasnitsky 1936; Skabichevsky 1936). Then, for a long time, studies of the bottom microflora of the deepest lake on the planet (as well as the other freshwater or marine ecosystems) were restrained, mainly by the limitations of light microscopy.

The potential of high-resolution electron optics in the application to diatom frustule morphology, has been realized since the end of the 1970s and has contributed to the revival of biologists' interest to the studies of benthic Bacillariophyta and their role in aquatic ecosystems. This is evident by the increase in the number of scientific publications in the world with the keyword "benthic diatoms," which has risen, for example, forty-four times in 2012 compared to 1972.

By the end 1980s on the basis of the Limnological Institute of the Siberian Branch of the Russian Academy of Sciences, the Baikal International Center for Environmental Research (BICER) was established to coordinate international research on Lake Baikal. Within the frameworks of BICER the Natural History Museum (London), University College (London) and the Limnological Institute (Irkutsk), have been cooperating on a "Darwin Initiative for the Survival of Species" project to carry out taxonomic and ecological research of benthic diatoms of Lake Baikal.

The primary objective of this initiative was to create a new reference collection of samples of Lake Baikal benthos, which would serve as a source of materials for further detailed study of bottom diatom assemblages. The sampling strategy included a large-scale spatial survey along the whole perimeter of the lake (about 2000 km) in the littoral and sublittoral zones. In joint expeditions of Russian and British scientists during two summer seasons (June and July, 1997, 1998), surveys were carried out along the entire coastline, divided into 53 stations located at intervals of about 35 km (Figure 1). At each station, benthic samples were taken with the help of scuba divers at 1–2 m from the coastal line and in the lower littoral zone at depths up to 20 m. At shallow waters of open shores covered with boulders, and on rocky headlands, epilithic samples were taken from a stone substrate. In deeper bottom areas lined with silted sand or gravel, epipsammon/epipelon was sampled using an Ekman sampler (Flower et al. 2004; Flower and Chambers 2004). All samples were taken in three repeats.

In addition, two transects were selected in Southern Baikal for seasonal monitoring of benthic diatoms (Fig. l): station 1 in the reference area close to the village of Bolshie Koty on the rocky western shore and station 40 near the city of Baikalsk on the eastern cost.

In total, over 500 integral samples preserved in alcohol, characterized granulometrically, by depth, location, and GPS coordinates, formed the basis of the collection "Darwin Initiative. Benthic samples of Lake Baikal", which will be further in the text abbreviated as the "DI collection". Each of the samples was divided in half to form two copies of the DI collection. One exemplar of the DI collection is kept in the Natural History Museum, London, UK, and the other is stored in the Limnological Institute SB RAS, Irkutsk, Russia.

For light microscopy, a permanent slide with cleaned diatom material processed from any initial sample of the DI collection was mounted using Naphrax. For scanning electron microscopy an aliquot of the suspension of cleaned valves was placed on an aluminium stub, dried on air, coated with colloid gold, and examined. All the permanent slides and stubs for SEM prepared in this way are marked and included in the collection.

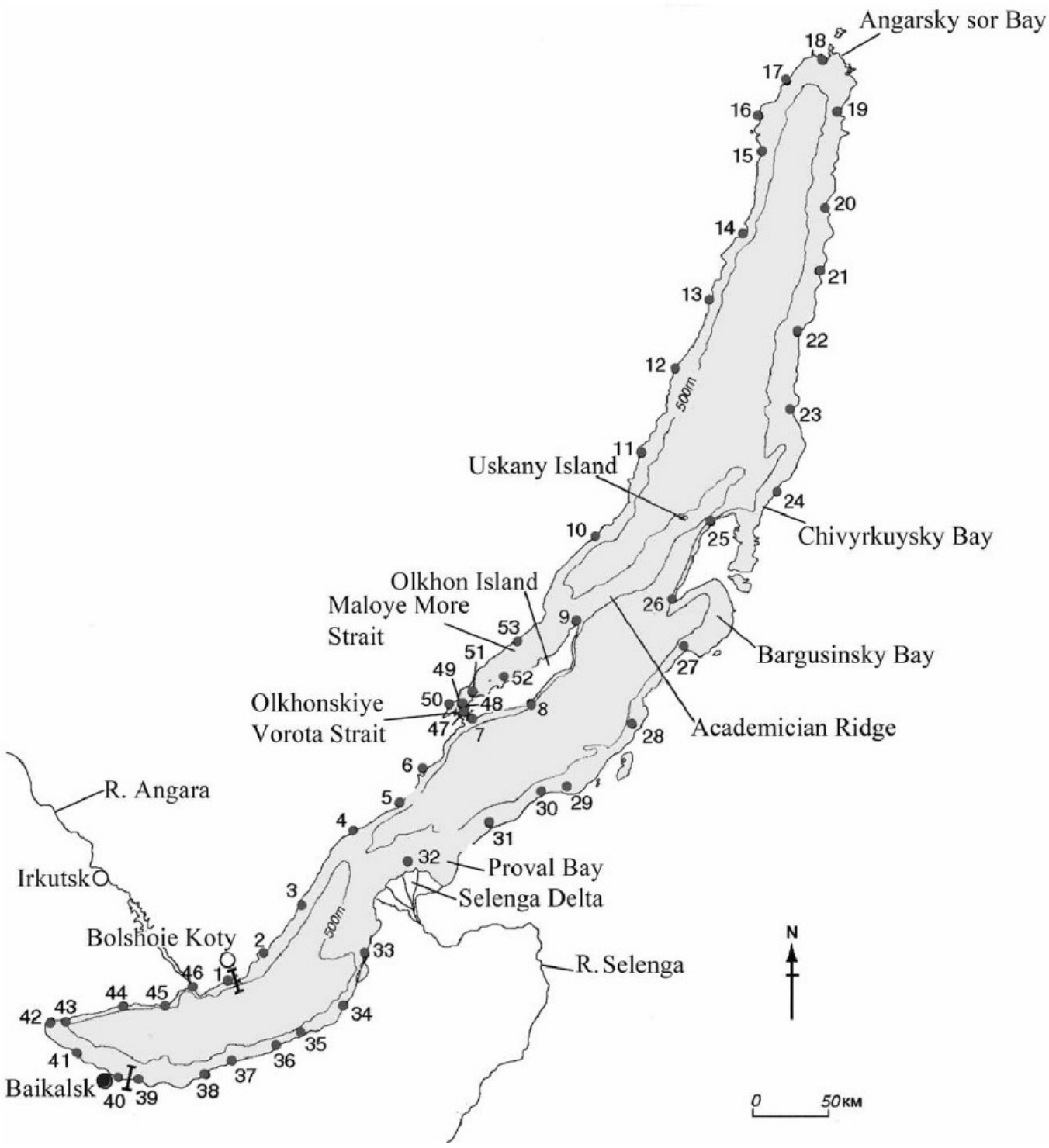

Figure 1. *Sampling stations around Lake Baikal littoral zone.*

The DI collection compiled in this way makes it possible to examine diversity, taxonomic composition, distribution, and other features of the nature of Lake Baikal benthic diatom communities.

The initial studies of Lake Baikal diatom flora based on materials of the DI collection brought some considerable results. In one of first works co-authored by English and Russian researchers (Flower et al. 2004), the patterns of distribution of benthic diatoms in shallow areas of the lake were studied. The diatom flora in these areas was not diverse and consisted largely of cosmopolitan taxa

or taxa closely related to them. The highest species richness was detected in the area of the Selenga River delta, as well as in the northern extremity of the lake. The number of almost the same dominant species in the samples varies from 1 to 4, regardless of the sample locality. All differences in species composition between stations were due to rare taxa (comprising less than 1% of the total number of valves) which varied between sampling points. In the littoral of the eastern and western shores of all three basins the distribution of dominant, widespread, or rare taxa does not form large-scale trends. This follows common trend for ancient lakes which "... provide little evidence for a predominant role of geography in speciation" (Critescu et al. 2010).

The study of seasonal samples taken regularly at fixed stations in Lake Baikal littoral zone, and also included in the DI collection, found more species compared to single surveys in the spatial research around the lake. The transect work on successional changes of diatom assemblages inhabiting the bottom from the 1 to 20 m in depth, revealed variation in the composition of abundant indicator species. At the area under human activity near the city of Baikalsk, there was a bias towards taxa belonging to o-β- and o-α-mesosaprobionts against the check point on the west coast, where xeno- and oligoxenosaprobes still prevailed (Pomazkina and Rodionova 2003; Pomazkina and Sherbakova 2011).

The initial examination of the DI collection has shown that the shallow water benthic diatom communities were dominated by forms thought to be cosmopolitan in distribution. However, there were subtleties of morphological difference from the widely spread types. This is exemplified by studying *Eunotia clevei* Grunow species complex which included some taxa united by a number of morphological features and ecological preference unusual for the genus *Eunotia* Ehrenberg. *E. clevei* was originally described from fossil material collected in Sweden and appears to be closely related to forms described by Skvortzov as endemic to Lake Baikal (*E. baicalensis* Skvortzov and K.I. Meyer, *E. clevei* var. *hispida* Skvortzov). After studying a large number of *E. clevei* specimens from various localities, fossils and other collections, a new genus, *Amphorotia* D.M. Williams and G. Reid, was established. Along with a dozen taxa transferred from other genera, the new genus contained five endemic Lake Baikal species, including two new to science (Williams and Reid 2003, 2006).

Studies of large scale distribution of several diatom species brought some important results and simultaneously showed extreme complexity of proving taxonomic status of very similar infraspecific subgroups. In the lack of molecular data one may rely only on the morphological features of baikalian forms which needed SEM investigations for precise identification. The necessity has closely joined the primary task of the project - studying the diversity of benthic diatoms within the lake.

After the acquisition in 2011 by the Limnological Institute of the scanning electron microscope Quanta 200 FEI (SEM), it became possible to conduct the priority task of the inventory of benthic taxa and the revision of previously described taxa according to actual taxonomy. The investigation of low-littoral samples using high-resolution electron microscopy revealed a huge unexpected morphological and species diversity of Lake Baikal benthic diatoms and shifted the main interest in the study of the DI collection to the biodiversity research.

The scope of diatom species variety becomes evident due to the establishment, based on the material of both exemplars of the DI collection, over the past decade of more than 20 diatom genera new to science and the description of over 750 new taxa belonging to the main taxonomic groups of naviculoid, cymbelloid, achnatoid, and nitzschioid diatoms (Kulikovskiy et al. 2012, 2015; Bukhtiyarova and Pomazkina 2013; Pomazkina and Rodionova 2014; Pomazkina et al. 2016, 2018, 2021; Rodionova et al. 2022).

In a number of widespread genera substantial species diversification was observed. For example, in the Naviculaceae Kützing family which plays a key role in benthic communities of Lake Baikal, out of the more than two hundred taxa identified in our DI collection, 125 were new to science leading

to a notable increase in the proportion of endemism in the genera. The following genera of the family are enriched both in terms of the total number of taxa and the proportion of endemics (in brackets, the number of new species and percent of endemics among the total are shown): *Navicula* Bory (104/ 75%), *Placoneis* Mereschkowsky (59/100%), *Hipodonta* Lange-Bertalot, Witkowski and Metzeltin (39/78%), *Paraplaconeis* Kulikovskiy, Lange-Bertalot, Metzeltin (20/94%).

The family Cymbellaceae Kützing, an important component of the summer microphytobentos, has been enriched with two new generic names and 52 new species found in the DI collection, belonging to *Cymbella* Agardh, *Encyonema* Kützing, and *Cymbopleura* (Krammer) Krammer making up to 62% of the total number of the genera species found (Kulikovskiy et al. 2012; Pomazkina and Rodionova 2014). The survey of the DI collection has also revealed 29 new species in the genus *Amphora* Kützing, in addition to the 77 taxa already known in the lake, increasing the endemism of the taxon to 49% (Skvortzov and Meyer 1928; Skvortzov 1937; Levkov 2009; Pomazkina and Rodionova 2014).

An example of one of the genera showing substantial species diversification in Lake Baikal is *Neidium* Pfitzer (Neidiaceae). In the early diatom flora lists 25 names belonged to the genus were reported, out of which only eight were widespread taxa (Skvortzov and Meyer 1928; Jasnitsky 1936; Skvortzov 1937). However, in samples of our DI collection, we found 94 species belonging to the genus *Neidium*, all of which were classified as "rare" or "very rare", with 91% of the taxa currently not found in other freshwater ecosystems. Impressively, the number of *Neidium* species in Lake Baikal even exceeds the total number of the genus species known in all freshwater bodies of North America (Kociolek 2005; Stachura-Suchoples et al. 2010; Pomazkina et al. 2021).

The genus *Diploneis* Ehrenberg also may be referred to the raw of species-rich genera in Lake Baikal. To date 41 taxa found in the DI collection were described as new to science (Kulikovskiy et al. 2015; Rodionova et al. 2019). Our recent study has shown that, in addition to seven common species, the morphology of the 89 *Diploneis* taxa found in the DI collection did not fit any existing diagnosis. Studies of *Diploneis* in ancient lakes such as Ohrid, Prespa (Macedonia) and Hubsugul (Mongolia) have revealed unexpected morphological diversity, new species and relict taxa from sediments (Jovanovska et al. 2013, 2015; Jovanovska and Levkov 2020; Lange-Bertalot et al. 2020). However, a comparison the total number of *Diploneis* species from early (Skvortzov and Meyer 1928; Skvortzov 1937; Meyer 1930) and recent sources (Kulikovskiy et al. 2015; Rodionova et al. 2019), including our own recent findings, suggests that the scale of species radiation of *Diploneis* in Lake Baikal is exceptional and exceeds that in all of the aforementioned lakes combined.

The observed species richness of distinct diatom taxa is unevenly distributed along the Lake Baikal littoral zone. Much of the intralacustrine endemicity relates to species with highly restricted geographic distributions, with some populations occupying only a few kilometers of shoreline. The western rocky shore of the lake is home to a greater number of taxa belonging to the family Cymbellaceae, compared to the eastern coast (Pomazkina and Rodionova 2014). However, the "hotspot" for species of this family may be attributed to the Maloe More Strait in the central basin and, in particular, to the small area of Olkhon Gates Strait. More than a third of all new species belonging to *Cymbella*, *Amphora*, *Encyonema* were found right there. Meanwhile, the greatest diversity of the genus *Geissleria* Lange-Bertalot and Metzeltin (45 new species) was found only along the coastline of Southern Baikal (Figure 1) from the city of Baikalsk to the Kultuk Bay (Bukhtiyarova and Pomazkina 2013; Pomazkina et al. 2018). Similarly, the southern extremity of Lake Baikal especially the western side of the Kultuk Bay may be attributed to the "center of speciation" for the genus *Neidium*. There in the silted sands of the lower littoral were found 82 out of 91 new *Neidium* taxa (Pomazkina et al. 2021). Diatoms belonging to the genus *Diploneis* were more common in the benthos of the eastern than the western coast, while up to 80% of new *Diploneis* species were found at depths of 10–20 m in the southern tip of the lake. The same general pattern distinguishing Maloe More Straight, Kultuk Bay and also Chivyrkuy Bay as the hotspots of species diversity is known for at least several Lake Baikal animal groups: amphipods (Bazikalova, 1945), molluscs (Koshova and Izmesteva 1997), ostracods (Schön et al. 2017). Interestingly, these

areas marked as hot spots all belong to the most ancient regions covered by water continuously (Mats et al. 2011).

The expected feature of Lake Baikal benthic diatom flora specific to all ancient lakes of the world, are "species flocks" – monophyletic groups of closely related species originated due to rapid radiation and occupied a large number of niches in the limited area (Brooks 1950; Wilke et al. 2009; Kociolek et al. 2017). "Species flocks" have been established in many groups of Lake Baikal hydrobionts such as fish, mollusks Baikaliidae, crustaceans, ostracods, dinoflagellates (Martens 1997; Sherbakov 1999; Kontula et al. 2003; Schön and Martens 2012; Daneliya et al. 2014; Annenkova et al. 2015; Kovalenkova et al. 2015; Schön 2017; Martin et al. 2019). In survey of the DI collection species series consisting of a few entities up to a few dozen relative organisms combined by a distinctive or derived character(s) (synapomorphy) which distinguishes them from a widely distributed closely related species, have been observed, for example, in the genera *Diploneis*, *Gomphoneis* Cleve, *Navicula*, *Neidium*. The "putative species flocks" mentioned below are currently only based on their morphological characteristics and do not have genetic evidence that they are of monophyletic origin. The recent great example of diatom species flock was proved using molecular and morphological data for twenty-five Diploneis species from Lake Tanganjika (Jovanovska et al. 2023). For Lake Baikal animal groups mentioned the mechanisms generating local cladogenesis remain obscure as well as for benthic diatoms, but in the latter case there is a possibility to use the DI collection for deeper further studies of local hyper-endemicity when found.

In 1999, D. Mann, observing valves of *Navicula lacus-baicali* Skvortzov and K.I. Meyer from Lake Baikal samples, suggested the taxon is a complex of reproductively isolated sympatric species, which can be distinguished from all freshwater *Navicula* by the presence of lateral hyaline areas (Mann 1999). Proving reproductive isolation between morphologically different forms in benthic organisms, including diatoms, is still challenging due to the lack of molecular data. Later, based on distinct morphological patterns of lateral non-pored areas, forms of apices, and areolation (Fig. 2) nine new species and intraspecific taxa were isolated from this group (Kulikovsky et al. 2012; Pomazkina et al. 2018).

In the species complex *Navicula baicalensis* Skvortzov and K.I. Meyer, the distinctive feature of large (more than 100 µm long) lanceolate valves with long protracted apices was the inflated valve central part. Specific differences that made possible to identify five new taxa baring the synapomorphy in this group concerned the density of striation, disproportional width of the valves, and the structure of the raphe (Pomazkina et al. 2018).

Twenty-two species of the genus *Gomphoneis* Cleve were described on the basis of historical collections including the DI collection, and some recent samples. They all are endemic to Lake Baikal. The group comprises two independent lineages of closely related species that originated during the radiations of two different ancestors that invaded the lake (Kociolek et al. 2013).

One more case of a group of closely related taxa is *Neidium baicalense* Jasnitsky species complex. Taxa of this group are distinguished by strongly silicified protruding longitudinal canals, a conopeum, extremely long proximal ends of the raphe. These traits are unique to the genus *Neidium* but are found to be present simultaneously in the species commonly distributed across Northern hemisphere *Neidium hitchcockii* (Ehrenberg) Cleve. In our DI collection 15 taxa closely related to *N. baicalense* were found, all having the unique diagnostic features, but differing from each other in the structure of the conopeum, as well as by the morphology and relief of the surface of longitudinal canals (Sherbakova et al. 2021; Pomazkina et al. 2021).

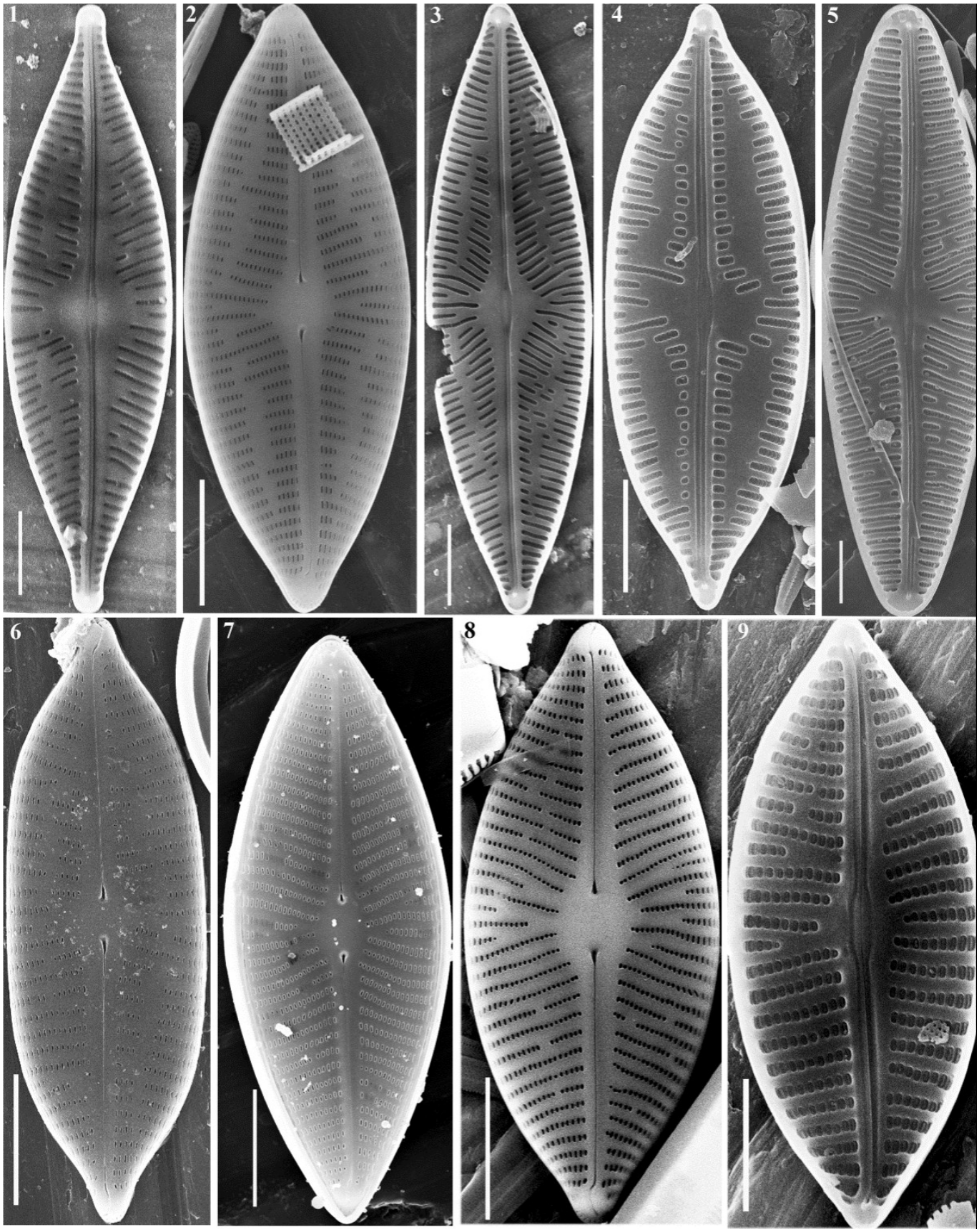

Figure 2. *Differences in the location and form of hyaline areas in species complex Navicula lacus-baicali: 1 – Navicula rhombicinsolitum Pomazkina, Rodionova and Sherbakova; 2 – N. caudata var. elliptica Pomazkina, Rodionova and Sherbakova; 3 − N. caudata Kulikovskiy, Metzeltin and Lange-Bertalot; 4 – Navicula sp.; 5 – N. lacus-baicali; 6 − N. caudata*

var. austrolacustris Rodionova and Pomazkina; 7 − N. caudata var. romboidea Pomazkina, Rodionova and Sherbakova; 8 – N. caudata var. skvortzowii Rodionova and Pomazkina; 9 − N. lacus-baicali var. ottochuschinica Pomazkina, Rodionova and Sherbakova. Scale bars: 1−8 – 10 μm; 9 – 5 μm.

Diploneis finnica (Ehrenberg) Cleve, the cosmopolitan species, and the endemic species *Diploneis baicalensis* Skvortzov and K.I. Meyer, were described in the first summary of diatom flora of Lake Baikal (Skvortzov and Meyer 1928). Both species have wide lanceolate or elliptical-lanceolate longitudinal canals and widely spaced external proximal ends of the raphe. The features distinguishing them are striae with an irregular arrangement of areolae in *D. finnica* and the absence of biseriate striae in *D. baicalensis*. We have found in our DI collection and formally described 13 taxa of *D. finnica*/*D. baicalensis* complex, representing some kinds of transient forms between the two taxa differing each other in size, outline, striation, and areola structure.

The importance of the "Darwin Initiative" collection for Lake Baikal diatoms cannot be overstated. The creation of DI collection has been instrumental in furthering our understanding and description of benthic diatom communities. The examination of DI collection has revealed an incredible richness of benthic diatoms in Lake Baikal, which has greatly expanded Bacillariophyta with numerous new species and genera. It has also revealed that certain genera have diversified extensively in the lake, resulting in an endemic flora of remarkable diversity and volume, while many other genera have not been more diversified, and are mainly represented by cosmopolitan taxa. Diatom assemblages inhabiting low littoral zone are more diverse, rich in species composition and contain much more new and endemic taxa in comparison with shallow waters. The morphology of Lake Baikal diatoms has added new and distinct structural elements and combinations to the current knowledge of diatom morphology. Over the past decade, data from the DI collection survey has been published in six monographs and atlases, as well as more than 20 scientific papers.

Since 2011, significant ecological changes have been observed in Lake Baikal due to anthropogenic stressors at both global and regional scales. In certain areas of the littoral zone, the initial stages of eutrophication or benthic degradation have been noted (Kravtsova et al. 2014; Timoshkin et al. 2016). Diatom species and their communities being biological indicators of aquatic ecosystems, respond to ecological fluctuations by changing the dominant complex, decreasing diversity, primarily due to lost rare taxa and local endemics. The DI collection of benthic diatoms that was collected during 1996–1997 represents the diatom diversity from a successful period in the history of Lake Baikal. The presence of regional and local endemics in benthic communities can serve as an indicator of the ecological conditions. The universal retrospective information of the DI collection has no analogues in other groups of Lake Baikal hydrobionts, and serves as a unique reference for future monitoring studies or environmental measures. Species of «putative species flocks» have detailed morphological descriptions and may be useful in molecular investigation both as this phenomenon and mechanisms of the origin of the exceptional diversity of diatoms in Lake Baikal. The diversity of diatoms, both in time and space, has and will continue to contribute significantly to environmental and evolutionary studies.

The DI collection for Lake Baikal has large potential in providing a validated taxonomic framework, and this potential is far from being exhausted and there is much more to be explored.

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