Are the Lake Baikal diatoms endemic?

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Abstract

An electron-microscopy study of *Aulacoseira baicalensis*, *A. islandica* (*A. skvortzowii*), *Cyclotella baicalensis*, *C. minuta*, and *Stephanodiscus meyerii* in phytoplankton samples from some mountain lakes of Zabaikalye (an area north and east of Lake Baikal) shows that these algae possess morphological similarities with the algae inhabiting Lake Baikal, including some elements of their ultra-structure. We hypothesise that they were more widespread in the past and persist today in mountain lakes along the Baikal rift zone owing to certain features of their biology. We conclude that these baikalian diatom algae, previously regarded as endemic, should be re-assigned to relict status.

Introduction

In Lake Baikal, about 10% of planktonic algae have been found to be endemic (Kozhov, 1962, 1972). These are mostly diatoms, mainly *Aulacoseira baicalensis* (K. Meyer) Simonsen, *Cyclotella baicalensis* Skvortzow, *C. minuta* (Skvortzow) Antipova, and *Stephanodiscus meyerii* Popovskaya et Genkal. The problem of endemism among dominant algae in Lake Baikal plankton has long been discussed in the literature.

One of them, *A. baicalensis*, was considered to be a baikalian endemic, but after it was found as a fossil in sediments of Lake Medvezhie (Moscow Province) (Wertebnaja, 1928, 1929), Meyer (1922) proposed it was of relict status. Subsequent findings of living *A. baicalensis* in other water bodies were regarded as methodical errors. Skabichevsky (1960) proposed that the finding of *A. baicalensis* in Lake Dalai Nor in Manchzhuria (Skvortzow, 1937) indicated that the status of *A. baicalensis* as a relict endemic species, formerly widely spread, should be reviewed. Recently, valves of an alga very similar to *A. baicalensis* were found in deep

layers of bottom sediments in Lake Washington (Abella, 1988) and may be a variety of *A. baicalensis*. Other authors now suggest a relatively young age of the present endemic species in Lake Baikal plankton, either that *A. baicalensis* originated in the lake 122 thousand years (Khursevich et al., 2001), or 107 thousand years ago (Grachev et al., 1998).

Spore forming *Aulacoseira islandica* from Lake Baikal was described as a new species *A. skvortzowii* Edlund, Stoermer et Taylor (Edlund et al., 1996) not found in other water bodies. However, spore-forming *A. islandica* was observed in Lake Khanka, Primorskiy Province, Russia (Skvortzow, 1929; Genkal & Schure, 2000). The taxonomic position of this alga seems to require more study (Popovskaya et al., 2002).

S. meyerii was earlier referred to as *Melosira binderana*, and presently has been shifted to the genus *Stephanodiscus*. Differing from the typical variety, it was described as *S. binderanus* var. *baicalensis* Popovskaya et Genkal (Genkal & Popovskaya, 1990), but later was given species rank as *S. meyerii* (Popovskaya et al., 2002).

Findings have been reported (Rozhkova et al., 2000) of dinoflagellates of the genus *Gymnodinium* considered earlier as Lake Baikal endemic species, in the plankton of large mountain and alpine lakes of Zabaikalye (located in the River Lena basin). Other endemic species, namely diatoms from the genera *Cyclotella* and *Melosira*, have been found in the Pliocene flora of the Tunkinskaya depression adjacent to Lake Baikal (Cheremisinova, 1966, 1968, 1973), in Neogene deposits from the Tunkinskaya depression and Zabaikalye (Popova et al., 1989; Chernyaeva et al., 2000; Chernyaeva & Moiseeva, 2003; and others), as well as in present plankton of Lake Khubsugul in Mongolia (Kozhova et al., 1977; Genkal et al., in press). Last, electron-microscopy studies of species composition of planktonic diatoms from the lakes of Zabaikalye, were reported by Genkal & Bondarenko (2001, 2004).

This paper focuses on morphological features of algal forms similar to the Lake Baikal endemic species, from the Zabaikalye lakes using electron microscopy.

Sites studied

The lakes are located on the Sayano–Baikal highland east and north-east of Lake Baikal, stretching

to the Kodar and Udokan ranges (Fig. 1). The Sayano–Baikal highland is an area of neotectonic activity and sharp orographic contrasts, with manifestations of volcanism and wide occurrence of glacial morpho-structures. It includes the Baikal rift zone as a whole morpho-structural complex (Logachev et al., 1974). The formation of the present relief was greatly affected by the Pleistocene glaciations, and seismic processes in Pleistocene and Holocene (Vdovin, 1976). Bazarov (1986) thought that the key moments in changes of palaeoclimate in the region have been cooling and Quaternary glaciations. The origin of the studied lakes is associated with glacial modifications of relief and melting of glaciers (Geologiya i seismichnost' zony BAM, 1983; Enikeev, 1998). Deposits of the second half of the Late Pleistocene are mainly glacial and aqua-glacial. Some of the lake depressions, for instance Oron and Tokko, have tectonic origins. Lake basins situated in river valleys lie along the tectonic break.

The lakes we studied are of ultra-oligotrophic type having relatively low temperatures and high oxygen content. They are covered with ice for 8–9 months a year. Destruction of ice-cover occurs most frequently during the first half of June, and the ice forms again in October. Water temperature rises until mid August, after that steadily decreases. All the lakes are flow-through. Soli, Tokko, Kamkanda give rise to rivers. Ogiendo,

Figure 1. Scheme of the lake location. 1 – Ogiendo lakes; 2 – Lake Soli; 3 – Lake Oron; 4 – Amalyk lakes; 5 – Kiryalta lakes; 6 – Lake Tokko; 7 – Lake Kamkanda.

Table 1. Composition of the Baikal endemic species in the studied lakes

	Ogiendo	Soli	Amalyk	Oron	Kamkanda	Tokko	Kiryalta
<i>A. baicalensis</i>	+	+	+		+	+	+
<i>A. islandica</i> (vegetative cells)	+	+	+		+		+
<i>A. islandica</i> (spores)	+	+			+		
<i>C. baicalensis</i>	+					+	
<i>C. minuta</i>	+		+			+	
<i>S. meyerii</i>	+	+		+	+		

Kiryalta, Amalyk are chains of lakes connected by surface water-flows, with elevation differences reaching 150–180 m. Except Lake Oron (19 km long and 184 m maximum depth), all the lakes are small, from 0.6 to 4.6 km long and 11–52 m deep.

Methods

Phytoplankton was sampled during the open water period over 1997–2001 in all the lakes. In Lake Ogiendo samples were also taken during the iced period. Net and water-sampler were used. The samples fixed with Utermohl solution were concentrated using sedimentation. Samples were first examined in a 0.1 ml chamber by “Pereval” microscope at magnifications $\times 720$ and $\times 1200$. The cells were separated from organic material by wet digestion (Balonov, 1975). Algae preparations were examined by electron microscope SEM “JSM-25 S”.

Results

All the known baikalian planktonic endemic species of Bacillariophyta were found in 7 of the 30 lakes sampled (Table 1). As the taxonomic status of baikalian spore-forming algae required additional study, we bracketed all samples of this species as *A. islandica*. According to the most recent opinion of Popovskaya et al. (2002), previously described intra-species taxa in *A. baicalensis*, *C. baicalensis*, and *C. minuta* may now be considered as synonyms. A complex of endemic species was recorded in Ogiendo lakes (Table 1). In Lake Soli, four endemic species were recorded, three in Amalyk, Kamkanda, and Tokko, two in Kiryalta, and only one in Oron (Table 1).

S. meyerii and *C. minuta* abounded mainly in the Ogiendo lakes (Table 2). *C. baicalensis* was represented only by solitary valves in Tokko and Ogiendo, which probably reflected scanty phytoplankton at the sampling time. In Lake Baikal, this alga thrives in spring, while *C. minuta*, which reaches its development maximum in autumn, is encountered all the year round (Popovskaya et al., 2002). The most widespread species in the lakes, *A. baicalensis* (Table 1), showed highest abundance in Lake Soli (Table 2). *A. islandica* was found in five lakes: Ogiendo, Soli, Kamkanda, Kiryalta, and Amalyk, and its spores in the first three of these (Table 1). The greatest number of spores was recorded in Kamkanda (Table 2).

The morphological characters, including some elements of ultra-structure, viz. shape of spines, structure and location of fulcra and rimoportulae, areols and alveols in the endemic species (Figs. 2 and 3) agree completely with taxonomic diagnoses (Genkal & Popovskaya, 1990, 1991; Likhoshway et al., 1992; Babanazarova et al., 1996; Edlund et al., 1996; Popovskaya et al., 2002). *S. meyerii* is the exception, having fewer numbers of striae per 10 microns and spine appendages (Table 2). This deviation may be related with geographic variability. As regards spine appendages, the diagnosis covers their usual number, though the baikalian forms of this species also have valves with spines possessing 3 or 4 appendages (Popovskaya et al., 2002; Table 11, 1–3).

Discussion

Occurrences of baikalian organisms in other lakes, distant from Lake Baikal, have been discussed in the literature for a long time. Several suggestions

Table 2. Morphological characters of the species studied

Water-body	Valve diameter, microns	Valve height, microns	Number of areol rows at the mantle, per 10 microns	Number of areols per 10 microns of the row	Number of valves found
<i>A. baicalensis</i>					
Tokko	12.6–30.0	18.8–40	7–8	5–7	3
Kamkanda	17.7	17.7	8	6	1
Amalyk	17.3–22.2	18.6–43.5	6–9	5–7	4
Ogiendo	13.3–20	22.2–53.3	6–8	4–6	3
Kiryalta	14–18.6	25.5–28	8	4–6	6
Soli	11.3–18	25.3–68.8	7–10	3–6	27
Diagnosis	6–37	10–72	6.5–11	3–13	Popovskaya et al. (2002)
<i>A. islandica</i> (vegetative cells)					
Ogiendo	11–13.5	10.7–20	12–14	12–18	3
Soli	12.1–20	12.1–25	9–12	11–13	3
Amalyk	12.8	13.5	14	16	1
Diagnosis	3–28	4–30	9–18.3	11–26	Popovskaya et al. (2002)
<i>A. islandica</i> (spores)					
Ogiendo	12.8	17.1	12	14	1
Soli	9.2	17.1	12	14	1
Kamkanda	7.7–14.6	10–17.8	12–16	14–16	5
Diagnosis	5–18.7	10.3–24.2	10.8–16.5	12–17	Popovskaya et al. (2002)

Water-body	Valve diameter, microns	Number of striae per 10 microns	Number of central fultoportulae	Presence of spines	Number of valves found
<i>C. baicalensis</i>					
Tokko	77.7	11	24	–	1
Ogiendo	~100		>50		1
Diagnosis	44–150	7–12	15–160	–	Popovskaya et al. (2002)
<i>C. minuta</i>					
Amalyk	46.6	10	16		1
Tokko	21.2–58.8	10–13	6–24	+	6
Ogiendo	17.8–40	10–14	1–9	+	8
Diagnosis	7–60	9–16	1–30	+	Popovskaya et al. (2002)
Water-body	Valve diameter, microns	Number of striae per 10 microns	Number of areols at the stria end	Number of spine appendages	Number of valves found in the preparation
<i>S. meyerii</i>					
Ogiendo	8.8–10.9	10–12	2–3	3–5	12
Soli	9.4	12		5	1
Oron	11.3	10	2	3–5	2
Kamkanda	7.7–11.4	10–12	2	3–5	9
Diagnosis	7.5–12.3	12–14	2–3	5	Popovskaya et al. (2002)

Figure 2. Electronic microphotographs of valves (SEM): 1–7 – *A. baicalensis*; 8–12 – *A. islandica*. 1 – colony; 2 – valves of this colony; 3 – spines in this colony; 4, 5, 8–10 – valves; 6 – girdle band; 7 – rimoportula of the inner surface; 11, 12 – spores. Scale bars: 1–50 μm ; 2, 4–6, 8, 10–12 – 10 μm ; 3, 9 – 5 μm ; 7 – 1 μm .

Figure 3. Electronic microphotographs of valves (SEM): 1 – *C. baicalensis*; 2–7 – *C. minuta*; 8–12 – *S. meyerii*. 1, 3, 4, 7 – valves from the inner surface; 2, 9 – valves from the outer surface; 5 – fultoportulae on a valve from the inner surface; 6 – rimoportula from the inner surface; 7 – marginal fultoportulae on a valve from the inner surface; 8 – colony; 11 – fultoportula on a valve from the inner surface; 12 – spines and marginal fultoportulae from the outer surface. Scale bars: 1–4 – 10 μm ; 5–7, 11, 12 – 1 μm ; 9, 10 – 5 μm .

have been made. Tomilov (1954) thought the Zabaikalye lakes, located in basins of two River Lena tributaries, Vitim and Olyokma, have a similar origin; it is possible to consider them as an inheritance of the last phase of the Glacial period. According to this view, the presence of some baikalian endemic and relict species in certain of the lakes indicates they existed as water bodies before the Glacial period. During the interglacial or some later time before the present, they were connected with other large basins. In the past, there was a chain of gigantic lakes in Baikal-type depressions populated by elements, which had invaded from Lake Baikal. Such dispersal of baikalian elements took place at the end of Neogene and early Quaternary along the river system directed towards the Lena through these ancient lakes (Kozhov & Tomilov, 1949). Kozhov (1950, 1962) also thought that the Zabaikalye lakes represented depressions of the Baikal system, which were an integral system in the past, or were closely connected with each other through short rivers. He regarded them as successors of an ancient Baikal multi-lake country.

According to Karasiov (1987), geological and biological data do not support the hypothesis of Kozhov (1950, 1962). Moreover, Baikal transgression into Zabaikalye and the resulting formation of a vast “Zabaikalye multi-lake country” was refuted by Florensov (1960), who showed there had not been a significant rise of Lake Baikal level and thus no transgression. So, a significant fraction of the so-called “Baikal hydro-fauna” must have been common to the rift (Karasiov, 1987). In later time, this fauna persisted to a greater extent in Lake Baikal (ecologically more diverse) and to a lesser extent in the relict margin lakes of the rift zone. In Neogene, before a period of rapid rise of the ranges in the vicinity of Lake Baikal on the watershed of the Olyokma–Vitim highland, there was an ancient lake district with water discharge towards both palaeo-Baikal through the palaeo-Barguzin and palaeo-basins of Vitim and Olyokma. The Neogene and Early Quaternary watershed lakes were deeper than 200 m and had diverse autochthonous floras and faunas.

In Karasiov's (loc. cit.) view, there are no grounds for believing that all so-called “Baikal” species living outside Lake Baikal, evolved in the lake and spread from it. These forms and their predecessors inhabited the Baikal rift as early as

the Tertiary period before the formation of Lake Baikal itself. In the Quaternary, the remains of the hydro-fauna of the mountain belt became isolated in separate refuges, which presumably maintained environmental conditions similar to former epochs. These relict bodies preserved some Tertiary hydrobionts till the present.

From Miocene deposits located in the Tunkinskaya depression (south-west of Lake Baikal along the Baikal rift zone), Likhoshway et al. (1997) used electron microscopy to describe representatives of the genus *Aulacoseira*. Some of them show similarity with *A. baicalensis* in their areol structure, location frequency and spine shape. These forms were thought to be ancestral to *A. baicalensis*. In the Pliocene deposits of Lake Baikal, *Aulacoseira* valves similar to those of *A. baicalensis* were also found (Likhoshway, 2004). In Pleistocene deposits of the Upper Angara depression (north-east part of the Baikal rift zone), valves of the Lake Baikal endemics *A. baicalensis*, *C. baicalensis*, and *C. minuta* were found by Kulchitsky et al. (1993) who explain their presence by repeated transgressions of Lake Baikal into the depression.

Investigations on Vitim highland revealed deposits of large deep lakes, which had passed through repeated phases of deposition (Chernyaeva et al., 2000). Rich diatom complexes including *A. baicalensis* were found in these deposits. It was suggested this species developed in lakes in the Zabaikalye area and lakes formerly occupying present Baikal. Later it disappeared over most of its distribution area, persisting only in Lake Baikal.

Ancient lake deposits formed prior to glacial periods have also been found in the trough of the Baikal rift at the south-west end of the Baikal rift at the south-west end of the Muysko-Kuandinskaya depression, between the Upper Angara River and Muysko-Kuandinskaya depression. Analysis has shown they contain valves of extant diatoms, baikalian endemic *A. baicalensis*, *C. baicalensis* Skv., *C. aff. minuta* Antip., as well as *A. aff. islandica* ssp. *helvetica* (O. Müll.) Sim.; and spores of *Aulacoseira* (Kulchitsky et al., 1993). It was suggested these Baikal endemic diatoms were earlier distributed in lakes close to it in the rift trough, and later penetrated into Lake Baikal. Favourable environmental conditions have preserved these species in Lake Baikal.

Deposits of the Charskaya depression (Zabaikalye, north-east of the Baikal rift zone) have revealed diatom complexes of ancient lakes, which now have disappeared (Chernyaeva & Moiseeva, 2003). In the Upper Miocene–Early Pliocene complexes, algae occur together with other representatives of the genus *Aulacoseira* identified as *A. aff. baicalensis*. From this and other findings it was proposed that the spread of *A. baicalensis* into East Siberia lakes started not from Lake Baikal but rather from the Zabaikalye lakes, which existed during the Neogene on the Vitim highland where the species occurred in sediments dated around the Mid Miocene. These authors believe it is incorrect to refer to *A. baicalensis* as a Baikal endemic.

Our study supports the latter conclusion and agrees with Skabichevsky (1960). In the past, *A. baicalensis* or (and) its close relatives appear to have occupied a vast area, including North America, Europe, and the Far East. At present this alga, as the other planktonic diatoms cited here, inhabits, beside Baikal, the Zabaikalye lakes in the north of the Baikal rift zone from the North Baikal highlands to the Kodar and Udokan ranges. Three representatives occur also in the south-west of the rift zone in Lake Khubsugul (Genkal et al., in press). So, *A. baicalensis* and the spore forming *A. islandica* are quite common in the region.

How have these algae persisted through many climatic and geological changes? In our view, certain biological peculiarities may help provide an explanation. First, they are meroplanktonic organisms: after growth in the water column they produce a resting stage that falls to the bottom where they can remain a long time. Furthermore they are ice organisms; their life cycle begins in the interstitial water in ice. In fact, the most productive bloom, in spring, takes place there (This was recently shown for the baikalian *Aulacoseira* species – Bondarenko, 2002; Obolkina et al., 2000 – and for *A. islandica*, living in the river Amur – Yuriev & Lebedev, 1988). The phenomenon suggests an underlying cause for their survival in the East Siberia lakes. Concerning to the other three representatives, *S. meyerii*, *C. baicalensis*, and *C. minuta*, their propagation in interstitial ice water has not yet been recorded, but it is well known that being meroplanktonic they can persist

frozen into the ice until spring. Tolerance of ice conditions may have played a main role in the survival of these algae during Pliocene–Pleistocene glaciations.

Conclusion

We conclude that all these baikalian planktonic diatom algae, previously regarded as endemic, should be reassigned to relict status. High mountain lakes of Pribaikalye and Zabaikalye presently serve as refuges for species widespread during past geological epochs. Researchers of the higher terrestrial vegetation have come to a similar conclusion: i.e. that prolonged influence of low temperatures, orographic and ecological isolation of separate inter-mountain lowlands and highlands, which originated during the Neogene–Pleistocene tectogenesis, facilitated formation of a great number of new endemics and the preservation of relicts in the high mountain flora (Predbaikalye and Zabaikalye, 1965; Peshkova, 2001).

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