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EXPERIMENTAL ARTICLES

Taxonomic and Ecological Characterization of Cyanobacteria from Some Brackish and Saline Lakes of Southern Transbaikal Region

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Abstract—The species composition of cyanobacteria from 12 lakes of Southern Transbaikal Region was studied. In the studied lakes, a total of 28 species of cyanobacteria were detected, including 10 species previously not retrieved from the lakes of Southern Transbaikal Region. The morphological and ecophysiological characteristics, as well as the phylogenetic position, of pure cyanobacterial cultures were determined. According to the results of 16S rRNA sequencing, the Cya 1, Cya 2, and Cya 10 cultures were identified as representatives of the genus *Phormidium*; the Cya 5 and Cya 6 cultures were assigned to the genus *Nodularia*. On the basis of its morphological properties, the Cya 4 culture was identified as *Pseudanabaena frigida*. The studied microorganisms were moderate alkaliphiles and could grow within a broad salinity range (0–100 g/l NaCl).

Keywords: saline lakes, Southern Transbaikal, cyanobacteria, ecophysiology, taxonomy.

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Brackish and saline lakes are common in the arid zones of the Earth. They are unique ecosystems with extremely high pH values and high mineralization levels (up to saturating concentrations) [1]. These lakes are inhabited by alkaliphilic microorganisms, including cyanobacteria [2]. This extensive group of photosynthetic prokaryotes often plays a key role in production of organic matter in soda, brackish, and saline lakes [3]. The high level of functional activity of cyanobacteria in extreme ecosystems is due to their physiological plasticity and quick response to changes in the physicochemical environmental parameters.

Until recently, only traditional methods were used for studying cyanobacteria. However, numerous works on the application of molecular biological techniques to cyanobacteria were presently published. Isolation of axenic cultures is the main problem that complicates thorough investigation of cyanobacteria. The first stage, without which isolation of pure cyanobacterial cultures is impossible, is investigation of their ecology and species diversity in natural environments.

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The species diversity and the ecophysiology of the cyanobacteria inhabiting some lakes of the Transbaikal region was previously investigated [4, 5], and the present work is a continuation of these studies. The aim of the present work was to analyze the species composition of the cyanobacteria inhabiting the brackish and saline lakes of Southern Transbaikal region and obtain pure cyanobacterial cultures, as well as to determine their ecophysiological properties and taxonomic position.

MATERIALS AND METHODS

The subjects of this study were two groups of brackish and saline lakes of Southern Transbaikal located in Selenga Dauria (Buryatia) and the Onon-Borza basin (Transbaikal region). Lakes Sul'fatnoe, Beloe (Orongoiyskoe), Verkhnee Beloe, and Solenoe (Kiran) are located in Selenga Dauria. The lakes of the Onon-Borza basin are divided into three subgroups: Onon, Borza, and Agin. The Agin subgroup includes Lakes Gorbunka, Khilganta, Zun Kholvo, and Ekhe Torom; Lake Zun Torei belongs to the Onon subgroup; and the Borza subgroup includes Lakes Borzinskoe, Bab'e,

and Tsagan Nuur. The studies were carried out in 2001–2007.

Methods of analysis. Determination of the physicochemical parameters and sampling for microbiological investigation were carried out using traditional techniques [6].

Determination of the species composition of cyanobacteria according to the standard morphological characteristics. Microscopic examination of cyanobacteria was carried out under an Axiostar plus microscope (Carl Zeiss, Germany). Determination of the taxonomic position of cyanobacteria was carried out according to Elenkin and Hollerbach [7, 8] and verified according to Komárek and Anagnostidis [9, 10].

Statistical analysis of the distribution of cyanobacterial taxa in the studied lakes. In order to assess the similarity or to determine differences in the taxonomic spectra of the cyanobacteria inhabiting the lakes, Jacquard's floristic similarity coefficient modified by Malyshev was applied [11]. The results obtained were treated using the Statistica 6.0 software package. The dendrograms were constructed by using the unweighted pair-group method with arithmetic mean.

Isolation of the cultures. Active enrichment cultures of cyanobacteria were isolated on a modified M medium containing the following (g/l): Na_2CO_3, 5.0; $NaHCO_3$, 5.0; NaCl, 5.0; K_2PO_4, 0.5; $MgSO_4 \times 7H_2O$, 0.5; $NaNO_3$, 1.5; KCl, 0.5; Na_2SO_4, 2.0; $FeCl_3$, 0.5; A5 trace element solution (H_3BO_3, 2.86; $MnCl_2 \times 4H_2O$, 1.81; $ZnSO_4 \times 7H_2O$, 0.222; $Na_2Mo_4 \times 2H_2O$, 0,39; $CuSO_4 \times 5H_2O$, 0.079; $Co(NO_3)_2 \times 6H_2O$, 0.0494), 1 ml; and vitamin B_{12}, 20 μg.

Monocultures of cyanobacteria were isolated on agarized media using an MS-2 stereomicroscope (Russia) at ~7–90× magnification. The cultures were grown under laboratory conditions at 20–25°C under continuous illumination in a luminostat (2000 lx). The culture purity was confirmed by microscopic examination.

Cyanobacterial growth across the pH–mineralization gradient. The experiment was carried out under laboratory conditions with a cyanobacterial mat from Lake Khilganta sampled when the lake dried up (2006), as well as with cyanobacterial monocultures isolated from the water samples. Within the pH–mineralization gradient, pH ranged from 7.5 to 9.5. The following NaCl concentrations were used: 0, 1, 5, 10, 20, 50, 100, 150, 200, 250, and 300 g/l. The pH values were adjusted by changing the ratio between 10% solutions of sodium carbonate and bicarbonate; pH was measured with a Hanna Instrument pH 211 pH meter (Russia). Cyanobacterial cultures were grown under laboratory conditions in a luminostat at illumination intensity of 2000 lx. The biomass yield was assessed by the optical density of the cell suspension measured on a CECIL 1021 spectrophotometer (United States). The duration of the experiment was 4–8 weeks. The Microsoft Excel software package was used for statistical analysis of the results obtained.

Determination of the phylogenetic position of cyanobacteria by 16S rRNA gene sequencing. To disintegrate the cell walls of cyanobacteria, the cell biomass was treated with 10% sarcosyl and liquid nitrogen. Then sodium dodecyl sulfate (SDS) and proteinase K were added. DNA was extracted with a mixture of phenol–chloroform and chloroform and precipitated with 96% ethanol. Nucleotide sequences of 16S rRNA gene fragments (1400 bp) were analyzed. PCR amplification of the 16S rRNA gene was carried out with the universal eubacterial primers 27f (5'-AGAGTTTGATCCTGGCTCAG-3') and 1492r (5'-TACGGYTACCTTGTTACGACTT-3'). The polymerase chain reaction (PCR) was carried out on a GeneAmp PCR System 2700 thermocycler (Applied Biosystems, United States). Analysis of the PCR products was carried out by electrophoresis in 1% agarose gel. The restriction analysis was performed using the *Hin*61 restriction enzyme. Determination of the 16S rRNA gene sequences was carried out on a CEQ 2000 XL automatic sequencer (Beckman Coulter, United States) according to the manufacturer's instructions. For identification of microorganisms closely related to the obtained strains, the RDBII (http://rdp.cme.msu.edu) and NCBI (http://www.ncbi.nlm.nih.gov) databases were used. The obtained 16S rRNA gene sequences were aligned using the CLUSTALX software package. The phylogenetic trees were constructed by methods implemented in the TREECON software package.

RESULTS AND DISCUSSION

Physicochemical properties of the studied lakes. The majority of the studied lakes are shallow water bodies with relatively small areas of the water surface (Table 1). In terms of the mineralization level of their waters [6], Lakes Beloe, Sul'fatnoe, Solenoe, Verkhnee Beloe, Ekhe Torom, Zun Kholvo, and Zun Torei are brackish (1–25 g/l). The water mineralization in Lake Khilganta during the high water period (1998) was similar to that of seawater (25–50 g/l). The waters of Lakes Tsagan Nuur, Borzinskoe, and Bab'e, as well as the silt waters of Lakes Gorbunka and Khilganta, are brine with mineralization levels of more than 50 g/l. The lake waters are alkaline. The majority of the studied lakes are characterized by an unstable hydrological regime due to the sharply continental climate of Southern Transbaikal, differing in this respect from the more stable lakes of the East African Rift Zone [12].

The effect of climatic conditions was studied in detail for Lake Khilganta. Analysis of the physicochemical parameters of the lake determined in differ-

Table 1. Physicochemical parameters of the studied lakes

Location	Lake	Date	h, m	S, km^2	T, °C	M, g/l	pH
Buryatia	Beloe	05.2006	2.0	0.6	12	1.7	9.0
	Sul'fatnoe	07.2001	8.0	9.0	24	5.8	9.0
		07.2005	7.0	12.0	17	7.5	9.1
	Solenoe	06.2004	3.0	1.0	22	5.6	9.9
	Verkhnee Beloe	05.2001	2.0	4.5	17	7.1	9.8
Transbaikal region	Ekhe Torom	07.2005	5.0	2.5	18	9.7	8.4
	Zun Kholvo	08.2006	1.5	150.0	20	10.0	9.2
	Zun Torei	08.2006	4.0	300.0	28	5.0	9.7
	Gorbunka*	08.2006	*	*	27	90.0	7.5
	Tsagan Nuur	"	2.0	150.0	26	268.0	9.9
	Borzinskoe	"	3.0	110.0	27	155.0	9.9
	Bab'e	08.2006	2.0	85.0	25	276.0	8.7
	Khilganta**	08.1998	0.4	0.5	25	40.0	9.5
	Khilganta**	08.2001	0.1	0.15	26	82.0	9.0
	Khilganta*, St. 1	08.2006	*	*	34	128.0	8.6
	St. 2				20	152.0	8.4

Note: h, maximal depth of the lake; S, water surface area; M, total mineralization; St., station; * the lake was dry during the period of observation and therefore silt water samples were taken; ** data obtained by B.B. Namsaraev [13].

ent years revealed that, during the high-water period (1998), the water mineralization in Lake Khilganta was 40 g/l, pH was 9.5, and lake depth was 37 cm. During the drought season (2001), the water mineralization increased up to 82 g/l, pH was 9.0, and the lake depth decreased to 10 cm. In 2006, the lake dried up and was occasionally replenished by rainfall. The silt water (pH 8.4–8.6) detected at a depth of 35–80 cm w**as** found to be salt brine (128–152 g/l).

Species composition of cyanobacteria. In the saline and brackish lakes of Southern Transbaikal, a total of 28 species of cyanobacteria were detected. Most of them (11 species) were detected in lakes with water mineralization ranging from 5 to 7 g/l (Lakes Sul'fatnoe, Verkhnee Beloe, and Solenoe); 2 species were detected in the brines of Lakes Bab'e and Tsagan Nuur (Table 2). The genus *Leptolyngbya* (seven species) was predominant. Other genera were less abundant.

We detected ten more species—namely, *Leptolyngbya valderiana, L. voronichiniana, Phormidium breve, Ph. retzii, Anabaena bergii, Arthrospira jenneri, Chroococcus minutus, Jaaginema woronichinii, Pseudanabaena frigida*, and *Trichodesmium lacustre*—in addition to the cyanobacterial species previously detected in the brackish and saline lakes of Southern Transbaikal [6, 8]. The study of this group of microorganisms revealed some deviations from the typical descriptions. For instance, the majority of members of the genera *Leptolyngbya, Phormidium*, and *Oscillatoria* were represented by transitional forms, differing in the length of their filaments and trichomes, as well as in the cell size.

Table 2. Taxonomic spectrum of cyanobacteria inhabiting the studied lakes

Taxa	Lakes												
	1	2	3	4	5			6	7	8	9	10	11
					HW	D	DRY						
Aphanothece salina Elenk. et Danil.					+	+							
Anabaena variabilis Kutz.			+										
A. variabilis f. *tenuis* Pop.	+	+	+	+						+			
***A. bergii* (Küts.) Gom.**				+									
***Arthrospira jenneri* Stizenb. ex Gom.**				+									
Calothrix sp.									+				
***Chroococcus minutus* (Kütz.) Näg.**							+					+	
***Jaaginema woronichinii* (Anis.in Elenk.) Anagnost. et Komár.**		+	+										
Leptolyngbya fovelarium (Rabench. ex Gom.) Anagnost. et Komár.		+	+										
L. tenuis (Gom.) Anagnost. et Komár.	+		+	+			+						
L. woronichinii (Anos.) Anagnost. et Komár.					+	+	+						
L. komarovii (Anos.) Anagnost. et Komár.	+	+	+										
L. laminose (Gom.) Anagnost. et Komár.									+				
***L. valderiana* (Gom.) Anagnos. et Komár.**													+
***L. voronichiniana* Anagnost. et Komár.**									+			+	+
Nodularia sp.						+			+	+			
Nostoc sp.	+		+										
Microcoleus chthonoplastes (Fl. Dan.) Thur.				+	+	+	+						
Oscillatoria tenuis Agard. et Gom.						+							
Oscillatoria sp.				+				+					
***Phormidium breve* (Kütz. et Gom.)**	+			+				+		+		+	
Ph. molle Gom.	+			+	+	+	+						
***Ph. retzii* (Agard.) Gom. ex Gom.**				+					+				
Phormidium sp.								+			+		
***Pseudanabaena frigida* (Fritsch) Anagnost.**	+		+	+				+			+	+	
Synechocystis sp.												+	
Spirulina major Kützing ex Gom.				+				+				+	
***Trichodesmium lacustre* Kleb.**	+												
Total	8	4	8	11	4	6	5	5	5	3	2	6	2

Notes: 1, Sul'fatnoe; 2, Beloe; 3, Verkhnee Beloe; 4, Solenoe; 5, Khilganta; HW*, high water period (1995–1996), data obtained by Kompantseva et al. [14]; D, drought season (2001–2004); DRY, dry season (2006); 6, Zun Kholvo; 7, Gorbunka; 8, Zun Torei; 9, Bab'e; 10, Ekhe Torom; 11, Tsagan Nuur. The cyanobacterial species not isolated previously from these habitats are shown in bold.

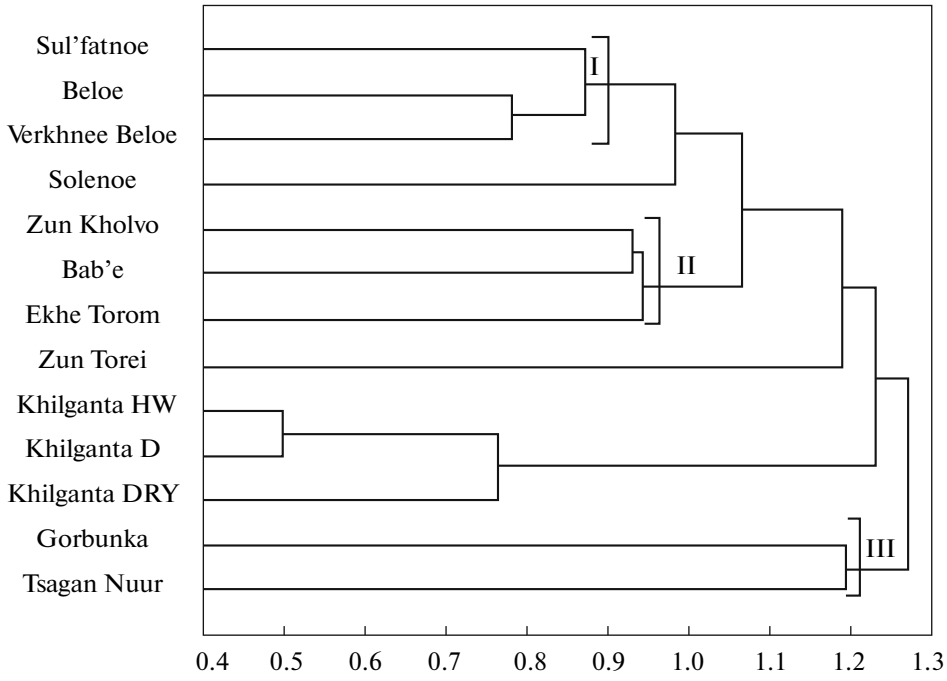

Fig. 1. Dendrogram constructed on the basis of cluster analysis of the cyanobacterial complexes of the brackish and saline lakes of Southern Transbaikal. The ordinate shows the coefficients of similarity calculated for the species spectra; the abscissa shows the Euclidean distance). I, II, III—clusters.

The effect of climatic conditions on the species composition of cyanobacteria was studied for Lake Khilganta. This lake is of special interest due to the fact that a layered cyanobacterial mat developed on the surface of its bottom sediment. This mat is a modern analogue of the ancient stromatolites that dominated the Precambrian Earth.

During the high-water period (1995), four cyanobacterial species, *Aphanothece salina*, *Leptolyngbya woronichinii, Microcoleus chthonoplastes*, and *Phormidium molle*, were detected at a water mineralization of 46 g/l and pH 9.8 [14] (Table 2). During the drought season (2001–2004), when the water mineralization increased up to 82 g/l, the highest diversity of cyanobacterial species was observed and *Nodularia* sp. and *Oscillatoria tenuis* appeared. The development and distribution of cyanobacterial communities in the lake may be attributed to their adaptation to considerable fluctuations in water mineralization. A further increase in water mineralization up to 152 g/l (2006) was followed by the development of a dry layered cyanobacterial mat with heterogeneous content and structure. Considerable diversity of cyanobacterial (*M. chthonoplastes, Ph. molle, L. tenuis, L. woronichinii, Ch. minutes*) and algal (*Oocistis* sp., *Dunaliella salina*) morphotypes was observed.

Statistical analysis of the distribution of cyanobacterial taxa in the studied lakes. Using Jacquard's floristic similarity coefficient (k), the frequency ranges of cyanobacterial taxa at the species and generic levels were determined for the brackish and saline lakes of Southern Transbaikal. As a result, it was demonstrated that, within the "species–mineralization" coordinate system, the coefficients of similarity varied within a wide range ($k = 0$–0.667). The lowest coefficient of similarity for cyanobacteria ($k = 0.063$) was obtained when comparing the species spectra for the cyanobacteria inhabiting the low- and high-mineralized waters of Lakes Verkhnee Beloe and Khilganta (dry season), respectively. This indicates that cyanobacterial communities adapted to extremely high or low mineralization levels differ significantly.

The levels of similarity between the communities of Lakes Sul'fatnoe–Verkhnee Beloe and Beloe–Verkhnee Beloe with similar physicochemical characteristics were highest ($k = 0.46$ and $k = 0.50$, respectively). This may be attributed to the presence of representatives of the genera *Anabaena, Leptolyngbya, Nostoc*, and *Pseudanabaena* in Lakes Sul'fatnoe–Verkhnee Beloe, as well as to the presence of members of the genera *Anabaena, Jaaginema*, and *Leptolyngbya* in Lakes Beloe–Verkhnee Beloe.

In the cases in which the level of similarity between the cyanobacterial complexes of the lakes is high, they cluster together (Fig. 1). The first cluster includes the cyanobacterial complexes of Lakes Sul'fatnoe, Beloe,

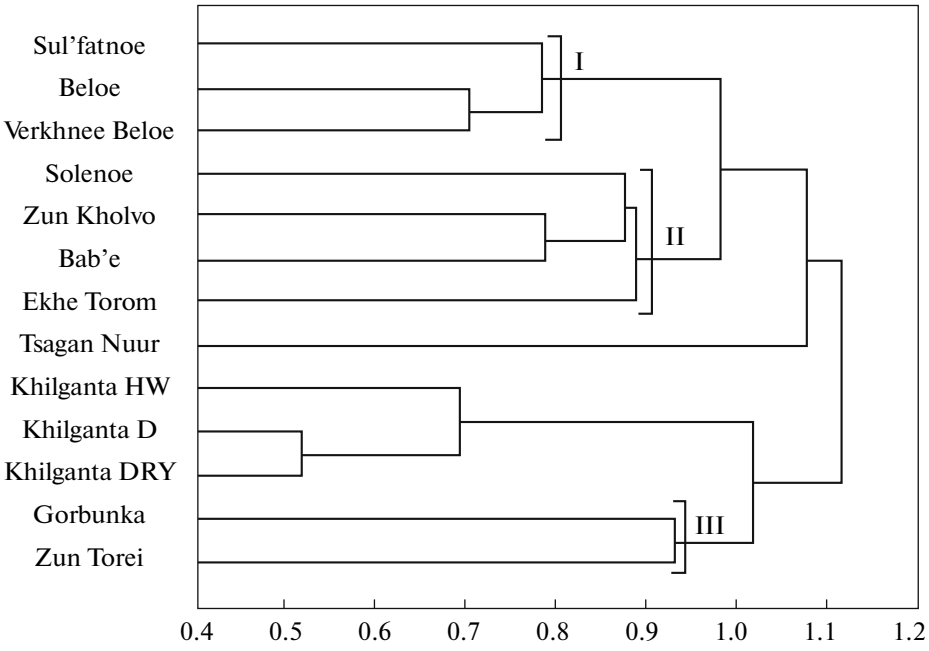

Fig. 2. Dendrogram constructed on the basis of cluster analysis of the cyanobacterial complexes of the brackish and saline lakes of Southern Transbaikal. The ordinate shows the coefficients of similarity calculated for the genus spectra; the abscissa shows the Euclidean distance). I, II, III—clusters.

and Verkhnee Beloe. The second cluster contains the cyanobacterial complexes of Lakes Zun Kholvo, Ekhe Torom, and Bab'e. The level of similarity between the cyanobacterial complexes of Lakes Gorbunka and Tsagan Nuur was high; however, these complexes displayed the lowest similarity to the complexes of other lakes. The cyanobacterial complexes of Lakes Solenoe and Zun Torei did not fall into any of the clusters, although they showed high similarity to the complexes of clusters I and II, respectively.

Importantly, the revealed patterns correlate well with the physicochemical conditions of the lakes inhabited by these cyanobacterial complexes. For instance, the first cluster of the dendrogram includes cyanobacterial complexes of the low-mineralized lakes of the Selenga group, whereas the second cluster includes the cyanobacterial complexes of the Onon–Borza group.

Analysis of the species composition of cyanobacteria using the "genera–mineralization" coordinate system revealed that Jacquard's floristic similarity coefficient varied within a wider range (0.083–0.5) than within the "species–mineralization" coordinate system. The highest k values were obtained when comparing the cyanobacterial complexes of Lakes Khilganta (drought and dry seasons), Sul'fatnoe–Verkhnee Beloe, and Solenoe–Gorbunka (0.75, 0.571, and 0.5, respectively). This may be due to the presence of representatives of the genera *Anabaena, Leptolyngbya, Nostoc*, and *Pseudanabaena* in Lakes Sul'fatnoe–Verkhnee Beloe, as well as to the presence of members of the genera *Oscillatoria* and *Phormidium, Pseudanabaena*, and *Spirulina* in Lakes Solenoe–Gorbunka. The lowest value of the coefficient of similarity (k = 0.083) was obtained when comparing the genus spectrum of cyanobacteria of Lakes Verkhnee Beloe–Khilganta during the dry season.

The dendrogram constructed on the basis of cluster analysis demonstrates that the clusters formed at the species level remain unchanged, except for cluster II, which was supplemented with Lake Solenoe (Fig. 2). At the genus level, the diversity spectrum of cyanobacteria decreases; therefore, the level of similarity between the studied lakes increases.

Thus, depending on the geochemical conditions, diverse cyanobacterial communities that differ at the species and genus levels develop in the studied ecosystems.

Ecophysiology and phylogenetic position of cyanobacterial cultures. Six monocultures of cyanobacteria were isolated from the bottom sediments and microbial mats of four lakes (Sul'fatnoe, Ekhe Torom, Khilganta, and Gorbunka) of the Southern Transbaikal Region (Table 3). Three of them (Cya 1, Cya 2, and Cya 10) were classified with the genus *Phormidium*, two monocultures (Cya 5 and Cya 6) were assigned to the genus *Nodularia*, and one monoculture (Cya 4) was assigned to the genus *Pseudanabaena*.

Table 3. Cultures of cyanobacteria isolated from the studied lakes

Culture	Isolation source	Identification according to Elenkin (1949) and Hollerbach et al. (1953)	Identification according to Komárek and Anagnostidis (1999, 2007)	Identification based on the 16S rRNA sequence analysis
Cya 1	Mat, Lake Sul'fatnoe	*Oscillatoria brevis* (Kütz.) Gom.	*Phormidium breve* (Kütz. et Gom.)	*Phormidium* sp.
Cya 2	Mat, Lake Ekhe Torom	*Oscillatoria brevis* (Kütz.) Gom.	*Phormidium breve* (Kütz. et Gom.)	*Phormidium* sp.
Cya 4	Mat, Lake Sul'fatnoe	*Phormidium frigidum* Fritsch.	*Pseudanabaena frigida* (Fritsch) Anagnost.	–
Cya 5	Crust, Lake Khilganta	*Anabaena sibirica* (Pop. et Degt.) Elenk.	*Nodularia* sp.	*Nodularia* sp.
Cya 6	Silt, Lake Gorbunka	*Anabaena sibirica* (Pop. et Degt.) Elenk.	*Nodularia* sp.	*Nodularia* sp.
Cya 10	Crust, Lake Khilganta	*Phormidium* sp.	*Phormidium* sp.	*Phormidium* sp.

The Cya 1 and Cya 2 cultures were isolated from the cyanobacterial mats of Lakes Sul'fatnoe and Ekhe Torom, respectively. The cell length (0.6–1.25 μm) was four times less than the cell width (5–5.6 μm). The terminal cells were rounded or curved and tapered. The terminal cells of mature trichomes were oblong and rounded. Biconcave cells darker than the main cells were often detected. The morphological properties of these cells were similar to those of *Oscillatoria brevis* [7] or *Phormidium breve* [10], except for some differences in size (Fig. 3a).

The Cya 4 culture was isolated from a cyanobacterial mat from Lake Sul'fatnoe. Trichomes (0.63–1.25 μm in width) were interweaved at the septa; the cells were square or barrel-shaped and not tapered. In most cases, the cells had the same length and width; sometimes, the cell length was greater. The terminal cells were rounded. According to the cell morphology, the culture was identified as *Phormidium frigidum* [7] or *Pseudanabaena frigida* [9] (Fig. 3b).

The Cya 5 and Cya 6 cultures were isolated from the dry crust of Lake Khilganta and from Lake Gorbunka silt, respectively. The trichomes were 3–3.13 μm in width, single or in parallel bundles, usually straight, without sheaths. The cells (up to 4.4 μm) were tapered, square, or oblong. The terminal cells were cone-shaped or rounded. The heterocysts were single, cylindrical or rounded, 3.13–4.4 μm in width and 4.4–5.6 μm in length, and located at the ends or in the middle of the trichomes. Spores (6.25 μm in diameter) were very scarce, single, spherical, surrounded by smooth capsules, and not attached to heterocysts. According to the cell morphology, the cultures were identified as *Anabaena sibirica* [8] or *Nodularia* sp. (Z. B. Namsaraev, unpublished data) (Fig. 3c).

The Cya 10 culture was isolated from a dry mat from Lake Khilganta. The filaments were blue-green and elongated; they were often bundled together and enclosed in sheaths. The cells were 5 μm in width. In most cases, they had the same length and width; sometimes, the cell width was greater. The terminal cells were rounded and not tapered. According to the cell morphology, the culture was identified as *Phormidium* sp. [10] (Fig. 3d).

To determine the phylogenetic position of the cultures, nucleotide sequences of the 16S rRNA gene fragments (1400 bp) were analyzed. Comparative phylogenetic analysis of the obtained 16S rRNA gene sequences revealed the greatest similarity of the Cya 10 culture to *Oscillatoria* cf. *laetevirens* Baja-Osc-1 (99.0%) and *Phormidium* sp. UTCC 487 (98.9%) (Table 4, Fig. 4). Importantly, the nomenclature of cyanobacteria is currently being revised to include the results of recent phylogenetic studies. In this work, the Cya 10 culture was tentatively described as a representative of the genus *Phormidium* rather than *Oscillatoria*. Interestingly, both *Oscillatoria* cf. *laetevirens* Baja-Osc-1 and *Phormidium* sp. UTCC 487 were isolated from highly mineralized lakes [15].

The restriction profiles of the 16S rRNA gene fragments of the cultures Cya 1 and Cya 2 amplified with the 27f and 1492r primers were found to be identical.

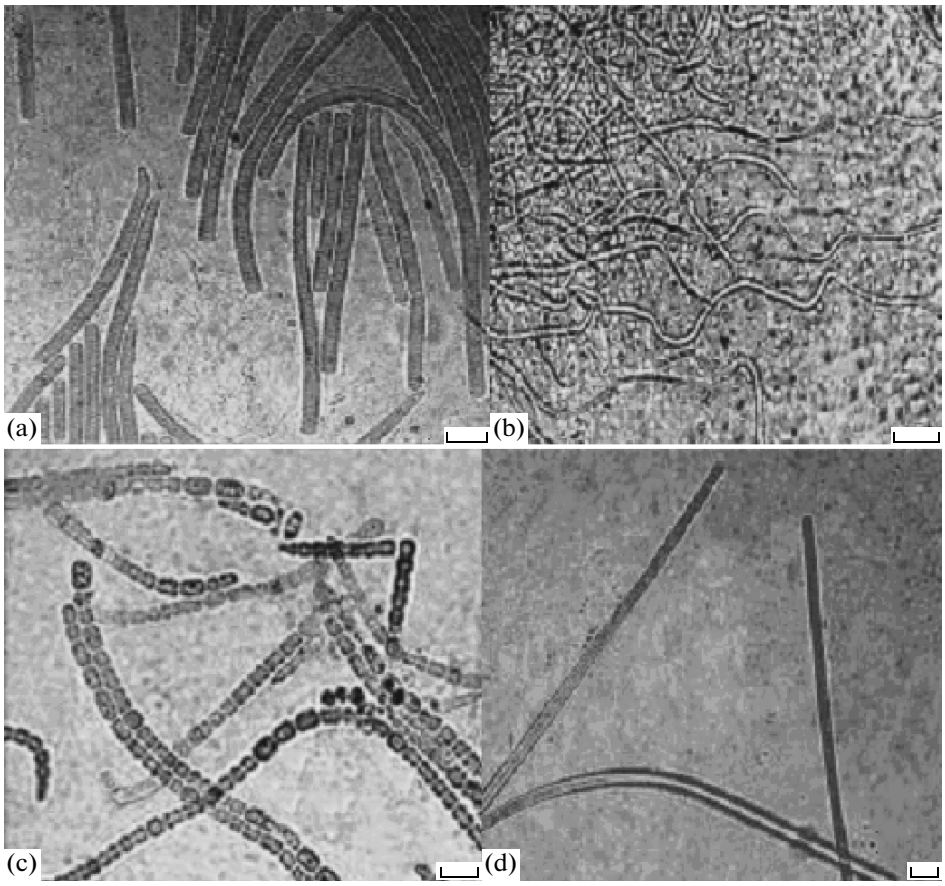

Fig. 3. Morphological properties of the studied cyanobacterial cultures: Cya 1 (a), Cya 4 (b), Cya 5 (c), and Cya 10 (d). Scale bar, 10 μm.

The morphological properties of these cultures were similar as well. Analysis of the 16S rRNA gene sequences demonstrated that the Cya 1 culture was closely related to *Phormidium* sp. NIVA-CYA 202 (99.2% similarity) (Table 4). Most of the cultures closely related to Cya 1 were isolated from the saline lakes of Antarctica [16]. On the basis of their phylogenetic and morphological characteristics, the Cya 1 and Cya 2 cultures were classified into the genus *Phormidium*.

Growth across the pH–mineralization gradient. The studied cultures were shown to grow within a broad salinity range: from complete absence of NaCl in the medium to 100 and 150 g/l NaCl.

The Cya 1 and Cya 2 cultures had the same growth optimum at pH 9.5 and salinity of 5 g/l NaCl. The cultures were able to grow at NaCl concentrations of up to 50 g/l, which corresponds to the conditions of their natural habitats (Fig. 5).

The results of our study revealed that the Cya 5 and Cya 6 cultures (*Nodularia* sp.) were alkaliphilic and halotolerant microorganisms. The pH optima of the Cya 5 and Cya 6 cultures were 8.5 and 9.5, respectively, at 20 (Cya 5) and 50 g/l NaCl (Cya 6). The cultures were able to grow in a salinity range of 0–100 g/l NaCl (Figs. 6, 7). This is the highest mineralization level at which the growth of heterocyst-forming cyanobacteria was observed. It is known from the literature that some *Nodularia* cultures are able to grow at NaCl concentrations not exceeding seawater concentrations [17]; however, these organisms were detected in some natural samples with a higher mineralization level [18].

The Cya 10 culture was able to grow within a salinity range of 0–50 g/l NaCl with an optimum at 5 g/l (Fig. 8). The NaCl content in the media above this level inhibited growth. The maximum biomass yield was detected at pH 8.5; the growth of the culture was weak under neutral or highly alkaline conditions.

Hence, the majority of the studied lakes were characterized by an unstable hydrochemical regime due to the sharply continental climate of the Southern Transbaikal Region. The waters (brackish and saline) of the majority of the studied lakes are of chloride–sodium and bicarbonate–sodium types. The lake waters are alkaline.

Table 4. Close relatives of the Cya 1, Cya 2, and Cya 10 cultures (according to the results of 16S rRNA sequencing)

Cultures	Phylogenetically related microorganisms	16S rRNA similarity, %	GenBank accession numbers
Cya 1, Cya 2	*Phormidium* sp. NIVA-CYA 202	99.2	Z82794
	Oscillatoria sp. Ant-G17	98.9	AF263334
	Oscillatoria sp. Ant-Salt	98.9	AF263337
	Phormidium sp. Ant-Brack-3	98.9	AF263332
	Phormidium lumbricale UTCC 476	98.6	AF218375
	Phormidium pseudopristleyi ANT.ACEV5.3	98.9	AY493600
Cya 10	*Oscillatoria* cf. *laetevirens* Baja-Osc-1	99.0	AF268490
	Phormidium sp. UTCC 487	98.9	AF218376

A total of 28 species of cyanobacteria were detected. The majority of them were found in low-mineralized lakes, and the smallest number were detected in highly mineralized lakes. The list of cyanobacteria inhabiting the lakes of the Southern Transbaikal Region includes ten species that have not been previously detected in these lakes. Analysis of the species composition of the cyanobacteria inhabiting the studied lakes using the Jacquard's floristic similarity coefficient showed that, depending on the physicochemical conditions, diverse cyanobacterial communities were formed in the studied ecosystems, differing at the species and genus levels.

Six cyanobacterial monocultures were isolated. The isolated microorganisms were moderate alkaliphiles with growth optima at alkaline pH. They were able to grow in the complete absence of NaCl in the medium and at NaCl concentrations of up to 100 g/l. The Cya 1, Cya 2, and Cya 10 cultures were classified into the genus *Phormidium*. The Cya 4 culture was classified into the species *Pseudanabaena frigida*. The Cya 5 and Cya 6 cultures were members of the genus *Nodularia*. They were able to grow at NaCl concentrations of up to 100 g/l, which was not previously reported for this genus.

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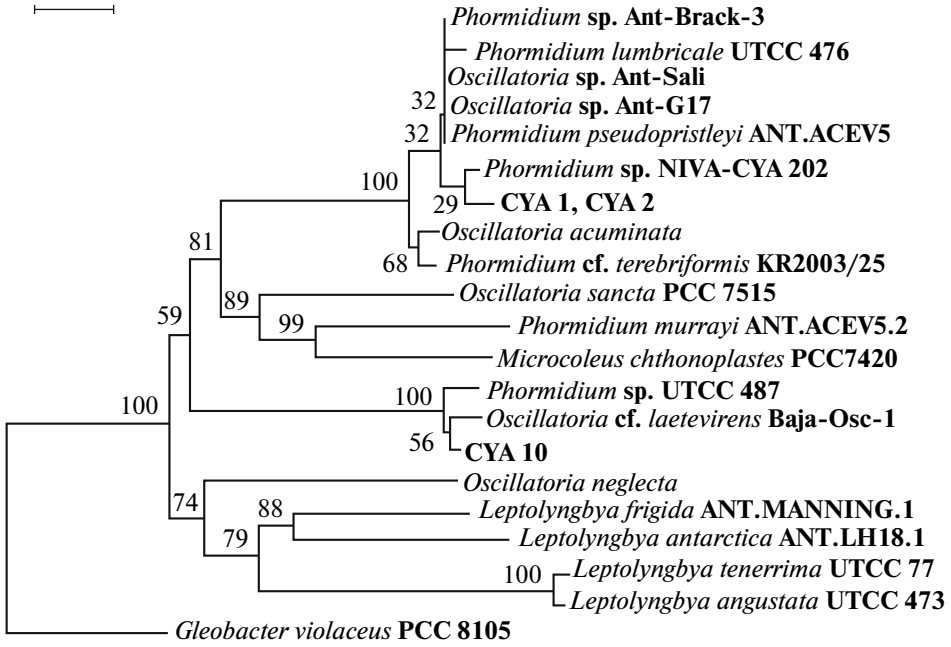

Fig. 4. Phylogenetic position of the cultures Cya 1, Cya 2, and Cya 10. Scale bar corresponds to two nucleotide replacements per 100 nucleotides.

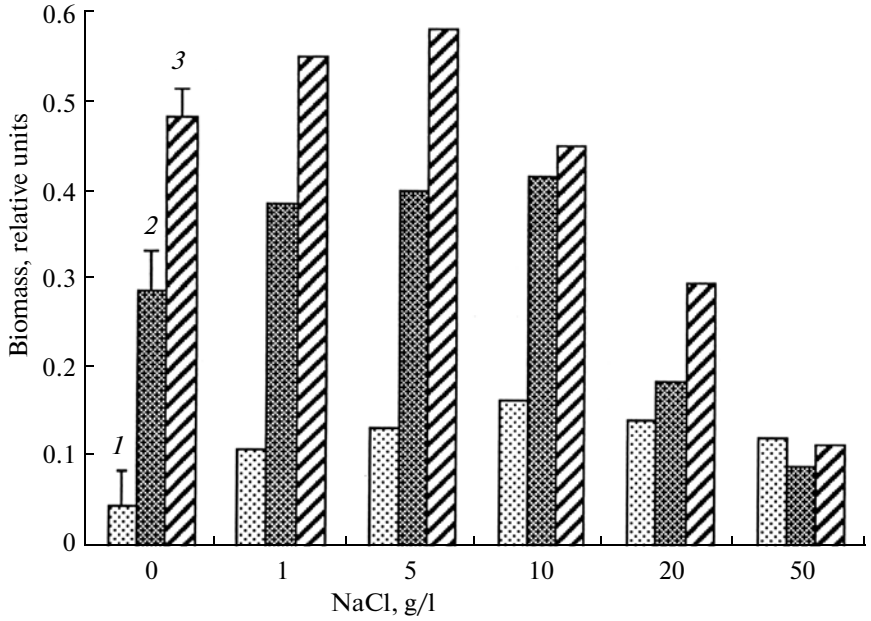

Fig. 5. Biomass yield of the Cya 1 culture across the pH-mineralization gradient: pH 7.5 (*1*), pH 8.5 (*2*), and pH 9.5 (*3*).

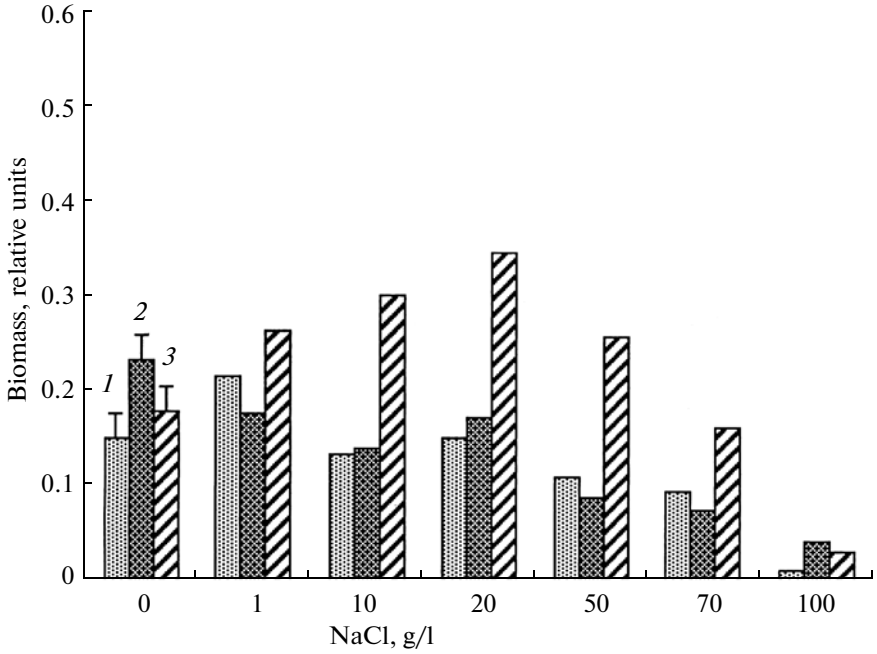

Fig. 6. Biomass yield of the Cya 5 culture across the pH-mineralization gradient: pH 7.5 (*1*), pH 8.5 (*2*), and pH 9.5 (*3*).

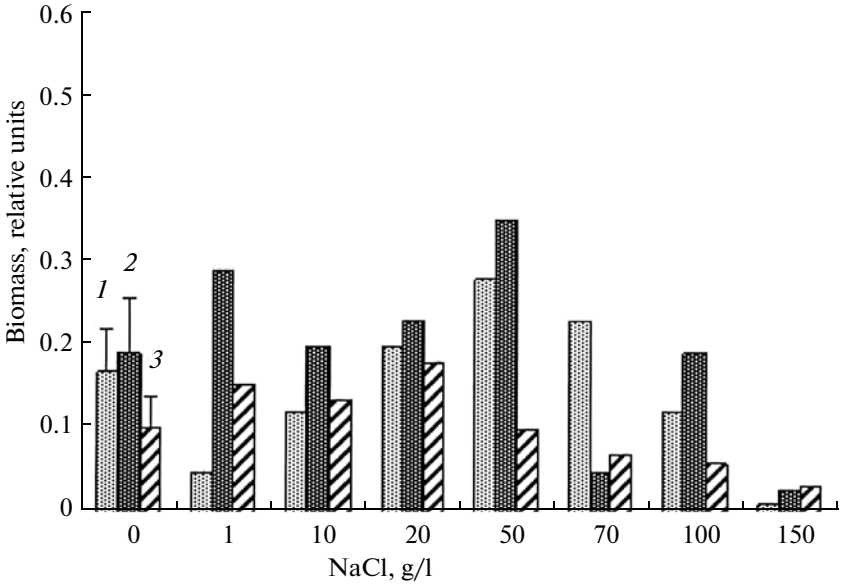

Fig. 7. Biomass yield of the Cya 6 culture across the pH-mineralization gradient: pH 7.5 (*1*), pH 8.5 (*2*), and pH 9.5 (*3*).

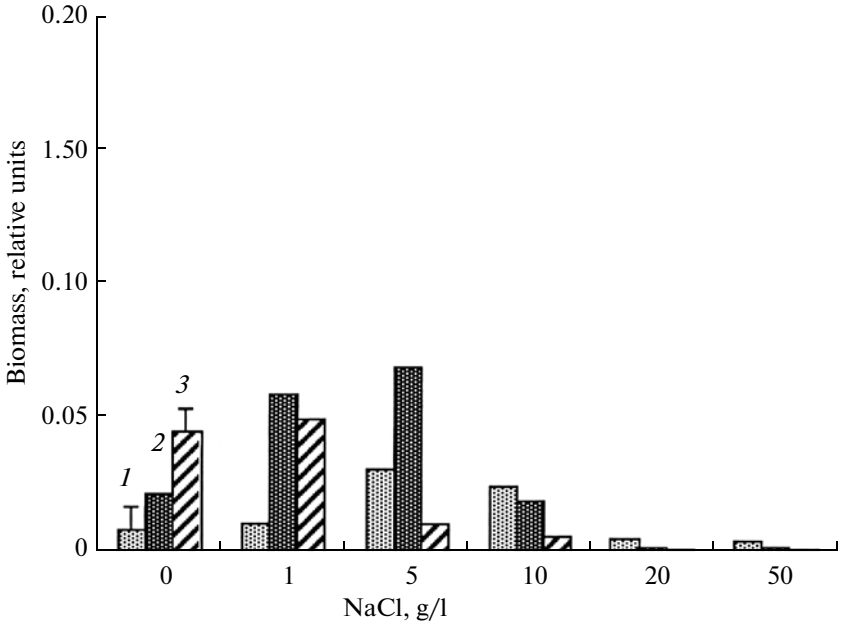

Fig. 8. Biomass yield of the Cya 10 culture across the pH-mineralization gradient: pH 7.5 (*1*), pH 8.5 (*2*), and pH 9.5 (*3*).

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