ISSN 0026-2617, Microbiology, 2018, Vol. 87, No. 4, pp. 583–590. © Pleiades Publishing, Ltd., 2018.
Original Russian Text © Z.B. Namsaraev, T.V. Kolganova, E.O. Patutina, D.D. Tsyrenova, O.S. Samylina, 2018, published in Mikrobiologiya, 2018, Vol. 87, No. 4.

EXPERIMENTAL ARTICLES

Cyanobacterial Diversity in the Alkaline Lake Khilganta during the Dry and Wet Periods

Z. B. Namsaraev[a, *], T. V. Kolganova[b], E. O. Patutina[b], D. D. Tsyrenova[c], and O. S. Samylina[d]

[a] *NRC Kurchatov Institute, Moscow, Russia*
[b] *Institute of Bioengineering, Research Center of Biotechnology, Russian Academy of Sciences, Moscow, Russia*
[c] *Institute of General and Experimental Biology, Siberian Branch, Russian Academy of Sciences, Ulan-Ude, Russia*
[d] *Winogradsky Institute of Microbiology, Research Center of Biotechnology, Russian Academy of Sciences, Moscow, Russia*
**e-mail: zorigto@gmail.com*

Received March 15, 2018

Abstract—Clone libraries and morphological analysis were used to investigate cyanobacterial diversity in the cyanobacterial mat and dry crust at the bottom of the shallow, saline, alkaline Lake Khilganta (Southern Siberia, Russia). Filamentous cyanobacteria belonging to *Phormidium* genus and *Coleofasciculus chthonoplastes* were found to predominate during the dry period (2006) and the wet periods (1995 and 2012), respectively. Community composition during the dry and wet periods differed significantly. While 11 operational taxonomic units of cyanobacteria were revealed, only 3 occurred during both dry and wet periods. Occurrence of cosmopolitan *C. chthonoplastes,* which is common in neutral saline environments, is not typical of a continental alkaline lake and may be explained by the similarity of the dominant ions composition in lake water and in seawater.

Keywords: cyanobacteria, saline lakes, alkaline lakes, cyanobacterial mat, *Coleofasciculus chthonoplastes*
DOI: 10.1134/S0026261718040136

Cyanobacterial mats are multilayered organomineral formations with predominance of cyanobacteria, which are mostly found in extreme environments (saline and soda lakes, hydrothermal vents, etc.). Cyanobacterial mats of soda lakes are considered as modern analogues of the stromatolite-forming communities predominant on Earth in the Proterozoic era (2500–541 Ma ago) (Zavarzin, 1993). Soda lakes are formed as a result of carbonate erosion of silicate rocks, causing accumulation of bicarbonate water in drainless areas. Extrapolating this mechanism to Precambrian conditions, Zavarzin suggested wide occurrence of large, shallow water bodies of the soda type in epicontinental areas and their major role in formation of terrestrial biota (the soda continent hypothesis). This theory is supported by the data on considerably heavier nitrogen isotopic composition ($\delta^{15}N$) of the lake rocks of the Tumbiana formation (2.72 Ga ago) compared to Archaean marine sediments, probably due to ammonium dissociation under anoxic alkaline conditions. Continental soda lakes are thought to be widespread in the late Archaean (Stüeken et al., 2015).

Lake Khilganta (Southern Siberia, Russia) was used as a model for investigation of the possible mechanisms of silicate erosion and stromatolite formation in epicontinental Precambrian water bodies (Zavarzin, 1993; Alekseeva et al., 2009). Depending on climatic conditions, the lake has salinity of 40 to 260 g/L and pH from 7.1 to 9.9. A cyanobacterial mat up to 2–3 cm thick is formed at the bottom of the lake (Namsaraev et al., 2010). Microscopic investigation of the phototrophic community of the lake revealed *Coleofasciculus chthonoplastes* to be one of the dominant cyanobacterial morphotypes in the mat (Gerasimenko et al., 2003), while cyanobacteria of the genera *Geitlerinema, Nodularia*, *Phormidium* and anoxygenic phototrophic bacteria of the genera *Ectothiorhodospira, Allochromatium, Thiocapsa*, and *Rhodovulum* were isolated from this community (Kompantseva et al., 2005; Tsyrenova et al., 2011).

Coleofasciculus chthonoplastes is the new name of *Microcoleus chthonoplastes*, a well-known species of mat-forming cyanobacteria (Siegesmund et al., 2008). This species has characteristic morphology (bundles of closely interwoven trichomes surrounded by a common sheath) and is cosmopolitan, occurring in saline and hypersaline conditions, at near-neutral pH and usually associated with marine environments (Oren, 2010). Thus, development of *C. chthonoplastes* within the phototrophic community of the alkaline continental Lake Khilganta is not typical and as yet has not been explained. This situation is complicated further by the absence of molecular genetic data on cyanobacterial diversity in the lake and by the contradictory

data on identification of the *Microcoleus* (*Coleofasciculus*) *chthonoplastes* strain isolated from Lake Khilganta. The goal of the present work was to carry out comprehensive investigation of cyanobacterial diversity in the Lake Khilganta phototrophic community under varying climatic conditions using morphological and molecular genetic approaches.

MATERIALS AND METHODS

Subject of research. Lake Khilganta (50°42.535′ N, 115°06.086′ E) is located in the steppe zone in the southeastern Transbaikal area, 76 km south to the Aginskoe settlement. The lake is drainless, round, with inclined shores. The water belongs to the chloride-sulfate-sodium type. The maximal water area during the moist period is up to 0.3 km^2, the greatest water depth is 64 cm. The temperature and pH were determined at the sampling site, as well as carbonate concentration (by titration) and salinity (refractometrically). The data on the total annual amount of precipitation, starting from 2005, were obtained from the World Meteorological Organization database, Aginskoe weather station, WMOID 30859 (https://www.ncdc.noaa. gov/data-access/land-based-station-data/land-based- datasets).

Morphological diversity of cyanobacteria. For determination of cyanobacterial species composition, the samples were fixed with 4% formalin. For microscopy of dry crust and cyanobacterial mat samples, they were homogenized on a slide, covered with 5% HCl for carbonate removal, and examined under a light microscope at ×400–1000. Morphological identification of cyanobacteria was carried out using identification manuals (Gollerbakh et al., 1953; Komàrek and Anagnostidis, 2005).

Analysis of diversity of cyanobacterial 16S rRNA genes. DNA was isolated from environmental samples according to Wilson et al. (1992) with cetyl trimethylammonium bromide (CTAB). PCR was carried out using Kapa Taq polymerase and cyanobacterial primers CYA106F and CYA781R (Nübel et al., 1997). Ligation of PCR products was carried out using the pGEM-T Vector System kit (Promega). Sequencing of the clonal inserts was carried out according to Sanger et al. (1977) using the Big Dye Terminator v. 3.1 kit (Applied Biosystems, Inc., United States) on the equipment of the Biotechnology Center, Russian Academy of Sciences. Sequencing was carried out using the universal plasmid primer. Cyanobacterial 16S rRNA gene sequences were analyzed for the presence of chimeras using DECIPHER (Wright et al., 2012). The remaining sequences were analyzed using the USEARCH software package (Edgar, 2010). At the first stage, the sequences were aligned using the MUSCLE algorithm. Cluster analysis of aligned sequences was carried out at 97% similarity level. For each operational taxonomic unit (OTU), a representative centroid nucleotide sequence corresponding to the cluster center was chosen. Taxonomic classification of the representative sequences was carried out by comparison with the GenBank database using the BLAST protocol. The sequences occurring only once (singletons) were excluded from subsequent analysis (Brown et al., 2015). The sequences were deposited to GenBank under accession nos. MH211207-MH211220. Phylogenetic trees were constructed using the FastTree v. 2.1.10 algorithm by the maximal likelihood method with distance assessment according to Jukes-Cantor (Price et al., 2010). Local support values were determined using the Shimodaira-Hasegawa test and 1000 replications. The trees were visualized using FigTree v. 1.4.3. (http://tree.bio.ed.ac.uk/software/figtree/).

RESULTS

Hydrological regimen of Lake Khilganta. Investigation of Lake Khilganta were carried out during the dry and wet periods. In 2006, the total precipitation measured at the Aginskoe meteorological station was 259 mm (Fig. 1). At the sampling time (June 21, 2006), the lake basin was completely dry, with the crusts of cyanobacterial mats on the surface of the bottom sediments (Fig. 2b). In 2012, the total precipitation was 342 mm, and at the sampling time (June 30, 2012) the basin was filled with water with 6.5 g/L salinity and pH 9.5. A multilayered cyanobacterial mat 0.5 to 3 cm thick developed on the bottom (Fig. 2a). Both the dry crust and the cyanobacterial mat exhibited pronounced layers, with darker layers containing microorganisms alternated with the lighter ones enriched with mineral components.

Morphological diversity of cyanobacteria. Species diversity of cyanobacteria was studied using their morphological parameters. In the dry crust (2006), five morphotypes were revealed: unicellular cyanobacteria *Chroococcus minutus* and filamentous cyanobacteria *Leptolyngbya tenuis, Leptolyngbya woronichinii, Coleofasciculus chthonoplastes*, and *Phormidium breve* (Fig. 2). *Ph. breve* was the dominant morphotype. In the cyanobacterial community studied in 2017, *C. chthonoplastes* predominated. Other morphotypes detected were identified as unicellular cyanobacteria *Chroococcus minutus* and filamentous cyanobacteria *Oscillatoria* sp. and *Lyngbya* sp. Layer-by-layer analysis of the dry crust and the cyanobacterial mat revealed the highest diversity of cyanobacterial morphotypes in the uppermost layer of the sample, while in deeper layers cyanobacterial cells degraded and the number of empty cyanobacterial sheaths increased.

Molecular diversity of cyanobacteria. From the dry crust collected in 2006, 91 nucleotide sequence was retrieved, which belonged to cyanobacteria and contained no chimera. Cluster analysis revealed 13 OTUs, of which 6 OTUs were represented by single sequences (singletons). These ones were excluded from analysis. The most represented one (41 sequences) was the OTU with the representative nucleotide sequence

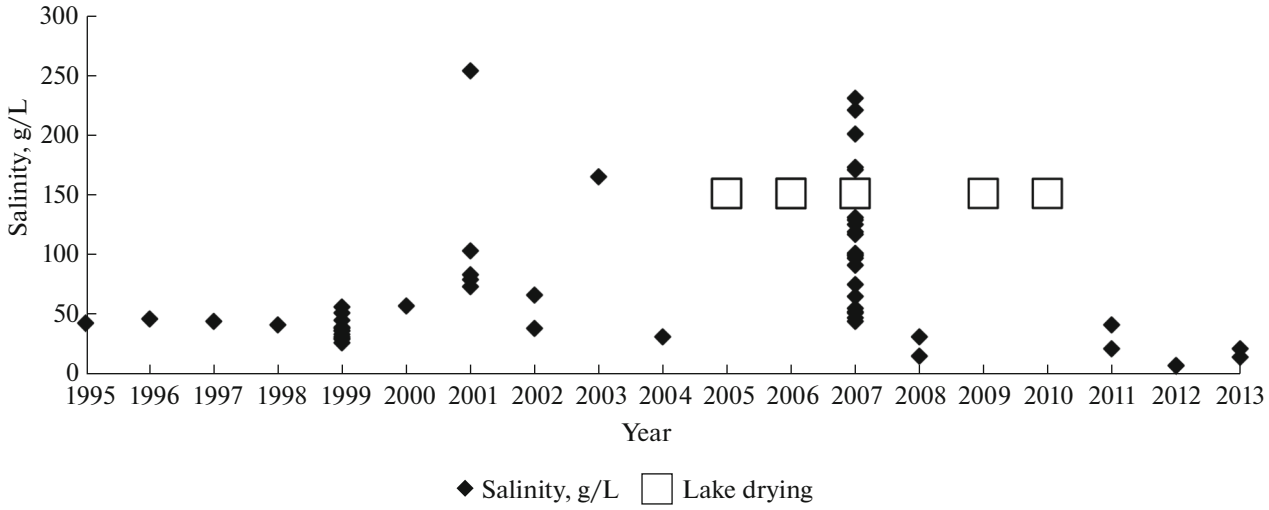

Fig. 1. Water salinity and drying episodes in Lake Khilganta from 1995 to 2013.

"Dry mat, clone F07," which according to the results of BLAST analysis was most closely related (over 97% similarity) to *Phormidium etoshii* and the cosmopolitan species *Phormidium autumnale* (Fig. 3). The second most numerous (21 sequences) was the OTU with the "Dry mat, clone G07" representative sequence, which exhibited over 97% similarity to the sequences of members of the genera *Geitlerinema, Leptolyngbya, Oscillatoria*, and *Phormidium*, as well as to *Microcoleus* sp. strain IPPAS B-353 (GenBank no. KU375124), previously isolated from Lake Khilganta (Kupriyanova et al., 2016). The remaining five OTUs, which contained over one nucleotide sequence (2 to 6), were closely related to members of the heterocystous cyanobacterial genera *Nodularia* and *Anabaena* ("Dry mat, clone G02"), the genera of filamentous cyanobacteria *Lyngbya* and *Planktothrix* ("Dry mat, clone G01"), *Leptolyngbya* and *Nodosilinea* ("Dry mat, clone G09"), unicellular cyanobacteria of the genera *Aphanothece, Synechococcus,* and *Cyanobacterium* ("Dry mat, clone H09"). The OTU with the "Dry mat, clone A09" representative sequence had no closely related cultured members.

From the cyanobacterial mat collected in 2012, 89 nucleotide sequences were retrieved, which belonged to cyanobacteria and contained no chimera. Cluster analysis revealed 8 OTUs, of which one contained a single sequence and was excluded from analysis. The most represented OTU (38 sequences) with the "Wet mat, clone H01" representative sequence, which according to the results of BLAST analysis was most closely related to *C. chthonoplastes*. The second most represented one (26 sequences) was the OTU exhibiting over 97% similarity to filamentous cyanobacteria of the genera *Leptolyngbya* and *Nodosilinea* ("Wet mat, clone H05" sequence). Other five OTUs, comprising 2 to 12 sequences, were related to filamentous cyanobacteria of the genera *Leptolyngbya* and *Nodosilinea* ("Wet mat, clone A01"), *Leptolyngbya* ("Wet mat, clone F09"), *Phormidium* and *Oscillatoria* ("Wet mat, clone C11"), and heterocystous cyanobacteria *Nodularia* and *Anabaena* ("Wet mat, clone E07"). The OTU with the representative sequence "Wet mat, clone A05" had no closely related cultured members.

Comparison of the OTUs revealed in the 2006 and 2012 samples revealed relatively low cyanobacterial diversity in Lake Khilganta. During both the dry and wet periods, 7 cyanobacterial OTUs were found, with only three of them occurring in both periods. These are the OTUs with the "Dry mat, clone G02" and "Wet mat, clone E07" representative sequences and related to heterocystous cyanobacteria of the genera *Nodularia* and *Anabaena*, as well as two OTUs of filamentous cyanobacteria related to *Leptolyngbya* and *Nodosilinea* species (the "Dry mat, clone G09" and "Wet mat, clone A01" sequences) and to members of the genus *Phormidium* (the "Dry mat, clone F07" and "Wet mat, clone C11" sequences). Thus, the overall number of unique OTUs revealed in Lake Khilganta was 11. All OTUs studied were cosmopolitan, with their members occurring within a broad geographical range.

DISCUSSION

In the alkaline Lake Khilganta, cyanobacterial communities develop as multilayered mats with predominance of filamentous cyanobacteria. Morphological and molecular genetic investigation of cyanobacteria revealed the differences in cyanobacterial composition between the dry and wet periods. Thus, a filamentous cyanobacterium morphologically identified as *Phormidium breve* predominated during the dry period (2006). This was in agreement with the results of molecular genetic analysis, which revealed predominance of the "Dry mat, clone F07" sequence related

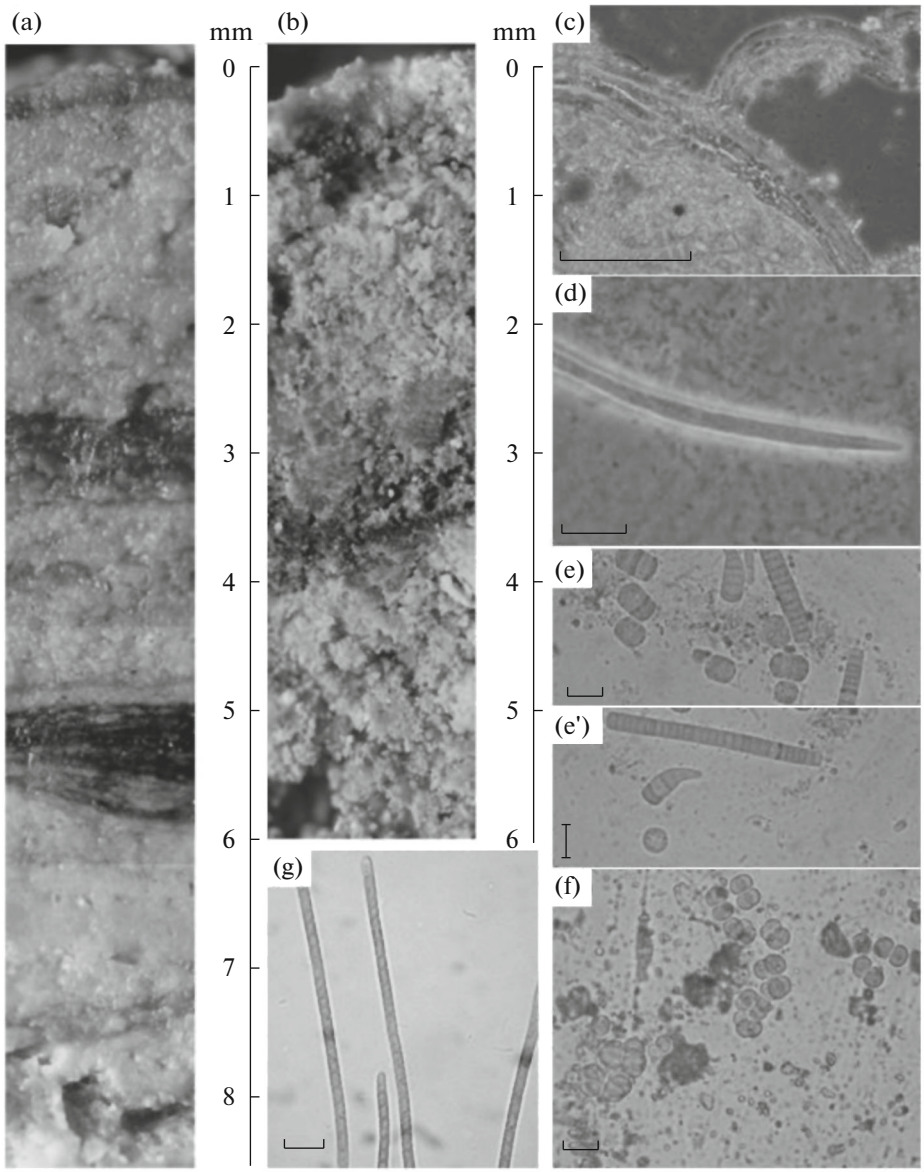

Fig. 2. Lake Khilganta cyanobacterial mat and cyanobacterial diversity: mat structure during the 2012 wet period (a); structure of the dry crust during the 2006 dry period (b); *Coleofasciculus chthonoplastes* in 2012 (c, d); *Phormidium breve* in 2006 (e, e'); *Chroococcus minutus* in 2006 (f); and *Microcoleus* sp. IPPAS B-353 (h). Scale bar is 10 μm.

to the 16S rRNA gene sequence of *Phormidium etoshii* KR2008/49 (NR_125647.1) in the dry crust sample. *Ph. breve* from Lake Khilganta (Fig. 2e) was morphologically and ecologically similar to *Ph. etoshii* described for saline, alkaline environments in Etosha-Pan solonchak, Namibia (Dadheech et al., 2013).

During the wet period of 2012, both morphological and molecular biological data indicated predominance of *C. chthonoplastes* "Wet mat, clone H01." While individual filaments of *C. chthonoplastes* were revealed by microscopy of the dry crust collected in 2006, its nucleotide sequences were not present in the clone library.

Taking into account the earlier contradictory reports of the presence of *C. chthonoplastes* in Lake Khilganta, we carried out a retrospective analysis of the data obtained during investigation of the samples collected in summer 1995. Gerasimenko et al. (2003) performed layer-by-layer investigation of these samples by transmission electron microscopy. Filamentous nonheterocystous forms identified as *Phormidium molle* and *Microcoleus chthonoplastes* (*C. chthonoplastes*) were found to predominate in different layers of the mat. Ultrastructural properties of cyanobacterial cell sections reported by Gerasimenko et al. (2003) confirm the taxonomic identification of *C. chthonoplastes*. The taxonomically important features charac-

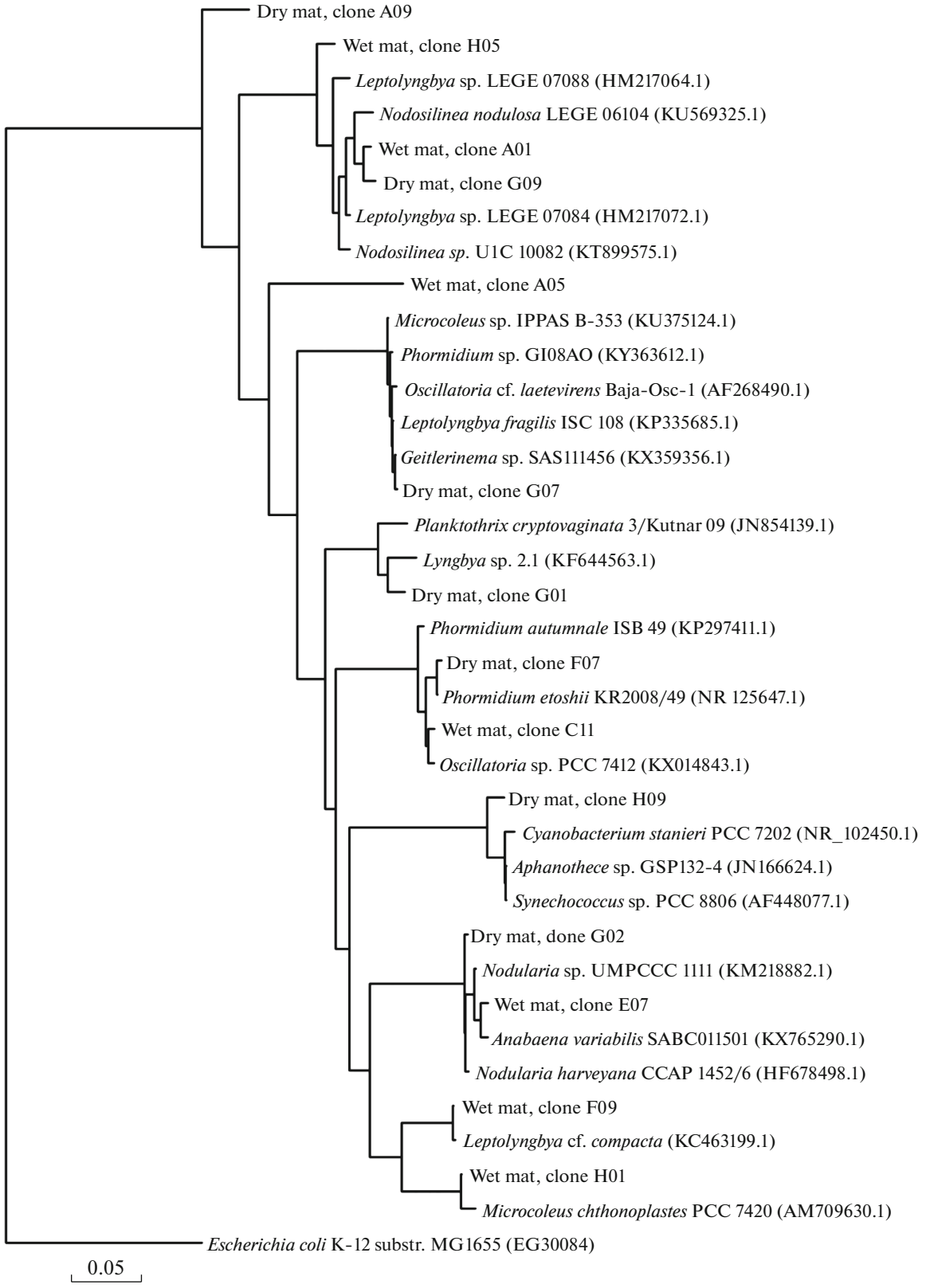

Fig. 3. Phylogenetic tree of the representative nucleotide sequences of the 16S rRNA genes of the cyanobacterial operational taxonomic units retrieved from Lake Khilganta and of the homologous sequences with similarity over 97%. "Dry mat, clone XXX" designates the nucleotide sequences from the 2006 dry crust, "Wet mat, clone XXX" designates the nucleotide sequences from the 2012 cyanobacterial mat. The phylogenetic tree was constructed using the approximate maximum likelihood method.

terizing this species were the bundles of parallel trichomes bound by a common mucous sheath and radial thylakoid arrangement in the cells (Gerasimenko et al., 2003).

From this mat, the strain Z-9627 was isolated, which was identified as *Microcoleus chthonoplastes* and became a model organism for investigation of the components of the CO_2-concentrating mechanism in haloalkaliphilic cyanobacteria (Kupriyanova et al., 2004, 2011, 2016; Kupriyanova and Samylina, 2015) and for modeling of the transformations of minerals under alkaline conditions (Alekseeva et al., 2009; Zavarzin et al., 2003; Zaitseva et al., 2007). The strain was deposited to two collections: the Microalgae Collection, Timiryazev Institute of Plant Physiology, Russian Academy of Sciences (*Microcoleus* sp. IPPAS B-353) and Culture collection of Autotrophic Organisms, Institute of Botany, Czech Republic (*Microcoleus chthonoplastes* CCALA 1011). Investigation by transmission electron microscopy (Kupriyanova et al., 2011) revealed the ultrastructural features of this strain to be different from those observed on the photographs of intact Lake Khilganta mats published by Gerasimenko et al. (2003). Thus, the cells of strain B-353 were characterized by parietal thylakoid arrangement, which is an important feature in cyanobacterial taxonomy, not depending on the growth phase and cultivation conditions. Analysis of the 16S rRNA gene sequence of this strain suggested its identification as a member of the *Geitlerinema* phylogenetic group, group IV (by Perkerson et al., 2010) or of marine *Geitlerinema* (by Strunecký et al., 2017). The sequences of this phylogenetic group form a close cluster and may be later described as a new taxon of the genus level. The nucleotide sequences of this cluster were also detected in the sample collected at Lake Khilganta in 2006, with the "Dry mat, clone G07" representative sequence, where they were the second most abundant group.

Thus, the data obtained during Lake Khilganta study show that during the wet periods (1995 and 2012) *C. chthonoplastes* was one of the dominant cyanobacteria in the lake, while during the dry period (2006) its role in the community was less pronounced.

Analysis of biogeographical distribution of 4700 nucleotide sequences with over 97% similarity to that of the type strain *C. chthonoplastes* SAG 2209 (NR_125521.1) revealed members of this species to occur mainly in the coastal zones of seas and oceans, saline soils, salterns, and saline lakes (Fig. 4). This finding does not contradict the earlier conclusion on its cosmopolitan occurrence and association with halophilic habitats with near-neutral pH, which was made based on the morphological and molecular genetic data (Garcia-Pichel et al., 1996; Oren, 2010). However, periodic predominance of *C. chthonoplastes* in an alkaline continental lake located at least 1200 km from the nearest sea requires additional discussion. Importantly, *C. chthonoplastes* was predominant in the cyanobacterial community during the wet period when pH was in the range from 9.5 to 9.9.

The hydrochemical data on lake water obtained by Namsaraev et al. (2010), show that the chemical composition of Lake Khilganta water was similar to marine conditions, unlike the typical soda lakes, in which carbonates are responsible for over 30% of the total anions (Namsaraev et al., 2015). During the wet period, the water of the lake, similar to seawater, belongs to the chloride-sulfate-sodium type, with carbonate content not exceeding 3.5% of the total amount of ions. However, during the wet period the water of the lake is alkaline with a stable high pH. This may be explained by the ratio of the carbonate and calcium ions according to the Hardie–Eugster equation: $2mCa^{2+} = mHCO_3^- + 2mCO_3^{2-}$ (Hardie and Eugster, 1970). During the wet period carbonate content in lake water exceeds that of calcium, which results in high pH values. However, the ratio of carbonates to chlorides and sulfates remains low, with probably no significant effect on *C. chthonoplastes*. Importantly, this cyanobacterial species has as yet not been found in classical soda lakes with high carbonate levels. At the same time, marine *Geitlerinema,* which comprise *Microcoleus* sp. IPPAS B-353, as well as members of the OTU with the "Dry mat, clone G07" representative sequence, from Lake Khilganta, are widespread in classical soda lakes (Samylina et al., 2015).

Our data on the composition of the Lake Khilganta cyanobacterial community support two different scenarios of development of the lake community depending on climatic and weather conditions in the southeastern Transbaikal region. Since in this area ~70% of precipitation occurs in summer, the water level in the lake basin in summer depends on the net annual precipitation. At relatively high amount of precipitation in the area (e.g., 342 mm in 2012), the lake basin is filled with water, and the water has low salinity (6.5–55 g/L) and pH from 9.5 to 9.9. During such periods, filamentous cyanobacteria *C. chthonoplastes* are among the dominant forms. At relatively low annual precipitation (259 mm in 2006 and 152 mm in 2007), the lake basin is filled only during short-term rains, followed by rapid water evaporation, and the lake bottom is covered with a dry crust. During this period, filamentous cyanobacteria of the genus *Phormidium*, as well as marine *Geitlerinema*, predominate in the cyanobacterial community, while the role of *C. chthonoplastes* is less pronounced than in more humid years.

Thus, it may be suggested that formation of the thick multilayer cyanobacterial mat in Lake Khilganta, which was of considerable interest to researchers, may be explained by the chemical composition of lake water, which is close to that of seawater and makes it possible for the filamentous cyanobacterium *C. chthonoplastes* to form cyanobacterial mats on the lake bottom.

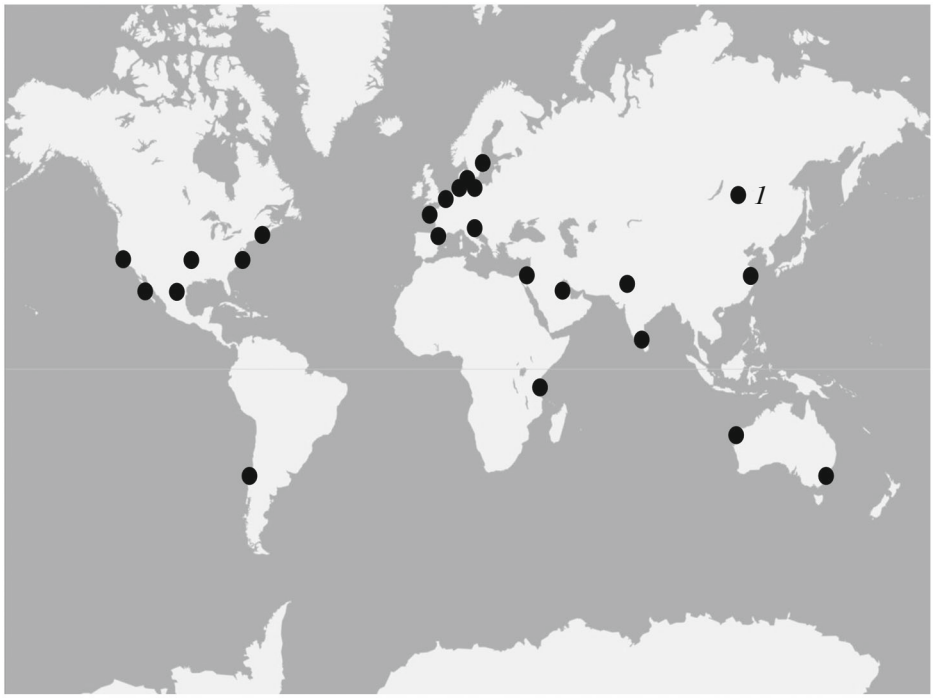

Fig. 4. The map showing the distribution of the 16S rRNA gene sequences with similarity of at least 97% to the sequence of the type strain *C. chthonoplastes* SAG 2209 (NR_125521.1). Lake Khilganta (*1*). The data on the geographical sources of the following sequences were used: AB784075, AF210048, AM709630.1, AY500274.1, DQ058853, EF160050.1, EF654025.1–EF654089.1, EU251080.1, FN678385.1, GQ402017.1, GQ441199.1, GU213185.1, HG938320.1, HM628456.1, HQ343413.1, JN166563.1, JN427152.1, JX002103.1, KJ998017.1, KT037024.1, NR_125521.1, X70770.1.

ACKNOWLEDGMENTS

The article is dedicated to the memory of B.B. Namsaraev, L.M. Gerasimenko, B.B. Kuznetsov, and B.K. Bumazhkin, who participated in the research of cyanobacterial diversity in Lake Khilganta. The work was supported by Russian Academy of Sciences and Federal Agency of Scientific Organizations (project no. AAAA-A17-117011810034-9) and NRC "Kurchatov Institute."

REFERENCES

Alekseeva, T.V., Alekseev, A.O., Sapova, E.V., and Gerasimenko, L.M., Transformation of clay minerals caused by an alkaliphilic cyanobacterial community, *Microbiology* (Moscow), 2009, vol. 78, pp. 776–784.

Brown, S.P., Veach, A.M., Rigdon-Huss, A.R., Grond, K., Lickteig, S.K., Lothamer, K., Oliver, A.K., and Jumponen, A., Scraping the bottom of the barrel: are rare high throughput sequences artifacts?, *Fungal Ecol.*, 2015, vol. 13, pp. 221–225.

Dadheech, P.K., Casamatta, D.A., Casper, P., and Krienitz, L., *Phormidium etoshii* sp. nov. (Oscillatoriales, Cyanobacteria) described from the Etosha Pan, Namibia, based on morphological, molecular and ecological features, *Fottea*, 2013, vol. 13, pp. 235–244.

Edgar, R.C., Search and clustering orders of magnitude faster than BLAST, *Bioinformatics*, 2010, vol. 26, pp. 2460–2461.

Garcia-Pichel, F., Prufert-Bebout, L., and Muyzer, G., Phenotypic and phylogenetic analyses show *Microcoleus chthonoplastes* to be a cosmopolitan cyanobacterium, *Appl. Environ. Microbiol.*, 1996, vol. 62, pp. 3284–3291.

Gerasimenko, L.M., Mityushina, L.L., and Namsaraev, B.B. *Microcoleus* mats from alkaliphilic and halophilic communities, *Microbiology* (Moscow), 2003, vol. 72, pp. 71–79.

Gollerbakh, M.M., Kosinskaya, E.K., and Polyanskii, V.I., *Sinezelenye vodorosli. Opredelitel' presnovodnykh vodoroslei SSSR* (Blue-Green Algae. Manual for Identification of Freshwater algae of the USSR), Moscow: Sov. Nauka, 1953, vol. 2.

Hardie, L.A. and Eugster, H.P., The evolution of closed-basin brines, *Mineralog. Soc. America*, 1970, pp. 253–273.

Komàre, J. and Anagnostidis, K., *Süsswasserflora von Mitteleuropa. 19/2. Cyanoprokariota. 2. Teil: Oscillatoriales* / Büdel, B., Gärtner, G., Krienitz, L., and Schagerl, M. Eds. Heidelberg: Elsevier, 2005.

Kompantseva, E.I., Sorokin, D.Yu., Gorlenko, V.M., and Namsaraev, B.B., The phototrophic community found in Lake Khilganta (an alkaline saline lake located in the southeastern Transbaikal Region), *Microbiology* (Moscow), 2005, vol. 74, pp. 352–361.

Kupriyanova, E.V. and Samylina, O.S., CO_2-concentrating mechanism and its traits in haloalkaliphilic cyanobacteria, *Microbiology* (Moscow), 2015, vol. 84, pp. 112–124.

Kupriyanova, E.V., Cho, S.M., Park, Y.-I., Pronina, N.A., and Los, D.A., The complete genome of a cyanobacterium from a soda lake reveals the presence of the components of

CO_2-concentrating mechanism, *Photosynth. Res.*, 2016, vol. 130, pp. 151–165.

Kupriyanova, E.V., Markelova, A.G., Lebedeva, N.V., Gerasimenko, L.M., Zavarzin, G.A., and Pronina, N.A., Carbonic anhydrase of the alkaliphilic cyanobacterium *Microcoleus chthonoplastes, Microbiology* (Moscow), 2004, vol. 73, pp. 255–259.

Kupriyanova, E.V., Sinetova, M.A., Markelova, A.G., Allakhverdiev, S.I., Los, D.A., and Pronina, N.A., Extracellular β-class carbonic anhydrase of the alkaliphilic cyanobacterium *Microcoleus chthonoplastes, J. Photochem. Photobiol. B: Biology*, 2011, vol. 103, pp. 78–86.

Namsaraev, Z.B, Zaitseva, S.V, Gorlenko, V.M, Kozyreva, L.P, and Namsaraev, B.B., Microbial processes and factors controlling their activities in alkaline lakes of the Mongolian plateau, *Chinese J. Oceanol. Limnol.*, 2015, vol. 33, pp. 1391–1401.

Namsaraev, Z.B., Gorlenko, V.M., Buryukhaev, S.P., Barkhutova, D.D., Dambaev, V.D., Dulov, L.E., Sorokin, V.V., and Namsaraev, B.B., Water regime and variations in hydrochemical characteristics of the soda salt lake Khilganta (Southeastern Transbaikalia), *Water Res.* (Moscow), 2010, vol. 37, pp. 513–519.

Nübel, U., Garcia-Pichel, F., and Muyzer, G., PCR primers to amplify 16S rRNA genes from cyanobacteria, *Appl. Environ. Microbiol.*, 1997, vol. 63, pp. 3327–3332.

Oren, A., Mats of filamentous and unicellular cyanobacteria in hypersaline environments, in *Microbial Mats*, Seckbach, J. and Oren, A., Eds., Springer, 2010, pp. 387–400.

Perkerson, R.B., III, Perkerson, E.A., and Casamatta, D.A., Phylogenetic examination of the cyanobacterial genera *Geitlerinema* and *Limnotrix* (*Pseudanabaenaceae*) using 16S rDNA sequence data, *Algol. Studies,* 2010, vol. 134, pp. 1–16.

Price, M.N., Dehal, P.S., and Arkin, A.P., FastTree 2—Approximately Maximum Likelihood Trees for large alignments, *PLoS One*, 2010, vol. 5, p. e9490.

Samylina, O.S., Sapozhnikov, F.V., Gainanova, O.Yu., Ryabova, A.V., Nikitin, M.A., and Sorokin, D.Yu. Algo–bacterial communities of the Kulunda Steppe (Altai Region, Russia) soda lakes, *Microbiology* (Moscow), 2014, vol. 83, pp. 849–860.

Siegesmund, M.A., Johansen, J.R., Karsten, U., and Friedl, T., *Coleofasciculus* gen. nov. (Cyanobacteria): morphological and molecular criteria for revision of the genus *Microcoleus* Gomont., *J. Phycol.*, 2008, vol. 44, pp. 1572–1585.

Strunecký, O., Markéta, M., Johansen, J.R., Čapková, K., Raabová, L., Dvořák, P., and Komárek, J., A revision of the genus *Geitlerinema* and a description of the genus *Anagnostidinema* gen. nov. (Oscillatoriophycidae, Cyanobacteria), *Fottea*, 2017, vol. 17, pp. 114–126.

Stüeken, E.E., Buick, R., and Schauer, A.J., Nitrogen isotope evidence for alkaline lakes on late Archean continents, *Earth Planetary Sci. Lett.*, 2015, vol. 411, pp. 1–10.

Tsyrenova, D.D., Bryanskaya, A.V., Namsaraev, Z.B., and Akimov, V.N., Taxonomic and ecological characterization of cyanobacteria from some brackish and saline lakes of Southern Transbaikal region, *Microbiology* (Moscow), 2011, vol. 80, pp. 216–227.

Wilson, H.D., Doebly, J., and Duvall, M., Chloroplast DNA diversity among wild and cultivated members of *Cucurbita* (Cucurbitaceae), *Theor. Appl. Genet.*, 1992, vol. 84, pp. 859–865.

Wright, E.S., Yilmaz, L.S., and Noguera, D.R., DECIPHER, a search-based approach to chimera identification for 16S rRNA sequences, *Appl. Environ. Microbiol.*, 2012, vol. 78, pp. 717–725.

Zaitseva, L.V., Orleanskii, V.K., Gerasimenko, L.M., Alekseev, A.O., and Ushatinskaya, G.T., Transformation of carbonate minerals in a cyano-bacterial mat in the course of laboratory modeling, *Microbiology* (Moscow), 2007, vol. 76, pp. 342–356.

Zavarzin, G.A., Epicontinental soda lakes as probable relict biotopes of terrestrial biota formation, *Microbiology* (Moscow), 1993, vol. 62, pp. 473–479.

Zavarzin, G.A., Orleanskii, V.K., Gerasimenko, L.M., Pushko, S.N., and Ushatinskaya, G.T., Laboratory simulations of cyanobacterial mats of the alkaline geochemical barrier, *Microbiology* (Moscow), 2003, vol. 72, pp. 80–85.

Translated by P. Sigalevich