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EXPERIMENTAL ARTICLES

Prokaryotic Communities in Saline Soils of the Lake Elton Area in a Soil Catena along the Khara River

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Abstract—Analysis of the taxonomic structure of prokaryotic microbial complexes of the saline soils in the Lake Elton area and their comparative characteristics were carried out for a soil catena along the Khara River flowing into the hypersaline Lake Elton. High-throughput pyrosequencing detected 11 bacterial and 2 archaeal phyla. Comparative analysis of community structure revealed the differences between *Solonchaks* located at the river flood land and *Kastanozems* at the slope and top of the river terrace. The patterns of occurrence were described for six predominant phyla (*Euryarchaeota, Thaumarchaeota, Proteobacteria*, *Firmicutes, Bacteroidetes*, and *Actinobacteria*). For the floodplain soils, the relations between the distribution of *Euryarchaeota, Thaumarchaeota, Firmicutes, Actinobacteria, Proteobacteria* and soil salinity as well as soil pH were described. Occurrence of members of the phyla *Euryarchaeota*, *Thaumarchaeota*, *Firmicutes, Actinobacteria*, and *Proteobacteria* in flood land soils was shown to depend on the soil salinity and pH. Members of the phyla *Actinobacteria* and *Firmicutes* were shown to predominate in *Gleyic Kastanozems* . Cloning of the 16S rRNA gene revealed high diversity within the genus *Streptomyces* (*Actinobacteria*). A number of the isolated streptomycete clones were homologous to the known antibiotic producers, which indicates that soils of this area are promising for further biotechnological screening.

Keywords: microbial diversity, saline soils, arid ecosystems, *Streptomyces*, Lake Elton, high-throughput sequencing pyrosequencing, microbial biotechnology

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Microbial diversity in the communities of dry and saline habitats is of special interest both in relation to the problems of global climate changes and for assessment of the biotechnological utility of these habitats. Global climate change and increasing anthropogenic load result in desertification and higher shares of saline soils in natural ecosystems worldwide (Rengasamy, 2006). The presently urgent tasks are investigation of succession of microbial communities under conditions of arid climate and of changes in the microbiome composition, ecological functions, and mechanisms of adaptation to changing regimes of salinization, alkalization, plant cover, and other characteristics of the soils of dry habitats. These data may be subsequently used to investigate the effect of global climatic processes on natural microbial ecosystems. By now, several integrated phylogenetic studies of prokaryotic communities from saline soils have been carried out in China (Xie et a., 2017), United States (Hollister et al., 2010), Pakistan (Mukhtar et al., 2017), Saudi Arabia (Bibi et al., 2018), and Mexico (Navarro-Noya et al., 2015).

Lake Elton area is a unique natural object located in the Caspian Depression in the southeastern part of the East European Plain (Volgograd oblast, Russia). Lake Elton is the most saline lake in Europe and one of the largest hypersaline lakes in the world. Its area is 155 km^2, and its salinity varies from 300 to 613 g/L (Argaman et al., 2012). The lake is located in a depression between large salt domes, which developed in the course of salt dome tectonic processes at the north of the Caspian depression. It is located 15 m below the sea level, while Mount Ulagan, the highest point of the Lake Elton area, is 68 m above sea level. Seven mineralized rivers flow into Lake Elton: Khara, Lantsug, Solyanka, Chernavka, Bol'shaya and Malaya Smorogda, and Karantinka. Apart from M. Smorogda, all these rivers are mesohaline (Kanapatskiy et al., 2018).

Table 1. Characterization of Lake Elton area soils

Sample	P1 = H1	P5 = H2	P9	H3	H4	H5
Location in the catena	Flood-land at the shoreline	Flood-land	Slope foot		Slope	Slope top
Salt crust	Yes	Yes	Yes (with sand inclusions)		No	No
Vegetation	None	Onset of halophyte vegetation growth	Halophyte vegetation		Wormwood-halophyte vegetation	Motley grass on top of the slope
Salts (TDS, g/L)	4.5	1.2	6.6		Not measured	
Acidity (pH)	6.3	7.8	6.4			

The soils of the region was formed under conditions of harshly continental dry climate with hot summer (average July temperature 25°C) and moderately cold winter (average January temperature –11°C) and annual precipitation of ~300 mm. The soils of this region are represented by *Haplic Solonchaks*, salt-dome structures, automorphic *Solonchaks* and *Kastanozems*, with ~10–25% contribution of accompanying soil (Shishov and Pankova, 2006).

Posthydromorphic soil evolution is pronounced in the Lake Elton area, when soil dealkalinization and desalinization occurs from the shore line to watershed areas (Andreeva et al., 2010). Thus, this region presents a unique ability to monitor the effect of natural soil changes on the composition of soil microbial communities.

Microbiological research in this area dealt mostly with aquatic ecosystems (Kanapatskiy et al., 2018). The only work on soil microbial diversity in the Lake Elton area revealed that abundance and genus diversity of actinomycetes increased along the Khara River with distance from the lake in the course of soil change (Zenova et al., 2016). Thus, microbial diversity of the soils of this area is presently almost unstudied.

The goal of the present work was to describe the phylogenetic diversity of prokaryotic communities in the soils along the Khara River (Lake Elton area).

MATERIALS AND METHODS

Research subjects and sampling. Research subjects were the soils located along Khara, the river inflowing into Lake Elton from the north (Figs. 1a–1b, Table 1). Five samples were collected in August 2013 in the direction from the shore line to the top of the river terrace: H1, H2, H3, H4, and H5 (Figs. 1c–1e). The area of sampling stations was 100 × 100 cm for every sampling point. Samples for molecular analysis were collected from the upper soil layer, 10 cm from the surface. In the case of soil crust covering the soil, samples were collected after crust removal from their surface. All samples were collected into sterile containers with cooling agents and transported to the laboratory, where they were stored at –20°C prior to DNA isolation.

Since flood-plain soils are most prone to changes due to draining and flooding, soil sections P1, P5, and P9 were established, which corresponded to points H1, H2, and H3, and physicochemical properties of the upper soil horizons were determined (Fig. 1). Types of soils at P1, P5, and P9 were determined using both the WRB international classification (IUSS Working Group WRB, 2014). More stable soils corresponding to points H4 and H5 were characterized using the literature data (Averianov and Sokhina, unpublished).

Salt composition of the upper 10-cm soil horizon was analyzed in water extracts (1 : 5), for which pH and TDS (Total Dissolved Solids) of samples P1, P5, and P9 was determined. The measurements were carried using stationary equipment: Expert-pH and Mettler Toledo Seveneasy, respectively.

DNA isolation, amplification, and pyrosequencing. DNA was extracted from soil samples (0.2 g) using the PowerSoil DNA Isolation Kit (Mobio Laboratories, United States). The samples were homogenized using Precellys 24 (Bertin Technologies, France). Purification degree and quality of isolated DNA were tested by electrophoresis in 0.5× TAE buffer in 1% agarose gel.

For construction and sequencing of the amplicon libraries, the purified DNA preparation (10–15 ng) was used as a template. The PCR temperature profile was as follows: 30 s at 95°C; 30 s at 50°C; 30 s at 72°C; a total of 30 cycles). PCR was carried out using Encyclo polymerase (Evrogen, Russia) and universal primers to the V4 variable region of the 16S rRNA gene: F515 (GTGCCAGCMGCCGCGGTAA) and R806 (GGACTACVSGGGTATCTAAT) (Bates et al., 2010). The primers were supplemented with unique barcodes for each sample (2 barcodes) and the service sequences required for pyrosequencing according to the Roche protocol. Sample preparation and sequencing were carried out on GS Junior (Roche, Switzerland) according to the manufacturer's recommendations.

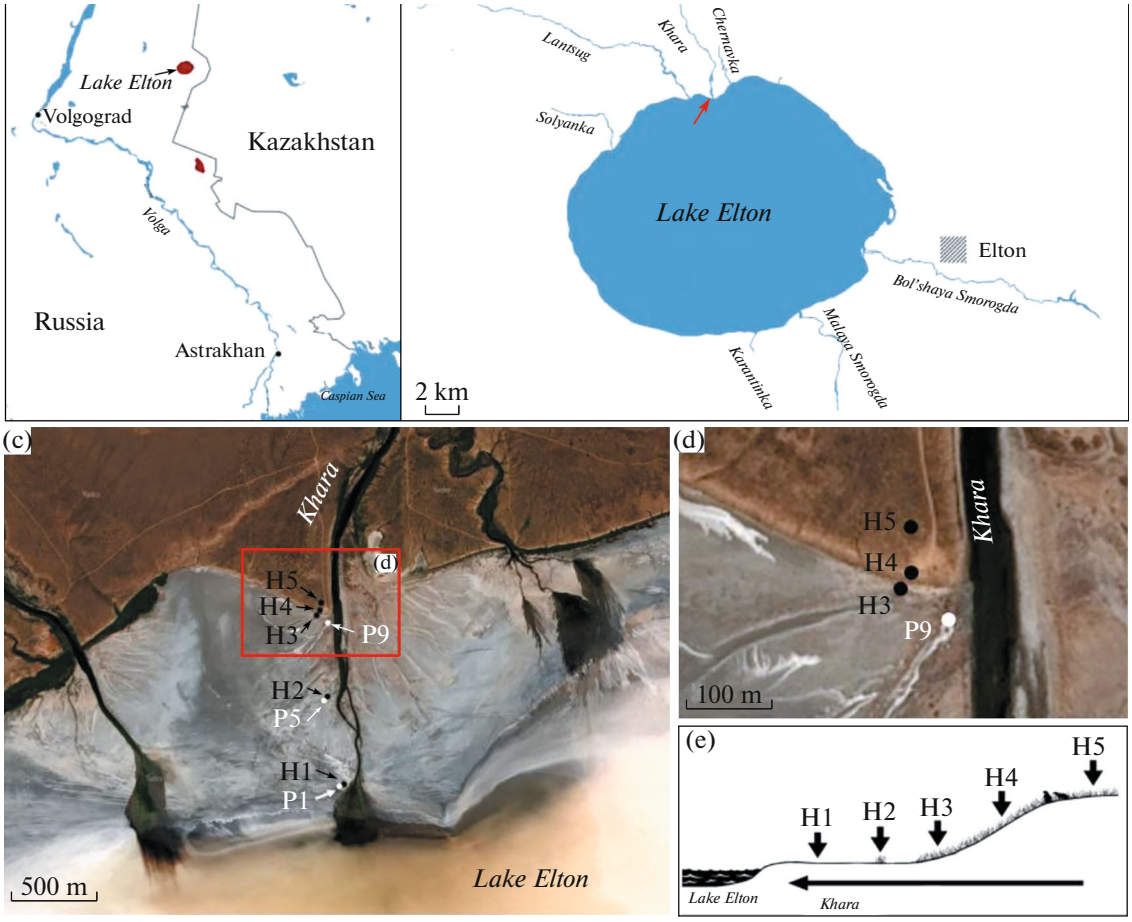

Fig. 1. Studied area and location of the sampling points: geographic position of Lake Elton (a); Lake Elton and inflowing rivers (the studied area is marked with a red arrow) (b); location of transverse sections (P1, P5, P9) and sampling station (H1–H5), Yandex maps (c, d); Khara River catena and location of stations H1–H5 (river flow direction is indicated by an arrow) (e).

Processing of the pyrosequencing data. Raw sequences were analyzed using QIIME ver. 1.9.0 (www.qiime.org). To decrease the errors, multiplex reads were initially filtered by quality and grouped according to the barcode sequences. The sequences with the length <200 bp and quality below 25, as well as those containing incorrect barcodes, primers, ambiguous symbols, or homopolymer length of 8 bp or more, were excluded from further analysis. The sequences not belonging to prokaryotes, chimeric sequences, and singletons were also removed from the studied data set.

Further steps included grouping of the sequences into operational taxonomic units (OTUs) with 97% similarity threshold using the uclust algorithm with selection of the representative sequences using the "most_abundant" algorithm. The sequences were aligned according to the PyNast algorithm, and the matrix of genetic distances was constructed. For these assessments, the number of sequences was normalized according to the minimal sample. The sequences were classified using the RDP database (Ribosomal Database Project) available at http://rdp.cme.msu.edu/. Comparative analysis of microbial communities from the soil samples and taxonomic identification of the nucleotide sequences were carried out using the QIIME 1.9.0 software package. All sequences were deposited at NCBI Sequencing Read Archive (SRA) (http://trace.ncbi.nlm.nih.gov/Traces/sra/) with the identifier (BioProject ID) PRJNA315964.

Microbial communities were compared using the values of alpha- and beta-diversity. Analysis of alpha-diversity included calculation of the following indices: Shannon ($H = -\sum p_i \ln p_i$, where p_i the share of the ith species in the community), phylogenetic diversity (Faith index, calculated as a sum of the lengths of the phylogenetic tree connecting all species in the community), and Chao1 (Chao1 = Sobs + a/b, where Sobs is the total OTU number, a and b are the numbers of OTUs containing 1 and 2 sequences, respec-

tively). For beta-diversity assessment, weighted UniFrac (Lozupone et al., 2011) was used to calculate the distances between all pairs of prokaryotic communities. The results were represented as cluster analysis with bootstrap support for confirmation of the branching order. All assessments were carried out for normalized data (normalization was performed to the smallest number of sequences present in the analyzed data set). Analysis of dependence between taxonomic diversity and chemical properties of the soils for samples H1, H2, and H3 was carried out with the StatPlus software package using Pierson linear correlation.

Amplification, cloning, and sequencing of streptomycete 16S rRNA genes. Analysis of streptomycete diversity was carried out for the soil sample H4. Total DNA was isolated as described previously (Boulygina et al., 2001). The total DNA preparation was used for PCR with streptomycete-specific 16S rRNA primers StrepB (ACAAGCCCTGGAAACGGGGT) and StrepF (ACGTGTGCAGCCCAAGACA) (Rintala et al., 2001). The PCR temperature profile was as follows: 5 min at 98°C; 40 s at 95°C—30 cycles; 40 s at 58°C; 2 min at 72°C; 10 min at 72°C. The reaction was carried out according to the previously described protocol for these primers (Rintala et al., 2001). PCR fragments were purified by electrophoresis in 0.7% agarose gel using the Wizard SV Gel and PCR Clean-Up System (Promega, United States) and cloned with the pGEM-T Easy Vector System I (Promega, United States). The pGEM-T vector ligated to the PCR fragments was used for *Escherichia coli* DH10B transformation by electroportation. Nucleotide sequences of the clonal inserts was determined from the StrepB primer by Sanger using the BigDye Terminator v3.1 Cycle Sequencing Kit in ABI3730 DNA Analyzer (Applied Biosystems, United States).

A total of 96 streptomycete clones were obtained from the library of the 16S rRNA gene fragments. The sequences were edited using BioEdit (Hall et al., 1999) and checked for chimeras with Bellerophon (Huber et al., 2014). Primary comparative analysis of the sequences was carried out with the NCBI BLAST online service (http://www.ncbi.nlm.nih.gov/blast). After elimination of short, nonspecific, and chimeric sequences, the remaining 63 streptomycete clones were used for further analysis. The length of these sequences was >600 bp. Phylogenetic reconstructions were carried out using MEGA 5.0 (Tamura et al., 2011). The sequences were deposited to GenBank under accession nos. KU951599–KU951661.

RESULTS

Characterization of soils of the studied area. During movement along Khara from the lake to the slope, soil change occurred in the following order (Fig. 1, Table 1): (1) samples P1, H1 (46°39′52″ N, 46°39′52″ E) *Fluvic Solonchak Clayic Evapocrustic Sulfidic* (*IUSS Working Group WRB*, 2014); (2) samples P5, H2 (49°12′13″ N, 46°39′46″ E) *Fluvic Gleyic Solonchak Clayic Evapocrustic Sulfidic*; (3) samples P9, H3 (49°12′26″ N, 46°39′47″ E) *Fluvic Gleyic Solonchak Clayic Evapocrustic*; (4) samples H4 (49°12′28″ N, 46°39′45″ E) and H5 (49°12′30″ N, 46°39′45″ E) *Gleyic Kastanozem*.

In soil section P1, which was established in the flood land 100 m from the shore line, *Sulfidic Solonchak* was formed. All soil surface was covered with a whitish salt crust. No vegetation occurred. Soil sample H1 was collected from the wet, black, unstructured horizon with scarce plant debris and smell of hydrogen sulfide located below. The P5 section was located 100 upstream from P1. The surface of this site was also completely covered by a salt crust. While higher plants were absent, halophyte vegetation occurred in some places. Below the salt crust was a horizon represented by wet, loose, black-gray silted loam with remains of half-decomposed plants. Soil sample H2 was collected from this horizon. Soil section P9 was established at the foot of the slope 200 m from inflow of the Khara River into Lake Elton. The salt crust with inclusions of sandy material formed a complete cover of whitish color. The lower loose, unstructured horizon, from which soil sample H3 was collected, had granulometric composition of medium loam and was characterized by nonuniform coloration: black and rusty spots occurred against the background of whitish-dove-colored soil mass. Rarefied *Solonchak* vegetation occurred at this site. Full descriptions of soil profiles P1, P5, and P9 are presented in the supplementary materials (Figs. S1–S3). Samples H4 and H5 were collected from the slope and top of the river terrace, respectively, where *Kastanozems* with chloride or chloride-sulfate salinization occurred (Averianov and Sokhina, unpublished). Soils of these sites were characterized by lower moisture content and better drainage properties. No salt crusts were present, and halophyte vegetation was replaced by wormwood-halophyte on the slope and motley grass at the top of the slope.

Characterization of diversity in soil microbial communities according to the 16S rRNA gene pyrosequencing data. A total of 8558 prokaryotic 16S rRNA gene sequences were obtained. The number of sequences varied from sample to sample from 1454 to 2214. The number of phylotypes (OTUs) in the samples varied from 117 to 276. Coverage (C) calculated for each sample based on these data varied from 89.1 to 98.2%. This value indicated that the sample size was sufficient to cover the soil microbial diversity (Table 2). The Chao1 index varied from 120.918 to 294.14.

In soil samples, 11 bacterial and 2 archaeal phyla were revealed (Fig. 2). Phylogenetic analysis showed that archaea of soil prokaryotic communities along the Khara catena belonged to the phyla *Euryarchaeota* (6.3%) and *Thaumarchaeota* (1.9%), while bacteria belonged to the phyla *Proteobacteria* (27.8%), *Bacte-*

Table 2. Major biodiversity indices for soil samples collected at the Khara catena

Sample no.	Faith index	OTU number	Chao1	C, %	Shannon index
H1	13.763	117	120.918	96.3	4.460
H2	22.053	234	241.198	89.1	6.626
H3	13.696	131	148.491	96.2	4.891
H4	22.764	276	294.140	89.7	7.068
H5	13.353	141	169.920	98.2	4.738

roidetes (21.0%), *Actinobacteria* (19.2%), *Firmicutes* (13.2%), *Gemmatimonadetes* (2.4%), *Acidobacteria* (0.9%), *Candidate phylum* Acetothermia (OP1) (2.2%), *Chloroflexi* (1.2%), *Planctomycetes* (1.3%), *Verrucomicrobia* (0.5%), and *Cyanobacteria* (0.3%). Unidentified bacteria (N/A, 1.4%) and rare phyla (RP, 0.2%) were also detected.

Based on these data, two archaeal phyla (*Euryarchaeota* and *Thaumarchaeota*) and four bacterial ones (*Proteobacteria*, *Firmicutes, Bacteroidetes*, and *Actinobacteria*), which were responsible for 89.5% of the sequences, were characterized in detail.

In the H1 sample collected at the shore line below the salt crust, archaea constituted 0.8% of all prokaryotes and were represented by the phylum *Euryarchaeota*, mainly by the family *Halobacteriaceae* (Figs. 2, 3). Members of the phylum *Proteobacteria* predominated in the sample (66.9%) (Fig. 4), with the families *Sphingomonadaceae* (3.3%), *Enterobacteriaceae* (56.8%), and *Pseudomonadaceae* (29.1%) being the most numerous. Among members of the phylum *Firmicutes*, the families *Planococcaceae* (0.39%) and *Gemellaceae* (0.44%) predominated (Fig. 6). The phylum *Actinobacteria* was responsible for 9.39% of the total bacterial diversity and was mostly represented by the families *Corynebacteriaceae* (3.3%) and *Micrococcaceae* (1.6%) (Fig. 7).

In the sample H2, collected in the zone of the first growth of halophyte plants, archaea were numerous, with their highest share among the samples (up to 23% of prokaryotic sequences). They belonged to the phyla *Euryarchaeota* (19.9%) (families *Halobacteriaceae* (18.8%) and MSP41 (1.1%)) and *Thaumarchaeota* (2.7%) (family *Cenarhaeaceae*) (Fig. 3). The share of *Proteobacteria*, on the contrary, decreased significantly, to 25.5% of the total microbial diversity. This phylum was represented by the families MND4 (1.1%), *Alteromonadaceae* (2.3%), *Ectothiorhodospiraceae* (2.2%), *Piscirickettsiaceae* (0.9%), and *Halomonadaceae* (2.9%) (Fig. 4). Members of the phylum *Bacteroidetes* were also abundant (36.8%), especially the family *Balneolaceae* (30%) (Fig. 5). Abundance of *Firmicutes* decreased to 0.58%. They were mainly represented by members of the family *Bacillaceae* (0.4%), and by members of the order *Bacillales* not identified at the family level (0.1%) (Fig. 6). The share of *Actinobacteria* phylotypes in this sample (4.1%) was two times lower than in the H1 sample. Actinobacteria

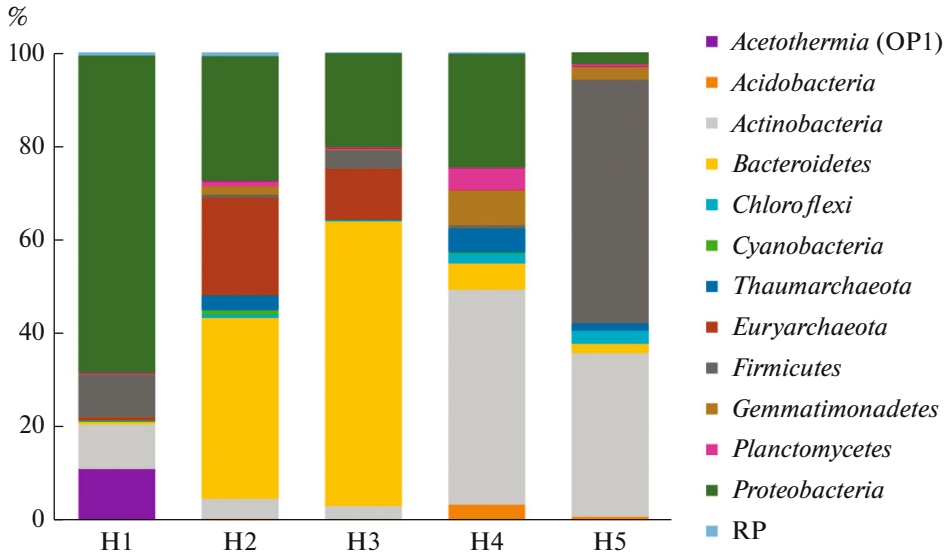

Fig. 2. Taxonomic structure of microbiomes along the Khara River at the phylum level for all samples. RP designates rare phyla, which constituted less than 1% of the total number of prokaryotic sequences.

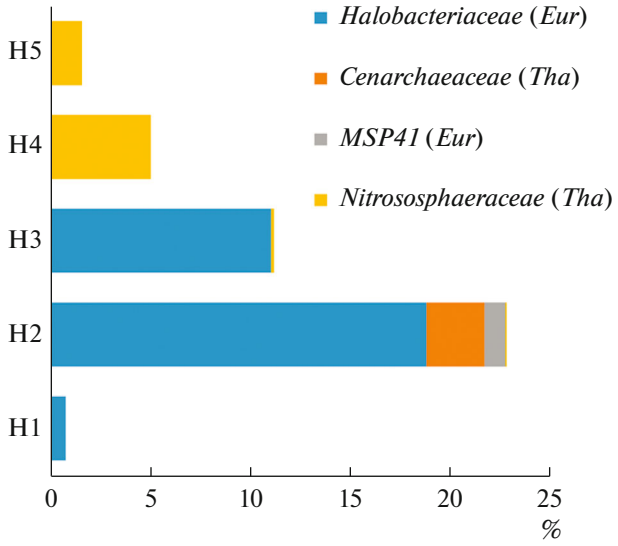

Fig. 3. Taxonomic structure of the soil archaeal community along the Khara River at the family level.

were mainly represented by members of the order *Acidimicrobiales* not identified at the family level (3.7%), as well as by the families *Micrococcaceae* (0.1%) and *Microbacteriaceae* (0.1%) (Figs. 7, 9).

In the H3 sample collected at the foot of the slope, archaea constituted 11.14% of all detected prokaryotes. Phylogenetic diversity of archaea changed in this sample. Thus, the shares of the phyla *Euryarchaeota* and *Thaumarchaeota* were 11.04 and 0.1%, respectively. The phylum *Thaumarchaeota* was represented by the family *Nitrososphaeraceae* (Fig. 3). Abundance of the phylum *Proteobacteria* decreased to 20.13%; it was represented by the families *Sphingomonadaceae* (1.4%), *Rhodobacteriaceae* (1.8%), *Halomonadaceae* (0.2%), *Enterobacteriaceae* (0.01%), and *Xantomonadaceae* (2.9%) (Fig. 4). The share of *Bacteroidetes* (60.46%) was two times higher than in the H2 sample (Fig. 5). This phylum was represented by the families *Flammeovirgaceae* (9.7%), *Cytophagaceae* (0.28%), and *Flavobacteriaceae* (46.5%). The phylum *Firmicutes* (3.9%) was represented by the families *Bacillaceae* (0.1%), *Paenibacillaceae* (0.1%), and *Planococcaceae* (3.4%) (Fig. 6). The share of *Actinobacteria* (2.96%) was the lowest among the studied samples, with *Micrococcaceae* (0.5%) and *Microbacteriaceae* (1.3%) being the most numerous families (Fig. 7).

In the H4 sample collected at the slope of the river terrace below wormwood-halophyte vegetation, archaea (5.0% of all prokaryotes) were represented only by the phylum *Thaumarchaeota* and the family *Nitrososphaeraceae* (Fig. 3). The share of *Proteobacteria* was higher than in the H3 sample (up to 23.8%). Phylogenetic diversity of proteobacteria was significantly higher in this sample, with the following families detected: *Beijerinkiaceae* (1.0%), *Bradyrhizobiaceae* (5.1%), *Hyphomicrobiaceae* (1.0%), *Sphingomonadaceae* (2.1%), *Commamonadaceae* (2.2%), *Enterobacteriaceae* (2.1%), *Pseudomonadaceae* (1.1%), and *Rhodobacteriaceae* (0.6%) (Fig. 4). The share of *Bacteroidetes* decreased sharply to 5.4%; this phylum was represented by the families *Chitinophaga-*

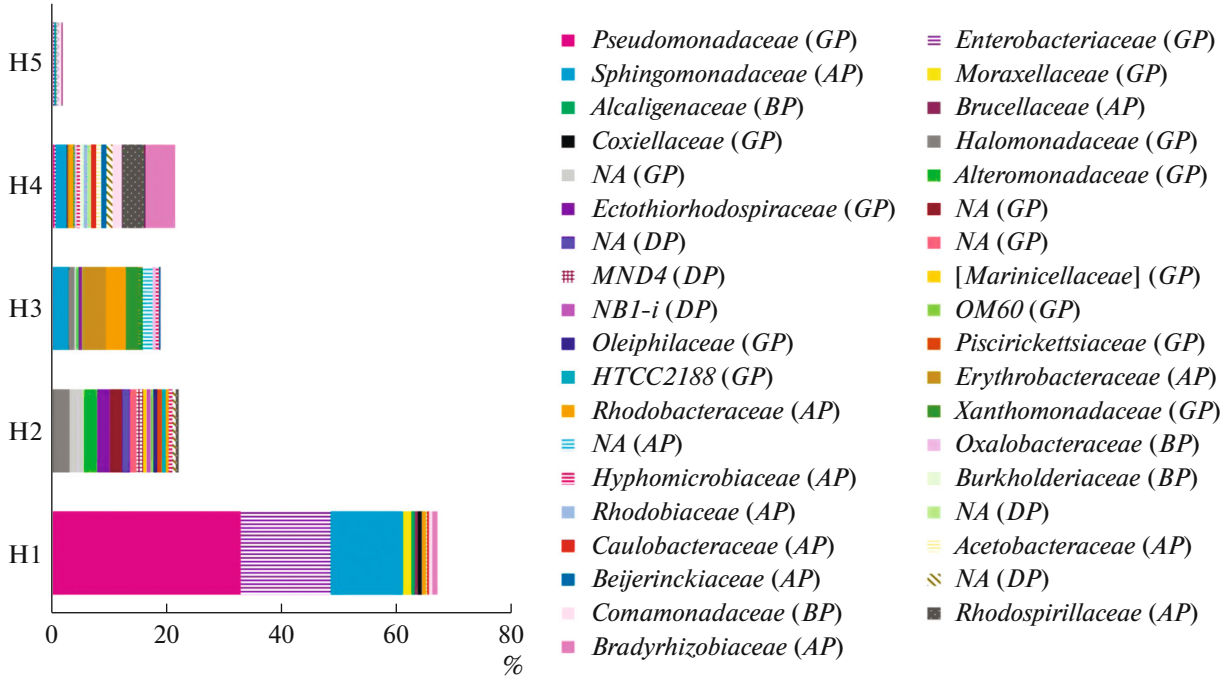

Fig. 4. Taxonomic structure of the phylum *Proteobacteria* in soil samples along the Khara River at the family level.

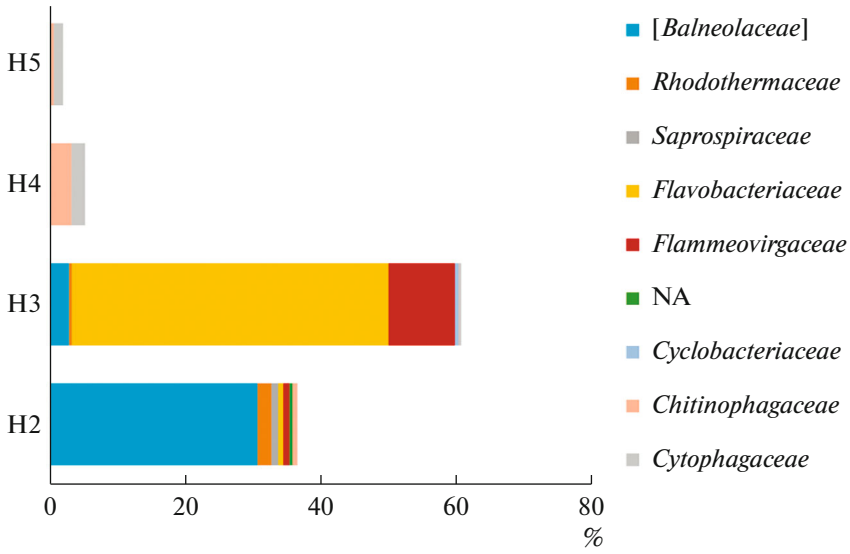

Fig. 5. Taxonomic structure of the phylum *Bacteroidetes* in soil samples along the Khara River at the family level.

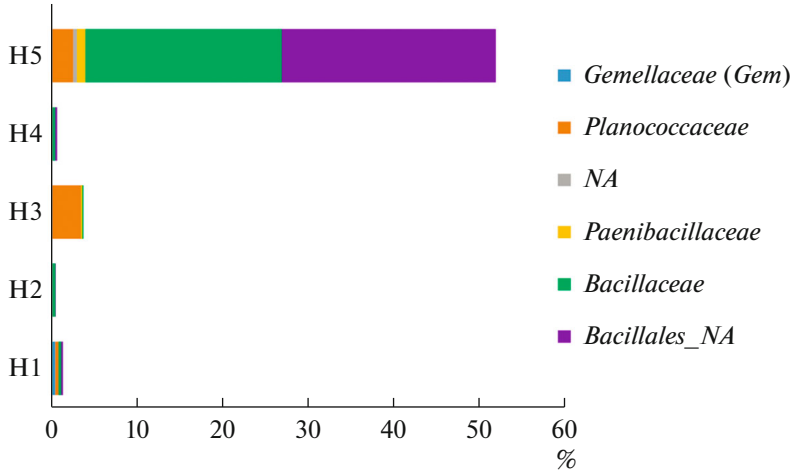

Fig. 6. Taxonomic structure of the phylum *Firmicutes* in soil samples along the Khara River at the family level.

ceae (3.1%) and *Cytophagaceae* (2.0%) (Fig. 5). Abundance of *Firmicutes* was 0.69%; the phylum was represented by the families *Bacillaceae* (0.34%) and *Planococcaceae* (0.1%), as well as members of the order *Bacillales* not identified at the family level (0.25%) (Fig. 6). The share of *Actinobacteria* was the highest among the studied samples (44.73%). Abundance and diversity of the order *Actinomycetales* were significantly higher in this sample (Figs. 7, 9, S7): apart from the families *Micrococcaceae* (3.2%) and *Microbacteriaceae* (4.1%), which occurred in other samples as well, the families *Geodermatophilaceae* (6.2%), *Streptomycetaceae* (0.4%), *Nocardioidaceae* (2%), *Pseudonocardiaceae* (2%), *Micromonosporaceae* (4%), and *Cellulomonadaceae* (1%) were also revealed. The dominant actinobacteria in this sample belonged to the family *Rubrobacteraceae* (5.7%) an order *Solirubobacteriales* (9.1%) (families *Solirubrobacteriaceae* and *Conexibacteraceae*) (Figs. 7, 9).

Similar to the H4 sample, in the H5 sample with chloride or chloride-sulfate salinization collected at the top of the river terrace below motley grass, wormwood and halophytes, archaea were represented only by the phylum *Thaumarchaeota* (1.6%) and family *Nitrososphaeraceae* (Fig. 3). The share of *Proteobacteria* decreased sharply (to 2.64%). Proteobacteria were represented by the families *Enterobacteriaceae* (0.2%), *Rhodobiaceae* (0.2%), and *Commamonadaceae* (0.4%); relative abundance of other proteobacterial families did not exceed 0.1% (Fig. 4). The share of *Bacteroidetes* in this sample was 1.6%; they belonged to the families *Chitinophagaceae* (0.3%) and *Cytophagaceae* (1.3%) (Fig. 5). On the contrary, abun-

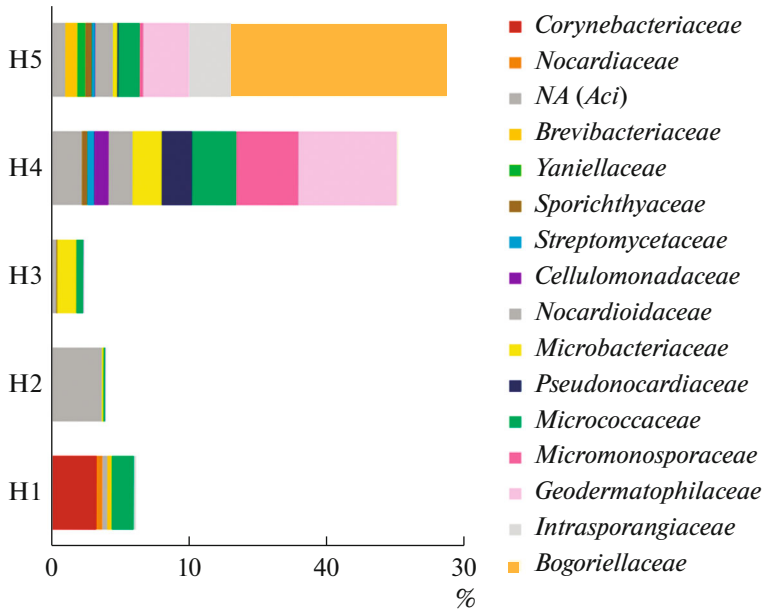

Fig. 7. Taxonomic structure of the phylum *Actinobacteria* in soil samples along the Khara River at the family level.

dance of the phylum *Firmicutes* increased sharply (51.74%), reaching the highest value for all studied samples. Firmicutes were represented by the families *Bacillaceae* (22.9%), *Paenibacillaceae* (1.0%), *Planococcaceae* (2.5%), and by unidentified members of the order *Bacillales* (24.9%) (Fig. 6). The share of *Actinobacteria* slightly decreased (to 34.56%) compared to the H4 sample. While the taxonomic diversity of actinobacteria in this sample was similar to that in H4, the families *Brevibacteriaceae* (1.0%), and *Yaniellaceae* (0.6%) were revealed in H5 (Fig. 7).

Thus, with increasing distance from the lake, soil types and therefore microbial communities changed. While archaeal phyla *Euryarchaeota* and *Thaumarchaeota* and bacterial phyla *Proteobacteria* and *Bacteroidetes* predominated in soil samples collected in the flood-plain, on the slope and top of the river terrace *Euryarchaeota* disappeared completely, abundance of *Proteobacteria* and *Bacteroidetes* decreased, and abundance of *Firmicutes* increased.

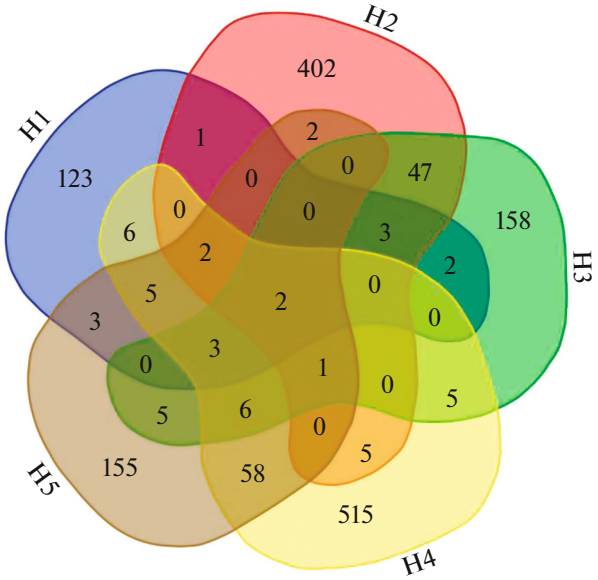

Fig. 8. The core and accessory components of prokaryotic complexes along the Khara River at the phylotype level.

Ecological characterization of soil microbial communities along the Khara River. Detection of the stable and unique microbial taxa in the studied soil samples was carried out by investigating the core microbiome (Shade and Handelsman, 2012). This analysis showed that the number of phylotypes in the studied samples was 1509 (Fig. 8). The highest number of shared OTUs was found for samples H2 and H3 (47 phylotypes) and H4 and H5 (58 phylotypes). The phylotypes of actinobacteria of the family *Microbacteriaceae* and bacteria of the genus *Bacillus* were present in the core microbiome. The share of common OTUs occurring in all samples from the studied soil catena did not exceed 1%. Thus, the microbial community of each studied soil was unique.

Cluster analysis revealed the differences between the studied soil microbial communities (Fig. 9). Microbiomes of the soil samples H1 and H2 were found to differ from all others. The samples H3, H4, and H5 formed a separate cluster, with H3 and H4 being closer to each other than H5. These differences probably resulted from different conditions at the sampling sites. Bootstrap support values indicated

Phylum	Class	Order	Family	H1	H2	H3	H4	H5
Acidobacteria	*Solibacteres*	*Solibacterales*	NA					
Actinobacteria	*Acidimicrobiia*	*Acidimicrobiales*	NA					
	Actinobacteria	*Actinomycetales*	*Bogoriellaceae*					
			Corynebacteriaceae					
			Cellulomonadaceae					
			Geodermatophilaceae					
			Intrasporangiaceae					
			Microbacteriaceae					
			Micrococcaceae					
			Micromonosporaceae					
			Nocardioidaceae					
			Pseudonocardiaceae					
			Streptomycetaceae					
	MB-A2-108	0319-7L14	NA					
	Nitriliruptoria	*Euzebyales*	*Euzebyaceae*					
	Rubrobacteria	*Rubrobacterales*	*Rubrobacteraceae*					
	Thermoleophilia	*Solirubrobacterales*	NA					
			Solirubrobacteraceae					
Bacteroidetes	[*Saprospirae*]	[*Saprospirales*]	*Chitinophagaceae*					
	Cytophagia	*Cytophagales*	*Cytophagaceae*					
	Flavobacteriia	*Flavobacteriales*	*Flavobacteriaceae*					
Chloroflexi	*Thermomicrobia*	AKYG1722	NA					
		JG30-KF-CM45	NA					
Firmicutes	*Bacilli*	*Bacillaceae*	NA					
			Bacillaceae					
Gemmatimonadetes	*Gemmatimonadetes*	*Gemmatimonadales*	NA					
	NA	NA	Ellin5301					
	NA	NA	NA					
Planctomycetes	*Phycisphaerae*	WD2101	NA					
	Planctomycetia	*Gemmatales*	*Isosphaeraceae*					
Proteobacteria	*Alphaproteobacteria*	*Rhizobiales*	NA					
			Beijerinckiaceae					
			Bradyrhizobiaceae					
			Hyphomicrobiaceae					
		Sphingomonadales	*Sphingomonadaceae*					
	Betaproteobacteria	*Burkholderiales*	*Comamonadaceae*					
	Deltaproteobacteria	*Myxococcales*	NA					
	Gammaproteobacteria	*Enterobacteriales*	*Enterobacteriaceae*					
		Pseudomonadales	*Pseudomonadaceae*					
Verrucomicrobia	[*Spartobacteria*]	[*Chthoniobacterales*]	[*Chthoniobacteraceae*]					
Euryarchaeota	*Halobacteria*	*Halobacteriales*	*Halobacteriaceae*					
Thaumarchaeota	*Thaumarchaeota*	*Nitrososphaerales*	*Nitrososphaeraceae*					

Fig. 9. Taxonomic structure of soil microbiomes along the Khara River at the family level. Cluster analysis was carried out using pairwise distances according tho the Bray-Curtiss algorithm. Only the families constituting at least 1% in at least one samples are presented. The tree was constructed using the pairwise distances matrix between the studied samples calculated by weighed UniFrac; the numerals indicate clusterization reliability (bootstrap support).

both high validity (at least 90%) of revealed clusters and uniqueness of the studied biotopes.

The samples H1 and H3 exhibited the lowest levels of biodiversity, with 117 and 131 phylotypes, respectively (Table 2). The highest species diversity was found in the sample H2, collected in the first growth of halophyte vegetation, and H4, collected on the slope under meadow vegetation (Fig. S5). The number of phylotypes in these samples was 216 and 249, respectively.

This difference may be explained by higher salt content in the samples H1 and H3 compared to H2 (4.5, 6.6, and 1.2 g/L, respectively). High salt content in the sample H3, collected at the foot of the river terrace, may be a result of salt accumulation caused either by flooding or by wash-out from the top of the terrace due to erosion processes at the slope. Analysis of predominant prokaryotic forms revealed the highest diversity of the *Proteobacteria* and *Bacteroidetes* in the samples H2 and H4 (Fig. S4); the highest *Actinobacteria diversity* occurred in H4 and, to a lesser extent, H5. The highest diversity of *Firmicutes* was found in H1 and H5, with a comparatively higher share of closely related phylotypes in H5.

Apart from population studies, dependence between the taxonomic diversity and chemical properties of the soils was investigated for the samples H1, H2, and H3. A statistically significant negative correlation with salinity was revealed for *Euryarchaeota* (–0.81) and *Actinobacteria* (–0.99), as well as positive correlation with salinity for *Firmicutes* (0.88). In the case of pH, the dependence was inverse, with positive correlations for *Actinobacteria* (0.91), *Euryarchaeota* (0.97), and *Thaumarchaeota* (0.93) and a negative correlation for *Firmicutes* (–0.99) (Fig. S6).

Members of the phylum *Euryarchaeota* are known to be halotolerant and halophilic, capable of growth at salt concentrations close to NaCl precipitation (Mwirichia et al., 2010). Some works reported preferential isolation of this prokaryotic group from soda lakes with pH up to 10. The latter indicates that the presence of cations, including Na^+ (which occurs in the *Solonchak* soil absorbent complex) is more important to this group than salt concentration (León-Lorenzana, 2017). Moreover, numerous works confirm that the level of salinization and ambient pH are the main factors determining development of specific microbial communities with predominance of the phyla *Actinobacteria* and *Firmicutes* (Zvyagintsev and Zenova, 2007; Zhang et al., 2019); these factors also affect the distribution of some *Thaumarchaeota* species (Navarro-Noya et al., 2015).

Thus, apart from the taxonomic differences between the soil samples, some patterns were revealed in the distribution of predominant phyla depending on salinity and pH of the water extracts from the relevant soils.

Phylogenetic characterization of *Streptomycetaceae* species in the *Gleyic Kastanozem* of the slope of the river terrace. While members of the phylum *Actinobacteria* were revealed in all studied soil samples, they were quantitatively predominant in the samples H4 and H5 (Fig. 2). According to molecular genetic data, the share of the family *Streptomycetaceae* in these samples was as high as 3.5 and 1%, respectively (the values are given as percentages of each family of the number of sequences in *Actinomycetales*, the dominant order of actinobacteria in the H4 and H5 samples, which constituted 52.5 and 80%, respectively) (Fig. S7). Thus, according to our data, the share of this bacterial family in the studied soil catena was 0.1%. This underestimate was probably due to specificity of investigation of this microbial group. Thus, metagenomic studies are known to reveal actinobacterial phylogenetic diversity in soil only incompletely (Schwientek et al., 2011). Application of universal primers, which may exhibit insufficient affinity to high-GC DNA (which is common in actinobacteria, including streptomycetes) may be one of the reasons. Diversity of mycelial actinobacteria (including members of the family *Streptomycetaceae*) is, however, an important characteristic of *Gleyic Kastanozem* (H4 and H5). Thus, pyrosequencing of the 16S rRNA genes from samples H4 and H5 revealed only 5 and 4 OTUs, respectively, of the family *Streptomicetaceae*. All of them belonged to the genus *Streptomyces*. More complete assessment of *Streptomyces* diversity was therefore carried out by cloning the 16S rRNA gene fragments using streptomycete-specific primer pairs. The H4 sample with the highest share of *Streptomyces* was chosen for this study (Fig. 7). Analysis revealed 63 clones, which formed 18 clusters with the most closely related type strains of *Streptomyces* species (Fig. 10). Predominant sequences were related to *Streptomyces chartreusis* ISP 5085^T (group 1a) and *Streptomyces flaveolus* NRRL B-1334^T (group 12b). Some of the sequences belonged to streptomycetes isolated from various soils, including arid ones (groups 1a, 3b, 8).

DISCUSSION

Unique geomorphological structure of the Lake Elton area makes it possible to carry out analysis of microbial communities from different soils within a single natural object. The soils in this region are differentiated according to height tiers of the coastal terraces and form a regular change (catena) of zonal and azonal soils. Replacement of calcium by sodium in the direction from the slope top to the lake shore indicated beginning of solonetz formation. *Fluvic Solonchak Clayic Evapocrustic Sulfidic* circling the lake are replaced by *Fluvic Gleyic Solonchak Clayic Evapocrustic* at the top of lakeside terraces (Averianov and Sokhina, unpublished). In the present work, changes in prokaryotic microbial communities of soils in this area

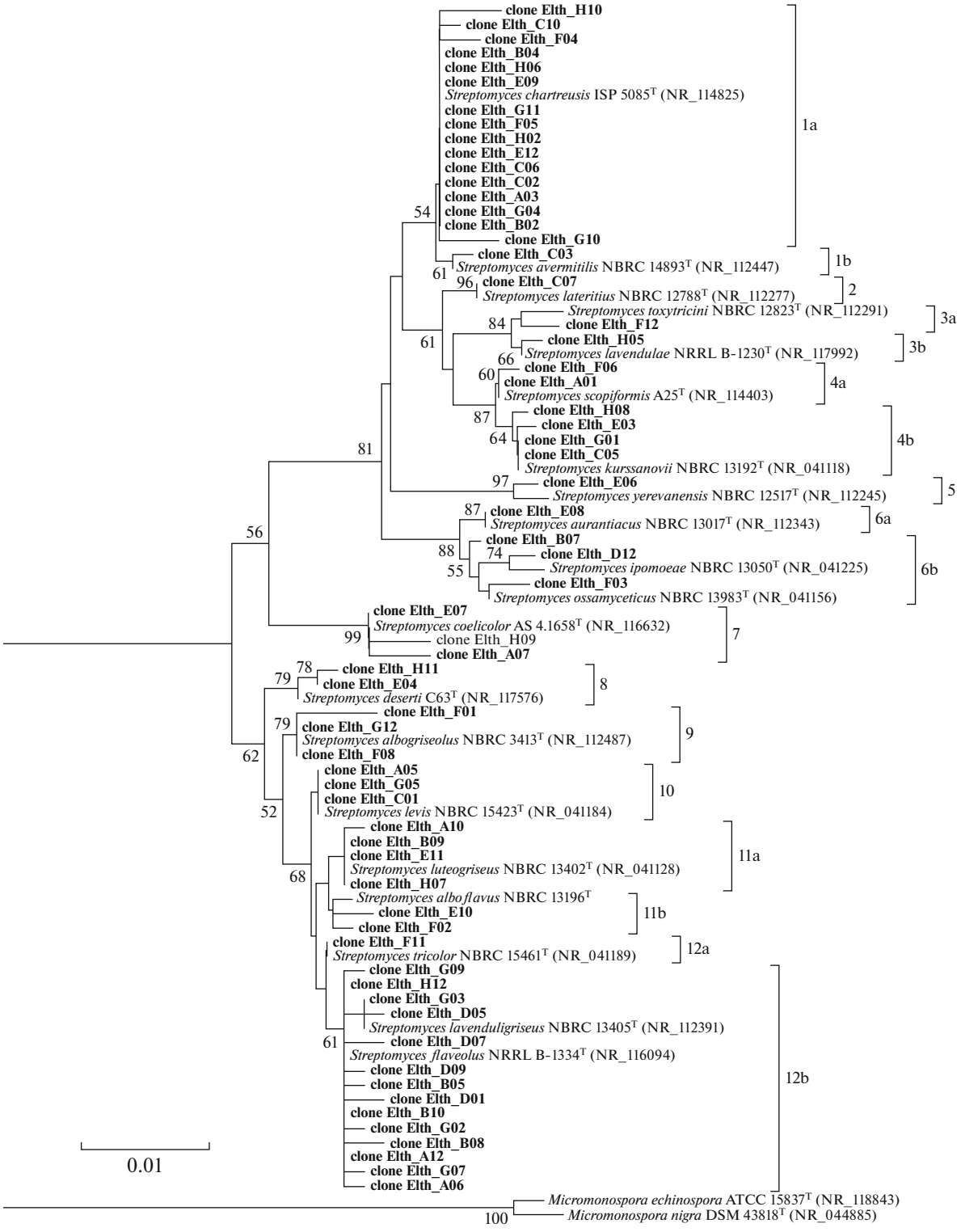

Fig. 10. Phylogentic tree constructed base on comparative analysis of the 16S rRNA gene sequences for actinomycete clones from the H4 soil sample (in boldface) and of the most closely related cultured representatives. The tree was constructed using the neighbor-joining algorithm. Scale bar indicates the evolutionary distance corresponding to 1 replacement per 100 nucleotides. The *Micromonospora* sequences were used as a root. The numerals indicate branching accuracy determined by bootstrap analysis of 1000 alternative trees (the values above 50 are shown).

was characterized for the catena along the Khara River.

Apart from soil types, vegetation, salinity, and pH changed from the lake shore to the top of the river terrace. The composition of microbial communities of each soil was unique. In the flood-land soils, members of the phylum *Proteobacteria* were better represented in the soils with high salinity (1.2 to 6.6 g/L) and slightly alkaline soils (pH 6.3 to 7.8). Members of the phyla *Thaumarchaeota*, *Firmicutes*, and *Actinobacteria* were associated with *Gleyic Kastanozems* of the river terrace. Such patterns are known in the literature and were reported for other environments. Thus, a similar dependence of *Actinobacteria* on soil alkalinity was established for soil samples collected in North and South America (Lauber et al., 2009), in the soils along the hypersaline Lake Ebinur, China (Zhao et al., 2018), and in various soils in Russia and Mongolia (Zvyagintsev and Zenova, 2007). In saline soils at the lake La Sal Del Rey (United States), members of the phyla *Proteobacteria, Bacteroidetes*, and *Firmicutes* were predominant (Hollister et al., 2010), which also correlates with our results. Phylotypes of the genus *Bacillus* (*Firmicutes*) are spore-forming and therefore easily survive unfavorable conditions, including elevated salt concentration in the soil, desiccation, insolation, etc. (van Djil and Hecker, 2013). These bacteria are also known to be involved in the first stages of decomposition of organic matter formed, for instance, out of microbial biomass killed by unfavorable environmental conditions (Hu et al., 2015).

According to the Faith's index, the highest biodiversity was observed in the soil samples collected at the first outgrowth of halophyte vegetation and on the slope of the river terrace. Predominant phyla in these samples were *Proteobacteria* and *Bacteroidetes*. Members of the phylum *Actinobacteria* were mainly associated with *Gleyic Kastanozems* at the slope and on the top of the river terrace, where wormwood-halophyte growth was also considerable. Molecular investigation of bacterial symbionts of *Salsola stocksii*, collected at Khewra Salt Mines (Pakistan), revealed predominance of the phyla *Proteobacteria* and *Actinobacteria* in soils associated with plant root system. Members of the phyla *Firmicutes, Acidobacteria, Bacteroidetes, Planctomycetes, Euryarchaeota*, etc. were also detected (Mukhtar et al., 2017). Similar data on soil microbial diversity below halophyte vegetation were obtained for coastal soils collected at Jeddah (Saudi Arabia) (Bibi et al., 2018). Thus, our results on microbial diversity of soils collected below halophyte vegetation at the Lake Elton area are in agreement with the data for halophyte vegetation in other regions.

Along the soil catena, the main trends were decreasing abundance of the phyla *Proteobacteria* and *Euryarchaeota* from the lake to the terrace top. Representation of the phyla *Bacteroidetes*, *Actinobacteria*, *Firmicutes,* and *Thaumarchaeota*, on the contrary, increased in the same direction. More detailed analysis of soil microbial communities revealed differences not only at the phyla level, but at the family level as well.

The phylum *Euryarchaeota* was revealed only in flood-land soil samples. Its highest share was found in the H2 sample, while the lowest occurred in the H1 sample. In flood-land samples the phylum *Euryarchaeota* was represented by the family *Halobacteriaceae*, which comprises typical inhabitants of saline soils (Xie et al., 2017). Members of the phylum *Thaumarchaeota* were revealed in all soil samples except H1. In the community of H2 sample this phylum was represented by the family *Cenarhaeaceae*, which has also been detected in saline-alkaline soils of the former lake Texcoco, Mexico (Navarro-Noya et al., 2015).

Abundance of proteobacteria was the highest in the H1 sample and decreased gradually along the soil catena with distance from the lake. The lowest *Proteobacteria* abundance was revealed in the H4 sample from the top of the river terrace. Predominant families were *Sphingomonadaceae*, *Enterobacteriaceae*, *Halomonadaceae*; halotolerant species are known within these families (de la Haba et al., 2014; de Vries et al., 2019). They are known to be widespread in saline soils (Bilal et al., 1990).

Members of the phylum *Firmicutes* were found in all studied samples. Their highest share in the overall microbial community was revealed in the H5 sample from the top of the river terrace, while their lowest abundance occurred in the H3 sample. The main families of this phylum were *Bacilliaceae*, *Paenibacillaceae*, and *Planococcaceae.* Investigation of response of microbial soil communities to addition of salts revealed that the distribution of these families exhibited positive correlation with both soil salinity and emergence of vegetation (Szoboszlay et al., 2019).

Members of the phylum *Bacteroidetes* were revealed in four out of five studied samples. The H1 sample collected at the shore line was an exception. Diversity within the phylum at the family level also increased with distance from the lake along the soil catena. The highest share of members of this phylum was found in the H1 sample, while the lowest occurred in the H2 sample. A noticeable change in microbial compositions was observed on transition from the H2 to the sample H4. Thus, the families *Flammeovirgaceae*, *Chitinophagaceae*, and *Flavobacteriaceae* were detected in the sample H2 while the families *Chitinophagaceae* and *Cytophagaceae* predominated in the samples H4 and H5. Investigation of the effect of drought on soil along the Rhine River in The Netherlands revealed predominance of the families *Flavobacteriaceae*, *Chitinophagaceae*, and *Cytophagaceae* under conditions of soil dehydration (Meinser et al., 2018) similar to arid conditions of the Elton area *Gleyic Kastanozems* (samples H4 and H5). Similar patterns

were observed in soils along Lake O'Connor, western Australia (Rath et al., 2019).

Members of the phylum *Actinobacteria* were revealed in all studied samples. Their lowest abundance was revealed in the H2 sample, while the sample H4 exhibited their highest abundance. Phylogenetic diversity of actinobacteria in flood-land samples was low, with predominance of the families *Corynebacteriaceae*, *Micrococcaseae*, and *Microbacteriaceae*. However, in the sample from the terrace slope, apart from these families, numerous mycelial and nonmycelial *Actinobacteria* were revealed. It was shown for Lake Akkol (Kazakhstan) that taxonomic diversity was somewhat higher on less saline sites than on more saline ones. Transition from *Solonchaks* to *Kastanozems* with emergence of steppe vegetation resulted in a change in the composition of the microbial community, with the typical soil *Actinobacteria* species gaining predominance (Pershina et al., 2012).

The patterns of changes in microbial communities of the Khara soil catena are in agreement with those described in the literature. Predominance of *Gammaproteobacteria*, *Actinobacteria*, *Firmicutes*, *Alphaproteobacteria*, *Bacteroidetes*, and *Betaproteobacteria* was established for soil near a saline lake Ebinur, China (Zhao et al., 2018). For soils close to Lake Qarhan (the largest salt lake in China), a pattern of changes in microbial communities depending on salinity gradient was revealed, and the effect of salinization on microbial communities was shown to be more pronounced in saline soils than in saline water or lake sediments (Xie et al., 2017).

Investigation of microbial communities of saline soils is also promising for search and isolation of new producers of antibiotics, enzymes, bioplastic, biofuel, etc. Actinomycetes of the genus *Streptomyces* are of special interest, since, apart from antibiotics, they are producers of compounds with antiviral, antitumor, antifungal, and other properties (Newman et al., 2007). Using soils for the search of streptomycetes producing biologically active compounds requires characterization of the streptomycete complexes of these soils using both the classical culture-based approaches and streptomycete-specific primer pairs.

Abundance and structure of actinomycete complexes have been previously determined for the soils studied in the present work using traditional techniques of plating on solid media (Zenova et al., 2016). Cultured members of the genera *Streptomyces* and *Micromonospora* were found to predominate in all samples from the Khara catena. Abundance of mycelial bacteria determined using culture-based techniques varied from 1×10^3 to 1×10^4 CFU/g soil. In the present work, significant streptomycete diversity was revealed in the sample of *Gleyic Kastanozem* soil. Some of the clones were homologous to known antibiotic producers. Thus, 1a, the most numerous group of clones, was homologous to *Streptomyces chartreusis*, isolated from African soils (Leach et al., 1953) and described as a producer of an antitumor antibiotic chartreusin. Groups 1b and 6b were homologous to *S. avermitilis* and *S. ossamyceticus*, producers of avermectin and ossamycin, respectively (NBRC collection, https://www.nite.go.jp/). Thus, based on comparison of different approaches to description of streptomycete complexes of the Elton area soils, it may be concluded that Gleyic Kastanozems are potentially promising for further biotechnological screening.

Thus, regular soil change along the ecological gradient and the change of microbial communities were shown for the Khara River catena. Some patterns in the changes of microbial diversity on transition from one soil to another were shown, and dependence of the composition of microbial complexes upon salinity, pH, vegetation, and relief was established.

Population analysis of the Elton area soil microbial communities revealed the similarities and differences between the studied samples, while determination of accessory components associated with a specific habitat may be promising for bioindication of specific environmental conditions: salinization/desalinization anaerobiosis, humidity, etc. It was also shown that *Gleyic Kastanozem* soils at the Khara River have a potential for isolation of streptomycetes which may subsequently be used in biotechnological research.

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COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

SUPPLEMENTARY MATERIALS

Supplementary materials are available for this article at doi 10.1134/S0026261720060119 and are accessible for authorized users.

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