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Biodiversity of terrestrial cyanobacteria of the South Ural region

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Abstract – South Ural is a territory with a unique geographical position and heterogeneous natural conditions. Unexplored biodiversity of the terrestrial cyanobacteria of this territory is very high. We undertook a floristic study covering all botanical-geographical zones of the Bashkiria and Bredinskiy district of the Chelyabinsk region. In a total of 85 soil samples collected, 56 species of cyanobacteria were identified. The number of cyanobacteria was highest in the boreal-forest zone (39 species) and notably lower in the other zones (18, 29, and 24 species for broad-leaved forest, forest steppe and steppe regions, respectively). *Leptolyngbya voronichiniana*, *Leptolyngbya foveolarum*, cf. *Trichocoleus hospitus*, *Pseudophormidium hollerbachianum*, *Nostoc* cf. *punctiforme*, *Microcoleus vaginatus*, *Phormidium breve*, *Phormidium dimorphum*, *Phormidium corium*, and *Leptolyngbya* cf. *tenuis* were detected in all studied zones. *Trichormus variabilis* and *Cylindrospermum majus* were detected in the forest zone, *Phormidium ambiguum* was typical for forest-steppe and steppe zones, *Pseudophormidium hollerbachianum* and *Nostoc* cf. *commune* were most abundant in the steppe. Humidity and heterogeneity of the substrate were likely the most important factors influencing terrestrial cyanobacteria diversity. For full understanding of the biodiversity of cyanobacteria in the South Urals, future molecular-genetic research is necessary.

Bashkiria / *Leptolyngbya* / *Oculatella* / *Phormidium* / soil / *Trichocoleus*

INTRODUCTION

Despite the large number of floristic studies of terrestrial cyanobacteria already published (e.g. Adhikary, 2000; Vinogradova *et al.*, 2000; Hauer, 2007, 2008; Neustupa & Škaloud, 2010; Davydov, 2013), we still lack sufficient information about cyanobacterial biodiversity of many territories. This problem is very actual for many regions of Eurasia, including the mountain range of the South Urals.

The region of the South Ural is situated on the border of Europe and Asia and is characterized by unique natural conditions. The Republic of Bashkortostan (Bashkiria) occupies a large part of the South Ural between 51°31'N and 56°25'N, and 53°10'E and 60°00'E (Alekseev *et al.*, 1988) with an area of 143,000 km² (Akhmadeyeva, 2003). Climatic features of Bashkortostan are explained by its position within the continent and the influence of geology that causes significant daily and annual amplitudes of temperature and precipitation (Tahaev, 1959).

Investigations of terrestrial cyanobacteria in the territory of the South Ural (mostly in Bashkiria) started in the 1960's. During long-term studies since the 1970s, phycologists from Bashkiria investigated cyanobacteria of agricultural lands (Sayfullina & Minibaev, 1980), urban territories (Sukhanova & Ishbirdin, 1997; Khaibulina *et al.*, 2005), polluted areas (Kabirov & Lubina, 1988; Kireeva *et al.*, 2007; Sharipova, 1997, 2007; Kabirov *et al.*, 2010), eroded lands (Dubovik, 2000, 2001, 2010), and caves (Abdullin & Sharipova, 2004; Abdullin, 2009). However, the overall biodiversity of the cyanobacteria in natural ecosystems in the South Urals was studied very irregularly. Floristic studies were conducted mostly on forest-steppe, steppe zones and mountains (Kuzyakhmetov, 1981, 1992, 1998; Shmelev & Kabirov, 2007; Bakieva *et al.*, 2012). For example, up until the present we lacked information about cyanobacteria of the northern part of Bashkiria in the zones of boreal-forest and forest-steppe.

The aim of this paper is to study cyanobacterial communities in different types of ecosystems in the South-Ural.

MATERIALS AND METHODS

Study sites

Soil samples including soil crusts where available were taken in May-August 2010 according to standard methods of soil phycology (Gollerbach & Shtina, 1969) from various botanical-geographical regions (zones), covering boreal and broad-leaved forests, forest-steppe, and steppes of the South Ural region. Botanical-geographical regions of Bashkiria were established based on peculiarities of vegetation cover and geographic features (longitude, latitude, terrain, elevation and land use) (Alekseev *et al.*, 1988). Each sample was a composite of seven subsamples collected from the site of around 2 m² to a depth of 5 cm. Samples were taken from the typical biotopes of the region as well as from the sites with heterogenic ecological conditions (e.g. riversides, ravines, paths), and sites with visible cyanobacterial growth and microbiotic crusts. A total of 81 samples were collected from 11 localities in the Republic of Bashkortostan. An additional four samples were taken in the steppes of the Bredinskiy district of the Chelyabinsk region (Fig. 1). Altogether,

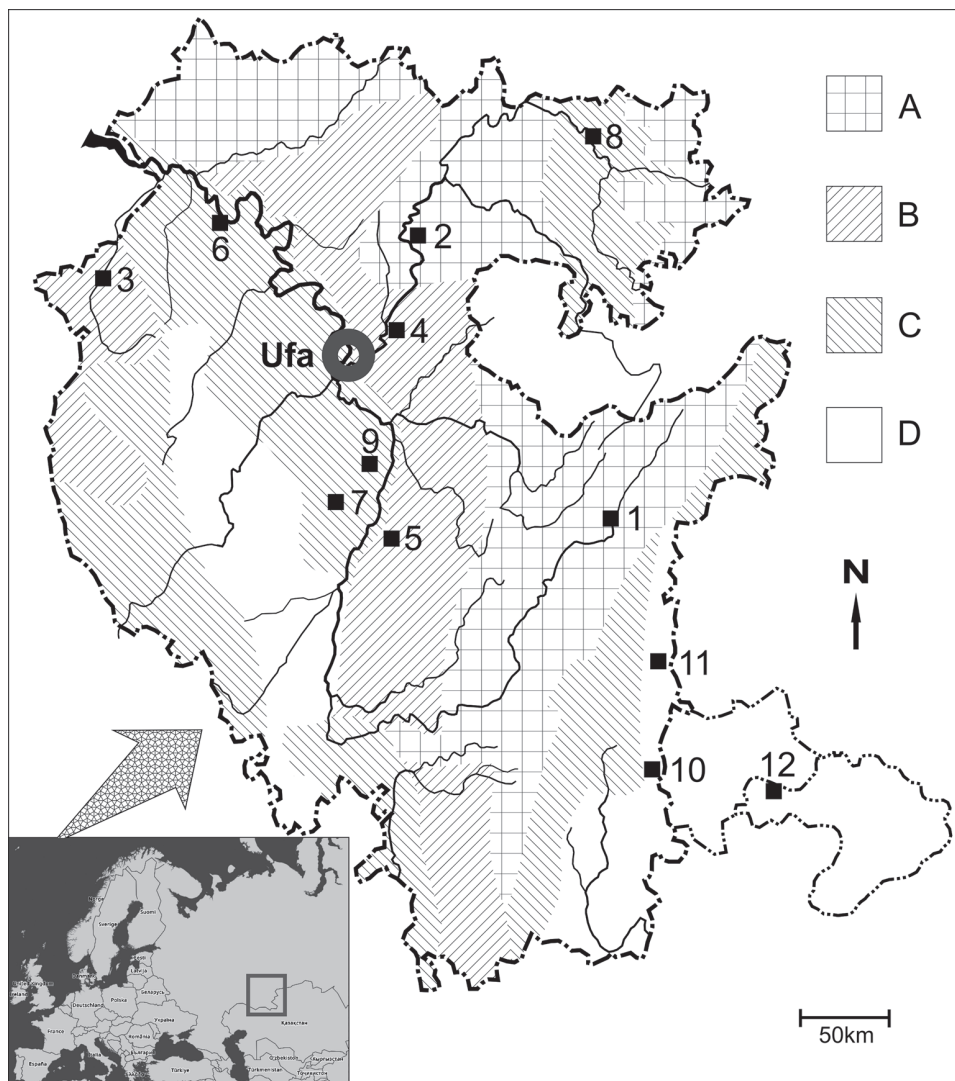


Fig. 1. Terrestrial cyanobacteria of the South Ural region: map of the sampling sites. Boreal forest zone (A): 1 – Beloretsk region, 2 – near Pavlovka village; Broad-leaved forest zone (B): 3 – Bakaly, 4 – Igolino, 5 – Krasnounsolskiy; Forest-steppe zone (C): 6 – near Dyurtyuli town, 7 – near Tolbazy village, 8 – edge of Bolsheustikinskoye village, 9 – near Georgievka village; Steppe zone (D) of Bashkiria and Bredinskiy district of Chelyabinsk region: 10 – near Sibay town, 11 – near Yangelskiy village, 12 –near Arkaim monument.

85 samples of soil and microbiotic crusts from 12 localities were studied: 17 collected from boreal forests, 21 from broad-leaved forests, 29 from forest-steppes, and 18 from steppes (Table 1).

Table 1. Comparisons of cyanobacteria in different zones in the territory of Bashkiria and the Bredinskiy district of the Chelyabinsk region, South Ural region, Russia. Frequency of occurrence is expressed using Braun-Blanquet scale with modifications: 1 = 0.1-5%; 2 = 6-10%; 3 = 11-20%; 4 = 21-40%; 5 = 41-60%; 6 = 61-80%; 7 = 81-100%. BoF = boreal forest, BrF = broad-leaved forest, FS = forest steppe, S = steppe, * = including the Bredinskiy district of the Chelyabinsk region

Taxon	Botanical-geographical region (zone)			
	BoF	BrF	FS	S*
Synechococcales				
Pseudanabaenaceae				
<i>Pseudanabaena papillaterminata</i> (Kiselev) Kukk			1	
Leptolyngbyaceae				
<i>Leptolyngbya foveolarum</i> (Rabenhorst ex Gomont) Anagnostidis & Komárek	5	4	5	4
<i>Leptolyngbya</i> cf. <i>fragilis</i> (Gomont) Anagnostidis & Komárek	2			2
<i>Leptolyngbya</i> cf. <i>hansgirgiana</i> Komárek in Anagnostidis	4			
<i>Leptolyngbya</i> cf. <i>subtilissima</i> (Kützing ex Hansgirg) Komárek in Anagnostidis	3		2	2
<i>Leptolyngbya</i> cf. <i>tenuis</i> (Gomont) Anagnostidis & Komárek	3	1	2	3
<i>Leptolyngbya</i> cf. <i>nostocorum</i> (Bornet ex Gomont) Anagnostidis & Komárek	2			
<i>Leptolyngbya</i> cf. <i>notata</i> (Schmidle) Anagnostidis & Komárek				2
<i>Leptolyngbya voronichiniana</i> Anagnostidis & Komárek	4	6	5	5
<i>Oculatella</i> sp. 1			2	
<i>Oculatella</i> sp. 2			2	
<i>Oculatella</i> sp. 3				2
cf. <i>Trichocoleus hospitus</i> (Hansgirg ex Forti) Anagnostidis	2	6	4	4
Pleurocapsales				
Hyellaceae				
<i>Myxosarcina</i> cf. <i>tatrica</i> (Starmach) Komárek & Anagnostidis		1		
Chroococcales				
Aphanothecaceae				
<i>Aphanothece stagnina</i> (Spreng.) A.Braun	2			
Chroococcaceae				
<i>Chroococcus varius</i> A.Braun in Rabenhorst			1	
Entophysalidaceae				
<i>Chlorogloea</i> cf. <i>purpurea</i> Geitler		1	1	3
Oscillatoriales				
Cyanotheceaceae				
<i>Cyanothece aeruginosa</i> (Nägeli) Komárek				2
Borziaceae				
<i>Borzia trilocularis</i> Cohn ex Gomont			2	
Microcoleaceae				
<i>Kamptonema animale</i> (Agardh ex Gomont) Strunecký, Komárek & Šmarda	2			
<i>Kamptonema laetevirens</i> (Crouan & Crouan ex Gomont) Strunecký, Komárek & Šmarda	2			
<i>Microcoleus autumnalis</i> (Gomont) Strunecký, Komárek & Johansen	3	3	2	
<i>Microcoleus vaginatus</i> (Vaucher) Gomont ex Gomont	5	3	4	5
<i>Microcoleus</i> sp. 1	2			

Taxon	Botanical-geographical region (zone)			
	BoF	BrF	FS	S*
<i>Microcoleus</i> sp. 2		2		
<i>Microcoleus</i> sp. 3	2			
<i>Oxynema</i> cf. <i>acuminatum</i> (Gomont) Chatchawan, Komárek, Strunecký, Šmarda & Peerapornpisal	2			
<i>Pseudophormidium hollerbachianum</i> (Elenkin) Anagnostidis	4	4	4	6
Oscillatoriaceae				
<i>Lyngbya martensiana</i> Meneghini ex Gomont	4		1	3
<i>Phormidium aerugineo-caeruleum</i> (Gomont) Anagnostidis & Komárek	2			
<i>Phormidium ambiguum</i> Gomont ex Gomont			2	2
<i>Phormidium breve</i> (Kützing ex Gomont) Anagnostidis & Komárek	4	2	3	4
<i>Phormidium corium</i> Gomont	3	1	4	2
<i>Phormidium dimorphum</i> Lemmermann	2	3	3	3
<i>Phormidium</i> cf. <i>jadinianum</i> Gomont	3			3
<i>Phormidium</i> cf. <i>retzii</i> (Agardh) Gomont ex Gomont	3			
<i>Phormidium tergestinum</i> (Kützing) Anagnostidis & Komárek	2			
<i>Phormidium uncinatum</i> (Agardh) Gomont	2			
<i>Phormidium</i> sp. 1	2			
<i>Phormidium</i> sp. 2				2
Gomontiellaceae				
<i>Hormoscilla pringsheimii</i> Anagnostidis & Komárek	2			
Nostocales				
Scytonemataceae				
<i>Scytonema</i> sp.	2			
Rivulariaceae				
<i>Roholtiella bashkiriorum</i> Gaysina & Bohunická			2	
<i>Roholtiella edaphica</i> Bohunická & Lukešová	2		2	2
<i>Roholtiella fluviatilis</i> Johansen & Gaysina			1	
<i>Roholtiella</i> sp.	2			
Nostocaceae				
<i>Cylindrospermum majus</i> Kützing ex Bornet & Flahault	3	3	4	
<i>Cylindrospermum</i> sp.			1	
<i>Desmonostoc</i> cf. <i>muscorum</i> (Agardh ex Bornet & Flahault) Hrouzek & Ventura	2	1		4
<i>Nostoc</i> cf. <i>calicicola</i> Brébisson ex Bornet & Flahault	3		3	2
<i>Nostoc</i> cf. <i>commune</i> Vaucher ex Bornet & Flahault				4
<i>Nostoc</i> cf. <i>ellipsosporum</i> Rabenhorst	2			
<i>Nostoc</i> cf. <i>microscopicum</i> Carmichael ex Bornet & Flahault	3	2	1	
<i>Nostoc</i> cf. <i>punctiforme</i> Kützing (Hariot)	6	4	4	4
<i>Trichormus variabilis</i> (Kützing ex Bornet & Flahault) Komárek & Anagnostidis	4	3	4	
<i>Trichormus</i> sp.	2			
Number of samples	17	21	29	18
Number of species	39	18	29	24
Minimum/maximum species per site	0/13	0/9	0/14	1/10

Descriptions of the studied zones are as follows (taken from Alekseev *et al.*, 1988):

1. *Boreal forest zone* – characterized by humid conditions and prevalence of coniferous trees *Picea obovata* Ledeb. and *Abies sibirica* Ledeb., with rare deciduous trees *Tilia cordata* Mill., *Acer platanoides* L., *Ulmus glabra* Huds. and *Quercus robur* L. Sample sites were in Beloretskiy region and near Pavlovka village (Fig. 1, sites 1 and 2). Soils in sites in the Beloretskiy region are podzolized chernozem, near Pavlovka village – dark gray forest and floodplain soils (Table 2) (Khaziyeu, 2012).
2. *Broad-leaved forest zone* – contains mixed forests of *Quercus robur* L., *Tilia cordata* Mill., and *Ulmus glabra* Huds. This zone is one of the most damaged parts of Bashkortostan as a result of anthropogenic influence. Samples were taken near Bakaly, Iglino, and Krasnounsolskiy villages (Fig. 1, sites 3, 4, 5). All samples in this zone were from sites with podzolized chernozem (Table 2) (Khaziyeu, 2012).
3. *Forest-steppe zone* – combination of forest and steppe communities. Most of the territory is characterized by forest-steppe of European type with broad-leaved trees like *Quercus robur* L., *Tilia cordata* Mill., and *Acer platanoides* L. In only the north-eastern part of this zone (site 8), forests are dominated by *Betula pendula* Roth, *Betula pubescens* Ehrh. and *Pinus sylvestris* L. Samples were taken near Dyurtyuli town, and Tolbazy, Bolsheustikinskoye, and Georgievka villages (Fig. 1, sites 6, 7, 8, 9). Soils in sample sites near Dyurtyuli and Tolbazy were leached chernozems, Bolsheustikinskoye – gray forest soils and floodplain soils (Table 2) (Khaziyeu, 2012).
4. *Steppe zone* – originally, the basis of the vegetation in this zone within Bashkiria were steppes with dominance of *Stipa pulcherrima* K.Koch in the north, *Stipa lessingiana* Trin. & Rupr. in the south, and *Stipa zalesskii* Wilensky in the middle part. Currently, steppes are almost completely destroyed by human activities. Small areas of the forest vegetation remain situated in more humid conditions in the valleys, on the slopes of ravines and floodplains. Samples were taken near Sibay town, Yangelskiy village, and Arkaim monument (Fig. 1, sites 10, 11, 12). Soils in study sited near Sibay were characterized as south chernozem, near Yangelskiy and Arkaim – as ordinary chernozem (Table 2) (Khaziyeu, 2012; Prikhod'ko *et al.* (2012).

Strain isolation and culture observation

For isolation of pure strains, enrichment cultures on solidified BBM medium (Bischoff & Bold, 1963; Kostikov *et al.*, 2001) and the dilution method of Bohunická *et al.* (2015) were used. For obtaining additional information about cyanobacterial biodiversity, direct observation of cyanobacteria on cover slips was also used (Lund, 1945; Hoffmann *et al.*, 2007). For this purpose, about 15-20 grams of soil were placed into a Petri dish and moisturized until 80% of full moisture capacity. The next day, four sterilized cover slips were put onto the surface of the soil and slightly pressed. After that between soil surface and cover slip small wet chambers arose, where cyanobacteria started to grow after 2-4 weeks of cultivation. During strain isolation, petri dishes with soil placed onto agar solidified media (1.5%) were incubated at room temperature on an illuminated shelf with 12h:12h light:dark regime. Pure cultures in tubes on 1.5% agar-solidified media slants were then stored at 4°C in a refrigerator with transparent door (natural daylight regime).

Table 2. Characteristics of sites and samples collected within the present study

Sample No	Sample name	Species found	Locality	GPS coordinate	Microhabitat	Substrate and soil type*	Vegetation cover	Litter	Higher plants at the site
Boreal forest zone									
Site 1 – Beloretsk region									
1	Be1	0	Edge of Revet station	54°11'27.1"N 57°37'18.6"E	Slope of the mountain, mixed forest	Soil, podzolized chernozem	100%	Deciduous and coniferous litter	<i>Tilia cordata</i> Mill., <i>Betula pendula</i> Roth, <i>Populus tremula</i> L., <i>Corylus avellana</i> L., <i>Pinus sylvestris</i> L., <i>Rubus saxatilis</i> L., <i>Fragaria vesca</i> L., Poaceae.
2	Be2	4	Edge of Revet station	54°11'24.4"N 57°37'16.1"E	Slope of the mountain, meadow near edge of mixed forest	Stony substrate, podzolized chernozem	100%	–	<i>Tilia cordata</i> Mill., <i>Betula pendula</i> Roth, <i>Pinus sylvestris</i> L.
3	Be3	8	Near Kulmas village	54°19'34.8"N 57°09'52.8"E	Meadow	Wet soil, podzolized chernozem	100%	–	<i>Trifolium pratense</i> L., <i>Equisetum arvense</i> L., <i>Sonchus</i> L., Bryophyta
Site 2 – near Pavlovka village									
4	P1	11	Near Pavlovka cemetery	55°25'47.2"N 56°33'44.2"E	Near the puddle	Wet dark gray forest soils	100%	–	<i>Taraxacum officinale</i> Web ex Wigg., <i>Alchemilla</i> L., Poaceae, Bryophyta
5	P2	7	Near Pavlovka cemetery	55°25'48.5"N 56°33'40.5"E	Edge of spruce forest	Wet dark gray forest soils	70%	Deciduous and coniferous litter	<i>Picea obovata</i> Ledeb., <i>Tilia cordata</i> Mill., <i>Betula pendula</i> Roth, <i>Anemone nemorosa</i> L., <i>Alchemilla</i> L.
6	P3	5	Near Red Rocks	55°25'28.3"N 56°34'36.8"E	Spruce forest	Wet dark gray forest soils		Deciduous and coniferous litter	<i>Picea obovata</i> Ledeb., <i>Tilia cordata</i> Mill., <i>Betula pendula</i> Roth, <i>Anemone nemorosa</i> L.
7	P4	3	Near Red Rocks	55°25'24.2"N 56°34'36.9"E	Glade on spruce forest on the south slope of the hill	Wet dark gray forest soils	60%	–	<i>Fragaria viridis</i> Duch., <i>Taraxacum officinale</i> Web ex Wigg., <i>Anemone ranunculoides</i> L., <i>Alchemilla</i> L., Poaceae
8	P5	1	Near Red Rocks	55°25'21.4"N 56°34'38.7"E	Glade on the on spruce forest on south slope of the hill	Wet dark gray forest soils	40-50%	–	<i>Corydalis solida</i> (L.) Swartz, <i>Anemone nemorosa</i> L.
9	P6	1	Near Red Rocks	55°25'21.3"N 56°34'43.0"E	Shrubs on spruce forest the south slope of the hill	Wet dark gray forest soils	20%	Deciduous and coniferous litter	<i>Picea obovata</i> Ledeb., shrubs
10	P7	7	Near Red Rocks	55°25'19.0"N 56°34'42.3"E	Glade on the on spruce forest on south slope of the hill	Wet dark gray forest soils	60%	–	<i>Picea obovata</i> Ledeb., <i>Corydalis solida</i> (L.) Swartz, <i>Anemone nemorosa</i> L.

Table 2. Characteristics of sites and samples collected within the present study (continued)

Sample No	Sample name	Species found	Locality	GPS coordinate	Microhabitat	Substrate and soil type*	Vegetation cover	Litter	Higher plants at the site
11	P8	1	Near Red Rocks	55°25'18.8"N 56°34'40.6"E	Under the spruce	Wet dark gray forest soils	1-5%	Coniferous litter	<i>Picea obovata</i> Ledeb., <i>Anemone nemorosa</i> L.
12	P9	1	Near Red Rocks	55°25'27.4"N 56°34'33.0"E	Spruce forest on the east slope of the hill	Wet dark gray forest soils	80%	–	<i>Abies sibirica</i> Ledeb., <i>Picea obovata</i> Ledeb., <i>Corydalis solida</i> (L.) Swartz, <i>Primula veris</i> L., <i>Gagea lutea</i> (L.) Ker-Gaw., <i>Viola canina</i> L.
13	P10	9	Edge of Pavlovka village	55°25'28.8"N 56°34'33.6"E	Ravine near spruce forest	Wet dark gray forest soils	10%	–	<i>Fragaria vesca</i> L., <i>Tussilago farfara</i> L., <i>Polygonum aviculare</i> L., <i>Elyngia repens</i> (L.) Nevski, <i>Taraxacum officinale</i> Web ex Wigg., <i>Sedum</i> L., Bryophyta
14	P11	12	Edge of Pavlovka village	55° 25'29"N, 56° 34'31"E	Slope of the hill	Wet dark gray forest soils	50%	–	<i>Taraxacum officinale</i> Web ex Wigg., <i>Fragaria viridis</i> Duch., <i>Artemisia</i> L., <i>Sedum</i> L., Bryophyta
15	P12	9	Near Krasnyy Kluch rill	55°22'42.6"N 56°40'26.5"E	Meadow near the road	Wet dark gray forest soils	60%	Dry grass	<i>Tussilago farfara</i> L., <i>Alchemilla</i> L.
16	P13	8	Riverside of Saldubash river	55°09'46.4"N 56°40'20.2"E	Riverside	Wet floodplain soils	5%	–	Poaceae
17	P14	13	Riverside of Saldubash river	55°09'46.5"N 56°40'17.5"E	Near the puddle	Wet floodplain soils	0%	Deciduous litter, dry grass	Poaceae
Broad-leaved forest zone									
Site 3 – near Bakaly village									
18	Ba1	3	Between Bakaly and Kilkabuzovo villages	55°09'00.6"N 53°51'16.6"E	Spruce forest	Soil, podzolized chernozem	40%	Coniferous litter	<i>Picea obovata</i> Ledeb., <i>Arctium tomentosum</i> Mill., <i>Urtica dioica</i> L., Poaceae
19	Ba2	4	Between Bakaly and Kilkabuzovo villages	55°09'10.0"N 53°50'52.2"E	Young pine forest	Soil, podzolized chernozem	60%	–	<i>Pinus sylvestris</i> L., <i>Arctium tomentosum</i> Mill., <i>Urtica dioica</i> L.
20	Ba3	1	Between Bakaly and Kilkabuzovo villages	55°09'15.2"N 53°51'04.5"E	Mixed forest with a predominance of lime tree	Soil, podzolized chernozem	70%	Deciduous litter	<i>Tilia cordata</i> Mill., <i>Corylus avellana</i> L., <i>Acer</i> sp.
21	Ba4	2	Between Bakaly and Kilkabuzovo villages	55°09'33.6"N 53°50'54.8"E	Mixed forest with a predominance of birch	Soil, podzolized chernozem	65%	–	<i>Betula pendula</i> Roth, <i>Fragaria vesca</i> L., Poaceae
Site 4 – near Igino village									
22	Ig1	1	North-western edge of Igino village	54°51'22.4"N 56°22'17.7"E	Mixed forest	Soil, podzolized chernozem	5%	Deciduous litter	<i>Quercus robur</i> L., <i>Sorbus aucuparia</i> L., <i>Urtica dioica</i> L., <i>Acer</i> sp.

Sample No	Sample name	Species found	Locality	GPS coordinate	Microhabitat	Substrate and soil type*	Vegetation cover	Litter	Higher plants at the site
23	Ig2	8	North-western edge of Igino village	54°51'19.6"N 56°22'19.1"E	Meadow	Soil, podzolized chernozem	30%	Turf	<i>Taraxacum officinale</i> Web. ex Wigg., <i>Alchemilla</i> sp., Poaceae
24	Ig3	0	North-western edge of Igino village	54°52'44.8"N 56°21'21.0"E	Birch forest	Soil, podzolized chernozem	15%	–	<i>Betula pendula</i> Roth, <i>Sorbus aucuparia</i> L.
25	Ig4	0	North-western edge of Igino village	54°53'14.2"N 56°21'44.8"E	Pine planting	Soil, podzolized chernozem	20%	–	<i>Pinus sylvestris</i> L.
26	Ig5	5	North-western edge of Igino village	54°53'20.2"N 56°21'54.1"E	Near the Ufa river	Soil, podzolized chernozem	10%	Deciduous litter	<i>Padus avium</i> Mill., <i>Aegopodium podagraria</i> L.
Site 5 – near Krasnoursolskiy village									
27	Kr1	3	North-western part of Krasnoursolskiy district	53°59'29.2"N 56°20'12.8"E	Broad-leaved forest	Soil, podzolized chernozem	40%	–	<i>Quercus robur</i> L., <i>Sorbus aucuparia</i> L., <i>Rosa</i> sp.
28	Kr2	7	North-western part of Krasnoursolskiy district	53°59'29.4"N 56°20'10.4"E	Broad-leaved forest, near the road	Soil, podzolized chernozem	30%	–	<i>Quercus robur</i> L., <i>Sorbus aucuparia</i> L., <i>Rosa</i> sp.
29	Kr3	4	Near Krasnoursolskiy spa	53°55'32.4"N 56°30'52.4"E	Near the rill	Soil, podzolized chernozem	10%	–	<i>Tussilago farfara</i> L., <i>Arctium tomentosum</i> Mill.
30	Kr4	9	Near Krasnoursolskiy spa	53°55'35.6"N 56°31'17.5"E	Near the road	Microbiotic crust with prevalence of Bryophyta, podzolized chernozem	50%	–	Bryophyta
31	Kr5	6	Near Krasnoursolskiy spa	53°55'36.0"N 56°31'16.4"E	Alder forest	Soil, podzolized chernozem	40%	Deciduous litter	<i>Alnus glutinosa</i> (L.) Gaertn., Bryophyta
32	Kr6	5	Near Krasnoursolskiy spa	53°55'37.0"N 56°31'14.9"E	Meadow near the alder forest	Soil, podzolized chernozem	50%	–	<i>Rubus idaeus</i> L., <i>Sonchus arvensis</i> L., <i>Arctium tomentosum</i> Mill., <i>Inula helenium</i> L., <i>Cichorium intybus</i> L., <i>Artemisia absinthium</i> L., Bryophyta
33	Kr7	2	Near Krasnoursolskiy spa	53°55'37.6"N 56°31'13.7"E	Pine planting near rill	Soil, podzolized chernozem	5%	Coniferous litter	<i>Pinus sylvestris</i> L., Poaceae
34	Kr8	4	Near Krasnoursolskiy spa	53°55'41.7"N 56°31'23.5"E	Meadow near pine planting	Soil, podzolized chernozem	10%	–	<i>Artemisia absinthium</i> L., <i>Fragaria viridis</i> Duch., <i>Achillea millefolium</i> L.
35	Kr9	4	Near Krasnoursolskiy spa	53°55'43.6"N 56°31'24.2"E	Small ravine near pine planting	Soil, podzolized chernozem	5%	–	<i>Pinus sylvestris</i> L., <i>Artemisia absinthium</i> L.
36	Kr10	1	Near eastern part of Krasnoursolskiy village	53°53'15.4"N 56°30'38.5"E	Oak forest in the western part of Krasnoursolskiy village	Soil, podzolized chernozem	60-70%	–	<i>Quercus robur</i> L., <i>Rubus idaeus</i> L., <i>Ulmus</i> sp.

Table 2. Characteristics of sites and samples collected within the present study (continued)

Sample No	Sample name	Species found	Locality	GPS coordinate	Microhabitat	Substrate and soil type*	Vegetation cover	Litter	Higher plants at the site
37	Kr11	2	Near eastern part of Krasnourskiy village	53°53'18.2"N 56°30'41.6"E	Edge of the oak forest	Soil, podzolized chernozem	70%	–	<i>Quercus robur</i> L., <i>Padus avium</i> Mill., <i>Arctium tomentosum</i> Mill., <i>Taraxacum officinale</i> Web. ex Wigg., <i>Potentilla anserina</i> L.
38	Kr12	6	Near eastern part of Krasnourskiy village	53°53'18.8"N 56°30'38.2"E	Meadow near the road	Soil, podzolized chernozem	50%	–	<i>Cichorium intybus</i> L., <i>Taraxacum officinale</i> Web. ex Wigg
Forest-steppe zone									
Site 6 – near Dyutyuli town									
39	D1	0	Near the road Ufa-Dyutyuli	53°24'09.7"N 54°49'25.7"E	Edge of the birch forest	Soil, leached chernozem	20%	Deciduous litter	<i>Betula pendula</i> Roth, <i>Taraxacum officinale</i> Web. ex Wigg., <i>Fragaria vesca</i> L., Poaceae
40	D2	3	Near the road Ufa-Dyutyuli	53°24'09.4"N 54°49'29.5"E	Edge of the birch forest	Soil, leached chernozem	15%	Deciduous litter	<i>Betula pendula</i> Roth, <i>Taraxacum officinale</i> Web. ex Wigg., <i>Fragaria vesca</i> L.
41	D3	1	Near the road Ufa-Dyutyuli	53°24'09.3"N 54°49'32.7"E	Poplar planting	Soil, leached chernozem	15%	–	<i>Populus</i> sp., <i>Taraxacum officinale</i> Web. ex Wigg., Poaceae
Site 7 – near Tolbazy village									
42	T1	5	Near Tretye pond	54°00'38.5"N 55°52'23.3"E	Ravine near the pond	Soil, leached chernozem	1%	–	<i>Fragaria viridis</i> L.
43	T2	4	Near Tretye pond	54°00'38.0"N 55°52'25.3"E	Slope near the pond	Microbiotic crust, leached chernozem	95%	–	<i>Artemisia absinthium</i> L., <i>Trifolium</i> sp., <i>Alchemilla</i> sp., <i>Galium</i> sp.
44	T3	5	Near Tretye pond	54°00'54.2"N 55°52'24.9"E	Betula forest	Soil, leached chernozem	1%	–	<i>Betula pendula</i> Roth, <i>Polygonum bistorta</i> L.
45	T4	7	Near Tretye pond	54°00'53.8"N 55°52'29.7"E	Slope near the pond	Soil, leached chernozem	2%	–	<i>Artemisia absinthium</i> L., <i>Verbascum thapsus</i> L., <i>Galium</i> sp.
46	T5	0	Near underground reservoir	54°00'49.2"N 55°52'36.6"E	Aspen planting	Soil, leached chernozem	40%	–	<i>Populus tremula</i> L., <i>Acer negundo</i> L., <i>Sorbus aucuparia</i> L., <i>Padus avium</i> Mill.
47	T6	1	Tolbazy village	54°01'02.9"N 55°53'28.6"E	Garden	Soil, leached chernozem	55%	–	<i>Malus domestica</i> Borkh., <i>Allium sativum</i> L.
Site 8 – near Bolsheustikinskoye village									
48	Bul	8	Hill near Nagornaya street	55°57'47.0"N 58°16'15.8"E	Small ravine near birch forest on the hill	Gray forest soil	1%	–	<i>Betula pendula</i> Roth, <i>Artemisia absinthium</i> L., <i>Convolvulus arvensis</i> L., <i>Ceranium sylvaticum</i> L.

Sample No	Sample name	Species found	Locality	GPS coordinate	Microhabitat	Substrate and soil type*	Vegetation cover	Litter	Higher plants at the site
49	Bu2	5	Hill near Nagornaya street	55°57'46"N, 58°16'18.0"E	Betula forest	Gray forest soil	40%	–	<i>Betula pendula</i> Roth, <i>Fragaria vesca</i> L.
50	Bu3	1	Hill near Nagornaya street	55°57'48.4"N 58°16'03.0"E	Pinery	Gray forest soil	30%	–	<i>Pinus sylvestris</i> L., <i>Peridium aquilinum</i> (L.) Kuhn., <i>Fragaria vesca</i> L.
51	Bu4	4	Slope to the Ik river, left bank	55°57'49.0"N 58°15'56.7"E	Slope in a pine forest	Floodplain soil	1%	Coniferous fall	<i>Pinus sylvestris</i> L.
52	Bu5	6	Slope to the Ik river, 15m to water, left bank	55°57'48.6"N 58°15'54.0"E	Slope in a pine forest	Floodplain soil	5%	–	<i>Alnus glutinosa</i> (L.) Gaertn., <i>Chelidonium majus</i> L., <i>Galium aparine</i> L., Poaceae
53	Bu6	13	Riverside of Ik river, left bank	55°57'47"N, 58°15'53.0"E	Path	Macroscopic cyanobacteria and algae growth on soil, floodplain soil	5%	–	<i>Plantago major</i> L., <i>Taraxacum officinale</i> Web. ex Wigg., <i>Polygonum aviculare</i> L.
54	Bu7	3	Riverside of Ik river, left bank	55°57'47"N, 58°15'52.0"E	Soil and water margin	Macroscopic cyanobacteria and algae growth on soil, floodplain soil	80%	–	<i>Tussilago farfara</i> L., <i>Potentilla anserina</i> L., <i>Aegopodium podagaria</i> L.
55	Bu8	3	Riverside of Ik river, left bank	55°57'39.5"N 58°15'53.4"E	Meadow near the river	Floodplain soil	90%	–	<i>Urtica dioica</i> L., <i>Arctium lappa</i> L., <i>Potentilla anserina</i> L., <i>Taraxacum officinale</i> Web. ex Wigg., <i>Trifolium pratense</i> L., <i>Onopordium acanthium</i> L.
56	Bu9	9	Riverside of Ik river, left bank	55°57'29"N, 58°15'50.0"E	Meadow near the river	Floodplain soil	100%	–	<i>Arenisia absinthium</i> L., <i>Sonchus olerensis</i> L., <i>Marricaria</i> sp.
57	Bu10	7	Riverside of Ik river, left bank	55°57'18.8"N 58°15'45.8"E	Willow forest	Macroscopic cyanobacteria and algae growth on soil, floodplain soil	80%	–	<i>Salix</i> sp., <i>Tussilago farfara</i> L.
58	Bu11	9	Riverside of Ik river, right bank	55°57'09.3"N 58°15'32.5"E	Meadow near floodplain forest	Floodplain soil	80%	Turf	<i>Taraxacum officinale</i> Web. ex Wigg., <i>Tussilago farfara</i> L.
59	Bu12	14	Riverside of Ik river, right bank	55°57'08.7"N 58°15'29.7"E	Road in floodplain forest	Macroscopic cyanobacteria and algae growth on soil, floodplain soil	80%	–	<i>Alnus glutinosa</i> (L.) Gaertn., <i>Padus avium</i> Mill., <i>Arctium lappa</i> L., <i>Urtica dioica</i> L., <i>Aegopodium podagaria</i> L., <i>Plantago major</i> L.
60	Bu13	5	Riverside of Ik river, left bank	55°57'07.8"N 58°15'42.6"E	Sandy substrate near the river	Floodplain soil	70%	–	<i>Arenisia absinthium</i> L., <i>Plantago major</i> L., <i>Taraxacum officinale</i> Web. ex Wigg.

Table 2. Characteristics of sites and samples collected within the present study (continued)

Sample No	Sample name	Species found	Locality	GPS coordinate	Microhabitat	Substrate and soil type*	Vegetation cover	Litter	Higher plants at the site
61	Bu14	4	Riverside of Ik river, left bank	55°57'13.1"N 58°15'49.8"E	Mound near the bridge	Floodplain soil	50%	–	<i>Artemisia absinthium</i> L., <i>Taraxacum officinale</i> Web. ex Wigg., <i>Arctium lappa</i> L., <i>Polygonum aviculare</i> L.
62	Bu15	4	Bolsheustikinskoye village	55°57'13.7"N 58°16'06.7"E	Garden	Floodplain soil	30%	–	<i>Malus domestica</i> Borkh., <i>Ribes nigrum</i> L.
63	Bu16	2	Bolsheustikinskoye village	55°57'12.8"N 58°16'06.0"E	Kitchen-garden	Floodplain soil	70%	–	<i>Daucus</i> L., <i>Beta</i> L.
Site 9 – near Georgievka village									
64	G1	2	Near the road	54°13'2.9"N 54°13'02.9"N	Ravine	Macroscopic growth of cyanobacteria and algae, leached chernozem	5%	–	<i>Potentilla anserina</i> L., <i>Geum rivale</i> L., <i>Plantago major</i> L., <i>Artemisia absinthium</i> L., <i>Cichorium intybus</i> L., <i>Atriplex</i> sp., <i>Maricaria</i> sp.
65	G2	3	Near the road	54°13'01.4"N 56°13'31.3"E	Ravine	Wet soil, leached chernozem	1%	–	<i>Potentilla anserina</i> L., <i>Plantago major</i> L., <i>Geranium pratense</i> L., <i>Dactylis glomerata</i> L., <i>Cichorium intybus</i> L., <i>Geum rivale</i> L., <i>Sanguisorba officinalis</i> L., <i>Trifolium pratense</i> L.
66	G3	3	Near the pond	54°12'55.8"N 56°13'44.7"E	Wetland	Wet soil, macroscopic growth of alga <i>Borjadium granulatum</i> (Linnaeus) Greville, leached chernozem	50%	–	<i>Equisetum arvense</i> L.
67	G4	7	Georgievka village	54°13'21.1"N 56°13'33.9"E	Garden	Soil, leached chernozem	50%	–	Garden flowers
Steppe zone									
Site 10 – near Sibay town									
68	S1	1	South part of edge of Sibay town	52°40'32.6"N 58°42'18.0"E	Forb-grass steppe	Vesicular microbiotic crust, south chernozem	90%	–	<i>Sipa capillata</i> L., <i>Plantago stepposa</i> Kuprian., <i>Arenisia sericea</i> Web. ex Stechm., <i>Festuca pratensis</i> Huds., <i>Hieracium virosum</i> Pall., <i>Trifolium montanum</i> L.
69	S2	4	South part of edge of Sibay town	52°40'30.0"N 58°42'17.4"E	Forb-grass steppe	Vesicular microbiotic crust, south chernozem	90%	–	<i>Sipa capillata</i> L., <i>Plantago stepposa</i> Kuprian., <i>Arenisia sericea</i> Web. ex Stechm., <i>Festuca pratensis</i> Huds., <i>Hieracium virosum</i> Pall., <i>Trifolium montanum</i> L.
70	S3	5	South slope of the hill near Kultuban lake	52°38'04"N, 58°43'42.0"E	Forb-grass steppe	Soil, south chernozem	90%	–	<i>Sipa capillata</i> L., <i>Dianthus acicularis</i> Fisch. ex Ledeb., <i>Helictotrichon desertorum</i> (Less) Nevskij, <i>Galium boreale</i> L., <i>Phlomis tuberosa</i> L., <i>Aster alpinus</i> L., <i>Seseli libanotis</i> (L.) Koch., <i>Sabia stepposa</i> Schost., <i>Plantago stepposa</i> Kuprian., <i>Arenisia sericea</i> Web. ex Stechm., <i>Onobrychis arenaria</i> (Kit) DC., <i>Festuca pratensis</i> Huds., <i>Hieracium virosum</i> Pall., <i>Trifolium montanum</i> L.

Sample No	Sample name	Species found	Locality	GPS coordinate	Microhabitat	Substrate and soil type*	Vegetation cover	Litter	Higher plants at the site
71	S4	6							<i>Stipa capillata</i> L., <i>Dianthus acicularis</i> Fisch. ex Ledeb., <i>Helictotrichon desertorum</i> (Less.) Nevskij, <i>Galium boreale</i> L., <i>Phlomis tuberosa</i> L., <i>Aster alpinus</i> L., <i>Seseli libanotis</i> (L.) Koch, <i>Salvia stepposa</i> Schost., <i>Plantago stepposa</i> Kuprian., <i>Artemisia sericea</i> Web. ex Stechm., <i>Onobrychis arenaria</i> (Kit.) DC., <i>Festuca pratensis</i> Huds., <i>Hieracium virosum</i> Pall., <i>Trifolium montanum</i> L.
72	S5	9							
73	S6	2	South slope of the hill near Kultuban lake	52°37'58.4"N 58°43'47.7"E	Forb-grass steppe	Various cyanobacterial crusts, south chernozem	90%	–	
74	S7	2							
75	S8	1							
76	S9	1							
Site 11 – near Yangelskiy village									
77	Ya1	4	Eastern part of edge of Yangelskiy village	53°15'24.8"N 58°51'11.2"E	Forb-grass steppe	Soil, ordinary chernozem	40-50%	–	<i>Stipa capillata</i> L., <i>Artemisia sericea</i> Web. ex Stechm., <i>Plantago stepposa</i> Kuprian.
78	Ya2	6	Eastern part of edge of Yangelskiy village	53°15'25.7"N 58°51'23.6"E	Abandoned marble quarry	Soil, ordinary chernozem	20-30%	–	<i>Convulvulus arvensis</i> L., <i>Cirsium arvense</i> (L.) Scop., <i>Artemisia</i> sp., Poaceae
79	Ya3	6	Western part of edge of Yangelskiy village	53°15'16.4"N 58°46'16.1"E	Forb-grass steppe	Soil, ordinary chernozem	50%	–	<i>Stipa</i> sp., <i>Artemisia</i> sp., <i>Plantago stepposa</i> Kuprian., <i>Galium boreale</i> L.
80	Ya4	10	Western part of edge of Yangelskiy village	53°15'12.5"N 58°44'19.1"E	Forb-grass steppe	Soil, ordinary chernozem	60%	–	<i>Stipa</i> sp., <i>Artemisia</i> sp., <i>Plantago stepposa</i> Kuprian., <i>Galium boreale</i> L.
81	Ya5	3	Western part of edge of Yangelskiy village	53°15'14.7"N 58°44'12.2"E	Floodplain of artificial pond	Soil, ordinary chernozem	95%	–	<i>Rumex confertus</i> Willd., Poaceae
Site 12 – near Arcaim monument									
82	Ar1	4	South-western edge of Arcaim monument	52°37'18.6"N 59°31'44.3"E	Forb-grass steppe	Soil, microbiotic crust with prevalence of lichens, cyanobacterial crust, ordinary chernozem	75-80%	–	<i>Stipa lessingiana</i> Trin. et Rupr., <i>Festuca valesiaca</i> Schleich. ex Gaudin, <i>Plantago stepposa</i> Kuprian., <i>Achillea millefolium</i> L.
83	Ar2	7	South-western edge of Arcaim monument	52°38'35.2"N 59°32'07.9"E	Forb-grass steppe	Microbiotic crust with prevalence of lichens, ordinary chernozem	75-80%	–	<i>Stipa lessingiana</i> Trin. et Rupr., <i>Festuca valesiaca</i> Schleich. ex Gaudin, <i>Plantago stepposa</i> Kuprian., <i>Achillea millefolium</i> L.
84	Ar3	1	South-western edge of Arcaim monument	52°38'48.2"N 59°32'46.1"E	Forb-grass steppe	Mosses, algae and cyanobacteria, ordinary chernozem	75-80%	–	<i>Stipa lessingiana</i> Trin. et Rupr., <i>Festuca valesiaca</i> Schleich. ex Gaudin, <i>Plantago stepposa</i> Kuprian., <i>Achillea millefolium</i> L.
85	Ar4	8	South-western edge of Arcaim monument	52°38'39.6"N 59°33'18.5"E	Forb-grass steppe	Cyanobacterial and algae crust, ordinary chernozem	75-80%	–	<i>Stipa lessingiana</i> Trin. et Rupr., <i>Festuca valesiaca</i> Schleich. ex Gaudin, <i>Plantago stepposa</i> Kuprian., <i>Achillea millefolium</i> L.

*According soil map for the territory of Bashkiriya (Khaziev, 2012) and the data of Prikhod'ko *et al.* (2012)

Observations of cyanobacteria were conducted using a Zeiss Axio Imager A2 microscope with DIC optics and Axio Vision 4.9 visualization system. Microphotographs were taken with an Axio Cam MRc camera on magnifications $\times 400$ and $\times 1000$. For identification of the taxa and classification, the relevant reference sources were used (Anagnostidis & Komárek, 1988; Guiry & Guiry, 2016; Komárek & Anagnostidis, 1999, 2005; Komárek, 2013; Komárek *et al.*, 2014). Typical morphological features of filamentous taxa, such as filament, trichome, and cell dimensions, sheath color, cell color, heterocyte and akinete dimensions, length of apical cells in filamentous taxa, degree of constriction at crosswalls, special features associated with end cells and necridia, filament polarity, tapering, and type of branching, when present, were observed and measured for each taxon and the proper identification was supplemented with the knowledge on the ecological data. For coccoid taxa, planes of cell division, cell shape, degree of lamellation of the cellular and colonial mucilage, sheath and cell color, and dimensions and shape of cells were used for identification.

The species list was created based on frequency of occurrence according Braun-Blanquet scale with modifications: 1 = 0.1-5%; 2 = 6-10%; 3 = 11-20%; 4 = 21-40%; 5 = 41-60%; 6 = 61-80%; 7 = 81-100% (Braun-Blanquet, 1951). Frequencies represent abundances in samples resulting from direct observation and from counting of cultures.

Statistical analysis

Using the R package ‘vegan’ (Oksanen *et al.*, 2017), a principle component analysis (PCA, Jolliffe, 1986) was performed to characterize compositional variation in soil cyanobacterial community data, using the combined data for each of the 12 sites. Species data were Hellinger transformed prior execution of the ordination. This transformation linearizes species data and alleviates the double zero problem, thereby allows analysis via Euclidean-based ordination methods, such as PCA (Legendre & Gallagher, 2001). Environmental factors were fitted onto the ordination using ‘envfit’ function, the goodness of fit was assessed using a permutation test ($n = 999$). All statistical analyses were performed in R software, version 3.4.0 (R Core Team, 2017).

RESULTS

Fifty-six cyanobacteria were identified. The total number of species was highest in the boreal-forest zone (39) and notably lower in the other zones (18, 29, and 24 for broad-leaved forest, forest steppe and steppe regions, respectively). Maximum species per site was higher in forest-steppe and boreal forests, and lower in steppes and broad-leaved forests (Tables 1, 2). Descriptions of all species encountered (Table 3) as well as images of most taxa (Figs 2-57) are presented so that evaluation of the taxonomy adopted in the study is possible.

Several species of cyanobacteria were detected in all studied zones: *Leptolyngbya voronichiniana* (Fig. 10), *Leptolyngbya foveolarum* (Fig. 3), cf. *Trichocoleus hospitus* (Fig. 14), *Pseudophormidium hollerbachianum* (Fig. 29), *Nostoc* cf. *punctiforme* (Fig. 55), *Microcoleus vaginatus* (Fig. 24), *Phormidium breve* (Fig. 32), *Phormidium dimorphum* (Fig. 34), *Phormidium corium* (Fig. 33), and *Leptolyngbya* cf. *tenuis* (Fig. 7) (Tables 2, 3). *Phormidium*, *Leptolyngbya* and *Nostoc* (including *Desmonostoc*, Figs 50-55) were the most abundant genera with 11, 8 and 6 species respectively.

Table 3. List of species collected within the present study with the sample numbers: Boreal forest zone = samples **1-17**, broad-leaved forest zone = samples **18-38**, forest steppe zone = samples **39-67**, steppe zone = samples **68-85**. The taxa are ordered based on taxonomic classification given in Table 1

<i>Species</i>	<i>Morphological features</i>	<i>Sample number</i>
<i>Pseudanabaena papillateterminata</i> (Kiselev) Kukku	Trichomes short, pale blue-green to pinkish, 1.7-2.1 µm wide, constricted at cross-walls. Cells isodiametric to twice longer than wide, 1.9-4.3 µm long. Small conical protrusion is present at the top of apical cell, probably with a ring-shaped aerotop.	FS: 64
<i>Leptolyngbya foveolarum</i> (Rabenhorst ex Gomont) Anagnostidis & Komárek	Filaments variously curved, sheaths thin, firm. Trichomes pale to bright blue-green, 1.6-2.8 µm wide, constricted at cross-walls, not attenuated at the ends. Cells isodiametric to twice longer than wide, 1.4-2.8 µm long.	BF: 4, 5, 13-17 BL: 23, 28, 31, 32, 38 FS: 44, 45, 48, 51, 52, 54, 56-59, 66-67 S: 68, 72, 80, 82, 83, 85
<i>Leptolyngbya</i> cf. <i>fragilis</i> (Gomont) Anagnostidis & Komárek	Filaments with thin, colorless sheaths. Trichomes pale blue-green, 1.2-2.3 µm wide, moniliform, distinctly constricted at cross-walls. Cells isodiametric to twice longer than wide, 1.5-2.2 µm long.	BF: 4 S: 80
<i>Leptolyngbya</i> cf. <i>hansgirgiana</i> Komárek in Anagnostidis	Trichomes pale blue-green, 1.1-1.3 µm wide, straight or slightly curved, not constricted at cross-walls. Cells cylindrical, 1.8-3.4 µm long.	BF: 4-6, 17
<i>Leptolyngbya</i> cf. <i>subtilissima</i> (Kützinger ex Hansgirg) Komárek in Anagnostidis	Filaments pale blue-green, 0.8-1.1 µm wide, slightly constricted at cross-walls. Cells isodiametric, 1.1-1.5 µm long.	BF: 4, 14, 17 FS: 48, 53 S: 80
<i>Leptolyngbya</i> cf. <i>tenuis</i> (Gomont) Anagnostidis & Komárek	Filaments with thin, colorless sheath. Trichomes pale blue-green, 0.6-0.8 µm wide, slightly constricted at cross-walls. Cells up to five times longer than wide, 2.0-3.2 µm long.	BF: 6, 14, 17 BL: 19 FS: 60, 67 S: 78, 80, 83
<i>Leptolyngbya</i> cf. <i>nostocorum</i> (Bornet ex Gomont) Anagnostidis & Komárek	Filaments flexuous, with thin, firm sheaths. Trichomes pale blue-green or brownish, 1.2-2.4 µm wide. Cells cylindrical, usually longer than wide, 2.5-3.5 µm long. Detected in the mucilage of <i>Nostoc</i> cf. <i>ellipso sporum</i> .	BF: 3
<i>Leptolyngbya</i> cf. <i>notata</i> (Schmidle) Anagnostidis & Komárek	Trichomes pale-blue green, constricted at cross-walls, 1.0-1.1 µm wide. Cells cylindrical up to three times longer than wide, 2.0-2.4 µm long.	77

Table 3. List of species collected within the present study with the sample numbers: Boreal forest zone = samples **1-17**, broad-leaved forest zone = samples **18-38**, forest steppe zone = samples **39-67**, steppe zone = samples **68-85**. The taxa are ordered based on taxonomic classification given in Table 1 (*continued*)

<i>Species</i>	<i>Morphological features</i>	<i>Sample number</i>
<i>Leptolyngbya voronichiniana</i> Anagnostidis & Komárek	Filaments with colorless, thin sheaths. Trichomes pale blue-green, 1.0-1.5 µm wide, without constrictions at cross-walls, not attenuated towards the ends. Cells cylindrical, two times longer than wide, with homogeneous content. Apical cells rounded.	BF: 2, 4, 7, 10, 11, 17 BL: 18-20, 22, 23, 27, 28, 30-34, 38 FS: 40, 42, 43, 45, 48-53, 55-57, 59, 61, 63, 67 S: 69, 70, 72, 77, 78, 80, 82, 85
<i>Oculatella</i> sp. 1	Filaments with colorless, thin sheaths. Trichomes blue-green, 1.1-1.9 µm wide, with constrictions at the cross-walls. Cells cylindrical, longer than wide, 2.1-4.0 µm. Apical cells with crystal-like spot in the apex.	FS: 53
<i>Oculatella</i> sp. 2	Filaments flexuous, in thin, attached sheath. Trichomes blue-green, 2.2-2.6 µm wide, with constrictions at cross-walls. Cells more or less isodiametric, 2.1-2.8 µm long. Apical cells widely rounded with crystal-like or orange spot in the apex of the cell.	FS: 54
<i>Oculatella</i> sp. 3	Filaments with thin, colorless sheaths. Trichomes green to blue-green, 1.6-2.0 µm wide, with constrictions at the cross-walls. Cells cylindrical, longer than wide, 2.2-3.9 µm. Apical cells conical, with crystal-like or orange spot in the apex of the cell.	S: 76
cf. <i>Trichocoleus hospitus</i> (Hansgrig ex Forti) Anagnostidis	Trichomes 0.6-0.7 µm wide, with cells 0.7-1.0 µm long, solitary or densely aggregated in sheaths, 2.5-3.9 µm wide. Apical cells rounded or thickened. Name refers to its growth on the sheaths of other cyanobacteria or in the mucilage of green algae.	BF: 13 BL: 19, 23, 26, 27, 29, 31-38
<i>Myxosarcina</i> cf. <i>tartica</i> (Starmach) Komárek & Anagnostidis	Forms small sarcinoid packets up to 25 µm in diameter. Cells dark blue-green, 5.3-7.4 in diameter.	BL: 28
<i>Aphanothece stagnina</i> (Spreng.) A. Braun	Colonies gelatinous, spherical, with loosely dispersed cells. Cells oval or spherical, blue-green, 5.4-8.3 µm long, 5.0-5.2 µm wide.	BF: 17
<i>Chroococcus varius</i> A. Braun in Rabenhorst	Cells in groups of two to four, each cell about 2 µm in diameter, spherical, hemispherical or with form of a section of a sphere, pale blue-green.	FS: 53
<i>Chlorogloea</i> cf. <i>purpurea</i> Geitler	Colonies mucilaginous, irregular, with pink cells 0.8-1.5 µm in diameter. Terrestrial species.	BL: 30 FS: 53 S: 80, 83, 85
<i>Cyanothece aeruginosa</i> (Nägeli) Komárek	Cells spherical, subspherical or oval, often in pairs, 10.3-20.8 µm long, 8.1-10.8 µm wide, blue-green, sometimes with yellow or brown tint, with granulation.	S: 69

<i>Species</i>	<i>Morphological features</i>	<i>Sample number</i>
<i>Borzia trilobularis</i> Cohn ex Gomont	Filaments blue-green, short, consist of few cells (mostly 2-8), constricted at cross-walls. Cells shorter than wide 2.8-3.5 µm long, 5.6-6.0 µm wide. Apical cells rounded.	FS: 59
<i>Kamptomena animale</i> (Agardh ex Gomont) Strunecký, Komárek & Šnarda	Filaments straight, in fine, diffuent sheaths. Trichomes blue-green, 4.1-4.2 µm wide, not constricted at the cross walls, attenuated and slightly bent at the ends, motile. Cells shorter than wide, 2.6-3.2 µm long. Apical cells acute-conical, without calyptra or thickened outer cell wall.	FS: 45
<i>Kamptomena laetevirens</i> (Crouan & Crouan ex Gomont) Strunecký, Komárek & Šnarda	Trichomes straight, blue-green, 2.3-3.0 µm wide, slightly constricted at cross-walls, attenuated towards the ends. Cells mostly isodiametric, rarely longer or shorter than wide, 2.5-4.2 µm long, cell content granular. Apical cells narrowed, bent, without calyptra.	BF: 6
<i>Microcoleus autumnalis</i> (Gomont) Strunecký, Komárek & J.R. Johansen	Trichomes bright blue-green, 5.5-6.3 µm wide, straight or slightly curved, apical region slightly curved. Cells half as long as wide to slightly longer than wide. Trichomes without constrictions at cross walls. Apical cells capitate, usually with rounded or conical calyptra.	BF: 4, 13 BL: 28, 30, 35 FS: 40, 57
<i>Microcoleus vaginatus</i> (Vaucher) Gomont ex Gomont	Usually many trichomes in common sheath, sometimes single. Trichomes dark-green to gray, 5.2-6.7 µm wide, without constrictions at cross walls. Cells 0.5-1.5 times longer than wide, with granulation. Apical cells capitate, usually with calyptra.	BF: 5-8, 10, 13-17 BL: 18, 23, 32 FS: 53, 56, 58, 59, 64, 66 S: 71, 72, 76-80, 82, 84, 85
<i>Microcoleus</i> sp. 1	Trichomes reddish in color, 6.7-7.1 µm wide, not constricted at the cross-walls, aggregated in sheaths. Cells almost isodiametric. Apical cells conical, without calyptra.	BF: 10
<i>Microcoleus</i> sp. 2	Trichomes blue-green or brownish, 7.4-8.2 µm wide, not constricted at the cross-walls, attenuated to ends, aggregated in sheaths. Cells almost isodiametric. Apical cells conical, slightly bent, without calyptra.	BL: 18
<i>Microcoleus</i> sp. 3	Trichomes blue-green or olive-green, 6.6-7.1 µm wide, not constricted at the cross-walls, aggregated in sheaths. Cells shorter than wide, rarely almost isodiametric. Apical cells conical, without calyptra.	BF: 13
<i>Oxynema</i> cf. <i>acuminatum</i> (Gomont) Chatchawan, Komárek, Strunecký, Šnarda & Peerapompisal	Trichomes blue-green, 3.9-4.3 µm wide, slightly constricted at the cross-walls, with ends abruptly briefly attenuated, pointed and bent, motile, with relatively rapid oscillation. Cells shorter than wide, 1.1-2.9 µm long. Apical cells acute-conical, pointed, 0.9-2.5 µm wide.	BF: 14
<i>Pseudophormidium hollerbachianum</i> (Elenkin) Anagnostidis	Thallus gelatinous, bright blue-green. Filaments curved, with pseudobranches. Trichomes pale or bright blue-green, 2.2-2.5 µm wide, constricted at cross-walls, with necridic cells. Cells barrel-shaped, usually shorter than wide or isodiametric, 1.0-2.6 µm long, not granulated. Apical cells rounded. Formation of hormogonia observed.	BF: 2, 5, 15-17 BL: 28, 31, 32, 34, 35 FS: 42, 43, 45, 48, 52, 61 S: 69-73, 75, 79, 80, 82, 84, 85

Table 3. List of species collected within the present study with the sample numbers: Boreal forest zone = samples **1-17**, broad-leaved forest zone = samples **18-38**, forest steppe zone = samples **39-67**, steppe zone = samples **68-85**. The taxa are ordered based on taxonomic classification given in Table 1 (*continued*)

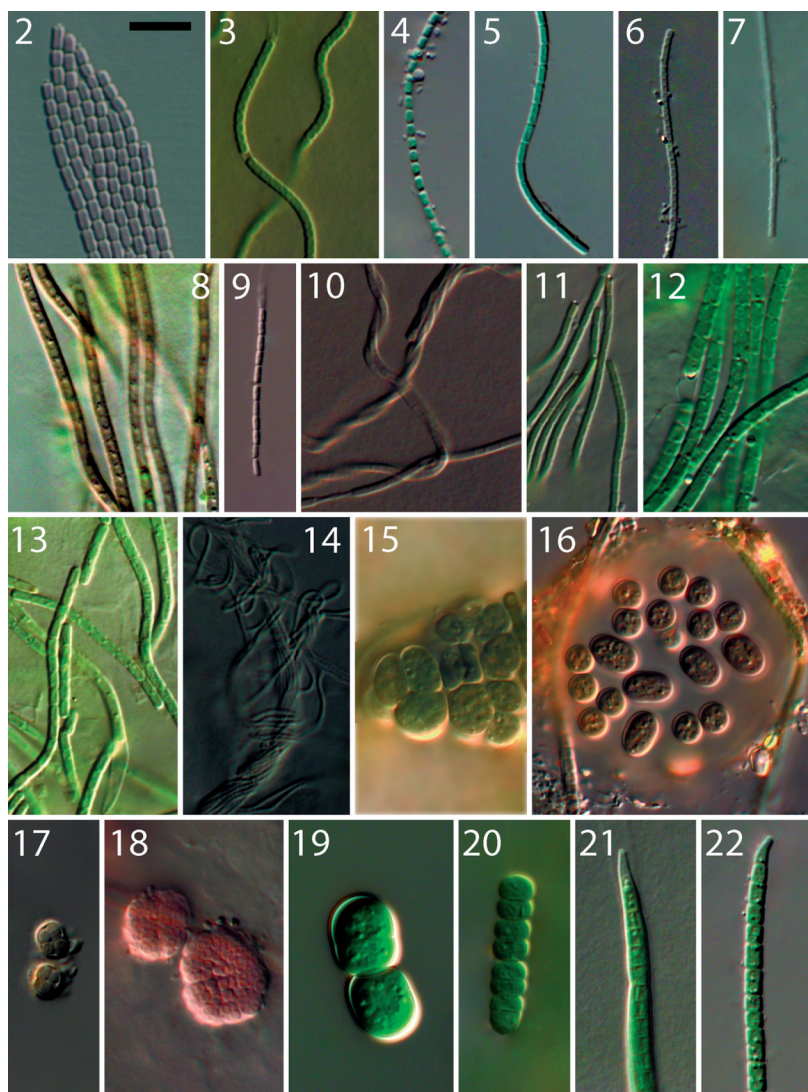
<i>Species</i>	<i>Morphological features</i>	<i>Sample number</i>
<i>Lyngbya marteniana</i> Meneghini ex Gomont	Filaments curved or straight, sheaths hyaline, thick, becoming thicker when aged. Trichomes blue-green to olive-green, 9.3-10.3 µm wide, cylindrical, not constricted at cross-walls, not attenuated. Cells significantly shorter than long, 0.8-1.5 µm long. Apical cells widely rounded, hemispherical, without calyptra or thickened outer cell wall.	BF: 14, 15, 17 FS: 42 S: 72, 78
<i>Phormidium ambiguum</i> Gomont ex Gomont	Filaments curved, rarely straight, with thin, slightly diffuent, colorless sheaths. Trichomes bright blue-green, 3.9-4.9 µm wide, slightly constricted at cross-walls, not attenuated at the ends. Cells shorter than wide, occasionally almost isodiametric, 1.1-1.3 µm long. Apical cells rounded, without calyptra.	FS: 44, 59, 67 S: 72
<i>Phormidium aeruginoso-caeruleum</i> (Gomont) Anagnostidis & Komárek	Filaments with thin, firm, colorless sheaths. Trichomes bright blue-green, sometimes with yellow tint, 6.3-7.2 µm wide, not constricted at cross-walls, not attenuated at the ends. Cells up to 1/3 as long as wide, 1.3-1.7 µm long, cell content with large, prominent granules. Apical cells obtusely conical or rounded, rarely weakly capitate, with slightly thickened outer cell wall.	BF: 3
<i>Phormidium breve</i> (Kützing ex Gomont) Anagnostidis & Komárek	Filaments straight or slightly curved. Trichomes bright blue-green, 4.0-4.7 µm wide, intensely motile and oscillating, not constricted at the granulated cross-walls, briefly attenuated at the ends, bent, hooked. Cells 1/2-1/3 time as long as wide, 1.4-2 µm long. Apical cells obtuse-conical or rounded-conical, rarely slightly depressed, without calyptra or thickened outer cell wall.	BF: 10, 14, 15, 17 BL: 32, 34 FS: 40, 41, 44, 56, 58, 59 S: 71, 72, 79, 80
<i>Phormidium corium</i> Gomont	Filaments curved, with thin, firm, colorless, sometimes diffuent mucilaginous sheaths. Trichomes bright blue-green or dark-green, 5.2-5.9 µm wide, not constricted at ungranulated cross-walls, not attenuated at the ends, straight. Cells nearly isodiametric up to two times longer than wide, 3.4-6.8 µm long. Apical cells obtuse conical.	BF: 10, 13 BL: 38 FS: 44, 52, 53, 57-59 S: 83
<i>Phormidium dimorphum</i> Lemmermann	Filaments with thin, firm sheaths. Trichomes blue-green, 3.9-4.9 µm wide, constricted at cross-walls, attenuated toward the ends when mature. Cells almost quadrate, sometimes shorter than wide, end cell longer than wide, 1.8-3.8 µm long. Apical cells conical, rounded after fragmentation.	BF: 16 BL: 28-30 FS: 45, 48, 66 S: 78, 79
<i>Phormidium cf. jadinianum</i> Gomont	Filaments with firm, colorless sheaths. Trichomes blue-green, 5.9-6.1 µm wide, constricted at cross-walls. Cells shorter than wide, 3.2-4.9 µm long. Apical cells acute-conical.	BF: 13, 15 FS: 81

Species	Morphological features	Sample number
<i>Phormidium cf. rezitii</i> (Agardh) Gomont ex Gomont	Filaments straight with thin, firm to diffuent sheaths. Trichomes blue-green, 7.7-8.5 wide µm, not constricted at cross-walls, not attenuated at the ends. Cells almost isodiametric or slightly shorter than wide, 5.7-6.5 µm long. Apical cells obtuse-rounded or truncate, without calyptra.	BF: 10, 13, 14
<i>Phormidium tergestinum</i> (Kützinger) Anagnostidis & Komárek	Filaments long, straight or irregularly curved, with thin, firm sheaths. Trichomes olive-green, 4.3-4.6 µm wide, with counter-clockwise (?) or undetermined rotation, not constricted at cross-walls, not attenuated at the ends. Cells usually shorter than wide or rarely isodiametric, 2.1-4.8 µm long. Apical cells rounded.	BF: 3
<i>Phormidium uncinatum</i> (Agardh) Gomont	Filaments straight or slightly bent with mucilaginous firm or diffuent sheaths. Trichomes blue-green or dirty green, 3.7-4.8 µm wide, not constricted at cross-walls, briefly attenuated toward ends, hooked or slightly coiled, rapidly motile. Cells 1/2-1/3 times as long as wide, 1.0-1.9 µm long. Apical cells capitate, mostly with obtuse or rounded-conical calyptra.	BF: 14
<i>Phormidium</i> sp. 1	Filaments straight with very firm sheaths. Trichomes blue-green or olive-green, 7.9-11.2 µm wide, sometimes constricted at cross-walls, not attenuated at the ends. Cells almost isodiametric, shorter or longer than wide, 6.2-11.4 µm long. Apical cells capitate, obtuse-conical.	BF: 10
<i>Phormidium</i> sp. 2	Filaments with thin, firm sheaths. Trichomes bright blue-green, 2.5-3.2 µm wide, constricted at cross-walls, not attenuated towards ends. Cells almost isodiametric, 1.8-3.8 µm long. Apical cells conical, rounded after fragmentation.	S: 79
<i>Hormosilla pringsheimii</i> Anagnostidis & Komárek	Trichomes short, 2-3.2 celled, rarely consisting of more cells, with fine mucilage, straight or slightly curved, blue-green or yellow-green, 3.3-5.8 µm wide, constricted at the granulated cross-walls, not attenuated towards ends. Cells shorter than wide to nearly isodiametric, 1.2-3.3 µm long, barrel-shaped. Apical cells widely rounded.	BF: 15, 16
<i>Scytonema</i> sp.	Filaments isopolar, with false branching and colorless attached sheaths. Trichomes cylindrical along the whole length, 5.5-8.0 µm wide. Cells almost isodiametric, or slightly shorter or longer than wide, 3.8-7.1 µm long. Apical cells usually rounded. Heterocytes intercalary, solitary, quadrate or cylindrical, 5.8-7.3 µm long, 3.0-5.5 µm wide.	BF: 3
<i>Roholtiella bashkiri</i> Gomont & Bohunická	Filaments short to long, single or double false branched, with thin, colorless, attached or diffuent sheath. Trichomes olive-green to orange-green, 6.6-9.8 µm wide, constricted at cross-walls, not tapered to distinctly gradually tapered. Cells shorter than wide to isodiametric, 2.1-8.5 µm long, barrel-shaped to rounded. Apical cells conical rounded. Heterocytes terminal hemispherical or intercalary cylindrical. Arthrospores or short rows of arthrospores released from the ends of the filaments.	FS: 53

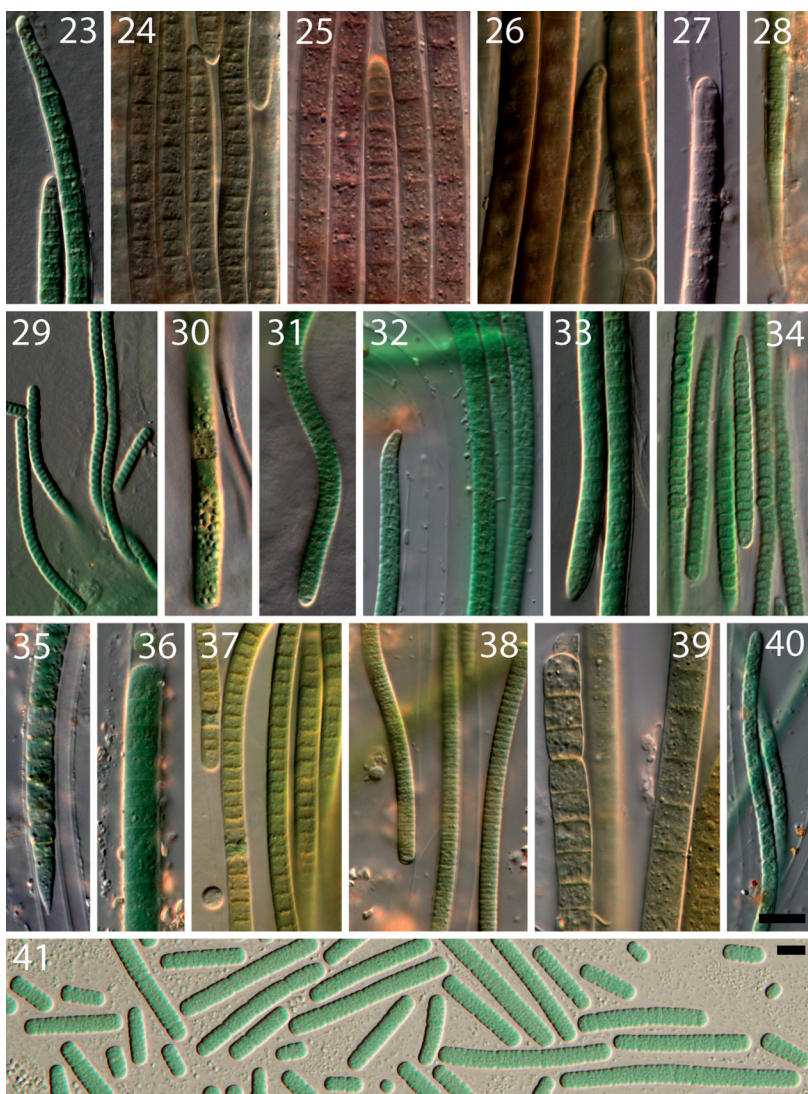
Table 3. List of species collected within the present study with the sample numbers: Boreal forest zone = samples **1-17**, broad-leaved forest zone = samples **18-38**, forest steppe zone = samples **39-67**, steppe zone = samples **68-85**. The taxa are ordered based on taxonomic classification given in Table 1 (*continued*)

<i>Species</i>	<i>Morphological features</i>	<i>Sample number</i>
<i>Roholtiella edaphica</i> Bohunická & Lukešová	Filaments isopolar or heteropolar, with false branching and thin, firm sheaths, colorless to reddish brown. Trichomes typically olive green, 6.2-12.3 µm wide at the swollen base, constricted at cross-walls, not tapered, or distinctly gradually tapered. Cells shorter than wide, sometimes isodiametric or slightly longer than wide, 1.6-8.2 µm long, barrel-shaped to almost spherical. Apical cells conical, conical rounded or rounded. Heterocytes both intercalary and terminal. Hornogonia short, arthrospores released from the end of the filament by dissociation.	BF: 14 FS: 48, 49 S: 70
<i>Roholtiella fluvialis</i> Johansen & Gaysina	Filaments short to long, single or double false branched with thin, attached, colorless to reddish sheaths, with basal heterocyte. Trichomes blue-green, olive-green to orange, 7.9-9.8 µm wide, constricted at cross-walls, not tapered to clearly tapered. Cells shorter than wide up to longer than wide, 2.8-10.8 µm long, barrel-shaped. Apical cells rounded or conical. Heterocytes terminal hemispherical or intercalary rounded cylindrical, yellowish, 4.3-7.4 µm wide, 3.2-6.8 µm long. Arthrospores or short rows of arthrospores released from the ends of the filaments.	FS: 54
<i>Roholtiella</i> sp.	Filaments with thin, firm, colorless sheaths, with basal heterocyte. Trichomes bright blue-green, 4.3-12.2 µm wide, constricted at cross-walls, tapered towards ends, with slightly widened base. Cells shorter than wide, rarely longer than wide, 2.4-7.1 µm long, cylindrical, barrel-shaped or compressed spherical. Apical cells conical-rounded or conical. Heterocytes terminal, hemispherical or slightly conical, or intercalary, yellow or tan, 4.4-6.2 µm wide, 2.1-6.87 µm long.	BF: 3
<i>Cylindrospermum majus</i> Kützing ex Bornet & Flahault	Trichomes bright blue-green, 3.7-4.9 µm wide, flexuous, constricted at cross-walls, cylindrical. Cells isodiametric or slightly longer than wide, 3.8-5.8 µm long, cylindrical to slightly barrel-shaped. Heterocytes oval, slightly elongated, 7.9 µm long, 3.9-5.1 µm wide. Akinetes solitary, ellipsoid to oval or widely oval, 10.5-14.5 µm long, 5.0-8.0 µm wide, with granular to warty exospore.	BF: 2, 4 BL: 23, 26, 37 FS: 49, 53, 55, 56, 58, 60, 62
<i>Cylindrospermum</i> sp.	Trichomes bright blue-green, 3.1-3.7 µm wide, flexuous, constricted at cross-walls, cylindrical. Cells almost isodiametric, 2.5-5.7 µm long, cylindrical. Heterocytes oval, sometimes elongated, 4.9-9.5 µm long, 3.4-4.3 µm wide. Akinetes solitary, ellipsoid to oval or widely oval, 13.6-15.6 µm long, 5.0-6.1 µm wide, with granular to warty exospore.	FS: 59

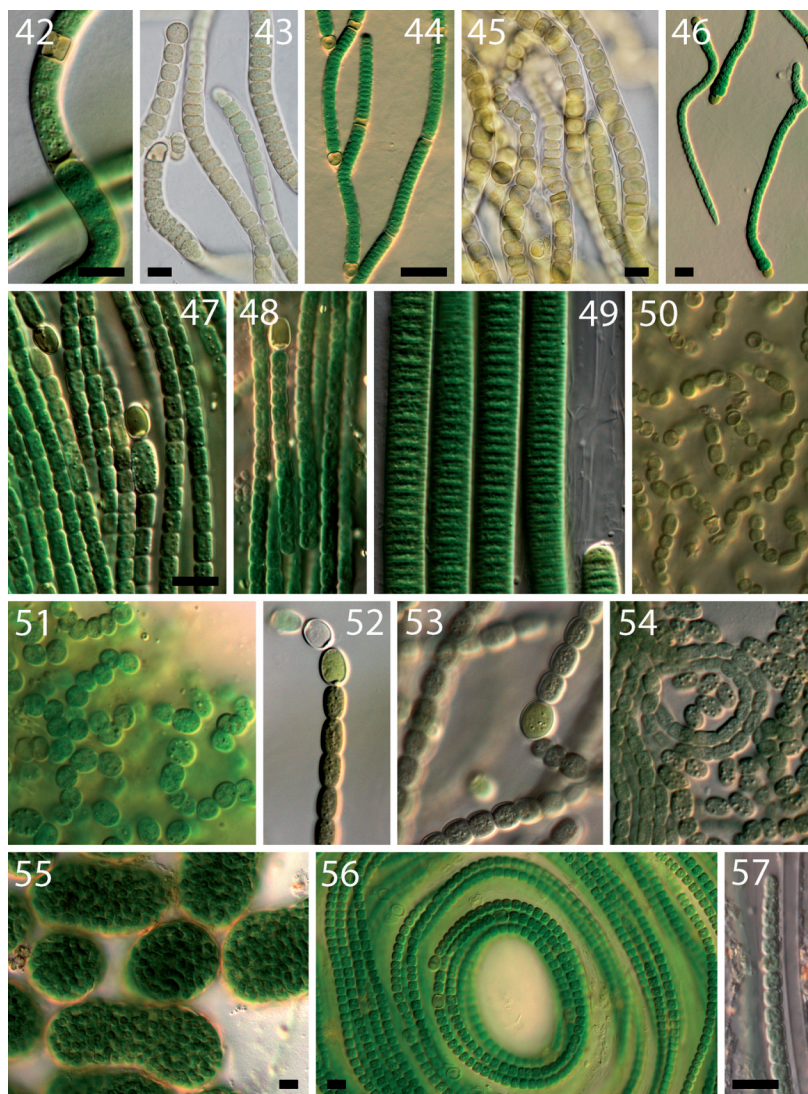
<i>Species</i>	<i>Morphological features</i>	<i>Sample number</i>
<i>Desmonostoc</i> cf. <i>muscorum</i> (Agardh ex Bornet & Flahault) Hrouzek & Ventura	Young colonies almost hemispherical, later forming mucilaginous mats, blue-green, later yellow-brown to olive-green, with densely entangled filaments. Trichomes 2.7-5.3 µm wide. Cells isodiametric or slightly longer or shorter than wide, 2.4-5.4 µm long, shortly barrel-shaped to cylindrical. Heterocytes spherical or barrel-shaped, 4.0-5.7 µm in diameter. Akinetes oval, 5.1-7.8 µm long, 3.1-5 µm wide.	BF: 7 BL: 27 S: 69, 70, 74
<i>Nostoc</i> cf. <i>calicicola</i> Brebisson ex Bornet & Flahault	Colonies irregular, flat, gelatinous, olive-green with filaments loosely entangled. Trichomes pale blue-green, 2.4-3.0 µm wide. Cells 2.5-3.1 µm long, barrel-shaped or almost spherical. Heterocytes spherical, 2.9-3.6 µm in diameter. Akinetes elongated or almost spherical, 4.3-5.2 µm long, 2.7-3.4 µm wide.	BF: 4, 16 FS: 42, 48, 57, 58 S: 71
<i>Nostoc</i> cf. <i>commune</i> Vaucher ex Bornet & Flahault	Colonies macroscopic, gelatinous, initially spherical, later irregularly flattened, crispy or wavy, olive-green or dark brown. Filaments flexuous, densely entangled. Trichomes pale olive-green, 3.2-4.6 µm wide. Cells slightly shorter or longer than wide, 2.2-4.4 µm long shortly barrel-shaped or almost spherical. Heterocytes spherical, both terminal and intercalary, 4.3-5.2 µm in diameter. Akinetes slightly larger than vegetative cells, 3.7-6.4 µm long, 3.3-4.8 µm wide.	S: 69, 70, 72, 79, 83, 85
<i>Nostoc</i> cf. <i>ellipsosporum</i> Rabenhorst	Colony brown, filaments flexuous. Trichomes olive-green, 4.3-5.0 µm. Cells 6.3-8.8 µm long, cylindrical. Heterocytes almost spherical or elongated, 5.1-7.7 µm long, 4.8-5.6 µm wide. Akinetes not observed.	BF: 3
<i>Nostoc</i> cf. <i>microscopicum</i> Carmichael ex Bornet & Flahault	Filaments flexuous, freely entangled. Trichomes blue-green or olive-green, 5.5-6.4 µm wide. Cells 3.6-6.8 µm long, barrel-shaped or almost spherical. Heterocytes spherical or elongate, 5.4-8.3 µm long, 4.5-5.4 µm wide. Akinetes not observed.	BF: 4, 5 BL: 26, 30 FS: 60
<i>Nostoc</i> cf. <i>punctiforme</i> Kützing (Hariot)	Colonies small, spherical, dark blue-green or blackish, later confluent into a blackish gelatinous mass. Filaments very densely entangled, coiled, in young stages agglomerated together. Trichomes blue-green, 2.9-4.8 µm wide. Cells shortly barrel-shaped, irregularly spherical to ellipsoidal. Heterocytes spherical or slightly elongate, 4.2-5.2 µm long, 3.9-4.2 µm wide. Akinetes spherical or slightly elongated, 4.8-6.8 µm long, 3.5-5.6 µm wide.	BF: 2, 3, 4-6, 9, 10, 12, 14, 15 BL: 23, 26, 28-30, 35, 38 FS: 43, 49, 53-55, 59, 60, 62 S: 71, 74, 83, 85
<i>Trichormus variabilis</i> (Kützing ex Bornet & Flahault) Komárek & Anagnostidis	Filaments coiled. Trichomes 5-5.8 µm wide, constricted at cross-walls, cylindrical, not attenuated or slightly narrowed at the ends. Cells almost isodiametric, 4.1-7.3 µm long, barrel-shaped or subspherical. Apical cells conical-rounded. Heterocytes intercalary, solitary, spherical or slightly elongated oval, 7.6-9.1 µm long, 5.7-7.5 µm wide. Akinetes not observed.	BF: 4, 14, 16, 17 BL: 23, 26, 31 FS: 53-57, 59, 62
<i>Trichormus</i> sp.	Trichomes 3.1-3.6 µm wide, cylindrical, constricted at cross-walls, slightly narrowed at the ends. Cells almost isodiametric, 2.3-4.1 µm long, barrel-shaped or subspherical. Apical cells conical-rounded. Heterocytes and akinetes not observed.	BF: 13



Figs 2-22. **Terrestrial cyanobacteria of the South Ural region:** 2. *Pseudanabaena papillaterminata* (Kiselev) Kukk, 3. *Leptolyngbya foveolarum* (Rabenhorst ex Gomont) Anagnostidis & Komárek, 4. *Leptolyngbya* cf. *fragilis* (Gomont) Anagnostidis & Komárek, 5. *Leptolyngbya* cf. *hansgirgiana* Komárek in Anagnostidis, 6. *Leptolyngbya* cf. *subtilissima* (Kützinger ex Hansgirg) Komárek in Anagnostidis, 7. *Leptolyngbya* cf. *tenuis* (Gomont) Anagnostidis & Komárek, 8. *Leptolyngbya* cf. *nostocorum* (Bornet ex Gomont) Anagnostidis & Komárek, 9. *Leptolyngbya* cf. *notata* (Schmidle) Anagnostidis et Komárek, 10. *Leptolyngbya voronichiniana* Anagnostidis & Komárek, 11. *Oculatella* sp. 1, 12. *Oculatella* sp. 2, 13. *Oculatella* sp. 3, 14. cf. *Trichocoleus hospitus* (Hansgirg ex Gomont) Anagnostidis, 15. *Myxosarcina* cf. *tatica* (Starmach) Komárek & Anagnostidis, 16. *Aphanothece stagnina* (Spreng.) A. Braun, 17. *Chroococcus varius* A. Braun in Rabenhorst, 18. *Chlorogloea* cf. *purpurea* Geitler, 19. *Cyanothece aeruginosa* (Nägeli) Komárek, 20. *Borzia trilocularis* Cohn ex Gomont, 21. *Kamptonema animale* (C. Agardh ex Gomont) Strunecký, Komárek & Šmarda, 22. *Kamptonema laetevirens* (Crouan & Crouan ex Gomont) Strunecký, Komárek & Šmarda. Scale bar = 10 µm, applies to all figures.



Figs 23-41. **Terrestrial cyanobacteria of the South Ural region:** 23. *Microcoleus autumnalis* (Gomont) Strunecký, Komárek & Johansen, 24. *Microcoleus vaginatus* (Vaucher) Gomont ex Gomont, 25. *Microcoleus* sp. 1, 26. *Microcoleus* sp. 2, 27. *Microcoleus* sp. 3, 28. *Oxynema* cf. *acuminatum* (Gomont) Chatchawan, Komárek, Strunecký, Šmarda & Peerapornpisal, 29. *Pseudophormidium hollerbachianum* (Elenkin) Anagnostidis, 30. *Phormidium aerugineo-caeruleum* (Gomont) Anagnostidis & Komárek, 31. *Phormidium ambiguum* Gomont ex Gomont, 32. *Phormidium breve* (Kützing ex Gomont) Anagnostidis & Komárek, 33. *Phormidium corium* Gomont, 34. *Phormidium dimorphum* Lemmermann, 35. *Phormidium* cf. *jadinianum* Gomont, 36. *Phormidium* cf. *retzii* (Agardh) Gomont ex Gomont, 37. *Phormidium tergestinum* (Kützing) Anagnostidis & Komárek, 38. *Phormidium uncinatum* (Agardh) Gomont, 39. *Phormidium* sp. 1, 40. *Phormidium* sp. 2, 41. *Hormoscilla pringsheimii* Anagnostidis & Komárek. Scale bars = 10 µm, for figures 23-40 the bar is placed in figure 40.



Figs 42-57. **Terrestrial cyanobacteria of the South Ural region:** 42. *Scytonema* sp., 43. *Roholtiella bashkiriorum* Gaysina & Bohunická, 44. *Roholtiella edaphica* Bohunická & Lukešová, 45. *Roholtiella fluvialis* Johansen & Gaysina, 46. *Roholtiella* sp., 47. *Cylindrospermum majus* Kützing ex Bornet & Flahault, 48. *Cylindrospermum* sp., 49. *Lyngbya martensiana* Meneghini ex Gomont, 50. *Nostoc* cf. *calcicola* Brébisson ex Bornet & Flahault, 51. *Nostoc* cf. *commune* Vaucher ex Bornet & Flahault, 52. *Nostoc* cf. *ellipsosporum* Rabenhorst, 53. *Nostoc* cf. *microscopicum* Carmichael ex Bornet & Flahault, 54. *Desmonostoc* cf. *muscorum* C.Agardh, 55. *Nostoc* cf. *punctiforme* Kützing (Hariot), 56. *Trichormus variabilis* (Kützing ex Bornet & Flahault) Komárek & Anagnostidis, 57. *Trichormus* sp. Scale bars = 10 µm, for figures 47-54 the bar is placed in figure 47.

Many species were found only in the boreal-forest zone: *Aphanothece stagnina* (Fig. 16), *Hormoscilla pringsheimii* (Fig. 41), *Leptolyngbya* cf. *hansgirgiana* (Fig. 5), *Leptolyngbya* cf. *nostocorum* (Fig. 8), *Kamptomena animale* (Fig. 21), *Kamptomena laetevirens* (Fig. 22), *Microcoleus* sp. 1 (Fig. 25), *Microcoleus* sp. 3 (Fig. 27), *Oxynema* cf. *acuminatum* (Fig. 28), *Phormidium aerugineo-caeruleum* (Fig. 30), *Phormidium* cf. *retzii* (Fig. 36), *Phormidium tergestinum* (Fig. 37), *Phormidium uncinatum* (Fig. 38), *Phormidium* sp. 1 (Fig. 39), *Nostoc* cf. *ellipsosporum* (Fig. 52), *Scytonema* sp. (Fig. 42), *Trichormus* sp. (Fig. 57) (Tables 2, 3). *Lyngbya martensiana* was detected in all zones, excluding the broad-leaved forest zone; it was most abundant in the boreal forest zone (Fig. 49) (Tables 2, 3).

The broad-leaved forest was characterized by the wide distribution of cf. *Trichocoleus hospitus* (Tables 2, 3). *Myxosarcina* cf. *tatrica* (Fig. 15) and *Chroococcus varius* (Fig. 17) were also detected only in this type of ecosystem.

Trichormus variabilis (Fig. 56), *Cylindrospermum majus* (Fig. 47), *Microcoleus autumnalis* (Fig. 23), and *Nostoc* cf. *microscopicum* (Fig. 53) were widely distributed in forest and forest-steppe zones.

Phormidium ambiguum (Fig. 31), was typical for forest-steppe and steppe zones. In the forest-steppe zone, some rare species, like *Borzia trilocularis* (Fig. 20), and *Pseudanabaena papillaterminata* (Fig. 2), were detected. *Cylindrospermum* sp. was also found in forest-steppe (Fig. 48) (Tables 1, 2, 3).

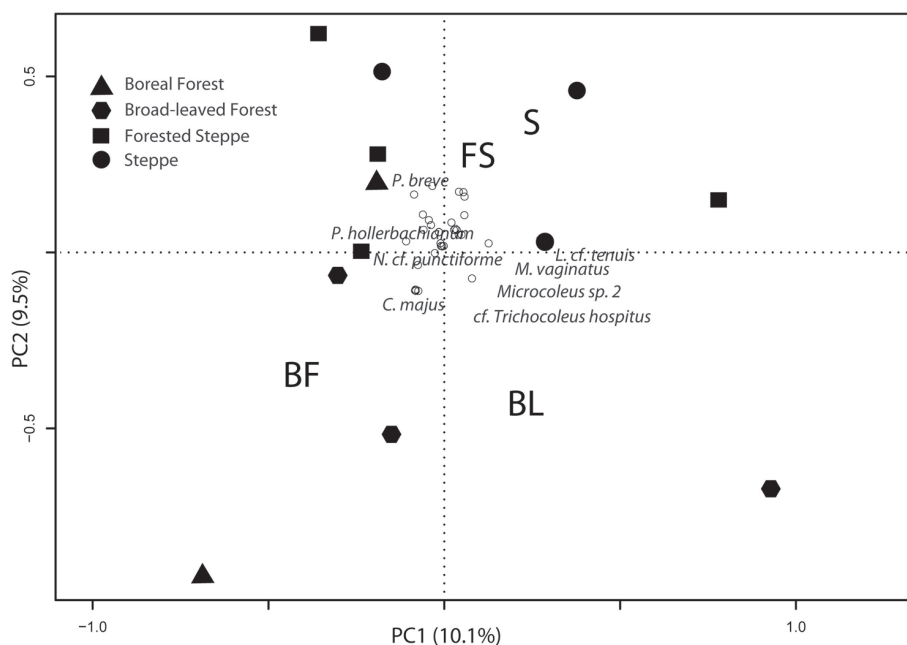


Fig. 58. Principal Component Analysis using Hellinger transformed species data for the combined data from the 12 sites. Community codes (BF, BL, FS, S) are placed in the centroid position of their respective data clouds. Hollow circles represent species, the outer taxa only being named. PC axis 1 roughly corresponds to an aridity gradient (high humidity to left, low humidity to the right), while PC axis 2 roughly corresponds to an organic matter/leaf litter gradient (high organic matter at the bottom, mineral soil at the top).

Pseudophormidium hollerbachianum and *Nostoc* cf. *commune* (Fig. 51) were most abundant in steppe. *Leptolyngbya* cf. *notata* was found only in steppe (Fig. 9). *Cyanothece aeruginosa* was also found in steppe in a sample collected from a forb-grass steppe near Sibay town (Fig. 19, Tables 2, 3). *Phormidium* cf. *jadinianum* was detected in the steppe and boreal-forest zones (Fig. 35) (Tables 2, 3).

The principal components analysis (PCA) of the 12 sites suggested that the boreal forest and broad-leaved forest communities were floristically separate, while significant overlap occurred between the forest-steppe and steppe communities (Fig. 58). The centroids for the boreal forest and broad-leaved forest were well away from each other and the forest-steppe and steppe regions. One boreal forest site (site 2) was close to the forest-steppe swarm of sites, while the other boreal forest site (site 1) was very distant from all other sites. The broad-leaved forest has considerably more leaf litter cover than the other three zones, and so it is not surprising to see that this zone is floristically separate. Forest-steppe and steppe zones are more arid and have higher irradiance due to less leaf litter cover. The first two axes of the PCA together explain almost 20% of the total variation in the community composition. Correlation between PCA scores and factors was not significant ($r^2 = 0.376$, $p = 0.186$).

DISCUSSION

In this study of terrestrial cyanobacteria of the South Ural region, in which 56 taxa of cyanobacteria were identified and documented, several unusual taxa were encountered. For example cf. *Trichocoleus hospitus* is very interesting. It is characterized by thin trichomes (0.6-0.7 μm wide), with cells 0.7-1 μm long, solitary or densely aggregated in sheaths 2.5-3.9 μm wide. Apical cells are round or thickened. It prefers to grow on the sheaths of other cyanobacteria or in the mucilage of green algae. The assignment of our finding to the genus *Trichocoleus* could not be confirmed with certainty, because typical cyanobacteria of this genus lack a calyptra or the thickened apical cell observed in the investigated specimen (Fig. 14). Another unusual cyanobacterium found in our sampling area is *Chlorogloea* cf. *purpurea* (Fig. 18). This taxon is similar to the description of *Chlorogloea purpurea* (mucilaginous irregular colonies with pink cells), but it possess smaller cells (0.8-1.5 μm in diameter compared with 1.5-2.5 in *Chlorogloea purpurea*). Additionally, *Chlorogloea purpurea* is a freshwater species, while our population is from a terrestrial habitat. *Myxosarcina* cf. *tatrica* was morphologically similar to the description published by Komárek & Anagnostidis (1999), but *M. tatrica* was originally described from a moist rock in Poland. *Phormidium* cf. *jadinianum* has trichomes about 6 μm wide, constrictions at cross-walls, with acute end cells. It is an unclear, incompletely described species, which was originally described from India (Komárek & Anagnostidis, 2005). *Oxynema* cf. *acuminatum* is also possibly another species, new to science. The morphological features of this species are similar to descriptions: trichomes 3.9-4.3 μm wide, attenuated motile with a relatively rapid oscillation, acute-conical long end cell (Komárek & Anagnostidis, 2005). But it differs by short cells and very different ecology. *Oxynema acuminatum* inhabits thermal springs high in salinity or sulfur, whereas this taxon is terrestrial. Several species of the genus *Microcoleus* were recorded (Table 2, Figs 23-27). *Microcoleus* sp. 1 is a cyanobacterium putatively new to science. It has long trichomes, 6.7-

7.1 μm wide, is unconstricted at the cross-walls, is aggregated within sheaths, and is reddish in color. Cells are almost isodiametric. Apical cells are conical, without calyptra. All of the above mentioned unclear species are putative new taxa that should be studied in detail, including molecular characterization in future studies.

Three species of *Oculatella* (Figs 11-13) were identified and are potentially new to science. Especially interesting is *Oculatella* sp. 2 with flexuous filaments and sheaths, 2.2-2.6 μm wide, with constrictions at the cross-walls, with more or less isodiametric cells, and with the apical cell widely rounded with slightly sloped crystal-like or orange spot in the apex of the cell (Fig. 12). Despite morphological similarity with some previously described taxa (Zammit *et al.*, 2012; Osorio-Santos *et al.*, 2014), these populations are likely to be separate species based on ecology. *Oculatella* has a wide distribution in the studied area. Possibly, it was earlier incorrectly identified as *Leptolyngbya foveolarum*. We found many other populations of *Leptolyngbya*, which fit *Leptolyngbya foveolarum* in the keys (blue-green, curved, flexuous, constricted at the cross-walls of the trichomes). Possibly, they represent several cryptic species of this genus. A similar situation occurs in the case of *Leptolyngbya voronichiniana* with colorless thin sheaths. Another group problematic for identification were *Phormidium* and *Phormidium*-like taxa, especially morphotypes with acute-conical apical cells, for example *Oxynema* cf. *acuminatum* and *Phormidium* cf. *jadinianum*. For correct identification of these taxa, observation of all stages of the life cycle together with understanding of their ecology is crucial.

Interesting findings also include *Kamptonema animale* and *K. laetevirens*. *Kamptonema* was recently separated from *Phormidium* (Strunecký *et al.*, 2014) and this is the first record of these species in the territory of South Ural. Observation of the aquatic *Cyanothece aeruginosa* in a steppe region is unusual. This taxon is widely distributed in aquatic habitats around the world, but is not common in terrestrial ecosystems (Komárek & Anagnostidis, 1999). It was reported as *Synechococcus aeruginosus* Nägeli from shrub-steppe soils in the Great Basin and Columbia Basin of North America (Johansen, 1993). Our finding is a significant addition to the knowledge of the ecology of *Cyanothece aeruginosa*.

During our investigations, several strains were identified as *Scytonema* and *Tolypothrix*. These strains were described in detail by a polyphasic approach in a separate study (Bohunická *et al.*, 2015). It was found that they belong to the new genus *Roholtiella*, which contained 4 new species, 3 of which were found in the territory of South Ural: *Roholtiella bashkirorum*, *R. edaphica*, and *R. fluviatilis* (Figs 43-46). An interesting observation was the additional discovery of another *Roholtiella* type within our collections, characterized by bright green filaments (Fig. 46). It is similar to *Roholtiella mojaviensis*, but it was isolated from a very different habitat (Bohunická *et al.*, 2015); we provisionally name it here as *Roholtiella* sp.

Many species of cyanobacteria were previously mentioned in lists of cyanobacteria compiled during floristic studies in the territory of the South Ural. For example, *Phormidium ambiguum*, *Phormidium breve*, *Phormidium dimorphum*, *Phormidium retzii*, *Phormidium tergestinum*, *Phormidium uncinatum*, *Leptolyngbya foveolarum*, *Leptolyngbya voronichiniana*, *Nostoc commune*, *Nostoc microscopicum*, *Nostoc punctiforme*, *Microcoleus vaginatus*, *Pseudophormidium hollerbachianum* and several other species were recorded in flora of steppe and forest-steppe zones of Bashkiria (Kuz'yakhmetov, 1992; Khaibullina *et al.*, 2005; Bakieva *et al.* 2012). But unfortunately these publications lack information about morphology of taxa, and the taxonomy of many genera has since been revised. This circumstance prevents comparison of previous results with our data. *Microcoleus vaginatus*, *Leptolyngbya*

foveolarum, and *Phormidium breve* characterized by wide distribution in this study are congruent with previous studies of other regions in Russia (Aleksakhina & Shtina, 1984) and territories of other countries (Kostikov *et al.*, 2001; Komárek & Anagnostidis, 2005; Škaloud, 2009; Neustupa & Škaloud, 2010; Davydov, 2013; Strunecký *et al.*, 2013). *Pseudophormidium hollerbachianum*, frequently found in this study, is a widely distributed taxon in soils, and was previously found in Russia, Austria, Czech Republic, Denmark, Greece, Poland, and Sweden (Komárek & Anagnostidis, 2005). *Trichormus variabilis*, *Cylindrospermum majus*, *Microcoleus autumnalis*, and *Nostoc microscopicum* also have wide distribution, but are possibly sensitive to deficiency of water and high solar insolation.

The combined use of several methods during floristic studies allows identification of more taxa. In our study, cyanobacteria were isolated into strains as well as directly observed on cover slips. It is difficult to isolate some cyanobacteria into pure culture, and the spectrum of species obtained might be limited by this method if used in isolation. For example, cf. *Trichocoleus hospitus* lives in the mucilage of other organisms, and it is impossible to divide it from those other species. In this case, the cover slip method was useful, because it allowed us to observe the cyanobacterium and to make preliminary identification of the taxon. We also found most of the species of *Leptolyngbya* only on cover slip surfaces, for example, *Leptolyngbya* cf. *fragilis* (Fig. 4), *Leptolyngbya* cf. *subtilissima* (Fig. 6), and *Leptolyngbya* cf. *tenuis* (Fig. 7).

The differences in the taxonomic composition found in each zone can be attributed to the influence of zonal factors, which have an effect on climate, soil type, and higher plant communities. In this connection, the most important factor was humidity of the substrate. The heterogeneity of the substrate had also considerable impact on the occurrence of the cyanobacterial taxa. In our study, the samples from humid and/or heterogenic conditions were characterized by the highest cyanobacterial diversity (Table 1). The highest number of cyanobacteria, (14 species), was found in sample 59 (Bu12) with visible cyanobacteria and algae growth on the road in the floodplain of the forest-steppe zone. Thirteen species were detected in two samples: sample 17 (P14) from the boreal-forest zone, taken from the riverside of Saldubash river, and sample 53 (Bu6) from forest-steppe zone from path from the riverside of the Ik River. Twelve species were identified in sample 14 (P11) from a ravine in the boreal-forest zone (Table S1). The importance of humidity as one of the most important ecological factors affecting the soil cyanobacteria was discussed by Gollerbach & Shtina, (1969). According to their data, the optimal humidity for typical soil algae (including cyanobacteria) is 60-80 % of the full moisture capacity. However, in some species of nitrogen-fixing cyanobacteria, maximal growth was observed at 80-100% soil humidity.

Species detected only in the boreal-forest zone, such as *Aphanothece stagnina*, *Leptolyngbya* cf. *hansgirgiana* and *Kamptomonas animale*, in general are moisture-loving cyanobacteria (Komárek & Anagnostidis, 1999, 2005). Cyanobacteria distributed in forest and forest-steppe zones such as *Trichormus variabilis* and *Cylindrospermum majus*, were previously reported as more drought-tolerant (Komárek, 2013). *Pseudophormidium hollerbachianum* and *Nostoc* cf. *commune*, abundant in steppes, belong to the subaerophytic species, resistant to water deficiency (Komárek & Anagnostidis, 2005; Komárek, 2013). *Microcoleus vaginatus* was dominant in dry soils of steppes, which is in agreement with previous observations that filamentous cyanobacteria from the order Oscillatoriales are the most resistant to drought. *Nostoc commune*, *Scytonema ocellatum* and *Microcoleus vaginatus* form so called “*Nostoc-Scytonema* coenoses of steppes and semi-deserts” (Gollerbach &

Shtina, 1969). Species of *Microcoleus* were also frequent in the boreal-forest zone, but the population density in steppes was much higher.

The PCA reveals, that steppe and forest-steppe zones were characterized by very similar biodiversity of cyanobacteria (Fig. 58). Species composition of the broad-leaved forest zone is very different. The boreal forest has only two sites, one that is very different from all sites, and one that shares species with the forest-steppe community. The surface soils of these biomes vary along two gradients, soil organic matter/surface leaf litter and humidity, with the most organic and humid soils being boreal forest and the most mineral and dry soils being within steppe.

Influence of microhabitat conditions including heterogeneity of the substrate on terrestrial cyanobacterial diversity has been little studied. E.A. Shtina (1976) mentioned that visible growth of algae and cyanobacteria was detected mostly on sites with irregularities in microtopography. The strong influence of ecotope conditions on soil algae and cyanobacteria has been discussed in several publications (Kuz'yakhmetov, 1981, 1992). Possibly, in heterogenic conditions, the cyanobacteria thrive from less competitive conditions with higher plants.

Higher plant communities also may have an impact on the cyanobacterial flora. We did not detect any cyanobacteria in five of the 85 samples (1, 24, 25, 39, 45). These samples were collected in different types of forests and plantings (Table 1). Rarity of cyanobacteria in forest soils was also reported by Gollerbach & Shtina, 1969; Hoffmann *et al.*, 2007 and Khaybullina *et al.*, 2010.

Our results confirm the known assumption that cyanobacteria play an important role in primary colonization of various substrates. In this connection, most prominent are filamentous species. For example, in sample 78 from an abandoned marble quarry in the steppe zone, *Leptolyngbya voronichiniana*, *Leptolyngbya* cf. *tenuis*, *Microcoleus vaginatus*, *Lyngbya martensiana*, *Phormidium dimorphum* and cf. *Trichocoleus hospitus* were all detected (Tables 1, 3).

Our study reveals that the territory of the South Ural hosts a wide variety of soil cyanobacteria including several taxa potentially new to science. For future molecular-genetic research, the frequently encountered representatives of the genus *Microcoleus* (Figs 25-27) and *Phormidium* (Figs 39-40) could be especially interesting.

CONCLUSIONS

Floristic studies should be the first step in the investigation of biodiversity of cyanobacteria. This type of research allows us to make preliminary assessment of dominant taxa, identify potentially new species and even new genera, and creates a strategy for further molecular-genetic research. To our knowledge, for *Chlorogloea* cf. *purpurea* and several species of *Oculatella*, this is the first record of their presence in the territory of the South Ural region. Strains obtained in this study will provide a valuable starting point for future molecular studies.

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