POLISH POLAR RESEARCH
vol. 33, no. 4, pp. 347–368, 2012 doi: 10.2478/v10183-012-0024-1

Cyanobacterial diversity of Petuniabukta, Billefjorden, central Spitsbergen

Jiří KOMÁREK[1,2], Lubomír KOVÁČIK[3], Josef ELSTER[1,2] and Ondřej KOMÁREK[4]

[1]*Faculty of Science, University of South Bohemia,*
Branišovská 31, CZ-37005 České Budějovice, Czech Republic
<komarek@butbn.cas.cz>

[2] *Institute of Botany, Academy of Sciences of the Czech Republic,*
Dukelská 135, CZ-379 82 Třeboň, Czech Republic

[3] *Comenius University in Bratislava, Faculty of Natural Sciences, Department of Botany,*
Révová 39, SK-811 02 Bratislava, Slovakia

[4] *Institute of Microbiology, Academy of Sciences of the Czech Republic,*
Opatovický Mlýn, CZ-379 81 Třeboň, Czech Republic

Abstract: The diversity of cyanobacterial assemblages from various microhabitats in the Arctic area of Petuniabukta, Billefjorden, central Svalbard, was described. The present article contains the introductory common review of the cyanobacterial diversity and ecological data concerning main habitats, while the characteristics of individual taxonomic groups will be presented in following specific studies. Eight distinct main habitats were recognized, which differed in their species composition and especially the dominant species. More than 80 morphospecies were registered during our investigation, but only about 1/3 of them could be assigned to known and described taxa. The others require additional analyses based on modern taxonomic methods (the polyphasic approach). The composition of cyanobacterial microflora was comparable with assemblages in coastal Antarctica. The diversity of unicellular and colonial morphotypes (36 taxa) was higher than other groups. The number of filamentous species without heterocytes and akinetes, with 30 species, and heterocytous types, with only 20 species, were similar in both of these ecosystems. These numbers will be surely changed in the future, but the overall proportion of different groups will likely stay the same. In contrast to the limited species diversity, simple filamentous aheterocytous species were dominant and formed massive populations. Few heterocytous taxa, mostly grouped within the genus *Nostoc* (*N. commune*–complex), were dominant in tundra soils.

Key words: Arctic, Svalbard, Cyanobacteria, diversity, ecology.

Introduction

Freshwater and terrestrial algal microflora are important particularly for extreme polar ecosystems (Walton 1987; Vincent 1988; Friedmann 1993; Priscu 1998; Elster 2002; Elster and Benson 2004). Cyanobacteria are prominent phototrophic components of biocenoses in almost all polar habitats. They are intense producers of organic biomass during the polar summer season. In the Arctic tundra, with developed communities of higher vegetation, the importance of cyanobacteria is not so striking as in Antarctic habitats, but they play a significant role particularly due to the rapid asexual reproduction of various species and their succession and decomposition during each vegetation period. Also important is the ability for the fixation of atmospheric nitrogen, of which common morphotypes from the *Nostoc commune*-complex and several other heterocytous species play a considerable role.

The specificity of cyanobacterial communities in various regions and habitats was already proven, in spite of the hypothetical easy transfer of diaspores (Whelden 1947; Garcia Pichel *et al.* 1998; Richert *et al.* 2006; Rejmánková *et al.* 2004; Komárek 1999; Komárek *et al.* 2008). Widely distributed morphospecies exist, but they are closely connected with specialized habitats. Specialized cyanobacterial communities develop in circumpolar ecosystems, in which numerous morpho- and ecospecies play a substantial role. These are sometimes similar to known types from temperate zones, but their ecology is different and they usually slightly differ morphologically. Cyanobacteria are morphologically simple and the relations between various populations can be solved only by help of molecular methods. Therefore, careful evaluation of morphological and ecological characters of different populations is an inevitable part of this work.

There are several urgent objectives in the study of cyanobacteria from polar regions:

(i) Description and revision of all morphotypes and genotypes, occurring in polar areas.

(ii) The study of ecological specificities of different genotypes and morphospecies. The various cyanobacterial taxa from polar habitats are specialized to distinct habitats (streams, seepages, wet rocks, flooded tundra, *etc.*) and the autecological demands of their genotypes must be studied.

(iii) It is necessary to investigate the geographic distribution of dominant and characteristic species from polar biocenoses, the identification of endemic and ecologically distinct species and species with wider (up to almost cosmopolitan) distributions. This problem is connected with the study of the autecology of different species.

(iv) The relations between ecologically and morphologically similar populations from Antarctic and Arctic habitats should be studied in detail. Similar habitats occur in both polar regions (which are sometimes similar also to high mountains), but relations between similar populations from all these habitats are not known up to now.

There are numerous publications concerning the diversity of cyanobacterial microflora from the high Arctic (*e.g.*, Elster *et al*. 1994, 1997, 1999; Vincent *et al*. 2000; Villeneuve *et al*. 2001; Matula *et al.* 2007, *etc.*) and especially from Antarctica (see in Prescott 1979, and, *e.g.*, of Broady 1989, 2005; Ohtani 1986; Mataloni and Pose 2001; Mataloni and Tell 2002; Taton *et al.* 2006; Komárek *et* *al.* 2008; Callejas *et al.* 2011 and many others). Also, there are numerous published studies based on molecular methods, which presented the numbers of genotypes in the studied samples, but provided little knowledge about the ecological function of different genotypes (and species with distinct morphological markers) in different microhabitats. The literature from Arctic regions is particularly restricted up to now. Therefore, the study of cyanobacterial microflora is urgent for understanding circumpolar freshwater and terrestrial ecosystems. Taxonomic revisions are necessary especially in connection with modern revisions based on the molecular re-evaluation of cyanobaterial taxa. The ecological situation of different taxa, supported by phylogenetic criteria, is particularly urgent. This paper concerns the introductory, first review and basic description of the phenotypic diversity of cyanobacteria, dominant or characteristic in various habitats in the tundra region of Petuniabukta, Billefjorden, central Svalbard.

Description of the area

The investigation area is located in the central part of Spitsbergen, Svalbard. Petuniabukta is a northward oriented fjord, connected with the Billefjorden and Isfjord (78°40'–78°44.5'N, 16°26'–16°40'E). It is enveloped by mountains which reach hights from 265 up to 935 m a.s.l. and by slopes covered with typical Arctic tundra vegetation (Figs 1, 2)). In the area there are several habitats in which characteristic cyanobacterial communities develop.

The geology in the vicinity of Petuniabukta is very diverse. The Billefjorden Trough (including Petuniabukta) is one of several half-graben structures, which developed alongside large fault zones in Svalbard during the middle Carboniferous. The trough accumulated more than 1000 m of sediments in its central part. The succession starts with red-colored clastic rock and continues through several sections of evaporites (gypsum/anhydrite and limestone), sandstone and carbonate rocks (Dallmann *et al.* 1999).

The northern parts of Isfjorden, Billefjorden and Petuniabukta belongs to the climatically mildest (maritime high Arctic climate) part of the Svalbard archipelago. The mean temperature in Isfjord is -7.5°C. July is the warmest month (5 to 6°C in average). Detail analysis of climatic conditions at Petuniabukta was based on the evaluation of several meteorological data sets acquired from July 1, 2009 to June 29, 2010 (Láska *et al.* 2012 this issue). During the investigated period the mean air temperature was -3.6°C, a little bit cooler than for Isfjord (Longyearbyen area). The mean global shortwave radiation was 95.1 Wm^{-2} for the entire time period. The mean surface temperature of the tundra vegetation (-4.0°C) corresponded to the length of the permanent snow cover which existed for 8 months in the coastal zone of Petuniabukta. In contrast, the maximum surface temperature rose to 26.5°C during the short summer period (more in detail Láska *et al.* 2012 this issue).

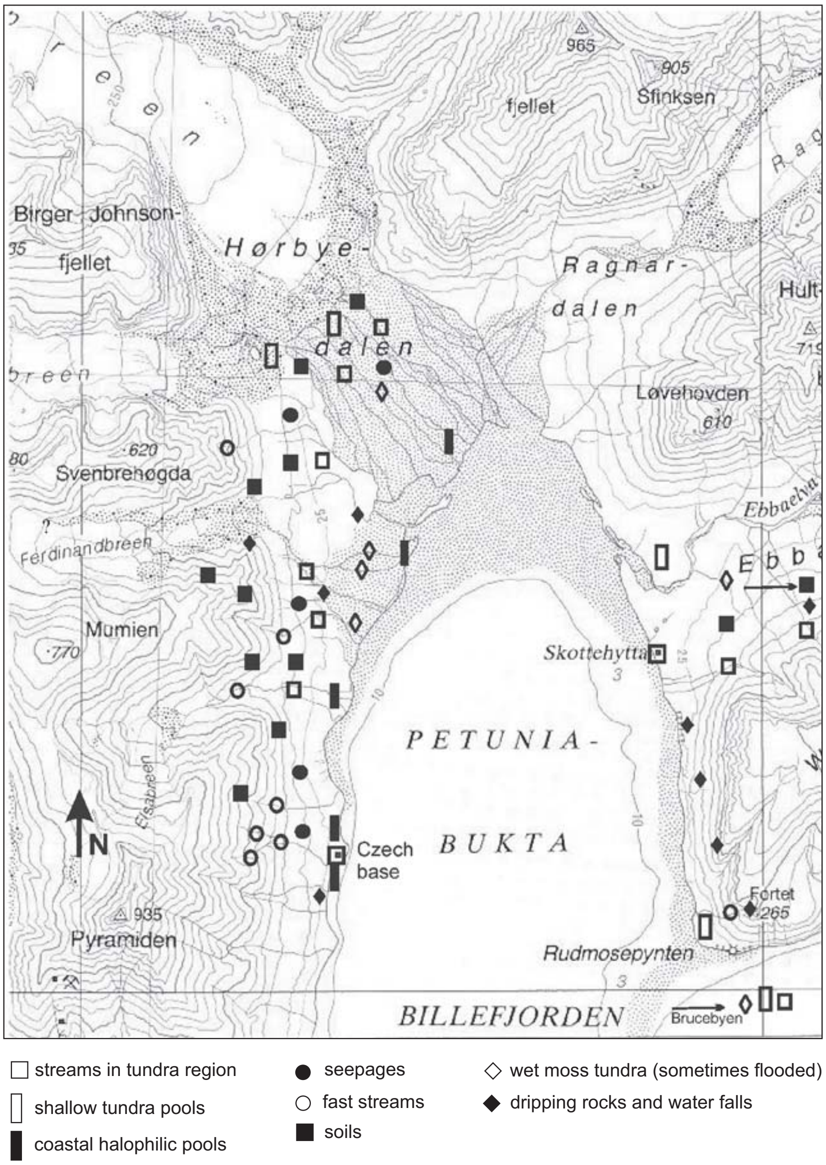

Fig. 1. Map of Petuniabukta with main habitats.

The physico-chemical parameters of water and soil correspond to the high diversity of geological types of substrata. In the upper parts of fast flowing streams, close to snow fields and glacial fronts, water temperatures are low, fluctuating between 2.2 to 4.6°C, with pH between 5.6 to 6.8 and conductivity of 34–166 μScm^{-1}. In lower parts of the streams, which flow through seepages covered with mosses and higher plants, water temperatures fluctuated between 4.6 to 10.7°C, with pH 6.8 to 7.38 and conductivity 166 to 606 μScm^{-1}. Water physico-chemical parameters in wet

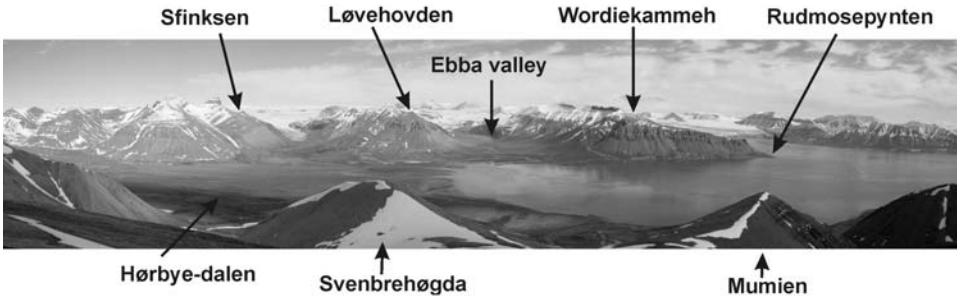

Fig. 2. Petuniabukta, the area of investigation. View from W to E. (All photos orig. Kováčik.)

and flooded moss tundra, shallow pools, seepages and wet, dripping rocks were studied in detail (see Elster *et al*. 2012 this issue). In these habitats, temperature fluctuated between 4.2 to 9.4°C, with pH 7.15 to 7.86 and conductivity 502 to 1215 µScm^{-1}. Soil climactic parameters were measured in detail by several automatic stations (Láska *et al.* 2012 this issue).

The physico-chemical parameters of soil were analyzed in the vicinity of all four automatic microclimatic stations. All microclimatic stations (AWS1, AWS2, AWS3, AWS4) (Láska *et al.* 2012 this issue), are located in the west coastal part of Petuniabukta and cover the whole soil diversity occurring in this part of Petuniabukta. Table 1 introduces the physico-chemical parameters of soil.

pH values are neutral to slightly alkaline in the western part of Petuniabukta in respect to limestone substrate in this area. Conductivity values show that, in sites covered by vascular plants, most of the mineral substances are fixed in the plant biomass. In contrast, more free mineral substances are in barren soils. These sites are rich in cyanobacteria communities. The soils of the second terrace, together with the summit of Mumien Peak, are richer in nitrogen and phosphorus content.

Table 1

Main chemical characters from soil extracts of four localities in the vicinity of Petuniabukta. The types AWS1 and AWS2 belong to Arctic brown soils, AWS3 to Arctic barren soils (according to Tedrow 1977, 1991).

	pH in dest. water	pH in KCl	Cond. [µScm^{-1}]	N-NH$_4$ [mgkg^{-1}]	N-NO$_3$ [mgkg^{-1}]	P-PO$_4$ [mgkg^{-1}]	Organic matter %	Dry matter %
AWS1 – first coastal terrace, covered by vascular plants and lichens	8.30	7.66	59.9	0.606	0.674	0.115	9.36	49.398
AWS2 – second coastal terrace, covered by vascular plants and lichens	8.27	7.75	61.1	1.206	3.243	0.122	8.89	64.664
AWS3 – close to front of Hørbyebreen glacier, microbial soil crust	8.51	8.49	214.0	0.723	0.495	0.080	3.03	98.508
AWS3 – top of first summit of Mumien Peak, microbial soil crust	8.71	8.70	171.1	1.346	1.216	0.078	3.75	77.781

The first and second terraces with vascular ground cover showed the highest content of soil organic matter and highest water content. This is a regular trend which follows vegetation development.

Coastal, halophilic shallow puddles, streams and seepages with the influence of sea water occur mainly in the north-west part of Petuniabukta (Hørbydalen). Similarly as for the lower part of stream and seepages, the water temperatures fluctuated between 4.6 to 10.7°C, with pH between 7.2 to 8.4 and conductivity from 941 to 1584 μScm^{-1}. From the above data, it follows that the vegetation period starts in June and ends in September, when the average temperature decreases below 0°C.

Methods

Natural populations were studied by optical microscopy, measured and documented by drawing and microphotography techniques. In this article are included only the basic identifications for common review. The analyses of different groups, genera and species with corresponding photodocumentation will be published in special studies. The studied sites are reviewed in Table 2. The soil characteristics are described in Table 1. Physico-chemical analyses of water and soil were performed by the analytical laboratory of the Institute of Botany, Academy of Science of the Czech Republic in Třeboň using standardised procedures, as defined by the Czech National Standards – ASTM (ISO 10390, ISO 10523, ČSN EN 27 888, ISO 11 465, ČSN EN ISO 11 732, ČSN EN ISO 13395 and ČSN EN ISO 15681-1).

Selected samples were preserved in 2% formaldehyde and deposited at the Institute of Botany of the Academy of Sciences of the Czech Republic in Třeboň. The species were identified according to modern taxonomic literature (particularly Komárek and Anagnostidis 1998, 2005). The species composition in various types of habitats was evaluated by Detrended Correspondence Analysis (DCA).

Types with mass development were cultured and transferred to agar plates. Cultivation was conducted in temperature boxes (5–8°C) using solidified BG11 medium (Rippka *et al.* 1979) used and illuminated by fluorescent tubes with intensity of 18–23 $\mu mol\ m^{-2}s^{-1}$ on the surface of Petri dishes at temperatures of 10–12°C. However, the cultivation was successful only in several cases (mainly in the *Phormidium autumnale*-complex); these cultures were used for further studies (Strunecký *et al.* 2012 this issue).

Results

Cyanobacterial vegetation

Up to now 85 morphospecies were recognized in the studied area (Tables 2–4). The majority of taxa were identified from coccoid, mostly colonial forms (36 taxa,

Table 2

List of coccoid cyanobacterial taxa (36) found in hydroterrestrial, freshwater habitats in the vicinity of Petuniabukta: a = fast glacial streams and waterfalls, b = slow tundra streams, c = wet moss tundra, d = tundra pools, e = seepages on slopes, f = tundra soils, g = wet and dripping rocks, h = coastal brackish puddles.

Names of taxa	Abbr.	a	b	c	d	e	f	g	h	Note
Anathece sp.	AntD			×	×					endogloeic
Aphanocapsa sp. 1	Apc1	×								
Aphanocapsa sp. 2	Apc2			×				×		
Aphanocapsa cf. *muscicola*	Apc3			×	×	×	(×)	×		
Aphanocapsa cf. *fonticola*	Apc4			××	×	×	×			
Aphanocapsa cf. *hyalina*	Apc5			××		×	××			
Aphanothece microscopica	Aptm		×	×××	(×)		×			
Asterocapsa sp.	Astc			×		(×)		××		
Chamaesiphon cylindricus	Chmc	×								epiphytic
Chamaesiphon rostafinskii	Chmr	×								epiphytic
Chamaesiphon (*Godlewskia*) sp.	ChmG	×	×							epilithic
Chlorogloea sp. 1	Chg1						×			
Chlorogloea sp. 2	Chg2				××			×		
Chlorogloea sp. 3	Chg3							××		
Chlorogloea sp. 4	Chg4	×	×					×		
Chlorogloeopsis sp.	Chgl							(×)		
Chroococcus sp. 1	Chr1		×			×				
Chroococcus sp. 2	Chr2				(×)					
Chroococcus cf. *helveticus*	Chrh			×	×	×	×	×		
Chroococcus cf. *prescottii*	Chrp		×	×	×	×	××			
Chroococcidiopsis sp.	Cccp				×××					in green mats
Clastidium cylindricum	Clas				×					
Cyanosarcina cf. *chroococcoides*	Cyas			(×)						
Cyanothece aeruginosa	Cyth			×			×	(×)		
Eucapsis minor	Eucm			×	××	(×)	×			
Geminocystis sp.	Gemi							×		
Gloeocapsa cf. *alpina*	Glov	×	×	(×)		×	(×)	××		
Gloeocapsa cf. *nigrescens*	Glon						×	×		
Gloeocapsa cf. *rupestris*	Gloy					×		×		
Gloeocapsa cf. *sanguinea*	Glor							×		
Gloeocapsa sp. 1	Gloc							×		
Gloeocapsa sp. 2	Glom							×		
Gloeothece cyanochroa	Gltc							×		
Gomphosphaeria aponina	Gomp		×	×	×					
Merismopedia sphagnicola	Mers			×	×	×	×			
Woronichinia tenera	Wort			×	×					

40%), which belong to 19 traditional genera. However, they are usually distributed over all habitats without forming the mass production of various populations and without dominance in different biocenoses. Oscillatorialean taxa (trichal species

Table 3

List of oscillatorialean cyanobacterial taxa (30) found in hydroterrestrial, freshwater habitats in the vicinity of Petuniabukta: a = fast glacial streams and waterfalls, b = slow tundra streams, c = wet moss tundra, d = tundra pools, e = seepages on slopes, f = tundra soils, g = wet and dripping rocks, h = coastal brackish puddles.

Names of taxa	Abbr.	a	b	c	d	e	f	g	h	Note
Ammatoidea sp.	Amma							×		marine influence
Geitlerinema sp.	Geit		×	×			×			
Heteroleibleinia sp.	Htlb		×		×	×				epiphytic (*Zygnema*)
Komvophoron sp.	Komv		×	×				(×)		
Leptolyngbya sp. 1	Lly1		×××	××	×					
Leptolyngbya sp. 2	Lly2		×××	××	×		×			
Leptolyngbya sp. 3	Lly3			××			×	×		
Leptolyngbya sp. 4	Lly4	×				(×)	×	×		
Leptolyngbya sp. 5	Lly5								×	halophilic
Leptolyngbya sp. 6	Lly6		×		×					endogloeic
Microcoleus sp.	Micc		×	×		×	×	×		
Oscillatoria sp. 1	Osc1							×		*Blennothrix* like
Oscillatoria sp. 2	Osc2		×		×					
Oscillatoria sp. 3	Osc3								××	
Phormidesmis sp.	Phds		×			×				
Phormidium cf. *autumnale* 1	Pha1	××	××			×				black mats
Phormidium cf. *autumnale* 2	Pha2		×	××		×				
Phormidium cf. *autumnale* 3	Pha3								×××	halophilic
Phormidium sp. 1	Phos			×		×	×			
Phormidium sp. 2	Phmr			×			×			*Wilmottia* like
Plectolyngbya sp.	Plec			×						
Porphyrosiphon sp.	Porp								××	
Pseudanabaena sp.	Psan	×			(×)	(×)			(×)	sp. div.?
Schizothrix facilis	Schf	××								
Schizothrix sp. 1	Sch1							××		blackish colonies
Schizothrix sp. 2	Sch2		×	×		×				colourless sheaths
Spirulina cf. *major*	Spmj								××	
Spirulina cf. *tenerrima*	Sptc								×	
Trichocoleus "*abiscoensis*"	Trab		×	×			×			
Tychonema sp.	Tycs				×	×				

without heterocytes and akinetes) comprise 29 species (33%), but contain several types which are distinctly dominant in several very specialized biotopes (*Leptolyngbya* sp. div. in tundra streams and wet moss tundra, one ecotype of *Phormidium autumnale* in coastal salinic pools, and *Schizothrix facilis* in rapid streams and waterfalls). Also, heterocytous types (20 species from 9 genera, 24%) have several dominant species, from which the most important are several ecotypes of *Nostoc* from the complex *N. commune*. This species (*sensu lato*) is the most common and most striking in the tundra biome in Petuniabukta.

Table 4

List of heterocytous cyanobacterial taxa (20) found in hydroterrestrial, freshwater habitats in the vicinity of Petuniabukta: a = fast glacial streams and waterfalls, b = slow tundra streams, c = wet moss tundra, d = tundra pools, e = seepages on slopes, f = tundra soils, g = wet and dripping rocks, h = coastal brackish puddles.

Names of taxa	Abbr.	a	b	c	d	e	f	g	h	Note
Anabaena cf. *jonssonii*	Anjo		(×)	×						
Anabaena sp. 1	Ansp			×	×	×				without akinetes
Calothrix sp. 1	Cal1		×	×			×	××		brown sheaths
Calothrix sp. 2	Cal2							×		yellow sheaths
Dichothrix sp.	Dich		×	×	×		×	××		
Hassallia sp.	Hass							×		
Microchaete cf. *tenera*	Mcht			××		×				
Nostoc cf. *commune* 1	Nos1		×	××	×	×				
Nostoc cf. *commune* 2	Nos2			×××		××				
Nostoc cf. *commune* 3	Nos3	×		××		×		×		
Nostoc sp. 1	Nos4			(×)			×××			lichenized
Nostoc sp. 2	Nos5						×			lichenized
Nostoc sp. 3	Nos6		(×)							± spher. colonies
Nostoc cf. *flagelliforme*	Nosf						×			
Rivularia borealis	Rivb	×	××	×		(×)				lower streams
Scytonema sp. 1	Scy1			××						
Scytonema sp. 2	Scy2		×				×	×		
Scytonema cf. *incrustans*	Scyi		×	×		×	×			
Scytonema "*hollerbachii*"	Scyh			(×)	×	×		×		
Tolypothrix tenuis	Tolt		×	××			×			

Several species must be studied in detail in the future. We present notes on selected genera (Tables 2–4):

Ammatoidea sp. – one unknown species occurs on wet rocks on the sea shore, forming black mats. It represents evidently a new species, not described in previous literature.

Aphanocapsa sp. div. – several morpho- and ecotypes are common, but occur in small quantity in particular habitats. The morphology is very simple and identity with phenotypically related morphotypes should be therefore confirmed in future by molecular methods.

Aphanothece microscopica – both morphologically and ecologically similar to the type from peaty localities in the temperate zone, but confirmation by molecular methods is required.

Anabaena jonssonii and *Anabaena* sp. – typical species from moss tundra. In *Anabaena* sp. no akinetes were found; its identification is, therefore, still open.

Anathece sp. – a little known genus, the members of which characteristically occur mostly in plankton of eutrophic reservoirs. Our population grows endogloeic in the mucilage of *Dichothrix* sp. and its close relation to the genus *Cyanobium* is possible.

Asterocapsa sp. – was found among subaerophytic populations of epilithic *Gloeocapsa* sp. div. The existence of this type as a special taxon or as a stage of any *Gloeocapsa* is not yet solved. Our populations occur among typical *Gloeocapsa* stages over the whole vegetation season. Clear transition stages were not recognized.

Calothrix sp. div. – studied populations from this genus were not rich. The specimens from both morphospecies cannot be identified with any described species.

Chamaesiphon sp. div. – three species from this traditional form-genus were identified. Two of them grow epiphytically, mostly on filaments of *Schizothrix facilis* in rapid streams and waterfalls. The third species form flat mats covering surface of stones, also in fast glacial streams. This species resembles mostly *C. polonicus* (subg. *Godlewskia*), but the identity was not proved.

Chlorogloea sp. div. – this genus was found in several different populations, which differ slightly morphologically and ecologically (in lichens, on the bottom of tundra pools, soils, *etc.*). Interesting was a morphospecies with coloured envelopes from dripping rocks. Relations among the species found and the up to now described morphospecies are unclear.

Chroococcus sp. div. – this polymorphic genus was registered in several morphotypes (morphospecies?) in various habitats of the tundra biome. Among the few morphospecies there were both morphological and ecological transitions. As usual, a majority of specimens did not correspond exactly with the described species.

Chroococcidiopsis sp. – only one population is developed among mosses on the bottom of a shallow tundra pool. Evidently a specific morpho- and ecospecies, characteristic of this habitat. Isolation and further study is required.

Dichothrix sp. – not identifiable according to all keys available (*e.g.*, Geitler 1932; Desikachary 1959; Starmach 1966; and others). Up to now only restricted populations have been found in wet tundra habitats and less frequently on wet rocks.

Eucapsis minor –wide morphological variation range, but the ecology corresponds more or less to the type material and genetic identity with this species is probable.

Gloeocapsa sp. div. – the variable community of epilithic *Gloeocapsa*-species from wet (dripping) rocks occurs commonly in many localities. The intense coloration of envelopes in the Svalbard populations was stable and did not change in different localities. However, the pH in the whole area was more or less higher than 7. The different morphotypes have not yet been identified with certainty and the majority of the populations were characterized by their blue, violet or blackish sheaths. The identity of similar assemblages from various high mountains and wet rocks over the world is also still questionable, mainly due to the difficulties in cultivation of the different types. From the whole set of various morphotypes, the most common is especially *Gloeocapsa* cf. *alpina*, which has violet envelopes and occurs also commonly on the surface of wet stony blocks near streams or solitary in communities from moss tundra.

Leptolyngbya sp. div. – this very simple morphotype occurs, as in numerous other biotopes, with very thin and ensheathed trichomes and forms several morpho- and ecotypes in various habitats of the tundra biome. A few slightly morphologically different types form relatively high biomass in rapid streams, stagnant puddles and pools in moss tundra, and in coastal saline puddles.

Nostoc commune-complex – the various morphotypes belong to the most common cyanobacteria in the tundra biome, both in aquatic and soil biotopes. It forms several indistinct morphotypes, which are also distinguishable ecologically. Their identity is possible to be solved only with the help of molecular analyses. Special forms include: (i) large macroscopic, flat and smooth, wavy colonies, commonly distributed in puddles of wet moss tundra, (ii) more concentrated and smaller macroscopic clusters from wet soils and seepages, and (iii) flat, blackish mats, which usually lichenize in soil ecosystems. Rare populations from soils should be designated as a special morphotype, which morphologically corresponds mostly to *N. flagelliforme*. This morphospecies was described mainly from deserts in central Asia, but similar populations were registered also in Scandinavia, and the Svalbard populations can be identical with this Scandinavian type. The relation to the typical *N. commune* and Asian populations is still an open question. *N. commune* sensu lato is an intense N-fixator and its substantial function in the tundra biome is extremely important. Therefore, the study of its diversity by more precise, molecular methods is also important.

Phormidium sp. div. – populations of this genus are very common, particularly in its morphospecies *P. autumnale* sensu lato, which occurs in several different microhabitats. Comparison of blackish mats from rapid oligotrophic, glacial streams and salty coastal pools, where it forms extensive mats and produces large biomass, must be studied both ecologically and genetically. *Phormidium autumnale*-type (and similarly also the *Nostoc commune*-complex) has a similar, important function in Antarctic and Arctic ecosystems, but their genetic identity has not yet been confirmed and definitely solved (*cf.* Novis and Smissen 2006; Strunecký *et al.* 2010).

Plectolyngbya sp. – the genus *Plectolyngbya* (with the type species *P. hodgsonii*) was recently described on the basis of combined molecular and phenotype analyses from Antarctica, as endemic and ecologically distinct species (Taton *et al.* 2010). The Svalbard population is morphologically similar to this species, but their relation should be studied by molecular methods.

Schizothrix facilis and sp. div. – the species *S. facilis* was described originally from N Scandinavia by Skuja (1964) and is commonly distributed also in Svalbard in very specialized ecological niches. It occurs exclusively in very rapid parts of oligotrophic, glacial streams and waterfalls. It seems to be endemic to Europe and Svalbard, and is ecologically restricted in this biotope. However, two more species of the genus *Schizothrix* were found in Petuniabukta, which are, however, distinctly different both ecologically and morphologically: (i) one species with colourless sheaths in wet, moss tundra, and (ii) a species forming macroscopic,

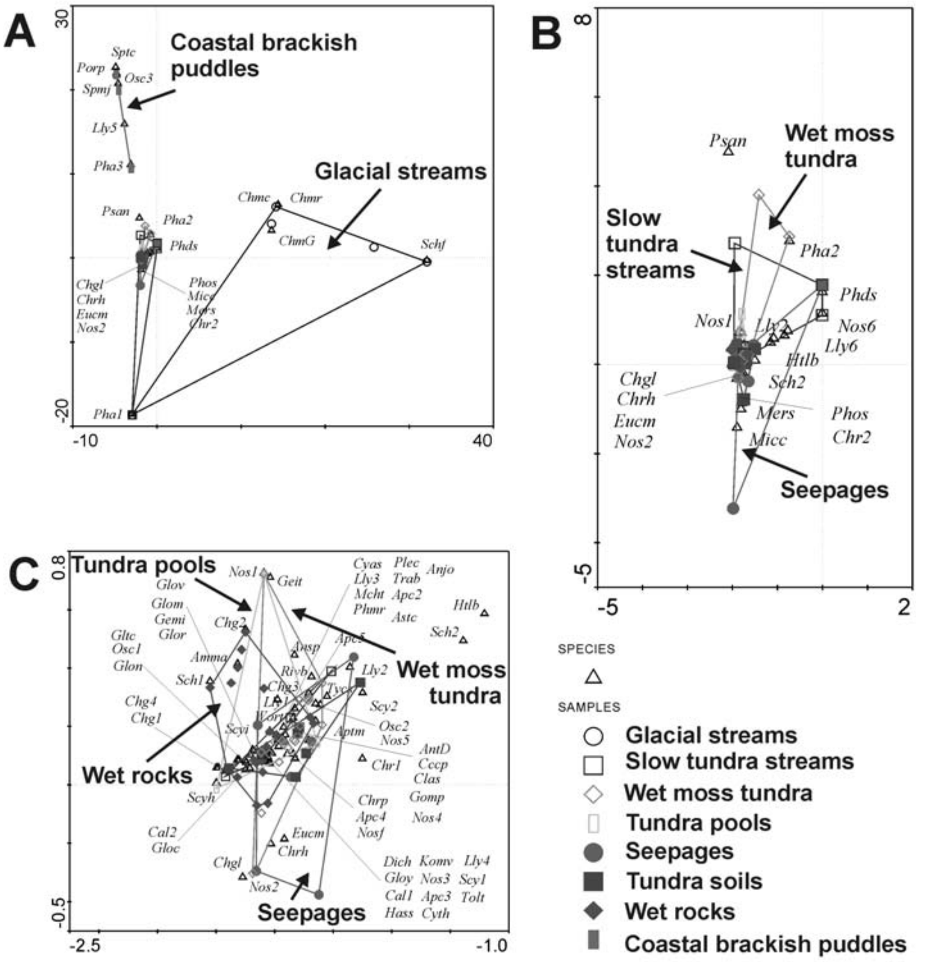

Fig. 3. **A**. The species and samples distributed over full scale of the first and second axis of DCA. **B**. The species and samples distributed over central 10×10 part of the first and second axis of DCA. **C**. The species and samples distributed over central 1×1 part of the first and second axis of DCA. The classification is made by the localities character of habitat.

hemispherical, black pillow-like colonies on dripping rocks (which is evidently up to now an unknown species).

Scytonema crustaceum and *Scytonema* sp. – two very similar *Scytonema* types occur in several wet tundra habitats and seepages, which correspond mostly to the different concepts of *Scytonema crustaceum*. According to our investigation, transitions do not exist between these types, which differ also slightly morphologically and ecologically. Similarity with the genus *Petalonema* is also questionable. The ecology and taxonomy of both these types should be studied by the polyphasic approach.

Trichocoleus abiscoensis – described originally as *Microcoleus sociatus* var. *abiscoensis* in N Scandinavia (Skuja 1964). It corresponds rather to the recently defined genus *Trichocoleus* (see review in Komárek and Anagnostidis 2005) and must be considered as a special species. The localities in Svalbard represent confirmation of this taxon from the first description.

Woronichinia tenera – described from moss tundra in Swedish Lappland (Skuja 1964) and commonly occurs (but not in masses) in the same habitats in Svalbard. Its geographic distribution is therefore analogous as in *Schizothrix facilis* (up to now known only from specialized biotopes in N Scandinavia and Svalbard).

Main habitats

Eight main microhabitats were recognized in the studied area, in which the assemblages of species differed not only by community structure, but also by species composition and dominant species (Fig. 3). Saline pools, separate from all others, and glacial streams are unique due to their very extreme conditions considering temperature, low nutrients and high flow velocity. The rest of the freshwater (slower) flow system is within the continual spectrum of conditions. The other two groups separated from each other inside the central cluster are “water” *vs* “soil” localities. “Water” habitats are slow tundra streams, wet rocks and wet moss tundra. “Soil” habitats are tundra soils and margins of seepages. However, specific species occur also in different tundra habitats. Several characteristic species occur particularly on wet, dripping rocks.

Fast streams with rapid water current and stony bottom, and waterfalls (Fig. 4). All streams flow from melted glaciers. Geothermal springs are very rare in Svalbard (Krawczyk and Pulina 1980, 1982) and do not occur in Petuniabukta.

Fig. 4. Examples of fast streams and waterfalls.

Schizothrix facilis is very characteristic and occurs as the dominant type in the most rapid sections of streams, sometimes with epiphytic *Chamaesiphon* morphospecies (*C. cylindricus, C. rostafinskii*). Another dominant species in fast streams is one morphotype from the *Phormidium autumnale*-complex, the identity of which will be studied by molecular methods along with other populations of this species from other habitats (Strunecký *et al.* 2012 this issue).

Streams in the tundra region have relatively slower current and pass sometimes fluently in wide seepages or places with a stony bottom mixed with wider places covered with mosses and higher plants (Fig. 5).

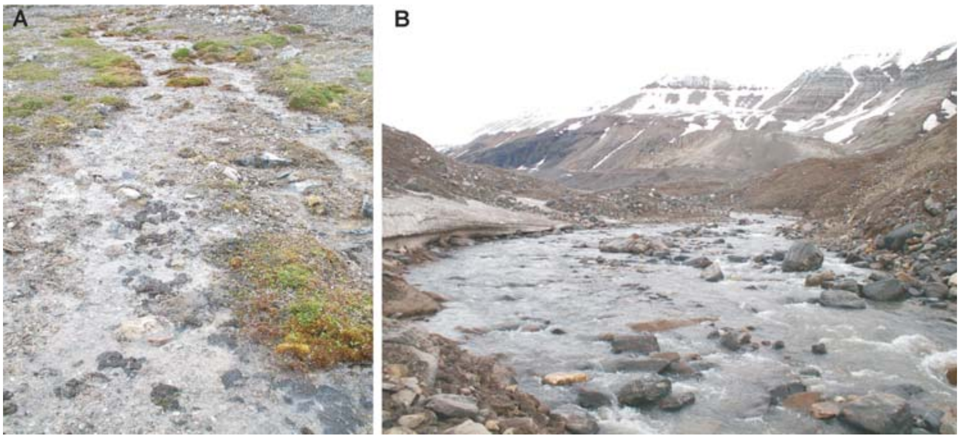

Fig. 5. Streams in tundra region.

Dominant cyanobacterial vegetation are again (less frequently) *Phormidium* mats (mostly from the *Phormidium autumnal*e-complex) and particularly 2–3 morphotypes from the *Nostoc commune*-complex. The *Nostoc* populations are probably genetically identical, but this state must be confirmed. The reasons for certain morphological differences are unclear. Species diversity is richer than in fast streams, but *Schizothrix facilis* is quite lacking here. Rich populations of two types of *Leptolyngbya* occur locally and sometimes colonies of *Rivularia borealis* develop on the bottom with small stones and shallow water.

Wet and flooded moss tundra is one of the most specialized biotopes with numerous species (Fig. 6).

Large macroscopic colonies of *Nostoc* grow here in several characteristic morphotypes, especially in large flat, gelatinous colonies up to several cm in diameter, which are especially dominant. Other characteristic species, occurring predominantly in this biotope, are several types of *Leptolyngbya*, *Schizothrix* with colourless sheaths, heterocytous *Anabaena jonssonii*, *Anabaena* sp., *Scytonema* sp., and *Tolypothrix tenuis*. Numerous coccoid types occur here, however, only

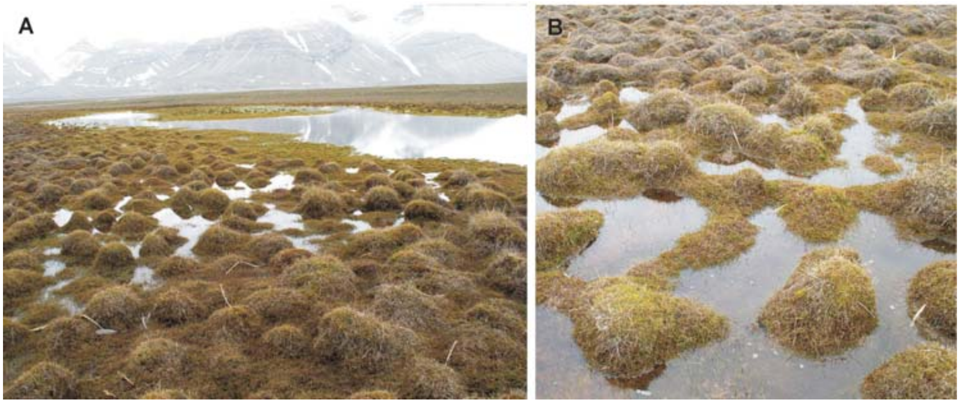

Fig. 6. Wet and flooded moss tundra.

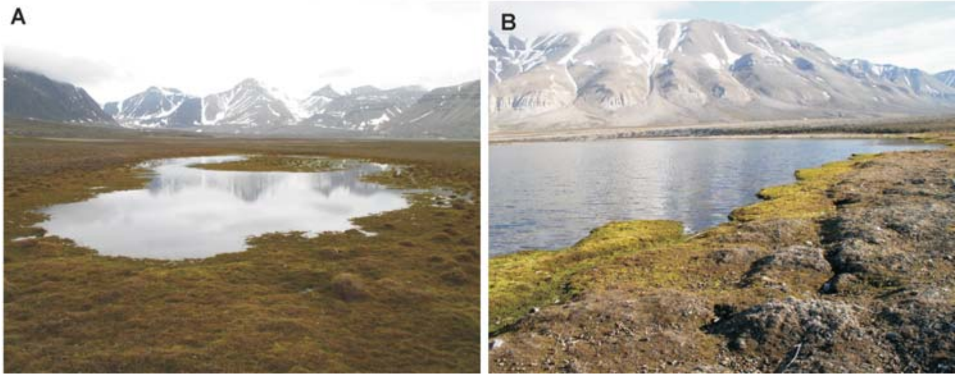

Fig. 7. Shallow pools in tundra biome.

very sporadically (*Woronichinia tenera*, *Gomphosphaeria aponina*, *Merismopedia sphagnicola*, few types of *Aphanothece*). *Aphanothece microscopica*, which is almost restricted only to this habitat, grows here in larger quantity.

Shallow pools in the tundra biome (Fig. 7) have somewhat similar vegetation as described for wet moss tundra (several coccoid types) with several dominant characteristic species (*Aphanothece microscopica*, *Microchaete* cf. *tenera*, *Tolypothrix tenuis*, but almost with absence of *Nostoc*-species).

On the other hand, the bottom is covered by several specific coccoid types, which were found exclusively in this habitat and occur here in higher quantity (one unknown morphospecies of *Chlorogloea, Chroococcidiopsis* sp., *Eucapsis minor*).

Seepages occur usually on slopes at the boundary between mountains, slopes and plains with tundra vegetation, but this area is not strictly delimited (Fig. 8).

The microvegetation is not as characteristic and well developed as in similar habitats in Antarctica (*cf.* Komárek 1999; Komárek and Elster 2008; Komárek *et*

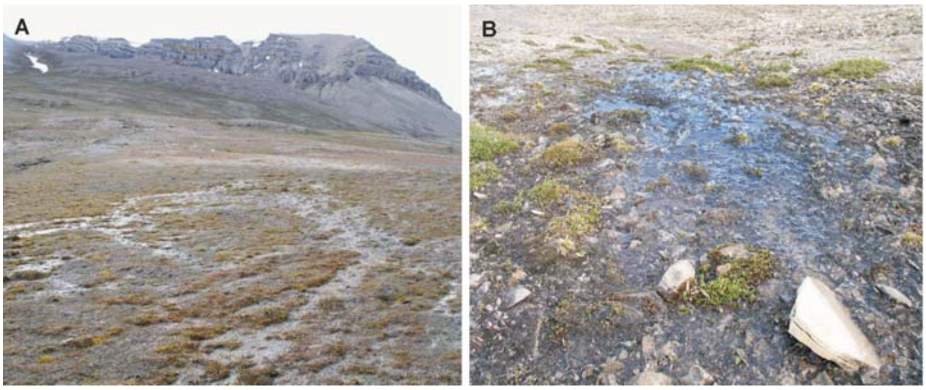

Fig. 8. Seepages on slopes with tundra vegetation.

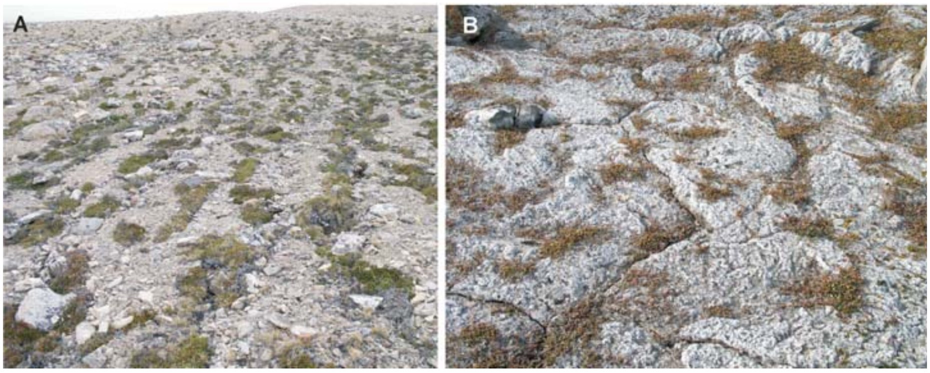

Fig. 9. Soils with crusts.

al. 2008), and has more of a transient community character. Small populations of soil species occur here, as well as in the tundra biome and the flooded tundra. It is not possible to designate any species as typical and dominant for this habitat, but sometimes there are more colonies of one morphotype of *Nostoc*.

Soils in the tundra (Fig. 9) are characterized by drastic fluctuations in temperature and drying. In spite of this, several algal and cyanobacterial communities develop specific crusts, which can be quickly colonized by more stable lichens.

Cyanobacterial communities develop more in places with higher humidity. The community is characterized by the common presence of lichens, in which there occurs commonly one *Nostoc*-type as phycobiont. The lichenized mats of *Nostoc* belong to the commonest members of the microphyte community. Coccoid species are commonly presented in small quantity, with the exception of a small-celled *Gloeocapsa* sp. with violet envelopes (*G.* cf. *nigrescens*), *Aphanocapsa* sp. (cf. *hyalina*) and 2 types of *Chroococcus*. Also, oscillatorialean types are rare. Heterocytous colonies of *Scytonema* occur in a small frequency, as well as the solitary *Tolypothrix tenuis.*

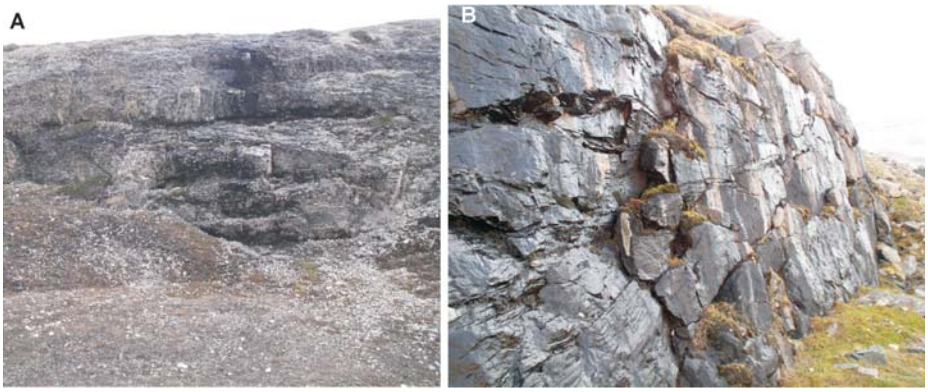

Fig. 10. Wet, dripping rocks.

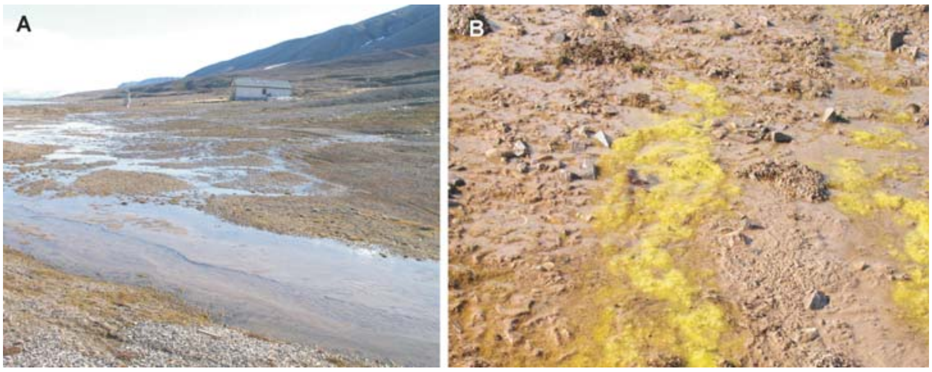

Fig. 11. Coastal halophilic shallow puddles, streams and seepages.

Wet, dripping rocks (Fig. 10) and wet surface of stony blocks in streams (above water level, in a spray zone) have quite special communities of cyanoprokaryotic vegetation. The ecological conditions are very unique. The temperature of the water, which springs usually from melted glaciers or permafrost, is only 0-3^{o}C, and the communities periodically freeze and dry.

There are sometimes also differences between different localities of the same character. Several species of *Gloeocapsa* are dominant, of which *G.* cf. *alpina* with violet envelopes is common; it occurs sometimes also in other similar microhabitats. Also characteristic are a few morphologically different types of *Chlorogloea* (one with coloured envelopes), *Aphanocapsa* with relatively large cells and macroscopic colonies, containing the heterocytous species *Dichothrix* sp., *Calothrix* and interesting populations of *Nostoc* and *Scytonema*. An unidentifiable *Schizothrix* species, forming large, blackish, hemispherical colonies, was found on small rocks in tundra with dripping water. On rocks influenced by the marine spray-zone there occurs an unknown and unidentifiable morphospecies of *Ammatoidea* with blackish sheaths.

Coastal, halophilic shallow puddles, streams and seepages influenced by sea water are another biotope with specific cyanobacterial vegetation (Fig. 11).

Extensive mats of oscillatorialean filamentous types, particularly from the complex *Phormidium autumnale,* are quite dominant in these habitats. Characteristic species include two species of *Spirulina* and one species of *Oscillatoria* with distinct calyptra. The biomass produced by cyanobacteria is very rich in this ecosystem, but the diversity is low. There was almost the complete absence of unicellular morphotypes. Mats of *Phormidium* are mixed with rich populations of green filamentous algae (*Zygnema, Klebsormidium*) and diatoms.

Discussion

The cyanobacterial microflora is an important component of plant communities in polar regions. In comparison with Antarctica, where the higher tundra vegetation is lacking and communities of mosses are less developed, the cyanobacterial communities are connected more with vegetation of higher plants. In spite of this, the cyanobacterial assemblages play an important role in plant communities in the whole deglaciated Arctic ecosystem. Quite indisputable is the role of heterocytous cyanoprokaryotes in the supply of nitrogen (nitrogen fixation) into polar soils (*cf*. Granhall and Lid-Torsvik 1975; Karagatzides *et al*. 1985; Lennihan *et al*. 1994; and many others). In several extreme Arctic deglaciated areas cyanobacteria-dominant communities develop especially in streams, on wet rocks and in coastal brackish pools.

The cyanobacterial flora of Svalbard is less isolated than those in Antarctic habitats and contains several distinct species, known also from localities in N Europe (N Scandinavia). However, species known from more southern European ecosystems live in similar habitats (peaty bogs, wet rocks in mountain areas) on Svalbard. In spite of this, the cyanobacteria of Svalbard are still relatively unknown, particularly in the context of modern taxonomic classification. The older literature about Svalbard microflora or from the Canadian high Arctic contains only several papers, from which only a few are focused on Cyanobacteria. Particularly lacking are ecological data about the main algal and cyanobacterial communities, and autecological characteristics of dominant species in tundra soils, streams, seepages, puddles, *etc*. There exist only a few lists of Cyanobacteria, which are based on the old morphological systems and in which keys for identification were used, in which the hypothesis of ubiquitous distribution of a majority of cyanobacterial species was often accepted. Examples of such studies from Arctic regions are, *e.g.*, the papers of Whelden (1947), Croasdale (1973), Elster *et al*. (1997) and Villeneuve *et al*. (2001) from the Canadian Arctic, or Thomasson (1958), Matula (1982), Oleksowicz and Luścinska (1992), Skulberg (1996), Matula *et al.* (2007), Kim *et al.* (2008) and Richter *et al.* (2009) from Svalbard. These papers present an important basic picture about the diversity of the Arctic cyanobacterial microflora (mostly only at the generic level); therefore they also yield basic information about the ecological significance of various morpho- and ecotypes, but the used system should be modernized in agreement with modern studies.

Almost 90 species were registered in the previous most important review from Svalbard (Skulberg 1996) . This corresponds more or less with our results from Petuniabukta, but the cyanobacterial flora of all of Svalbard will be surely richer. The future revisions should respect particularly the following problems:

(i) The cyanobacterial system was corrected and changed substantially in the last few decades. The identification of Svalbard populations should be corrected according to these modern conclusions.

(ii) Many species, which were identified according to keys based on morphological taxonomy (*e.g*., Geitler 1932; Desikachary 1959; Starmach 1966; Kondrateva 1968; and others), cannot be found in Svalbard ecosystems, because their ecology is distinctly different. This pertains to *e.g.*, *Anabaena planctonica*, *Phormidium ambiguum*, *Dermocarpa pseudoxenococcoides* and others.

(iii) The same species occur in the previous lists under two different synonymic names, *e.g*., *Chroococcus turgidus/Gloeocapsa turgida*, *Calothrix gypsophila/ Dichothrix gypsophila*, *Chroococcus sanguinea/Gloeocapsa sanguinea.*

(iv) There are numerous mistakes in identification: *Dactylococcopsis acicularis* = green alga (Drouet and Daily 1956), *Chroococcus compactus* = very unclear taxon, *Oscillatoria splendida* belongs to the genus *Geitlerinema* (Anagnostidis and Komárek 1988), *etc*.

(v) There are already serious data showing that numerous specific cyanobacterial species exist in polar regions. Arctic populations are more related to the flora of the connected continents, while the Antarctic communities are more isolated. Some relations between Svalbard and N Scandinavia are interesting. Several species (*Schizothrix facilis*, *Microcoleus sociatus* var. *abiscoensis*, *Woronichinia tenera*) were detected in Svalbard, which were described from Swedish Lappland by Skuja (1964) and found up to now only in these two areas. Modern investigations must be focused also on this problem. Comparison with Antarctic cyanobacterial populations is necessary (cf. lists of Ohtani 1986; Komárek 1999; Komárek and Elster 2008; Komárek *et al*. 2008). An important problem is, therefore, genetic comparison of morphologically similar genotypes from both polar regions. Only a few studies have been conducted up to now (Comte *et al*. 2007; Strunecký *et al*. 2010); these authors only very rarely found identical genotypes of cyanobacteria from both polar regions.

(vi) All recognized cyanobacterial species are delimited ecologically and also grow only in specific and different microhabitats in Svalbard (*cf.* Table 1). Ecological variability and specificity data have not yet been published. Ecological specificity of the majority of Svalbard cyanoprokaryotes is probable, but the types distributed in all microhabitats are rare.

Acknowledgements. — This study was conducted with the support of grants from Project Czech Polar INGO LA 341, LM2010009, KONTAKT ME 934, Grant Agency VEGA No. 1/0868/11 (L. Kováčik) and AV0Z60050516 (J. Komárek). The authors are indebted to all, who have helped them during the organization of the expedition. We thank particularly to Dana Švehlová and Jana Šnokhousová (Třeboň laboratory) for technical help, especially in the isolation and careful cultivation of strains.

References

ANAGNOSTIDIS K. and KOMÁREK J. 1988. Modern approach to the classification system of cyanophytes 3 – *Oscillatoriales*. *Algological Studies* 50–53: 327–472.

BROADY P.A. 1989. Broadscale patterns in the distribution of aquatic and terrestrial vegetation at three ice-free regions on Ross Island, Antarctica. *Hydrobiologia* 172: 77–95.

BROADY P.A. 2005. The distribution of terrestrial and hydro-terrestrial algal associations at three contrasting locations in southern Victoria Land, Antarctica. *Algological Studies* 118: 95–112.

CALLEJAS C., GILL P.R., CATALÁN A.I., AZZIZ G., CASTRO-SOWINSKI S. and BATISTA S. 2011. Phylotype diversity in a benthic cyanobacterial mat community on King George Island. *World Journal of Microbiology & Biotechnology* 27 (6): 1507–1512.

COMTE K., ŠABACKÁ M., CARRE-MLOUKA A., ELSTER J. and KOMÁREK J. 2007. Relationships between the Arctic and the Antarctic cyanobacteria; three *Phormidium*-like strains evaluated by a polyphasic approach. *FEMS Microbiology Ecology* 59 (2): 366–376.

CROASDALE H. 1973. Freshwater algae of Ellesmere Island, N.W.T. *Natural Museum of Natural Sciences, Publications of Botany* 3: 1–131.

DALLMANN W.K. ed. 1999. Lithostratigraphic Lexicon of Svalbard. Upper Palaeozoic to Quaternary bedrock. Review and recommendations for nomenclature use. *Committee on the Stratigraphy of Svalbard/Norsk Polarinstitutt*: 320 pp.

DESIKACHARY T.V. 1959. *Cyanophyta*. ICAR Monographs on Algae, New Delhi: 686 pp.

DROUET F. and DAILY W.A. 1956. Revision of the coccoid Myxophyceae. *Butler University Botanical Studies* 12: 1–218.

ELSTER J. 2002. Ecological classification of terrestrial algal communities in polar environments. *In*: L. Beyer and M. Bölter (eds) *Geoecology of Antarctic ice-free coastal landscapes*. Springer, Berlin, Heidelberg, New York: 303–326.

ELSTER J. and BENSON E.E. 2004. Life in the polar terrestrial environment with a focus on algae and cyanobacteria. *In*: B. Fuller, N. Lane and E. Benson (eds) *Life in the Frozen State*. Taylor and Francis Book, London: 110–150.

ELSTER J., KOMÁREK J. and SVOBODA J. 1994. Algal communities of polar wetlands. *Scripta Facultas Scientiarum Nauralium Universitatis Masarykiane Brunensis 24 (Geography)*: 13–24.

ELSTER J., LUKEŠOVÁ A., SVOBODA J., KOPECKÝ J. and KANDA H. 1999. Diversity and abundance of soil algae in the polar desert, Svedrup Pass, central Ellesmere Island. *Polar Record* 35 (194): 231–254.

ELSTER J., SVOBODA J., KOMÁREK J. and MARVAN P. 1997. Algal and cyanoprocaryote communities in a glacial stream, Sverdrup Pass, 79°N, Central Ellesmere Island, Canada. *Algological Studies* 85: 57–93.

FRIEDMANN E.I. 1993. *Antarctic Microbiology*. John Wiley & Sons, Inc., New York: 634 pp.

GARCIA-PICHEL F., NÜBEL U. and MUYZER G. 1998. The phylogeny of unicellular, extremely halotolerant cyanobacteria. *Archiv für Microbiologie* 169: 469–482.

GEITLER L. 1932. Cyanophyceae. *In*: L. Rabenhorst (eds) Kryptogamen-Flora von Deutschland, Österreich und der Schweiz. *Akademische Verlagsgesellschaft, Leipzig* 14: 673–1056.

GRANHALL U. and LID-TORSVIK V. 1975. Nitrogen fixation by bacteria and free-living blue-green algae in tundra areas. *Ecological Studies* 16: 305–315.

KARAGATZIDES J.D., LEWIS M.C. and SCHULMANN H.M. 1985. Nitrogen fixation in the high Arctic tundra at Scarpa Lake, Northwest Territories. *Canadian Journal of Botany* 63: 974–979.

KIM G.H., KLOCHKOVA T.A. and KANG S.H. 2008. Notes on freshwater and terrestrial algae from Ny-Ålesund, Svalbard (high Arctic sea area). *Journal of Environmental Biology* 29(4): 485–491.

KOMÁREK J. 1999. Diversity of cyanoprokaryotes (cyanobacteria) of King George Island, maritime Antarctica – a survey. *Algological Studies* 94: 181–193.

KOMÁREK J. and ANAGNOSTIDIS K. 1998. Cyanoprokaryota 1. Teil: Chroococcales. *In*: H. Ettl, G. Gärtner, H. Heynig and D. Mollenhauer (eds) *Süsswasserflora von Mitteleuropa 19/1*. Gustav Fischer, Jena-Stuttgart-Lübeck-Ulm: 548 pp.

KOMÁREK J. and ANAGNOSTIDIS K. 2005. Cyanoprokaryota – 2. Teil/2nd Part: Oscillatoriales. *In*: B. Büdel, L. Krienitz, G. Gärtner and M. Schagerl (eds) *Süsswasserflora von Mitteleuropa 19/2*. Elsevier/Spektrum, Heidelberg: 759 pp.

KOMÁREK J. and ELSTER J. 2008. Ecological background of cyanobacterial assemblages of the northern part of James Ross Island, NW Weddell Sea, Antarctica. *Polish Polar Research* 29 (1): 17–32.

KOMÁREK J., ELSTER J. and KOMÁREK O. 2008. Diversity of the cyanobacterial microflora of the northern part of James Ross Island, NW Weddell Sea, Antarctica. *Polar Biology* 31: 853–865.

KRAWCZYK W. and PULINA M. 1980. Hydrochemical investigation carried out on the northern shore of Hornsund. *Field investigations performed during the Spitsbergen Expedition of the Silesian University in the summer of 1979*, Katowice.

KRAWCZYK W. and PULINA M.1982. Preliminary results of hydrological and hydrochemical investigations in Fugleberget basin (SW Spitsbergen). *Prace naukowe Uniwersytetu Śląskiego* 543: 167–180.

LÁSKA K., WITOSZOVÁ D. and PROŠEK P. 2012. Weather patterns of the coastal zone of Petuniabukta, central Spitsbergen in the period 2008–2010. *Polish Polar Research* 33 (4): 297–318.

LENNIHAN R., CHAPIN D.M. and DICKSON L.G. 1994. Nitrogen fixation and photosynthesis in high Arctic forms of *Nostoc commune*. *Canadian Journal of Botany* 72: 940–945.

MATALONI G. and POSE M. 2001. Non-marine algae from islands near Cierva Point, Antarctic Peninsula. *Cryptogamie Algologie* 22 (1): 41–64.

MATALONI G. and TELL G. 2002. Microalgal communities from ornithogenic soils at Cierva Point, Antarctic Peninsula. *Polar Biology* 25: 488–491.

MATULA J. 1982. Investigations on the algal flora of West Spitsbergen. *Acta Universitatis Wratislaviensis* 525: 173–187.

MATULA J., PIETRYKA M., RICHTER D. and WOJTUŃ B. 2007. Cyanoprokaryota and algae of Arctic terrestrial ecosystems in the Hornsund area, Spitsbergen. *Polish Polar Research* 28 (4): 283–315.

NOVIS P.M. and SMISSEN R.D. 2006. Two generic and ecological groups of *Nostoc commune* in Victoria Land, Antarctica, revealed by AFLP analysis. *Antarctic Science* 18 (4): 573–581.

OHTANI S. 1986. Epiphytic algae on mosses in the vicinity of Syowa Station, Antarctica. *Memoirs of Natural Institute of Polar Research* (Special Issue) 44: 209–219.

OLEKSOWICZ A.S. and LUŚCIŃSKA M. 1992. Occurrence of algae on tundra soils in Oscar II Land, Spitsbergen. *Polish Polar Research* 13 (2): 131–147.

PRESCOTT G.W. 1979. A contribution to a bibliography of Antarctic and Subantarctic algae. *Bibliotheca Phycologica* 45: 312 pp.

PRISCU J.C. (ed.) 1998. Ecosystem dynamics in a polar desert. *Antarctic Research Series* 72: 369 pp.

REJMÁNKOVÁ E., KOMÁREK J. and KOMÁRKOVÁ J. 2004. Cyanobacteria – a neglected component of biodiversity: patterns of species diversity in inland marshes of northern Belize (Central America). *Diversity and Distributions* 10: 189–199.

RICHERt L., GOLUBIC S., LE GUÉDÈS R., HERVÉ A. and PAYRI C. 2006. Cyanobacterial populations that build "kopara" microbial mats in Rangiroa, Tuamotu Archipelago, French Polynesia. *European Journal of Phycology* 41: 259–279.

RICHTER D., MATULA J. and PIETRYKA M. 2009. Cyanobacteria and algae of selected tundra habitats in the Hornsund fiord area (West Spitsbergen). *Oceanological and Hydrobiological Studies* 38 (2): 65–70.

RIPPKA R., DERUELLES J., WATERBURY J.B., HERDMAN M. and STANIER R.Y. 1979. Generic assignments, strain histories and properties of pure cultures of cyanobacteria. *Journal of General Microbiology* 111: 1–61.

SKUJA H. 1964. Grundzüge der Algenflora und Algenvegetation der Fjeldgegenden um Abisco in Schwedisch-Lappland. *Nova Acta Regiae Societatis Scienciarum Upsaliensis, Sér. 4* 18 (3): 1–465.

SKULBERG O.M. 1996. Terrestrial and limnic algae and cyanobacteria Part 9. *In*: A. Elvebakk and P. Prestrud (eds), A catalogue of Svalbard plants, fungi, algae and Cyanobacteria. *Norsk Polarinstitut, Skrifter* 198: 383–395.

STARMACH K. 1966. *Cyanophyta – sinice. Glaucophyta – glaucofity. Flora słodkowodna Polski 2*. PWN Warszawa: 807 pp.

STRUNECKÝ O., KOMÁREK J. and ELSTER J. 2012. Biogeography of *Phormidium autumnale* (Oscillatoriales, Cyanobacteria) in western and central Spitsbergen. *Polish Polar Research* 33 (4): 369–382.

STRUNECKÝ O., ELSTER J. and KOMÁREK J. 2010. Phylogenetic relationships between geographically separate *Phormidium* cyanobacteria: is there a link between north and south polar regions? *Polar Biology* 33: 1419–1428.

TATON A., GRUBISIC S., BRAMBILLA E., DE WIT R. and WILMOTTE A. 2003. Cyanobacterial diversity in natural and artificial microbial mats of Lake Fryxell (McMurdo Dry Valleys, Antarctica): a morphological and molecular approach. *Applied and Environmental Microbiology* 69: 5157–5169.

TATON A., WILMOTTE A., ŠMARDA J., ELSTER J. and KOMÁREK J. 2011. *Plectolyngbya hodgsonii*: a novel filamentous cyanobacterium from Antarctic lakes. *Polar Biology* 34: 181–191.

TEDROW J.C.F. 1977. *Soils of the polar landscapes*. Rutgers University Press, New Brunswick: 664 pp.

TEDROW J.C.F. 1991. Pedogenic linkage between the cold desert of Antarctica and the polar desert of the high Arctic. *Antarctic Research Series II* 53: 1–17.

THOMASSON K. 1958. Zur Planktonkunde Spitzbergen. *Hydrobiologia* 12 (2–3): 226–236.

VILLENEUVE V., VINCENT W.F. and KOMÁREK J. 2001. Community structure and microhabitat characteristics of cyanobacterial mats in an extreme high Arctic environment: Ward Hunt Lake (lat. 82.8°N). Beih. *Nova Hedwigia* 123: 199–223.

VINCENT W.F. 1988. *Microbial Ecosystem of Antarctica*. Cambridge University Press, Cambridge: 304 pp.

VINCENT W.F., BOWMAN J.P., RANKIN L.M. and MCMEEKIN T.A. 2000. Phylogenetic diversity of picocyanobacteria in Arctic and Antarctic ecosystems. *In*: R. Bell, C.M. Brylinski and M. Johnson-Green (eds) Microbial biosystems: new frontiers. *Proceedings of the 8th International Symposium on Microbial Ecology, Halifax, Canada*: 317–322.

WALTON D.W.H. (ed.) 1987. *Antarctic Science*. Cambridge University Press, Cambridge: 280 pp.

WHELDEN R.M. 1947. Algae. *In*: Botany of eastern Arctic, II: Thallophyta and Bryophyta. *Bulletin of Natural Museum of Canada* 97: 13–127.

WILLÉN T. 1970. Phytoplankton from Björnöya, Svalbard. *Norwegian Journal of Botany* 17 (1): 17–24.

Received 28 June 2011
Accepted 21 May 2012