

Taxonomic and Ecological Structure of Basidial Macromycetes Biota in Polar Deserts of the Northern Hemisphere

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Received February 18, 2018; in final form, April 3, 2018

Abstract—The results of a study of the more than century-long history of taxonomic and ecological structures of basidial macromycete biota in polar deserts of the Northern Hemisphere are discussed. Nowadays, 77 species of macromycetes are known from this region, 40 species of which are agaricoid fungi, 30 are aphyllophoroid, and 7 are gasteromycetes. The highest number of species is known for the Franz Josef Land archipelago and Severanya Zemlya. All the identified species of agaricoid and 86% of gasteroid fungi are native representatives from extremely high latitudes collected under natural conditions, whereas 80% of the aphyllophoroid fungi are alien elements. All alien species are able to exist in the region exclusively in human-modified habitats, colonizing anthropogenic woody and grass substrates, and they disappear with the depletion of these resources. Despite the existence of mycobiota at the limit of the global thermal gradient, a specific species complex of macromycetes that does not occur anywhere in the world is formed here. Symbiotic species (basidial lichens and mycorrhiza-formers) are the most adaptable to such extreme conditions. General features of the organization with Antarctic mycobiota are established. The possibility that new species will appear in the region is discussed in connection with the intensification of human economic activity and global climate change.

Keywords: Arctic, adaptation, biogeography, diversity, fungal ecology, extreme climate, Basidiomycota

DOI: 10.1134/S1995425518050086

INTRODUCTION

Changes that occur as a result of global warming and industrial development in the Arctic regions primarily affect the soil cover, of which fungi are an important component. The composition and response of various taxonomic and ecological groups of Arctic plants and animals to such changes have been studied quite well, but fungi have been undeservedly given little attention, while the cenotic role of this group of organisms in high-latitude biomes is high (Dahlberg et al., 2013). Fungal organisms are the main component of the regeneration block of Arctic terrestrial ecosystems. They, together with lichens and bryophytes, determine the productivity of the tundra and especially the polar-desert biome.

Basidial macromycetes (Basidiomycota, Agaricomycetes) is one of the largest groups of fungi, uniting important ecological groups such as agaricoid, aphyllophoroid, and gasteroid fungi. They are distributed on all continents from polar glaciers and high mountains to tropical deserts and equatorial rain forests and

are involved in all three main functional blocks of the biosphere, participating in soil formation and the ascending flow of basic nutrients. This determines their role as significant indicators of climatic, anthropogenic, and invasive processes of high-latitude biota. These fungi are a long-standing research object in tundra ecosystems, whereas in polar deserts located at the edge of the global temperature gradient they were studied fragmentarily. Macromycetes in the polar deserts develop under the most favorable conditions of marine terraces on polygonal soils with associated algae, mosses, and lichens groups, where the arctic poppy, whitlow grass, and saxifrage grow, creating the mortmass as a result of the die-off. Under warm conditions and good drainage, polar willow can be detected, which is obligate in its development from the fungal symbiont.

The history of the study of Arctic basidial macro-mycetes in the Northern Hemisphere is reflected in a number of studies (Karatygin et al., 1999; Knudsen, 2003; Dahlberg et al., 2013), emphasizing the poverty of their species composition when compared with

more southern regions. Studies of agaricoid fungi of the polar deserts (within the boundaries according to Aleksandrova (1983)) within the Canadian Arctic Archipelago have been going on for a century (Dearness, 1923; Redhead, 1989). Recently, studies of agaricoid basidiomycetes have not been performed in these territories. The mycobiota of Greenland tundra were studied for more than a century, but data on fungi of the polar deserts of Peary Land are very limited (Borgen et al., 2006). The combined list of species is known for the Svalbard Archipelago (Gulden and Torkelsen, 1996). On Frantz Josef Land Archipelago, fungi have been studied for more than 50 years (Ezhov et al., 2012, 2014, 2016; Zmitrovich and Ezhov, 2015). Agaricoid fungi were collected on the Severnaya Zemlya islands by Nezdoiminogo (1982, 2002). Agaricoid fungi were not known in the regions of Novaya Zemlya, Chelyuskin Peninsula, and the De Longa Islands.

Information is also extremely limited for the aphyllophoroid fungi of the polar deserts. In Greenland, fungi from various tundra regions are known, but only one species was identified in Peary Land—*Multi-clavula vernalis* (Borgen et al., 2006). On the Svalbard Archipelago, extensive mycological studies were conducted in the tundra of Western Spitsbergen Island (Gulden and Torkelsen, 1996; Kosonen and Huhtinen, 2008; Mattsson at al., 2010; Shiryaev and Mukhin, 2010), whereas there is no data for the polar deserts of Nordaustlandet. Until the beginning of the 21st century, the aphyllophoroid fungi were not mentioned for the polar deserts of the Russian Arctic (Karatygin et al., 1999), but over the past two decades expeditions in all parts of the region have been conducted. Results of the collection of aphyllophoroid fungi on the Frantz Josef Land Archipelago were published (Ezhov et al., 2012, 2016). There is a series of publications on the composition of clavarioid fungi collected on Novaya Zemlya (Shiryaev, 2006, 2013), Severnaya Zemlya, and the Chelyuskin Peninsula (Shiryaev, 2011). Information is not available for the Canadian Arctic Archipelago and the De Long Islands.

Data for the third group—gasteroid basidiomycetes—have been published for the polar desert zone of Greenland (Lange, 1987, 1990). There is no data for other regions. In general, it can be stated that the information on the studied groups of fungi in this natural zone is extremely limited. A detailed history of the study of basidial macromycetes in Russian regions can be found in our recent studies (Zmitrovich and Ezhov, 2015; Shiryaev, 2015).

In the 20th century the increase in economic activity in the Arctic led to the emergence of a large number of settlements, the livelihood of which required a significant amount of raw materials, in particular timber. Along with timber the aphyllophoroid fungi functionally adapted to development in the wood substrate (poroid and corticioid) penetrate to the extreme north. Such anthropogenic migration of fungi and their pos-

sible ecological consequences for northern ecosystems have not yet been adequately reflected in mycological studies. In the last two decades, the number of publications on the study of alluvial aphyllophoroid fungi in the Arctic has significantly increased (Gulden and Torkelsen, 1996; Kotiranta and Mukhin, 2000; Kosonen and Huhtinen, 2008; Mattsson et al., 2010, etc.), but attempts to establish naturally existing species are still limited (Shiryaev and Mikhaleva, 2013).

This study is a continuation of ecological and biogeographical studies of biota of agaricoid (Ezhov et al., 2012, 2014, 2016; Zmitrovich and Ezhov, 2015) and aphyllophoroid fungi (Shiryaev, 2013, 2014, 2015) of the polar deserts of the Northern Hemisphere.

The goal of this study is to accumulate all possible information about agaricoid, aphyllophoroid, and gasteroid fungi in the polar desert zone of the Northern Hemisphere at the present and establish the species composition of fungi in individual longitude regions; identify the group of native species, separating them from alien ones; determine the features of the geographical and ecological structure for the natural component of mycobiota; determine whether there is a similarity between the mycobiota of the polar deserts of the Arctic and Antarctic; and predict which species and functional groups can potentially still be found in this natural zone.

MATERIALS AND METHODS

In this study, the boundaries of natural zones in the Arctic are shown according to the regionalization of Aleksandrova (1983). It should be noted that in this study the southern boundary of the polar desert zone is further north in comparison with the map of the CAVM Team (2003), which is widely used in Europe. The distribution of the three largest groups of basidial macromycetes (agaricoid, aphyllophoroid, and gasteroid fungi) was studied within eight regions located in close proximity to the North Pole: (1) the extremely northern territories of the Canadian Arctic Archipelago, (2) in Greenland—Peary Land and neighboring territories (further north of 82° N), (3) on the Svalbard Archipelago—Nordaustlandet, (4) the whole of the Franz Josef Land Archipelago, (5) the northern extremity of the Northern Island of Novaya Zemlya, (6) Severnaya Zemlya Islands, (7) Chelyuskin Peninsula on the Taimyr Peninsula, and (8) within the boundaries of the New Siberian Islands (the northernmost part, De Long Island (see Fig. 1)).

The authors of the study reviewed all available literature and herbarium fungi specimens and performed expeditions to various high latitude regions. Targeted studies of agaricoid fungi were conducted in 2010–2016 on the Franz Josef Land Archipelago. We collected the aphyllophoroid and gasteroid fungi in the regions of Svalbard Archipelago, Franz Josef Land, Novaya Zemlya, Severnaya Zemlya, Chelyuskin Pen-

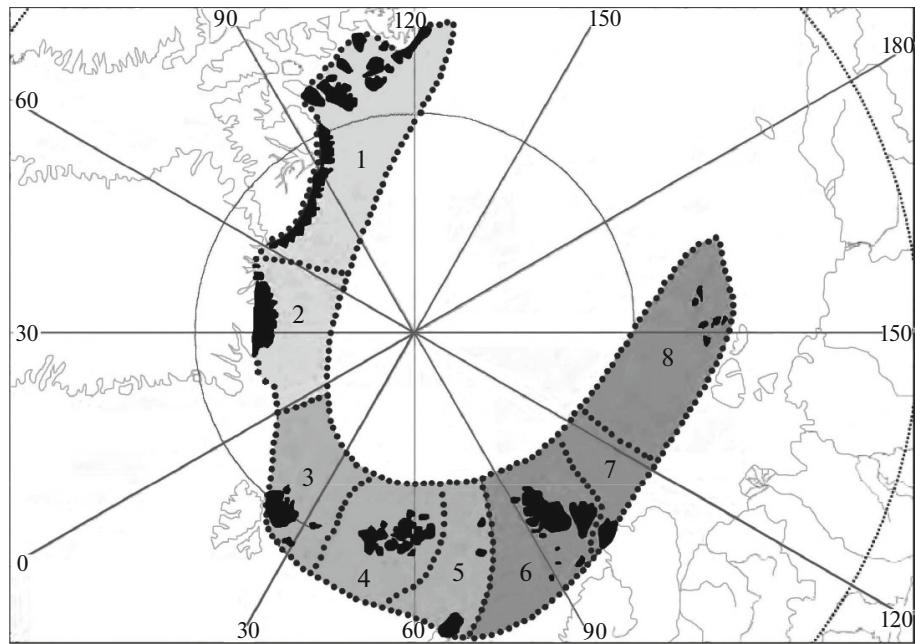


Fig. 1. Eight longitude regions of the polar desert zone of the Northern Hemisphere.

insula, and the New Siberian Islands. The materials are stored in the mycological collections of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences (SVER); the Komarov Botanical Institute (LE); and the Laverov Federal Research Center for Integrated Studies of the Arctic (AR). For Greenland, in addition to the published materials, samples of gasteroid fungi deposited in the Mycology Department of the University of Copenhagen (C) were analyzed. The names of the fungi species were given according to the database (<http://www.indexfungorum.org>).

RESULTS AND DISCUSSION

As of now, 77 species of basidial macromycetes have been identified in the polar deserts of the Northern Hemisphere, including 40 species of agaricoid fungi, 30 species of aphyllophoroid fungi, and 7 species of gasteromycetes (Table 1). In this study, 14 fungi species are shown for the first time for the polar desert zone: six species of aphyllophoroid fungi: *Cerrena unicolor* was found on the Chelyuskin Peninsula; *Dacrymyces stillatus* on Frantz Josef Land, Chelyuskin Peninsula, and the De Long Islands; *Dititola radicata* on Severnaya Zemlya; *Eichleriella deglubens* on Svalbard and Chelyuskin Peninsula; *Tubulicrinis calothrix* on Svalbard and the Chelyuskin Peninsula; and *Tulasnella violea* on Svalbard, Novaya Zemlya, Severnaya Zemlya, Chelyuskin Peninsula, and the De Long Islands. Six species of agaricoid fungi were found: *Hebeloma monticola* was collected on the Peary Land Peninsula in Greenland (Peary

Land, Jørgen Brønlund Fjord, 82°16' N, 07.VIII.1947, collected by K. Holmen, Jan Vesterholt/Herbarium specimen at the Museum of the University of Copenhagen no. KH 47.076) (personal communication by H. Knudsen), and *Cortinarius decipiens*, *C. obtusus*, *C. polaris*, *Deconica montana*, and *Galerina subclavata* were found on Franz Josef Land. Two new species of gasteroid fungi have been collected, out of which *Lycoperdon* sp. was found in Greenland (stored in the Mycological Department of the University of Copenhagen; basidiomata were found on Nansen Land island (Nansen Land, Brainard Sund, 82°95' N, 41°67' W, 05.08.1991 C. Bay) and probably represents the species *L. frigidum* Demoulin, or *L. niveum* Kreisel (personal communication of H. Knudsen). *Crucibulum laeve* was collected on Chelyuskin Peninsula.

Among the fungi previously identified in the studied natural zone, there are a number of new species for individual sectoral regions. Thus, the following species were detected for the first time: for Greenland, *Hebeloma monticola*, *Inocybe dulcamara* s.l., and *Lycoperdon* sp.; for Svalbard, *Multiclavula corynoides*, *M. vernalis*, *Peniophorella praetermissa*, *Tomentella atramentaria*, and *Typhula crassipes*; for Novaya Zemlya, *Arrhenia lobata* and *Bovista tomentosa*; for Severnaya Zemlya, *Multiclavula vernalis*; for Chelyuskin Peninsula, *Coniophora puteana*, *Crucibulum laeve*, and *Typhula crassipes*; for the New Siberian Islands (De Long Island), *Amylocorticiellum molle*, *Antrodia serialis*, *Gloeophyllum sepiarium*, *Hyphoderma setigerum*, *Multiclavula corynoides*, *Tubulicrinis sororius*, and *Typhula crassipes*. For De Long Islands the

Table 1. Distribution of basidial macromycetes in eight regions of polar desert zone of the Northern Hemisphere

Species	Region								Information about the finding of species
	Canadian Archipelago	Green-land	Svalbard	Franz Josef Land	Novaya Zemlya	Severnaya Zemlya	Taimyr	New Siberian Islands	
Agaricoid fungi									
<i>Arrhenia auriscalpium</i> (Fr.) Fr.		+		+					2 (Borgen et al., 2006; Zmitrovich and Ezhov, 2015)
<i>A. lobata</i> (Pers.) Kühner & Lamoure ex Redhead		+		+	+	+			4 (Borgen et al., 2006; Zmitrovich and Ezhov, 2015)
<i>A. obatra</i> (J. Favre) Redhead, Lutzoni, Moncalvo & Vilgalys				+		+			2 (Zmitrovich and Ezhov, 2015)
<i>A. retiruga</i> (Bull.) Redhead			+						1 (Gulden, Torkelsen, 1996; Zmitrovich and Ezhov, 2015)
<i>A. rickenii</i> (Hora) Watling				+					1 (Zmitrovich and Ezhov, 2015)
<i>A. spathulata</i> (Fr.) Redhead				+					1 (Ezhov et al., 2016)
<i>Clitocybe dryadicola</i> (J. Favre) Harmaja				+					1 (Zmitrovich and Ezhov, 2015)
<i>C. festiva</i> J. Favre				+					1 (Ezhov et al., 2016)
<i>Coprinopsis martinii</i> (P.D. Orton) Redhead, Vilgalys et Moncalvo					+				1 (Zmitrovich and Ezhov, 2015)
<i>Cortinarius alpinus</i> Boud.					+				1 (Zmitrovich and Ezhov, 2015)
<i>C. decipiens</i> (Pers.) Fr.				+					1 AR 2819
<i>C. obtusus</i> (Fr.) Fr.				+					1 AR 2882
<i>C. oreobius</i> J. Favre					+				1 (Zmitrovich and Ezhov, 2015)
<i>C. polaris</i> Høil.				+					1 AR 1732, 2428, 2818
<i>C. subtoryus</i> Lamoure					+				1 (Zmitrovich and Ezhov, 2015)
<i>Cystoderma arcticum</i> Harmaja					+				1 (Zmitrovich and Ezhov, 2015)
<i>Deconica coprophila</i> (Bull.) P. Karst.				+					1 (Ezhov et al., 2016)
<i>D. montana</i> (Pers.) P. Kumm.				+					1 AR 2816
<i>Galerina arctica</i> (Singer) Nezdojm.	+			+	+				3 (Borgen et al., 2006; Zmitrovich and Ezhov, 2015)
<i>G. embolus</i> (Fr.) P.D. Orton					+				1 (Zmitrovich and Ezhov, 2015)
<i>G. mniophila</i> (Lasch) Kühner					+				1 (Zmitrovich and Ezhov, 2015)
<i>G. pseudocerina</i> A.H. Sm. & Singer				+	+				2 (Zmitrovich and Ezhov, 2015)
<i>G. pseudomycenopsis</i> Pilát			+	+	+				3 (Gulden and Torkelsen, 1996; Ezhov et al., 2012, 2016)
<i>G. pumila</i> (Pers.) M. Lange				+		+			2 (Zmitrovich and Ezhov, 2015) AR 2823, 2829
<i>G. tibiicystis</i> (G.F. Atk.) Kühner				+					1 (Zmitrovich and Ezhov, 2015)

Table 1. (Contd.)

Species	Region									Information about the finding of species
	Canadian Archipelago	Green-land	Svalbard	Franz Josef Land	Novaya Zemlya	Severnaya Zemlya	Taimyr	New Siberian Islands	total	
<i>G. subclavata</i> Kühner				+					1	AR 2826
<i>G. vittiformis</i> (Fr.) Singer				+					1	(Zmitrovich and Ezhov, 2015)
<i>Hebeloma gigaspernum</i> Gröger & Zschiesch.				+					1	(Zmitrovich and Ezhov, 2015)
<i>H. marginatum</i> (J. Favre) Bruchet				+					1	(Zmitrovich and Ezhov, 2015; Ezhov et al., 2016)
<i>H. monticola</i> Vesterh.		+							1	see information in the text
<i>H. remyi</i> Bruchet				+					1	(Zmitrovich and Ezhov, 2015)
<i>Inocybe dulcamara</i> (Pers.) P. Kumm. <i>sensu lato</i>		+	+						2	(Gulden and Torkelsen, 1996; Zmitrovich and Ezhov, 2015)
<i>Laccaria pumila</i> Fayod						+			1	(Zmitrovich and Ezhov, 2015)
<i>Lepista multiformis</i> (Romell) Gulden	+								1	(Redhead, 1989)
<i>Lichenomphalia alpina</i> (Britzelzelm.) Redhead, Lutzoni, Moncalvo & Vilgalys	+	+		+		+			4	(Redhead, 1989; Knudsen, 2003; Borgen et al., 2006; Zmitrovich and Ezhov, 2015)
<i>L. velutina</i> (Quél.) Redhead				+		+			2	(Zmitrovich and Ezhov, 2015) AR 2827
<i>L. umbellifera</i> (L.) Redhead, Lutzoni, Moncalvo & Vilgalys				+		+			2	(Zmitrovich and Ezhov, 2015)
<i>Naucoria salicis</i> P.D. Orton				+					1	(Zmitrovich and Ezhov, 2015)
<i>Pseudolaccaria pachyphylla</i> (Fr.) Vizzini & Contu				+					1	(Ezhov et al., 2016)
<i>Russula cf. chamiteae</i> Kühner					+				1	(Zmitrovich and Ezhov, 2015)
Total:	2	6	3	27	1	18	0	0		
Aphyllophoroid fungi										
* <i>Amylocorticiellum molle</i> (Fr.) Spirin & Zmitr.				+	+	+	+	+	5	(Shiryaev, 2015); SVER(F) 32350
* <i>Antrodia serialis</i> (Fr.) Donk				+	+	+		+	4	(Shiryaev, 2015); SVER(F) 33006
* <i>A. xantha</i> (Fr.) Ryvarden					+		+		2	(Shiryaev, 2015); SVER(F) 32383
* <i>Cerrena unicolor</i> (Bull.) Murrill							+		1	SVER(F) 33417
* <i>Coniophora puteana</i> (Schumach.) P. Karst.				+	+		+		3	(Shiryaev, 2015); SVER(F) 31969
* <i>Dacrymyces stillatus</i> Nees: Fr.				+			+	+	3	SVER(F) 31845
* <i>Dacryobolus sudans</i> (Alb. & Schwein.) Fr.						+	+		2	SVER(F) 33286
* <i>Ditiola radicata</i> (Alb. & Schwein.: Fr.) Fr.							+		1	SVER(F) 31841
* <i>Eichlerella deglubens</i> (Berk. & Broome) D.A. Reid			+				+		2	SVER(F) 31852
* <i>Funalia trogii</i> (Berk. in Trog) Bondartsev et Singer				+					1	(Ezhov et al., 2012)
* <i>Gloeophyllum sepiarium</i> (Wulfen) P. Karst.					+			+	2	(Shiryaev, 2015); SVER(F) 32388

Table 1. (Contd.)

Species	Region								Information about the finding of species	
	Canadian Archipago	Green-land	Svalbard	Franz Josef Land	Novaya Zemlya	Severnaya Zemlya	Taimyr	New Siberian Islands		
* <i>Hypoderma setigerum</i> (Fr.) Donk					+	+		+	3	(Shiryaev, 2015); SVER(F) 32786
* <i>Hypodontia alutacea</i> (Fr.) J. Erikss.					+				1	(Shiryaev, 2015)
<i>Multiclavula corynoides</i> (Peck) R.H. Petersen		+	+	+	+	+	+	+	6	(Shiryaev, 2011, 2014, 2015); SVER(F) 56304
<i>M. vernalis</i> (Schwein.) R.H. Petersen	+	+	+	+	+	+	+		6	(Shiryaev, 2011, 2014, 2015); SVER(F) 56301
* <i>Peniophora incarnata</i> (Pers.) P. Karst.							+		1	(Shiryaev, 2015)
* <i>P. pithya</i> (Pers.) J. Erikss.				+		+			2	(Shiryaev, 2015)
* <i>Peniophorella praetermissa</i> (P. Karst.) K.H. Larss.		+	+	+	+	+	+		5	(Shiryaev, 2015)
* <i>Stereum sanguinolentum</i> (Alb. & Schwein.) Fr.					+	+			2	(Shiryaev, 2015)
* <i>Tomentella atramentaria</i> Rostr.		+	+			+			3	(Shiryaev, 2015)
* <i>T. badia</i> (Link) Stalpers					+		+		2	(Shiryaev, 2015)
* <i>Trametes ochracea</i> (Pers.) Gilb. & Ryvarden			+			+			2	(Ezhov et al., 2012; Shiryaev, 2015)
* <i>Tubulicrinis calothrix</i> (Pat.) Donk		+			+				2	SVER(F) 32389
* <i>T. sororius</i> (Bourdot & Galzin) Oberw.							+	+	2	(Shiryaev, 2015); SVER(F) 32382
<i>Typhula caricina</i> P. Karst.						+			1	(Shiryaev, 2015)
<i>T. crassipes</i> Fuckel		+	+	+	+	+	+	+	6	(Shiryaev, 2011, 2013); SVER(F) 56324
<i>T. culmigena</i> (Mont. & Fr.) Berthier					+	+	+		3	(Shiryaev, 2011, 2013)
<i>T. lutescens</i> Boud.		+	+	+		+			4	(Shiryaev, 2011, 2013)
* <i>Tulasnella violae</i> (Quél.) Bourdot & Galzin		+			+	+	+	+	5	SVER(F) 31857
* <i>Veluticeps abietina</i> (Pers.) Hjortstam & Tellería						+			1	(Shiryaev, 2015)
Total:	0	1	8	13	17	17	17	9		
Gasteroid fungi										
<i>Bovista tomentosa</i> (Vittad.) De Toni	+				+				2	(Lange, 1987); SVER(F) 38491
<i>Calvatia bellii</i> (Peck) M. Lange	+								1	(Lange, 1990)
<i>Calvatia connivens</i> M. Lange	+								1	(Lange, 1990)
<i>Calvatia cretacea</i> (Berk.) Lloyd Lange	+								1	(Lange, 1990)
<i>Calvatia septentrionalis</i> M. Lange	+								1	(Lange, 1990)
* <i>Crucibulum laeve</i> (Huds.) Kambly					+				1	SVER(F) 39168
<i>Lycoperdon</i> sp.		+							1	see information in the text
Total:	0	6	0	0	2	0	0	0	1	
Amounting to all fungi species:	2	13	11	40	19	33	16	9		

Asterisk indicates alien species.

data regarding macromycetes are presented for the first time.

The highest number of species is known for Franz Josef Land archipelago (40) and Severnaya Zemlya (33), from 19 to 9 were detected on Novaya Zemlya, Chelyuskin Peninsula, Greenland, Svalbard, and De Long Islands, while for the Canadian Archipelago only 2 species are known (Table 1).

Three groups of fungi are considered separately due to the significant differences in their ecology and spatial development of the territory of the polar deserts: agaricoid and gasteroid fungi form fruiting bodies found mainly on the soil, and aphylophoroid fungi found on imported wood and various plant remains. This allows us to distinguish the two groups among the fungi of the polar deserts: species collected only under natural conditions and alien species (alien, anthropogenic).

Taxonomic structure of native mycobiota. The taxonomic richness of the biota of the agaricoid basidiomycetes of the polar deserts is extremely low. All 40 species of agaricoid fungi were collected in the native conditions of the polar deserts, and no alien taxa were identified. The proportion of fungi from the total species diversity of this combined group (14000 species, according to Kirk et al., 2008) in the studied ecosystems was about 0.2%. The polar desert zone is characterized by the low species richness of agaricoid basidiomycetes at all levels of the taxonomic hierarchy, even in comparison with the tundra zone with substantially impoverished microbiota.

Based on abundance, the leading genus is *Galerina* (9 species), followed by the genera *Arrhenia*, *Cortinarius* (6 species), and *Hebeloma* (4 species). The genus *Lichenomphalia* contains three species, and the remaining genera (*Cystoderma*, *Laccaria*, *Inocybe*, *Coprinopsis*, *Naucoria*, *Clitocybe*, and *Lepista*) in the studied territory were represented by one or two species (Table 1). Such a generic spectrum of agaricoid fungi of the polar desert zone in general is typical for the Arctic, although it represents a degenerate spectrum of the tundra mycobiota.

At the moment, the highest number of species is known on Franz Josef Land (27) and Severnaya Zemlya (18), while in other regions this index is much lower, and for Chelyuskin Peninsula and De Long Islands, agaricoid fungi species were not known, which is due to a lack of regular mycological studies in these regions (Table 1).

An analysis of data on agaricoid fungi of some islands of the continental shelf of Eurasia, the Svalbard Archipelago, and Greenland Island, as the most studied in the mycological relation (Gulden, Torkelsen, 1996; Karatygin et al., 1999; Borgen et al., 2006; Geml et al., 2011; Zmitrovich and Ezhov, 2015), showed the transformation of the taxonomic structure of the mycobiota during the transition from tundra to polar deserts. In the tundra, all leading taiga genera were still represented—*Agaricus*, *Lepiota*, *Entoloma*,

Marasmius, *Hypholoma*, *Pholiota*, *Collybia*, *Melanoleuca*, *Tricholoma*, *Boletus*, *Leccinum*, *Suillus*, and *Lactarius*, even though each of them, in contrast to the taiga zone, was represented by a low number of species. These genera were not represented in the polar deserts; e.g., the generic variety of families in the polar desert zone is also low in comparison with the tundra zone. The decrease in the generic variety of the family Tricholomataceae is especially noticeable. According to the data available for the Eurasian sector of the polar desert zone, the species richness of the order Agaricales decreased from 287 to 30 species, i.e., 10 times; in the polar deserts of Greenland, the species richness of this order (6 species) in comparison with the tundra zone (447 species) decreased 75 times; and, on Svalbard (4 against 126 species), it decreased 32 times.

The simplification of the taxonomic structure of the biota of agaricoid basidiomycetes of the polar desert zone is associated with both pessimal abiotic conditions and a weak niche differentiation of primitive periglacial ecosystems. The groups of acidophilic psychrotolerant saprotrophic taxa adapted to development in the moss turf (*Clitocybe*, *Galerina*, and *Lepista*), ephemeral saprotrophs colonized dead grasses and eutrophic (often zoogenic) microsites (*Coprinopsis* and *Cystoderma*), bryophilic biotrophs (*Arrhenia*) and symbiotrophs were associated with *Salix polaris* (*Hebeloma*, *Naucoria*, and *Inocybe*), and fungi formed symbiotic associations with aerophyte algae and protonemata of bryophytes.

The following species were identified in the maximal number of regions (Table 1): *Arrhenia lobata* (4 regions), *Lichenomphalia alpina* (4 regions), *Galerina arctica* (3 regions), and abundant species by the number of findings are as follows: *Clitocybe dryadicola*, *Cortinarius polaris*, and *Hebeloma gigaspernum* (Ezhov et al., 2012; Zmitrovich and Ezhov, 2015). It can be assumed that the number of widespread and active species in this natural zone is actually much higher, and the lack of data is only a consequence of the small attention of mycologists to this region.

Aphylophoroid fungi also are rarely found in polar deserts in comparison with tundra and especially forest ecosystems. In the study zone, 30 species of the aphylophoroid fungi were identified (Table 1): most on Novaya Zemlya, Chelyuskin Peninsula and Severnaya Zemlya (17 species each), 13 on Franz Josef Land Archipelago, and somewhat fewer on De Long Islands (9) and the Northeastern Svalbard Island (8). The lowest number is currently known for Peary Land (1 species), and there are no data for Canadian archipelago. Definitely, most species are known for regions where mycologists have worked longer.

Under natural conditions, on the soil, among mosses and lichens, as well as on dead flowering plants, six species were identified (Table 1), i.e., only a fifth of the species composition. Four times as many species (24) were collected on the introduced substrate

Table 2. Distribution of native and alien species of basidial macromycetes in eight regions of polar desert zones of the Northern Hemisphere

Fungi group	Regions															
	1 (n = 2)		2 (n = 13)		3 (n = 11)		4 (n = 40)		5 (n = 19)		6 (n = 33)		7 (n = 16)		8 (n = 9)	
	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Agaricoid	2	0	6	0	3	0	27	0	1	0	18	0	0	0	0	0
Aphyllophoroid	0	0	1	0	3	5	4	9	5	11	5	10	5	11	2	7
Gasteroid	0	0	6	0	0	0	0	0	1	1	0	0	0	0	0	0
Total:	2	0	13	0	6	5	31	9	7	12	23	10	5	11	2	7

(1) Canadian Arctic Archipelago, (2) Greenland, (3) Svalbard, (4) Franz Josef Land, (5) Novaya Zemlya, (6) Severnaya Zemlya, (7) Taimyr Peninsula, and (8) New Siberian Islands. The total number of fungi species in the region is indicated in brackets. (A) Native species, (B) alien species

(wood, building materials, old abandoned buildings, etc.). Thus, under natural conditions, only six species of the investigated group of fungi were capable of forming fruiting bodies at the northern limit of the existence of life (Table 2). As the conditions were optimized, the number of species increased, for example, in the hypoarctic tundra in the Uralian longitude transect, 60 species were identified and, in the southern taiga, 745 species. The study of this problem using example of localities along the latitudinal temperature gradient on the Ural transect revealed a similar tendency: in the localities on Novaya Zemlya, on average, 2 species were identified, whereas in the hemiboreal regions of the Southern Urals it increased to 78 species (Shiryaev, 2018).

It should be noted that the native species of aphyllophoroid fungi are characterized exclusively by clavarioid life forms, whereas the stranger species are representatives of the corticioid and poroid life forms. Undoubtedly, tree dwelling fungi are an imported element brought into high latitudes along with timber: the forest zone where these fungi grow are many hundreds and thousands of kilometers from the polar deserts. Thus, species collected exclusively from the imported substrate are classified as imported, whereas species that represent the natural element of the polar-deserted mycobiota (forming basidiomata on soil and higher plants) are considered native.

Among aphyllophoroid fungi, under extreme polar desert conditions, only two genera of clavarioid fungi are able to form fruiting bodies under native conditions (Table 1): the basidial lichen genus *Multiclavula* unites two species (*M. corynoides* and *M. vernalis*) and the genus *Typhula* includes four species (*T. caricina*, *T. crassipes*, *T. culmigena*, and *T. lutescens*) and is distinguished by the presence of sclerotial resting stages in the ontogenesis, allowing them to survive unfavorable weather conditions. No such range of genera or species was found in any other natural zone on the planet. Thus, basidial lichen and sclerotial life strategies proved to be the most effective for the reclamation of aphyllophoroid fungi in polar deserts with their severe

cryothermal conditions (Shiryaev, 2006; Shiryaev and Mukhin, 2010; Shiryaev and Mikhaleva, 2013).

The highest number of native species was collected on Novaya Zemlya, Severnaya Zemlya, and Chelyuskin peninsula, where the studies were the most prolonged. Five types of clavarioid species were identified here (Table 2). In the largest number of regions (in six), the following species were identified: *Multiclavula corynoides*, *M. vernalis*, and *Typhula crassipes* (Table 1).

Thus, at the moment, only representatives of the clavarioid morphogroup were identified in the native biota of aphyllophoroid fungi of the polar deserts. Further south, in the mycobiotic tundra, single species of corticioid fungi are added to this group. In the hypoarctic tundra, poroid and telephoroid fungi form the fruiting bodies on the trunks of dwarf birches and willows. In the forest zone, the share of the clavarioid morphogroup decreased, but the share of the poroid and, especially, corticioid morphogroups increased in the taiga and nemoral forests (Shiryaev, 2007; Shiryaev and Mukhin, 2010).

Out of the seven gasteromycetes species, six species, representing three genera were found in nature: *Calvatia* unites four species, and two genera (*Bovista* and *Lycoperdon*) are single species genera. Only one species (*Crucibulum laeve*) was collected under anthropogenic conditions—on decomposing woody-plant remains in an abandoned village on the Novaya Zemlya Archipelago.

The following question arises: why are so many native gasteromycetes that are known in Greenland absent in the Eurasian sector? On the other hand, many agaricoid and aphyllophoroid fungi were found in the Eurasian sector, but very few in Greenland. It is likely that new studies will reveal the same species in all regions of the zone or provide proof of longitude differences in the formation of the diversity of myco-biota of the polar deserts.

Geographical analysis of native mycobiota. One important feature of the landscape profile of biota of agaricoid fungi of the polar desert zone is the prevalence of species with arctic and arctic-alpine distribu-

tion (the total proportion of which reaches 65%) over arctic boreal and plurizonal species (total share reaches 35%). For comparison, in all studied areas of the Northern Hemisphere forest belt, the share of multizonal species was either half of all species diversity or higher. Species with a strictly arctic distribution include *Cortinarius polaris*, *Cystoderma arcticum*, *Galerina arctica*, and *G. pseudocerina*. In comparison with the closely related taxa of the northern hemisphere forest belt, they are characterized by a “strong” addition—a slightly shortened and thickened stipe and pileus moderately opening in a mature state. Arctic-alpine species are confined, apart from arctic landscapes, to altitudinal analogs of tundra and polar deserts, and some of them (*Galerina pseudomycenopsis*, *Lichenomphalia alpina*, etc.) are connected through a series of corresponding mountain habitats with Antarctica (Pegler et al., 1981; Redhead, 1989). The strict absence of arctic-alpine fungi species in the low forests of the forest zone and the continuous zonal extent of their areas indicates the leading role of ecological isolation mechanisms in their ecotype and taxonomic differentiation. Arctic boreal species with a cenogenetic association to the temperate zone penetrated into the specific habitats of the polar deserts either in the mycorrhizal association (*Naucoria salicis*) or as saprotrophic r-strategists (*Coprinopsis martinii*) capable of the rapid colonization of zoogenic microsites rich in easily immobilized detritus.

Most agaricoid fungi of the polar deserts have circumpolar areas (42%). Species with bipolar distribution account for about 10%. The share of European species (*Cortinarius polaris*, *Naucoria salicis*, and a number of species of the genus *Arrhenia*) is 25%; that of pangolarctic species is 16%. The nature of the general distribution of species found in various parts of the polar deserts and the prevalence of taxa with circumpolar distribution among them allow predicting the species composition of the underexplored areas of the Canadian provinces.

All species of clavarioid fungi in the polar deserts are widespread—holarctic, cosmopolitan, and multi-zone. There are no “true” Arctic species whose range would be limited by the tundra zone among them (Shiryaev, 2006, 2014). In the tundra zone, there are a number of arctic-alpine species common in the zonal and mountain tundra and entering the forest zone; in the Arctic they occur mainly in the hypoarctic tundra, but not further north (*Clavaria sphagnicola*, *Ramariopsis subarctica*, *Typhula chamaemori*, etc.).

All native species of clavarioid fungi are Arctic and arctic-alpine elements, while the alien *Crucibulum leave* is ubiquist, found in various regions of the planet. It is too early to judge the distribution of this group in polar deserts. Five out of six native species were identified in only one region (Greenland).

In total, the list of macromycetes of natural habitats comprises 52 species, out of which two-thirds (35)

were collected in only one region. Based from the prevailing now and reasonable ideas about the prevalence of species with wide areas in the Arctic, a similar result indicates a fragmented detection of the species composition of mycobiota in various high latitude regions.

Trophic structure of native mycobiota. Among agaricoid fungi of the polar desert zone, saprotrophs numerically predominate over symbiotrophs and biographs (Table 1), which is also characteristic for mycobiota of the forest belt; however, in the polar deserts, against the background of the predominance of saprotrophs (42%), in comparison with forest mycobiota, the proportion of biotrophs was significantly higher (16%). This is a specific group of agaric fungi adapted to parasitize on moss shoots (the genus *Arrhenia*). In forest mycobiota, the proportion of biotrophs rarely exceeds 3%. Under the harsh conditions of the tundra, and especially the polar deserts, this percentage increases and the role of symbiotic associations increases as well: the total share of symbiotrophs here was 42%, which is on average higher than in forest mycobiota.

Ectomycorrhizal formers (32.3%) were associated with *Salix polaris*. Such species are *Cortinarius polaris*, *Hebeloma gigaspermum*, *H. marginatum*, *H. remyi*, *Inocybe dulcamara*, and *Naucoria salicis*. For *Inocybe dulcamara*, the possibility of mycorrhizal symbiosis with *Dryas octopetala* was also indicated (Ohenoja et al., 1998), which, however rarely, can also exist under polar desert conditions.

Agaricoid fungi, establishing a symbiotic relation with soil algae and moss protonemata, perform an exceptionally important function in the “chronically pioneering” communities of polar deserts on polygonal substrates, forming a kind of “stroma” regulating the surface moisture supply of algal mats and optimizing the extraction of key mineral elements from colloidal soil systems. These are species of the genus *Lichenomphalia*. *L. alpina* develops on poor soils. Upon the extensive growth of autotrophic symbiont biomass, dark green granular thallus known to lichenologists as *Botrydina vulgaris* is formed at the bases of fruiting bodies of this species. The species *Lichenomphalia umbellifera* was often found in pioneer moss communities and *Botrydina* thallus type forms less often. For *Lichenomphalia umbellifera*, various chemotypes, the differentiation of which is also preserved in the cold belt of the planet, were described (Høiland, 1987).

All native species of gasteromycetes are saprotrophs on soil, although to the south, in the forest zone, the proportion of species on deadwood and herbaceous plants increases.

Among the aphyllophoroid fungi under the native conditions of the polar desert, fruiting bodies of typically “forest” groups have not been identified: poroid (bracket fungi) and corticioid fungi—traditional wood-destroying fungi in forest communities. Among

the native fraction of clavarioid fungi in the polar deserts, representatives of two trophic groups develop. Symbiotrophs, forming symbiosis with algae of the genus *Coccomyxa*, include 2 species: *Multiclavula corynoides* and *M. vernalis*, growing on the soil as basidial lichens. A saprotrophic way of life is characteristic of two-thirds of the aphylllophoric fungi species of the polar desert (four species): *Typhula caricina*, *T. crassipes*, *T. culmigena*, and *T. lutescens*, forming basidiomata on the dead parts of grassy plants, and few shrubs—dwarf willows and mountain avens. For this trophic group, the presence of sclerotial structures in the ontogenesis, serving for survival in an unfavorable period for fruiting, is one possible way to maintain viability under such extreme conditions.

Thus, for the polar desert zone, a specific set of trophic groups of the native fraction, limited by symbiotic ground sclerotial and sclerotial saprotrophs on grasses and leaves, was established. Such a set of species and proportions of functional groups are not known anywhere else on the planet, which undoubtedly determines the specificity of the mycobiota of the polar deserts. Further south, in the tundra, with the appearance of a larger set of accessible substrates and an increase in soil fertility, the fruiting bodies form various mycorrhiza-forming species and humus saprotrophs. A higher number of litter saprotrophs appears, developing on the dead birch and willow leaves and xylosaprotrophs.

Diversity of alien fungi species. The problem of alien species in the Arctic mycobiota is widely discussed (Kotiranta and Mukhin, 2000; Arentz et al., 2011; Shiryaev and Mikhaleva, 2013; Held and Blanchette, 2017), but information on their presence in the polar deserts is very limited (Shiryaev, 2015; Blanchette et al., 2016). As the results of this study indicate, in the studied natural zone, all species of agaricoid and 86% of gasteroid fungi are native, while 80% of the species of aphylllophoroid fungi are alien (Table 2).

On the polar desert islands, located hundreds and thousands of kilometers from the mainland, the fruiting bodies of aphylllophoric fungi on sunken timber have not yet been identified. However, in the mainland part of the Arctic, a few species of wood-destroying fungi were collected on driftwood that was transported along rivers in fresh water or for a short time stayed in seawater with significantly lower salinity than in the open ocean (Kotiranta and Mukhin, 2000). Many months and years in salt water probably did not contribute to the conservation of a viable active mycelium of fungi within the wood (Kosonen and Huhtinen, 2008; Shiryaev and Mukhin, 2010; Shiryaev, 2015). Although there were examples showing that some fungi species can survive swimming in ocean waters, these species did not form fruiting bodies and were identified only through genetic studies of wood (Blanchette et al., 2016).

Among the aphylllophoroid fungi, 24 species were identified on the introduced substrate, among which 18 species from 15 genera are corticioid fungi (*Peniophora*, *Tomentella*, *Tubulicrinis*, etc.), while poroid fungi were represented by 6 species from 5 genera (*Antrodia*, *Cerrena*, *Funalia*, *Gloeophyllum*, *Trametes*).

Studies in the tundra zone of Svalbard (Kosonen and Huhtinen, 2008) and Tiksi Bay (Kotiranta and Mukhin, 2000; Shiryaev and Mikhaleva, 2013) showed that corticioid fungi predominate 2.5–4 times in the imported mycobiota over the poroid fungi based on number of species. In our study for polar deserts in general, this ratio was 3.0 (Table 1). For individual regions this parameter varies significantly: from 4.0 (12 corticioid fungi species/3 poroid fungi species) on Severnaya Zemlya to 2.0 (6/3) on Franz Josef Land. These results suggest that the study of the species composition and its distribution according to the morphological groups of the natural zone is at a level similar to similar tundra mycobiota, but individual longitudinal regions require additional studies.

In our study, the following imported species were identified in the highest number of regions: *Tulasnella violea* (five regions), *Peniophorella praetermissa* (five regions), *Amylocorticellum molle* (= *Hypochnicellum molle*) (five regions), *Antrodia serialis* (four regions). Two-thirds of all alien species in the polar deserts (16 species) were collected only 1–2 times: *Conio-phora puteana*, *Funalia trogii*, *Gloeophyllum sepiarium*, *Peniophora incarnata*, *P. pithya*, *Tomentella atramentaria*, *T. badia*, *Trametes ochracea*, and *Veluticeps abietina*. All these fungi have annual fruiting bodies, although in the forest zone they form perennial basidiomata (*Antrodia*, *Funalia*, *Gloeophyllum*, and *Trametes*). In the case of imported species, areas are broad: cosmopolitan and multizone, and there are no specific Arctic species among them.

On the similarity with Antarctic mycobiota. The territory of the Antarctic Peninsula and the nearby islands belong to the zone of polar deserts. *Multiclavula vernalis* was collected on the soil under the natural conditions of the Antarctic Peninsula (Shiryaev, 2014); this species was also found in the polar deserts of the Northern Hemisphere (Table 1). On the dead plant remains in Antarctica, *Typhula subvariabilis* (Yajima et al., 2017), also known in the European Arctic (Shiryaev, 2017), was collected. Thus, despite the fact that, under native conditions of the Antarctic only two species of aphylllophoric fungi were identified, they were both characterized by clavarioid biomorphs and represent the same two genera (*Multiclavula* and *Typhula*) and life strategies (basidial lichen and sclerotial) as in the Arctic polar deserts. Other native species of aphylllophoric fungi have not yet been identified under the native conditions of Antarctica.

In the tundra of the South Shetland Islands, with a more diverse substrates, the number of clavarioid species was higher (Pegler et al., 1981), and here typical

“forest” species—*Typhula capitata* and *T. hyalina* (Smith, 1994)—were identified which are widespread in the tundra and taiga of the Northern Hemisphere (Shiryaev and Mukhin, 2010; Shiryaev, 2013, 2014).

Among alien species, porous fungus *Cerrena unicolor* was collected on introduced hardwood in Antarctica and the Arctic (Arenz et al., 2011) (Table 1). In Antarctica, other wood-destroying corticoid and poroid fungi (*Bjerkandera adusta*, *Chondrostereum purpureum*, *Cylindrobasidium evolvens*, *Peniophora cinerea*, *Trametes hirsuta*, *T. versicolor*, *Schizophora paradox*, *Stereum hirsutum*, and *Thanatephorus* spp.), widely known in the Arctic were also collected (Pegler et al., 1980; Smith, 1994; Osyczka et al., 2012).

Like in Antarctica, *Amylocorticiellum molle* and *Tulasnella violea* (Held and Blanchett, 2017) were found in the polar Arctic deserts among species, most frequently detected on introduced timber (Table 1). Examples of corticoid and agaricoid species on introduced timber are given, indicating that, under native actual climatic conditions, such species cannot be found and their adaptation to Antarctic conditions is impossible.

A number of arctic–alpine agaricoid species associated with the polar deserts of Antarctica were also characteristic for the corresponding zone of the Arctic: *Arrhenia auriscalpium*, *A. lobata*, *Coprinopsis martinii*, *Galerina pseudomycenopsis*, *G. pumila*, and *G. vitiformis* (Bridge et al., 2010). However, in the Arctic, a number of species of Antarctic or American genesis uncharacteristic for the Arctic were detected (*Arrhenia antarctica* (Singer) Redhead & Lutzoni, *A. salina* (Høil.) Bon & Courtec., *Galerina antarctica* Singer, *G. austrocalyprata* A. H. Sm. & Singer, *G. longinqua* A. H. Sm. & Singer, *G. macquariensis* A. H. Sm. & Singer, *G. perrara* Singer), as well as cosmopolitans, the presence of which in the Arctic was not determined presumably due to the still fragmented study of the territory (*Agaricus arvensis* Schaeff., *A. campestris* Schwein., *Agrocybe praecox* Pers., *Cystoderma amianthinum* (Scop.) Fayod, *Coprinopsis atramentaria* (Bull.) Redhead, Vilgalys & Moncalvo), *Galerina hypnorum* (Schrad.) Kühn., *Tubaria furfuracea* (Pers.) Gillet, and *Naucoria glebarum* (Berk.) Sacc.).

Which fungi species can be identified in the aboriginal conditions of the polar deserts? For fungi obligately associated with certain elements of communities (for example, bryophilic biotrophs and mycorrhizal-formers), a prognostic assessment of their presence is possible due to the availability of suitable ecotopes. It can be assumed that the number of species of the genus *Arrhenia*, upon a detailed study of moss communities (intrazonal under the conditions of polar deserts), can increase to 19, the index known for Greenland. The species diversity of the genera *Hebeloma* and *Inocybe* has the potential to increase by about ten species in each genus due to species forming mycorrhiza with willow, present in tundra ecosystems.

The increase in the number of ephemeral saprotrophs associated with eutrophic elements of plant mosaics, up to three species in the genus *Cystoderma* and about the same number in the genus *Coprinopsis*, is also possible. The high diversity in the genera *Agaricus* and *Lepiota*, represented in the tundra zone, cannot be expected under the conditions of polar deserts, because a sufficient stock of mortmass for their development is not accumulated in this zone. For the same reason, a high number of new species of the genus *Clitocybe* associated with development in the moss sod should not be expected; probably no more than ten species can be detected (Zmirovich and Ezhov, 2015).

Thus, according to preliminary estimates, and based on the representation of the niches occupied by agaricoid fungi under conditions of maximal niche differentiation of the optimum zone (coniferous–broadleaf forests zone), the total species composition of the agaricoid basidiomycetes of the polar desert is unlikely to exceed 75 species. Based on this assessment, the degree of detection of this group is currently about 1/3.

As the study of the territories of various polar desert regions intensifies, the differences in their species composition and among themselves will be leveled. This conclusion follows from the nature of the areas of currently identified species, among which taxa with circumpolar (and bipolar) distribution prevail.

For aphyllophoroid fungi, under modern native bioclimatic conditions of polar deserts, probably only clavarioid fungi can form fruiting bodies. It can be assumed that, in the Barents Sea region, due to the milder climate and more precipitation, it is possible to find some other species of clavarioid fungi, in particular, on the dead leaves of the polar willow (*Salix polaris*). This is possible due to the fact that some species of the genus *Typhula* (for example, *T. setipes*) are confined to this substrate in their development and widely represented in the tundra of the Arctic (Shiryaev, 2013) or have already been identified on willow leaves under similar conditions, for example, in the immediate proximity to the glaciers of Western Spitsbergen (*T. crassipes* and *T. lutescens*) (Shiryaev and Mukhin, 2010).

It can be noted that, in some anthropogenically altered habitats of the tundra zone, alien vascular plants and associated fungi appear. In the village of Dikson (Taimyr), basidiomata of *Typhula micans* and *T. variabilis* were collected on the dead parts of *Artemisia tilesii*. It is worth mentioning that, in Dixon and on the New Siberian Islands (Kotelny Island), *Artomyces pyxidatus* and *Ramaria stricta* were detected on imported logs of coniferous species and firewood. It can be assumed that the distribution of some clavarioid fungi to the Arctic is limited by the absence of a necessary substrate. A similar conclusion was made for the analysis of the distribution of other fungi group in tundra (Kotiranta and Mukhin, 2000; Borgen et al., 2006;

Shiryaev and Mikhaleva, 2013). As the predicted warming of the climate happens, these species may be able to form basidiomata under polar desert conditions.

However, the question of species of the genus *Tomentella*, which form mycorrhizas with a few arctic willows and mountain avens (Ryberg et al., 2009), remains open. In the hypoarctic tundra, *Tomentella* species sometimes form fruiting bodies on the litter and tree waste under the mentioned plants. In particular, in the tundra of Kotelny Island (New Siberian Islands) on the dead parts of the *Salix polaris* and on the soil beneath it, as well as on the introduced wood substrate (destroyed), at the place of direct contact with polar willow, *Tomentella atramentaria* formed fruiting bodies (Shiryaev and Mikhaleva, 2013). The question of whether this species was introduced together with timber or is a permanent natural element of the tundra forming fruiting bodies only in a short period of optimum hydrothermal conditions remains unclear. A similar situation was established in this study (for example, on Severnaya Zemlya, Table 1). Further research will probably solve this issue, and possibly the species of the genus *Tomentella* described in this study will be attributed to the natural element in the polar deserts. In studies of Antarctica, an example of the detection of an ubiquist of *Sistotrema brinkmannii* was demonstrated (Hao et al., 2010), and it allows the expectation that this species can be found in the Arctic.

CONCLUSIONS

At the polar limit of life, communities of basidial macromycetes are characterized by their structural simplicity and economy. The need for a close spatial and functional association of organisms is determined by pessimal hydrothermal conditions. For the communities of the periglacial zone, the development of mycorrhizal and lichenlike symbioses is very characteristic. The absence of any significant reserve of unreduced biomass is a characteristic feature of periglacial biomes. In communities of polar deserts nothing is “superfluous,” and the number of organisms of practically all systematic groups is rigidly regulated.

For macromycetes, the absence of depots of lignin and other polyphenolic composites (blowdown soil complexes in the forest zone and a sufficiently developed moss sod in many types of tundra communities) is significant in the polar desert zone. The biomorphological structure of the vegetation cover of the polar desert restrict the development of this zone by fungi as mycorrhizal symbionts. This niche is limited to polar willows and mountain avens. These conditions mainly determine the peculiarities of the taxonomic composition and trophic structure of the biota of the basidial macromycetes of the polar deserts. Taxa, the diversification of which is associated with the development of woody and littered meganiches, as well as mycorrhizal specialization on “forest” types of cenosis-forming species, are absent in this zone.

The following specific features of the taxonomic and ecological structure of the mycobiota of the polar desert zone can be listed.

(1) Very poor species composition of basidial macromycetes is formed here in comparison with southern biomes. In this natural zone, 77 species of fungi were identified, which is three orders of magnitude lower than in the taiga biome. The highest number of species is currently known for Franz Josef Land archipelago (40) and Severnaya Zemlya (33)—from 18 to 9 species identified on the Northeastern Land of Svalbard, Novaya Zemlya, Chelyuskin Peninsula, Peary Land, and De Long Islands—whereas only 2 species were collected in the Canadian Arctic Archipelago. For the polar desert zone, 14 species were reported for the first time. Information on the findings of macromycetes on De Long Islands is presented for the first time.

(2) The species composition of the agaricoid fungi of the polar deserts consists of 40 species, all of which are identified under natural conditions. Out of the 7 species of gasteroid fungi, 84% were collected under natural conditions, and among the 30 species of the aphylophoroid, only 6 can be attributed to the natural component of the biota (20%), while the remaining species were collected on an alien wood substrate.

(3) Under the natural conditions of polar deserts, among agaricoid fungi, the following groups can be clearly distinguished: (a) psychrotolerant saprotrophic taxa adapted to development in the moss sod (*Clitocybe*, *Galerina*, and *Lepista*), (b) ephemeral saprotrophs colonizing dead grasses and eutrophic (often zoogenic) microsites (*Coprinopsis* and *Cystoderma*), (c) bryophilic biotrophs (*Arrhenia*), (d) symbiotrophs associated with *Salix polaris* (*Hebeloma*, *Naucoria*, and *Inocybe*), and (e) fungi forming symbiotic associations with aerophyte algae and protonemata of bryophytes. The group of aphylophoroid fungi is represented here exclusively by the clavarioid morphological group (genera *Multiclavula* and *Typhula*). In general, for basidial macromycetes of polar deserts, in comparison with forest ecosystems, the prevalence of saprotrophic species on the dead parts of flowering plants is typical, although the share of symbiotrophs (mycorrhiza-formers and basidial lichens) is also high. Basidial lichens and sclerotial life strategies, undoubtedly, contribute to the reclamation under extreme conditions of the polar deserts. All aboriginal species of gasteromycetes are saprotrophs on soil, where the species of the genus *Calvatia* predominate. Such a set of species and genera reflects the specificity of the high-latitude mycobiota, and the established set of taxa can be given the status of a zonal mycological standard.

(4) The chorionic profile of aboriginal biota of agaric fungi has a pronounced arctic–alpine character (more than 74% of species are characterized by arctic or arctic–alpine distribution; the area of about 42% of species is circumpolar), and bipolar species account

for 10%. This, in fact, is a group of “marginals”; most of them not represented in the flat spaces of the temperate and arid belts. All native species of gasteromycetes are typical arctic–alpine species. In contrast, all species of clavarioid fungi of the polar deserts are widespread—holarctic, cosmopolitan, and multizonal. Among them there are no “true” Arctic species, the area of which would be limited to the tundra zone. Typical arctic–alpine species are not found here—they are distributed to the south, in the zonal and mountain tundra.

(5) A number of arctic–alpine and bipolar species of the Arctic, associated with polar deserts, is also characteristic of the corresponding zone of Antarctica. However, in Antarctica there are also a number of species that are uncharacteristic for the Arctic of Antarctic or American genesis (*Arrhenia antarctica*, *A. salina*, *Galerina antarctica*, *G. austrocalyptata*, etc.), as well as cosmopolitans, the presence of which in the Arctic was not detected presumably due to the still fragmentary study of the territory (*Agaricus arvensis*, *A. campestris*, *Agrocybe praecox*, *Cystoderma amianthinum*, etc.). Gasteromycetes have not yet been identified in Antarctica. For aphylllophoroid fungi under the natural conditions of Antarctica, the same set of genera (*Multiclavula* and *Typhula*), respectively, also represented only by clavarioid bimorphs, basidial lichens, and sclerotial life strategies, as in the polar deserts of the Arctic, was identified. No other native species of aphylllophoroid fungi under the native conditions of the Arctic and Antarctic have been identified. The established mycological standard for aphylllophoroid fungi in polar deserts is probably also relevant for Antarctica.

(6) Agaricoid fungi were not found in the Arctic on an introduced substrate, whereas among the alien fraction of these fungi in Antarctica, a species of the genus *Pholiota* was identified on the introduced wood. The probability of finding representatives of this genus in the Arctic is high. Among the aphylllophoroid fungi, 24 species from 20 genera were identified on the imported substrate. In Antarctica there are also about 20 species known from the same genera (*Bjerkandera adusta*, *Chondrostereum purpureum*, *Cylindrobasidium evolvens*, *Peniophora cinerea*, *Trametes hirsuta*, *T. versicolor*, *Stereum hirsutum*, etc.). These species are often found on household buildings in the tundra zone of the Arctic, but they have not yet been identified in polar deserts. The set of genera and the most common species largely coincides with the results obtained in Antarctica. In the two compared regions, *Amylocorticium molle* and *Tulasnella violea* are among the most frequently detected on imported wood. In Antarctica and the Arctic, the cosmopolitan poroid fungus *Cerrena unicolor* was collected. Among the morphological groups in both regions, the number of species of corticoid fungi exceeds the poroid fungi by 3–4 times and distinguishes high-latitude mycobiota from forest mycobiota. The list of alien species found in both regions consists entirely of ubiquist taxa, which

suggests the stochastic nature of the formation of the imported mycobiota developing on the polar limits of the global temperature gradient.

The dominant opinion is that the high-latitude mycobiota is characterized by the predominance of species with wide areas. However, in this study, two-thirds of native fungi species were identified in only one region. Undoubtedly, such a result indicates the fragmented detection of the mycobiota species composition at the present and requires additional studies in various regions of the polar desert zone.

ACKNOWLEDGMENTS

We are grateful to O.G. Dobrovolskii (Norilsk), A.N. Shuman (Krasnoyarsk), S.V. Malen’kikh (Yekaterinburg), H. Kotiranta (Helsinki), E. Okhenoiya (Oulu), H. Knudsen (Copenhagen), and M. Skierli (Tromso) for help in collecting material and information on the occurrence of some species. We are grateful to R.V. Ershova and M.V. Gavrilov for help in organizing research. The research by A.G. Shiryaev was supported by the Russian Foundation for Basic Research, project no. 18-05-00398. The study by I.V. Zmitrovich was carried out within the framework of the state task of the Komarov Botanical Institute, Russian Academy of Sciences Biodiversity and Spatial Structure of Fungi and Myxomycete Communities in Natural and Anthropogenic Ecosystems.” The study by O.N. Ezhev was conducted as part of topic no. 0409-2015-0141 “Structure and Variability of Populations of Forest Communities in the Northern Arctic Regions of the Russian Plain” (state registration no. AAAA-A18-118011690221-0).

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Translated by V. Mittova