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EXPERIMENTAL ARTICLES

The Structure of Micromycete Complexes in Permafrost and Cryopegs of the Arctic

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Abstract—A comparative study of the structure of micromycete complexes has been performed. The samples of micromycetes were taken by boring from unique habitats: cryopegs (lenses of non-freezing hypersaline water in ancient permafrost horizons) and permafrost Arctic sediments of different age enclosing these cryopegs. The possibility of characterizing the above habitats by the structure of specific complexes of microscopic fungi using qualitative and quantitative indices at extremely low numbers of these organisms was demonstrated.

Key words: cryopegs, permafrost sediments, mycelial fungi.

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It is known that eukaryotes, including mycelial fungi, are able to exist in an active state at low positive and weakly negative temperatures [1, 2]. The quantity and biodiversity of mycelial fungi in extreme habitats are determined by the efficiency of adaptive mechanisms of individual fungal species and by the presence of environmental protection factors. Our results show that the time limits of viability preservation in eukaryotes, including fungi, are very broad. Fungi have been found in deep permafrost sediments of the age embracing the entire Pleistocene and even late Pliocene periods [3, 4], which is evidence of their high adaptive abilities. It is now well known that eukaryotes are able to survive the action of multiple stressors [5]. In this respect, it is particularly interesting to study the microscopic fungi in cryopegs, which are a unique habitat characterized by permanently negative temperatures, high salinity, and the absence of external action during the geological time period. Eukaryotes are rather diverse in the microbial communities formed in cryopegs [6].

The data on the diversity of mycelial fungi in permafrost habitats available in the literature are usually descriptive and concern surface horizons. They contain only lists of isolated fungal species [7], which give no information about the domination of one or another species in different samples and are even less informative concerning the occurrence of individual species in deep horizons.

We have therefore attempted for the first time to determine the structure of the complexes of microscopic fungi isolated from cryopegs and the sediments that enclose them. In this work, specific complexes of microscopic fungi are determined as certain sets of micromycete species isolated in this research by the applied methods of sample treatment on the applied nutrient media. They were characterized by the frequency of occurrence of individual species.

MATERIALS AND METHODS

Mycelial fungi were studied in cryopegs and in the covering, enclosing, and underlaying permafrost sediments of the Arctic. Soil and water samples of the cryopegs opened by boring in the area of continuous occurrence of permafrost sediments were taken from four boreholes close to each other (14/99, 15/99, 16/99, and 17/99). The boreholes were located in the tundra zone of the Kolyma lowland near the East Siberian Sea coast (69°59′ N, 159°30′ E) (Fig. 1). The total of 4 samples of cryopeg water, 4 samples of suspension (cryopeg water contaminated with upper soil layers), and 23 samples of the covering, enclosing, and underlaying grounds was studied (Table 1). The cryopegs in these boreholes are at the sea horizon level of the end of Middle Pleistocene, which marks the boundary of the Polar basin before the decrease of its level and recession to the north in Late Pleistocene [8]. The average annual temperature of permafrost sediments and brine in this area is –9°C; their salinity is 170–300 g/l.

In order to recover the highest possible number of viable microscopic fungi occurring under conditions of natural permafrost cryopreservation, different temperatures of ground samples thawing were applied: 20, 35,

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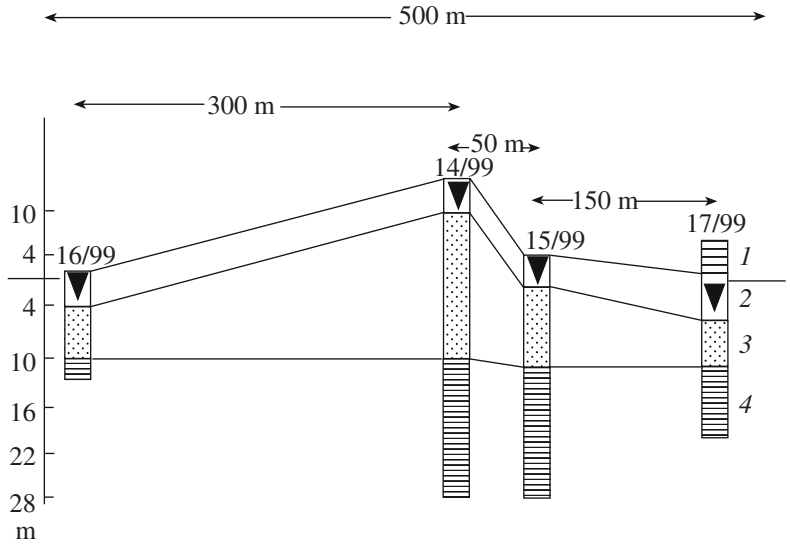

Fig. 1. Characteristics of the boreholes used for sampling. The line on the *Y* axis indicates the level of Lake Yakutskoye. *1*, alass sediments; *2*, late Pleistocene ice complex; *3*, sea sediments; *4*, terrigene sands.

and 52°C, similar to the procedure used previously in analogous studies [3]. Moreover, different nutrient media were used for the most thorough enumeration of mycelial fungi both in grounds and in cryopegs: malt agar (MA), Czapek agar with 2% sucrose (Cz 2), and Czapek agar with 0.1% sucrose (Cz 0.1) (for oligotrophs), without NaCl or with different NaCl concentrations (1, 5, 10, 15, and 20%), as well as different incubation temperatures (4 and 25°C). The number of experimental variants per one sample was up to 65.

The pure cultures of isolated microscopic fungi were identified on the basis of their cultural and morphological characteristics using modern guides for particular taxonomic groups [9, 10].

The qualitative similarity index of the samples was calculated according to the formula [11] $S = 2C/(A + B)$, where A is the total number of micromycete species of the first sample, B is the total number of micromycete species of the second sample, and C is the total number of species common for both samples.

The quantitative similarity index of the samples was calculated according to the formula [12] $S = 2\Sigma C_{min}/(A + B)$, where A is the sum of occurrence frequencies of micromycetes of the first sample, B is the sum of occurrence frequencies of micromycetes of the second sample, and C is the sum of occurrence frequencies of the species common for both samples (taking the least of the two values).

The indexes of similarity were calculated and the corresponding charts were plotted using the Biomatrix software package applying the elements of cluster analysis [13].

RESULTS AND DISCUSSION

Our studies revealed the presence of viable mycelial fungi both in some ground horizons of the examined boreholes and in cryopegs. The number of fungi in the cryopegs and enclosing permafrost sediments varied from several CFU (colony-forming units) to hundred thousand CFU per 1 g of air-dry soil or per 1 ml of cryopeg water (Table 1). Only single colonies were revealed in saline sediments, but in the upper freshwater horizons their number was sometimes much higher. The change of fungal CFU by profile is evidence of micro-focal distribution of mycelial fungi in this habitat. Distribution of the fungi may be irregular even within a single horizon. This is confirmed by the significant difference (five- to tenfold in some samples) between the maximal quantity revealed in one of the experimental variants and the average value for all variants of cultivation and thawing.

The species composition of mycelial fungi from the cryopegs and enclosing sediments is presented in Table 2. A total of 46 fungal species (23 genera) was identified and considerable amounts of dark and light sterile mycelium were isolated. Comparison of species compositions of the fungi showed that an almost equal number of micromycete species was isolated on nutrient media of different composition. However, the similarity of the micromycete complexes isolated on rich media (MA and Cz 2) did not exceed 60%; this observation confirms the necessity of using different nutrient media in such studies. At the same time, representatives of only three species were revealed on a deficient medium (Cz 0.1); these species were isolated also on MA and Cz 2. This fact does not contradict the data of the Arctic ice studies showing more successful reactivation of microorganisms from frozen samples on nutrient media with high content of sugars, amino acids, and

Table 1. The quantity of mycelial fungi in cryopegs and enclosing permafrost sediments

Borehole no.	Horizon	Age (thousands of years)	Depth (m)	Quantity (CFU/g (ml))	
				Average	Maximal
14/99	Holocene freshwater terrigene sediments	6.48	1.00	5.6×10^2	6.8×10^3
	Late Pleistocene ultrafresh ice complex	30.19–36.40	8.95–9.00	0	0
		30.19–36.40	15.42–15.46	6.4×10^2	3.3×10^3
		43.32	19.10–19.17	0.3×10^2	1.9×10^2
	Middle Pleistocene saline sea sediments	100–120	21.00–24.00*	0.3×10^2	0.6×10^2
		100–120	21.00–24.00**	0.2×10^2	0.2×10^2
		100–120	21.85–21.90	0.7×10^2	4.4×10^2
		100–120	24.40–24.45	0	0
	Late Pliocene freshwater terrigene sediments (?)	~3000	27.50–27.70	0	0
15/99	Late Pleistocene ultrafresh ice complex	15–40	1.00–1.10	7.8×10^3	1.5×10^4
		15–40	5.35–5.40	0.8×10^2	2.1×10^2
	Middle Pleistocene saline sea sediments	100–120	10.95–11.00	0.3×10^2	2.2×10^2
		100–120	17.00–21.00*	1.1×10^2	2.1×10^2
		100–120	17.00–21.00**	4.0×10^2	4.0×10^2
		100–120	14.15–14.25	0.2×10^2	0.7×10^2
		100–120	21.00–21.20	0.1×10^2	0.7×10^2
	Late Pliocene freshwater terrigene sediments (?)	~3000	24.15–24.25	0.2×10^2	0.6×10^2
16/99	Holocene freshwater terrigene sediments	2.9	1.95–2.00	0.1×10^2	1.0×10^2
		5–10	3.35–3.40	0.1×10^2	0.6×10^2
	Late Pleistocene ultrafresh ice complex	15–20	4.90–4.95	4.9×10^3	1.4×10^4
		26.4	7.67–7.70	0.1×10^2	0.6×10^2
	Middle Pleistocene saline sea sediments	100–120	11.00–12.00*	0	0
		100–120	11.00–12.00**	0.1×10^2	0.3×10^2
17/99	Holocene freshwater terrigene sediments	5–10	3.20–3.30	1.3×10^5	1.9×10^5
	Late Pleistocene ultrafresh ice complex	15–40	6.70–7.00	3.4×10^2	1.7×10^3
		15–40	12.50–13.00	0.6×10^2	1.5×10^2
		15–40	14.90–14.95	0.4×10^2	1.4×10^2
	Middle Pleistocene saline sea sediments	100–120	15.80–16.00	0.2×10^2	0.4×10^2
		100–120	17.00–17.30*	0.1×10^2	0.2×10^2
		100–120	17.00–17.30**	0.4×10^2	1.2×10^2
		100–120	17.30–17.40	0.3×10^2	0.5×10^2

Notes: * indicates brine.
** indicates suspension.

Table 2. The species composition of micromycetes in cryopegs and enclosing permafrost sediments (frequency of occurrence, %)

Fungal species	Cryopegs		Permafrost sediments			
	Water	Suspension	Holocene	Pleistocene		Late Pliocene
				Late	Middle	
Acremonium pteridii W. Gams et Frankland			20.0			
A. salmoneum W.Gams et Lodha		25.0				
Alternaria alternata (Fr.) Keissl.	50.0					
Aspergillus fumigatus Fresen.				9.0		
A. niger Tiegh.					20.0	
A. sydowii (Bainier et Sartory) Thom et Church				9.0		
A. versicolor (Vuill.) Tirab.					20.0	
Aureobasidium pullulans (de Bary) G. Arnaud var. *pullulans*	25.0				40.0	
A. pullulans (de Bary) G. Arnaud var. *melanogenum* Herm.-Nijh.				18.0		
Botrytis cinerea Pers.				18.0		
Chaetomium globosum Kunze					20.0	
Chrysosporium merdarium (Ehrenb.) J.W. Carmich.				9.0		
Cladosporium cladosporioides (Fresen.) G.A. de Vries		25.0	20.0	27.0	20.0	
C. herbarum (Pers.) Link	75.0	25.0	40.0	27.0	20.0	
Coelomycetes sp. (I)				9.0		
Coelomycetes sp. (II)					20.0	
Eurotium amstelodami L. Mangin				9.0		
E. herbariorum (F.H. Wigg.) Link			20.0	9.0		
Fusarium solani (Mart.) Sacc.	25.0	25.0				
Geomyces pannorum (Link) Sigler et J.W. Carmich.	75.0	50.0	40.0	18.0		
G.vinaceus Dal Vesco	25.0		20.0			
Gliocladium sp.				9.0		
Lecythophora mutabilis (J.F.H. Beyma) W. Gams et McGinnis			20.0			
Monodictys sp.				9.0		
Penicillium aurantiogriseum Dierckx	25.0	25.0				50.0
P. chrysogenum Thom				9.0	20.0	
P. glabrum (Wehmer) Westling				9.0		
P. granulatum Bainier				9.0	20.0	50.0
P. griseofulvum Dierckx	25.0					
P. minioluteum Dierckx	25.0	50.0		9.0	40.0	
P. rugulosum Thom				9.0		
P. simplicissimum (Oudem.) Thom			20.0	9.0		
Penicillium sp.					20.0	
P. variabile Sopp		25.0			20.0	
P. verrucosum Dierckx		25.0				
Phialophora melinii (Nannf.) Conant			20.0			
Phoma destructiva Plowr.				9.0		
Ph. jolyana Piroz. et Morgan-Jones var. *jolyana*					20.0	

Table 2. (Contd.)

Fungal species	Cryopegs		Permafrost sediments			
	Water	Suspension	Holocene	Pleistocene		Late Pliocene
				Late	Middle	
Ph. nebulosa (Pers.) Berk.			20.0			
Phoma sp.			20.0			
Thysanophora penicillioides (Roum.) W.B. Kendr.					20.0	
Ulocladium atrum Preuss			20.0	9.0		
U. botrytis Preuss		25.0				
Valsa sordida Nitschke	25.0					
Xylohypha nigrescens (Pers.) E.W. Mason				9.0		
Light sterile mycelium	50.0	25.0		27.0	40.0	
Dark sterile mycelium	25.0	50.0	20.0	32.0	40.0	
Dark sterile mycelium with sclerotia				9.0		
Total number of species	12	12	13	25	16	2

Table 3. The species composition of cryopeg micromycetes isolated on different nutrient media at both cultivation temperatures, 4 and 25°C

Taxon	Nutrient media								
	MA	MA + 1% NaCl	MA + 5% NaCl	Cz 0.1	Cz 0.1 + 1% NaCl	Cz 0.1 + 5% NaCl	Cz 0.1 + 20% NaCl	Cz 2.0	Cz 2.0 + 5% NaCl
Alternaria alternata				V	V			V	
Aureobasidium pullulans		V							
Cladosporium herbarum	V							V	
Geomyces pannorum var. *pannorum*	V		V	V	V	V	V	V	V
G. vinaceus					V				
Light sterile mycelium		V							

vitamins [14]. This is apparently the result of the fact that most of the fungi in permafrost sediments exist in a dormant state and growth initiation requires a rather rich nutrient medium. Representatives of the species *Geomyces pannorum* dominating in the cryopegs were isolated on almost all of the used media, including oligotrophic ones (Table 3), which probably results from the absence of microfocality in the liquid medium or points to the possibility of their presence in this habitat in an active state.

Determination of occurrence frequency for individual micromycete species made it possible to establish the structure of specific complexes, i.e., to determine dominant, frequent, and rare species (Table 4).

According to our data, the fungi *Cladosporium herbarum* and *G. pannorum* are dominant in the cryopegs. The frequency of occurrence of these species in most of the studied water samples is 75%. Species such as *Alternaria alternata*, *Penicillium minioluteum*, and, probably, as yet unidentified strains of sterile light mycelium may be also termed frequent species.

In grounds, the diversity of mycelial fungi is much higher. Here, explicitly dominating species are absent, but representatives of the species *C. herbarum*, *G. pannorum*, and *P. minioluteum* have the highest frequency of occurrence. Twenty-six species were found solely in permafrost sediments and 6 species were found solely in the water of cryopegs. Representatives of micromycete species typical of both the water and grounds were isolated from suspension samples, which is in agreement with the results of the study of prokaryotic microorganisms from the same boreholes [15].

Specific complexes of microscopic fungi in saline grounds were represented by a lower number of species than those from freshwater sediments: *G. pannorum*, five species of the genus *Penicillium* (*P. aurantiogriseum*, *P. chrysogenum*, *P. granulatum*, *P. minioluteum*, *P. variabile*), two species of the genus *Cladosporium* (*C. cladosporioides* and *C. herbarum*), *Chrysosporium merdarium, Aureobasidium pullulans* var. *pullulans*, and sterile mycelium.

Table 4. The structure of micromycete complexes from cryopegs and permafrost sediments

Species category	Cryopegs		Permafrost sediments			
	Water	Suspension	Holocene	Pleistocene		Late Pliocene
				Late	Middle	
Dominant (occurrence frequency >70%)	*C. herbarum* *G. pannorum*	No	No	No	No	No
Frequent (occurrence frequency >25%)	*A. alternata* Light sterile mycelium	*G. pannorum* Dark sterile mycelium *P. minioluteum*	*C. herbarum* *G. pannorum*	Dark sterile mycelium Light sterile mycelium *C. cladosporioides* *C. herbarum*	*A. pullulans* var. *pullulans* Dark sterile mycelium Light sterile mycelium *P. minioluteum*	*P. aurantiogriseum* *P. granulatum*
Rare (occurrence frequency 25% or less)	*A. pullulans* var. *pullulans* *F. solani* *G. vinaceus* Dark sterile mycelium *P. aurantiogriseum* *P. griseofulvum* *P. minioluteum* *V. sordida*	*A. salmoneum* *C. cladosporioides* *C. herbarum* *F. solani* Light sterile mycelium *P. aurantiogriseum* *P. variabile* *P. verrucosum* *U. botrytis*	*A. pteridii* *C. cladosporioides* *E. herbariorum* *G. vinaceus* *L. mutabilis* Dark sterile mycelium *P. simplicissimum* *P. melinii* *P. nebulosa* *Phoma* sp. *U. atrum*	*A. fumigatus* *A. sydowii* *A pullulans* var. *melanogenum* *B. cinerea* *C. merdarium* *Cladosporium* sp. *Coelomycetes* sp. (I) *E. amstelodami* *E. herbariorum* *G. pannorum* *Gliocladium* sp. *Monodictys* sp. *P. chrysogenum* *P. glabrum* *P. granulatum* *P. minioluteum* *P. rugulosum* *P. simplicissimum* *P. destructiva* *U. atrum* *X. nigrescens*	*A. niger* *A. versicolor* *C. globosum* *C. cladosporioides* *C. herbarum* *Coelomycetes* sp. (II) *P. chrysogenum* *P. granulatum* *P. variabile* *P. jolyana* var. *jolyana* *T. penicillioides*	Not detected

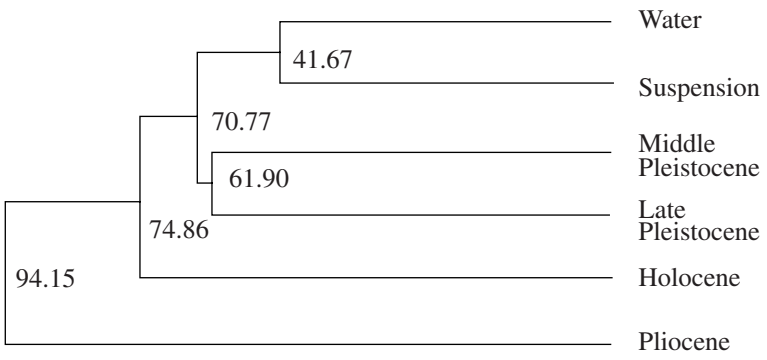

Fig. 2. Similarity of permafrost sediments, cryopeg water, and suspension samples by the qualitative characterization of occurrence of different micromycete species.

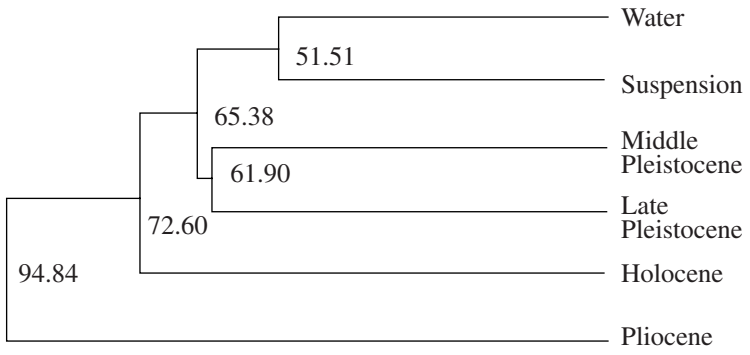

Fig. 3. Similarity of permafrost sediments, cryopeg water, and suspension samples by the quantitative characterization of occurrence of different micromycete species.

Comparison of the species diversity of mycelial fungi in the cryopegs and enclosing layers showed that the index of similarity of specific micromycete complexes revealed in these habitats was 30% or less. These results do not depend on the method of index calculation, whether it is based on registration of only the species composition of micromycetes (qualitative characteristic, Fig. 2) or whether it uses the quantitative indices of species occurrence (Fig. 3). The figures show that the samples of cryopeg water and suspensions have the greatest similarity to each other. Such results could be easily foreseen, as suspensions were formed by the substance from the walls of the rocks enclosing the lenses with brines.

It has been shown that, the common species notwithstanding, specific halopsychrotolerant communities of mycelial fungi are formed under the conditions of cryopegs; they significantly differ in species composition and structure from the communities of permafrost sediments. Figures 2 and 3 also show the results of similarity testing of the structure of complexes of mycelial fungi in the samples of permafrost sediments of different age. It can be seen that the similarity indices for the samples of different age are rather low and do not exceed 38.2%. The lowest values were noted for the sediments of Holocene and Late Pliocene, which are the most distant from each other in geological time. This indicates that the proposed method of integral characterization of the set of species found in the samples of different age makes it possible to determine the differences between samples containing low numbers of micromycetes.

Our data on the domination of members of the genera *Cladosporium, Geomyces*, and *Penicillium* in the isolated complexes are in good agreement with the previous data on the ability of *Penicillium* fungi isolated from the Arctic sea ice and sea water to develop at low water activity and relatively low (10°C) temperatures [16]. Previously, we have shown a distinct tendency for the predominant development of *Penicillium* and *Cladosporium* cultures isolated from permafrost sediments at low temperatures [4]. This is manifested by the shift of growth limits of the above fungi towards low positive temperatures and by an increase in the radial growth rate at 5–12°C (as compared with present-day isolates). Subsequent investigation of the physiological peculiarities of the fungi dominating in cryopegs showed that *Geomyces* fungi, which are often isolated from Arctic and Antarctic habitats in great amounts, are capable of

active growth under the joint action of low temperature and high salinity of the medium [17].

Thus, in spite of the extremely low occurrence of mycelial fungi in permafrost sediments and cryopegs, our results demonstrate that it is possible to isolate specific complexes of micromycetes and to estimate their species composition using diverse nutrient media, a significant number of repeated samples, and different cultivation conditions. It was shown that the qualitative and quantitative indices characterizing the above micromycete complexes provide an opportunity for comparative assessment of the samples of permafrost sediments and cryopegs of different ages.

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