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NEW RECORDS OF *ARCHAEORHIZOMYCETES* FROM RUSSIA REVEALED BY METAGENOMIC APPROACH

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The class *Archaeorhizomycetes* (*Taphrinomycotina*, *Ascomycota*) is a cosmopolitan group of fungi associated with the plant root system. Representatives of this class are extremely poorly studied due to the difficulty of cultivation, but sequences belonging to *Archaeorhizomycetes* are often detected during sequencing of natural substrates. Four unique sequences belonging to *Archaeorhizomycetes* were obtained during a study of the diversity of fungi associated with the orchid *Goodyera repens* by next-generation high-throughput sequencing of the ITS2 site. One sequence identical to *Archaeorhizomyces borealis* was identified in Russia for the first time, while two sequences presumably belong to a yet undescribed genus. One sequence belonging to an undescribed species of the genus *Archaeorhizomyces* is the most frequently detected in all types of samples (sod-podzolic soil, coniferous tree roots, rhizosphere, and orchid roots). The presence of nucleotide sequences of representatives of this class in the root system of *Goodyera repens* was shown for the first time, and the presence of one sequence in free soil was shown for the first time. The sequences were deposited in the GenBank database.

Keywords: *Archaeorhizomyces borealis*, environmental sequencing, ITS2, OTUs

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INTRODUCTION

Class *Archaeorhizomycetes* Rosling et T.Y. James (*Taphrinomycotina*, *Ascomycota*) was coined in 2011 and currently comprises a single order *Archaeorhizomycetales* with a monotypic family *Archaeorhizomyce-taceae* presented by *Archaeorhizomyces* genus with only two known species, *A. finlayi* Rosling et T.Y. James and *A. borealis* Menkis, T.Y. James et Rosling (Menkis et al., 2014). Both species were revealed in pine roots, but did not produce recognizable mycorrhizal structures (Rosling et al., 2011; Menkis et al., 2014). Despite of small number of species described, direct sequencing and metagenomic approaches applied to environmental samples often allow to detect archaeorhizomycete OTUs (operational taxonomic units) thus implying high hidden diversity within the class (Taylor et al., 2014; Schadt, Rosling, 2015).

Archaeorhizomycetes species are supposed to be globally distributed with higher abundance in boreal forests (Rosling et al., 2013). Some archaeorhizomycete OTUs were recently recorded from the Subarctic (Miyamoto et al., 2022). These fungi are considered to be associated with ectomycorrhizal tree roots, but their OTUs are detected either in bulk soil (Prenafeta Boldú et al., 2014) or non-ectomycorrhizal plants, e.g. *Orchidaceae*, roots too (Qin et al., 2019). Orchid mycobionts are known to form mycorrhizal networks linking orchid

plants to neighboring trees thus providing nutrient sharing (Genre et al., 2020). This implies some common mycobionts shared between ectomycorrhizal trees and orchids and allows assuming *Archaeorhizomycetes* association with orchids' roots too. Revealing of *Archaeorhizomycetes* in roots of *Orchidaceae* species typical for boreal forests, such as *Goodyera repens* (L.) R. Br. can contribute to more full recognition of archaeorhizomycete ecology.

Currently, eight archaeorhizomycete sequences from Russian territory are available in GenBank database, and four of them are resulted from this study. According to data on biodiversity retrieved from UNITE, there are no confirmed records on *Archaeorhizomycetes* from Russia but they are presented for a number of both North and South European countries (Fig. 1). Besides, *Archaeorhizomyces* OTUs have been reported from North America, Africa, Eastern and South-Eastern Asia and Australia.

Considering wide distribution, understudied ecology and physiology, lacking data on distribution in Russia, and potential significance of *Archaeorhizomycetes* for forest ecosystem performance, the study was aimed at revealing the biodiversity of this taxon and its occurrence estimation in different habitats within pine forest with spruce: *Goodyera repens* roots and rhizosphere, conifer roots and bulk soil.

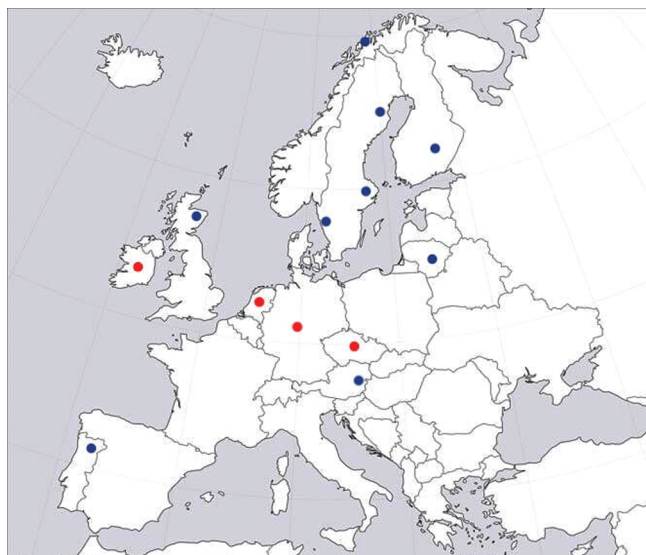


Fig. 1. *Archaeorhizomyces* records in Europe according to UNITE (Kõljalg et al., 2020). Blue marks indicate defined localities; red marks point the countries for which OTUs are available.

MATERIALS AND METHODS

Sampling and sample preparation. Environmental sampling was carried out in November 2021 at the territory of MSU Zvenigorod biological station (MSU ZBS, Moscow Region, Russia) in conifer forest dominated by *Pinus sylvestris* and *Picea abies* underlied by podzol soil. In total 22 samples (from 11 habitats with two replicas) were collected and analyzed (Table 1).

Plant roots were freed from adjacent soil particles by rinsing in water and surface sterilized by serial dipping in 70% ethanol, surfactant, and amoxicillin solution. Prepared samples were stored at 4°C until were analyzed.

Amplification and metagenom analysis. Environmental DNA was extracted by means of FastDNA SPIN Kit (MP), ITS2 region was amplified with NR_5.8SR (forward) and NR ITS4R (reverse) primers. Real-time PCR and genomic library construction were accomplished using a CFX96 Touch (Bio-Rad) amplifier. Next-generation sequencer Illumina MiSeq generating more than 5000 reads per sample was applied for genome library analysis. The analysis was carried out by BioSpark Company (Troitsk, Moscow Region).

Data procession. QIIME 1.9.1 algorithm was employed for sequence segregation, forward and reverse read consolidation and chimeric sequence removal. Taxonomy of OTUs revealed was established according to references from UNITE and GenBank databases. Samples were compared, and OTUs were subset into classes of occurrence by means of quartile analysis made with Microsoft Excel. Sequence processing, phylogenetic trees construction, and sequence deposition into GenBank was accomplished with MEGA-X.

RESULTS AND DISCUSSION

To explore fungal biodiversity 11 samples with two replicas from sites with *Goodyera repens* plants at the territory of MSU ZBS was subjected to metagenom analysis by high-throughput sequencing.

Archaeorhizomyces diversity on the territory of Russia

Four different archaeorhizomycete OTUs, named A1, A8, A10 and A12, were detected. Two OTUs were identified as “*Archaeorhizomyces*”, two were ascribed to *Archaeorhizomyces* genus, and one of them demonstrated conspecificity with *Archaeorhizomyces borealis*. All sequences were deposited into GenBank (Table 2).

There are eight archaeorhizomycete sequences from Russia available in GenBank up to date. Five OTUs are known from samples collected in the Moscow Region (MSU ZBS), four of them are revealed within this study. One OTU conspecific with *A. finlayi* derived from Leningrad Region (Nizhnesvirsky Nature Reserve), *Archaeorhizomyces* sp. OTU was revealed in Sakha Republic (Chokurdakh village proximities), and *Archaeorhizomyces* gen. sp. ined. OTU originated from Karachay-Cherkess Republic (Teberda Nature Reserve). All OTUs were revealed in conifer root or conifer forest soil samples: *Pinus* and *Picea* for Moscow Region, *Pinus* for Leningrad Region, *Larix* for Sakha Republic, and soil for Karachay-Cherkess Republic. OTUs A1, A8, A10 and A12 were detected in *Goodyera repens* roots, and A1 and A8 were revealed in soil samples too (Table 3).

Phylogenetic analysis was applied to clarify relationship between archaeorhizomycete taxa represented by OTUs revealed and previously known for Russian territory. The results were visualized as a maximum-likelihood cladogram with 1000-fold bootstrap-test based on the sequences aligned according to MAFFT

Table 1. Sample sites characteristics

Site N	Coordinates	Sample types
1	55.691680 N; 36.715776 E	bulk soil ^{2*} , conifer roots ² , <i>Goodyera repens</i> roots ² and rhizosphere ²
2	55.691485 N; 36.714948 E	bulk soil ² , <i>G. repens</i> roots ² and rhizosphere ²
3	55.694775 N; 36.739656 E	bulk soil ² , conifer roots ² , <i>G. repens</i> roots ² and rhizosphere ²

*Number of samples collected.

Table 2. Archaeorhizomycete OTUs revealed

OTU	Taxon	GenBank accession number
A1	<i>Archaeorhizomyces</i> sp.	ON819605.1
A8	<i>Archaeorhizomyces borealis</i>	ON714642.1
A10	<i>Archaeorhizomyces</i> gen. sp. ined.	ON819606.1
A12	<i>Archaeorhizomyces</i> gen. sp. ined.	ON819607.1

algorithm. *Archaeorhizomyces borealis* (NR_126144.2) from Lithuania (Menkis et al., 2014) was included too. *Taphrinomycotina* species from *Neoelectomyces* (*Neoelecta vitellina* FJ171855.1), *Taphrinomyces* (*Taphrina carpini* NR_119488.1), *Schizosaccharomyces* (*Schizosaccharomyces pombe* OW983270.1), and *Pneumocystidomycetes* (*Pneumocystis carinii* U07226.1) were chosen for outgroup (Fig. 2).

The sequences analyzed demonstrated *Archaeorhizomyces* affinity forming a monophyletic group within *Taphrinomycotina*. A8 turned out to be conspecific with *A. borealis* (NR_126144.2). This is the first confirmed report of the species from the territory of Russia. *A. finlayi* from Leningrad Region comprises the sister clade to *A. borealis*. A1 sequence is identical to *Archaeorhizomyces* sp. (MH248043.1) formerly reported for Moscow Region (Voronina et al., 2018) and is close to *Archaeorhizomyces* sp. (LC574773.1, Sakha Republic). A10 and A12 represent a separate clade rather distant from the other taxa. Besides, A12 OTU is identical to OP750444.1 (Karachay-Cherkess Republic, not included).

According to references, A1 sequence can be ascribed to some unknown *Archaeorhizomyces* species, A8 conspecific with *A. borealis*; and A10 and A12, clustered together and standing apart from other taxa, can

be identified only as *Archaeorhizomyces* members, and presumably represent species from some other than *Archaeorhizomyces* genus.

Global distribution of archaeorhizomycete taxa matching OTUs revealed

Reference sequences for OTUs revealed (GenBank, 100% overlap and match) were studied to define its global distribution. For *Archaeorhizomyces* sp. A1 7 references meeting the conditions were found. They all are reported from Europe (Finland, Sweden, the Netherlands) or European Russia (Moscow Region) conifer forests. OTU was detected in conifer roots, but also in roots of other plants typical for boreal forests, such as *Goodyera repens* and *Vaccinium myrtillus* (Table 4).

Archaeorhizomyces borealis (A8) matched 24 suitable references. The species is known from the north of Moscow Region, Lithuania, Scotland and Austria (*Pinus sylvestris* roots), Portugal (*P. pinaster* roots), Japan (*P. densiflora* and *Castanopsis cuspidata* roots), Chinese provinces Guizhou, Jiangsu and Hunan (*Pinus* sp., *P. tabulaeformis* and *P. massoniana* roots accordingly). Besides, the species was revealed in bottom soil of Indian Ocean near Sumatra at the more than 4000 m depth (Table 4).

Only one reference was found for A10, the sequence was obtained from conifer forest soil sample (Table 4).

A12 OTU is identical to OP750444.1 revealed in conifer forest soil in Teberda Nature Reserve (Karachay-Cherkess Republic) (Table 4).

No matching references were revealed for LC574773.1 (Sakha Republic) and MG597442.1 (Leningrad Region).

Thus *Archaeorhizomyces* sp. A1 is known from conifer forests of Northern Europe, and *A. borealis* A8 has wider distribution and is reported from conifer forests

Table 3. Archaeorhizomycete diversity in Russia based on GenBank data

Taxon	GenBank accession number	Sample origin	Sample type	Reference
<i>Archaeorhizomyces</i> sp.	LC574773.1	Sakha Republic	<i>Larix gmelinii</i> roots	Miyamoto et al. (2022)
<i>A. finlayi</i>	MG597442.1	Leningrad Region	<i>Pinus sylvestris</i> roots	Malysheva et al. (2018)
<i>Archaeorhizomyces</i> gen. sp. ined.	OP750444.1	Karachay-Cherkess Republic	Conifer forest soil	—
<i>Archaeorhizomyces</i> sp.	MH248043.1	Moscow Region	<i>Picea abies</i> and, <i>Pinus sylvestris</i> roots	Voronina et al. (2018)
<i>Archaeorhizomyces</i> sp.	ON819605.1		<i>Picea abies</i> , <i>Pinus sylvestris</i> , and <i>Goodyera repens</i> roots; conifer forest soil	current study
<i>A. borealis</i>	ON714642.1			
<i>Archaeorhizomyces</i> gen. sp. ined.	ON819606.1, ON819607.1		<i>Picea abies</i> , <i>Pinus sylvestris</i> , and <i>Goodyera repens</i> roots	

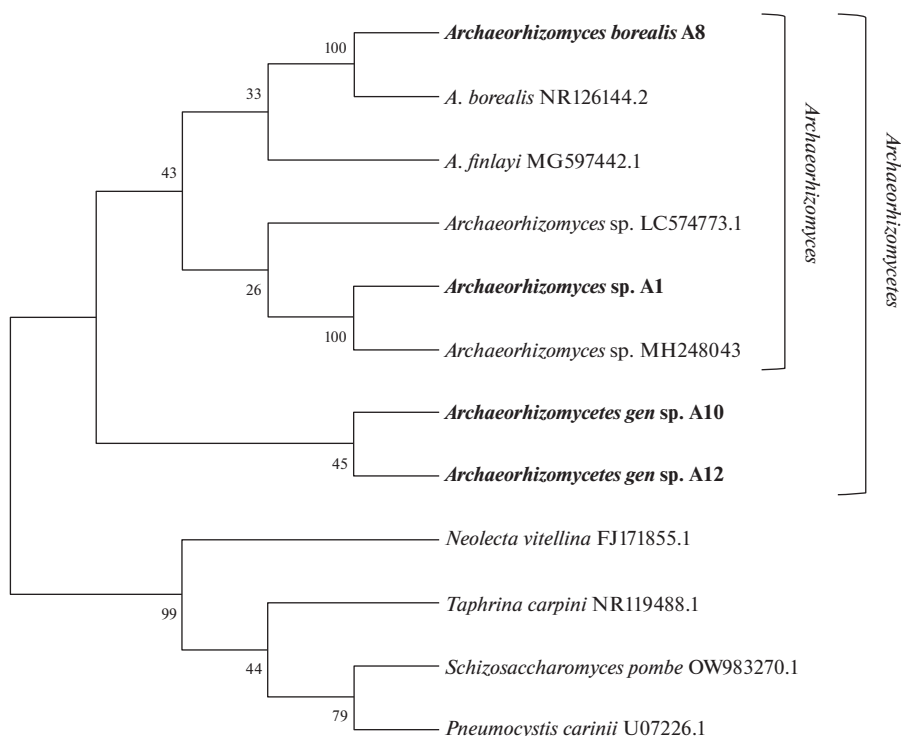


Fig. 2. Phylogeny of OTUs revealed and *Archaeorhizomyces* taxa known from Russia. OTUs revealed in the current research are marked in bold.

of both Northern and Southern Europe up to Japan and Southern China, and inhabits broadleaved forests too.

OTUs occurrence at the study site

Metagenomic approach allows not only to reveal taxonomic diversity, but also to estimate the occurrence of OTUs detected. The quartile analysis was applied to raw data obtained, and all OTUs were ranked and ascribed to one of categories followed: I (minor), II (rare), III (frequent), and IV (dominant taxa). For revealed archaeorhizomycete taxa occurrence ranks in samples studied see Table 5.

Archaeorhizomyces sp. A1 was detected in 10 of 11 habitats studied. In 9 samples A1 belongs to dominant taxa, in one *Goodyera repens* rhizosphere sample it is frequent, and it is absent from one soil habitat. *Archaeorhizomyces borealis* A8 was revealed in 5 habitats. The species is dominant in two soil samples, is frequent in one *Goodyera repens* rhizosphere sample, and represents minor element in fungal community of two *G. repens* root samples. *Archaeorhizomyces borealis* was not found in conifer roots samples. A10 OTU was detected in 3 habitats, always in association with plant roots: as a dominant species in one conifer roots sample, and as a rare or minor species in two *Goodyera repens* root samples. A12 OTU was registered in 3 samples: as a rare species in a conifer roots sample and a *G.*

repens root sample, and as a frequent species in a *G. repens* rhizosphere sample.

CONCLUSION

Four archaeorhizomycete OTUs were revealed by metagenomic approach in the samples collected in the conifer forest at the territory of MSU ZBS. Phylogeny of taxa revealed is presented as a cladogram, global distribution and occurrence are discussed.

OTU A1 is ascribed to an unknown species of *Archaeorhizomyces*. Matching sequences were detected in boreal conifer forests, and revealed at MSU ZBS territory previously (Voronina et al., 2018). A1 is the most frequent archaeorhizomycete species at the study site, the OTU revealed in 9 of 11 habitats. In bulk soil in Russia and in *G. repens* roots it was found for the first time. With the high occurrence and predisposition to plant roots this species can possibly have yet unrevealed symbiotic function probably related to conifer ectomycorrhiza.

OTU A8 is conspecific with *Archaeorhizomyces borealis*. This species is known both from Northern and Southern Europe and Asia up to south of China and Sumatra coast. *A. borealis* was revealed not only in conifer roots, but also in roots of broadleaved mycorrhizal tree *Castanopsis cuspidata*. This tree species shares its habitat with *Pyrola japonica*, a mixotrophic pyroloid with similar to *Orchidaceae* strategy to establish common mycorrhizal networks with ectomycorrhizal trees

Table 4. GenBank references matching revealed OTUs

Taxon	GenBank accession number	Sample origin	Sample type	Reference
<i>Archaeorhizomyces</i> sp. A1 (ON819605.1)				
<i>Archaeorhizomyces</i> sp.	MH248043.1	Moscow Region	<i>Picea abies</i> and <i>Pinus sylvestris</i> roots	Voronina et al. (2018)
no data	JN032485.1	Sweden	<i>Pinus sylvestris</i> roots	Lindahl et al. (2007)
	JQ312829.1		<i>Picea abies</i> roots	Menkis et al. (2012)
	HM069407.1	Finland	<i>Pinus sylvestris</i> roots	–
	HQ873359.1	the Netherlands	Soil	Prenafeta Boldú et al. (2014)
	JN006468.1	–	<i>Pinus sylvestris</i> roots	Rosling et al. (2011)
	DQ309123.1	–	<i>Vaccinium myrtillus</i> roots	–
<i>Archaeorhizomyces borealis</i> A8 (ON714642.1)				
<i>A. borealis</i>	MW793985.1, MW793987.1, MW793988.1	Lithuania	<i>Pinus sylvestris</i> roots	Motiejūnaitė et al. (2021)
	DQ068979.1, NR_126144.2			Menkis et al. (2014)
<i>Archaeorhizomyces</i> sp.	MW793931.1			Motiejūnaitė et al. (2021)
No data	MW793990.1, MW793915.1			
	MW215135.1		–	–
	FN811925.1	Scotland	<i>P. sylvestris</i> roots	–
	GQ205364.1, HQ625454.1	Portugal	<i>P. pinaster</i> roots	Buscardo et al. (2012)
	EU046019.1, EU046062.1, EU046087.1	Austria	<i>P. sylvestris</i> roots	Urban et al. (2008)
<i>A. borealis</i>	MT522544.1, MT678866.1	China, Guizhou	<i>Pinus</i> sp. roots	–
no data	AB873202.1	China, Jiangsu	<i>Pinus tabulaeformis</i> roots	–
	AB769883.1	China, Hunan	<i>P. massoniana</i> roots	Huang et al. (2014)
	LC096916.1, LC096889.1	Japan, Aichi	<i>Castanopsis cuspidata</i> roots	Uesugi et al. (2016)
	KJ173584.1	Indian Ocean	bottom soil	Zhang et al. (2014)
	JN006466.1, JN032575.1	–	conifer forest soil	Rosling et al. (2011)
<i>Archaeorhizomyces</i> gen. sp. A10 (ON819606.1)				
No data	JN032571.1	–	conifer forest soil	Rosling et al. (2011)
<i>Archaeorhizomyces</i> gen. sp. A12 (ON819607.1)				
<i>Archaeorhizomyces</i> gen. sp. ined.	OP750444.1	Karachay-Cherkess Republic	conifer forest soil	–

Table 5. Archaeorhizomycete OTUs occurrence (quartiles) in samples studied

Sample	<i>Goodyera repens</i> roots			<i>G. repens</i> rhizosphere			Conifer roots		Bulk soil		
	1	2	3	1	2	3	1	3	1	2	3
A1	IV	IV	IV	IV	IV	III	IV	IV	–	IV	IV
A8	I	–	I	III	–	–	–	–	–	IV	IV
A10	I	–	II	–	–	–	IV	–	–	–	–
A12	–	–	I	–	–	III	–	I	–	–	–

(Uesugi et al. 2016; Suetsugu et al., 2021). Wide distribution of *Archaeorhizomyces borealis* and high diversity of substrates occupied along with the shown ability for asymbiotic growth (Menkis et al. 2014) indicate this species as ubiquitous. On the territory of Russia it was revealed in *Goodyera repens* roots for the first time.

OTUs A10 and A12 were reported from Russia for the first time. They were also detected in association with *G. repens* roots. Currently it is impossible to define distribution of these taxa due to lack of data. These OTUs comprise a separate clade probably representing the second yet undescribed genus within *Archaeorhizomycetes*. At present they cannot be identified other than species belonging to the class mentioned.

The study presented broadens current recognition of biodiversity and ecology of *Archaeorhizomycetes* at the territory of Russia. The detection of provisional genus requires further global inventory to contribute to knowledge on biodiversity of this ubiquitous and abundant but critically understudied fungal group. *Archaeorhizomycetes* are not known to form mycorrhizas, but their regular presence in roots of mycorrhizal plants engaged in shared mycelial networks (conifers, orchids etc.) indicates their potential to contribute somehow to common nutrient transfer between plants and requires more research to enlighten their real ecological roles in forest communities.

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Новые находки представителей *Archaeorhizomycetes* на территории России на основании результатов метагеномного анализа

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Класс *Archaeorhizomycetes* (*Taphrinomycotina*, *Ascomycota*) представляет собой космополитную группу грибов, ассоциированных с корневой системой растений. Представители этого класса крайне мало изучены в силу трудности культивирования, однако при секвенировании природных субстратов нередко выявляются относящиеся к *Archaeorhizomycetes* последовательности. В ходе исследования разнообразия грибов, ассоциированных с орхидеей *Goodyera repens*, методом высокопроизводительного секвенирования нового поколения по участку ITS2 получены четыре уникальные последовательности, относящиеся к классу *Archaeorhizomycetes*. Одна последовательность, идентичная *Archaeorhizomyces borealis*, выявлена на территории России впервые, две последовательности предположительно относятся к еще не описанному роду. Одна последовательность, относящаяся к неопisanному виду рода *Archaeorhizomyces*, является наиболее часто обнаруживаемой во всех типах образцов (дерново-подзолистой почве, корнях хвойных деревьев, ризосфере и корнях орхидеи). Впервые было показано наличие нуклеотидных последовательностей представителей этого класса в корневой системе *Goodyera repens*, впервые показано присутствие одной последовательности в свободной почве. Последовательности депонированы в базу данных GenBank.

Ключевые слова: секвенирование природных субстратов, *Archaeorhizomyces borealis*, ITS2, OTUs