

First carnivorous fungus from Santonian Taimyr amber

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ABSTRACT: Mycelium from the Yantardakh Lagerstätte (Santonian of Taimyr) is reported. Its hyphae are arranged mostly parallel, weakly branched and septated. The clamp connections indicate the Basidiomycota affinity. Two types of outgrowths are formed on the mycelium, located perpendicular to the parent hypha: the former rather long and common; and the latter are short peg-shaped, formed with a lower frequency. Arthroconidia and large spherical structures, looking like exudate drops are observed upon hyphae. Hyphae rings similar to the trapping loops of extant Basidiomycota have been found. Altogether, these rings, numerous drops and peg-like hyphal outgrowths may be interpreted as this mycelium belongs to nematophagous fungus of Agaricomycetes. Thus, this is the first finding of mycelium putatively nematophagous Basidiomycota from the Cretaceous of North Asia, which also implies the presence of nematodes in the Taimyr amber forest.



KEY WORDS: Basidiomycota, clamp connections, Cretaceous, mycelium, nematophagous fungi.

Taimyr amber is known from many localities (Rasnitsyn *et al.* 2016; Perkovsky & Vasilenko 2019) ranging in age from late Albian to Santonian (Perkovsky & Wegierek 2017; Gumovsky *et al.* 2018). History and recent results in the Taimyr amber studies were summarised by Perkovsky & Vasilenko (2019) added by Azar & Maksoud (2020), Kolibáč & Perkovsky (2020), Fedotova & Perkovsky (2020), Hakim *et al.* (2021), Melnitsky & Ivanov (2021), Giřka *et al.* (2022), Oglęza *et al.* (2022a, 2022b) and Perkovsky (2022).

Several plant fossils were observed in the amber bearing sediments. These include spores attributed to various leptosporangiate ferns, peat mosses as well as pollen of several gymnosperms and angiosperms (Saks *et al.* 1959). Golovneva (2012) reported leaf fragments of the gymnosperm *Taxodium* sp. and the angiosperm *Trochodendroides* sp. in formations above and below the Kheta Formation. Furthermore, fossils of *Sequoia tenuifolia* Schmalhausen 1890 and the large-leaved Platanaceae *Pseudoprotophyllum hatangaense* Abramova 1983 were observed. The single plant inclusion described from Taimyr amber was bryophyte *Taimyrobryum martynoviorum* Ignatov *et al.* 2016.

Cretaceous mycetophages are rather numerous in tropical burmite, suggesting a high diversity of agaricomycetes in Kachin amber forest (Blagoderov & Grimaldi 2004; Cai *et al.* 2017; Peris 2020 and references therein). Unlike these, much more northern Taimyr amber inclusions are poorer in mycetophages, both in number and taxonomic diversity (Blagoderov & Grimaldi 2004; Makarov & Perkovsky 2020). This paper describes the first fungus from the Taimyr amber, except a supposed fungus upon beetle *Paleobiphyllus ponomarenkoi* Makarov & Perkovsky, 2020 (Biphyllidae) collected in the same Lagerstätte in 2012 (Makarov & Perkovsky 2020, Fig. 1a).

1. Materials and methods

Amber sample was collected in Yantardakh in 1970 by the expedition of V.V. Zherikhin and I.D. Sukacheva.

Yantardakh Lagerstätte is situated in Krasnoyarsk Krai: Taymyrsky Dolgano-Nenetsky District: Taimyr Peninsula: right bank of the Maimecha River, 3 km upstream of its confluence with the Kheta River (a left tributary of Khatanga River), Yantardakh Hill; Kheta Formation, Santonian, Upper Cretaceous.

The sample with the mycelium was collected in 1970, and is kept in the Borissiak Paleontological Institute of the Russian Academy of Sciences (PIN) with inventory number PIN 3130/222. For microscopy, a sample of 4 × 3.2 × 2 mm was prepared. According to Alexander Rasnitsyn (personal communication, 2023), the sample was manually processed with a safety razor blade and polished on a woolen cloth. After that, it was immersed in a Canadian balsam melt on a glass slide and covered with a cover glass. The micrographs were taken by compound light microscope Olympus CX41 equipped with digital camera Infinity 2–2 (2080 × 1536 px) and processed by software LAS V3.8 and Primo Star microscope (Carl Zeiss, Germany) equipped with a Canon A 300 camera and processed with software AxioVision 4.7.

2. Results

Mycelium was found deeply embedded in an amber piece (Fig. 1). Fruit bodies are absent. Mycelium is relatively unbranched and its hyphae, 2–4 μm wide, are arranged mostly in one direction, generally parallel to each other (Fig. 1a, b). Hyphae are branched at acute angle, and branches keep direction of the frontal expansion of the mycelium, sometimes forming bundles (Fig. 1c, d, e). Drop-like spherical bodies are scattered upon the mycelium, reminiscent of the liquid and oil exudate in fungi (Fig. 1f, g). Drop-like spherical bodies are in average in 12.5 μm in diameter, while some are up to 15 μm.

Septae are well-seen in several hyphae (Fig. 2a, b). Clamps are regularly present in mycelium (Fig. 2b, c, d). Clamps are of

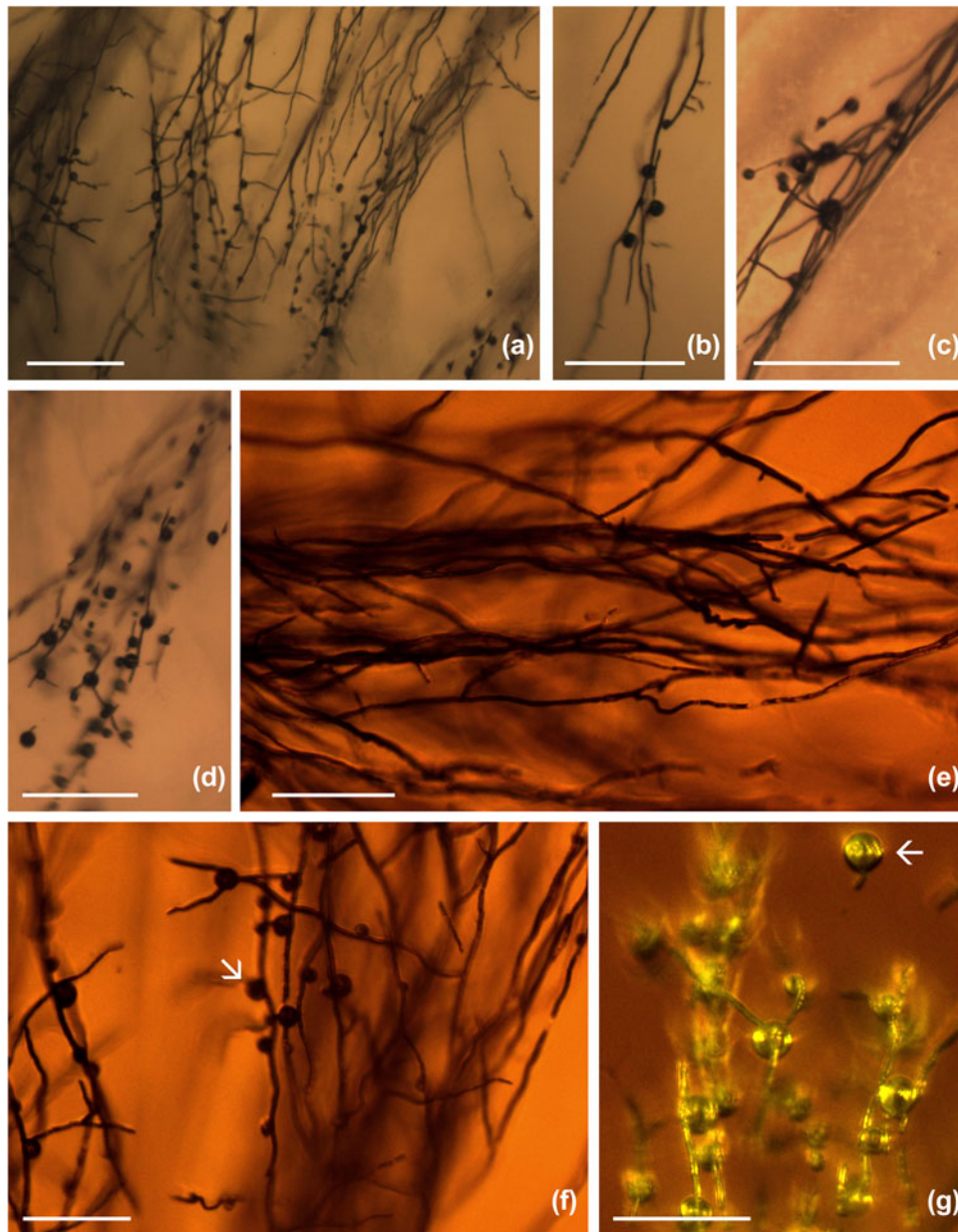


Figure 1 Mycelium of the Taimyr amber sample. (a–e) Fungal hyphae. (f, g) Drop-shaped formations. Scale bars: (a–d) 100 μm ; (e–g) 50 μm .

medallion type, where there is an obvious space between anastomosis and hypha. Clamps are 6–7 μm broad and up to 12 μm long. Two types of offshoots were found in the Taimyr amber: short and long. Both are perpendicularly arranged to the maternal hypha. The long ones are rather numerous (Fig. 2e); they are mostly 35 μm long, the longest being 45 μm long. Most of the long outgrowths extend from the clamps. Similar outgrowths on clamps have modern species *Amylostereum areolatum* Boidin 1958 (Baxter *et al.* 1995). The short off springs are rarer; they are peg-like, 12–16 μm long (Fig. 2f). Arthroconidia are seen in the Taimyrian mycelium as well (Fig. 2g–j).

Ring-like structures were seen among the mycelium hyphae. They are quite similar to the trapping loops of extant basidiomycetes (Fig. 2k). Inner diameter of this structure can reach 24 μm , the outer one 33 μm .

3. Discussion

Mycelium fragments are a rather common part of palinospectra. Their identification even at the level of the largest groups of fungi is impossible due to the almost complete absence of any

morphological differences (Maslova *et al.* 2021). However, the presence of septae and clamp connections in the Taimyr mycelium definitely indicates its belonging to Basidiomycota.

Mycelium clamps were found in late Albian Álava amber from Spain (Ascaso *et al.* 2005). In these specimens clamp connections were found in non-septate hyphae.

Other Cretaceous Basidiomycota have been reported from many localities. *Archaeomarasmius leggetti* Hibbett *et al.* 1997 was found in Turonian New Jersey amber, 90–94 Mya. Many basidiomycetes were described from the Cenomanian Kachin amber (Poinar & Brown 2003; Poinar *et al.* 2014; Poinar 2016). More recently, mycelium with clasps' connections has been discovered from the Cretaceous of Northeast China (Tian *et al.* 2020).

The combined presence of the putative trapping loops, clavate hyphae ends with drops, peg-like offshoots, which all are indicative for nematophagous fungi, suppose that the Taimyrian mycelium also belong to nematophagous fungi.

Nematophagous fungi are known in fossil state.

There is a certain similarity between our Taimyrian specimen and one mid-Cretaceous fungus, *Palaeodikaryomyces baueri*

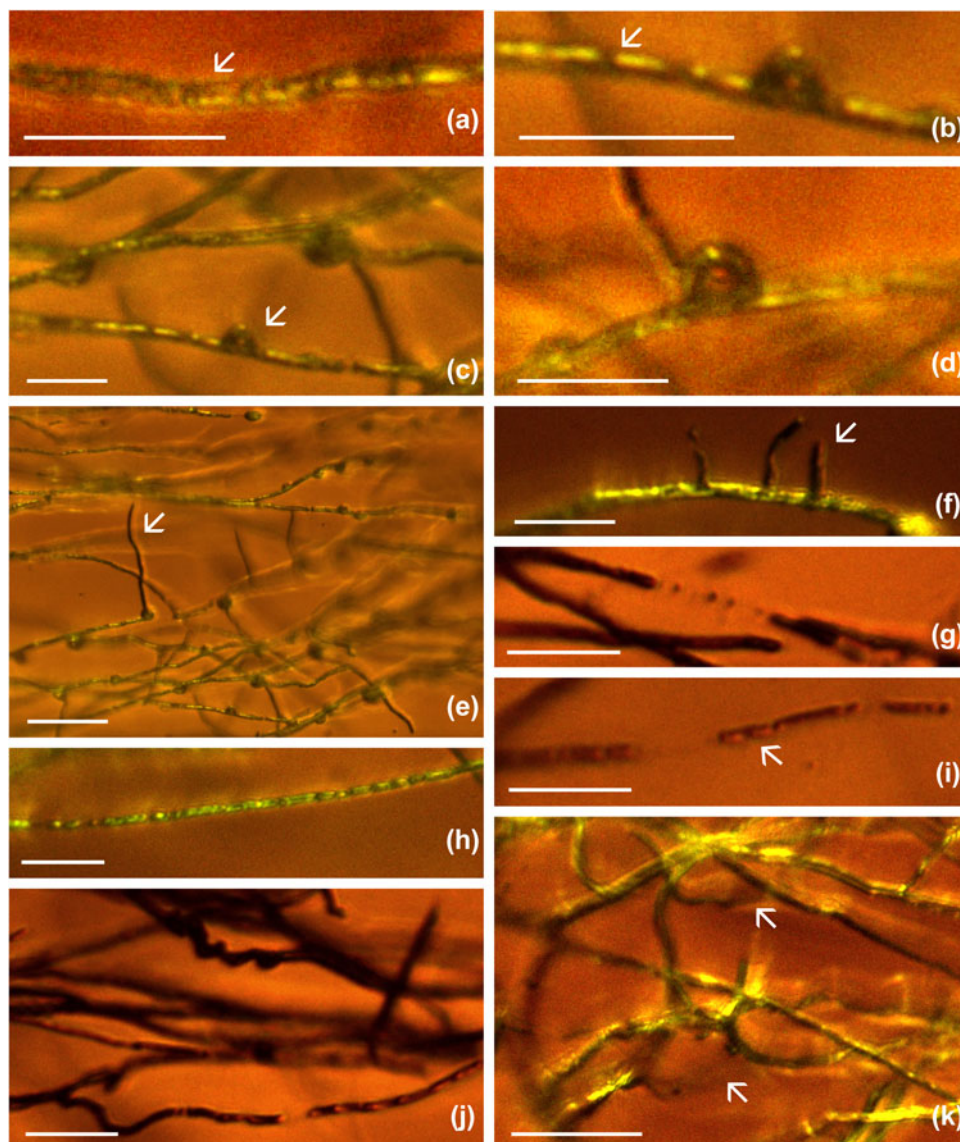


Figure 2 Mycelium of the Taimyr amber sample. (a, b) Septa on hyphae. (c, d) Clamp connections. (e, f) Outgrowths on the mycelium. (g–j) Arthroconidia. (k) Annular loops (arrowed). Scale bars: (a, b) 10 μm ; (c, d) 20 μm ; (e) 50 μm ; (f–j) 20 μm ; (k) 20 μm .

Dörfelt & Schäfer 1998. It was collected in Cenomanian (~99–93 Mya) Schliersee amber (Dörfelt & Schäfer 1998). Taimyrian mycelium however, unlike *P. baueri*, has obvious medallion-like clamps and septate hyphae.

We compared the similarity of the Taimyrian specimen with the extant nematophagous fungi from various groups. Today, nematophagous fungi belong to various taxonomic groups: Chytridiomycota; Ascomycota; Basidiomycota; Zoopagomycotina; and Mucoromycotina. About 200 nematophagous species of fungi are known in extant fauna according to Yang *et al.* (2007), although later publications increased this number to 700 species and also report this in species of the order Oomycota (Li *et al.* 2015; de Soares *et al.* 2018). The ability of Basidiomycetes to consume nematodes has been reported by Drechsler (1941).

The basidium fungi found to date that are capable of trapping nematodes or releasing substances that kill nematodes number more than 200 species and belong to three classes: Agaricomycetes; Dacrinomycetes; and Tremellomycetes (see Online supplementary material available at https://www.iceenas.org/site/assets/files/3971/sukhomlyn_supplementary_table.docx) – the former class including the main species diversity. Nematophagous fungi of Dacrinomycetes do not develop clamps. Species identity

of a nematophagous fungus from Tremellomycetes remains unknown, thus a comparison with it cannot be provided.

The classification of the nematophagous species is based on the capturing mechanisms and includes the following groups: (a) fungi, using adhesive and mechanical hyphal traps; (b) endoparasitic fungi, destroying nematodes by means of spores; and (c) fungi that are parasites of eggs and females (Barron & Thorn 1987; Dackman *et al.* 1992; Askary 1996; Jansson *et al.* 1997; Liu *et al.* 2009; Swe *et al.* 2011; Devi 2018). Recently two additional groups were discovered for: (d) toxin-producing fungi, immobilising nematodes before invading their bodies; and (e) fungi that produce structures to damage the nematode cuticle mechanically (Siddiqui & Mahmood 1996; Kerry 2000; Lopez-Llorca & Jansson 2006; Liu *et al.* 2009). Basidiomycetes include species of all the above mentioned groups.

The Taimyrian mycelium unlikely belong to the groups b and e, as both develop quite specific structures for nematode capturing, which are not observed in Taimyrian specimen. Group e has attacking structure, such as spiny propagulae, for example, in *Coprinus comatus* Persoon, 1797 (Luo *et al.* 2004, 2007); acanthocysts, for example, in *Stropharia rugosoannulata* Murrill 1922 (Luo *et al.* 2006); and stephanocysts, for example, in *Hyphoderma rude* Hjortstam & Ryvarden 1980 (= *Peniophorella*

rude Larsson, 2007) (Liou & Tzean 1992; Barron 2003). Endoparasitic fungi (group b) are also rather rare among basidial fungi: for example, species of *Hohenbuehelia* Schulzer *et al.* 1866 (anamorpha *Nematoctonus* Drechsler 1949), the trapping apparatus of which are represented by adhesive outgrowths such as an hourglass and adhesive spores (Karakas 2020).

Our specimen is especially similar to the xylophagous toxin-producing nematophagous representatives of Agaricomycetes.

Most of the specimens belong to the family Pleurotaceae: genera *Hohenbuehelia* (with anamorpha *Nematoctonus*) and *Pleurotus* Kummer 1871 (Thorn *et al.* 2000; Kirk *et al.* 2008). Carnivorous species of the genus *Nematoctonus* capture many nematodes by means of hypha projections of hourglass shape, whereas species of *Pleurotus* produce non-adhesive small drops containing toxic compounds from small peg-like offsprings on hyphae (Kwok *et al.* 1992; Koziak *et al.* 2007). Our sample is one of those which have drop-like structures on their mycelium, but does not form hourglass-shaped structures, characteristic for *Hohenbuehelia*.

Secretory structures, similar to that in *Pleurotus* were found in hyphae of Agaricales: *Conocybe lactea* Métrod 1940 (Hutchison *et al.* 1996) and *Flammulina velutipes* Singer 1951 (Ferreira *et al.* 2019). Their way to attack nematodes is similar to *Pleurotus* (Hutchison *et al.* 1996). However, in *Conocybe lactea* the stalk of the drop-producing glands is high and broadened to the stalk base (Hutchison *et al.* 1996).

More recently, nematophagous activity has been found in a number of species of various genera from the same order (Thorn & Barron 1984; Mamiya *et al.* 2005; Ishizaki *et al.* 2015; Balaeş & Tănase 2016; de Soares *et al.* 2019; Hahn *et al.* 2019). Fungi of other orders were found to have a similar ability (Mamiya *et al.* 2005, Balaeş & Tănase 2016). In these nematophagous fungi the hyphae grow upon the nematode body, leading with time to the degrading of its body, both cuticle and internal structures. Dense hyphae assemblages in proximity to nematodes possess abundant chlamydospores and conidia. Thus, the mechanism of nematode damage in these species differs from that in *Pleurotus* (Mamiya *et al.* 2005; Balaeş & Tănase 2016).

There is the only report of the secretory cells that immobilise nematodes among non-agaricoid, polyporoid fungi, that causes white rot: *Climacodon septentrionalis* Karsten 1881b of the family Meruliaceae (Tanney & Hutchison 2012; de Soares *et al.* 2018). However these secretory cells in *C. septentrionalis* differ markedly from secretory cells of agaricoid fungi, described by Hutchison *et al.* (1996) for cultures of *Panaeolina foenicicii* Maire 1933 and *C. lactea*, and also in cultures described by Barron & Thorn (1987) and *Pleurotus ostreatus* Kummer 1871. The secretory structures of *C. septentrionalis* are wide, and produced on tall, septate, single-celled stalks that branched (Tanney & Hutchison 2012). Droplets formed by species of the order Agaricales are much smaller than the drops of *C. septentrionalis*.

Some aphylloroid fungi are similar to our Taimyrian specimen. They have clamps, arthroconidia and oil drops in mycelium (Stalpers 1978). However, most of them have one or two of these three characters, or sometimes they have additional features that are absent in our specimen (e.g., chlamydospores, reindeer-horn-shaped hyphae, etc.).

In our specimen, drops and the putative trapping loops were observed.

The arthroconidia (oidia) found on the mycelium of Taimyr amber do not make it possible to unambiguously determine the fungus even to the familiar level, because such asexual spores were noted in many representatives of basidiomycetes. Reshetnikov (1991) listed as many as 151 species of Agaricales and 73 species of aphylloroid basidiomycetes known to develop arthroconidia. Among them are the species, potentially similar to our sample: *Pleurotus cystidiosus* Miller 1969 (Buchalo 1988) and mentioned

above *Flammulina velutipes* (Reshetnikov 1991; Borhani *et al.* 2011); and many aphylloroid fungi, including the earlier mentioned species of the genus *Amylostereum* Boidin 1958.

Whereas Taimyr amber has a gymnosperm origin, the restriction to the fungi that inhabit gymnosperms allows us to confine the comparison for fungi living on the trees of this group and having ability for capturing nematodes from conifer forests. Mamiya *et al.* (2005) reported a number of fungi that are able to capture pinewood nematodes being cultivated on agar medium in Petri dishes: *Pleurotus pulmonarius* Quélet 1872; *Pleurotus eryngii* Quélet 1872; *Lentinula edodes* Pegler 1975; *Neolentinus lepideus* Redhead & Ginns 1985; *Pholiota nameko* Imai 1933; *Omphalotus guepiniformis* Neda 2004; *Trichaptium abietinum* Ryvarden 1972; and *Cryptoporus volvatus* Shear 1902.

It should be noted that many nematophagous basidial fungi associated with conifers have many features characteristic of the studied sample: clamp connections; outgrowths on clamp connections; and the presence of arthroconidia (for example, *Bjerkandera adusta* Karsten 1879, *Pycnoporus cinnabarinus* Karsten 1881a, *Amylostereum areolatum* whose mycelial features are described by Stalpers (1978)). The fact that it is a parasite of exclusively coniferous trees can also speak in favour of the latter. Extant species of *Amylostereum* usually develop cystidia, which were not noticed in our specimen. However, lack of cystidia could be because this mycelium was fossilised when quite young, before forming cystidia that appear usually after several weeks of growth. An alternative explanation could be that an ancient relative of *Amylostereum* simply lacks cystidia.

4. Conclusion

The representative of the Basidiomycota is found in the Taimyr amber for the first time. Such taxonomic attribution is based on the presence of mycelium septae and clamp connections. Hyphal rings similar to trapping loops in combinations with peg-like outgrowths and drops of the putative exudate support a hypothesis that this mycelium belongs to the wood-destroying nematophagous species.

Altogether, these rings, numerous drops and peg-like hyphal outgrowths may be interpreted as this mycelium belongs to nematophagous fungus of Agaricomycetes. Furthermore, it is the first indication of the presence of nematodes in the Taimyr amber forest.

Summing up, the described Taimyrian mycelium of the Cretaceous age likely belongs to one of the orders of Agaricomycetes. Barron (1992) proposed that nematophagous fungi evolved from cellulolytic or ligninolytic fungi in response to the deficiency of nourishments in nitrogen-poor environments. In such conditions with the high carbon content, the nematode nitrogen may be an important addition. It was wood-destroying fungi that we considered among the most similar to the found sample. However, it is still difficult to give an unambiguous answer regarding whether a sample belongs to a certain family or even order. Nonetheless, this finding may help to estimate the origin of carnivory in Basidiomycota, where the diversity of trapping structures is much more limited as compared to Ascomycota.

This is the first Cretaceous record of the carnivorous Basidiomycota in the warm-temperate region (Perkovsky *et al.* 2018) and the first indirect evidence of the nematode presence in the Taimyr amber forest. The results presented by us will be useful for tracing the evolution of nematophagous fungi and their trapping devices for inhibiting nematodes and are a contribution to documenting the stages of the formation of the Earth's mycobiota as a special evolutionary group of organisms, providing important evidence in favour of not only individual groups of fungi that appeared at the early stages of historical development, but also the co-evolutionary relationships of fungi and representatives of other Kingdoms of living beings (Maslova *et al.* 2021).

5. Supplementary material

Supplementary material is available online at https://www.iceenas.org/site/assets/files/3971/sukhomlyn_supplementary_table.docx.

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8. Competing interests

None.

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