



## YEAST FUNGI IN THE EDIACARAN STROMATOLITES OF THE SIBERIAN PLATFORM

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**ABSTRACT** – Yeast fungi are extremely diverse, very widespread, and have a long history of industrial use; however, the time of their origin and early ecology on Earth remain unclear. This work fills this gap in scientific research, and, for the first time, descriptions are given with the allocation of new taxa of discovered yeast fungi in the Ediacaran (635–538 Ma). They are perfectly preserved in the form of microfossils and participated in the development of silicified columnar stromatolites (reef-like organogenic formations). The rock material was collected from the Byuk Formation (about 550 Ma) in the Berezovsky trough in the east of the Siberian platform. It was studied in thin sections of stromatolites on a scanning electron microscope. Microfossils were studied using standard comparative morphological methods. Their biological interpretation and systematic identification were conducted using analogy, the most widespread and efficient method of scientific research. The fungal (yeast) nature of the microorganisms discovered is indicated by the following features: reproduction by budding, sporulation, and division of individuals (cells), and properties of cell growth and their ecology (parasitization on the green algae thalli). New taxa of fossil yeast fungi have been identified: genus *Tungusia*, type-species *Tungusia mane*. We suggest that these microorganisms were the early ancestors of the modern yeast fungi.

**Keywords:** *Tungusia*, green algae, Ediacaran, Byuk Formation, Siberian platform.

**RESUMO** – Os fungos de levedura são extremamente diversos, muito difundidos e têm uma longa história de uso industrial; entretanto, sua origem e ecologia inicial permanecem desconhecidas. Este trabalho preenche essa lacuna na pesquisa científica e, pela primeira vez, são apresentadas descrições com a alocação de novos táxons de fungos de levedura descobertos no Ediacarano (635–538 Ma). Eles estão perfeitamente preservados na forma de microfósseis e participaram do desenvolvimento de estromatólitos colunares silicificados (formações organogênicas semelhantes a recifes). O material rochoso foi coletado da Formação Byuk (cerca de 550 Ma) na calha de Berezovsky, no leste da plataforma siberiana. Ele foi estudado em seções delgadas de estromatólitos em um microscópio eletrônico de varredura. Os microfósseis foram estudados usando métodos morfológicos comparativos. Sua interpretação biológica e identificação sistemática foram realizadas por meio de analogia, o método mais difundido e eficiente de pesquisa científica. A natureza fúngica (levedura) dos microrganismos descobertos é indicada pelas seguintes características: reprodução por brotamento, esporulação e divisão de indivíduos (células) e propriedades de crescimento celular e sua ecologia (parasitização nos talos de algas verdes). Foram identificados novos táxons de fungos de levedura fósseis: gênero *Tungusia*, espécie-tipo *Tungusia mane*. Nós sugerimos que esses microrganismos foram os primeiros ancestrais dos fungos de levedura modernos.

**Palavras-chave:** *Tungusia*, algas verdes, Ediacarano, Formação Byuk, plataforma siberiana.

### INTRODUCTION

The research of the early (Precambrian, *i.e.*, up to 538 Ma) evolution stages of life on Earth is the basis for the study of the Phanerozoic evolution paths of the organic world. The authors' research aims to search for very rare, well-preserved remains of life in the form of microfossils in the Precambrian, their biological interpretation, and systematic identification. Although phylogenetically fungi are “relatives” of animal organisms (*e.g.*, Woese *et al.*, 1990), they have been largely overlooked by paleontologists and paleobotanists. Nonetheless, terrestrial fungi were the most important components of ecosystems throughout the entire Phanerozoic.

Starting in the mid-1950s, during the formation stage of the Precambrian paleobiology, numerous Proterozoic microfossils were mistakenly identified as potential filamentous “fossil fungi”, mainly through the hyphae-like morphology of partially preserved individuals (Djakov & Sidorova, 2012). Notable examples include Paleoproterozoic “hyphae”, “mycelia” and “spores” of fungal origin (Taylor & Barghoorn, 1954); Neoproterozoic filamentous taxon *Eomycetopsis*, described as “*Eumycophyta?*” (Schopf, 1968); and numerous other examples (*e.g.*, Hofmann, 1971; Hermann, 1979; Mikhailova, 1986). The “hyphae”, “mycelia” and other organic residues presented in the publications were considered to be fungus-like microfossils but not fungi

(Meyen, 1987). Although some of the data presented are not sufficiently convincing, most researchers began to believe that the ancestry of fungi goes far back to the Precambrian (Knoll, 1992; Schopf, 1993; Heckman *et al.*, 2001; Rozanov, 2003; Hedges *et al.*, 2004), while the data on the molecular clock allowed scientists to assume that the invasion of ancestral forms of fungi on the Earth's surface could have occurred 2.4 Ga (Schopf, 1993; Rozanov, 2003) or 1000 Ma (Heckman *et al.*, 2001; Hedges *et al.*, 2004). The reliable fossil evidence of their Proterozoic presence is limited.

Karatygin (2007) summarized to a certain extent the paleomycological data accumulated in the press up to 2006. Prior to our research, there was little data on Ediacaran fungi (Burzin, 2003). Presumably, a few Late Precambrian acritarches of irregular and spherical shape with protrusions of cell walls are comparable to yeast fungi (Retallack, 2015). Calcareous lump-like small (up to 1–2 mm) formations referred to as catagraphites (microphytolites) are widespread in carbonate deposits on the Siberian platform in the Ediacaran (Mikhailova, 1986; Kolosov, 2003). They are primarily of organosedimentary origin. Some of these formations have protrusions of a smooth contour and are somewhat similar to yeast in morphology. There is no data indicating the methods of reproduction of potential microorganisms in the form of catagraphites. Therefore, only some external similarities between these formations and large individuals of yeast fungi can be claimed.

Perhaps, the most documented organisms are microfossils from the Ediacaran of the European part of Russia, which resemble rhizoids and sporangia of fungal thalli (Burzin, 1995, 2003), as well as fossils interpreted as symbiotic algal-fungal lichens from phosphorites of the Doushantuo Formation in Southern China (Yuan *et al.*, 2005). In recent years, indubitable marine fungi of excellent preservation have been found in the Ediacaran stromatolites in Yakutia, *i.e.*, in the east of the Siberian platform. Description of mycelial (filamentous) fungi *Surninia implicata* and yeast-mycelial / mycelial-yeast (yeast with mycelial structures) fungi *Sakhi solomonovi* have been compiled (Kolosov, 2016a, b, 2021, 2022). These types of fungi are characterized by diverse morphology. Considering this, it can be assumed that the main lineages of fungi diverged approximately 1 billion years ago (Knoll, 1992). Fossil evidence suggests that fungi colonized the Earth in the Cambrian (Taylor & Osborn, 1996; Kolosov, 2013; Kolosov & Sofroneeva, 2014).

The discovery of microfossils in the Ediacaran (635–538.8 Ma) as well as the establishment of their systematic position as fungi may contribute to the elucidation of the evolution and ecology of these eucaryotes in subsequent periods (Karatygin, 2007; Kolosov, 2016a, b, 2019). For example, a large group of researchers cited biomorphic structures from the Early Cambrian Bokson bauxites of the Eastern Sayan of Russia referring to them as biomorphoses (Shkol'nik *et al.*, 2004). Some of them, depicted on tables LXI–LXII, are presumably mineralized yeast and mycelial fungi. In the Cambrian, only hypothetical fungi existed, whereas later, in Devonian sediments (400 Ma), a mass of fossils identified as fungi was discovered (Taylor *et al.*, 2005; Dyakov & Sidorova, 2012).

We also note the prospects of micropaleontological (paleoalgal and paleomycological) studies of the Ediacaran in the east of the Siberian platform (the territory of Western Yakutia). Here, these age deposits are mainly represented by carbonate rocks that have experienced almost no secondary changes. The deposits occur on the Cryogenian sedimentary strata and directly underlying strata of carbonate-clay sediments containing well-studied Early Cambrian faunal assemblages (Rozanov, 1980; Kolosov, 2003; Rozanov *et al.*, 2008).

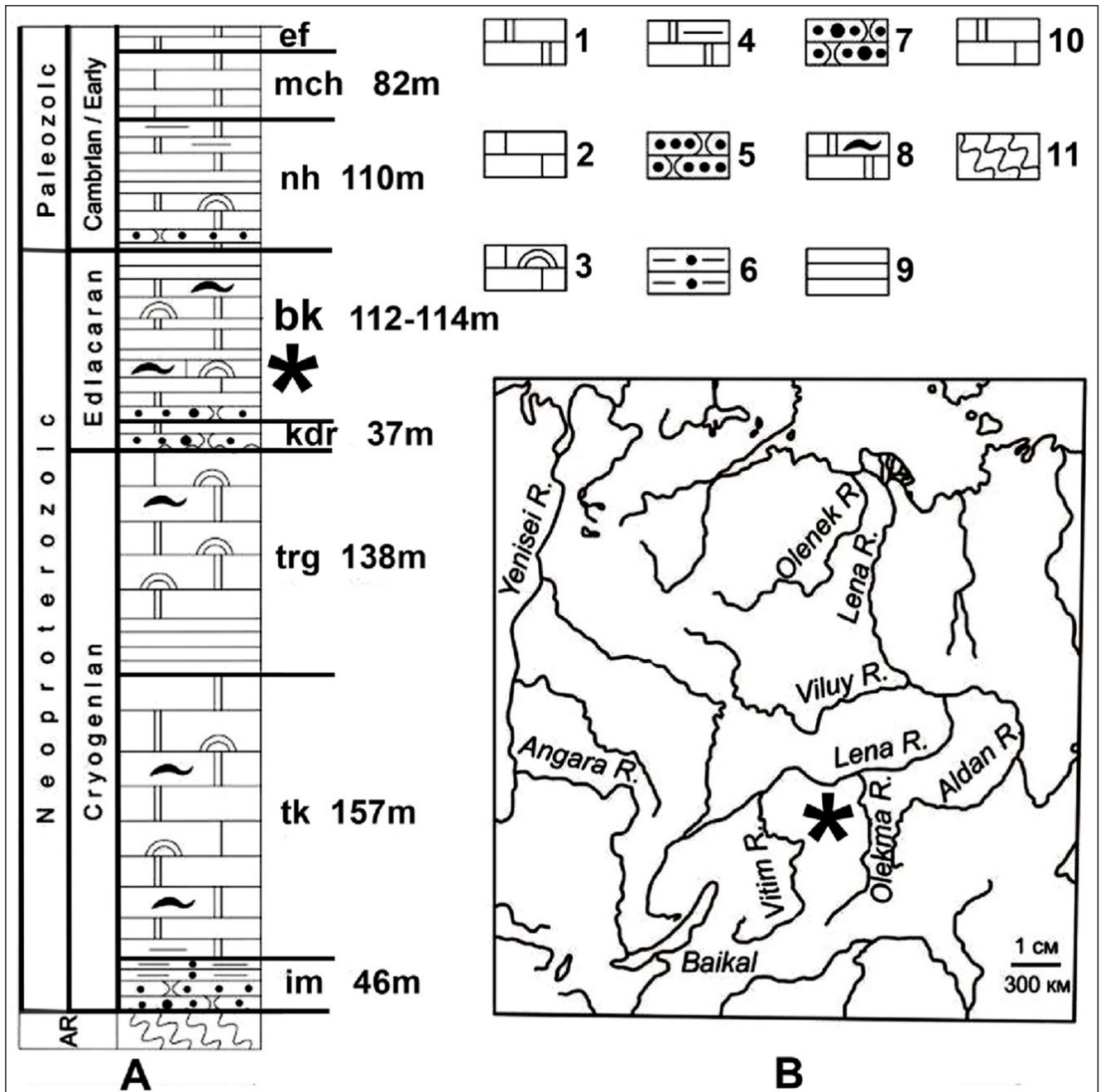
It is difficult to precisely identify the taxonomic affiliation of the Precambrian residues. In classifying microfossils, paleomycologists primarily use their morphology, vegetative structures (formations), and ecological characteristics, which are additionally considered for the taxonomy of recent fungi (Alexin *et al.*, 2007; Wijayawardene *et al.*, 2020).

## GEOLOGICAL SETTING

The Berezovsky trough is composed of the Neoproterozoic and Early Paleozoic deposits (Figure 1A–B). It is located on the territory of Western Yakutia, between the Aldan antecline and the Baikal–Patom folded region. Its basement is comprised of the Early Proterozoic and Archean metamorphosed strata. All geologists (Rozanov, 1980; Semikhatov, 2000; Kolosov, 2003; Semikhatov *et al.*, 2004; Khomentovskiy, 2008; Rozanov *et al.*, 2008) that develop the stratigraphy of the Upper Precambrian deposits of the south-east of the Siberian platform unambiguously compare the Byuk (Porokhtakh) Formation with the Ust-Yudoma Ediacaran Formation of the Uchur-Maya region; its base in the Ulakhan-Ytyga section (the Yudoma river) provides a dating of 553±23 Ma, obtained by the Pb–Pb method (Semikhatov, 2000; Semikhatov *et al.*, 2004; Khomentovskiy, 2008). Based on the stratigraphic position (occurrence under the earliest Cambrian strata) and the mentioned dating, the Ediacaran age of the Byuk Formation has been established (Semikhatov, 2000; Semikhatov *et al.*, 2004; Khomentovskiy, 2008). Its section consists of (from bottom to top) basal gravelite-sandstones of quartz composition (not exceeding 3 m), dolomites, occasional stromatolite silicified limestones, as well as rare thin interlayers of mudstones. The Byuk Formation is well studied, horizontally bedded, not metamorphosed and is not disrupted by faults. The thickness of the Byuk Formation is 112–114 m. A sketch map of Western Yakutia, which marks the collection site of the studied stromatolite samples and section (lithology column) of the Neoproterozoic deposits from the south of the Berezovsky trough, is shown in (Figure 1A–B).

## MATERIAL AND METHODS

Well-preserved microfossils, interpreted as yeast fungi and described in the article, are present in the lower half of the Byuk Formation of the Ediacaran (Figure 1A, bk) in the Berezovsky trough in the southeast of the Siberian platform. They are found in densely packed, thinly layered,



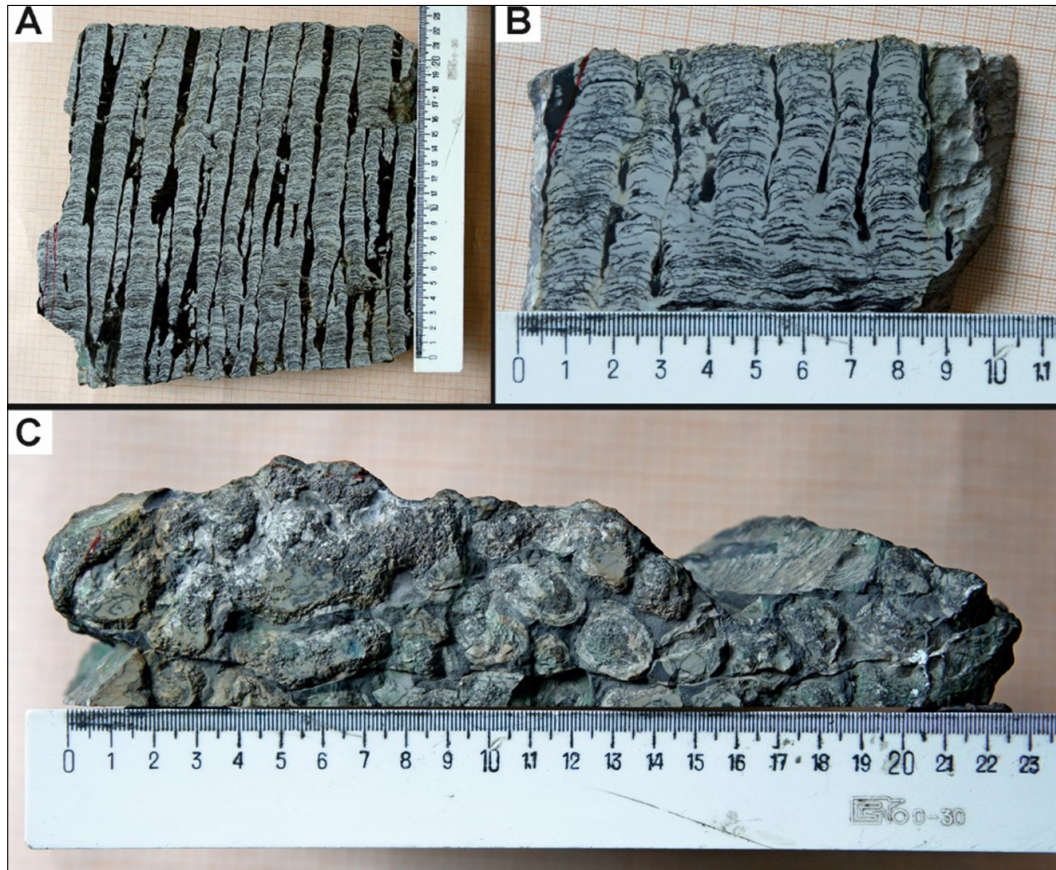
**Figure 1.** Stratigraphic and geographical location of the Byuk stromatolites containing algae and fungi, indicated by an asterisk (\*) both in the stratigraphic section (A) and on the terrain map (B). **Abbreviations for the formation names:** ef, Elgyan; mch, Macha; nh, Nokhtui; bk, Byuk; kdr, Kederga; trg, Torgo; tk, Tokko; im, Imalyk. **Lithological symbols shown in the stratigraphic column are presented in the upper right corner:** 1, dolomites; 2, limestones; 3, organogenic carbonate rocks; 4, argillaceous dolomites; 5, sandstones; 6, siltstones; 7, sand sandstones; 8, lenses of dark gray cinder; 9, mudstones; 10, calcareous dolomites and dolomitic limestones; 11, rocks of the crystalline basement.

silicified columnar stromatolites (Figure 2), which are the origin of the previously described mycelial (filamentous) fungi *Surninia implicata* Kolosov, 2016 (Kolosov, 2016a, b) and yeast-mycelial / mycelial-yeast (yeast with mycelial structures) fungi *Sakhi solomonovi* Kolosov, 2021 (Kolosov, 2021). The affiliation with the lamellar form of green algae of microfossils present in the same sample of stromatolites, to which we refer, is substantiated in another article, in which a new genus *Paleoulvaria*, with its type species *Paleoulvaria plate* is established by Kolosov (2023).

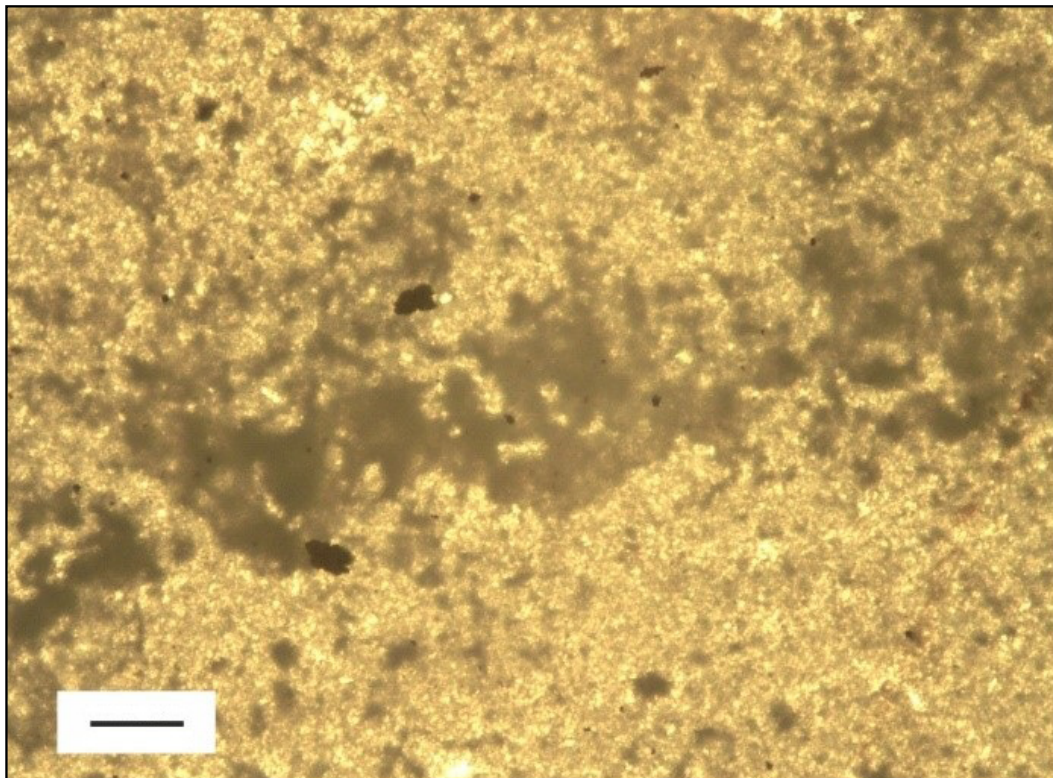
The columnar stromatolites of the Byuk Formation have dark, thin layers (Figure 2) that are represented by dark brown kerogenic organic masses (Figures 3, 9), and therefore they are distinctly visible. Microfossils in stromatolites on Figure 9 have high carbon contents.

These layers primarily consist of perfectly preserved yeast fungi of a mineralized state (Figure 4). Mycelial and yeast-mycelial/ mycelial-yeast fungi are uncommon in them. An explanation for the excellent preservation of microorganisms in the dark layers of stromatolites (Figure 2) includes the





**Figure 2.** A sample of columnar silicified stromatolites of the Byuk Formation of the Ediacaran: **A**, longitudinal section; **B**, base of columns (A); **C**, cross-section of columns (A).



**Figure 3.** In the photo of the petrographic thin section, dark brown algae-fungal (shown by an arrow) associations are visible with light passing through; they form dark microlayers of the stromatolite sample from the Byuk Formation, shown in Figure 2. Scale bar = 100  $\mu\text{m}$ .

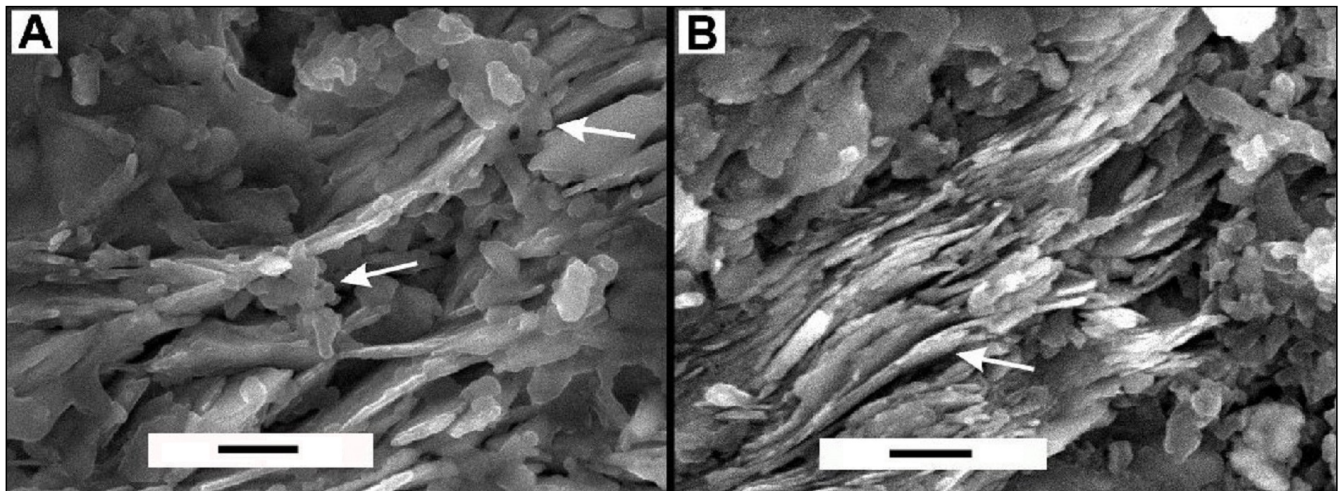


following: their microscopic size, which determines the complete preservation of individuals; a possible oxygen “starvation” caused by intensive consumption of oxygen by rapidly growing yeast fungi, as a result of which the organic matter of microorganisms was not oxidized; potential silicification of microorganisms due to the presence of their own silicon; and, lastly, the rapid silt burial of some stromatolites during their formation as a result of the well-known Late Ediacaran transgression of the sea on the Siberian platform (Kolosov, 2021).

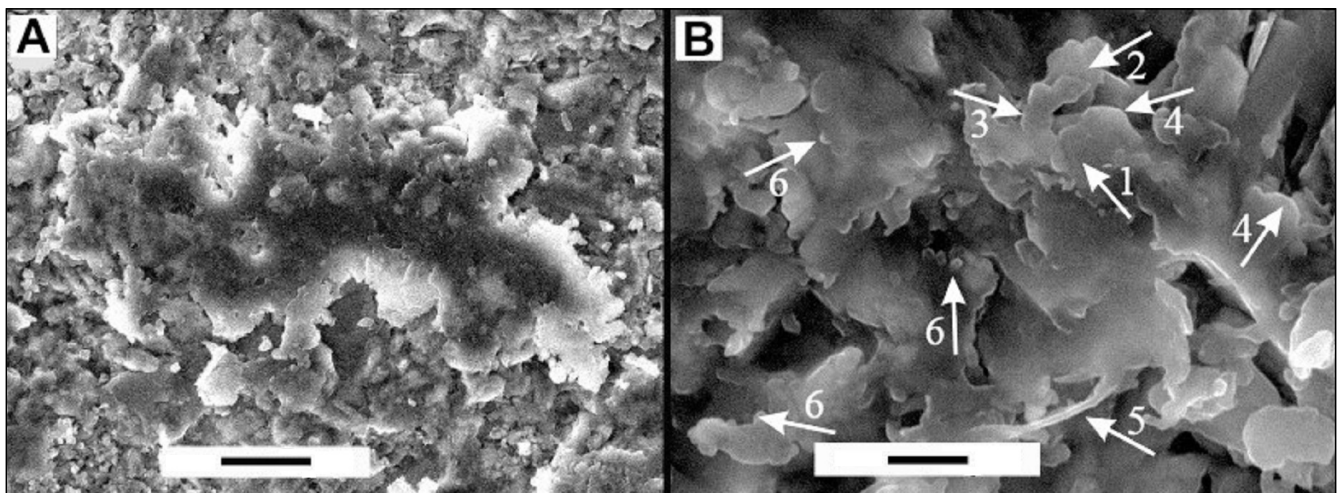
The studied yeast fungi are clearly preserved in situ, as evidenced by their occurrence in the above-mentioned translucent petrographic thin sections (Figure 3), in which parts of the preserved cells are immersed in the host rock and are closely related to it (Figure 5). Lamellar green algae (Figures 3, 4) also penetrate the underlying rock matrix of stromatolite (Figure 4B). At the same time, the silicified stromatolite containing microfossils is evenly compact and devoid of microcracks and cracks near the fossils.

Microfossils were studied using scanning electron microscopy (SEM) in 11 thin sections of stromatolites, oriented vertically in reference to their layering. The surface of the sections was processed on a rotating disk using fine powder, thoroughly washed with distilled water, dried, and coated with gold under sterile conditions. Following this process, polished sections (plates) were produced, which were examined by the authors with a JEOL JSM-6480LV SEM microscope. Under high vacuum conditions with the use of an accelerating voltage of 10 kV, a diaphragm of 2, a SEI signal, and a working distance of 10 mm, SEM images were obtained utilizing secondary electrons. More than 200 high-quality photos of microfossils were taken at magnifications ranging from 100 to 30,000. The Axioscop 40 light photomicroscope was also utilized to initially determine the location of the mass of microscopic organic residues in the studied samples.

The standard comparative morphological method was applied during the microfossils study. Their biological interpretation and systematic identification were performed



**Figure 4.** Green lamellar siphon algae of the Byuk Formation: **A**, yeast fungi (**arrows**) are distinct, parasitizing on algae thalli; **B**, algae have a lamellar shape (**arrow**), the lower parts of the plates are immersed in the rock matrix. Scale bars: A = 5  $\mu$ m; B = 1  $\mu$ m.



**Figure 5.** Yeast fungi *Tungusia mane* gen. et sp. nov. of the Byuk Formation: **A**, occurred within the kerogen layer shown in Figure 3 in a petrographic thin section; **B**, holotype. **1**, mother cell (individual); **2**, formation of daughter cells; **3**, bridge connecting daughter cell to the mother cell; **4**, cell growth via protrusion of its shell; **5**, mycelial structure (formation) of a tubular shape in one of the yeast cells; **6**, buds. Scale bars = 1  $\mu$ m.

using the analogy method, which is the most common and effective method in scientific research (Sukhotin, 1988). Classification of microfossils as yeast marine fungi is based on their morphological comparison with their recent counterparts, with reference to the ecosystem of stromatolites (Figure 2).

### BASIS FOR THE YEAST NATURE OF MICROFOSSILS

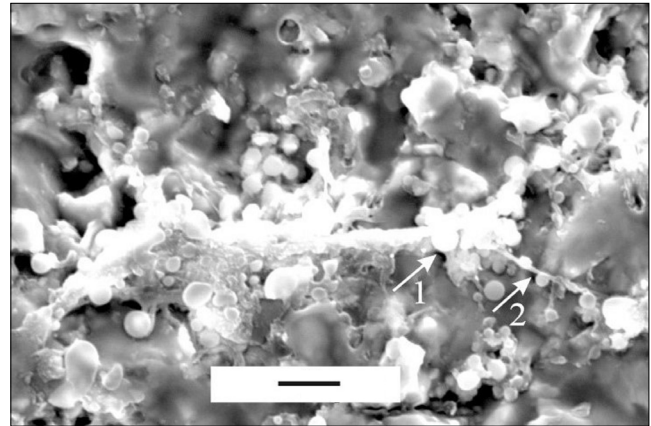
The biological interpretation of several Byuk microfossils as siphon green algae was performed by the author earlier (Kolosov, 2021, 2023). It has been shown that algae have thalli of a lamellar shape with reproductive organs on stalks, which are one of the distinctive characteristics of siphons (Kolosov, 2021, 2023, fig. 1d). In the paleoecosystem of columnar stromatolites of the Byuk Formation, yeast fungi (Figures 4A, 8A) fed on the organic material of these green algae (Figure 5).

From the materials on recent green algae (Kondratieva *et al.*, 1989), it is known that the environment of these lower marine plants is favorable for heterotrophs; their cell covers contain polysaccharides (starch, sucrose, hemicelluloses). Some species of these organisms have malic, oxalic, lactic, formic, acetic, glycerol, citric, and other acids found among extracellular products.

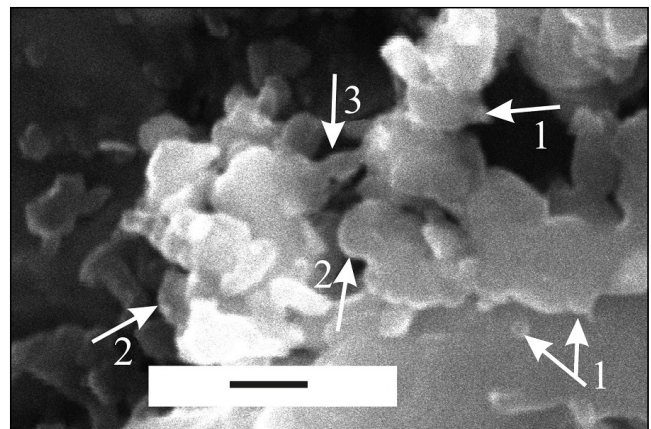
Next, a basis for the yeast nature of the Byuk microfossils is provided. In mycology, “each yeast cell represents a separate individual” in unicellular yeast (Djakov, 2013). Similar to cells / individuals of recent yeast, Byuk Formation vary widely in shape, such as round, oval, elliptical, or occasionally strongly elongated in the form of mycelium, etc. In size (yeast individual length – 6.9  $\mu\text{m}$ , diameter 8.35  $\mu\text{m}$ ; elongated forms length 1.09–1.18  $\mu\text{m}$ , diameter 0.03  $\mu\text{m}$ ).

Recent unicellular fungi reproduce vegetatively, predominantly by budding. On the surface of the studied cells, nanoscale bodies are present, which are similar to buds in their location, shape and size. The buds are characterized by a convex globular shape (Figure 5B). Their size ranges from 0.04 to 0.18  $\mu\text{m}$ . Reproduction specifics of fungi by budding and their overgrowth via protrusion of the shell on any part of the surface (Figures 5B: 4 and 7: 2) explicitly distinguish Byuk yeasts from bacterial cells. This difference between yeast cells (individuals) and bacterial cells has been frequently stated by Professor Yu. T. Djakov, 2013 (Velikanov *et al.*, 2007).

The Byuk yeasts are also reproduced by sporulation. Formation of spores also often occurs on mycelia or pseudomycelia (blastospore) and on hyphae of mycelia, arranged in a chain (conidia) (Djakov, 2013). Spores are also present in the stromatolites studied (Figure 2) (Kolosov, 2022). As in the recent yeast, they occasionally formed blastospores and conidia (Figure 6). The yeast actively reproduced by sporulation. The growth of the individuals / cells was rapid and led to their increase in size (Figures 5, 7). The formation of blastospores is a characteristic feature of recent yeasts (for example, the genus *Candida*). The cells studied are not bacterial. As it is known, bacterial spores



**Figure 6.** Reproduction of yeast fungi via spore formation on mycelia and hyphae: 1, blastospore (mycelium with multiple spores); 2, conidium (hypha at the end of the mycelium, with a chain of spores). Scale bar = 2  $\mu\text{m}$ .



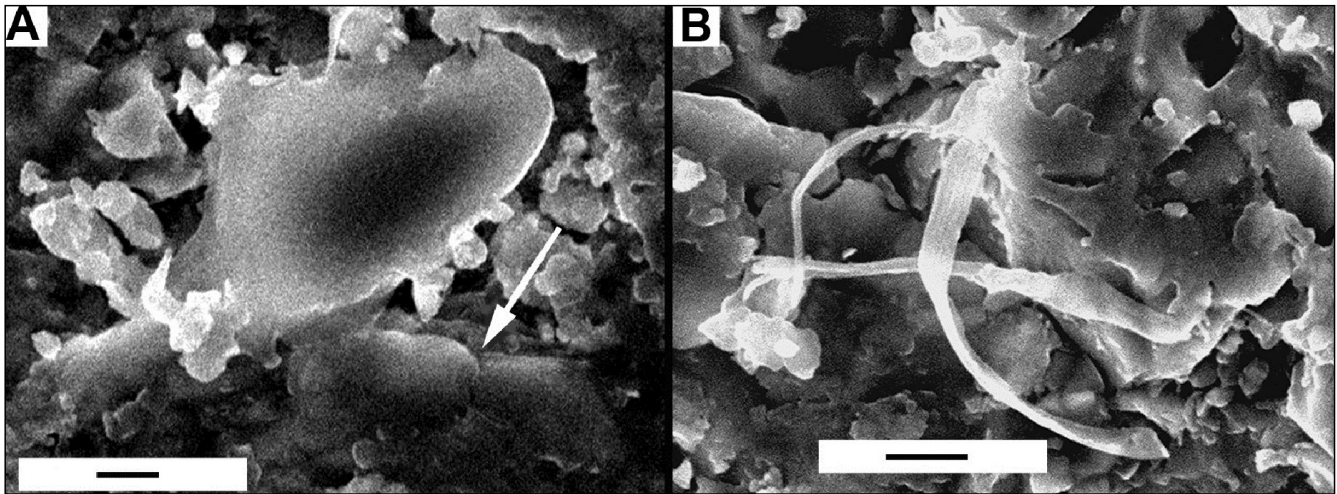
**Figure 7.** Yeast fungi *Tungusia mane* gen. et sp. nov.: 1, buds; 2, growth of a cell / individual through protrusion of its shell; 3, bridge connecting the cells. Scale bar = 0.5  $\mu\text{m}$ .

do not serve as a means of cell reproduction. Similar to the recent fungi, the spores presumably contributed to the Byuk fungi endurance of the occasionally unfavorable conditions occurring in the stromatolite paleoecosystems.

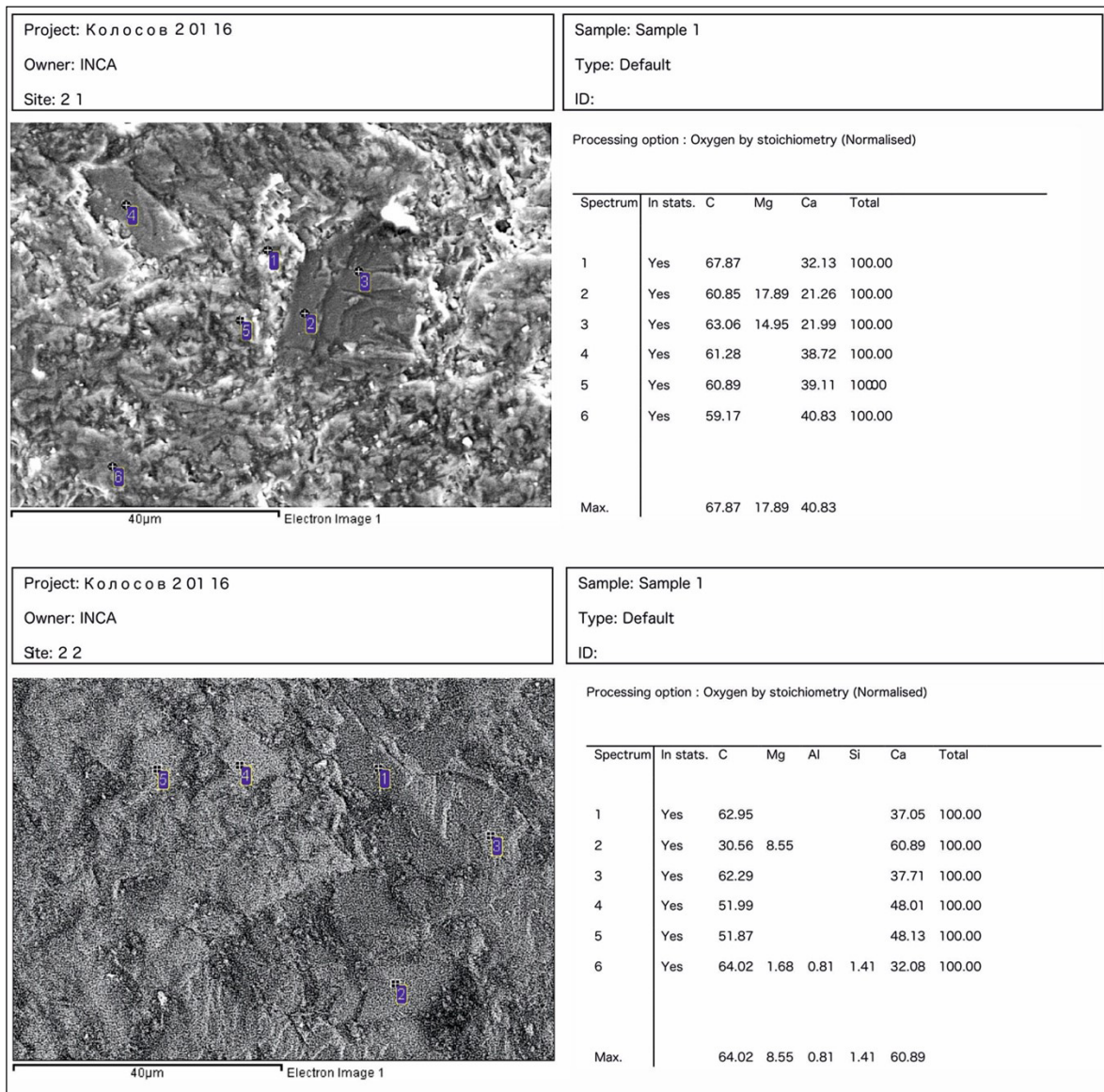
In addition to budding and sporulation, the Byuk yeast also reproduced by cell division. The shell / wall of the mother cell bent outward and formed the wall of the daughter cell (Figures 5B, 7). The size of individuals increased via protrusion of the shell (Figures 5B, 7). In the tidal zone of the seacoast, the surface of stromatolites was periodically exposed, which led to changes in the environmental conditions, as previously reported (Kolosov, 2021). In these cases, yeast produced yeast-mycelial forms, *i.e.*, yeast with mycelial structures (Figure 8B). The same process occurs in recent yeast (Djakov, 2013). Mycelial fungi were discovered in the studied sample of stromatolites (Figure 2) (Kolosov, 2016a, b). In cases where the surface of stromatolites was below the water level, their hyphae, similarly to the recent forms, presumably disintegrated thus leading to yeast formation.

Above, in the same section, it is noted that the studied yeast was located within the paleoecosystem of columnar stromatolites, which was rich in organic matter (polysaccharides) of green algae, wherein the yeast reproduced





**Figure 8.** Yeast. **A**, *Tungusia mane* gen. et sp. nov. Reproduction by budding is illustrated by small and two large buds that have turned into daughter cells (arrow indicates a small separation between the two daughter cells); **B**, yeast-mycelial fungi, i.e., yeast with mycelial structures (Kolosov, 2021, fig. 3: fungi *Sakhi solomonovi*). Scale bars = 1  $\mu$ m.



**Figure 9.** Carbon content in microfossils studied in stromatolites (Figure 2).

rapidly. It is known that under favorable conditions, *e.g.*, on saccharine substrates, blast-like growth of the modern yeast biomass occurs. It appears that a similar pattern occurred in the Ediacaran during the Byuk period in the paleoecosystem of stromatolites (Figure 2). Presumably, the Byuk yeasts of Ediacaran age were chemoorganotrophs, with organic matter obtained from algae through parasitism. Like recent fungi, the yeast probably released certain enzymes (external fermentation) into the intracellular medium to break down the potential starch and sucrose of the thallus into low-molecular soluble compounds. The yeast absorbed the resulting acids through their entire surface. The presence of yeast fungi on lamellar algae thalli observed in the Byuk stromatolites is neither commensalism nor mutualism. Based on how the Byuk yeasts corroded the thalli (Figure 4A), they were parasitic osmotrophs. This type of nutrition is characteristic of yeast fungi. It is well known that yeast typically parasitizes the thalli of green algae.

Modern fungi use mycelium and hyphae for nutrition in terrestrial ecosystems where there is no ready-made dissolved organic substances (Djakov, 2013). Precambrian lands were deficient in ready-made organic matter; it was caused by the fact that some Byuk yeasts used mycelial structures in order to obtain nutriment (Figure 8B; Kolosov, 2021, fig. 2b; Kolosov, 2023, tab. I, fig. 1). The rock-forming function of recent fungi in biosphere is well-known. The Byuk stromatolites are primarily composed of fossilized yeasts that do not have mycelia. Therefore, yeast were not secondarily unicellular forms, as is commonly believed (Figures 7 and 8A). It is more reasonable to assume that after Ediacaran (Vendian), after millions of years, yeast fungi did not need mycelial structures. This was due to the transition of inhabitation to substrates that were rich in ready-made organic matter.

To summarize, all the facts presented in the section of the Byuk stromatolites are characteristic of recent yeast fungi. Based on this, the absolute majority of the studied Byuk microfossils have been biologically interpreted and classified as yeast fungi. Presumably, these microfossils were the early ancestors of budding saccharomycete yeast fungi. (Fungi, class *Saccharomycetes*, division *Ascomycota*, subdivision *Saccharomycotina*).

The studied collection No. 87 is kept in the Geological Museum of the Diamond and Precious Metal Geology Institute SB RAS (Russia, Yakutsk).

## PALEOMYCOLOGICAL DESCRIPTION

### FUNGI INCERTAE SEDIS

*Tungusia* Kolosov et Okhlopko, gen. nov.

**Type species.** *Tungusia mane* Kolosov et Okhlopko, gen. et sp. nov.

**Etymology.** The genus name derives from the word “Tungus” (ethnic group of the East of Russia).

**Diagnosis.** Single marine yeast fungi. Cells (individuals) are mainly lumpy or slightly elongated with many outgrowths that increase their size. They reproduce through budding and sporulation. Some buds are separated from the mother cells, others are not. The cells are arranged mostly in large quantities together, thereby creating, as it were, aggregates. Separate cells infrequently produce rudimentary short single mycelial structures (formations) of a tubular shape. The fungi represent components of the stromatolite ecosystem and other bottom formations of organosedimentary origin; they parasitize the thalli of the lamellar green algae (Figures 5, 7, 8).

**Species composition.** Type species only.

*Tungusia mane* Kolosov et Okhlopko,  
gen. et sp. nov.

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(Figures 5, 6, 7, 8A)

**Etymology.** The name of the species comes from the word “early”.

**Holotype.** DPMGI SB RAS, n° 87/187; Eastern Siberia, Western Yakutia, the Tokko River basin (right tributary of the Chara River in the Olekma River basin); Neoproterozoic, Ediacaran, Byuk Formation.

**Diagnosis.** As in genus.

**Description.** The following is a description of the holotype (Figure 5B): yeast cells (individuals) of different shapes, primarily rounded or slightly elongated, are present in large numbers together, creating aggregates. This is explained by their intensive reproduction that forms many new (daughter) cells, some of which remain associated with the mother for a certain period. The sizes of the cells, as well as their shape, vary greatly. The daughter cells are extended by 1.44 (here and further in  $\mu\text{m}$ ) and are 0.73 in thickness. The cell membrane protrudes from 0.56 to 0.57. One of the cells has a mycelial structure of a tubular shape with a length of 1.64 and thickness of 0.07. Depending on the degree of maturity, buds of various dimensions protrude by 0.10–0.17, with a thickness of 0.11–0.18. Figure 7 shows: buds with a length ranging from 0.08 to 0.13, and a thickness ranging from 0.10 to 0.16; the size of the cell growth because of its protrusion from the shell ranges from 0.34 to 0.37 in length and 0.10 to 0.18 in thickness. A 0.27-long and 0.17-thick bridge connecting the cells is present. Presumably, reproduction by division is observed. Reproduction of yeast fungi by the formation of spores on mycelia (Figure 6: 1) with a length of 15.22, on which there are large spores of 1.05–1.19 in diameter and small spores of 0.217–0.225 in diameter. The average spore size of the longitudinal mycelium varies from 0.7 to 0.715. Reproduction of yeast fungi also occurs on hyphae (Figure 6: 2) of 3.60 in length, their spore size ranging from 0.362–0.392. The sizes of mycelium and hyphae, as well as spores, vary quite a lot. Figure 8A: like the recent yeast fungi, the wall of the Byuk cell is smooth; probably it was elastic during the lifetime of the organism. It has an oval shape and outgrowth,



occasionally in the form of a “tail”. The presence of a “tail”, an apically located outgrowth, presumably, as with the recent counterparts (Djakov, 2013), is explained by the necessity to better digest the substrate. On the “tail” there are many very small round formations, *i.e.*, incipient buds. On one side of the described yeast cell (Figure 8A), there are buds and daughter cells, and on the other side, there are outgrowths, through which the individual gradually increases in size. Two daughter cells of smaller size are not separated from the mother cell. They are arranged sequentially one after another, with a bridge between them. Dimensions of an oval cell with a “tail”: cell length 10.7 (without a “tail” 6.0, “tail” part 4.7); thickness: maximum 4.0, “tail” part 0.8–1.2; bud height 0.4–0.8; length of daughter cells 3.3, thickness 1.6.

Rod-like rudimentary mycelial structure in individual yeast cells (Figure 5B), presumably, is formed sporadically because of changes in the environment conditions of the stromatolite ecosystem. This also explains why the further development of yeast occurs in the mycelial-yeast habitat (Figure 8B; Kolosov, 2021). The described Byuk yeast fungi are primarily characterized by a lumpy shape with many outgrowths, elongated forms with a length of up to 1.09–1.18  $\mu\text{m}$  and a thickness of 0.03  $\mu\text{m}$  are observed less often.

**Comparison.** The only species of the genus.

**Material.** 219 SEM images of 11 thin sections of stromatolites in a large number (rock-forming = stromatolite-forming) of excellent preservation.

## CONCLUSIONS

For the first time, columnar stromatolites of the Ediacaran of the Siberian Platform have been found to contain microfossils, which are undoubtedly perfectly preserved cells (individuals) of yeast fungi. The evidence of such systematic identification of cells lies in their asexual reproduction by budding, sporulation (including the location of spores in the form of blastospores and conidia), division, and protrusion at any point of the shell, as well as the type of nutrition (they were chemoorganoheterotrophs and parasites on the thalli of green algae). The Ediacaran-aged Byuk yeast originated in an aqueous medium and had no mycelium. The mycelium was formed only in an environment that was poor in ready-made organic matter. It is conceivable that further research will reveal that they are the early (or one of the) ancestors of budding saccharomycete yeast fungi.

The rock representing the studied stromatolites is composed almost entirely of fossilized yeast fungi and algae. The spread of green algae in the Ediacaran in the east of the Siberian platform and their increasing presence in the stromatolite paleoecosystem led to the prospering of aquatic yeast fungi in the Byuk period in the Berezovsky trough. It is possible that during the Ediacaran period, not only columnar yeast but also yeast of other forms participated in the formation of the bottom sediments of organogenic-sedimentary origin on the Siberian platform. From the studied samples of stromatolites (Figure 2), as noted above, mycelial

and yeast-mycelial/ mycelial-yeast fungi were previously described. However, their biomass in the mineralized state is insignificant in comparison with yeast. Consequently, they made a minor contribution to the development. Yeast has good preservation, which can be explained to some extent by the silicification of the calcareous-dolomite composition of the rock that contains it.

The results on yeast presented in the article complement the reliable data previously obtained in Yakutia on the origin of mycelial and yeast-mycelial marine fungi on Earth within the Ediacaran. In addition, including the aforementioned other fungi, yeast indicates the prospects of paleomycological studies of the Ediacaran. The Siberian platform is one of the most suitable large geological structures for searching for the Late Precambrian microfossils of fungal origin.

The detection of microfossils in Ediacaran (635–538.8 Ma) and the establishment of their systematic position – fungi, can contribute to elucidating the evolution and ecology of these eukaryotes in subsequent periods (Karatygin, 2007; Kolosov, 2016a, b, 2019).

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## REFERENCES

- Alexin, A.I. *et al.* 2007. *Mycology today*. Vol. 1. Moscow, National Academy of Mycology, 376 p.
- Burzin, M.B. 1995. Most ancient organisms – sources of oil in the Russian platform. *Priroda*, 2:38–44 (in Russian).
- Burzin, M.B. 2003. *Microorganisms in the fossil record: A teaching manual*. Moscow, MAKS-Press, 27 p.
- Djakov, Yu.T. 2013. *Recreational mycology*. Moscow, Librokom, 240 p.
- Djakov, Yu.T. & Sidorova, I.I. 2012. Possible role of fungi in the early colonization of land. *In: S.V. Rozhnov (ed.) Geo-biological processes in the past*, PIN RAN, p. 120–137.
- Heckman, D.S.; Geiser, D.M.; Eidell, B.R.; Stauffer, R.L.; Kardos, N.L. & Hedges, S.B. 2001. Molecular evidence for the early colonization of land by fungi and plants. *Science*, **293**:1129–1133. doi:10.1126/science.1061457
- Hedges, S.B.; Blair, J.E.; Venturi, M.L. & Shoe, J.L. 2004. A molecular timescale of eukaryote evolution and the rise of complex multicellular life. *BMC Evolutionary Biology*, **4**:2. doi:10.1186/1471-2148-4-2
- Hermann, T.N. 1979. Fungus records in the Riphean. *In: B.S. Sokolov (ed.) Paleontology of the Precambrian and Early Cambrian*, Nauka, p. 129–136.

- Hofmann, H.J. 1971. Polygonomorph acritarch from the gunflint formation (Precambrian), Ontario. *Journal of Paleontology*, **45**:522–524.
- Karatygin, I.V. 2007. Mycofossils: current state and problems. In: Yu.T. Djakov & Yu.V. Sergeev (eds.) *Mycology today*, National Academy of Mycology, p. 10–28.
- Khomentovsky, V.V. 2008. The Yudomian of Siberia, Vendian and Ediacaran systems of the International stratigraphic scale. *Stratigraphy and Geological Correlation*, **16**:581–598. doi:10.1134/S0869593808060014
- Knoll, A.H. 1992. The early evolution of eukaryotes: a geological perspective. *Science*, **256**:622–627. doi:10.1126/science.1585174
- Koloso, P.N. 2003. *Late Precambrian microfossils and stratigraphy of oil-and-gas-bearing strata in the eastern Siberian platform*. Yakutsk, Yakut Branch of Russian Academy of Sciences, 164 p.
- Koloso, P.N. 2013. Fungiform organisms from the Early Cambrian of the Northern Tien Shan. *Paleontological Journal*, **47**:549–553. doi:10.1134/S0031030113050080
- Koloso, P.N. 2016a. New microorganisms from the Vendian (Ediacaran) of the Berezovsky Trough, Southern Siberian platform. *Paleontological Journal*, **50**:549–556. doi:10.1134/S0031030116060071
- Koloso, P.N. 2016b. Fungi in the Vendian of Yakutia. In: READINGS IN MEMORY OF KRISHTOFOVICH. A.N., IX, 2016. Komarov Botanical Institute of the Russian Academy of Sciences, Saint-Petersburg, p. 11–12.
- Koloso, P.N. 2019. Fungal spores in the stromatolites of the Vendian (Ediacaran) of Yakutia. In: READINGS IN MEMORY OF KRISHTOFOVICH. A.N., X, 2019. Komarov Botanical Institute of the Russian Academy of Sciences, Saint-Petersburg, p. 33.
- Koloso, P.N. 2021. Uniquely preserved fungi in the Vendian (Ediacaran) of Yakutia. *Paleontological Journal*, **55**:455–461. doi:10.1134/s0031030121040080
- Koloso, P.N. 2022. The ancestors of Cryptococci appeared on Earth 600 million years ago. *Open Access Library Journal*, **9**:1–8. doi:10.4236/oalib.1109125
- Koloso, P.N. 2023. *Paleoulvaria* green algae of the Vendian (Ediacaran) Berezovsky trough (South of the Siberian platform). *Paleontological Journal*, **57**:231–234. doi:10.1134/S0031030123020090
- Koloso, P.N. & Sofroneeva, L.S. 2014. Microorganisms in the zone of submarine volcanic eruptions at 535–513 Ma. *American Journal of Plant Sciences*, **5**:2464–2471. doi:10.4236/ajps.2014.515261
- Kondratieva, E.N.; Maksimova, I.V. & Samuilov, V.D. 1989. *Phototrophic microorganisms: Textbook*. Moscow, Moscow University Press, 376 p.
- Meyen, S.V. 1987. *Fundamentals of paleobotany*. Moscow, Nedra, 403 p.
- Mikhailova, N.S. 1986. New records of microfossils from Upper Riphean beds in Krasnoyarsky Krai. In: B.S. Sokolov (ed.) *Topical problems of present-day paleoalgology*, Naukova Dumka, p. 31–37.
- Retallack, G.J. 2015. Acritarch evidence of a late Precambrian adaptive radiation of fungi. *Botanica Pacifica*, **4**:19–33. doi:10.17581/bp.2015.04203
- Rozanov, A.Yu. 1980. Centers of origin of the Cambrian faunas. In: SESSION OF THE INTERNATIONAL GEOLOGICAL CONGRESS, 26, 1980. Nauka, Moscow, p. 30–34.
- Rozanov, A.Yu. 2003. Fossil bacteria, sedimentogenesis and early evolution of biosphere. *Paleontological Journal*, **37**:41–49.
- Rozanov, A.Yu.; Parkhaev, P.Yu.; Shabanov, Yu.Ya.; Pegel, T.V.; Raevskaya, E.G.; Zhuravlev, A.Yu.; Gamez Vintaned, J.A. & Yergaliev, G.Kh. 2008. The 13th International field conference of the Cambrian stage subdivision working group (Siberian platform, Western Yakutia Russia). *Episodes*, **31**:440–441. doi:10.1134/S0031030109030150
- Schopf, J.W. 1968. Microflora of the Bitter Springs formation, Late Precambrian, Central Australia. *Journal of Paleontology*, **42**:651–688.
- Schopf, J.W. 1993. Microfossils of the early Archean Apex chert: new evidence of the antiquity of life. *Science*, **260**:640–646. doi:10.1126/science.260.5108.640
- Semikhatov, M.A. 2000. Refined estimates of the isotope age of lower boundaries of the Upper Riphean, Vendian, Upper Vendian, and Cambrian. In: *Additions to the Stratigraphic Code of Russia*, Russian Geological Research Institute, p. 95–107.
- Semikhatov, M.A.; Kuznetsov, A.B.; Podkovyrov, V.N.; Bartley, J. & Davydov, Yu.V. 2004. The Yudoman complex of a stratotype area: C-isotopic chemostratigraphic correlations and relation to the Vendian. *Stratigraphy and Geological Correlation*, **12**:435–459.
- Shkol'nik, E'.L. et al. 2004. *Biomorphic structures in bauxites*. Moscow, Eslan, 112 p.
- Sukhotin, A.K. 1988. Methodology of Science: Problems and Solutions. *Voprosy Filosofii*, **3**:120–123.
- Taylor, T.N.; Hass, H.; Kerp, H.; Krings, M. & Hanlin, R.T. 2005. Perithecial ascomycetes from the 400 million year old Rhynie chert: an example of ancestral polymorphism. *Mycologia*, **97**:269–285. doi:10.1080/15572536.2006.11832862
- Taylor, T.N. & Osborn, J.M. 1996. The importance of fungi in shaping the paleoecosystem. *Review of Paleobotany and Palynology*, **90**:249–262. doi:10.1016/0034-6667(95)00086-0
- Tyler, S.A. & Barghoorn, E.S. 1954. Occurrence of structurally preserved plants in pre-Cambrian rocks of the Canadian Shield. *Science*, **119**:606–608. doi:10.1126/science.119.3096.606
- Velikanov, L.L.; Garibova, L.V.; D'jakov, Yu.T.; Prohorov, V.P.; Sidorova, I.I.; Kamnev, A.N.; Tolpysheva, T.Yu.; Belyakova, G.A. & Tarasov, K.L. 2007. *Botany: Course of Algology and Mycology*. Moscow, Moscow University Press, 558 p.
- Wijayawardene, N.N. et al. 2020. Outline of Fungi and fungus-like taxa. *Mycosphere*, **11**:1060–1456. doi:10.5943/mycosphere/11/1/8
- Woese, C.R.; Kandler, O. & Wheelis, M.L. 1990. Towards a natural system of organisms: proposal for the domains Archaea, Bacteria, and Eucarya. *Proceedings of the National Academy of Sciences of the USA*, **87**:4576–4579. doi:10.1073/pnas.87.12.4576
- Yuan, X.; Xiao, S. & Taylor, T.N. 2005. Lichen-like symbiosis 600 million years ago. *Science*, **308**:1017–1020. doi:10.1126/science.1111347

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