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Fungal Remains from the Late Riphean

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Abstract—The paper describes organic remains of one billion years old from the Lakhanda microbiota of the Uchur-Maya Region of southeastern Siberia. The microfossils were discovered on organic sapropelic films. The preserved morphological characters and some developmental stages of the ancient organisms, which are fixed in fossil state, suggest that some of them resembled zygomycetes. Other microfossils under consideration are comparable to reproductive structures of myxomycetes in the type of fusion of spheroid cells and formation of various types of aggregation (sori). Colonies of unicellular microfossils that are arranged in a branching pseudomycelium superficially resemble yeasts. The presence in the same biota of fungal remains belonging to the Myxomycota and Mycota, as well as members of xanthophyte vaucherian algae, indicates that various branches of eukaryotes might have developed in parallel even earlier than the Late Riphean.

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INTRODUCTION

For our understanding of the history of the organic world, the evolutionary chronology of taxa needs further elucidation. This is important for the taxonomy of ancient organisms and for determination of the times when biologically complex organisms appeared. The overwhelming majority of Late Proterozoic microfossils are microscopical unicellular remains that lack diagnosable morphological characters. A large number of formal taxa of microfossils have been described, thus suggesting a considerable biodiversity. Butterfield (2004) believes that only four pre-Ediacaran genera of microfossils can with certainty be shown to have affinity with extant taxa. These are the genus *Palaeovaucheria*, which is comparable with modern xanthophyte algae (Hermann, 1981); *Proterocladus*, which is assigned to siphonaceous algae (Butterfield *et al.*, 1994); vase-shaped protists *Melanocyrillium* (Porter *et al.*, 2003); and algae *Bangiomorpha*, which are close to modern red algae (Butterfield, 2000). Hermann (1979) discovered from the Late Riphean of the Siberian Platform (Meso/Neoproteozoic boundary, Lakhanda microbiota) microfossils that, in our opinion, are at least equally important from a paleobiological perspective. The preserved morphological characters and particular stages of the life cycle of these organisms show them to be comparable with modern zygomycetes, myxomycetes, and yeasts. It is important to pay more attention to the group that is morphologically distinct from other Late Riphean microfossils. In order to provide an apt illustration of the degree of complexity that fungi had reached in the Late Riphean, photomicrographs of fossil fungi are accompanied by drawings of modern fungi that are close to them in morphology and in some stages of the life cycle.

The first record of fungi from the Late Riphean (Hermann, 1979) was long doubted because it contradicted the generally accepted concept of fungal phylogeny. The internationally known German mycologist Anton de Bary believed that fungi appeared relatively late in the history of the organic world and derived (in particular, zygomycetes) from green algae of the modern vaucherian algae-type, since both groups show some degree of similarity in their life cycles (Parnes, 1972). We should note, however, that fossil vaucherian algae (Figs. 1a–1f) were found in the same Lakhanda microbiota (Hermann, 1981) as the fungal remains under description (Pl. 11), and these two groups of microfossils differ considerably in morphology.

There are several opinions about the time of the origin of fungi. Malakhov (2003) reviewed the main evolutionary stages of eukaryotes and concluded that fungi could not have appeared earlier than higher plants and, consequently, the time of their origin should have been in the Ordovician–Silurian. Molecular phylogeny and biogeochemistry show that the differentiation of eukaryotes took place during the early history of the Earth (Javaux *et al.*, 2001), and astonishing recent data have suggested that the phylogenetic tree of eukaryotes should be revised and that its "roots" (including fungi) should even be sunk into the Archean (Martin *et al.*, 2003).

Reports of Precambrian fungal remains are still rare. According to the paleomycologist Popov (1965), the

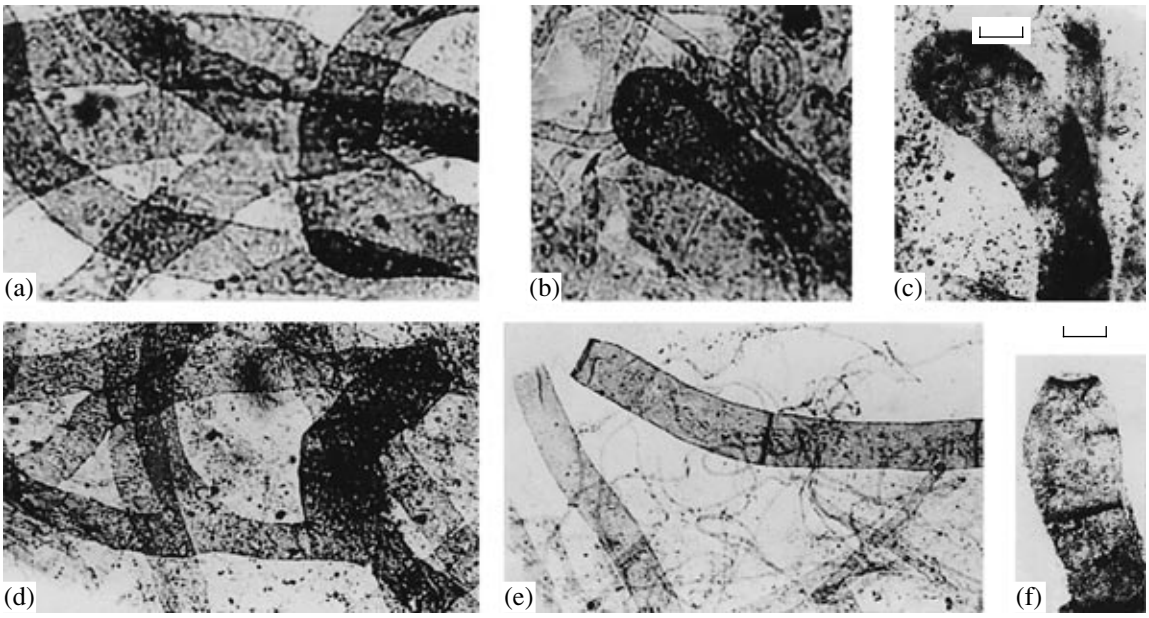


Fig. 1. *Palaeovaucheria clavata* Hermann, 1981: (a) branching filament, IGGP, no. 28/1-12.1.78; (b, c) clavate endings of filaments, IGGP, no. 28/1-12.1.78; (d) branching filament and a horn-shaped antheridium, IGGP, no. 28/4-10.1.78; (e) filament with occasional septa, cyanobacteria form a background, IGGP, no. 27/14-26.X1.77; (f) open ending of a filament, IGGP, no. 28/1-12.1.78. Scale bar 50 μm.

fact that records of fungi from Precambrian rocks are rare suggests a lack of recording effort rather actual scarcity or absence. Indeed, Butterfield (2005) restudied an extensive heterogeneous population of acanthomorphic acritarchs of the formal genus *Tappania* and concluded that these microfossils may belong to a sister group of "higher fungi." The acritarchs come from the Early Neoproterozoic (Late Riphean) Wynniatt Formation (Victoria Island, northwestern Canada, 723 million year old). In addition, Butterfield believes that some other Proterozoic acritarchs, *Trachyhystrichosphaera, Shuiyousphaeridium, Dictiosphaera*, and *Foliomorpha*, show some affinity with fungi. Acritarchs of the genus *Tappania* were first described from the Meso-Neoproterozoic deposits of the Ruyang Group, northern China (Yin, 1997). Similar microfossils were reported from the Sanda Formation of the Ganga Basin of India (Javaux *et al.*, 2004), which is correlated with the Tottinskaya Formation of Siberia (1.3 million years). The earliest records of *Tappania* come from the Mesoproterozoic of the Roper Group of Australia, their age is 1430 million years (Javaux *et al.*, 2004). These finds of supposed fungal fossils imply the early appearance of this group and its broad geographic distribution.

THE LOCALITY OF THE MICROBIOTA AND DEPOSITIONAL ENVIRONMENT OF THE LAKHANDA PALEOBASIN

The microbiota comes from clayey facies of the Neryuenskaya Formation of the Lakhanda Series in the middle course of the Maya River (Uchur-Maya Region of the southeastern Siberia).

The exceptionally good state of preservation and high diversity of organic remains of the Lakhanda microbiota are the result of a combination of several favorable factors (Davydov, 1975; Hermann and Podkovyrov, 2002b). The accumulation of the clayey deposits that contain the organic remains under description occurred in the quiet conditions of a shallow sea basin (below the level of storm waves). The rapid development of organic life in the Lakhanda paleobasin was facilitated by well-aerated waters and input of nutritive substances from the continent, including the products of synchronous volcanic activity (Ivanovskaya *et al.*, 1988). Dead organic material was buried under a cover of fine clayey particles, in a nearly neutral medium, lacking in oxygen and having excess reactive iron (an environment resembling that of the Burgess-Shale). This guaranteed a uniquely high level of preservation of microfossils.

Originally, the Lakhanda Series was established as the Lakhanda Formation with four subformations (from bottom to top): Kumakhinskaya, Mil'konskaya, Nel'kanskaya, and Ignikanskaya (Nuzhnov, 1967). Later, it was proposed that this formation was should be considered as a series with two formations: Neryuenskaya Formation (with Lower Lakhanda deposits of the Kumakhinskaya, Mil'konskaya, and Nel'kanskaya subformations) and Ignikanskaya Formation, which included Upper Lakhanda deposits (Semikhatov and Serebryakov, 1983). In her original description of fungal remains,

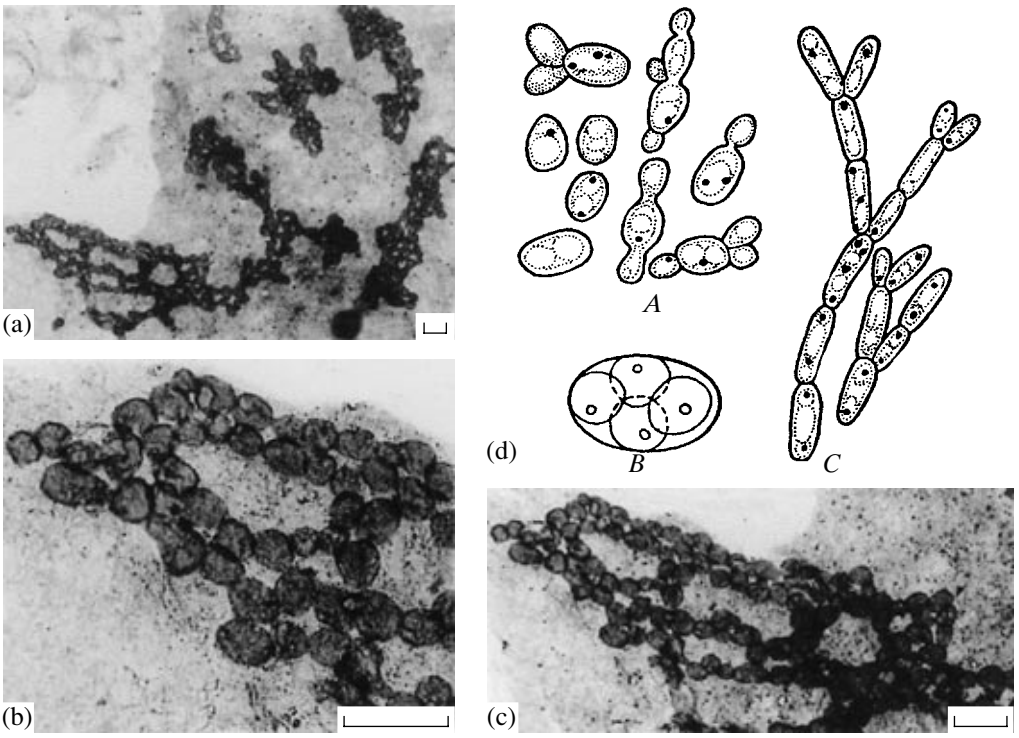


Fig. 2. *Eosaccaromyces ramosus* Hermann, 1979: (a) colonies on an organic film that were formed as gemmation of unicellular microfossils; (b, c) microfossils in the form of a branching mycelium, IGGP, no. 19/1-U.75; (d) gemmation in the modern *Saccharomyces cerevisiae.* Scale bar 50 μm.

Hermann (1979) used the chart that was developed by Nuzhnov. According to the currently adopted stratigraphic chart, the microfossils under study come from the lower part of the Neryuenskaya Formation of the Lakhanda Series. The age of the deposits is 1020–1030 million years (Semikhatov, 2000).

On the left bank of the Maya River, 25 km downstream from the village of Aim, near the mouth of Ytyrynda Creek, the lower beds of the Neryuenskaya Formation are exposed. The outcrop is 350 m long; 27-m-thick beds of variegated silt-clayey deposits are exposed. Above the water level, dark gray clayey shales crop out. Their thin-bedded varieties appear as slightly altered laminated claystones and contain numerous organic remains of different nature that are perfectly preserved (Hermann, 1979, 1981, 1990; Timofeev and Hermann, 1979; Hermann and Timofeev, 1985).

MATERIAL AND METHODS

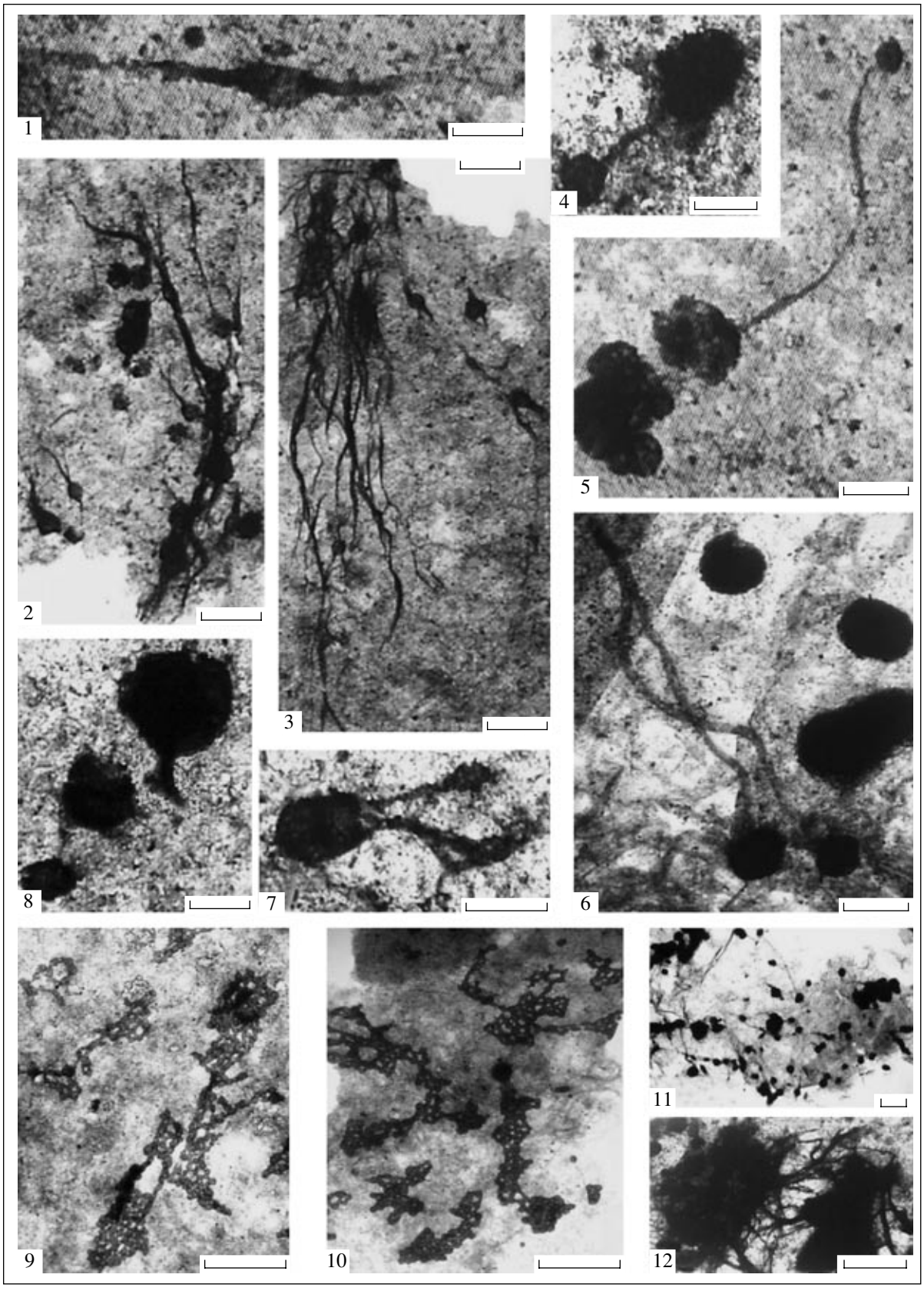
Before dissolution with hydrofluoric acid, pieces of rock were studied under a binocular microscope in reflected light. Along the lamination of organic-rich shales, large fragments of sapropelic films are visible. They are dark brown with silvery spots. Such films usually contain diverse fossils. Pieces of rock of more than 1 cm thick were carefully cleaved along the lamination for rapid dissolution with HF. The films were washed with caution to separate the organic films that held fossils together undamaged. Again, with caution, the films were transmitted (with a needle or pipette) to a slide. Then, permanent slides were made (Hermann, 1974; Hermann and Podkovyrov, 2002a). The microfossils were studied with a light microscope (Ergaval) at magnifications of 400× and 1000×.

Two samples (no. 19 and, particularly, no. 22) contained, among abundant organic remains, microfossils that were not comparable with either known acritarchs or filamentous organisms. Nonetheless, the fossil remains showed characters that reflected the developmental histories of the organisms. The microfossils are preserved at various stages of the life cycle: fusion, division, growth, formation of specific colonies, and formation of reproductive structures (fungal sori). The study of the individual morphology of fossil organisms and comparison between revealed stages of the life cycle and those in some modern lower organisms indicate relationships between these fossils and fungi. Morphological characters that serve as a basis for our interpretation of the fossil remains are described below.

MATERIAL

The collection is housed at the Institute of Geology and Geochronology of the Precambrian in St. Petersburg (IGGP).

Plate 11



THE MORPHOLOGY AND PRESERVATION OF THE MICROFOSSILS

The organic film preserved several stages in the life cycle of some fossil organisms that are morphologically different, but related. These stages are comparable with those of the life cycles of some modern Mucorales (zygomycetes). Figure 4 (after Borodin, 1897) provides a comparison with modern zygomycetes and shows types of zygospore formation in modern Mucorales. There is a phase of copulation of adjacent hyphae in their life cycle. In the point where fossil hyphae are fused, a zygospore (75 × 50 μm) is formed. Laterally, remains of copulating hyphae of 350 and 450 μm long are preserved (Pl. 11, fig. 1; compare with types of formation in modern fungi, Figs. 4a–4d). The type of formation of a fossil zygospore (Pl. 11, fig. 8) is virtually identical to that observed in the modern *Mucor tenuis* (Fig. 4f), in which zygospores can develop without copulation (Figs. 4g, 4h). Numerous ancient zygospores were discovered in proximity to remains of copulating hyphae-suspensors (Pl. 11, figs. 2, 3). In places, suspensors are destroyed and spores released (Pl. 11, fig. 3, top right), but, more often, suspensors are preserved, become thicker, denser, and darker (Kursanov, 1953). We found many fossil zygospores with an envelope of suspensors, a characteristic of Mucorales (Pl. 11, fig. 12). After the dormancy phase, the zygote may grow into a long non-branching filament terminating in an incipient sporangium. There is a fossil showing an analogous type of germination: the incipient sporangium is 37.5 μm in size, and the germinated cell is 125 μm (Pl. 11, fig. 5; Fig. 4e shows the same process in modern organisms). Two long fragmentary sporangiophores were also found (Pl. 11, fig. 6). Zygotes were discovered to germinate with a short filament (Pl. 11, fig. 4) or short forking filaments (Pl. 11, fig. 7). The characteristic morphology of ontogenetic stages of the ancient organisms proves their relationship to zygomycetes. The microfossils were described as *Mucorites ripheicus* Hermann (Hermann, 1979). It is pertinent to note that nonflagellate fungi, zygomycetes including, are traditionally placed near the roots of eukaryotes (Starobogatov, 1986), and zygomycetes are considered within the systems of fungi as a group that evolved terrestrial adaptations (*A Course* …, 1981).

One more group of fossil organic remains that was discovered was related to the modern yeast *Saccharomyces*, based on cell gemmation and the mode of colony formation.

The colonies that appear as reticulate "tissue" were composed of regularly oriented cells and exhibit a more complicated level of connection and relation of cells. The cells of the colonies are devoid of mucous covers and are aligned in one row. Different outlines of the colonies are explained by the mode of the cell gemmation, which is either irregular or successive gemmation of parent and daughter cells, which have spherical, oval, or, more rarely, a rodlike or oval-triangular shape. The cells are 10–40 μm, sharply constricted, but did not separate, in the form of a branching mycelium (Pl. 11, figs. 9, 10; Figs. 2a–2c, compare the gemmation in modern yeast, Fig. 2d). The microfossils were described as *Eosaccharomyces ramosus* Hermann (Hermann, 1979). The discovery of fossil remains of budding cells is important from the theoretical point of view. Endomycetes, which include fungi of the Saccharomycetaceae, are supposed to be a transitional link between ascomycetes and their possible ancestors, relatives of modern zygomycetes (*A Course* …, 1981).

The third group of extremely numerous microfossils was also discovered on organic films in the form of sori. The sori consist of thick-walled spheroid cells that vary in size and number; hence, different shapes and sizes of the sori. The films are heavily dotted with sori and separate dark cells, which are fused into aggregations under a sort of a joint cover (Fig. 3a). Short and tapering bars occasionally branch from the microfossils, resembling remains of mucous mass (Pl. 11, fig. 11). The presence of thick resistance coat in this group of microfossils and the fusion of cells into aggregations, sori, allow us to putatively consider them as reproductive structures of myxomycetes without a true mycelium. Additional evidence that these microstructures are of myxomycete origin are plasmodium-like organic remains (Figs. 3c–3e). We found pseudopodium-like protuberances, which suggest that the organisms could have moved. Their plasticity and fluidity is expressed in the morphology. These organisms apparently were a fixed mucous mass of varying and changing shape. Morphologically, these formations resemble the plasmodiocarp of myxomycetes. In modern myxomycetes,

Explanation of Plate 11

Figs. 1–8. *Mucorites ripheicus* Hermann: (1) fossil zygospore, which is laterally borne by remains of copulating hyphae, IGGP, no. 22/24-U75; (2, 3) fragments of numerous branching hyphae (suspensors), attached to zygospores, note partial degradation of the suspensors, IGGP, no. 22/1-14.11.76; (4) zygospore that grows in a short filament terminating in a sporangium, IGGP, no. 22/24-U.75; (5) zygospore that grows in a long non-branching filament terminating in an incipient sporangium, IGGP, no. 22/24-V.75; (6) two long sporangiophores terminating in spherical sporangia, IGGP, no. 22/1-29.IX.75; (7) zygospore grows with two tubes, at their ends sporangia develop, IGGP, no. 22/24-U.7; (8) zygospore that developed without copulating branches, IGGP, no. 22/1-12.IX.75.

Figs. 9, 10. *Eosaccharomyces ramosus* Hermann, colonies of budding cells form a branching pseudomycelium, IGGP, no. 19/1-V.76.

Fig. 11. *Mycosphaeroides aggregatus* Hermann, individual and fused spheroid cells of diverse shapes, remains of plasmatic filaments are visible, IGGP, no. 19/1-V76a.

Fig. 12. fossil zygospores enveloped with suspensors, IGGP, no. 22/1-14.11.76.

Scale bar 100 μm (1, 4–8) and 200 μm (others).

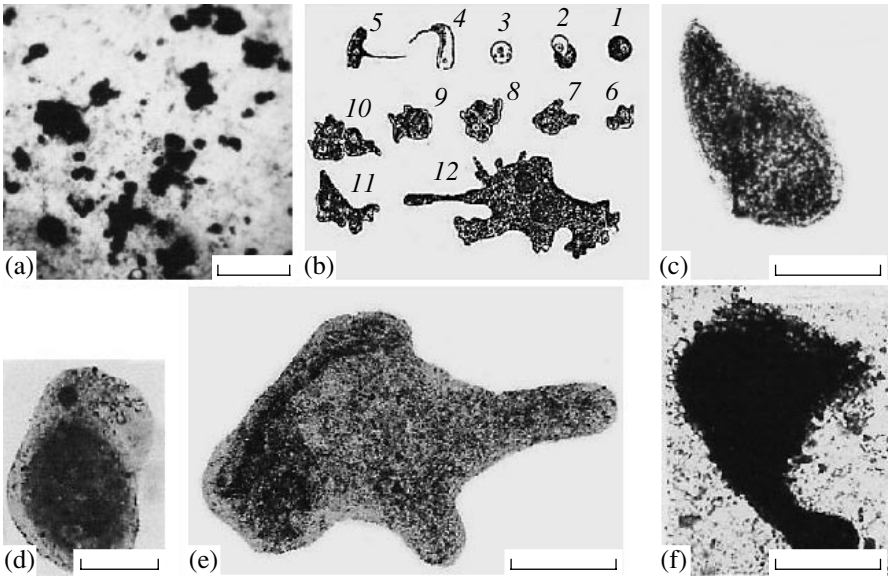


Fig. 3. *Mycosphaeroides aggregatus* Hermann, 1979: (a) fossil reproductive structures fused into aggregations (sori), IGGP, no. 19/1; (b) ontogenetic stages of the plasmodium development in modern myxomycetes; (c) change of the spheroid shape of a cell resulting in a protuberance, IGGP, no. 22/10-26.11.75; (d) outflow of the inner fluid content of a spore, IGGP, no. 22/2-21.X.75; (e) opening of a reproductive organ that resembles capillitium, IGGP, no. 22/1-12.1X.75. Scale bar (a, d) 100 μm, (b, c, e) 200 μm.

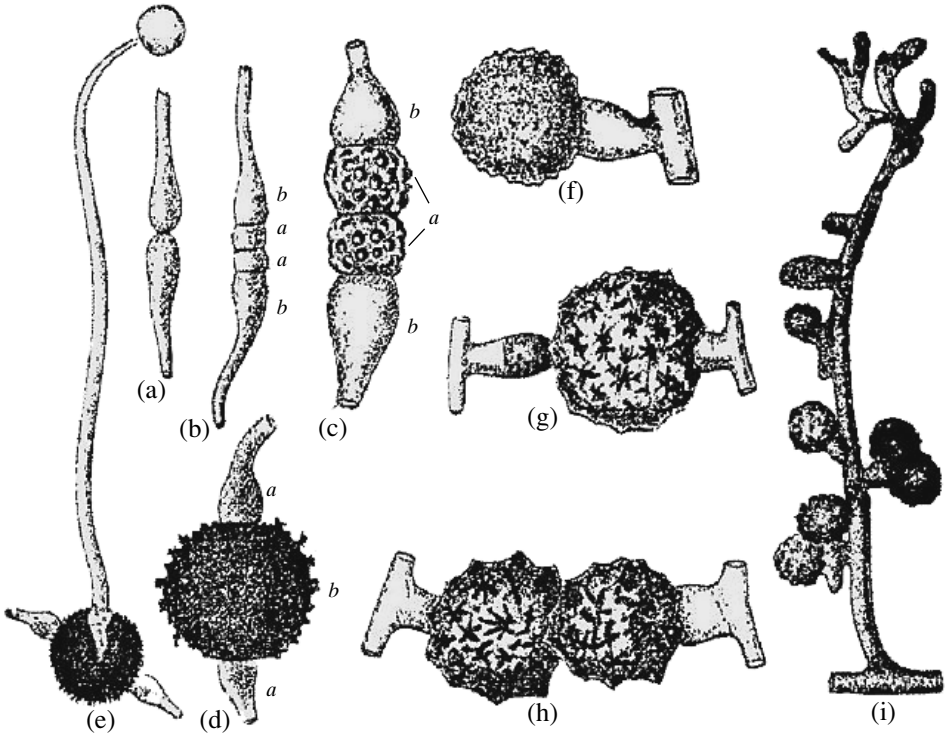


Fig. 4. Development of zygospores in modern *Mucor mucedo* (according to Borodin, 1897): (a) copulating cells of mycelium; (b) copulating cells "*a*" separated from hyphae "*b*"; (c) later stage, fusion of the cells "*a*" has not finished, but these cells are being covered with a patterned coat; (d) mature zygospore "*b*" between two suspensors, hyphae "*a*; (e) zygospore germinates, a growing end terminates in a sporangium, ×60; (f, g) formation of zygospores in *Mucor erectus*, both copulated branches have formed a spore without copulation; (f) two zygospores; (g) one zygospore; (h, i) development of zygospores in *Mucor tenius*, no copulated branches form to be directed towards each other.

the plasmodiocarp is covered with a membranous or cartilage-like peridium, whereas the cytoplasm within the coat is divided into spores with a hard coat (*A Course* …, 1981). The fossil formations apparently had a thin but resistant elastic outer membrane, which was able to fossilize. The ability of the vegetative body of myxomycetes to transform totally into spore organs explains the extreme multiplicity of the dark fossil cells fused into sori (Figs. 3a, 3b show a comparable stage in modern fungi). The dark color of the reproductive structures of fossil fungi is explained by the presence of melanin and other brown pigments—a character of fungal fossils (Elsik, 1982). We found a fossil with an opening of a reproductive organ, capillitium, which is characteristic of myxomycetes and serves as an additional proof of the relationship between the group under consideration and myxomycetes. Such fructifications in myxomycetes have special filaments within them. These filaments may be branching, solid, or form a network. Usually, filaments are tightly coiled in a capillitium and uncoil rapidly like a steel spring when they rupture (Kursanov, 1953).

CONCLUSIONS

According to the modern system of fungi (*A Course* …, 1981), some of the fossil remains under consideration (*Mycosphaeroides*) should apparently be assigned to the division Myxomycota and class Myxogasteromycetes. The microfossils of the genus *Mucorites* should be placed in the division Mycota (class Zygomycetes), and the microfossils of *Eosaccharomyces* in the class Ascomycetes. We hope that this information about fossil fungal remains contributes to the understanding of phylogenetic relationships (as yet unclear) within this extensive, metabolically diverse group of eukaryotes.

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