

Recent Studies of Co-Evolutionary Relationships of Fossil Plants and Fungi: Success, Problems, Prospects

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Abstract—A study of the history of consortial relationships between plants and fungi facilitates our understanding of the patterns and processes associated with evolutionary history of the members of these two kingdoms, their ecosystem function, and the formation of existing biodiversity. This paper is a review of recent paleomycological research focusing on the analysis of its main directions, objectives and prospects. Here we consider the main preservation types of fossil micromycetes and their study using modern research techniques. The significance of paleomycological research for paleoecological interpretations and paleoclimatic reconstructions is discussed. We also focus on further improvements of the classification systems to damage types on plant fossils by different agents, particularly fungi.

Keywords: Fungi, paleomycology, micromycetes, classification of damage types on plant fossils, paleophytopathology

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INTRODUCTION

Plants and fungi, representatives of two kingdoms of living organisms, Plantae and Fungi, belong to fundamentally different, auto- and heterotrophic components of ecosystems, and are characterized by significant differences in the structural and physiological organization, feeding strategies, and roles in biospheric processes. They have a long history of coexistence and the development of complex interactions, which largely determine the evolutionary pathways of both groups, as well as the formation of existing biodiversity. While plants were traditionally assigned the most important role in the formation of the biota and the formation of the Earth's biosphere, the participation of fungi in these processes has not been properly confirmed or recognized for a long time. Nevertheless, fungi are an integral component of Earth's modern biocenoses, and can play a fundamental role in the function and sustainability of ecosystems. Various fungi are responsible for decomposition of the substrate they have assimilated, acting as intermediaries between organic and inorganic substances of the biosphere, in connection with which it was proposed to consider them within the framework of a special ecohorizon (Karatygin, 1994).

The co-evolutionary relationships of fungi and plants are based on trophic relationships. The evolution of the substrate (plants) determined the evolution of decomposing organisms (fungi) and, conversely, fungi, exerting a direct or indirect influence on the metabolic processes of the host plant, determined their multivariant adaptations to various ecological environments. In addition, it should be noted that the concept of a role of horizontal gene transfer between different species and even kingdoms of living organisms, including plants and fungi, in the evolution of the biota, is gaining momentum (e.g., Marienfeld et al., 1997; Rosewich and Kistler, 2000; Richards et al., 2009; Li et al., 2018).

The transition of fungi to land in the late Precambrian (about 720 Ma) contributed to the further colonization of land by embryophytes (Pirozynski and Malloch, 1975; Heckman et al., 2001; Lutzoni et al., 2018). Molecular genetic studies have established that the appearance of arbuscular mycorrhizal fungi (Glomeromycotina) in geological history coincided with diversification of embryophytes (Lutzoni et al., 2018). Modern glomeromycetes are terrestrial fungi, of which almost all (except for one species associated with cyanobacteria of the genus *Nostoc*) form arbuscular mycorrhiza (AM) with roots of higher plants or

AM-like associations with non-root structures, for example, rhizoids of bryophytes (Lutzoni et al., 2018). Fossil spores of Glomeromycotina are known from the Ordovician (Redecker et al., 2000), but the earliest paleobotanical evidence of symbiosis between arbuscular mycorrhizal fungi and terrestrial plants dates back to the Early Devonian (Remy et al., 1994). According to Karatygin (2007), it was in the Devonian ecosystems that all the main mechanisms of relationships between auto- and heterotrophs were formed, which are decisive for the function of terrestrial ecosystems. The appearance and diversification of various ecological groups of fungi are correlated with several key events in plant evolution, including the origin of forest vegetation, true roots, seeds, and, finally, angiosperms (Lutzoni et al., 2018). By the end of the Cretaceous, angiosperms became the main constituents of terrestrial ecosystems. The diversity of life forms of flowering plants, their taxonomic diversity and high plasticity, as well as the ability to adapt to existence in a variety of biocenoses, have largely determined the formation of ecological niches for fungi of various taxonomic categories and trophic preferences. At the same time, fungi capable of living and developing in a wide variety of environments, including at high and low temperatures, with waterlogging and drought, under aerobic conditions and with extremely low oxygen content, can colonize various niches in almost any environment.

To date, about 100 thousand species of living fungi have been described, which, according to mycologists, is only a small part of the available diversity (Taylor et al., 2015a, 2015b; Hawksworth and Lücking, 2017). The first attempt at a quantitative analysis of the modern mycobiota was made based on the ratio of fungi and plant species known by that time in those regions where fungi were considered well studied (Hawksworth, 1991). The result of this study was an estimate of a possible 1.5 million species of modern fungi. Since, by the beginning of the 1990s, only about 70 thousand species had been described, such a high estimated total number motivated mycologists to search for previously unknown taxa. Later data based on molecular genetic studies showed the existence of about 5.1 million species in the modern mycobiota (O'Brien et al., 2005; Taylor et al., 2010; Blackwell, 2011). This number, however, was adjusted based on a combination of different methods (estimation of known fungal diversity, extrapolation of this data to plant diversity, and sequencing methods), and the actual number of species was estimated at 2.2 to 3.8 million (Hawksworth and Lücking, 2017).

A cursory glance at the history of the study of the biodiversity of modern fungi shows, on the one hand, how numerous this group of organisms is today, and on the other hand, how recently they have become intensely studied. Only in recent decades, the development of new technologies in light microscopy (LM) and scanning electron microscopy (SEM) has pro-

vided additional opportunities for a detailed study of the morphology of microscopic fungi. To identify modern fungi, it is often necessary to know their ontogeny. This primarily concerns the Ascomycota fungi. Ascomycota are pleomorphic, i.e., with morphologically different asexual (anamorphic) and sexual (teleomorphic) stages. However, the relationship between reproductive forms is often not obvious. In addition, morphologically different anamorphs can form under different conditions, at different times and in different geographic zones (Hughes, 1979). Often, morphologically similar anamorphic fungi can have teleomorphs belonging to different systematic groups of fungi, and, conversely, some teleomorphic groups are extremely rich in anamorphs of different morphology (Shenoy et al., 2007). The increasing use of molecular methods in recent decades has made it possible to correct the concept of the relationship between the teleomorphic and anamorphic stages of many ascomycetes, which in many cases entailed a change in ideas about the volume of genera and species and the position in the system of many representatives of anamorphic ascomycetes. Nevertheless, in most cases, the affiliation between teleomorphic and anamorphic stages remains undetected, and the avalanche of information coming from molecular phylogenetics and comparative genomics of fungi requires a comparison of these modern data with the results obtained by traditional comparative morphological methods, hence the latter also need further development.

Paleomycology studies fossil fungal remains, and according to Taylor et al. (Taylor et al., 2015a), is still at the initial stage largely due to the situation described above with the study of modern equivalents that serve as primary references when identifying fossils. In addition, the incompleteness of the fossil record, the preservation of scattered fungal structures in the fossil state, which does not allow the reconstruction of the whole fungal organism and the stages of its complete life cycle, and the impossibility of applying molecular methods to fossils, complicate this work. Nevertheless, from the first descriptions of fossil fungal remains at the beginning of the 19th century (e.g., Sternberg, 1820; Eichwald, 1830; Göppert, 1836), a substantial amount of data on the past biodiversity of almost all large taxonomic groups of fungi has become available (e.g., Karatygin and Snigirevskaya, 2004; Karatygin, 2007; Taylor et al., 2015a, 2015b; Samarakoon et al., 2019). A number of monographs and review articles are published on the history of the science of paleomycology, including a review of the known fungal remains in the fossil record, as well as the analysis of various aspects of co-evolutionary relationships between plants and fungi (e.g., Karatygin, 1993, 1994, 2007; Taylor et al., 2015a). The purpose of this paper is to review some problems in paleomycological studies concerning identification of microscopic fungi, their classification, interpretation of their possible paleoecological and paleoclimatic significance, as

well as the significance of the co-evolutionary relationships of fungi and plants for the phylogeny of both groups.

DISPERSED FUNGAL REMAINS IN THE PALYNOLOGICAL RECORD

The earliest fossil fungi so far known come from the Precambrian (e.g., Tyler and Barghoorn, 1954; Heckman et al., 2001; Horodyskyj et al., 2012), while a considerable increase in mycobiota diversity is recorded from the early Mesozoic (Kalgutkar and Jansonius, 2000; Tripathi, 2009; Taylor et al., 2015a). All the main morphological types of fungal spores known today were formed in the Mesozoic (Tripathi, 2009), and their increased morphological complexity and high frequency of occurrence are recorded in the Cenozoic assemblages (Elsik, 1970). The possibility of recognition dispersed fungal spores increases with the increased complexity of their morphology; therefore, their value for solving problems of paleoecology and paleoclimatology increases (Kalgutkar, 1993).

Micromycetes in fossil palynomorph assemblages are most often represented by individual hyphae, spores, less often fruiting bodies and their primordia. The cell walls of hyphae, spores and peridia of fruiting bodies of fungi include chitin, a natural biopolymer resistant to chemical reagents during maceration of fossil plant remains and processing of palynological samples. The presence of fungi in spore and pollen spectra can thus be very significant.

Identification of fungi is often difficult because of their convergent similarity, the absence of unique morphological features, or the similarity of some fungal structures to those of many other groups of organisms (mainly algae and protists). Hence, the importance of fungal remains found in palynomorph assemblages for solving problems of fungal taxonomy and assessing paleoecological and paleoclimatic conditions has long been underestimated.

Spores. Fossil fungal spores, found mainly in palynomorph assemblages, are used for biostratigraphic purposes and provide valuable information about paleoenvironmental conditions, including climate, hydrological conditions, vegetation type, and the nature of fungal interactions with other organisms (van Geel and Aptroot, 2006; Taylor et al., 2015a, 2015b). Numerous publications in recent years demonstrate a progressive increase in the morphological and taxonomic diversity of fossil spores in pollen spectra (e.g., Jansonius and Kalgutkar, 2000; Ferreira et al., 2005; van Geel and Aptroot, 2006; Kalgutkar and Braman, 2008; Singh and Chauhan, 2008; El Atfy et al., 2013; Sahay et al., 2016; Miao et al., 2017; Luz et al., 2019). The identification of the systematic affiliation of dispersed spores often causes difficulties due to the lack of distinctive characters. However, some fungal spores, mostly Cenozoic, due to their specific

characters, can be correlated with modern families and even genera of fungi. For example, bicellular spores with characteristic pores irregularly located along the equator, morphologically close to spores of the modern genus *Amphisphaerella* (Ascomycota, Sordariomycetes, Xylariomycetidae, Amphisphaeriales, Amphisphaeriaceae), were described from the Miocene of India as *Palaeoamphisphaerella keralensis* Ramanujam et Srisailam (Ramanujam and Srisailam, 1978), and from the Miocene of North America (Jarzen et al., 2010) as *Palaeoamphisphaerella* sp., while similar ascospores from the Lower Holocene of the Netherlands were assigned to the extant species *Amphisphaerella dispersella* (Nyl.) O. Eriksson (van Geel and Aptroot, 2006). However, most of the dispersed fossil fungal spores cannot be classified within the natural system; variants of artificial systems based on morphological characters have been proposed for them at different times (van der Hammen, 1956; Clarke, 1965; Elsik, 1968, 1976; Pirozynski and Weresub, 1979).

The use of fossil fungal spores in biostratigraphy becomes more complicated due to their already mentioned convergent similarity or wide temporal range of existence. However, many morphotypes of spores are distinguished by unique morphology and are restricted to a narrow stratigraphic interval, which, along with other palynomorphs, allows the host deposits to be dated (e.g., Kalgutkar, 1993; Visscher et al., 2011). Thus, the characteristic bicellular spores *Fusiformisporites* (anamorphic Ascomycota) with pronounced longitudinal ribs (e.g., Martínez-Hernández and Tomasini-Ortiz, 1989; Kumar, 1990; Parsons and Norris, 1999), as well as the complexly arranged spores *Pesavis* Elsik et Jansonius (Smith and Crane, 1979; Kalgutkar and Sweet, 1988), are not reported before the Paleogene and may be indicators of the Cenozoic age.

Light microscopy remains a traditional method for studying dispersed fungal remains in palynological samples; the potential of scanning electron microscopy has not yet been fully used. A number of structural features of fungal spores (for example, surface ornamentation) can be more informatively described only in studies using SEM. The study of the exine ultrastructure of fungal spores using transmission electron microscopy (TEM) may also become a promising direction in the future. There are virtually no such works on fungal remains; however, by analogy with the results of similar studies performed in recent decades for pollen grains and spores of higher plants, additional information that is essential for the identification of fungal spores can be expected.

Fruiting body primordia. The development of fungi from spores to fruiting bodies has not been sufficiently described and illustrated even for modern taxa of the kingdom Fungi. The formation of the fruiting body in fungi can occur in different ways. Thus, in representatives of the phylum Ascomycota, for example, the pat-

terns of formation of ascolocular stromata (pseudothecia) and true ascocarps differ significantly (Luttrell, 1951). The developmental variants of both pseudothecia and true fruiting bodies of ascomycetes in many cases remain unexplored since immature fruiting bodies are practically not taken into account in the taxonomy of modern micromycetes. In this respect, more progress has been made in paleomycology, where it is important to describe all the structures available to researchers. Dilcher (1965) described in detail early developmental stages of thyriothecia in Microthyriaceae, separating them into a formal group “Young forms (germlings) of microthyriaceous fungi” (Dilcher, 1965). The basis for isolation of such a group was the discovery of numerous primordia of micromycetes in different stages of development on one leaf of the angiosperm *Sapindus* Tourn. ex L. (Eocene, Tennessee, USA) together with mature thyriothecia belonging to various genera of Microthyriaceae. Since the initial stages of development of different thyriothecia are practically the same, it is not possible to determine at an early stage which fruiting body will eventually form. Before the publication of Dilcher’s (1965) work, germlings of fruiting bodies found in palynomorph assemblages were identified as algae (e.g., Köck, 1939) or were called by the generic name of mature fruiting bodies found in the same samples (e.g., Altehenger, 1959). Subsequently, in papers on the analysis of palynomorph assemblages, these structures began to be extensively described and defined as germlings of fruiting bodies in the understanding of the formal group proposed by Dilcher (e.g., Jain and Gupta, 1970; Ramanujam and Rao, 1973; Selkirk, 1975; Greenwood, 1994; Conran et al., 2016; Sahay et al., 2016). Note that almost all data concerning the primordia of fruiting bodies were obtained using the LM. It is obvious that in this case the use of SEM can provide new opportunities for studying the morphology and developmental patterns of these structures (Figs. 1a, 1b).

Fruiting bodies. The developed fruiting bodies of some micromycetes are confidently identified among other palynomorphs. First of all, this concerns representatives of Ascomycota from the order Microthyriales (Kar et al., 1972; Eriksson, 1978; Lange, 1978; Prasad, 1986; Saxena and Misra, 1990; Kalgutkar, 1997; Erdei and Lesiak, 1999–2000; García-Massini et al., 2004; Ferreira et al., 2005; Limaye et al., 2007; Kalgutkar and Braman, 2008; Singh and Chauhan, 2008; Jha and Aggarwal, 2011; El Atfy et al., 2013; Velayati, 2013; Worobiec and Worobiec, 2013, 2017; Alexandrova et al., 2015), in which fruiting bodies have a characteristic structure. Such characters of the structure of thyriothecia, as the mode of organizing the wall cells of the fruiting body, the size of cells and the features of cell walls, the presence/absence of pores on the anticlinal walls of cells, the type of the

edge of the fruiting body, as well as the way of releasing spores (absence/presence and way of organizing ostiole or the form of the excretory holes in ostiole lacking thyriothecia), make it possible to fairly accurately establish the systematic affiliation of such structures. Note that the study of fruiting bodies of micromycetes only using light microscopy is often insufficient. For example, the smallest pores in thyriothecium cells can sometimes only be visible when using SEM (Fig. 1c).

Hyphae. Fragments of fungal hyphae are a common and often significant component of palynomorph assemblages. It is almost impossible to attribute these remains to any taxonomic group of fungi due to their poorly informative morphology. Representatives of zygosporic fungi (in particular, micromycetes of the division Mucoromycota), as well as fungus-like organisms from the division Oomycota (Pseudofungi) have nonseptate hyphae, the rest of the fungi have septate hyphae, sometimes with multiple branching. Those elements of the palynomorph assemblages that can be attributed only to the kingdom of fungi, without a more precise taxonomic affiliation (for example, some morphotypes of spores and fruiting bodies, fragments of hyphae), nevertheless, deserve the attention of paleontologists. Based on the available characters (size and shape of spores and fruiting bodies, degree of septation and branching of hyphae), their diversity in the samples can be estimated, which will indicate the possible taxonomic diversity of mycobiota of the past and indirectly confirm the judgment about the diversity of substrates (plants, animals, etc.), on which these fungi could have developed.

MICROMYCETES ON FOSSIL PLANTS

In the fossil record, traces of interactions between plants and fungi are represented by impressions and can also be identified during microstructural studies of phytolite remains or mummified plant remains. Also of great interest are the remains of plants with fungi in amber (see the literature review in: Halbwachs, 2019; Tischer et al., 2019) and permineralized plant fossils that preserve host plants and accompanying fungi in an anatomical 3D form (e.g., Cevallos-Ferriz and Stockey, 1989; LePage et al., 1994; Klymiuk et al., 2013a, 2013b). Fungi are found on all organs of fossil plants: roots, stems, leaves, and various reproductive structures. There is an opinion that, for example, modern epiphytic micromycetes have no preferences in relation to the host plant or its organs (Phadtare, 1989); however, it seems obvious that the number of studied examples of the interaction of this group of fungi with the substrate is clearly insufficient for such general conclusions.

Mycorrhiza. In the final publication from a series of works by R. Kidston and W. Lang, on Devonian plants of the genera *Rhynia* Kidston et Lang, *Asteroxylon* Kidston et Lang and *Horneophyton* Barghoorn et

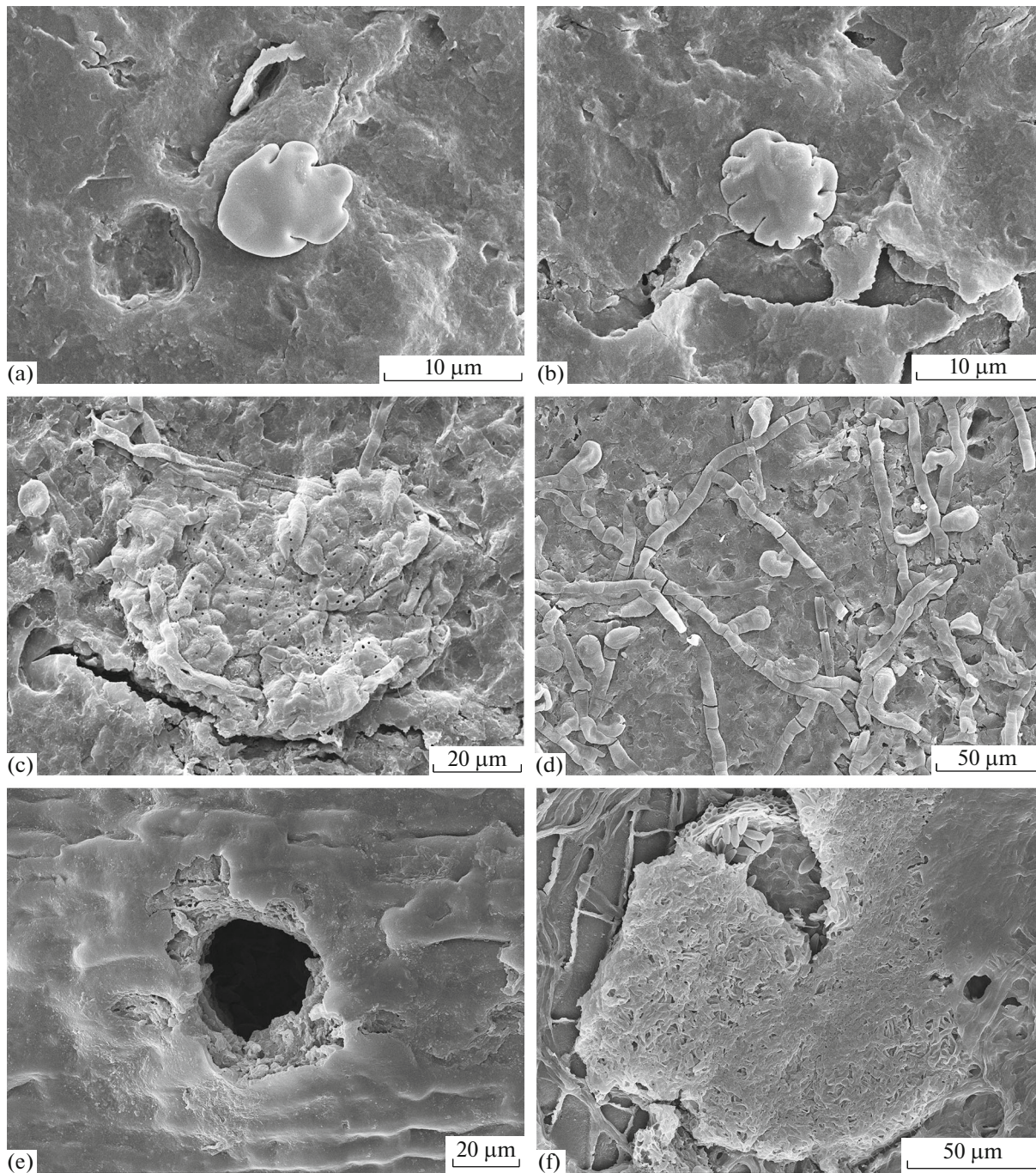


Fig. 1. Micromycetes on leaves of fossil plants, SEM: (a, b) primordia at different stages of development, specimen MMJ3-2346; (c) fruiting body of *Callimothallus* sp., specimen MMJ3-2371; (d) hyphae with appressoria, Melioliales, specimen MMJ3-2371; (e) the outer surface of a leaf of *Dacrycarpus*, the excretory pore of the fruiting body developed under the leaf cuticle is visible, Xylariales, specimen GP-198; (f) inner surface of the leaf cuticle of *Dacrycarpus*, fruiting body with spores, Xylariales, specimen GP-198; (a–d) South China, Maoming Basin; late Eocene; (e, f) South China, Guiping Basin; Miocene.

Darrah from the Rhynie chert in Scotland, Kidston and Lang (1921) described fungi discovered in the sedimentary matrix and in the tissues of these plants. Based on the presence of nonseptate hyphae, thick-walled resting spores, and vesicles in plant cells, Kidston and Lang were the first to note the similarity of

fossil fungi from Rhynie to modern endotrophic mycorrhizal fungi. Subsequent studies, continuing to this day, complement the concept of taxonomic diversity, morphology and ecological features of Devonian mycobiota from Rhynie (e.g., Taylor et al., 1992, 1995, 2004, 2005; Remy et al., 1994; Berbee and Taylor,

2007; Krings et al., 2007; Strullu-Derrien et al., 2017; Edwards et al., 2018).

It is known that the roots of 80–90% of species of modern higher plants are in symbiotic associations with the mycelia of fungi, which are diverse both in origin and in the nature of the relationships established between cobionts (Karatygin, 1994; LePage et al., 1997; Taylor et al., 2015a; Berruti et al., 2016), therefore, one can expect a wide variety of fossil forms of mycorrhizal relationships in the geological past. Along with studying the taxonomic diversity of fossil plants and mycorrhizal fungi, it is also important to assess symbiotic interactions at the level of vegetation and ecosystems in general.

Micromycetes on leaves and reproductive structures of plants. The finds of fossil micromycetes associated with plant organs are especially interesting, since they make it possible to more accurately determine their systematic affiliation, due to the potential possibility of studying different stages of fungal development and the nature of their relationship with the substrate. Fungi can be highly specialized or not strictly confined to the host plant; therefore, in-depth knowledge of the “host plant–micromycete” association in extant equivalents can facilitate identification of both the fossil plant and the fungus living on it. The problem is that not all, or rather, only some modern plants, primarily economically significant for humans, have been studied in terms of their relationship with fungi. Also, when analyzing existing ideas about the consort relationships of plants with the micromycetes developing on them in the historical aspect, it is necessary to consider a possible change of consorts in the modern biota.

To date, many fossil micromycetes have been described that live both on the surface of leaves (epiphytic fungi) and inside their tissues (endophytic fungi) (e.g., Cookson, 1947; Dilcher, 1965; Alvin and Muir, 1970; Phipps and Rember, 2004; Shi et al., 2010; Ding et al., 2011; Du et al., 2012). The most informative are the findings of fungal fruiting bodies with morphology allowing the most accurate taxonomic affiliation of micromycetes. Representatives of the order Microthyriales (in particular, the families Microthyriaceae and Micropeltidaceae), due to the traits of the structure of thyriothecia, can be easily diagnosed and therefore their evolutionary history is currently considered the best studied (e.g., Kalgutkar and Jansonius, 2000; Tripathi, 2009; Saxena and Tripathi, 2011).

Fossil micromycetes associated with the reproductive organs of plants are not so widely known, which is partly due to the scarcity of finds of these structures in comparison, for example, with leaves. Reproductive structures with preserved phytollems are promising in this respect. For instance, the fruiting bodies of endophytic ascomycetes have recently been found in the fruits of *Burretiodendron* from the Oligocene of South

China (Xu et al., 2020). Examples of damage by ascomycetes to permineralized fruits and seeds are known from the Cretaceous of India (hyphae and pycnidia on the fruits of the monocotyledon *Viracarpon*) (Kalgutkar et al., 1993), the Eocene of Canada (hyphae and pseudothecia on fruits and seeds of *Decodon* (Lythraceae), hyphae and sclerotia on seeds of *Allenbya* (Nymphaeaceae), hyphae and pycnidia on fruits and seeds of *Princetonia* (familia incertae sedis) (LePage et al., 1994). Representatives of Chytridiomycota were found inside saccate pollen grains from the Carboniferous of North America (Millay and Taylor, 1978) and from the Permian of India (Vijaya and Meena, 1996), as well as on the surface of saccate pollen grains from the Permian of India (Srivastava et al., 1999). It should be noted that the zoosporangia of Chytridiomycota are convergently very similar to orbicules, derivatives of tapetum, found on the surface of spores and pollen grains of a number of higher plants. The study of such structures using TEM can help to avoid errors. For example, Orlova et al. (in prep.) showed that spherical structures morphologically similar with zoosporangia Chytridiomycota (Figs. 2a–2c) found on the surface of micro- and megaspores *Svalbardia* (Archaeopteridales) from the Devonian of Northern Timan (Russia) have a homogeneous internal structure filled with sporopollenin, the electron density of which is identical to that of the sporoderm (Fig. 2d). and, therefore, are orbicules.

PROBLEMS OF IDENTIFICATION OF TRACES OF FUNGAL DAMAGE ON PLANT FOSSILS

Difficulties in identifying of damage types on plant fossils by various agents are largely due to insufficient knowledge of the phytopathological states of modern plants from the same taxonomic groups. Phytopathologists give preference to studying the causative agents of diseases of forage crops, trees and shrubs introduced for urban planting, as well as other economically significant plants. As a result, when determining the damage types on plant fossils, it is not always possible to obtain comparative information regarding the phytopathology of modern equivalents in natural habitats. At the same time, the identification of the contaminant that caused the damage largely depends on the knowledge of its consortium relationship with the host plant. The situation is complicated by the fact that different stages of the development of invasion by different agents, usually result in a morphologically similar plant response. Accordingly, a fixed stage in the development of an invasive process (the situation most often faced by a paleobotanist) often cannot be confidently identified.

To date, evidence has been found of the existence in the past of representatives of all phyla of the kingdom Fungi (Karatygin, 2007). The main characters distinguishing phyla are the traits related to reproduc-

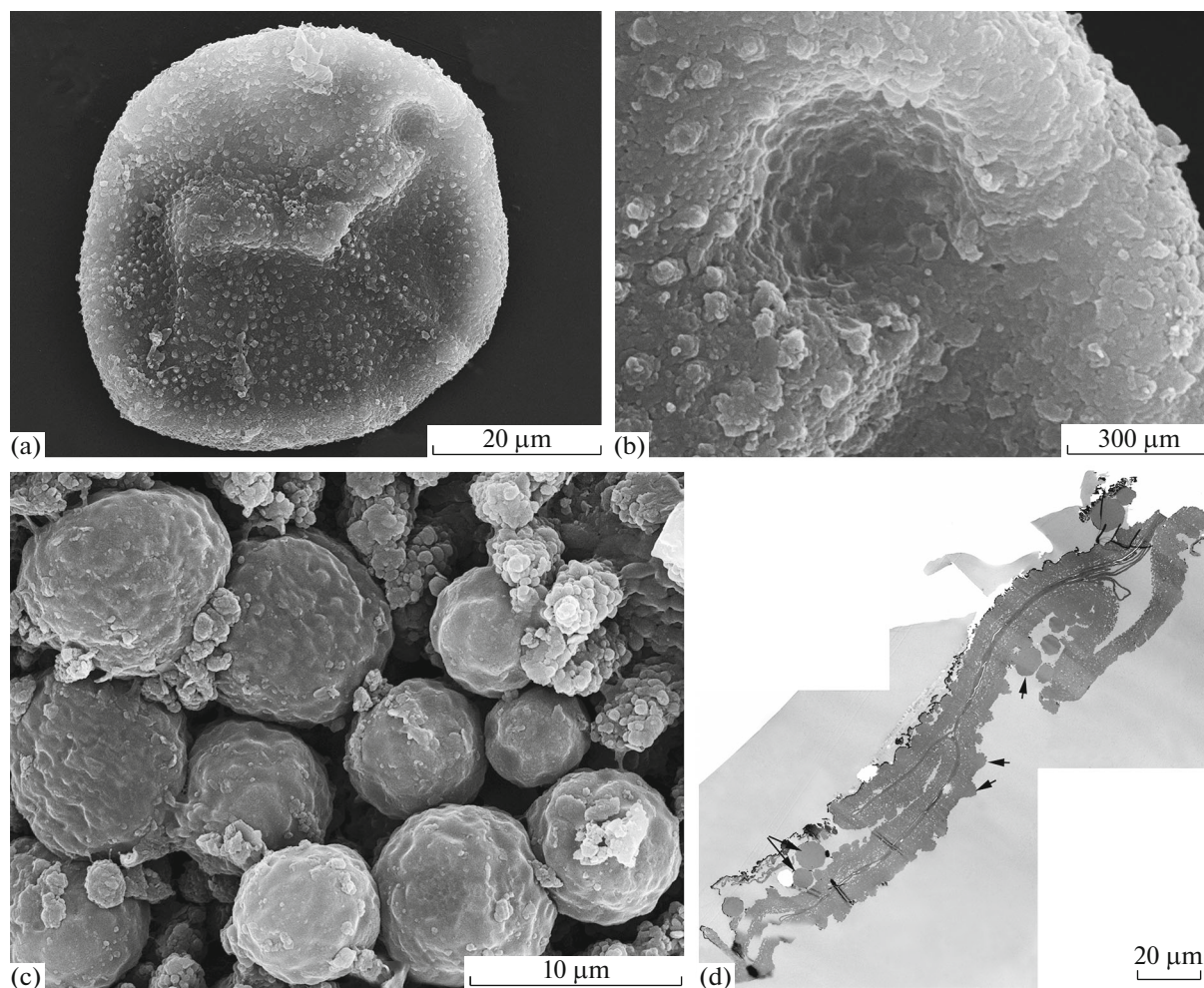


Fig. 2. Megaspores and microspores of *Svalbardia* sp., Archaeopteridales: (a, b) microspore, orbicular imprint is visible, specimen 88-04-01-11 (2), SEM; (c) orbicules on the surface of the megaspore, specimen 88-4-01-02 (2), SEM; (d) cut through the megaspore, visible orbicules identical in electron density to the sporoderm, specimen 88-4-01-02 (1), TEM; Russia, Northern Timan; Devonian.

tion, the structure and development of reproductive organs and characteristics of life cycles. Information on the methods of reproduction and life cycles in fossil fungi is very limited, more often it is simply not available. It is very difficult to determine the exact taxonomic affinity of fungal remains, since the vegetative structures of fungi are not very informative, and reproductive structures are less commonly preserved and are usually incomplete.

Traces of fungi on plant impressions. Traces of fungal damage to the organs of fossil plants, preserved as impressions, are rather difficult to diagnose. Even in modern plants, the determination of the agent that caused a number of pathological conditions of plant organs (in particular, various spots) causes difficulties due to the similarity of plant responses to the action of fungi, bacteria or viruses. Spotting is represented by presence of spots of various sizes, shapes, colors and structures on the affected organs. Relying solely on the

morphology of such spots, it is almost impossible to reliably identify their cause due to the overlap of phenotypic characteristics. To correctly identify the damaging agent that caused tissue modifications, special microbiological studies are required, which are only possible in modern plants.

An illustrated catalog of damage types on plant fossils was published by Labandeira et al. (2007). Based on the Permian, Late Cretaceous and early Paleogene floras of North America, as well as the Late Triassic floras of South Africa, 150 damage types (DT) were identified, briefly described and illustrated. Subsequently, the number of DTs described increased, which is reflected in a series of papers (e.g., Donovan et al., 2014; Adroit et al., 2018). The following characters were used to characterize the damage type: size, shape, features of the internal structure, position of damage on the surface of the organ, as well as the type and degree of development of the plant response to

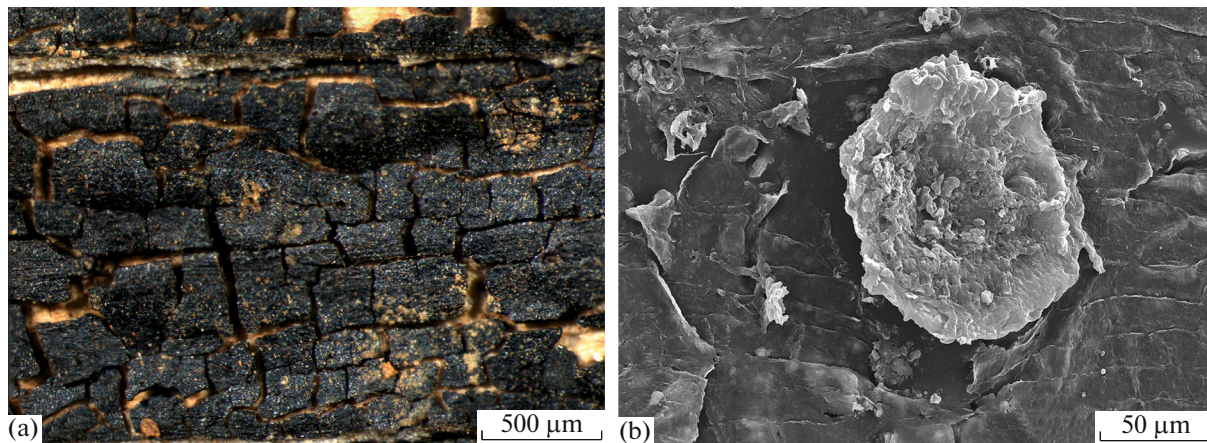


Fig. 3. Micromycetes on leaves of *Taxodium* sp.: (a) the outer surface of the leaf, rounded fruiting bodies under the cuticle are visible, specimen 5142/2, CM; (b) fruiting body; specimen 4867-AB1-606, SEM; Russia, Amur Region, Arkhara-Boguchan brown coal mine; early Paleocene.

damage and the presence of preserved coprolites. On the basis of these signs of damage, they are combined into the following groups: hole feeding, margin feeding, skeletonization, surface feeding, piercing-and-sucking, oviposition, mining, galling, seed predation, fungal and a group of damage of undetermined nature (*incertae sedis*).

The group of fungal damage in this catalog includes a type referred to as DT58. A morphological type of plant response to invasion similar to DT58 is also characteristic of bacterial and viral damage in modern plants. The necrotic surface of the leaf blade may be limited by a visible scar of the leaf tissue, or such a scar may be absent. The presence of a pronounced scar depends to a large extent on the specificity of the immune response of the plant itself.

A number of damage of the galling group (Labandeira et al., 2007) in the form of very small (about 1 mm or less), more often of different sizes, sometimes merging swellings on leaf impressions can be caused by gall midges (Sohn et al., 2017) or microscopic mites, as well as can indicate fruiting bodies of some epiphytic and endophytic micromycetes. The exit hole of the gall in the impressions is morphologically similar to the ostiolar pore of the fungal fruiting body. Structural analysis of these forms of damage is not possible in fossil impressions, but can be performed in phytolite, and then the determination of the type of damage will be verified. Similar structures (Fig. 3a) originally described based on external morphology as arthropod galls (Vasilenko et al., 2015), were later re-identified using microstructural study (Maslova et al., 2018) as results of micromycete infection. The shape of the fruiting body and the presence of a stoma-like pore facing the surface of the epidermis suggested that these fruiting bodies belong to Ascomycota fungi (Fig. 3b). Ascomata (perithecia or ascolocal stromata)

and pycnidial conidiomata can have such morphological features.

The external similarity of small galls and swelling of the leaf blade in the places of development of fruiting bodies of micromycetes was also noted for modern plants (Ho and Hyde, 1996). Microstructural examination of the leaves has shown that the gall-like structures are in fact caused by ascomata, belonging to the family Phyllachoraceae (class Sordariomycetes). Several examples illustrating the above are also published by Li et al. (2011).

It is not always possible to unambiguously identify some damage from the hole feeding and margin feeding groups (Labandeira et al., 2007). Leaves of the modern *Liquidambar chinensis* Champ. show various stages in the development of the plant responses to the damage caused by micromycetes (Fig. 4), the result of which can be holes after the loss of dried fragments of the leaf blade, both in its inner part and in the marginal part. They sometimes look like the damage caused by arthropods grazing or mining leaves. Morphologically similar damage is observed in the surface feeding group. Some circular punctures from the piercing-and-sucking group are similar to the fruiting bodies of micromycetes, while damage from the mining group in the form of rounded or polygonal mines with rare dispersed coprolites may in fact be damage of fungal origin with remnants of microscopic fruiting bodies (see, for comparison, Fig. 4e).

More generally, we note that the damage types on plant fossils, which are represented exclusively by impressions and are characterized only by external features of morphology, require a special approach to their identification and classification. Probably, it would be more reasonable to attribute this kind of damage in fossil plants to a general, wider morphological group, since it is impossible to accurately determine the invasive agent. It should be noted that micro-

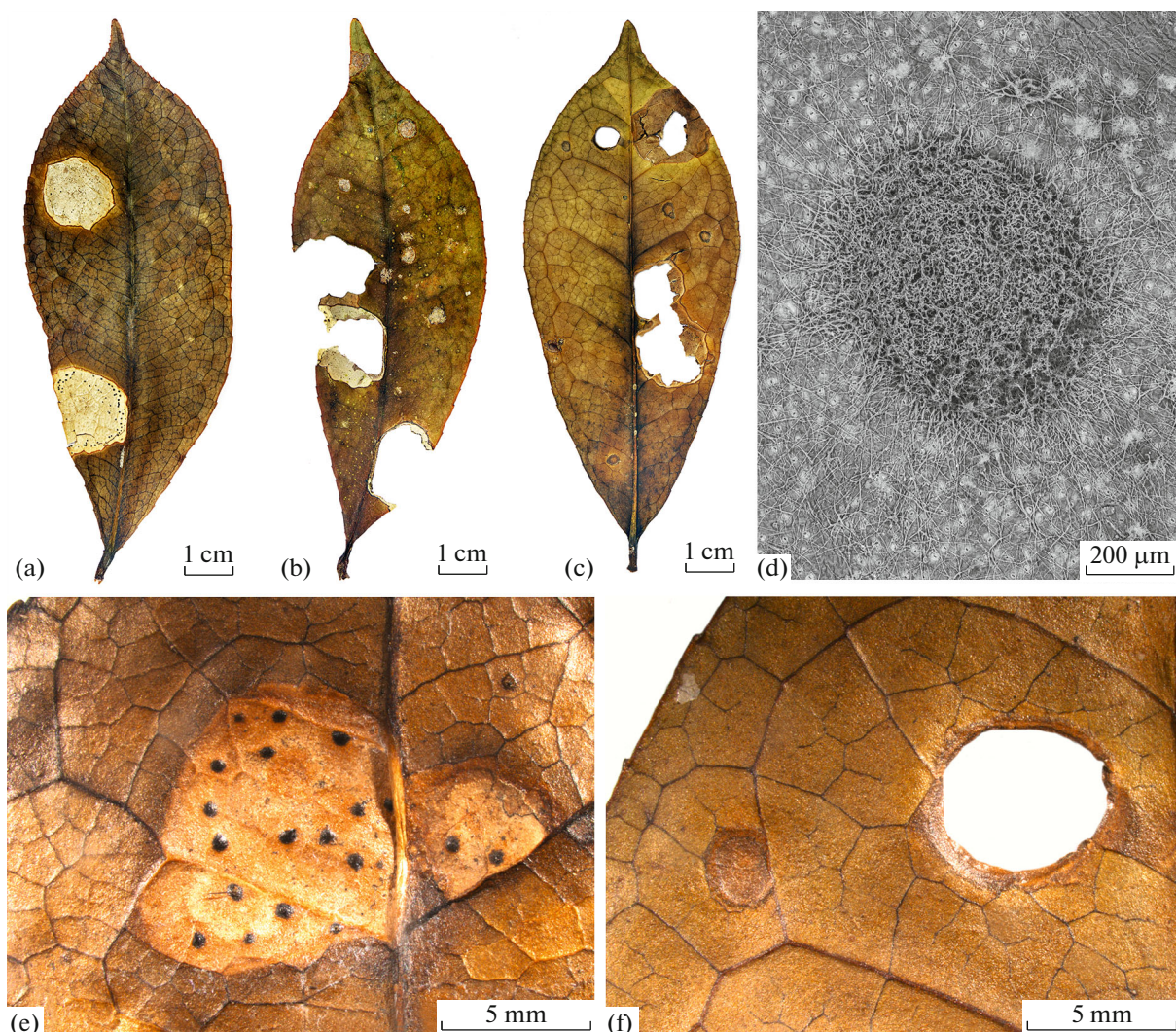


Fig. 4. *Liquidambar chinensis* Champ.: (a–c) leaves damaged by micromycetes, various stages of damage are visible; (d) lower surface of the leaf blade, a developed mycelium is visible, SEM; (e) micromycetes damage to the leaf, lower surface of the leaf blade, fruiting bodies are visible; (f) upper surface of the leaf blade, a rounded damage in the initial stage and a hole after the loss of the destroyed leaf tissue are visible. The authors' herbarium, collected in Nankun Mountain, Guangdong Province, South China.

mycetes can penetrate into plants, destroying plant epidermis by their own enzymatic effect, through epidermal structures (stomata, hydathodes, etc.), mechanical damage to the integrity of tissues, as well as punctures and wounds caused by insects or other pathogens. Therefore, the result of the plant responses can be integrated: insects can be carriers of fungal spores, bacteria, or viruses, which cause secondary damage to areas that were first attacked by insects. Some gall midges (Diptera: Cecidomyiidae) lay eggs in plant tissues together with conidia of symbiotic fungi that cause the formation of galls in which larvae develop (Rohfritsch, 2008; Kobune et al., 2012). Some criteria for distinguishing the types of damage caused by fungi, bacteria and viruses are presented by Labandeira and Prevec (2014). These authors note that new research methods in paleobotany, such as X-ray spec-

tral analysis, computed tomography, spectroscopy, etc. can significantly improve identification of damage.

Micromycetes preserved in phytolims and mummified and mineralized plant remains. The possibility of studying the microstructural organization of three-dimensionally preserved plant fossils has resulted in great progress in the identification of the fungal remains associated with them. Ascomycetes are considered the most studied group in terms of historical development (Kalgutkar and Jansonius, 2000; Taylor et al., 2015a). However, an important diagnostic feature of ascomycetes, the structure of asci, due to the very fine organization of the sac, which is not preserved during fossilization, is hardly accessible for study. Moreover, in the fossil state it is often difficult to determine even the stage of development of the ascomycete (anamorph/teleomorph), since the fruit-

ing bodies (primarily perithecia and pycnidia) are morphologically similar, and in the absence of sacs it is difficult to understand which of the structures are present.

When identifying fossil micromycetes that developed on plants, in addition to the set of characteristic features of the existing fungal structures, the analysis of the host plant in modern analogs is used. In the absence of close extant analogous fungi, a new genus of micromycete with an arbitrary name is recognized (e.g., Dilcher, 1965), and where possible, the generic name of the extant fungus is used with the addition of the suffix-ites (e.g., Currah et al., 1998; Phipps and Rember, 2004; Ma et al., 2015).

Finds of fungal fruiting bodies with spores preserved in them, which would give more complete information about the fossil micromycetes, are extremely rare. An example is the fruiting bodies of endophytic ascomycetes with spores inside, developing on the leaves of *Dacrycarpus* (Podocarpaceae) from the Miocene of Southern China (Wu et al., 2019; a detailed description of the findings will be presented in a separate publication). Rounded fruiting bodies with an ostiole have a multilayer wall formed by prosoplectenchyme; inside, there are unicellular fusiform, slightly unequal spores with a smooth exine and a noticeable longitudinal groove (Fig. 1f). The combination of characters allows these fruiting bodies to be attributed to the order Xylariales (Ascomycota, Sordariomycetes).

Fruiting bodies without accompanying hyphae and spores or in association with spores dispersed on the cuticles are more often described, often with different types of spores (e.g., Phipps and Rember, 2004; Shi et al., 2010; Saxena and Tripathi, 2011; Vishnu et al., 2017; Kodrul et al., 2018). We can assume that damage caused by micromycetes was more diverse and widespread in the biota of the past than is evident today. Of course, the identification of structurally preserved fossil fungal remains is the most accurate, and studies of such remains in the future will expand our understanding of the evolution of these organisms.

THE IMPORTANCE OF FOSSIL MICROMYCETES FOR SOLVING THE PROBLEMS OF PALEOECOLOGY AND PALEOCLIMATOLOGY

Paleoecological interpretations and paleoclimatic reconstructions rely to a large extent on the corresponding data concerning modern analogues. Fungi, along with bacteria, are of fundamental importance in terrestrial ecosystems, as active destructors of both organic and inorganic matter, and as connecting links in biological cycles. For example, soil micromycetes largely determine the structural and chemical characteristics of soils, and thus indirectly affect the compo-

sition of soil and terrestrial biota (Chernov and Marfenina, 2010).

According to the mode of feeding, fungi developing on a plant substrate are divided into two groups: biotrophs (obligate parasites and symbiotrophs) and saprotrophs (Levkina, 2010; Kemen and Jones, 2012). A special group is made up of necrotrophic fungi (Oliver and Ipcho, 2004), which settle on a living plant and kill its cells with secreted toxins, and then use dead and weakened host tissues as a food source. In addition, based on the potential of the fungal organism, it is possible to distinguish groups of facultative saprotrophs and facultative parasites (Agrios, 2005; Dyakov, 2007), which, under certain conditions, are capable of passing from parasitism to saprotrophy and vice versa. The transition conditions are determined by the state of the host plant, competitive relationships, and abiotic factors. Thus, one and the same fungus in different conditions can occupy different ecological niches, and its correct assignment to one or another ecological-trophic group often requires a study of the full development cycle, which is impossible for fossil fungi. Thus, it is extremely difficult to reliably assign a fossil micromycete to a particular ecological-trophic group.

The parasitic properties of fossil micromycetes can be more or less confidently assessed by the presence of haustoria in the cells of the host plant or by strongly altered cells of the host tissues (various kinds of growths, changes in cell walls, or specific damage). The actual location of the fruiting bodies and hyphae of micromycetes inside plant tissues cannot be unambiguously considered as a sign of the parasitic lifestyle of the fungus, since it is impossible to reliably determine the feeding strategy of this fungus, e.g., on the host's living cells, or on the cells that, for various reasons, sometimes not associated with the fungal activity, began to die off (necrotrophs and saprotrophs), or by absorbing substances accumulated in the intercellular spaces during the life of the plant (endophytes).

Some extant micromycetes, for example, species of the genus *Trichothyria* (Petr.) Petr. (Microthyriaceae) are hyperparasites, developing on other epiphytic micromycetes. At the same time, they can be found on plant substrates (Hughes, 1953; Ellis, 1977). Dilcher (1965) showed a variety of fossil epiphytic micromycetes, in particular, representatives of the families Microthyriaceae and Melioliaceae, on the leaves of the angiosperm *Sapindus* sp., and suggested that some of the forms described by him could be hyperparasites, but no solid evidence was found.

In most cases, it is impossible to determine the group of a fossil micromycete. The method of actualism, albeit with known assumptions, is widely used to assess the ecological preferences of fossil organisms, but mycological data in this aspect have been used relatively recently and require careful verification.

Phytopathogenic fungi are an important component of biocenoses, exerting a significant influence on the growth and development of plants at different stages of vegetation. Different fungi may prefer different life forms of plants, different layers in phytocenoses; the topography of micromycete development within the crown and/or leaf of a large tree may be different. In addition, fungi are often closely associated with specific plants. Thus, if we are dealing with the finds of certain micromycetes on fossil plants, in some cases it is possible to draw conclusions about the life form and habit of the plant, and assumptions can also be made whether the fossil plant was evergreen or deciduous. The discovery of associations of certain plants and fungi in a fossil state may suggest the existence of their consortium relations in the geological past (Leppik, 1973; Saxena and Tripathi, 2011). When comparing mycofossils with modern analogues, it should be borne in mind that information about the ecology of modern fungi is far from complete, new taxa of fungi are constantly being described, and knowledge about their host plants and geographical distribution is increasing.

An example of the use of the method of actualism in paleomycology can be the identification of the probable presence of poplar, the host plant, in the Holocene flora of the Netherlands, which has not been confirmed by finds of leaves or other organs, by the presence of spores of the fungus *Amphisphaerella dispersella* in the assemblages, which obligately develops on the leaves of extant *Populus* (van Geel and Aptroot, 2006). Since the life cycle of micromycetes can take a very long period of time, the presence or absence of fungal fruiting bodies and their primordia on leaves can be an additional indicator of the evergreen or deciduous status of the host plant (Sherwood-Pike and Gray, 1988).

The pattern of the vertical distribution of micromycetes within a single plant growing in conditions of modern tropical and subtropical forests were shown by Phadtare (1989). It was shown that epiphytic micromycetes prefer mainly the lower surface of the leaves located in the upper part of the crown, while they develop on both surfaces of the leaves located in the lower and central parts of the crown. Both direct sunlight and an open position in relation to air currents have a detrimental effect on the development of fungal primordia. Based on these data, it can be assumed that the topography of micromycetes on leaf surfaces is due to the arrangement of the leaves in the crown of a tree, and there is not a characteristic feature and not important for determining the systematic position of the fungus. Epiphytic micromycetes are also more diverse on the leaves located in the lower part of crown (Gilbert et al., 2007). There is also an opinion that humidity and temperature are decisive for the abundance of saprotrophic fungi, while the distribution of parasitic forms is more controlled by the hosts (Phadtare, 1989).

Since many organisms are characterized by a relatively limited ecological amplitude, changes in the state of the environment entail a change in the nature of the biota. Taking this into account, the ecological and climatic conditions of the past can be assessed on the basis of the presence of certain representatives of flora, fauna and microbiota, and especially associations of different groups of organisms. Analysis of communities of epiphytic micromycetes is important in reconstructing paleoclimates. Among them, the most studied are micromycetes of the orders Microthyriales and Melioliales, modern representatives of which are parasites on the leaves of higher plants in tropical and subtropical zones growing in areas with high humidity and relatively stable temperatures throughout the year (e.g., Kalgutkar, 1985; Prasad, 1986; Phadtare, 1989; Schmiedeknecht, 1995; Hosagoudar et al., 1998a, 1998b, 1998c; Tripathi, 2009; Piepenbring et al., 2011; Worobiec and Worobiec, 2013). Due to the specific morphology of fruiting bodies of modern representatives of Microthyriales (Fig. 1c), the characteristic features of mycelium with appressoria (Fig. 1d), fruiting bodies and spores inherent in Melioliales, as well as the confinement of these groups of fungi to tropical and subtropical regions, they are easily identifiable and potentially useful for paleoecological and paleoclimatic conclusions.

Thus, using the example of modern fungi of the family Microthyriaceae (Microthyriales), it was shown that their parasitic forms are usually found in the subtropics and tropics, while saprotrophic and hyperparasitic forms are found in temperate regions (Hofmann, 2009). Note, however, that identification of the fruiting bodies of Microthyriales can be difficult because of their morphological similarity, for example, with algae. Examples of such convergent similarities include green algae of the genus *Ulvelia* P. Crouan et H. Crouan (Hansen, 1980) and red algae of the genus *Caloglossa* (Harvey) G. Martens (Tripathi, 2009).

The use of comparative data on modern analogs of micromycetes for paleoclimatic constructions is somewhat limited due to the fact that modern fungi are best studied from regions with a temperate climate, while fossil micromycetes are described mostly from subtropical and tropical regions (Stubblefield and Taylor, 1988). Over the past decades, this gap has been substantially filled (e.g., Reynolds and Gilbert, 2005; Thaug, 2006; Hofmann, 2009; Piepenbring et al., 2011), however, Stubblefield and Taylor' view that this situation can limit possible conclusions concerning the evolution and diversity of microscopic fungi remains relevant.

Developing on the surface of plant organs, epiphytic micromycetes are found to be dependent not only on the state of the host plant itself, but also to a large extent on abiotic environmental factors, e.g., humidity and temperature. High humidity (high

annual precipitation rate, relatively long wet period) is critically important for the full growth of the fungal mycelium, the formation and development of fungal fruiting bodies from primordia (Selkirk, 1975; Limaye et al., 2007). The occurrence of fossil epiphytic micromycetes suggests the highly humid regional paleoclimate.

Fossil germlings of the microthyriaceous thyrithoecia are considered reliable indicators of paleoclimates (Lange, 1976). Germlings of microthyriaceous fungi at various stages of development have been used for paleoclimatic interpretations in a number of studies (e.g., Dilcher, 1965; Wells and Hill, 1993; Carpenter et al., 1994; Greenwood, 1994; Tripathi, 2009; Saxena and Tripathi, 2011; Du et al., 2012; Conran et al., 2016; Paruya et al., 2017) as indicators of tropical humid habitats of host plants.

As for the temperature factor, studies have shown (Dilcher, 1965; Selkirk, 1975; Tripathi, 2009) that epiphytic micromycetes of some modern genera are capable of developing at high latitudes. Dilcher (1965) and D. Selkirk (1975) were the first to point out that ecological interpretations of warm climate based on the findings of epiphytic micromycetes should be treated with caution. They noted that although most fossil epiphytic micromycetes are associated with subtropical vegetation, isolated fruiting bodies occur over a wide latitudinal range in the Pleistocene deposits of North America (Rosendahl, 1943), as well as in a wide range of climatic conditions in Britain (Godwin and Andrew, 1951).

Most researchers support the Dilcher's (1965) view that any paleoecological and paleoclimatic conclusions should be based not only on the ecological analysis of fossil and similar extant epiphytic fungi, but also on associated fossils, including palynomorphs, leaves, reproductive organs, wood, etc. However, according to Sherwood-Pike and Gray (1988), the abundance and diversity of epiphytic fungi is a more sensitive indicator of paleoclimate than the composition of palynomorph assemblages and leaf morphology.

The conclusions about warm and humid paleoclimates in numerous paleobotanical studies have been confirmed by the presence of fungal fruiting bodies and spores both in palynomorph assemblages and in association with host plants (e.g., Dilcher, 1965; Rao and Nair, 1998; Tripathi, 2009; Mandal et al., 2011; Du et al., 2012; Ma et al., 2015; Bannister et al., 2016; Paruya et al., 2017; Wang et al., 2017; Kodrul et al., 2018; Khan et al., 2019; Singh et al., 2019; Wu et al., 2019). Recently, the CLAMP (Climate Leaf Analysis Multivariate Program, <http://clamp.ibcas.ac.cn/>) method has been intensely used to reconstruct paleoclimatic conditions. Paleoclimatic reconstructions based on integrated studies of fossil plants and micromycetes using CLAMP data have been successfully presented in a number of works (e.g., Conran et al., 2016; Kodrul et al., 2018). Obviously, reconstructions

of paleoclimatic conditions should be based on a set of data obtained by various methods, taking into account the entire spectrum of available macrofossils and palynomorphs, including the remains of fungi.

CONCLUSIONS

Paleomycological studies, which have been developing most productively in recent decades, have shown the interaction of various taxonomic groups of fungi and plants throughout their historical development. Today, it is obvious that the coevolutionary relations of plants and fungi, probably still underestimated in their historical aspect, was a powerful factor that manifested itself at key moments in the development of the Earth's biota. Fungi played a significant role in the formation of paleosols, the formation and evolution of terrestrial plants, the emergence of the first phytocenoses, and the evolution of plant communities.

The evolutionary mechanisms of the formation of a group with such a high taxonomic and morphological diversity remain largely unknown. In this regard, paleomycological studies can be successfully used to assess the reliability of ideas about the systematics of the Fungi kingdom, the origin of fungi and the formation of the main branches of their phylogenetic tree, based on the results of classical morphological studies of modern mycobiota and genosystematics data. The paleomycological record, although not without significant shortcomings and limitations, documents the most important stages in the formation of the Earth's mycobiota as a special evolutionary group of organisms, providing important evidence in favor of the coevolutionary relationships between fungi and various representatives of other kingdoms, that appeared at the early stages of historical development. Further improvement of the scientific paleomycological direction, primarily through the wider application of modern research techniques, will undoubtedly shed light on the key issues of taxonomy and phylogeny of fungi, coevolution of fungi with other groups of organisms, which is also essential for the development of evolutionary theory.

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