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Fossil fungi in lignite-bearing deposits: An overview of Miocene lignites from Poland

Grzegorz Worobiec*, Elżbieta Worobiec

W. Szafer Institute of Botany, Polish Academy of Sciences, Lubicz 46, 31-512 Kraków, Poland
GW https://orcid.org/0000-0002-2916-9905, EW https://orcid.org/0000-0001-5997-9602
* corresponding author, e-mail: g.worobiec@botany.pl

Abstract

The present paper summarises results of studies into fungal microremains (non-pollen palynomorphs) encountered during palynological studies of Miocene lignite-bearing deposits in the Adamów-Konin Basin, the Bełchatów Lignite Mine, the Ruja lignite deposit and the lignite seam at Chłapowo. The Adamów-Konin lignite deposits turn out to be the richest site for fossil fungi within Neogene lignite-bearing strata in Poland. Fungal ecological groups (e.g., epiphyllous fungi, rhizosphere fungi and indigenous wetland fungi) and fungal taxa as environmental proxies were examined alongside plant pollen/spores in order to reconstruct ancient peat-forming environments. Fossil fungi are valuable palaeoclimatic indicators seeing that fungi are generally sensitive to environmental conditions. Fungal non-pollen palynomorphs found in lignite-bearing deposits can provide information on ancient wetland hydrology and conditions, vegetation structure and density, temperature and humidity, and even plant-fungal interactions. Coupled with other proxies, fungal remains can complement the palaeoenvironmental picture obtained from classic pollen analysis, creating a detailed picture of Miocene coal-forming environments.

Keywords: Fungal microremains, palynology, non-pollen palynomorphs, lignite deposits, palaeoenvironment, Neogene

1. Introduction

Fungi constitute one of the kingdoms of eukaryotic organisms, and are now found in every environment on Earth. It is estimated that there are between 2.2 and 3.8 million species of fungi that have been described (Hawksworth & Lücking, 2017). They are obligate heterotrophs, with saprotrophic fungi that acquire organic molecules typically by secreting enzymes into their environment (Deacon, 2006). Therefore, fungi play an essential role in biogeochemical cycles, including nutrient cycling, by degrading organic matter, and are the major decomposers in terrestrial and aquatic ecosystems (Tsui et al., 2016). Many fungi are parasites on plants, animals and other fungi and may lead to serious diseases in humans. The phyla Ascomycota and Basidiomycota are the most diverse in the kingdom Fungi; both reproduce sexually and asexually (Kirk et al., 2008). Fungi presumably first appeared in the late Proterozoic (Bonneville et al., 2020), whereas the first land plants (Embryophyta) originated in the early Palaeozoic, around 450 Ma ago (Gensel, 2021). Land plants and fungi have coexisted for hundreds of millions of years and, as a result, have established many ecological interactions, including competition, antagonism and various forms of mutualism (Strullu-Derrien et al., 2018). The commonly reported interactions between fossil plants and fungi are mutualistic mycorrhizal relationships between fungi and roots of land

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plants, as well as the presence of endophytic fungi (Taylor & Osborn, 1996; Strullu-Derrien et al., 2018). Traces of biotrophic fungi feeding on living plants have also been found in plant fossils. These traces cover a wide spectrum of morphological and anatomical abnormalities and modifications to plant tissues and organs caused by fungal pathogens (Taylor et al., 2015). Plant–fungal interactions have shaped plant communities and ecosystems (Taylor & Osborn, 1996). Moreover, interactions between fungi and plants have played a significant role in driving the evolution of life on land (Selosse & Strullu-Derrien, 2015; Strullu-Derrien et al., 2018). Root-associated fungi (mycorrhizal and endophytes) played a crucial role in the colonisation of terrestrial ecosystems by plants (Strullu-Derrien et al., 2018).

Since the cell walls of most fungi (particularly Ascomycota and Basidiomycota) contain the acid-resistant biopolymer chitin, a variety of fungal microremains, including spores, hyphae and reproductive structures, may be encountered during palynological investigations (Elsik, 1996; Worobiec et al., 2009). However, preservation bias remains a challenge as delicate hyphae and hyaline spores are easily degraded and therefore could not be preserved in a fossilised state. Fungal microremains are usually examined alongside other microfossils of various origins, collectively termed non-pollen palynomorphs (NPP) (Shumilovskikh & van Geel, 2020; Shumilovskikh et al., 2021). Fungal non-pollen palynomorphs are found during palynological studies in the form of dark-coloured, often strongly melanised structures (Nuñez Otaño et al., 2021). The fungal remains recorded in palynological studies belong mainly to the Ascomycota, Basidiomycota and Glomeromycota (Shumilovskikh et al., 2021). Many fungal NPP are used as palaeoecological proxies in reconstructions of palaeoenvironments and palaeoclimates (Shumilovskikh et al., 2021). Hence, unequivocal taxonomic interpretation of fossil fungal forms is crucial for such reconstructions (Saxena & Wijayawardene, 2022).

Although fungi are primarily terrestrial organisms, some can be found in aquatic habitats. The major groups of fungi occur in wetlands (swamps, bogs, fens, marshes and riparian communities), which represent habitats inhabited by both terrestrial and aquatic fungi (Stephenson et al., 2013). The majority of wetland fungi belong to the Ascomycota and Basidiomycota and to their anamorphs (hyphomycetes) (Goh & Hyde, 1996). The main ecological role of fungi in freshwater ecosystems, such as wetlands, is to decompose dead plant material, including woody and herbaceous remains such as leaf litter, twigs and trunks (Gessner et al., 2007; Stephenson et al., 2013). Fungal decay of plant tissues is due to the ability of fungi to degrade plant biopolymers such as cellulose and lignocellulose (Tsui et al., 2016). Accumulations of partly decomposed plant remains in the form of peat deposits in ancient swamps and bogs were the source of coal/lignite formation. Notwithstanding the fact that the process of coalification causes significant changes to plant material, leading to the decomposition of cellular structures, various identifiable remains of plants are often preserved in lignite. These are mostly remains of the vegetation from which the peat formed as well as remains of other components of ancient wetland communities, such as fungi (Worobiec et al., 2021, 2022d). Pollen, spores and other microremains (e.g., fungi) can be studied in lignite by means of palynological analysis. Various microremains of fungi have been often noted in the course of palynological investigations of lignite deposits, and are widely used as proxies for reconstructing ancient peat-forming environments (e.g., Saxena & Tripathi, 2011; Worobiec & Worobiec, 2017; Khanolkar & Sharma, 2019; Worobiec et al., 2022a, c, 2025a).

2. Geological background

Microfossils of fungi discussed in the present paper were found in Miocene lignite-bearing sedimentary series of the Adamów–Konin Basin, the Bełchatów Lignite Mine in central Poland, the Ruja lignite deposit in south-west Poland, and the lignite seam from Chłapowo in northernmost Poland (Fig. 1). The lignite deposits at the Adamów–Konin area in central Poland occur within shallow tectonic grabens. Fungal remains were collected from Middle Miocene strata at three opencast pits: the Adamów opencast mine of the Adamów Lignite Mine (52°01'N, 18°37'E), as well as the Drzewce (52°16'N, 18°31'E) and Tomisławice (52°27'N, 18°31'E) opencast pits of the Konin Lignite Mine. The Neogene strata sampled originated in the Polish Lowlands. Fungal remains were found in palynological samples collected from the 1st mid-Polish lignite seam (MPLS-1), which is assigned to the Grey Clay Member, which constitutes the lower part of the Poznań Formation (Piwocki & Ziembińska-Tworzydło, 1997; Widera et al., 2021a, b). The 1st mid-Polish lignite seam is up to several metres thick. Its accumulation started during the last peak of the Miocene Climatic Optimum (MCO) (Kasiński & Słodkowska, 2016; Bechtel et al., 2019, 2020; Słodkowska & Widera, 2021, 2022; Worobiec et al., 2021, 2022a). The age of MPLS-1 is determined as middle Middle Miocene, dated as ~15.1–14.3 Ma (Piwocki & Ziembińska-Tworzydło, 1997; Kasiński & Słodkowska, 2016; Widera et al., 2021a, b). The overlying deposits of the Wielkopolska Member (upper part of the Poznań Formation), so-called 'green clays' and 'flame clays' that represent deposition in a late Neogene fluvial system, were laid down between the late Middle Miocene to Early Pliocene (Zieliński & Widera, 2020; Kędzior et al., 2021; Słodkowska & Widera, 2022). The Neogene strata are capped by Quaternary deposits such as glaciogenic tills, gravels, sands and muds (Słodkowska & Widera, 2022).

The lignite deposits at the Bełchatów Lignite Mine, central Poland (51°14'N, 19°17'E, Fig. 1), occur within the Kleszczów Graben filled with Neogene lignite-bearing sedimentary sequence dominated by Miocene fluvial–lacustrine and peat-forming deposits. Fungal microremains from Bełchatów were taken from collections of plant macroremains KRAM-P 210, KRAM-P 214, KRAM-P 218, KRAM-P 225 and KRAM-P 226. They were found in the Bełchatów opencast pit in overburden deposits belonging to the clayey-coal and clayey-sandy units and are considered to be of Early to Late Miocene age (Worobiec & Lesiak, 1998; Worobiec, 2003; Worobiec & Worobiec, 2016, 2019, 2022). According to Krzyszkowski and Winter (1996) deposits of the lower part of the clayey-sandy unit formed in a fluvial environment of braided to meandering rivers with dense vegetation along riverbanks.

Fig. 1. Map of Poland showing localities yielding fungal microremains from Miocene lignite-bearing deposits (The map's cartographic base is sourced from: Open Data Commons Open Database License, OpenStreetMap Foundation (OSMF), www.OpenStreetMap.org, © Authors OpenStreetMap (CC BY-SA 2.0).

Fungal remains from the Ruja lignite deposit were collected from the Komorniki 97/72 borehole located in the southernmost part of the Legnica–Ścinawa lignite resource complex in Lower Silesia, south-west Poland (51°11'N, 16°23'E; see Fig. 1). Fungal microfossils were found in a palynological sample taken from the 2nd Lusatian lignite seam (LLS-2) of latest Early to early Middle Miocene age. The lignite-bearing strata of the Ruja deposit infill a widespread system of tectonic depressions related to Late-Alpine post-Cretaceous tectonic movements (Worobiec et al., 2022b).

Palynological samples with fungal remains from Chłapowo (54º48'N, 18º21'E) originate from the Miocene lignite layer exposed in the so-called Chłapowo Cliff on the coast of the Baltic Sea (Fig. 1). These deposits represent the Ścinawa Formation with the lignite seam considered to be equivalent to the 2nd Lusatian lignite seam (LLS-2) and thus estimated as latest Early Miocene to early Middle Miocene in age (Piwocki & Ziembińska-Tworzydło, 1997; Widera, 2021). The sedimentary environment of the peat from which the studied lignite was formed was loosely associated with the overbank zone of a meandering or anastomosing river system (Widera, 2019; Worobiec et al., 2025a).

3. Material and methods

Fungal microremains, including spores (conidia and rare ascospores), sporocarps, hyphal fragments and microsclerotia, were identified during palynological studies of samples taken from Miocene deposits at the Adamów, Drzewce, Tomisławice, Bełchatów opencast pits, the Komorniki 97/72 borehole core from the Ruja lignite deposit, and the Miocene lignite seam exposed in Chłapowo (Fig. 1). Most samples were processed at the Laboratory of the W. Szafer Institute of Botany, Polish Academy of Sciences in Kraków, using 10% hydrochloric acid, 10% potassium hydroxide, 40% hydrofluoric acid, and subsequently 10% hydrochloric acid. The residuum was sieved at 5 µm on a nylon mesh (Moore et al., 1991; Worobiec & Worobiec, 2016, 2022; Worobiec et al., 2021, 2022a, b, 2025a).

One sample from the Tomisławice opencast mine was processed at the Laboratory of the Polish Geological Institute – National Research Institute in Warsaw, using hydrochloric acid, and subsequently a potassium hydroxide and zinc chloride ($ZnCl_2$) solution with a density of 2.21 g/cm^3 (Słodkowska & Widera, 2022). From each sample microscope slides were made, using glycerine jelly as a mounting medium. Fossil fungal microremains, especially slides with holotypes of new taxa are stored in the W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków. Selected important fungal taxa are presented in graphic form (Figs. 2–4).

4. Results – fossil fungi in Miocene lignites

4.1. Adamów–Konin Basin – hotspot of biodiversity of Miocene wetland fungi

The Adamów–Konin lignite deposits are the richest in fossil fungi within lignite-bearing Miocene strata of Poland. Altogether one new fossil-genus and six new fossil-species of fungi were found in the 1st mid-Polish lignite seam (MPLS-1) and accompanying Miocene strata in the Adamów, Drzewce and Tomisławice opencast mines.

The Adamów opencast pit is the richest in fungal taxa in Poland, with fungi associated with wetland vegetation predominating. Five new fossil-species, namely *Canalisporium lignitum*, *Dictyosporites muriformis*, *Dictyosporites zeaformis*, *Microthyriacites radiatus* and *Pleosporomyces adamowiensis*, as well as a new fossil-genus, *Pleosporomyces*, have been described (Worobiec et al. 2022d). A mixture of terrestrial and aquatic anamorphic fungi and ascomycetes (*Canalisporium lignitum, Cephalothecoidomyces neogenicus*

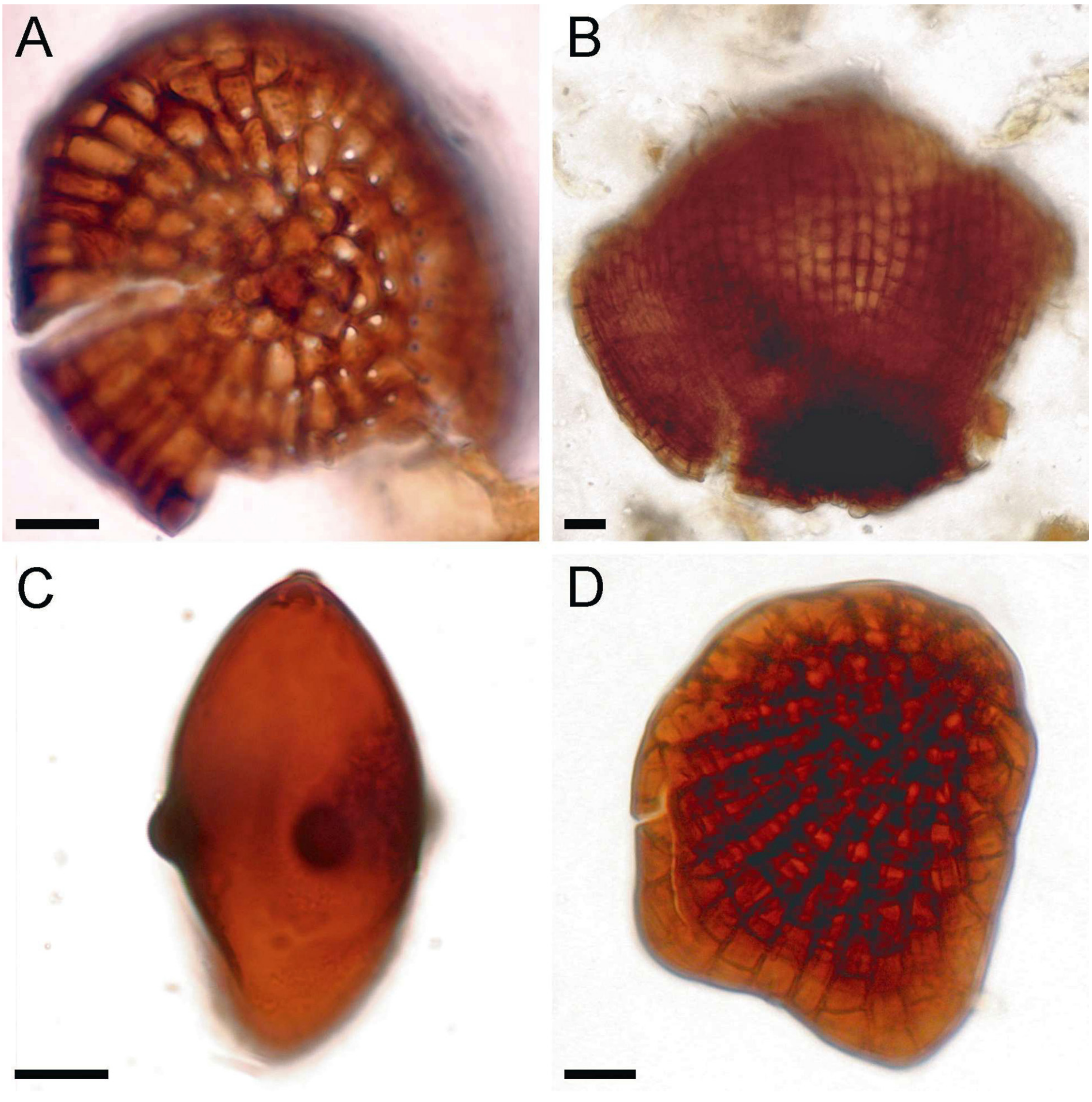

Fig. 2. Selected fungal microfossils from Miocene lignite-bearing deposits in Poland. **A –** Sporodochium of *Neomycoleptodiscus pertusus*, Bełchatów opencast mine; **B –** Conidium of *Cancellidium intergraniferum*, Tomisławice opencast mine; **C –** Ascospore of *Potamomyces* sp. ex gr. *P. armatisporus*, Bełchatów opencast mine; **D –** Conidium of *Mycoenterolobium eccentricum*, Bełchatów opencast mine. Scale bars equal 10 µm.

[Fig. 3D], *Dictyosporites muriformis*, *D. zeaformis*, *Pleosporomyces adamowiensis* and *Potamomyces* sp. ex gr. *P. armatisporus*) was presumably growing on decaying wood (Worobiec et al., 2022c, d). Epiphyllous fungi (*Isthmospora* cf. *spinosa*, *Microthyriacites radiatus*, *Neomycoleptodiscus pertusus*, *Plochmopeltinites* cf. *masonii*, *Trichothyrites* cf. *kiandrensis* and *Trichothyrites* spp.) probably were saprophytic on leaf litter. These fungi most probably grew on dead plant parts that accumulated in the Middle Miocene peatlands from which the Adamów lignite seam was formed (Worobiec et al., 2021, 2022d).

The fungal assemblage from Drzewce includes terrestrial epiphyllous, mycorrhizal and helicosporous aero-aquatic fungi. Epiphyllous fungi that inhabited surfaces of living leaves or, possibly, those decaying as leaf litter, are represented by sporocarps of the fossil-genera *Plochmopeltinites* and *Trichothyrites* (Fig. 3A). Remains of *Cenococcum*-like mycorrhizal fungus and microsclerotia identical to modern dark septate endophytic (DSE) fungi represent rhizosphere fungi associated with root systems of Neogene plants (Worobiec et al., 2022a, 2025b). The helicosporous mitosporic aero-aquatic fungi from Drzewce are similar to species of the extant genera *Helicoon* and *Helicodendron* (Fig. 3B).

The only fossil-species found in the single sample studied from the Tomisławice opencast mine is *Cancellidium intergraniferum* (Fig. 2B). In fact, remains of this aero-aquatic hyphomycete document

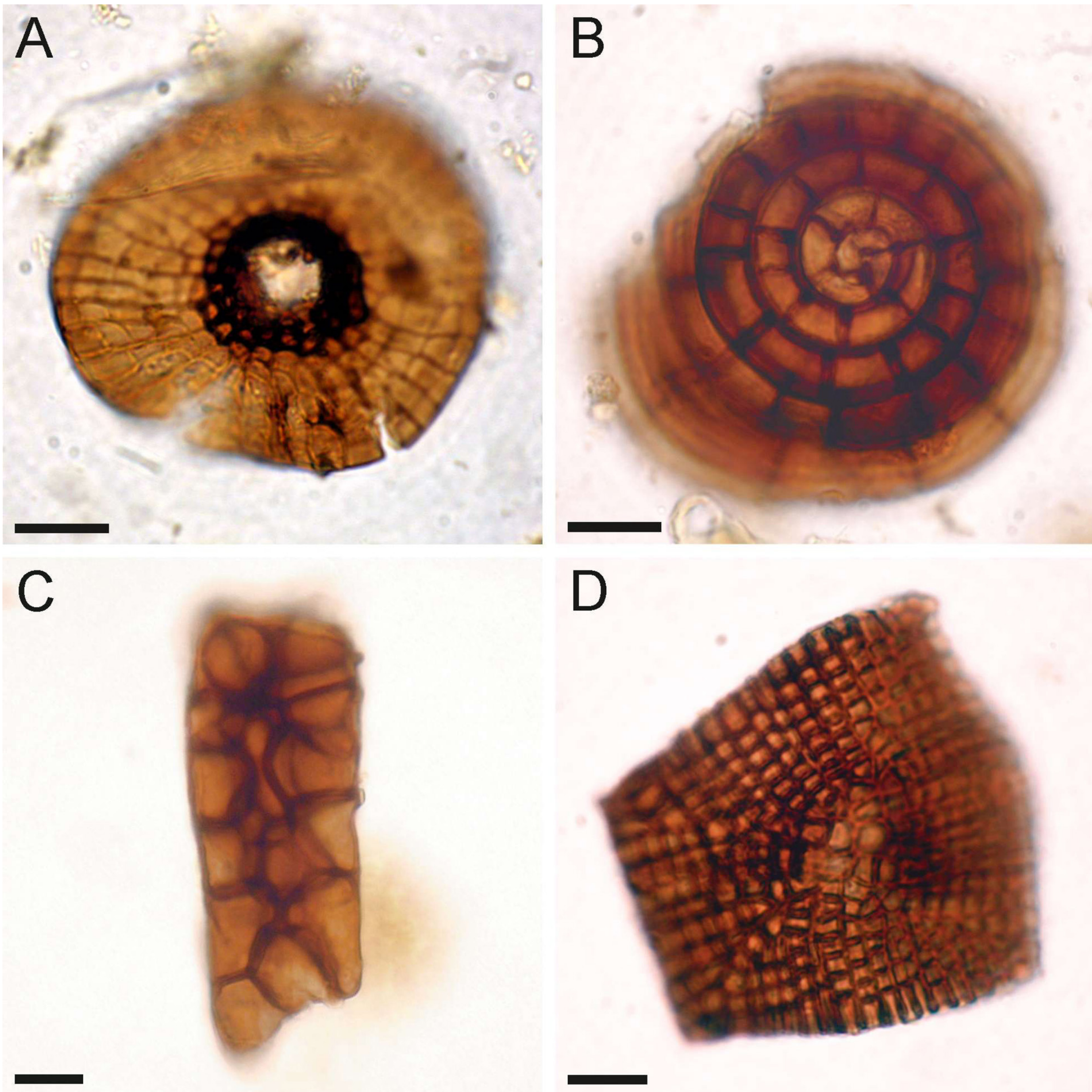

Fig. 3. Selected fungal microfossils from Miocene lignite-bearing deposits in Poland. **A –** Epiphyllous sporocarp of *Trichothyrites* sp., Drzewce opencast mine; **B –** Conidium of helicosporous aero-aquatic hyphomycete, Drzewce opencast mine; **C –** Microsclerotium of dark septate endophytic fungus, Chłapowo lignite seam; **D –** Isolated fragment of cephalothecoid peridium of *Cephalothecoidomyces neogenicus*, Adamów opencast mine. Scale bars equal 10 µm.

the first fossil record of the genus *Cancellidium* outside of Asia, its first documentation from Europe, as well as the northernmost fossil occurrence of *Cancellidium* to date (Worobiec et al., 2024).

4.2. Bełchatów, Ruja and Chłapowo

Fungal assemblages from the Bełchatów opencast pit consist mostly of remains of epiphyllous fungi. Encountered were sporocarps of *Phragmothyrites* cf. *lutosus*, *Phragmothyrites* spp., *Trichothyrites* cf. *hordlensis* and *Trichothyrites* sp., and sporodochia of *Neomycoleptodiscus pertusus* (Fig. 2A; Worobiec & Worobiec, 2017; Worobiec et al., 2020). *Mycoenterolobium eccentricum* (Fig. 2D), classified as an aero-aquatic hyphomycete, was a saprophytic fungus occurring on decaying wood or leaves (Worobiec et al., 2023b). Another saprotrophic fungus found in Bełchatów is *Potamomyces* sp. ex gr. *P. armatisporus* (Fig. 2C), which may be classified as a facultative-aquatic or terrestrial-aquatic fungus (Worobiec et al., 2022c). Of particular interest is the presence of conidia of *Asterosporium asterospermum* (Fig. 4). Nowadays, this fungus with staurosporous, tetrahedral conidia is strictly host-specific and found only on branches or bark of various species of beech in Europe, Asia and North America. Conidia of *Asterosporium asterospermum* found in the Bełchatów opencast mine were associated with remains of beech (leaves and fruits of *Fagus*, as well as pollen grains belonging to the fossil-genus *Faguspollenites*), similar to other localities in Germany and Poland from where *Asterosporium asterospermum* has been recorded (Worobiec et al., 2023a). This confirms the host-specific relationship between *Asterosporium asterospermum* and beech in the past (Worobiec et al., 2023a).

Fig. 4. Conidium of *Asterosporium asterospermum*, Miocene of Bełchatów opencast mine. Scale bar equals 10 µm.

Fungal spores, sporocarps and microsclerotia were found in palynological samples from the Miocene lignite seam from Chłapowo. Epiphyllous fungi are represented by the fossil-genera *Phragmothyrites*, cf. *Plochmopeltinites* and *Trichothyrites*. Microsclerotia of dark septate endophytic fungi found in Chłapowo correspond to those of modern dark septate root endophytic fungi (Fig. 3C). Mitosporic helicosporous fungi are represented by conidia similar to representatives of the extant genus *Helicoma* (Worobiec et al., 2025a).

Finally, in the core of the Komorniki 97/72 borehole (Ruja lignite deposit, part of Legnica–Ścinawa lignite deposit complex) only ascospores of *Potamomyces* sp. ex gr. *P. armatisporus*, a saprotrophic fungus occurring today in freshwater or damp terrestrial environments (Worobiec et al., 2022c) have been noted to date.

5. What do fossil fungi tell us about past vegetation, climate and environment?

Fungal microremains, forming part of the broader group of non-pollen palynomorphs, can be used to infer aspects of past vegetation and climate. The nearest-living relative (NLR) approach is used for this purpose. This approach uses the idea of physiological uniformitarianism, the assumption that ecological tolerances and requirements of fossil taxa were much the same as those of present-day relatives (Tiffney, 2008). The NLR approach links fossil fungal taxa to ecological preferences of their modern relatives, providing a path towards palaeoecological reconstructions (comp. Utescher et al., 2014).

In the case of palynological studies of Miocene lignite-bearing deposits in Poland, fungal microremains were used alongside plant pollen/spores and algal remains in order to reconstruct ancient peat-forming environments. As fungi are usually sensitive to moisture, their presence often indicates a humid environment typical of swamp forests and shrub bogs, where fungal activity was part of decomposition and nutrient cycling processes (Tsui et al., 2016). Many fungal taxa reflect interactions with plants and substrates. For example, the presence of fungal spores of wood-decomposing taxa may indicate substantial woody biomass at the time of deposition, which is typical of a peat-forming environment (Shearer, 1992). The characteristic spores of helicosporous aero-aquatic fungi, which thrive in waterlogged soils with water bodies that have a variable water level, enable the reconstruction of wetland hydrology, indicating the presence of small, shallow ponds or even periodic reservoirs (Goh & Hyde, 1996; Yamaguchi, 2023).

5.1. Fossil fungi in reconstructions of Miocene peat-forming environments in Poland

Rich assemblages of fungal remains from the Adamów opencast mine were collected from the Middle Miocene 1st mid-Polish lignite seam (MPLS-1), originating from peat-forming wetland vegetation. Fungal associations from Adamów opencast mine are represented by remains of indigenous fungal taxa of wetland communities, but some of them might be allochthonous and brought in by water or wind from other, albeit mostly wetland, habitats. Fossil-taxa such as *Canalisporium lignitum, Cephalothecoidomyces neogenicus*, *Dictyosporites muriformis*, *D. zeaformis*, *Pleosporomyces adamowiensis* and *Potamomyces* sp. ex gr. *P. armatisporus*, represent a mixture of submerged-aquatic and terrestrial fungi and, similar to modern counterparts, were most probably growing on plant debris such as branches and trunks that accumulated during peat formation (Worobiec et al., 2017, 2022c, d). *Canalisporium lignitum* and *Potamomyces* sp. ex gr. *P. armatisporus* indicate that the wood debris accumulated in a very humid environment (Schlütz & Shumilovskikh, 2013, Worobiec et al., 2022c, d). Epiphyllous fungi such as *Isthmospora* cf. *spinosa*, *Microthyriacites radiatus*, *Neomycoleptodiscus pertusus*, *Plochmopeltinites* cf. *masonii* and *Trichothyrites* cf. *kiandrensis*, were presumably saprophytic on the litter of fallen leaves or on living leaves (Worobiec & Worobiec, 2017; Worobiec et al., 2022a, c, 2025a). Therefore, fungal taxa found in lignite at the Adamów opencast mine indicate abundant accumulations of woody plant debris such as branches and trunks and litter of fallen leaves in a very humid environment typical of swamp forests or shrub bogs. The palaeoenvironment reconstructed on the basis of fungal taxa found in MPLS-1 at Adamów is consistent with results of palynological studies that documented the presence of pocosin-like shrub bog plant communities (Worobiec et al., 2021).

The assemblage from the Drzewce opencast mine consists of fungal spores, sporocarps and remains of terrestrial epiphyllous fungi, rhizosphere fungi and helicosporous aero-aquatic fungi. Epiphyllous fungi inhabited surfaces of leaves, both living and those decaying as leaf litter and indicate the accumulation of leaf litter. Rhizosphere fungi represented by remains of the mycorrhizal fungus *Cenococcum* and microsclerotia similar to modern root-associated dark septate endophytic fungi confirm the presence of dense vegetation during the time of peat deposition (Worobiec et al., 2022a, 2025b). Finally, helicosporous conidia of mitosporic aero-aquatic fungi, along with above-mentioned fungi, are indicative of dense vegetation on damp, swampy soils and the presence of small, shallow-water bodies with variable water level or even periodic reservoirs existing only during the wet season or after floods (Worobiec et al., 2022a). The palaeoenvironment reconstructed on the basis of fossil fungi is consistent with results of spore-pollen analysis of the 1st mid-Polish lignite seam from Drzewce. The analysis indicates that the area was overgrown by palustrine wetland communities, similar in composition to the modern pocosins with members of the families Ericaceae, Cyrillaceae and Clethraceae, as well as the genera *Ilex* and *Myrica* (Worobiec et al., 2022a).

The fossil-species *Cancellidium intergraniferum* was the sole fungal species found in a sample taken from the Tomisławice opencast pit (Fig. 2B). Considered an aero-aquatic hyphomycete, this fungus presumably was saprotrophic on decaying wood or on decaying leaves, in a freshwater environment. It might be indicative of the presence of a shallow-water reservoir (small water body or margins of lake), probably with a variable water level in a peat-forming environment (Worobiec et al., 2024). This is in accordance with results of palynological analysis of the sample from the Tomisławice, which yielded the conidium of *Cancellidium intergraniferum*. The palynological spectrum of this sample indicates the presence of a shallow body of water characterised by stagnant or slow-flowing conditions (Słodkowska & Widera, 2022).

Assemblages from the Bełchatów opencast mine consist mostly of remains of epiphyllous fungi (Worobiec & Worobiec, 2017, 2022). Additionally, saprotrophic fungi that occur on decaying wood, namely the aero-aquatic hyphomycete *Mycoenterolobium eccentricum* (Fig. 2D) and the facultative-aquatic or terrestrial-aquatic ascomycete *Potamomyces* sp. ex gr. *P. armatisporus* (Fig. 2C), have been recognised. Fungal microremains from Bełchatów suggest the presence of shallow water bodies and confirm the dense vegetation and accumulation of leaf litter in the peat-forming plant communities (Worobiec & Worobiec, 2017). Palynological spectra and plant macroremain assemblages of Miocene lignite-bearing deposits of fluvial–lacustrine and peat-forming sedimentary sequences at Bełchatów have revealed the dominant role of wetland vegetation of swamp forests, bush swamps and riparian forests and mixed mesophytic upland communities (Worobiec & Lesiak, 1998; Worobiec, 2003; Worobiec & Szynkiewicz, 2016; Worobiec & Worobiec, 2016, 2019, 2022). Therefore, palaeovegetation inferred from fungal remains that accompanied plant assemblages from the lignite-bearing deposits at Bełchatów matches the spore-pollen and plant macroremain analysis well.

Fungal spores, sporocarps and indeterminate fungal hyphae were found in palynological samples from Chłapowo. They represent indigenous fungal taxa of peat-forming communities of the 2nd Lusatian seam. Remains of three ecological groups of fungi were encountered: conidia of helicosporous fungi similar to the modern genus *Helicoma*, epiphyllous fungi (*Phragmothyrites*, *Plochmopeltinites* and *Trichothyrites*) and microsclerotia of root-inhabiting dark septate endophytic fungi (Worobiec et al., 2025a). Helicosporous fungi may be suggestive of the presence of small, shallow water bodies on peat bogs, while the occurrence of microsclerotia of dark septate endophytes points to well-developed plant root systems in the peat layer. This is indicative of a dense vegetation cover including trees and shrubs during the time of peat deposition. The presence of epiphyllous fungi that inhabited the phyllosphere of leaves confirms the dense vegetation and accumulation of leaf litter (Worobiec et al., 2025a). The results of the spore-pollen study of the 2nd Lusatian seam from Chłapowo point to bottomland wetland vegetation, including communities from which lignite was formed (mainly shrub bogs and swamp forests) and upland mesophilous communities occurring in the vicinity. Shrub bogs, similar to the modern pocosins, comprised various representatives of the families Cyrillaceae, Clethraceae and Ericaceae, as well as the genera *Myrica* and *Ilex*. Less humid places in the area, such as river terraces and upland localities, may have been covered by mesophilous communities. The variability of other palynomorphs (freshwater algae including *Botryococcus*, *Closterium* and Zygnemataceae) and the sequence of palynofacies indicate significant habitat modification, including trophic changes and drainage (Worobiec et al., 2025a). Therefore, results of fungal microremain studies and the classic palynological analysis of the Miocene peat-forming communities from Chłapowo are consistent and complement one another.

Potamomyces sp. ex gr. *P. armatisporus*, a saprotrophic fungus probably related to a freshwater to moist to damp terrestrial environment, was found in the 2nd Lusatian lignite seam at the Komorniki 97/72 borehole of the Ruja lignite deposit (Worobiec et al., 2022c). Similar to cases from the Adamów and Bełchatów opencast pits, ascospores of wood-inhabiting, saprotrophic *Potamomyces* suggest the accumulation of dead plant litter (branches, leaves) in damp, terrestrial to freshwater environments (Worobiec et al., 2022c). Accordingly, the floristic composition of the Miocene plant macro- and microremain assemblages from the Komorniki borehole is characterised by the predominance of wetland, swamp and riparian vegetation (Worobiec et al., 2008, 2022b).

5.2. Palaeoclimate of Miocene wetlands in Poland based on fungal microremain data

Fungi are valuable palaeoclimatic indicators because extant taxa are generally sensitive to moisture, and the occurrence of many forms is directly linked to temperature (Talley et al., 2002; Deacon, 2006; Tripathi, 2009). Thus, the presence of abundant and diverse fungal microremains could suggest a humid palaeoenvironment. Some fossil fungi, found as non-pollen palynomorphs in Neogene deposits, are good indicators of a warm, humid climate (Tripathi, 2009; Musotto et al., 2013; Conran et al., 2016). In the Miocene lignite-bearing formations in the Adamów–Konin area, the Bełchatów opencast mine and the Ruja lignite deposit, fungal microremains of *Cancellidium intergraniferum* (Fig. 2B), *Mycoenterolobium eccentricum* (Fig. 2D), *Neomycoleptodiscus pertusus* (Fig. 2A) and representatives of the genus *Potamomyces* (Fig. 2C) constitute proxies for a warm, humid climate (Worobiec et al., 2020, 2022c, 2023b, 2024).

The presence of sporodochia of *Neomycoleptodiscus pertusus* and ascospores of *Potamomyces* sp. ex gr. *P. armatisporus* at the Adamów pit indicates warm (subtropical) and humid climatic conditions (Schlütz & Shumilovskikh, 2013; Worobiec et al., 2020, 2022c, d). Accordingly, epiphyllous fungi found in the lignite seam from Adamów may indicate a rather high mean annual precipitation (probably over 1,000 mm) during the formation of the 1st mid-Polish lignite seam (Worobiec et al., 2022d). Results of pollen analysis of the lignite seam from Adamów suggest that at the time of sedimentation the climate was warm temperate and humid (favourable for development of peat bogs and swamp forests) with estimated mean annual temperature of between 15.7 and 18.0°C (Worobiec et al., 2021).

Hence, palaeoclimate estimates obtained from an analysis of the fungal assemblage from Adamów is fully confirmed by spore-pollen investigations.

The saprotrophic aero-aquatic hyphomycete *Cancellidium intergraniferum*, whose modern relatives are found exclusively in warm, tropical to subtropical regions of the world, was found in lignite from the Tomisławice opencast mine. Its presence suggests warm climatic conditions that accompanied peat formation of the 1st mid-Polish lignite seam at Tomisławice (Worobiec et al., 2024). Indeed, MPLS-1 there formed during the last peak of the Miocene Climatic Optimum (MCO), when the climate was warm temperate to subtropical and humid (Mosbrugger et al., 2005; Romero et al., 2021; Steinthorsdottir et al., 2021). These conclusions are consistent with results of previous palaeobotanical studies of the accompanying vegetation which is dominated by warm temperate and thermophilous species (Kowalski, 2008; Kowalski & Fagúndez, 2017; Słodkowska & Widera, 2022).

Mycoenterolobium eccentricum, *Neomycoleptodiscus pertusus* and *Potamomyces* sp. ex gr. *P. armatisporus* found in Miocene deposits at Bełchatów, along with remains of epiphyllous fungi, again point to a warm temperate to subtropical and humid climate that prevailed in this area during the Miocene (Worobiec & Worobiec, 2017; Worobiec et al., 2020, 2022c, 2023b). The floristic composition of the plant macro- and microremain assemblages from Bełchatów points to a warm, temperate to subtropical and moderately wet climate, with mild winters (Worobiec, 2003; Worobiec & Szynkiewicz, 2016; Worobiec & Worobiec, 2016, 2019). In this case climatic inferences based on plant and fungal remains are fully consistent as well.

Ascospores of *Potamomyces* sp. ex gr. *P. armatisporus* found in the 2nd Lusatian lignite seam in the Komorniki borehole (Ruja lignite deposit) clearly indicate warm and humid climate (Worobiec et al., 2022b, c), which is in accordance with results of studies of plant assemblages from this borehole. An analysis of floristic composition points to warm temperate climate conditions with mild winters (Worobiec et al., 2008), with a mean annual temperature in the range of 15.7–17.8 °C. The climate was generally described as humid based on the vegetation, including the presence of swamp forests and peat bogs (Worobiec et al., 2022b).

The fungal assemblages from lignite deposits at the Drzewce opencast pit and Chłapowo do not comprise taxa that could be used as direct proxies of warm climate. However, numerous remains of epiphyllous fungi (sporocarps of the fossil-genera *Phragmothyrites*, *Plochmopeltinites* and *Trichothyrites*) may suggest a humid palaeoenvironment (Worobiec et al., 2022a, 2025a). Modern epiphyllous fungi show the highest abundance and taxonomic diversity in humid regions across the globe, because high annual rainfall and elevated air moisture are important for their growth (Tripathi, 2009; Piepenbring et al., 2011; Conran et al., 2016; Worobiec & Worobiec, 2017). Accordingly, results of palynological investigations indicate a warm and humid climate during the formation of these lignite seams (Worobiec et al., 2022a, 2025a).

6. Conclusions

Palynological studies of coal-bearing deposits are a crucial tool to reconstruct the palaeoenvironment of peat-forming ancient wetlands. Classic palynological analysis (pollen and spores) is key to determining the composition and ecology of peat-forming plant communities and changes during the formation of peat deposits, as well as concomitant climatic conditions. Fungal non-pollen palynomorphs are also potentially valuable palaeoenvironmental indicators. However, pre-Quaternary fungal NPP are rarely investigated, and their potential as a source of data for palaeoecological interpretations of Neogene coal-forming environments is often overlooked.

Studies of fungal non-pollen palynomorphs from Miocene lignite deposits in Poland clearly demonstrate that, when coupled with other proxies, fungal remains can add to the palaeoenvironmental picture obtained from classic pollen analysis. Fossil fungi play a significant role in multiproxy reconstructions, providing information on wetland hydrology, vegetation structure and density, temperature, humidity and plant-fungal interactions. They may confirm and complement palaeovegetational and palaeoclimatic inferences derived from classic palynology, creating a comprehensive picture of Miocene coal-forming environments. This is clearly visible, for example, in the case of the Chłapowo lignite seam, where changes in the abundance of ecological groups of fungi, in correlation with the variability of other palynomorphs and palynofacies, clearly indicate changes in plant communities associated with palaeoenvironmental variability (Worobiec et al., 2025a).

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Authors' contributions

G.W.: conceptualization, methodology, original draft preparation, writing, review, editing, investigation, supervision; E.W.: original draft preparation, writing, review, editing, investigation. All authors have read and agreed to the published version of the manuscript.

Conflicts of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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