Fossils of parasitic fungi

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Abstract

Parasitic fungi occur in virtually every ecosystem, where they can significantly affect the functions of other organisms. Fungal parasites were probably also widespread in the geologic past. However, evidence of fossil fungi and their ecological roles is relatively rare. Here we demonstrate a spectrum of (putative) parasitic relationships in ancient continental ecosystems, using fossil examples of Chytridiomycota, zygomycetous fungi, Basidiomycota, and Ascomycota, along with several fungal fossils whose affinities remain unknown, from different periods of the Phanerozoic. Although many of the hosts no longer exist, the fungi involved mostly appear morphologically very similar to extant forms.

Introduction

The kingdom Fungi comprises an estimated 2 to 13 million extant species, many of which play important roles as constituents of continental ecosystems (Blackwell, 2011; Hawksworth and Lücking, 2017; Wu *et al.*, 2019; Cheek *et al.*, 2020). Fungi exhibit an extensive diversity of morphologies, reproductive strategies, and metabolic pathways; moreover, they enter into a broad spectrum of ecological relationships with other organisms, which may be dead or alive at the time of colonization (Willis, 2018). The ecological role of the common ancestor of the true Fungi remains elusive. However, early-diverging branches of the fungal stem lineage are parasites (Anderson *et al.*, 2010).

Fossil fungi have been documented throughout the Phanerozoic (Taylor *et al.*, 2015a), but fungal relationships with land plants and other fungi from the Lower Devonian, Carboniferous, Triassic, Cretaceous, and Cenozoic have attracted increased attention. The simple reason for this is the existence of exceptional rock or amber deposits from these periods of time that faithfully preserve numerous fungi together with their hosts, and thus provide direct insights into different levels of fungal interaction with other organisms in ancient ecosystems (Taylor and Krings, 2010; Taylor *et al.*, 2015a, 2015b; Krings *et al.*, 2017b, 2018; Halbwachs *et al.*, 2021).

Documented fossil evidence of parasitic fungi in general is relatively rare, due primarily to the fact that, of all the potential levels of fungal interaction, parasitism is probably the most difficult to demonstrate based on fossils (Harper and Krings, 2021). Cherts, which are a dense microcrystalline or cryptocrystalline type of sedimentary rock deposits that may preserve organisms three-dimensionally and down to the finest

cellular details, represent the most important sources of new evidence of fossil parasitic fungi. Coal balls, which typically are concretions of calcium carbonate, are another matrix that may yield exquisite fossils of parasitic fungi. A third copious source of information on parasitic fungi since the Cretaceous is fossilized plant resin called amber.

The fossil record of fungi as parasites was recently reviewed by Harper and Krings (2021). While these authors focus on the hosts, and describe fungal parasites of fossil land plants, algae, other fungi, and animals, here we use the (assumed) systematic affinities of the parasites as the guiding thread. This book chapter is aimed primarily at students and colleagues interested in having a concise overview of fossil parasitic representatives of the major lineages of fungi, and is complementary to the Harper and Krings (2021) review.

Fossils of parasitic fungi

Because not all branches of the fungal tree of life have a fossil record (Taylor *et al.*, 2015a, 2015b; Krings *et al.*, 2017b), and not all fungal lineages with a fossil record include parasites, the following compilation is limited to those lineages for which parasitism has been documented or suggested based on fossils, namely Chytridiomycota, zygomycetous fungi, Basidiomycota, and Ascomycota. Several fossil fungi that probably were parasites, but whose systematic affinities remain unresolved, are also included. Examples of fungal parasitism have been documented throughout the Phanerozoic (Harper and Krings, 2021). However, the Lower Devonian Rhynie chert of Scotland (~410 Ma), which is the oldest rock deposit containing comprehensive information on fungal life in a continental palaeoecosystem (Taylor *et al.*, 2003, 2015a), and also several Mississippian and Pennsylvanian cherts (~331 Ma and ~304 Ma, respectively) from France and Early Pennsylvanian coal balls (~319 Ma) from England have been more systematically studied to date, and thus have yielded the largest number of examples.

Chytridiomycota (chytrids)

Rhynie chert

The oldest fossil bona fide parasitic chytrids come from the Rhynie chert, and include holocarpic and eucarpic forms as parasites of land plants, charophytes, and other fungi (Kidston and Lang, 1921; Taylor *et al.*, 1992b, 2015a; Krings *et al.*, 2018). Three different forms have been identified as parasites of the charophyte *Palaeonitella cranii* (**Fig. 1A**; Taylor *et al.*, 1992a). One of them, *Milleromyces rhyniensis*, is characterized by an endobiotic zoosporangium with a discharge tube extending out from the host cell wall. The other chytrids associated with *P. cranii* are *Lyonomyces pyriformis* and *Krispiromyces discoides*, which differ from one another in thallus morphology, but are comparable with several extant chytrid parasites of freshwater algae, including members of *Entophlyctis* and *Phlyctochytrium*. The host response in *P. cranii* is visible as a massive hypertrophy of cells, which grow to approximately five times the diameter of normal cells (**Fig. 1B**).

Rhizophydites matryoshkae is a monocentric chytrid from the Rhynie chert that parasitizes spores of the land plant *Horneophyton lignieri* (**Fig. 1C**; Krings *et al.*, 2021). Zoosporangia are epibiotic, inoperculate, and possess 1–4 discharge papillae or short tubes. Several specimens comprise two or more successive generations of zoosporangia occurring one inside another (**Fig. 1D**), a feature that allows for a direct comparison with the extant genus *Rhizophydium* (Rhizophydiales).

Perhaps the most impressive parasitic chytrid from the Rhynie chert occurs on propagule clusters of unknown nature and affinity that are frequently encountered in microbial mats (Krings and Harper, 2019). Thalli consist of a robust, endobiotic or intramatrical rhizoidal system and an epibiotic sporangium, which is situated on the surface of the host cluster and arises from a prominent subsporangial inflation or apophysis (**Fig. 1E**). Some of the distal rhizoidal branches penetrate individual propagules and extend into their lumen.

The rhizoid first forms a distally inflated, appressorium-like structure from which a narrow penetration peg is then pushed through the host wall.

Other monocentric and polycentric chytrids are colonizers and likely parasites of spores of arbuscular mycorrhizal fungi (Glomeromycota) in the Rhynie chert (Hass *et al.*, 1994; Krings, 2022). Most are characterized by epibiotic zoosporangia and rhizoidal systems extending into the host spore lumen, others develop entirely within the spore lumen. An example of the former is *Illmanomyces corniger*, which consists of a zoosporangium with 4–5 conical discharge tubes (**Fig. 1F**) and a rhizoidal system that originates from a proximal protrusion on the sporangium (Krings and Taylor, 2014). Conversely, *Globicultrix nugax* is a polycentric thallus comprised of branched filaments and apophysate sporangia that are exclusively terminal (**Fig. 1G**; Krings *et al.*, 2009b). The form has been compared with the extant genera *Nowakowskiella* and *Cladochytrium* (both Cladochytridiales). Finally, *Brijax amictus* develops largely within the wall of certain glomeromycotan aculospores (**Fig. 1H**; Krings and Harper, 2020). Thalli consist of an inoperculate sporangium (zoosporangium or resting spore stage) located in the outer, ephemeral host spore wall component, and a rhizoidal system that extends into the inner, persistent spore wall. *Briax amictus* resembles certain present-day species of *Phlyctochytrium* (Chytridiales) and *Rhizophydium* (Rhizophydiales).

Hass *et al.* (1994), Krings and Harper (2018), and Krings (2022) describe penetration rhizoids of Rhynie chert mycoparasitic chytrids on glomeromycotan spores that extend into the host spore lumen and, once inside the lumen, become encased in a prominent, elongate-conical formation of newly synthesized spore wall material, termed a callosity (**Fig. 1I**). This host response is believed to prevent the rhizoid from extracting nutrients from the host. However, callosities in longitudinal section view reveal series of convex and concentric layers of varying thickness. This configuration indicates that the rhizoids continued to grow longer in spite of the presence of the callosity, and that the spores responded to the continued growth of the rhizoid by addition of new layers to the callosity. Krings and Harper (2018) regard callosity formation as evidence of biotrophy. Biotrophic relationships represent physiologically balanced systems, in which the parasite coexists with the host for an extended period of time and often forms specialized infection structures or host-parasite interfaces (Jeffries and Young, 1994; Jeffries, 1995). The arms race between the penetration rhizoid and the callosity can be viewed as a specialized host-parasite interface, in which the parasite is contained to a certain extent by the host, but is still able to grow and extract sufficient nutrients to provide for sporangium development and maturation. The consecutive layers comprising the callosities indicate that the host remained viable for an extended period of time while being parasitized.

Carboniferous, Mesozoic, and Cenozoic records

Fossil chytrids have also been reported from several Mississippian (Visean, ˜331 Ma) and Late Pennsylvanian (˜304 Ma) chert deposits in France. For example, *Grilletia spherospermii* and *Oochytrium lepidodendri* are two chytrid parasites of gymnosperms and arborescent lycophytes that have been described from these cherts more than 120 years ago (Renault and Bertrand, 1885; Renault, 1895, 1896). Additional evidence of chytrids has more recently been documented in (degrading) vascular plant tissues (xylem, periderm, cortical parenchyma, leaf mesophyll) and sporangia, as well as in various plant and fungal spores (Krings *et al.*, 2007a, 2009a, 2009c, 2011b; Dotzler *et al.*, 2011). Host responses possibly linked to chytrid infection occur in the form of callosities, some with a distinct penetration canal, in lycophyte xylem and periderm (**Fig. 1J**), as well as in glomeromycotan spores (Krings *et al.*, 2009a).

Conspicuous spheroidal inclusions are sometimes present in gymnosperm pollen grains from the Upper Permian (˜265 Ma) of India (Aggarwal *et al.*, 2015). They occur in the corpus of the pollen grain, and have been interpreted as the remains of a pollen-colonizing organism, perhaps the endobiotic zoosporangia of a chytrid (**Fig. 1K**). Another putative endoparasitic chytrid, *Synchtrium permicus*, occurs in silicified plant remains from the Upper Permian of Antarctica (˜255 Ma) (García Massini, 2007). The thallus is holocarpic and consists of thick-walled resting sporangia, thin-walled sporangia, and zoospores in different stages of development. The host cells are often hypertrophied. Morphology and development of the fossil suggest similarities with the extant genus *Synchytrium* (Chytridiales). Other fossils resembling *Synchytrium* have

been reported from the roots of a Pennsylvanian calamite (~310 Ma) (Agashe and Tilak, 1970). They consist of mostly intercellular, oval to spheroidal sporangium-like structures containing numerous globular bodies.

The record of Mesozoic and Cenozoic chytrid parasites is exceedingly meagre. Pollen grains and spores obtained through palynological sampling sometimes contain structures that may represent chytrids. However, these structures do not normally receive attention because the focus of the research is directed at the pollen and spores, rather than their contents (Taylor *et al.*, 2015a). A Mesozoic example of such an occurrence is *Rhizophidites triassicus*, a putative chytrid parasite of some Triassic spores that resembles the extant *Globomyces pollinis-pini*, which is a parasite of pine pollen (Daugherty, 1941).

Zygomycetous fungi

Fossil evidence of zygomycetous fungi and their interactions with other organisms is rare. Not even the famous Rhynie chert has produced conclusive evidence of them (Krings *et al.*, 2013a). The oldest bona fide fossils of zygomycetous fungi come from the Lower Pennsylvanian of England (~319 Ma) and occur in the form of several types of structurally preserved reproductive units interpreted as zygosporangia with attached gametangia (Krings and Taylor, 2012a, 2012b; Krings *et al.*, 2013b). These fossils all have been discovered within the confines of plant parts, such as ovules and degraded wood. This is unusual since most modern zygomycetes produce zygospores aerially, on or in the soil, or on organic debris (Benny *et al.*, 2001). As to whether the occurrence within plant parts reflects some life history strategy of Carboniferous zygomycetous fungi, perhaps plant parasitism, cannot be determined.

There are a few reports of putative parasitic zygomycetous fungi preserved in amber. For example, aseptate hyphae that resemble the assimilative hyphae of certain modern nematophagous zygomycetes occur in Miocene amber fossils of nematodes from Mexico (~20 Ma) (**Fig. 1L**; Jansson and Poinar, 1986). Another example is present in Cretaceous amber from Spain (~120 Ma) (Speranza *et al.*, 2010), and occurs in the form of a thrip containing hyphae and reproductive structures similar to those seen in certain extant zygomycetes. Moreover, Poinar and Thomas (1982) describe an entomophthoralean fungus from a termite preserved in amber from the Miocene Dominican Republic (~18 Ma). The body of the animal is covered with a white mat composed of closely appressed (**Fig. 1M**), supposedly coenocytic hyphae. A layer of conidia lines the surface of the mycelial covering. Some of the conidia are budding and a number of smaller conidia (secondary conidia) are present in the amber close to the mycelial covering.

Figure 1: Examples of fossil fungal parasites: Chytridiomycota and zygomycetous fungi. A. Portion of charophyte Palaeonitella cranii showing normal cell size from Lower Devonian Rhynie chert; colour version of fig. 1 in Taylor et al. (1992a); bar 100 μm. B. Hypertrophied cells of P. cranii from Lower Devonian Rhynie chert; colour version of fig. 26 in Taylor et al. (1992c); bar 200 μm. C. Partially degraded sporangia of Horneophyton lignieri colonized by Rhizophydites matryoshkae (arrows) from Lower Devonian Rhynie chert; fig. 1E in Krings et al. (2021); bar 100 μm. D. Rhizophydites matryoshkae with four generations of zoosporangia occurring one inside another from Lower Devonian Rhynie chert; fig. 5A in Krings et al. (2021); bar 10 μm. E. Fungal intruders of enigmatic propagule clusters in microbial mats from Lower Devonian Rhynie chert; fig. 2a in Krings and Harper (2019); bar 10 μm. F. Illmanomyces corniger zoosporangium on host spore from Lower Devonian Rhynie chert; fig. 2a in Krings and Taylor (2014); bar 50 μm. G. Globicultrix nugax in glomeromycotan spore from Lower Devonian Rhynie chert; fig. 2.2 in Krings et al. (2009b); bar 20 μm. H. Thalli of Brijax amictus in ephemeral outer wall component of glomeromycotan acaulospore from Lower Devonian Rhynie chert; pl. III, fig. 8 in Krings and Harper (2020); bar 25 μm. I. Callosity (white arrows) in glomeromycotan spore; note sporangium of parasite on host spore surface (black arrow) from Lower Devonian Rhynie chert; fig. 31 in Krings (2022); bar 10 μm. J. Callosities in lycophyte periderm from Visean (Mississippian) chert deposits in France; pl. II, fig. 12 in Krings et al. (2009a); bar 20 μm. K. Chytrid-like inclusions in gymnosperm pollen grain from Upper Permian of India; fig. 2C in Aggarwal et al. (2015); bar 20 μm. L. Developing spore of a fungal pathogen inside a nematode from Miocene Mexican amber; fig. 2A in Jansson and Poinar (1986); bar 10 μm. M. Termite bearing white colonies of an entomophthoralean fungus (arrow) from Miocene Dominicam amber; colour version of fig. 1 in Poinar and Thomas (1982); bar 1.0 mm. A, B. Courtesy of Hagen Hass and Hans Kerp, University of Münster. L, M. Courtesy of George O. Poinar, Oregon State University.

Basidiomycota

The oldest basidiomycetous fossils occur in a structurally preserved fern stem from the Upper Mississippian (˜331 Ma) of France, and comprise septate hyphae with clamp connections that pass from cell to cell (Krings *et al.*, 2011a). The clamp-bearing hyphae co-occur with elongate callosities in several of the host cells (**Fig. 2A**); however, hyphae and callosities have not been observed physically connected. If the callosities in fact formed in response to invading clamp-bearing hyphae, then this host response would be evidence of a parasitic interaction, which would support the hypothesis that ancestral Basidiomycota were parasites (Oberwinkler, 2012). Hyphae with clamp connections co-occurring with callosities have also been described in an Early Permian *Psaronius* tree fern root mantle from Germany (Krings *et al.*, 2017a).

Fossilized wood-rot also provides possible evidence of basidiomycetous parasitism and pathogenicity. Tracheids and vessels of extant plants have a diversity of passive defense mechanisms to ward off or contain microbial attacks (Blanchette, 1992), while living cells may also employ active mechanical defences in the form of appositions, tyloses, and chemical defence strategies (Schwarze and Baum, 2000). Silicified *Glossopteris* wood from the upper Permian (˜255 Ma) of Antarctica show irregular areas lacking cells, and septate hyphae with clamp connections (Harper *et al.*, 2016). The decay pattern in this fossil is comparable to present-day rots caused by Basidiomycota. Moreover, the lumina of some of the tracheids are sealed by opaque matter, while the cell walls of other tracheids are swollen and partially occlude the lumen (**Fig. 2B**). Both types of occlusion could have developed to contain antagonistic fungal expansion. Basidiomycota have also been identified as the causal agents for decay in conifer wood from the Jurassic (˜160 Ma) and Cretaceous (˜75 Ma) of Argentina (Sagasti *et al.*, 2019; Greppi *et al.*, 2022) and the Cretaceous (˜120 Ma) of China (Tian *et al.*, 2020), either directly based on the presence of clamp-bearing hyphae in the decayed areas of the wood, or indirectly based on micro-patterns that are consistent with patterns generated by xylophagous Basidiomycota in present-day conifer wood.

Another structural detail of fossil woods that has been discussed in connection with fungal infection is tyloses (Decombeix *et al.*, 2022). Harper *et al.* (2012) describe a Jurassic permineralized conifer axis from Antarctica (˜180 Ma) in which tylosis formation co-occurs with abundant fungal remains, suggesting that the tyloses served as mechanical barriers against the advancing hyphae (**Fig. 2C**). However, the fact that the hyphae also occur within and around the tyloses, as well as in the rays and phloem, suggests that the fungus was able to surmount this barrier. A similar interpretation has been offered by Khan *et al.* (2018) for Plio-Pleistocene (˜2.5 Ma) angiosperm wood from Tibet that also contains both tyloses and fungal remains.

Ascomycota

The bulk of evidence of fossil parasitic Ascomycota comes from amber fossils and cuticle preparations of compressed leaves. However, the hitherto oldest putatively parasitic Ascomycota, *Paleopyrenomycites devonicus*, is from the Lower Devonian Rhynie chert, and is preserved in leaf-like enations, stems, and rhizomes of the early lycophyte *Asteroxylon mackiei*, where it produced ostiolate perithecia in substomatal chambers just beneath stomatal pores (Taylor *et al.*, 1999, 2005). Necrotic areas in the host suggest that the fungus was a parasite. Hyphae and spores of another fungus, probably a mycoparasite, occur in several of the perithecia.

Amber fossils, and a permineralization

Fossils of parasitic fungi associated with animals primarily come from specimens enshrined in Cretaceous and Cenozoic amber. Perhaps the most spectacular example is a fungus described as *Paleoophiocordyceps coccophagus*, which was a parasite of scale insects and morphologically similar to present-day *Ophiocordyceps* (Sung *et al.*, 2008). This fossil occurs in mid-Cretaceous Kachin amber (˜100 Ma) from Myanmar in the form of synnemata emerging from the head of the insect (**Fig. 2D**). Another possible fungal parasite has recently been described from a *Camponotus* ant in Baltic amber (˜45 Ma) as *Allocordyceps baltica* (Hypocreales:

Clavicipitaceae) (Poinar and Maltier, 2021). The fungus is characterized by a stalked, cup-shaped ascoma with partially immersed perithecia that emerges from the rectum of the ant, two separate stromata with septate mycelium that emerge from the base of the neck and the abdomen of the ant, respectively, and free-standing putative perithecia bearing putative asci with multicellular ascospores. A third remarkable amber fossil preserving a fungus–animal interaction is a springtail (Collembola) covered in hyphae and conidiophores of an *Aspergillus* species that is also preserved in Eocene Baltic amber (Dörfelt and Schmidt, 2005). Most conidiophores extend directly from the host surface. The fungus may have penetrated and parasitized the living organism, and may have sporulated after the host had become entangled in liquid resin. The dominance of a single insecticolous fungus, together with the excellent preservation of the springtail, suggest a parasitic mode of life of the fungus (**Fig. 2E**).

A fossil member of the order Laboulbeniales, which are obligate ectoparasites (Haelewaters *et al.*, 2021), is preserved on the thorax of a stalk-eyed fly in Bitterfeld amber (~24 Ma) from Germany (Rossi *et al.*, 2005). The authors stated that the fungus is preserved in Baltic amber, but it is actually Bitterfeld amber (Perreau *et al.*, 2021). This fossil was assigned to the extant genus *Stigmatomyces*, of which representatives are parasites of Diptera, and described as *S. succinii*. It is the oldest bona fide fossil representative of the class Laboulbeniomycetes (**Fig. 2F, G**). Another fossil attributed to the Laboulbeniales with confidence has recently been discovered in Miocene Dominican amber (~18 Ma) (Perreau *et al.*, 2021). This fungus, *Columnomyces electri*, occurs on the leg of a leiodid beetle, and its discovery indicated that these beetles and their parasitic Laboulbeniales have coevolved at least since the Miocene (**Fig. 2H, I**).

A parasitic relationship involving an ascomycete has also been suggested for what has been interpreted as a *Claviceps*-like sclerotium, *Palaeoclaviceps parasiticus*, that occurs on a grass floret in Kachin amber (**Fig. 2J**; Poinar *et al.*, 2015). The fossil is believed to demonstrate the existence of intricate interactions between Clavicipitaceae and the plant family Poaceae in the Cretaceous. Recently, Poinar (2020) reported on epiphyllous pycnidia, formally described as *Palaeomycus epallelus*, from an angiosperm leaf in Kachin amber, and suggested that, albeit no modern equivalents to these pycnidia are known, they are most similar to leaf spot-producing Coelomycetes (**Fig. 2K**). Finally, lichenicolous fungi of the genus *Lichenostigma* (Lichenostigmatales) occurring on the apothecial margin and crustose thallus of two lichen fossils preserved in Paleogene Baltic amber (~45 Ma) have been interpreted as parasites (Kaasalainen *et al.*, 2019).

Examples of putative mycoparasitism and hypermycoparasitism have been reported from Kachin amber by Poinar and Buckley (2007). The gilled mushroom *Palaeoagaracites antiquus* is parasitized by an ascomycete, *Mycetophagites atrebora*. The mycelium of the parasite overgrows the pileus of *P. antiquus* and its hyphae also occur within the host tissue (**Fig. 2L**). A third organism involved in this interaction is *Entropezites patricii*, which appears to be a necrotrophic hyperparasite based on hyphae invading and apparently destroying the mycelium of *M. atrebora* (Fig. 2M). Another report of a fungal hyperparasite comes from the Eocene Princeton chert of Canada (Currah *et al.*, 1998). *Paleoserenomyces allenbyensis* is an ascomycete preserved on permineralized leaves of the palm *Uhlia allenbyensis*. The fossil fungus shares certain features with extant *Serenomyces* (Phyllachorales), which also forms spots on palms (Hyde and Cannon, 1999). Present in some of the locules of *P. allenbyensis* are globose ascomata formally described as *Cryptodidymosphaerites princetonensis* (Melanommatales) that share morphological traits with *Didymosphaeria*, a genus of plant pathogens in Pleosporales.

Plant cuticles

The oldest fossil evidence in plant cuticles of a host response to the presence of a fungus comes from the Mississippian of Germany (~350 Ma) (Hubers *et al.*, 2011). Pronounced cuticle rims bordering the margins of fungal thalli are interpreted as a host response suggestive of parasitism. A similar host response has been observed in a Jurassic *Sphenobaiera* (Ginkgophyta) leaf from China (~170 Ma) (**Fig. 2N**; Sun *et al.*, 2015). Cuticle alterations probably linked to a fungal colonization have also been observed in Cenozoic angiosperm leaves from Australia (~30 Ma) (Tarran *et al.*, 2016). Cuticular rims present on these leaves appear to have directed fungal hyphae away from the stomata, and thus away from the entry points into the

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leaves. *Pteropus brachyphylli* (Pleosporales) is a fossil ascomycete that occurs on leaves of a conifer from the Upper Cretaceous of Belgium (˜67 Ma). Nearly all stomata of the host leaves are occupied by the fungus, suggesting that the association was parasitic rather than saprotrophic (van der Ham and Dortangs, 2005).

Compression fossils of Paleocene conifers of the Cupressaceae and Pinaceae from Russia (˜60 Ma) show various types of damage, most of which were caused by Ascomycota (Maslova *et al.*, 2021). Fungal remains obtained through cuticle preparations of the damaged areas include hyphae, chains of conidia, various types of fruiting bodies, and dispersed spores. The diversity of Ascomycota on these Paleocene conifers is consistent with previously obtained data on the existence of these plants in a temperate humid climate with a hot summer and without a dry season. There is astonishing diversity of fungal hyphae, fruiting bodies (e.g., thyriothecia, pycnidia), and hyphopodia, mostly of microthyriaceous fungi, also on Cenozoic angiosperm leaves. The vast majority of these remains have been obtained through maceration of compression fossils (e.g., Dilcher, 1965; Bannister *et al.*, 2016). The nutritional modes of most of these fungi remain unknown; however, some authors have noted morphological similarities to present-day plant parasites and pathogens, such as *Asterina*, *Vizella*, and *Trichothyrina* (Taylor *et al.*, 2015a).
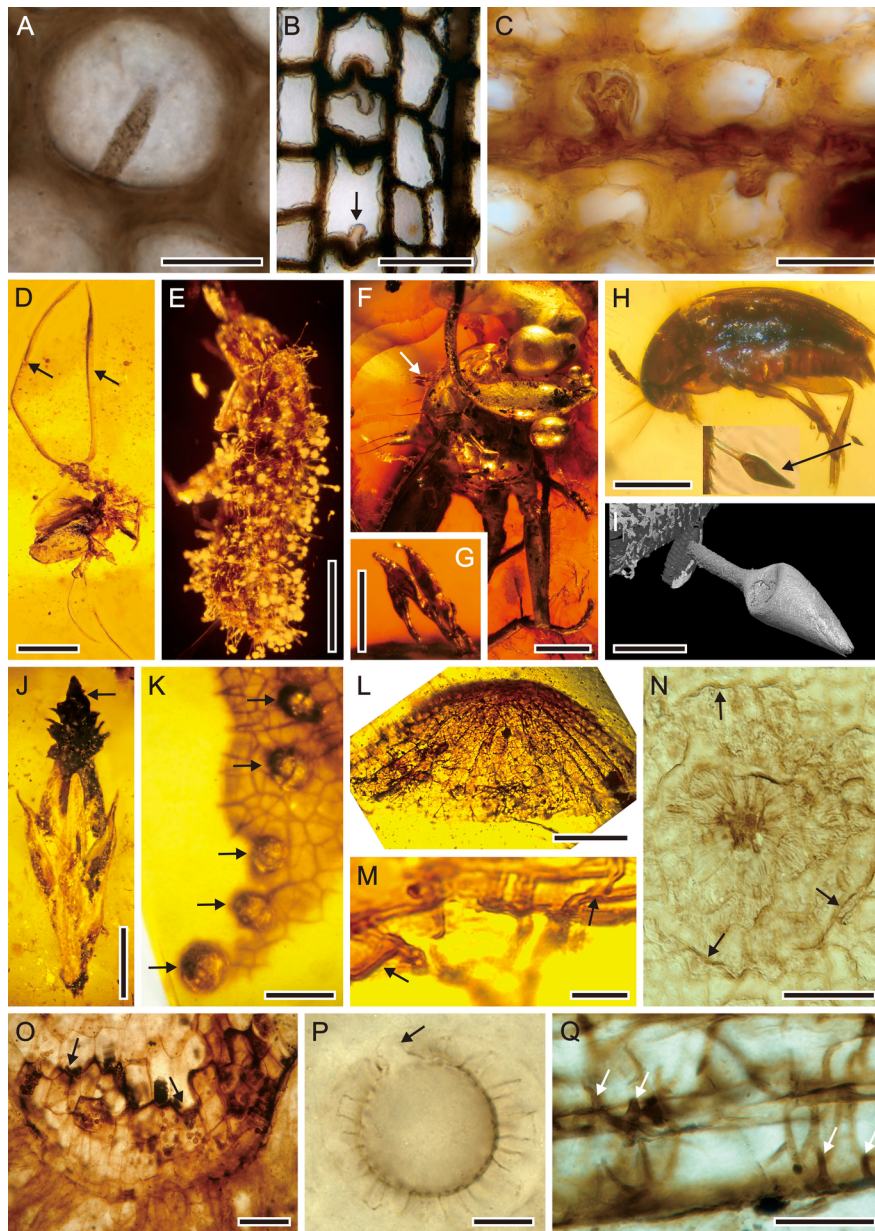
Figure 2: Examples of fossil fungal parasites: Basidiomycota, Ascomycota, and unclassified fungi. A. Callosity extending into lumen of Botryopteris antiqua cortical cell from Visean (Mississippian) chert deposits in France; fig. 1n in Krings et al. (2011a); bar 20 μm. B. Swollen tracheid wall extending into cell lumen (arrow) adjacent to ray from Upper Permian of Antarctica; fig. 2A in Harper et al. (2017); bar 25 μm. C. Transverse section of wood from Jurassic of Antarctica showing crushed vascular ray (dark line in center), with tyloses in adjacent tracheids; bar 25 μm. D. Paleoophiocordyceps coccophagus with two synnemata (arrows) arising from head of a scale insect from mid-Cretaceous Kachin amber of northern Myanmar; fig. 1A in Sung et al. (2008); bar 1.0 mm. E. Conidial heads of Aspergillus collembolorum extending from surface of a springtail from Eocene Baltic amber; fig. 2 in Dörfelt and Schmidt (2005); bar 500 μm. F. Stalk-eyed fly Prosphyracephala succini with tuft of Stigmatomyces succini (arrow) attached to thorax from Oligocene Bitterfeld amber, colour version of fig. 1 in Rossi et al. (2005); bar 1.0 mm. G. Detail of S. succini, colour version of fig. 2 in Rossi et al. (2005); bar 250 μm. H. Proptomaphaginus alleni with Columnomyces electri located on the right leg from Miocene Dominican amber; fig. 1a in Perreau et al. (2021); bar 500 μm. I. Propagation phase-contrast synchrotron X-ray microtomography (PPC-SRμCT) image of mature thallus of C. electri; fig. 5a in Perreau et al. (2021); scale bar 50 μm. J. Grass spikelet with sclerotium (arrow) of Palaeoclaviceps parasiticus from mid-Cretaceous Kachin amber of northern Myanmar; fig. 1 in Poinar et al. (2015); bar 2.0 mm. K. Angiosperm leaf portion with dorsal view of 5 pycnidia (arrows) of Palaeomycus epallelus from mid-Cretaceous Kachin amber of northern Myanmar; fig. 1 in Poinar (2020); bar 1.0 mm. L. Pileus of Palaeoagaricites antiquus overgrown by mycoparasite Mycetophagites atrebora from mid-Cretaceous Kachin amber of northern Myanmar; fig. 1A in Poinar and Buckley (2007); bar 0.5 mm. M. Mycetophagites atrebora parasitized by Entropezites patricii (arrows); fig. 1C in Poinar and Buckley (2007);

Other unidentified fungi

Very often it is impossible to determine the systematic affinities of a parasitic fungus based on fossils. For instance, three morphologically different types of endophytic fungi occur in the prostrate axes of the Rhynie chert land plant *Nothia aphylla* (Krings *et al.*, 2007b, 2007c). In spite of the exquisite preservation of the fungi, their affinities remain unclear. The association is nevertheless noteworthy because axes heavily infected by one of these fungi show a hypodermal zigzag line composed of secondarily thickened cell walls that appears to represent a specific host response effective in separating infected from uninfected tissues (**Fig. 2O**). Another fungus in *N. aphylla* triggers a host response in the form of encasement layers consisting of cell wall material that exclusively form around hyphae of this endophyte.

A truly enigmatic fossil from the Rhynie chert is *Triskelia scotlandica*, an acritarch-like structure with a prominent surface ornamentation. The form had been initially described as a green algal resting stage (Strullu-Derrien *et al.*, 2021), but the subsequent discovery of specimens that occur in situ in prominent swellings of fungal hyphae provided strong evidence that it was not algal, but rather fungal in nature (Krings, 2021). Moreover, specimens with a discharge tube suggest that *T. scotlandica* may be a zoosporangium or resting spore stage of an endoparasite (**Fig. 2P**), perhaps with affinities to holocarpic Oomycota (e.g., *Olpidiopsis*), Cryptomycota (e.g., *Rozella*), or zoosporic Fungi (e.g., *Olpidium*), in which case the hyphal swellings would be either dilatations resulting from the expansion of the parasite inside, or a host response (hypertrophy).

A geologically younger, presumably parasitic fungus of unknown affinity is *Cashhickia acuminata*, which is preserved in permineralized calamite roots from the Upper Pennsylvanian of central France (~304 Ma) (Taylor *et al.*, 2012). Infected roots contain intracellular hyphae in the outer cortex that arise from a meshwork-like mycelium extending between cortical cells. All intracellular hyphae are oriented towards the root centre. Within the cortical cells are host responses in the form of callosities that indicate the roots were alive at the time of infection (**Fig. 2Q**). Fossils similar to *C. acuminata* have been described in roots from the Triassic of the Svalbard archipelago by McLoughlin and Strullu-Derrien (2016). Other evidence of fungal parasitism in Pennsylvanian plants occurs in a *Lasiostrobus polysaccii* cone from Illinois, USA (~310 Ma) (Stubblefield *et al.*, 1984). On the inner surface of cortical cells containing fungal hyphae are peculiar swellings that appear to represent wall appositions produced by the host in response to the infection.

Septate fungal hyphae present in silicified *Agathoxylon* (Araucariaceae) wood from the Upper Cretaceous (~84 Ma) of South Africa have been compared with blue-stain fungi colonizing the wood of present-day *Pinus strobus* (Strullu-Derrien *et al.*, 2022). They represent the first documented evidence of these wood-colonizing Ascomycota in the geological record. Structures interpreted as fungal mycelia of uncertain affinity have also been found in sections of dinosaur egg shells from the Upper Cretaceous (~80 Ma) of central China (Gong *et al.*, 2008). Based on fungal morphology and the areas in the shells in which the fungi occur, it has been hypothesized that the fungi were parasitic and invaded the eggs before they became lithified.

Concluding Remarks

Fungi today master very different levels of interaction with various other organisms. They form lichens, enter into mutualistic relationships with plants and animals, occur as endophytes in virtually all land plants, and negatively affect the functions of other microorganisms, plants, animals, and even humans as parasites and pathogens (Kaishian *et al.*, 2022). Fungi probably had similar roles in the geologic past. Documenting these roles based on fossils is a challenging task, foremost because of the low preservation potential of most fungal life cycle stages, and because the majority of fungal fossils occur dispersed and are fragmented (Taylor *et al.*, 2015a). It is clear from the examples of fossil fungal parasitism presented in the sections above that the key to understanding fungi as constituents of past ecosystems is the extraordinary preservation found in certain rock deposits. While the Rhynie chert of Scotland is perhaps the prime illustration of this, there are other fossil ecosystems that have been preserved in a similar manner, but to date have received less attention (e.g.,

García Massini *et al.*, 2012; Klymiuk *et al.*, 2012; Harper *et al.*, 2016). As more information is gathered on the fungi preserved in these deposits, and as further rock deposits containing well preserved fungi are unearthed, additional examples of fungal parasitic interactions will be discovered and described. This will provide increasing opportunities to relate fossils to extant analogues to better understand the past diversity, evolutionary history, and past ecological functions of parasitic fungi.

Acknowledgments

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