

Chapter 3

Fungi as Parasites: A Conspectus of the Fossil Record



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Abstract Fungal parasites are important drivers in ecosystem dynamics today that can have far-reaching effects on the performance and community structure of other organisms. Knowledge of the fossil record and evolution of fungal parasitism is therefore a key component of our understanding of the complexity and functioning of ancient ecosystems. However, the fossil record of fungi as parasites remains exceedingly incomplete for several reasons. This chapter provides selected fossil examples of (putative) fungal parasites in association with land plants, algae, other fungi, and animals, and elucidates the inherent problems that often render interpretation of even the most exquisite fungal fossils difficult. Of all the potential levels of fungal interaction, parasitism is perhaps the most difficult to demonstrate in the fossil record. Different lines of evidence obtained from both the host and fungus are required to safely discriminate parasitic fungi from saprotrophs and even mutualists when examined in fossils.

Keywords Chert · Disease symptom · Host response · Interaction · Mycoparasitism · Preservation · Rhynie chert

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3.1 Introduction

Fungi occur in next to every ecosystem of the world, colonizing numerous substrates and performing multiple functions (Treseder and Lennon 2015; Dighton and White 2017). As carbon heterotrophs, they have, by necessity, evolved several different nutritional modes and mastered various levels of cooperation with, and exploitation of, other organisms to acquire carbon (Lewis 1973). Many fungi degrade complex organic compounds such as lignin and cellulose and, through this recycling, are important in returning minerals to the soil and CO₂ to the atmosphere (Hatakka 2005; Baldrian and Valášková 2008). Others partner with certain types of algae and cyanobacteria to form lichens (Nash 2008), while still others enter into mycorrhizal associations with non-vascular and vascular land plants (Brundrett and Tedersoo 2018). Fungi have also evolved mutualistic associations with animals; some even thrive within the animal, in anaerobic environments (Orpin and Joblin 1997; Dollhofer et al. 2015). On the other hand, what has been termed the “dark side” of the fungal Kingdom (Taylor et al. 2015) is that, as parasites and pathogens, fungi negatively affect the performance of other microorganisms, plants, animals, and even humans and are causative agents of many diseases (e.g., Sharon and Schlezinger 2013; Köhler et al. 2015; Hall and Noverr 2017; Möller and Stukenbrock 2017).

Parasitic fungi live and derive the majority of their nutrients at the expense of other organisms that are alive at the time of infection (Deverall 1969; Zelmer 1998). Biotrophic parasitic relationships represent physiologically balanced systems, in which the parasite coexists with its host for an extended period of time, whereas necrotrophic parasites kill host tissue and then feed saprotrophically on the dead remains (Glazebrook 2005; Delaye et al. 2013). However, it is known today that, while this subdivision is generally accurate, the actual situation is more complex because many fungi behave as both biotrophs and necrotrophs, depending on the conditions in which they find themselves or the stages of their life cycles (Glazebrook 2005).

The origin of the true fungi is estimated at between 660 Ma and up to 2.6 Ga ago based on molecular clock data and some paleontological evidence (for details on early fungal fossils, see Krings et al. 2017c; Loron et al. 2019; Bonneville et al. 2020), and the divergence of the fungal-animal lineage from the plant lineage at between 780 Ma and up to 2.5 Ga ago (e.g., Altermann and Schopf 1995; Martin et al. 2003; Taylor and Berbee 2006; Blair 2009; Lücking et al. 2009; Sharpe et al. 2015; Bengtson et al. 2017; Berbee et al. 2017). The nutritional mode of the common ancestor of the true fungi remains elusive. However, early-diverging branches of the fungal stem lineage include the Aphelida, which are parasites of planktonic algae (Letcher et al. 2013, 2017; Karpov et al. 2014, 2017), and the animal-endoparasitic Cryptomycota and Microsporidia (Keeling and Fast 2002; James et al. 2006; Jones et al. 2011a, b; Vávra and Lukeš 2013; Han and Weiss 2017; Bass et al. 2018), suggesting that the evolutionary arms race of fungi as parasites of other organisms is of ancient origin (Anderson et al. 2010). Unfortunately, none of these early-diverging lineages (except possibly Aphelida; see Krings and Kerp 2019) have

been documented in the fossil record, due probably to the simple fact that it is very difficult to recognize these life forms as fossils because of their diminutive size (e.g., Garcia 2002). Moreover, they lack structural features that could be used to safely identify them, with one possible exception. Xenomas (or xenoparasitic complexes; see Chatton 1920; Weissenberg 1968) are tumor-like growths caused by a variety of parasitic protists and fungi, including Microsporidia. They can occur on numerous organisms such as oligochaetes, insects, and crustaceans; however, they are predominantly found on fishes (Matos et al. 2003; Lom and Dyková 2005; Weiss and Becnel 2014). It might therefore be worth looking for such abnormal growths also in well preserved fossil fish specimens, although it will most likely be very difficult to positively identify the actual causative agent(s) (e.g., Petit 2010; Petit and Khalloufi 2012).

Fungal parasites can have profound influence on the performance and community structure of other organisms, and thus are important players in ecosystem functioning today (e.g., Marcogliese 2004; Skerratt et al. 2007; Sime-Ngando 2012; Frenken et al. 2017). Knowledge of their fossil record, evolution, and the roles they played in biological and ecological processes in the past is therefore a key component of our understanding of the complexity and functioning of ancient ecosystems. However, the fossil record of fungi as parasites remains incomplete and is often difficult to interpret for several reasons as explained in the following section (Fig. 3.1a, b).

3.2 Identifying Fungal Parasitism in the Fossil Record

3.2.1 *Finding Fossil Fungi*

The success of finding fungi from the geologic past heavily relies on the way the fossils are preserved (Krings et al. 2012), even more so if nutritional modes and interactions with other organisms are to be resolved, too. Cherts certainly represent the most important sources of evidence of fossil fungi (Taylor et al. 2015). Chert deposits occur at various points in geologic time and typically represent an extremely dense microcrystalline or cryptocrystalline type of sedimentary rock (Laschet 1984; Hesse 1989). Some cherts may be fossiliferous and demonstrate not only three-dimensional and structural preservation of the organisms (sometimes even in situ), but often also details of individual cells and subcellular structures. As a result of faithful fossil preservation, cherts provide an ideal matrix from which to extract information about fungi and fungal interactions with other organisms. Moreover, cherts provide the only source of direct evidence of the fungal world within the context of ecosystem complexity, versatility, and dynamics. Foremost among the chert deposits yielding evidence of fungi is the Lower Devonian (~410 Ma) Rhynie chert from Aberdeenshire, Scotland (Trewin and Kerp 2017; Garwood et al. 2020), that contains representatives of all major fungal lineages except Basidiomycota (Taylor et al. 2004; Krings et al. 2017a). The Rhynie chert is perhaps best known

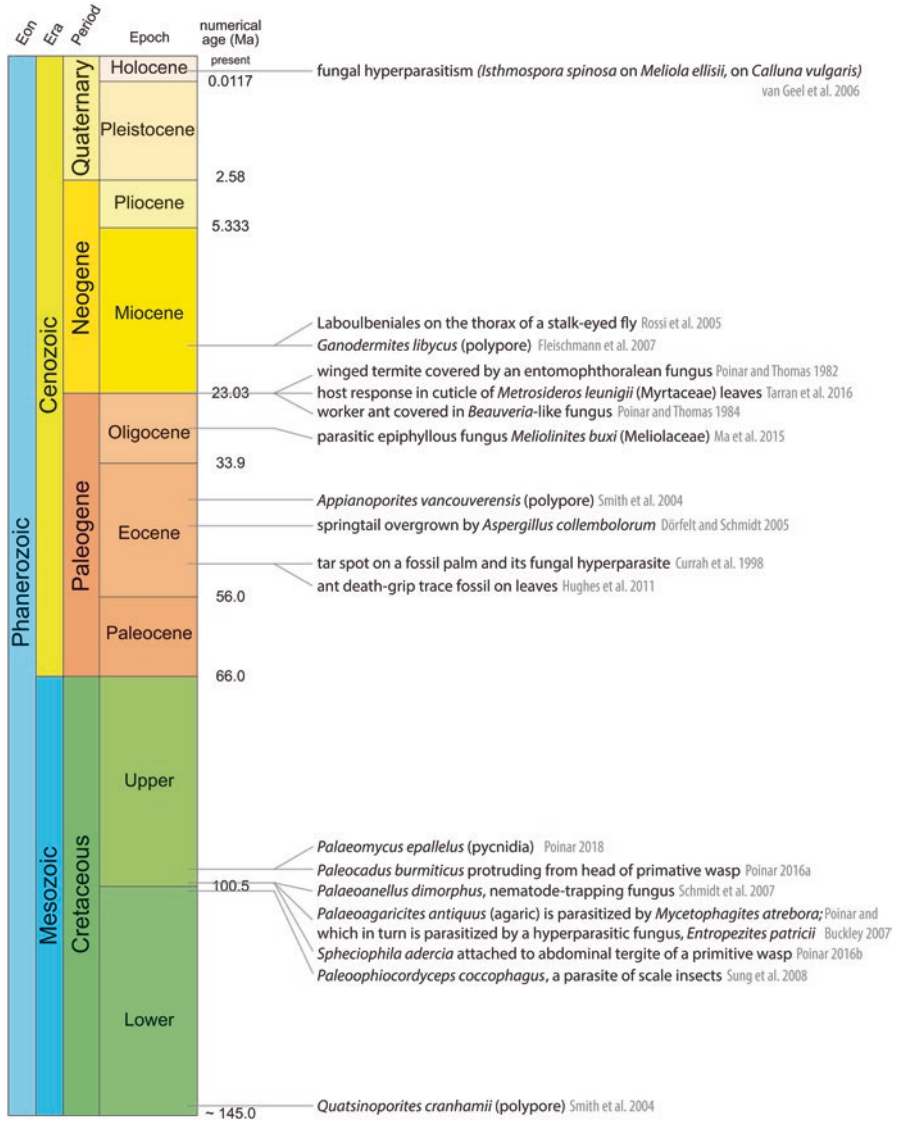


Fig. 3.1 (a) Selected fossils of fungi as parasites plotted on the Cretaceous to Holocene stratigraphic chart. Stratigraphic chart based on Cohen et al. (2013). (b). Selected fossils of fungi as parasites plotted on the Devonian to Jurassic stratigraphic chart. Stratigraphic chart based on Cohen et al. (2013)

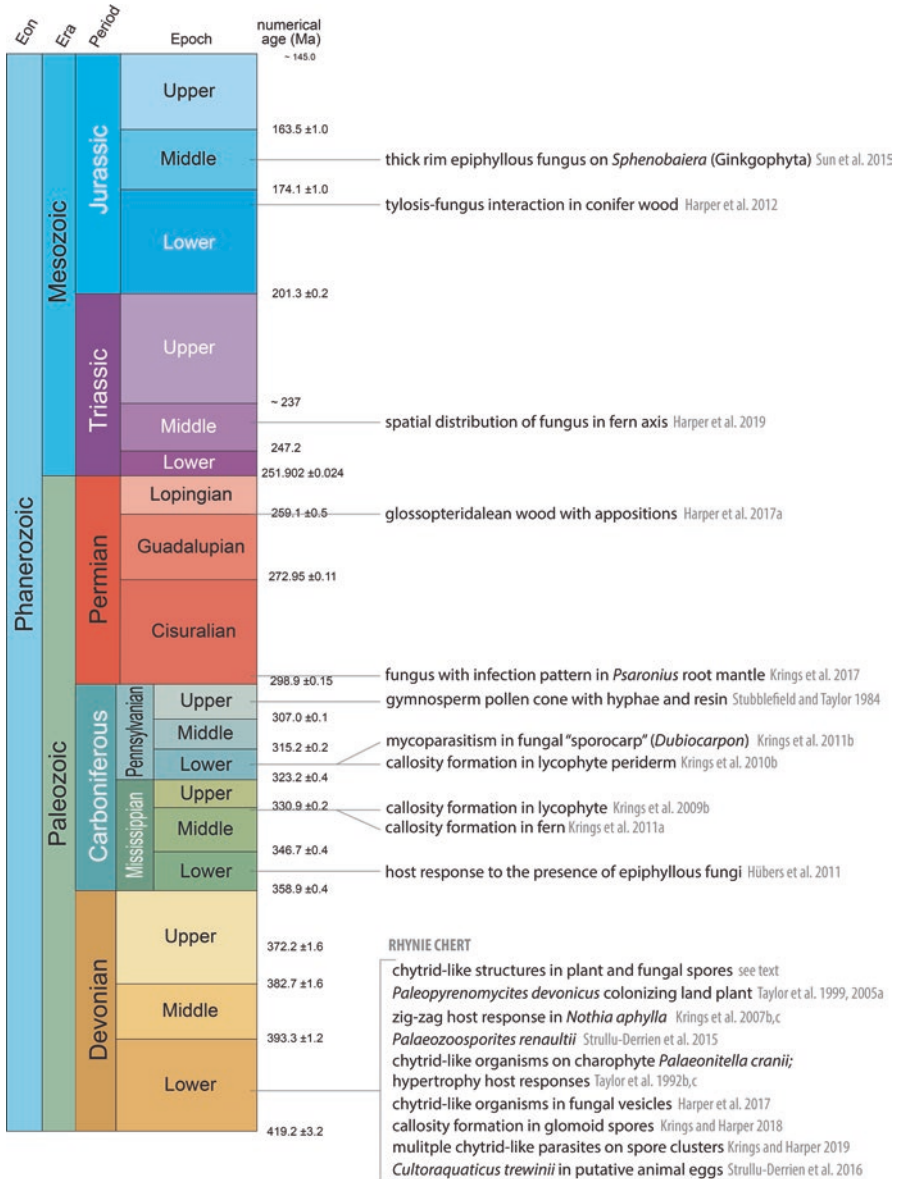


Fig. 3.1 (continued)

among mycologists for several specimens of fungi that are exquisitely preserved in situ together with their host organisms and demonstrate the existence of different types of fungal associations and interactions, including arbuscular mycorrhizas (Taylor et al. 1995, 2005b; Brundrett et al. 2018; Walker et al. 2018), and parasitism of land plants, algae, other fungi, and possibly animals (see below).

Permineralized peat and coal balls are two other rock matrices that may contain abundant fossil evidence of fungi (e.g., Williamson 1878, 1880, 1883; Stubblefield and Taylor 1988; Harper et al. 2015, 2016; Slater et al. 2015). However, the organic remains in these matrices are usually compacted and partially to largely degraded, and hence render it more difficult, but not impossible, to safely identify fungal interactions (e.g., Knoll 1985; Krings et al. 2014). Various types of fungi and fungal interactions, as well as indirect evidence of fungal activities such as microborings and chemical traces (Golubic et al. 1975; Marynowski et al. 2013), have also been exquisitely preserved by other preservation modes, including silicified wood, animal hard parts, and amber (Taylor et al. 2015). However, the ecological configuration of the community in which these organisms lived is often less completely known.

3.2.2 *Tracing Fungal Parasitism in the Fossil Record*

Parasitic fungi exploit carbon sources that are, by definition, alive at the time of infection. However, fossils represent snap-shots in time, with no long-term and follow-up studies available to determine the condition of the host before and after fungal colonization. This raises the question how, if at all, parasitic fungi can be recognized as fossils and distinguished from epi-/endophytes and saprotrophs? In other words, how can we tell if a fossil containing evidence of the presence of a fungus was (part of) a living organism at the time of fungal colonization, and how can we determine whether the fungus thrived at the host's expense?

If the host organism is preserved in pristine condition, then this could mean that it was alive at the time of fungal colonization. Conversely, a host that is tattered, fragmented, and shows tissue disruption and disintegration might have been in the process of decay when colonized. Nevertheless, it is not normally possible to determine whether fragmentation and tissue destruction were initiated before or after the fungus colonized the host, or are preservation artifacts (Krings et al. 2009b, 2010b). Somewhat more reliable is perhaps the spatial distribution of fungi within the host. A fungal distribution pattern within an intact host that reflects forced entry and a consistent pathway of colonization (e.g., along the vascular bundles in plants; see Harper et al. 2019), or is restricted to certain body parts or tissue types of the host, is suggestive of colonization of a living host, while colonization of dead and decaying matter more likely results in random fungal distribution.

Structural features suggestive of parasitism and pathogenicity in fossil organisms include disease symptoms and host reactions such as cell and tissue alteration or local necroses (e.g., Mendgen et al. 1996; Pearce 1996). In rare instances, the fungal perpetrator and the disease symptom/host response even co-occur, providing additional lines of direct evidence (Taylor et al. 1992b, c; Krings and Harper 2018). For example, a common type of host response to fungal intrusion is the formation of callosities, which are inwardly directed projections consisting of newly synthesized cell wall material that encase the parasite's penetration device, and thus may reduce or inhibit nutrient extraction from the host (Akai 1959; Aist 1976, 1977). Callosities

have been observed in fossil plants belonging to several different lineages, including lycophytes (Krings et al. 2009b, 2010b), sphenophytes (Taylor et al. 2012), ferns (Krings et al. 2011a), and gymnosperms (Stubblefield et al. 1984), but have also been recorded in fossil fungi (Hass et al. 1994). Several of the latter records even provide evidence of a biotrophic relationship, in which the parasite was contained to a certain extent by the callosities, but was still able to grow and extract nutrients, while the host remained demonstrably viable for an extended period of time while being parasitized (Krings and Harper 2018). However, not all parasites elicit host responses, and it may therefore be difficult, if not impossible, to determine the nutritional modes of asymptomatic fossil fungi associated with intact hosts. For example, commonly present within structurally preserved plants throughout the Phanerozoic are small fungal reproductive units (e.g., spores, sporangia, cleistothecia, pycnidia) and mycelia that are randomly distributed; no evidence of host responses has been found (Magnus 1903; Stubblefield and Taylor 1986; LePage et al. 1994; García Massini et al. 2012; Klymiuk et al. 2013). Some of these fungal remains, including ascomycotan hyphae, pseudothecia, pycnidia, and hyphomycetous spores, have nonetheless been interpreted as parasites because their (presumed) modern equivalents are parasites of plants (LePage et al. 1994; García Massini et al. 2012). Finally, many of the host responses known in extant organisms (e.g., chemical responses; see Swain 1977; Langenheim 1994) cannot be identified in fossils or are easily mistaken for natural decay (e.g., necroses; see Van Loon et al. 2006).

Evidence of fungal parasitism in ancient ecosystems also occurs in the form of fungal structures that are found as detached fossils (i.e. with no information on the host available), but that can be directly compared to modern fungal taxa known to be parasites. For example, polyporous fungi or polypores (Basidiomycota) today thrive as saprotrophs in decaying wood or as parasites and perpetrators of diseases in conifers and hardwoods (Blanchette 1991; Ryvarden 1991; Schwarze et al. 2000). The Cretaceous and Cenozoic record of these fungi is quite extensive and consists primarily of basidiocarps (conks) that usually can be assigned to modern families and genera with some confidence based on morphology and spore structure (e.g., Smith et al. 2004; Fleischmann et al. 2007). The inventory of fossil polypores suggests that these fungi were widely distributed and diverse in Neogene and Quaternary forest paleoecosystems and significant in delignification processes and as pathogens of woody plants.

Of all the potential levels of interaction between fungi and other organisms, parasitism is perhaps the most difficult to demonstrate in the fossil record. Without a combination of different lines of evidence obtained from both the host and fungus, this type of interaction cannot be discriminated from saprotrophism and even mutualism when examined in fossils (Taylor et al. 2009). Excellent examples illustrating this problem occur in the form of structurally preserved remains of *Lepidodendrales* (arborescent lycophytes) from the Carboniferous of central Europe that contain diverse assemblages of fungal mycelia and reproductive units (Krings et al. 2007a, 2009b, 2010b, 2011d; summarized in Fig. 3.2). Some of these fungi have been interpreted as parasites based on morphology and distribution (Fig. 3.2j) or the presence of host responses (Fig. 3.2f), while others were probably mutualists (mycorrhizal

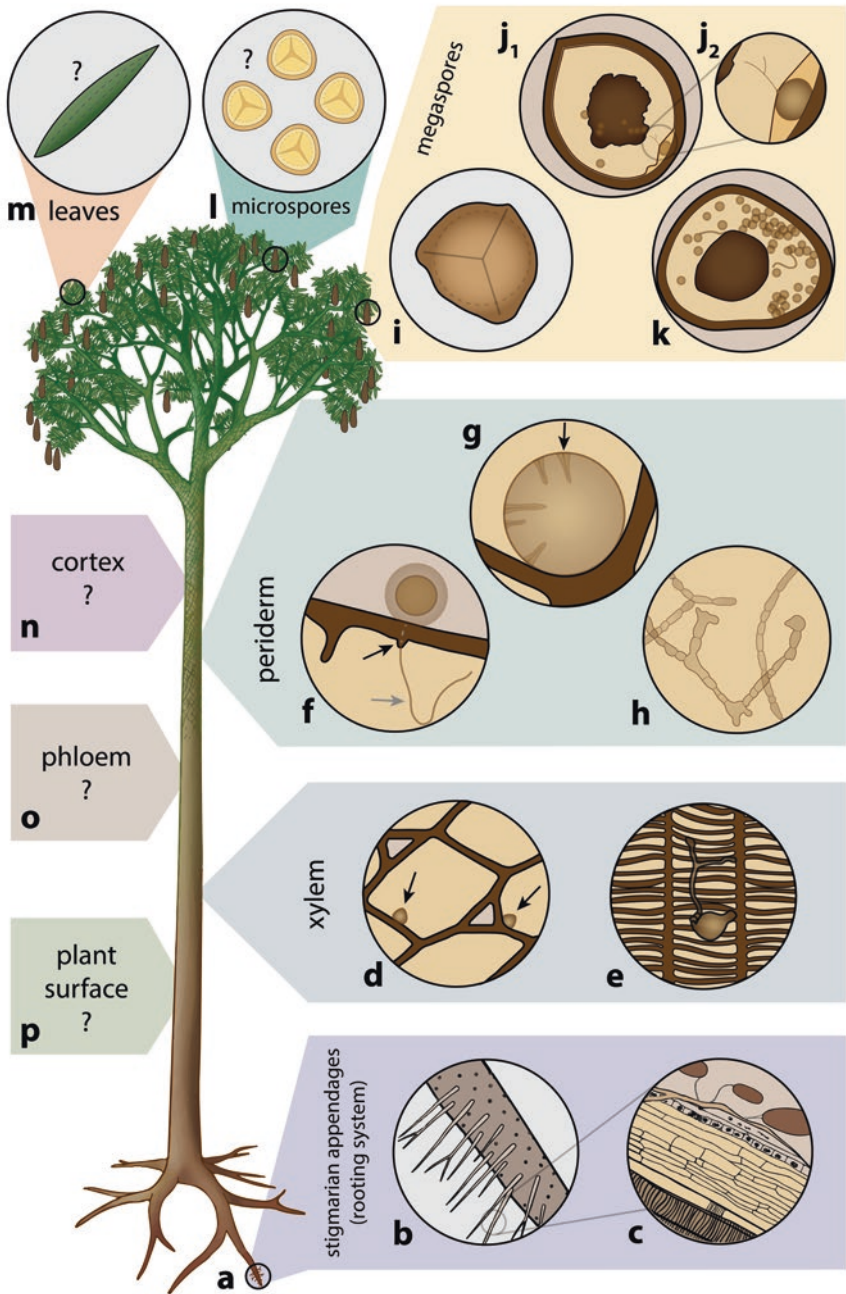


Fig. 3.2 Synopsis of documented evidence of fungi associated with Carboniferous arborescent lycophytes (*Lepidodendrons*). Some of these fungi, especially those eliciting host responses, were probably parasites, whereas others were mutualists or saprotrophs. (a) Stigmarian appendages

fungi; Fig. 3.2a–c) because their morphology parallels that seen in present-day mycorrhizal fungi (Glomeromycota). However, the nutritional modes of most fungal remains associated with Carboniferous Lepidodendrales remain elusive.

3.3 Fossils of Fungi as Parasites

Fossil evidence of fungi has been documented throughout the Phanerozoic (Taylor et al. 2015), but it is fungal associations with land plants and other fungi from the Early Devonian, Carboniferous, Triassic, and Cenozoic that have to date been examined more systematically. As a result, there are several well-documented examples of fungal parasites of plants and other fungi from these periods of geologic time. On the other hand, the fossil record of parasitic fungi of animals is scanty throughout for several reasons (see Sect. 3.3.4 below). The purpose of this chapter is to portray the fossil record of fungi as parasites. In the sections below, we have not attempted to provide exhaustive coverage, but rather have selected fossil examples of (putative) fungal parasites in association with plants (i.e. land plants and a few algae), other fungi, and animals, with a slight emphasis on the Rhynie chert, and have elucidated the inherent problems that often render interpretation of even the most exquisite fungal fossils difficult.

3.3.1 Fungal Parasites of Land Plants

Land plants today are exposed to a wide variety of different fungi, many of which are parasites (Cannon and Hawksworth 1995). Although one can only speculate about the events during the terrestrialization of plants some 515–485 Ma ago (Morris et al. 2018), the conquest of the terrestrial realm has likely been profoundly influenced by interactions with saprotrophic, parasitic, and mutualistic fungi

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Fig. 3.2 (continued) (below-ground rooting system). **(b)** Higher magnification of Fig. 3.3a, focusing on appendages. **(c)** Higher magnification of Fig. 3.3b, showing mycorrhizal association in cortex of appendage; based on fig. 2a in Krings et al. 2011d. **(d)** Chytrid-like sporangia (arrows) attached to tracheid walls; based on pl. II, 1 in Krings et al. 2009b. **(e)** Pear-shaped sporangium with narrow, aseptate subtending hypha growing along inner surface of tracheid; based on fig. 1j in Krings et al. 2007a. **(f)** Putative chytrid resting sporangium with primary rhizoidal axis (gray arrow) and early stage in callosity development (black arrow); note another, more prominent callosity to left; based on fig. 4j in Krings et al. 2010b. **(g)** Glomeromycotan spore with callosities (arrow); based on pl. III, 10 in Krings et al. 2009b. **(h)** Septate, irregularly swollen hyphae; based on figs 1e, f in Krings et al. 2010b. **(i)** Surface view of megaspore. **(j₁)** Megaspore with large chytrid zoosporangium between wall layers; based on pl. I, 7 in Krings et al. 2009b. **(j₂)** Higher magnification of chytrid, showing rhizoidal system extending into spore lumen; based on pl. I, 8 in Krings et al. 2009b. **(k)** Megaspore containing numerous spheres (?zoosporangia of a polycentric chytrid) and tenuous hyphae; based on pl. I, 1 in Krings et al. 2009b. **(l–p)** Lepidodendraleans organs, tissues, and reproductive structures for which there is currently no documented evidence of associated fungi

(Chisholm et al. 2006). To become effective as a plant parasite, a fungus must access the plant interior, either by actively penetrating the surface or by finding, recognizing, and entering through wounds or natural openings such as stomata (Hoch and Staples 1991; Knogge 1996; Mendgen et al. 1996; Szabo and Bushnell 2001). Alternatively, a fungus on the plant surface may produce substances that kill (parts of) the host and subsequently feed on the decaying tissue (Berrocal-Lobo et al. 2002; Dean et al. 2012). Fungal parasites today are found on all parts of plants, including roots, stems, leaves, reproductive structures, and pollen grains (Money 2016). Interestingly, there are also some 400 species of plants that parasitize fungi and exploit them as their principle source of carbon (Leake 2005; Merckx 2013), but that's another story.

3.3.1.1 Early Land Plants

Several (putative) fungal parasitic interactions with early land plants have been reported from the Lower Devonian Rhynie chert, including chytrid-like fungi interpreted as parasites that are associated with the spores of several early land plants (Fig. 3.3a) (Kidston and Lang 1921; Harvey et al. 1969; Illman 1984; Taylor et al. 1992a), and *Paleopyrenomycites devonicus*, a perithecial ascomycete colonizing the land plant *Asteroxylon mackiei* (Taylor et al. 1999, 2005a). Although no host response has been found, Taylor et al. (2005a) submit that *P. devonicus* colonized *A. mackiei* while it was alive based on the fact that the perithecia often occur within the substomatal chambers of the host plant, with the ostioles directly beneath the stomata to facilitate spore dissemination (Fig. 3.3b). Moreover, some of the perithecia contain remains of other fungi believed to represent mycoparasites (Taylor et al. 2005a: fig. 41). Another example of fungal parasitism has been described in rhizomes of the land plant *Nothia aphylla* (Krings et al. 2007b, c), but this time the fungal intruders elicit host responses in the form of characteristic cell and tissue alterations. A hypodermal zigzag line composed of secondarily thickened cell walls characterizes heavily infected rhizomes (Fig. 3.3c). This line marks the outer

Fig. 3.3 (continued) from ray (r), with fungal hyphae (white arrows) penetrating through tylosis (Jurassic); University of Kansas paleobotanical collection slide TS-GIX-SB-036-01; scale bar = 20 μ m. (g) Fungus extending into, and subsequently forming coralloid branching systems within, lumen of *Psaronius* root mantle cell (Permian); pl. IV, fig. 3 in Krings et al. 2017b; scale bar = 20 μ m. (h) Ascoma surrounded by incompletely thickened ring (arrowheads) formed by host leaf cuticle (Jurassic); pl. II, fig. 15 in Sun et al. 2015; scale bar = 100 μ m. (i) Higher magnification of Fig. 3.2h, focusing on thickened rim; scale bar = 20 μ m. (j) Chytrid-like inclusions in pollen grain of *Striatopodocarpites multistriatus* (Permian); fig. 2D in Aggarwal et al. 2015; scale bar = 20 μ m. (k) Angiosperm leaf portion with 5 pycnidia (arrows) of *Palaeomyces epalleus* in Myanmar amber (Cretaceous); fig. 1 in Poinar 2018; scale bar = 1 cm. (l) *Milleromyces rhyniensis* chytrid zoosporangium extending through cell surface (arrowhead) of the charophyte *Palaeonitella cranii* (Devonian); color version of fig. 10 in Taylor et al. 1992b; scale bar=10 μ m. (m) Two *Palaeonitella cranii* cells showing extensive enlargement (hypertrophy host response; h) when compared with normal cells at base (Devonian); color version of fig. 26 in Taylor et al. 1992b; scale bar = 100 μ m. (n) Longitudinal section of normal cells (n) of *Palaeonitella cranii* (Devonian); color version of fig. 1 in Taylor et al. 1992b; scale bar = 100 μ m

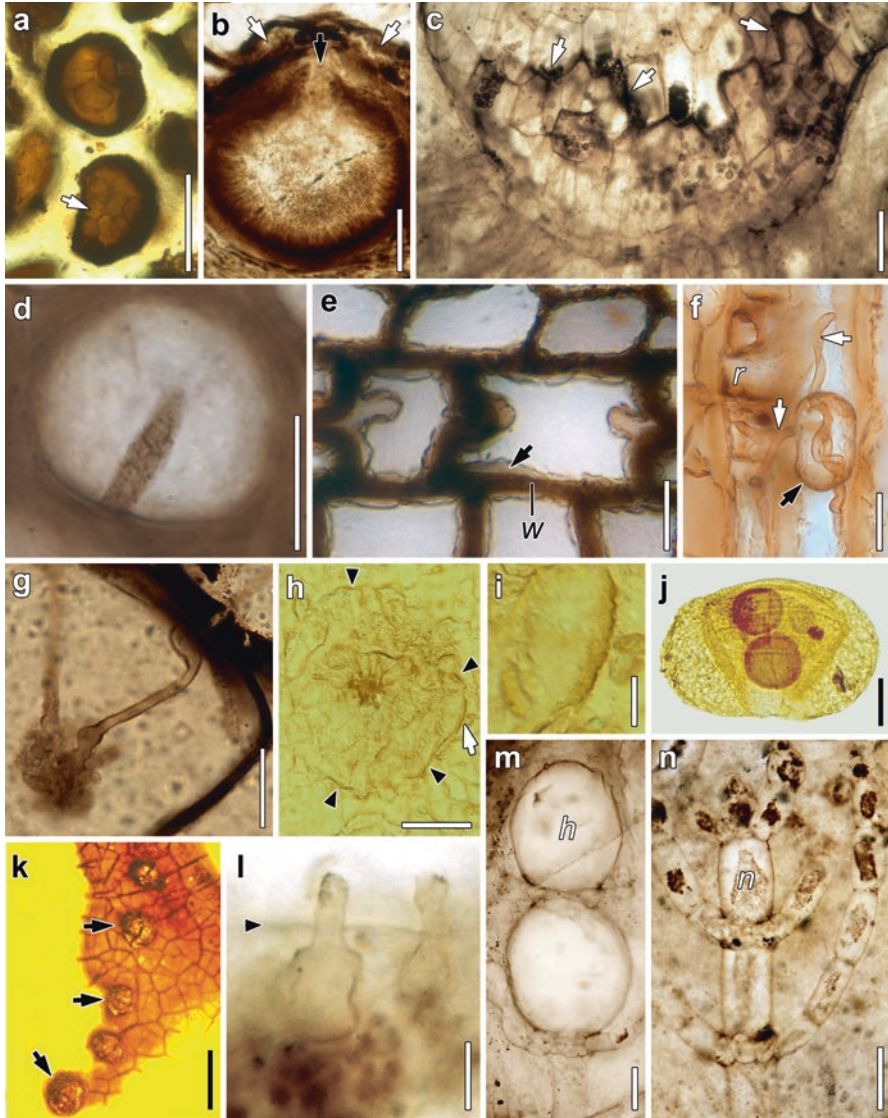


Fig. 3.3 Fossils of fungus-land plant and fungus-alga (putatively) parasitic interactions (detailed explanations in the text). (a) Endobiotic fungi (arrow) in spores of *Horneophyton lignieri* (Devonian); Munich collection, slide SNSB-BSPG 1964 XX 24; scale bar = 50 μm . (b) *Paleopyrenomycites devonicus* perithecium with ostiole (black arrow) in sub-stomatal chamber; white arrows indicate guard cells (Devonian); color version of fig. 7 in Taylor et al. 2005a; scale bar = 100 μm . (c) Zig-zag host response (arrows) in *Nothia aphylla* (Devonian); color version of fig. 2e in Krings et al. 2007c; scale bar = 100 μm . (d) Callosity extending into lumen of *Botryopteris antiqua* cortical cell (Carboniferous); color version of fig. 1n in Krings et al. 2011a; scale bar = 20 μm . (e) Glossopteridalean cell walls (w) with appositions and wall swellings (arrow) (Permian); fig. 2E in Harper et al. 2017a. (f) Conifer wood with tylosis (black arrow) extending

boundary of cells containing one of the intrusive fungi, and hence probably represents a host response effective in separating infected from uninfected tissues. Moreover, several of the infected rhizomes contain peripheral regions that are devoid of cells. Krings et al. (2007c) suggest that this tissue degradation may have been effective as a defense mechanism based on the fact that, in some extant plants, phytopathogenic microorganisms are deterred by programmed cell death around the infected areas that inhibit the microbes from spreading (Hammond-Kosack and Jones 1996; Veronese et al. 2003; Glazebrook 2005; Anderson et al. 2010).

Clusters of globose vesicles attached to branching hyphae characterize *Palaeozoosporites renaulatii*, another fungus in *Asteroxylon mackiei* (Strullu-Derrien et al. 2015). These authors suggest that *P. renaulatii* was a parasite with affinities to the Chytridiomycota, and report, but do not illustrate, a host response in the form of secondarily thickened cell walls. We hold the opinion that *P. renaulatii* represents a cluster of glomoid spores; however, Strullu-Derrien et al. (2015) reject affinities to the Glomeromycota because “hyphal structures...narrow progressively as they branch”, which is in fact a common morphology within the Glomeromycota (Walker et al. 2018).

3.3.1.2 Plant Structural Alterations in Response to Fungal Intrusion

The previous section provided examples of structural defense mechanisms effective in slowing down or deterring “unwanted” fungal colonization or spreading that were in place in early land plants by the Devonian. A little later, in the Carboniferous, vascular plants showed host responses against fungal intrusion in the form of callosities (also called appositions, lignotubers, or papillae, among other terms; see Stubblefield et al. 1984) that closely resemble defenses employed by plants today (Akai 1959; Pearce 1996; Schwarze et al. 2000; Schulze-Lefert 2004). One example of callosity formation occurs in a rachis of the filicalean fern *Botryopteris antiqua* (Krings et al. 2011a) from the Mississippian of France (Fig. 3.3d), while another has been reported in a lycophyte (*Lepidodendron* sp.), also from the Mississippian of France (Krings et al. 2009b: pl. II, figs 12–17). The latter specimen even contains two different types of callosities, namely a narrow form that does not show evidence of a penetration canal, and a larger form that may be straight or curved and usually contains a central penetration canal. The presence of two different types of callosities may be evidence that this host recognized two different intruders. Although putative chytrid zoosporangia occur in the same tissue samples as the callosities, they have not been found in organic connection, and thus cannot be positively linked to one another. Other documented evidence of callosity formation in Carboniferous plants includes lycophyte periderm from the Pennsylvanian of Great Britain (Krings et al. 2010b: fig. 4J–M) and sphenophyte rootlets from the Pennsylvanian of France (Taylor et al. 2012: pl. I, fig. 1, pl. II, fig. 9, pl. III, figs 1–3). Finally, the gymnosperm pollen cone *Lasiostrobus polysacci* from the Carboniferous of North America contains septate fungal hyphae in the cortex and microsporophylls (Stubblefield et al. 1984). The host cells are sometimes accompanied by opaque

matter interpreted as resin that might represent a host response. In addition, on the inner surface of the cells are swellings suggestive of some type of wall apposition. Although fungi today frequently target the nutritional density in reproductive structures of plants (Vujanovic et al. 2009), the preceding is one of the few persuasive fossil examples of this fungal strategy.

3.3.1.3 Host Responses in Woody Plants

Woody plants have a long evolutionary and antagonist history with fungi (Schwarze et al. 2000; Vacher et al. 2008). Wood-degrading fungi encompass a heterogeneous assemblage of basidiomycetes and ascomycetes, and constitute one of the major drivers of carbon cycling in forest ecosystems today (Lindahl et al. 2002; van der Heijden et al. 2008). Some investigators have suggested that wood-rotting fungi begin their life cycle as parasites, but then, once the host is dead, switch to saprotrophism (Garrett 1970; Lewis 1973). Evidence of decay attributable to fungi is frequently encountered in fossil wood; however, studies focusing on fossil fungal wood degradation are rare (see Harper et al. 2016 for a review; Wan et al. 2017), and documented examples of (partially) decayed fossil wood containing well preserved fungal remains are even rarer. Harper et al. (2017a) report on decaying glossopterid wood from the Permian of Antarctica that contain fungal remains, symptoms of white pocket-rot decay, arthropod remains, and host-responses in the form of appositions (Fig. 3.3e). Appositions that occur at sites of infection or attempted penetration by a fungus (Pearce 1996) are composed of material and components not normally present in cell walls (e.g., phenolic compounds, callose, silicon) plus normal cell wall components, especially suberin (Pearce and Holloway 1984), that can partially to fully occlude cell lumina to contain or prevent further spreading of the intruder (Aist 1976, 1983). The lumina of some of the tracheids in the glossopterid wood are completely sealed by some opaque matter (Harper et al. 2017a: fig. 2F, J), while the cell walls of other tracheids are swollen and partially occlude the lumen (Harper et al. 2017a: fig. 2I). Both types of cell lumen occlusion might represent strategies of passive defense against antagonistic fungal expansion within the wood. Conspicuous swellings in extant wood have been interpreted as a reaction or barrier zone to penetration by delignifying fungi (Schwarze and Baum 2000). Similar appositions have also been documented in other Permian woods from Antarctica (Stubblefield et al. 1985; Stubblefield and Taylor 1986; Weaver et al. 1997). Other structures in fossil woods believed to represent host responses to fungi include ergastic substances and resin (Stubblefield et al. 1985; Gnaedinger et al. 2015). However, it is difficult to specifically attribute these formations to fungal parasitism because they are also known to be produced in response to damages caused by fire or mechanical injury (e.g., Shrimpton 1973; Blanchette and Biggs 1992). In rare cases, such as in a Jurassic conifer wood from Antarctica, the fungus is in direct contact with a possible host response in the form of tyloses (Fig. 3.3f) (Harper et al. 2012). Tyloses are bladder- or sac-like outgrowths (protoplasmic bulges) on parenchyma cells that extend into adjacent conducting cells (tracheids, vessels) via pits in

the cell walls and, in this way, can block the dead conducting cells to counteract the spreading of phytopathogenic organisms. They may be filled with various substances (tannins, gums, resins, etc.) as a result of physical damage or parasitic activity (Collins and Parke 2008; Feng et al. 2013; for an extensive review, see De Micco et al. 2016). Harper et al. (2012) hypothesize that the Jurassic tyloses formed a physical barrier to prevent the fungus from spreading. The morphology and pattern of colonization suggest that the fossil shares similarities with various extant Ascomycota, including sap-stain, blue-stain, and dark-stain fungi that are pathogens of various conifers (see Ballard et al. 1982; Hessburg and Hansen 1987). Last, in some extant gymnosperms, including *Pinus*, the number of resin ducts in the xylem may increase as a result of a fungal infection (Martín-Rodríguez et al. 2013). This is certainly a structural feature that can also be recognized in fossil wood. In addition, certain types of tissue disruption are caused by parasitic plants invading stem tissue, but may also be the result of fungal infection (Gomes and Fernandes 1994; do Amaral and Ceccantini 2011). However, no evidence of such tissue disruptions in fossil wood has been produced to date, which may be due in part to the fact that most investigators of fossil wood lack a search image for such structures, or perhaps attribute the disruptions to a different cause.

3.3.1.4 Host Plant Preservation and Fungal Distribution

While the evidence used to infer fungal parasitism in the fossils surveyed in the preceding sections largely consists of fossilized host responses, there is one example of a fossil fungus-land plant interaction that deserves special mention because in this case host plant preservation and fungal distribution within the host have been used to infer the nutritional mode of the fungus (Barthel et al. 2010; Krings et al. 2017b). This fungus occurs in a silicified Early Permian *Psaronius* root mantle from Germany, and displays a consistent pattern of host cell colonization that includes the formation of swellings effective in pushing a hyphal tip through the host cell wall and multi-branched structures remotely resembling arbuscules and certain haustoria that probably served in nutrient extraction or exchange (Fig. 3.3g). The different tissues of the host root mantle, including the fragile root aerenchyma, are exquisitely preserved, suggesting that the roots were intact, and thus probably alive at the time of fossilization. Moreover, the strictly intracellular growth pattern of the fungus seems implausible for a saprotroph that extends through moribund or dead and decaying plant tissue. However, the fungus did apparently not trigger any host response or disease symptom, suggesting it may have been a harmless endophyte or mild parasite, which extracted some nutrients, but not in an amount sufficient enough to cause notable damage. It is also possible, however, that the fungus was well adapted to its mode of life, rendering it “invisible” to the immune response of the plant, although this is virtually impossible to test in fossils.

3.3.1.5 Epiphyllous Fungi

The cuticle, a waxy coating of all aerial plant parts before secondary growth (Pollard et al. 2008), is the first line of physical defense and barrier against pathogenic fungi (Martin 1964; Serrano et al. 2014). However, many fungi have evolved strategies to breach this barrier, pass into the interior of the plant, and spread out (Kolattukudy 1985; Nicholson and Epstein 1991), while others grow on the plant surface and locally penetrate the cuticle to extract nutrients from the underlying tissues (Mendgen and Deising 1993; Tucker and Talbot 2001). Still other fungi reside on the plant surface without ever entering the host (e.g., Hongsanan et al. 2016). Fungi that grow on leaves are termed epiphyllous, regardless of whether they are parasites or just surface residents. Since leaf cuticles often survive fossilization and diagenesis relatively unaltered, they can be freed from the surrounding rock matrix and cleared through chemical maceration processes and studied in transmitted light (Kerp 1990; Kerp and Krings 1999). Fossil leaf cuticles provide information on epidermal anatomy, including cell pattern and stomatal morphology, but may also contain information on leaf-associated fungi. There are numerous reports of fossil epiphyllous fungi, mostly microthyriaceous types, for which details of the fungus and the host are known (e.g., Dilcher 1965; Elsik 1978; Phipps and Rember 2004; Limaye et al. 2007; Bannister et al. 2016). For the most part, the nutritional modes of these fungi remain unknown; some authors indicate there are morphological similarities to modern plant pathogens such as *Asterina*, *Vizella*, and *Trichothyria*, thus inferring the nutritional mode as parasitism (Ellis 1977; Phipps 2007; Khan et al. 2015). Evidence suggestive of a host response to the presence of an epiphyllous fungus in the form of a rim of thickened cuticle has been described in a Jurassic *Sphenobaiera* (Ginkgophyta) leaf from China (Fig. 3.3h, i) (Sun et al. 2015: pl. II, fig. 15). Other examples of cuticle alterations interpreted as a host response include *Metrosideros leunigii* (Myrtaceae) leaves from the Eocene-Oligocene of Australia that appear to have produced cuticle thickenings to divert the growth of the hyphae of a fungal parasite (Tarran et al. 2016: fig. 8A). Another interesting epiphyllous fungus, *Meliolinites buxi* (Meliolaceae), occurs on the cuticles of Oligocene *Buxus* leaves from China (Ma et al. 2015: fig. 3A–H). These authors offer the hypothesis that *M. buxi* is a parasite based on the thickening and twisting of epidermal cell walls in the host leaf, along with the parasitic life style of the extant Meliolaceae. The earliest fossil evidence in plant cuticles of a host response to the presence of epiphyllous fungi occurs in the form of impressions of rosette-like fungal thalli on a dispersed plant cuticle of unknown systematic affinity from the Carboniferous of Germany (Hübers et al. 2011). The host reaction occurs in the form of extensive cutinizations around the thallus margins. The thalli are interpreted as hyphopodia or some other epiphyllous structure of a parasitic fungus that facilitated host attachment and penetration.

3.3.1.6 Dispersed Remains and Plant Pathogens

The dispersed microfossil record yields a plethora of information on fungi and fungal interactions in the geologic past (Kalgutkar and Jansonius 2000). For example, small ‘spherules’ that are sometimes attached to the outer surface or occurring within the body of Carboniferous to Cenozoic land plant spores and pollen grains obtained through palynological sampling (Fig. 3.3j) (e.g., Daugherty 1941: pg. 43; Phipps et al. 2000: pl. 2, figs 5 and 6; Aggarwal et al. 2015: figs 2–4) are mostly interpreted as remains of fungi and compared to modern pollen-colonizing Chytridiomycota. On the other hand, Mesozoic and Cenozoic non-pollen palynomorph (NPP) assemblages frequently contain spores of microthyriaceous and other fungi that are morphologically similar to the spores produced by certain present-day fungal parasites and pathogens (e.g., Höhnelt 1924; Van Geel and Anderson 1988; Kalgutkar and Jansonius 2000; Van Geel 2002; Singh and Tripathi 2010; Kürschner et al. 2015; Schumilovskikh et al. 2015; Roth and Lorscheitter 2016).

There are certain fungal plant pathogens such as rusts (Pucciniomycetes), smuts (Ustilaginomycetes), and leaf spot diseases (e.g., *Alternaria*, *Cercospora*) (Agrios 2005) that are widespread today but rare or absent in the fossil record (reviewed in Taylor et al. 2015). This is surprising since innumerable fossils of leaves are available, and one would expect to find at least some showing evidence of these fungi in the form of lesions or galls (Callow and Ling 1978). However, there is likely a collection bias for undamaged leaves, thus probably discarding leaves with fungal remains (Taylor and Krings 2010; Krings et al. 2012). While no convincing evidence of fossil rusts has been documented, there are several reports of dispersed spores which are similar in morphology to extant *Puccinia*, *Gymnosporangium*, and *Uromyces* (Bradley 1931; Wolf 1969; Kalgutkar and Jansonius 2000). Documented evidence of fossil smuts is in a similar situation. Most of the reports of fossil smuts have later been dismissed or remain inconclusive. For example, fossils interpreted as spore clusters similar to *Ustilago* have been reported in degrading plant tissue from Deccan Intertrappean cherts (Cretaceous) from India (Kapgade 2016). However, none of the specimens figured display features of sufficient clarity to allow assignment to any group of fungi with confidence. The dispersed spore type *Ustilago deccanii* from the same beds was initially reported as a spore of a smut fungus (Chitale and Yawale 1976, 1978), but has subsequently been transferred to *Inapertisporites*, a taxon used for fossil amerospores of Fungi Imperfecti (Kalgutkar and Jansonius 2000). No information is available on the nutritional modes of these fossil fungi. In yet another case, small spores in *Saururus tuckerae* anthers from the Eocene of North America were initially identified as a smut fungus (Currah and Stockey 1991; LePage et al. 1994), but are now thought to represent minute pollen grains produced by the flower (Smith and Stockey 2007). Another important plant pathogen today are the leaf spot fungi (Agrios 2005). There are numerous reports of specks and dots on Mesozoic and Cenozoic plant remains (surveyed in Tiffney and Barghoorn 1974), and even one report of a putative Paleozoic leaf spot (Wang 1997). More recently, Poinar (2018) reported well preserved pycnidia, formally described as *Palaeomyces epalleus*, on an angiosperm leaf preserved in

mid-Cretaceous Myanmar amber (Fig. 3.3k). The author suggests that, although there are no modern equivalents to the pycnidia, they are most similar to leaf spot-producing members of the coelomyceteous fungi. Because the taxonomy and identification of modern rusts, smuts, and other fungal disease causative agents in plants is largely dependent on micromorphological characters of the spores, careful palynological preparations and/or examination of permineralized angiosperms are likely the keys to more accurately resolving the fossil history of these pathogens.

Another approach that has been employed to better understand the geologic history of fungus-plant parasitic interactions is to look for the host plants. For example, the Erysiphales (Ascomycota), or powdery mildews, produce cleistothecia with very characteristic appendages and are associated with specific angiosperm hosts (Braun 1987). Consequently, the presence of certain angiosperm hosts during the Late Cretaceous has been used as indirect evidence of the initial radiation of this group of fungi (Takamatsu et al. 2010; Takamatsu 2013). However, we feel that this approach, although interesting, is also problematic (see De Baets and Littlewood 2015). In the absence of a fossil record, how do we know if the ancestors of present-day (hyper-)host-specific fungal parasites parasitized the ancestors of the present-day hosts and elicited the same disease symptoms? Nevertheless, it should be possible to identify members of the Erysiphales on the surface of fossil leaf cuticles since many of the reproductive structures are highly ornamented.

3.3.2 *Fungal Parasites of Algae*

Algae are critical elements in modern aquatic ecosystems, not only in producing oxygen for other aquatic life, but also in serving as primary producers of organic matter at the base of the food chain (Round 1981). Some are pivotal in the biology of aquatic animals, while others are major structural contributors to the formation of reefs (Coates and Jackson 1987; Weiss and Martindale 2017). The fossil record of algae is extensive and dates back to the Late (perhaps even Middle) Proterozoic (Coniglio and James 1985; Graham and Wilcox 2000; Butterfield 2015; Bengtson et al. 2017). Fungal parasitism of algae today is common, and some fungi enter into complex relationships with their algal hosts (e.g., Kohlmeyer 1979; Kohlmeyer and Kohlmeyer 1979; Gachon et al. 2010). One interesting example consists of endolithic microscopic algae inhabiting coral skeletons as a convenient shelter and endolithic fungi colonizing the corals primarily for food and feeding on both the coral polyps and the endolithic algae (for details, see Le Campion-Alsumard et al. 1995; Golubic et al. 2005). Parasitic fungi can have a profound impact on freshwater and/or marine phytoplankton and algal populations (Ibelings et al. 2004; Kagami et al. 2007; Wang and Johnson 2009; Gleason et al. 2011); however, documented evidence of fungal parasites of fossil algae is very rare. This dearth of evidence is due probably to the fact that the most common modes of preservation of fossil algae (e.g., as cysts, calcareous skeletons, or thallus impressions) are not conducive to the preservation in recognizable form of microbial parasites associated with these

organisms *in vivo*. It is also possible that some researchers have noted fungi occurring with their algae fossils, but did not bother to address them because they were merely interested in the algae and/or lacked the expertise to adequately describe fungal remains.

Perhaps the best fossils of fungal parasites of algae come from the Lower Devonian Rhynie chert, together with the earliest evidence of hypertrophy (i.e. increase in cell size as a result of an external stimulus) in the fossil record. Chytrid-like organisms are common parasites of the Rhynie chert charophyte *Palaeonitella cranii* (Taylor et al. 1992b, c). One of these organisms, *Milleromyces rhyniensis*, is characterized by an endobiotic zoosporangium extending out from the charophyte cell wall (Fig. 3.31). At the base of the zoosporangium is a rhizoidal system. Other chytrid-like organisms associated with *P. cranii* include *Lyonomyces pyriformis* and *Krispiromyces discoides*, which differ from one another in thallus morphology. Both *M. rhyniensis* and *K. discoides* are associated with hypertrophic host cells (Fig. 3.3m), which grow to approximately five times the diameter of normal cells (Fig. 3.3n), and thus prove that colonization occurred while the host was alive. This same pattern in cell increase in response to chytrid parasitism has been reported in the modern genus *Chara* (Karling 1928), a distant relative of *P. cranii*.

3.3.3 Fungal Parasites of Other Fungi

The term mycoparasitism is used to describe the interfungal interrelationships of a fungus parasite and a fungus host (Barnett 1963; Jeffries and Young 1994). There are numerous examples of mycoparasitism in the fossil record, the majority of which come from the Lower Devonian Rhynie chert.

3.3.3.1 Rhynie Chert Interfungal Interactions

Rhynie chert evidence of interfungal associations ranges from fungal mycelia and reproductive units in the lumen of other fungal reproductive units (Kidston and Lang 1921; Krings et al. 2009a, 2010a, 2015, 2016), to fungal hyphae enveloping and subsequently penetrating fungal vesicles (Krings and Taylor 2014b), to fungal reproductive units developing in glomeromycotan vesicles (Fig. 3.4a) (Harper et al. 2017b). Moreover, numerous monocentric and polycentric chytrid-like organisms have been described as intruders of fungal hyphae and spores. Most of these organisms consist of epibiotic sporangia and rhizoidal systems extending into the host spore lumen (Fig. 3.4b) (Taylor et al. 1992a; Krings and Taylor 2014a; Krings and Harper 2019). Other chytrid-like intruders of fungal spores are found between particular wall layers of fungal spores or occupying the spore lumen (Hass et al. 1994). Unfortunately, the majority of fungi associated with other fungi in the Rhynie chert cannot be identified

as to their nutritional mode because there is no observable host response. Moreover, larger sample sets of specimens displaying consistent patterns of such associations are relatively rare. Spectacular exceptions include one particular type of glomoid spore located in degrading land plant axes that contains evidence of (simultaneous) colonization by three different intrusive fungi (Krings and Harper 2018). In this study, the authors report massive callosities that occur around the intrusion filaments of a chytrid-like parasite with epibiotic sporangia, while at the same time the penetration hyphae of another fungus can extend into the same spore without triggering a host response. Moreover, several of the spores show large numbers of short, inwardly directed projections, each consisting of a short hyphal branch of a third fungus encased in a callosity of host wall material (Fig. 3.4c). It should be noted that it is exceedingly rare to find the causative agent preserved in direct contact with the callosity (or any host response); typically, only evidence of the host response is found (Fig. 3.4d).

There are several reports of fungal mycelia and reproductive units occurring on the surface of or within other fungi also from geologically younger deposits (e.g., White and Taylor 1989: pl. 2, figs 1, 2, 6; 1991: pl. II, figs 1 and 3, pl. III, figs 1–5; Taylor et al. 1994: pl. I, fig. 2; Taylor et al. 2005c: fig. 7; Krings et al. 2011c: fig. 1L; Krings and Taylor 2012: pl. I, fig. 4; Harper et al. 2015: pl. 1, figs 13 and 14; White et al. 2018: pl. IV, figs 3–6). However, as with the Rhynie chert specimens, there is mostly no direct evidence of parasitism in the form of a host response.

3.3.3.2 Fossil Fungal “Sporocarps”

One group of fungal fossils that have received considerable attention are the so-called “sporocarps”, enigmatic structures, mostly from the Carboniferous and Triassic, that are composed of a walled cavity enveloped in an investment of interlacing or tightly compacted hyphae (surveyed in Krings et al. 2013; Taylor et al. 2015). In some specimens, the cavity is empty, but more often contains one to several spheres that have been the basis for several hypotheses regarding the affinities of these structures. One interprets them as cleistothecia and suggests affinities with the Ascomycota based on specimens containing one large sphere believed to represent an ascus that in turn contains several smaller spheres interpreted as ascospores (Stubblefield and Taylor 1983; Stubblefield et al. 1983). An alternative interpretation views the large sphere as a zygospore, and the entire structure accordingly as a reproductive structure (i.e. a mantled zygosporangium) of a member of the zygomycetous fungi (Pirozynski 1976; Taylor and White 1989). If this latter interpretation is accurate, then the smaller spheres found within the large sphere in some specimens would represent some type of mycoparasite. There is an increasing body of circumstantial evidence to corroborate the latter hypothesis. For example, a “sporocarp” specimen from the Carboniferous of Great Britain contains not only spherical structures, but also hyphae forming appressorium-like swellings at the contact region with host walls (Fig. 3.4e, f) (Krings et al. 2011b).

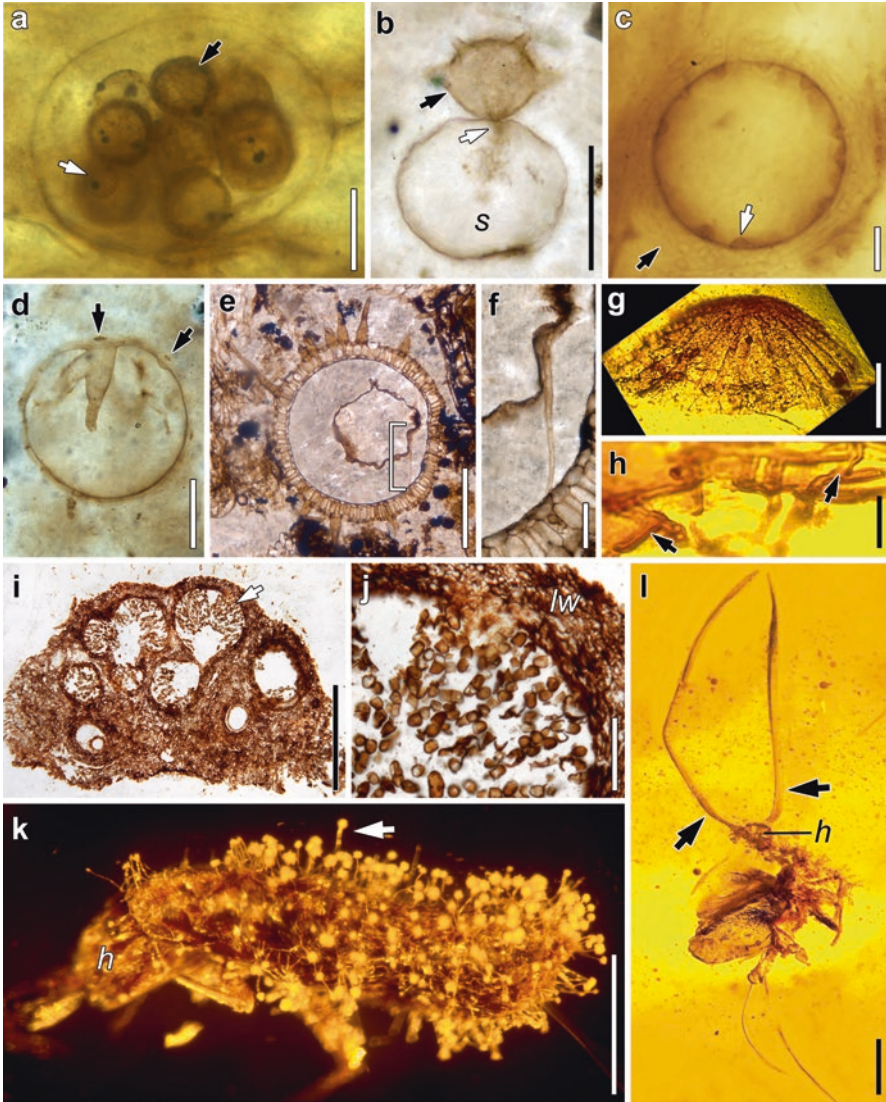


Fig. 3.4 Fossils of fungus-fungus and fungus-animal (putatively) parasitic interactions. (a) Thick-walled (black arrow) and smaller thinner-walled propagules (white arrow) of fungal intruder in glomeromycotan vesicle (Devonian); fig. 2, 5 in Harper et al. 2017b; scale bar = 20 μm . (b) *Illmanomyces corniger* zoosporangium (black arrow) with four discharge tubes and endobiotic rhizoidal system (white arrow) extending into lumen of host spore (s) (Devonian); color version of fig. 2f, g in Krings and Taylor 2014a; scale bar = 100 μm . (c) Glomeromycotan spore enveloped in a compact, multi-layered hyphal sheath and showing numerous penetration sites (white arrow) of another, parasitic fungus (black arrow) (Devonian); fig. 3F in Krings and Harper 2018; scale bar = 10 μm . (d) Massive, branched callosity in a glomeromycotan spore (Devonian); note parasite penetration sites on spore surface (arrows); Munich collection, slide SNSB-BSPG 2017 XXXII 1; scale bar = 50 μm . (e) Overview of fungal sporocarp *Dubiocarpon* sp. with mycoparasite (bracket) (Carboniferous); color version of fig. 1a in Krings et al. 2011b; scale bar = 250 μm . (f) Detail of

3.3.3.3 Hyperparasitism

A parasite that infects a host which is parasitizing a third organism is termed a hyperparasite (Parratt and Laine 2016). One of the oldest gilled mushrooms, *Palaeoagaricites antiquus*, comes from Myanmar amber that is Early Cretaceous in age (Fig. 3.4g) (Poinar and Buckley 2007). This fossil consists of a portion of a cap, 2.2 mm in diameter. Especially interesting is that this fossil agaric is parasitized by a mycoparasite, *Mycetophagites atrebora*, which in turn is parasitized by a hyperparasitic fungus, *Entropezites patricii* (Fig. 3.4h). A structurally preserved ascomycete, *Paleoserrenomyces allenbyensis* from the Eocene Princeton chert, occurs in leaf tissue of the palm *Uhlia allenbyensis* (Fig. 3.4i) (Currah et al. 1998). The fungus is composed of multiple locules lined by thin-walled hyphae. Present in some of the locules are globose ascomata interpreted as hyperparasites. The hyperparasite, formally described as *Cryptodidymosphaerites princetonensis* (Fig. 3.4j), shares structural details with certain present-day species in *Didymosphaeria*, a plant pathogen of multiple hosts that is included in the Pleosporales (Aptroot 1995). Last, an interesting report by Van Geel et al. (2006), which demonstrated the potential of examining multiple host–parasite interactions among organisms in the fossil record, noted the subfossil occurrence of *Isthmospora spinosa*, a hyperparasite of various genera within the Meliolaceae. Specimens were recovered from a Holocene bog and demonstrated the tripartite relationship between the host *Calluna vulgaris* (heather) and the parasitic fungus *Meliola ellisii*, which is in turn parasitized by *I. spinosa*.

3.3.4 Fungal Parasites of Animals

There is a diverse suite of fungi today that thrive as facultative and/or obligatory parasites of invertebrates and vertebrates (Ainsworth et al. 1973); some are also the causative agents of mild to severe diseases (Góralaska and Błaszowska 2015). Although there are fungal infections that elicit abnormal growth or tissue



Fig. 3.4 (continued) Fig. 3.3e, focusing on bracketed area, showing hypha of a parasite entering sporocarp cavity and extending to sac-like structure; color version of fig. 1C in Krings et al. 2011b; scale bar = 50 μm . (g) Pileus of *Palaeoagaricites antiquus* preserved in amber and covered with the mycelium of the mycoparasite *Mycetophagites atrebora* (Cretaceous); fig. 1a in Poinar and Buckley 2007; scale bar = 500 μm . (h) Mycoparasite *Mycetophagites atrebora* parasitized by the hyperparasite *Entropezites patricii* (arrows) (Cretaceous; fig. 1C in Poinar and Buckley 2007; scale bar = 20 μm). (i) Section of stroma of *Paleoserrenomyces allenbyensis* with endoparasite (arrow) in locules (Eocene); color version of fig. 13 in Currah et al. 1998; scale bar = 500 μm . (j) Section of *Paleoserrenomyces allenbyensis* locule (lw) containing asci of endoparasite *Cryptodidymosphaerites princetonensis* (Eocene); color version of fig. 15 in Currah et al. 1998; scale bar = 50 μm . (k) Conidial heads of *Aspergillus collebolorum* (arrow) attached to the surface of a springtail, head = h (Eocene); fig. 2 in Dörfelt and Schmidt 2005; scale bar = 500 μm . (l) *Paleoophiocordyceps coccophagus* showing two synnemata (arrows) arising from head (h) of a scale insect (Cretaceous); fig. 1 in Sung et al. 2008; scale bar = 500 μm

destruction in hard parts such as bones, tests, and shells (Meyers 1990; Stewart 1993; Cook et al. 2003), most host responses and disease symptoms (mycoses) that can develop in animals in response to fungal infections occur in the soft parts of the body, in non-mineralized tissues that are readily degraded by bacteria and other microorganisms. Because soft tissue preservation in animals is exceedingly rare in the fossil record (Allison and Briggs 1993), there is only a narrow chance for finding fossil evidence of fungal parasitism and pathogenicity in animals.

3.3.4.1 Rhynie Chert

Although the documented record of animals from the Rhynie chert is quite extensive and diverse (e.g., Anderson and Trewin 2003; Dunlop and Garwood 2017), there is only a single report to date of an ostensible interaction of fungi with animals. The co-occurrence of a chytrid-like organism, *Cultoraquaticus trewinii*, with peculiar spherules interpreted as resting eggs of the branchiopod crustacean *Lepidocaris rhyniensis*, is purported to represent compelling evidence of a role for chytrids in a mycocoloop (Kagami et al. 2014) that transferred nutrients obtained from a substrate to the crustacean (Strullu-Derrien et al. 2016). The spherules, which are of varying diameters and bear spines of varying lengths (Strullu-Derrien et al. 2016: fig. 4D, E, G, H, J, K), are compared to the resting eggs of the modern *Linderiella santarosae* (Anostraca) (Thiéry and Fugate 1994).

3.3.4.2 Amber Inclusions

Specimens enshrined in amber dominate the fossil record of parasitic and pathogenic fungi on insect hosts (Boucot and Poinar 2010). One report describes *Paleocadus burmiticus*, a member of the Eccrinales, which were previously thought to be zygomycetous fungi but are today considered members of the Mesomycetozoa (Opisthokonta), producing two types of sporangiospores on different thalli that protrude from a primitive wasp preserved in Cretaceous amber from Myanmar (Poinar 2016a). Present-day Eccrinales do not infect members of the Hymenoptera, suggesting a wider host range during the Mesozoic. Geologically younger (Eocene) Baltic amber has also yielded exquisite examples of insect colonization by fungi, including a springtail overgrown by conidiophores of the fossil fungus *Aspergillus collemborum* (Fig. 3.4k) (Dörfelt and Schmidt 2005). The authors suggest that *A. collemborum* was a facultative parasite because modern *Aspergillus* species usually are facultative parasites or saprotrophs. Another example of fossil *Aspergillus* comes from Dominican amber and occurs in the form of well-preserved tufts of catenulate chains of conidia covering the surface of the abdomen of a fly (Thomas and Poinar 1988). Although the authors do not comment on the nutritional mode of the fungus, it is likely that, similar to *A. collemborum*, it was a facultative parasite. Another example of fungal parasitism of animals in Dominican amber is a winged termite covered by an entomophthoralean fungus (Poinar and Thomas 1982). The

authors conclude that the fungus was parasitic based on the presence of conidia budding along with smaller secondary conidia adjacent to the main mycelial mat, a characteristic of modern Entomophthorales (Prasertphon 1963). In addition, a fossil member of the Laboulbeniales, which are obligate ectoparasites, has been discovered on the thorax of a fossil stalk-eyed fly (*Prospyracephala succini*) in Eocene Baltic amber (Rossi et al. 2005). An enigmatic fossil from Myanmar amber, *Spheciophila adercia*, also attributed to the Laboulbeniales, consists of a thallus with numerous perithecia and antheridia that is attached to the abdominal tergite of a primitive wasp (Poinar 2016b). This author suggests that *S. adercia* belongs to an extinct lineage because there are no other extant thallus-forming ectoparasitic fungi. Finally, an example of a special form of fungal parasitism, predation (carnivory), has also been fossilized in amber (Schmidt et al. 2007). Several specimens of a fungus that used hyphal rings as trapping devices occur in Late Cretaceous amber from France together with the fungus' prey, small nematodes. The fossil nematode-trapping fungus cannot be assigned to any recent taxon of carnivorous fungi, but rather suggests that different groups occupied this ecological niche in the Cretaceous and that trapping devices evolved independently multiple times in the course of Earth history. Predatory fungi catch microorganisms using a remarkable array of trapping devices; however, their primary ecosystem function appears to be that of wood decay, and hence they are saprotrophs that attack other organisms as sources of nitrogen to supplement a primarily carbohydrate (woody) diet (Barron 2003).

3.3.4.3 Cordycipitaceae Interactions with Arthropods

Fungi in the family Cordycipitaceae (Ascomycota) enter into several types of fascinating parasitic interrelationships with insects and other arthropods that usually, but not always, result in the death of the arthropod host (Sung et al. 2007). For example, *Ophiocordyceps unilateralis* enters ants and eventually takes control over the host's brain activities (commonly named 'zombie' infection) and manipulates its behavior. The manipulated ant, which becomes a so-called parasite-extended phenotype (Hughes 2014), is forced by the fungus to move to so-called death locations (usually plant parts) that represent ideal spots for fungal spore dispersal (de Bekker et al. 2014, 2015; Shang et al. 2015). Arrived at its death location, the fungus forces the ant to bite into the substrate (e.g., a leaf or small plant axis) and remain in that position until death arrives. These bites leave a characteristic scar in the plant known as the 'death-grip' (Anderson et al. 2009). Although it is exceedingly rare to capture multiple stages of fungal life histories in the fossil record, there are three documented examples of fossils displaying stages of the Cordycipitaceae life cycle. One includes an ant preserved in Dominican amber that is covered in a fungus morphologically similar to certain present-day species in *Beauveria* (Cordycipitaceae), which are obligate endoparasites (Poinar and Thomas 1984). The sexual stages (or teleomorphs) of *Beauveria*, where known, are species of *Cordyceps* (Rehner et al. 2011). The second example is a spectacular specimen of a fungus formally described as *Paleoophiocordyceps coccophagus*, which is a parasite of Cretaceous scale

insects (Fig. 3.41) (Sung et al. 2008). This fossil provides the oldest compelling evidence of animal parasitism by fungi, and is characterized by several synnemata emerging from the head of the host. However, there is no evidence indicative of host behavior manipulation. The third example is a trace fossil that occurs in the form of well-preserved death-grip scars in Eocene (48 Ma) angiosperm leaves from the Messel pit in Germany (Hughes et al. 2011b). The characteristic scars are remarkably similar to the death-grip scars produced by some present-day fungus-infected carpenter ants (Hughes et al. 2011a).

3.3.4.4 Dinosaurs

Some of the first animals that come to mind when we think of life in the geologic past are dinosaurs. There are limited reports of pathogenic fungi associated with dinosaur remains. One possible example is a *Tyrannosaurus rex* mandible that shows multiple erosive lesions (Rega and Brochu 2001; Wolff et al. 2009; but see Rothschild and Martin 2006; Watson and Rothschild 2021 for alternative interpretations). The authors postulate that such abscesses may eventually form large, localized caseous masses which would be susceptible to fungal parasitic infections, similar to those seen in modern crocodylians (Huchzermeyer 2003). Another interesting example includes fossilized Cretaceous sauropod dung from India that contains an array of fungal remains, including forms that are known to be plant parasites (e.g., *Colletotrichum*), thus indicating that some sauropods ate the leaves of fungus-infected plants as food (Kar et al. 2004). Other sauropod coprolites from India contain several different fungal remains characteristic of present-day plant pathogens, including *Colletotrichum*-like acervuli (leaf spot, red rot disease), *Erysiphe*- and *Uncinula*-like cleistothecia (powdery mildew), and black spot-producing microthyriaceous ascostromata (Sharma et al. 2005). A single specimen of an infected grass spikelet with similarities to extant *Claviceps purpurea* (commonly known as ergot) has been identified in Cretaceous Myanmar amber (Poinar 2015). The authors suggest that, if ergot-infected grass was ingested by herbivore animals, they may have felt the effects of the psychotropic compounds produced by the fungus in a similar way to that seen in livestock animals today (Bove 1970). Finally, numerous large coprolites from three different horizons (spanning at least 6 Ma) within the Upper Cretaceous Two Medicine Formation of Montana have revealed that some herbivorous dinosaurs sometimes consumed large amounts of fungus-infected wood (Chin 2007). This author states that decaying wood would have provided an assortment of nutritious foods, including cellulose from the wood, fungi, other microbes, and detritivorous invertebrates.

Some investigators even have suggested that fungal parasites may have contributed to the demise of the dinosaurs at the end of the Cretaceous. Several dinosaur eggs have been reported with mycelium-like structures or endolithic fungi in the eggshells (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. A very provocative hypothesis regarding the extinction of dinosaurs relating to fungal infections by Casadevall

(2005) suggests that the purported unprecedented accumulation of fungal spores after the global plant die-off at the end of the Cretaceous would have altered the usual balance of power, namely by delivering such massive concentrations of spores into the lungs of the dinosaurs that their immune defenses were overwhelmed. If the body temperature of dinosaurs was lower than that of mammals, then these reptiles might well have been susceptible to fungal infection, perhaps giving an advantage to early mammals to survive the KT-extinction event. While there are numerous censures surrounding this hypothesis, including the debate as to whether the spores that accumulated indeed are fungal in origin (Hochuli 2016) and the ongoing discussion of whether dinosaurs were warm- or cold-blooded (e.g., Grady et al. 2014), it nevertheless opens an interesting and thought-provoking new perspective on the end of the age of dinosaurs.

3.4 Concluding Remarks

Deciphering the roles of fungi colonizing other organisms in natural environments today is challenging because of the difficulties in making field observations (Jeffries 1995). Even more challenging is the analysis of fungal relationships from the geologic past. The lack of information that can be used to safely assign fungal fossils systematically is one of the principle problems exacerbating the assessment of fossil fungal associations (Krings et al. 2016). As we have tried to exemplify in this chapter, however, there are also persistent uncertainties with regard to determining the fungal nutritional modes that are connected to the inherent limitations of the fossil record (Fig. 3.5). Based on the examples of (assumed) fungal parasitism from the fossil record presented throughout the sections of this chapter, certain patterns nonetheless begin to emerge:

1. Sublime preservation (e.g., in amber or chert) is a precondition to identify direct features such as fungal mycelia spreading along consistent pathways in intact plant tissue, and indirect evidence such as host responses or death-grip scars in fossils that can be attributed to fungal parasitism.
2. Host responses currently represent the most reliable fossil evidence in support of fungal infection of a living host, albeit not necessarily of a parasitic nutritional mode of the intruder.
3. In the absence of host responses, the presence of certain structural features regularly seen in extant fungal parasites (e.g., haustoria, endobiotic rhizoidal systems, and holdfasts) can provide hints at parasitism in fossil fungi (see Karling 1932).
4. Fossils that can be attributed to present-day parasitic fungal families and genera with confidence are suggestive of fossil parasitism even if information on the hosts is not available. Unfortunately, fungal fossils older than Cretaceous cannot normally be attributed to modern families and genera with confidence.

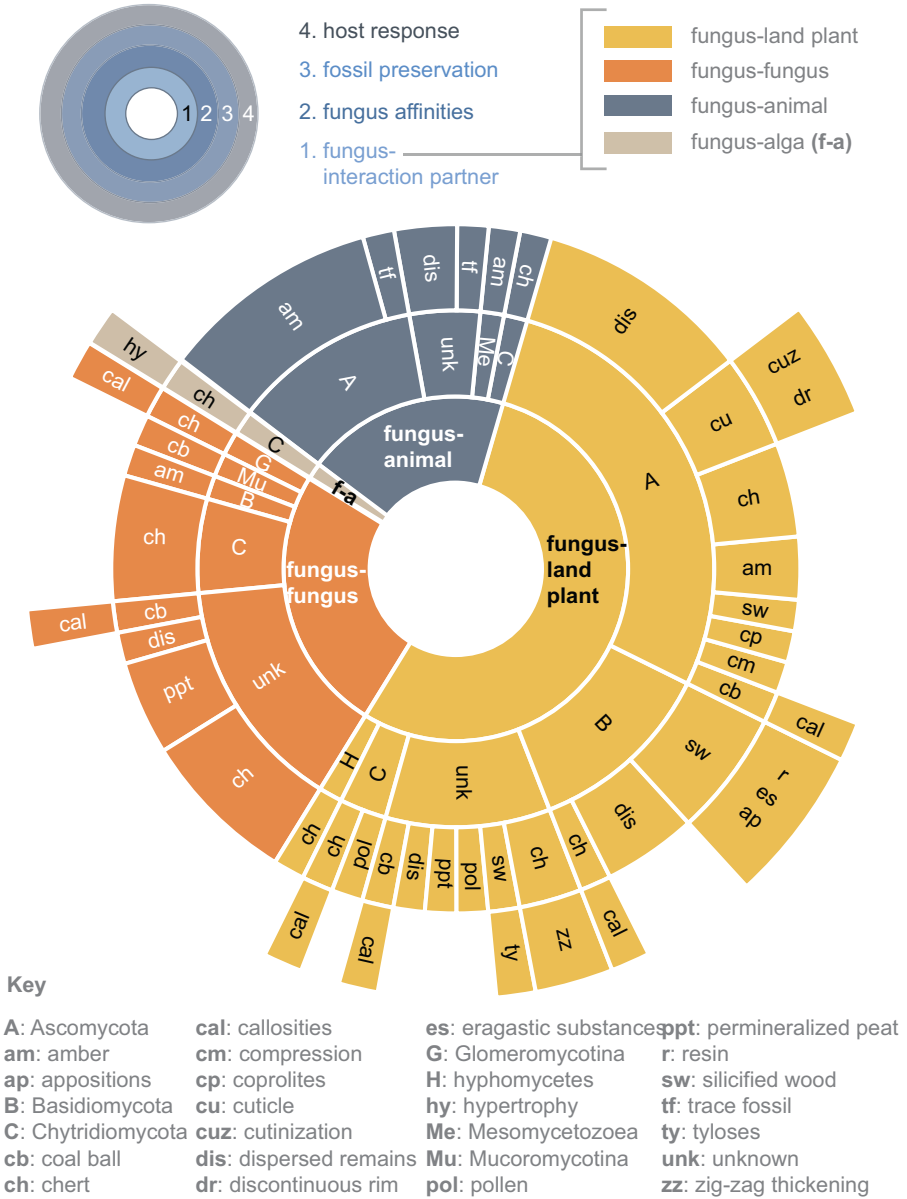


Fig. 3.5 Graphical synopsis of the information contained in the chapter, showing proportional abundance of (1) fossil hosts containing fungal parasites, (2) suggested affinities of the fungal parasites, (3) mode of fossil preservation, and (4) host response(s) if present. We acknowledge that the figure contains a prominent bias towards the paleobotanical evidence

For annotated version of Fig. 3.5 click [here](#).

The sobering truth is that, in most of the fossil record, we will never be able trace parasitic fungal interactions, simply because either the fungi are not preserved or the structural features required in determining the nutritional modes of the fungi cannot be resolved. On the other hand, we must not overhear the clarion call for concerted research efforts aimed at integrating other research fields such as geochemistry or biomarker analysis into paleomycology, because they might provide some of the information that cannot be obtained by using traditional paleontological techniques. More than anything, collaborative and synergistic research efforts are needed between neo-mycologists, pathologists, and paleontologists to accurately document fossil fungi and their many different interactions with other ecosystem components so that these fossils can be placed in a greater context such as (paleo-) ecosystem functioning and/or phylogenetic analyses.

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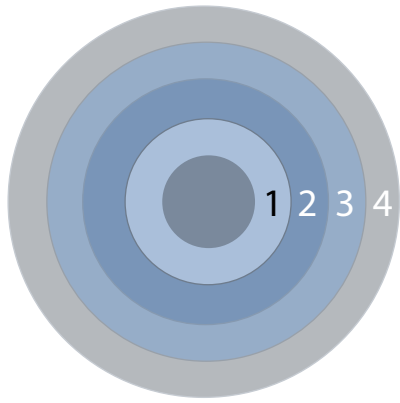
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4. host response
3. fossil preservation
2. fungus affinities
1. fungus-
interaction partner

