

A review of fossil fleshy fungi recovered from amber deposits around the world.

Britt A. Bunyard

How old are the oldest fungi? How far back into the geological record do fungi go ... and how do we know this? They surely do not fossilize, right?

It turns out that although soft fleshy fungi do not fossilize very well, we do have a fossil record for them. (Indeed, I can recommend an excellent book, *Fossil Fungi* by Taylor et al.; 2014; Academic Press.) The first fungi undoubtedly originated in water; estimates of their age mostly come from “molecular clocks” and not so much from fossils. Based on fossil record, fungi are presumed to have been present in Late Proterozoic (900-570 MYA) (Berbee and Taylor, 1993). The oldest “fungus” microfossils were found in Victoria Island shale and date to around 850M-1.4B years old (Butterfield, 2005), though the jury is still out on if truly fungal. The first terrestrial plants date to around 700 million years ago (MYA) and the consensus seems to be that fungi probably arrived on land just ahead of them and paved the way for plants to move from marine to ever drier habitats. The first “lichen-like” organisms we see date to around 600 MYA. At about 550 MYA is when chytrids and higher fungi split from a common ancestor (Berbee and Taylor, 1993). The first taxonomically-identifiable fungi are from 460 MYA, and seem similar to modern Glomeromycota, ubiquitous but still poorly known fungi that now thrive in all terrestrial biomes of the planet. At about 400 MYA is when the Basidiomycota and Ascomycota split from a common ancestor. The first insects came onto the scene around 400 MYA; the first beetles and flies came

onto the scene around 245 MYA.

Much of what we know of extinct fungi comes from specimens found in amber. Amber is one medium that preserves delicate objects, such as fungal bodies, in exquisite detail (Poinar, 2016). This is due to the preservative qualities of the resin when contact is made with entrapped plants and animals. Not only does the resin restrict air from reaching the fossils, it withdraws moisture from the tissue, resulting in a process known as inert dehydration. Furthermore, amber not only inhibits growth of microbes that would decay organic matter, it also has properties that kill microbes. Antimicrobial compounds in the resin destroy microorganisms and “fix” the tissues, naturally embalming anything that gets trapped there by a process of polymerization and cross-bonding of the resin molecules (Poinar and Hess, 1985).

George Poinar is the world’s authority on mushrooms found in amber and generously contributed a wonderful collection of images (and a wealth of information) for this review. The evolutionary history of gilled mushrooms is restricted to the relatively few fossils from Cenozoic and Cretaceous amber, with the oldest specimen, *Palaeoagaricites antiquus* 100 MYA (Figure 1), in Myanmar amber showing an affinity to members of the family Tricholomataceae (Taylor et al., 2015). Excellent examples of gilled mushrooms in amber have been published by David Hibbett and others, including *Archaeomarasmius legetti* from 90 MYA and *Protomyces electra* from 20 MYA (Hibbett et al., 1997), and *Aureofungus yaniguaensis* (Hibbett et al., 2003). Gilled mushrooms



Figure 1. *Palaeoagaricites antiquus* from Burmese amber, 100 MYA. This is the oldest-known fossilized mushroom. Photo courtesy G. Poinar.



Figure 2. *Coprinites dominicana* from Dominican amber, 20 MYA. Photo courtesy G. Poinar.

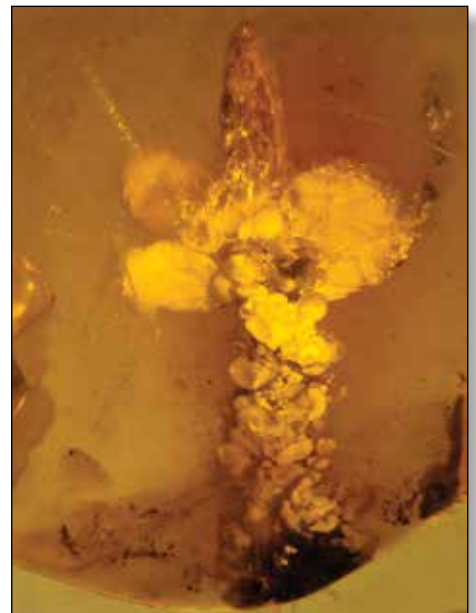
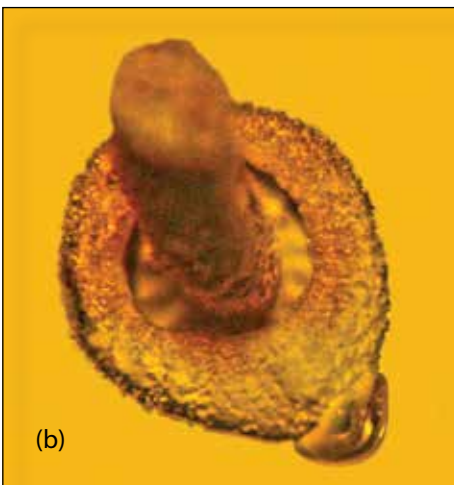


Figure 3. Sporocarps of a wood-inhabiting species tentatively identified as *Favolaschia* sp. Photo courtesy G. Poinar.



(a)



(b)

Figure 4. *Gerontomyces lepidotus* from Baltic amber found in Russia. a) shows side view; b) shows ventral view. Photo courtesy G. Poinar.

such as *Coprinites dominicana* from 20 MYA (Figure 2), along with sporocarps of a wood-inhabiting species tentatively identified as *Favolaschia* sp. (Mycenaceae) (Figure 3), appear

to share characteristics found in their descendants today (Boucot and Poinar, 2010; Poinar and Singer, 1990). Recently discovered in Baltic amber from the Samland Peninsula of Russia is an organism given the name *Gerontomyces lepidotus* (Poinar, 2016) (Figure 4). The specimen was small (1.8 mm total length) but well-preserved and includes a complete pileus (cap) just 1 mm in diameter. The stipe (stem) is broken at the base but still attached to the cap. Due to the absence of spores and the basal portion of the stipe, it is difficult to align *Gerontomyces lepidotus* with any modern genus or even family. The combination of such a small size, dry, brownish, scaly surface, broad, distant to subdistant lamellae (gills) and a straight, solid stipe are not common characters in gilled mushrooms, although some of these features do occur in a few genera in the family Tricholomataceae (Poinar, 2016).

There are gasteromycetes known

from amber; sporophores of the puffball, *Lycoperdites tertarius*, in Mexican amber (Figure 5) (Poinar, 2001) and the first known fossil bird's nest fungi (Figures 6 and 7), where you can see the peridioles at the base of the peridia (Poinar, 2014b). The clavarioid fungus, *Palaeoclavaria burmitis*, in Burmese amber (Figure 8) represents the first fossil record of the non-gilled mushrooms. Not only were sclerified generative hyphae with clamp connections present, but spores borne externally on basidia could be observed (Poinar and Brown, 2003).

What about ascomycetes? Yes, there have been fossils recovered that have been identified as members of the Ascomycota, even from well-known modern groups like morels and Dead Man's Fingers. An early form of the latter, *Xylaria antiqua* (Figure 9), is well-preserved with organized layers of conidiophores still retaining their conidia as well as perithecia filled with ellipsoid ascospores adjacent to the ostioles (Poinar, 2014a). From Dominican Republic amber we see *Paleomorchella dominicana* (Figure 10) (Boucot and Poinar, 2010). The specimen is a mere 2 mm in length, and thus very immature, which could account for why it does not much resemble extant morels (note that there are no sponge-like pits or sterile ridges of more familiar morels, instead this ancient specimen has longitudinal ridges more reminiscent of striate or sulcate basidiomycete mushroom caps). And this is something worthy of pointing out: most fleshy fungi (or objects thought to be fleshy fungi) found in amber are very small, typically just a few millimeters, and don't exhibit many easily discerned morphological characteristics.

Also of interest are various arthropods and mycoparasites associated with fossil fleshy fungi. Leaving the cap of *Coprinites dominicana* in Dominican amber is a mite that was trapped when the mushroom was preserved (Poinar and Singer, 1990) (Figure 2). Adjacent to the Baltic amber *Gerontomyces lepidotus* was an exuvia of a nymph of a Phasmatodea (and strand of mammalian hair) (Figure 4). It was assumed that the insect was feeding on the mushroom (Poinar, 2016). A small polypore in Dominican amber that was tentatively identified as a *Ganoderma* sp. is partly



Figure 5. *Lycoperdites tertarius*, a puffball from Mexican amber. Photo courtesy G. Poinar.



Figure 6. Fossil bird's nest fungus, *Cyathus dominicanus*. Photo courtesy G. Poinar.

eaten by an unknown agent, but still shows the outer rounded margin and faint pores on the undersurface (Figure 11) (Boucot and Poinar, 2010). Two insects were associated with the fruiting bodies of *Palaeoclavaria burmitis* in Burmese amber (Figure 8). One was a fungus gnat in the family Mycetophilidae that appears to have been in the process of depositing eggs on a sporocarp. The other was a larva of a phlebotomine fly that was probably developing in one of the fruiting bodies (Poinar et al., 2006). The Burmese amber *Palaeoagaracites antiquus* (Figure 1) mentioned above is so well-preserved that it led to the discovery of mycoparasites in amber. This is the oldest fossil mushroom, and only the second described from the Cretaceous (along with *Archaeomarasmius leggetti*) (Hibbett et al., 1997). You can

make out (Figure 1) the presence of mycelial strands of a parasitic fungus, *Mycetophagites atrebora*, that ramify through the cap. Furthermore, inside the hyphae of the latter are hyphal strands of a hyperparasite, *Entopezites patricii* (Poinar and Buckley, 2007).

Mycorrhizal relationships are believed to have arisen more than 400 MYA as plants began to colonize terrestrial habitats – indeed, these fungi are thought to have facilitated plants' move to land – and are seen as a key innovation in the evolution of vascular plants. There are two primary types of mycorrhizae: the more ancestral and predominant is called endomycorrhiza (“arbuscular mycorrhizae”), found in over 80% of all plant species studied. The less common form is called ectomycorrhiza (ECM), occurring in roughly 10% of plant species, and

includes many well-known mushroom-producing groups like *Amanita*, *Russula*, chanterelles, and boletes. Additional mycorrhizal associations have arisen as well, including a special kind of mycorrhizae between orchids and fungi. More on orchid fungi in the fossil record, below.

Recently, the first fossil ectomycorrhiza associated with flowering plants (angiosperms) was discovered (Beimforde et al., 2011) (Figure 12, courtesy of P. Nascimbene). The fossils were found in a piece of Lower Eocene (52 MYA) Indian amber, from a time only 13 million years after the demise of the dinosaurs. The ECM inclusions show various stages of development and reveal a variety of morphological details. “Mycorrhizae are extremely rare in the fossil record – in fact, only one other fossil ECM has ever

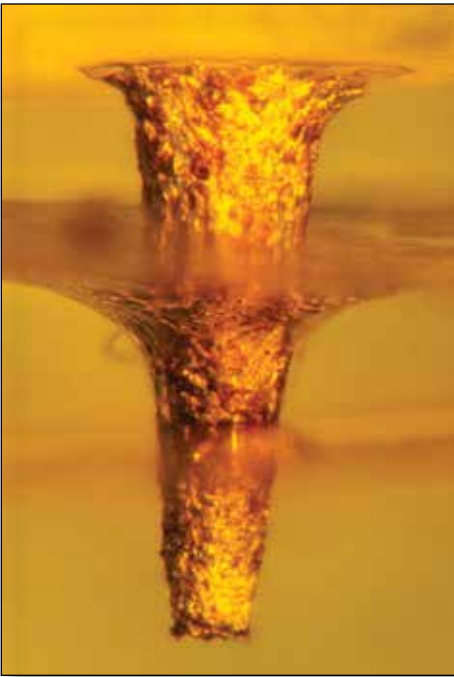


Figure 7. Fossil bird's nest fungus, *Nidula baltica*. Photo courtesy G. Poinar.

been found," Dr. Alexander Schmidt from Göttingen University (Germany), the senior author of the study, told FUNGI back in 2011 when the discovery was made. "The Indian amber containing the ECM was produced by the dominant trees of an early tropical rain forest." Paul C. Nascimbene of the American Museum of Natural History in New York, a coauthor of the study, added: "Based on the amber's very specific chemistry, as well as on analyses of pollen and fossil wood found in association with the amber, the tree that produced the resin is likely a member of the dipterocarps (Dipterocarpaceae), which are ectomycorrhizal, and are the prevalent overstory trees in Southeast Asia today. The discovery of a 52 million-year old mycorrhizal association illustrates the morphological stability of terrestrial ecosystems."

Synaptomitius orchiphilus was described as a mycorrhizal fungus of a germinating orchid seed, *Mycophorus elongatus*, in Dominican amber dating from 30-45 MYA (Poinar, 2017a; 2017b). The discovery noted additional features of *Synaptomitius orchiphilus* in cells of the orchid host seed, including intracellular hyphae, moniliform cells and basidiocarps with basidia and basidiospores. This is the first record of the teleomorphic stage of a basidiomycete occurring in an angiosperm seed. An

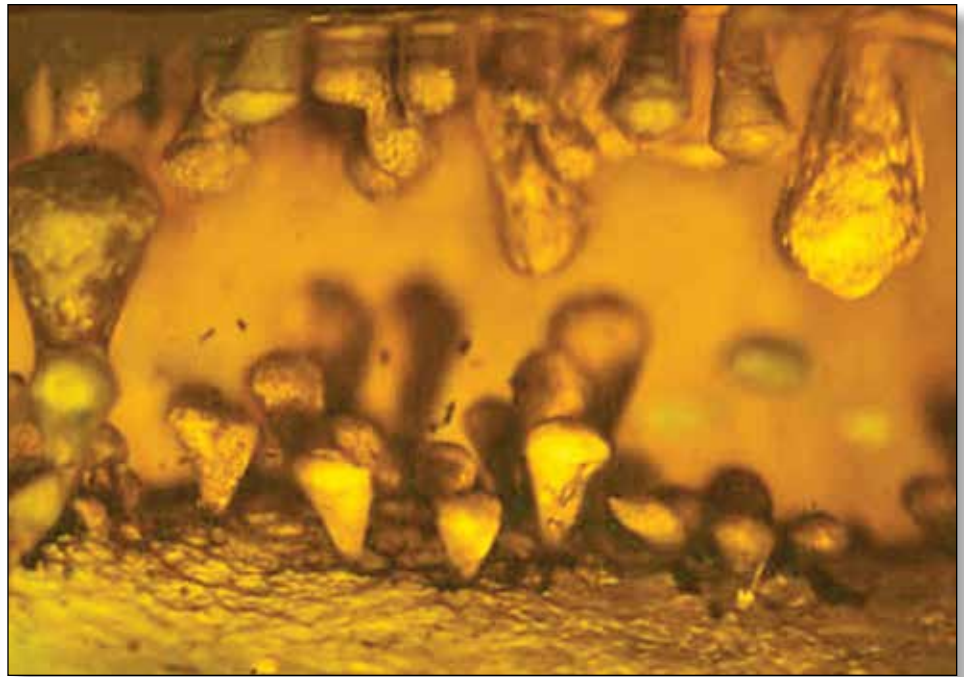


Figure 8. The clavarioid fungus, *Palaeoclavaria burmitis*, in Burmese amber. Photo courtesy G. Poinar.

examination of the posterior end of the seed of *M. elongatus* showed that hyphae of *S. orchiphilus* had entered the seed through the suspensor cells. Rhizoid-like bodies emerging from the germinating seed indicate that the seed was viable when it entered the resin. Further evidence of seed viability are dividing nuclei, some of which are still connected by spindles, in uninfected embryo cells of *M. elongatus*. Developing hyphae of *S. orchiphilus* were observed within embryo cells of *M. elongatus*. In several instances, fungal strands from different points of origin united, providing evidence of plasmogamy, followed by karyogamy and the initiation of the teleomorph stage of *S. orchiphilus*. The hemispherical basidiocarps have basal walls ranging from 30 to 40 μm in thickness with the hymenial layers ranging from 385 to 420 μm in thickness. Basidia are at different stages of development. Some are in the initial stages of formation, while others have immature basidia with sterigmata and immature spores and a few had mature basidiospores.

Due to the age of the fossil and having to take the photo through a layer of amber, the hyphae in the fossil orchid cells are not as distinct as those in the prepared and stained slide of the extant orchid cells. Indeed, it's led some researchers to doubt the



Figure 9. *Xylaria antiqua*, a precursor to modern-day Dead Man's Fingers. Photo courtesy G. Poinar.

veracity of the "discovery" altogether. Selosse et al. (2017) in a paper titled "Why *Mycophorus* is not an orchid seedling, and why *Synaptomitius* is not a fungal symbiont within this fossil" argued that Poinar's discovery, while seemingly exciting is baseless in their opinion. Analyzing Poinar's data, point by point, Selosse et al. explain their conclusions that *Mycophorus* may not be an orchid seed (instead dust seed of any number of plant groups), why *Mycophorus* is not a germinating



Figure 10. A fossilized morel? *Paleomorcella dominicana*. Photo courtesy G. Poinar.

seed, why fungal hyphae and a symbiotic fungus are absent in Poinar's *Mycophoris*, and why *Synaptomitius* is likely not a fossil basidiomycete.

More recently Poinar (2017b) has supplied additional data to support his previous report of a fossilized orchid fungus. The debate continues.

References Cited

- Beimforde, C., N. Schäfer, H. Dörfelt, P.C. Nascimbene, H. Singh, J. Heinrichs, J. Reitner, R.S. Rana, and A.R. Schmidt. 2011. Ectomycorrhizas from a Lower Eocene angiosperm forest. *New Phytologist* 192(4): 988-996.
- Berbee, M.L., and J.W. Taylor. 1993. Dating the evolutionary radiations of the true fungi. *Canadian Journal of Botany* 71: 1114-1127.
- Boucot, A.J., and G.O. Poinar. 2010. *Fossil Behavior Compendium*. CRC Press, 424 pp.
- Butterfield, N.J. 2005. Probable Proterozoic fungi. *Paleobiology* 31: 165-183.
- Hibbett, D.S., M. Binder, Z. Wang, and Y. Goldman. 2003. Another fossil agaric from Dominican amber. *Mycologia* 95: 685-687.
- Hibbett, D., D. Grimaldi, and M. Donoghue. 1997. Fossil mushrooms from Miocene and Cretaceous ambers and the evolution of Homobasidiomycetes. *American Journal of Botany* 84: 981-991.

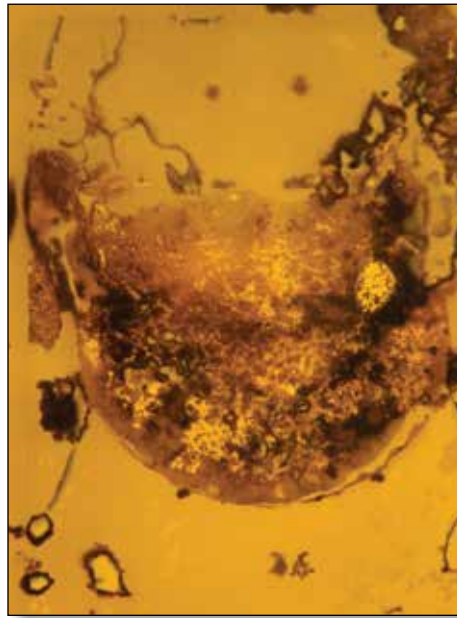


Figure 11. A small polypore in Dominican amber that was tentatively identified as *Ganoderma* sp. Photo courtesy G. Poinar.

- Poinar Jr., G. 2017a. Developmental stages of the fungus, *Synaptomitius orchiphilus*, in the germinating seed, *Mycophoris elongatus* (Orchidaceae), in Dominican amber. *Historical Biology* DOI: 10.1080/08912963.2017.1411352
- Poinar Jr., G. 2017b. Two new genera, *Mycophoris* gen. nov., (Orchidaceae) and *Synaptomitius* gen. nov. (Basidiomycota) based on a fossil seed with developing embryo and associated fungus in Dominican amber. *Botany* 95(1): 1-8.
- Poinar Jr., G. 2016. Fossil fleshy fungi ("mushrooms") in amber. *Fungal Genomics and Biology* 6: 142. doi:10.4172/2165-8056.1000142
- Poinar, G.O. 2014a. *Xylaria antiqua* sp. nov. (Ascomycota: Xylariaceae) in Dominican amber. *Journal of the Botanical Research Institute of Texas* 8(1): 145-149.
- Poinar, G.O. 2014b. Bird's nest fungi (Nidulariales: Nidulariaceae) in Baltic and Dominican amber. *Fungal Biology* 118(3): 325-329.
- Poinar, G.O. 2001. Fossil puffballs (Gasteromycetes: Lycoperdales) in Mexican amber. *Historical Biology* 15(3): 219-222.
- Poinar, G.O., and A. Brown. 2003. A non-gilled hymenomycete in Cretaceous amber. *Mycological Research* 107(6): 763-768.
- Poinar Jr., G.O., and R. Buckley. 2007. Evidence of mycoparasitism and



Figure 12. The first fossil ectomycorrhiza ever discovered, and a likely dipterocarpaceae associate. Photo courtesy of P. Nascimbene.

- hypermycoparasitism in Early Cretaceous amber. *Mycological Research* 111: 503-506.
- Poinar, G.O., and R. Hess. 1985. Preservative qualities of recent and fossil resins: electron micrograph studies on tissue preserved in Baltic amber. *Journal of Baltic Studies* 16: 222-230.
- Poinar, G.O., and R. Singer. 1990. Upper Eocene gilled mushroom from the Dominican Republic. *Science* 248(4959): 1099-1101.
- Poinar Jr., G.O., R.L. Jacobson, and C.L. Eisenberger. 2006. Early Cretaceous phlebotomine sand fly larvae (Diptera: Psychodidae). *Proceedings of the Entomological Society of Washington* 108: 785-792.
- Selosse, M.A., M. Brundrett, John Dearnaley, V.S.F.T. Merckx, F. Rasmussen, L.W. Zettler, and H.N. Rasmussen. 2017. Why *Mycophoris* is not an orchid seedling, and why *Synaptomitius* is not a fungal symbiont within this fossil. *Botany* 95(9): 865-868.
- Taylor, T.N., M. Krings, and E.L. Taylor. 2015. *Fossil Fungi*. Elsevier, Inc., Amsterdam, 382 pp. 7