



The Devonian enigma: *Prototaxites*. Already during the 19th century, fossils several meters high were detected. Initially, they were interpreted as archaic plants, then as algae, rolled liverworts, or giant lichens (Moore et al., 2011). Recently, evidence has been mounting that they may have been ascomycetes, possibly lichenized (Retallack and Landing, 2014; Honegger et al., 2017). More information on *Prototaxites* (and much more) can be found in www.davidmoore.org.uk. Painting image courtesy Geoffrey Kibby (British Mycological Society).

Fungi in the rear mirror

A brief history of the fungi during the last two billion years

Hans Halbwachs

ABSTRACT

Fungal evolution goes back for at least two billion years. From flagellate marine Chytridiomycota to terrestrial Asco- and Basidiomycota, fungal speciation—and the radiation of those species—occurred through multiple steps that were mainly triggered by key morphological (often symbiotic) innovations. The fossil record does document such evolutionary steps, albeit incompletely due to the scarcity

of fossils; what evidence we have is preserved geological strata or amber. Through molecular analysis methods (examining the “molecular clock”), the fungal pathway through Earth’s history can be amended and ancestral relationships elucidated. In the following historical review, important, history-illuminating fossils are depicted and put into evolutionary context. It also describes the delicate dependencies of

fungal evolution on biotic and abiotic environmental circumstances, which sheds some light on the consequences of the present degradation of nature.

Keywords: Basidiomycetes, ascomycetes, fossils, amber, evolution, symbiosis, Agaricomycotina

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The mysteries of fungal evolution

The sheer magnitude of extant fungal diversity, with probably more than 2.2 million species, is baffling (Hawksworth and Lücking, 2017). This number indicates that fungi are an old kingdom, perhaps one of the oldest among eukaryotes (organisms with a distinct nucleus in their cells). The magic of the fungal kingdom's diversity becomes particularly visible, specifically, in the "higher" fungi, with its enormous but unevenly distributed phylogenetic and morphological diversity. For example, why does genus *Marasmius* includes approximately 500 species, but *Agrocybe* only 35 (Kirk et al., 2011)?

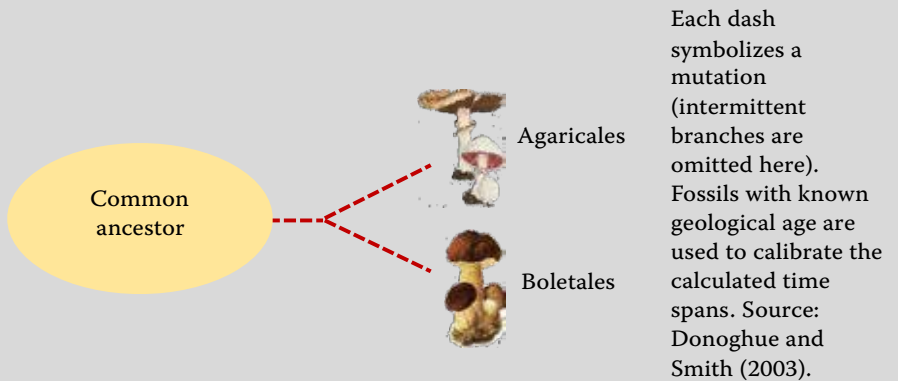
Apart from the question of how fungi emerged, the observed diversity patterns beg for explanations. In other words, what were (and are) the drivers of speciation and associated phylogenetic peculiarities? This review aims to present a synopsis of the evolution of fungi as well as to cast a little light onto some darker corners of fungal phylogeny.

How it (perhaps) began

To be clear right from the beginning, how the first fungi evolved remains largely unknown. Science is not at all sure what appeared first on the evolutionary scene: plant? or fungus? (Hedges et al., 2006). Or if both at the same time? A visionary British mycologist even assumed that LUCA (the "Last Universal Common Ancestor"), the forebear of all eukaryotic living things, was a fungus (Moore, 2013). Widely accepted now is the view that ancestral plants and fungi developed in the primeval seas of the Precambrian, namely algae and flagellate fungi (*Chytridiomycota sensu lato*) (Hedges et al., 2006). The current oldest fungal fossil is probably 2.4 billion years old (Paleoproterozoic) (Bengtson et al., 2017). The first fungal steps on land took place circa one billion years ago, likely before plants (Hedges et al., 2006). The still-quite-hostile terrestrial habitat (little oxygen, intense UV radiation) only allowed an expansion of biocrusts, which were composed of heterotrophic bacteria and cyanobacteria (Taylor et al., 2015). These biocrusts, together with first terrestrial fungi, could have formed a mutualistic-lifestyle organism similar to lichens (Yuan et al., 2005; Strullu-Derrien et al., 2018).

Box 1: How is the molecular clock ticking?

Each organism is subject to alterations of its DNA and proteins. Mutations also occur in neutral sequences, which do not affect the phenotype, i.e., do not underlie selective pressure. Given that the mutation rate of such neutral sequences remains the same through time, they can be used to estimate the point when two species diverged in the course of the evolution.



If it only were that simple! Sadly, the mutation rates are not so constant as initially assumed (Bromham, 2016). For instance, Beimforde et al. (2014) showed an uncertainty of 100 million years on the divergence of *Helvella* and *Gyromitra* towards the end of the Cretaceous. Finally, one should realize that cladistic methods are based on statistics, which are inevitably accompanied by uncertainties (Nagy et al., 2012).

Where did these authors get their data? First of all, fossils are recovered from sediments and other rocks and, notably, from amber; I will come back to the issue of fossilized fungi in more detail later on. The second and most important source of data are molecular clocks. Despite some uncertainties (see Box 1), the method has become indispensable for elucidating the evolutionary pathway of fungi.

The more one goes back in time, the more inherently dubious the inferences, because fossils for calibrating the molecular clock are seldom available. One should not be surprised that the suggested divergence time between basidio- and ascomycetes varies between 900 million (Hedges et al., 2006) and 650 million years (Tedersoo et al., 2018).

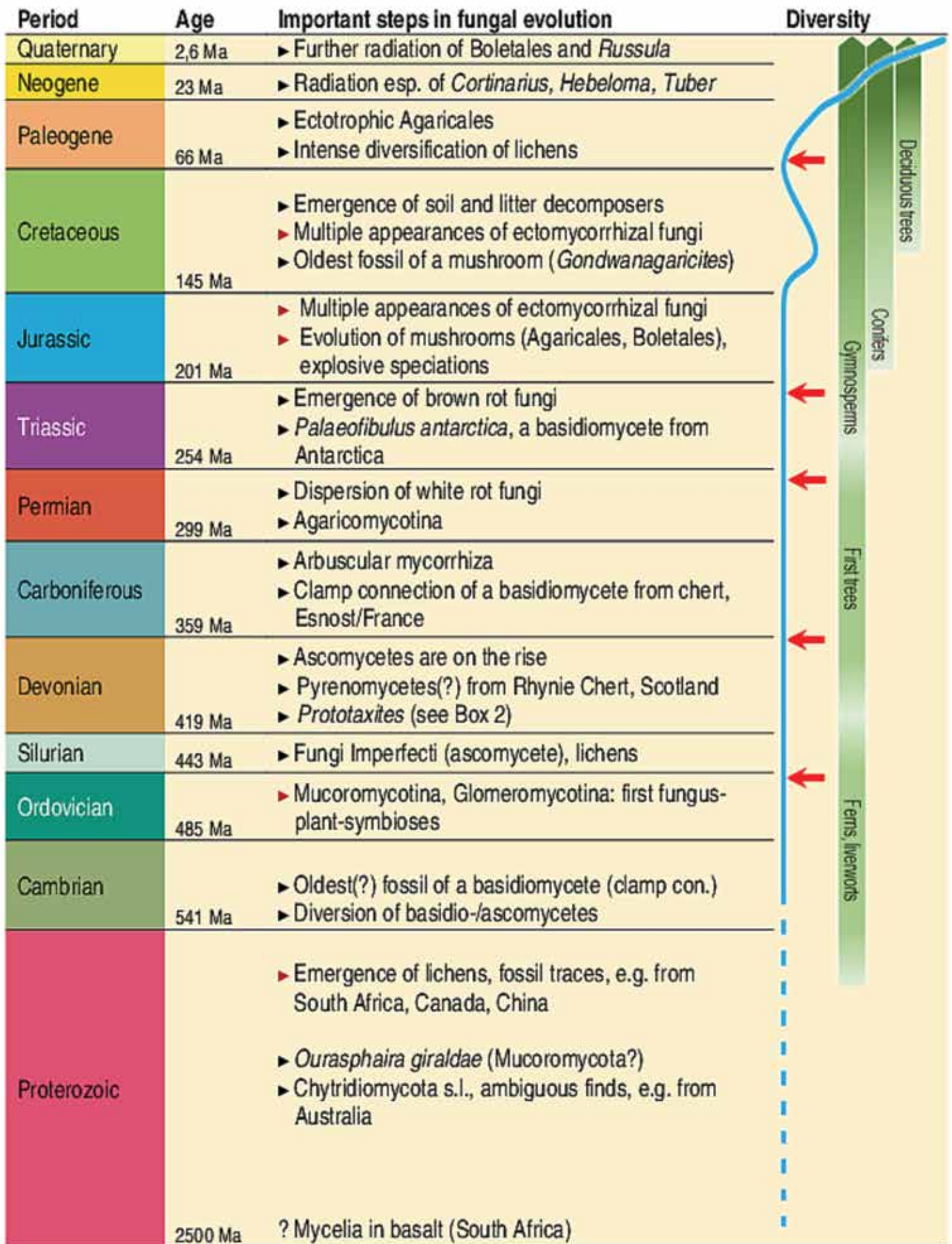
Back to conquering land. We had unruly times in those days towards the end of the Ordovician (ca. 450 MYA). Wildly oscillating sea levels, high carbon dioxide concentrations, and fierce volcanic activities (Edwards et al., 2015), paradoxically created a concoction of circumstances that accelerated speciation through selective forces and geographical isolation (Levin, 2004; Mayhew, 2006; Schluter, 2017). The onward march of the fungi is paved with

speciation surges ("radiations"), rather uneventful periods, and extinctions (Boenigk et al., 2015).

Diversity and extinction

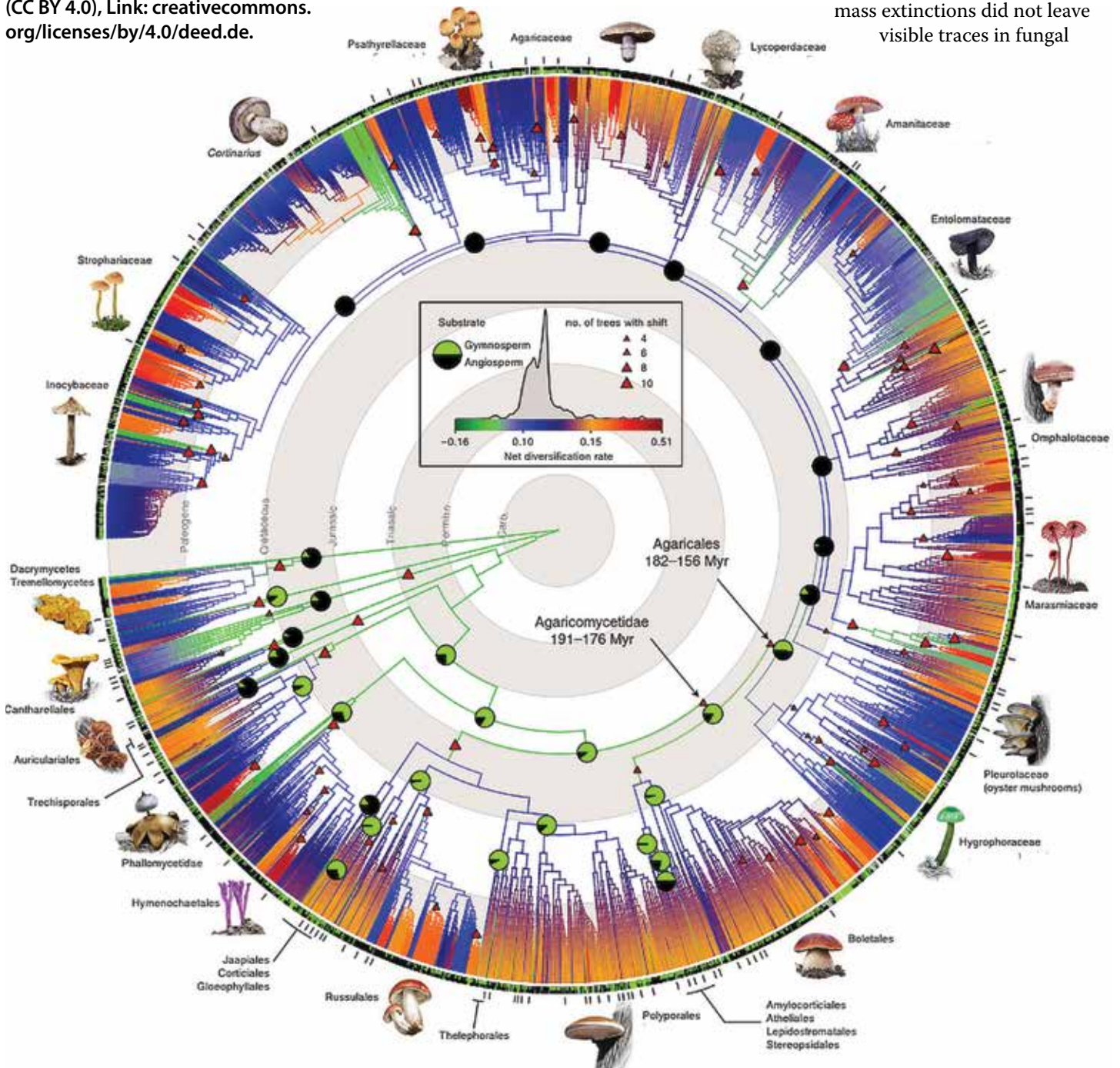
As I have noted, the history of the Earth is a turbulent one. Above all, volcanic and tectonic forces shaped a mosaic of land and sea. The period when life emerged was particularly uncomfortable for sure because of frequent meteorite impacts (Boenigk et al., 2015). What we would consider extreme environmental upheaval may have contributed to the lack of observable specimens along the evolutionary path that led to the advent of fungi. The further evolution can be inferred with the help of fossils and the molecular clock. It should be noted that during this process, fungi and plants are usually found in association with one another shortly after the "conquest" of land (Boenigk et al., 2015). The somewhat erratic fungal paleohistory is presented in Table 1.

The diversity graph (based on the currently described taxa from amber, see Halbwachs, 2019b) in Table 1 depicts the evolutionary steps only in a flashlight fashion. Still, the key events become clear. Red bullets flag particularly



← Table 1. Compilation of fungal evolution in the course of Earth's history based on fossil and molecular data. In the last column, the accompanying dynamics of fungi (blue) and plant (green) evolution is schematically depicted. Red arrows denote mass extinctions. The color code and the classification follow the International Commission on Stratigraphy (www.stratigraphy.org). Sources: Berbee and Taylor (2001); Wellman (2003); Wikström et al. (2003); Binder and Hibbett (2006); Matheny et al. (2006); Miller et al. (2006); (2008); Soltis et al. (2008); Bidartondo et al. (2011); Krings et al. (2011); Ryberg and Matheny (2011); Bonito et al. (2013); Boenigk et al. (2015); Taylor et al. (2015); Bengtson et al. (2017); Lutzoni et al. (2018); Seyfullah et al. (2018); Strullu-Derrien et al. (2018); Loron et al. (2019); Varga et al. (2019).

Figure 1. Cladogram illustrating mushroom radiation, beginning with the Carboniferous (depicted as root of the phylogenetic tree in the center) (modified after Varga et al., 2019). The explosive split-ups of the lineages within the Agaricomycotina mainly took place at the beginning of the Paleogene (ca. 60 MYA). The insert in the center shows the diversification rates as hues (the warmer, the higher). License: Attribution 4.0 International (CC BY 4.0), Link: creativecommons.org/licenses/by/4.0/deed.de.



innovative developments which, for the most part, resulted in intense radiations. I want to highlight the first fungus-plant symbioses because they likely triggered co-evolution and thus contributed to the acceleration of adaptations to changing environmental conditions (Thompson, 2017). In the same way, the emergence of mushrooms ca. 180 MYA sparked explosive radiation of species, possibly due to the lifting of spore production above the substrate surface, making spore dispersal significantly more effective (Varga et al., 2019). The staggering diversification becomes evident with a cladogram (Fig. 1).

It seems rather remarkable that mass extinctions did not leave visible traces in fungal

Period	Ma	General effects	Effects on fungi
Ordovician/ Silurian	~444	85% of all species died out, mainly marine taxa.	Unknown
Devonian	~360	75% of all species died out, mainly reef-building organisms.	Due to the decreasing oxygen content of seas, possibly selective pressure to become terrestrial occurred.
Permian/ Triassic	260–252	96% marine and 65% of terrestrial species perished, probably because of a dramatic rise of temperature between 5° and 10°C.	Especially plants were affected. A rapid rise of fungal species because of the enormous masses of plant remains (white and brown rot) (Steiner et al., 2003). In the aftermath, fungal diversity and abundance could have collapsed again due to the depletion of the substrate. Beimforde et al. (2014) suggested that the ecological diversity in all ascomycete lineages was responsible for the survival of at least some taxa of each group, despite global crises.
Triassic/ Jurassic	~210	Probably triggered by massive volcanism, ca. 80% of all species perished.	Changes in the prevailing modes of primary production could have compromised fungal diversity (Pieńkowski et al., 2011).
Cretaceous/ Paleogene	~66	Probably triggered by a colossal meteorite impactation, ca. 75% of all organisms died out (dinosaurs!).	Probably only temporary effects on fungi (Sweet and Braman, 2001).

Table 2. The “Five Big Mass Extinctions” (Boenigk et al., 2015).

radiation (Table 2). However, it may not have been that simple. The “Big Five” may have led to drastic transformations of the environment and species spectra, at least regarding plants (McElwain and Punyasena, 2007). It also should have affected fungi, which depend on plants in multifaceted ways. Such allegedly catastrophic events may lead to the creation of new environmental niches, among other things, and explosive species diversifications. One starting point could have been the last extinction episode ca. 60 MYA. It is apparent that mushrooms made a jump ahead, as shown in Fig. 1. It appears that massive speciation events are a result of specific genetically induced morphological innovations that are connected to the dispersal fitness of fungi (Lomolino et al., 2006). In the meantime, the Big Five are under dispute; it is argued that fossil records have been misinterpreted (Racki, 2019).

In any case, another radiation event refers to the conspicuously multiple diversifications of some ectomycorrhizal groups, which it seems have developed pronounced ornamentation as key innovations in

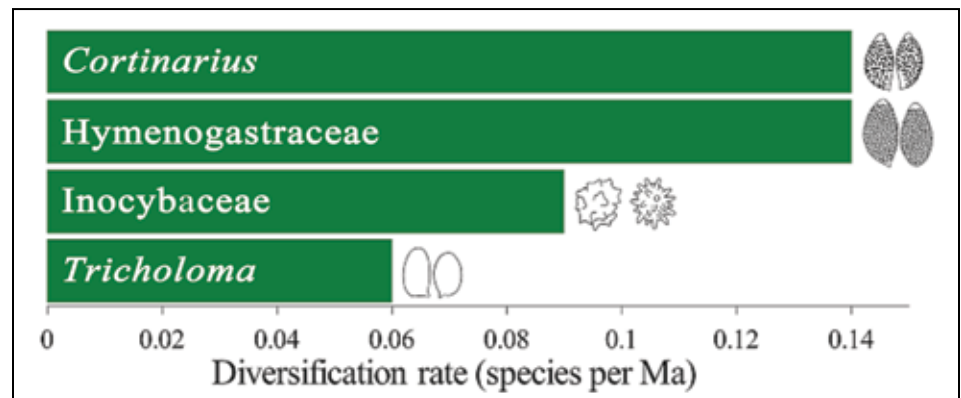


Figure 2. The strongly ornamented *Cortinarius*, Hebelomataceae and Inocybaceae have significantly higher diversification rates than, e.g., *Tricholoma*. Sources: Ryberg and Matheny (2011), spore images Knudsen and Vesterholt (2012), courtesy Henning Knudsen.

dispersal (Fig. 2). Spore ornamentation could imply advantages in dispersal by invertebrates such as collembola, because spores may better get into the soil and close to host roots with such vectors (Halbwachs et al., 2015; Halbwachs and Bässler, 2015; Calhim et al., 2018). Whether such a connection is real, remains speculative to date.

Now, another key innovation in the evolution of fungi: sex! Initially, it only

entailed differing DNA codes (“Mating System”), which essentially served to avoid detrimental inbreeding (Box 2). Which key innovations or their combinations led to notable speciation boosts is still largely unknown. Also, not only the already-mentioned lineages were subject to intense radiations. Some other macromycetes show similar dynamics (Fig. 3). *Marasmius* is such a candidate with high diversity, despite

Box 2: Mating systems.

Fungi being eukaryotes (having cells with a nucleus) are generally not able to reproduce under the exchange of genes (recombination) by fusing hyphae, and their cell nuclei (karyogamy) followed by nuclear division. This process shuffles the genetic attributes of two individuals resulting in an offspring that recombines the characteristics of the parents. It creates a genetic diversity that better enables fungi to adapt, e.g., to changing environmental conditions. Therefore, an exchange of identical or similar genetic information would be of little use (Fraser and Heitman, 2004). To avoid this, mating systems ensure that only recombination can take place if allowed by specific gene markers (see Moore et al., 2011). Precursors of such a mechanism are already present in zygomycetes (Dyer, 2008), which putatively originated during the Precambrian (Taylor et al., 2015).

an inconspicuous morphology and a saprobic lifestyle.

Additional approaches to explaining differences in species numbers relate to ecological and regional factors (Rabosky, 2009). Moreover, some chromosomal mechanisms, e.g., transposons (“jumping genes,” which may accelerate evolution) (Bromham, 2016), may be relevant to help explain the erratic speciation patterns in fungi. All this diversity demands research concerning, e.g., the effects of morphological traits on the fungal reproductive and dispersal fitness

or the evolvability of fungi.

Fossil witnesses

A great deal of what we know of the fungal past, we owe to fossils even if, due to their ephemeral nature, only a few have persisted (Taylor et al., 2015). However, such fossils often have the disadvantage of being preserved merely as imprints, which only allow limited interpretations. Therefore, errors are preprogrammed, even for experienced paleontologists and mycologists. Due to the three-dimensional nature of

fungal inclusions in amber, taxonomic attributes are better discerned. Still, even supposedly well-preserved morphological traits of fungi in amber may lead down a wrong interpretive track: a mushroom-shaped specimen was classified as *Palaeocybe striata* by Dörfelt and Striebig (2000), which Schmidt and Dörfelt (2007) several years later identified as an extinct member of Matoniaceae, a dwarf fern. However, such errors do not negate the work of scientists nor the value of fungal fossils, especially in the case of higher fungi found in amber (Poinar Jr, 2016) (Box 3). The state of preservation is mostly better than of fossils from sediments and rocks, even if they are often not easily investigated by optical means (Penney and Green, 2010).

Ascomycota

Since the Cambrian (ca. 530 MYA, Prieto and Wedin, 2013) sac fungi have become a substantial part of the present fungal flora with 64,000 described species (Kirk et al., 2011). Unequivocal records from earlier periods are rather meager and of little informative value. Only the already mentioned find in Rhynie Chert provides definite proof (Fig. 4a). Another example is an

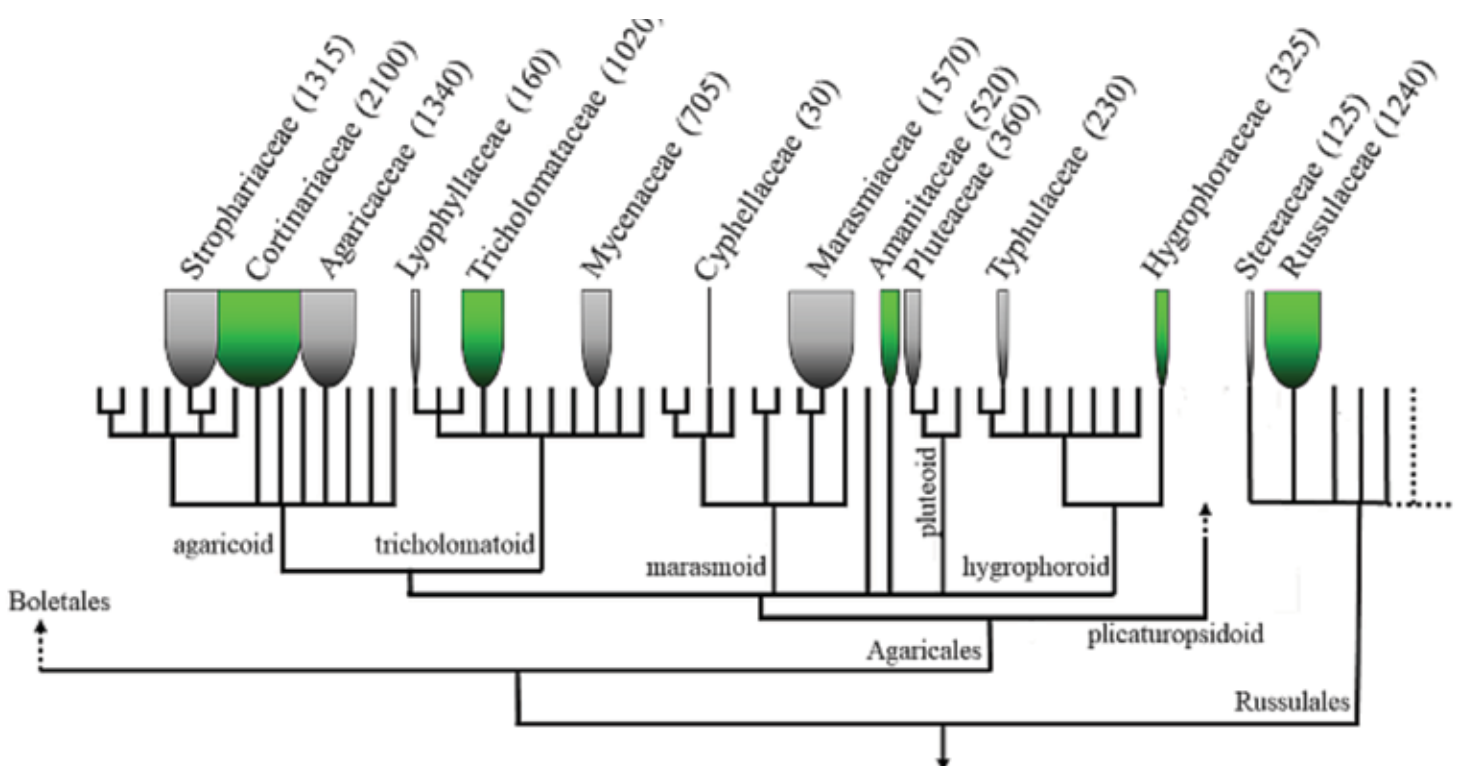


Figure 3. Diversity patterns of some agaricomycete lineages (tree based on Matheny et al., 2006; Miller et al., 2006; Matheny et al., 2007). The approximate species numbers in brackets behind the family names have been taken from Kirk et al. (2011). Green symbols denote wholly or partially ectotrophic families, grey denotes saprobic groups.

Box 3: Entombed in amber.

Amber is the fossilized resin of various trees from almost all geological periods since the Carboniferous. Most of the ca. 35 deposits originate from the epochs since the Cretaceous, i.e., starting ca. 145 MYA (Krumbiegel and Krumbiegel, 1994). Younger (<1 MYA), subfossil amber is called copal (Penney and Preziosi, 2010). Insect inclusions are not really rare, depending on the origin of the amber. In Dominican amber we find insects >75% of the time; fungi are barely represented with 1% (Poinar Jr and Poinar, 1999).



On the left Baltic pebbles; in the center Myanmar specimens with tiny insect inclusions; on the right copal from Madagascar (author's collection).

What about embedded DNA (Greetings from Jurassic Park)? Lamentably, one has to accept that DNA in anything older than 1M years is too degraded for molecular analyses (Penney and Green, 2010).

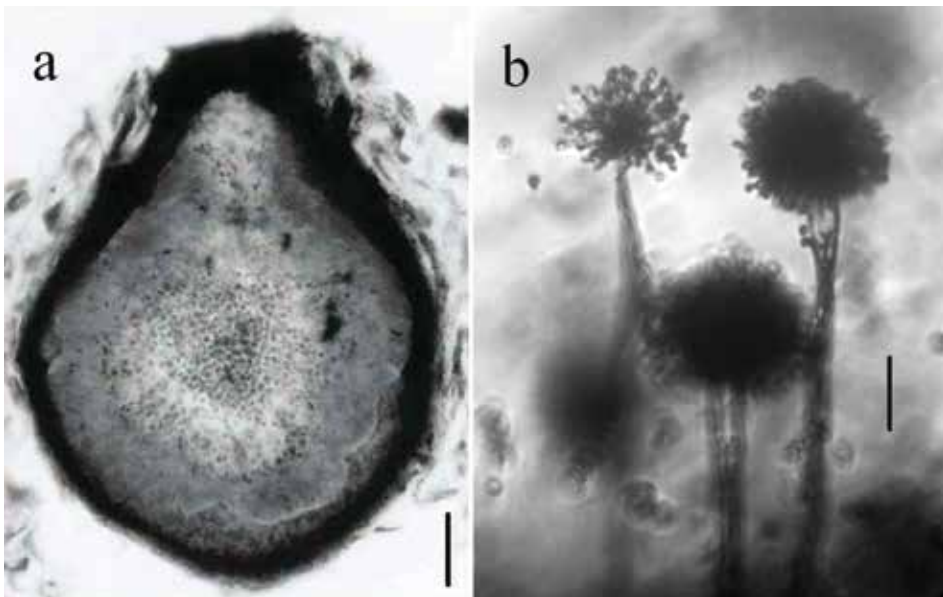


Figure 4. a) Longitudinal section of a perithecium of *Paleopyrenomyces devonicus* Taylor, Hass, Kerp, Krings et Hanlin from Rhynie Chert (ca. 400 MYA). Source: Taylor et al. (1999), Springer license No. 4558171315501; bar 50 μm . b) Conidia of an *Aspergillus* (Lower Miocene, ca. 17.5 MYA). Source: Thomas and Poinar Jr (1988), courtesy George Poinar; bar 100 μm .

Aspergillus in Dominican amber (Fig. 4b).

Basidiomycota

The Basidiomycota are ca. 60M years older than the Ascomycota (Taylor and Berbee, 2006). By 2011, almost 32,000 species had been described (Kirk et al., 2011). The determinants of Basidiomycota, being more species-poor than Ascomycota, are multifaceted. For one, the evolutionary pace (speciation rate) is about 20% higher in ascomycetes, in which the species-rich sordariomycetes evolve particularly fast (Wang et al., 2010). Conspicuously, ascomycetes possess, on average, a 20% larger genome than basidiomycetes, without any clues as to why (Mohanta and Bae, 2015). For whatever reason, some organismal groups with large genomes do have a higher speciation rate (e.g., some fish, Kraaijeveld, 2010), and this is perhaps the case with the ascomycetes. In the end, speciation rates cannot be explained by a single

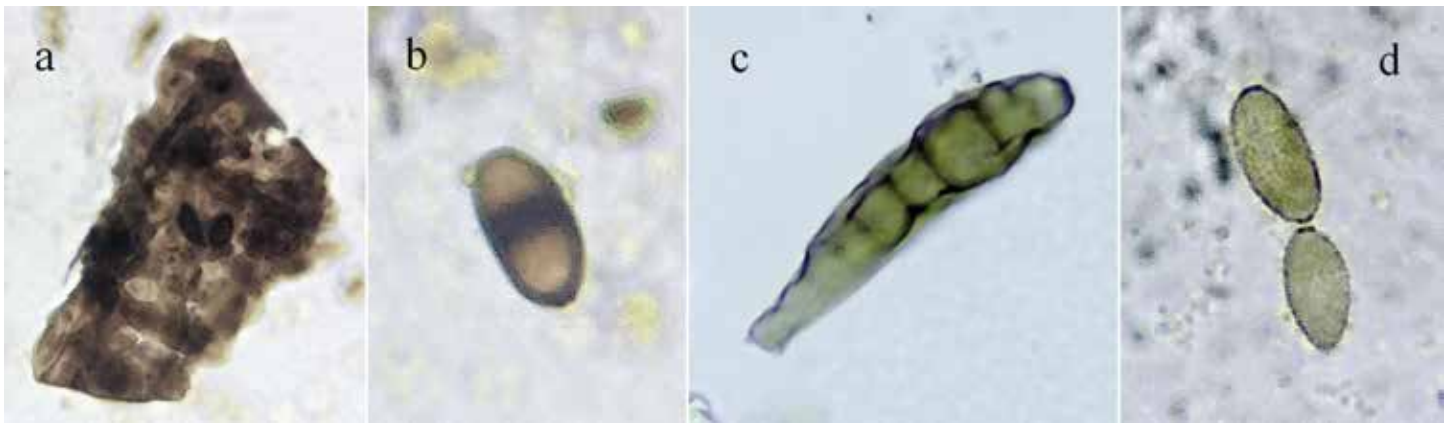


Figure 5. a and b) Ascospores in a plant fragment (Sumatra, Miocene ~23 MYA), 6.5x13 μm and 10x18 μm . c) Conidium (Mexico, ~16 MYA), 13x35 μm . d) Ascospores cf. *Peziza* sp. (Mexico, ~16 Ma), 10x20.5 μm . All images by the author.



Figure 6. *Gondwanagaricites magnificus* from Chapada do Araripe, Ceará, Brazil. Gill remains are identifiable on the left upper part. Source: Heads et al. (2017), License: Attribution 4.0 International (CC BY 4.0). Link: creativecommons.org/licenses/by/4.0/deed.de.

factor. The interrelations and causalities are too complex and, therefore, require more intense research, especially at the molecular level. Currently, the oldest known fossil of a macro-basidiomycete originates from the Cretaceous (ca. 115 MYA). It is a gilled mushroom, described as *Gondwanagaricites magnificus*, belonging to the Agaricales (Heads et al., 2017). The fossil exhibits the typical architecture of a mushroom (Fig. 6).

So far, the oldest known hyphae of a white rot fungus with clamp connections were described from the Lower Cambrian (Fig. 7).

Some micro-fossils have been isolated by the solvent method and these specimens can be attributed to basidiomycetes (Halbwachs, 2019a) (Fig. 9).

One can be sure that more finds of this kind will appear, which may fill gaps in the fossil record.

Parasites and symbioses

Fungal endophytes have apparently played a crucial role in the conquest of land, with a fuzzy passage from parasites to mutualists (see Box 4) (Krings et al., 2012). Arbuscular hyphal structures from strata of the German Lower Permian are one example (Fig. 10).

Associations with animals are likewise rather old. In the Burgsvik Sandstone (Gotland, Sweden, Upper Silurian ~425 MYA) Sherwood-Pike and Gray (1985) found coproliths (fossil excrements) of soil arthropods (springtails, mites or millipedes) associated with masses of hyphae and spores of ascomycetes (Fig. 11). In this case, the evidence points to fungi as a nutrient source.

It should also be noted that most of the “mosquitos” found in amber are fungus gnats (Ross, 2010), which points to a rich fungal flora in humid-temperate to tropical amber forests at that time.

In early terrestrial Earth history, symbiotic associations (parasitism to mutualism, see Box 4) are known first to occur together with plants, a condition which may have been required in order for fungi to colonize land (Selosse and Strullu-Derrien, 2015). In the process, lichens took an exceptional position because of their extreme adaptability (Taylor et al., 2015). They count as forebears of fundamental ascomycete groups as *Aspergillus* and *Penicillium* (Lutzoni et al., 2001). The alliance between fungi, cyanobacteria, and also algae is an evidently successful symbiosis because it arose independently around 30 times (!) during Earth’s history (Lücking and Nelsen, 2018). Particularly intense radiations began by the Paleogene ca. 50 MYA (Kettunen et al., 2017), as is evidenced from Bitterfeld amber (Fig. 12).

However, parasitic associations, e.g., between fungal pests and plants, can cause an accelerated evolution. Parasitic associations induce the syndrome of the so-called “Red Queen,” a character in Lewis Carroll’s

Box 4: Symbiosis, a stretchy affair.

First of all, a clarification: when do we speak about symbiosis, and when about mutualism? Or are both the same? In both the German and the English language usage, it gets merrily mixed up; the more so intermediate forms exist. *Sensu* Lewis (1985), it concerns the various relationships (symbiosis) of two or more organisms:

	+	*	-	
+	Mutualism			Species 1
-	Parasitism		Competition	Species 2

*Effect: - negative, + positive
Simplified after Bronstein 1994)

Fungal examples:

Competition	Displacement of <i>Xylaria hypoxolon</i> by <i>Megacollybia platyphylla</i> in deadwood (Rayner and Webber, 1984)
Parasitism	<i>Armillaria</i> sp. on living trees (Jahn, 1979)
Mutualism	Ectomycorrhiza of <i>Gomphidius maculatus</i> with larch

What is more, there are additional combinations that show that symbiosis is not a firmly defined lifestyle but forms a continuum (Bronstein, 1994).

Symbioses are evidently an evolutionary propellant. One of the most eminent biologists of our times, Lynn Margulis, even proposed that mutualistic symbioses were and are omnipresent and indispensable for the emergence and persistence of life (Margulis, 1998).

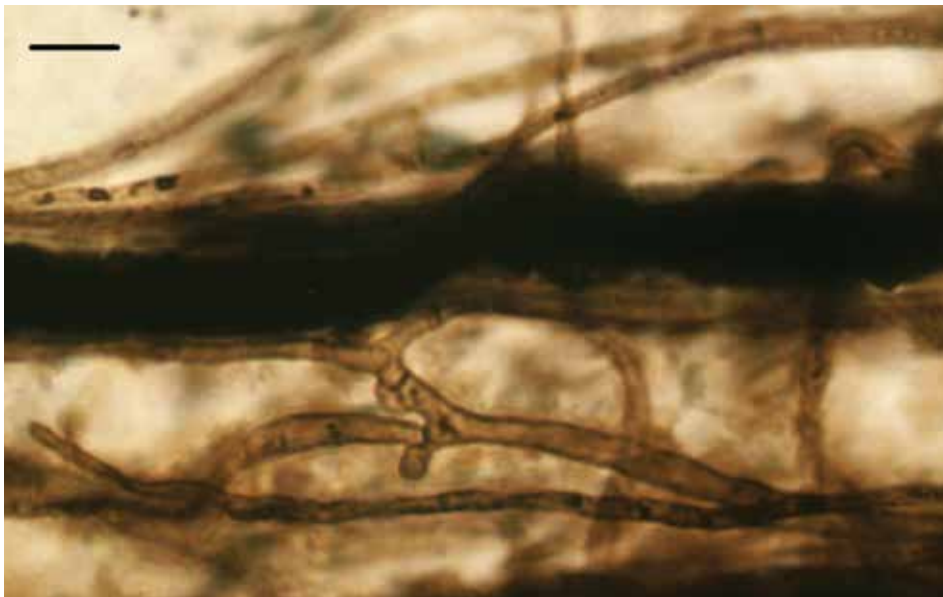


Figure 7. Hyphae of a ca. 135M old basidiomycete with clamp connections. Source: (Tian et al., 2018), courtesy Ning Tian; bar 10 µm.

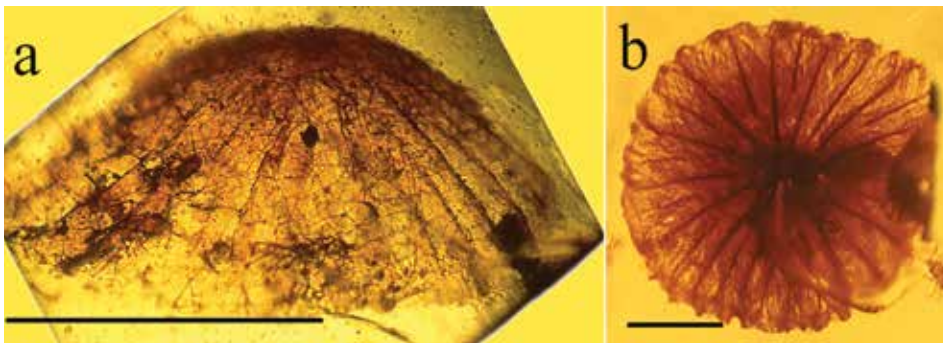


Figure 8. Basidiomycete fossilized in amber. a) *Nidula baltica* (Baltic, Eocene ~36 MYA); b) *Palaeoagaracites antiquus* (Myanmar, Upper Cretaceous ~100 MYA); c) *Coprinites dominicana* (Dominican Republic, Miocene ~18 MYA). Source: Poinar Jr (2016), all images courtesy George Poinar; bars 1 mm.

parable *Alice Through the Looking Glass*, who was forced to run ever faster to keep in place. Parasites trigger defense responses in the host, which in turn provoke adaptations by the parasite to breach the host's improved armament. Thus, an evolutionary chain reaction is initiated that leads to accelerated speciation (Van Valen, 1977). A further pivotal development, which began ca. 200 MYA, was the multiple emergences of ectotrophic associations between woody plants and asco- or basidiomycetes. A spectacular example has been detected in Indian amber ("Cambay amber") (Fig. 13).

The multiple emergences of a mutualistic lifestyle during the evolution of fungi (primarily mycorrhizae) entail new ecological opportunities and hence lead to significant radiations (Lutzoni and Pagel, 1997; Hoysted et al., 2018).

Impulses

What does the neverending story of fungi teach us? There were conspicuous speciation bursts, a phenomenon in line with the theory of the "Punctuated Equilibrium" of Eldredge and Gould (1972), who postulated that evolution occurs in erratic jumps. The erratic radiations of fungi were mainly sparked off by:

- Symbiotic associations, primarily with plants as endophytes (Krings et al., 2012).
- The emergence of the lichens (Lücking and Nelsen, 2018).
- Mycorrhizae were exceedingly innovative and successful in shaping and boosting resilience of ecosystems (van der Heijden et al., 2015).
- The emergence of mushrooms in the Agaricomycotina, which led to higher reproductive and dispersal fitness (Varga et al., 2019). This interpretation may well be too simplistic because this radiation involved a variety of morphological traits and combinations (Zmitrovich and Wasser, 2011).
- (Partial) extinctions like those documented towards the end of the Cretaceous, during which two-thirds of all life perished.

What's next? Evolution is not a directional force that only proceeds towards "improvement." Evolution is a tinkerer (Jacob, 1977) that works with

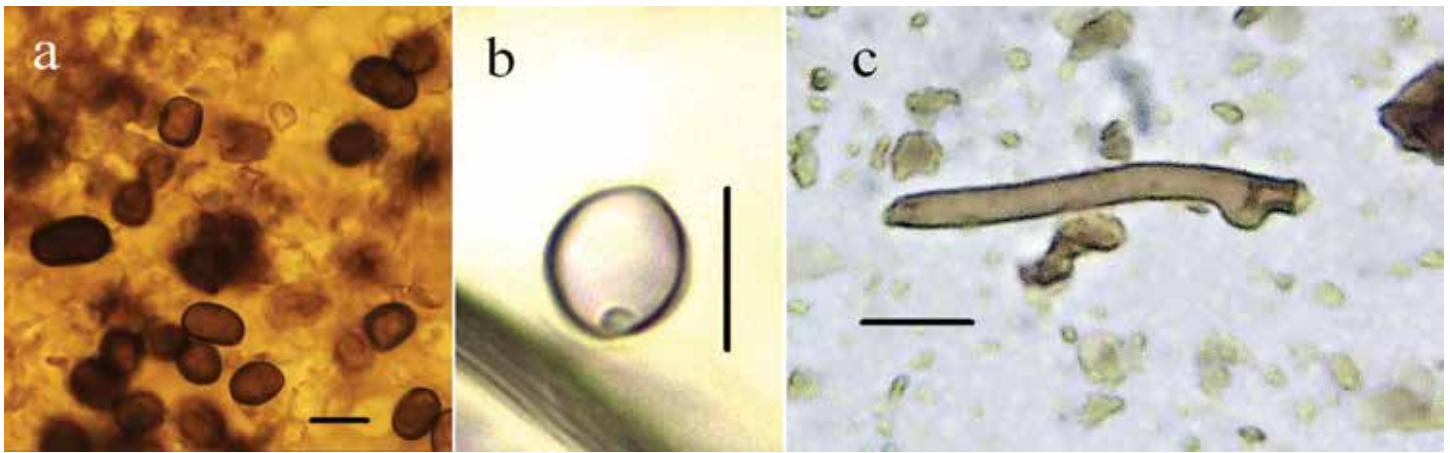


Figure 9. Micro-fossils of basidiomycetes isolated from amber. a) Basidiospores cf. *Psathyrella* (Baltic, Eocene ~36 MMY); b) Basidiospore cf. *Coprinus sensu lato* (Baltic, Eocene ~36 MYA); c) Hypha with clamp connection (Sumatra, Miocene ~23 MYA); bars 10 μm . All images by the author.

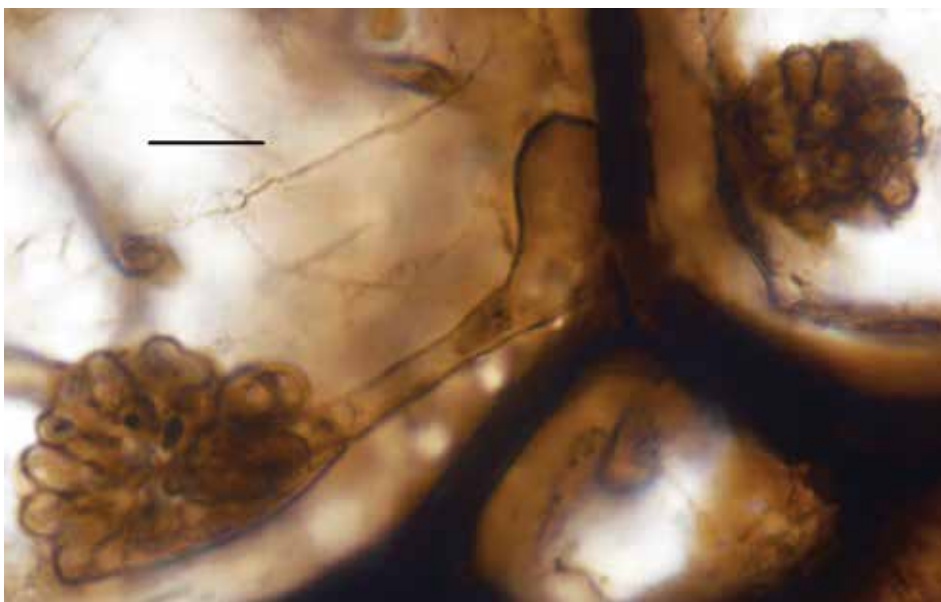


Figure 10. Arbuscular hyphal structures with appressoria at a *Psaronius* root (a tree fern). Image courtesy Michael Krings; bar 10 μm .

trial and error, leading to adaptation and speciation. Therefore, it cannot be predicted which new impulses will drive the ongoing evolution of fungi. One thing is clear: the progressive destruction of our natural environment spells trouble because the reduction of ecological diversity does at least impair evolutionary opportunities (see, e.g., stateoftheworldsfungi.org/2018/). The evidence presented herein is reason enough for mycologists to be engaged in combating this detrimental process.

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Literature cited

Beimforde, C., Feldberg, K., Nylander, S., Rikkinen, J., Tuovila, H., Dörfelt, H., Gube, M., Jackson, D.J., Reitner, J., and L.J. Seyfullah. 2014. Estimating the

Phanerozoic history of the Ascomycota lineages: combining fossil and molecular data. *Molecular Phylogenetics and Evolution* 78: 386–398.

Beimforde, C., Schäfer, N., Dörfelt, H., Nascimbene, P.C., Singh, H., Heinrichs, J., Reitner, J., Rana, R.S., and A.R. Schmidt. 2011. Ectomycorrhizas from a Lower Eocene angiosperm forest. *New Phytologist* 192(4): 988–996.

Bengtson, S., Rasmussen, B., Ivarsson, M., Muhling, J., Broman, C., Marone, F., Stampanoni, M., and A. Bekker. 2017. Fungus-like mycelial fossils in 2.4-billion-year-old vesicular basalt. *Nature Ecology & Evolution* 1: 141.

Berbee, M.L., and J.W. Taylor. 2001. Fungal molecular evolution: gene trees and geologic time. In: *Systematics and Evolution*, edited by Esser K., and P.A. Lemke. Springer: 229–245.

Bidartondo, M.I., Read, D.J., Trappe, J.M., Merckx, V., Ligrone, R., and J.G. Duckett. 2011. The dawn of symbiosis between plants and fungi. *Biology Letters* 7(4): 574–577.

Binder, M., and D.S. Hibbett. 2006. Molecular systematics and biological diversification of Boletales. *Mycologia* 98(6): 971–981.

Boenigk, J., Wodniok, S., and E. Glücksman. 2015. *Biodiversity and Earth History*. Springer Berlin Heidelberg.

Bonito, G., Smith, M.E., Nowak, M., Healy, R.A., Guevara, G., Cázares, E., Kinoshita, A., Nouhra, E.R., Domínguez, L.S., and L. Tedersoo. 2013. Historical biogeography and diversification of truffles in the Tuberales and their newly identified southern hemisphere sister lineage.

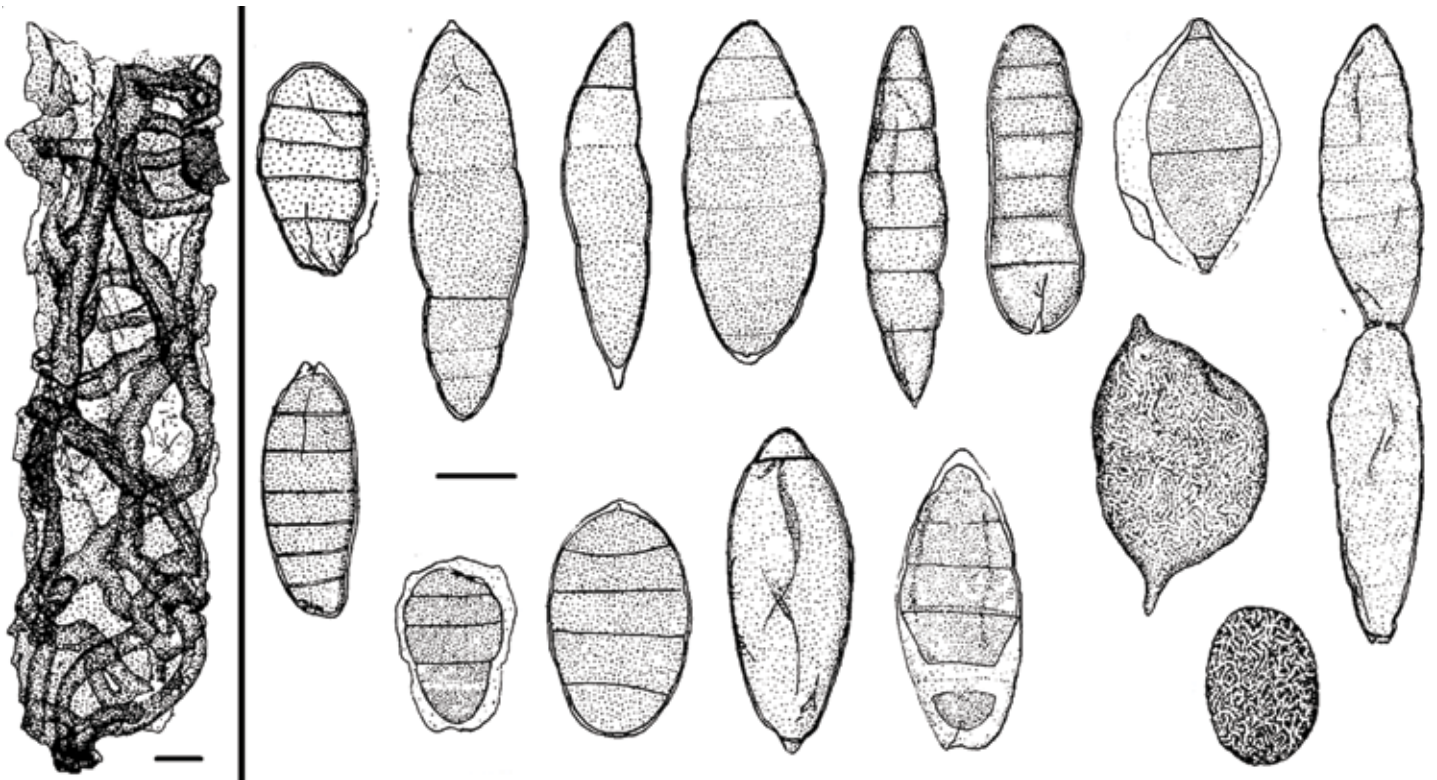


Figure 11. Fungal fragments from coproliths (Upper Silurian ~425 MYA); left) fragment with hyphae; right) various ascospores. Source: Sherwood-Pike and Gray (1985), license no. 4560231088779 (J. Wiley); bar 10 μm .

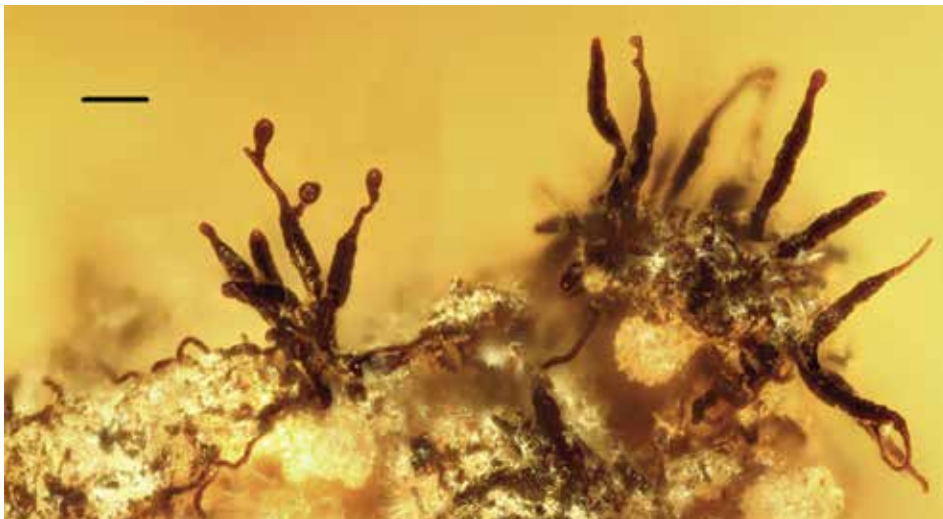


Figure 12. Conidia of a lichen from the Oligocene (ca. 25 MYA) (aff. *Sporidesmium*); Source: Kettunen et al. (2016), license no. 4561960273780 (J. Wiley); bar 50 μm .

PLoS One 8(1): e52765.
 Bresinsky, A., Körner, C., Kadereit, J.W., Neuhaus, G., and U. Sonnwald. 2008. *Lehrbuch der Botanik, 36. edition*. Spektrum Akademischer Verlag, Heidelberg.
 Bromham, L. 2016. *An Introduction to Molecular Evolution and Phylogenetics*. Oxford University Press.
 Bronstein, J.L. 1994. Conditional outcomes in mutualistic interactions. *Trends in Ecology & Evolution* 9(6): 214–217.

Calhim, S., Halme, P., Petersen, J.H., Læssøe, T., Bäessler, C., and J. Heilmann–Clausen. 2018. Fungal spore diversity reflects substrate-specific deposition challenges. *Scientific Reports* 8(1): 5356.
 Donoghue, P.C.J., and M.P. Smith. 2003. *Telling the Evolutionary Time: Molecular Clocks and the Fossil Record*. CRC Press.
 Dörfelt, H., and B. Striebich. 2000. *Palaeocybe striata*, ein neuer fossiler Pilz in Bernstein des Tertiär. *Zeitschrift*

für Mykologie 66(1): 27–34.
 Dyer, P.S. 2008. Evolutionary biology: genomic clues to original sex in fungi. *Current Biology* 18(5): R207–R209.
 Edwards, D., Cherns, L., and J.A. Raven. 2015. Could land-based early photosynthesizing ecosystems have bioengineered the planet in mid-Palaeozoic times? *Palaeontology* 58(5): 803–837.
 Eldredge, N., and S.J. Gould. 1972. Punctuated equilibria: an alternative to phyletic gradualism. In: *Models in Paleobiology*, edited by Schopf T. Freeman, Cooper & Company, San Francisco: 82–115.
 Fraser, J.A., and J. Heitman. 2004. Evolution of fungal sex chromosomes. *Molecular Microbiology* 51(2): 299–306.
 Halbwachs, H. 2019a. Detecting fungal spores and other micro-fossils in amber and copal by solvent treatment. *Palynology*: DOI 10.1080/01916122.2019.1633436.
 Halbwachs, H. 2019b. Fungi trapped in amber: a fossil legacy frozen in time. *Mycological Progress* 18(7): 879–893.
 Halbwachs, H., Brandl, R., and C. Bäessler. 2015. Spore wall traits of ectomycorrhizal and saprotrophic agarics may mirror their distinct lifestyles. *Fungal Ecology* 17: 197–204.

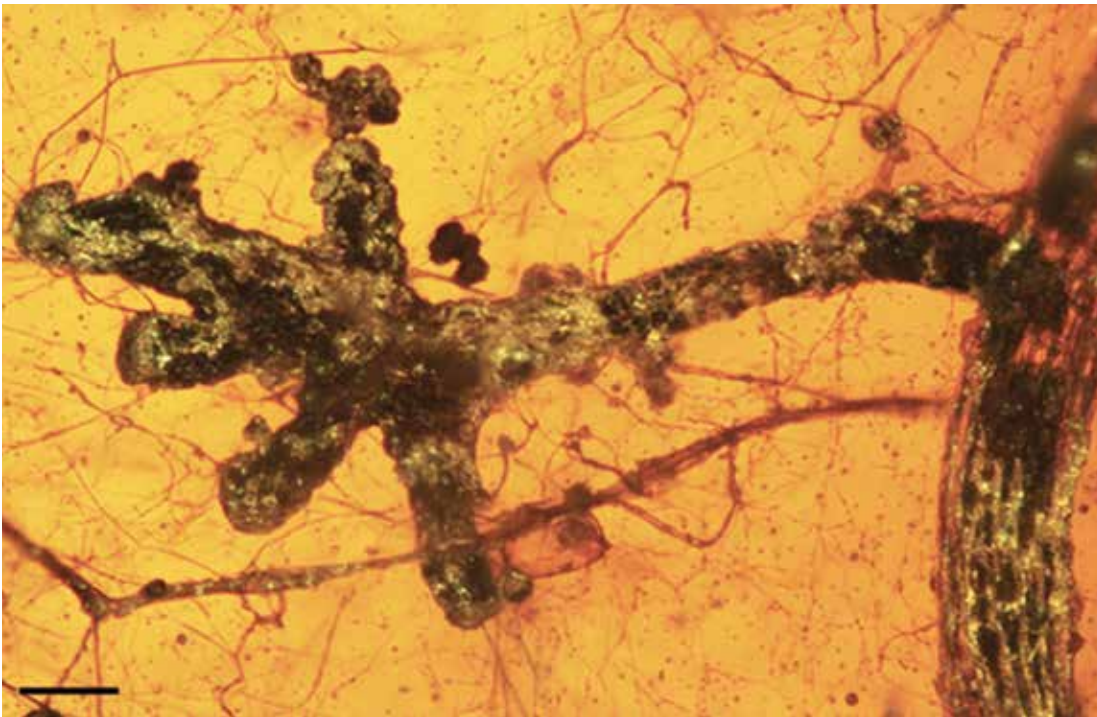


Figure 13. Rootlet of a dipterocarp tree from the Indian Lower Eocene (ca. 52 MYA) wrapped in a hyphal mantle typical for ectomycorrhiza. It is an ascomycete (*Eomelanomyces cenococcoides* Beimforde, Dörfelt et A.R. Schmidt). Source: Beimforde et al. (2011), license no. 4560630539390 (J. Wiley); bar 100 μm .

Halbwachs, H., and C. Bässler. 2015. Gone with the wind: a review on basidiospores of lamellate agarics. *Mycosphere* 6: 78–112.

Hawksworth, D.L., and R. Lücking. 2017.

Fungal diversity revisited: 2.2 to 3.8 Million Species. *Microbiology Spectrum* 5(4).

Heads, S.W., Miller, A.N., Crane, J.L., Thomas, M.J., Ruffatto, D.M., Methven,

A.S., Raudabaugh, D.B., and Y. Wang. 2017. The oldest fossil mushroom. *PloS One* 12(6): e0178327.

Hedges, S.B., Battistuzzi, F.U., and J.E. Blair. 2006. Molecular timescale of

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- evolution in the Proterozoic. In: *Neoproterozoic Geobiology and Paleobiology*, edited by Xiao S., and A.J. Kaufman. Springer: 199–229.
- Honegger, R., Edwards, D., Axe, L., and C. Strullu-Derrien, 2017. Fertile *Prototaxites taiti*: a basal ascomycete with inoperculate, polysporous asci lacking croziers. *Philosophical Transactions of the Royal Society B: Biological Sciences* 373(1739): 20170146.
- Hoysted, G.A., Kowal, J., Jacob, A., Rimington, W.R., Duckett, J.G., Pressel, S., Orchard, S., Ryan, M.H., Field, K.J., and M.I. Bidartondo. 2018. A mycorrhizal revolution. *Current Opinion in Plant Biology* 44: 1–6.
- Jacob, F. 1977. Evolution and tinkering. *Science* 196(4295): 1161–1166.
- Jahn, H. 1979. *Pilze die an Holz wachsen*. Buchdruckerei und Verlag Busse, Herford.
- Kettunen, E., Schmidt, A.R., Diederich, P., Grabenhorst, H., and J. Rikkinen. 2016. Lichen-associated fungi from Paleogene amber. *New Phytologist* 209(3): 896–898.
- Kettunen, E., Schmidt, A.R., Diederich, P., Grabenhorst, H., and J. Rikkinen. 2017. Diversity of lichen-associated filamentous fungi preserved in European Paleogene amber. *Earth and Environmental Science Transactions of The Royal Society of Edinburgh* 107(2–3): 311–320.
- Kirk, P.M., Cannon, P.F., Minter, D.W., and J.A. Stalpers. 2011. *Ainsworth & Bisby's Dictionary of the Fungi, 10th edition*. Cabi Publishing.
- Knudsen, H., and J. Vesterholt. 2012. *Funga Nordica: Agaricoid, Boletoid, Clavarioid, Cyphelloid and Gastroid Genera*. Nordsvamp, Copenhagen.
- Kraaijeveld, K. 2010. Genome size and species diversification. *Evolutionary Biology* 37(4): 227–233.
- Krings, M., Dotzler, N., Galtier, J., and T.N. Taylor. 2011. Oldest fossil basidiomycete clamp connections. *Mycoscience* 52(1): 18–23.
- Krings, M., Taylor, T.N., and N. Dotzler. 2012. Fungal endophytes as a driving force in land plant evolution: evidence from the fossil record. In: *Biocomplexity of Plant-Fungal Interactions*, edited by Southworth D. John Wiley & Sons: 5–27.
- Krumbiegel, G., and B. Krumbiegel. 1994. *Bernstein-Fossile Harze aus aller Welt*. Goldschneck Verlag, Weinstadt.
- Levin, D.A. 2004. Ecological speciation: the role of disturbance. *Systematic Botany* 29(2): 225–233.
- Lewis, D.H. 1985. Symbiosis and mutualism: crisp concepts and soggy semantics. In: *The Biology of Mutualism: Ecology and Evolution*, Boucher D.H. Oxford University Press, USA: 29–39.
- Lomolino, M.V., Riddle, B.R., and J.H. Brown. 2006. *Biogeography*. Sinauer Associates, Sunderland, Mass.
- Loron, C.C., François, C., Rainbird, R.H., Turner, E.C., Borensztajn, S., and E.J. Javaux. 2019. Early fungi from the Proterozoic era in Arctic Canada. *Nature* 570: 232–235.
- Lücking, R., and M.P. Nelsen. 2018. Ediacarans, protolichens, and lichen-derived Penicillium: a critical reassessment of the evolution of lichenization in fungi. In: *Transformative Paleobotany*, edited by Krings M., Harper C.J., Cúneo NR, and G.W. Rothwell. Elsevier: 551–590.
- Lutzoni, F., Nowak, M.D., Alfaro, M.E., Reeb, V., Miadlikowska, J., Krug, M., Arnold, A.E., Lewis, L.A., Swofford, D.L., Hibbett, D., Hilu, K., James, T.Y., Quandt, D., and S. Magallón. 2018. Contemporaneous radiations of fungi and plants linked to symbiosis. *Nature Communications* 9(1): 5451.
- Lutzoni, F., and M. Pagel. 1997. Accelerated evolution as a consequence of transitions to mutualism. *Proceedings of the National Academy of Sciences* 94(21): 11422–11427.
- Lutzoni, F., Pagel, M., and V. Reeb. 2001. Major fungal lineages are derived from lichen symbiotic ancestors. *Nature* 411(6840): 937–940.
- Margulis, L. 1998. *Symbiotic Planet*. Basic Books, New York.
- Matheny, B., Moncalvo, J.-M., and S.A. Redhead. 2007. *Agaricales*. Version 09 May 2007. <http://tolweb.org/Agaricales/20551/2007.05.09> in The Tree of Life Web Project, <http://tolweb.org/>.
- Matheny, P.B., Curtis, J.M., Hofstetter, V., Aime, M.C., Moncalvo, J.-M., Ge, Z.-W., Yang, Z.-L., Slot, J.C., Ammirati, J.F., Baroni, T.J., Bougher, N.L., Hughes, K.W., Lodge, D.J., Kerrigan, R.W., Seidl, M.T., Aanen, D.K., DeNitis, M., Daniele, G.M., Desjardin, D.E., Kropp, B.R., Norvell, L.L., Parker, A., Vellinga, E.C., Vilgalys, R., and D.S. Hibbett. 2006. Major clades of Agaricales: a multilocus phylogenetic overview. *Mycologia* 98(6): 982–995.
- Mayhew, P.J. 2006. *Discovering Evolutionary Ecology: Bringing Together Ecology and Evolution*. Oxford University Press Oxford.
- McElwain, J.C., and S.W. Punyasena. 2007. Mass extinction events and the plant fossil record. *Trends in Ecology & Evolution* 22(10): 548–557.
- Miller, S.L., Larsson, E., Larsson, K.–H., Verbeken, A., and J. Nuytinck. 2006. Perspectives in the new Russulales. *Mycologia* 98(6): 960–970.
- Mohanta, T.K., and H. Bae. 2015. The diversity of fungal genome. *Biological Procedures Online* 17(1): 8.
- Moore, D. 2013. *Fungal Biology in the Origin and Emergence of Life*. Cambridge University Press.
- Moore, D., Robson, G.D., and A.P.J. Trinci. 2011. *21st Century Guidebook to Fungi*. Cambridge University Press.
- Nagy, L.G., Papp, T., and C. Vágvölgyi. 2012. Comparative methods in fungal evolutionary biology: theory, examples and potential applications. In: *Systematics and Evolution of Fungi*, edited by Misra J., Tewari J., and S. Deshmukh. CRC Press: 363–397.
- Penney, D., and D.I. Green. 2010. Introduction, preparation, study and conservation of amber inclusions. In: *Biodiversity of Fossils in Amber from the Major World Deposits*, edited by Penney D. Siri Scientific Press, Manchester: 5–21.
- Penney, D., and R.F. Preziosi. 2010. On inclusions in subfossil resins (copal). In: *Biodiversity of Fossils in Amber from the Major World Deposits*, edited by Penney D. Siri Scientific Press, Manchester: 299–303.
- Pieńkowski, G., Niedźwiedzki, G., and M. Waksmundzka. 2011. Sedimentological, palynological and geochemical studies of the terrestrial Triassic-Jurassic boundary in northwestern Poland. *Geological Magazine* 149(2): 308–332.
- Poinar Jr, G., and R. Poinar. 1999. *The Amber Forest: A Reconstruction of a Vanished World*. Princeton University Press, Princeton, New Jersey.
- Poinar Jr, G.O. 2016. Fossil fleshy fungi (“mushrooms”) in amber. *Fungal*

- Genomics & Biology* 6(2): DOI 10.4172/2165-8056.1000142.
- Prieto, M., and M. Wedin. 2013. Dating the diversification of the major lineages of Ascomycota (fungi). *PLoS One* 8(6): e65576.
- Rabosky, D.L. 2009. Ecological limits and diversification rate: alternative paradigms to explain the variation in species richness among clades and regions. *Ecology Letters* 12(8): 735–743.
- Racki, G. 2019. Big 5 Mass Extinctions. *Paleobiology* 30: 522–542.
- Rayner, A.D.M., and J.F. Webber. 1984. Interspecific mycelial interactions: an overview. In: *The Ecology and Physiology of the Fungal Mycelium*, edited by Jennings D.H., and A.D.M. Rayner. Cambridge University Press: 383–417.
- Retallack, G., and E. Landing. 2014. Affinities and architecture of Devonian trunks of *Prototaxites loganii*. *Mycologia* 106(6): 1143–1158.
- Ross, A. 2010. *Amber: The Natural Time Capsule*. Firefly Books.
- Ryberg, M., and P.B. Matheny. 2011. Asynchronous origins of ectomycorrhizal clades of Agaricales. *Proceedings of the Royal Society B: Biological Sciences* 279(1735): 2003–2011.
- Schluter, D. 2017. Speciation and macroevolution. In: *The Princeton Guide to Evolution*, edited by Losos J.B. Princeton University Press: 485–489.
- Schmidt, A.R., and H. Dörfelt. 2007. Evidence of Cenozoic Matoniaceae from Baltic and Bitterfeld amber. Review of *Palaeobotany and Palynology* 144(3–4): 145–156.
- Selosse, M.-A., and C. Strullu-Derrien. 2015. Origins of the terrestrial flora: a symbiosis with fungi? *BIO Web of Conferences*, EDP Sciences: 00009.
- Seyfullah, L.J., Beimforde, C., Dal Corso, J., Perrichot, V., Rikkinen, J., and A.R. Schmidt. 2018. Production and preservation of resins—past and present. *Biological Reviews* 93: 1684–1714.
- Sherwood-Pike, M.A., and J. Gray. 1985. Silurian fungal remains: probable records of the class Ascomycetes. *Lethaia* 18(1): 1–20.
- Soltis, D.E., Bell, C.D., Kim, S., and P.S. Soltis. 2008. Origin and early evolution of angiosperms. *Annals of the New York Academy of Sciences* 1133(1): 3–25.
- Steiner, M.B., Eshet, Y., Rampino, M.R., and D.M. Schwindt. 2003. Fungal abundance spike and the Permian-Triassic boundary in the Karoo Supergroup (South Africa). *Palaeogeography, Palaeoclimatology, Palaeoecology* 194(4): 405–414.
- Strullu-Derrien, C., Selosse, M.-A., Kenrick, P., and F.M. Martin. 2018. The origin and evolution of mycorrhizal symbioses: from palaeomycology to phylogenomics. *New Phytologist* 220(4): 1012–1030.
- Sweet, A., and D. Braman. 2001. Cretaceous-Tertiary palynofloral perturbations and extinctions within the Aquilapollenites Phytogeographic Province. *Canadian Journal of Earth Sciences* 38(2): 249–269.
- Taylor, J.W., and M.L. Berbee. 2006. Dating divergences in the Fungal Tree of Life: review and new analyses. *Mycologia* 98(6): 838–849.
- Taylor, T., Hass, H., and H. Kerp. 1999. The oldest fossil ascomycetes. *Nature* 399(6737): 648.
- Taylor, T.N., Krings, M., and E.L. Taylor. 2015. *Fossil Fungi*. Elsevier Science, London.
- Tedersoo, L., Sánchez-Ramírez, S., Kõljalg, U., Bahram, M., Döring, M., Schigel, D., May, T., Ryberg, M., and K. Abarenkov. 2018. High-level classification of the fungi and a tool for evolutionary ecological analyses. *Fungal Diversity* 90(1): 135–159.
- Thomas, G.M., and G.O. Poinar Jr. 1988. A fossil *Aspergillus* from Eocene Dominican amber. *Journal of Paleontology*: 62(1): 141–143.
- Thompson, J.N. 2017. Coevolution and speciation. In: *The Princeton Guide to Evolution*. Losos J.B. Princeton University Press: 537–544.
- Tian, N., Wang, Y., Zheng, S., and Z. Zhu. 2018. White-rotting fungus with clamp-connections in a coniferous wood from the Lower Cretaceous of Heilongjiang Province, NE China. *Cretaceous Research* DOI 10.1016/j.cretres.2018.11.011.
- van der Heijden, M.G.A., Martin, F.M., Selosse, M.-A., and I.R. Sanders. 2015. Mycorrhizal ecology and evolution: the past, the present, and the future. *New Phytologist* 205(4): 1406–1423.
- Van Valen, L. 1977. The Red Queen. *The American Naturalist* 111(980): 809–810.
- Varga, T., Krizsán, K., Földi, C., Dima, B., Sánchez-García, M., Sánchez-Ramírez, S., Szöllösi, G.J., Szarkándi, J.G., Papp, V., Albert, L., Andreopoulos, W., Angelini, C., Antonín, V., Barry, K.W., Bougher, N.L., Buchanan, P., Buyck, B., Bense, V., Catcheside, P., Chovatia, M., Cooper, J., Dämon, W., Desjardin, D., Finy, P., Geml, J., Haridas, S., Hughes, K., Justo, A., Karasiński, D., Kautmanova, I., Kiss, B., Kocsubé, S., Kotiranta, H., LaButti, K.M., Lechner, B.E., Liimatainen, K., Lipzen, A., Lukács, Z., Mihaltcheva, S., Morgado, L.N., Niskanen, T., Noordeloos, M.E., Ohm, R.A., Ortiz-Santana, B., Ovrebo, C., Rácz, N., Riley, R., Savchenko, A., Shiryaev, A., Soop, K., Spirin, V., Szebenyi, C., Tomšovský, M., Tulloss, R.E., Uehling, J., Grigoriev, I.V., Vágvölgyi, C., Papp, T., Martin, F.M., Miettinen, O., Hibbett, D.S., and L.G. Nagy. 2019. Megaphylogeny resolves global patterns of mushroom evolution. *Nature Ecology & Evolution* 3: 668–678.
- Wang, H., Guo, S., Huang, M., Lumbsch, H.T., and J. Wei. 2010. Ascomycota has a faster evolutionary rate and higher species diversity than Basidiomycota. *Science China Life Sciences* 53(10): 1163–1169.
- Wellman, C.H. 2003. Dating the origin of land plants. In: *Telling the Evolutionary Time*, edited by Donoghue P.C.J., and M.P. Smith. CRC Press, Boca Raton: 119–141.
- Wikström, N., Savolainen, V., and M.W. Chase. 2003. Angiosperm divergence times: congruence and incongruence between fossils and sequence divergence estimates. In: *Telling the Evolutionary Time*, edited by Donoghue P.C.J., and M.P. Smith. CRC Press, Boca Raton: 142–165.
- Yuan, X., Xiao, S., and T.N. Taylor. 2005. Lichen-like symbiosis 600 million years ago. *Science* 308(5724): 1017–1020.
- Zmitrovich, I.V., and S.P. Wasser. 2011. Phylogenetic conundrum of the mushroom-forming fungi (Agaricomycetes). In: *Systematics and Evolution of Fungi*, edited by Misra J., Tewari J., and S. Deshmukh. CRC Press: 206–252.

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