

Origin and evolution of fungus farming in wood-boring Coleoptera – a palaeontological perspective

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ABSTRACT

Insect–fungus mutualism is one of the better-studied symbiotic interactions in nature. Ambrosia fungi are an ecological assemblage of unrelated fungi that are cultivated by ambrosia beetles in their galleries as obligate food for larvae. Despite recently increased research interest, it remains unclear which ecological factors facilitated the origin of fungus farming, and how it transformed into a symbiotic relationship with obligate dependency. It is clear from phylogenetic analyses that this symbiosis evolved independently many times in several beetle and fungus lineages. However, there is a mismatch between palaeontological and phylogenetic data. Herein we review, for the first time, the ambrosia system from a palaeontological perspective. Although largely ignored, families such as Lymexylidae and Bostrichidae should be included in the list of ambrosia beetles because some of their species cultivate ambrosia fungi. The estimated origin for some groups of ambrosia fungi during the Cretaceous concurs with a known high diversity of Lymexylidae and Bostrichidae at that time. Although potentially older, the greatest radiation of various ambrosia beetle lineages occurred in the weevil subfamilies Scolytinae and Platypodinae during the Eocene. In this review we explore the evolutionary relationship between ambrosia beetles, fungi and their host trees, which is likely to have persisted for longer than previously supposed.

Key words: ambrosia, mutualisms, fossil, amber, Lymexylidae, Bostrichidae, Cretaceous

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I. INTRODUCTION

Wood is one of the most abundant natural organic compounds on Earth and a huge potential source of energy for

heterotrophic organisms. However, the lignocellulosic matrix precludes access to carbohydrates for many organisms because they do not have the necessary enzymatic machinery to digest it. Many fungi have cellulolytic enzymes, but may be

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limited in terms of their access to wood. Mutualistic associations between animals and fungi can unify their capacities for transport, dispersal, access to the source and its digestion, and shape one of the most advanced solutions for access to woody substrates (Mueller *et al.*, 2005). *Flavodon* (Basidiomycota), for example, is an ambrosia fungus that digests cellulose and lignin within wood (Kasson *et al.*, 2016). Wood-boring insects are important early decomposers of dead woody plant material and play a central role in nutrient cycling in forests, with fungal association complementing or improving the catabolic capacity of these beetles (Geib *et al.*, 2008) and facilitating the ecological and evolutionary success of both parties. Beetles, the largest group of eumetazoans on Earth, were among the first insects to colonize the wood of dead and dying trees, to which they brought communities of symbiotic fungi (Kirkendall, Biedermann & Jordal, 2015). These beetle–fungus relationships can be hugely destructive to forests, but also serve as an extremely informative model system in ecology and in understanding the evolution of symbioses. While most symbiotic beetles and fungi are important early decomposers of dead wood, in some contexts this symbiosis may reduce decay rates by outcompeting other wood-decaying fungi (Skelton *et al.*, 2019b). Research on the beetle–fungus symbiosis has advanced greatly during the last decade (Hulcr & Stelinski, 2017), however many unanswered questions remain, and we still lack a solid theoretical background and mechanistic understanding (Hulcr *et al.*, 2020).

The origins of insect–fungus mutualisms are unclear. Herein we present an evolutionary overview of the tree–beetle–pathogenic fungus system by analysing data from the fossil record. This is the first time that the evolutionary histories of ambrosia beetles and ambrosia fungi have been compared and analysed in a wide context including fossils of the groups involved. We suggest that Lymexylidae and Bostrichidae should be considered facultative ambrosia beetles, because some extant species in these families cultivate ambrosia fungi, and that they were potentially early vectors for ambrosia fungi, which have an older origin than ambrosia beetles.

We use definitions of bark beetles and ambrosia beetles provided by Kirkendall *et al.* (2015). Ambrosia beetles have larvae that feed primarily on symbiotic ambrosia fungi cultivated by the parent beetle in tunnels or caves in woody tissues. With the inclusion of Lymexylidae as facultative ambrosia beetles, we suggest that cultivation of fungi is not limited only to adult beetles as in Scolytinae or Platypodinae, but also includes cultivation by larvae (the farming stage in Lymexylidae). Whether or not farming beetles also consume wood in the cultivation process is not known (Kirkendall *et al.*, 2015), but this is not important in defining fungus cultivation. Bark beetles refers to groups of beetles that breed in the inner bark and feed primarily on phloem or inner bark, where fungi may be beneficial dietary supplements, but are not actively cultivated.

We suggest that new data from the fossil record should be used to recalibrate the phylogenetic analyses, potentially affecting the ecological interpretations. Analysing current data within this new context, we suggest that Lymexylidae and Bostrichidae, which are relatively abundant in the

Cretaceous fossil record, were likely among the earliest vectors of ambrosia fungi. The symbiosis evolved later in Scolytinae and Platypodinae between the late Cretaceous and the Eocene. Many new fungal lineages were adopted by multiple lineages of these ambrosia beetles, thereby reaching the advanced level of specificities that we see today.

II. FUNGUS-FARMING BEETLES

Ectosymbioses between beetles and fungi are known in detail from relatively few taxa (Biedermann & Vega, 2020). The best studied group are the scolytine ambrosia beetles (Curculionidae: Scolytinae), which receive much attention due to their economic significance. Several other beetle groups evolved fungal mutualisms, but are generally poorly investigated: the weevil subfamily Platypodinae (Curculionidae) and some species of Lymexylidae and Bostrichidae (Fig. 1). Additional beetle groups use fungi as a food resource, either feeding on fungi externally on the wood as in some Attelabinae (Curculionidae), Languriinae (Erotylidae) and Silphidae, or

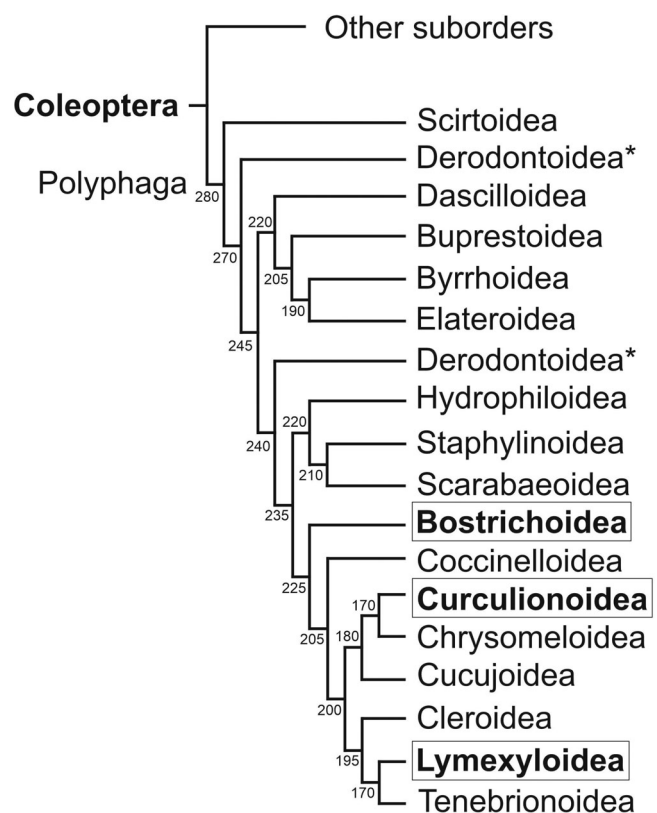


Fig 1. Phylogeny of Coleoptera extracted from Zhang *et al.* (2018). Superfamilies with ambrosia representatives are shown in rectangles and highlighted in bold. Numbers on nodes are estimated age in millions of years, following Zhang *et al.* (2018). *Derodontoidea is nested in two alternative positions.

using fungi as a supplementary food to the bark or phloem as in true bark beetles (Scolytinae).

Ambrosia beetles are a polyphyletic group of ecologically similar insects which are obligately dependent on nutritional fungal symbionts (Kirkendall *et al.*, 2015) (Fig. 1). Because of their diversity and economic importance, historically they were placed in an obviously polyphyletic group (*ca.* 3400 species) containing many independently evolved clades within the weevil subfamilies Scolytinae and Platypodinae (Hulcr & Stelinski, 2017). Ambrosia beetles live inside the plant host, inoculating their tunnel walls with fungal spores that the adults transport in their mycetangia, a variety of cuticular invaginations in their exoskeleton (Six, 2003). The fungal inoculum grows in the tunnel walls and serves as the sole source of food for the ambrosia beetles (Batra, 1963b; Harrington, 2005).

The Scolytinae (commonly known as bark and ambrosia beetles) utilize a variety of plant tissues for reproduction and feeding (Jordal, 2014a; Kasson *et al.*, 2016; Simmons *et al.*, 2016). Inner bark, or phloem, is more nutritious than bark or wood and is the most common food source for bark beetles, although some use leaf petioles, seedlings or seeds. Many bark beetles are known to benefit from fungal growth in the phloem which adds nutrients to their diet (Six & Paine, 1998). Ambrosia beetles, on the other hand, exploit Ascomycota and, to a lesser degree, Basidiomycota fungi as their sole food source (Kirisits, 2004; Hulcr & Stelinski, 2017). The Platypodinae occupy a similar niche to scolytine ambrosia beetles (Raffa, Grégoire & Lindgren, 2015). Platypodines comprise almost 1500 mostly tropical and subtropical species (Wood & Bright, 1992). With the exception of two basal taxa in this subfamily, all species are ambrosia beetles (Jordal, 2014b), cultivating ambrosia fungi (Ascomycota: Ophiostomatales and Saccharomycetales) in galleries bored into the wood (Li *et al.*, 2018).

Besides the ambrosia beetles in Scolytinae and Platypodinae other groups of beetles have symbiotic associations with fungi (Fig. 1), but the obligatory nature of their symbiosis is not well studied. Following Wilson (1971), who defined all beetles that cultivate fungi in wood as a food source (especially for larvae) as “fungus growing”, we include these as

ambrosia beetles. The family Lymexylidae contains less than 100 known species (Paulus, 2004), including forms known only from fossils (Fig. 2A), and their ambrosia habit has often gone unnoticed. Adult lymexylids are found in decaying wood, under bark, or on tree trunks, but their larvae are wood borers (Francke-Grosmann, 1967). In this group, it is the larvae that carry the fungal spores on their bodies into the wood and feed primarily on the fungi that grow in the walls of their galleries (Wheeler, 1986). Adult females emerge from the wood carrying spores in special invaginated pouches (Francke-Grosmann, 1967; Toki, 2021), which are eventually deposited in a slimy matrix with eggs. First-instar larvae display a characteristic prolonged twisting behaviour, ensuring contact of the larva with siblings and eggs, and resulting in the transfer of fungal spores onto the integument (Wheeler, 1986). Invaginated pockets on adult females have been described as mycetangia and illustrated in some species (Buchner, 1928; Francke-Grosmann, 1953, 1967; Toki, 2021). The fungi (Ascomycota: Saccharomycetales) associated with the larvae cover the walls of the tunnels (Batra, 1963b, 1967).

Another family of wood-boring beetles with a close relationship with fungi are the Bostrichidae. Their symbiosis with *Geosmithia* fungi (Kolarik, Kostovik & Pazoutova, 2007; Kolarik *et al.*, 2017) and with *Ophiostoma* fungi (Nel *et al.*, 2021) (both Ascomycota: Sordariomycetes) has only been reported anecdotally, explaining its omission from a previous review (Biedermann & Vega, 2020). Nevertheless, all obligate ambrosia relationships begin with a facultative association and we therefore include bostrichid beetles herein, as potentially representing an early stage in a symbiosis with ambrosia fungi (Figs 1, 2B). Bostrichidae are a small family of beetles containing about 570 species (Lawrence, 2010). They are wood borers in small to large tree trunks, branches or dead trees, digging galleries in which they lay eggs (Lawrence, 2010). They enter the phloem or xylem as adults and reproduce within the tree hosts. The larvae and adults of those that live in wood generally infest dead and dry wood (Ivie, 2002), but sometimes the larvae require the wood of freshly killed trees. Adult females may, in some cases, cause the death of the trees due to mechanical injury before colonization by the larvae (Wolcott, 1950).



Fig 2. Wood borers preserved in Cenomanian (Late Cretaceous) Kachin amber from Myanmar. (A) Picture of the holotype of *Raractocetus fossilis* Yamamoto, 2019, FMNHINS-3965990 (Lymexylidae); kindly provided by Dr Shuhei Yamamoto. (B) Wood borers (potential Bostrichidae). Previously unpublished specimen. Scale bars: (A) 3 mm, (B) 0.5 mm.

The Ptinidae, phylogenetically close relatives of Bostrichidae, have recently been rediscovered in a “forgotten system of symbiosis” with *Symbiotaphrina* (Ascomycota) (Martinson, 2020). However, this facultative relationship between the symbionts has extracellular and intracellular stages during the life cycle of their beetle hosts and the beetles do not truly farm these fungi. There are also examples of beetle families that farm fungi outside the wood, such as Attelabinae (Curculionidae) (Wang *et al.*, 2015), Languriinae (Erotylidae) (Toki *et al.*, 2012) and Silphidae (Shukla *et al.*, 2018). Because the symbiotic farming occurs exclusively outside the wood, these systems are not considered further herein.

III. EVOLUTION OF AMBROSIA BEETLES

Fungus farming provides efficient and rapid access to nutrition and allows the colonization of a broad diversity of host plants (Ayres *et al.*, 2000; Bleiker & Six, 2007). Unlike typical wood-boring species that specialize on a few host plants, fungus-farming species are largely generalists, and are able to breed successfully in a wide range of tree genera and families (Beaver, 1979). Thus, the specificity of the host plant seems to be determined by the symbiotic fungi and not the vectored beetle (Harrington, 2005; see Section V). Wherever moist and warm climates make fungus farming optimal, scolytine ambrosia beetles tend to be more abundant than bark beetles (Hulcr & Stelinski, 2017). Environmental conditions appear to be more favourable in the tropics, with high temperatures and humidity (Bentz & Jönsson, 2015).

By far the largest diversity of independently evolved ambrosia beetle lineages is seen in Scolytinae (Jordal & Cognato, 2012), with at least 11 independent transitions to fungus farming reported in this subfamily (Gohli *et al.*, 2017; Johnson *et al.*, 2018) as opposed to a single origin in Platypodinae (Jordal, 2015). There are many species in the various ambrosia beetle lineages in which this fungal relationship has never been investigated, with fungus farming often assumed but not proven (Hulcr & Stelinski, 2017). In Lymexylidae, fungus-farming symbiosis has only been studied in detail in females of a few species (Francke-Grosmann, 1967; Toki, 2021). Interestingly, there are no known cases of reversion from a fungus farming to non-farming habit in any beetle lineage (Jordal & Cognato, 2012; Vanderpool, Bracewell & McCutcheon, 2018), although recent research on fungal evolution suggests otherwise (Mayers *et al.*, 2020).

Conifers originally were thought to be the ancestral host for bark and ambrosia beetles, but this is unlikely to be true as they diversified in conjunction with the more recent angiosperm radiation (McKenna *et al.*, 2009). Within bark beetle genera, most species tend to specialize on either angiosperm or gymnosperm hosts, although some genera utilize host trees from both subdivisions (Gohli *et al.*, 2017). The many origins of conifer feeding in bark beetles all appeared within angiosperm-associated clades, probably no earlier than the late Cretaceous (Pistone, Gohli & Jordal, 2018). Fungus

farming in scolytine ambrosia beetle lineages evolved even later, and exclusively in angiosperm host plants (Farrell *et al.*, 2001; Jordal & Cognato, 2012; Raffa *et al.*, 2015; Gohli *et al.*, 2017). The use of conifer hosts occurred only recently in ambrosia beetles, and very few species specialize on these plants. Even though angiosperms were still early in their radiation at the beginning of the late Cretaceous (Friis, Crane & Pedersen, 2011; Doyle, 2012), they may have been more widespread than previously appreciated (Sauquet & Magallón, 2018; Li *et al.*, 2019).

Morphological differences between Scolytinae and true weevils (Curculionidae) gave rise to an interesting debate regarding the evolutionary affiliations of scolytine beetles (Jordal, Smith & Cognato, 2014). However, DNA sequencing data places Scolytinae firmly within Curculionidae (McKenna *et al.*, 2009; Gillett *et al.*, 2014; Shin *et al.*, 2017; Mugu, Pistone & Jordal, 2018), as do morphological characteristics of the larvae (Marvaldi *et al.*, 2002). The same data show that Platypodinae are not closely related to Scolytinae. The origin of Scolytinae has been estimated to be as late as the early Cenozoic (Shin *et al.*, 2017) but several studies indicate an older origin at 82 million years ago (Ma) (Gunter, Oberprieler & Cameron, 2016) or 112 Ma (Pistone *et al.*, 2018). Whichever estimate is correct, it seems that the largest radiation of scolytine beetles had occurred by the Eocene–Oligocene, apparently coinciding with the earliest estimated origin of fungus farming in this group at around 50 Ma (see Section V) (Jordal & Cognato, 2012; Gohli *et al.*, 2017; Pistone *et al.*, 2018) (Fig. 3).

The phylogenetic placement of Platypodinae was long debated. However, three recent in-depth analyses based on phylogenomic data reject a close relationship to Scolytinae and strongly support a sister relationship to Dryophthorinae (Curculionidae) (Gillett *et al.*, 2014; Shin *et al.*, 2017; Mugu *et al.*, 2018). This group is likely to have originated before Scolytinae, in the mid-Cretaceous, about 119–88 Ma (Jordal, 2015), even though the oldest fossils are much younger. Recent phylogenies suggest a similar age as Scolytinae, at least 75 Ma (Shin *et al.*, 2017), during the Campanian (Fig. 3). Limited availability of suitable growth conditions for the fungi may have contributed to the low initial rate of ambrosia beetle diversification during the first half of this lineage’s lifetime (Jordal, 2015). Diversification in Platypodinae only gained real momentum during the Late Palaeocene and Eocene with the origin of the clade Platypodini, coinciding with diversification of half of the known lineages of the ambrosia beetles in Scolytinae (Jordal & Cognato, 2012) during the Palaeocene–Eocene Thermal Maximum (PETM).

Lymexylidae are taxonomically distant from the previous two groups. Their phylogenetic position varies according to different studies, but the most recent and thoroughly sampled studies have suggested a close relationship to (or even within early-divergent) Tenebrionoidea (Bocak *et al.*, 2014; Gunter *et al.*, 2014; McKenna *et al.*, 2015; Zhang *et al.*, 2018) (Fig. 1). They show a mid-Jurassic origin, around 170 Ma (Zhang *et al.*, 2018) (Fig. 3). Bostrichidae are similarly distant from the weevils and from Lymexylidae. This beetle family

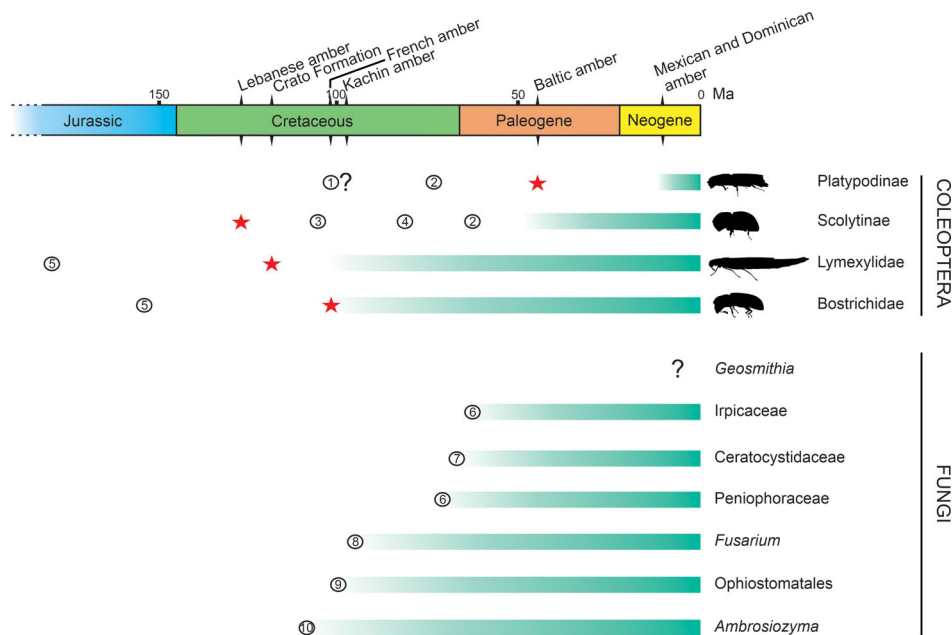


Fig 3. Geochronological ranges of ambrosia beetles, facultative ambrosia beetles and ambrosia fungi. The stars indicate the oldest fossil described for each taxon. The circles indicate the suggested divergence time of the taxon, which differs according to different sources: 1, Jordal (2015); 2, Shin *et al.* (2017); 3, Pistone *et al.* (2018); 4, Gunter *et al.* (2016); 5, Zhang *et al.* (2018); 6, He *et al.* (2019); 7, Mayers *et al.* (2020); 8, O'Donnell *et al.* (2013); 9, Vanderpool *et al.* (2018); 10, Shen *et al.* (2018). The bars indicate the range with an abundant fossil record for each coleopteran taxon and the suggested divergence for each fungal taxon (fossil records are scarce for fungal taxa).

belongs to Bostrichiformia, which diverged phylogenetically from Ptinidae about 157 Ma (Zhang *et al.*, 2018) (Fig. 3).

As Bostrichidae and Lymexylidae have not been recognized as true ambrosia beetles previously, claims that Platypodinae were the earliest ambrosia group currently prevail (Jordal & Cognato, 2012; Hulcr *et al.*, 2015; Jordal, 2015; Hulcr & Stelinski, 2017; Pistone *et al.*, 2018; Vanderpool *et al.*, 2018). Paradoxically, they are the latest of the four beetle groups known from the fossil record (Fig. 3). The earliest Scolytinae are from Early Cretaceous (~125 Ma, Barremian) Lebanese amber (Kirejtshuk *et al.*, 2009), the earliest Lymexylidae are from an Early Cretaceous (~120 Ma, Aptian) compression fossil from the Crato Formation of Brazil (Wolf-Schwenninger, 2011), the earliest Bostrichidae are from Late Cretaceous (~100 Ma, Cenomanian) French amber (Peris *et al.*, 2014) and the earliest Platypodinae are from Eocene (~45 Ma) Baltic amber (Peris *et al.*, 2017; Legalov, 2020) (Fig. 3). A hypothetical fossil platypodine was proposed from Kachin amber (Myanmar, ~99 Ma, Cenomanian), without description of the specimen (Cognato & Grimaldi, 2009), and this record is cited as the oldest record of this subfamily in some phylogenies (Jordal, 2015). Recently, Poinar, Vega & Legalov (2020) described a new platypodine from Kachin amber, but it was not accepted in Platypodinae or in Curculionoidea and was placed tentatively in Zopheridae (Clarke *et al.*, 2019). These authors also proposed that the platypodine cited by Cognato & Grimaldi (2009) was probably an odd bostrichid.

Fortunately, several phylogenetic analyses of weevils without calibration using these questionable fossils have resulted in fairly similar estimates of Platypodinae age (Shin *et al.*, 2017). There are also uncertainties associated with the age estimation for Scolytinae. The latest phylogenies of weevils (e.g. Shin *et al.*, 2017) excluded the Lebanese fossil scolytine, which may have led to an unrealistically recent estimation for Scolytinae. By contrast, the earliest Lymexylidae are described from the Aptian period, and these beetles are relatively abundant in Kachin amber of Cenomanian age (Yamamoto, 2019) but are also found in more modern Eocene Baltic and Miocene Dominican ambers (Wolf-Schwenninger, 2011; Yamamoto, 2019). A similar situation also occurs for Bostrichidae (Peris *et al.*, 2014; Legalov & Hava, 2020).

In conclusion, molecular phylogenies indicate a Mesozoic origin for all four groups of ambrosia and facultative ambrosia beetles (Jordal, 2015; Shin *et al.*, 2017; Pistone *et al.*, 2018; Zhang *et al.*, 2018), even though this is not always supported by the fossil record. None of these families are known from the Jurassic fossil record. Lymexylidae and Bostrichidae are abundant and diverse from the Cretaceous, mainly the late Cretaceous (Peris *et al.*, 2014; Clarke *et al.*, 2019; Yamamoto, 2019; Legalov & Hava, 2020), scolytine fossils are scarce in the Cretaceous (Cognato & Grimaldi, 2009; Kirejtshuk *et al.*, 2009, but see Clarke *et al.*, 2019) and not abundant until the Eocene (Hieke & Pietrezeniuk, 1984), and platypodines occurred in the Eocene (Peris *et al.*, 2017; Legalov, 2020),

but not abundantly until the Miocene (Bright & Poinar, 1994; Peris *et al.*, 2015) (Fig. 3). Therefore, the fossil record conflicts with estimates from molecular results. It must be noted, however, that fossil sources are scarce during the late Cretaceous, which may partly explain the absence of platypodine and scolytine fossils during their early diversification.

Both Scolytinae and Platypodinae have an estimated origin during the Cretaceous which, in the case of Platypodinae, does not agree with their fossil record – whereas two fossil scolytines, one definite (Lebanese amber) and one dubious (Kachin amber), are known to be from the Cretaceous. The small size of many species together with their cryptic lifestyle probably preclude their preservation in compression deposits of aquatic origin. Regarding amber deposits, all of the Cretaceous ambers originated from gymnosperms, where these beetle groups are absent (Platypodinae) or under-represented (Scolytinae) for different reasons. The ancestral association of these beetle groups is thought to be with angiosperm hosts (Pistone *et al.*, 2018) and thus they would have been absent from resiniferous gymnosperm forests. Resiniferous deposits seem to entrap arthropod fauna living primarily in or near the resiniferous tree (Solórzano Kraemer *et al.*, 2018), potentially explaining why these two groups of beetles are mostly absent from the fossil record until the Eocene (Cognato & Grimaldi, 2009), despite diversifying during the Cretaceous. The secondary adaptation of these beetles to gymnosperms around this time promoted their entrapment in the Eocene resins of gymnosperm origin. It is also likely that at least some groups of ambrosia beetles, Platypodinae in particular, were less diversified and perhaps less abundant in the Cretaceous, and therefore less likely to leave evidence as fossils, while they are well represented in Miocene and younger angiosperm resins.

IV. EVOLUTION OF AMBROSIA FUNGI

Ambrosia fungi, all of which depend on beetle vectors for transmission of propagules between trees, consist of a restricted set of unrelated species mainly from Ascomycota and some Basidiomycota (Mayers *et al.*, 2020) (Fig. 4). It is an active field of research where many more species and entirely new ambrosia lineages remain to be discovered (Batra, 1967; Hulcr & Stelinski, 2017). The phylogeny and evolution of fungi that have obligate arthropod associations is a focus of ongoing research (Mayers *et al.*, 2015, 2020; Skelton *et al.*, 2019a). Morphological and biological traits favouring insect dispersion have evolved many times in the Ascomycota (De Beer, Seifert & Wingfield, 2013; Mayers *et al.*, 2020).

Past efforts to reconstruct the evolutionary relationships in Ophiostomatales (Ascomycota: Sordariomycetes) have been inconclusive (Vanderpool *et al.*, 2018) and this phylogenetic uncertainty makes it difficult to address a long-standing question regarding the timing and number of domestication events for ambrosial cultivars in this group (Dreaden *et al.*,

2014). Ophiostomatoid fungi (Fig. 4) are a polyphyletic group of wood-infecting fungi that arose for the first time around 101 Ma, in the Albian (Early Cretaceous) (Vanderpool *et al.*, 2018) (Fig. 3). Over time, this group evolved multiple independent associations with arthropods (Vanderpool *et al.*, 2018). The two main genera of ambrosia fungi, *Raffaelea* and *Ambrosiella*, are both polyphyletic, and ambrosia lineages currently included in each of these genera arose independently at least five times (Cassar & Blackwell, 1996). A fossil of likely ophiostomatoid affinity was described in association with a fossil zopherid beetle (Clarke *et al.*, 2019) from Kachin amber (Poinar & Vega, 2018). The placement of this fossil in Ophiostomatales is controversial; genetic data indicate that classifications of ophiostomatoid fungi based on morphology are unreliable (Massoumi Alamouti, Tsui & Breuil, 2009; Dreaden *et al.*, 2014). For example, beetle-associated fungi in the two unrelated orders Ophiostomatales and Microascales (Ascomycota: Sordariomycetes) independently evolved nearly identical long-necked perithecia that attach sticky ascospore masses onto insect cuticles (De Beer *et al.*, 2013). Furthermore, the hypothetical mycetangial structure described in the femora of the fossil beetle from Kachin amber would be new in insect morphology.

Ambrosia fungi in the Microascales are all in the family Ceratocystidaceae (Fig. 4), which has received much attention in recent phylogenetic analyses (De Beer *et al.*, 2014, 2017; Mayers *et al.*, 2015; Nel *et al.*, 2017). However, the phylogenetic relationships of the ambrosia symbionts to the rest of the family remain poorly resolved. It is suggested that the clade accommodating all ambrosia fungi in this family had an estimated crown age of 62.4 Ma, in the Palaeocene (Fig. 3), and that, subsequently, three evolutionary events led to ambrosia symbiosis in Ceratocystidaceae (Mayers *et al.*, 2020).

The Hypocreales (Ascomycota: Sordariomycetes) have two known genera of ambrosia fungi: *Geosmithia* and *Fusarium* (Fig. 4). *Geosmithia* is an ascomycete genus of worldwide distribution, regularly found in association with phloem-feeding bark beetles in dry microhabitats (Kolarik & Kirkendall, 2010; Kolarik *et al.*, 2017). Spores of *Geosmithia* are thought to be transmitted by adhering to the exterior surfaces of their beetle vectors and are not known to be carried in mycetangia, as is the case for most mutualistic fungal associates of bark and ambrosia beetles (Huang *et al.*, 2019). Some are generalists, living in association with insects on a variety of plant hosts, while others are specialists restricted to wood-boring beetles living on Pinaceae conifers (Kolarik *et al.*, 2004, 2007; Veselská *et al.*, 2019). Species in this genus possess characteristics also found in several different ambrosia lineages of Ophiostomatales, Microascales and Saccharomycetales, probably as a result of convergent evolution (Kolarik & Kirkendall, 2010). Phylogenetic analyses using morphology and DNA sequences show that *Geosmithia* ambrosia fungi arose from various phloem-associated ancestors in the Hypocreales at least twice independently during the evolution of this genus (Kolarik & Kirkendall, 2010). A more specific analysis indicated that ecology has a greater effect on phenotype in *Geosmithia* species than does their

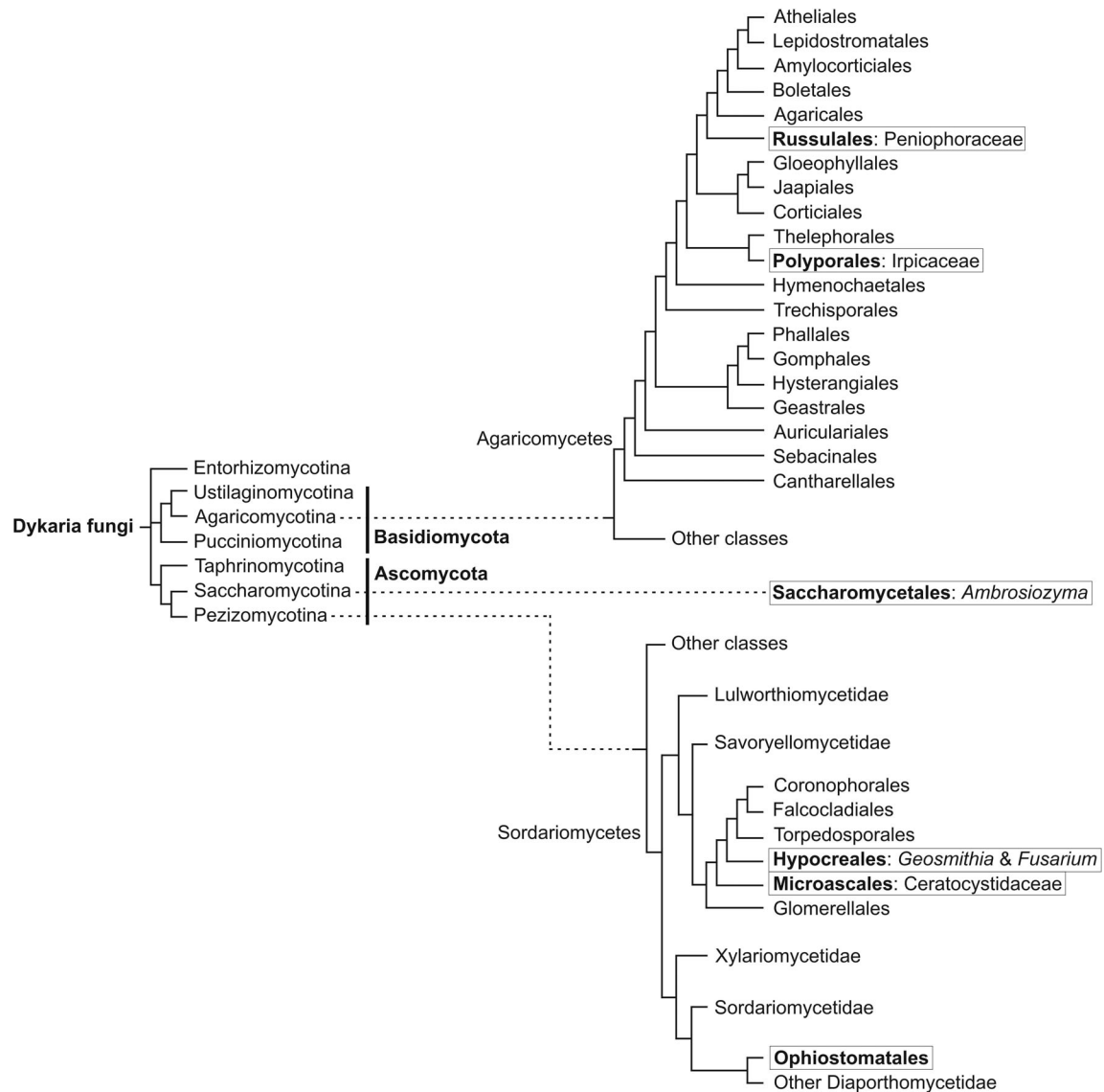


Fig 4. Phylogeny of Dykaria fungi extracted from Naranjo-Ortiz & Gabaldón (2019), Hibbett *et al.* (2014) (Agaricomycetes) and Hongsanan *et al.* (2017) (Sordariomycetes). Orders with ambrosia representatives are shown in rectangles and highlighted in bold.

phylogenetic relationships (Veselská *et al.*, 2019). Unfortunately, a time-calibrated phylogeny is not available for this genus (Fig. 3). Most species are saprotrophic, although two species are pathogens of oaks and walnut trees (Tisserat *et al.*, 2009; Lynch *et al.*, 2014). Due to frequent taxonomic misidentification, it is possible that nutritional symbiosis between *Geosmithia* and ambrosia beetles is more common than previously thought (Kolarik & Kirkendall, 2010), and it may be one of the most prevalent ambrosia fungi in the Neotropics (Hulcr & Stelinski, 2017; Kolarik *et al.*, 2017).

The massive fungal genus *Fusarium* contains over 300 species that occupy a broad array of ecological niches worldwide (Aoki, O'Donnell & Geiser, 2014). Many of these species are plant pathogens, and some *Fusarium* species are capable of causing disease and death of healthy trees when inoculated

by Xyleborini (Scolytinae) beetles in sufficient quantities (Brayford, 1987; Mendel *et al.*, 2012; Kasson *et al.*, 2013). Ambrosia fusaria form a strongly supported monophyletic group, designated the Ambrosia Fusarium Clade (AFC) (Kasson *et al.*, 2013). Mutualism between scolytine ambrosia beetles and *Fusarium* is thought to have originated near the Oligocene–Miocene boundary ~19–24 Ma. Cophylogenetic analyses indicated that the *Fusarium* phylogeny is largely incongruent with the adaptive radiation of the Xyleborini (O'Donnell *et al.*, 2015), contradicting previous suggestions (Kasson *et al.*, 2013). This incongruence is apparently due to the beetles switching fusarial symbionts at least five times during the evolution of this mutualism (O'Donnell *et al.*, 2015). Five of the agronomically most important and species-rich clades, including most of the mycotoxigenic

and phytopathogenic fusaria, began to diversify during the middle-to-late Miocene (O'Donnell *et al.*, 2013). The symbiosis between *Fusarium* and their vectors is relatively young compared to fungiculture in other ambrosia beetle groups that employ ophiostomoid and microascalean fungi (Fig. 3). A comprehensive and well-supported phylogenetic hypothesis of evolutionary relationships estimated the origin of the genus at approximately ~90 Ma, in the Turonian (Late Cretaceous), when the four most basal lineages diversified (O'Donnell *et al.*, 2013).

Yeasts have consistently been reported from both galleries and mycetangia of ambrosia beetles. The only true ambrosial clade in Saccharomycetales (Ascomycota) (Fig. 4) seems to be the genus *Ambrosiozyma* (Baltra, 1963a; Endoh, Suzuki & Benno, 2008; Hulcr & Stelinski, 2017), but the recent suggestion that lymexylids have an obligate relationship with *Alloascoidea* (Toki, 2021) might increase the number of ambrosia fungal clades. Other types of yeasts often are routinely reported (Berkov *et al.*, 2007; Davis, 2015; Toki, 2021), but these are probably non-specific commensals or parasites, occurring in subcortical spaces created by the wood-boring beetle (Hulcr & Stelinski, 2017). Multigene phylogenetic analyses have placed *Ambrosiozyma* as an early-diverging (~110 Ma, Albian) member (Fig. 3) of a clade formed by six other genera (Shen *et al.*, 2018). Many deep relationships in the subphylum Saccharomycotina are weakly supported, with most genera being paraphyletic or polyphyletic (Shen *et al.*, 2016), but not *Ambrosiozyma* (Shen *et al.*, 2018). Similarly, Alloascoideaceae is a small fungal family located in a phylogenetically basal position of the Saccharomycotina (Shen *et al.*, 2018) that consists of just two described species in one genus (*Alloascoidea*) that are suspected to have obligate relationships with lymexylids. If finally confirmed, this might represent the most ancient origin of an ambrosia fungus; *Alloascoidea* is thought to have diverged from other Saccharomycotina more than 200 Ma in the Triassic.

Basidiomycota fungi are rarely found in ambrosial association with beetles. Such associations were, until recently, only reported from a few species of bark and ambrosia beetles, with uncertain symbiotic interactions (see references in Whitney, Bandoni & Oberwinkler, 1987; Harrington, 2005). During the last 5 years, research on the genus *Flavodon* (Basidiomycota: Polyporales: Irpicaceae) has demonstrated a range of new characteristics for ambrosia symbiosis, typically associated with scolytine ambrosia beetles in the genera *Ambrosiodmus* and *Ambrosiophilus* which breed in white-rot decayed wood (Li *et al.*, 2015; Simmons *et al.*, 2016). *Flavodon ambrosius* is the only known ambrosial fungus that can digest both cellulose and lignin within wood, allowing for unique long-lived, communal colonies of beetles with overlapping generations (Kasson *et al.*, 2016). *Flavodon* is likely to have arisen recently in Irpicaceae; this family is thought to have a Palaeocene origin, around 62 Ma (He *et al.*, 2019) (Fig. 3). Another basidiomycete group, *Entomocorticium* (Russulales: Peniophoraceae) (Fig. 4), contains a single formally described species (Whitney *et al.*, 1987) and several undescribed species that specialize on decaying phloem of

conifers, primarily Pinaceae (Hsiau & Harrington, 2003; Hulcr & Stelinski, 2017). *Entomocorticium* is a nutritional symbiont of the mountain pine beetle *Dendroctonus ponderosae* (Whitney *et al.*, 1987). Phylogenetic analyses strongly support the monophyly of *Entomocorticium* and suggest a rapid radiation of this presumably very young clade (Hsiau & Harrington, 2003); the whole family Peniophoraceae is thought to have diverged around 70 Ma (He *et al.*, 2019) during the Maastrichtian (Fig. 3).

Mutualistic nutritional associations with a beetle as a vector thus have evolved repeatedly among distantly related fungal lineages. The earliest origin of Ascomycota ambrosia fungi is in *Ambrosiozyma* (~110 Ma; Shen *et al.*, 2018), followed by the Ophiostomatales (~101 Ma, Vanderpool *et al.*, 2018), both during the Albian, followed by *Fusarium* during the Turonian (~90 Ma; O'Donnell *et al.*, 2013), and later by emergence of the Ceratocystidaceae during the Danian (62.4 Ma; Mayers *et al.*, 2020). The age of the Hypocreales genus *Geosmithia* is not yet available. In Basidiomycota, ambrosia fungi are found in two families whose estimated familial origin, from molecular studies, occurred around the Cretaceous–Paleogene (K–T) boundary (70 Ma in the Peniophoraceae and 62 Ma in the Irpicaceae; He *et al.*, 2019). With the likely presence of some ambrosia fungal lineages from around 110 Ma, at least some of the oldest lineages must have used different insect vectors from those we know today (Fig. 3; see Section V).

V. EVOLUTION OF FUNGUS-FARMING BEHAVIOUR

Bark beetle–fungal interaction has been widely considered to be mutualistic, where one or several fungi benefit from transportation and inoculation in wood by the beetles, and the fungi provide beetles with essential vitamins, amino acids and sterols in return (Batra, 1967; Beaver, 1989; Paine, Raffa & Harrington, 1997; Krokene, 2015). The prevalent view of a one-to-one relationship between the acting symbionts has recently been challenged by observations of a multitude of fungal species occurring in a fungal community associated with a beetle, where one fungus often dominates and other community members demonstrate different degrees of specificity and mechanisms in the maintenance of community symbioses (Bracewell & Six, 2015; Kostovcik *et al.*, 2015; Skelton *et al.*, 2019a). Although physiological conditions in the beetle mycetangia possibly facilitate species-level specificity, the broader ecology of the association is determined by the symbiotic fungi, which are evolutionarily more specific to the host plant than to the beetle (Harrington, 2005; Six, 2012). The degree of selectivity in the mycetangium is nevertheless significant and was found to be correlated with fungus lineage in both ambrosia beetles and bark beetles (Bracewell & Six, 2015; Skelton *et al.*, 2019a). However, a shift of the main symbiont is not

impossible, and has been described under specific circumstances (O'Donnell *et al.*, 2015; Six, 2020).

Molecular data suggest an origin of the farming behaviour of Ophiostomatales ambrosia fungi by Platypodinae, at about 86 Ma, during the Santonian (Vanderpool *et al.*, 2018). The early origin of this group is long before the oldest known fossil of their beetle associates (Platypodinae). Similarly, the origin of fungus farming in Scolytinae is estimated at about 50 Ma (Jordal & Cognato, 2012; Pistone *et al.*, 2018), during the Eocene, long after the origin of this subfamily, and also long after the estimated origin for many of their associated ambrosia fungi (Fig. 3). Fungus farming in Scolytinae is estimated to have evolved after an increase in global temperatures during the PETM around 55.5 Ma, which possibly created more favourable conditions for moisture-requiring symbiotic fungi to diversify (Jordal & Cognato, 2012; Jordal, 2015; Gohli *et al.*, 2017). How the ambrosial fungal lineages were transmitted in the absence of ambrosia beetles, and whether other beetle groups were involved early in their evolutionary history, remains unknown. Lymexylidae and Bostrichidae, with an older origin and diversification than other ambrosia beetles, could potentially have played this role, but their time of origin and fungal associates are not known in any detail.

Ambrosia beetle groups in the Scolytinae evolved from bark beetle ancestors (Hulcr & Stelinski, 2017). Likewise, members of Platypodinae, appear to have originated from phloem-feeding weevils (Jordal, 2015). Therefore, differences between bark and ambrosia beetles may fall along a continuum of degrees of mycophagy (Hulcr & Stelinski, 2017). In light of the fossil record for various beetle groups, the phylogenetically derived position of ambrosia cultivation, and evidence that some beetle–fungus symbioses appear to be facultative (Kirisits, 2004), it must be assumed that early fungal associations occurred with as yet unknown ancient groups, in contrast to previous suggestions that Platypodinae are the oldest known group of farming insects (Vanderpool *et al.*, 2018) (Fig. 3). It is likely that these hypothetical ambrosial lineages became extinct because reversal to a phloem-feeding habit is not known in any current ambrosia beetle lineages.

The Ophiostomatales originated during the mid-Cretaceous (Vanderpool *et al.*, 2018). The fossil record available for beetles suggests that groups of beetles other than Platypodinae were most probably their earliest vectors (Fig. 3). Indeed, today, Ophiostomatales are not only associated with ambrosia beetles but are frequent facultative associates of bark beetles (Raffa *et al.*, 2015). Ophiostomatoid fungi provide supplementary food for bark beetles (Raffa *et al.*, 2015), and from such simple associations may have evolved the more intimate symbioses seen in farming ambrosia beetles (Batra, 1963b; Farrell *et al.*, 2001; Biedermann & Vega, 2020).

We suggest that the early presence of fungal species with the potential for cultivation facilitated the evolution of farming in beetles by serendipitous nutrient supplementation and subsequent modification towards an ambrosial lifestyle.

These fungi must have initially inhabited the same substrate as the beetle. Irrespective of the immediate benefit to the beetle, fungal spores can be transported by the beetle from one dead tree to another, representing potential fungal phoresy. Eventually, this association evolved into a more intimate symbiosis in which fungi are inoculated into a newly colonized tree, mycelia grow, and the beetle larvae then consume the long conidia. Vectoring of fungi within the gut may have been the ancestral mode of spore transmission (Kirkendall *et al.*, 2015). Later, various lineages of ambrosia beetles evolved an impressive array of different mycetangia as a means to ensure reliable fungus transmission. Indeed, almost all fungi involved in insect mutualisms are actively dispersed by their hosts, with the exception of fungus-growing termites (Biedermann & Vega, 2020). Variations within a species of beetles may nevertheless depend on their ecology and the surrounding host tree community, with climatic factors also playing an important role (Six & Bentz, 2007; Jankowiak *et al.*, 2017).

VI. CONCLUSIONS

- (1) The ambrosia beetles have been considered as comprising various lineages in the curculionid subfamilies Scolytinae and Platypodinae. Less well known is the facultative ambrosia symbiosis in some species of the wood-borer families Lymexylidae and Bostrichidae, and further studies on the ecology of these lymexylid or bostrichid species are much needed. It is likely that further examples of obligate fungus farming will be found in these two groups.
- (2) Molecular studies propose origins of the Scolytinae, Platypodinae, Lymexylidae and Bostrichidae at different times during the Mesozoic, in some cases conflicting with their fossil record.
- (3) Almost all known fossils of these four families of ambrosia beetles are from amber deposits. While there is a relatively abundant and diverse record of Lymexylidae and Bostrichidae starting from the Cretaceous, there is only a vague and dubious record of Scolytinae. A relatively abundant record of lymexylids and bostrichids from Kachin amber (99 Ma, Cenomanian) (Fig. 2) is currently under investigation. Scolytines are, by contrast, abundant only from the Eocene, the period in which the earliest Platypodinae are found. It should be noted that one of the two oldest platypodine fossils represents a derived modern lineage, strongly implying a much older age for the subfamily as a whole. It is also likely that Cretaceous and Eocene ambers of gymnosperm origin do not provide representative records of angiosperm-associated beetles and therefore we are likely to underestimate their existence.
- (4) Inference of ecological interactions and behaviour based on the fossil record is both challenging and controversial. However, some of the most typical ambrosia

fungi originated during the Cretaceous (Fig. 3), when groups of unknown insects may have acted as early vectors until their close relationship with Scolytinae and Platypodinae evolved. Those early vectors could include representatives of the more ancient families Lymexylidae and Bostrichidae (Fig. 3). Both beetles and fungi are therefore suspected of being involved in symbiotic relationships from the Early Cretaceous.

- (5) The ubiquitous presence of fungi and wood-boring beetles from the Early Cretaceous promoted the early domestication of some cultivars, such as *Raffaelea s.lat.* for example. The evolution of new lineages of ambrosia beetles and ambrosia fungi, and the capacity for symbiont shifting under specific conditions, will have favoured different fungus-farming associations, and facilitated different evolutionary pathways. In this sense, different mycophagous bark beetles independently exploited different fungi, leading to dramatic and perhaps irreversible morphological adaptations, and finally to successful symbioses.
- (6) Future studies dating the origins of all fungal cultivars in both Ascomycota and Basidiomycota divisions will help to clarify the evolution of the ambrosial lineages. More detailed study of the ecology and life cycles of lymexylids and bostrichids will open new lines of research and will better support our conclusions. Potential discoveries of new fossil material in future years could extend the fossil history of Scolytinae and Platypodinae deeper into the past, and could explain their early evolutionary associations with fungal symbionts. It remains necessary to update the calibration of beetle phylogenies using appropriate fossils in order to define the historical context of this particular symbiosis with more accuracy.
- (7) The search for the origin and explanation of the fungus-farming symbiosis is an interesting research theme that is receiving increasing attention from the scientific community (Hulcr *et al.*, 2020).

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