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Review

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The origin and evolution of mycorrhizal symbioses: from palaeomycology to phylogenomics

Author for correspondence:
Christine Strullu-Derrien
Tel: +33 (0)6 15 88 24 36
Email: c.strullu-derrien@nhm.ac.uk

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Christine Strullu-Derrien[1,2], Marc-André Selosse[3,4], Paul Kenrick[1] and Francis M. Martin[2]

[1]Department of Earth Sciences, The Natural History Museum, Cromwell Road, London, SW7 5BD, UK; [2]Interactions Arbres/Microorganismes, Laboratoire d'excellence ARBRE, Centre INRA-Lorraine, Institut national de la recherche agronomique (INRA), Unité Mixte de Recherche 1136 INRA-Université de Lorraine, 54280, Champenoux, France; [3]Institut Systématique Evolution Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE, 57 rue Cuvier, CP39, 75005 Paris, France; [4]Department of Plant Taxonomy and Nature Conservation, Faculty of Biology, University of Gdańsk, Wita Stwosza 59, 80-308 Gdansk, Poland

Contents

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Summary

The ability of fungi to form mycorrhizas with plants is one of the most remarkable and enduring adaptations to life on land. The occurrence of mycorrhizas is now well established in *c.* 85% of extant plants, yet the geological record of these associations is sparse. Fossils preserved under exceptional conditions provide tantalizing glimpses into the evolutionary history of mycorrhizas, showing the extent of their occurrence and aspects of their evolution in extinct plants. The fossil record has important roles to play in establishing a chronology of when key fungal associations evolved and in understanding their importance in ecosystems through time. Together with calibrated phylogenetic trees, these approaches extend our understanding of when and how groups evolved in the context of major environmental change on a global scale. Phylogenomics furthers this understanding into the evolution of different types of mycorrhizal associations, and genomic studies of both plants and fungi are shedding light on how the complex set of symbiotic traits evolved. Here we present a review of the main phases of the evolution of mycorrhizal interactions from palaeontological, phylogenetic and genomic perspectives, with the aim of highlighting the potential of fossil material and a geological perspective in a cross-disciplinary approach.

I. Introduction

In modern terrestrial ecosystems, plants, algae and cyanobacteria develop vital symbiotic associations with soil fungi and these relationships are known to be ancient. Pirozynski & Malloch (1975) hypothesized that 'terrestrial plants are the product of an ancient and continuing symbiosis of a semi-aquatic ancestral green alga and an aquatic fungus (. . .), and indeed the very evolution of plants was possible only through such mutualistic partnerships'. Usually the fungus receives carbon from the photosynthetic host, which in return is supplied with essential soil elements (e.g. nitrogen (N), phosphorus (P)). Other benefits include protection against biotic and abiotic adversities (e.g. drought, toxic compounds, parasites). Associations involving green algae or cyanobacteria take the form of lichens (Selosse & Le Tacon, 1998), whereas mycorrhizas are mutualistic relationships that develop exclusively with plants, being found in an estimated 85% of living plant species (Brundrett, 2004; Smith & Read, 2008; van der Heijden *et al.*, 2015; Brundrett & Tedersoo, 2018). Mycorrhizas are the main focus of the present review.

Mycorrhizal associations in living species take several forms that involve different plant and fungal clades (van der Heijden *et al.*, 2015). Endomycorrhizas, the most widespread associations, include the arbuscular mycorrhizas (AM) formed by the Glomeromycotina. These fungi commonly colonize roots and sometimes also the rhizomes (Wang & Qiu, 2006; Smith & Read, 2008; Pressel *et al.*, 2016) of vascular plants and the thalli of early-diverging land plants, namely liverworts (Marchantiophyta) and hornworts (Anthocerotophyta) (e.g. Strullu, 1985; Read *et al.*, 2000; Selosse, 2005; Duckett *et al.*, 2006; Pressel *et al.*, 2010; Desirò *et al.*, 2013). The AM symbiosis is thus phylogenetically widespread in plants. Hyphae grow in the apoplastic space between plant cells and they penetrate cells where they form arbuscules (i.e. branched structures involved in nutrient exchange between the plant and the fungus; Bonfante & Genre, 2010). They may also form vesicles (i.e. enlarged intraradical hyphae storing reserves; Smith & Read, 2008). Coil-forming endomycorrhizas similar to those formed in other groups were recently recognized in the Mucoromycotina (CMm). These take the form of intracellular hyphal coils, lumps and intercellular thick-walled and thin-walled fungal structures (Bidartondo *et al.*, 2011; Field *et al.*, 2012, 2015, 2016; Strullu-Derrien *et al.*, 2014). Mucoromycotina and Glomeromycotina are sister clades within the phylum Mucoromycota (Spatafora *et al.*, 2016; Tang *et al.*, 2016). Like AM, CMm develops in the thalli of early-diverging land plants, as well as in the roots of lycopods and ferns (Rimington *et al.*, 2015), sometimes simultaneously with Glomeromycotina (Bidartondo *et al.*, 2011; Desirò *et al.*, 2013; Strullu-Derrien *et al.*, 2014; Field *et al.*, 2016).

Another type, the ectomycorrhiza (ECM), is distinguished on the basis of a sheath of fungal hyphae enveloping the root and an intercellular penetration pattern where the hyphae form a network between cortical cells called a Hartig net (Strullu, 1985; Smith & Read, 2008). Many species of Ascomycota, Basidiomycota and a few members of the genus *Endogone* (Mucoromycotina) form ECMs (Yamamoto *et al.*, 2017). The associated plants are mostly shrubs and trees from temperate, boreal and Mediterranean regions, but there are also some ecologically important tropical families, including Dipterocarpaceae, Myrtaceae, Caesalpinioideae and Fagaceae (e.g. Alexander, 2006; Smith & Read, 2008; Tedersoo & Brundrett, 2017).

Finally, two plant families display endomycorrhizas involving Basidiomycota and Ascomycota, namely Orchidaceae (Dearnaley *et al.*, 2013) and one subclade of Ericaceae (Lallemand *et al.*, 2016). Here, a fungal sheath is absent, and the root cells are colonized by hyphal coils (Strullu, 1985; Smith & Read, 2008).

Because they are widespread, ancient, taxonomically diverse, and have arisen several times by convergence in plants and fungi, mycorrhizal symbioses provide an opportunity to investigate the evolution of plant—fungus interactions. Their long evolutionary history enables an analysis of their interactions and diversity in both modern and long extinct ecosystems. In this review, we summarize the palaeobotanical (including palaeomycological) knowledge in the light of recent plant and fungal phylogenomic studies, and we discuss the potential for interaction between these disciplines. From the fungal perspective, recent genomic advances have stimulated interest in understanding how and when fungal genomes evolved to adapt to mycorrhizal symbiosis and what genetic traits in plants and fungi make the symbiosis possible. Moreover, the transition from the ancestral, free-living niche to mycorrhizal status in fungal partners raises questions about intermediate steps and underlying evolutionary mechanisms. Finally, knowledge of the chronology of the events is important for investigating potential environmental drivers of the many independent acquisitions of mycorrhizal symbioses (Selosse *et al.*, 2015). The fossil record has an important role to play in establishing this chronology. It can also provide insights into ancestral traits and associations. Recent articles or reviews of the origin and evolution of mycorrhizal symbioses have focused on genomics of CMm and AM (Rimington *et al.*, 2016; Delaux, 2017; Kamel *et al.*, 2017) and ECM (Martin *et al.*, 2016, 2017), evolution and ecology (van der Heijden *et al.*, 2015) and responses of AM and CMm to environmental changes (Field *et al.*, 2015, 2016). Here, we explore the potential for dialogue between the fossil record, phylogenetics and genomics, which are complementary ways of seeing into the past (Selosse *et al.*, 2015; Strullu-Derrien *et al.*, 2016b; Berbee *et al.*, 2017).

This review follows a chronological description of the fossil record. We first discuss the oldest AM and CMm fungi and their evolution, based on fossils and sequenced genomes. Second, we analyse the emergence of plant roots in the context of the AM symbiosis in the Late Palaeozoic. Third, we report the diversification of the AM symbiosis after the Late Palaeozoic. Fourth, we discuss fossil evidence for the Mesozoic emergence of ECMs and the fungal genomic data that allow us to understand the iterative nature of their evolution. Lastly, we consider more recently evolved endomycorrhizas specific to Orchidaceae and Ericaceae. Based on this analysis, we discuss the limits of palaeontological vs genetic approaches and suggest some perspectives for cross-disciplinary research.

II. The mycorrhizal symbiosis at the dawn and rise of the land flora

Genetic evidence points to an early symbiotic interaction between the algal ancestors of plants (the Charophycean algae) and primitive fungi; however, compelling fossil evidence from fully aquatic environments is lacking (see Supporting Information Notes S1). Early continental fossils are scant and inconclusive in terms of evidence for symbiosis. Spores and hyphae of glomeromycotan affinity were documented from 460 million-yr-old sediments, but these fossils were not directly associated with plants (Redecker *et al.*, 2000). The earliest direct fossil evidence for plant–fungal interactions comes from the 407-million-yr-old Rhynie chert (Trewin & Rice, 2004) (Boxes 1, 2). Several types of endomycorrhizal associations have been documented and these were already diverse (Taylor & Krings, 2005; Strullu-Derrien *et al.*, 2014; Taylor *et al.*, 2015; Figs 1–4a–c, 5). The land vegetation in the Rhynie chert was characterized by plants of small stature (< 20 cm) with rhizoid-based rooting systems (Kenrick & Strullu-Derrien, 2014; Box 2). AM associations attributable to Glomeromycotina (Fig. 1) have long been known, but the first credible evidence for arbuscules was documented by Remy *et al.* (1994; see also Taylor *et al.*, 1995) in the aerial axes of the primitive plant *Aglaophyton majus* (Figs 3, 4a, 5). Arbuscules were also recorded in the haploid gametophyte phase of the life cycle (Taylor *et al.*, 2005b). Another plant species (*Rhynia gwynne-vaughanii*) only presented vesicles (Boullard & Lemoigne, 1971; Karatygin *et al.*, 2006). Although rhizoids are common entry points for fungi in many modern liverworts (Pressel *et al.*, 2010), the path of colonization was not observed in either fossil. In a third plant (*Nothia aphylla*), intercellular vesicles and spores were produced, but not arbuscules (Krings *et al.*, 2007). Here, the rhizoids were infected; however, as three different fungal species have been described in this plant (Krings *et al.*, 2007), it is uncertain that the rhizoids were colonized by the putative symbiotic fungus.

Multiple colonizations by different types of mycorrhiza have been recorded in Rhynie chert plants (Fig. 1). Strullu-Derrien *et al.* (2014) described a new species of Glomeromycotina colonizing the outer cortex at the base of the aerial axes of the fossil plant *Horneophyton lignieri* (Figs 2, 3). This fungus produced arbuscules, vesicles and spores, and probably entered the cortex through the epidermis (Fig. 3). Moreover, a Mucoromycotina colonization was found in the corm (Figs 2, 3) that developed densely packed thin-walled, nonseptate hyphae, thick-walled fungal structures in intercellular spaces, and intracellular coils typical of CMm (Fig. 4b,c). The mode of penetration of the corm by Mucoromycotina hyphae remains unclear, as all rhizoids were fungus-free. In both *Aglaophyton* and *Horneophyton*, all fungal structures developed in well-preserved, thin-walled turgescent cells, which is evidence that they were alive at the time of infection. These early fungal associations are often called mycorrhiza-like (Smith & Read, 2008) or paramycorrhizas (Strullu-Derrien & Strullu, 2007) because the plants had no true roots. This colonization of diverse organs, even photosynthetic ones, resembles that seen in modern liverwort and hornwort thalli (Strullu-Derrien & Strullu, 2007; Pressel *et al.*, 2010; Desirò *et al.*, 2013; Strullu-Derrien *et al.*, 2014; Field *et al.*, 2015, 2016).

While the mutualistic nature of these plant–fungal interactions cannot be demonstrated in fossils from a physiological perspective, the presence of key anatomical features (e.g. intracellular arbuscules and coils) clearly implies physiological exchange between partners. Furthermore, the distribution of fungi in restricted zones of tissues within the plant axis together with the absence of associated necrosis is consistent with mutualism. Recent physiological studies performed on modern analogues with paramycorrhizal associations (i.e. liverworts and hornworts) demonstrated the extent of plasticity of the functioning of the associations under simulated CO_2 concentrations of the mid-Palaeozoic (Field *et al.*, 2015, 2016). While recognizing that these experiments were done on living species adapted to modern CO_2 atmospheres, they nevertheless strengthen the case for mutualism in the early fossils.

The origin of modern fungus–plant associations, or at least of the evolutionary potential for such relationships, was probably established in the last common ancestor of Mucoromycotina and Glomeromycotina (Spatafora *et al.*, 2017), but the extent to which this ancestor would resemble its modern relatives remains an open question. The ubiquity and importance of Glomeromycotina have

Box 1 Geological and palaeoenvironmental context of the evolution of mycorrhizas

The early evolution of endomycorrhizas took place in a world in which land masses were configured into a massive Gondwanan element, extending from the equator to the South Pole, and several smaller blocks, the largest of which was Laurussia. The Early Palaeozoic commenced with an exceptionally high CO_2 atmosphere that declined to values close to those of today by the latter part of the Carboniferous (Franks *et al.*, 2014). One of the principal causes of falling atmospheric CO_2 was the development of land plants and the rise of forest ecosystems (Morris *et al.*, 2015). This enhanced two key drivers of the geochemical carbon cycle: weathering of calcium-magnesium silicates in rocks and carbon sequestration. The burial of vast amounts of organic carbon led to a rapid rise in atmospheric oxygen (Glasspool *et al.*, 2015). Therefore, the transition to root colonization by endomycorrhizas (in earlier fossils, they colonized aerial axes) occurred during declining levels of atmospheric CO_2 and increasing O_2 levels that probably enhanced respiration in soils (Fig. 3).

During the mid-Jurassic, the supercontinent Pangaea started to rift, giving rise to modern continents and ocean basins (Torsvik & Cocks, 2016). Geochemical models indicate a high CO_2 atmosphere through the period with a maximum of four to seven times the present-day level (Franks *et al.*, 2014). Ectomycorrhizal (ECM) symbiosis in Pinaceae probably originated in the continent of Laurasia during this period (Lin *et al.*, 2010; Rothwell *et al.*, 2012). 'Greenhouse' conditions prevailed through the Cretaceous and Paleogene, attaining peaks of short duration at the Paleocene–Eocene Thermal maximum (*c.* 55 million yr ago (Ma)) and in the Early Eocene (*c.* 51 Ma), before declining to present-day levels (Zachos *et al.*, 2001). Evidence from the fossil record of charcoal indicates that atmospheric O_2 remained at fairly constant levels (*c.* 20–21%) during the past 40 Ma (Glasspool *et al.*, 2015). Angiosperms expanded into high latitudes in Laurasia and Gondwana during the early part of the Upper Cretaceous (Francis *et al.*, 2008; Friis *et al.*, 2011). Rosids were part of this diversification. Thus ECM symbiosis probably originated under a high CO_2 atmosphere and tropical to subtropical climates.

Box 2 The early terrestrial communities

Early terrestrial communities most closely resembled modern Cryptogamic ground covers (CGCs; Edwards *et al.*, 2015; Mitchell *et al.*, 2016), a type of biological soil crust comprising varied and mixed associations of bacteria, arthropods, lichens, fungi, green algae and bryophytes. The plant component comprised cryptophytes – a poorly documented grade of extinct bryophyte-like plants belonging to land plants (Edwards *et al.*, 2014) – and later stem-group vascular plants (e.g. *Aglaophyton majus*, *Horneophyton lignieri*, *Nothia aphylla*) which differed significantly from modern forms. Many of these were leafless and rootless. They were anchored to the substrate by rhizoids. A simple vascular system comprising xylem cells with unthickened or helically thickened walls connected rhizoids to aerial axes that bore stomata in low densities (Edwards *et al.*, 2014; Kenrick & Strullu-Derrien, 2014). These plants displayed an intermediate level of complexity between bryophytes and vascular plants. Collembolans, mites, myriapods, trigonotarbid arachnids and possibly nematodes formed the soil fauna (Labandeira, 2005; Poinar *et al.*, 2008)

Lichen-like associations are recognized as a component of early terrestrial ecosystems, although apparently with a limited abundance (Selosse & Strullu-Derrien, 2015). Some of these were very simple and possibly they represent loose consortia of fungi and cyanobacteria rather than a proper mutualism (e.g. Taylor *et al.*, 1997). Others are more compelling as macrolichens because they contain plausible ascomycetes associated with either cyanobacterial or green algal photobionts and the thalli are dorsiventral with internal stratification (Edwards *et al.*, 2013; Honegger *et al.*, 2013). Earlier records of fossils assigned to the lichens lack credibility because details of anatomical structure are absent and they are plausibly interpreted as a variety of other things, ranging from inorganic sedimentary features to biofilms or early metazoans. Devonian Period ecosystems also contained important and unique organisms whose affinities and biology remain obscure. *Prototaxites* and related fossils, which were up to 8–10 m tall, may represent gigantic algal–fungal symbioses (Selosse, 2002; Selosse *et al.*, 2015; Honegger *et al.*, 2017). They disappeared when the first trees evolved, in the Mid-Devonian (350 million yr ago).

been understood for some time, but the significance of the Mucoromycontina in mycorrhizal symbioses has only recently been established. The discovery that Mucoromycotina form mycorrhizal associations was first made in the earliest diverging group of liverworts (Haplomitriopsida; Bidartondo *et al.*, 2011). Mucoromycotina resemble Glomeromycotina in having aseptate hyphae, endosymbiotic bacteria and asexual reproduction by chlamydospores, but they differ principally in having a broader ecology (i.e. saprotrophs, endomycorrhizal and ectomycorrhizal species) and, for some species, the ability to grow *in vitro* and develop sexually (Spatafora *et al.*, 2016, 2017). By contrast, Glomeromycotina are considered as asexual (however, this view has recently been challenged; Riley *et al.*, 2014) – and they are strict AM biotrophs on plants (or cyanobacteria; Schüßler, 2012). Further investigations revealed CM-forming Mucoromycotina in other early-diverging embryophytes (liverworts, most hornworts, and some early-branching vascular plants, e.g. lycophytes), sometimes in association with Glomeromycotina (Desirò *et al.*, 2013, 2014; Rimington *et al.*, 2015). Also, some species have been misattributed: the fungus commonly known as '*Glomus tenue*' might belong to Mucoromycotina (Orchard *et al.*, 2016). Both groups of fungi appear to be implicated in the early colonization of the land by plants, and it might be that terrestrialization involved an ancestral group from which Glomeromycotina and Mucoromycotina later diverged (Selosse & Strullu-Derrien, 2015; Field *et al.*, 2016). The idea that some early Paleozoic endomycorrhizas were formed by stem group Glomeromycotina and Mucoromycotina is consistent with a cross-species mutant rescue experiment (Wang *et al.*, 2010), where genes from Mucoromycota-associated liverworts can rescue AM formation in *Medicago*, suggesting that aspects of the CMm and AM symbioses share a common origin. Yet, this remains to be confirmed, especially by molecular clock dating of the divergence between Mucoromycotina and Glomeromycotina.

The recent discovery of homologues to plant hormone receptors in early-diverging fungi suggests the participation of plant sensing proteins (histidine kinases) in fungus–plant interaction processes, which may have helped the early-diversifying fungal lineages to colonize land (Hérivaux *et al.*, 2017). This study shows that phytohormone receptor homologues are present in both fungi that behave as plant root symbionts (i.e. Glomeromycotina, Mucoromycotina) and in early-diverging fungi that colonize decaying plant material (i.e. Blastocladiomycota, Chytridiomycota). Interestingly, Dotzler *et al.* (2006, 2009) found fossil spores in the Rhynie chert that are related to extant Diversisporales, which is a mycorrhizal sister group to Glomerales. Unlike related living species, these spores were found in degraded aerial axes of plants, indicating a possible ancestral saprotrophic mode of existence. Early fossils are consistently attributed to Glomeromycotina or Mucoromycotina (Strullu-Derrien *et al.*, 2014; Taylor *et al.*, 2015 and references therein), but we should be open to the possibility that some might be extinct stem group Mucoromycota. Continued investigation of the Rhynie chert land plants and other Palaeozoic remains will provide further evidence of the diversity of primitive plant–fungal relations and their status.

Genomics studies carried out on *Rhizophagus irregularis* (Tisserant *et al.*, 2013; Lin *et al.*, 2014), *Rhizophagus clarus* (Sędzielewska Toro & Brachmann, 2016) and *Gigaspora rosea* (Tang *et al.*, 2016) highlighted several genetic features of these obligate AM biotrophs that testify to their highly developed and long-standing relationships with plants. Although their gene repertoires are amongst the largest in Fungi (> 25 000 genes), they have lost several genes involved in major metabolic activities, including degradation of lignocellulose, and synthesis of polyketides, thiamine and fatty acids (Fig. 1). By contrast, they contain a striking overrepresentation of proteins predicted to play a role in signalling pathways (e.g. protein kinases), protein–protein interactions (e.g. Sel1-, BTB-, and WD-40 domain containing proteins), and sex (HMG-box containing proteins) compared with known fungal gene repertoires. These genes could facilitate their adaptation to fluctuating environments and different plant hosts. Additional evidence of a long-standing interaction with plants is the occurrence of dozens of mycorrhiza-induced small secreted proteins (MiSSPs) in *R. irregularis*, *R. clarus* and *G. rosea*. Some of these small proteins probably control plant immunity and development (Kloppholz *et al.*, 2011; Tsuzuki *et al.*, 2016) during

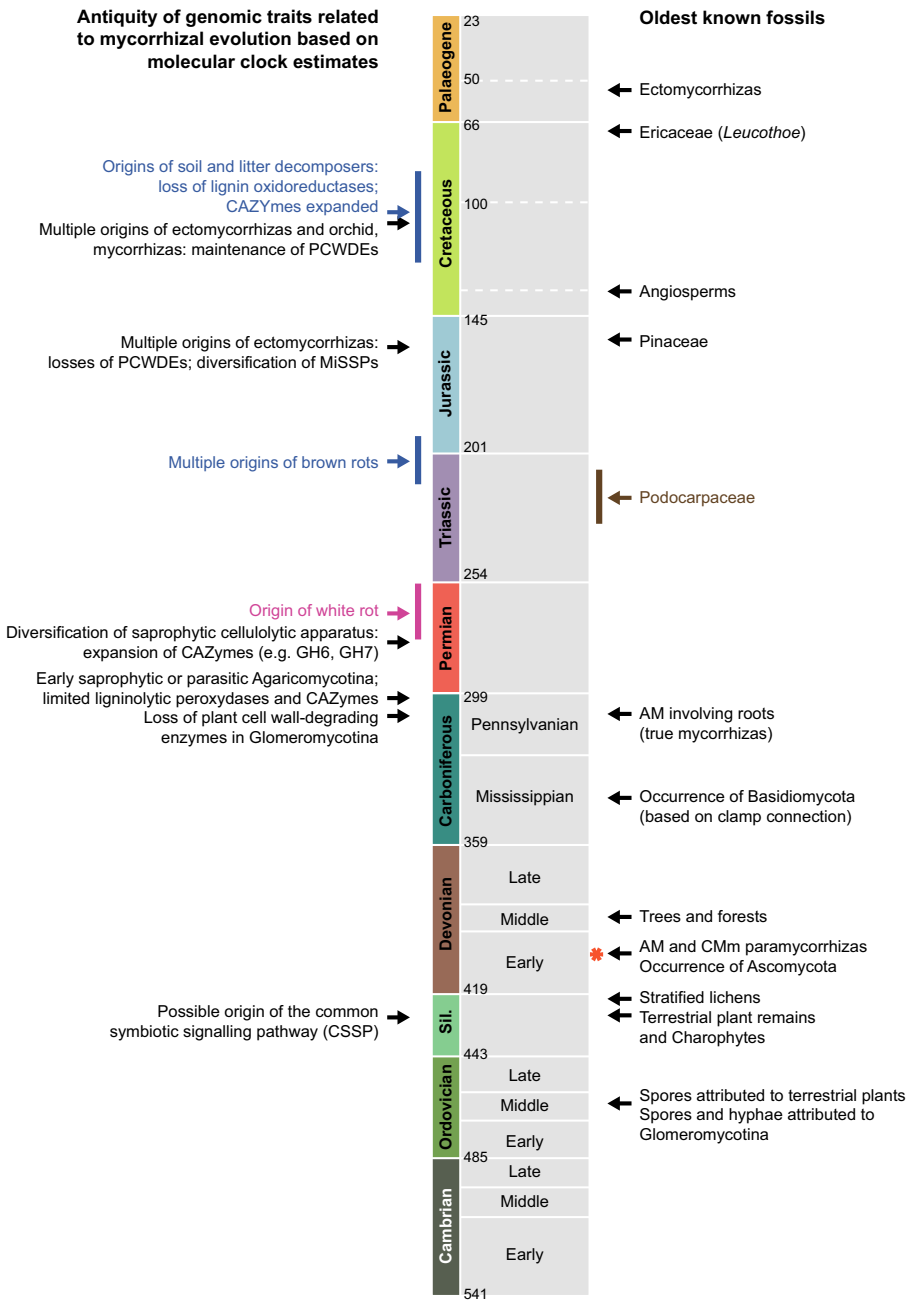

Fig. 1 Geological timescale with oldest known fossils (right: Feist *et al.*, 2005; Friis *et al.*, 2011; Honegger *et al.*, 2013; Krings *et al.*, 2011a,c; LePage *et al.*, 1997; Redecker *et al.*, 2000; Remy *et al.*, 1994; Rothwell *et al.*, 2012; Stein *et al.*, 2012; Strother *et al.*, 1996; Strullu-Derrien *et al.*, 2009, 2014; Taylor *et al.*, 1999) and antiquity of genomic traits based on molecular clock estimates (left: Floudas *et al.*, 2012; Kohler *et al.*, 2015; Martin *et al.*, 2016). The asterisk represents the Rhynie chert. AM, arbuscular mycorrhizas; CAZymes, Carbohydrate-Active enZYmes; CMm, coil-forming mycorrhizas in Mucoromycotina; MiSSPs, mycorrhiza-induced small secreted proteins; PCWDEs, plant cell wall-degrading enzymes.

the establishment of the symbiosis. Another striking feature of sequenced AM fungi is the lack of genes coding for the lignocellulose decay machinery, meaning that most of cell wall reshaping during the interaction, intercellular growth and intracellular penetration is carried out by the plant host. Characterization of the genomic diversity (and similarities) within Glomeromycotina should be pursued with the sequencing of a wider range of taxa. The absence of published CMm genomes leaves unresolved the nature of the acquisition of mycorrhizal abilities in Glomeromycotina and Mucoromycotina (i.e. common vs convergent). The sequencing of Mucoromycotina genomes will shed new light on the origins of mycorrhizal associations in early-diverging fungi.

III. From early land plants to early trees: the origin of roots and true mycorrhizas

Roots evolved at least twice during the early radiation of vascular plants (Tracheophytes; Kenrick & Strullu-Derrien, 2014; Hetherington *et al.*, 2016), namely in Lycophytes and Euphyllophytes (Fig. 5). In contrast to the wealth of information from plants with rhizoid-based rooting systems from the Rhynie chert, knowledge of fungal symbioses associated with the primitive roots remains surprisingly limited. Nothing is known about fungal mycorrhizal symbionts in the rooting systems of the trees in the earliest forests of the Mid and Late Devonian (398–359 million yr ago (Ma); Morris *et al.*, 2015). These forests were formed by Cladoxylales (an extinct

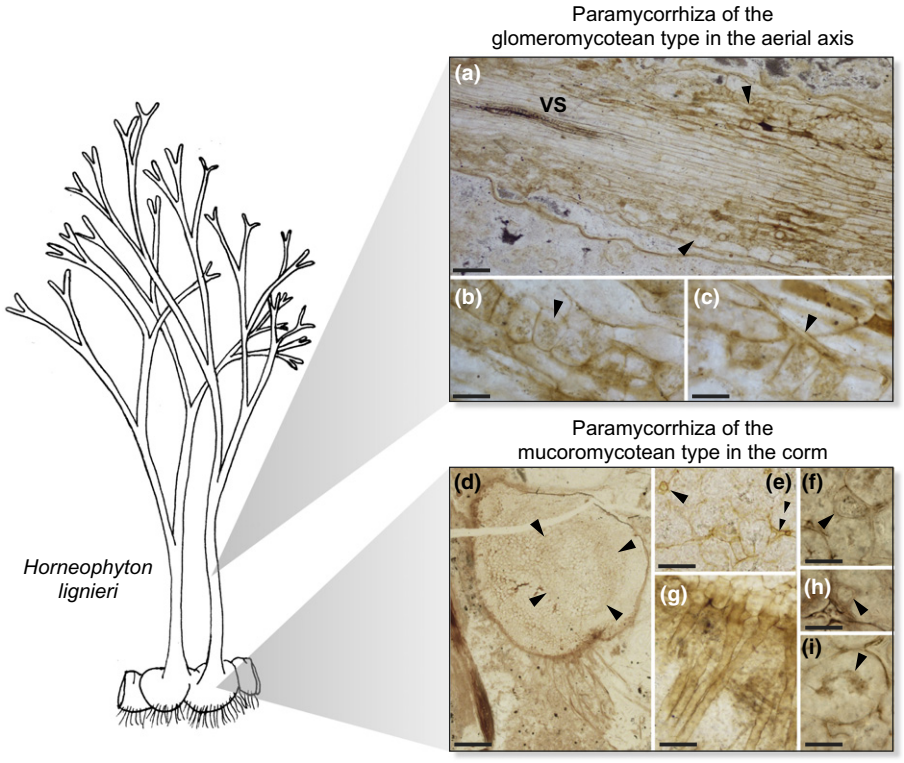

Fig. 2 Dual colonization in the Rhynie chert plant *Horneophyton lignieri* (Strullu-Derrien *et al.*, 2014). Left, interpretation of plant habit (*c.* 5–10 cm height). Right, plant anatomy with fungal infection (transmitted light microscopy). (a–c) Colonization of the outer cortex of the aerial axes by Glomeromycotina-forming vesicles, arbuscule-like structures and spores. (a) Longitudinal section of an axis. Hyphal colonization occurs in a discontinuous zone of cortical parenchyma (arrowheads). VS, vascular strand. (b) Cells containing arbuscular structures (arrowhead). (c) Intra-axial hypha (arrowhead) from which arbuscules developed. (d–i) Fungal colonization in the corm by Mucoromycotina. (d) Zone of fungal colonization is visible within the corm (arrowheads). (e) Intercellular branched thin-walled (double arrowheads) and intercellular thick-walled hyphae (arrowhead) are present. (g) Rhizoids devoid of colonization. (f, h) Intercellular thick-walled hyphae (arrowhead). (i) Intercellular coil-like structure (arrowhead). Bars: (a) 220 μm; (b, c) 60 μm; (d) 700 μm; (e) 80 μm; (f) 20 μm; (g) 30 μm; (h) 24 μm; (i) 26 μm.

group of uncertain affinities, reproducing by spores) (Xu *et al.*, 2017) and progymnosperms, (a group of plants reproducing by spores but with secondary growth of the vascular tissues similar to true gymnosperms; Figs 3, 5). Improving our knowledge of early root symbionts would benefit from an approach that targets specifically permineralized rooting systems (e.g. specimens from China; Xu *et al.*, 2017) and focuses on documenting the fungal component.

By the Carboniferous Period (359–299 Ma), forests containing extinct vascular plants, including arborescent Lycopsida (clubmosses), ferns, sphenopsids, pteridosperms (or seed ferns, a polyphyletic collection of distinct groups of extinct seed plants with fern foliage), *Cordaites* (sister group to conifers) and conifers (Taylor *et al.*, 2009; Fig. 5) were well established in lowland coastal sites. The earliest evidence of mycorrhizas confined to roots comes from fossils preserved in carbonate concretions of Late Carboniferous age (*c.* 315 Ma; Box 3). An AM fungus was reported colonizing the tips of the rootlets of an arborescent clubmoss (Krings *et al.*, 2011c) (Figs 1, 3, 4d, 5). Large vesicles or spores were attached to hyphal threads, while other hyphae penetrated cortical cells where they formed arbuscules. AM fungi were also documented in a *Cordaites* tree (Strullu-Derrien *et al.*, 2009) preserved in cherts from the Late Carboniferous (Figs 1, 3, 4e, 5). The fungus developed an extensive intracellular phase without vesicle formation. Small arbuscules formed within the cortical cells, except for those that developed bands of secondary wall ('phi thickenings') reinforcing the primary wall (Idris & Collins, 2015). A key difference between the rootlets of the lycophyte and those of the *Cordaites* is that the latter possess an endodermis, which is a ring of cells surrounding the vascular system whose cell walls contain hydrophobic substances. The endodermis is speculated to have been important in the evolution of true mycorrhizas by acting as a barrier to the fungal colonization of the vascular system (Strullu-Derrien *et al.*, 2009). As roots in lycophytes and other vascular plants evolved independently (Kenrick & Strullu-Derrien, 2014), mycorrhizas in both Lycophytes and *Cordaites* may indicate at least two separate origins for root colonization. The shift from paramycorrhizas to true mycorrhizas (i.e. fungi harboured in root cortex exclusively) occurred in the rooting systems of the sporophytic (diploid) generation of vascular plants. While extant roots are sometimes viewed as organs exploiting soil autonomously, and they perform this function in nonmycorrhizal plants, it has been hypothesized that roots first evolved as symbiotic axes, interacting with soil fungi (Brundrett, 2002). Strikingly, similar underground interaction organs also evolved in some liverworts, namely the underground 'flagelliform axes' that are densely colonized by soil fungi (Read *et al.*, 2000; Selosse, 2005).

Our understanding of the evolution of roots has greatly benefited from advances in our understanding of the developmental genetics of plant rhizoids in bryophytes (*Physcomitrella*) and root hairs in vascular plants (*Arabidopsis*). Their development is now known to be controlled by the same group of transcription factors (Menand *et al.*, 2007) and similar controls regulate their initiation from epidermal cells (Proust *et al.*, 2016). In other words, although the fossil evidence points to at least two independent origins of roots in the vascular plants, root hairs share a similar origin with rhizoids (Jones & Dolan, 2012; Kenrick & Strullu-Derrien, 2014). Rhizoids frequently

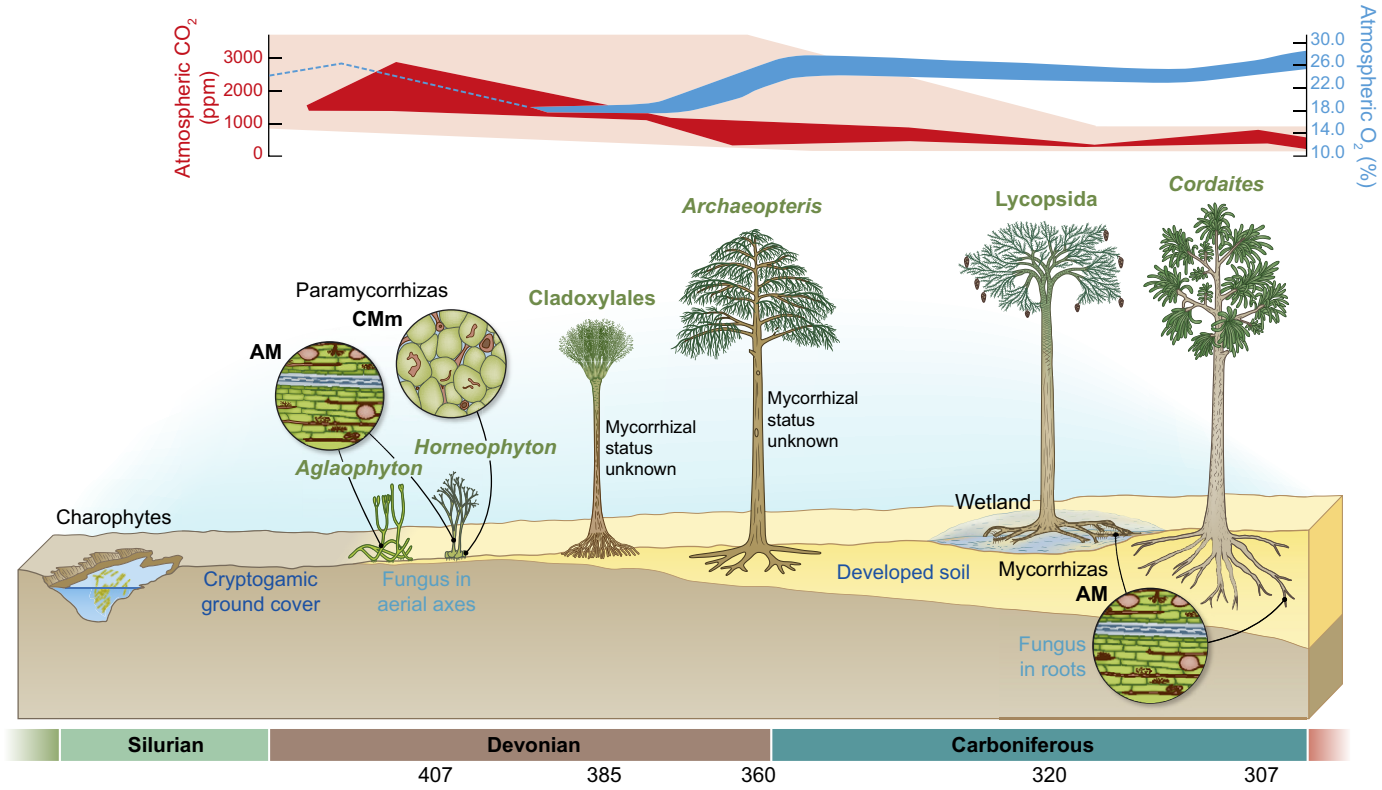

Fig. 3 Evolution of the endomycorrhizal symbioses during the Palaeozoic, from early plants to trees. Left to right, early life on land was mostly microbial. Elements of the common symbiotic signalling pathway developed first in charophycean algae (courtesy Jean-Michel Ané and Anthony Bortolazzo, University of Wisconsin, USA). The first window onto the evolution of mycorrhizas is the exceptional preservation of the 407 million-yr-old Rhynie chert. Paramycorrhizas (i.e. mycorrhizal-like structures) involving Mucoromycotina and Glomeromycotina were well developed in small (*c.* < 20 cm tall) rootless stem group vascular plants (*Aglaophyton majus*, *Horneophyon lignieri*). Soil depths were of the order of millimetres to centimetres. By *c.* 385 million yr ago (Ma), tree-like growth forms (*c.* 8 m tall) evolved in the fern stem group (Cladoxylales) and by 370 Ma arborescence had evolved independently in several groups, including progymnosperms (*Archaeopteris*, which were > 30 m tall). Soil depths were of the order of decimetres to a metre. The second window on the evolution of endomycorrhizas is the preservation in 315–303 million-yr-old deposits. Glomeromycotina developed in the rooting systems of large swamp-dwelling tree lycopods (*Lepidodendron* > 30 m tall) and trees in the conifer stem group (*Cordaites c.* 20–40 m tall). Soil depths could exceeded several metres. Atmospheric O_2 increased from 0.9 present atmospheric level (PAL) *c.* 400 Ma to *c.* 1.3 PAL *c.* 300 Ma. Models of atmospheric CO_2 indicate that the Early Palaeozoic interval commenced with an exceptionally high CO_2 atmosphere; concentrations during the latter part of the Carboniferous Period were close to modern values (Royer, 2014; Glasspool *et al.*, 2015; Wilson *et al.*, 2017. Part of the figure adapted from Fig. 1, Montañez, 2016 and Fig. 4, Wilson *et al.*, 2017; courtesy Royer, 2014, reprinted with permisssion from Elsevier). AM, arbuscular mycorrhizas; CMm, coil-forming mycorrhizas in Mucoromycotina.

act as an entry point for endomycorrhizal fungi, but it remains unclear whether this was the original mode of infection for the mycorrhizal symbiosis.

Our current understanding of the nature, function and diversity of fungal associations in extant lycophytes and ferns is surprisingly patchy (Strullu-Derrien & Strullu, 2007; Pressel *et al.*, 2016; Lehnert *et al.*, 2017). Molecular ecology could shed further light on the diversity of fungal endophytes and putative symbionts (Rimington *et al.*, 2015). We need to develop an understanding of how precisely Glomeromycotina and Mucoromycotina function in basal extant vascular plants, i.e. lycophytes, ferns and seeds plants (Field *et al.*, 2015). Another question concerns how the mycorrhizal symbiosis works in the haploid (gametophytes) and diploid (sporophytes) phases of their life cycles. In living vascular plants, sporophytes are root-bearing plants with root hairs, whereas gametophytes are rootless but possess rhizoids. Our understanding of how this functions within an individual life cycle remains mostly unknown. Where it has been studied, the same AM fungus colonizes both phases of the life cycle (Winther & Friedman, 2008, 2009). Gene expression patterns in infected sporophytes and gametophytes could be instructive regarding their function in the life cycle. Genomic-wide transcript profiling of plants with and without roots is desirable, together with transcriptomic analyses of gene expression involving Glomeromycotina vs Mucoromycotina. To date, the available tools have long limited the study of lycophyte and fern development, but now transcriptomic analyses, genomic and stable genetic transformation are available, for example in ferns (Plackett *et al.*, 2014), as they are in the liverwort *Marchantia* (Bowman *et al.*, 2017). In parallel, stronger efforts are required with regard to the fossil record of mycorrhizal associations in lycophytes, ferns and gymnosperms (Strullu-Derrien & Strullu, 2007). Indeed, large museum collections of exceptionally well preserved Late Carboniferous (*c.* 320–300 Ma) plant petrifactions can provide remarkable information on root anatomy and they can be studied from a mycological perspective.

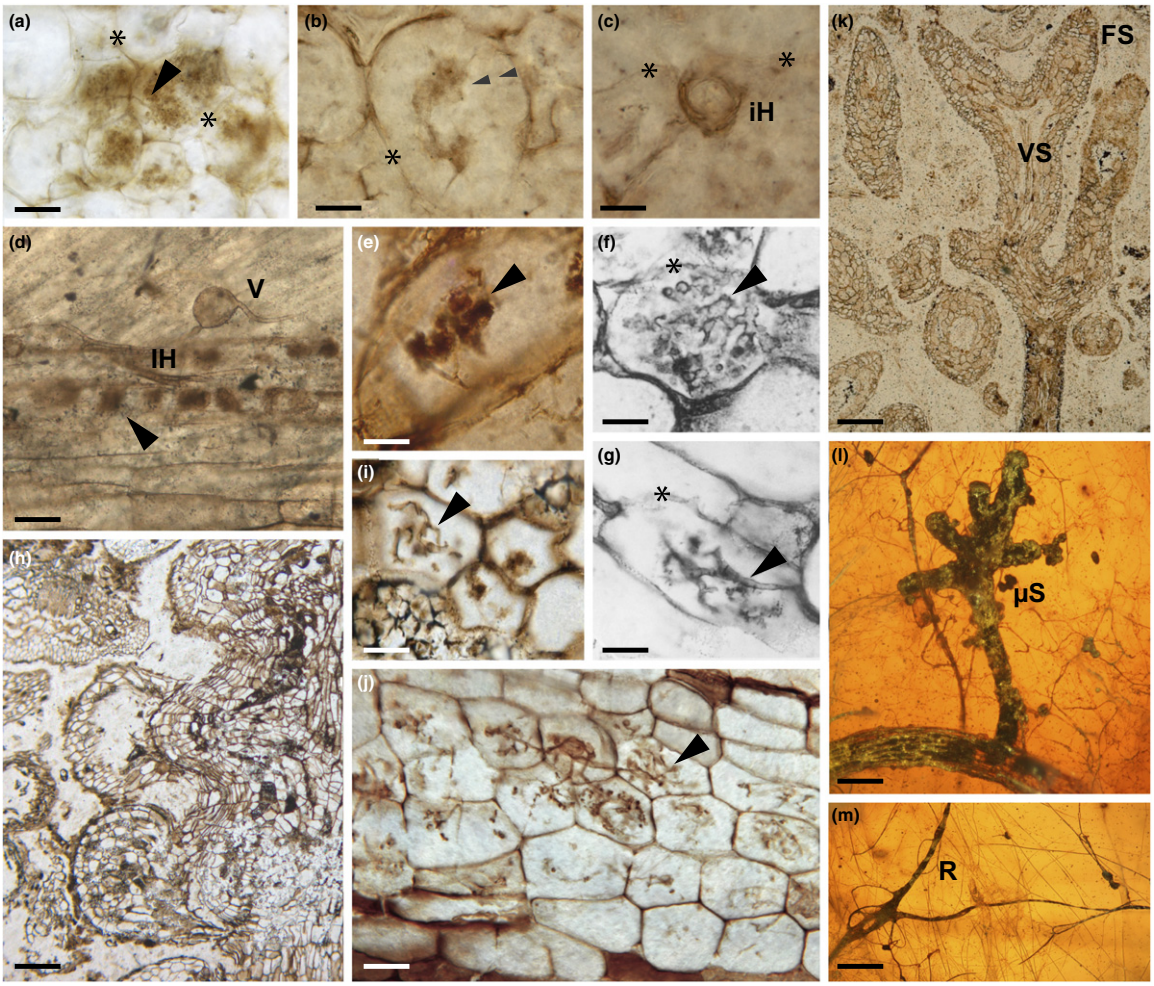

Fig. 4 Fossil mycorrhizas. (a) Arbuscules of *Glomites rhyniensis* (Glomeromycotina) in the cortical cells of an aerial axis of *Aglaophyton major* (*c*. 407 million yr ago (Ma)) (photograph courtesy of H. Kerp, Taylor *et al*., 1995; reprinted with permission from *Mycologia*, © The Mycological Society of America). (b, c) Colonization by Mucoromycotina in the cortical cells of the corm of *Horneophyon lignieri* (*c*. 407 Ma) (Strullu-Derrien *et al*., 2014); Coil (b) and intercellular (c) thick-walled hyphae. (d) Arbuscular mycorrhizal (AM) fungus in rooting system of tree lycophyte (*c*. 315 Ma). Trunk hyphae, intercalary vesicle and arbuscules (photograph originally published in Krings *et al*. (2011c) in *New Phytologist*, reprinted with permission). [Correction added after online publication 24 March 2018: text relating to the permission has been amended in the preceding sentence.] (e) Detail of arbuscules in *Cordaites* rootlet (*c*. 303 Ma). The hyphal trunk of the arbuscule branches repeatedly to form a bush-like tuft within the cell (Strullu-Derrien *et al*., 2009). (f, g) Details of arbuscule of *Gigasporites myriamyces* (f) and arbuscule of *Glomites cycestris* (g) in the cortical cell of a root of *Antarcticycas schopfii* (*c*. 240 Ma) (Phipps & Taylor, 1996; reprinted with permission from *Mycologia*, © The Mycological Society of America). (h, i) Three developing root nodules attached to a conifer root (*c*. 240 Ma) (in longitudinal section) (h) with probable arbuscules in the cortex (i) (photographs courtesy A. Schwendeman, Schwendemann *et al*., 2011; reprinted with permission from *Proceedings of the National Academy of Sciences, USA*, © National Academy of Sciences). (j) Branching hyphae and arbuscules in the root cortex of the *Metasequoia milleri* (*c*. 48.7 Ma) (photograph courtesy of Ruth Stockey). (k) Longitudinal section through a *Pinus* rootlet with ectomycorrhizas (*c*. 48.7 Ma) (photograph courtesy of Eva Koppelhus; LePage *et al*., 1997; reprinted with permission from *American Journal of Botany*). (l, m) Monopodial-pinnate ectomycorrhiza in an angiosperm forming microsclerotia (l) with surrounding branched rhizomorphs (m) preserved in amber (*c*. 52 Ma) (photographs courtesy Alexander Schmidt, Beimforde *et al*., 2011; reprinted with permission from *New Phytologist*). Bars: (a, e) 12 μm; (b, j) 14 μm; (c) 5 μm; (d) 9 μm; (e, i) 15 μm; (f, g) 18 μm; (h) 50 μm; (k) 280 μm; (l) 150 μm; (m) 190 μm. *, host cell wall; arrowhead, arbuscule; double arrowheads, coil; iH, intercellular thick-walled hyphae; VS, vascular strand; FS, fungal sheath; V, intercalary vesicle; IH, intraradical hyphae; μS, microsclerotia; R, rhizomorph.

IV. The diversification of the AM symbiosis

The ecosystems of the Late Palaeozoic and Mesozoic contained many plants that are now extinct. Gymnosperms, including conifers, were much more diverse at that time, and they were accompanied by extinct pteridosperms (Bateman *et al*., 2006). These plants were the most prominent shrub and tree elements in many climatic zones. Mycorrhizas have been reported in the extinct pteridosperm *Glossopteris* (Glossopterids; Fig. 5) based on fossils preserved in a permineralized peat from the Upper Permian of Antarctica (260–252 Ma; Harper *et al*., 2013; Box 3). The fungus has septate hyphae but was attributed to *Glomites* (Taylor *et al*., 1995; genus amended by Harper *et al*., 2013), which, if correct, contrasts with the aseptate condition of modern AM Glomeromycotina. The fungus colonized cortical cells of rootlets in a helical pattern that the authors suggested resembled modern *Paris*-type AM mycorrhizas. Rootlets of *Antarcticycas* (Cycadophytes; Fig. 5) preserved in a siliceous chert from the Middle Triassic of Antarctica

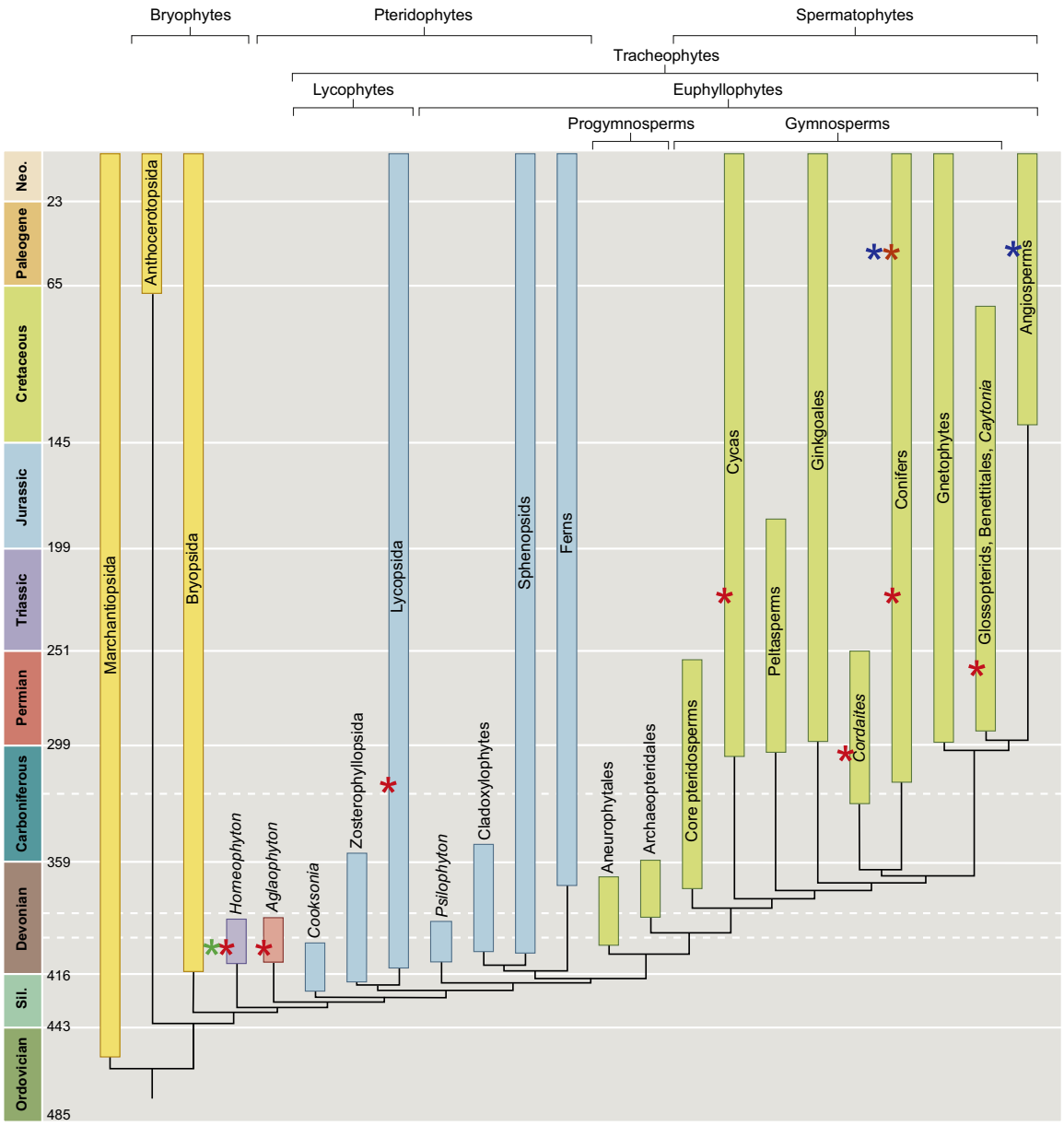

Fig. 5 Simplified phylogenetic tree showing the minimum stratigraphic ranges of selected groups based on fossils (thick bars) and their minimum implied range extensions (thin lines). Extinct and living plant groups are shown. Adapted from Kenrick & Crane (1997, with permission from *Nature*) and C. Strullu-Derrien (unpublished DPhil thesis). Sil, Silurian; Neo, Neogene. Asterisks show the earliest fossil mycorrhizas: green, coil forming mycorrhizas in Mucoromycotina (CMm); red, arbuscular mycorrhizas (AM); blue, ectomycorrhizas (ECM).

(Box 3) harbour two putative mycorrhizal fungi (Stubblefield *et al.*, 1987; Phipps & Taylor, 1996; Fig. 4f,g), sometimes even colonizing the same root. The absence of reproductive spores meant that these could not be assigned to modern taxa (Stubblefield *et al.*, 1987). Here again, hyphae showed frequent septa, and they developed throughout the cortex, especially in the central region (Phipps & Taylor, 1996). One fungus (*Gigasporites myriamyces*) had inter- and intracellular hyphae forming loops and coils in cells, while the second (*Glomites cycestris*) had slightly narrower hyphae associated with thick-walled hyphal swellings, forming terminal or lateral vesicles of variable size (Phipps & Taylor, 1996). In modern Cycadophytes, a clear AM fungal zone exists in some species, and arbuscules arise from typically aseptate intercellular hyphae (Fisher & Vovides, 2004).

This Antarctica site provided a second example of multiple AM fungi developing in the rooting system of an extinct conifer (Bomfleur *et al.*, 2013). The fungus was observed within a discrete cortical zone of young roots (Harper *et al.*, 2015) that appears opaque because of densely packed, multi-branched intracellular arbuscules that are difficult to distinguish, but devoid of vesicles. Other roots characterized by a nodular shape harbour a fungus forming both arbuscules and small vesicles in the outer cortex (Schwendemann *et al.*, 2011) (Figs 4h,i, 5). Interestingly, the roots of the three extant gymnosperm families, Araucariaceae,

Box 3 Fossil mycorrhizal associations – a patchy record linked with exceptional geological conditions

Fossil evidence of mycorrhizas is very patchy because of the exceptional conditions required to preserve cellular and subcellular details of plant tissues (e.g. rapid permineralization). The earliest such environment is the Rhynie chert (407 million yr ago (Ma)), which is interpreted as a tropical, seasonally arid, geothermal wetland that was located on the southern margin of the palaeocontinent of Laurussia (Trewin & Rice, 2004). Plants and their fungal symbionts were preserved *in situ* by low-temperature silicification in a hot-spring system, providing unique insights into these associations before the evolution of forests (Edwards *et al.*, 2017). Conditions suitable for preserving roots became very widespread in the equatorial belt tropical wetlands of the Late Carboniferous through the earliest Permian (310–295 Ma). Here, special environmental conditions prevailed, enabling carbonate concretions to form within wet organic rich soils preserving rooting systems in remarkable detail (e.g. Hetherington *et al.*, 2016). A similar quality of preservation is known from the Late Carboniferous Grand-Croix chert (France, Strullu-Derrien *et al.*, 2009). Fossil soils are relatively common, so our knowledge of mycorrhizal evolution could be improved by targeting suitably preserved soils from particular time intervals, palaeogeographic areas and environments (Kenrick & Strullu-Derrien, 2014). For example, Upper Permian (260–252 Ma) and Middle Triassic (247–237 Ma) silicified peats from Antarctica and Upper Triassic (237–227 Ma) sites in the Svalbard archipelago (Arctic) provide our first glimpse of exceptionally well preserved high-latitude forest soils that formed under the warm-temperate climates that prevailed at the time (Schwendemann *et al.*, 2011; Strullu-Derrien *et al.*, 2012; Harper *et al.*, 2013). Permineralized Eocene roots from Canada (48.7 Ma) shed light onto mycorrhizal development in a shallow freshwater ecosystem under 'greenhouse' Earth conditions (Stockey, 2001; Greenwood *et al.*, 2005). Although amber preservation of roots is rarely reported, an Early Eocene (52 Ma) lignite from India captured exceptionally preserved ectomycorrhizas from a tropical forest soil (Beimforde *et al.*, 2011). Also, there is much potential in existing museum collections, whose materials frequently preserve plant-associated microbiota (e.g. Strullu-Derrien *et al.*, 2011).

Podocarpaceae, and Phyllocladaceae, possess similar small nodular roots (Duhoux *et al.*, 2001; Russell *et al.*, 2002 and references therein) containing Glomeromycotina that enter from the soil through epidermal cells (Russell *et al.*, 2002). The exact role or function of these specialized nodular roots remains unclear, but they perhaps increase the contact surface between partners. Finally, AM fungi were reported in the conifer *Metasequoia milleri* (Cupressaceae) (Fig. 5) from the Eocene (48.7 Ma) Princeton chert of Canada (Box 3). The inner cortex of fine roots contains branched aseptate hyphae and arbuscules arising from intracellular coils (Stockey *et al.*, 2001; Fig. 4j). As in modern *Metasequoia* roots (e.g. Böcher, 1964), AM hyphae appear to be exclusively intracellular.

Arbuscular mycorrhizas have thus been documented in fossil Mesozoic cycads and conifers, and possibly in one extinct pteridosperm of the Late Palaeozoic, showing that they were present in the diverse gymnosperm trees and shrubs of the mid-northern latitude and high southern latitude polar forests that developed in the 'greenhouse' climates of the Mesozoic and Cenozoic eras. However, the patchy record of fossil mycorrhizas in gymnosperms presents huge gaps (Fig. 5) and needs to be improved. Also, we are not aware of AM fossils in any primitive angiosperms, and post-Rhynie chert evidence for CMm associations is also lacking, so their diversification and continuity in the fossil record remains unknown. Moreover, endomycorrhizas are not that well studied in modern gymnosperms. New data on AM and CMm diversity in living species would help with the recognition of mycorrhizas in the fossil record.

V. The ECM symbiosis

The oldest known ECM fossils were found in *Pinus* roots preserved in the Princeton chert of Canada (Eocene, 48.7 Ma) (Boxes 1, 3). Here roots were colonized by a pseudoparenchymatous fungal sheath and a hyphal network (Hartig net) that extended intercellularly through the cortex to the endodermis (LePage *et al.*, 1997; Figs 4k, 5). Hyphae were septate as in current ECM Dikarya (Asco- and Basidiomycota). In response to colonization, roots formed dichotomously branched secondary rootlets as often observed in modern ECM associations on *Pinus* (Smith & Read, 2008). Other structures sometimes attached to ECM roots, such as rhizomorphs, sclerotia or fruiting bodies, were not observed. The fungus was reminiscent of extant *Rhizopogon* and *Suillus* spp. specific to *Pinus*. ECMs were reported from Early Eocene (52 Ma) amber from western India (Beimforde *et al.*, 2011) (Boxes 1, 3). Unramified, cruciform and monopodial-pinnate ECMs are fossilized adjacent to rootlets and display different developmental stages (Fig. 4l,m). Although the fungal mantle is excellently preserved, the root tissues decayed so that no Hartig net is documented. The mycobiont is speculated to belong to the Dothideomycetes (Ascomycota), because of morphological similarity to the extant genus *Cenococcum*, and the host to Dipterocarpaceae (currently, tropical lowland rainforest trees) (Fig. 5), although the numerous angiosperm families known from this period in India leave other possibilities open. The only two ECM fossils known to date are therefore from regions with tropical or warm temperate climates, whereas ECM symbiosis nowadays dominates in temperate and boreal regions. The dearth of direct fossil evidence for ECM belies its broad distribution among plants today and its ecological prominence in modern ecosystems.

Timetrees and palaeogeographic distributions of plant hosts and fungi provide an alternative means of estimating the origins of ECM that could also inform our targeting of the fossil record. The first ECM may have evolved in stem group Pinaceae, between their split from Gnetophytes (Fig. 5; possibly Mid Permian, *c.* 270 Ma) and the radiation of the Pinaceae crown group (possibly in the mid-to-late Jurassic, < 174 Ma; Lin *et al.*, 2010; Rothwell *et al.*, 2012). Indeed, *Gnetum* (Gnetophyte) forms ECM and this association might have originated in the common ancestor with Pinaceae, although convergence cannot be excluded. ECM symbiosis might even have emerged convergently in extinct pteridosperm groups (e.g. Benettitales, a sister group to the angiosperms, which was an important component of floras during Triassic-Cretaceous times). A plausible maximum age for the origin of ECM in Angiosperms is the first appearance of rosids (100–109 Ma based on molecular calibrations; Hibbett & Matheny, 2009), an age range consistent with the earliest fossils attributable to this clade (*c.* 105–90 Ma;

Friis *et al.*, 2011). Moyersoen (2006) hypothesized an earlier ECM origin at 135 Ma based on a vicariance model in Dipterocarpaceae, but this should be treated with caution as the role of vicariance vs long-distance dispersal has to be considered (Alexander, 2006). These meagre fossil findings have been largely serendipitous, and the field would benefit from a targeted study of permineralized plants and soils of Mesozoic age.

Ectomycorrhizas evolved independently numerous times, not only in plants (> 18 times in angiosperms; Koele *et al.*, 2012), but also in fungi (78–82 times; Tedersoo & Smith, 2017) and also over an extended geological period. It may even be that some current lineages of fungi are shifting (or able to shift) to the ECM niche (Baldrian & Kohout, 2017). Multiple origins of ECM indicate the action of important evolutionary drivers. Switching of nutritional mode is considered to be a key driver, but there are others that are still poorly understood. The spread of cooler temperate climates has been suggested as a potential driver for diversification during the early to mid-Cenozoic (Bruns *et al.*, 1998; Selosse & Le Tacon, 1998; Ryberg & Matheny, 2012). Many ECM fungal lineages have a tropical origin (Buyck *et al.*, 1996; Matheny *et al.*, 2009; Smith *et al.*, 2011), a finding that seems paradoxical if we consider that current ECM fungal diversity is higher in temperate regions (e.g. Tedersoo *et al.*, 2014). This paradox may be explained if basal lineages were preferentially conserved in the tropics, whereas a more recent Late Paleogene–Neogene diversification was driven by global cooling and the spread of temperate biomes (Selosse & Le Tacon, 1998). This diversification of ECMs out of the tropics is exemplified by plant host switching from tropical to temperate observed in various fungi (Looney *et al.*, 2016; Sato *et al.*, 2016). Other corroborating evidence comes from phylogenetic studies of particular clades. For example, Sánchez-Ramírez *et al.* (2015) recently showed that the ECM fungus *Amanita caesarea* and its allies were ancestrally Palaeotropical (Eocene to late Miocene), reaching temperate regions during the late Miocene and Pliocene. ECM fungi themselves probably contributed to the acceleration of this long-term cooling trend. Plant roots and their associated mycorrhizal fungi enhance the weathering of calcium-magnesium silicates, which draws CO_2 out of the atmosphere. This phenomenon is one of the key regulators of the geochemical carbon cycle (Bergman *et al.*, 2004). ECM fungi are known to have higher weathering capacity than AM fungi (Thorley *et al.*, 2015). So, the emergence and subsequent diversifications of ECM fungi may have contributed to episodes of global climate cooling observed during the Cretaceous and over the past 120 million yr (Taylor *et al.*, 2012; Quirk *et al.*, 2014). In addition to environmental conditions, plants themselves are key to deciphering the origins of ECM interactions. Van de Peer *et al.* (2017) recently reviewed the accumulating evidence that correlates polyploidization with environmental change, leading to an increased recognition of its short-term adaptive potential. Analyses of sequence data from a large number of plant genomes and transcriptomes suggest that a wave of whole-genome duplications (WGDs) occurred in angiosperms close to the Cretaceous–Paleogene (K–Pg) boundary. Changes such as these could have been an influential driver of adaptive success in both plant and fungi, facilitating the diversification of ECM interactions in parallel.

Phylogenomic analyses based on a dozen sequenced ECM fungal genomes confirmed the convergent evolution of ECM fungi from white- and brown-rot fungi and from soil saprotrophs (Kohler *et al.*, 2015). Several orders of fungi are involved, which facilitates the unravelling of the shared genetic traits leading to the evolution of ECM fungal species. This is marked by gene decay with extensive loss of genes involved in plant cell wall-degrading enzymes (PCWDEs) and lignin-oxidizing class II peroxidases, as well as sucrose invertase, all of which existed in ancestral saprotrophs (Fig. 1). Losses are most pronounced in genes that encode class II peroxidases and cellulases, notably those that encode the families of cellobiohydrolases GH6 and GH7. However, all sequenced ECM fungi have maintained genes that encode lytic polysaccharide monooxygenases, laccases, dye-decolorizing peroxidases and haem-thiolate peroxidases (Kohler *et al.*, 2015), which may be involved in the decomposition of soil organic matter to scavenge organic N and P (Rineau *et al.*, 2013; Lindahl & Tunlid, 2015). Lacking the ability to decompose lignocellulose and cleave sucrose, ECM fungi have become highly reliant on their hosts' photoassimilates, while preserving plant cell integrity (Martin *et al.*, 2016). A similar evolutionary trend has been observed in Ascomycota (e.g. *Tuber melanosporum* (Martin *et al.*, 2010); *Cenococcum geophilum* (Peter *et al.*, 2016)) and Glomeromycotina (see Part II). An additional shared evolutionary feature of mycorrhizal fungal genomes is the induction of MiSSP gene expression upon symbiosis (Martin *et al.*, 2010; Kohler *et al.*, 2015; Peter *et al.*, 2016). As shown in *R. irregularis* (see Part II), MiSSPs can modulate the host gene expression and dampen defence reactions triggered by root colonization. Symbiosis-related orphan genes, coding for effector-like MiSSPs, might arise from duplication, rearrangement processes and *de novo* evolution out of noncoding genomic regions (Martin *et al.*, 2008, 2017). This genetic material probably played a role in lineage-specific adaptations required for symbiosis development (Martin *et al.*, 2016).

It has also been proposed that an endophytic niche, possibly even facultative, could act as a symbiotic 'waiting room', predisposing the fungus to evolve a tighter mutualism with some hosts (Selosse *et al.*, 2009; van der Heijden *et al.*, 2015). Indeed, endophytism is increasingly reported for some saprotrophic fungal genera (e.g. Vasiliauskas *et al.*, 2007; Kernaghan & Patriquin, 2011; Davey *et al.*, 2013; Smith *et al.*, 2017). Furthermore, in at least two fungal orders where endophytism is well documented, namely Sebacinales (Basidiomycota; Selosse *et al.*, 2009; Weiss *et al.*, 2016) and Helotiales (Ascomycota; Tedersoo & Smith, 2013), ECM species arose repeatedly from endophytic ancestors. Yet, in other lineages, the ECM lifestyle appears to be derived directly from litter-degrading ancestors (e.g. in Amanitaceae) or brown rotters (Kohler *et al.*, 2015). Although we cannot exclude the possibility that endophytic behaviour was a secondary loss in these lineages, it is likely that several evolutionary pathways allow the transition from saprotrophy to ECM status. Unfortunately, the fossil record of endophytism in roots is even scarcer than that of ECM associations, so that palaeontology can hardly contribute to this discussion.

Linking the shift from saprotrophic to ECM nutrition in fungi to particular environmental changes and evolutionary events in plant hosts requires an increase in fungal species sampled for genome

sequencing and further refinement of tree calibration. The origin of white and brown rots – the background mode of life to ECM Basidiomycota – is itself an interesting question. Analyses of fungal genomes again set some broad constraints, suggesting an origin of lignin-degrading capability in Agaricomycetes around the end of the Carboniferous period, but error margins are large (Floudas *et al.*, 2012). Knowledge of the early fossil record of wood decay is meagre despite the fact that permineralized woods are common (Taylor *et al.*, 2009). The earliest evidence of wood decay reported as white rot involving Basidiomycota comes from late Devonian (*c.* 372–359 Ma) permineralized wood (*Callixylon newberry,* Archeopteridales; Fig. 5) (Stubblefield *et al.*, 1985). However, neither clamp connections typical of Agaricomycetes hyphae nor fruiting body were observed, leaving open the possibility that another type of fungus was responsible for the decay. A more focused study of patterns of decay in fossil woods would help to refine our knowledge of the origins of various types of rot. To date, the existence of white rot-like traits in Ascomycota (Schwarze, 2007) is not confirmed by genomic data. An analysis of the phylogenetic distribution of white rot (and other types of rot, e.g. soft, grey) in Ascomycota would be beneficial. Moreover, an origin from soil saprotrophs has been proposed for ECMs involving Ascomycota, and scenarios for the evolution of the ECM lifestyle in Basidiomycota differ depending on the group of fungi involved: Sebacinales, Tulasnellales and Cantharellales vs Agaricomycotina (Martin *et al.*, 2016). More genomic data are needed to fully understand the evolution of decay mechanisms and consequently the evolution of ECM fungi from soil saprotrophs or white rot fungi.

Extending genomic-scale comparisons to ECM fungal species in Mucoromycotina (Endogonales; Smith & Read, 2008) and endophytic fungi related to ECM fungal lineages could also provide further insights into large-scale changes accompanying the evolution of this trait. On the plant side, the convergent evolution of the ECM symbiosis facilitates comparative genomic analyses to determine the existence and nature of a putative ECM toolbox (Delaux *et al.*, 2015). Thus, how plants access their ECM fungal partners deserves further study in the near future. In this context, the phylogenetic proximity of *Gnetum* to Pinaceae makes this group especially relevant for investigation.

VI. The recently evolved ericoid and orchid mycorrhizas

Orchidaceae and Ericaceae independently evolved endomycorrhizas with Basidiomycota (Dearnaley *et al.*, 2013) and Ascomycota and Sebacinales (Smith & Read, 2008; Weiss *et al.*, 2016), respectively, in which fungal hyphae form coils in cortical root cells. The fossil record of the Orchidaceae is scant. The oldest fossils, a pollinarium attached to a preserved bee (Ramirez *et al.*, 2007) and a debated seed (Poinar, 2017; see discussion in Selosse *et al.*, 2017), are from Dominican Republic amber (15–20 Ma). Calibrated molecular phylogenies suggest a Cretaceous origin of orchids (76–84 Ma in Ramirez *et al.*, 2007; 76–112 Ma in Givnish *et al.*, 2015) coupled with a Cenozoic radiation of the species-diverse epiphytic clades. Mycorrhizas are an ancestral state shared by the whole Orchidaceae family (Yukawa *et al.*, 2009; Dearnaley *et al.*, 2013), including the very specific germination where the future mycorrhizal fungus acts as a carbon source to support the early development of reserveless seeds (Dearnaley *et al.*, 2016).

By contrast, Ericaceae has an extensive fossil record (Friis *et al.*, 2011; Schwery *et al.*, 2015), with fossils assignable to the modern ericoid genus *Leucothoe* dating from the Late Cretaceous (66–72 Ma; Fig. 1). In this family, two new mycorrhizal types evolved secondarily from AM ancestors (Freudenstein *et al.*, 2016; Lallemand *et al.*, 2016): the family diverged into two lineages, one associated with ECM fungi, and another forming the typical 'ericoid' endomycorrhizas with a specific set of fungi. Calibrated phylogenies indicate that this occurred during the mid-Cretaceous (*c.* 100–110 Ma; Schwery *et al.*, 2015). Similarly to ECMs, mycorrhizas in Orchidaceae and ericoid mycorrhizas in Ericaceae probably originated under the warm climates that prevailed at the time. Yet, Ericaceae now dominate at high latitudes and altitudes where they are adapted to poorly mineralized soils (Smith & Read, 2008), but whether this ecological niche is primarily or secondarily evolved remains unclear. Fossil mycorrhizas are lacking for these two groups, although amber-preserved specimens (especially for epiphytic orchids) could prove to be a source of materials (e.g. Ramirez *et al.*, 2007).

In contrast to ECM fungi, ericoid and orchid mycorrhizal fungi retained an extensive decay apparatus that is probably exploited indirectly by the plant for N and P supply (Kohler *et al.*, 2015; Martino *et al.*, 2018), and even C supply in orchids (Dearnaley *et al.*, 2013; Selosse & Martos, 2014). This explains their saprotrophic ability (Smith & Read, 2008; Dearnaley *et al.*, 2013), although it remains to be confirmed through genome sequencing of more species. Extensive phylogenetic studies demonstrate that Serendipitaceae (Sebacinales; Agaricomycetes) evolved ericoid or orchid mycorrhizal abilities from endophytic ancestors (Selosse *et al.*, 2007, 2009; Weiss *et al.*, 2016), providing further examples of where endophytism could act as a 'waiting room' for the evolution of true mycorrhizal associations (Selosse *et al.*, 2009; van der Heijden *et al.*, 2015). Further corroborating evidence comes from comparisons of the repertoire of enzymes active on plant carbohydrates (CAZymes) in Helotiales that are pathogenic and endophytic in *Arabis alpina* (Almario *et al.*, 2017): plant-beneficial Helotiales contain an overall larger CAZyme repertoire than do pathogenic and saprotrophic species. These genomic features are very similar to those found in ERM fungi (Martino *et al.*, 2018) and support the 'waiting room' hypothesis. Although aspects of the exact ecology of the fungi remain unclear, another major orchid mycorrhizal group, the Tulasnellales, probably possess similar endophytic abilities (Girlanda *et al.*, 2011). Yet other taxa might exhibit more direct transitions from different lifestyles, and a full picture of the evolution of ericoid and orchid mycorrhizas will necessitate not only the sequencing of more fungi involved in these relationships, but also a better understanding of their ecology.

VII. Limits of paleontological vs genetic approaches and perspectives

Mycologists make a plea for more genomes and genome-wide transcript profilings to understand how fungi live, adapt and

evolve (Aylward *et al.*, 2017). As obligate biotrophs, AM Glomeromycotina cannot be cultivated axenically and can only be propagated with plant roots in pot culture or *in vitro* on root organ culture, their genetic structure remains poorly documented (Kamel *et al.*, 2017). Spatafora *et al.* (2016) and Tang *et al.* (2016) reported a clustering of Mucoromycotina and Mortierellomycotina in sister position to Glomeromycotina, based on the few genomes available to date. This challenges the usual view of Glomeromycotina as sister group to Ascomycota + Basidiomycota (Hibbett *et al.*, 2007). Since increased sampling changed the accepted view, acquisition of new genomes (including for CMm fungi such as '*Glomus tenue*') may further help to refine our understanding of the Mucoromycota clade (Tang *et al.*, 2016), and delineate its exact composition. To reconstruct more fully the mode of transition from free-living saprotoph to ECM fungus and to better understand the specific traits characterizing each mycorrhizal type, more genomic data are needed from several fungal clades, including ECM (mainly in Ascomycota), ericoid and orchid mycorrhizal fungal lineages, together (in the context of the waiting-room hypothesis) with a richer set of endophytic lineages. Expanded genome sampling and phylogenomic analyses are required to assess the generality of the mechanisms that are described based on model systems and to assess the timing of the evolution of the ECM symbioses. To provide a global picture, several questions need to be answered (Martin *et al.*, 2017): do the effectors used by evolutionary distant ECM fungal species target similar host proteins and how did these effector proteins evolved? How do orphan genes that are up-regulated in symbiosis evolve and how quickly are they modified? Why are some ectomycorrhizal fungal species able to colonize diverse hosts, whereas other species have a more restricted host range? Do all the ECM fungi species use the same signalling pathways?

Better resolved phylogenies pave the way to building the fungal tree of life, but the accuracy and precision of the dates assigned to nodes are dominated by the quality and quantity of the fossil calibrations (Warnock *et al.*, 2017). For fungi this is a challenge, because the number of fossils that can be placed with confidence on deep nodes is comparatively few (Berbee & Taylor, 2010). For example, *Paleopyrenomycites devonicus* (Taylor *et al.*, 2005a) from the Rhynie chert is a key fossil for dating the origin of Ascomycota. Yet, although clearly related to Ascomycota it does not fit comfortably within an extant taxonomic group. Douzery *et al.* (2004) took a conservative approach (minimizing the effect of the constraint), assigning it to the stem lineage of the Ascomycota subphylum Pezizomycotina, a placement later endorsed by Lücking *et al.* (2009) and Beimforde *et al.* (2014). However, the ascus tip in *P. devonicus* may not display the opercule typical of modern Pezizomycotina (Berbee & Taylor, 2010), so its placement remains debatable. A similar situation occurs in dating of the origin of the Basidiomycota. The oldest fossils of Basidiomycota are clamp connections from the Carboniferous (*c.* 330 Ma, Krings *et al.*, 2011a, c), which are far younger than the oldest fossil of its sister group Ascomycota (407 Ma). Furthermore, Basidiomycota fruiting bodies are unknown before the Early Cretaceous (113–120 Ma) (Heads *et al.*, 2017). Key issues, therefore, are the quantity of fossils available for calibration and our capacity to place those that are known with precision on the phylogenetic tree. The latter requires the building and analysis of morphological datasets alongside molecular datasets. Whereas this issue is less critical for node-based approaches to tree calibration, it is essential to total evidence dating (Ronquist *et al.*, 2012), which is arguably a more objective and theoretically sound method. Combining morphological and molecular data has additional benefits for understanding the evolution of fungal traits. Strullu-Derrien *et al.* (2017) compared a new fossil fungus with cultures of putative living relatives and character state reconstructions on molecular phylogenies of 24 modern zoosporic fungi. This approach supported an affinity of the fossil with Blastocladiomycota shedding light on the origin of hyphae. This new fossil fungus is the earliest known to develop hyphae and these probably served as a saprotrophic adaptation to patchy resource availability.

There are two main issues regarding the fossil record of mycorrhizas, and more generally plant–fungal interactions (including endophytism). The first concerns determining the nature of the interaction between plant and fungus. The presence and distribution of fungal structures within the host, the response of the host and the nature of the immediate host environment can provide physiological indicators and clues. For example, the presence of decay in the cells of a restricted host tissue might be indicative of parasitic infection (Krings *et al.*, 2011b; Taylor *et al.*, 2015), whereas the colonization of turgescent cells with thin cell walls is more consistent with symbiotic colonization, particularly when associated with features like intracellular fungal arbuscules or coils (Remy *et al.*, 1994; Taylor *et al.*, 1995; Krings *et al.*, 2007, 2011c; Strullu-Derrien *et al.*, 2014). Greater attention needs to be paid to potential physiological clues associated with fungi in fossil materials; for example, the division of the plant cell perpendicularly to its main axis associated with hyphal penetration in AM (Strullu-Derrien *et al.*, 2014; Fig. 3b,c; G. Russo *et al.*, unpublished) or the cortical cell elongation typical of ECM (Strullu, 1985). Second, although the fossil record of mycorrhizas has increased greatly over the past two decades this record is still sparse. Research on key fossils should target permineralized soils from new sites and make greater use of large resources already present in museums, especially historic collections of thin sections, which harbour abundant microorganisms including fungi (e.g. Dotzler *et al.*, 2006, 2009; Krings *et al.*, 2007; Krings *et al.*, 2009; Krings *et al.*, 2011c; Strullu-Derrien *et al.*, 2011, 2014). X-ray synchrotron microtomography and confocal laser scanning microscopy also provide new ways of investigating these materials (Strullu-Derrien *et al.*, 2015, 2016a).

Plant fossils should now be considered as palaeoholobionts. The idea that plants harbour a dense and diverse microbial community that shapes most of its functions (e.g. Selosse *et al.*, 2004) now gains momentum under the umbrella of the holobiont concept (Vandenkoornhuyse *et al.*, 2015). By holobiont, it is acknowledged that the functional (if not evolutionary) unit is not just the macroorganism (plant or animal), but also includes its microbiota (McFall-Ngai, 2015). In the last decade, this view originating from the microbial community has progressively invaded physiological studies, and microbes were discovered to make a crucial contribution to all the functions of the organism (Hacquard and Schadt,

2014; Selosse *et al.*, 2014). Researchers need to understand that the same applies to fossils of macroorganisms, and that well-preserved ones, allowing anatomical investigations, are palaeoholobionts in which microbial symbionts and interactions are preserved structurally.

It is also important to use and analyse metadata in the context of the knowledge of the origins and evolution of mycorrhizas. For example, comprehensive biogeography databases enable hypotheses of dispersal and distribution of mycorrhizas over geological timescales to be tested (Stürmer & Morton, 2015), or an evolutionary history of this symbiosis to be proposed (Brundrett & Tedersoo, 2018). Despite the fact that these studies face some issues, such as biased sampling (e.g. limited to the northern hemisphere) and misassignment of the types of mycorrhizas, which are common in publications (Brundrett & Tedersoo, 2018), they can be highly informative. Using metadata, Brundrett & Tedersoo (2018) recognized three waves of mycorrhizal evolution: AM evolution in early land plants; first nonmycorrhizal (NM) plants plus ECM, ericoid and orchid mycorrhizas in the Cretaceous; recent and ongoing evolution, resulting in root complexity linked to rapid diversification in biodiversity hotspots. A recent molecular study using a large number of fungal DNA samples from roots revealed very low endemism in AM fungi, suggesting that the biogeography of this group is driven by efficient dispersal, probably via both abiotic and biotic vectors (Davison *et al.*, 2015). Studies like these provoke interesting discussions between communities and can provide ideas to palaeomycologists about where to look for new fossil fungi.

Mycorrhizal antiquity and history should also be analysed through the lens of geochemistry. Mycorrhizas are not just passive responders to the environment; they are also active agents of environmental change. The likely effects of early fossil fungi are inferred from analyses based on field and laboratory studies that use modern analogues of early plants partnering with arbuscular mycorrhizal fungi (e.g. liverworts, hornworts) and lichens. These organisms influenced calcium-magnesium silicate weathering and cation mobilization, leading to CO_2 drawdown by carbonate precipitation during the Late Paleozoic (e.g. Lenton *et al.*, 2012), although the extent of the effects is debated (Edwards *et al.*, 2015; Quirk *et al.*, 2015; Porada *et al.*, 2016), and the respective impact of a varied community elements (fungi, bacteria, algae) is largely unknown (Mitchell *et al.*, 2016). Roots and mycorrhizal symbionts are thought to have a major impact on biogeochemical cycles (Taylor *et al.*, 2012); however, estimating the magnitude of these effects in the earliest forests is challenging. Experiments using extant mycorrhizal trees as analogues of past forests have been performed under elevated CO_2 atmosphere conditions approximating those of the middle Devonian (Morris *et al.*, 2015). This has demonstrated that under elevated atmospheric CO_2, trees support larger hyphal networks and AM fungi increase physical alteration of silicate mineral surfaces (Quirk *et al.*, 2014). The rationale for a cross-disciplinary approach integrating palaeontological, mineralogical and geochemical analyses of palaeosol sequences was recently presented (Morris *et al.*, 2015) and this type of approach needs to be developed.

Finally, fungal 'omics' studies also begin to offer insights into the genome signatures of different trophic strategies and the roles of mycorrhizal fungi in the carbon cycle. One of the most debated issues in the field of mycorrhizal research concerns the putative role of these fungi as soil saprotrophs (Lindahl & Tunlid, 2015; Marmeisse & Girlanda, 2016). Over geological timescales, we might therefore anticipate that mycorrhizas are driving environmental change on a large scale, themselves influenced by the major changes that they cause. Such potential geophysiological feedbacks between mycorrhizas, CO_2 and climate, and their influence on genome evolution are as yet unexplored but could be a fruitful area of research, to be elaborated in the ongoing dialogue between palaeomycology and phylogenomics.

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ORCID

Christine Strullu-Derrien http://orcid.org/0000-0003-1131-9546
Marc-André Selosse http://orcid.org/0000-0003-3471-9067
Paul Kenrick http://orcid.org/0000-0002-3626-5460
Francis M. Martin http://orcid.org/0000-0002-4737-3715

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Notes S1 The origin of the fungal symbiosis: out of the water?

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