Coal Measure formation and lignin-degrading fungi

The first speculation of which I am aware that the formation of the Carboniferous Coal Measures could be linked to the evolution of fungi able to decompose lignin was that of Corner (1964: 112), who in discussing the origins of fungi commented: "to judge from the great accumulation of plant debris which makes the Coal measures, either they were not then established or they were unable to cope with the chemistry of those plants". When I read this as an undergraduate it made a huge impression on me as to the importance of fungi in shaping the world we know today, and I have alluded to this from time to time in lectures and publications. Now, comparative genomics have shown Corner was, as in so many aspects of mycology, spot-on.

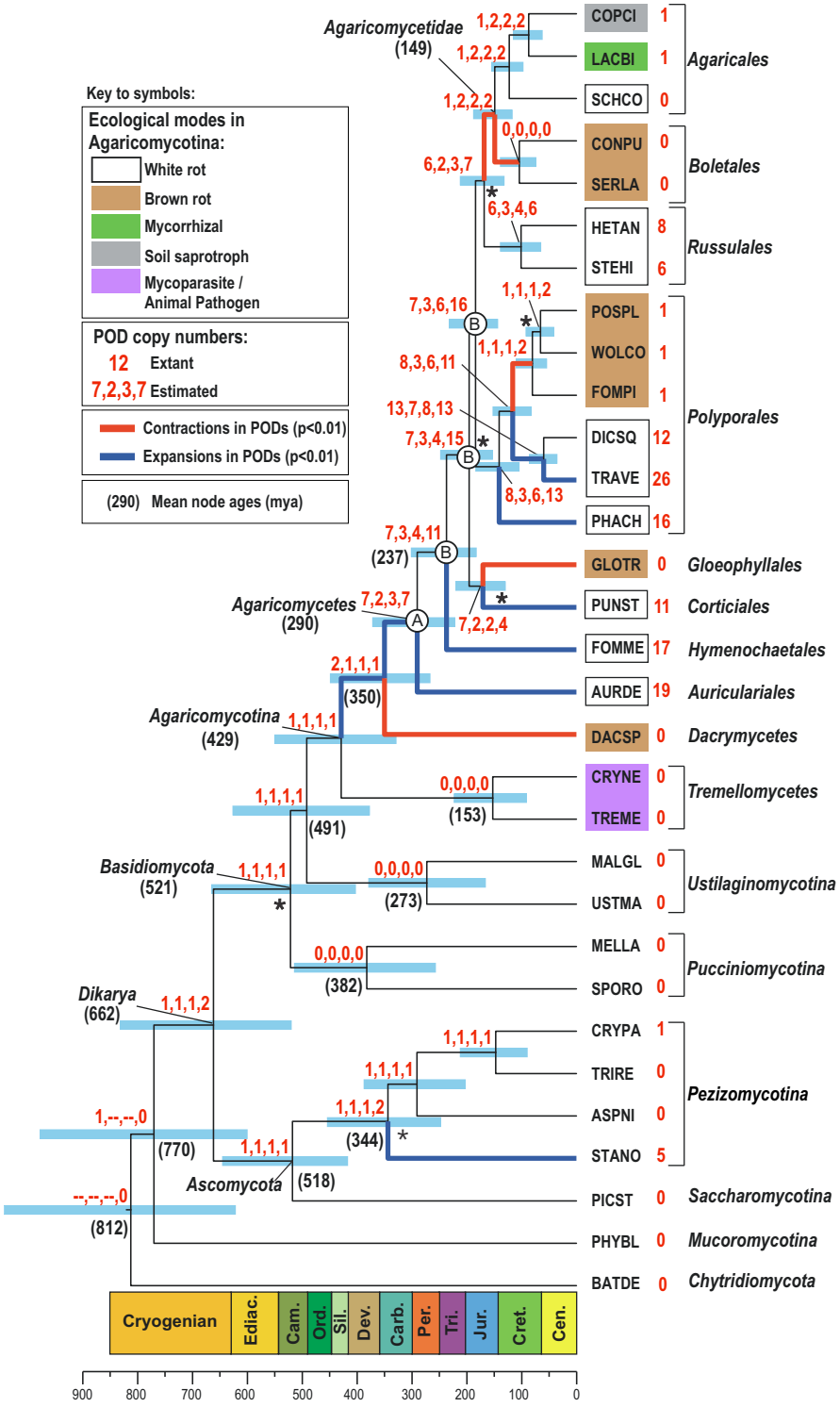
Floudas *et al.* (2012) analysed 31 fungal genomes, 12 of which were generated for their study, to ascertain when lignin decomposition had arisen within *Agaricomycotina*. They used a 26-gene data set and conducted molecular clock analyses. David S. Hibbett (Clark University, Worcester, MA) co-ordinated this massive team-effort, which achieved more than any lab could have contemplated doing alone. The results were striking, and suggest that both brown-rot and ectomycorrhizal fungi evolved from white-rot ancestors, with the origin of lignin-decomposing brown-rot fungi revealed as coinciding with a sharp decrease in the rate of organic carbon burial at the end of the Carboniferous period, at around 290 Myr ago. Their study also places the split between ascomycetes and basidiomycetes at 662 Myr, and diversification of the ascomycetes from the Cambrian period, 518 Myr ago.

Had lignin-decomposing fungi been around earlier, with no Coal Measures could there ever have been an Industrial Revolution in the 18th century and subsequent exponential development of the iron and steel industries that laid the foundations of the modern world? A worthy topic perhaps for an exam question to raise awareness of the relevance of fungi in the shaping of the world we live in today.

David S. Hibbett kindly supplied the figure reproduced here.

Corner EJH (1964) *The Life of Plants*. London: Weidenfeld and Nicolson.

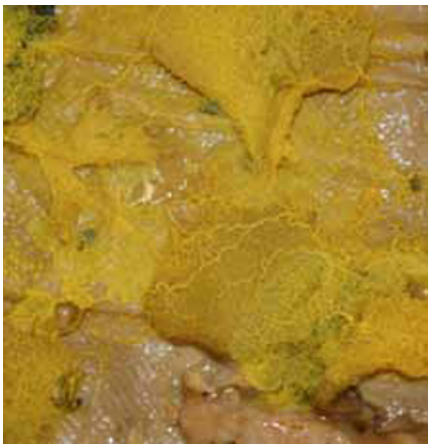
Floudas D, Binder M, Riley R, Barry K, Blanchette RA, *et al.* [and 66 others] (2012) The Palaeozoic origin of enzymatic lignin decomposition reconstructed from 31 fungal genomes. *Science* **336**: 1715–1719.



Chronogram produced with BEAST from a 26-gene data set. Light blue bars are 95 % highest posterior density intervals for node ages; mean ages of selected nodes (millions of years) are in parentheses. Blue and red branches indicate significant expansion and contraction, respectively. The node A is the ancestor of *Agaricomycetes*, and an asterisk (*) indicates nodes that did not receive maximal support. See Floudas *et al.* (2012) for more detailed explanation of figures and species names, from whom this figure has been adapted.

Slime mould navigation

Slime moulds, traditionally and still recorded and studied by mycologists despite their classification outside the kingdom *Fungi*, continue to amaze. Plasmodia migrating across dead wood are delightful to observe, not least when they are of brightly coloured species. But what controls the mycelium-like strands the colonies often express? Previous studies have shown abilities to negotiate complex mazes and discover the shortest paths, but the mechanisms have remained obscure. Just what happens in the case of *Physarum polycephalum* has now been investigated in the laboratory by Reid *et al.* (2012). Plasmodia were first presented with a choice between agar with extracellular slime from the mould and also blank agar in a Y-shaped maze, with a food source at the end of each arm. They had a most dramatic result; 39 of 40 plasmodia chose the blank arm. On blank agar with a U-shaped rather than a Y-shaped configuration, 96 % reached a glucose goal in 120 h, while on slime-coated agar only 33 % achieved that in the same time The authors concluded that the plasmodium was foraging, avoiding areas previously visited (i.e. those with slime formed by previous trips) in favour of ones that did not appear to have previously been explored, and thus were more likely to have untapped food resources. Complex navigational behaviour does not, therefore, necessarily depend on an organism having an internal memory, but can result from an externalized spatial memory based on signals left from previous roaming.

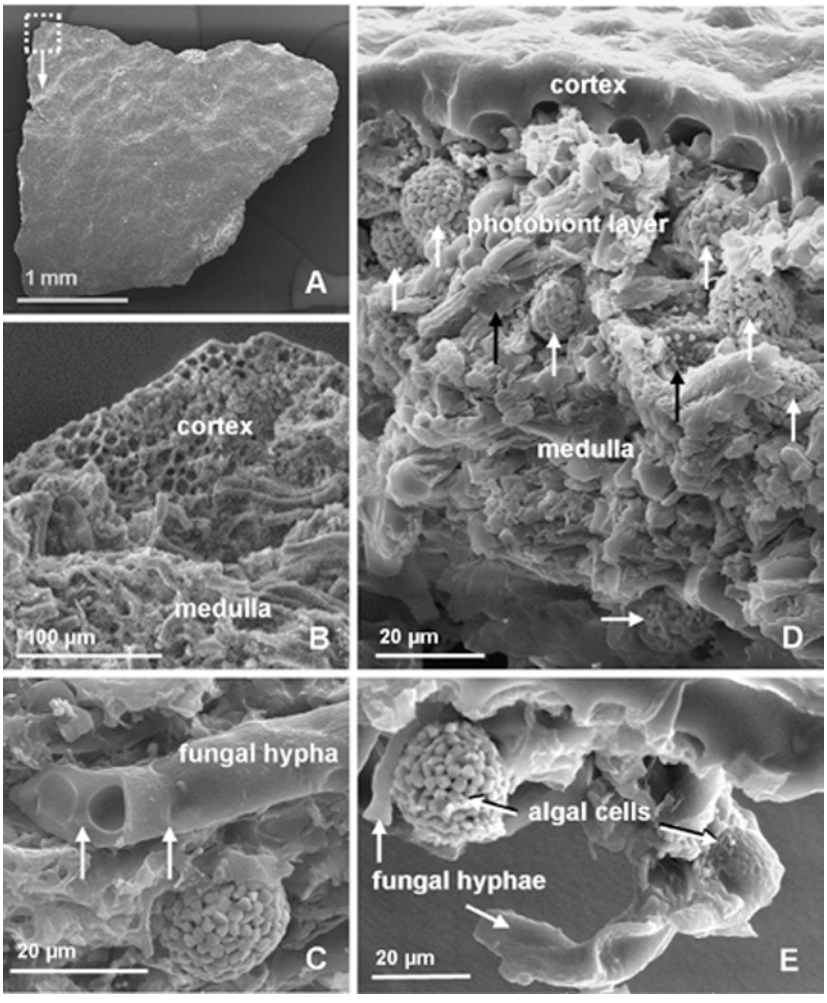


Foraging *Physarum polycephalum* in the laboratory. Photo: Steven L. Stephenson.

Reid CR, Latty T, Dussutour A, Beekman M (2012) Slime mold uses an externalized spatial "memorary" to navigate in complex environments. *Proceedings of the National Academy of Sciences, USA* **109**: 17490–17494.

Stratified algal and cyanobacterial lichens from the Lower Devonian

The search for the origins of lichenization as a biological strategy within fungi has taken a dramatic advance. Honegger *et al.* (2013) have discovered not loose associations between fungi and photosynthetic algae or cyanobacteria, but layered ("stratified") thalli strongly reminiscent of extant foliose lichens. These fossils come from the Lower Devonian in the borderland between England and Wales, which the second author, eminent palaeobotanist Dianne Edwards, has been investigating for several decades. Two new fossils reported on here are in deposits 415 Myr



Chlorolichenomycites salopensis. **A.** Entire fragment seen from the upper surface. **B.** Detail as marked in "A" seen from the lower surface, and showing hyphae of the alga and algal layer connected to the peripheral fungal cortex. **C.** Detail of a partly factored hyphae, the arrows pointing to a tangentially fractured septum and to a septum within the hypha. **D.** Thallus cross-section, with a cortex, algal layer, and medulla; the white arrows point to presumed green algal cells with framboidal pyrite contents, and black arrows to ones with lost contents. **E.** Fungal hyphae in contact with remains of globose algal cells, the right one having retained its delicate wall. Scanning electron micrographs by Rosmarie Honegger.

old, and are interpreted as representing stratified thalli, one with a cyanobacterial partner (*Cyanolichenomycites devonicus*) and one with a green algal partner (*Chlorolichenomycites salopensis*). The structures were compared with modern freshly collected lichens which had been "charcoalified" to facilitate comparison with the Lowe Devonian specimens. The results are remarkable and leave no doubt that complex stratified lichen thalli similar to that seen in extant *Lecanoromycetes* had already evolved by this early date. These predate the earliest previous reports of fossil stratified lichens from the Triassic by some 195 Myr. The paper is also of value in including a critical assessment of previously discovered fossils that have been interpreted as lichens, including citations of several papers scarcely known outside the palaeobotanical community.

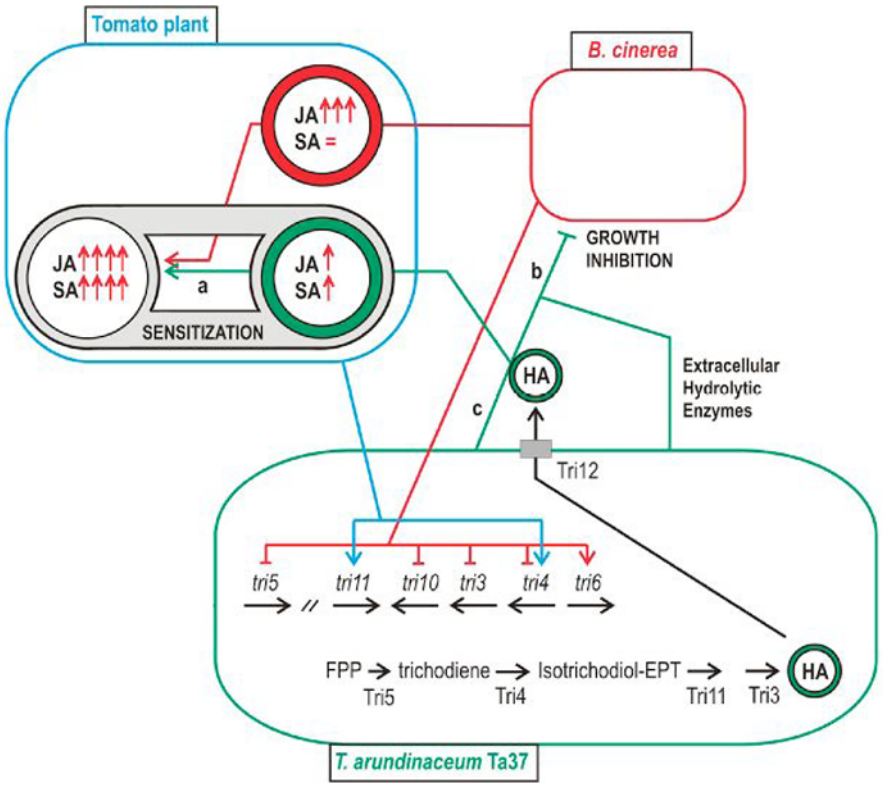
Of further interest is that while no ascomata were found, the *Cyanolichenomycites* had what is clearly a pycnidium, within which young conidia and conidiophores were visualized by superbly skilled scanning electron microscopy.

This is an extraordinarily meticulously executed and elegant study, and I understand that there will be future papers documenting other fascinating fungal fossils from these ancient deposits. Such fossils have major implications for the calibration of molecular clocks and the dating of divergence points in phylogenetic trees. In this case the authors are confident their two fossils belong to *Pezizomycotina*, but, perhaps over-cautiously, prefer not to refer them to a class in the absence of any sexual reproductive structures despite the obvious structural similarity to extant *Lecanoromycetes*. However, I do feel that possible classification now needs to be considered in future attempts to reconstruct and date the origins of that class, and of lichenization itself, even in the absence of ascomata. Structurally differentiated lichen thalli had clearly started to develop well before the Lower Devonian to enable such complex fossil to have been around by that time.

Honegger R, Edwards D, Axe L (2013) The earliest records of internally strafified cyanobacterial and algal lichens from the Lower Devonian of the Welsh borderland. *New Phytologist* **197**: 264–275; DOI 10:1111/nph.12009.

Trichoderma trichothecenes in biocontrol and plant defence gene induction

Molecular tools are increasingly enabling us to understand something of the complexity of interactions between different fungi and plants. Some *Trichoderma* species produce trichothecenes, most importantly trichodermin and harzianum A (HA), but the genes encoding these have a different genomic organization from that seen in trichothecene producing gene clusters of *Fusarium* species. There have been some previous studies on the effects of trichodermin produced by *T. brevicompactum* on plants, but the role of harzianum A had remained obscure. Now, the pertinent genes in a transformed strain of *T. arundinaceum*, labelled *tri4* and involved in HA biosynthesis, were silenced, enabling Malmierca *et al.* (2012) to explore its effects and possible relevance to the use of the fungus in biocontrol. They demonstrated that disruption of this gene led to reduced antifungal activity against both *Botrytis cinerea* and *Rhizoctonia solani*, and further to a reduced ability to induce the expression of plant defence related genes in tomato plants compared to the wild-type *Trichoderma* strain. Their experiments lead to the conclusion that harzianum A has a role in sensitizing the tomato plants to attack by other fungi, as well as in its antifungal mycoparasitic activity. They also found that the plant pathogenic fungi and the tomato plants had a role in regulating the expression of the *tri* genes in *T. arundinaceum*.



Schematic representation of the network of interactions established among *Trichoderma arundinaceum* (Ta37), *Botrytis cinerea,* and tomato plants deduced from the present work. Arrows indicate response stimulation or gene upregulation, and blunt-ended lines indicate gene repression or growth inhibition. Red, blue, and green lines indicate interactions mediated by *B. cinerea*, tomato plant, and the *Trichoderma*, respectively. a, sensitizing effect of *Trichoderma*-pretreated tomato plants mediated by the trichothecene harzianum A (HA); b, coupled action of HA and extracellular hydrolytic enzymes to inhibit *B. cinerea* growth; c, other metabolites produced by *T. arundinaceum* that, in addition to HA, would also affect its interaction with plants and with its fungal targets. Reproduced from Malmierca *et al.* (2012).

This appears to be the first report of an interaction between trichothecenes and plant defence responses, indicating that these compounds are involved in a complex network of interactions in which each partner regulates the other. The complexity of this particular situation is indicated in the accompanying figure, but it seems probable that extrolites from other fungi may also have similar roles in biocontrol scenarios.

Malmierca MG, Cardoza RE, Alexander NH, McCormick SP, Hermosa R, Monte E, Gutiérrez SW (2012) Involvement of *Trichoderma* trichothecenes in the biocontrol activity and induction of plant defense-related genes. *Applied and Environmental Microbiology* **78**: 4856–4868.