Pre-war, Gwynne-Vaughan & Barnes (1937) *The Structure and Development of the Fungi* had been a standard text in Departments of Botany in Britain, but post-war it had become completely out-of-date. Cambridge University Press, in seeking a replacement, wondered if I might undertake the job. However, knowing my limitations, I had no hesitation in rejecting the idea and suggested that they should approach John. It seems to me that in sowing the seeds of his *Introduction to Fungi* (Webster 1970) I performed a major contribution to mycology. This remarkable book, profusely illustrated by the author's own drawings, has over 1600 references. It is incredible that it should be the work of one man.

Although hardly more than jottings, it has been an honour to contribute to this celebration issue of *Mycological Research*, but it is for others and over time to make a scholarly appraisal of his researches. Over many years John and I have shared the same attitude to mycology, never losing sight of the whole living fungus, and inspired by giants such as de Bary and Buller. May this approach never be extinguished.

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FIRE, HYPOGEOUS FUNGI AND MYCOPHAGOUS MARSUPIALS

In their interesting research on post-fire foraging behaviour of northern bettongs (*Bettongia tropica*) in tropical Queensland, Australia, Vernes *et al.* (2004) used forage-diggings of their study animals to locate plots for estimating biomass of hypogeous fungi on prescribed-burnt sites in comparison with unburnt control sites. They concluded that '… within a few weeks after each experimental fire, biomass on burnt sites peaked at very high levels compared with unburnt sites, and then decreased markedly to very low levels within 2–3 months post-fire. The peak in biomass on burnt sites was largely due to increased biomass of species within the family *Mesophelliaceae* …' They noted that '… the density of *B. tropica* forage-diggings did not increase after fire, suggesting that the intensity of foraging did not change. However, the rate at which *B. tropica* foraged for sporocarps (diggings made per metre travelled) was significantly higher on burnt ground compared with adjacent unburnt ground, suggesting that foraging efficiency increased following fire, presumably due to increased biomass of sporocarps'. Vernes *et al.* reasoned that the post-foraging biomass in the plots centered at forage-digging sites reflected real changes in the availability of the fungal resource 'as perceived by *B. tropica*'.

We appreciate that Vernes *et al.* (2004) acknowledged the 'scholarly criticisms and suggestions' of two of us (A.W.C. & J.A.T.) in reviewing an early draft of their manuscript. We here express some of the points included in that prepublication review in a spirit of friendly discourse. We offer some alternative conclusions based on their data and suggest additional ways to analyse their data. Such an exchange of views is of more than academic interest, because some forest management agencies in Australia have used the notion that fire enhances the hypogeous fungal food resource for small marsupials as one justification for their policy of frequent prescribed burning; the topic is reviewed elsewhere (Claridge & Trappe 2004).

It is important to note that use of bettong forage-digging sites to locate plots can yield interesting information, but it is not a random sampling system. Lack of randomness necessarily limits the inferences that can be drawn about biomass of fungi in burnt vs. unburnt sites. Alternative possibilities for the phenomenon identified by Vernes *et al.* 2004 include: (1) the bettongs can more readily detect colonies of *Mesophelliaceae* in burnt sites than unburnt because heating intensifies the aroma of fruit-bodies already present at time of burning (Millington *et al.* 1997, Claridge & Trappe 2004), and (2) suppression of fruiting of other, more fleshy hypogeous fungi by burning forces the bettongs to focus on *Mesophelliaceae* for lack of alternative food sources (Claridge & Trappe 2004). In other words, the data of Vernes *et al.* (2004) allow interesting inferences about the behaviour of the bettongs, but their design does not support statistical comparison of overall hypogeous fungus biomass on burnt *vs* unburnt sites or between sampling dates. True estimators of hypogeous fungus biomass may only be obtained *via* a randomized sampling and design. Furthermore, a detailed review of fungal fruit body morphogenesis by Claridge & Trappe (2004) suggests that production and maturation of sporocarps of the structure of the *Mesophelliaceae* within a few weeks is highly unlikely. Thus, the significant peaking of biomass of the *Mesophelliaceae a* few weeks after the burn treatment reflects bettong foraging behaviour but not treatment effects on biomass *per se*.

To use forage-diggings of bettongs as a basis for plot location and then assume that this reflects fungal biomass *per se* rests on the assumption that the detectability of fungal fruit bodies does not differ between

burnt and unburnt sites. Our research offers no reason to believe that this is so. Fruit bodies of *Mesophellia* from burnt sites are typically strongly aromatic, whereas those from unburnt sites are not. This could simply mean that bettongs detect *Mesophellia* fruit bodies more easily and can access them more readily on burnt than on unburnt sites. This hypothesis needs testing, but it seems reasonable (Claridge & Trappe 2004). Some of the plots in our long-term studies of hypogeous fungi in south-eastern Australia burned in the wildfires of 2003 and were sampled 3 months later (Claridge & Trappe 2004). In plots that contained *Mesophellia* spp., the fruit bodies near the surface where scorched and smelled intensely of rotten onions, whereas underlying, well matured fruit bodies a few cm deep were undamaged and had a mild, nutty aroma.

Vernes *et al.* (2004) noted that in burnt sites the bettongs discarded the peridium and powdery spore mass of *Mesophellia* fruit bodies and ate only the nutritious inner core, a feature not observed in their unburnt sites. They repeated Johnson's (1995) suggestion that the fruit bodies on the burnt sites were so abundant that '… bettongs had discarded all but the most nutritionally valuable portions'. Such a feeding behaviour is common among many marsupials in eastern Australia and better reflects a 'natural' feeding behaviour rather than a 'frenzied' or 'wasteful' feeding behaviour. In captivity, for example, long-nosed potoroos (*Potorous tridactylus*) will always discard the outer, dry and brittle peridium and spore powder of *Mesophellia* fruit bodies in the process of getting to the nutritious core (Claridge & Cork 1994). Discarded peridia and spores of *Mesophellia* are commonly seen at forage-diggings of bandicoots and potoroos at unburnt sites in the wild (Claridge 1993, Claridge & May 1994), so this behaviour is not exclusive to burned areas.

Similar economical feeding behaviour is observed among mycophagous mammals elsewhere. For example, in North America small rodents that feed on *Elaphomyces* eat only the outer, fleshy peridium of fruit bodies of that genus, discarding the inner powdery spore mass (Trappe & Maser 1979), which is essentially indigestible (Cork & Kenagy 1989). Johnson's (1994a) data on Tasmanian bettongs (*B. gaimardi*) suggest an analogous behaviour: *Elaphomyces* fruit bodies were plentiful in his study sites, but *Elaphomyces* spores were rare in the bettong feces. A major dispersal strategy of hypogeous fungi that produce a powdery spore mass is to be dug up by the animal, which then releases most of the spores to the air or to be attached to whiskers, fur and paws of the mycophagist in the course of accessing the more nutritious sporocarp tissues (Trappe & Claridge 2005).

Another critical feature of the data presented by Vernes *et al.* (2004) is that burning appeared to have no long-term benefit in terms of ongoing bettong post-foraging site biomass of hypogeous fungi. Overall, the burnt and unburnt sites did not differ. Vernes *et al.* (2004) do not show the separate ANOVA tables for each of the sites in 1995 and 1996, but their Figs 3 and 4 suggest that the bettong post-foraging site overall mean biomass may be higher in the unburnt than burnt sites, whereas in 1996 the unburnt and burnt sites do not differ. This raises the question of under what circumstances would forest managers use fire to benefit either the bettong or its key food resources? The answer, in part, would be when fire is necessary to re-create preferred vegetation types or seral stages of vegetation for the species, rather than to expect increased hypogeous fungus sporocarp biomass.

Although the biomass data and determining the effects of prescribed burning on the bettong detection of two selected hypogeous species (*Mesophellia* and *Gummiglobus*) are interesting from an autecological point of view, the relevance of such results and analyses in regard to maintaining the fitness of mycophagous small mammal populations is questionable. First, the lack of analysis of fungus diversity data in the study by Vernes *et al.* (2004) is a critical omission. Johnson (1997) found that species richness on sites burnt 1–4 years prior to sampling was low compared to sites not burnt for 10 or more years. Small mammals tend to feed on a variety of taxa and not rely on a single taxon for nutrition (Maser, Trappe & Nussbaum 1978, Johnson 1994a, b, Claridge & Trappe 2005). Judging from differences in contents of carbohydrates, amino acids, proteins, vitamins, etc, between fungal species, this diet diversity probably represents a nutritional imperative (Claridge & Trappe 2005). Thus, bettong populations may not benefit in the long run from accessibility of only *Mesophellia* and *Gummiglobus* spp., no matter how great their abundance. Second, Vernes *et al.* do not test whether the *occurrence* of the two taxa that contributed greatly to the bettong post-foraging site biomass also changed in response to fire. Simple logistic regression analyses using binary (presence/absence) data on *Mesophellia* and *Gummiglobus* sporocarps might elucidate if indeed the bettongs detected a greater number of fruiting colonies of these species. Use of binary data provides a robust tool that avoids problems of the gregarious fruiting common to hypogeous fungi. Finally, an interesting alternative to the design presented would be a random sampling for hypogeous fruit bodies before and after fire on adjacent paired plots. Such a design would resolve the above-discussed issues on detectability resulting from sporocarp responses to heating.

Regardless of how one decides to interpret the results of Vernes *et al.* (2004), a main point not to be overlooked is that marsupials such as the northern bettong play a critical role in dispersing spores of hypogeous, mycorrhizal fungi such as *Mesophellia* spp. in recently burnt habitats. Indeed, nowhere is this role more critical than where fire has damaged the mycorrhizal (perennial) portion of the fungus. With this in mind, forest managers would do well to put in place measures that help protect species such as the northern bettong

as well as the myriad other terrestrial mammals that perform this vital, spore-dispersing function.

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PALAEOPYRENOMYCITES DEVONICUS: A 400 MYR OLD PYRENOMYCETE

The 400 Myr old Early Devonian Rhynie Chert deposits in Aberdeenshire (UK) have already yielded an amazing array of fossil fungi, including chytrids, a blastocladialean fungus, mycoparasites, endomycorrhizal zygomycetes, and a cyanobacterial lichen. Now, Taylor *et al.* (2005) report a pyrenomycete from just beneath the epidermis of the aerial stems and rhizomes of the lycopod *Asteroxylon mackeri*. The degree of preservation leaves no doubt about this being an ascomycete as asci with up to 16 ascospores, and also paraphyses, could be distinguished. The perithecia are almost globose and ostiolate with a collar, and the ascospores are at first rounded but become elongate and 1–5 celled. There is also an associated arthrosporic anamorph. The asci appear to be unitunicate in structure. This is the first indisputable evidence for an early-Devonian pyrenomycete, at least superficially resembling modern *Sordariomycetes* (Eriksson 2005), and suggests that the ascomycetes were already very diverse 400 Myr ago and consequently may be a very much older phylum than suggested by molecular clock estimates.

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