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FOSSIL MUSHROOMS FROM MIOCENE AND CRETACEOUS AMBERS AND THE EVOLUTION OF HOMOBASIDIOMYCETES[1]

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Two species of fossil mushrooms that are similar to extant Tricholomataceae are described from Cretaceous and Miocene ambers. *Archaeomarasmius leggetti* gen. et sp. nov., from mid-Cretaceous amber of New Jersey, resembles the extant genera *Marasmius* and *Marasmiellus*. Two fruiting bodies of *Archaeomarasmius* were found. One consists of a complete pileus with stipe, and the other consists of a fragment of a pileus. The latter was accidentally exposed, and zxsubsequently was used for molecular systematics studies (attempts to amplify ribosomal DNA were unsuccessful) and electron microscopy. The spores are smooth and broadly elliptic with a distinct hilar appendage. *Protomycena electra* gen. et sp. nov., which is represented by a single complete fruiting body from Miocene amber of the Dominican Republic, is similar to the extant genus *Mycena*. Based on comparison to extant Marasmieae and Myceneae, *Archaeomarasmius* and *Protomycena* were probably saprophytes of leaf litter or wood debris. The poor phylogenetic resolution for extant homobasidiomycetes limits the inferences about divergence times of homobasidiomycete clades that can be drawn from *Archaeomarasmius* and *Protomycena*. The ages of these fossils lend support to hypotheses that the cosmopolitan distributions of certain mushroom taxa could be due to fragmentation of ancestral ranges via continental drift. Anatomical and molecular studies have suggested that there has been extensive convergence and parallelism in the evolution of homobasidiomycete fruiting body form. Nevertheless, the striking similarity of these fossils to extant forms suggests that in certain lineages homobasidiomycete macroevolution has also involved long periods during which there has been little morphological change.

Key words: amber; *Archaeomarasmius*; basidiomycetes; evolution; fossil fungi; paleomycology; *Protomycena*; Tricholomataceae.

Despite the recent proliferation of molecular studies in fungal systematics, basic taxonomy and identification of homobasidiomycetes (which include the mushroom-forming fungi) still rely heavily on morphological characters from fruiting bodies. These are the most conspicuous phase of the homobasidiomycete life cycle and encompass a broad spectrum of morphological variation. In terms of complexity, they range from simple, resupinate forms that have traditionally been placed in the ''Corticiaceae'' sensu lato, to elaborate, developmentally integrated forms, such as those in the mushroom genus *Amanita*, or the veiled stinkhorn genus *Dictyophora*. Most are ephemeral, but the fruiting bodies of certain wood-rotting bracket fungi can persist for years. In addition to their taxonomic importance, fruiting bodies also provide information—in most cases the only information—about the temporal and spatial distributions of homobasidiomycete individuals. For these reasons, fossils of fruiting bodies could contribute greatly to hypotheses about the phylogeny and paleoecology of homobasidiomycetes.

Regrettably, homobasidiomycete macrofossils are extremely rare, although fungal spores and hyphae are often encountered in association with plant remains (e.g., Stubblefield, Taylor, and Beck, 1985; Kalgutkar and Sigler, 1995). As a result, almost everything that is known about the evolution of homobasidiomycetes is based on comparative studies of extant taxa. In recent years, the combination of molecular techniques and rigorous methods of phylogenetic inference has provided significant insight into patterns of evolution in homobasidiomycetes. Nevertheless, many unanswered questions remain concerning the phylogeny of the homobasidiomycetes, the ages of homobasidiomycete clades, the relationship between the evolution of homobasidiomycetes and the radiation of angiosperms, the relative importance of vicariance and long-distance dispersal in homobasidiomycete distribution, and macroevolutionary patterns of morphological change in homobasidiomycetes. Paleomycological data have the potential to address these issues, especially when combined with phylogenetic hypotheses based on molecular characters (e.g., Berbee and Taylor, 1993). In this paper we describe two fossil mushrooms that appear to be closely related to certain extant genera and consider their significance for homobasidiomycete evolution. One of these fossils was reported previously (Hibbett, Grimaldi, and Donoghue, 1995), but there was no taxonomic diagnosis.

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MATERIALS AND METHODS

New Jersey amber—Atlantic coastal plain amber occurs in a band of Cretaceous exposures that strikes northeast from just below the Raritan River, and extends from the Delaware River to the Atlantic coast (Grimaldi, Beck, and Boon, 1989). The piece of amber that contained the mushrooms was found in East Brunswick, New Jersey, in November 1994, by G. R. Case, P. D. Borodin, and J. J. Leggett. At this site, the amber erodes out of rills along a barren, exposed hillside. The amber deposits are interspersed in layers of fine clay, sand, and highly compacted lignitic peat, all of which are the products of deltaic deposition. Fine structure of the lignite occurring in the amber indicates a coniferous origin, as is expected for all Cretaceous amber (Langenheim, 1969). The amber that contained the mushrooms lay just above the South Amboy Fire Clay of the Raritan Formation, thus making it Turonian in age [90–94 million years ago (mya)].

The fossils were contained in a hemispherical piece of clear, light yellow amber ~ 6 cm in diameter (AMNH NJ-90). Exposure had caused the piece to fracture along flow lines into ~ 80 thin chips that were placed into a single container and transported to the laboratory at AMNH (American Museum of Natural History). The thin pieces from the original lump of amber actually facilitated screening for inclusions. Two of the amber fragments contained mushroom pieces. One piece, AMNH NJ-90Y (Fig. 1), contained a complete pileus with a central stipe that was broken off below the underside of the cap. The top of the pileus was located along an exposed, opaque surface of the amber and was not visible. To limit oxidative degredation, a thin layer of synthetic resin was applied to the flat surfaces of the amber, and this improved visibility somewhat. Another piece, AMNH NJ-90Z (Fig. 2), contained a wedge-shaped fragment of a pileus. The New Jersey Cretaceous amber is extremely brittle. In the course of preparing AMNH NJ-90Z for viewing, the piece was inadvertently fractured along a flow line that split the inclusion in half (Fig. 2). Initially there was no intention of performing any destructive sampling, but the accidental exposure of the inclusion, and the consequent threat of oxidative damage, warranted that parts of the inclusion be sacrificed for ultrastructural studies and molecular systematics.

For scanning electron microscopy (SEM), fragments of the amber of AMNH NJ-90Z and small pieces of the inclusion were mounted directly on SEM stubs with double-sided tape, and sputter-coated with gold-palladium. For transmission electron microscopy (TEM), a small piece of the inclusion was embedded in Spurr's resin, and sectioned with a diamond knife. The embedded inclusion was oriented so that vertical tangential sections of the hymenophore would be produced.

DNA extraction was attempted using part of the inclusion of AMNH NJ-90Z. Handling of materials for molecular systematics was organized to minimize the likelihood of DNA contamination in polymerase chain reaction (PCR) amplifications. DNA isolation was performed in the molecular systematics laboratory of AMNH, which previously had never been used for fungal molecular studies. A small piece of the inclusion was extracted overnight at 55°C in 900 μL 100 mmol EDTA, 10 mmol/L Tris pH 7.5 with 1 μL 20 μg/μL proteinase K, and 100 μL 10% SDS, extracted twice with equilibrated phenol and once with chloroform, and purified using Centricon 30 tubes (Amicon, Beverly, MA). In addition to the extraction from the inclusion, a control extraction was performed using a piece of the amber that contained no visible fungal material. The putative DNA extract was stored in a laboratory in the Peabody Museum, Harvard University, which also had never been used for fungal molecular studies. PCR reactions were set up in the Peabody Museum laboratory and the tubes containing the reaction cocktail were transported to a laboratory in the Harvard University Herbaria (which is in a separate building) for amplification. Post-PCR solutions, potentially containing amplified fungal rDNAs, were never taken into the Peabody Museum laboratory.

Three regions of nuclear ribosomal DNA were selected for amplification: (1) a 122-bp (base pair) fragment near the 5′ end of the nuclear large-subunit rDNA that is part of a highly variable eukaryote-specific ''divergent domain'' region; (2) the internal transcribed spacer 1 (ITS 1); and (3) the ITS 2. The primers for the large subunit divergent domain were designed based on previously published homobasidiomycete large subunit rDNA sequences (Hibbett and Vilgalys, 1993); the primer sequences are (5′→3′) CCC TAG TAA CTG CGA GTG AAG CGG and CCA (AG)G(AG) (GA)AC TT(AG) TAC ACG GTC C. The ITS 1 and ITS 2 were separately amplified using primer pairs ITS 5 and ITS 2, and ITS 3 and ITS 4 of White et al. (1990). Each amplification was performed using three different templates: the extract from the inclusion, the extract from the amber, and a negative control blank in which the DNA extract was replaced by water. In a separate set of reactions, aliquots of the fossil extracts (from both the inclusion and the amber alone) were combined with an equal volume of dilute DNA from the homobasidiomycete *Lentinula edodes* and used as a PCR template with the same set of primers. The goal of this exercise was to determine whether there are PCR-inhibiting substances present in the amber extracts.

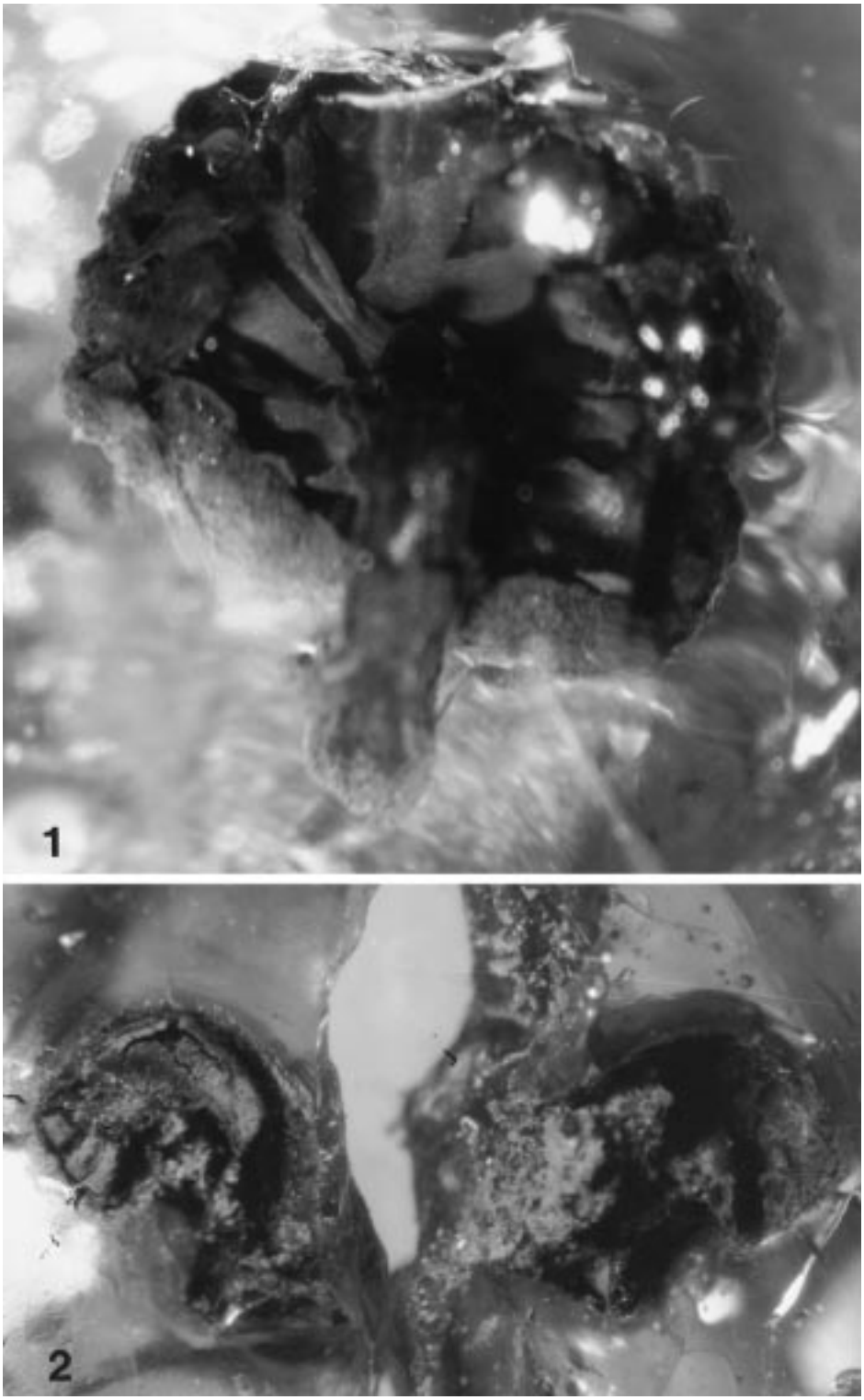
Dominican amber—Dominican amber is derived from resin of *Hymenaea* (Leguminosae), and is primarily found in an area of ~ 400 km^2 at an elevation between 500 and 1000 m in the Cordillera Septentrional (Grimaldi, 1995). The exact location where the piece that contained the mushroom fossil was found is not known. The amber piece measures ~ 4.5 × 2.5 cm, is clear and light yellow, and has been polished.

Dominican amber has already yielded one fossil mushroom. *Coprinites dominicana* was described by Poinar and Singer (1990) in amber, reportedly from the La Toca mines in the Cordillera Septentrional. *Coprinites* was originally estimated to be ~ 40 million years old (Eocene), based on a ^{13}C nuclear magnetic resonance (NMR) study of Dominican amber by Lambert, Frye, and Poinar (1985). This age estimate has been disputed by two recent studies, including a critique of the NMR data of Lambert, Frye, and Poinar, which suggests that the Dominican amber actually dates from the lower Miocene to mid Oligocene (23–30 mya; Grimaldi, 1995), and an analysis of biostratigraphic and paleogeographic data, which suggests that the Dominican amber is from the late Early Miocene to early Middle Miocene (15–20 mya; Iturralde-Vinent and MacPhee, 1996).

DESCRIPTION OF NEW JERSEY FOSSIL MUSHROOMS

Kingdom—Fungi
Phylum—Basidiomycota
Order—Agaricales
Family—Tricholomataceae
Archaeomarasmius leggetti Hibbett, Grimaldi & Donoghue gen. et sp. nov.

Description—Basidiomata medium-dark brown. Pileus 3.2 mm (AMNH NJ-90Y) to 6.0 mm (AMNH NJ-90Z) diameter, circular, plano-convex, thin-fleshed (< 1 mm), radially sulcate (Figs. 1–3); margin incurved; surface glabrous to minutely textured; veil absent; context thin. Lamellae distant to subdistant (12), without lamellulae, less than 1 mm wide at the widest point, attached to stipe apex; noncollariate, nonanastomosed; edges entire. Stipe 2.2 × 0.5 mm, base broken, insertion central, cylindrical, smooth, exannululate. Basidiospores 6.5–8.3 × 4.0–5.2 μm (mean dimensions = 7.3 × 4.7 μm, N = 4 spores and 4 spore casts in amber), broadly ellipsoid to ovoid, smooth or possibly minutely textured, with a distinct hilar appendage (Figs. 4–7).



Figs. 1, 2. *Archaeomarasmius legettii* gen. et sp. nov. Holotype. **1**. AMNH NJ-90Y. View of undersurface of intact pileus with radial lamellae and stipe (which is broken). Pileus diameter = 3.2 mm. **2**. AMNH NJ-90Z. Fragment of pileus. View of two halves of inclusion split open along flow line in amber. The plane of the fracture has produced a vertical, radial section of the hymenophore and pileus. Remains of face of one lamella are visible in the fragment on the left. Pileus radius = 3 mm.

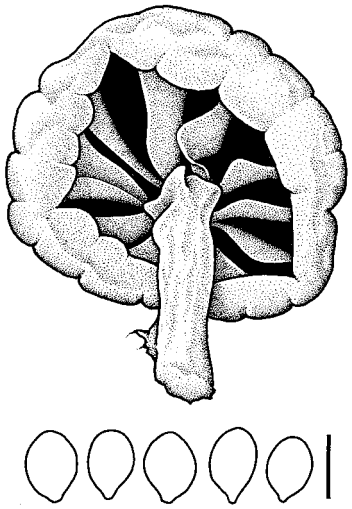


Fig. 3. *Archaeomarasmius legettii* gen. et sp. nov. Sketch of fruiting body from AMNH NJ-90Y and spores from AMNH NJ-90Z. Pileus diameter is 3.2 mm. Scale bar for spores = 7 μm.

Locality—East Brunswick, New Jersey, USA, close to site number 5 on the map in fig. 4 of Grimaldi, Beck, and Boon (1989).

Holotype—American Museum of Natural History, Department of Entomology, collection numbers AMNH NJ-90Y and AMNH NJ-90Z.

Etymology—The generic epithet means ''ancient *Marasmius.*'' The specific epithet honors J. J. Leggett and colleagues, without whose alertness this specimen might never have been discovered.

DESCRIPTION OF DOMINICAN FOSSIL MUSHROOM

Kingdom—Fungi
Phylum—Basidiomycota
Order—Agaricales
Family—Tricholomataceae
Protomycena electra Hibbett, Grimaldi & Donoghue gen. et sp. nov.

Description—Basidiome pale, appearing yellowish through amber. Pileus 5 mm diameter × 4 mm height (optical distortion induced by the amber makes precise measurements difficult), circular, convex, surface glabrous at the center, becoming striate and translucent (pellucid) toward the margin; margin slightly flared; veil absent; context thin (Figs. 8–10). Primary lamellae distant (6–8), moderately broad, broadly attached to stipe apex, anastomosed with lamellulae of several lengths; edges entire. Stipe curved, ~ 1 cm × 0.75 mm, cylindrical, smooth or minutely textured (gas and liquid filled bubbles, apparently drawn out of the mushroom, impair observations of the surface textures), exannulate; stipe base abrupt. Basal mycelium, rhizoids, or other anchoring structures absent.

Locality—Northern amber mines of the Dominican Republic.

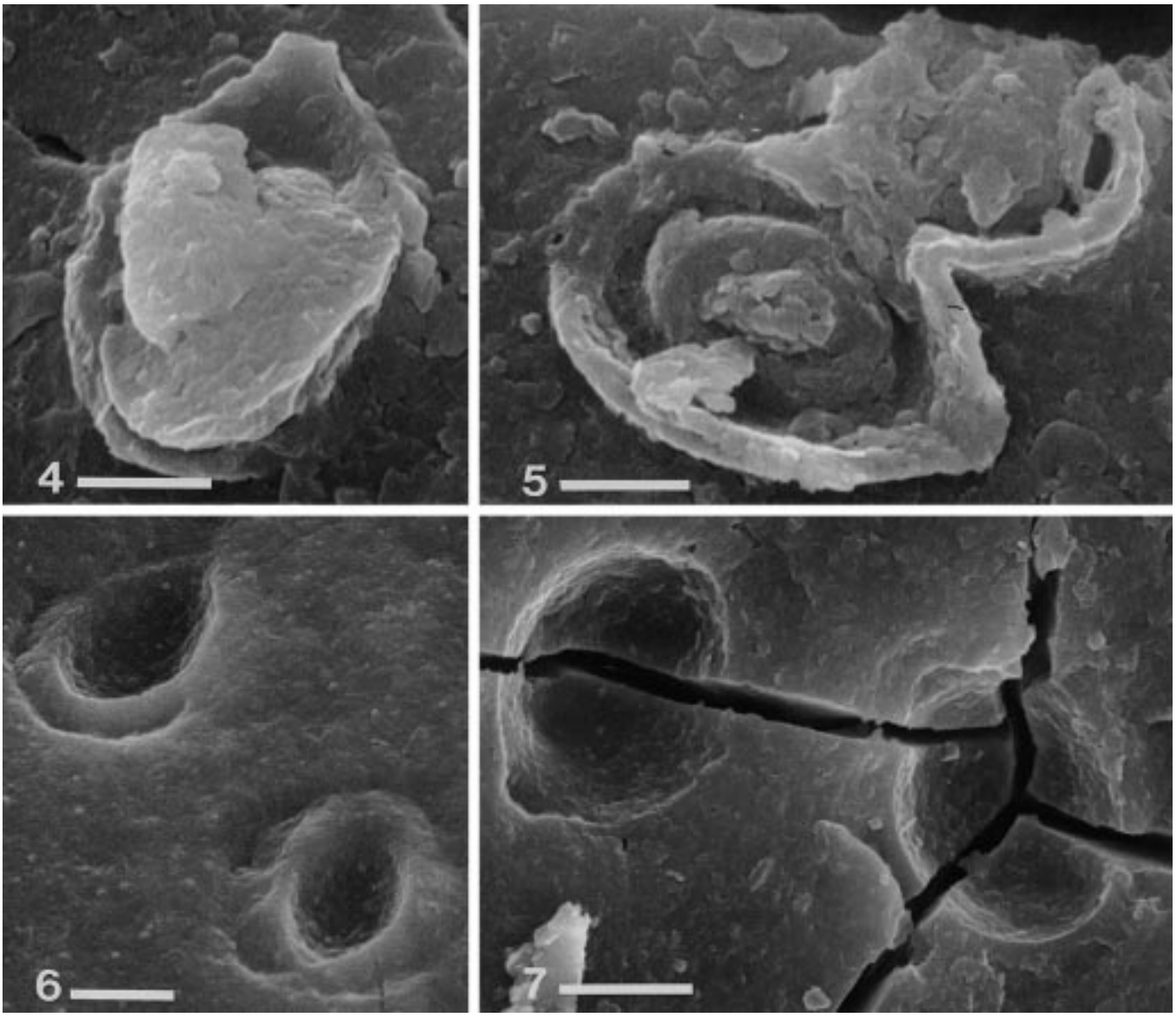
Holotype—In private collection of Ettore Morone, Turin, Italy (on loan to D. Grimaldi).

Etymology—The generic epithet means ''first *Mycena.*'' The specific epithet refers to amber.

RESULTS AND DISCUSSION

Taxonomy and preservation of Archaeomarasmius—In overall habit the New Jersey fossils are similar to the extant genera *Marasmius* and *Marasmiellus,* which include minute agarics that often have radially sulcate pilei. A diagnostic character of typical *Marasmius* and *Marasmiellus* species is that their fruiting bodies are not putrescent, but rather become tough with drying and can revive upon rewetting. This attribute would probably increase the likelihood that fruiting bodies could become entombed in amber before they decayed, and further suggests that the fossil mushrooms are related to *Marasmius* or *Marasmiellus.* Nevertheless, there are other genera that include small, ''marasmioid'' agarics, which could be plausible candiates for the closest relatives of *Archaeomarasmius.* The majority are hyaline-spored members of the Tricholomataceae, such as *Mycena, Collybia* and *Crinipellis,* but certain pigmented-spored species, such as *Phaeomarasmius rimulincola* of the Strophariaceae (Singer, 1986) are also marasmioid. To rigorously discriminate among these taxa it is necessary to make observations of anatomical characters that are often subtle and that unfortunately could not be seen in the fossils. For example, according to Singer (1986, p. 320), ''*Marasmiellus* differs from *Marasmius* in the structure of the epicutis of the pileus and the inamyloid [=nondextrinoid] hyphae'' (in response to potassium iodide, amyloid cells stain blue, whereas dextrinoid cells stain reddish-brown). The paucity of consistent, qualitative characters for these genera has resulted in considerable taxonomic disagreement (reviewed by Antonín and Noordeloos, 1993). For example, Singer (1986) classified *Marasmius, Marasmiellus,* and *Collybia* in three separate tribes of the Tricholomataceae, the Marasmieae, Myceneae, and Collybieae, respectively, whereas Kühner (1980) placed all three in the Marasmieae of the Marasmiaceae. Of the Marasmiaceae, Kühner wrote, ''All the Marasmiaceae herein are found in Singer's tribes Marasmieae, Collybieae and Myceneae but only the names are accepted not the limits. . . The genus *Collybia* passes into the genus *Marasmius* in such an unnoticeable way. . .that the delimitation of the two genera is arbitrary; placing these two genera into different tribes as proposed by Singer cannot be supported'' (Kühner, 1980, p. 950).

Spores are the only anatomical features that can be observed in the fossils. The hilar appendages indicate that the spores are those of a basidiomycete. Although the spores were not observed attached to basidia of the fruiting body, their proximity to the fossils strongly suggests that they were produced by the now-fossilized mushrooms. Macrochemical reactions and the color of spores in mass are important taxonomic characters in homobasidiomycetes, but these could not be observed in the fossils. No germ pores or ornamentation could be seen. Spore wall thickness, which can also be taxonomically informative, is difficult to judge because the fossils con-

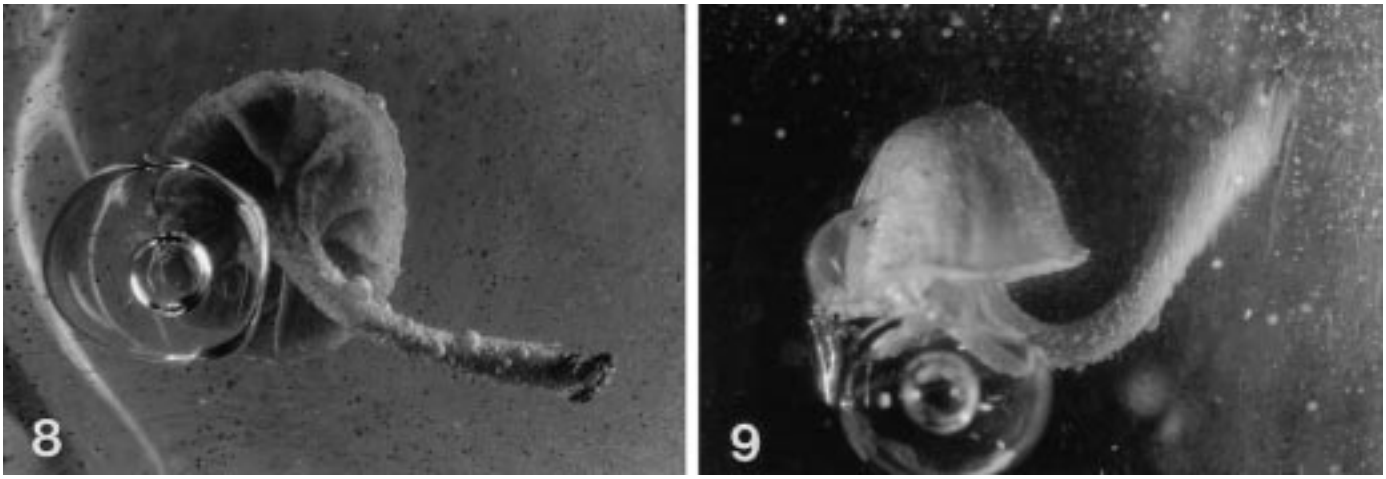


Figs. 4–7. *Archaeomarasmius legettii* gen. et sp. nov. Spores and spore casts from AMNH NJ-90Z. **4, 5**. Spore fragments. **6, 7**. Spore casts. Note halos surrounding spore casts. Scale bars: Figs. 4, 5 = 2 μm, Fig. 6 = 1.5 μm, Fig. 7 = 4 μm.

tain only fragmented spores, which were visualized with SEM, whereas this character is usually viewed using light microscope observations of intact spores. Furthermore, it is not clear whether the spore fragments are composed only of original cell wall material, or whether substances derived from the cytoplasm or amber matrix also contribute to the thickness of the spore fragments. All that we know about the spores with certainty is that they were $\sim 7 \times 5$ μm, broadly elliptic with hilar appendages, and more or less smooth. Spores with this combination of characters are found in *Marasmius, Marasmiellus, Mycena, Collybia,* and elsewhere (Gilliam, 1976; Singer, 1976, 1986).

The lack of informative anatomical characters in the fossils and the present contoversy over the limits and relationships of extant marasmioid agarics make it difficult to assign *Archaeomarasmius* to a group with precision or confidence. Nevertheless, the majority of extant species that agree with the fossils (marasmioid habit, small size, and smooth, elliptic spores) are found in *Marasmius, Marasmiellus, Mycena, Collybia* and other Tricholomataceae (i.e., the Marasmiaceae sensu Kühner), which are generally thought to be closely related. This is our best estimate of the group that includes *Archaeomarasmius*—and this conclusion forms the basis for later discussion—but more conservative workers may prefer to place *Archaeomarasmius* as incertae sedis among the Tricholomataceae, Agaricales, or homobasidiomycetes.

Ultrastructural observations indicate that there is little intact tissue remaining of *Archaeomarasmius.* The surfaces and exposed interior portions of the inclusion showed only an amorphous, irregular structure. No hyphae were discernible. The only clearly biological struc-



Figs. 8, 9. *Protomycena electra* gen. et sp. nov. Holotype in private collection of Ettore Morone. **8**. View from underside of pileus. **9**. Side view of fruiting body. Pileus is 5 mm in diameter and ~ 4 mm tall.

tures that could be seen were spores and spore fragments, which were embedded in amber chips adjacent to the inclusion. Spores appeared to have been subject to considerable stress inside the amber; most spores had been either crushed, sheared, or fractured (Figs. 4, 5). Some of this damage may have been caused by the fracturing of the amber after it was collected, but some kinds of damage could not be attributed to fracturing of the amber. Spore casts showed halo-like impressions around the periphery of the spores (Figs. 6, 7). The halos suggest that gaseous or liquid substances were drawn out of the spores into the amber, or alternately that some property of the spores inhibited the transformation of the resin into amber.

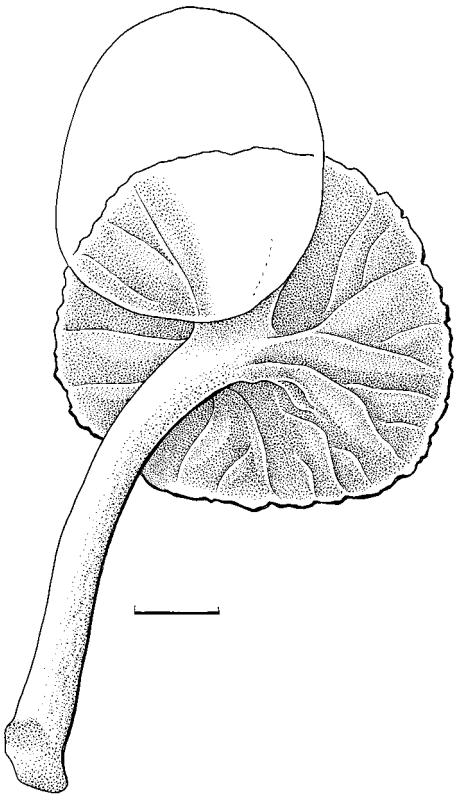


Fig. 10. *Protomycena electra* gen. et sp. nov. Sketch of holotype.

TEM observations also revealed no recognizable biological structures. Amber fragments were visible as overlapping rhomboidal structures ~ 0.5 × 2.5 μm. The area of the inclusion was filled with amorphous granular material or irregular, elongate, angular structures less than 0.25 μm wide and up to 1 μm long. Although it was difficult to precisely locate the edge of the inclusion, it appears that the inclusion was permeated by resin that had turned into amber.

No products were obtained in PCR amplifications of rDNA. The nuclear rDNAs are present as tandem repeats, which makes them easy targets for PCR or cloning and accounts in part for their popularity in molecular systematics studies. Amplifications performed with a template mixture of amber extracts and dilute DNA of *Lentinula edodes* yielded the expected products, which indicate that soluble inhibitors of PCR are not present at significant concentrations in the amber extracts. Taken together, the ultrastructural observations and results of the PCR suggest that there is little or no high molecular mass DNA remaining in this specimen of *Archaeomarasmius.* The fact that this specimen split open so readily suggests that fissures in the amber along flow lines may have penetrated to the inclusion. If so, then the inclusion would not have been hermetically sealed, and there would be little reason to expect DNA or organic tissue to have been preserved.

Nonfungal inclusions and ecology of Archaeomarasmius—In addition to the mushrooms, AMNH NJ-90 contains ~ 40 insects, including Diptera (three Ceratopogonidae, seven Chironomidae, one empidioid, one Tipulidae, and two rhagionids), two Heteroptera, one nymphal homopteran, three thrips, two spiderlings, one pseudoscorpion, one mite, three parasitoid wasps, two male *Sphecomyrma* ants, three elaterid and one unidentified beetle, one caddisfly (Trichoptera), one partial cockroach nymph, and one partial termite (the nonfungal in-

clusions will be described elsewhere). The presence of the ceratopogonid and chironomid midges and the caddisfly suggests a proximity to fresh water, and the presence of the pseudoscorpion, elaterid beetles, and termite—and the mushrooms themselves—indicates a proximity to rotten wood. Fibers in the amber appear to be from bark or wood of Cupressaceae. In addition, leafy shoots of Cupressaceae are present in other pieces of New Jersey amber from a close contemporaneous site. Extant Marasmieae are common, widespread saprophytic decayers of wood and leaf litter, and so it is most likely that *Archaeomarasmius* was also a saprophyte. Collectively, these observations suggest that *Archaeomarasmius* had been growing as a saprophyte on or near a member of the Cupressaceae adjacent to a freshwater body when it became entrapped in that plant's resin.

Taxonomy and preservation of Protomycena—The assignment of *Protomycena* to an extant group, in this case the Myceneae, is based solely on macromorphology. Similarities of *Protomycena* to extant *Mycena* species include the convex, slightly campanulate pileus with striate-pellucid margin, and the absence of veils. The limitations discussed above with regard to the placement of *Archaeomarasmius* also apply to *Protomycena*. Although *Protomycena* has the overall habit of a *Mycena,* other small Tricholomataceae, such as *Marasmius,* could also be closely related. *Protomycena* is clearly distinct from *Coprinites,* however. The latter differs from *Protomycena* in its possession of a plicate-pectinate pileus and nonanastomosing lamellae.

Protomycena is extremely well preserved. Unlike the New Jersey amber, the amber containing *Protomycena* has no apparent fissures or flow lines. The cavity just below the pileus of *Protomycena* contains liquid and has a small gas bubble that moves freely when the piece is turned, suggesting that the inclusion is completely sealed.

Minimum age estimates for homobasidiomycete families—The discovery of even a single fossil has the potential to provide minimum age estimates for the origins of multiple evolutionary lineages (e.g., Doyle and Donoghue, 1993). To realize this potential, two things are required: (1) accurate taxonomic placement of the fossil (difficult for fungi because of the taxonomic importance of soft anatomical characters, which may not be preserved); and (2) phylogenetic resolution for the fossil-bearing lineage (still lacking for many groups of homobasidiomycetes). In this section, we briefly review the fossil record of homobasidiomycetes, and, to the extent possible, infer minimum divergence times for certain lineages, taking into consideration recent phylogenetic hypotheses based on molecular studies of extant taxa. For more complete reviews of the paleomycological record, see Tiffney and Barghoorn (1974), Stubblefield and Taylor (1986, 1988), Sherwood-Pike (1991), Taylor and Taylor (1992), and Taylor (1993).

The age of the homobasidiomycetes is controversial. The hyphal form taxa *Palaeancistrus martinii* and *Palaeosclerotium pusillum* from Pennsylvanian (~ 300 mya) coal balls have well-preserved clamp connections like those of extant homobasidiomycetes (Dennis, 1970, 1976). Clamp connections, however, are also produced by certain heterobasidiomycetous ''jelly fungi,'' such as the Dacrymycetales and Tremellales (Wells, 1994), which have been shown through phylogenetic studies of 18S rDNA sequences to be basal to the homobasidiomycetes (Swann and Taylor, 1993). Thus, clamp connections alone do not tell which group of basidiomycetes is most closely related to *Palaeosclerotium* and *Palaeancistrus.*

Palaeosclerotium was initially interpreted (Dennis, 1976) as a morphological intermediate between the ascomycetes and basidiomycetes on the basis of its apparent connection to a cleistothecium-like fruiting body and the presence of both clamped and simple septa. This interpretation was challenged by McLaughlin (1976), who suggested that the fossil could actually be composed of more than one organism. Although its exact identity is problematic, the presence of clamp connections strongly suggests that *Palaeosclerotium* is composed (at least in part) of basidiomycetous hyphae.

In addition to clamp connections, the hyphae of *Palaeancistrus* produced terminal and intercalary swellings that are strikingly similar to asexual propagules called chlamydospores, which are produced by certain extant homobasidiomycetes. (The term ''chlamydospore'' has been widely applied to a variety of spores produced on vegetative fungal hyphae, including structures produced by ascomycetes and zygomycetes.) Dennis (1970) compared the hyphal swellings of *Palaeancistrus* to the chlamydospores of the mushroom *Lentinus tigrinus* (as *Panus tigrinus*), but numerous other species of wood-decaying homobasidiomycetes produce similar structures in culture (Nobles, 1965). In contrast, we are aware of only a single report of chlamydospores in heterobasidiomycetes, by Bulat (1953), who noted chlamydospores in cultures of *Dacrymyces ellisii*. Nevertheless, there have been far fewer cultural studies in heterobasidiomycetes than in homobasidiomycetes. Although definitive fossil evidence for the existence of homobasidiomycetes would require either basidial or fruiting body morphology (or septal pore ultrastructure, which may never be observable in fossils), the combination of clamp connections and the putative chlamydospores suggests, albeit weakly, that *Palaeancistrus,* from the Carboniferous, was a homobasidiomycete. A molecular phylogenetic study by Berbee and Taylor (1993), however, suggested that the divergence of the homobasidiomycetes occurred in the Triassic, ~ 220 mya, plus or minus 50 million years. *Palaeancistrus* is ~ 30 million years older than the early limit of this range, which was based on molecular clock dating of nuclear small-subunit ribosomal DNA (rDNA) sequences.

Fossils of ectomycorrhizal plants provide indirect evidence for the existence of their fungal partners (Pirozynski and Hawksworth, 1988). The mycobionts of extant ectomycorrhizae are either homobasidiomycetes or ascomycetes, with the former being the more diverse and abundant. Unfortunately, we still know too little about the distribution of ectomycorrhizae among living and extinct seed plants and other vascular plants to make an accurate reconstruction of the evolution of ectomycorrhizal associations (cf. Newman and Reddell, 1987; Fitter and Moyersoen, 1996). Despite these ambiguities, the Pinaceae are noteworthy because they are a presumably monophyletic group of conifers whose extant members

are almost entirely ectomycorrhizal (Newman and Reddell, 1987). If the Pinaceae are assumed to be plesiomorphically ectomycorrhizal, then *Compsostrobus,* a late Triassic fossil that is thought to be an ovulate cone of Pinaceae (Delevoryas and Hope, 1987), suggests that ectomycorrhizal homobasidiomycetes, or possibly ascomycetes, had arisen by ~ 200 mya. The oldest ectomycorrhizae fossils are 50 million-year-old associates of *Pinus* roots from the Princeton chert of British Columbia (Ben LePage, University of Alberta, Edmonton, personal communication). The Princeton chert ectomycorrhizae are morphologically similar to ectomycorrhizae of the extant homobasidiomycete *Rhizopogon,* but they are not connected to a fruiting body and cannot be identified with confidence.

The oldest generally accepted homobasidiomycete macrofossil is *Phellinites digiustoi,* from the Jurassic (~ 167 mya), which was interpreted as a perennial bracket fungus (Singer and Archangelsky, 1958). The description of *Phellinites* was accompanied by a photograph of the putative fruiting body (which to us does not strongly suggest a fungus) and drawings of the hymenophore and sterile hymenial cells (Singer and Archangelsky, 1958). No spores, basidia, or hyphae were described. We are studying the type material of *Phellinites* and will publish our findings elsewhere. Our preliminary observations cast doubt on the identity of *Phellinites* as a homobasidiomycete.

Even if *Phellinites* were accepted as a homobasidiomycete, it would provide little information about minimum ages of nodes within the homobasidiomycetes. The name *Phellinites* alludes to the extant genus *Phellinus,* which includes saprophytic and pathogenic wood-decaying polypores that form tough, persistent ''conks.'' Similar perennial polypores also occur, however, in the genera *Fomes, Ganoderma,* and *Fomitopsis* (Ryvarden, 1991). Recent molecular phylogenetic studies emphasizing polypores (Hibbett and Donoghue, 1995; Hibbett, 1996) suggest that *Fomes* and *Ganoderma* are closely related, but that *Fomitopsis* and *Phellinus* are in separate lineages. Thus, *Phellinites* could belong to any one of at least three distinct lineages of homobasidiomycetes in which perennial bracket fungi have been independently derived.

Macromorphology suggests that *Archaeomarasmius* and *Protomycena* are members of the Tricholomataceae (Figs. 1–3, 8–10). Singer (1986) divided the Tricholomataceae into 12 tribes, which other authors have sometimes classified as separate families (e.g., Kühner, 1980; Jülich, 1981). If the taxonomy of the present paper is accepted, then *Archaeomarasmius* in the mid-Cretaceous establishes a minimum age estimate for the divergence of the Tricholomataceae. For reasons given earlier, it is especially difficult to assign *Archaeomarasmius* and *Protomycena* to infrafamilial taxa. Even if the closest extant relatives of the fossils were unambiguous, however, the lack of phylogenetic resolution within the Tricholomataceae—and serious questions about the monophyly of the Tricholomataceae and its relationships to other groups—would limit the utility of these fossils for estimating divergence dates. Although a few molecular systematics studies have included certain genera of the Tricholomataceae along with other homobasidiomycetes (e.g., Chapela et al., 1994, see below; Hibbett and Vilgalys, 1993; Hibbett and Donoghue, 1995; Cullings, Szaro, and Bruns, 1996), so far there has been no detailed phylogenetic study of the Tricholomataceae. Until such an analysis has been performed, the full value of *Archaeomarasmius* and *Protomycena* for estimating divergence dates in homobasidiomycetes cannot be realized.

Coprinites, from the Miocene to Oligocene (perhaps Eocene), was interpreted as a representative of the Coprinaceae, which includes the genus *Coprinus* (Poinar and Singer, 1990). *Coprinus* mushrooms dissolve into a black, slimy liquid as they mature, and are commonly known as ''inky caps.'' *Coprinites* is apparently not deliquescent (indeed, it is hard to imagine how a deliquescent fruiting body could ever become fossilized). Although deliquescence is not an invariant character of the Coprinaceae (e.g., *C. disseminatus*; Singer, 1986; Hopple and Vilgalys, 1994), its absence, and the morphology of the fruiting body, suggest that *Coprinites* may be related to members of the genus *Leucocoprinus,* such as *L. fragilissimus,* with which it shares a thin-fleshed, plicate-pectinate pileus that has some radial splitting along the margin (Singer, 1986; Singer and Poinar, 1990). The gross similarity of *Leucocoprinus* to certain species of *Coprinus* was noted by Singer, who described *Leucocoprinus* with the phrase ''habit of the carpophores much like that of the thinner *Coprini*'' (Singer, 1986, p. 479). Nevertheless, Singer placed the genus in the tribe Leucocoprineae of the Agaricaceae. Thus, *Coprinites* could represent either the Agaricaceae sensu Singer, or a nondeliquescent member of the Coprinaceae.

Relationships of the Coprinaceae and Agaricaceae sensu Singer were evaluated in a molecular phylogenetic study by Chapela et al. (1994) that was centered on homobasidiomycetes that are obligate symbionts of attine ants. *Coprinites, Archaeomarasmius,* and fossils of attine ants can be used to estimate minimum divergence dates for certain nodes of the molecular cladogram (Fig. 11). Chapela et al.'s (1994) results suggest that the Agaricaceae sensu Singer (represented by exemplars of Singer's tribes Agariceae, Lepioteae, and Leucocoprineae) are monophyletic, and that the Coprinaceae plus Cortinariaceae are its sister group (other taxa that could also be closely related to the Agaricaceae, such as the Strophariaceae, were not included, however). Most of the attine ant symbionts are nested within a terminal clade of the Agaricaceae that includes representatives of the Leucocoprineae and Lepioteae, but a second group of attine ant symbionts is weakly supported as being closely related to certain Tricholomataceae (Fig. 11). By comparing independent phylogenetic hypotheses for the ants and the fungi, Chapela et al. concluded that the original ant–fungus symbiosis involved fungi derived from the Agaricaceae.

The symbiosis of attine ants and fungi has been estimated to be ~ 50 million years old, but this was based only on biogeography and climatic history, not fossil evidence (Weber, 1958). The oldest actual fossils of attine ants are from Dominican amber (Wilson, 1985), thus making them contemporary with *Coprinites,* or ~ 15–30 million years old (Grimaldi, 1995; Iturralde-Vinent and MacPhee, 1996). If it is accepted that attine ants have always been fungus gardeners, then the Dominican fossil

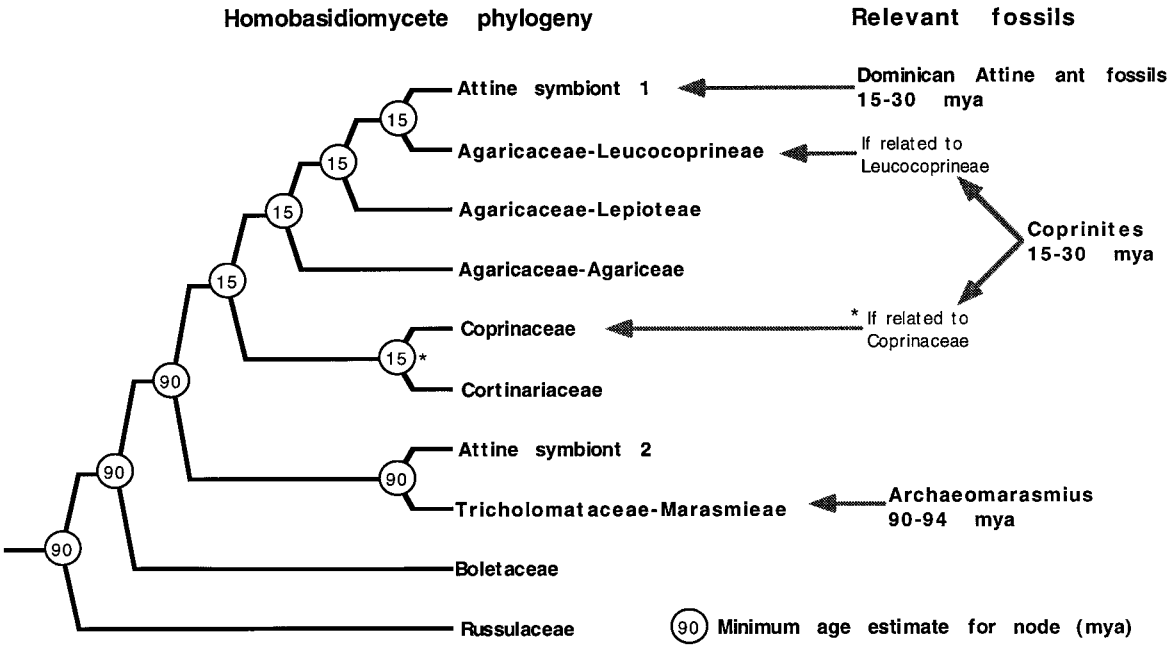


Fig. 11. Phylogenetic hypothesis for agaricoid and attine ant symbiont homobasidiomycetes, with fossils used to estimate minimum divergence dates for nodes. The tree is a simplified representation of the molecular phylogeny of Chapela et al. (1994). Fossil taxa listed to right of tree are assigned to lineages represented in the sample of extant taxa used to generate phylogeny (*Coprinites, Archaeomarasmius*) or are related to symbionts of fungi in the phylogenetic analysis (attine ant fossils and Leucocoprineae). Circled numbers at nodes.

ants set the minimum divergence date for the terminal clade of the Agaricaceae that includes the Lepioteae and Leucocoprineae (Fig. 11). Placement of *Coprinites* in the Leucocoprineae would corroborate this minimum age estimate. On the other hand, if *Coprinites* is interpreted as a member of the Coprinaceae, then it provides a minimum age estimate of 15 million years for the split between the lineages leading to the Coprinaceae and Cortinariaceae (Fig. 11). In Chapela et al.'s (1994) cladogram, the Tricholomataceae, including *Marasmius delectans,* are basal to the Agaricaceae, Coprinaceae, and Cortinariaceae. The Boletaceae are the next most basal lineage in the tree, which is rooted with Russulaceae. Based on *Archaeomarasmius,* a minimum age estimate of 90–94 million years can be inferred for these three basal nodes (Fig. 11). Although there are only three relevant fossils, it is possible to place minimum divergence dates on many nodes of Chapela et al.'s (1994) cladogram.

In addition to the fossils discussed above, other relatively recent homobasidiomycete macrofossils that can be assigned to extant groups include *Geastrum tepexensis,* which is an earthstar from the Miocene or Pleistocene of Mexico (Magallon-Puebla and Cevallos-Ferriz, 1993), *Ganoderma adspersum,* from the Miocene of the Netherlands (Fraaye and Fraaye, 1995), and others, mostly polypores, from the Oligocene and later (see Tiffney and Barghoorn, 1974).

Biogeography—Many homobasidiomycete species and genera have broad, cosmopolitan distributions. One obvious explanation for this pattern would be that homobasidiomycetes are freely dispersed over long distances by airborne spores. Nevertheless, the occurrence of *Phellinites* in the Jurassic and *Archaeomarasmius* in the Cretaceous holds open the possibility that the cosmopolitan distributions of certain homobasidiomycetes are due to fragmentation of ancestral ranges via continental drift. This is consistent with the findings of Redhead (1988), who studied the biogeographic relationships of North American indigenous mushroom species and concluded that vicariance must have played a role in creating the present distributions of numerous taxa. Among the species cited by Redhead as having circumpolar or circumboreal distributions are *Marasmius epidryas, M. epiphyllus, M. androsaceus,* and *Marasmiellus candidus.* The putative close relationship between these species and *Archaeomarasmius* adds support to the hypothesis that the present distributions of certain Marasmieae could be relicts of ancient Laurasian ranges.

Pace of homobasidiomycete morphological evolution—*Archaeomarasmius, Protomycena,* and *Coprinites* are strikingly similar to extant agarics in the Marasmieae, Myceneae, and Leucocoprineae (or Coprinaceae). The simplest explanation for this is that the morphologies of the fossils are homologous to the morphologies of their extant putative relatives. If so, then there must have been conservation of form in these lineages for many millions of years. At the same time, molecular and morphological studies of extant taxa suggest that there has been extensive convergence and parallelism in gross morphology of homobasidiomycete fruiting bodies (c.f., Petersen, 1971; Hibbett and Vilgalys, 1993; Hibbett and Donoghue, 1995). For example, molecular characters have corroborated anatomically based hypotheses of close relationships between fungi as dissimilar as polypores and gilled mushrooms (*Lentinus* and *Polyporus*), and gilled mush-

rooms, toothed fungi, and coral fungi (*Lentinellus, Auriscalpium,* and *Clavicorona*; Hibbett and Donoghue, 1995; Hibbett, 1996). Some of the most dramatic examples of macromorphological transformations in homobasidiomycetes involve the secotioid fungi. Secotioid fungi have gasteromycete-like fruiting bodies (e.g., resembling puffballs or truffles) but have anatomical features that suggest that they are closely related to typical mushroom-forming fungi (Thiers, 1984). Molecular studies have confirmed putative relationships between secotioid and agaricoid forms in the Boletales (Bruns et al., 1989; Baura, Szaro, and Bruns, 1992), Coprinaceae (Hopple and Vilgalys, 1994), and Tricholomataceae (Pine and Mueller, 1993). In several cases (Bruns et al., 1989; Baura, Szaro, and Bruns, 1992; Hopple and Vilgalys, 1994), comparison of rates of molecular and morphological evolution has suggested that the derivation of secotioid forms from agaricoid forms has involved rapid morphological evolution relative to molecular evolution. The genetic basis for the derivation of secotioid forms is not understood, but in *Lentinus tigrinus,* a species with naturally occurring agaricoid and secotioid forms, it appears that the secotioid phenotype is conferred by a single, recessive Mendelian factor (Hibbett, Tsuneda, and Murakami, 1994).

The studies discussed above suggest that fruiting body morphology in homobasidiomycetes is evolutionarily flexible, and that in at least some cases small genetic changes can result in major morphological transformations. In contrast, the fossils suggest that certain fruiting body morphologies have remained unchanged over tens of millions of years. Taken together, these observations suggest that homobasidiomycete morphological evolution is characterized by periods of rapid change as well as long periods in which there is little or no morphological change. Unfortunately, the fossil record is still too incomplete to provide a detailed picture of the history of morphological evolution in homobasidiomycetes. To understand the macroevolutionary patterns of morphological change in homobasidiomycetes, it will be necessary to generate a detailed phylogenetic hypothesis for the homobasidiomycetes, infer the distribution of ancestral character states, and estimate the timing of branching events.

Conclusions—It would be easy to dismiss fossil mushrooms as being too few in number to be significant for understanding the evolution of homobasidiomycetes. This would be unfortunate, however, because theories about homobasidiomycete evolution must at least be consistent with the fossil record. Furthermore, having even a small number of relevant fossils makes it possible to put minimum age estimates on multiple nodes of a cladogram, as was demonstrated in the example based on Chapela et al.'s (1994) molecular phylogenetic study (Fig. 11). The broad phylogenetic relationships of homobasidiomycetes are not well understood, but with the further development of the molecular phylogenetic database this situation should improve. As it does, fossils will become increasingly useful for dating divergences and calibrating molecular clocks, as was done by Berbee and Taylor (1993). In addition to the fossils of the fungi themselves, fossils of obligate symbionts of particular homobasidiomycetes will provide minimum divergence dates for some nodes. Plate tectonic events may also provide minimum divergence dates for certain lineages whose distributions are best explained in terms of vicariance. Through a combination of phylogenetic, paleontological, and biogeographic studies, it may be possible to achieve an understanding of both the phylogeny and the actual timing of homobasidiomycete evolution.

Information on the timing of branching events can be used not only to estimate the ages of clades, but also to increase the power of tests designed to determine if shifts in diversification rates are localized in a phylogeny (Sanderson and Donoghue, 1996). Such tests can be used to evaluate hypotheses that particular radiations were associated with the evolution of specific intrinsic characters (''key innovations''), or extrinsic factors, such as changes in climate or the radiations of other groups of organisms. In conjunction with molecular phylogenetic studies, the homobasidiomycete fossil record—although still very limited—may ultimately enable us to determine whether shifts in rates of homobasidiomycete diversification have been correlated with the evolution of particular characters of the fungi, such as lamellate hymenophores or the ability to form ectomycorrhizae, or extrinsic factors, such as the radiation of the angiosperms.

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Note added in proof: Readers may also be interested in a Brief Communication entitled ''Is *Phellinites digiustoi* the oldest homobasidiomycete?,'' which appears on pp. 1005–1011 in this issue. It was submitted after this article was accepted for publication.