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Fossil Fleshy Fungi ("Mushrooms") in Amber

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Abstract

A survey of fleshy fungi from amber deposits around the world is presented. Included are representatives of gilled fungi, puffballs, bird's nest fungi, gasteroid fungi, xylaroid fungi, hymenomycetes, polypores and morels. Also included is a description of the first fossil morel, *Paleomorchella* dominicana gen. et sp. nov. from Dominican Republic amber. Several arthropods that were associated with the fossil fungi are figured and discussed.

Keywords: Fossil mushrooms; Amber deposits; Tertiary; Cretaceous

Introduction

Most consider mushrooms as gilled fungi that grow in yards and are available for purchase in stores; however mycologists consider these table mushrooms as just one group of fleshy fungi, along with coral fungi, jelly fungi, bracken fungi, puffballs, earthstars, gastroids and bird's nest fungi [1]. Due to the delicate nature of most fleshy fungi, the fossil record of such forms is quite limited. Amber is one media that preserves delicate objects, such as fungal bodies, in exquisite detail. This is due to the preservative qualities of the resin when contact is made with entrapped plants and animals. Not only does the resin restrict air from reaching the fossils, it withdraws moisture from the tissue, resulting in a process known as inert dehydration. This together with antimicrobial compounds in the resin that destroy decay- causing microorganisms and terpenoids and resin acids that fix the tissues, a natural embalming process occurs during the process of polymerization and cross-bonding of the resin molecules [2]. The present work reviews fossil fleshy fungi recovered from amber deposits around the world.

Materials and Methods

Provinces of amber deposits with fleshy fungi

The Mexican amber specimen, *Lycoperdites tertiarius* (Figure 1) was found in the Positos mine occurring in lignitic beds in association with the Balumtun Sandstone of the early Miocene and the La Quinta formation of the Late Oligocene, dating the deposits to 22.5 to 26 mya. The Dominican specimens were obtained from mines in the Cordillera Septentrional of the Dominican Republic. Using foraminifera in the bed rock, Dominican amber has been dated at 15-20 mya [3]. However, when dating was based on coccoliths, a range of 30-45 mya was obtained [4].

The Baltic amber specimen originated from the Samland Peninsula in the Kalinin District of the Russian Federation. These deposits are considered to range from 45 to 55 mya [5]. Bitterfeld amber is similar to Baltic but is located in more southern areas of northern Europe [5]. New Jersey amber from the Atlantic coastal plain that extends from the Delaware River to the Atlantic coast is mid-Cretaceous and has been dated at 90-94 mya [6,7]. The Burmese specimens originated from the Noije Bum 2001 Summit Site mine excavated in the Hukawng Valley in 2001 and located southwest of Maingkhwan in Kachin State (26°20´N, 96°36´E) in Myanmar. Based on paleontological evidence this site was dated to the Upper Albian of the Early-Mid Cretaceous [8], placing the age at 97 to 110 mya. A more recent study using U-Pb zircon dating determined the age to be 98.79 ± 0.62 Ma [9]. Since samples in the latter study were taken from matrix containing redeposited amber, the age is obviously older than this date.

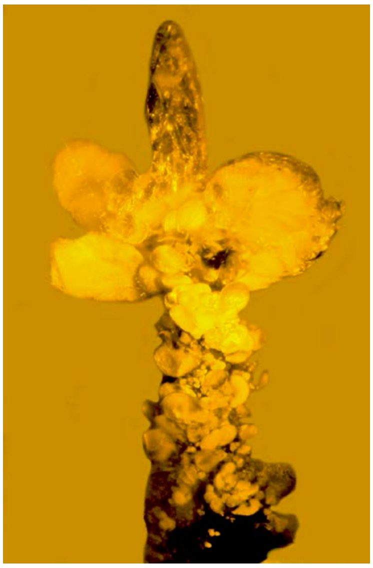

Figure 1: A Mycenaceae, *Favolaschia* sp., in Dominican amber.

Results

Fleshy fungi ("mushrooms") reported from amber deposits around the world are presented in Table 1. Gilled mushrooms in Tertiary and Cretaceous amber (Figures 1-4), including sporocarps of a wood-inhabiting species tentatively identified as *Favolaschia* sp. (Mycenaceae) do not appear to have characteristics unknown in their descendants today [10]. This can also be said of the sporophores of the puffball, *Lycoperdites tertiarius*, in Mexican amber (Figure 5) [11].

The preservative qualities of Dominican and Baltic amber also captured the first fossil bird's nest fungi. Not only are the fruiting bodies preserved but also peridioles at the base of the peridia [12] (Figures 6 and 7).

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A. Gilled fungi		
Specimen	**Amber source**	**References**
Coprinites dominicana (Figure 2)	Dominican	Poinar and Singer [16]
Protomycena electra	Dominican	Hibbett et al. [6]
Aureofungus yaniguaensis	Dominican	Hibbett et al. [20]
Palaeocybe striata	Bitterfeld	Dörfelt and Striebich [21]
Gerontomyces lepidotus (Figure 3)	Baltic	Poinar [17]
Archaeomarasmius leggetti	New Jersey	Hibbett et al. [7]
Palaeoagaracites antiquus (Figure 4)	Burma (Myanmar)	Poinar and Buckley [15]
Favolaschia sp. (Figure 1)	Dominican	Boucot and Poinar [10]
B. Puffballs		
Lycoperdites tertiarius (Figure 5)	Mexican	Poinar [11]
C. Bird's nest fungi		
Cyathus dominicanus (Figure 6)	Dominican	Poinar et al. [22]
Nidula baltica (Figure 7)	Baltic	Poinar [12]
D. Gasteroid fungi		
Palaeogaster micromorpha (Figure 8)	Burma (Myanmar)	Poinar et al. [22]
E. Xylaroid fungus		
Xylaria antiqua (Figure 9)	Dominican	Poinar [13]
F. Hymenomycetes		
Palaeoclavaria burmitis (Figure 10)	Burma (Myanmar)	Poinar et al. [22]
G. Polypores		
Ganoderma sp. (Figure 11)	Dominican	Boucot and Poinar [10]
H. Morels		
Paleomorchella dominicana sp. nov. (Figure 12)	Dominican	Boucot and Poinar [10]

Table 1: Fleshy fungi ("mushrooms") reported from amber deposits.

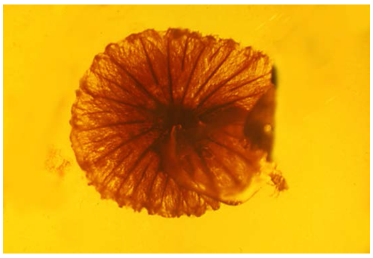

Figure 2: Cap of the gilled mushroom, coprinites dominicana in Dominican amber.

Figure 3: Cap of the gilled mushroom, *Gerontomyces lepidotus*, in Baltic amber.

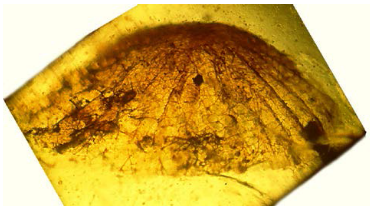

Figure 4: Cap of the gilled mushroom, *Palaeoagaracites antiquus,* in Burmese amber.

Figure 5: Sporophore of the puffball, *Lycoperdites tertiarius*, in Mexican amber.

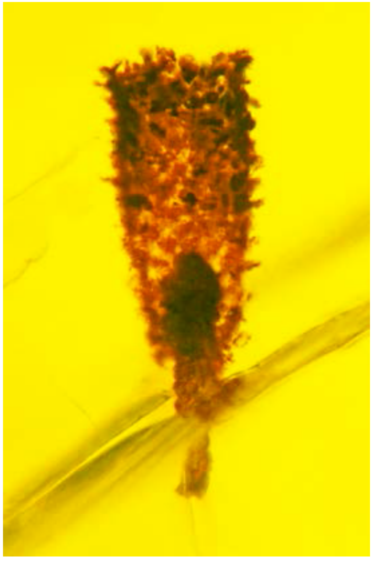

Figure 6: Sporophore of the bird's nest fungus, *Cyathus dominicanus,* in Dominican amber.

Some of the Cretaceous fossils are unique in possessing unknown features without any direct descendants. Of note is the gasteroid fungus, *Palaeogaster micromorpha* (Figure 8), which represents the first fossil Sclerodermatineae and oldest gasteroid fungus. The shape of its small

Figure 7: Sporophore of the bird's nest fungus, *Nidula baltica*, in Baltic amber.

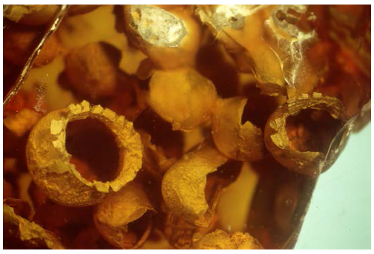

Figure 8: Sporophores of the gasteroid fungus, *Palaeogaster micromorpha,* in Burmese amber.

Figure 9: The xylaroid fungus, *Xylaria antiqua*, in Dominican amber.

yellow to orange fruiting bodies and subglobose spores distinguish it from extant members of the Sclerodermatineae [12]. The "Dead-Man's Fingers" fungus, *Xylaria antiqua*, (Figure 9) is equally well preserved with organized layers of conidiophores still retaining their condia as well as perithecia filled with ellipsoid ascospores adjacent to the ostioles [13]. The clavacoid fungus, *Palaeoclavaria burmitis,* in Burmese amber (Figure 10) represents the first fossil record of the Aphyllophorales. Not only were scleritified generative hyphae with clamp connections present, but spores borne externally on could basidia be observed [14].

A small polypore in Dominican amber that was tentatively identified as a *Ganoderma* sp. is partly eaten by an unknown agent, but still shows the outer rounded margin and faint pores on the undersurface (Figure 11) [10].

The Burmese amber *Palaeoagaracites antiquus* further shows a high degree of preservation. Not only is the pileus of this oldest fossil gilled mushroom preserved, but also present are mycelial strands of a parasitic fungus, *Mycetophagites atrebora*, that ramify through the cap. Inside the hyphae of the latter are hyphal strands of the hyperparasite, *Entropezites patricii* [15].

Of special interest does the discovery of a small morel resemble a *Morchella* sp. in Dominican amber (Figure 12) [10]. There are no previous descriptions of fossils of this group and the present specimen is described below.

Order: Pezizales

Family: Morchellaceae

Figure 10: The clavacoid fungus, *Palaeoclavaria burmitis,* in Burmese amber.

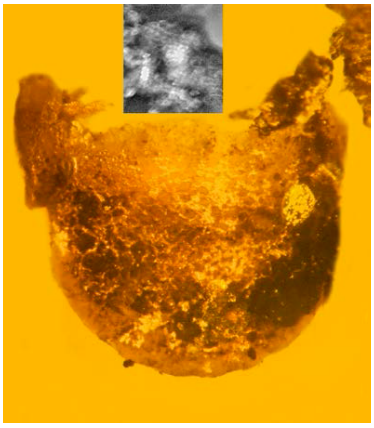

Figure 11: A polypore, *Ganoderma* sp., in Dominican amber. Insert shows pores on undersurface.

Figure 12: The morel, *Paleomorchella dominicana* gen. et sp. nov., in Dominican amber.

Type genus *Paleomorchella* Poinar gen. nov.

Diagnosis: As for type species (monotypic)

Genus *Paleomorchella* Poinar, gen. nov. (MycoBank # = 819168)

Type species: *Paleomorchella dominicana* Poinar gen. et sp. nov.

Paleomorchella dominicana Poinar gen. et sp. nov. (MycoBank # = 819169) (Figure 12)

Description: Specimen straight, small, total length, 2.0 mm; cap brown, oval-shaped, bearing closely adjacent longitudinal ridges; cap margin joined to stalk; stalk whitish, broken off at base; sac absent.

Holotype: No. AF-9-10 deposited in the Poinar amber collection maintained at Oregon State University.

Etymology: Generic name from Latin "paleo"=old and name of extant genus Morchella. Specific epithet is based on the origin of the fossil.

Type locality: Cordillera Septentrional of the Dominican Republic.

Diagnosis: The closely appressed longitudinal ridges on the cap distinguish the fossil from extant species of Morchella and other members of the family, most of which have pitted or honeycombed caps. The fossil has some similarities to members of the *M. elata* group that have brownish-black caps bearing dark ridges. However the ridges in members of the *M. elata* group are not closely appressed and the cap width ranges from 20-60 mm [1]. It is possible that the fossil is immature and if so, the final configuration of the mature cap would be unknown.

Also of interest are various arthropods associated with fossil fleshy fungi. Leaving the cap of *Coprinites dominicana* in Dominican amber is a mite that was trapped when the mushroom was preserved [16] (Figure 13). Adjacent to the Baltic amber *Gerontomyces lepidotus* was an exuvia of a nymph of a Phasmatodea. It was assumed that the insect was feeding on the mushroom [17] (Figure 14).

Two insects were associated with the fruiting bodies of *Palaeoclavaria burmitis* in Burmese amber. One was a fungus gnat (Diptera: Mycetophilidae) that appears to have been in the process of depositing eggs on a sporocarp (Figure 15). The other was a larva of a

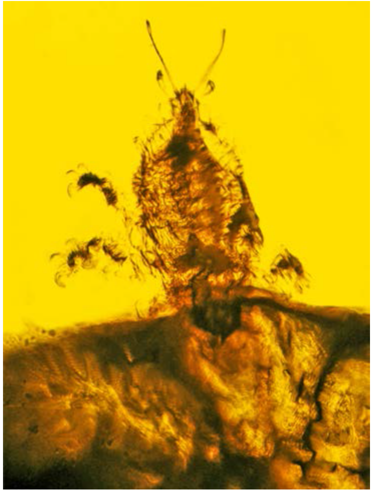

Figure 13: A mite leaving the cap of *Coprinites dominicana* in Dominican amber.

Figure 14: An exuvia of a nymph of a Phasmatodea adjacent to the gilled mushroom, *Gerontomyces lepidotus*, in Baltic amber.

Figure 15: A fungus gnat (Diptera: Mycetophilidae) ovipositing in a sporocarp of *Palaeoclavaria burmitis* in Burmese amber.

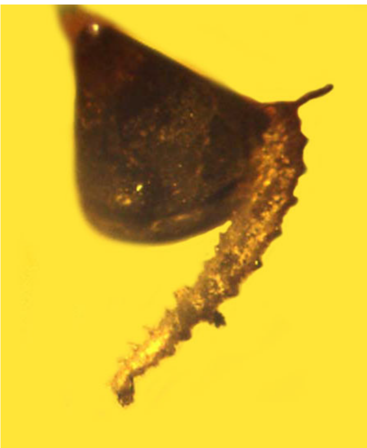

Figure 16: A larva sand fly (Diptera: Phlebotomidae) adjacent to a fruiting body of *Palaeoclavaria burmitis* in Burmese amber.

phlebotomine fly that was probably developing in one of the fruiting bodies (Figure 16) [18].

The above specimens show how important amber deposits are in documenting ancient lineages of fleshy fungi.

Discussion

Previous studies using nuclear and mitochondrial ribosomal DNA to comprehend the evolutionary history of Homobasidiomycete fungi, including gilled mushrooms and puffballs, indicated that gilled mushrooms evolved from structurally diverse precursors at least 6 times [6]. With the fossil forms presented in the present study, it is likely that *Favolaschia* sp. evolved from a separate lineage from those of *Coprinites dominicana, Gerontomyces lepidotus* and *Palaeoagaracites antiquus*.

Apparently puffballs, represented by the fossil *Lycoperdites tertiarius*, also evolved at least 4 times. Bird's nest fungi like *Cyathus dominicanus* and *Nidula baltica* have uniquely evolved fruiting structures that differ from other lineages of Gasteromycetes. From the studies of Hibbett et al. [7], it is clear that the origins of various lineages of fleshy fungi are quite complicated.

It is also clear that while many of the fossil lineages presented here represent the oldest members of the group, these lineages are much older than the fossils indicate. It is interesting that while the nutritional mode of the common ancestor of fungi is unknown, the common ancestors of Basidiomycota lineages are considered to have been parasites with numerous transitions from pathogenic to saprophytic lifestyles [19]. Unfortunately it is not possible to determine if any of the fossil fleshy fungi presented here started their growth processes by invading healthy plant tissues.

Conclusion

Certainly, amber from various regions around the world contains more evidence of fleshy fungi than any other type of deposits. This is due to the ability of amber to preserve delicate material that quickly deteriorates under environmental conditions. Also many fleshy fungi are associated with the bark, flowers and fruits of resin-producing trees, which make it easier for them to encounter the resin deposits that occur on the branches and trunks of the host trees.

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