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Research Paper

Amber fossils of sooty moulds

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ABSTRACT

Sooty moulds are saprophytic ascomycetes with brown hyphae, often forming extensive subicula on living plant surfaces. These fungi grow on plant exudates and honeydew secreted by sap sucking insects and are ubiquitous in many humid terrestrial ecosystems. Here, we review previously published specimens of sooty moulds and provide new fossil evidence that traces the fossil record of these fungi for about 100 million years, from the early Miocene (17 million years) to the Early Cretaceous (Albian, about 100 to 113 million years). Investigation of Mesozoic and Cenozoic ambers from different parts of the world revealed sooty moulds from eight northern hemisphere amber deposits. Fragments of superficial subicula composed of smooth brown moniliform hyphae with tapering distal ends identical to those produced by extant species in the family Metacapnodiaceae (Capnodiales) are recorded since the Albian. The fossil fungi originate from tropical to temperate coastal forests where they grew on leaves and bark of different conifer and angiosperm trees. This indicates that capnodialean sooty moulds have occupied their specialized niche since at least from when early angiosperms appeared in the fossil record.

1. Introduction

The term sooty moulds is used in a vernacular sense for an ecological group of epiphytic ascomycetes with dark-coloured hyphae that often produce conspicuous black growth on the leaves and other surfaces of living plants (Hughes, 1976; Seifert et al., 2011). Sooty moulds are not parasitic but get their nutrition from insect excretions, especially the honey dew produced by sap sucking aphids and scale insects, and from plant leachates and exudates, such as the nectar secreted by extrafloral nectaries. They tend to form diverse assemblages that may encompass capnodialean (Capnodiales, Dothideomycetes) species within the families Antennulariellaceae, Capnodiaceae, and Metacapnodiaceae, but also ecologically and morphologically similar fungi from other distantly related groups. For example, some species in the Chaetothyriaceae (Eurotiomycetes) share the same niche and convergent morphology; they also appear as melanized, usually anamorphic epiphytes (e.g. Chomnunti et al., 2012a, 2012b). The main differences are in the characteristics of the ascomata, which are not necessarily produced in most specimens. As many sooty mould species are highly pleomorphic and do not readily grow in culture, their identification is quite challenging (e.g. Hughes, 1976; Reynolds, 1986; Sugiyama and Amano, 1987; Reynolds, 1998; Faull et al., 2002; Hughes, 2003, 2007; Cheewangkoon et al., 2009; Crous et al., 2009; Chomnunti et al., 2011).

The Capnodiales, centering on Capnodiaceae, currently contain eight families (Kirk et al., 2008; Lumbsch and Huhndorf, 2010). Capnodialean sooty moulds produce superficial ascomata with fasciculate asci, and have hyaline to dark, septate ascospores. Their anamorphs are dematiaceous, and may include both mycelial (phragmo- to dictyoconidia), as well as spermatial and pycnidial synanamorphs (Hughes, 1976; Crous et al., 2009; Chomnunti et al., 2011). Some species within the family Metacapnodiaceae produce extensive spongy mycelia of darkly pigmented, densely interwoven and often anastamosing, monilioid, distally tapering hyphae, which are strongly constricted at the septa. This unique habit is characteristic enough to have given rise to the descriptive term 'metacapnodiaceous hyphae' (Hughes, 1976).

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Species of the genus *Metacapnodium* Spegazzini are not presently available in culture collections and no sequences of species within the Metacapnodiaceae have yet been deposited in GenBank. Thus, the exact placement of the family among other capnolialean sooty moulds still waits to be confirmed by molecular methods.

The overall prospects for finding fossils of sooty moulds in amber, which is fossilized exudate of ancient gymnosperm and angiosperm trees, are good. The brittle and often rather loose epiphytic colonies growing on trees, especially those secreting exudates, almost predestine them for preservation in resin. Finding an extant species of sooty mould entrapped in fresh resin of *Pinus elliottii* Engelmann in a Florida swamp forest (see Schmidt and Dilcher, 2007) demonstrates that also in modern forests sooty mould are entrapped in plant exudates (Plate I). Indeed, metacapnodiaceous sooty moulds have already been reported from several pieces of Eocene Baltic and Oligocene Bitterfeld amber (Rikkinen et al., 2003), and recently small hyphal fragments and conidia were identified on the cuticle of a thrips in early Eocene amber from the Paris Basin (Nel et al., 2013). Other amber inclusions of possible sooty moulds have been mentioned from the Albian of France (Girard et al., 2009a) and Myanmar (Hentschel et al., 2009) as well as from the Cenomanian of Ethiopia (Schmidt et al., 2010a).

Here, we describe and discuss the fossil evidence of sooty moulds based on both previously published findings and recently discovered fossils from a total of eight Albian to Miocene amber deposits from the northern hemisphere. Sooty moulds now appear to represent the first fungi with a more or less continuous fossil record since the Early Cretaceous. These fungi were relevant components of palaeoecosystems in that their presence indicates interactions of plants, animals, and fungi. In the present study we evaluate these fossil fungi with respect to their different ancient forest ecosystems.

2. Materials and methods

The amber pieces investigated originate from eight northern hemispheric amber deposits. Table 1 provides data about provenance, age and the repository of the pieces investigated, and Fig. 1 illustrates the age of the findings through the Cretaceous and Cenozoic. Amber pieces containing previously published findings from Baltic and Bitterfeld ambers were further prepared and imaged in order to elucidate relevant features.

The amber pieces were ground and polished manually using a series of wet silicon carbide papers [grit from FEPA P 600–4000 (25.8 μm to 5 μm particle size), Struers]. A fraction of a millimeter of amber surface was gradually removed from each amber piece, while frequently checking the preparation under a stereoscope to ensure that the inclusions were not damaged. The flattened surface of the amber was brought to about 100 μm of the inclusions, if no valuable syninclusions were affected (see Schmidt et al., 2012, for protocols).

Prepared specimens were placed on a glass microscope slide with a drop of water applied to the upper surface of the amber, covered with a 0.06–0.08 mm thick glass coverslip (Menzel Inc., Braunschweig). This reduces light scattering from fine surface scratches and improves optical resolution. Amber from the Austrian Traunsee locality is very brittle and thus fragments of a size of less than 1 mm were placed in water on concave glass microscope slides (Menzel Inc., Braunschweig) and covered by a glass coverslip to reduce light scattering.

The preparations were examined under a Carl Zeiss AxioScope A1 compound microscope equipped with a Canon 450D digital camera. Sometimes incident and transmitted light were used simultaneously. The images of Plates I, II, 2–7, III, 1–6, 8, 9, and IV–VI were obtained from several focal planes using the software package HeliconFocus 5.0 to enable a better illustration of the three-dimensional inclusions.

3. Results

3.1. Recent discoveries of metacapnodiaceous sooty moulds that have not been identified to genus level

3.1.1. Àlava amber

Phylum Ascomycota Cavalier-Smith 1998
Class Dothideomycetes O. E. Erikss. et Winka 1997
Order CAPNODIALES Woron. 1925
Family cf. METACAPNODIACEAE Hughes et Corlett 1972

Museo de Ciencias Naturales de Àlava, no. MCNA 9495 (Plate II, 1). Several dark brown moniliform hyphae up to 280 μm in length are attached to spider silk. The cells are smooth, globose to subglobose and about 12 μm in diameter with apical cells being slightly smaller. Syninclusions are fragments of a spider web and the paratype of the stigmaphronid wasp *Hippocoon basajauni* Ortega-Blanco, Delclòs et Engel (Ortega-Blanco et al., 2011).

3.1.2. Charentes amber

Phylum Ascomycota Cavalier-Smith 1998
Class Dothideomycetes O. E. Erikss. et Winka 1997
Order CAPNODIALES Woron. 1925
Family METACAPNODIACEAE Hughes et Corlett 1972

Amber collection of Géosciences Rennes at the University Rennes 1, no. IGR.ARC-115.3b (Plate II, 2); and Muséum National d'Histoire

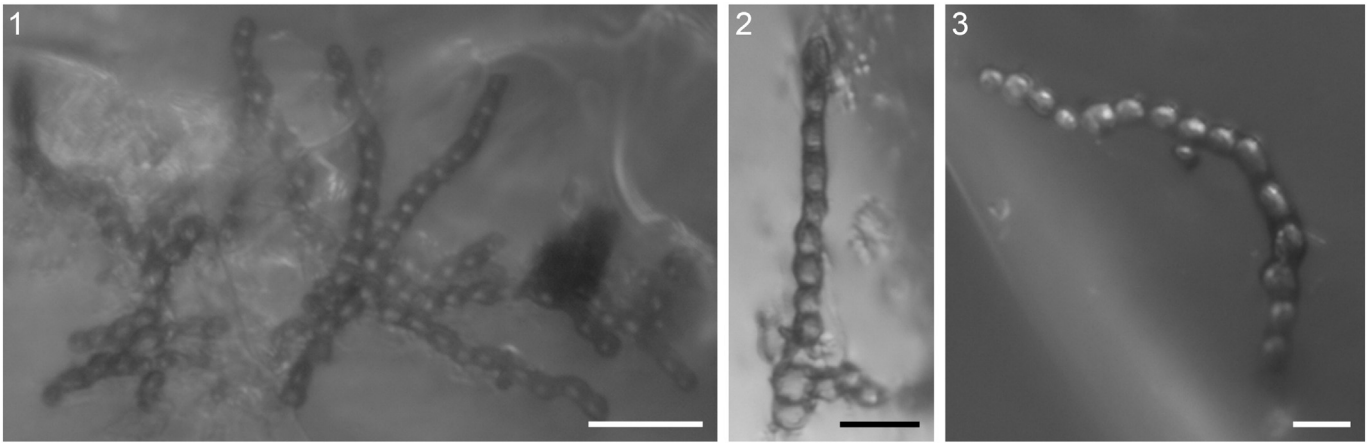

Plate I. Fragments of a subiculum of an extant sooty mould in resin of *Pinus elliottii* in a swamp forest east of Gainesville, Florida. Geoscientific Collections of the Georg August University Göttingen, Germany; GZG.BST.27287. Scale bars: 20 μm.