Fossilised fungal mycelium from Tertiary Dominican amber

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Received 28 October 2000; accepted 13 February 2001.

A fossilised fungal colony is described and illustrated from Dominican amber dating back 15–45 Myr. Many hyphae in the coenocytic mycelium had produced terminal or intercalary protuberances resembling the sporangia of some extant zygomycetes and oomycetes. Other hyphae had produced cylindrical arthroconidia similar to those of *Geotrichum* and related extant yeasts. Many fossilised diaspores had germinated prior to preservation. The fungus seems to have been a rapidly growing saprophyte, utilising fluid substrates, possibly plant exudate. The palaeoenvironment proposed for the mycelium, namely that of a moist epiphytic or epixylic microhabitat, supports earlier conclusions that the original Dominican amber forest possessed a tropical moist forest biome.

INTRODUCTION

The invertebrates and plant parts conserved in amber from the Dominican Republic represent one of the world's most complete fossil records of terrestrial life in a tropical region. However, even from these deposits only a very limited number of fungi have been recovered. The macroscopic taxa include two species of mushrooms, a species of *Xylaria*, and two foliose macrolichens (Poinar & Singer 1990, Hibbett, Grimaldi & Donoghue 1997, Poinar & Poinar 1999, Poinar, Peterson & Platt 2000). The microfungi include *Geotrichum glaesarius* (Stubblefield *et al*. 1985), one species each of *Entomophthorales*, *Beauveria*, and *Aspergillus*, and one unidentified synnematous entomopathogen (Poinar & Thomas 1982, 1984, Thomas & Poinar 1988, Poinar & Poinar 1999). In addition to these true fungi, also one plasmodial slime mould has been reported (Waggoner & Poinar 1992).

Here we describe a well preserved fungal mycelium found among other biological inclusions in a piece of Dominican amber. This amber is fossilised exudate of leguminous trees of the genus *Hymenaea*, especially of the now extinct *H. protera* (Poinar 1992). During fossilisation terpenoid materials of the exudate were progressively oxidised and polymerised to a point where they became resistant against chemical and biological degradation.

MATERIAL AND METHODS

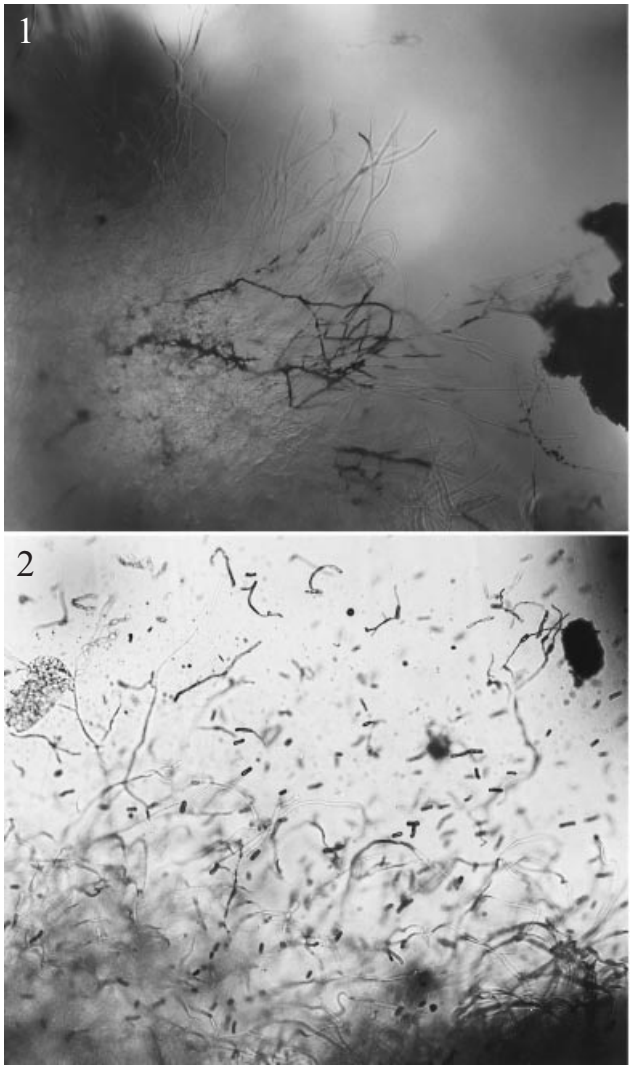
The fossilised mycelium is contained in large fragment (40 × 36 × 3 mm) of clear light yellow amber (Poinar B 1–23). The specimen originated from the amber mines in the Cordillera Septentrional of the Dominican Republic, and is preserved in the amber collections at Oregon State University. These mines are in the El Mamey Formation (Upper Eocene), which is a shale-sandstone interspersed with a conglomerate of well-rounded pebbles (Eberle *et al*. 1980). The exact age of Dominican amber is unknown, with estimates ranging from 15–20 Myr on the basis of foraminifera counts to 30–45 Myr from studies with coccolith fossils (Schlee 1990, Iturralde-Vincent & MacPhee 1996).

The amber piece had been previously cut and polished to facilitate screening for inclusions. In this study no further destructive sampling was performed. All measurements and photographs were taken from the intact specimen under transmitted and/or incident light. Optical distortions were neutralised by coating the specimen in vegetable oil.

RESULTS

Preservation of mycelium

The amber fragment contains a multitude of biological inclusions, including well preserved fungal mycelium, approx. 2.0 × 1.75 mm diam. The peripheral, expanding regions of the mycelium are composed of hyaline, moderately branched hyphae. In the central parts of the colony the hyphae are replaced by unicellular yeasts, embedded in an amorphous, rather cloudy matrix. Although in close proximity of hyphae, the yeast cells are not attached to the mycelium. The hyphae themselves do not show evidence of budding, but have instead produced arthroconidia by fragmentation. Thus, the



Figs 1–2. Fossilised mycelium in amber. **Fig. 1.** Moderately branched, expanding hyphae. Bar = 0.2 mm. **Fig. 2.** Detached arthroconidia at the edge of the mycelium. Bar = 0.1 mm.

hyphae and the yeast cells seem to represent two different organisms which lived and were preserved together.

The fossilised hyphae are largely coenocytic; septa are mainly present to delimit reproductive structures. In addition, a few isolated septa occur in large, presumably old hyphae. Expanding main hyphae had produced long, thin lateral and terminal branches with gradually tapering apexes; the main hyphae are 2–4 μm wide, finer branches are 0.5–3 μm wide. Most hyphae are transparent, but some contain opaque or dark regions of variable size (Fig. 1). The alternating hyaline and dark zones probably reflect partial evacuation of condensed cytoplasmic cell contents, while the refractive zones indicate the presence of gas within the hyphal inclusions. The general structure of the hyphae is well preserved, but due to the refractive properties of the amber, it is not possible to define the thickness of the hyphal wall. The hyphae are smooth and without conspicuous thickenings or accretions of extracellular material. Some hyphae have been brought to the surface and sectioned during polishing. In cross-section they appear opaque with small translucent central areas, possibly indicating the presence of a central vacuole or lumen.

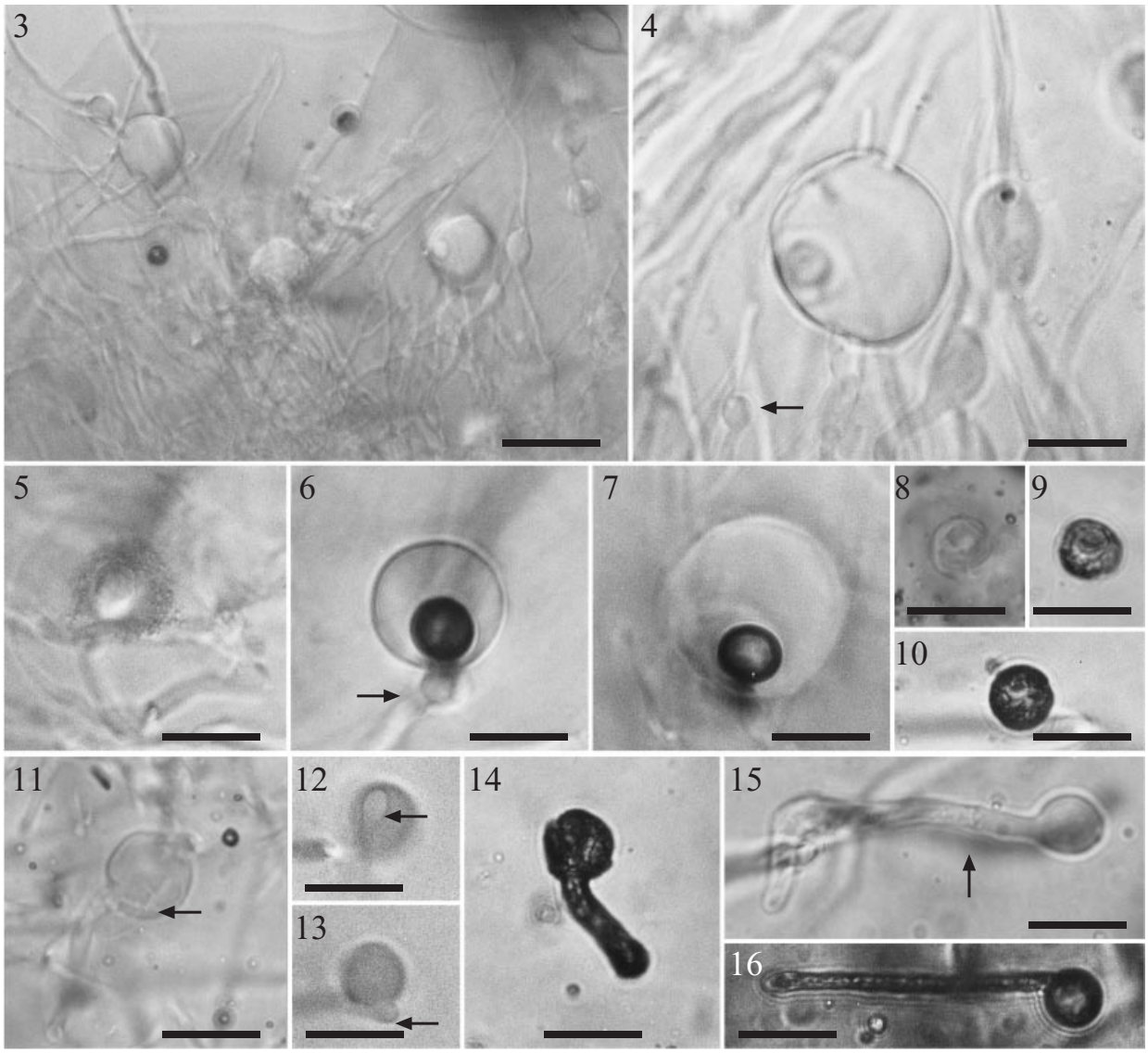
Some hyphae at the edges of the mycelium had developed abruptly expanded apical or subapical enlargements, 5–20 μm diam, apparently representing gametangia and/or sporangia. Also intercalary protuberances had developed on several hyphae and some hyphae appear to have several protuberances in a row, with sections of undifferentiated hyphae separating individual enlargements (Figs 3–11). Some hyphae deep within the colony have subapical protrusions with prominent hyphal pegs, possibly corresponding to early stages in the formation of proliferating hyphal enlargements (Figs 12–13). Also the thin-walled apical protuberances are at an angle to the main axes of subtending hyphae.

Some hyphal protuberances contain single spore-like objects, *ca* 6 μm diam (Figs 3–7). These objects are smooth, eccentrically arranged and rather small compared to the diameter of the protuberances. One globular object is surrounded by dense granular material (Fig. 5). There is also a small inflated cell at the base of at least one apical enlargement (Fig. 6). The cell, which in many ways resembles an antheridium, is separated from the subtending hypha by a septum. There is also some evidence of recognition reactions between small apical protuberances on the other hand, and very thin, branched hyphae on the other. The thin hyphae had grown close to and partly enveloped some apical protuberances (Fig. 11).

The amber matrix also contains many detached globular spores. Most of them are very small, 1–4 μm diam, and were probably produced by the yeasts in the centre of the colony. However, some correspond both in size and shape with the globular objects inside the hyphal protuberances (Figs 8–10). Some of the spores have thickened walls and others appear to have germinated by producing stout germ tubes with abruptly tapering apices (Figs 14–16). There may be a septum delimiting the hyphal tube from the empty spore (Fig. 15).

Other hyphae in the fossilised mycelium had disarticulated into catenulate hyphal elements or arthroconidia. Hundreds of detached conidia occur in the amber matrix. Most of them had been encapsulated into a fan-like formation extending from the edge of the mycelium to a region of solid amber with many air bubbles (Fig. 2). The conidia had usually developed next to each other, without intermediary zones (Figs 17–19). However, sometimes an isthmus seems to have formed between two presumptive cells, leading to a short connective between adjacent conidia (Figs 17, 20–21). Also some longer connectives occur, but they all seem to represent collapsed conidia (Fig. 18). The fragmentation of hyphae had been random and the renewal of vegetative hyphae had taken place by cymose branching under the conidia (Fig. 18). The detached conidia are elongate to cylindrical, or sausage-shaped, 2–5 × 3–20 μm, with rounded ends, although less regular shapes also occur (Figs 21–25). While some conidia may have been preserved intact, in most cases only shrivelled cellular remains are enclosed in highly refractive casts.

Many arthroconidia had germinated prior to preservation, confirming their function as reproductive units. The germinated conidia include all stages of development from the production of peg-like germ tube initials from non-inflated conidia to the elongation and branching of new hyphae (Figs 23–28). The germinated cells had produced slender germ



Figs 3–16. Sporangia and spore-like objects. **Fig. 3.** Sporangia at the edge of the mycelium. Bar = 30 µm. **Fig. 4.** Terminal and intercalary sporangia. Note young terminal protuberance (arrow). Bar = 10 µm. **Fig. 5.** Granular material within sporangium. Bar = 10 µm. **Figs 6–7.** Apical sporangia with spore-like objects and an inflated basal cell (arrow). Bars = 10 µm. **Figs 8–10.** Detached spore-like objects. Bars = 10 µm. **Fig. 11.** Thin hyphae partly enveloping sporangium (arrow). Bar = 10 µm. **Figs 12–13.** Young sporangia. Note prominent hyphal tips (arrows). Bars = 10 µm. **Figs 14–16.** Spore-like objects with hyphal appendices. Note septum in the hyphal tube (arrow). Bars = 10 µm.

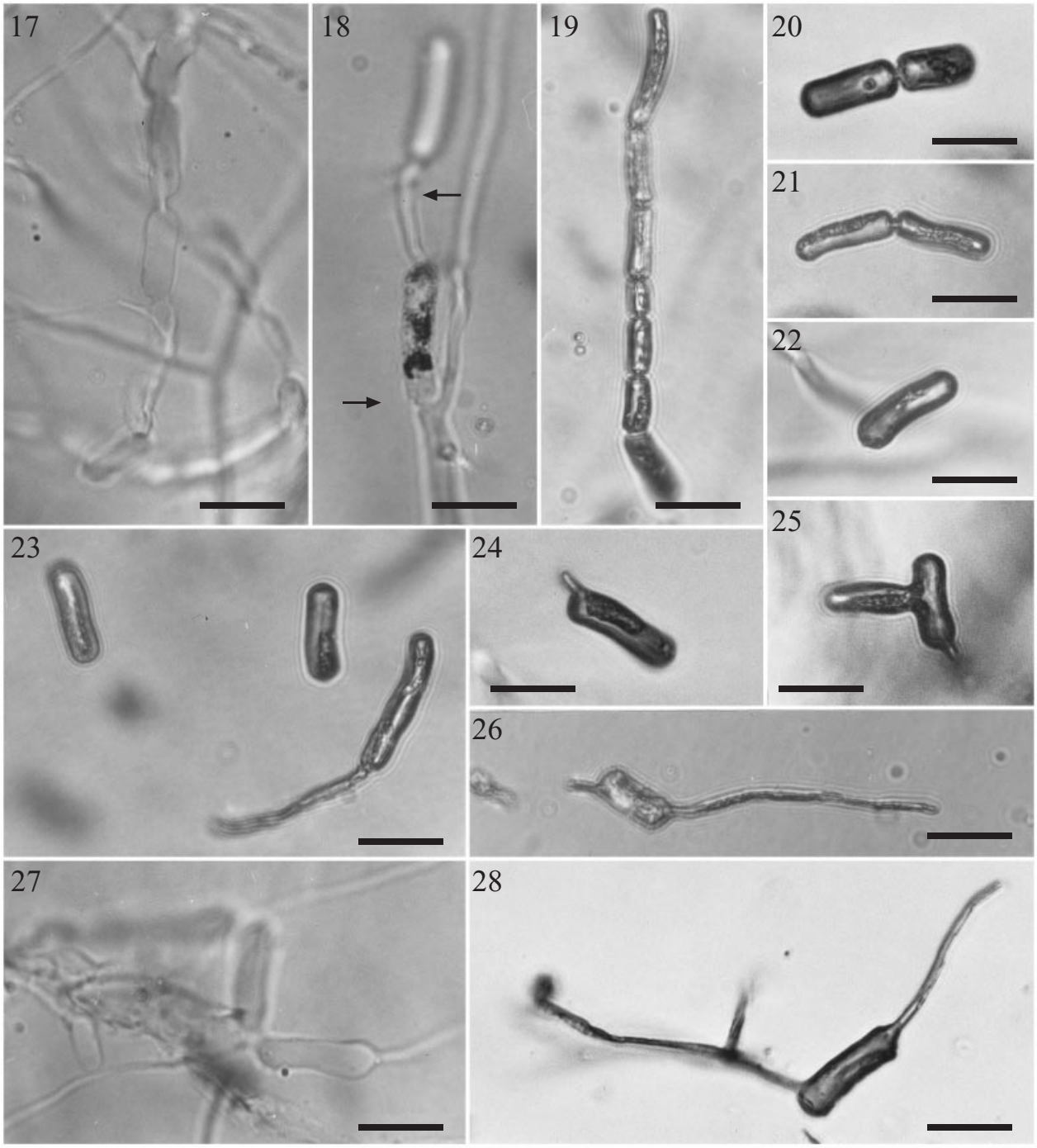
tubes close to or through one or both terminal scars. Both germ tubes and young hyphae taper gradually towards the apex. In one region of the mycelium short irregularly swollen hyphae form profusely branched clusters. These structures seem to have developed from arthroconidia which failed to completely detach from parental hyphae and/or each other prior to germination (Fig. 27).

DISCUSSION

Comparison with modern analogues

Many extant fungi produce hyphae, sporangial structures and/or arthroconidia quite similar to those of the fossil. However, we have not yet been able to find a modern organism which would perfectly combine all the preserved features. Thereby, we will refrain from assigning the fossilised mycelium to any extant group. Instead we will compare it with several potential analogues. This is the safest approach, especially since all structures in the mycelium do not necessarily represent the same organism.

At least two fungal organisms were involved in producing the fossilised colony, i.e. the mycelial fungus described here and an unicellular yeast, which will be discussed in more detail in a separate paper. It is possible that all hyphae in the mycelium were produced by only one organism. However, convincing evidence of this would require at least confirmation that individual hyphae had been able to produce both arthroconidia and sporangia. The fact that this could not be done is hardly surprising, as even in gross cultures of extant



Figs 17–28. Production and germination of arthroconidia. **Figs 17–19.** Disarticulating hyphae. Note collapsed gemma (upper arrow in Fig. 18) and renewal of hypha by cymose branching (lower arrow in Fig. 18). Bars = 10 μm. **Figs 20–21.** Short connectives between adjacent conidia. Bars = 10 μm. **Fig. 22.** Typical detached arthroconidium. Bar = 10 μm. **Figs 23–28.** Germinating gemmae at different stages of development. Germ tubes are formed from close to or through one or both terminal scars. Bars = 10 μm.

fungi it is often impossible to trace assuredly the connections between different reproductive phases of individual species.

In an earlier draft of this paper we suggested that while the fossilised arthroconidia are very similar to those of some extant hemiascomycetes, the fossil as a whole could most convincingly be placed in the *Oomycota*. The co-occurrence of coenocytic hyphae, oogonium- and antheridium-like structures, and the production of catenulate conidia (gemmae) were seen to support this hypothesis. Accordingly, the detached thick-walled spores would be oospores, some of which had germinated. The germtubes, in turn, might have had the potential of developing terminal zoosporangia. However, an anonymous referee, a leading expert on oomycetes, had grave doubts about this hypothesis. He emphasised that all the fossilised structures are significantly smaller than those of most extant oomycotes, particularly those of saprolegnian species. He also pointed out that the purported oosphere/oospore occupies a suspiciously small proportion of the

oogonium volume, and that the oospores of extant oomycetes are not usually released from oogonia, but come in a functioning package with the oogonium wall. Apparently, it is also rare to see germinating oospores in living material.

Another possibility is that the sporangia were produced by a zygomycete, which also have coenocytic hyphae and are known to produce sporangial structures resembling those of the fossilised specimen. Many zygomycetes also produce chlamydospores or conidia, sometimes in catenulate chains. While the sporangia of most extant zygomycetes are relatively huge, some species produce sporangiola of comparable size to the fossilised structures (Beakes & Campos-Takaki 1984, Beakes *et al*. 1984). The zygomycete hypothesis would be especially appealing if the globular objects inside the fossilised sporangia were to represent columellae. In accordance, the structure in Fig. 14 could represent a detached sporangiophore with fragments of the sporangium wall remaining at the base of the columella after dehiscensce. Concurrently, the circular structures seen in some globular 'spores' could represent detachment scars (Figs 8–9). However, the presence of many non-columellate and proliferating sporangia, the lack of spores in the sporangia with purported columellae, and the germinated globular spores, provide contrasting evidence. Still, the sporangium with granular contents could represent an early stage in spore differentiation (Fig. 5). There are also countless tiny spore-like particles, 1–2 μm diam, in the amber matrix and some of these could represent released zygomycete spores.

Because of the presence of cylindrical arthrospores, the fossilised sporangia should also be compared with the asci and chlamydospores of filamentous yeasts, although these fungi tend to produce septate hyphae. Especially the asci of *Galactomyces* species are quite similar in being subspheroidal and containing only one or two ascospores. However, their ellipsoidal spores tend to have rough inner walls and an irregular, locally inflated exospore with a pale median furrow. Furthermore, the spores tend to more or less fill their asci (de Hoog, Smith & Guého 1986).

The fossilised arthroconidia are definitely very similar to those produced by extant *Galactomyces* and *Dipodascus* species and their *Geotrichum* anamorphs (de Hoog, Smith & Guého 1998a, b, c). These filamentous yeasts have often been used to demonstrate arthric conidiogenesis, that is, the formation of conidia by fragmentation of pre-existing hyphae (e.g. Cole & Kendrick 1969, Cole 1975, Alexopoulos, Mims & Blackwell 1996). The fossilised conidia are also very similar to those of *Geotrichites glaesarius*, a fossil fungus described by Stubblefield *et al*. (1985) from an arachnid cadaver in Dominican amber (*cf*. Taylor & Taylor 1993: fig. 3.48). Ting & Nissenbaum (1986) mention finding *Geotrichum* arthroconidia also in Miocene amber from Chiapas, Mexico. All these fossils should be critically compared, but despite several efforts we have not been able to obtain the type specimen of *Geotrichites glaesarius* on loan for examination.

The most important difference between *G. glaesarius* and our fossil is that the mycelium of the former species is said to be septate. Also, *Geotrichum* and related yeasts have septate hyphae; while their expanding hyphae may initially be only remotely septate, mature hyphae have thickened septa every 20–60 μm. The main hyphae of most *Geotrichum* species tend to also be wider (5–12 μm) than those of the fossil (2–4 μm). In further contrast with the fossil, the arthroconidia of *Geotrichum* usually inflate before germination. Also many extant euascomycetes and basidiomycetes produce arthroconidia; for example *Moniliella* and *Trichosporon* are well known arthrosporous, mitosporic heterobasidiomycetes (de Hoog 1979, de Hoog & Smith 1998, Guého, Smith & de Hoog 1998). However, also these fungi have septate hyphae.

Among extant fungi with coenocytic hyphae, the cylindrical conidia of some zygomycetes (*Zoopagales*) may resemble arthroconidia. However, these diaspores develop through the partial evacuation of the parent hypha and are separated by hyaline zones (Benjamin 1979). Also, saprolegnian oomycetes may produce catenulate units of asexual reproduction. Their gemmae contain a dense accumulation of protoplasm, and are capable of functioning directly as zoosporangia or germinating into new hyphae (Johnson 1956, Sparrow 1960). However, these organisms tend to be quite large and their gemmae rarely detach from the parent mycelium.

Some hyphae of the fossilised mycelium give the impression of being divided into segments by constrictions rather than distinct septa (Figs 17, 20–21). This type of compartmentalisation brings into mind the pseudoseptate hyphae of extant *Leptomitales*. The hyphae of these oomycetes are constricted at more or less regular intervals, the constrictions being partly plugged by highly refractive cellulin granules, similar to the bead-like particles seen in some fossilised conidia (Fig. 20). Also *G. glaesarius* is said to have connectives between some of its arthroconidia (Stubblefield *et al*. 1985). De Hoog *et al*. (1986) noted that while such structures are not typical of *Geotrichum* or its teleomorphs, *Geotrichites* otherwise closely resembles *Geotrichum* and *Galactomyces* species, especially *Galactomyces reesii*. The arthroconidia of these extant fungi develop without connectives and their disarticulation is effected by the breakage or lysis of the hyphal wall at the septum.

Palaeoecology

Associated organisms in the same amber specimen, including several species of bryophytes and a small foliose lichen, indicate a moist forest environment. The lack of mineral particles among the detritus suggests an epiphytic or epixylic, rather than a soil substratum. The lack of algal and cyanobacterial fossils, on the other hand, does not indicate a permanently wet, semi-aquatic habitat. The fossilised bryophytes belong to extant genera, which are widely distributed in the tropics and quite characteristic of rainforests (Frahm 1993, Gradstein 1993, Frahm & Reese 1998). As a whole, the palaeoenvironment proposed for the fossilised mycelium supports earlier conclusions that the original Dominican amber forest possessed a tropical moist forest biome (Poinar & Poinar 1999).

The presence of many germinating cells suggests a sudden preservation event during moist conditions, otherwise favourable for fungal growth. The community appears to have been entrapped *in situ*, probably by viscous exudate running down a tree trunk or dripping from the forest canopy. This scenario

is supported, for example, by the natural orientation of bryophytes in the amber. It seems unlikely that this life-like composition would have resulted from random deposition of bryophytes into a stationary pool of exudate. Flowing exudate would also account for the innumerable bubbles inside the amber. Some of the bubbles may initially have contained water, which diffused out as the exudate solidified.

The fossil provides few details regarding the nutrition of the fossilised fungus. The lack of a solid food source indicates that it was a rapidly growing saprophyte, utilising fluid or semisolid substrates. The abrupt transition from hyphae to yeast cells may have been stimulated by microaerobic conditions inside the colony. Also, the occurrence of many rod-shaped bacteria and bubbles indicates that fermenting conditions may have existed inside the colony. Some expanding hyphae at the edge of the mycelium have grown through a small piece of amorphous, opaque matter, which may represent a fragment of the original food source. There are also some larger opaque globules close to the mycelium, which might represent fossilised droplets of plant exudate. Some globules have deep wrinkles, indicating that inert dehydration had removed water from their contents. There are also some bryophyte and lichen fragments and small pieces of unidentified plant tissue close to the mycelium. However, the only recognisable particles inside the colony are a detached, morbid moss leaf and a fragment from the leg of a small invertebrate, possibly a mite. Although some hyphae had grown along the surfaces of the moss leaf, they do not seem to have penetrated into bryophyte cells.

Despite amber's extraordinary qualities as a medium for preservation, germinated fungal diaspores have only rarely been reported. We have previously seen germinated fungal spores in Baltic amber (Rikkinen & Poinar 2000). Their occurrence in solid amber was accounted for by the rearrangement of germinated spores by flowing exudate, rather than from germination within the exudate itself. Similar events may also explain the distribution of germinated conidia in the present fossil. Most germinated conidia are in a fan-shaped formation extending from the edge of the mycelium to a region of solid amber with many air bubbles. Thus, flowing exudate seems to have lifted germinated conidia from the mycelium and moved them into their current position. However, it is also possible that some germ tubes continued to grow after the cells had already been engulfed by exudate. Somewhat similar phenomena are known from other types of amber fossils. For example, internal parasites are known to have made their exit out of insect hosts after these had become immersed in exudate and microbial activity in insect guts had often continued for some time after the insects had been encapsulated (Poinar & Poinar 1999). Ting & Nissenbaum (1986) proposed that some morphological features in their fossils might have developed specifically because the micro-fungi had continued to grow after being enclosed by exudate.

ACKNOWLEDGEMENTS

This study was made possible by grants from the Academy of Finland and The Council for International Exchange of Scholars. We thank the anonymous reviewers for their helpful comments.

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Corresponding Editor: D. L. Hawksworth