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Fungi of the Bitterfeld amber forest

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Summary

Fungi have only rarely been reported from Bitterfeld amber, and only four taxa, *Chaenothecopsis bitterfeldensis*, *Chaenothecopsis* aff. *proliferatus*, *Metacapnodium succinum*, and *Stigmatomyces succini*, have been published, so far. This situation recently changed due to the discovery of a plethora of new fungal inclusions from private amber collections which shows that fungi (including lichen-forming ascomycetes) from Bitterfeld amber are much more abundant than previously recognized. Here, we provide an overview of the systematics and ecological diversity of fungi that have been studied from the Bitterfeld amber deposit until now.

Kurzfassung

Pilze sind aus Bitterfelder Bernstein bisher nur selten bekannt geworden. Lediglich vier Taxa, *Chaenothecopsis bitterfeldensis*, *Chaenothecopsis* aff. *proliferatus*, *Metacapnodium succinum* und *Stigmatomyces succini*, wurden publiziert. Die gründliche Durchsicht von privaten Bernsteinsammlungen brachte jedoch zahlreiche Neufunde (inklusive Flechten) zum Vorschein. Wir geben einen Überblick über die Systematik und ökologische Diversität der bisher aus Bitterfelder Bernstein untersuchten Pilze (siehe Abb. 1–9):

Bei *Metacapnodium succinum* handelt es sich um einen Vertreter der Rußtaupilze, einer ökologischen Gruppe saprophytischer Pilze, welche die Oberflächen lebender Pflanzen besiedelt und ihre Nährstoffe von Insektenexkretionen oder von Pflanzensaftausscheidungen bezieht. Die charakteristischen kettenförmigen und oft anastomosierenden Hyphen verschmälern sich distal und weisen apikale Zellteilungsstadien auf. Im Bitterfelder Bernstein konnte erstmals das *Capnophialophora*-Stadium als Fossil nachgewiesen werden (Rikkinen et al. 2003, Schmidt et al. 2013).

Vertreter der Gattung *Torula sensu* Caspary (1886) sind ebenfalls im Bitterfelder Bernstein erhalten. Die Fossilien bestehen aus dunklen kettenartigen Filamenten, die denen von Vertretern der Gattung *Metacapnodium* ähneln, jedoch aus septierten Einheiten aufgebaut sind. Ihr Wachstum erfolgt zudem nicht apikal sondern durch interkalare konidiogene Zellen. Die Beziehung der Fossilien zur rezenten Gattung *Torula* Pers. bleibt aufgrund der Merkmalsarmut der Fossilien ungeklärt.

Bitterfelder Bernstein beherbergt den einzigen Nachweis der Klasse der Laboulbeniomyceten, einer hochspezialisierten Entwicklungslinie, die ektoparasitisch auf Arthropoden lebt. Drei Thalli von *Stigmatomyces succini* sind auf dem Thorax einer Stielaugenfliege (Diopsidae) erhalten (Rossi et al. 2005).

Baumharze dienen unter anderem der Abwehr von Mikroorganismen und Insekten. Einige hochspezialisierte Pilze sind jedoch in der Lage, auf Harzausflüssen zu wachsen. Dazu gehören mehrere Vertreter der Gattung *Chaenothecopsis*, die fossil auch im Bitterfelder Bernstein gefunden worden sind (Rikkinen & Poinar 2000, Tuovila et al. 2013). *Chaenothecopsis bitterfeldensis* bildete unverzweigte Ascomata, die auf dem Substrat, einem Harzfluss auf einem im Bernstein konservierten Rindenstück, konserviert sind. *Chaenothecopsis* aff. *proliferatus* weist proliferierende und oft verzweigte Ascomata auf. Das Fossil ist morphologisch nicht von der rezenten resinicolen Art *Chaenothecopsis proliferatus* zu unterscheiden, welche in China auf Harz von *Cunninghamia lanceolata* (Cupressaceae) gesammelt wurde (siehe Abb. 10–13). Die Ausbildung übereinander angeordneter Ascomata wird als eine Anpassung an das Leben auf Harzflüssen interpretiert, da sich die relativ hohen Fruchtkörper nach partieller Überflutung durch frisches Harz wieder regenerieren können.

Ein Vertreter der Gattung *Aspergillus* wurde auf einem Insektenrest identifiziert. Diese Gattung ist fossil bisher aus Baltischem und Dominikanischem Bernstein belegt.

Etwa 40 Bitterfelder Bernsteinstücke enthalten bisher noch weitgehend unbearbeitete Einschlüsse von Flech-

ten. Aufgrund der hohen Anzahl dieser neu entdeckten Einschlüsse und ihrer Diversität kann derzeit noch keine Übersicht über die Flechtenflora des Bitterfelder Bernsteins gegeben werden. Es zeichnet sich jedoch bereits ab, dass sich diese von der heutigen europäischen deutlich unterscheidet. So sind zum Beispiel Vertreter der rezenten Gattung *Anzia*, die bisher fossil nur aus dem Baltischen Bernstein bekannt war, im Bitterfelder Bernsteinwald sehr häufig gewesen. Heute kommt diese Gattung in Europa nicht mehr vor.

1. Introduction

Fungal inclusions are quite common in amber from almost any deposit. Despite their abundance, however, the vast majority of these fossils cannot be determined due to the absence of diagnostic features in sterile mycelia. Exceptions are some anamorphic and teleomorphic stages of the Ascomycota and Basidiomycota.

Fungi are known from Baltic amber since the mid-19th century (e.g., Berkeley 1848, Menge 1858, Caspary & Klebs 1907, Grüss 1931, Domke 1952). Compared to Baltic amber, however, Bitterfeld amber was discovered and mined much later (see Eißmann et al. 2008). Not until about 20 years after the first description of Bitterfeld amber inclusions by Barther & Hetzer (1982) were three fungi described (Rikkinen & Poinar 2000, Rikkinen et al. 2003, Rossi et al. 2005). These fungi were discovered in the private collections of George O. Poinar Jr. (Corvallis), Volker Arnold (Heide), and Manfred Kutscher (Sassnitz), respectively.

Likewise all subsequent specimens of fungi from Bitterfeld amber became known thanks to careful screening of private collections by their owners for any minute inclusions. Some of these newly discovered fungi have recently been described (Tuovila et al. 2013, Schmidt et al. 2013), but a plethora of inclusions still awaits study. These new undescribed findings include about 40 amber pieces with lichens and lichenicolous fungi. Because of the high number of specimens and their diversity, the completion of their scientific descriptions will still take several years. This means that it is currently impossible to provide a complete overview of all fungal inclusions from Bitterfeld amber and that we have to restrict this present overview to the non-lichenized ascomycetes.

2. Methods

The amber pieces were ground and polished manually with a series of wet silicon carbide abrasive papers [FEPA P 600–4000 (25.8 µm to 5 µm particle size), Struers company, Germany] to remove the weathered crusts and to minimize light scattering for the investigation. An exception is the piece containing the *Stigmatomyces* inclusion since this specimen was already sufficiently prepared and embedded in epoxy resin for conservation. Prepared specimens were placed on a glass microscope slide with a drop of water applied to the upper surface of the amber, and covered with a glass coverslip. The inclusions were studied using a Carl Zeiss AxioScope A1 compound microscope. In most instances, incident and transmitted light were used simultaneously (see Schmidt et al. 2012, for protocols). All images except of Fig. 8 are digitally-stacked photomicrographic composites obtained from several focal planes using the software package HeliconFocus 5.0 for a better illustration of the three-dimensional objects.

3. Results and discussion

3.1. *Metacapnodium succinum*

Phylum Ascomycota Cavalier-Smith 1998
Class Dothideomycetes O. E. Erikss. et Winka 1997
Order Capnodiales Woron. 1925
Family Metacapnodiaceae Hughes et Corlett 1972
Genus *Metacapnodium* Speg. 1918

***Metacapnodium succinum* (Dörfelt, A. R. Schmidt et Wunderlich) Rikkinen, Dörfelt, A. R. Schmidt et Wunderlich 2003**

Holotype: from Baltic amber, Senckenberg collection SMF Be 526a (formerly collection Jörg Wunderlich F70/BB/PL/CYA/CJW).

Bitterfeld amber inclusions investigated: Geoscientific Collections of the Georg August University Göttingen GZG.BST.27291-27292 (formerly collection Volker Arnold 1900 and 1908), and GZG.BST. 27293-27294 (formerly collection Heinrich Grabenhorst Li-3 and 122).

Description and discussion: Representatives of the genus *Metacapnodium* belong to the so-called sooty moulds, an ecological group of saprophytic ascomycetes with brown hyphae. They often form 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 (Hughes 1976, Seifert et al. 2011). Fossils of the genus *Metacapnodium* have been discovered in several pieces of Bitterfeld amber (Rikkinen et al. 2003, Schmidt et al. 2013). The moniliform hyphae of the fossils possess globose to subglobose cells of 10–13 x 7–10 µm size. One Bitterfeld amber piece (GZG.BST.27291) contains a *Capnophialophora* conidial state (Fig. 1) which has not been recorded from any other amber, so far. The *Capnophialophora* conidiogenous cells are developed singly or in groups of 2–4 on subterminal sections of hyphal branches and are 8–10 µm in height and 6–8 µm wide. The phialides

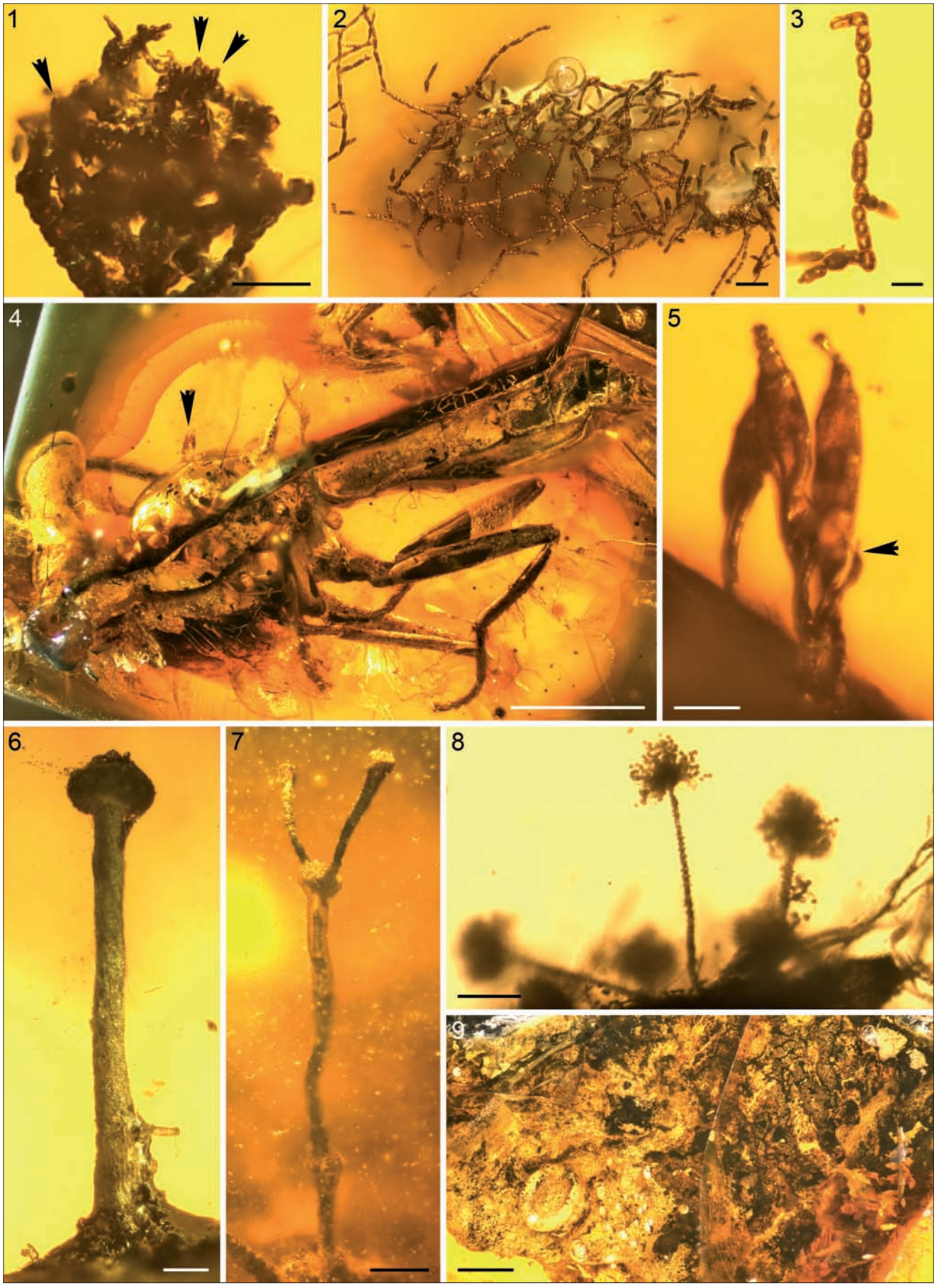

Plate I

are pale brown, more or less spherical or obpyriform with a flattened base, the distal end possesses a single subhyaline collarette. Amber piece number GZG. BST.27292 contains networks of hyphae of *Metacapnodium* that grew on bark and on a corticolous *Cavernularia*-like lichen. As the Baltic amber fossils, the Bitterfeld inclusions are morphologically assignable to the extant genus *Metacapnodium* based on their moniliform and sometimes anastomosing hyphae with tapering distal ends and apical dividing stages. The occurrence of sooty moulds in Bitterfeld amber indicates a certain humidity in the forests from which the amber derives. Capnodialean sooty moulds are recorded from the Early Cretaceous (Schmidt et al. 2013). They are an example of the apparent morphological stability of taxa which, once adapted to particular microhabitats such as bark of trees, preserved their morphological features over more than 100 million years.

3.2 *'Torula' sensu Caspary 1886*

Phylum Ascomycota Cavalier-Smith 1998
Genus cf. *Torula* Pers. 1794

Cf. *Torula globulifera* Caspary 1886

Holotype: from Baltic amber, Museum für Naturkunde Berlin, Künow amber collection, number 153.

Bitterfeld amber inclusions investigated: collection Heinrich Grabenhorst M-4, and five further pieces *sine numero.*

Description and discussion: Caspary (1886) described two microscopic fungi from Baltic amber as *Torula globulifera* Caspary and *T. heteromorpha* Caspary. These fungi share a moniliform appearance of the dark filaments and a similar cell size with the metacapnodiaceous sooty moulds mentioned above. However, these fungi do not possess distally tapering filaments with apical dividing stages nor anastomosing hyphae (Figs 2–3). The short branched cell chains are rather fragile. Most probably, these inclusions represent chains of conidia with intercalary conidiogenous cells that initiate branchings. The units forming the cell chains are about 6–11 µm in size and, contrary to the metacapnodiaceous hyphae mentioned above, mostly septate (Fig. 3). Fungi similar to Caspary's *Torula globulifera* are abundant in several pieces of Bitterfeld amber. The true nature and possible affiliation of the fossils to the problematic extant genus *Torula* remains unclear currently, due to the very few available morphological features in these fossil fungi.

3.3. *Stigmatomyces succini*

Phylum Ascomycota Cavalier-Smith 1998
Class Laboulbeniomycetes Engl. 1897
Order Laboulbeniales Lindau 1897
Family Laboulbeniaceae G. Winter 1886
Genus *Stigmatomyces* H. Karst. 1869

***Stigmatomyces succini* W. Rossi, Kotrba et Triebel 2005**

Holotype: from Bitterfeld amber, Zoologische Staatssammlung München, *sine numero.*

Bitterfeld amber inclusion investigated: Zoologische Staatssammlung München, *sine numero.*

Description and discussion: Laboulbeniomycetes are highly specialized fungi that live as obligate ectoparasites on different arthropods, especially on insects. Unlike most other ascomycetes, they lack a typical mycelium, instead they possess a minute compact thallus that is attached to the host cuticle. Bitterfeld amber contains the only fossil record of the highly specialized lineage of the Laboulbeniomycetes. The title of the Rossi et al. (2005) paper suggests Baltic amber as origin of this fungus. However, the description reveals that the specimen was discovered by the fossil collector Manfred Kutscher in material from the Bitterfeld amber deposit. Three thalli are preserved attached to the thorax of *Prosphyracephala succini*, a stalk eye fly (Diptera, Diopsidae) representative (Figs 4–5). The

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Plate I: Ascomycetes from the Bitterfeld amber forest (Fotos: Schmidt).

Fig. 1: *Capnophialophora* conidial state of *Metacapnodium succinum.* Some phialides are indicated by arrowheads. Geoscientific Collections of the Georg August University Göttingen GZG.BST.27288. Scale bar: 50 µm.

Fig. 2: Dark branched moniliform cell chains of *'Torula' sensu* Caspary (1886). Collection Heinrich Grabenhorst. Scale bar 50 µm.

Fig. 3: Single moniliform filament of '*Torula*' composed of mostly septate units. Collection Heinrich Grabenhorst. Scale bar 10 µm.

Fig. 4: *Prosphyracephala succini* (Diptera, Diopsidae) parasitized by *Stigmatomyces succini.* The arrowhead indicates the thalli at the surface of the thorax. Zoologische Staatssammlung München. Scale bar 1 mm.

Fig. 5: Three thalli of *Stigmatomyces succini.* The arrowhead indicates two antheridia. Zoologische Staatssammlung München. Scale bar 50 µm.

Fig. 6: Ascoma of *Chaenothecopsis bitterfeldensis.* GZG.BST.27286. Scale bar 200 µm.

Fig. 7: Branched ascoma of *Chaenothecopsis* aff. *proliferatus.* GZG.BST.27285. Scale bar 200 µm.

Fig. 8: Conidiophores of an *Aspergillus* representative with conidia. Collection Heinrich Grabenhorst Li-5. Scale bar 50 µm.

Fig. 9: Association of several lichens and lichenicolous fungi. GZG.BST.27293-27294. Scale bar 1 mm.

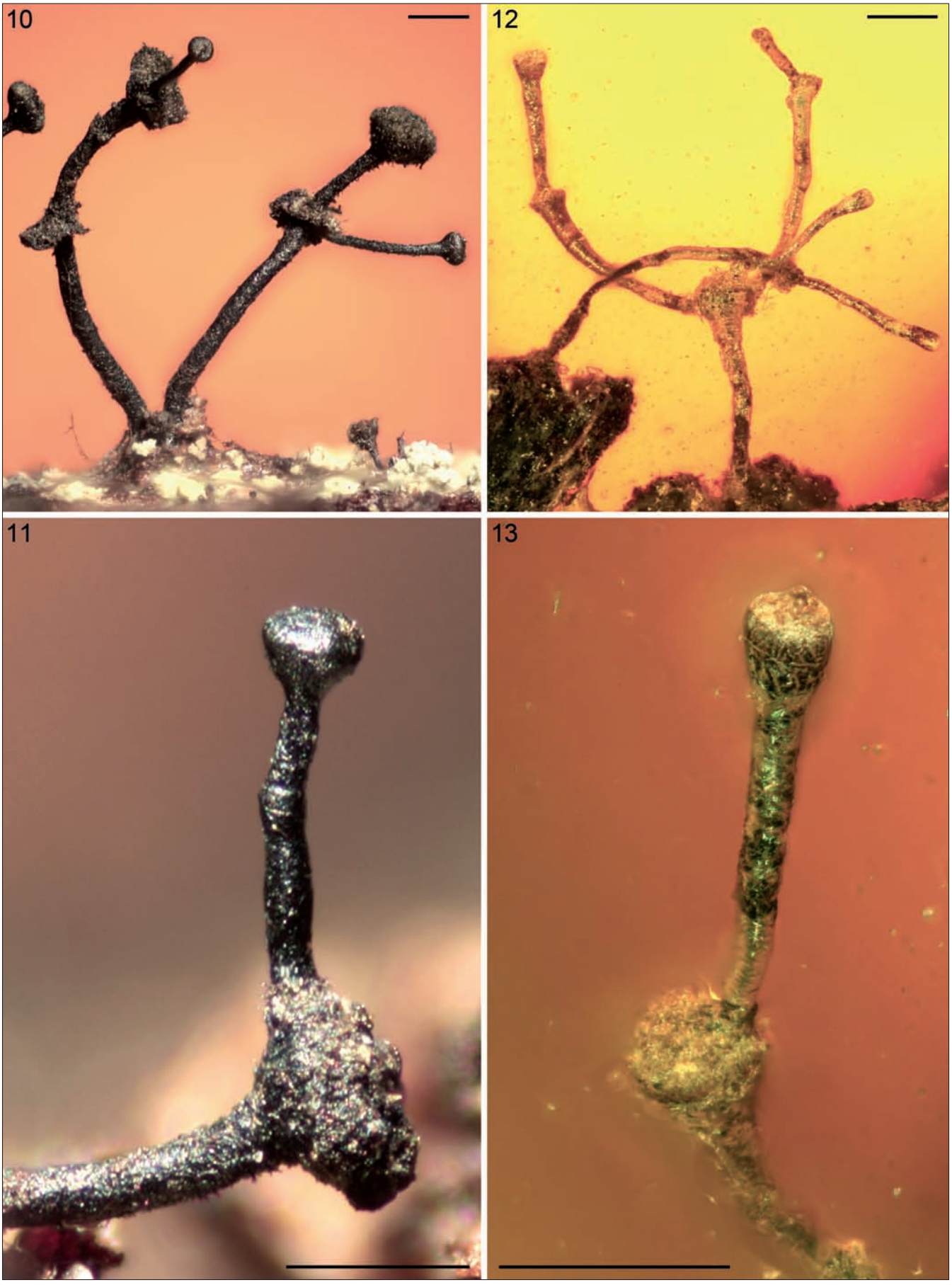

Plate II

fossil thalli are 300 µm in length and possess a slender receptacle, a perithecium, and an appendage with antheridia. The antheridia have slightly curved and unusually long necks. *Stigmatomyces succini* differs from the known extant species of *Stigmatomyces* in the very low number of antheridia and the elongation of their efferent tube. In addition, it differs from extant *Stigmatomyces* species that parasitize Diopsidae representatives in the short perithecial neck (Rossi et al. 2005).

3.4. *Chaenothecopsis bitterfeldensis and Chaenothecopsis aff. proliferatus*

Phylum Phylum Ascomycota Cavalier-Smith 1998
Class Eurotiomycetes O.E. Erikss. & Winka 1997
Order Mycocaliciales Tibell et Wedin 2000
Family Mycocaliciaceae A.F.W. Schmidt 1970
Genus *Chaenothecopsis* Vain. 1927

Tree resins provide plants with protection against pathogens and parasites, but some highly specialized fungi are also known to grow exclusively on resin substrates. Examples are several extant species of the genus *Chaenothecopsis*. Two fossil representatives of this genus have been described from Bitterfeld amber, so far (Rikkinen & Poinar 2000, Tuovila et al. 2013).

Chaenothecopsis bitterfeldensis Rikkinen et Poinar 2000

Holotype: from Bitterfeld amber, Poinar amber collection AF 9-26.

Bitterfeld amber inclusion investigated: Poinar amber collection AF 9-26.

Description and discussion: The ascomata are 300 to 700 µm in height and develop obconical to narrowly lenticular capitulate (Fig. 6). Their stalks are erect and 50–75 µm in diameter. About 20 ascomata are preserved in this amber piece. The mycelium that developed the fruiting bodies grew on resin flows on the surface of a remnant of bark that is enclosed in this amber piece.

Chaenothecopsis aff. *proliferatus*

Bitterfeld amber inclusion investigated: Geoscientific Collections of the Georg August University Göttingen GZG.BST.27285 (formerly collection Heinrich Grabenhorst Li-83).

Description and discussion: Tuovila et al. (2013) described the extant resinicolous species *Chaenothecopsis proliferatus* Rikkinen, A. R. Schmidt et Tuovila 2013 from resin of the conifer *Cunninghamia lanceolata* (Cupressaceae) from the Hunan Province in China (Figs 10–11). The authors also presented morphologically indistinguishable fossils from Bitterfeld amber (see Figs 7 and 12–13). 45 stipitate fossil ascomata are preserved in the amber piece. The individual ascomata are erect and 250–1100 µm high. They form stacks of up to three ascomata of different ages by proliferating and branching. These proliferating ascomata are morphologically virtually identical to those of the newly described extant species. The extant and the fossil fungi share (1) relatively slender, mostly branched and proliferating fruiting bodies, (2) the shape and general appearance of the capitula of young fruiting bodies, and (3) a network of arching hyphae at the surface of the stipes. The distinction between the extant *Chaenothecopsis proliferatus* and closely related species such as C*haenothecopsis hunanensis* requires study of anatomical details and chemical features that cannot be observed from fossil specimens embedded in amber. Hence, despite their excellent preservation, Tuovila et al. (2013) did not assign the new fossil from Bitterfeld amber to the extant *Chaenothecopsis proliferatus*. The development of branched proliferating ascomata may represent an adaptation to growing near fresh resin flows since the proliferating ascomata can effectively rejuvenate if they are partially overrun by fresh, sticky exudate.

3.5. *Aspergillus sp.*

Phylum Phylum Ascomycota Cavalier-Smith 1998
Class Eurotiomycetes O.E. Erikss. & Winka 1997
Order Eurotiales G.W. Martin ex Benny & Kimbr. 1980
Family Trichocomaceae E. Fisch. 1897
Genus *Aspergillus* P. Micheli ex Haller 1768

Bitterfeld amber inclusions investigated: collection Heinrich Grabenhorst Li-5.

Description and discussion: Fig. 8 shows a preliminary illustration of a conidial state of an *Aspergillus*

Plate II: Comparison of *Chaenothecopsis proliferatus* from modern *Cunninghamia* resin (left) with its fossil ancestor from Bitterfeld amber (right). Scale bars 200 µm (Fotos: Schmidt).

Fig. 10: Proliferating ascomata of *Chaenothecopsis proliferatus* growing on resin of *Cunninghamia lanceolata*. University Herbarium Helsinki, Rikkinen JR990061.

Fig. 11: Young ascoma of the extant fungus. University Herbarium Helsinki, Rikkinen JR990061.

Fig. 12: Proliferating ascomata inside Bitterfeld amber. Geoscientific Collections of the Georg August University Göttingen GZG. BST.27285.

Fig. 13: Young ascoma of the fossil. GZG.BST.27285.

which is attached to a decayed insect leg. The conidiophores are 140–170 µm in height and about 3–4 µm in diameter. The conidia are about 3–4 µm in size. This fossil represents the third find of a fossil *Aspergillus* as amber inclusion. The other finds are inclusions of Miocene Dominican amber (Thomas & Poinar 1988) and Eocene Baltic amber (Dörfelt & Schmidt 2005). The Bitterfeld amber fossil is distinguished from other two amber-preserved *Aspergillus* specimens by possessing rough conidiophores.

4. Outlook: lichenized fungi from Bitterfeld amber

We have recently also identified several well preserved fragments of lichens in Bitterfeld amber. These include specimens of the foliose macrolichen genus *Anzia* that have previously been only been known from Baltic amber (Rikkinen & Poinar 2002). While none of the modern species of *Anzia* occur in Europe, this genus seems to have been remarkably common in the ancient amber forests of the region. It appears that several different species are present in the amber flora. Also other parmelioid macrolichens and fertile crustose lichens quite similar to some extant *Ochrolechia* species await more detailed study. The thalli of many fossil lichens had supported the growth of dark lichenicolous hyphomycetes and sometimes also of sooty moulds (Fig. 9).

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