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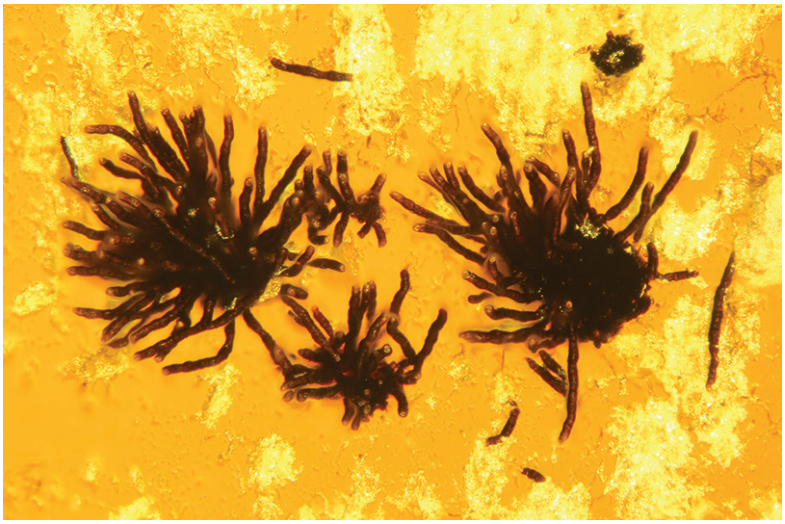
ELINA KETTUNEN

Diversity of Microfungi Preserved in European Palaeogene Amber



FACULTY OF BIOLOGICAL AND ENVIRONMENTAL SCIENCES
DOCTORAL PROGRAMME IN PLANT SCIENCES
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Faculty of Biological and Environmental Sciences
University of Helsinki
Helsinki

DIVERSITY OF MICROFUNGI PRESERVED IN EUROPEAN PALAEOGENE AMBER

Elina Kettunen

ACADEMIC DISSERTATION

To be presented for public examination, with the permission of the Faculty of Biological and Environmental Sciences of the University of Helsinki, in lecture room 105 (B6), Viikki B building, on 4th of May 2018, at 12 noon.

Helsinki 2018

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ABSTRACT

Fungi are one of the most diverse groups of organisms, but their fossil record is scarce compared with that of plants and animals. However, many fossils of microfungi have survived as inclusions in amber, which is fossilized resin produced by ancient trees millions of years ago. Some of these fossils were already discovered and described during the 19th century. There are important sources of Palaeogene amber in Europe: the Baltic and Bitterfeld deposits. Baltic amber is about 43–25 Ma old (Eocene), whereas Bitterfeld amber is slightly younger (approx. 24 Ma, Oligocene).

The aim of this thesis was to increase our knowledge of the microfungi preserved in the Baltic and Bitterfeld ambers. The material studied included both historic collections and previously unstudied amber specimens.

The approach led to several advances in the field of palaeomycology. The systematic affinities of the microfungi described by Robert Caspary and Richard Klebs over a century ago were reassessed. None of these historical specimens belong to the extant fungal genera they were originally assigned to. Amended descriptions were provided for the historical specimens, and several new types of fungi were described from novel amber specimens. These included the first fossils of lichen-associated filamentous fungi.

The results demonstrate that relatively few fossil microfungi in amber can be identified accurately enough to be used as minimum age constraints in dating phylogenetic trees of different fungal lineages. All the fossil fungi studied grew either on or in the immediate vicinity of resin-producing trees, which made them likely candidates for preservation in amber.

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications:

I Kettunen, E., Grabenhorst, H., Gröhn, C., Dörfelt, H., Sadowski, E.-M., Rikkinen, R., & Schmidt, A. R. 2015. The enigmatic hyphomycete Torula sensu Caspary revisited. Review of Palaeobotany and Palynology 219, 183–193.

II Kettunen, E., Sadowski, E.-M., Seyfullah, L. J., Dörfelt, H., Rikkinen, J. & Schmidt, A. R. Caspary's fungi from Baltic amber: historic specimens and new evidence (manuscript).

III Kettunen, E., Schmidt, A. R., Diederich, P. Grabenhorst, H. & Rikkinen, J. 2016. Lichen-associated fungi from Paleogene amber. New Phytologist 209, 896–898.

IV Kettunen, E., Schmidt, A.R., Diederich, P., Grabenhorst H. & Rikkinen, J. 2017. Diversity of lichen-associated filamentous fungi in European Paleogene amber. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 107, 311–320.

The publications are referred to in the text by their roman numerals.

Authors contributions to the publications:

I AS, EK and JR designed the study. The specimens were prepared by AS, EMS, HG and CG. EK, AS and JR analysed and imaged the fungi. EK, JR and AS wrote the species descriptions. EK wrote the article as the main author, together with AS, JR and EMS. All authors commented on the manuscript.

II AS, EK and JR designed the study. The specimens were prepared by AS and EMS. EK, AS and JR analysed and imaged the fungi. EK, JR and AS wrote the species descriptions of the fungi. EMS and LJS identified the substrates of the fungi. EK wrote the article as the main author, together with AS, JR, EMS and LS. All authors commented on the manuscript.

III AS, JR and EK designed the study. The specimens were prepared by AS and HG. EK, AS and JR analysed and imaged the fungi. EK, JR and AS wrote the descriptions. EK wrote the article as the main author, together with AS, JR and PD. All authors commented on the manuscript.

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Cover photo by Alexander Schmidt

SUMMARY

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1. INTRODUCTION

AMBER

Amber has been known since ancient times and has been used for amulets, jewellery and even medicine for millennia. Several gymnosperms and angiosperms produce resins containing terpenoid compounds that can polymerize and harden into a solid resinous mass. Under the right conditions, the hardened resin can be preserved in sediments and eventually matures into fossilized resin, i. e. amber (Langenheim 2003, Bray & Anderson 2009).

The oldest evidence for resin production in plants dates back to the Carboniferous (320 Ma); several well-preserved droplets of amber have been found in Illinois, USA. The botanical origin of this amber is as yet unknown. The amber was probably produced by a preconifer gymnosperm, but it has several chemical characteristics in common with the resin produced by extant angiosperms. No fossils were discovered inside these tiny amber pieces (Bray & Anderson 2009). So far, the oldest amber fossils come from Triassic amber discovered in the Dolomites of northern Italy. Fossils of algae, amoebae, mites and also conidial fungi have been found in these amber droplets (Schmidt et al. 2006, 2012).

There are approximately 100 known amber deposits on Earth, and amber has been found in all continents except Antarctica. About 20 amber deposits are rich enough for commercial use. The Baltic amber deposit (Eocene) is the largest and most famous individual amber deposit, and it has also been the most studied deposit since the 19th century (Weitschat & Wichard 2002, Langenheim 2003, Anderson 2006). Another important fossiliferous European amber deposit from the Palaeogene is in Bitterfeld (Germany), and significant European Mesozoic amber deposits have been found in Italy (Triassic), France and Germany (Cretaceous). Recently Neri et al. (2017) reported a new Jurassic amber deposit from northern Italy. In other regions, remarkable amber deposits are located in the Dominican Republic (Miocene), Myanmar (Burma) (Cretaceous) and Lebanon (Cretaceous). Most of the known amber deposits are located in the Northern Hemisphere, but fossiliferous amber has also been found in Africa (Cretaceous), South America

(Miocene), Australia (Palaeogene) and New Zealand (Miocene) (Antoine et al. 2006, Hand et al. 2010, Schmidt et al. 2010a, 2018).

Amber is named after its location, and its properties vary between different deposits. For example its colour may vary greatly within a single deposit. More significant for the preservation of amber and its inclusions are the chemical properties of resin. For example, Baltic amber is widely known for its ability to preserve organisms so well that even cellular-level structures are visible (Poinar & Hess 1982, Weitschat & Wichard 2002, Langenheim 2003, Anderson 2006). Fossilized resin is divided into several different types according to its chemical properties and age. There are differing views on when subfossil resins (copal) become amber, but usually only fossil resin dating back millions of years is considered true amber (Anderson 1996, Weitschat & Wichard 2002, Langenheim 2003).

Dating of amber fossils is challenging, since individual amber pieces cannot be dated with any physical or chemical method. The only radioactive element in amber is radiocarbon-14, and it cannot be utilized for dating samples that are millions of years old. Usually, the only way to date amber is to measure the age of the sediments from which the fossil resin is recovered. In some cases the index fossils inside the amber can also be used for relative dating estimates (Anderson 1996, Weitschat & Wichard 2002, 2010, Dunlop 2010).

Amber can be preserved only under anoxic conditions in seafloor sediments. In the presence of oxygen, amber starts to deteriorate, and all natural raw amber pieces have a weathered crust. The thickness of the crust is dependent on the conditions under which the amber has been preserved. Some of the old amber collections from the 19th century are already damaged, and efforts to preserve them by methods such as submerging the specimens in water, mineral oil or alcohol have destroyed several specimens. Currently, amber specimens are usually embedded in synthetic resins to prevent oxidative damage (Weitschat & Wichard 2002, Penney & Green 2010, Schmidt et al. 2012).

Plant resins are chemically complex and consist of several compounds. The chemical properties of amber have been studied using various techniques (Fourier-transform infrared (FTIR) analysis etc.) based on the infrared spectra of resins (Langenheim & Beck 1965, Weitschat & Wichard 2002, Wolfe et al. 2009, 2016). Pyrolysis-gas chromatography-mass spectroscopy (Py-GC-MS) has also been used to distinguish resins of different botanical origins. One problem with chemical analyses of amber is convergent evolution on the molecular level, which often prevents the identification of amber producing trees solely by chemical methods. In practice identifiable plant fossils must be found in association with amber to reliably determine the biological origin of the ancient resin (Anderson 2006, Grimaldi 2009).

Baltic and Bitterfeld ambers

Baltic amber has been found in many locations throughout the Baltic Sea area in sediments that were formed between the middle Eocene (approx. 43 Ma) and the late Oligocene (approx. 25 Ma). The oldest amber bearing sediments are located in eastern Scania (Skåne) in southern Sweden and the Samland Peninsula (Kaliningrad region). Most of the amber mining today occurs in the Samland area. According to some estimates the 'Baltic amber forests' grew somewhere in the area that might extend from Scania to the Ural Mountains (Weitschat & Wichard 2002). However, the idea of the Fennoscandian origin of the Baltic amber has been challenged, and the exact geographical location of the amber forests is still debated (Standke 2008, Sadowski 2017). So far shore-washed or redeposited Baltic amber has been found in Denmark, southern Sweden, Germany, Poland, Russia, Ukraine and the Baltic countries. The huge amounts of amber excavated from the Baltic deposits must only be a tiny fraction of the massive amounts of resin once produced by the ancient amber forests. Most of the resin decomposed and never reached the sedimentation sites (Weitschat & Wichard 2002, 2010, Standke 2008, Wolfe et al. 2009).

The botanical origin of Baltic amber is still unclear, and several gymnosperms have been suggested as the amber producing trees. The strongest candidates based on similarities of chemical properties and infrared spectra have been trees of the families Pinaceae and Araucariaceae, but so far fossils of Araucariaceae trees have not been found in European amber, and it is unclear how similar the resins of extant members of the Pinaceae are to Baltic amber (Weitschat & Wichard 2002, Langenheim 2003, Wolfe et al. 2009, Sadowski 2017, Sadowski et al. 2017a). Based on FTIR-analysis of extant and fossil resins and palaeobotanical evidence species of the gymnosperm genus *Sciadopitys* (Sciadopityaceae) have also been suggested as potential sources of Baltic amber. In comparison to the resinous exudates of extant conifers Baltic amber contains much higher levels of succinic acid, for which reason Baltic amber has sometimes been called succinate (Wolfe et al. 2009, 2016). However, conifers such as *Pseudolarix* (Pinaceae) and the extinct *Cupressospermum saxonicum* (Geinitziaceae) cannot be ruled out as potential sources of Baltic amber, and for now the exact botanical origin of Baltic amber remains a mystery (Sadowski 2017).

The Bitterfeld amber deposit in the state of Saxony-Anhalt in Germany is another important Palaeogene amber deposit in Europe. The first amber findings at this site were made in association with coal mining and date back to at least the 19th century (Fuhrmann & Borsdorf 1986, Dunlop 2010). In 1955, an extremely rich amber deposit was found in the Goitzsche brown coal mine, and hundreds of thousands of tonnes of raw amber were mined from there until the closure of the mine in 1993. Currently the mine is filled with water, and thus the amber left cannot be accessed (Dunlop 2010). The amber-bearing sediments have been dated to the upper Oligocene with an absolute age of 25.3–23.8 million years (Knuth et al. 2002).

The origin and exact age of the Bitterfeld amber have been widely debated and, based on fossil inclusions (especially arthropod fossils), Bitterfeld amber has been interpreted as redeposited Baltic amber (Weitschat & Wichard 2002, Dunlop 2010, Hoffeins et al. 2010). Most of the Bitterfeld amber contains large amounts of succinate, as does Baltic amber (Fuhrmann & Borsdorf 1986, Wolfe et al. 2016). However, several different types of amber have been found in the Bitterfeld deposit, and chemical analyses indicate that the Bitterfeld amber containing succinate was probably produced by a different tree species than Baltic amber (Yamamoto et al. 2006, Wolfe et al. 2016). There are no signs in the local sediment stratigraphy of an event that would explain the redeposition or accumulation of a large amber deposit in Bitterfeld during the Oligocene (Fuhrmann & Borsdorf 1986). Recently the view of the Bitterfeld amber as an independent upper Oligocene amber deposit has gained support (Dunlop & Giribet 2003, Schmidt & Dörfelt 2007, Dunlop 2010, Wolfe et al. 2016).

The traditional views of the 'Baltic amber forest' as a tropical forest with some mountainous, more temperate regions have been challenged by studies that have focused on the plant inclusions. According to Sadowski (2017) there is no palaeobotanical or geographical evidence that would support the idea of mountainous forests, and there is considerable ambiguity regarding the presumed tropical plant fossils that have been discovered in Baltic amber. The climate in middle or late Eocene Europe was warm-temperate, and the Baltic amber flora contains fossils of conifer species from the families Pinaceae, Cupressaceae, Geinitziaceae and Sciadopityaceae. Angiosperm fossils from several families have been found, and stellate hairs of Fagaceae are among the most common plant remains in Baltic amber (Caspary & Klebs 1907a, b, Weitschat & Wichard 2002, Wolfe et al. 2009, Sadowski 2017, Sadowski et al. 2017a). Fossils of graminids (Cyperaceae and possibly Poaceae), carnivorous plants (Roridulaceae), dwarf mistletoes and epiphytic lichens clearly indicate that there were also open and well-illuminated habitats in the European Eocene amber forests (Sadowski et al. 2015, 2016, 2017b, Kaasalainen et al. 2017). Near forest areas there were likely heterogenous habitats that included swamps, riverbeds and alluvial meadows (Sadowski 2017). The morphologies of lichen fossils in Baltic amber also indicate moist and most likely temperate forest habitat (Kaasalainen et al. 2017).

Resins from coastal or lowland forests are more likely to become preserved and fossilized in marine near-shore sediments than resins from more inland areas. Bitterfeld amber is also assumed to have originated in Oligocene coastal forests. The plant families Pinaceae, Cupressaceae, Geinitziaceae and Fagaceae were represented in the Bitterfeld amber forest, and chemical analyses suggest that some of the amber may have been produced by members of the family Betulaceae (Schmidt et al. 2001, 2013, Yamamoto et al. 2006, Sadowski 2017).

Study and challenges of amber

Fossils in amber, especially those of insects, have been known for centuries and the systematic scientific study of amber inclusions already began in the 19th century. Amber inclusions can be mere hollow casts, and even in well-preserved insect fossils only the exoskeleton often remains (Weitschat & Wichard 2002). Researchers have tried various methods to dissolve amber to gain a better access to the fossils inside, but usually such attempts have only led to the destruction of fossils. However, some ambers dissolve readily, and researchers have successfully extracted plant and insect remains from Cretaceous Lebanese amber by dissolving the amber in chloroform (Azar 1997). Beimforde et al. (2011) dissolved Indian Eocene amber (52 Ma) and extracted pieces of ectomycorrhizal specimens, which were then studied under a scanning electron microscope (SEM). SEMs have also been used to image lichen-forming fungi preserved in amber (Hartl et al. 2015, Kaasalainen et al. 2015, 2017). X-ray high-resolution computed tomography (HR-CT) and X-ray synchrotron imaging have also been used to produce detailed three-dimensional (3D) images of amber fossils (Penney & Green 2010). Raman spectroscopy can be used to study the chemical compositions of fossils in amber, and it has been used to demonstrate the presence of melanin in a fossil fungus (Beimforde et al. 2011, Hartl et al. 2015).

Features of organisms inside resin may become distorted due to desiccation and decomposition processes. When an organism trapped in resin dies, microbes are still able to decompose its tissues even if the organism is completely submerged in resin. Microbial activity often releases gasses and liquids from the inclusion to the surrounding resin, and when the resin is still liquid small gas bubbles can form an opaque and milky layer that often surrounds parts of or even the whole organism. This phenomenon is well known in Baltic amber, and in some cases it makes detailed morphological observations impossible (Weitschat & Wichard 2002). Attempts can be made to remove this milky layer by subjecting the amber to increased pressure and temperature in an autoclave, but this treatment can easily distort the fossil's features (Szwedo & Sontag 2009).

Several reports have documented DNA extraction from amber fossils of different ages (see Hamamoto & Horikoshi 1994, Lambert et al. 1998) and even cultivation of ancient bacteria found inside amber (Greenblatt et al. 1999, 2004). The temptation to undertake these type of experiments is understandable, since DNA would greatly aid in species identification, especially with micro-organisms (Girard & Adl 2011). However, the results of ancient DNA extractions have been strongly disputed, and attempts to replicate the results have failed. Supposedly live fossil bacteria inside amber are most likely the results of recent contaminations. Extant bacteria and other microorganisms are known to grow both on and inside amber pieces (Girard et al. 2008, Beimforde & Schmidt 2011). The current view is that it is highly unlikely that DNA could survive millions of years inside amber (Austin et al. 1997, Girard & Adl 2011).

Amber fossils are remarkable in that many of the organisms that became entrapped in the resin were still alive and only died after being engulfed by the resin. Thus, many amber specimens that contain multiple fossils can provide 'snapshots' of ancient communities of living organisms. Amber is a particularly excellent source of various micro-organisms, such as fungi, bacteria and unicellular eukaryotes, and of course various arthropod findings from amber are well known. Amber has also preserved macroscopic plant remains, bryophytes, lichens and even small basidiomycetes (e. g. Caspary & Klebs 1907a, b, Hibbet at al. 1997, 2003, Schmidt & Dörfelt 2007, Saint Martin et al. 2012, Heinrichs et al. 2015, Cai et al. 2017). Even though larger animals have better chances of escaping from the resin, small vertebrate animals, such as lizards, have been found at least partially preserved in amber (Weitschat & Wichard 2002). Some of the latest and most spectacular findings include Cretaceous bird wings and even a tail of a dinosaur (Xing et al. 2016a, b, 2017).

It should be noted that not all plant exudates become fossilized, and thus amber can only provide an incomplete picture of all those ancient trees that produced resins or similar exudates (Langenheim 2003). One must also account for other preservation bias, since organisms with exoskeletons or robust cell walls are much more likely to be preserved than soft-bodied organisms (Adl et al. 2011). One of the problems, especially regarding microorganisms, is pseudo-inclusions, i.e. inclusion-like structures in amber that are not of biological origin, but artefacts of desiccation processes within the resin itself. Fossils of soft-bodied unicellular organisms such as amoebae are rare, but some have survived as amber inclusions. However, inclusions of pseudo-protists in amber are likely to be far more numerous than real protist fossils at least in Cretaceous ambers. Many pseudo-inclusions may have been described as real organisms, which can seriously distort the fossil record of these groups (Schmidt et al. 2010b, Girard et al. 2011).

FUNGI AND THEIR FOSSIL HISTORY

Fungi comprise one of the most diverse groups of organisms on Earth – the total number of species is estimated to be in the millions (Hawksworth 2001, 2004, Blackwell 2011). So far, about 100 000 species of fungi have been described from diverse environments and habitats throughout the world (Ainsworth & Kirk 2008, Blackwell 2011). Due to the rarity of identifiable fungal fossils, the study of fungal evolution has mainly relied on the extant species and their phylogenetic relationships. However, well-preserved fossils can offer valuable information on the divergence of fungal lineages (Taylor et al. 2015), and they can be used as calibration points in molecular systematics (see Taylor & Berbee 2006, Prieto & Wedin 2013, Beimforde et al. 2014).

Fungi do not preserve as fossils as readily as some animal parts (e.g. bones of vertebrates) and plant remains, and well-preserved fungal fossils have mainly been found in silicified certs and amber. The first fossils of fungi were already described in the 19th century, but generally research has strongly

focused on the more readily available plant fossils. Fossil fungi are usually found during studies of plant fossils, and quite often partially damaged leaves with signs of fungal infestation have been ignored in favour of better-preserved specimens (Taylor & Krings 2005). Most fungal fossils are small and difficult to recognize as such, and if there are no reproductive structures present, their identification is in most cases impossible. Often, studies of fossil fungi have focused on the diversity and stratigraphy of fungal spores in palynology (Stubblefield & Taylor 1988, Taylor et al. 2015). Since the 1980s interest in fossil fungi has increased, and more emphasis placed on the interactions between ancient fungi and their environment. Currently, there is abundant evidence for the associations between fungi and the earliest land plants, and since their first emergence, fungi have played an important role in the carbon cycle and formation of the first soils (Stubblefield et al. 1985, Stubblefield & Taylor 1988, Taylor & Osborn 1996, Taylor & Taylor 1997, Selosse & Le Tacon 1998, Taylor & Krings 2005, Krings et al. 2007, Selosse et al. 2015).

Constructing the early history of fungal lineages, based on molecular and fossil evidence, has been challenging, and several estimates of the divergence times of fungi have been presented over the years. Molecular evidence suggests that the divergence of the Ascomycota and Basidiomycota may have already occurred in the Proterozoic, about 1000–900 Ma ago, but so far the oldest unequivocal fungal fossils come from the Palaeozoic (541–251.9 Ma) (Taylor & Berbee 2006, Lücking et al. 2009, Berbee & Taylor 2010, Prieto & Wedin 2013, Taylor et al. 2015). However, the recently published filamentous, fungal-like fossils from 2.4-billion-year-old basalt from South Africa may drastically change traditional views on the evolution of the Eukaryota (Bengtson et al. 2017).

Ascomycetes are the most diverse fungal group, comprising a total of about 65 000 described species (Ainsworth & Kirk 2008). Hyphae and spores that resemble those of extant anamorphic ascomycetes have been found in Silurian limestone in Gotland, Sweden (Sherwood-Pike & Gray 1985), but the oldest unequivocal ascomycete fossils are from the Rhynie chert, the famous Early Devonian fossil Lagerstätte in Scotland. *Paleopyrenomycites devonicus* from the Rhynie chert is so far the oldest fossil fungus that has perithecia, asci and ascospores preserved (Taylor et al. 2005). The Rhynie chert has also yielded several chytridiomycetes and mycorrhizal fungi (mainly Glomeromycotina) that occur in association with some of the earliest land plants (Taylor et al. 1992, 2015). Vesicles and spores of glomeromycotan fungi are very common in plant fossils from the Rhynie chert, and some of these arbuscular mycorrhizal fungi are colonized by other microfungi, already indicating complex interfungal interactions in the earliest terrestrial ecosystems (Krings et al. 2015, Harper et al. 2017). The oldest evidence for lichen-like symbioses between fungi and algae also originate in the Devonian (Taylor et al. 1997, Karatygin et al. 2009, Honegger et al. 2013). Enigmatic, tree-trunk-like fossils assigned to the genus *Prototaxites* (Silurian to Upper Devonian) have been interpreted as conifer trunks, algae, rolled mats of liverworts and finally as

gigantic basidiomycetous fungi. However, recent findings indicate that *Prototaxites* may belong to the basal ascomycetes (Honegger et al. 2017).

In comparison to the ascomycetes, basidiomycetes are rare in the fossil record, with the oldest direct evidence for them being from the Carboniferous. Krings et al. (2011) found septate hyphae with clear clamp connections associated with a fern leaf from central France. There are Devonian plant remains with fungal hyphae showing signs of decay very similar to the white rot caused by certain modern basidiomycetes (Stubblefield et al. 1985), but in the absence of clamp connections or reproductive structures it remains unclear to which fungal group the hyphae belonged to. Often evidence of fungi in ancient ecosystems is indirect; various signs of fungal activity in plant fossils are far more common than fully preserved fossil fungi (Stubblefield & Taylor 1986). Recently a new fossil agaric was described from Lower Cretaceous limestone in Brazil (Heads et al. 2017), but generally the fruiting-bodies of basidiomycetes are rarely preserved as fossils (Cai et al. 2017).

Fungi in amber

Fungal spores and hyphae have been found as amber inclusions since the 19th century, although some of the structures described as fungal hyphae were probably actinobacteria (Girard & Adl 2011). The oldest descriptions of hyphomycete or mould fossils are from the mid-19th century, all from Baltic amber. In 1845 Heinrich Göppert and Georg Karl Berendt described a basidiomycete and a microfungus (*Sporotrichites heterospermus*), and a few years later Miles Joseph Berkeley described three species of moulds also from Baltic ('Prussian') amber (Göppert & Berendt 1845, Berkeley 1848). Anton Menge (1858) described a further filamentous fungus by the name *Sphaerophorus moniliformis*. Unfortunately, all these early amber fungi specimens appear to have been lost.

For over a century the largest collection of fossil fungi from Baltic amber was that described and illustrated by Robert Caspary and Richard Klebs (1907a, 1907b). Some of the fungi had already been described by Caspary in an earlier publication (Caspary 1886). These fossils are reanalysed and discussed in detail in my thesis (I, II). For several decades after these early 20th century studies, there was a hiatus in the study of amber fungi. The study only picked up again in the 1980s, and since then fossils of fungi have been found and described in several amber deposits throughout the world (see Girard & Adl 2011 for a review). Most Mesozoic fossil fungi come from Cretaceous ambers (e.g. Schmidt et al. 2001, 2008, 2010a, 2014, Girard et al. 2009, Saint Martin et al. 2012), but so far the oldest unequivocal amber fossils of fungi were discovered in Triassic amber from Italy. These filamentous, conidial microfungi resemble species of the extant genus *Ramularia* (Schmidt et al. 2006).

Basidiomycetous hyphae have been found in Cretaceous amber from France (Girard et al. 2009, Adl et al. 2011), and even some mushroom fruiting-

bodies have been described in New Jersey and Burmese (Cretaceous) and Dominican Republic (Miocene) ambers (Poinar & Singer 1990, Hibbet et al. 1997, 2003, Poinar & Buckley 2007, Cai et al. 2017). These fossil agarics are very small, which has significantly aided in their preservation inside amber (Cai et al. 2017). The majority of fungal remains in amber are vegetative hyphae, and in the absence of clear clamp connections or reproductive structures it is impossible to assign them to any single fungal group.

During recent years several types of fungi have been described in European Palaeogene amber. These discoveries include representatives of the Capnodiales (*Metacapnodium succinum*, Rikkinen et al. 2003; Schmidt et al. 2014), Laboulbeniales (*Stigmatomyces succini*, Rossi et al. 2005) and resinicolous Mycocaliciales (*Chaenothecopsis bitterfeldensis*, Rikkinen & Poinar 2000, and *Chaenothecopsis* spp. Tuovila et al. 2013). Dörfelt and Schmidt (2007) described two anamorphic fungi from a conifer seedling in Baltic amber and an *Aspergillus*-like anamorph (Eurotiales) was mentioned by Schmidt et al. (2013).

Lichen fossils have been regarded as extremely rare, compared with those of plants and animals, and lichen-associated microfungi have not had a fossil record. However, the number and diversity of recognized lichen fossils in amber has increased rapidly during recent years, and research on these specimens has also led to the discovery of the first lichen-associated fungi from Baltic and Bitterfeld ambers, discussed in detail in my thesis (III, IV) (Hartl et al. 2015, Kaasalainen et al. 2015, Kettunen et al. 2016, 2017).

The compositions of the microbial communities in ambers of different ages and origins vary considerably. For example, in French Cretaceous amber the most abundant microinclusions appear to be sheathed prokaryotes (Cyanobacteria) and Actinobacteria. The majority of microorganisms found are believed to represent litter- or soil-living taxa, although some marine and epiphytic taxa are also present (Girard et al. 2009, Girard & Adl 2011). These 'litter amber' microfossils have been used for reconstructing ancient soil food webs (Adl et al. 2011).

Distinguishing fungal hyphae from the filaments produced by eubacteria and actinobacteria can be difficult. Especially some actinobacteria (Actinomycetales) can produce hyphae that are superficially very similar to fungal hyphae. However, the actinomycete filaments are usually thinner than fungal hyphae, and tend to show fragmentation patterns that are not typical of fungi (Waggoner 1994). In Palaeogene amber eukaryotic microorganisms are usually more common than prokaryotes, and the majority of filamentous structures can be attributed to fungi rather than to bacteria (Schmidt et al. 2013).

Hyphomycetes

Hyphomycetes are asexually (mitotically) reproducing states (anamorphs) of various ascomycetes and basidiomycetes. They do not represent a monophyletic group and their identification and traditional classification have been based purely on morphology and culture characteristics. There are two other major groups of anamorphic fungi; blastomycetes (asexual yeasts, both ascomycetes and basiodiomycetes) and coelomycetes (reproduction by pycnidia and acervuli, mostly ascomycetes, some basidiomycetes). The morphological distinction between the anamorph groups is not always clear, since some fungi could be considered either blastomycetes or hyphomycetes (Seifert et al. 2011).

Hyphomycetes produce conidia (asexual spores) openly, without forming true fruiting bodies (conidiomata). Most of the microfungi commonly known as 'moulds' belong to this group. Some anamorphs of zygomycetes and related fungi are morphologically similar to hyphomycetes (Seifert et al. 2011). Traditionally anamorphic fungi have been referred to as Fungi Imperfecti or Deuteromycota, but these are obsolete terms, referring to the absence of sexual reproduction in these fungi. Many hyphomycetes have been associated with their sexually reproducing counterparts (teleomorphs), and together they are referred to as the holomorph of the fungus. However, for most hyphomycetes the teleomorph is not known (Seifert et al. 2011), and up to one fifth of all fungi described are known only as asexual states (Shenoy et al. 2007). Hyphomycetes are an ecologically and economically important group including many pathogens and parasites, as well as primary decomposers in ecosystems throughout the world.

Before the rise of the molecular era the classification of hyphomycetes was based solely on the morphology of the conidia and conidiophores, and the method of conidiogenesis (Subramanian 1972). In many cases, convergent evolution has led to the development of similar morphological structures in unrelated fungal lineages. This has led to an artificial classification of anamorphic fungi, and many anamorph genera are highly polyphyletic (Shenoy et al. 2007). Molecular methods have made it possible to assign anamorphs to different fungal families (Hyde et al. 2011). The dual nomenclature system for fungi was officially terminated in 2011 (18th International Botanical Congress in Melbourne, Australia) and the naming follows the 'One Name = One Fungus' policy. However, for fungi with many anamorphic states there are several name options to consider (Hawksworth 2012).

Since DNA extraction is not a viable option in the study of fossil hyphomycetes, we can only rely on morphological characters, and it is often difficult if not impossible to assign fossil microfungi reliably to any one modern group. However, in some fungal groups such as the sooty moulds of the family Metacapnodiaceae (Capnodiales, Ascomycota), even anamorphs can sometimes be identified to family level. Many dematiaceous (darkly-pigmented) hyphomycetes have conidia and conidiophores with thick cell

walls, which increases the likelihood of preservation. The dark colour also makes them easier to detect when screening for biological inclusions in amber.

2. AIM OF THE THESIS

The aim of this thesis was to produce new information on the diversity and ecologies of the microfungi that grew in the ancient amber forests of Europe during the Palaeogene. One of the specific goals was to investigate the historical specimens of fossil fungi described by Robert Caspary in 1886 from Baltic amber (I, II), provide amended descriptions and to re-evaluate their affinities in light of what is currently known about fungal systematics.

In Articles III and IV the specific aim was to analyse and describe the first ever discovered fossils of lichen-associated fungi and discuss their affinities and ecology. The latter line of research had its roots in my Master's thesis project, during which I discovered the first specimen of these microfungi.

3. MATERIAL AND METHODS

MATERIAL

The specimens of Baltic and Bitterfeld ambers examined for this thesis were acquired from museums and private collectors. The age of the amber specimens from the Baltic region is approximately 43–25 Ma and the age of those from Bitterfeld approximately 24 Ma. Table 1 shows all the amber specimens examined in this thesis, together with their current repositories.

Table 1. *Specimens of fossil fungi addressed in this thesis.*

Fossil	Specimen number(s)	Affiliation	Source	Article (I-IV)
Casparyotorula globulifera	MB 1979/696 [1]	Ascomycota	Baltic amber	I, II
Casparyotorula globulifera	GZG.BST 24340[2]	Ascomycota	Baltic amber	I, II
Casparyotorula heteromorpha	MB 1979/636 [1]	Ascomycota	Baltic amber	I, II
Casparyotorula heteromorpha	3628 [3]	Ascomycota	Baltic amber	I, II

Casparyotorula heteromorpha	GZG.BST.27302 [2]	Ascomycota	Bitterfeld amber	I, II
Casparyotorula heteromorpha	GZG.BST.27303 [2]	Ascomycota	Bitterfeld amber	I, II
Casparyotorula heteromorpha	Mi-19 to Mi-32 [4]	Ascomycota	Bitterfeld amber	I, II
Casparyotorula heteromorpha	Mi-47 to Mi-50 [4]	Ascomycota	Bitterfeld amber	I, II
Casparyotorula arnoldii	GZG.BST.27301 [2]	Ascomycota	Bitterfeld amber	I
Filamentous organism (‘*Fungites capillaris*’)	F158 [5]	Prokaryota	Baltic amber	II
Fungites pullus	GZG.BST.2 4340 [2]	Ascomycota	Baltic amber	II
Fungites hirtus	MB 1979/614 [1]	Ascomycota	Baltic amber	II
Fungites macrochaetus	GZG.BST.24490 [2]	cf. *Gonatobotryum*	Baltic amber	II
Condial fungus (‘*Acremonium succineum*’)	GZG.BST.24479 [2]	Ascomycota	Baltic amber	II
Gonatobotryum primigenium	GZG.BST.24367 [2]	*Gonatobotryum*	Baltic amber	II
Metacapnodium succinum	GZG.BST.24348 [2]	*Metacapnodium*	Baltic amber	II
Conidial fungi (‘*Ramularia oblongispora*’ and ‘*Ramularia* sp.’)	None	Ascomycota	Baltic amber	II
Calicium succini	MB 1979/838 [1]	*Calicium*	Baltic amber	II
Fruticose lichen (‘*Cetraria* sp.’)	Casp. 108 BST 24489 [2]	Ascomycota	Baltic amber	II
Gonatobotryum-like fungus	1422-2 [6]	cf. *Gonatobotryum*		II
Trichopeltina-like fungi	G15 BST 24658 [2], B583 BST 24611 [2], Casp 38 BST 24470 [2], 2678[3], 4B107 BST 24592 [2], G4.507 BST 24346 [2]	cf. *Trichopeltina*	Baltic amber	II
Conidial fungi	Casp 38 BST 24470 [2], G59 BST 24619 [2]	Ascomycota	Baltic amber	II
Sooty mould	G59 BST 24619 [2]	cf. Capnodiales	Baltic amber	II

Sporidesmium-like fungus, conidial fungi	GZG.BST.27298 [2]	*Sporidesmium* (sensu lato)	Bitterfeld amber	III, IV
Sporidesmium-like fungus, Metacapnodiaceae, conidial fungi	GZG.BST.27294 [2]	*Sporidesmium* (sensu lato)	Bitterfeld amber	III, IV
Taeniolella-like fungus, conidial fungi	GZG.BST.27299 [2]	cf. *Taeniolella*	Bitterfeld amber	III, IV
Conidial fungi	GZG.BST.27293 [2]	Ascomycota	Bitterfeld amber	IV
Taeniolella-like fungus	Ri-49 [4]	cf. *Taeniolella*	Bitterfeld amber	IV
Taeniolella-like fungus	Le-91 [4]	cf. *Taeniolella*	Bitterfeld amber	IV
Conidial fungus	Ri-30 [4]	Ascomycota	Bitterfeld amber	IV
Metacapnodiaceae	Ri-35 [4]	Metacapnodiaceae	Baltic amber	IV
Conidial fungus	Ri-54 [4]	Ascomycota	Baltic amber	IV
Conidial fungus	Ri-51 [4]	Ascomycota	Baltic amber	IV

[1] Museum für Naturkunde zu Berlin (Germany)
[2] Geoscientific Collections of the Georg August University (Göttingen, Germany)
[3] Carsten Gröhn Amber Collection (Glinde, Germany)
[4] Heinrich Grabenhorst Amber Collection (Wienhausen, Germany)
[5] Jörg Wunderlich Amber Collection (Senckenberg Museum in Frankfurt am Main, Germany)
[6] Hoffeins Amber Collection (the specimens studied are now part of the Geoscientific Collections of the Georg August University)

METHODS

To remove the weathered crust and obtain a better view of the inclusions, the amber pieces were ground and polished manually with a series of wet silicon carbide papers (grit from the Federation of European Producers of Abrasives (FEPA), grain size P 600 – 4000 (25.8 µm to 5 µm particle size), Struers GmbH, Willich, Germany). After the investigations, most of the amber pieces were embedded in epoxy resin to ensure the preservation of the fossils.

The amber inclusions were first examined with a stereomicroscope (Carl Zeiss Stemi 508) to observe and document the macromorphological features of the fossil fungi. The micromorphology was examined under a compound microscope (Carl Zeiss AxioScope A1), using a drop of water and a cover glass on the amber specimen to minimize light scattering and reflections. The measurements were done under 20× and 40×objectives, often with additional 1.6× magnification resulting in 200- to 640-fold magnifications. If the fossil

consisted of just a few fungal structures, all available individuals were measured. In larger colonies, a sample of at least 10–20 individual objects was measured.

The specimens were imaged with a Canon 5D digital camera attached to the compound microscope. A software package Helicon Focus 5.0 was used to construct digitally stacked photomicrographic composites that consist of up to 70 individual focal planes. This technique was used in the illustrations of all four original articles of this thesis to better show the three-dimensional structures of the inclusions. In Article IV a field-emission scanning-electron microscope (Carl Zeiss LEO 1530 Gemini) was also used to confirm the identity of the lichen substrate.

4. MAIN RESULTS

In Article I we provided amended descriptions of the dematiaceous hyphomycete fossils that Robert Caspary originally assigned to the modern genus *Torula*. We discovered that the fungi were not assignable to this or any other extant genus, and they were placed in a new fossil genus *Casparyotorula*. In addition to *C. globulifera* and *C. heteromorpha*, the two species described by Caspary from Baltic amber, we described a third species, *C. arnoldii*, from Bitterfeld amber. Caspary's original specimens showed no indication of the substrate of these fungi, but we were able to locate a new specimen of *C. globulifera* growing on an angiosperm leaf. The other two species probably also shared a similar ecology. Fragmentary fossils of *Casparyotorula* are common in Baltic and Bitterfeld amber, which is probably explained by their epiphytic lifestyle and subsequent high preservation potential. We also discovered arthropod faecal pellets containing conidia of *C. heteromorpha*, which is clear evidence of fungivory in the European amber forests.

In Article II we re-examined the historical collection of fungi described and illustrated in Baltic amber by Caspary and Klebs (1907a, b). We reassessed the taxonomic affinities of the six remaining specimens and presented amended descriptions. Another seven of the original specimens have been lost, but we provided descriptions of new similar fossils from Baltic amber. Most of the historical specimens were impossible to assign with certainty to any modern fungal genus, and the remaining original type specimens did not represent the modern genera they had been assigned to. One of the specimens turned out to be a fossil *Calicium* (originally described as *Stilbum succini*), and one filamentous fungus was reassigned to the genus *Metacapnodium* (originally described as *Torula*). Based on the original description and illustration we were able to reassign *Gonatobotrys primigenia* to the genus *Gonatobotryum*. The fungus described as *Acremonium succineum* does not belong to this extant genus, but its systematic position remained uncertain. The specimen

described as *Fungites capillaris* was probably a filamentous prokaryote instead of a fungus. In addition to re-evaluating the historical specimens located we described several new specimens of microfungi in Baltic amber and discussed their ecologies. These included Trichopeltinaceae-like thalloid fungi, sooty mould ascomata, and a *Gonatobotryum*-like hyphomycete growing on a dwarf mistletoe. Trichopeltinaceae-like fungi or sooty mould ascomata have not been previously described in European ambers.

In Articles III and IV we described the first-ever discovered fossils of lichen-associated microfungi. Lichens have remained largely undetected in amber studies and are thus underrepresented in the fossil record. Previous to our studies, no fossils of microfungi associated with lichens had been found. We described several morphologies growing on lichens or lichen remains preserved in Baltic and Bitterfeld ambers. These included fossil hyphomycetes that closely resemble some species of the extant genera *Sporidesmium* and *Taeniolella*. While both genera include some extant species that have been reported growing on lichens, we do not believe that the fossils represent obligate lichenicolous fungi. We rather interpret the fungi as opportunistic saprotrophs or parasites that probably exploited a variety of substrates and were also able to grow on dead or dying lichen thalli.

5. DISCUSSION AND CONCLUSIONS

All the fungal fossils addressed in this thesis were undoubtedly genuine Palaeogene fungi and not younger contaminants – modern microorganisms can sometimes grow inside amber specimens, which can lead to false interpretations (Girard et al. 2008, Beimforde & Schmidt 2011). Before polishing, the fossils were embedded deep in the amber matrix, and there were no signs of fungal hyphae growing from the surface into the amber. Some of the fossils (I) had preserved conidia that had germinated after being embedded in liquid resin, and such germinating conidia were invariably fully enclosed by amber.

Amber specimens provide unique opportunities to study the growth habit and 3D structures of minute fossil fungi. In many cases we were able to observe structural details of conidiophores and the septation of conidia and sometimes several developmental stages of conidia were visible in the amber fossils (I). Such features could usually only be seen if the conidia were preserved in large numbers, and many of the fossils were comprised of only a few preserved colonies or individual conidiophores. Species of *Casparyotorula* usually are present in the amber specimens as numerous fragments of conidial chains and hyphae, which made it possible to document intricate features of conidiogenesis. This was especially the case in the holotype specimen of *C. arnoldii*, in which the pull of the resin flow revealed the breakage points in the

conidial chains, which made it easier to observe the formation of the conidia in this fungus.

The majority of fossils studied represented anamorphic states of various ascomycete lineages. All of the fungi grew most likely in close proximity to resin-producing conifer trees, either on the bark or on epiphytic lichens, while others grew on stems, leaves or fruits of neighbouring angiosperms. Some of the fungi most likely were able to grow on solid or solidifying resin, which significantly increased their chances of being preserved as amber inclusions. For example, many detached conidia of *Casparyotorula heteromorpha* germinated after first being trapped in liquid resin (I). The apical cells of some hyphae also started to produce new conidial initials, and often such conidia and hyphae were moved and reorganized by the resin flow before it solidified. The germination of conidia clearly indicates that *C. heteromorpha* had tolerance for resin compounds that prevent the growth of many other micro-organisms (Langenheim 2003). *Casparyotorula* species likely grew as dense epiphyllous and corticolous colonies that were grazed by small arthropods such as mites.

In addition to resin, lichen thalli are also often challenging substrates for micro-organisms, due to the presence of different types of lichen compounds that can inhibit the growth of bacteria and fungi (e.g. Lawrey 1986, Halama & Van Haluwyn 2004). Some fungi have evolved to tolerate lichen compounds, and our findings demonstrated that lichen thalli have provided a habitat for several different types of microfungi, at least since the Palaeogene (III, IV). Considering the long evolutionary history of lichens, the associations between lichen-forming fungi and the microfungi growing on lichen surfaces likely evolved much earlier, but our findings represent the first concrete evidence of such interactions.

Sooty moulds of the family Metacapnodiaceae are common in European Palaeogene ambers, and we found several specimens growing on plant leaves and lichen thalli. These fungi use as their nutrition source honeydew that is excreted by sap-feeding insects such as scale insects and aphids. Since these fungi are able to grow on various surfaces as long as there is honeydew present, they are very likely candidates for preservation in amber. In our study, we discovered clear growth patterns, because sooty mould hyphae were commonly found growing in small valleys or cavities between leaves. These were areas in which honeydew most likely accumulated (II). In the canopy the epiphytic fungi are exposed to UV-radiation, and the lack of available water can limit the growth of colonies. The presence of sooty moulds and other epiphytic fungi indicate humid conditions in the 'Baltic amber forest'.

Well-preserved, reliably identifiable fossils can provide a minimum age for the divergence time of a specific lineage, which can then be used in molecular systematics for dating phylogenetic trees (Padovan et al. 2005, Taylor & Berbee 2006, Beimforde et al. 2014, Liu et al. 2017). Many of the historical specimens studied in Articles I and II were originally assigned to modern fungal genera. Our results indicate that none of them actually belong to the

modern genera they were originally assigned to, and in most cases the many uncertainties regarding phylogenetic position do not allow them to be used for dating phylogenies. Only two fossils (*Calicium*, *Metacapnodium*) were unequivocally identifiable to modern genera (II). Since identifying hyphomycetes is often difficult, we have been cautious and avoided naming fossil fungi that do not show all the characters necessary for reliable identification. Such fossil names could easily be misinterpreted as solid evidence and used as false calibration points, which would lead to unreliable phylogenetic trees (Rutschmann et al. 2007, Forest 2009, Beimforde et al. 2014, Kaasalainen et al. 2015). For example, a presumed lichen fossil originally described as *Alectoria succini* was used as an age constraint for the genus *Alectoria* in phylogenetic studies (Amo de Paz et al. 2011, Prieto & Wedin 2013), but subsequent analysis revealed that the fossil was in fact a decomposed plant part rather than a lichen (Kaasalainen et al. 2015). If possible, all fossil specimens, especially those from historical collections, should be re-investigated before using them in phylogenetic studies.

In addition to the challenges concerning the identification of fossil hyphomycetes, the naming of anamorphic fossil fungi is also often difficult, because the delimitations of extant species are not clear. For example, over 400 species of hyphomycetes have been assigned to the genus *Torula*, but the vast majority of these species are not related to the type species *T. herbarum* (I). Many other genera, such as *Sporidesmium* and *Taeniolella* are also highly polyphyletic (III, IV). Many of the fossils described and illustrated in this thesis are morphologically almost identical to some species in modern genera, but convergent evolution in unrelated lineages may well have resulted in similar morphologies. Keeping this in mind, we mainly refrained from making formal assignments to specific genera. This helps to avoid the controversies that would almost certainly arise from the hasty use of such fossils as minimum age constraints for dating phylogenies.

Despite the many practical problems involved in the study and accurate identification of fossil microorganisms, it is clearly worthwhile to document and study their diversity, palaeoecology and evolutionary history. Information on ancient microbial life is crucial to achieving a more complete picture of ancient ecosystems. For example, very little is known so far about the possible effects of global extinction events on microfungi and bacteria (Girard & Adl 2011). The European Palaeogene amber forests housed diverse communities of microfungi that represented several morphologies and ecologies, and my thesis demonstrates that careful reanalysis of historical amber specimens can provide valuable new information and give fresh insights into the systematic affinities of fossil fungi.

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