

Chapter 22

Morphological Convergence in Forest Microfungi Provides a Proxy for Paleogene Forest Structure

Jouko Rikkinen and Alexander R. Schmidt

1. INTRODUCTION

Amber, fossilized plant resin from gymnosperms and angiosperms, is renowned for preserving a wide range of organisms in microscopic fidelity. These so-called amber inclusions comprise many groups of organisms, ranging from bacteria to arthropods and vertebrates (Penney, 2010; Ragazzi and Schmidt, 2011; Grimaldi and Ross, 2017). Organisms trapped in amber typically derive from forest ecosystems where they became stuck to resin outpourings in their habitats (Seyfullah and Schmidt, 2015). In addition, ambers are prime examples of chemical fossils that are relatively resistant to diagenesis and can retain their original chemical and isotopic compositions. Therefore, chemical profiles of ambers may support the detection of the resin-bearing plants and the reconstruction of the paleoenvironment and paleoclimate (Langenheim, 2003; Dal Corso et al., 2017). The study of amber and its inclusions should consequently enable the reconstruction of past forest ecosystems and even prevailing climatic conditions.

However, several constraints exist for this approach. Much amber from the hundreds of worldwide localities does not contain notable inclusions or predominantly preserved arthropods, prokaryotes, and fungal mycelia (Martinez-Delclòs et al., 2004; Labandeira, 2014). Arthropods are indeed the most commonly studied amber inclusions, whereas fossil plant remains and palynomorphs, on which reconstructions of Cenozoic forests and derived climate estimates are typically based on (Ferguson et al., 1998; Bruch and Mosbrugger, 2002; Kunzmann and Walther, 2012), are relatively rare in amber. Only six worldwide amber deposits harbor plenty of plant inclusions, so far: Miocene Dominican and Mexican ambers, Paleogene Baltic, Bitterfeld, and Rovno ambers, and mid-Cretaceous Burmese amber (Penney, 2010).

Further hurdles are linked to the physical properties of amber. Once reworked from the original sediment, amber may float or drift in sea water, and the notion exists that even amber specimens forming large deposits may have been reworked and transported, originally belonging to older and possibly geographically distinct sediments (Weitschat and Wichard, 2010).

Baltic and Bitterfeld ambers constitute the largest Paleogene amber deposits worldwide, with estimated 640,000 tons of fossil resin for the Baltic deposit (Weitschat and Wichard, 2010) and approximately 3000 tons for the central German Bitterfeld locality (Liehmann, 2013). Hundreds of thousands of inclusions were found in Baltic amber, with >3000 species described from Baltic amber (Weitschat and Wichard, 2010) and >700 species reported from Bitterfeld amber (Rappsilber, 2016).

Uncertainties regarding botanical provenance, age, and geographical origin are particularly associated with these two amber deposits. Langenheim (2003) introduced the term “Tertiary Baltic Amber Mystery” to refer to the conflicting evidence about the botanical source of succinite, which is the main resin variety of Baltic

and Bitterfeld amber. Suggested source plants of succinite include representatives of the Araucariaceae, Cupressaceae, Pinaceae, and Sciadopityaceae (Langenheim, 2003; Yamamoto et al., 2006; Wolfe et al., 2009; Seyfullah et al., 2018).

Baltic amber primarily derives from the marine Blue Earth layer that is predominantly exposed on the Samland Peninsula northwest of Kaliningrad (Russia) and contiguous areas. Baltic amber eroded from sediments is also frequently found washed ashore along the coast of the Baltic Sea, particularly on the Samland Peninsula and in the Baltic States, Poland, Denmark, Germany, and southern Sweden (Standke, 2008; Weitschat and Wichard, 2010). The absolute age of Baltic amber is still under debate. Palynological data suggest an upper Eocene (Priabonian) age (c. 38e34 million years) of the Blue Earth (Kosmowska-Ceranowicz et al., 1997; Standke, 1998, 2008). Fewer amounts of amber also occur in Lutetian (middle Eocene) sediments including the Lower Blue Earth and even in the upper Oligocene Lower Gestreifter Sand, leading to a possible age range of approximately 47e 24 million years before present for all Baltic amber-bearing strata (Kosmowska-Ceranowicz et al., 1997; Standke, 1998, 2008; Kasinski and Kramarska, 2008).

The frequently cited Lutetian age of the Blue Earth was originally suggested by Ritzkowski (1997), who dated glauconites from the amber-bearing layer. However, Clauer et al. (2005) showed that the applied dating methods can lead to older age estimates if the glauconites have been reworked or if nonglauconized detrital mica contaminated the glauconite splits. Redeposition of the Baltic amber into the Blue Earth layer has also been suggested (Weitschat and Wichard, 2010). However, typical signs of erosion which normally occur if amber has been reworked, such as “pebble-shaped” amber pieces or a dark oxidized crust, are absent in the material from the Blue Earth layer. The majority of amber from the Blue Earth is rather of a fresh lemon yellow color and unoxidized (Grimaldi and Ross, 2017). Bitterfeld amber derives from the Goitzsche open cast mine near the city of Bitterfeld in central Germany where it was mined from the 1970s to the 1990s (Liehmann, 2013). The amber-bearing sediment of this locality is the Bernsteinschluff Horizon, located in the upper part of the Cottbus Formation, and it has been dated as upper Oligocene with an absolute age of 25.3–23.8 million years (Knuth et al., 2002; Blumenstengel, 2004). A notion that Bitterfeld amber represents redeposited Eocene Baltic amber is based on the significant proportion of identical arthropod morphologies in amber from both localities (Weitschat, 1997). However, redeposition of Baltic amber is unlikely based on the reconstruction of the sedimentary environment of this amber deposit (Standke, 2008). In addition, chemical differences have been detected between Baltic and Bitterfeld succinite (Yamamoto et al., 2006; Vávra, 2008), and more additional resin types occur in the Bitterfeld area, compared with the Baltic region (Kosmowska-Ceranowicz and Vávra, 2015), which makes an identical provenance unlikely. A local reworking of pre- Chattian amber, however, has not been dispelled so far (see Dunlop, 2010 and Wolfe et al., 2016, for discussion). In any case, Bitterfeld amber is Paleogene in age and its minimum age is approximately 24 million years.

Given these uncertainties, assumptions about forest composition, forest structure and climate of the source area of these ambers vary considerably, depending on the assumed age, origin and source plants (Sadowski et al., 2017). The search for amber inclusions that are indicative for certain forest types and forest structures is a logical consequence (Kaasalainen et al., 2017; Sadowski et al., 2017).

Inclusions of filamentous fungi are common in amber from many deposits around the world (Beimforde and Schmidt, 2011). However, in most cases, only vegetative mycelia are preserved without any reproductive

structures. As the accurate taxonomic assignment of such specimens is usually impossible, relatively few amber-preserved fungal fossils have so far been assigned to extant lineages (Beimforde et al., 2014; Kettunen et al., 2015, 2018). However, recent studies have demonstrated that European Paleogene amber is a valuable source of fossils in some taxonomic and ecological groups within the Ascomycota. Such findings have already provided valuable new insights into the diversity and evolutionary history of sooty molds (Schmidt et al., 2014), lichen-symbiotic and lichen-associated fungi (Hartl et al., 2015; Kaasalainen et al., 2015, 2017; Kettunen et al., 2016, 2017), and calicioid lichens and fungi (Rikkinen and Poinar, 2000; Rikkinen, 2003b; Tuovila et al., 2013; Rikkinen et al., 2018).

Calicioid lichens and fungi, which are from now on referred to as “calicioids,” constitute a diverse group of tiny ascomycetes with superficially similar, usually well-stalked ascomata and which often accumulate mature ascospores on top of the apothecial disk to form a true mazaedium (Plates I, II, and III). Because the ascospores of most calicioids are dark, the mazaedium stains the finger if touched. The Finnish term for calicioids (*nokinuppinen*) is a diminutive of “smut-knob,” which accurately describes the smearing property of the persisting spore mass. Calicioids include both lichen-symbiotic, parasitic and saprotrophic species and include genera from several classes of Ascomycota. The polyphyletic nature of the group was first demonstrated by Tibell (1984) on morphological grounds and has since been confirmed in many molecular studies (Wedin and Tibell, 1997; Tibell and Wedin, 2000; Wedin et al., 2000, 2002; Tibell, 2003; Hibbett et al., 2007; Prieto et al., 2013; Prieto and Wedin, 2013, 2017; Beimforde et al., 2014; van den Broeck et al., 2017). Traditionally, *Sphaerophorus* Pers. and some other genera of fruticose macrolichens with mazaediate apothecia also were included in “calicioid lichens.” However, as their morphology, size, and ecology differ drastically from those of crustose species, they are not discussed further here.

The aim of this study is to use all available information on the morphology and ecology of extant calicioids to reconstruct the substrate and habitat ecology of known fossil calicioids and then to use this information to open new insights into the stand structure and ecological conditions of European Paleogene amber forests. First, we introduce the morphology of extant calicioids and demonstrate that their structural features are intimately linked to habitat ecology and are instrumental for successful dispersal; we also explain the conspicuous morphological convergence between phylogenetically distant calicioid fungi. Then, we show that the adaptive traits of calicioids have not changed since at least the Eocene, and argue that their fundamental niches also have remained unchanged. Finally, we summarize what the diversity and relative abundance of fossil calicioids in amber tells us about the ecological conditions that once prevailed in European amber forests.

2. MORPHOLOGY, DISTRIBUTION, AND ECOLOGY OF EXTANT CALICIOIDS

2.1 Morphology and Anatomy

Most nonlichenized calicioids have immersed mycelia and produce ascomata only on the surface of their substrate. While the vegetative thalli of some calicioid lichens also are endosubstratic, most of them produce episubstratic crustose thalli (Plate I). Depending on the species, the thallus can be smooth, squamulose,

verrucose, granular, or farinaceous, and in some species, the structure of the thallus is partly determined by growth conditions.

The most conspicuous features of calicioids are the upright ascomata, which are invariably produced on the substrate surface (Plates I, II, and III). The size and shape of ascomata vary between different genera and species as can be expected in light of the highly polyphyletic nature of the group. In several genera, the ascomata are always stalked, while in others, they can be either stalked or sessile or always sessile. Even when mature, the ascomata are small, typically <1.2 mm high, and sometimes tiny, only 0.1–0.3 mm high. The stalks of some resinicolous species can rarely elongate to 20 mm or even more, and in many cases the stalk length is quite variable and partly dependent on the environment (Yahr, 2015). The outermost stalk hyphae of all extant *Chaenotheca* (Th. Fr.) Th. Fr. (Coniocybaceae, Coniocybomycetes) and *Phaeocalicium* A.F.W. Schmidt (Mycocaliciaceae, Eurotiomycetes) are periclinally arranged, while those of *Calicium* Pers. (Caliciaceae, Lecanoromycetes) and *Chaenothecopsis* Vain. (Mycocaliciaceae, Eurotiomycetes) are irregularly arranged. The excipulum surface is usually formed by isodiametric cells in *Calicium*, while those of *Chaenotheca*, *Chaenothecopsis*, and *Phaeocalicium* typically consist of elongated cells (Tibell, 1984, 1999).

When mature, most calicioids have open apothecial disks covered by a layer of ascospores forming a true mazaedium. The spore mass sticks together remarkably well and can in some species protrude as a column easily two or three times longer than the width of the capitulum. A true mazaedium is defined to consist of both ascospores and sterile elements, which together form a powdery but cohesive mass. The ascospores are released “passively” through disintegrating ascus walls and continue to mature in the mazaedium. This feature (prototunicate ascus) is unusual among Ascomycota and has evolved independently in several different lineages from ancestors with apical dehiscence apparatus (Wedin and Tibell, 1997; Wedin et al., 2000; Prieto et al., 2013).

The mazaedium is black in *Calicium* (Plate II, 1 and 2) and medium to dark brown in *Chaenotheca* (Plate II, 3 and 4), with the color being largely determined by the surface color of mature ascospores. The ascospores of most *Chaenotheca* species are nonseptate and essentially spherical, while those of *Calicium* are one-septate. The often very rough surface ornamentation of ascospores, together with sclerotized paraphyses and refuse matter, helps to keep the spore mass intact, and some force is typically needed to remove spores from the mazaedium.

The ascospores of *Chaenothecopsis*, *Phaeocalicium*, and other Mycocaliciales are discharged through the ascus apex and do not form a true mazaedium (Plate II, 5 and 6). However, some species in these genera effectively accumulate a layer of ascospores on their apothecial surfaces. In such fungi, the paraphysis tips can form a more or less solid epithecium and the ascospores discharged are released through pores in this structure. Often the released ascospores stick together due to amorphous substances (Schmidt, 1970; Tibell, 1984; Rikkinen, 2003c; Tuovila, 2013).

Ascomata of many *Calicium* and *Chaenotheca* lichens have crystallized secondary metabolites forming a distinct ring along the excipulum margin and sometimes also covering the lower side of the capitulum (Plates II, 1,3 and III, 1,2). Especially on young ascomata, the pruina can also extend to the stalk, and in some species, the stalk remains distinctly pruinose even when mature. The pruina can consist of various substances including anthraquinones or vulpinic acid, and some *Calicium* and *Chaenotheca* species also accumulate the same or related compounds in their thalli (Plate II, 1,3). The characteristic ring of pruina might simply reflect high metabolic activity in the maturing capitulum and the resulting discharge of waste products on the excipulum

surface. However, the conspicuous accumulation of specific metabolites in highly specific locations does not really support this simple explanation. Vulpinic acid and anthraquinones have antimicrobial and antiherbivore qualities and they might thus give protection against grazing invertebrates (Asplund and Wardle, 2013; Nguyen et al., 2013; Gaya et al., 2015). Still, even more likely is that these hydrophobic substances help to keep the mazaedium dry. A hydrophobic pruina on the excipulum edge effectively helps to remove all water droplets from the mazaedial surface, which itself is distinctly hydrophobic. This function promotes mazaedial integrity and thus is consistent with the spore-saving strategy of calicioid mazaedia (Rikkinen, 1995).

Most calicioid lichens have ascospores with strongly thickened and darkly pigmented walls. The melanin pigments in the spore wall protect ascospores in the mazaedium from ultraviolet radiation, this again being constituent with the spore-saving strategy. The typical spore wall ornamentation of different genera is achieved via different ontogenetic processes as summarized in Tibell (1984). In *Chaenotheca*, the primary wall of the ascospore increases in thickness and its outer surface is finally ruptured by irregular cracks. The resulting ornamentation ranges from weak to very coarse in some species. In *Calicium* a secondary wall is deposited beneath the primary wall. The secondary wall increases in thickness and finally forms the bulk of the spore wall, with the ruptured primary wall forming the surface ornamentation. The spore walls of most *Chaenothecopsis* and *Phaeocalicium* species are not very strongly thickened. The spore wall is typically pale or lightly pigmented, and any surface ornamentation, if present, is formed by internal irregularities in the outer layer of the spore wall (Tibell, 1975, 1980, 1984).

The mycobionts of calicioid lichens establish symbiotic associations with green algae (Raths, 1938; Tschermak- Woess, 1978a; Tibell, 1984, 1999). The diversity of photobionts is high but as yet poorly known. For example, different species of *Chaenotheca* are known to associate with species of *Symbiochloris* Skaloud, Friedl, A. Beck et Dal Grande, *Trebouxia* Puymaly or *Stichococcus* Nägeli (Microthamniales), or *Trentepohlia* Martius (Trentepohliales). Each fungal species is believed to usually associate with only one photobiont genus, but levels of specificity have as yet hardly been studied with modern methods (Tibell, 2001; Tibell and Beck, 2002; López-Bautista et al., 2006; Hodac et al., 2016; Skaloud et al., 2016).

Several calicioid fungi produce coelomycetous and/or hypomycetous conidial states in culture, and in some cases such anamorphs can even be recognized in the field. The ecological role of the anamorphs is poorly understood, but they may function in reproduction or dispersal or both. They might play a role in the establishment of biotic associations in lichen-symbiotic and parasitic species, and it is possible that some species can survive as saprotrophes or commensals before entering into more specific relationships with optimal photobionts or hosts (Bonar, 1971; Vobis, 1980; Hawksworth, 1981; Samuels and Buchanan, 1983; Honegger, 1985; Tibell, 1990, 1991b, 1993, 1997; Tibell and Constantinescu, 1991; Beimforde et al., 2017b).

2.2 Distribution

The vast majority of extant calicioids live in forests, share similar habitat requirements, and can form characteristic communities in specific types of microhabitats (e.g., Tibell, 1999; Titov, 2006; Rikkinen, 2003a; Selva, 2013). For example, epiphyte communities rich in calicioid species are remarkably similar in composition

over the entire circumpolar belt of boreal coniferous forests and adjoining areas of temperate coniferous-deciduous forests (Tibell, 1975, 1980, 1999; Peterson and Rikkinen, 2003; Titov, 2000, 2001, 2006; Rikkinen, 2003a; Selva, 2010, 2013, 2014). A number of calicioid species have bipolar distributions and thus also occur in temperate forests of the southern hemisphere (Tibell, 1987, 1994, 1998). Some species extend their range into subtropical and tropical regions, where they typically occur at high altitudes and occupy zones corresponding to their latitudinal range (Tibell, 1981b, 1982, 1984, 1996a, 2006; Sparrius et al., 2002; Tibell and Thor, 2003; Thor et al., 2008; Tibell and Frisch, 2010). In addition to widely distributed taxa, many regional endemics also exist (Tibell, 1994; Titov, 2006). One problem presently hindering the accurate evaluation of calicioid distributions is that the species delimitations of very few widely distributed taxa have as yet been studied with the use of DNA methods (Tibell, 2001, 2002, 2006; Vinuesa et al., 2001; Tibell and Beck, 2002; Tibell and Vinuesa, 2005; Yahr, 2015).

The macroclimatic optima of many boreal and temperate calicioids seem to be in subcontinental regions, and a number of widely distributed *Chaenotheca* species, for example, are rare in the most oceanic sections of northwestern Europe and western North America (Tibell, 1980; Middelborg and Mattsson, 1987; Rikkinen, 2003a). This may more reflect the lack of suitable substrate than the climate per se. In temperate rainforests, the calicioids, which depend on hard lignum, can be in short supply of suitable substrate as dead tree trunks tend to decompose rapidly and the lignum formed is soft and very rapidly overgrown by bryophytes. Also, mollusk grazing can be a major threat. This may explain why many lignicolous calicioids are most commonly found in slightly continental and indifferent sections of the boreal zone and in corresponding altitudinal belts in mountain regions of the temperate zone.

2.3 Ecology

Despite their wide ranges, individual calicioid species often occur only in rather restricted and specialized microhabitats. Most species grow on either bark or hard lignum and are found on basal tree trunks in temperate and boreal forests (Middelborg and Mattsson, 1987; Tibell, 1992; Selva, 1994, 2003, 2013, 2014; Rikkinen, 1995, 2003a; Holien, 1996, 1998; Titov, 1998, 2000, 2001; Titov et al., 2004; McMullin and Arsenault, 2016). Others are substrate specialists that only grow on resinous exudates of conifers (Bonar, 1971; Titov and Tibell, 1993, 1999; Rikkinen, 1999, 2003c,d; Tuovila et al., 2013, 2014; Rikkinen et al., 2014, 2016; Selva and Tuovila, 2016) or angiosperms (Tibell and Titov, 1995; Selva and Tibell, 1999; Tuovila et al., 2011a, 2014; Tuovila, 2013; Beimforde et al., 2017b), on thalli of calicioid or other lichens (Hawksworth, 1978; Löfgren and Tibell, 1979; Tibell and Ryman, 1995; Titov, 2006), on basiomata of polyporoid fungi (Hawksworth, 1980; Tibell, 1981a; Hutchison, 1987; Muñiz et al., 2013; Hawksworth et al., 2014; Allen and McMullin, 2015; Suija et al., 2015), on leafy liverworts (Øvstedal and Vevle, 1967; Döbbeler and Feuerer, 2004), and even on bark or thin twigs of woody plants (Tibell, 1991a, 1996b; Kalb and Hafellner, 1992; Titov, 1994; Peterson and Rikkinen, 1998; Berglund et al., 2004). The range of nutritional ecologies is concurrently wide as the group includes both lichensymbiotic, parasitic and saprotrophic species (Tschermak- Woess, 1978b, 1980; Lücking et al., 2017).

While saprotrophic and parasitic calicioids are obviously restricted to their particular hosts, the substrate requirements of calicioid lichens are somewhat wider. Many bark-inhabiting species grow on the basal trunks of conifers or deciduous trees, especially old and slow-growing trunks. They frequently grow on the rough edges of bark fissures, but under favorable conditions, they also extend onto smooth bark and can sometimes cover large surfaces. With respect to substrate chemistry, most species are clearly acidiphytic and anitrophytic, which gives them an advantage in competition for space against some rapidly growing macrolichens. Species-specific differences in substrate preferences are seen as clear difference in calicioid community composition between different tree species (Räsänen, 1927; Koskinen, 1955; Halonen, 1990; Halonen et al., 1991; Hyvärinen et al., 1992; Rikkinen, 2003a; Bäcklund et al., 2016; Hardman et al., 2017).

Some calicioids only grow on standing hard lignum, which represents a characteristic and often abundant substrate type in many natural boreal and temperate forests (Löhmus and Löhmus, 2001; Niemelä et al., 2002; Nascimbene et al., 2008; Spribille et al., 2008; Svensson et al., 2016; Santaniello et al., 2017). Calicioids can grow on either bark or lignum or both, and the degree of preference varies between different taxa. Some species that regularly grow on hard old lignum can also colonize old log buildings, fence posts, and other worked wood (Areskoug and Thor, 2005; Svensson et al., 2005; Petersen et al., 2017). Patches of exposed lignum on scarred trees provide enough substrate for numerous lignum-inhabiting calicioids, and even the deep scars left by woodpeckers can offer an ideal microhabitat for some species (Plate IV, 1). The basiomata of polypores represent yet another unusual substrate and microhabitat type exploited by some specialized calicioids (Hawksworth et al., 2014; Allen and McMullin, 2015; Suija et al., 2015).

The microclimatic conditions prevailing within a forest stand, which are often closely correlated with successional age, are more important determinants of calicioid species richness than any single macroclimatic parameter (Tibell, 1992; Selva, 1994, 2003; Rikkinen, 1995, 2003a; Löhmus and Löhmus, 2011; Dymytrova et al., 2016). A number of calicioid species are restricted to mature and old-growth forests, these being rich in appropriate substrates and having a favorable forest microclimate. Some calicioid species, among other epiphytic lichens, have been successfully used as indicators for identifying forest stands with long habitat continuity and subsequently high conservation value (Tibell, 1992; Kuusinen and Siitonen, 1998; Selva, 2002, 2003; Ranius et al., 2008). However, the specific reasons for the old-growth dependence can vary between different forest types and regions (McMullin et al., 2008; Berglund et al., 2009; Nascimbene et al., 2010; Löhmus and Löhmus, 2011; Löhmus et al., 2007, 2012; Marmor et al., 2013; Lättman et al., 2014; Selva, 2016) and between different groups of lichen epiphytes (Johansson, 2008; Rheault et al., 2009; Hauck, 2011; Ellis, 2012; Hauck et al., 2013; Nascimbene et al., 2013).

While not all reasons for the old-growth dependence calicioids are necessarily known, both substrate factors and high air humidity are clearly important for explaining the habitat preferences of many old-growth associated species; in addition, light conditions are important for lichensymbiotic species. Some calicioids grow only in deeply shaded microhabitats that are also well protected from rain but promote a high and constant atmospheric humidity. For example, some *Chaenotheca* species grow in deep trunk crevices and root overhangs that are dimly lit and well protected from rain. Such species also occur on humus in rock crevices and caves, especially under north-facing cliff overhangs, again in microhabitats that retain high atmospheric humidity throughout the year.

Barkman (1958) noted that some calicioid lichens were found only from the northern edges of forests bordering marshes, bogs, and riparian habitats and at the southwestern edges of forest glades, where they typically grew on the northeastern sides of mature tree trunks. Also, James et al. (1977) noted that these species mainly grew on the northeastern sides of deciduous trees. As explained in detail by Rikkinen (1995), the calicioid lichens that grow on northfacing surfaces of tree trunks at the northern edges of woods bordering forest glades very frequently experience “open shade” conditions. The remarkably cool microclimate of such sites is caused by the radiation conditions that regularly develop in the close vicinity of open vertical north-facing surfaces where there is a constant outgoing flux of long-wave radiation to the open sky and only diffuse radiation from the northern sky can compensate for the heat loss. The surface temperatures of epiphytic lichens in such open shade habitats often remain considerably below air temperature, while the lichens still receive considerable amounts of diffuse light, which is relatively rich in blue wavelengths. In suitable environments of the boreal and temperate zones, the open shade effect can be experienced at any time of the year, but such conditions are only rarely experienced in oceanic regions with cloudy and foggy climates. During the winter, the open shade effect is more pronounced and, because of the low elevations of the sun, more extended as well. It is especially characteristic for areas where areas of low vegetation occur among taller canopies. Also, small forest glades are typical open shade environments and often remain relatively cool and moist for most of the day.

During the winter season, open shade conditions are experienced in a range of sites that would be characterized as deeply shaded in the summer. Light reflection from snow may be very important for calicioid lichens at such sites, on the condition that they can photosynthesize at low temperatures. Many calicioid lichens grow on the basal trunks of trees, on slanting tree trunks, and on the undersides of overhanging logs and branches. In these microhabitats, light intensity is typically low in the summer but can be high at times in late winter and early spring due to intense light reflection from snow. Such calicioid-rich microhabitats can thus be described as distinctly cheimophotophytic. There is evidence that both symbionts of some boreal and temperate calicioid lichens are able to grow under low temperatures and that the photobionts of some temperate and tropical species may be relatively susceptible to frost (Tschermak-Woess, 1984, 1989; Nash et al., 1987; Tibell, 1991b; Rikkinen, 1995, 2003a; Marini et al., 2011).

As a whole, there is ample evidence that many boreal and temperate calicioid lichens benefit from open shade conditions. This influences their habitat selection and distribution on many spatial scales. On individual tree trunks, they prefer expositions where open shade conditions are most likely to occur. Also, within individual forests, they show a preference for similar locations and thus directly benefit from the structural variability of old-growth stands, which offer a wide range of microhabitats that combine favorable light conditions with high atmospheric humidity. On wider geographical scales, calicioid communities tend to be most diverse and abundant in regions where macroclimate favors the development of open shade conditions (Rikkinen, 1995, 2003a). Forest-inhabiting calicioids suffer from major disturbances, such as forest fires, but clearly benefit from small and medium scale disturbances, such as isolated treefalls and limited insect outbreaks. Moderate disturbances can promote calicioid diversity both by increasing substrate availability for lignum-dependent species and by improving light conditions within the lower canopy, without still jeopardizing the humid forest microclimate. Differences in disturbance history are likely to explain many patterns in calicioid diversity both on

the landscape level and even between adjacent forest stands (Rikkinen, 1995, 2003a; Lõhmus et al., 2007, 2012; Lõhmus and Lõhmus, 2011; Vehkaoja et al., 2017).

Tibell (1994) found that calicioid species with wide distributions have significantly smaller ascospores than do those with more restricted distributions. The obvious explanation would be that long-range dispersal by wind is more likely for species with small spores. While wind undoubtedly plays a central role in the dispersal of many calicioid species, there is growing evidence that dispersal by wood-inhabiting insects and other animals may be more important for others. Invertebrates crawling over calicioid ascomata can easily act as vectors that transport the ascospores directly into new habitats (Plate III, 3). Many woodboring insects have similar habitat requirements to those of calicioid species and can easily come into contact with the staining mazaedia. Some such insects are strong fliers and can transport ascospores over long distances directly into specific new microhabitats. Also, woodpeckers and other birds and even some mammals are likely to promote the dispersal of some calicioid species (Rikkinen, 1995, 2003a; Tuovila et al., 2011b; Messuti et al., 2012; Rikkinen et al., 2016; Beimforde et al., 2017a).

3. FOSSIL CALICIOIDS PRESERVED IN AMBER

Many extant resinicolous species regularly colonize semisolid resin and produce their ascomata on hardened resin or resin-impregnated wood and bark (Plate IV). Also, some calicioid lichens frequently grow in or around resinproducing cankers and sometimes produce ascomata on hardened resin (Plate V). Because their ascomata are tiny, they are easily engulfed by subsequent flows of fresh exudate and are then fossilized if the resin turns into amber (Plates V, VI, VII, and VIII). Due to all these characteristics, the overall prospects for finding fossil calicioids in amber are good.

Indeed, no fewer than six specimens of resinicolous *Chaenothecopsis* have been found from Baltic and Bitterfeld ambers (Rikkinen and Poinar, 2000; Tuovila et al., 2013; Rikkinen et al., 2018). Also, three specimens of *Calicium*, five fossil specimens of *Chaenotheca*, and one specimen of *Phaeocalicium* have so far been found (Rikkinen, 2003b; Kaasalainen et al., 2017; Kettunen et al., 2018; Rikkinen et al., 2018). Some of these fossils have since been used as minimum age constraints for dating phylogenies of Ascomycota (Prieto and Wedin, 2013, 2017; Beimforde et al., 2014).

The first fossil of *Chaenothecopsis* was found from Bitterfeld amber and described as *Chaenothecopsis bitterfeldensis* by Rikkinen and Poinar (2000). The ascomata of the type specimen represent different developmental stages from small initials to mature ascomata, some with a well developed spore mass on top of the capitulum. The preservation of ascospores is excellent, and as some of the spores had germinated before preservation, they reveal different stages of development from germ tube formation to hyphal elongation. The ascomata arise from a superficial hyphal mat, but also the original resin substrate is infested with hyphae, often with irregularly thickened hyphal walls and spirally twisted regions (Plate VI).

In its overall morphology and anatomical details, *Chaenothecopsis bitterfeldensis* closely resembles some extant resinicolous species of the genus. Apart from being slightly larger, the ascospores of the fossil are identical to extant taxa of *Chaenothecopsis* Group D (Tuovila et al., 2014). While there is some variation in the size and

shape of ascomata in the five other *Chaenothecopsis* fossils found from European amber, also all of them are very similar to *C. bitterfeldensis* and to each other, and most probably all represent the same lineage. The full range of morphological variation revealed by the six fossils is comparable to that of extant species, and scanning electron microscopic images of fragmented ascospores isolated from two of the fossils demonstrate that even ultrastructural details of spores are identical to those of extant species (Rikkinen et al., 2018).

The first fossil of a calicioid lichen from Baltic amber was described by Robert Caspary in 1886 as *Stilbum succini* and recently transferred to the genus *Calicium* in Kettunen et al. (2018). The ascospores of this fossil are similar to those of another *Calicium* specimen recently found from Bitterfeld amber, which also revealed many details in ascospore ultrastructure (Rikkinen et al., 2018). The preserved features of the two fossils correspond with those of extant species in *Calicium* Clade A (Prieto and Wedin, 2017). A third *Calicium* specimen from Baltic amber does not belong to the same clade but cannot be safely assigned to any one extant group because species of two extant lineages produce comparable ascomata and similar ascospores (Rikkinen et al., 2018).

In addition, four of the five *Chaenotheca* fossils from European amber are very similar to their extant relatives. The first fossil specimen (Plate VII, 1) was reported by Rikkinen (2003b) as *Chaenotheca* sp. and the others were described in Rikkinen et al. (2018) and found to represent one or possibly two additional species. However, many extant *Chaenotheca* species are notoriously plastic and their accurate identification requires examination of ascus and photobiont characteristics that cannot be seen in the fossils. Furthermore, as intrageneric relationships within *Chaenotheca* have not yet been comprehensively analyzed with DNA methods, the *Chaenotheca* fossils cannot as yet been assigned to specific lineages within their genus (Rikkinen et al., 2018).

The fifth *Chaenotheca* fossil (Plate VII, 3) deviates from all extant species in important anatomical details and was described as a fossil species, *Chaenotheca succina* Rikkinen et A.R. Schmidt, in Rikkinen et al. (2018). The three features that characterize the fossil species (intertwining hyphae of stipe surface, persisting paraphyses of mazaedium, continuous outer layer of ascospore wall) may represent ancestral features that have not been preserved in modern species of the genus.

The overall morphology of the two ascomata preserved in the single *Phaeocalicium* fossil is similar to those of extant species of the genus but does not reveal details of ascospore morphology (Rikkinen et al., 2018).

The calicioid fossils demonstrate that key features in the morphology of *Calicium*, *Chaenotheca*, *Chaenothecopsis*, and *Phaeocalicium* ascomata have remained unchanged at least since the Paleogene. One *Chaenotheca* fossil differs from extant species in some anatomical details, but these differences do not change the general observation that all four genera have very conservatively maintained key morphological features that are relevant for their sporesaving strategy and the long-term maintenance of specialized niches in their forest habitat.

One prime example of maintenance of ecologically important adaptations is given by the branching and proliferating ascomata of several *Chaenothecopsis* fossils (Tuovila et al., 2013; Rikkinen et al., 2018). The ascomata of several extant species in the genus occasionally produce apothecial disks divided into distinct regions or lobes. Some species can also produce branched ascomata, and this feature is especially common among resinicolous taxa with long and slender stipes. In some species, the branching occurs close to the tip of the stipe, with each short branch forming a separate apothecial disk. This type of branching can lead to compound capitula, in some cases with up to a dozen partially contiguous apothecial disks (Rikkinen, 2003c).

The stipes of some resinicolous *Chaenothecopsis* species branch low and hence tend to have long branches, and the ascomata of others form multilayered groups via branching and proliferation directly through the hymenium. This morphology, which is also preserved in two amber fossils, is restricted to resinicolous species that often live on cankers and wounds that exude resin over extended periods. The unusual morphology is a specific adaptation to growing near active resin flows: the perennial fungi can continue growth after commonly reoccurring incidents where their ascomata are overrun and partially covered by fresh exudate (Tuovila et al., 2013).

Mycocalicium sequoiae Bonar, an extant resinicolous calicioid that, despite its current name, belongs to the same lineage as some resinicolous *Chaenothecopsis* species (Tuovila et al., 2014), only grows on exudate that issues from the exposed heartwood of living specimens of *Sequoiadendron giganteum* (Lindl.) J. Buchholz and *Sequoia sempervirens* Endl. in western North America (Bonar, 1971; Tibell and Titov, 1995; Rikkinen, 2003a). This relationship is likely to date back to at least the Paleogene, when both host genera were more widely distributed on the Northern Hemisphere. Also, the close relationship of resinicolous *Chaenothecopsis* fossils from European Paleogene amber to extant taxa from East Asia and eastern and western North America suggests that the current distribution of these fungi is strongly relictual. The current European distribution, with a main population in the boreal forests of northern Europe and some small populations in the montane forests of central and Mediterranean Europe, indicates that they survived the last glacial maximum together with *Picea* A. Dietr. and *Abies* Mill. Taking into consideration what is now known of their past and present distribution, one can safely assume that the resinicolous species were more widespread in Europe during the early and middle Weichselian, when *Picea abies* (L.) H. Karst. was widely distributed and common in central and southeastern Europe (Tuovila et al., 2011b, 2013).

4. DISCUSSION

Baltic amber forms the largest amber deposit on Earth, and assumptions about the locality, geographic extent, structure, and floral composition of its source forests have been a matter of debate since the launch of the intensive study of Baltic amber inclusions in the 19th century. The assumptions about the source forests of Baltic amber have generally been based on the ecological interpretations of inclusions of plants and animals (Sadowski et al., 2017). While Conwentz (1890) assumed dense humid and warm pine forests with only a few deciduous trees, other authors of the 19th century distinguished the source area into lowlands with subtropical to warm-temperate plant taxa and mountains in which taxa having extant analogues in the northern high latitudes occurred (Göppert, 1853; Caspary, 1872; Göppert, 1883). These authors saw affinities to extant floras of northern America, East Asia, and Europe.

Ander (1942) interpreted the presence of various climatic indicator taxa of plants and animals as being a result of the vertical stratification of the forest into different altitudinal zones and described the “Baltic amber forest” as a warm-temperate, moist, and dense “jungle” mainly composed of conifer trees. In Ander’s opinion (1942), the climate was predominantly humid, warm-temperate, and only locally subtropical. A similar picture of

the “Baltic amber forest” was suggested by Bachofen-Echt (1949), who emphasized the different climatic implications of taxa from the Baltic amber flora and fauna.

Czeczott (1961) provided a compilation of described Baltic amber plants and highlighted the high proportion of presumed tropical and subtropical plant taxa (23% of the total number of species) in the Baltic amber flora and agreed with the suggestions of a moist and dense amber forest. She further suggested the presence of open forest glades.

Schubert (1953, 1961) and Ruffle and Helms (1970) proposed drier conditions for the Baltic amber source area and suggested similarities to the “hammocks” of Florida and the mountain steppe forests of Cuba. They assumed that the “Baltic amber forest” was generally dominated by pines and palms, that hard-leaved woods occurred along rivers, and that the higher mountains were covered by pine-oak forests. Kohlman-Adamska (2001) suggested such pine-oak steppe forests in the foothills, supposed the presence of humid swamps along the rivers in lower elevations and suggested that pure conifer forests were located in higher altitudes. She concluded that the spatially structured topography of the area as well as the location of the “Baltic amber forest” in the transition of the temperate to subtropical zone led to a high diversity of the flora.

Other recent publications (Weitschat, 1997; Wichard et al., 2009; Weitschat and Wichard, 2010) regard the “Baltic amber forest” as tropical, combined with mountainous subtropical rain forests, a notion that is mainly based on the interpretation of arthropod inclusions. In contrast, coleopteran inclusions from Baltic amber studied by Alekseev and Alekseev (2016) hint of a plain landscape with a thermophilic, humid-mixed climax forest community.

The East European Craton is a prime example of longterm geologic stability (Nikishin et al., 1996), and no orogenic events occurred in the Baltic region before or during the Paleogene. Hence, there is no geological evidence for the presence of any mountains of any height in the Baltic amber source area, which makes any perception of mountain taxa obsolete.

Sadowski et al. (2017) evaluated previously described and recently found inclusions of conifers from Baltic amber taxonomically and paleoecologically and used these fossils along with ecological data from their closest fossil and extant analogues to reconstruct habitats and climate of the source area of the Baltic amber. The findings indicate heterogeneous warm-temperate humid forest types and point to a “horizontal” stratification of the Baltic amber source area into various habitat types, comprising coastal lowland swamps, back swamps, riparian forests, mesophytic mixed conifer-angiosperm forests, and meadows. Lichen assemblages from Baltic and Bitterfeld ambers suggest that the climate of European Paleogene amber forests was relatively humid and most likely temperate. The morphological adaptations observed in the fossil lichens are most consistent with a humid and moderately wellilluminated temperate forest (Kaasalainen et al., 2017).

As demonstrated by our present analysis, the conspicuously prominent presence of calicioid lichens and fungi among the amber inclusions provides strong support to the emerging perception of European Paleogene amber forests as structurally variable mosaics of dense and more open forest stands. There is full reason to believe that the calicioid lichens preserved in amber preferred similar open shade habitats as their modern relatives (Plate IX). On individual trees, they mainly grew on trunk surfaces that regularly experienced open shade conditions. Also within the forest landscape, they preferred structurally variable old-growth stands, which offered abundant lignum, bark and resin substrates, and a plethora of microhabitats that combined favorable

light conditions with high atmospheric humidity (Plate IX). On the basis of what is known about the substrate preferences and overall ecological requirements of extant calicioids, we propose a likely microhabitat of each fossil and by combining all these data produce an idealized model of forest stand where all these fossils could even have lived side by side. This model may represent the best presently available proxy for European Paleogene amber forest structure (Plate X).

ACKNOWLEDGMENTS

This study would not have been possible without the generous support of amber enthusiasts who detected amber inclusions of calicioid fungi and lichens in their collections and made them available for research. We especially thank Volker Arnold (Heide), Heinrich Grabenhorst (Wienhausen), Carsten Gröhn (Glinde), Max Kobbert (Münster), George O. Poinar, Jr. (Corvallis), and Jörg Wunderlich (Hirschberg an der Bergstraße) for providing amber specimens with inclusions of calicioids. Bruce McCune and Patricia Muir (Corvallis) kindly supported our field work in Oregon. Stella Kristin Louise Meinke (Göttingen) imaged the specimens illustrated in Plate II, 1, 3, and 5.

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FIGURES



Plate I. Morphology of extant calicioid lichens of the genus *Chaenotheca*. 1. *Chaenotheca trichialis* (Ach.) Hellb. with minutely squamulose thallus. 2. *Chaenotheca stemonea* (Ach.) Müll. Arg. with farinaceous thallus. 3. *Chaenotheca brunneola* (Ach.) Müll. Arg. with immersed, endosubstratic thallus. All lichens were photographed in the field in central Finland. Scale bars = 2 mm.

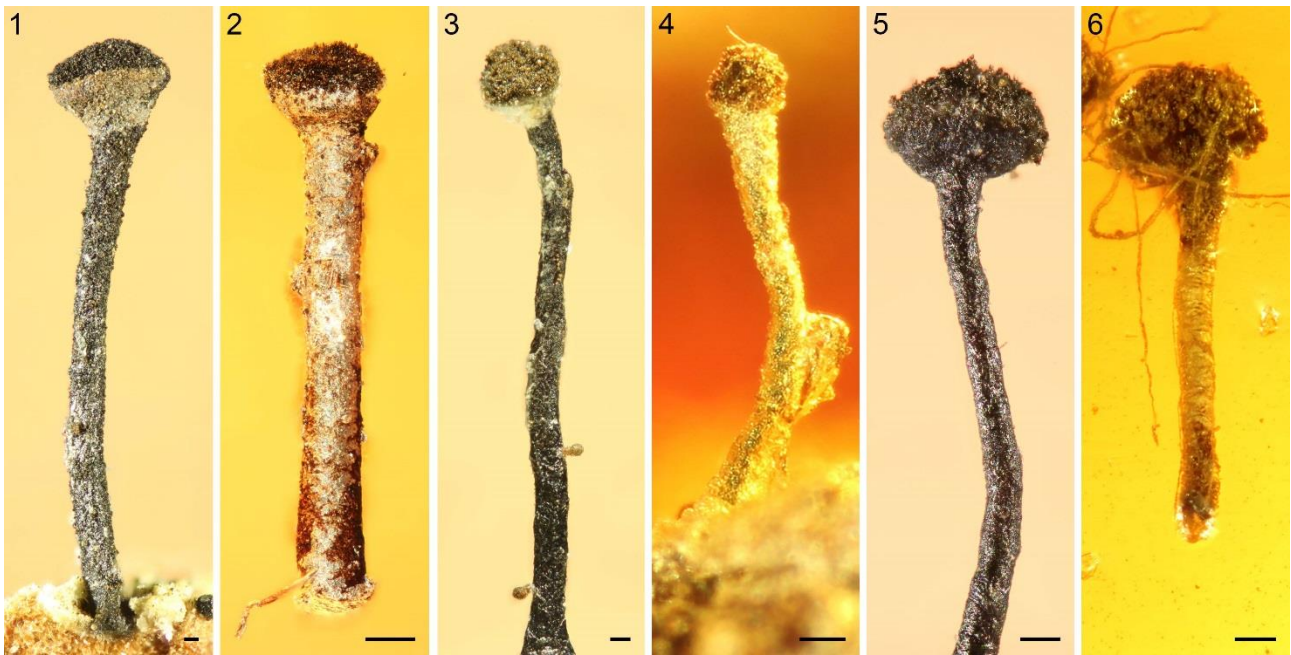


Plate II. Capitula and mazaedia of extant (1, 3, and 5) and fossil (2, 4, and 6) calicioids. The superficial similarity of ascoma morphology among phylogenetically distant fungi is a product of convergent evolution within calicioid communities towards a common spore-saving strategy and animal dispersal. 1. *Calicium viride* from Oregon. 2. *Calicium* sp. in Baltic amber (Geoscientific Collections of the University of Göttingen, GZG.BST.27296). 3. *Chaenotheca brunneola* from Oregon. 4. *Chaenotheca* sp. in Bitterfeld amber (Heinrich Grabenhorst Amber Collection, Le-75). 5. *Chaenothecopsis proliferatus* Rikkinen, A.R. Schmidt et Tuovila from China. 6. *Chaenothecopsis* cf. *bitterfeldensis* in Bitterfeld amber (Heinrich Grabenhorst Amber Collection, Mi-55). Scale bars = 50 μ m.

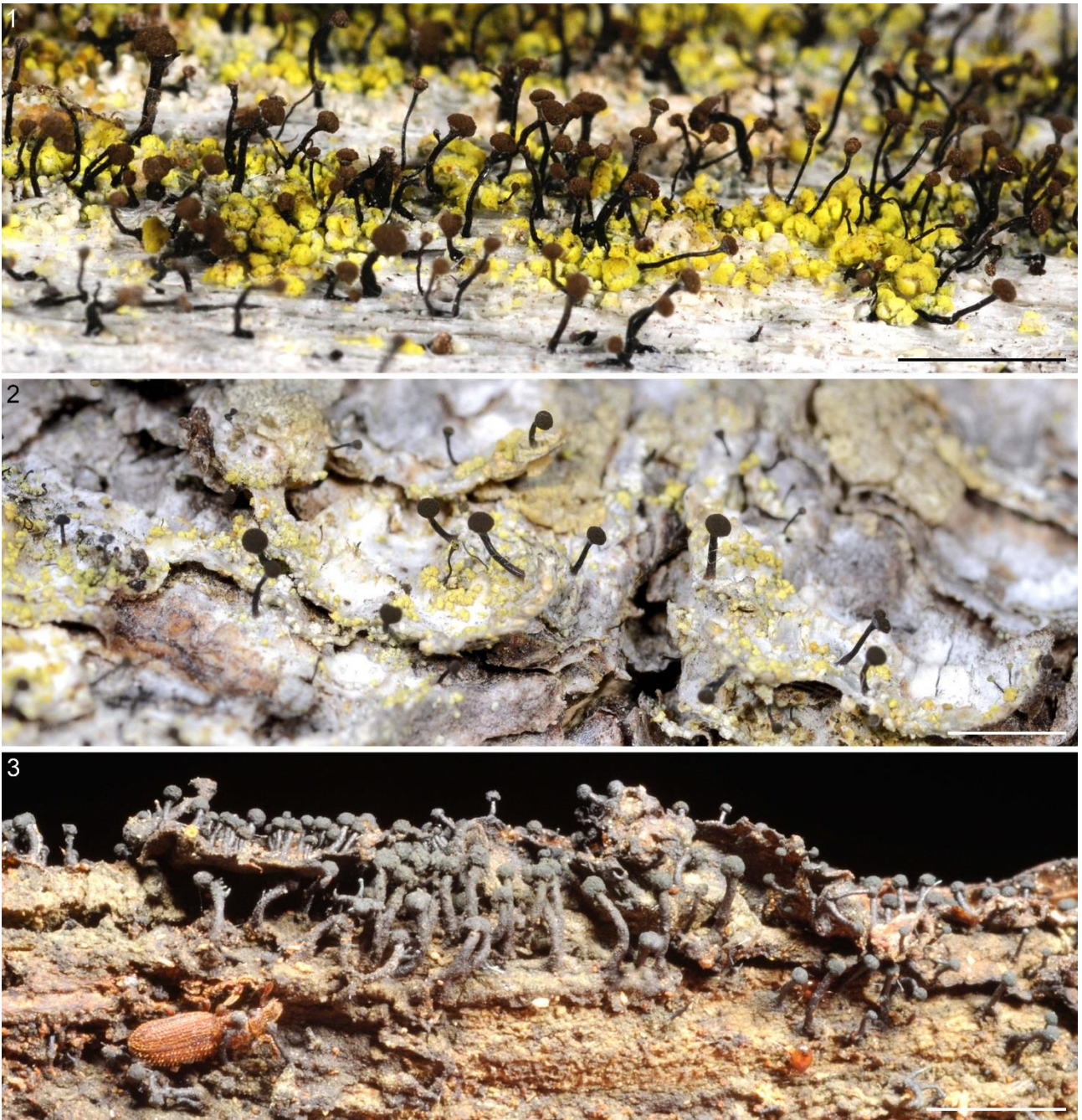


Plate III. Ecology of extant calicioid lichens and fungi. 1. *Chaenotheca chrysocephala* (Ach.) Th. Fr. has vulpinic acid and other yellow pulvinic acid derivatives in its thallus. In ascomata the same secondary metabolite accumulates to form a narrow ring along the excipulum margin and sometimes also covers the lower side of the capitulum. 2. *Chaenothecopsis consociata* (Nádv.) A.F.W. Schmidt only grows on *Chaenotheca chrysocephala* and produces its large black ascomata on the thallus of its host. The *Chaenotheca* species suffers from the association as indicated by its pale color and limited production of host ascomata. 3. *Chaenothecopsis schefflerae* growing in a canker caused by wood-boring insects on the stem of *Pseudopanax colensoi* K. Koch. Note small beetle seeking shelter between the ascomata (lower left) Invertebrates crawling over calicioid ascomata can transport the ascospores directly into new habitats. Also birds and even mammals promote the dispersal of some calicioid species. *Chaenotheca chrysocephala* and *Chaenothecopsis consociata* were photographed in central Finland and *Chaenothecopsis schefflerae* in New Zealand. Scale bars = 2 mm.



Plate IV. Ecology of extant resinicolous calicioids. 1. Resinous scars left by large woodpeckers can develop into ideal microhabitats for resinicolous *Chaenothecopsis* species. This deep scar on the basal trunk of *Picea abies* was produced by a black woodpecker (*Dryocopus martius* L.) in Finland. 2. *Chaenothecopsis sitchensis* Rikkinen grows on thick deposits of resin and organic debris that accumulate on soil within shady trunk base overhangs of huge old-growth *Picea sitchensis* in coastal forests of Oregon. 3. *Chaenothecopsis sitchensis* can produce much larger ascomata than most of its relatives, the longest stipe so far measured was 16 mm long. 4. Three species of resinicolous *Chaenothecopsis* were found growing together in this canker on the basal trunk of *Abies pinsapo* Boiss. in southern Spain. 5. *Chaenothecopsis tsugae* Rikkinen and several other resinicolous species sometimes produce extensive hyphal mats especially behind bark slabs and in other sheltered microhabitats with high atmospheric humidity. This specimen was photographed in the Oregon Cascades. 6. *Chaenothecopsis schefflerae* (Samuels et D.E. Buchanan) Tibell grows on the exudates of several *Pseudopanax* species (Araliaceae) in New Zealand.



Plate V. Extant calicioid lichens and fungi in resinous microhabitats. 1. Patches of exposed lignum on scarred conifers provide an ideal habitat for many calicioid lichens and fungi. 2. Both resinicolous and lignum-inhabiting calicioids grow together in such habitats and can be easily engulfed by any subsequent flows of fresh exudate. 3. Running resin can also engulf calicioids growing on conifer bark, note the two *Chaenotheca* ascomata that have only narrowly escaped this fate (arrowheads). 4. Ascomata of *Chaenotheca ferruginea* (Turner) Mig. growing immediately adjacent to active resin flow are under high risk of being covered by fresh exudate. 5. *Chaenotheca trichialis* (Ach.) Hellb. starting to colonize the surface of dry, hardened resin flow. 6. *Chaenotheca trichialis* producing ascomata on old and weathered resin flow. Images 1, 3 and 6 were photographed on *Picea abies* in central Finland and images 2, 4 and 5 of *Sequoia sempervirens* in northern California.

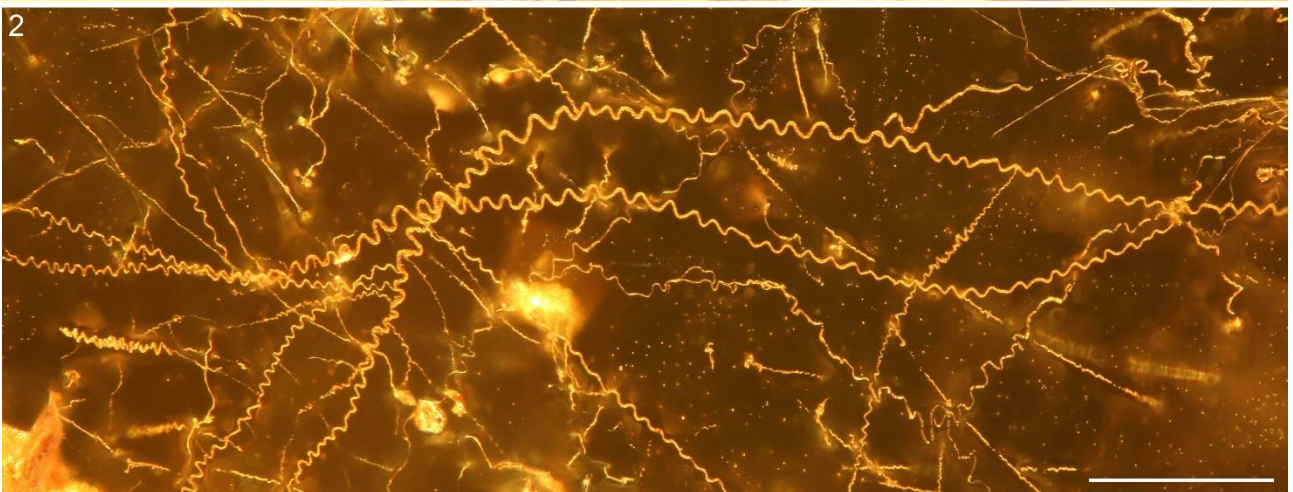


Plate VI. *Chaenothecopsis bitterfeldensis* in Bitterfeld amber. 1. The fungus had produced an extensive mycelium over an old resin surface, partly superficial and penetrating into the substrate. Ascospores emerge from the dense hyphal mat, and many detached ascospores occur in the surrounding amber matrix (George O. Poinar Amber Collection, AF 9-26). 2. The resin substrate of the fungus is completely infested with hyphae, often with spirally twisted regions (Heinrich Grabenhorst Amber Collection, Le-127). Scale bars = 200 μm .

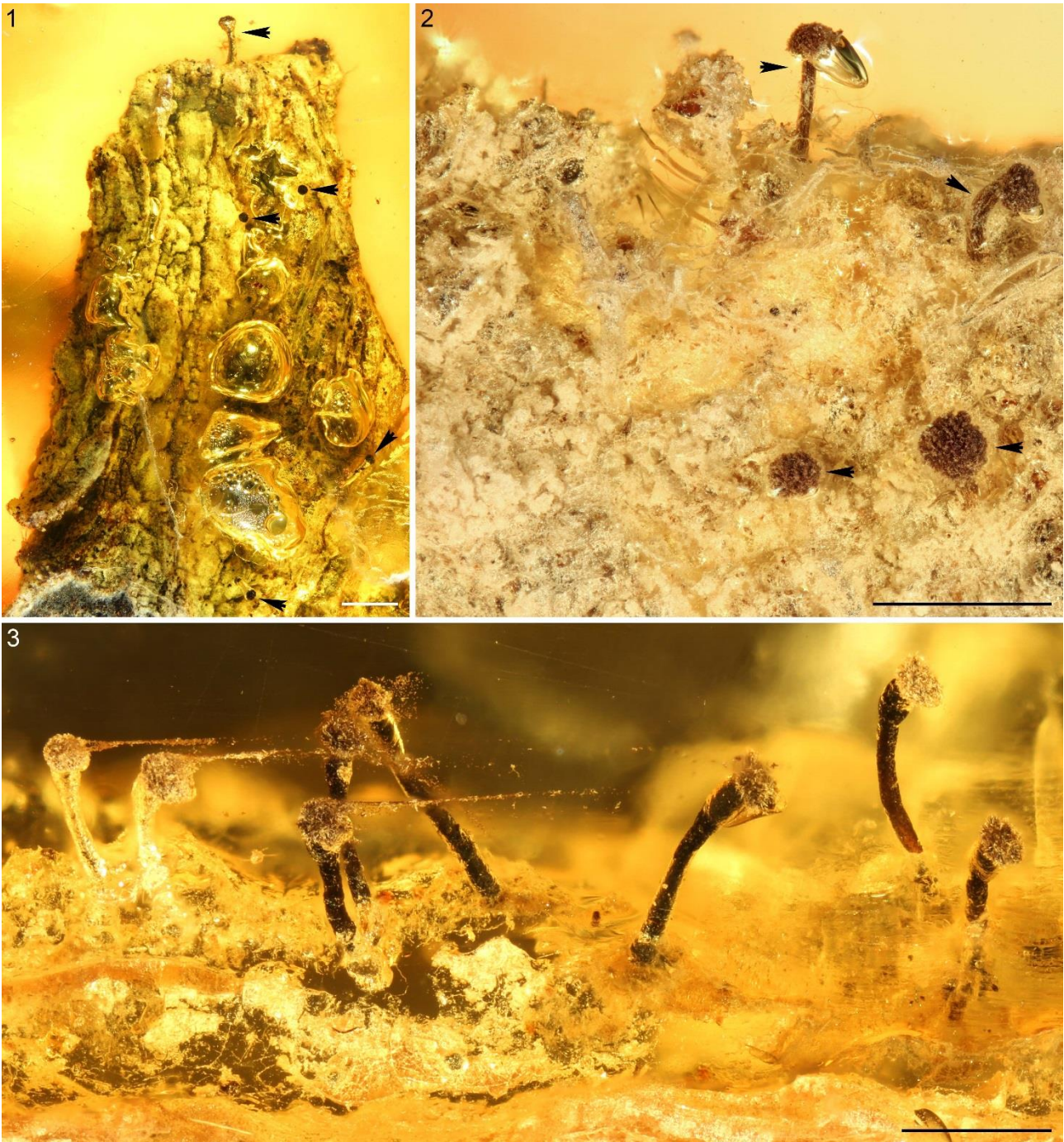


Plate VII. Morphology of fossil calicioid lichens of the genus *Chaenotheca*. 1. *Chaenotheca* sp. in Baltic amber (Geoscientific Collections of the University of Göttingen, GZG.BST.27297). Note verrucose thallus covering substrate and several ascomata (arrowheads). 2. *Chaenotheca* sp. in Baltic amber (Max Kobbert Amber Collection, *sine numero*). Note coarsely granular to minutely squamulose thallus on substrate and four ascomata with well-developed mazaedia (arrowheads). 3. *Chaenotheca succini* in Baltic amber (Carsten Gröhn Amber Collection, P 5377). Scale bars = 500 μ m.

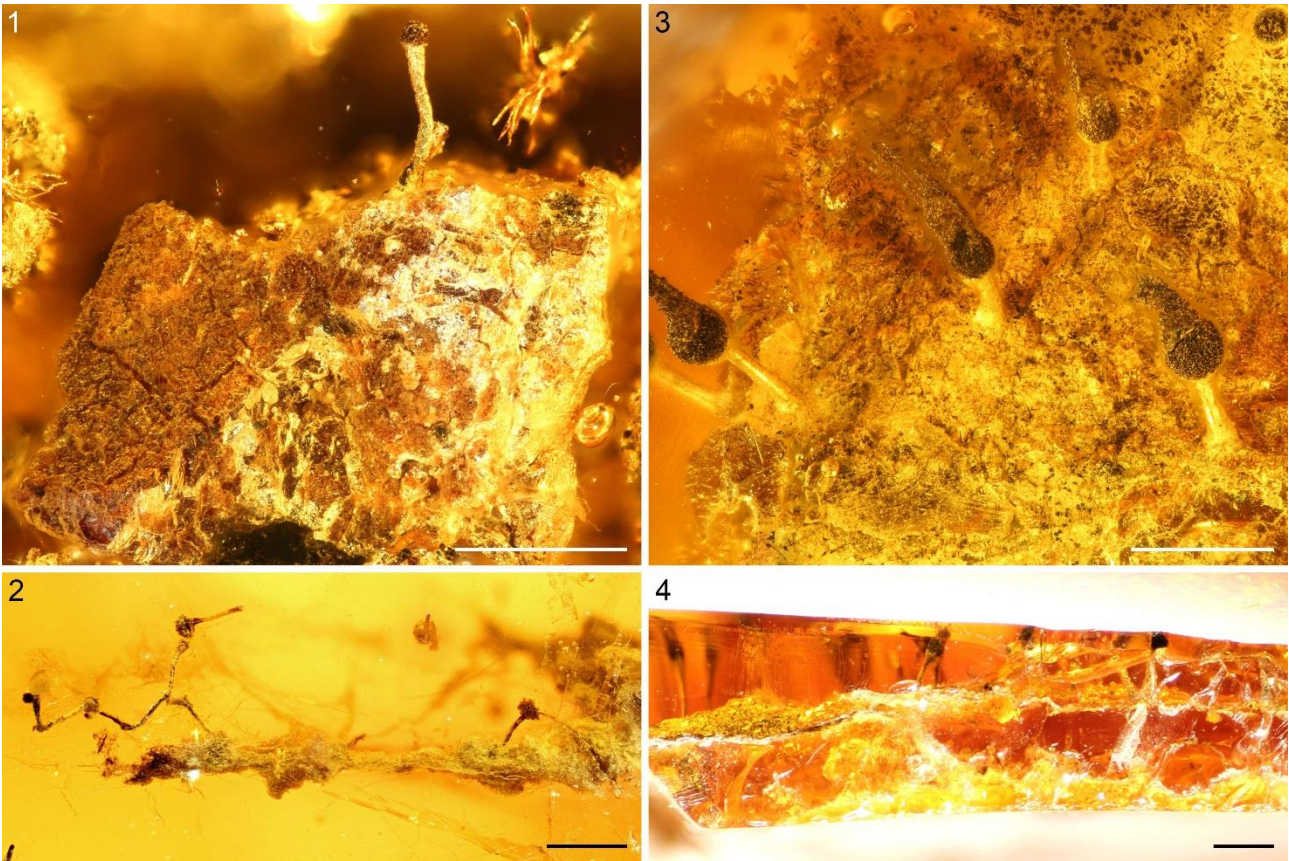


Plate VIII. Preservation of fossil calicioid lichens and fungi in amber. 1. A small detached resin fragment with a single ascoma of *Chaenotheca* sp. attached is preserved together with bark fragments, stellate plant hairs and other debris in Bitterfeld amber (Grabenhorst Amber Collection, Le-75). 2. Ascomata of *Chaenothecopsis* cf. *bitterfeldensis*, some attached to mycelium and others caught in an overlying spider web preserved in Bitterfeld amber (Grabenhorst Amber Collection, Mi-55). 3. Ascomata of *Calicium* cf. *succini* in Bitterfeld amber (Geoscientific Collections of the University of Göttingen, GZG.BST.27300). Mature ascospores were organized into elongated fans in the amber matrix after being pulled from the mazaedium by a slow and unidirectional flow of resin. 4. Piece of Bitterfeld amber composed of three successive resin flows that preserved ascomata of *Calicium* cf. *succini* (Geoscientific Collections of the University of Göttingen, GZG.BST.27300). Scale bars = 500 μm .



Plate IX. Relationship between forest structure and calicioid diversity in extant temperate conifer forests as illustrated by two surveyed forest stands in western Oregon (data from Rikkinen 2003a). 1. Old-growth mixed conifer forest in Hackleman Grove in the Cascades. Mixed montane conifer forests of suboceanic and subcontinental temperate regions represent an optimal habitat for many calicioid lichens and fungi. This is because they offer a wide range of microhabitats that combine favorable light conditions with high atmospheric humidity and also an abundant supply of hard lignum. Consequently, both calicioid diversity (26 species found) and the overall abundance of dominant species are relatively high. 2. Old-growth Sitka spruce forest in Cummins Creek in the Coast Range. Temperate rainforests represent a suboptimal habitat for most calicioid lichens and fungi and consequently species diversity (13 species found) and the overall abundance of dominant species are relatively low. The reasons for this include excessive humidity and shading, the lack of hard lignum, competition for space by bryophytes, and intense mollusk grazing.

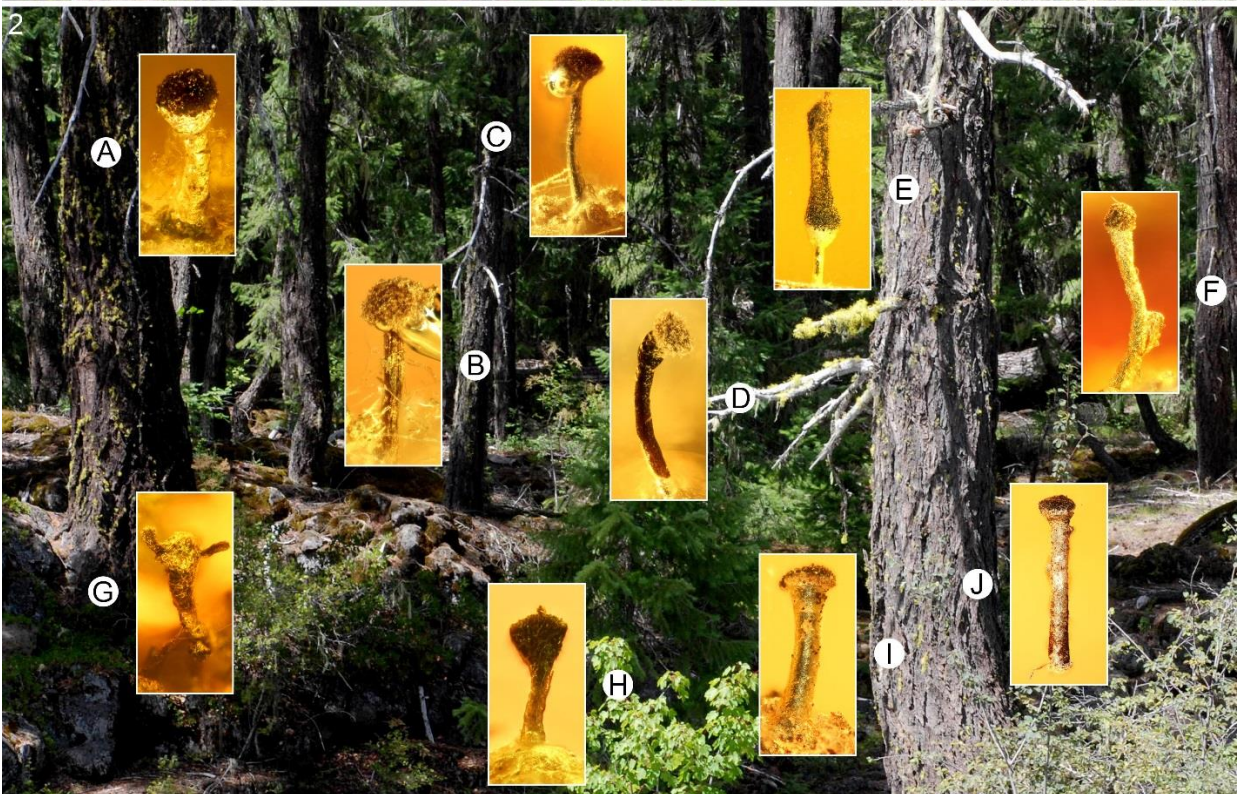


Plate X. Many extant calicioid lichens and fungi in temperate forests have specialized habitat requirements. They represent an important functional group in old-growth forests where diverse communities are found in humid microhabitats that receive plenty of diffuse light, but not much direct sunlight. As the abundance and diversity modern calicioids is climate and habitat dependent, and as the calicioids in amber probably exhibited congruent habitat preferences, the fossils provide rare insights into the habitat quality. 1. On the basis of what is known about the ecological requirements of extant calicioids we propose a model of a forest stand where all the known fossil

specimens could have existed side by side. The reconstruction is based on an extant humid-temperate mixed conifer forest from the Oregon Cascades, western North America. 2. Within the habitat model we indicate a possible microhabitat for all fossil specimens so far found from European Paleogene amber. A. *Chaenotheca* sp. (Baltic amber, Geoscientific Collections of the University of Göttingen, GZG.BST.27297). B. *Chaenotheca* sp. (Baltic amber, Max Kobbert Amber Collection, sine numero). C. *Chaenotheca* sp. (Baltic amber, Carsten Gröhn Amber Collection, P 6463). D. *Chaenotheca succini* (Baltic amber, Carsten Gröhn Amber Collection, 5377). E. *Calicium* cf. *succini* (Bitterfeld amber, Heinrich Grabenhorst Amber Collection, Li-22). F. *Chaenotheca* sp. (Bitterfeld amber, Heinrich Grabenhorst Amber Collection, Le-75). G. *Chaenothecopsis* cf. *bitterfeldensis* (Baltic amber, Jörg Wunderlich Amber Collection, F2026). H. *Phaeocalicium* sp. (Bitterfeld amber, Heinrich Grabenhorst Amber Collection, Le-10). I. *Calicium succini* (Baltic amber, Museum für Naturkunde zu Berlin, MB.Pb.1979/838). J. *Calicium* sp. (Baltic amber, GZG.BST.27296).