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CONTRIBUTIONS TO THE PALEOGENE LICHEN FLORA OF EUROPE: CRUSTOSE AND FRUTICOSE LICHENS

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Paleogene Baltic and Bitterfeld ambers are currently the most important source of Cenozoic fossil lichens. The lichen assemblage suggests that the climate of the European amber forests 41−23 million years (Ma) ago was relatively humid and most likely temperate. In addition to the climatic inference, the lichen fossils reveal information about the divergence and age of lineages and the interactions in the past epiphytic communities. As most crustose lichens are relatively obscured and closely attached in their substrate, calicioid taxa (*Calicium*, *Chaenotheca*) were previously the only crustose lichens known as amber inclusions. However, our recent survey demonstrated that further crustose lichens are preserved in European Paleogene ambers. Three of the fossil crustose lichens from Baltic (41−34 Ma) and Bitterfeld (23 Ma) amber belong to the extant genus *Ochrolechia* (Ochrolechiaceae, Lecanoromycetes) and one possessed conidiomata similar to those produced by modern fungi of the order Arthoniales (Arthoniomycetes). Most intriguingly, two of the fossil *Ochrolechia* specimens host lichenicolous fungi of the extant genus *Lichenostigma* (Lichenostigmatales, Arthoniomycetes). The finding confirms that *Ochrolechia* and *Lichenostigma* already diversified in the Paleogene. Our study of fruticose lichens from Paleogene amber revealed diverse finely pendulous and more robust morphologies. Among them, the genus *Usnea* is identifiable from late Eocene Baltic amber, based on general morphology and annular cortical fragmentation. The unique type of cortical cracking suggests the presence of a central cord that keeps the branch intact even when its cortex is split into segments. This evolutionary innovation has remained unchanged since the Palaeogene and likely contributed to the considerable ecological flexibility that allows *Usnea* species to flourish in a wide variety of ecosystems and climate regimes. Funding: UK (Alexander von Humboldt Fellowship).

Contributions to the Paleogene lichen flora of Europe: Crustose and fruticose lichens

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Paleogene amber is currently the most important source of Cenozoic fossil lichens and, to date, over 150 lichen inclusions have been found from Baltic and Bitterfeld ambers. The lichen assemblage suggests that the climate of the Paleogene European amber forests was relatively humid and most likely temperate. Additionally, the lichen fossils reveal information about the divergence and age of lineages and the interactions in the past epiphytic communities, which also included representatives of extant lichenized and lichenicolous fungal genera *Anzia*, *Ochrolechia*, *Usnea*, and *Lichenostigma*.

Amber is fossilized resin and famous for its lifelike preservation of even soft-bodied microorganisms, and the fossil record of many lineages of fungi, plants, and arthropods is actually restricted to amber inclusions. **Baltic amber** has a **minimum age of 41–34** and **Bitterfeld amber 23 million years**; both originate from Europe.

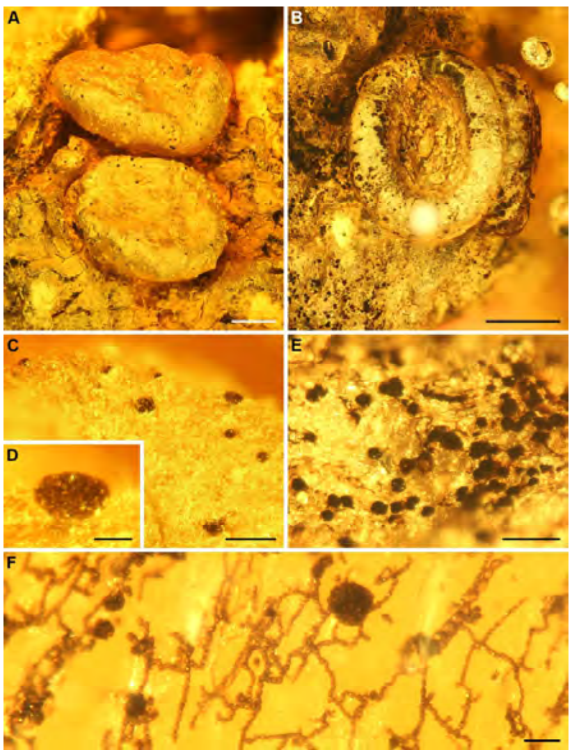


Figure 1. **Crustose *Ochrolechia* specimens with lichenicolous *Lichenostigma* from European Paleogene amber.** A) *Ochrolechia* with apothecia, growing together with a foliose lichen. The black dots on the apothecial margin (C, D) are conidiomata and/or ascomata of the lichenicolous fungi *Lichenostigma*. B) Another fossil specimen of *Ochrolechia* with apothecia and E) *Lichenostigma* on the specimen's crustose thallus. F) Branched moniliform hyphae and conidiomata/ascomata of a putative lichenicolous fungus. Scales 500 µm in A and B, 100 µm in C and E, 20 µm in D and F. (Kaasalainen *et al.* 2019)

Figure 2. A further crustose lichen from European Paleogene amber: Specimen of **Arthoniales** (Arthoniomycetes) with byssoid thallus and conidiomata. The optical sections of immersed conidiomata are svisible from the lower side and show hyphae and masses of conidia preserved within the conidiomata (not visible here). Scale 200 µm. (Kaasalainen *et al.* 2019)

Several modern lichen genera had already diversified in the Paleogene, setting **the minimum age for *Ochrolechia* (Ochrolechiaceae, Lecanoromycetes), *Usnea* (Parmeliaceae, Lecanoromycetes), and the lichenicolous fungus *Lichenostigma* (Lichenostigmatales, Arthoniomycetes) in 34 million years**. Also the specific **lichenicolous association between *Lichenostigma* and *Ochrolechia*** existed already in the Paleogene, as well as the **evolutionary innovation of central cord**, contributing to the considerable ecological flexibility that allows *Usnea* to flourish in a wide variety of ecosystems and climate regimes.

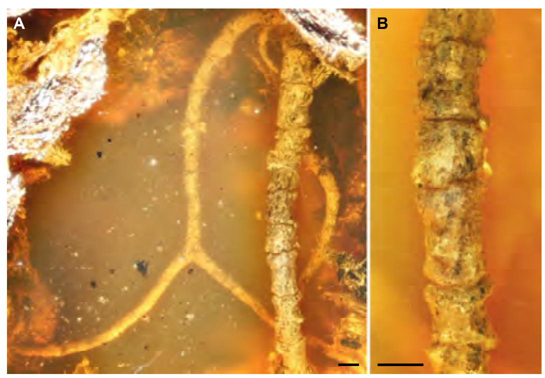
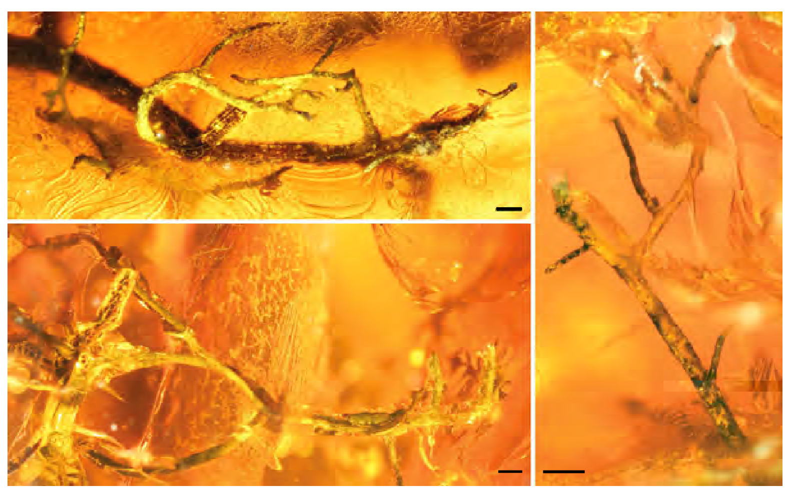


Figure 3 (left). **Fossil *Usnea* in Baltic amber.** A) Fruticose thallus with terete and tapering branches. B) Annular cracks in the cortex dividing the main branch into vertebrae-like segments, characteristic also to extant *Usnea* species. Scales 200 µm. (Kaasalainen *et al.* 2020)

Figure 4 (below). Further fruticose lichens in European Paleogene amber. Scales 200 µm. (Kaasalainen *et al.* 2020)



Material and Methods. The presented fossil lichens are among **150 screened lichen inclusions in altogether 122 Baltic and Bitterfeld amber specimens**. The specimens are mainly deposited in the Geoscientific Collection of the University of Göttingen or in other museum collections in Germany (Kaasalainen *et al.* 2017, 2019, 2020). The manually ground and polished amber pieces were studied under dissection and compound microscopes equipped with digital cameras using simultaneous incident and transmitted light. For an enhanced illustration of the three-dimensional inclusions, the light-microscopical images were digitally stacked from individual focal planes to photomicrographic composites.

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