

Towards a new picture of the ‘Baltic amber forest’ – flora, habitat types, and palaeoecology

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- [1] Seyfullah, L. J., **E.-M. Sadowski**, and A. R. Schmidt. 2015. Species-level determination of closely related araucarian resins using FTIR spectroscopy and its implications for the provenance of New Zealand amber. *PeerJ* 3:e1067, doi: 10.7717/peerj.1067.
- [2] Kettunen, E., H. Grabenhorst, C. Gröhn, H. Dörfelt, **E.-M. Sadowski**, J. Rikkinen, and A. R. Schmidt. 2015. The enigmatic hyphomycete *Torula* sensu Caspary revisited. *Review of Palaeobotany and Palynology* 219:183-193.
- [3] **Sadowski, E.-M.**, A. R. Schmidt, L. Kunzmann, C. Gröhn, and L. J. Seyfullah. 2016a. *Sciadopitys* cladodes from Eocene Baltic amber. *Botanical Journal of the Linnean Society* 180:258-268.
- [4] **Sadowski, E.-M.**, A. R. Schmidt, P. J. Rudall, D. A. Simpson, C. Gröhn, J. Wunderlich, and L. J. Seyfullah. 2016b. Graminids from Eocene Baltic amber. *Review of Palaeobotany and Palynology* 233:116-168.
- [5] **Sadowski, E.-M.**, A. R. Schmidt, L. J. Seyfullah, and L. Kunzmann. 2017a. Conifers of the ‘Baltic amber forest’ and their palaeoecological significance. *Stapfia* (in press).
- [6] **Sadowski, E.-M.**, L. J. Seyfullah, C. A. Wilson, C. L. Calvin, and A. R. Schmidt. 2017b. Diverse early dwarf mistletoes (*Arceuthobium*), ecological keystones of the Eocene Baltic amber biota. *American Journal of Botany* 104: 1-25. doi:10.3732/ajb.1600390.

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Summary

Amber is fossilized resin that was excreted by conifers or angiosperms. Plant and animal remains which got caught inside of these ancient resin flows are called ‘inclusions’ and are often preserved with high fidelity. Amber deposits which are remarkably rich in inclusions mainly occur in Cretaceous and Cenozoic sediments. The Eocene Baltic amber is a prominent example which constitutes the largest amber deposit worldwide and is famous for its plenitude of inclusions that mainly comprise arthropod taxa.

This thesis, however, focuses on plant inclusions from Baltic amber, which are rare, and less studied than the arthropod inclusions. Despite their rareness, plant inclusions are significant for the reconstruction of the palaeoecosystem from which the amber derives, the so-called ‘Baltic amber forest’. Up to now, knowledge about the ‘Baltic amber forest’ is mainly based on historic descriptions of plant inclusions from the 19th century and on the interpretation of animal inclusions. Contradictory pictures of the ‘Baltic amber forest’ exist, ranging from tropical lowland rainforests with neighbouring subtropical to temperate mountain forests to steppe forests and pure, dense conifer stands that only intermingled with angiosperm trees along their margins. The topography of the Baltic amber source area is mainly interpreted as mountainous, but also theories about a plain landscape exist. Further debates are related to the age of Baltic amber, as well as the locality of its source forests and its botanical origin. These questions were summarized as ‘Baltic amber mysteries’.

The primary focus of this thesis is to achieve a new picture of the ‘Baltic amber forest’ by predominantly using plant inclusions. Amber inclusions from museum and private collections were used to revise described historic specimens and to identify undescribed plant taxa from Baltic amber. Identified plant taxa were then compared to their fossil and extant analogues. This comparison served to reconstruct the potential palaeoecology of plant taxa, as well as their habitat preferences and palaeoclimatic requirements. With this information, plant diversity, habitat types and their structure were reconstructed, thus synthesising a new picture of the ‘Baltic amber forest’.

In this thesis, ten conifer genera were identified from Baltic amber: *Calocedrus*, *Quasisequoia* and *Taxodium* (Cupressaceae), *Cupressospermum* (Geinitziaceae), *Abies*, *Cathaya*, *Nothotsuga*, *Pseudolarix* and *Pinus* (Pinaceae), and *Sciadopitys* (Sciadopityaceae). The diversity of Cupressaceae is actually higher, since three morphological complexes of Cupressaceous twig fragments and pollen cones were also classified. The majority of all identified conifers has not been verified from Baltic amber before; thus, new candidates for a Baltic amber source plant should be restudied. In addition, newly discovered or revised angiosperm inclusions confirm the presence of Poaceae, Cyperaceae (*Rhynchospora*), Roridulaceae, Myricaceae (*Comptonia*), Viscaceae (six species of *Arceuthobium*), Ericaceae (*Cassiope* or *Calluna*), and Fagaceae (quercooid and castaneoid taxa) in the

‘Baltic amber forest’. The named conifers and angiosperms allowed the reconstruction of several habitat types with their respective plant communities from the Baltic amber source area: coastal lowland swamps under brackish-water influence, raised bog habitats, non-brackish inundated back swamps and riparian forests, non-inundated mixed-mesophytic angiosperm-conifer forests with both open habitat patches (such as meadows) and canopy gaps. Moreover, different life forms could be reconstructed, such as parasitic (dwarf mistletoes, *Arceuthobium*) and carnivorous (Roridulaceae) plants. Previous studies about ferns, bryophytes, liverworts, fungi and lichens from Baltic amber were also considered in the interpretation of the microhabitats of the ‘Baltic amber forest’. They indicated complex and highly diverse communities with epiphytic, terrestrial, saprophytic and parasitic components.

From a palaeobotanical perspective, there is neither evidence of a (sub)tropical ‘Baltic amber forest’, nor of an altitudinal stratification of the source area. This is supported by previous geological studies of the Baltic amber deposit, which suggest a local amber formation and deposition in the Baltic region during the late Eocene. No orogenic events took place in the Baltic region, precluding the presence of mountains in the Baltic amber source area. Comparisons of the Baltic amber flora with fossil assemblages from the central European Palaeogene showed clear differences to (sub)tropical fossil floras. Instead the Baltic amber flora indicates a warm-temperate palaeoclimate with affinities to the extant warm-temperate to temperate floras of East Asia and North America.

The thorough analyses of available plant inclusions from Baltic amber reveal a heterogeneous mosaic-like landscape of the Baltic amber source area in a coastal setting. This heterogeneity allowed the existence of diverse animal and plant taxa with different habitat preferences in close proximity to each other.

1. Introduction

1.1. What is amber?

Amber is defined as “fossilized resin from various botanical sources” (Ragazzi and Schmidt 2011, p. 25) and represents a “lipid-soluble mixture of volatile and non-volatile terpenoid and/or phenolic secondary compounds” (Langenheim 2003, p. 24). All extant Coniferales, as well as some angiosperm taxa [e.g. Fabaceae, Dipterocarpaceae, see Langenheim (2003) for an extensive list] synthesize, store and secrete resin, and have specialized structures, such as endogenous canals, cells and cysts or glandular trichomes serve for resin secretion (Langenheim 2003).

Different time frames have been suggested for defining when resins turn into amber. Using carbon 14 dating, Anderson (1996) defined any resin older than 40,000 years as amber; resins younger than that he termed as ‘subfossil resins’. Poinar (1992) applied physical tests, such as melting point, hardness and burning reactions, to differentiate between ambers and copal, a term that he used to describe immature amber. Following his results, copals are between three and four million years old, before they become amber. However, in other papers, the term copal is more related to its commercial use, for instance for incense resins utilized in pre-Columbian Mexico and Central America or for resin-based varnishes of the Fabaceae and Araucariaceae (Poinar 1992, Langenheim 2003). To avoid misunderstandings, I will follow Vávra (2009) and his suggestion, treating ‘fossil resin’ and ‘amber’ as synonyms, while the term ‘copal’ will be used for “any non-fossilised resin material whatever its geological age may be” (Vávra 2009, p. 220).

Reasons for resin release are complex, as is the importance of resins in plant ecology (Langenheim 1995). Resin serves as a defence and protection mechanism against pests, such as fungi (e.g. pitch-canker fungi, *Fusarium* sp.) and bark beetles (e.g. *Dendroctonus*) attacking pine trees (True and Snow 1949, Langenheim 2003, McKellar et al. 2011) or weevils whose infestations induce higher resin release in *Hymenaea courbaril* (Fabaceae) and *Araucaria humboldtensis* (Araucariaceae) (Janzen 1975, Beimforde et al. 2016). Wounds resulting from physical damage are sealed with resin (Farrell et al. 1991, Langenheim 1995). In arid habitats, resin coats leaves and stems of xeromorphic plants as protection against water loss and heat (Dell and McComb 1978). Terpenoids in resins not only attract pollinators but also predators which feed on insect pests infesting the tree (Langenheim 1994).

1.2 Amberization and the formation of an amber deposit

A specific set of processes and conditions are involved in the transformation of resin into amber. These processes are summarized with the term ‘amberization’ (Anderson et al. 1992, Tonidandel et al. 2008). Amberization is still not completely understood, but several key factors have been identified (Ragazzi and Schmidt 2011). First of all, the systematic affiliation of the source plant and thus, the chemical and physical resin properties are of great importance, since not all resins have the potential to become

amber. Resin needs to polymerize so that the resin monomers “form a complex compound of higher molecular weight” (Langenheim 2003, p. 144), while components of low molecular weight are lost with time (Ragazzi and Schmidt 2011). Further resin properties facilitating the amberization comprise the resistance to oxidative degradation and microbial decomposition (Langenheim 1969). The environment of the source plant also influences the resin composition (and its potential to become amber), for instance by climate and insolation. Moreover, resin must be protected from deterioration agents, such as UV light, precipitation, temperature, humidity fluctuations, and pressure facilitates amberization (Langenheim 2003, Ragazzi and Schmidt 2011, Bisulca et al. 2012, Labandeira 2014).

Resin either has been buried in situ (i.e. autochthonous) or, due to its buoyant properties, has been transported by streams and rivers. It then became deposited in the sediments of estuaries, deltas and bays along with logs and other plant remains which are turned into lignite while the resin may become amber (Poinar 1992, Grimaldi 1996, Langenheim 2003). If resin was transported before it was buried, the resulting amber deposit is an allochthonous primary deposit (Zherikhin 2002). It may also occur that after primary deposition, amber was eroded and subsequently re-deposited. This is termed an allochthonous secondary amber deposit (Zherikhin 2002). In cases where resin was first buried autochthonously, then transported by rivers and re-deposited, the amber deposit is termed a mixed allochthonous deposit (Zherikhin 2002).

Amber can be found in marine sediments, such as Baltic and Bitterfeld amber, indicating that the amber was deposited in a coastal setting (Standke 1998, 2008). Poinar (1992) discussed the importance of seawater for amberization, supposing that it inhibits the fluctuation of temperature and oxygen concentration and that seawater salts may drive the polymerization process. However, “transport and deposition of resins are [still] poorly understood” (Martínez-Delclòs et al. 2004).

1.3 Amber deposits worldwide and in the Baltic area

Amber deposits are widely distributed in geological time and space [for the most recent list of amber deposits worldwide see maps and references by Martínez-Delclòs et al. (2004) and Krumbiegel and Krumbiegel (2005)]. Except for Antarctica, amber deposits occur on each continent, and during the last few years even more amber localities have been discovered, such as Peruvian amber of the Amazon basin (Antoine et al. 2006), Cambay amber of Gujarat in western India (Rust et al. 2010) or Ethiopian amber of Northwest Ethiopia (Schmidt et al. 2010).

The oldest amber so far derives from Carboniferous sediments of the Tradewater formation of Illinois (USA) in very small amounts and without any inclusions (Bray and Anderson 2009). Further amber deposits with reported inclusions occur in the Mesozoic, such as Late Triassic amber of the Dolomites (Roghi et al. 2006, Schmidt et al. 2012), Early Jurassic amber from the Rotzo Formation in northern Italy (Neri et al. 2017) and Late Jurassic amber of Lebanon

(Azar et al. 2010). The Cretaceous deposits contain much higher amounts of amber, such as Early Cretaceous amber of the Middle East (several localities across Lebanon, Israel and Jordan) and of northern Spain (Álava, Basque county), as well as Albian amber from Myanmar (Kachin state) and Charente and Charente-Maritime amber from France (Albian-Cenomanian) (Perrichot et al. 2007, Azar et al. 2010, Ross et al. 2010). Many amber deposits are also reported from different time periods of the Cenozoic, such as Dominican (Dominican Republic) and Mexican amber (Chiapas, Mexico), both suggested to be Miocene in age (Langenheim 1995, Penney 2010, Solórzano Kraemer 2010).

Despite the high number of amber deposits, this thesis focuses on the by far largest amber deposit: the Baltic amber deposit of the Samland Peninsula (Kaliningrad, Russia). Between 1951 and 1988, around 17,705 tonnes of amber were mined in several open cast mines and other excavation pits of Samland (Kosmowska-Ceranowicz 1997a). The concentration of amber in the main amber bearing layer, the Blue Earth, is estimated between 45 to 2667 g/m³, but even higher concentrations of 10,000 g/m³ were reported (Kosmowska-Ceranowicz 1997a). The Samland amber bearing sediments also extend to Poland, and thus, further Baltic amber deposits exists, such as Chłapowo, the delta of Parczew, the region of Kurpie and Polesie Lubelskie in South Poland (Kosmowska-Ceranowicz 1997b). Besides these deposits, Baltic amber can also be found washed ashore along the coast of the littoral states of the North and Baltic Seas (Weitschat and Wichard 2010).

1.4 Amber classification

Although “ambers are not true minerals” (Labandeira 2014), they are often treated as such (King 2006) and mineral names were introduced to describe different types of ambers, based on their deposit and chemical-physical characteristics (see Vávra (2015) for an extensive list of mineral names for ambers and copals, including their properties).

The majority of Baltic amber is so-called succinite, which is distinguished from most amber by the incorporation of succinic acid (Rottländer 1970, Anderson et al. 1992, Tonidandel et al. 2009). Besides succinite, further amber types can be found in the Baltic amber deposit: beckerite, gedanite and stantienite; however, they all together only represent about 3% of all Baltic amber, while > 90% are succinite (Kosmowska-Ceranowicz 1992, Weitschat and Wichard 2010). Therefore, most authors mean ‘succinite’ when referring to ‘Baltic amber’. To avoid misunderstandings in the following text, the term ‘Baltic amber’ will be used synonymously with ‘succinite’.

Besides mineralogical classifications, a further classification system for ambers has been established, based on Pyrolysis-Gas Chromatographic-Mass Spectroscopic analyses (Py-GC-MS) of ambers (Anderson et al. 1992, Anderson and Botto 1993, Anderson and Crelling 1995, Bray and Anderson 2009). The macromolecular characteristics of ambers have been used to differentiate between five classes (Class I to V) and four subclasses (Class Ia to Id) which are listed in Tab.

1. Classes III to V are very rare, while the most abundant ambers belong to Class I (including succinite) and II with affinities to several conifer families, such as Araucariaceae, Cupressaceae and to angiosperm taxa of Fabaceae and Dipterocarpaceae.

Tab. 1: Classification system for ambers, taken from Anderson et al. (1992; and citations therein), Anderson and Botto (1993), Anderson (1994, 2006), and Anderson and Crelling (1995), Yamamoto et al. (2006), Bray and Anderson (2009), Rust et al. (2010), Vavra (2009; and citations therein), Ross et al. (2010) and Poulin and Helwig (2012).

Class	Characteristics	Selected examples	Botanical affinity
Class I	based on polymers of labdanoid diterpenes, including especially labdatriene carboxylic acids, alcohols and hydrocarbons		
Class Ia	based on polymers and copolymers of labdanoid diterpenes (regular configuration), including communic acid and communol; incorporation of significant amounts of succinic acid	succinite: Baltic area (shores), Samland	Pinaceae? Araucariaceae? Sciadopityaceae?
		glessite: Bitterfeld, Lusatia	Burseraceae, <i>Betula</i>
Class Ib	based on polymers and copolymers of labdanoid diterpenes (regular configuration), including/not limited to communic acid, communol and biformene; devoid of succinic acid	raritan amber (New Jersey)	Cupressaceae
		Burmese amber	<i>Agathis</i> (Araucariaceae)
		New Zealand amber	<i>Agathis</i> (Araucariaceae)
Class Ic	based on polymers and copolymers of labdanoid diterpenes (enantio configuration), including/not limited to of ozic acid, ozol and enantio bioformenes; devoid of succinic acid	Mexican amber	<i>Hymenaea mexicana</i> (Fabaceae)
		Dominican amber	<i>Hymenaea protera</i> (Fabaceae)
		African amber (Zanzibar, Kenya)	
		carboniferous amber from Illinois	preconifer gymnosperm
Class Id	based on polymers and copolymers of labdanoid diterpenes with <i>enantio</i> configuration; incorporation significant amounts of succinic acid	Canadian Arctic (Nunavut) and British Columbia	unknown
Class II	based on polymer of bicyclic sesquiterpenoid hydrocarbons, especially cadinene; triterpenoid including di-sesquiterpenoid component as occluded material	Indian amber	Dipterocarpaceae (<i>Shorea</i>)
Class III	basic structural feature is Polystyrene	siegburgite: Siegburg and Bitterfeld	Hammelidaceae (<i>Liquidambar</i>)
		some New Jersey ambers	
Class IV	basic structural feature is sesquiterpenoid, based on Cedrane (IX) skeleton, non-polymeric	ionite: Pliocene of California	unknown
Class V	non-polymeric diterpenoid carboxylic acid, especially based on the abietane, pimarane and iso-pimarane carbon skeletons	<u>Highgate copalite</u> : Eocene of Highgate Hill area, London <u>settlingite</u> : Northumberland, U.K.	Pinaceae

1.5 Abundance and formation of inclusions from Baltic amber

In Baltic amber, as it is the case for many other amber deposits, animal inclusions are more abundant than plant inclusions. Especially Arthropoda are very well represented, as they comprise 80% of all animal inclusions from Baltic amber. Following the most current numbers by Weitschat and Wichard (2010), 539 families of Arthropoda were hitherto described from Baltic amber. Diptera represent the by far most abundant group of arthropods with 800 species being described, followed up

by Araneae (587 species) and Hymenoptera (448 species; Weitschat and Wichard 2010). In contrast, there are only approximately 130 species of plants (conifers and angiosperms) that were described from Baltic amber so far [based on a species list by Czechtz (1961)]. This low species number of plants is strongly connected to the low percentage of botanical inclusions in unselected samples of Baltic amber, ranging from 0.6 % to 24.9 % (Hoffeins and Hoffeins 2003, Sontag 2003), depending whether stellate plant hairs were counted individually or not (Sontag 2003). Although these estimations vary, it is clear that plant inclusions from Baltic amber are very scarce. Reasons for this rareness may be collection bias (Szwedo and Sontag 2009), but could also be related to the taphonomy of plant inclusions which, however, has not been studied yet.

For animal inclusions, certain factors which bias trapping in resin have been discussed already (Martínez-Delclòs et al. 2004, Solórzano Kraemer et al. 2015) and some of them could be considered to be of similar importance for the formation of plant inclusions. Depending on the resin viscosity and stickiness, surface tension might be too high to allow the trapping of insects into the resin. In this case, the size of the insect is a crucial factor as well: too high surface tension inhibits the intrusion of very small insect into the resin, while larger insects may penetrate the resin. However, due to their larger size, they can escape more easily (Martínez-Delclòs et al. 2004); a similar situation could hold true for plant fragments: high surface tension of resin flows might prevent plant fragments getting stuck on the resin (pers. comm. M. M. Solórzano Kraemer, Frankfurt).

As it is the case for animals, the size of a plant fragment likely biases the trapping as well: depending on resin properties, small plant remains are probably more easily retained by resin than larger ones. The location of the source tree is another crucial factor: animals which occur close to the source tree and within its immediate environment are more likely to be captured than animals outside of this area (Martínez-Delclòs et al. 2004). However, animals which occur in habitats other than that of the resin bearing plant also may be captured in amber, since they can actively move around; anyhow, they are more scarce in amber than those animals which live in close proximity to the amber source plant (Martínez-Delclòs et al. 2004). For plant inclusions, a similar situation is possible: plants located close to the source trees or those which are even epiphytic on the resin secreting plant are more likely to be abundant in amber than other plant taxa with different ecologies. For instance, inclusions of bark overgrown with the leafy liverwort *Frullania* were recently reported from Burmese amber, indicating that the liverworts were likely epiphytic and removed from the bark by a resin flow (Heinrichs et al. 2012).

In contrast to animals, plants cannot ‘actively roam around’ and get stuck to fresh resin flows, thus plants become passively stuck to the resin outpourings. It is more likely that fresh resin drops covered plant remains coincidentally, while falling on the forest floor (pers. comm. M. M. Solórzano Kraemer, Frankfurt). So-called ‘litter amber’, which was reported from French Cretaceous amber deposits, could be an indicator for that since it contained taxa which were specific for soil biotas indicating its proximity to the forest floor (Perrichot 2004). Observations from extant

habitats with resin-releasing trees, such as Araucarian forests of New Caledonia, support this idea, showing that large fresh resin flows on the forest floor covered litter and entombed plant fragments (Girard et al. 2009). Thus, inclusions of plants more likely represent local floras, originating from the same environment. However, it is also possible that plant fragments were transported passively by wind into fresh resin flows, which however, depends on the vegetation structure, since very dense forests may inhibit wind transport (Martínez-Delclòs et al. 2004).

In contrast to plants, animal behaviour can strongly influence the probability whether they get caught by resin or not. For instance, insects maybe attracted by volatile terpenoids and then accidentally be trapped on the sticky resin (Martínez-Delclòs et al. 2004). Also swarming insects are more prone than others to become inclusions (Martínez-Delclòs et al. 2004). These factors favour the entrapment of animals in resin, and as a result, they are not only more abundant than plant inclusions, but also often represent heterogeneous taphocoenoses when occurring as syninclusions (Seredszus 2003). For instance, Seredszus (2003) studied inclusions of chironomid midges and their syninclusions from Baltic amber, reporting that terrestrial and aquatic taxa often co-occurred. Seredszus (2003) argued that the swarming behaviour of insects, but also the close proximity of habitat types likely was the reason for heterogeneous taphocoenoses from Baltic amber.

In summary, plant inclusions are rarer than animal inclusions, but have a great potential to portray the immediate environment they derive from. In comparison, animal inclusions might represent an assemblage of different habitats. However, these are hypotheses that still need verification by actualistic experiments, studying and comparing certain habitat conditions and how they may influence or even bias the trapping of plants and animals in resin. Biased preservation of certain organisms in amber should always be considered when reconstructing palaeohabitats on the basis of amber inclusions. Based on the recent knowledge of the taphonomy of plant inclusions, it is challenging to estimate these biases and which group of plants might be underrepresented in comparison to others.

After being embedded into resin, several processes facilitate the formation of amber inclusions. Dehydration of the organism, comparable to mummification, is crucial to inhibit the degradation of the tissue (Henwood 1992). In some cases, it is suggested that volatile compounds of the resin diffused through cell walls and replaced the cellular water, resulting in the high-quality preservation of internal tissues (Grimaldi et al. 1994, Stankiewicz et al. 1998). Antimicrobial compounds of the resin inhibit the degradation of the inclusions by fungi and bacteria, protecting the entombed organism from decay (Martínez-Delclòs et al. 2004). However, the preservation also depends on the amber type and the diagenetic processes discussed above (chapter 1.2).

1.6 The Baltic amber mysteries

Although Baltic amber derives from the largest amber deposit worldwide and is well-known for its plethora of inclusions, its botanical provenance is still unknown and this was termed the “Tertiary Baltic Amber Mystery” (Langenheim 2003). Besides its botanical origin, more questions or ‘mysteries’ about Baltic amber exist, since its precise age, the geographical location and the extent of the source forest, its vegetation and habitat types are unknown or ambiguous as well. I have summarized all these questions as additional ‘Baltic amber mysteries’ and describe and discuss them below.

1.6.1 Geographical location of the ‘Baltic amber forest’ and the age of Baltic amber

The main source of Baltic amber is the Blue Earth layer which is characterized by a high glauconite concentration and a dark-blue clayey silt (Kasiński and Kramarska 2008, Standke 2008). The Blue Earth layer is marine and its lithology indicates near-coaststagnant water conditions, such as in lagoons and bays with low sediment input (Standke 1998, 2008). The Baltic amber deposit represents an allocthonous deposit where the amber has been washed from its source forest into the Blue Earth layer (Standke 2008). Studies of pollen, spores and phytoplankton, as well as stratigraphic and lithological studies indicated a late Eocene (Priabonian) age of the Blue Earth layer. Further but fewer amounts of amber are deposited in the Lower Blue Earth (Lutetian) and in the Lower Gestreifte Sande (upper Oligocene), resulting in an age range of 23 to 48 million years for all strata yielding Baltic amber (Kosmowska-Ceranowicz et al. 1997, Standke 1998, Aleksandrova and Zaporozhets 2008a, b, Kasiński and Kramarska 2008, Standke 2008).

Another study suggested a Lutetian age for the Blue Earth amber, using K-Ar age estimations of glauconites deriving from the Blue Earth (Ritzkowski 1997). However, Clauer et al. (2005) criticized the reliability of glauconite-based chronometers, since they often result in older age estimations. Following Clauer et al. (2005), contamination of the glauconite splits or reworking processes of the glauconites can negatively influence the results.

Nonetheless, a Lutetian or even Ypresian age of Baltic amber from the Blue Earth is still under debate. For instance, Schulz (1999), Weitschat (1997), and Weitschat and Wichard (1998) believe that the amber was formed in the early to middle Eocene and then redeposited into late Eocene sediments. The named authors argue that Baltic amber originated in vast forests of the early to middle Eocene, with its western borders around South Sweden, expanding to the east until the Ural Mountains. The northern margins of the ‘Baltic amber forest’ were located somewhere in Scandinavia, while the southern border was defined by the northern margin of the Tethys. In these forests, resin accumulated autochthonously as soil deposits. Then, resin was transported from north to south via a hypothetical river that was called ‘Eridanos’, referring to a Greek myth of Phaeton that mentions this ‘amber river’ (Kosmowska-Ceranowicz 1997a, Schulz 1999). The Eridanos river finally terminated into a large delta, covering the entire area of the Samland

peninsula up to Chłapowo (Poland; Kosmowska-Ceranowicz and Konart 1989; Kosmowska-Ceranowicz 1997a). In this delta, the transported resin was re-deposited, forming a mixed allochthonous deposit (Weitschat and Wichard 1998, Zherikhin 2002). Larsson (1978) suggested a further similar delta which was located around Kattegat and northern Jutland (Denmark), as high amounts of Baltic amber are still found along the Westcoast of Jutland today.

Weitschat (1997) and Weitschat and Wichard (1998) justify the river transport of Baltic amber with arthropod inclusions which exhibit presumed affinities to extant tropical or subtropical taxa (e.g. Psocoptera, Diopsidae; Weitschat 1997), and thus, are interpreted as indicators of a (sub)tropical 'Baltic amber forest' (see chapters 5.2 and 5.3 for more details). Corresponding tropical to subtropical climatic conditions predominated during the Eocene Climatic Optimum [ECO; early to middle Eocene (Zachos et al. 2001, Mosbrugger et al. 2005, Zachos et al. 2008)], leading to the assumption that this must have been the time period where Baltic amber was originally formed (Weitschat 1997, Weitschat and Wichard 1998, Weitschat 2008). For justifying the late Eocene age of the Baltic amber bearing sediments, Weitschat (1997) and Weitschat and Wichard (1998) suggest that a river must have existed that redeposited the amber from the early Eocene Fennoscandian regions into the late Eocene sediments of the Chłapowo-Samland delta.

Further evidence for a Lutetian age of Baltic amber are based on comparisons of Baltic amber insect faunas to middle Eocene fossil localities of Germany. Wappler (2003) compared fossil taxa of Coleoptera, Hymenoptera and Hemiptera from Baltic amber and Eckfeld Maar (Eifel, western Germany), concluding that they share numerous insect taxa which were originally described from Baltic amber. The basalt inverse isochrone age of the Eckfeld Maar is 44.3 (+/- 0.4) million years (Mertz et al. 2000) and due to mentioned similarities of their insect faunas, a middle Eocene age was also suggested for Baltic amber (Wappler 2003). Further comparative studies, including fossil bees and water striders from the Eckfeld Maar and Messel (approximately 47 Ma, early to middle Eocene; Mertz and Renne 2005, Lenz et al. 2015) also exhibited similarities in the taxonomic composition to the Baltic amber fauna, again suggesting a similar age of all three fossil localities (Wappler and Engel 2003, Wappler and Møller Andersen 2004). Besides animal inclusions, several authors also named plant inclusions which were affiliated to tropical or subtropical extant families, such as Theaceae, Palmae, Apocynaceae and others (Czeczott 1961) and thus being indicative for early to middle Eocene age (Weitschat and Wichard 1998).

In contrast to these hypotheses, Standke (1998, 2008) showed evidence for a different scenario for the Baltic amber deposition and age, as well as for the geographical locality of the 'Baltic amber forest'. Standke (2008) provided palaeogeographic maps of northern Central Europe, showing the expansion of the Palaeo-North Sea from the upper Paleocene (Thaneltian) to the middle Miocene (Serravallian). According to Standke (2008), a 'Baltic amber forest' that exclusively occurred in Fennoscandian areas seems unlikely for the middle Ypresian, since these areas were partly covered by the Palaeo-North Sea. Contrarily, Standke (2008)

suggested areas eastwards from the Palaeo-North Sea as a putative locality of the ‘Baltic amber forest’. With time, these forest areas were successively inundated by the transgressing sea. As a result, amber was transported and deposited from the forest into stillwater sediments of bays or lagoons, in and close to the Baltic amber source area (Standke 2008).

According to Standke (2008), long-distance transport of amber by the hypothetical Eridanos river is doubtful. Such a river must have had an approximate length of at least 900 km; thus, it is surprising that there is no geological evidence of this river in Palaeogene sediments of the entire Baltic Sea coast. Assuming that a relocation of amber from early Eocene Fennoscandia into late Eocene sediments took place, the delta of Eridanos must have remained unchanged for a long time period, which, following Standke (2008), seems unlikely for a fluvial system. Furthermore, Standke (2008) raised the question: how such a high amount of amber (up to 2667 g of amber per m³, in the Blue Earth; Kosmowska-Ceranowicz, 1997a) was only deposited in one specific layer, while older and younger layers do not exhibit similar large amber amounts. However, it remains unresolved how similarities between insect faunas of Baltic amber and Central European faunas of early to middle Eocene emerged. Standke (2008) pointed out that plant inclusions from Baltic amber, especially pollen, needed more attention for understanding the provenance of the ‘Baltic amber forest’. Standke (2008) proposed that the age of the Blue Earth and of Baltic amber preserved in this specific layer is almost coeval, meaning that a Priabonian age is to be expected for the majority of Baltic amber. Based on her geological analyses, she concluded that there was no hiatus between the formation and deposition of Baltic amber (Standke 2008). Thus, Standke (2008) sees no reasonable evidence for 1) an early to middle Eocene age of Baltic amber; 2) the existence of a Palaeogene Eridanos river, including long-distance amber transport and 3) a Fennoscandian origin of the ‘Baltic amber forest’.

In conclusion, the debate about the age of Baltic amber is strongly connected to the geographical location of its source forest. Two main opinions are controversially debated: 1) Baltic amber originated in early Eocene forests of Fennoscandia and was transported by rivers to the Samland-Chłapowo delta. There, the amber was finally deposited into late Eocene sediments, versus 2) Baltic amber derives from late Eocene forests and was deposited in or nearby its source forest.

1.6.2 Putative source plants of Baltic amber

For decades, scientists made efforts to find the Baltic amber source tree, suggesting several plant taxa (see Tab. 2 for summary). At least an angiosperm origin of Baltic amber succinite can be excluded due to the structure of labdanoid diterpenes: in ambers of conifer origin (Class I, including Baltic amber succinite), the optical isomers possess a regular configuration, while in angiosperm ambers these isomers exhibit an enantio configuration (Anderson and Crelling 1995; Tab. 1 for further references). For inferring the Baltic amber provenance to genus or even species level, two main approaches exist which are presented in the following text: 1)

morphological-anatomical examinations: wood inclusions or amberized wood from Baltic amber deposits which contain amber in their tissues (in-situ amber) are of special interest, since they potentially allow the linking of the amber directly to its source plant. Morphological-anatomical features of the amberized wood are used for taxonomical identification. 2) Chemical analyses: extant conifer resins and the amber itself are examined and key features of their infrared spectra and chemical structures are compared to each other. Similarities between the bulk chemistry of extant resins and ambers can indicate taxonomic affinities between the source plants.

1.6.2.1 Morphological-anatomical implications from Baltic amber inclusions

To identify the Baltic amber source tree, wood inclusions of Baltic amber were studied by several researchers to find xylotomical evidence of its taxonomic affinities. Goeppert (Goeppert and Berendt 1845) searched for wood inclusions from Baltic amber which exhibited in-situ amber, indicating that the embedded wood must have come from an amber bearing tree. Based on his anatomical studies of amberized wood, he introduced the name *Pinites succinifer* Goepp. et Berendt for describing wood inclusions from Baltic amber. ‘*Pinites*’ is a fossil morphotaxon which encompasses specimens with affinities to conifers such as *Pinus* and *Taxus*. However, in his study, Goeppert (Goeppert and Berendt 1845) emphasized similarities of the wood inclusions to extant *Pinus* and *Picea* (especially *Picea abies*). In a further study by Goeppert (Goeppert and Menge 1883), he mentioned that *Pinites succinifer* was actually rarely found in the Baltic amber flora, while specimens of another species, *Pinites stroboides* with affinities to the extant resin-rich conifer *Pinus strobus*, were more abundant. Besides these two conifers, Goeppert (Goeppert and Menge 1883) described four further conifer species from Baltic amber (*Pinites mengeanus*, *P. radiosus*, *P. anomalus* and *Physematopitys succineus*) based on wood inclusions. Due to this coniferous diversity Goeppert (Goeppert and Menge 1883) concluded that possibly more than one amber bearing conifer species existed in the Baltic amber forest. Due to the higher occurrence of *Pinites stroboides* and *P. succinifer* in Baltic amber, he suggested that both represented the main producing trees of Baltic amber.

Later, Conwentz (1886b) transferred *Pinites succinifer* to *Picea succinifera*, as he discovered wood-anatomical features of *Picea* in wood inclusions from Baltic amber. In addition, he commented on the wood inclusions which Goeppert (Goeppert and Menge 1883) designated to four further conifer species. Conwentz (1886a) included these four species into *Pinus succinifera*, stating that they all represented different developmental stages or/and parts of the same taxon. In his subsequent publication, Conwentz (1890) changed *Picea succinifera* into *Pinus succinifera*, but stressing that the differentiation between *Picea* and *Pinus* was rather difficult, since the wood inclusions were in parts insufficiently preserved.

Many years later, Schubert (1961) studied newly discovered wood inclusions from Baltic amber and confirmed affinities to *Pinus*, and hence, suggested the retention of the taxon *Pinus succinifera*; contrary to Conwentz (1890), Schubert

(1961) could not confirm affinities to extant *Picea*. A reinvestigation of Conwentz' holotype of *Pinus succinifera* by Dolezych et al. (2011) once again confirmed similarities to *Pinus*, but with affinities to extant subgenus *Strobus* LEMMON and to sections *Parraya* and *Strobus*.

Tab. 2: Suggested source plants of Baltic amber. Adapted from Poinar (1992) and amended with more recent research results, taken from references indicated in the last column. + indicates the presence and – indicates the absence of the respective fossil evidence.

Suggested source plant	Type of examination	Suggested affinities to extant taxa	Confirmed fossil evidence from Baltic amber	References
Pinaceae				
<i>Pinus</i> sp.	morphological-anatomical chemical analysis	<i>Pinus</i>	+ <i>Pinus</i> spp. (wood, needles)	Aycke 1835; Schubert 1961; Rottländer 1970; Dolezych et al. 2011; Sadowski et al. 2017a
<i>Pinites succinifer</i> Goeppert	morphological-anatomical	Pinaceae	–	Goeppert 1836
<i>Abies bituminosa</i> Haczewski	morphological-anatomical	<i>Abies</i>	+ <i>Abies</i> sp. (needles)	Haczewski 1838; Sadowski et al. 2017a [5]
<i>Pinites succinifer</i> Goeppert et Berendt	morphological-anatomical	<i>Pinus</i> (especially <i>P. abies</i>) and <i>Picea</i>	–	Goeppert and Berendt 1845
<i>Pinites succinifer</i> Goeppert	morphological-anatomical	<i>Pinus, Abies, Larix</i>	+ <i>Pinus</i> spp. (wood, needles)	Goeppert and Menge 1883; Schubert 1961; Dolezych et al. 2011; Sadowski et al. 2017a [5]
<i>Pinites storobides</i> Goeppert		<i>Pinus strobus</i>	+ <i>Abies</i> sp. (needles)	
<i>Pityoxylon succiniferum</i> Kraus	morphological-anatomical	<i>Pinus</i> or <i>Picea</i>	–	Schimper 1870-72
<i>Picea succinifera</i> Conwentz	morphological-anatomical	<i>Picea</i>	–	Conwentz 1886a
<i>Pinus succinifera</i> (Göppert) Conwentz	morphological-anatomical	<i>Pinus</i> and <i>Picea</i>	+ <i>Pinus</i> spp. (wood, needles)	Conwentz 1890; Schubert 1961; Dolezych et al. 2011; Sadowski et al. 2017a [5]
<i>Pinus succinifera</i> (Conwentz) emd. Schubert	morphological-anatomical	<i>Pinus</i>	+ <i>Pinus</i> spp. (wood, needles)	Schubert 1961; Dolezych et al. 2011; Sadowski et al. 2017a [5]
<i>Pinus</i> sp.	resin analysis (?)	<i>Pinus halepensis</i>	+ <i>Pinus</i> spp. (wood, needles)	Schubert 1961; Mosini and Samperi 1985; Dolezych et al. 2011; Sadowski et al. 2017a [5]
<i>Pinuxylon succiniferum</i> (Goeppert) Kräusel emd. Dolezych	morphological-anatomical infrared spectroscopy	<i>Pinus</i> (section <i>Parrya</i> or <i>Strobus</i>)	+ <i>Pinus</i> spp. (wood, needles)	Kräusel 1949; Dolezych et al. 2011; Sadowski et al. 2017a [5]
<i>Cedrus</i> sp.	infrared spectroscopy	<i>Cedrus atlantica</i>	–	Stroganov 1987; Weitschat and Wichard 2010
<i>Pseudolarix</i> sp.	Py-GC-MS analyses	<i>Pseudolarix amabilis</i>	+ <i>Pseudolarix</i> sp.	Anderson and LePage 1995; Grimaldi 1996; Sadowski et al. 2017a [5]
Araucariaceae				
<i>Agathis</i> sp.	infrared spectroscopy, chemical analysis, pyrolysis mass spectrometry	<i>Agathis australis</i>	–	Langenheim 1969; Gough and Mills 1972; Poinar and Haverkamp 1985
Sciadopityaceae				
<i>Sciadopitys</i> sp.	FTIR microspectroscopy	<i>Sciadopitys verticillata</i>	+ <i>Sciadopitys</i> cf. <i>tertiaria</i>	Wolfe et al. 2009; Sadowski et al. 2016a [3]

1.6.2.2 Chemical analyses for inferring the Baltic amber tree

The most widely used method to study amber is infrared spectroscopy (IR). This method allows the characterizing and distinguishing of amber samples by their spectroscopic fingerprints (Lambert et al. 2008). For instance, Beck et al. (1964) applied IR analyses to ambers, showing that it is a useful tool to differentiate between ambers from various deposits. In later studies, IR spectra of ambers and extant resins were compared, showing correlations between extant *Hymenaea* resins (Fabaceae) and amber of Chiapas (Mexico), as well as affinities of Miocene amber of Sumatra to *Shorea* resins of the Dipterocarpaceae (Langenheim and Beck 1965). Thus, IR became a frequently used method to assess the botanical origin of amber (Kosmowska-Ceranowicz 1999, 2015).

In IR studies of Baltic amber, the spectra show a specific feature, ‘the Baltic shoulder’, which is an “easily recognizable absorption band of medium intensity [...] which is preceded by a more or less flat shoulder” (Langenheim and Beck 1965, p. 52). Despite this specific pattern, there was no extant conifer resin so far showing a similar IR spectrum (Langenheim 1969). Thus, Langenheim (1969) assumed that extant conifer resins may lack the Baltic shoulder due to evolutionary changes of the resin. Alternatively, Langenheim (1969) suggested *Agathis* (Araucariaceae) as source tree of Baltic amber, since extant *Agathis australis* is known to produce large resin amounts which formed extensive copal deposits in New Zealand (Langenheim 2003). She also mentioned similarities between the IR spectra of *Agathis* resins and Baltic amber, highlighting the presence of agathic acid type diterpenes in Baltic amber. Despite this chemical evidence, araucarian resins are devoid of succinic acid. Moreover, inclusions of Araucariaceae have not been reported from Baltic amber (Langenheim 1969), and there is no unambiguous fossil evidence of Araucariaceae from any other European fossil deposit of the Palaeogene yet (Eckenwalder 2009). Thus, the presumed affinities of Baltic amber to Araucariaceae were often questioned.

Previous studies and advanced methods provided new theories on the botanical origin of Baltic amber and how to assess it. A further method involving IR is Fourier transform infrared spectroscopy (FTIR) which allows studying resin and amber chemistry with even small sample sizes and without elaborated sample preparations (Wolfe et al. 2009, Tappert et al. 2011). In Seyfullah et al. (2015 [1]¹) FTIR was applied to extant resins taken from Araucariaceae (*Agathis australis*, *Ag. lanceolata*, *Ag. ovata*, *Araucaria heterophylla*, *Ar. humboldtensis*, *Ar. nemorosa* and *Wollemia nobilis*) in order to compare their resin spectra with the absorption spectra of Miocene ambers from the Idaburn coal mine of central Otago, New Zealand. Key features in the FTIR spectra of the extant araucarian resins and the amber were compared, revealing that FTIR is a useful tool to assess even interspecific variations in resin chemistry and to draw conclusions about the botanical affinities of amber. In

¹ References to papers included in this thesis are indicated by bold numbers in brackets after the year of publication which refers to the respective appendix.

this case, the Idaburn amber exhibits most similarities to extant *Agathis australis*, indicating that the amber source plant was affiliated to this taxon (Seyfullah et al. 2015 [1]).

Based on IR and FTIR studies, further conifers have been suggested as Baltic amber source plants, comprising several taxa of the Pinaceae and Sciadopityaceae (see Tab. 2 for extensive list and references and chapter 4.1.4 for detailed discussion). However, no consensus about the botanical provenance of Baltic amber has been found so far.

1.6.2.3 Succinic acid – key component or diagenetic product?

As already mentioned, succinic acid is a key feature of Class Ia (Baltic) and Id ambers, (Rottländer 1970, Anderson et al. 1992, Tonidandel et al. 2009). This key feature has been, however, widely discussed among scientists since its origin is unresolved. Therefore, the significance of succinic acid for assessing the Baltic amber source plant is not yet clarified.

In his study, Rottländer (1970) argued that succinic acid is part of the “soluble fraction of amber [which] is the result of degradation” and “thus, by no means [is] indicative of its origin” (Rottländer 1970, p. 35 and 48). It has further been suggested that succinic acid is a byproduct of the microbial degradation of phytosterols which are abundant in plants (Schubert et al. 1969, Szykuła et al. 1990). Kosmowska-Ceranowicz et al. (2008) reported microcrystals comprising succinic acid from Baltic amber and supposed that they must have been formed through high temperatures associated to climatic changes in the past. Also Wolfe et al. (2009) argue that succinic acid rather goes back to diagenetic and degradation processes after the burial of resin in its sediment.

The remarkably high percentage of succinic acid in Baltic amber (1-8%; Ragazzi and Schmidt 2011) is in contrast to its absence (or low concentration) in extant conifer and angiosperm trees. This fact supports the idea of its diagenetic origin (Wolfe et al. 2009); however, at the same time Wolfe et al. (2009) stated that they detected succinic acid in extracts of *Pinus ponderosa* needles. Hence, further studies are necessary to explain absence and presence of succinic acid in amber and extant resins, as well as its significance for identifying the botanical origin of Baltic amber.

1.6.3 The enigmatic ‘Baltic amber forest’

The ‘Baltic amber forest’ is a term describing the Baltic amber source vegetation. However, numerous perceptions about this palaeoecosystem exist, comprising partly contradictory opinions about its floristic composition, habitat types, climate and the topography of the source area (see Tab. 3 for summary and references). Thus, the ‘Baltic amber forest’ is a rather abstract term, representing one (or more) palaeoecosystem(s) which harboured the Baltic amber source plant(s). Therefore, the term ‘Baltic amber forest’ will be written in quotation marks in the following text.

Historic descriptions of the ‘Baltic amber forest’ divide the amber source area into lowlands and mountains in which subtropical to warm-temperate plant taxa inhabited lowland areas while plant taxa with extant analogues in the northern high latitudes grew in higher elevations (Goepfert 1853, Caspary 1872a, Goepfert and Menge 1883). Following these authors, the ‘Baltic amber forest’ had affinities to extant floras of northern America, East Asia and Europe. Contrarily, Conwentz (1890) highlighted the dominance of pines which formed pure and dense stands. In his opinion, further deciduous tree species were scarce and only located at the margins of pine forests. Also, Conwentz (1890) mentioned that it must have been a humid and warm forest in which, however, snowfall occurred.

Based on insect inclusions, Ander (1942) concluded that the Baltic amber source area harboured many kinds of aquatic habitats. He divided the ‘Baltic amber forest’ into altitudinal zones and based on studies of Baltic amber plant inclusions from the 19th century, Ander (1942) describes the ‘Baltic amber forest’ as dense and moist, with affinities to extant forests of Central China and North America. Following his interpretation, the forest was dominated by conifers, but intermingled with oaks. Further broad-leaved deciduous trees and shrubs were only located in open glades or along southern slopes. In Ander’s opinion (1942), the main climate was humid, warm-temperate and only locally subtropical. In a comprehensive review, Czechtz (1961) agreed with Ander’s (1942) interpretations, but highlighted the high proportion of tropical and subtropical plant taxa (e.g. Apocynaceae, Araceae, Lauraceae and Theaceae) which comprised 23 % of all plant taxa from Baltic amber while temperate taxa only constitute 12 %. Due to the presence of temperate taxa along with tropical ones, Czechtz (1961) concluded that the source area of Baltic amber was mountainous with a warm-temperate to subtropical climate. Further studies on the ‘Baltic amber forest’ by Bachofen-Echt (1949) and Larsson (1978) draw a similar picture and only differ from other interpretations in few details. Bachofen-Echt (1949) emphasized the diversity of the Baltic amber source area, comprising meadows, arid areas, but also stagnant waters and mixed forests. In contrast, Larsson (1978) underlined the diversity of *Quercus* species, but only saw little evidence for the presence of meadows.

Contrarily to these perceptions of the ‘Baltic amber flora’, Schubert (1953, 1961) and Ruffle and Helms (1970) found indicators for drier climates with affinities to ‘hammocks’ of Florida and mountain steppe forests of Cuba and Honduras. Following their interpretation, subtropical and sclerophyllous woods with pines and

palms dominated the lowland of the Baltic amber source areas, while mountainous sides were inhabited by pine-oak forests (Rüffle and Helms 1970). Kohlman-Adamska (2001) differentiated between altitudinal zones with specific vegetation types and climates: swamps habitats close to subtropical lowland river systems, pine-oak-steppe forests in mid-altitudinal warm-temperate zones and pure conifer stands on temperate high altitudes. Contrarily, Weitschat (1997), Wichard et al. (2009) and Weitschat and Wichard (2010) interpreted Baltic amber arthropod inclusions as evidence for tropical rain forests in lowland areas and subtropical to warm-temperate oak-pine forests at higher elevations of Fennoscandia.

The most recent summary on the 'Baltic amber forest' was published by Alekseev and Alekseev (2016) who used beetle inclusions from Baltic amber to estimate the habitat types. Along with historic and recent literature on the Baltic amber plants, they concluded that the forest was a climax community, located in a plain landscape. In contrast to the other mentioned interpretations above, they did not see evidence for mountain ranges in the Baltic amber source area, although hills (300 m above sea level) might have been present (Alekseev and Alekseev 2016). Based on their study, the 'Baltic amber forest' was thermophilous, moist and layered. Contrasting with Kohlman-Adamska (2001), Alekseev and Alekseev (2016) denied the presence of any inundated areas such as swamps, but instead underlined the presence of different kinds of stagnant waterbodies. As mentioned by other authors before, they also saw affinities to East and Southeast Asian forests.

In summary, the 'Baltic amber forest' is still controversial and strongly disparate theories about its vegetation exist. Most studies about the Baltic amber source area state that it was a humid, warm-temperate to 'subtropical' forest. Following these studies, conifers, especially pines, were dominant, while broad-leaved deciduous plant taxa intermingled (rarely) with pine forests or grew in more open areas. In contrast, other studies found evidence for tropical or dryer climates and vegetation (see Tab. 3 for summary). These conflicting theories also evoked speculative ideas about a Fennoscandian locality and a vast and mountainous distribution area of the 'Baltic amber forest', as well as different age estimations for Baltic amber. It is noteworthy that the majority of the mentioned studies are either based on analyses of arthropod inclusions or on interpretations of plant inclusions that were published much earlier by Goeppert and Berendt (1845), Goeppert (1853), Goeppert and Menge (1883), Conwentz (1886b, 1890), and Caspary and Klebs (1907). Since the 19th century, the majority of these plant inclusions have not been restudied. Besides literature based revisions by Czecczott (1961) and Spahr (1993), there were no new comprehensive studies about plant inclusions from Baltic amber. This lack of knowledge contributes to the vast number of contrasting theories about the 'Baltic amber forest'.

Tab. 3: Perceptions of the ‘Baltic amber forest’, taken from references indicated in the first column. Results of this thesis are indicated in the last row.

Reference	Particular characteristics	Topography	Habitats and vegetation	Climate		Affinities to extant floras	Age of Baltic amber
Dense and close pine forests, broad-leaved deciduous taxa scarce							
Conwentz 1890	pinus as dominant tree taxa	-	amber source trees (pinus) formed closed, pure stands; broad-leaved deciduous trees scarce and rarely intermingling with pine forests	humid, warm, but also snowfall		North America, East Asia	Eocene
Warm-temperate to subtropical forest, humid, mountainous							
Caspary 1872a Goepfert and Menge 1883 Goepfert 1853	-	lowlands	subtropical and warm-temperate species	subtropical or at least warm-temperate		floras of northern latitudes of the USA and Europe	middle Miocene or Pliocene
		mountains	plant taxa with extant analogues in northern high latitudes				
Ander 1942	different kinds of aquatic habitats	altitudinal zones	- broad-leaved deciduous trees and shrubs only in open glades or along southern slopes - dense moist forest	warm-temperate, only locally subtropical, humid		Central China North America	upper Eocene to lower Oligocene
Czeczott 1961	high proportion of tropical and subtropical plant taxa	mountainous	- conifers, mixed with <i>Quercus</i> species	subtropical to warm-temperate		-	Eocene
Bachofen-Echt 1949	diverse landscape and biota	lowlands mountains	- mixed forests with conifers and broad-leaved deciduous trees - meadows, arid areas - stagnant water bodies	-		‘Malaya’	early Eocene?
Larsson 1978	- conifers and <i>Quercus</i> species very dominant and diverse - few meadows - Holarctic and subtropical elements	lowlands mountains/hills	subtropical lowland flora temperate flora	seasonal		Assam-Burma-Yunnan flora	Eocene
Kohlman-Adamska 2001	<u>presence of two geofloras:</u> - Arcto-Tertiary geoflora - Palaeotropical geoflora	lowlands mountains	humid swamp habitats along river valleys pine-oak steppe forests in lower mountainous areas pure conifer forests at higher altitudes	subtropical warm-temperate temperate		-	early Palaeogene
Subtropical to cold-temperate forest, ‘hammock’-like, dry, mountainous							
Schubert 1953, 1961 Rüffle and Helms 1970	-	lowlands mountains	- pine-palm-woods - sclerophyllous pine woods along rivers - subtropical vegetation along coast pine-oak forests	warm, subtropical cold-temperate	dry	‘hammocks’ of Florida, mountain steppe forests of Cuba and Honduras	-
Tropical to subtropical rain forest, mountainous							
Weitschat 1997, 2008 Weitschat and Wichard 1998, 2010 Wichard et al. 2009	various aquatic habitat types	lowlands mountains	tropical rain forest subtropical to warm temperate oak-pine forests	tropical subtropical	extremely warm and humid	-	early Eocene to middle Eocene (Lutetian)
Thermophilous, humid, broad-leaved forest in a plain landscape							
Alekseev and Alekseev 2016	forest was a climax community	plain landscape to slightly hilly	- thermophilous, moist, broad-leaved forest - stagnant waterbodies (acidophilous, dystrophic, oligotrophic), streams, no inundated areas - layered forest	humid		plain forests of East and Southeast Asia, especially China	-
Humid, warm-temperate, heterogeneous mosaic-like, plain landscape							
Sadowski et al. 2016a [3], b [4]; 2017a [5], b [6]	- heterogeneous: various habitat types - high conifer diversity	plain landscape	- <u>coastal swamps</u> : brackish-water influenced areas and raised bogs - <u>back swamps and riparian forests</u> : inundated (non-brackish) - mixed-mesophytic conifer-angiosperm forests with meadows	humid, warm-temperate		East Asia, North America	late Eocene (Priabonian)

2. Aims of this thesis

As shown in the introduction, many questions or mysteries arise when studying Baltic amber inclusions, especially regarding the Baltic amber source area. These mysteries mainly comprise the following questions: What did the ‘Baltic amber forest’ look like in terms of its structure, habitats, and vegetation? Which palaeoclimatic conditions prevailed in the ‘Baltic amber forest’? Does the Baltic amber flora reflect an altitudinal stratification of its source ‘forest’? Where was the ‘Baltic amber forest’ located? What was the Baltic amber source plant? In order to contribute to solving these Baltic amber mysteries, it is the aim of this thesis to develop a new picture of the ‘Baltic amber forest’. As explained above, a huge gap in knowledge about plants from Baltic amber exists, as they are less studied than animal inclusions. However, botanical inclusions from Baltic amber are the key to understanding its source forest and therefore, are predominantly used in this thesis.

As the first step, descriptions and taxonomic identification of plant inclusions from Baltic amber are necessary. Therefore, described plant inclusions from historic museum collections are reinvestigated and described, and botanical inclusions of new specimens from private and museum collections are identified (Tab. 4 shows a complete list of these collections and their affiliations). This gives new insights into the Baltic amber flora and its diversity, and might even yield new candidates as possible Baltic amber source plant(s).

As the second step, a palaeobiological analysis of the plant inclusions is conducted. Identified plant taxa from Baltic amber are compared to their extant analogues (actualistic approach) and fossil relatives. With this comparison, the following information about certain plant taxa from Baltic amber are collected: ecosystem and habitat preferences, climatic requirements, and specific adaptations to their environment (e.g. life forms, associations). The results of this comparison are applied to the ‘Baltic amber forest’ to finally draw conclusions from habitat types and structure, palaeoecology and palaeoclimatic conditions of the Baltic amber source area. As last step, previous assumptions about the ‘Baltic amber forest’ are evaluated with respect to the new results of Baltic amber plant inclusions. It is tested whether these previous reconstructions of the ‘Baltic amber forest’ are still valid, and whether or how they should be improved and complemented.

A new perspective on the source area of Baltic amber supports interpreting the numerous arthropod inclusions from Baltic amber in terms of their palaeobiology and palaeobiogeography. Furthermore, fresh insights into the ‘Baltic amber forest’ contribute to the understanding of the European Palaeogene vegetation, and to the evolutionary and biogeographical history of certain plant taxa.

3. Material and methods

3.1 Specimens investigated

For revising and studying plant inclusions from Baltic amber, holotypes and further original specimens described and published by Goeppert and Berendt (1845), Goeppert (1853), Menge (1858), Goeppert and Menge (1883), Caspary (1872a, b, 1886), Conwentz (1886a, b, 1890), and Caspary and Klebs (1907) were reinvestigated and evaluated. Although their collections have been preserved over the last centuries, they are incomplete since many specimens were lost during World War II, including several type specimens (Kosmowska-Ceranowicz 1990).

In order to find holotypes of plant inclusions and non-described specimens from Baltic amber, several historic amber collections were screened. Private amber collections including recently found amber pieces provided by several private collectors were also used in this study (see Tab. 4 for an extensive list). For revising holotypes whose whereabouts are unknown, historic literature (cited above), which supplied detailed descriptions and illustrations of the respective specimen, was used.

Tab. 4: Baltic amber collections examined for this thesis.

Name of collection	Institution
Königsberg Amber Collection	Geoscientific Museum, Geowissenschaftliches Zentrum (GZG), University of Göttingen
Hoffeins Amber Collection	Geoscientific Museum, Geowissenschaftliches Zentrum (GZG), University of Göttingen
Berendt Amber Collection	Museum für Naturkunde Berlin (MB), Germany
Künow Amber Collection	Museum für Naturkunde Berlin (MB), Germany
Carsten Gröhn Amber Collection	Glinde; in parts at the Geological-Palaeontological Institute and Museum of the University of Hamburg (GPIH)
Jürgen Velten Amber Collection	Idstein, Germany
Jörg Wunderlich Amber Collection	Hirschberg an der Bergstraße, Germany

3.2 Preparation, microscopy and imaging

The majority of specimens used in studies involved in this thesis had already been prepared in the past by the respective collector(s) and/or former curators. However, some specimens showed scratches and fissures that cause light diffraction which does not allow an optimal visualization of the inclusions. For this reason, the respective amber specimens were carefully ground manually by using wet silicon carbide papers of different grit sizes (Struers company). The grinding was conducted in stages (500-800-1200-2400 grits) and terminated with a final polish, using a 4000-grit carbide paper and a leather polishing cloth with a tooth paste suspension (abrasive tooth pastes, e.g. Blend-a-med classic or Colgate). The ground facet had to be smooth and parallel orientated to the inclusion for an optimal view on its morphological details [see Nascimbene and Silverstein (2000) for detailed protocols on the grinding and polishing procedures]. For specimens that were embedded into high-grade epoxy resin (see chapter 3.3) a grinding machine (Buehler Eco Met 250) was used to create a smooth and even facet. The mechanical grinding procedure was

the same as already described for manual grinding; however, the grit sizes were different, ranging from 80-320-600-1200-2500 grits. The final polish was conducted with a polishing cloth (VerduTex, Buehler) and a polycrystalline diamond suspension (MetaDi Supreme, Buehler). The polishing was done in stages, starting with a procrystalline diamond particle size of 3 μm and terminating with 1 μm particle size.

Each specimen was placed on an object slide and topped by a drop of water and a coverslip. The specimens were examined with Carl Zeiss microscopes (stereo microscopes Stemi 508 and Stereo Discovery V8, and a compound microscope AxioScope A1), using incident and transmitted light simultaneously. Inclusions were photographed using Canon EOS 5D digital cameras installed on each microscope. To accommodate the three-dimensionality of the inclusions, the software package HeliconFocus 6.0 was used to digitally stack the individual focal planes (up to 120 single images) in to one photomicrographic composite. For overview images of large specimens, up to four photomicrographic composites of the respective specimen were merged, applying the Adobe Photoshop CS6 software. Using a micrometer eyepiece, important morphological characteristics of each specimen were measured.

3.3 Permanent preparation

Some amber specimens exhibited deep fissures and cracks that extended to the inclusion. This facilitates deterioration of the amber inclusions, destabilizes the entire specimen and also impairs the optimal view of the inclusion (Nascimbene and Silverstein 2000, Pastorelli 2009, Bisulca et al. 2012). To stabilize amber specimens and to fill deep fissures, some specimens were embedded in a mixture of high-grade Epoxy resin (EPO-TEK 301-2, Part A) and hardener (EPO-TEK 301-2, Part B), following in parts the protocol by Nascimbene and Silverstein (2000). Before mixing both components, they were stirred beforehand to re-disperse settled particles. 17.5 g of Epoxy resin was weighed out and placed in a small plastic container (volume 4 cl); 7 g of hardener was added and both components were mixed with a glass rod until striations disappeared. If numerous air bubbles occurred during the mixing process, the air was released by placing the container for a short time into a vacuum drying oven (VO 200, with pump module PM 200, Memmert company) until a vacuum of 50 mbar was reached.

Meanwhile, each amber specimen was glued into a chamber of silicon ice cube trays (Lurch company), using Epoxy-Minute Adhesive (Weicon company). This is a fast-curing transparent epoxy resin with double cartridges, containing adhesive resin and hardener. After rejecting the first amounts of the double syringe on a mixing pad (Omnicent company), both components were mixed thoroughly with a wooden pick. Very small drops of this mixture were applied into the silicon moulds to attach the specimen to the bottom. This prevents the ‘floating up’ of the specimens during the embedding process. The Epoxy-Minute Adhesive needs to cure for about 30 minutes for a handling strength of approximately 35 %.

Under a fume hood and using a plastic pipette, the epoxy resin-hardener mix was added to each chamber containing a specimen, covering the entire amber piece at least 1-2 mm above the upper facet. Then, the silicon mould was set into the vacuum chamber (adjust vacuum to 50 mb) and remained there for at least 15 minutes to ensure that the epoxy permeated the entire amber specimen. Air bubbles which remained in the epoxy resin were removed with a needle afterwards. For curing, the mould, including all embedded specimens, was placed into a fume hood for at least 3 days. Later, specimens were ground and polished, as described in chapter 3.2.

4. Plant inclusions: their contribution to the understanding of vegetation, palaeoecology and habitat structure of the ‘Baltic amber forest’

4.1 Conifers

4.1.1 Unexpected conifer diversity of the Baltic amber flora

Conifer inclusions from Baltic amber are of particular interest, since one (or several) of them might be the Baltic amber source plant. During the last centuries, numerous authors published comprehensive studies about coniferous inclusions from Baltic amber and described numerous taxa (Goeppert and Berendt 1845, Goeppert 1853, Goeppert and Menge 1883, Conwentz 1886a, 1890, Caspary and Klebs 1907). Czezzott (1961) revised this literature of plant inclusions from Baltic amber, including conifers, and established a list of fossil plants from Baltic amber. She further excluded synonyms and false identifications, as well as plant fossils which were listed as amber inclusions, but actually were found nearby or impressed on amber. Among conifers, Czezzott (1961) named 33 fossil species (see Tab. 5 for an amended list), including Pinaceae (3 genera, 11 species), ‘Taxodiaceae’ (2 genera, 4 species) and Cupressaceae (5 genera, 18 species). Taxa in addition to those listed by Czezzott (1961) were published by Pielńska (2001), Jähnichen (1998) and Dörfelt and Schmidt (2007) who described four additional taxa (*Cupressus* sp., *Picea baltica*, *Thuja* sp. and *Taiwania schaeferi*) from Baltic amber. A further literature-based summary was presented by Spahr (1993) who published a comprehensive bibliography about plant inclusions, including Baltic amber. However, until a recent study (Sadowski et al. 2017a [5]), no revision of coniferous plant inclusions, which was based on literature and amber specimens, including holotype material, was published.

Sadowski et al. (2016a [3], 2017a [5]) verified ten genera of four conifer families, including several holotype specimens (Tab. 5). In comparison to the revision of Baltic amber conifers by Czezzott (1961), new taxa were added to the list (Tab. 5). Czezzott (1961) named three genera of Pinaceae (*Abies*, *Pinus* and *Picea*) of which two (*Abies* and *Pinus*) were confirmed by Sadowski et al. (2017a [5]). These authors also added further genera which were previously unknown from Baltic amber. Thus, the number of pinaceous genera from Baltic amber increased to five (*Abies*, *Cathaya*, *Nothotsuga*, *Pinus* and *Pseudolarix*).

In their revision of needle inclusions of *Pinus* species, Sadowski et al. (2017a [5]) distinguished four species: *Pinus baltica*, *P. cembraefolia*, *P. serrata* and *P. aff. schiefferdeckeri*, including one species (*P. serrata*) that Czezzott (1961) had eliminated from her list. A further species, *P. silvatica*, was found to be synonymous with *P. cembraefolia* and can thus be excluded from the list of conifers from Baltic amber. Due to missing holotypes, Sadowski et al. (2017a [5]) could not revise four further pine species (*Pinus banksianoides*, *P. dolichophylla*, *P. künowii*, *P. triquetrifolia*) which were described from Baltic amber over 100 years ago (see Tab.

Tab. 5: Updated list of coniferous inclusions from Baltic amber, taken from Czezcott (1961; and references therein) and based on more recent studies (see references). Revised taxa are indicated by *; recently verified taxa are highlighted in blue; doubtful taxa are highlighted in red; taxa mentioned by Pielnińska (1990) in a shortened list without further details are indicated by †.

Name	Kind of remain	Comment	Reference	
Cupressaceae				
<i>Athrotaxis</i> †	?		Pielnińska 1990	
<i>Calocedrus</i> sp.	twig fragments		Sadowski et al. 2017a [5]	
<i>Chamaecyparis casparyi</i> *	twig fragment male cone	shoot type 2	Czezcott 1961; Sadowski and Kunzmann (unpublished)	
<i>Chamaecyparis massiliensis</i> *†	twig fragments	shoot type 1	Czezcott 1961; Pielnińska 1990; Sadowski and Kunzmann (unpublished)	
<i>Chamaecyparis mengineanus</i>			Czezcott 1961	
<i>Cupressus</i> sp.†			Pielnińska 2001	
<i>Cupressites linkianus</i> *	male cones	pollen cone type 1	Caspary and Klebs 1907; Czezcott 1961; Sadowski and Kunzmann (unpublished)	
<i>Cupressites schenkii</i>		<i>Cupressites</i> Brongniart 1828 is based on a vegetative shoot from the lower Triassic, and should not be retained for Eocene cones		
<i>Cupressites hartmannianus</i>				
<i>Cupressites sommerfeldii</i>				
<i>Cupressites sambiensis</i>				
<i>Cupressites conwentzii</i>				
<i>Cupressinanthus polysuccus</i>				
<i>Cupressinanthus magnus</i> *		affinities to ? <i>Glyptostrobus</i> (pollen cone type 3)		
<i>Glyptostrobus europaeus</i> *	twig fragments	affinities to ? <i>Cupressospermum saxonicum</i> (shoot type 3)	Caspary and Klebs 1907; Kunzmann 1999; Sadowski et al. 2017a [5]; Sadowski and Kunzmann (unpublished)	
<i>Juniperus major</i>	male cones		Caspary and Klebs 1907; Czezcott 1961	
<i>Juniperus minor</i>				
<i>Libocedrus subdecurrens</i>	twig fragments		Sadowski et al. 2017a	
<i>Quasisequoia couttsiae</i>			Caspary and Klebs 1907; Czezcott 1961	
<i>Sequoia sternbergii</i>			Caspary and Klebs 1907; Czezcott 1961; Sadowski et al. 2017a [5]	
<i>Sequoia couttsiae</i> *		? <i>Quasisequoia couttsiae</i>		
<i>Sequoia brevifolia</i>			Caspary and Klebs 1907; Czezcott 1961	
<i>Sequoia langsdorffii</i> †			Pielnińska 1990	
<i>Taiwania schaeferi</i> *			synonym of <i>Quasisequoia couttsiae</i>	Jähnichen 1998; Sadowski et al. 2017a [5]
<i>Taxodium</i> sp.				Sadowski et al. 2017a [5]
<i>Thuites succineus</i> *			shoot type 1	Caspary and Klebs 1907; Czezcott 1961; Knobloch 1971; Sadowski and Kunzmann (unpublished)
<i>Thuites carinatus</i>			<i>Thuites</i> introduced by Sternberg 1825 is not equivalent to <i>Thuites</i> from Baltic amber	
<i>Thuites lamelliformis</i>				
<i>Thuites borealis</i>				Pielnińska 1999, 2001
<i>Thuja</i> sp.†				
<i>Widdringtonites oblongifolius</i> *		synonym of <i>Quasisequoia couttsiae</i>	Caspary and Klebs 1907; Czezcott 1961; Sadowski et al. 2017a [5]	
<i>Widdringtonites oblongifolius</i> var. <i>longifolius</i>		type material of mid-Cretaceous <i>Widdringtonites</i> lacks confirmation	Caspary and Klebs 1907; Czezcott 1961; L. Kunzmann (pers. comm.)	
<i>Widdringtonites lanceolatus</i>				
Geinitziaceae				
<i>Cupressospermum saxonicum</i>	twig fragment	synonym of one specimen of ? <i>Glyptostrobus europaeus</i> , exclusively from Baltic amber	Caspary and Klebs 1907; Kunzmann 1999; Sadowski et al. 2017a [5]	
Pinaceae				
<i>Abies</i> sp.	needles		Sadowski et al. 2017a [5]	
<i>Abies obtusifolia</i> *		synonyms of <i>Dicotylophyllum</i> var. sp. (Angiospermae)	Goepfert and Menge 1883; Caspary and Klebs 1907; Czezcott 1961; Sadowski et al. 2017a [5]	
<i>Abies linearis</i> *				
<i>Abies suckerii</i> *				
<i>Picea engleri</i>		Conwentz 1890; Czezcott 1961		
<i>Picea baltica</i>	seedling	provisional description	Dörfelt and Schmidt 2007	
<i>Cathaya</i> sp.	needles		Sadowski et al. 2017a [5]	
<i>Nothotsuga protogaea</i>			Sadowski et al. 2017a [5]	
<i>Pinus baltica</i> *			Conwentz 1890; Czezcott 1961; Sadowski et al. 2017a [5]	
<i>Pinus banksianoides</i>			Goepfert and Menge 1883; Czezcott 1961	
<i>Pinus cembraefolia</i> *		synonym of <i>Pinus silvatica</i>		Caspary 1886; Conwentz 1890; Caspary and Klebs 1907; Czezcott 1961; Sadowski et al. 2017a [5]
<i>Pinus dolichophylla</i>				Caspary and Klebs 1907; Czezcott 1961
<i>Pinus künowii</i>				
<i>Pinus serrata</i> *				Caspary and Klebs 1907; Sadowski et al. 2017a [5]
<i>Pinus</i> aff. <i>schiefferdeckeri</i> *			synonyms of ? <i>Pinites rigidus</i> , ? <i>Pinus subrigida</i> , ? <i>Pinus rigida</i>	Goepfert and Berendt 1845; Goepfert 1853; Goepfert and Menge 1883; Caspary and Klebs 1907; Czezcott 1961; Sadowski et al. 2017a [5]
<i>Pinus silvatica</i> *			synonym of <i>Pinus cembraefolia</i>	Goepfert and Menge 1883; Czezcott 1961; Sadowski et al. 2017a [5]
<i>Pinus triquetrifolia</i>				Goepfert and Menge 1883; Czezcott 1961
<i>Pseudolarix</i>				Sadowski et al. 2017a [5]
Sciadopityaceae				
<i>Sciadopitys</i> cf. <i>tertiaria</i>	needles		Sadowski et al. 2016a [3]	
<i>Sciadopityes glaucescens</i> *		?angiosperm leaves	Goepfert and Menge 1883; Czezcott 1961; Sadowski et al. 2016a [3]	
<i>Sciadopityes linearis</i> *				

5). Czekcrott (1961) estimated that about eight *Pinus* species are to be expected from Baltic amber. However, Czekcrott (1961) only considered pine needle inclusions and excluded male cones and wood inclusions of *Pinus* from her list, arguing that they might represent the same species as the needles. This procedure is arguable, since specimens are excluded whose affinities are not clarified yet. This could artificially delimit the actual species number of *Pinus* from Baltic amber and thus, Czekcrott's (1961) list also needs further revisions in the future. Based on the new findings of Sadowski et al. (2017a [5]) it is evident that at least four *Pinus* species existed in the Baltic amber flora (Tab. 5). However, more studies on pine needle inclusions are needed to restudy all *Pinus* species that Czekcrott (1961) excluded from her list.

In the case of *Abies*, Sadowski et al. (2017a [5]) revised holotypes from historic amber collections along with literature descriptions and images. They showed that *Abies* species exclusively described from Baltic amber (*A. obtusifolia*, *A. linearis* and *A. suckerii*), are actually interpreted as angiosperm leaves (*Dicotylophyllum* var. sp.) and thus, should be removed, when updating Czekcrott's (1961) list (Tab. 5). However, Sadowski et al. (2017a [5]) found a non-described specimen in a private amber collection that exhibited clear affinities to *Abies* and thus, confirmed the occurrence of firs in the Baltic amber flora.

From nine listed cupressaceous genera from Baltic amber, Sadowski et al. (2017a [5]) only verified three genera (*Calocedrus*, *Quasisequoia* and *Taxodium*) that were not listed as such by Czekcrott (1961). Baltic amber inclusions with affinities to *Taxodium* were already published by Goeppert and Berendt (1845), and Goeppert and Menge (1883). Caspary and Klebs (1907), however, doubted affinities of the specimens to *Taxodium*. The respective specimens are currently lost, and therefore, the new fossil evidence represents the first unambiguous record of *Taxodium* from Baltic amber (Sadowski et al. 2017a [5]).

Czekcrott (1961) listed *Sequoia couttsiae* which is a basionym of *Quasisequoia couttsiae*. The particular specimen is a twig fragment inclusion which was described and pictured by Caspary and Klebs (1907) as *S. couttsiae*. Sadowski et al. (2017a [5]) reevaluated these descriptions and images, since the original specimen is currently lost. They showed that its assignment to *Q. couttsiae* cannot be clearly verified. However, Sadowski et al. (2017a [5]) presented unambiguous specimens of *Q. couttsiae*, confirming its occurrence in the Baltic amber flora.

Sadowski et al. (2017a [5]) further evaluated *Widdringtonites oblongifolius* and *Taiwania schaeferi* that were listed by Czekcrott (1961). These named taxa are synonymous with *Quasisequoia couttsiae* and thus, should be removed when updating Czekcrott's (1961) list. Further putative representatives of *Widdringtonites* (*W. lanceolatus*, *W. oblongifolius* var. *longifolius*) should be excluded from the list as well, according to preliminary research results of L. Kunzmann and J. Kvaček (pers. comm. L. Kunzmann, Dresden). Both authors are currently restudying type material of *Widdringtonites* from the Cenomanian Peruc-Corycany and Niederschöna formations in the Czech Republic and Germany. The leaf micromorphology of *Widdringtonites* is still poorly known and needs further investigation. When revisions of its type material are available, Paleogene fossils of *Widdringtonites* have

to be restudied and revised, as well. Hence, this mid-Cretaceous taxon should not be applied to accommodate cupressaceous twig remains from Baltic amber yet (pers. comm. L. Kunzmann, Dresden).

Including the new results, the number of Baltic amber Cupressaceae genera of Czeczott's amended list decreases from 16 to 14 (Tab. 5); however, the majority of cupressaceous amber genera still lack verification and thus, more research is needed to revise the remaining Cupressaceae taxa from Baltic amber. Preliminary results on cupressaceous inclusions from Baltic amber (established by L. Kunzmann and I; see chapter 4.1.2), however, already confirmed their high (taxonomic) diversity.

Besides Pinaceae and Cupressaceae, Sadowski et al. (2017a [5]) added a further family (and species) to the list of Baltic amber conifers, the extinct Geinitziaceae with *Cupressospermum saxonicum*. In addition, the new findings of *Sciadopitys* inclusions from Baltic amber (Sadowski et al. 2016a [3]) finally increased the number of conifer families from Baltic amber from two to four (Tab. 5). Although reports of *Sciadopitys* from Baltic amber were already published (Goepfert and Berendt 1845, Goepfert and Menge 1883), illustrations and descriptions of these specimens showed that their affinities were doubtful (Sadowski et al. 2016a [3]). Furthermore, the whereabouts of the respective type specimens are unknown. Thus, the new fossil evidence from Baltic amber presented by Sadowski et al. (2016a [3]) unambiguously proves the presence of *Sciadopitys* in the Baltic amber flora.

4.1.2 Indeterminable conifers – challenges and preliminary results

A definite identification of plant inclusions from Baltic amber can be challenging, even when the preservation is sufficient. This is especially true in the case of cupressaceous inclusions which are very abundant in Baltic amber. Extant Cupressaceae taxa are defined by a set of characters, comprising seed cone and leaf morphology (Farjon 2005). Typically, Cupressaceae exhibit polymorphic leaves, meaning that during the life-span of one individual plant different types of leaves occur: cotyledons, juvenile, transitional and mature leaves (Farjon 2005). These leaves differ in their shape (scale-like or linear), partly in their phyllotaxis (helically arranged but aligned in a plane or spreading) and in their orientation along the twig (leaves appressed to partly or non-appressed; Oladele 1983, Farjon 2005). Thus, when identifying disarticulated and small-sized twig inclusions of Cupressaceae difficulties may occur; particularly genera and species of the subfamilies Callitroideae and Cupressoideae are challenging to distinguish from one another without having information about the seed cone morphology. Also, the determination and affiliation of isolated Cupressaceae pollen cone inclusions are not yet resolved. In extant Cupressaceae, pollen cones are “uniform, simple, and terminal” and mostly singular with scale-like leaves (Schulz et al. 2014). As most pollen cone inclusions are detached from the twig, it is impossible to link morphological information of these cones with specific leaf types, which in combination could be helpful for

accommodation in respective genera. So how should the great amount of Cupressaceae inclusions from Baltic amber be systematically evaluated?

In a preliminary study, Lutz Kunzmann and I classified disarticulated twig fragment inclusions as well as isolated pollen cone inclusions of the Cupressaceae into morphotypes. Each type shows affinities to several extant taxa of the Cupressaceae, but cannot be assigned with certainty to one specific genus. These morphotypes can be distinguished from each other, based on morphological features of the leaves and cone scales (Tab. 6 and 7). The preliminary results of our study are presented in the following text, including descriptions of cupressaceous shoot and pollen cone types.

Cupressaceous shoot types

We differentiated between three shoot types of the Cupressaceae from Baltic amber. Shoot type 1-3 can be distinguished from another by the phyllotaxis of the leaves, the leaf shape, and the location and morphology of the stomata complexes.

Shoot type 1

Fig. 1

Description

Shoot type 1 comprises twig fragments which are different to all other cupressaceous twig inclusions from Baltic amber in the combination of the following features (Fig. 1, Tab. 6): complanate twig (Fig. 1A, B, F, G); dimorphic leaves (Fig. 1C, H); phyllotaxis: opposite-decussate leaf pairs (Fig. 1C, H); leaf apices appressed, incurved, acute-obtuse (Fig. 1D, H); one twig side without or only very few stomata (corresponding to the upper twig side; Fig. 1B, G), the lower twig side with triangular stomata patches on facial and stomata bands on lateral leaves (Fig. 1A, C, H); lobed, undercut Florin rings (Fig. 1E, F); papillae on subsidiary cells (Fig. 1E).

Comparison

There is no extant representative of Cupressaceae which combines all these features; however, *Thuja*, *Thujopsis*, *Chamaecyparis* and *Platyclusus* show at least some of the named characteristics (Florin 1931, Farjon 2005). Thus, we suggest possible affinities to these genera. Three of the studied specimens that were assigned to shoot type 1 represented original material of Caspary and Klebs (1907) who described and published them as *Thuites succineus* Casp. et R. Klebs (Fig 1F-I). Caspary and Klebs (1907) used the fossil taxon *Thuites* to summarize over 70 amber inclusions with similarities to the genera *Thuja*, *Thujopsis*, *Chamaecyparis* and *Biota* (= *Platyclusus* Spach. following recent taxonomy, Fu et al. 1999). Both authors already noticed that morphological features of these cupressaceous twig fragments were not sufficient or reliable to differentiate between the mentioned genera. *Thuites* with *T. alienus* as type species was introduced by Sternberg (1825) for cupressaceous fossils of the

Cretaceous and one century later, Knobloch (1971) assigned *T. alienus* to *Sequoia aliena*. Shoot type 1 (including *Thuites succineus*) is clearly different to *Sequoia*, e.g. in the phyllotaxy which is helical in *Sequoia*, but decussate in shoot type 1. Therefore, we concluded that the name *Thuites* should not be used for Baltic amber inclusions of cupressaceous shoot type 1.



Fig. 1: Cupressaceous twig fragment inclusions from Baltic amber, assigned to shoot type 1 (A-E: GZG.BST.24605; F-I: GZG.BST.24461, *Thuites succineus* Casp. et R. Klebs, from Caspary and Klebs 1907, pl. XIII). (A, F) Lower side of the twig fragments; note the stomata patches. (B, G) Upper side of the twig fragments; stomata patches only few to absent. (C) Twig apex, view from the lower twig side; leaf apices are incurved and appressed. (D) Lateral leaf with stomata band; leaf margin pectinate with acuminate papillae (arrowhead). (E) Stomata complexes with lobed, undercut floric rings (black arrowhead) and papillous subsidiary cells (white arrowhead). (H) Middle part of the twig (view from the lower twig side); black arrowhead indicates the facial stomata patch, white arrowhead indicates the stomata band on the lateral leaf. (I) Stomata band from a lateral leaf, partly covered by fungal hyphae, arrowhead indicates the pectinate leaf margin. Scale bars 1 mm (A, B, F, G), 500 μ m (C, H), 100 μ m (D), 50 μ m (E, I).

Tab. 6: Preliminary results of morphotypes of cupressaceous twig fragment inclusions from Baltic amber. – indicates features which were not discernible.

	Shoot type 1	Shoot type 2	Shoot type 3
Foliage branch	convex, complanate	complanate	not flattened
Leaf type	dimorphic, imbricate	heterophyllous, monomorphic to dimorphic, imbricate	monomorphic, imbricate
Leaf morphology			
Shape	obtrullate to rhombic	rhombic, trullate	rhombic
Apex	acute-obtuse, incurved, appressed	acute or obtuse with inconspicuous acuminate tip; incurved, spreading or appressed	obtuse, appressed
Margin	entire; pectinate with acuminate papillae	entire; pectinate with acute papillae	entire; pectinate with acute papillae
Phyllotaxis	decussate	decussate	spirally
Stomata			
Distribution	amphistomatic	amphistomatic	–
Stomata arrangement			
Upper twig side	few to absent	twig sides indistinguishable	twig sides indistinguishable
Lower twig side	facials: 2 triangular patches laterals: 2 bands along each side of midline		
Stomata complex			
Arrangement	abaxial and adaxial; irregular in patches or short rows	abaxial; inconspicuous, only at the base, small patches adaxial; 2 bands along each side of midline, proceeding up to the leaf tip	abaxial; in patches; proceeding from the base to the upper third of the leaves; complexes irregularly distributed
Subsidiary cells	–	–	monocyclic, 4-5 cells: roundish to slightly elliptic circle
Papillae	present on stomata complex	present on stomata complex and ordinary epidermal cells of the entire stomata patch/band	absent
Floral rings	lobed, undercut	pronounced, lobed, slightly undercut	absent
Stomatal pit			
Shape	elliptic to roundish	elliptic	elliptic to roundish
Orientation (towards longitudinal leaf axis)	facials: irregular laterals: parallel	parallel (rows) to slightly irregular (patches)	irregularly
Ordinary epidermal cells			
Shape and arrangement	narrow, rectangular, elongated; in regular rows orientated towards leaf tip	narrow, rectangular, elongated; in regular rows orientated towards leaf tip	rectangular to polygonal (mostly in stomata patches); in regular rows
Oxalate crystals	present	present to absent	present to absent
Affinities			
Extant taxa	<i>Thuja</i> , <i>Thujopsis</i> , <i>Chamaecyparis</i> , <i>Platycladus</i>	<i>Chamaecyparis</i> , <i>Cupressus</i> , <i>Xanthocyparis</i>	<i>Glyptostrobus</i> , <i>Cupressospermum</i>
Specimen investigated (collection number) and affiliation			
Museum für Naturkunde zu Berlin	MB.Pb.1979/508	–	–
Königsberg Amber Collection (GZG)	GZG.BST.24461; GZG.BST. 24471; GZG.BST.24605	GZG.BST.23520, GZG.BST.24487, GZG.BST.24600	GZG.BST.24347, GZG.BST.24611, GZG.BST.24631, GZG.BST.24624, GZB.BST.24658
Hoffeins Amber Collection (GZG)	1146-4	–	–
Carsten Gröhn Amber Collection	886	–	3588, 3678

Shoot type 2

Fig. 2

Description

Shoot type 2 (Fig. 2, Tab. 6) is different to other cupressaceous twig inclusions in its flattened heterophyllous monomorphic (to slightly dimorphic) decussate leaves with spreading apices at the lateral side of the twig (Fig. 2A, B, F); twig sides are indistinguishable from each other (Fig. 2A, B); stomata patches of abaxial leaf side are partly covered by neighbouring leaves or abaxial leaf side is stomata free (Fig. 2D, G); adaxial leaf side with two bands of stomata rows, located on each side of the longitudinal midline and proceeding to the leaf tip (Fig. 2C, H); numerous papillae on subsidiary cells and ordinary epidermal cells within each stomata patch or band (Fig. 2H, I); Florin rings pronounced and entire (Fig. 2E, I); parallel orientation of the stomatal pits towards the longitudinal leaf axis (Fig. 2H).

Comparison

Extant cupressaceous taxa with similar morphologies to shoot type 2 are *Cupressus arizonica* (abaxial side with partly covered stomata patches, adaxial side with stomata from base to apex, monomorphic leaves, apices spreading to appressed; Farjon 2005), *Chamaecyparis* (dimorphic leaves; mainly all abaxial stomata patches are covered; Florin rings and papillae present; Florin 1931, Farjon 2005) and *Xanthocyparis* (transitional leaves decussate, dimorphic but nearly of the same size, spreading leaf apices, stomata mostly adaxially; Farjon et al. 2002, Farjon 2005). Despite these similarities, these taxa also differ from the fossils, e.g. in the presence of glands (as in *Chamaecyparis lawsoniana* and *Cupressus arizonica*; Farjon 2005). Specimens which were assigned to shoot type 2 also contained original material of Caspary and Klebs (1907), namely *Chamaecyparis casparyi* R. Klebs (Fig. 2A-E); however, Caspary and Klebs (1907) did not discuss further affinities to *Cupressus* (*Xanthocyparis* was discovered in 1999; Farjon et al. 2002, Farjon 2005).



Fig. 2: Cupressaceous twig fragment inclusion from Baltic amber, assigned to shoot type 2 (A-E: GZB.BST.24347; *Chamaecyparis casparyi* R. Klebs, Caspary and Klebs 1907, pl. XVIII; F-I: no. 3678, Carsten Gröhn Amber Collection). (A and B) Overview of GZG.BST.24347 from both twig sides which are indistinguishable from each other; arrowheads in (B) indicate almost entirely covered stomata patches. (C) Lateral leaf from the side, arrowhead indicates the adaxial side with stomata band. (D) Facial leaf (abaxial). (E) Stomata with lobed Florin rings (black arrowhead) from abaxial side of leaf; note the pectinate leaf margin (white arrowhead). (F) Overview of specimen 3678. (G) Facial leaf (abaxial). (H) Adaxial side of a lateral leaf, showing two stomata bands on each side of the midline. (I) Adaxial stomata complexes with pronounced Florin rings (white arrowhead) and papillae (black arrowhead) on subsidiary cells. Scale bars 1 mm (A, B, F), 100 μm (C, H), 500 μm (D, G), 50 μm (E), 20 μm (I).

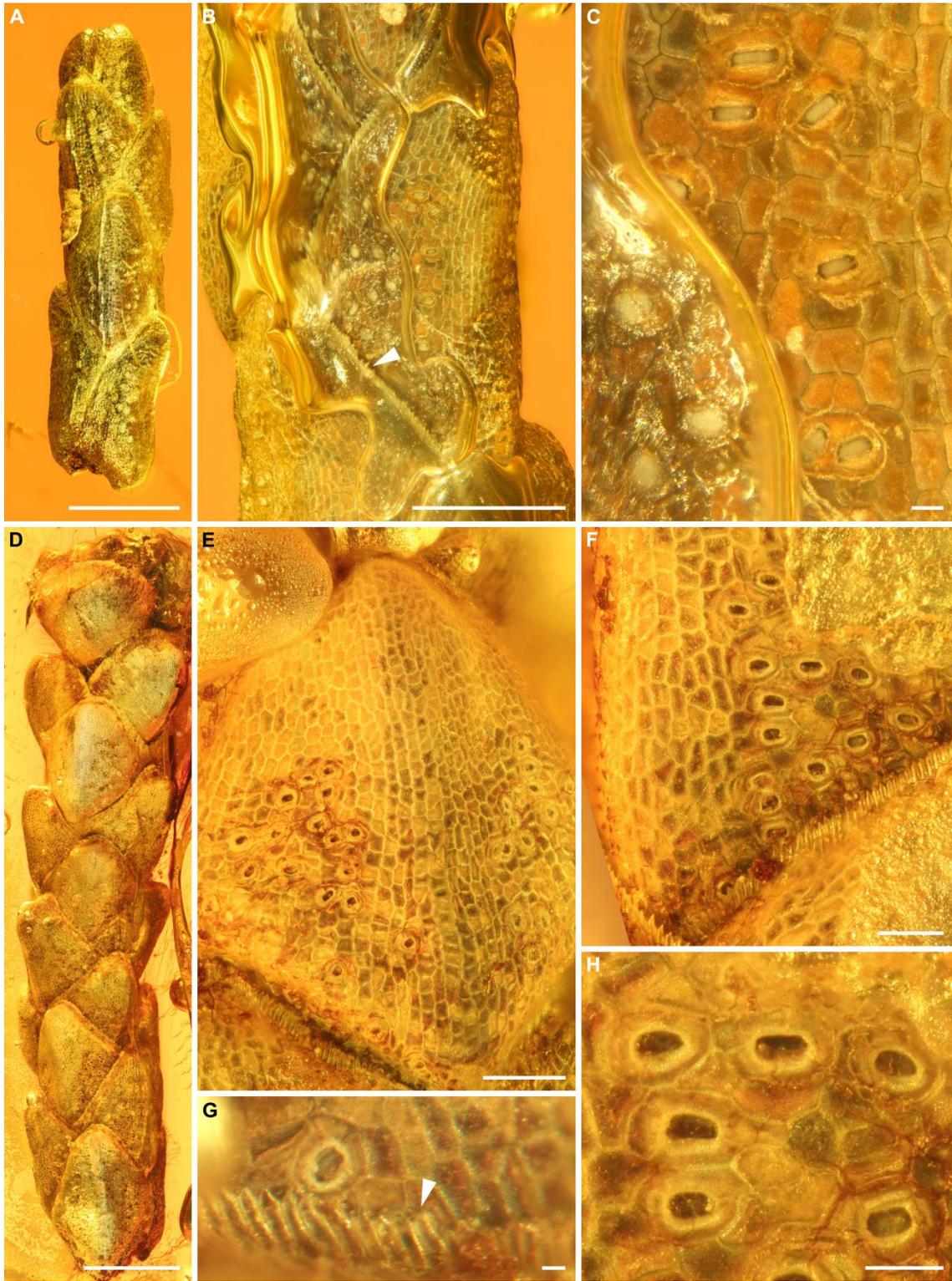


Fig. 3: Cupressaceous twig fragment inclusions from Baltic amber, assigned to shoot type 3 (A-C: GZG.BST.24487; D-H: GZG.BST.24600). (A, D) Overview of the twigs. (B, E) Spirally arranged leaves, addressed to the twig; arrowhead in (B) indicates pectinate leaf margin. (C, F-H) Stomata complexes with smooth subsidiary cells and without Florin rings; arrowhead (G) indicates pectinate leaf margin with acute papillae. Scale bars 1 mm (A, D), 500 μm (B), 20 μm (C, G), 200 μm (E), 100 μm (F), 50 μm (H).

Shoot type 3

Fig. 3

Description

The third shoot type (Fig. 3, Tab. 6) includes twig fragment inclusions combining morphological features of *Glyptostrobus pensilis*, *G. europaeus* and *Cupressospermum saxonicum*. Shoot type 3 can be distinguished from the other shoot types in the monomorphic, spirally arranged leaves (Fig. 3A, B); stomata in large patches that proceed to the upper third of the leaf (Fig. 3B, E, F); non-papillous subsidiary cells and the absence of Florin rings (Fig. 3C, G, H).

Comparison

Specimens of shoot type 3 share features with both *Glyptostrobus* (scale-like monomorphic adult leaves; spirally phyllotaxis; adpressed leaf apices; subsidiary cells non-papillous; Florin rings absent) and *Cupressospermum saxonicum* [non-decurrent leaf base, adpressed leaf apices; stomata patches broad but not reaching the leaf tip; cyclocytic stomata; see Sadowski et al. (2017a [5]) for a detailed table (tab. 4 and references therein), comparing *Glyptostrobus* and *Cupressospermum*]. However, the amber specimens of shoot type 3 also differ from both *Glyptostrobus* and *Cupressospermum*, since distinctive features of *C. saxonicum* (three subsidiary cells, ordinary epidermal cells at the leaf base are broader than long; Kunzmann 1999) were not observed in the specimens. They also did not show amphicyclocytic stomata arranged in bands which proceed to the tip, as it is the case for extant *G. pensilis* and the extinct *G. europaeus* (Florin 1931, Ma et al. 2013).

Cupressaceous pollen cone types

We defined three cupressaceous pollen cone types that can be distinguished from each other in shape and phyllotaxis of the sporangiophores, the position of sporangia, and the number of sporangia per sporangiophore (Tab. 7, Fig. 4).

Tab. 7: Preliminary results of cupressaceous pollen cone types from Baltic amber. + indicates the presence, – the absence of the respective feature; ‘NA’ indicates features which are not available.

	Pollen cone type 1	Pollen cone type 2	Pollen cone type 3
Cone distribution			
Solitary	+	NA	+
Clustered	–	NA	–
Sporangiophore			
Phyllotaxis	decussate	spiral	decussate, spreading in an angle of 90° from the longitudinal cone axis
Shape	widely ovate	almost triangular	triangular
Apex	drawn-out tip, obtuse	acute	acute-obtuse
Margin	irregularly lacerated, pectinate with elongated papillae	slightly lacerated, pectinate with papillae	irregular lacerated, pectinate with papillae
Hyposporangiate	+	+	+/-
Number of sporangiophores/cone	10	>10	>22
Number of sporangia/sporangiphore	2	5	8-9
Leaves	3 pairs of decussate monomorphic leaves	NA	2 pairs of decussate monomorphic leaves
Suggested taxonomic name	–	?	<i>Cupressinanthus</i>
Suggested affinities to extant	?	?Taxodiaceae	? <i>Glyptostrobus</i>
Specimens investigated (collection numbers) and affiliation			
Museum für Naturkunde Berlin	MB.Pb.1979/796, MB.Pb.1979/0511	MB.Pb.1979/0513	–
University of Göttingen			
Königsberg Amber Collection	GZG.BST.24620, GZG.BST.24604, GZG.BST.24350	–	GZG.BST.23519, GZG.BST.28823, GZG.BST.24353
Carsten Gröhn Amber Collection	6507	–	–

Pollen cone type 1

Fig. 4A, B

Description

Pollen cone type 1 (Tab. 7; Fig. 4A, B) encompasses solitary pollen cones with widely ovate sporangiophores which possess drawn-out obtuse apices and irregular lacerated, pectinate margins, as well as two sporangia per sporangiophore (Fig. 4B).

Comparison

Since numerous Cupressaceae possess male cones with two sporangia per sporangiophore (e.g. *Calocedrus*, *Cryptomeria*, *Chamaecyparis*, *Juniperus*, *Glyptostrobus*; Farjon 2005, Schulz et al. 2014), no affinities to a specific genus of

Cupressaceae were suggested so far. One of the assigned specimens is the original type of *Cupressites linkianus* Casp. et R. Klebs (Fig. 4A, B) (Caspary and Klebs 1907); both authors suggest affinities to *Chamaecyparis*, but considering the above mentioned similarities to other Cupressaceae, we refrain from assignment of morphotype 1 to *Chamaecyparis*. Nonetheless, the name ‘*Cupressites*’ that was suggested by Caspary and Klebs (1907) could not be retained either to summarize pollen cones with two sporangia per sporangiophore, as the type of *Cupressites* Brongniart 1828 is based on a vegetative shoot from the lower Triassic (Farr and Zijlstra 1996).

Pollen cone type 2

Fig 4C-E

Description

The second pollen cone type (Tab. 7; Fig. 4C-E) includes pollen cones with spirally arranged sporangiophores (Fig. 4C) which are triangular in shape with acute apices and slightly lacerated, pectinate margins (Fig. 4D). They show five sporangia per sporangiophore (Fig. 4E).

Comparison

We suggest affinities to ‘Taxodiaceae’, since the majority of taxodiaceous genera possesses more than two sporangia/sporangiphore, such as *Glyptostrobus* (2-9 sporangia/sporangiphore), *Athrotaxis* (1-5 sporangia/sporangiphore), *Cunninghamia* (1-10 sporangia/sporangiphore), *Sequoia* and *Sequoiadendron* (both 1-6 sporangia/sporangiphore; all numbers taken from Schulz et al. 2014).

Pollen cone type 3

Fig. 4F, G

Description

The third cupressaceous pollen cone type (Tab. 7; Fig. 4F, G) is very distinct from pollen cone types 1 and 2 since it possesses eight to nine sporangia per sporangiophore (Fig. 4G); sporangia are located under the abaxial side (hyposporangiate), however, also reaching the adaxial side (perisporangiate) (Fig. 4G); sporangiophores are decussate and spreading from the longitudinal axis at an angle of 90° (Fig. 4F); sporangiophores are only shortly peltate and triangular (Fig. 4F).

Comparison

This morphotype contains only one specimen which was originally described by Caspary and Klebs (1907) as *Cupressinanthus magnus* (Fig. 4F, G). *Cupressinanthus* was introduced to describe Baltic amber pollen cones with eight to nine sporangia per sporangiophore. The authors also mentioned that it was impossible to assign those male cones to extant Cupressaceae (Caspary and Klebs 1907).

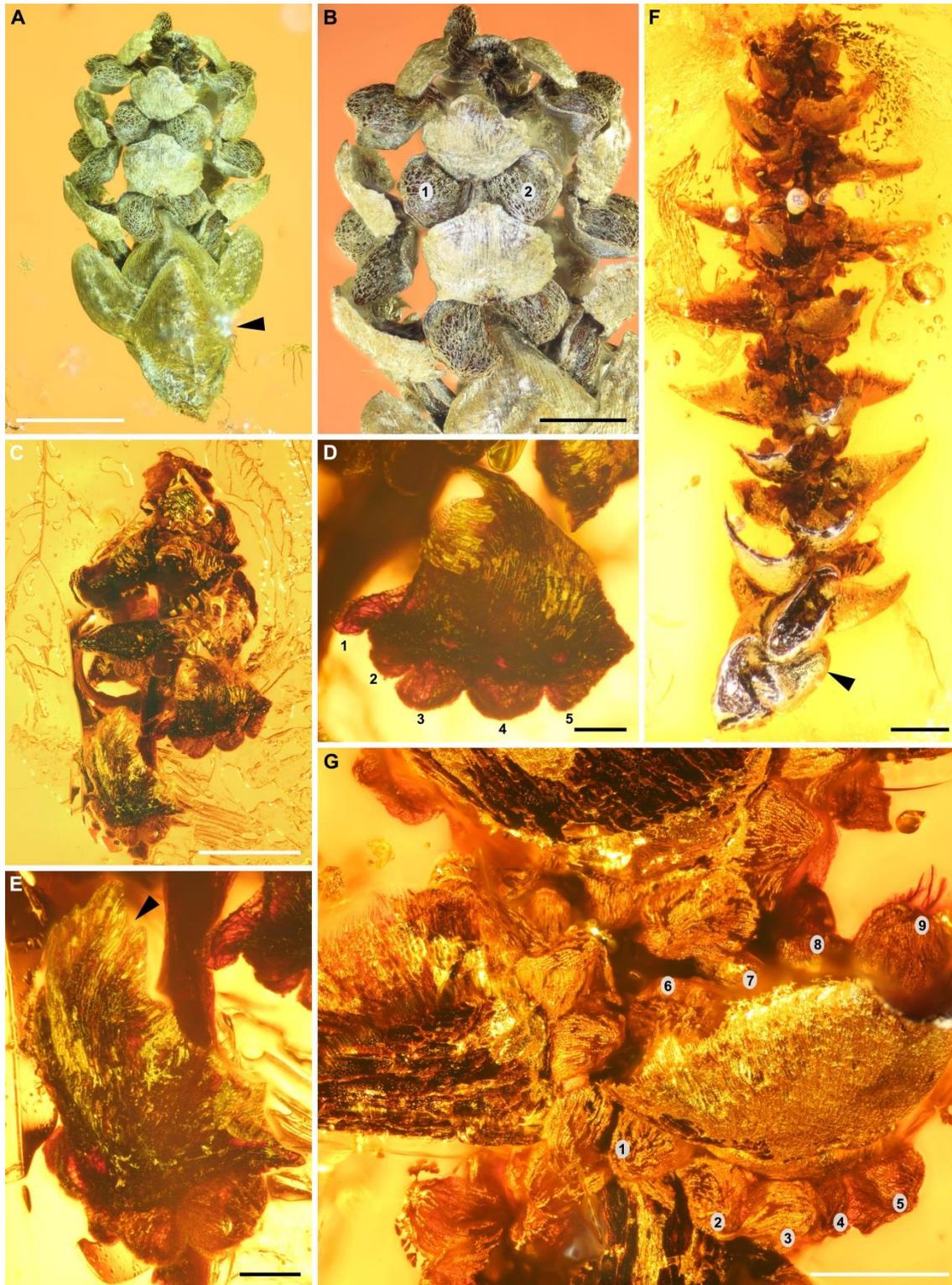


Fig. 4: Cupressaceous pollen cone inclusions from Baltic amber, assigned to pollen cone type 1 to 3: pollen type 1 (A and B: Mb.Pb.1979/796, *Chamaecyparis casparyi* R. Klebs, Caspary and Klebs, pl. XIX), pollen cone type 2 (C-E: Mb.Pb.1979/513) and pollen cone type 3 (F and G: GZG.BST.23519, *Cupressinanthus magnus* Casp., Caspary and Klebs 1907, pl. XXII). (A) Overview of Mb.Pb.1979/796, note the basal decussate leaves (arrowhead). (B) Magnification of (A), showing two sporangia (1-2) per sporangiophore. (C) Overview of Mb.Pb.1979/513. (D) Magnification of one sporangiophore, showing five sporangia (1-5) per sporangiophore. (E) Sporangiophore, arrowhead indicates the slightly lacerated margin. (F) Overview of GZG.BST.23519, note the basal decussate leaves (arrowhead). (G) Magnification of one sporangiophore with nine sporangia (1-9), located on the abaxial and adaxial side of the sporangiophore. Scale bars 1 mm (A, C, F), 500 μ m (B, G), 200 μ m (D, E).

Schulz et al. (2014) provided a comprehensive list of all conifers, including Cupressaceae, and their pollen cone features. Among Cupressaceae, the following taxa possess up to nine sporangia per sporangiophore: *Cupressus*, *Glyptostrobus*, *Taxodium* and *Tetraclinis*. Comparing the pollen cone inclusions to the named taxa, we suggest similarities to *Glyptostrobus*, since this taxon shares the following features with the fossil: two pairs of decussate monomorphic leaves beneath the male cone inclusion (Fig. 4G) and numerous sporangiophores (Fig. 4F; *Glyptostrobus pensilis* possesses 15-20 sporangiophores per cone; Farjon 2005). All the other mentioned taxa show characters different to the inclusion: dimorphic leaves underneath the pollen cones (*Cupressus*, *Tetraclinis*); pollen cones rather short and only abaxial sporangia (*Taxodium*). However, some morphological features are not in accordance with *Glyptostrobus*, such as the sporangia located on the adaxial side of the sporangiophores. According to Schulz et al. (2014), Taxaceae are the only coniferous family with perisporangiate sporangia (Schulz et al. 2014). However, none of the taxaceous genera possesses nine sporangia, although *Amentotaxus* and *Pseudotaxus* may exhibit up to eight sporangia per sporangiophore (Schulz et al. 2014). Based on these preliminary results, we decided that currently, it is impossible to be more definite regarding possible affinities of morphotype 3 to extant Cupressaceae (or even Taxaceae).

Based on our preliminary results we suggest distinguishing between three cupressaceous shoot types, and three pollen cone types from Baltic amber. All morphotypes are likely to represent different species, but studies on cupressaceous shoot and pollen cone inclusions from Baltic amber need to be continued to establish proper identification keys, synonymy lists and comprehensive descriptions of the respective specimens. Nonetheless, these preliminary results indicate a high diversity of Cupressaceae taxa in the Baltic amber flora, although definite assignments to a specific taxon are not yet possible.

4.1.3 Conifer inclusions revise our understanding of the Baltic amber source area

The results of Sadowski et al. (2017a [5]) not only showed the high conifer diversity of the Baltic amber flora, but also allowed conclusions about habitat types of the ‘Baltic amber forest’. It is noteworthy that these conclusions are not only based on an actualistic approach, but also include palaeoecological information of certain plant taxa for assuring that reliable habitat preferences are used for the reconstruction of the ‘Baltic amber forest’ (see chapter 2). Sadowski et al. (2017a [5]) distinguished between coastal lowland swamps, back swamps and riparian forests, as well as mixed mesophytic forests.

Cupressospermum saxonicum is an extinct conifer which is known from other Central European fossil localities, such as the Bitterfeld amber deposit [Upper Oligocene, Saxony, Germany; Barthel and Hetzer 1982) or the Mockrehna flora (earliest Miocene, Saxony, Germany; Mai and Walther 1991). These fossil localities give insight into the palaeoecology of *C. saxonicum* which was growing in coastal environments where it either occurred in eutrophic swamps or in swamps that were affected by brackish water flooding (Rascher et al. 2013). Thus, Sadowski et al. (2017a [5]) interpreted *C. saxonicum* as an indicator for the presence of these habitat type within the Baltic amber source area.

Recently found inclusions of *Sciadopitys* cf. *tertiaria* from Baltic amber gave further insight into the habitat diversity of the Baltic amber source area (Sadowski et al. 2016a [3]). During the European Palaeogene, *Sciadopitys terciaria* was an abundant tree species of raised bog habitats (Gothan 1936, Thiergart 1949, Dolezych and Schneider 2007). Based on this knowledge, Sadowski et al. (2017a [5]) argue that *S. terciaria* is a key taxon, indicating the presence of water-saturated peat habitats in the ‘Baltic amber forest’, occurring along coastal lowland swamps. From its fossil record, *Cathaya* is known to occur along the margins of raised bogs which were dominated of *Sciadopitys* (Dolezych and Schneider 2007). Referring to the ‘Baltic amber forest’, Sadowski et al. (2017a [5]) suggest that *Cathaya* either grew in similar localities or was intermingling within a mixed conifer-angiosperm forest. The latter was formed by *Abies*, *Nothotsuga*, *Pseudolarix*, *Pinus* and *Calocedrus*, along with angiosperm taxa (see chapter 4.2.2 for Baltic amber angiosperms) (Sadowski et al. 2017a [5]). Following the interpretation of Sadowski et al. (2017a [5]), inundated back swamps and riparian forest are indicated by *Quasisequoia couttsiae* and *Taxodium*. From their fossil record, both tree taxa are known to be typical constituents of swamps that however were not influenced by brackish water (Kunzmann 1999, Kunzmann et al. 2009).

In summary, Sadowski et al. (2017a [5]) showed that coniferous inclusions are a useful tool to reconstruct the habitat types of the ‘Baltic amber forest’. They found evidence for a very heterogeneous Baltic amber source area that was characterized by a high conifer and habitat diversity. Different swamp habitats existed in the Baltic amber source area, comprising coastal swamps under brackish and tidal water influence, raised bogs with water-saturated peat, back swamps which were not flooded with brackish water, as well as riparian forests. Besides inundated

habitats, non-flooded areas also existed which were covered by mixed mesophytic conifer-angiosperm forests (Sadowski et al. 2017a [5]).

4.1.4 New candidates for the Baltic amber source plant

Although a coniferous origin of Baltic amber was proven (chapter 1.6.2), the source plant is still a mystery. Regarding the newly described conifer taxa from Baltic amber presented in the previous chapters, new candidates should be further investigated for assessing the botanical origin of Baltic amber. Mostly, the Baltic amber source plant has been suggested as being pinaceous, such as *Pinus succinifera* which has been discussed as Baltic amber tree for almost two centuries. Besides numerous palaeobotanical studies (e.g. Schubert 1961, Dolezych et al. 2011) and chemical analyses of Baltic amber and extant resins (e.g. Kosmowska-Ceranowicz 2015, Wolfe et al. 2009), it is still unclear if Pinaceae resin is really suitable for the formation of amber or not. Several types of diterpene acids (e.g. abietic and pimaric acids), which are abundant in pinaceous resins do not polymerize and thus, are less likely to persist in the rock record and to form large amber deposits (Langenheim 2003, Ragazzi and Schmidt 2011). However, there is conflicting evidence from several studies discussing Pinaceae, especially *Pinus*, as Baltic amber source tree. For instance, Mosini and Samperi (1985) discovered correlations between Baltic amber and resin of extant *Pinus halepensis*, after they had artificially aged resin samples of four pine species by heating them at 110°C for 30 to 60 days maximum. A gas chromatography–mass spectrometry (GC/MS) analysis of the ‘aged’ resins and Baltic amber revealed similarities, especially in resin acids which were transformed during the aging process (Mosini and Samperi 1985).

A further study linking the amber to a pinaceous origin was published by Dolezych et al. (2011) who analysed in-situ amber of a wood inclusion from Baltic amber. The wood itself was assigned to *Pinus* (subgenus *Strobus*, section *Parraya* and/or *Strobus*), and by applying IR analyses the in-situ amber was identified as gedano-succinite (Dolezych et al. 2011). The latter is a ‘transitional type’ between succinite and gedanite, combining chemical properties of both amber types, such as specific peaks in their IR spectra and the amount of succinic acid (Stout et al. 1995, Vávra 2015). Stout et al. (1995) interpreted the similarities between gedanite, gedanite-succinite and succinite as indicator for a common botanical source and suggested that the structural differences between the named amber varieties are caused by diagenetic processes.

Another amber type with pinaceous affinities was suggested by Yamamoto et al. (2006) who identified *Pinus* or *Picea* as source tree for Bitterfeld succinite, indicating that Pinaceae taxa can be source trees of large amber deposits. This result has previously been supported by Wolfe et al. (2016) who applied along FTIR and isotope analyses, time of flight-secondary ion mass spectrometry (ToF-SIMS) to study Baltic and Bitterfeld amber. Structural and chemical characteristics of both ambers show similarities to resin properties of extant Pinaceae and Sciadopityaceae, but a definite taxonomic assignment to a source plant was still impossible. Although

both ambers are “broadly contemporaneous”, they are not equivalent to each other, meaning that succinite of the Bitterfeld and Baltic area derived from different botanical sources and localities (Wolfe et al. 2016). There is no doubt that numerous *Pinus* species existed in the Baltic amber flora (see chapter 4.1.1); however, based on the state of knowledge, the morphological-anatomical evidence, as well as structural and chemical indications are still too contradictory to consider or exclude *Pinus* species as Baltic amber source tree.

Among Pinaceae, *Pseudolarix* should again be considered as putative Baltic amber source tree, as it was already done by Anderson and LePage (1995) who discovered several conifer taxa on Axel Heiberg Island of the Canadian Arctic Archipelago (Anderson and LePage 1995). Middle Eocene sediments of the Buchanan Lake Formation preserved a coniferous swamp forest with in-situ amber, meaning that the amber was associated with identifiable plant fossils, which allowed the linking of the amber directly to its source plant (Anderson and LePage 1995). Pyrolysis-gas chromatography-mass spectrometry (Py-GC-MS) analyses were conducted to study the chemical properties of the ambers as well (Anderson and LePage 1995), and in combination with fossil evidence, revealed that the ambers originated from *Metasequoia*, *Pinus* and *Pseudolarix*. Interestingly, the *Pseudolarix* amber not only derived from polylabdanoid resins, but also contained succinic acid. Both features are two key characteristics of Class Ia resins, including Baltic amber (Tab. 1). Furthermore, Wolfe et al. (2009) found that resin of extant *Pseudolarix amabilis* exhibits a subdued ‘Baltic shoulder’ in its IR spectra, suggesting affinities of Baltic amber to *Pseudolarix*. But differences in the labdane configuration of both ambers and the absence of the ‘Baltic shoulder’ in the IR spectra of *Pseudolarix* amber, as well as lacking fossil evidence from Baltic amber raised doubts about *Pseudolarix* being a Baltic amber source tree (Anderson and LePage 1995, Langenheim 2003, Wolfe et al. 2009). Despite this, the recently described first record of *Pseudolarix* needle inclusions from Baltic amber by Sadowski et al. (2017a [5]) shows that *Pseudolarix* is not yet ruled out as a source tree of Baltic amber. Despite the differences between both ambers, the chemical similarities between the ambers and extant *Pseudolarix amabilis* supports the idea of Anderson and LePage (1995) that both amber source trees were not alike but at least shared a common ancestor.

A further pinaceous origin of Baltic amber was suggested by V. Katinas (Stroganov 1987) who considered the Atlas cedar *Cedrus atlantica* as Baltic amber source tree. However, besides a newspaper article by Stroganov (1987) no further details about Katina’s studies are available. Regarding the latest update of conifers from Baltic amber (Sadowski et al. 2017a [5]), inclusions with affinities to cedars have not been discovered yet, questioning whether *Cedrus* was a constituent of the Baltic amber forest at all.

Another conifer which should be considered as putative amber tree is *Cupressospermum saxonicum* of the extinct Geinitziaceae. Fossils of this ancient conifer were discovered in open cast mines of the Bitterfeld amber deposit (Upper Oligocene, Saxony, Germany), but also in the Lusatian Miocene of Saxony and Brandenburg (Barthel and Hetzer 1982, Kunzmann and Schneider 2013). In-situ

resin in wood remains, twigs and cone scales of *C. saxonicum* indicated excessive resin release in stands which were inundated by brackish waters (Barthel and Hetzer 1982, Sadowski et al. 2017a [5]). However, in inundated stands of *C. saxonicum*, which were non-tidal influenced, resin release was observed to be present, but not as pronounced as under brackish-water influence (pers. comm. Dr. Wilfried Schneider, Hoyerswerda). IR spectra of this in-situ resin were similar to Bitterfeld amber and thus, *C. saxonicum* was suggested as a source tree of Bitterfeld amber (Barthel and Hetzer 1982). However, Barthel and Hetzer (1982) did not clarify which type of Bitterfeld amber was used in their IR analyses for comparing it to the resin of *C. saxonicum*. Despite this, in a further publication about Bitterfeld amber by Krumbiegel and Kosmowska-Ceranowicz (2007), the authors were more precise and stated that Barthel and Hetzer (1982) had identified the amber type gedanite from fossil cone scales of *C. saxonicum*. But it remained unclear how Krumbiegel and Kosmowska-Ceranowicz (2007) knew that it was gedanite, since this was not mentioned by Barthel and Hetzer (1982). Gedanite is an amber variety which was first described from the Baltic amber deposit (Stout et al. 1995). Although gedanite was suggested to be related to *C. saxonicum* (Krumbiegel and Kosmowska-Ceranowicz 2007), its source plant is still not verified, and is further confused since Krumbiegel and Kosmowska-Ceranowicz (2007) also mention that IR spectra of gedanite were similar to extant resin of *Agathis australis* (Araucariaceae).

In contrast to Barthel and Hetzer (1982), Yamamoto et al. (2006) detected strong differences when comparing the chemical composition of *Cupressospermum* resin to Bitterfeld succinite (the main amber variety of the Bitterfeld deposit). But Yamamoto et al. (2006) discovered similarities of *Cupressospermum saxonicum* resin to stantienite, another rare form of amber, which also occurs in the Blue Earth layer (Vávra 2015). Despite of the conflicting chemical evidence, *C. saxonicum* was a resinous conifer and has been recently reported from Baltic amber (Sadowski et al. 2017a [5]), too. Although the chemical composition of *C. saxonicum* resin is different to Baltic amber, *C. saxonicum* still needs to be considered when discussing possible source plants of further amber varieties, besides succinite from the Baltic amber deposit.

Wolfe et al. (2009) used FTIR to compare extant resins of the suggested source conifers of Baltic amber to the amber itself (*Pinus contorta*, *Metasequoia glyptostroboides*, *Pseudolarix amabilis*, *Agathis australis*, and *Sciadopitys verticillata*). Moreover, the authors conducted FTIR for further amber types which had a similar age to Baltic amber and whose botanical affinities were also proven by palaeobotanical evidence, including *Pseudolarix* ambers from the Canadian Arctic (see above). Although Anderson and LePage (1995) highlighted the strong similarities of *Pseudolarix* amber from the Canadian Arctic and that of Baltic amber, Wolfe et al. (2009) underlined differences between both ambers, mainly the absence of the ‘Baltic shoulder’ in the absorption spectrum of the *Pseudolarix* amber. Following Wolfe et al. (2009), Baltic amber showed most similarities to the spectrum of *Sciadopitys verticillata*, including the ‘Baltic shoulder’. Hence, Wolfe et al. (2009) proposed *Sciadopityaceae* as source plant of Baltic amber, although extant *S.*

verticillata resin is devoid of succinic acid but contains verticillol, a typical compound found in cladodes of *S. verticillata* but which is missing in Baltic amber. The authors argued that diagenetic transformations of the amber explained these inconsistencies; however, they could not present unambiguous fossil evidence proving the presence of *Sciadopitys* in the Baltic amber flora.

Just recently, Sadowski et al. (2016a [3]) restudied a needle-shaped inclusion from Baltic amber, which was presented by Wolfe et al. (2009) showing sciadopitoid affinities. In their study, Sadowski et al. (2016a [3]) revealed that the putative sciadopitoid inclusion lacked specific features of cladodes of *Sciadopitys* (e.g. papillous groove on the underside, ‘double leaf tip’) and rather showed characteristics of an angiosperm leaf, especially in the morphology of the stomata complexes. However, Sadowski et al. (2016a [3]) found two Baltic amber inclusions of cladodes which possessed the unique features of *Sciadopitys* and thus clearly proved the presence of this taxon in the Baltic amber flora (Sadowski et al. 2016a [3]). Thus, there are chemical and structural indications, as well as palaeobotanical evidence for a potential sciadopitoid provenance of Baltic amber.

Besides Pinaceae and Sciadopityaceae, other conifer families also exhibit resin properties which facilitate amber formation. For instance, Cupressaceae resin possesses labdane-type acids which polymerize more easily and thus, are more likely to form amber (Langenheim 2003, Ragazzi and Schmidt 2011). As discussed in the previous chapters, Sadowski et al. (2017a [5]) proved the presence of the cupressaceous taxa *Calocedrus*, *Quasisequoia couttsiae* and *Taxodium* in the Baltic amber flora. Also, there are numerous Cupressaceae inclusions from Baltic amber, especially twig fragments and pollen cones (Figs 1-4) which, however, could not be assigned to specific taxa yet (see chapter 4.1.2 for details). Despite their abundant occurrence in Baltic amber, Wolfe et al. (2016) eliminated Cupressaceae as potential source of Baltic amber, based on recent chemical and structural analyses of extant resins. However, among 133 extant Cupressaceae species (Farjon 2005), the authors only analysed resin from 11 cupressaceous taxa. Considering the high diversity of extant and fossil Cupressaceae, especially in the Baltic amber flora, resins of more Cupressaceae genera should be examined, including the verified conifer taxa from Baltic amber, to test their affinities to the chemistry of Baltic amber.

In conclusion, despite using a wide range of techniques and new fossil data from Baltic amber, no consensus about the botanical origin of Baltic amber was found so far (see Tab. 8 as overview). For resolving the origin of Baltic amber, more data about chemical and structural properties of extant and fossil resins across all conifer taxa are needed. Another challenge which needs more attention is the unknown effect of diagenetic processes on amber and how they change its properties (Anderson et al. 1992). Furthermore, palaeobotanical evidence from Baltic amber should be included more often in those studies. Wood inclusions with in-situ amber are an especially promising tool to infer the Baltic amber source plant. Based on different types of amber from the Baltic region, as well as the high coniferous diversity, it also should be considered that there might be more than one amber source plant.

Tab. 8: Arguments for (in blue) and against (in red) different suggested source trees of Baltic succinite. Indistinct arguments were left blank. Table is adapted from Langenheim (2003) and extended with subsequent results, as indicated in the references. NA indicates information that was not available.

Suggested source	<i>Agathis</i>	<i>Pseudolarix</i>	<i>Pinus</i>	<i>Sciadopitys</i>
Family	Araucariaceae	Pinaceae		Sciadopityaceae
Chemical and structural resin and amber properties				
Molecules	labdane polymers are the same as in Baltic amber	labdane polymer enantiomeric and not regular	Verticillol	NA
Polymerization	polymerizes easily	polymerizes insufficiently	polymerizes insufficiently	NA
Baltic shoulder	absent	present absent	absent	present
Succinic acid	absent	present	present absent	absent
Positive wavenumber ratio (FTIR)	absent	absent	absent	present
FTIR spectra	dissimilar	dissimilar	dissimilar	correlating
Potential of accumulation	massive resin accumulation in extant trees	no massive resin accumulation in extant trees	no massive resin accumulation in extant trees	no massive resin accumulation in extant trees
Fossil record				
Presence in the Baltic amber flora	fossils absent	fossils present	fossils present	fossils present
Reports of in-situ amber	no	yes	yes	no
References	Langenheim 2003; Wolfe et al. 2009	Langenheim 2003; Wolfe et al. 2009	Dolezych et al. 2011; Ragazzi and Schmidt 2011; Wolfe et al. 2009, 2016; Sadowski et al. 2017a [5]	Wolfe et al. 2009, 2016; Sadowski et al. 2016a [3]

4.2 Angiosperms

4.2.1 Angiosperm diversity of the Baltic amber flora

The most recent update on angiosperm inclusions from Baltic amber was provided by Czezzott (1961) who revised identifications of angiosperm inclusions, mainly from Conwentz (1886b) and Kirchheimer (1937). Her list contains 43 families, 64 genera and 101 species from Baltic amber, of which she declares 11 species as doubtful (especially within the Fagaceae and Proteaceae). Since then, only few angiosperm taxa from Baltic amber have been revised or newly described [see Tab. 9 for a current list of angiosperms from Baltic amber, based on Czezzott (1961) and updated with current research results; families were updated, following APG (Stevens 2001 onwards) and Tropicos (2017)].

Sadowski et al. (2016b [4]) presented new evidence of graminids (a general term for Poaceae, Cyperaceae and Juncaceae) from Baltic amber. The authors discovered three inclusions of spikelets of which one was assigned to the genus *Rhynchospora* (Cyperaceae). A further spikelet showed affinities to Cyperaceae, while the third inclusion exhibited similarities to both families, Poaceae and Cyperaceae. Sadowski et al. (2016b [4]) highlighted that graminid inclusions from Baltic amber are extremely rare. Previous studies on Baltic amber graminids date back to the 19th century when Conwentz (1886b) published poaceous leaf inclusions (*Graminophyllum succineum*) which, however, could not be confirmed. A further Baltic amber fossil with graminid affinities was *Zeites succineus* (Caspary 1872a) whose real identity was also doubted (Schuster 1931, Kirchheimer 1937). Sadowski et al. (2016b [4]) restudied the type specimen of *Z. succineus*, showing that it most likely represents a cast of a coniferous cone and thus, must be excluded from the list of Baltic amber angiosperms.

A hitherto unknown angiosperm family from Baltic amber was presented by Sadowski et al. (2015) who found leaf inclusions of the carnivorous plant family Roridulaceae (Fig. 5A-C). Both leaf inclusions share numerous features with extant roridulid representatives (Fig. 5D-I), such as stalked glands (=tentacles) of different size classes (Fig. 5B, C, F), located along the margins and on the abaxial side of leaf (Fig. 5A, E); hyaline unicellular trichomes (Fig. 5B, F); as well as the specific micromorphology of the tentacles (Fig. 5C, G). Roridulaceae belong to the sarracenioid clade within Ericales, consisting of the Actinidiaceae and the carnivorous Sarraceniaceae (American pitcher plants) (Anderberg et al. 2002, Schönenberger et al. 2005). Interestingly, extant Roridulaceae are endemic to few localities of South Africa (Anderson 2006), while their closest related families are distributed in America (Sarraceniaceae: North and South America; Ellison et al. 2012) and Asia (Actinidiaceae: Central and South America, South East Asia; Stevens 2001 onwards). Therefore, extant distribution areas of the Roridulaceae in South Africa were interpreted as relictual, dating back to the break-up of Gondwana (Warren and Hawkins 2006). However, based on the first Roridulaceae fossils found in Baltic amber, Sadowski et al. (2015) concluded that this family must have had a

Tab. 9: Current list of angiosperms from Baltic amber, taken from Czecczott (1961; and references therein) and amended with indicated references. Families were updated, following APG (Stevensen 2001 onwards) and Tropicos (2017). Revised taxa are indicated by *; recently verified taxa are highlighted in blue; doubtful taxa are indicated by ?; taxa mentioned by Pielnińska (1990) in a shortened list without further details are indicated by †.

Family	Name	Kind of remain	Comment	Reference
-	<i>Dicotylophyllum</i> var. sp.	leaves	abundant angiosperm leaves, primarily described as 'Abies'; affinity unresolved	Sadowski et al. 2017a [5]
Adoxaceae	<i>Sambucus multiloba</i> , <i>S. succinea</i>	flowers		
Apiaceae	<i>Chaerophyllum dolichocarpum</i>	fruit		
Apocynaceae	<i>Apocynophyllum jentzschii</i>	leaf		
Aquifoliaceae	<i>Ilex prussica</i> , <i>I. minuta</i> , <i>I. aurita</i>	flowers		
Araceae	<i>Acoropsis minor</i> *	spadix infructescence	synonym of <i>Acoropsis eximia</i>	Bogner 1976
Arecaceae	? <i>Phoenix eichleri</i> *, <i>Palmophyllum kunowi</i> , <i>Bembergia pentataris</i> , ?palm flower (indet.)	male flower, leaves	due to stamen morphology, Daghlian doubts affinities of <i>Phoenix eichleri</i> to <i>Phoenix</i>	Daghlian 1981; Poinar 2002
Campanulaceae	<i>Carpolithus specularioides</i>	juvenile fruit		
Celastraceae	<i>Celastrinanthium hauchecornei</i>	inflorescence		
Cistaceae	<i>Cistinocarpum roemeri</i>	fruit		
Clethraceae	<i>Clethra berendtii</i>	fruit		
Commelinaceae	<i>Commelinacites</i>	flower		
Connaraceae	<i>Connaracanthium roureoides</i>	inflorescence		
Cyperaceae	<i>Rhynchospora</i> sp., Cyperaceous indet.	spikelets		Sadowski et al. 2016b [4]
Dilleniaceae	<i>Hibbertia latipes</i> , <i>H. tertiaria</i> , <i>H. amoena</i>	leaves		
Droseraceae	<i>Aldrovanda</i> †	-		Pielnińska 1990
Ericaceae	<i>Orphanidesites primaevus</i> , <i>Andromeda imbricata</i> *, <i>A. primaeva</i> *, <i>A. glabra</i> , <i>A. polytricha</i> , <i>A. brachysepala</i> , <i>A. goepperti</i> , <i>Ericiphyllum ternatum</i>	infructescence, flowers, fruits, foliage twig fragments	<i>Andromeda imbricata</i> and <i>A. primaeva</i> probably affiliated to <i>Cassiope</i> or <i>Calluna</i>	Sadowski (unpublished)
Fabaceae	<i>Dalbergia sommerfeldii</i>	leaves		
Fagaceae	<i>Quercus</i> sp., <i>Quercus meieriana</i> , <i>Q. mucronata</i> , <i>Q. subglabra</i> , ? <i>Q. capitato-pilosa</i> , <i>Q. henscheana</i> , ? <i>Q. macrogemma</i> , ? <i>Q. microgemma</i> , <i>Castanea longistaminea</i> , ? <i>C. brachyandra</i> , ? <i>Fagus succinea</i> *, <i>Dryophyllum berendtianum</i> , <i>D. furcinerve</i>	male flowers, male catkins, leaves, buds, juvenile fruit	<i>Fagus succinea</i> was assigned to <i>Trigonobalanus succinea</i> ; quercoid and castaneoid affinities of male inflorescences confirmed	Forman 1964; Mai 1967; Pielnińska 2001; Sadowski (unpublished)
Geraniaceae	<i>Geranium beyrichi</i> , <i>Erodium nudum</i>	awn		
Graminids	Graminoid indet.	spikelet	affinities to Poaceae and Cyperaceae	Sadowski et al. 2016b [4]
	<i>Zeites succineus</i> *	infructescence?	probably cast of a coniferous cone	
Hamamelidaceae	<i>Hamamelidanthium succineum</i> , <i>H. meii</i>	inflorescence, flower		
Hydrangeaceae	<i>Deutzia tertiaria</i> , <i>D. divaricata</i>	stamen		
Hydrocharitaceae	<i>Najas marina</i> †	-		Pielnińska 1990
Iteaceae	<i>Adenanthemum iteoides</i> *	flower	affinities to <i>Itea</i> were confirmed	Hermesen 2013
Lauraceae	<i>Trianthera eusideroxylon</i> , <i>Cinnamomum polymorphum</i> , <i>C. prototypum</i> , <i>C. felixii</i>	flower, leaf		
Liliaceae	<i>Simlax baltica</i>	female flower		
Linaceae	<i>Linum oligocenicum</i>	fruit		
Loranthaceae	<i>Loranthacites succinues</i>	twig		
Magnoliaceae	? <i>Magnolilepis prussica</i> , <i>Drimysophyllum succineum</i>	stipule, leaf		
Myricaceae	<i>Myrica linearis</i> , <i>M. casparyana</i> , <i>Myriciphyllum oligocenicum</i>	male flower, leaf		
	<i>Comptonia</i> sp.	leaves		Skadell 2016
Primulaceae	<i>Myrsinopsis succinea</i> , <i>Berendtia primuloides</i> , <i>Berendtia rotata</i>	flowers		
Oleaceae	<i>Oleiphyllum boreale</i>	leaf		
Oxalidaceae	<i>Oxalidites averrhoides</i> , <i>O. brachysepalus</i>	fruits		
Pentaphragaceae	<i>Pentaphragax oliveri</i>	leaf		
Phyllanthaceae	<i>Antidesma maximowiczii</i>	male flower		
Pittosporaceae	<i>Billardierites longistylus</i>	flower		
Poaceae	? <i>Graminophyllum succineum</i> *	leaves	<i>G. succineum</i> doubtful	Sadowski et al. 2016b [4]
Polygonaceae	<i>Polygonum convolvuloides</i>	seed		

Tab. 9 continued

?Proteaceae	<i>Persoonia subrigida</i> , <i>Lomalites</i> *, <i>Dryandra duisburgii</i> , <i>Proteacites pinnatipartitus</i>	leaves	Kirchheimer doubts Proteaceae affinities; <i>Lomalites</i> related to <i>Dryophyllum</i> (Fagaceae)	Kirchheimer 1937
Rhamnaceae	<i>Rhamnus apiculata</i>	fruit		
Rosaceae	<i>Mengea palaeogena</i>	flower		
Roridulaceae	Indet.	leaves		Sadowski et al. 2015
Rubiaceae	<i>Cephalanthus</i> †	–		Pielińska 1990
	<i>Enantioblastos viscoides</i> *	foliage twig fragment	<i>E. viscoides</i> is synonym of <i>Arceuthobium viscoides</i> (Viscaceae)	Sadowski et al. 2017b [6]
	<i>Sendelia ratzeburgiana</i>	flower		
Salicaceae	? <i>Saliciphyllum succineum</i>	leaf		
Sapindaceae	<i>Acer majus</i> , <i>A. micranthum</i> , <i>A. schumanni</i> , <i>A. succineum</i> , <i>A. scharlokii</i>	male flower		
Santalaceae	<i>Thesianthium incusum</i> , <i>Osyris schiefferdeckeri</i> , <i>O. ovata</i>	flowers		
Saxifragaceae	<i>Stephanostemon brachyandra</i> , <i>S. helmi</i>	flower-bud, flowers		
Theaceae	? <i>Stewartia kowalewskii</i> *	flower	doubtful	Mai 1971
	?Indet.	flower		Pielińska 2001
Thymelaeaceae	<i>Eudaphniphyllum nathorsti</i> , <i>E. rosmarinoides</i> , <i>E. oligocenicum</i> , <i>E. balticum</i>	leaves		
Urticaceae	<i>Forskaleanthium nudum</i>	male flower		
Viscaceae*	<i>Arceuthobium conwentzii</i> , <i>A. groehnii</i> , <i>A. johnianum</i> , <i>A. mengeanum</i> , <i>A. obovatum</i> , <i>A. viscoides</i>	foliage twig fragments, infructescences	originally included within Loranthaceae, with two species <i>Patzea johniana</i> and <i>P. mengeana</i>	Sadowski et al. 2017b [6]
Vitaceae†	?Indet.	–		Pielińska 1990
Ximeniaceae	<i>Ximenia gracilis</i>	fruit		

cosmopolitan distribution during the late Eocene, questioning the assumed Gondwanan origin of Roridulaceae (Warren and Hawkins 2006) and indicating that the extant relict areas are likely consequences of post-Eocene extinction events (Sadowski et al. 2015). Further angiosperm taxa from Baltic amber, which have been revised and restudied, belong to the Loranthaceae, namely *Patzea mengeana* and *P. johniana* (Sadowski et al. 2017b [6]). The authors presented evidence for assigning these species to the extant dwarf mistletoe genus *Arceuthobium* (Viscaceae) and found further amber specimens that they identified as *Arceuthobium* as well. In total, Sadowski et al. (2017b [6]) distinguished between six species, *A. conwentzii*, *A. groehnii*, *A. johnianum*, *A. mengeanum*, *A. obovatum*, and *A. viscoides*, including *Entantioblastos viscoides* which was assigned to the Rubiaceae by Conwentz (1886b), but actually is a further representative of *A. viscoides*.

Due to the high abundance of *Quercus*-like inclusions in Baltic amber (especially oak trichomes; Czechtz 1961), Fagaceae are of special interest when studying the Baltic amber flora. Czechtz (1961) listed 12 species of Fagaceae from Baltic amber of which she regarded five species as doubtful (*Quercus capitato-pilosa*, *Q. macrogemma*, *Q. microgemma* *Castanea brachyandra*, and *Fagus succinea*; Tab. 9). Forman (1964) and Mai (1967) evaluated illustrations of a fruit inclusion of *Fagus succinea* and assigned this species to *Trigonobalanus*. However, it is noteworthy that further extant species of the Trigonobalanoideae, *Colombobalanus excelsa* and *Formanodendron doichangensis*, were described more than 20 years later by Nixon and Crepet (1989). Therefore, a re-evaluation of the *Trigonobalanus* inclusion from Baltic amber is needed, reviewing its affinities to all Trigonobalanoideae species. I

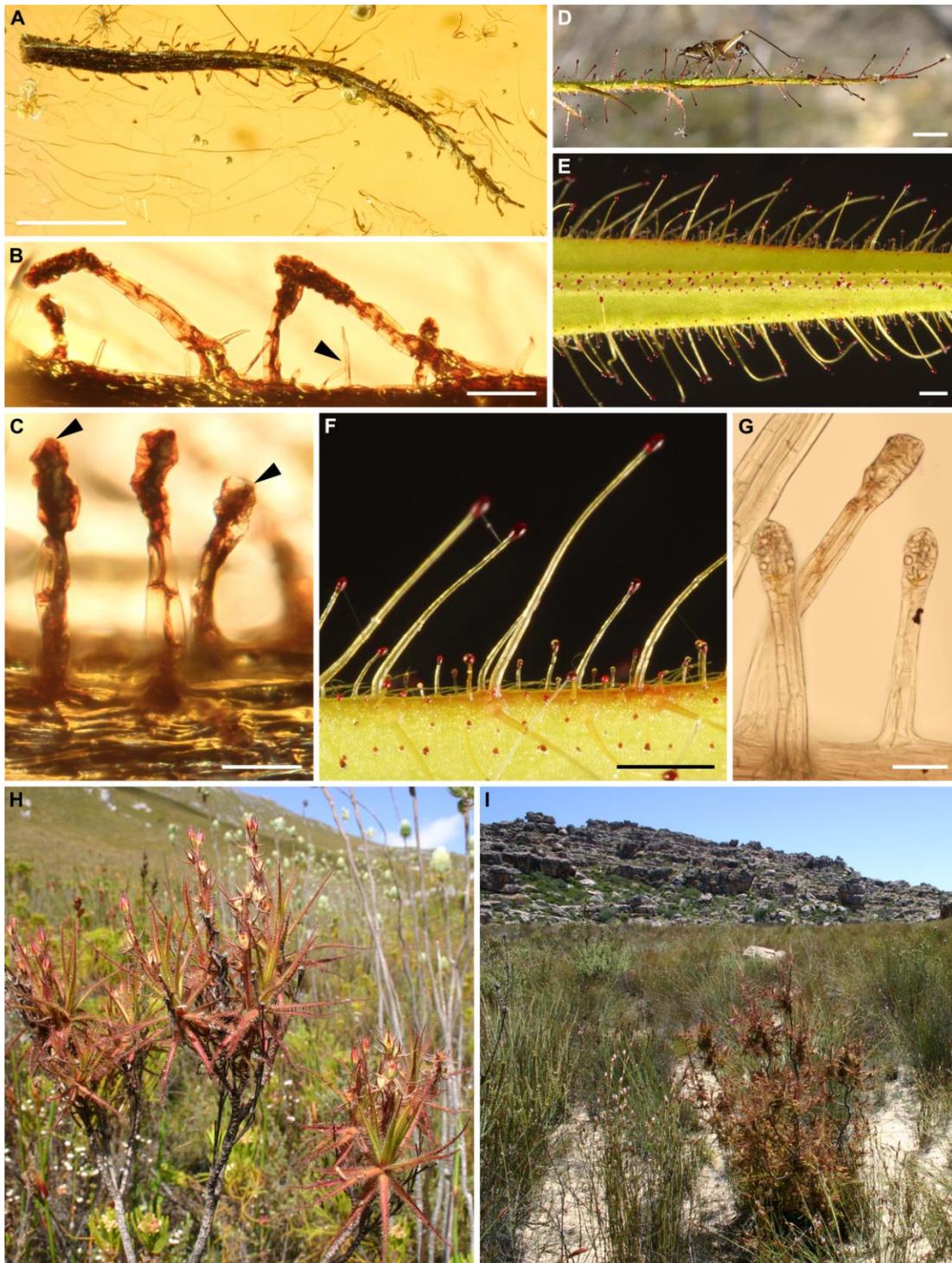


Fig. 5: A carnivorous leaf inclusion from Baltic amber and extant Roridulaceae. **(A)** Overview of GZG.BST.27310, showing numerous tentacles along the leaf margin and on the abaxial side of leaf. **(B)** Tentacles of different size classes and hyaline trichomes (arrowhead). **(C)** Magnification of tentacles composed of a multicellular stalk and a glandular head with a central porus (arrowheads). **(D)** Leaf tip of extant *Roridula dentata* with its hemipteran mutualist *Pameridea marlothi*. **(E)** Abaxial leaf side of *R. gorgonias*. **(F)** Magnification of the abaxial leaf margin of *R. gorgonias*, showing different tentacle size classes and hyaline trichomes. **(G)** Tentacles of *R. gorgonias* with multicellular stalks and glandular heads. **(H, I)** *R. gorgonias* (H) and *R. dentata* (I) in their natural well-lit and open habitat. (D, I: Cederberg Mountains ca. 6 km east of Clamwilliam, South Africa; E, F: cultured specimens by A.R. Schmidt; H: Fernkloof Nature Reserve near Hermanus, South Africa). Photos (D, H, I) A. R. Schmidt; (E, F) G. Hundertmark. Scale bars 1 mm (A, D, E, F), 100 µm (B), 50 µm (C, G).

further studied the morphology of fagaceous male inflorescences inclusions and compared them to male inflorescences of extant Fagaceae². According to my preliminary results, extant *Quercus* species, as well as *F. doichangensis* and *C. excelsa* possess pendulous, mostly unbranched catkins (Forman 1964, Nixon and Crepet 1989, Borgardt and Pigg 1999). In contrast, male inflorescences of Castanoideae are rigid spikes (Hjelmquist 1948, Kubitzki 1993). Thus, quercooid catkins can be easily distinguished from other fagaceous genera. Based on my preliminary results, I concluded that different quercooid (Fig. 6A-C) as well as castaneoid taxa (Fig. 6E-F) are present in the Baltic amber flora, confirming the high diversity of Fagaceae. However, it remains challenging to identify fagaceous inclusions of male inflorescences to genus level, since differentiating between Fagaceae genera and species requires further information about leaf and fruit morphology. Furthermore, extinct fagaceous genera need to be considered as well, such as *Eotrigonobalanus*, *Trigonobalanopsis* and *Dryophyllum* (Denk et al. 2012). These genera were widespread across Europe during the Palaeogene (Denk et al. 2012) and show that the diversity of ancient Fagaceae was even higher than today.

I further initiated a study on the Ericaceae of which numerous species from Baltic amber have been described (Tab. 9) but have not been restudied so far. Preliminary results of my study deal with a twig fragment inclusion (MB.Pb.1979/615, Fig. 7A-F) which I found in the historic Künow amber collection of the Museum für Naturkunde Berlin. This specimen was tagged with an historic label assigning the specimen to *Calluna primaeva* Menge (Fig. 7D). This is an ericoid species that A. Menge exclusively described from Baltic amber (Menge 1858). Specimen MB.Pb.1979/615 is described as it follows: leaves scale-like, rhombic, imbricate, sessile, non-petiolate and decussate (Fig. 7A, E); leaf margins are fimbriate-ciliate, possessing unicellular, long, acute trichomes (Fig. 7E, F); leaf apex obtuse (Fig. 7F). The most peculiar feature is a narrow groove at the abaxial leaf base, proceeding parallel to the longitudinal midline up to the middle of leaf (Fig. 7F). The groove is covered by acute papillae (Fig. 7F), likely hiding the stomata complexes. Regarding the shape of the leaves, the abaxial groove, the phyllotaxis and the fimbriate-ciliate leaf margins, specimen MB.Pb.1979/615 is in congruence with the species description and images of *Calluna primaeva* by Menge (1858). However, comparison of specimen MB.Pb.1979/615 with images of the holotype of *C. primaeva* from Menge (1858) (Fig. 7B, C) also revealed that both differ from each other: the twig inclusion of the holotype is sharply bent at an approximate angle of 90° (Fig. 7B); furthermore, the holotype is enclosed next to a syninclusion of an elongated linear leaf (mentioned by Menge 1858) which is not present in specimen MB.Pb.1979/615. This means that MB.Pb.1979/615 does not represent the holotype of *C. primaeva*. Conwentz (1886b), however, had access to the holotype of *Calluna primaeva* and discussed Menge's (1858) assignment. Conwentz (1886b) criticized

² For feasibility, I followed the classification system of the Fagaceae presented in Grímsson et al. (2016) who divided the Fagaceae into the subfamilies Fagoideae (*Fagus*), Trigonobalanoideae (*Colombobalanus*, *Formanodendron*, *Trigonobalanus*), Castanoideae (*Castanea*, *Castanopsis*, *Chrysolepis*, *Lithocarpus* and *Notholithocarpus*), and Quercoideae (*Quercus*).



Fig. 6: Inclusions of fagaceous male inflorescences from Baltic amber (A-C: GZG.BST.24414; D-F: no. 1037-2, Hoffeins Amber Collection). (A) Overview of GZG.BST.24414, a pendulous catkin with affinities to *Quercoidae*. (B, C) Magnification of singular staminate flowers. (D) Overview of specimen 1037-2, a rigid catkin with affinities to *Castaneoideae*. (E, F) Magnification of staminate flowers, arranged in clusters. Scale bars 5 mm (A), 1 mm (B-D), 500 μ m (E, F).

that Menge's image of *C. primaeva* showed furrows on the abaxial side of leaf (Fig. 7C). In his revision of this specimen, Conwentz (1886b) could not find such an abaxial furrow and thus, assigned *C. primaeva* to *Andromeda*, an ericoid genus which mostly lacks an abaxial groove. Conwentz's (1886b) results are in contrast to my preliminary results, since I clearly observed such a groove in the newly discovered specimen of *C. primaeva* (MB.Pb.1979/615). However, the holotype of *C. primaeva* that Conwentz (1886b) studied is lost and thus, it remains unclear how to evaluate his interpretation.

I examined a further ericoid twig inclusion from Baltic amber from the Carsten Gröhn Amber Collection (coll. number P1516; Fig. 7G-I). This specimen shows a similar morphology as specimen MB.Pb.1979-615, including an abaxial groove (Fig. 7I). But specimen P1516 is different from specimen MB.Pb.1979/615 in the more flattened leaf lamina (Fig. 7H, I), the shorter abaxial groove (Fig. 7I) and in the quadrangular shape of the twig (Fig. 7G). However, specimen P1516 is in congruence with descriptions and images of *Andromeda imbricata*, an ericoid species exclusively described from Baltic amber (Conwentz 1886b). Conwentz (1886b) highlighted the presence of an abaxial groove and long trichomes along the leaf margins of *A. imbricata*. Unfortunately the holotype of *A. imbricata* is lost, precluding further investigations of this holotype.

According to my preliminary results both specimens MB.Pb.1979/615 and P1516 are more likely related to *Calluna* or *Cassiope* (both belonging to the Ericaceae) which are defined by sessile, decussate leaves, possessing an abaxial groove and fimbriate-ciliate leaf margins (Stevens 1970, Stevens et al. 2004). This kind of leaf was termed "Calluna-leaf" by Hagerup (1953) who highlighted its morphological uniqueness in comparison to other ericoids. Also Watson (1964) underlined the peculiar morphology of *Calluna* and *Cassiope* which are conspicuously decussate, while other Ericaceae mostly exhibit a verticillate phyllotaxy. In contrast, extant *Andromedeae* (with *Andromeda*) possess petiolate, flat leaves (Stevens 1970), which are different to the fossils. Therefore, I would recommend rejecting the genus name *Andromeda* for the amber inclusions of *A. primaeva* and *A. imbricata*. Further studies will show whether both specimens are either affiliated to *Calluna* or *Cassiope*.

Within the Myricaceae, a new taxon was recently added to the angiosperm list from Baltic amber (Tab. 9). In the unpublished Bachelor thesis of L. Skadell (2016; supervised by A.R. Schmidt and I), the first evidence of *Comptonia* leaves from Baltic amber was described (Skadell 2016). However, further research is needed to ascertain the affinities of the inclusions to other Palaeogene species of *Comptonia*.

In summary, new knowledge about angiosperm taxa from Baltic amber was gained during the last years, showing that higher angiosperm diversity in the 'Baltic amber flora' is to be expected. However, many taxa still need revision, such as the Fagaceae, to further understand the floristic composition of the Baltic amber flora.



Fig. 7: Inclusions of ericoid twig fragments from Baltic amber [A, D-F: Mb.Pb.1979/615; B, C: historic drawings of *Calluna primaeva* Menge, from Menge (1858), figs 15-17; E-G: no. 1516, Carsten Gröhn Amber Collection]. (A, B, G) Overview of the twig fragments. (C) Magnification of the twig with scale-like decussate leaves, as well as a singular leaf with a fimbriate-ciliate margin and an abaxial furrow. (D) Historic label of Mb.Pb.1979/615, assigning the specimen to *Calluna primaeva*. (E, H) Magnification of each twig, showing scale-like, imbricate, decussate leaves. (F, I) Abaxial groove at the base of the leaf (arrowheads) covered with papillae; note the fimbriate-ciliate leaf margins. Scale bars 1 mm (A, D), 500 μ m (B, E), 100 μ m (C, G).

4.2.2 Angiosperm inclusions and their potential as palaeoecological key taxa

Czeczott (1961) assigned all angiosperm families from Baltic amber to a so-called geographical element, based on the occurrence of their extant analogues (Tab. 10). The majority of angiosperm families from Baltic amber exhibited a cosmopolitan distribution today (20 families, 46 %), while 10 families belonged to the ‘tropical-subtropical element’ (23 %) and only 5 families (12 %) were temperate. The remaining families either showed a discontinuous (12 %) or anomalous (7%) distribution, meaning that they could not be definitely assigned to one of the other ‘geographical elements’ (Tab. 10). Czeczott (1961) highlighted that “the tropical element is numerically almost double the temperate”. Considering revisions of some Baltic amber angiosperms, as well as newly discovered angiosperm taxa (see chapter 4.2.1), two questions arise: Are these confirmed angiosperms palaeoecological indicators for assessing the ‘Baltic amber forest’? Do these angiosperm taxa give new insights into Czeczott’s (1961) concept of geographical elements?

As described in chapter 4.1.3, conifer inclusions from Baltic amber already imply a complex picture of the ‘Baltic amber forest’, comprising the following habitat types: coastal lowland swamps under brackish and tidal water influence, raised bogs with water-saturated peat, inundated back swamps (not under brackish water influence), riparian forests, and non-flooded areas with mixed mesophytic conifer forests (Sadowski et al. 2017a [5]).

Angiosperm inclusions complete this picture; Sadowski et al. (2016b [4]) suggested graminid inclusions of Cyperaceae and Poaceae as valuable indicators for assessing habitat types in the ‘Baltic amber forest’. Extant Poaceae mostly prefer dry and sunny habitats, such as steppes and savannahs, while Cyperaceae were adapted to wetland habitats during the Eocene and thus, are nowadays highly diverse in swampy habitats (Linder and Rudall 2005, Bouchenak-Khelladi et al. 2014). Applying this knowledge to the ‘Baltic amber forest’ it is likely that the recently found cyperaceous taxa grew within swampy and riparian areas. Based on the graminid inclusions, Sadowski et al. (2016b [4]) further suggested that open, light areas, such as meadows, existed in the Baltic amber source area. This is supported by another study of Sadowski et al. (2015), reporting the presence of Roridulaceae in the Baltic amber flora. Extant representatives of this family grow on permanently humid or on sandy, drier areas which are open and light (Anderson 2006) (Fig. 5H, I). Hence, roridulid plants from Baltic amber also indicate the presence of open habitats within the ‘Baltic amber forest’.

It is probable, that these open dry areas were also inhabited by *Comptonia*. Extant *Comptonia* occurs in eastern North America and is known from forest understory and sandy dry soils (Pijut 2004). Moreover, Puijt (2004) highlights that extant *Comptonia* is intolerant of shade, preferring “full exposure to the sun”. From its fossil record in the European Palaeogene, several species of *Comptonia* are known from numerous fossil localities (e.g. middle Eocene floras of Eckfeld Maar, late Eocene assemblage Gîrbou/Romania; Kvaček 2010); one fossil species of

Tab. 10: Angiosperm families described from Baltic amber and their suggested geographical affinity, after Czecczott (1961). Percentage indicates portion of all angiosperm families from Baltic amber which belong to the respective geographical element. Families with the two highest species numbers (described from Baltic amber) are highlighted in green. Family names were adopted from Czecczott (1961) and not updated with current taxonomy.

Geographical element	Percentage	Family	Species no.
Cosmopolitan	46 %	Aquifoliaceae	3
		Campanulaceae	1
		Caprifoliaceae	2
		Celastraceae	1
		Ericaceae	8
		Euphorbiaceae	1
		Geraniaceae	2
		Graminae	1
		Liliaceae	1
		Linaceae	1
		Loranthaceae	3
		Oleaceae	1
		Oxalidaceae	2
		Papilionaceae	1
		Polygonaceae	1
		Rhamnaceae	1
		Rubiaceae	3
		Santalaceae	3
Thymeleaceae	4		
Urticaceae	1		
Tropical or subtropical	23 %	Apocynaceae	1
		Araceae	1
		Commelinaceae	1
		Connaraceae	1
		Dilleniaceae	3
		Lauraceae	4
		Myrsinaceae	3
		Olacaceae	1
		Palmae	3
		Theaceae	2
Temperate	12 %	Aceraceae	5
		Hamamelidaceae	2
		Rosaceae	1
		Saxifragaceae	5
		Umbelliferae	1
Discontinuous	12 %	Cistaceae	1
		Clethraceae	1
		Fagaceae	12
		Magnoliaceae	2
		Proteaceae	4
Anomalous	7 %	Myricaceae	3
		Pittosporaceae	1
		Salicaceae	1

Comptonia, *C. schrankii*, is part of xerophytic scrubs of extrazonal vegetation (e.g. early Eocene of Arceui, Calcaire Grossier; Eocene-Oligocene boundary of Häring, Austria; Kvaček 2010), indicating that fossil species of *Comptonia* also preferred dry habitats. The extant, as well as the fossil palaeoecological preferences of *Comptonia* could be an indicator that *Comptonia* from Baltic amber was part of dry and sunny habitats as well. However, *Comptonia* species were an abundant constituent in many other fossil assemblages across the European Palaeogene and thus, likely differed in their palaeoecological preferences. For a definite and more precise palaeoecological

interpretation of the Baltic amber *Comptonia*, more future studies are needed which clarify its affinities to other *Comptonia* species from the European Palaeogene.

Regarding preliminary results of ericoid inclusions from Baltic amber with affinities to *Cassiope* and *Calluna*, it is very probable that these two genera also indicate open habitats as well. Extant *Cassiope* and *Calluna* are shrubby; *Cassiope* mostly occurs in alpine and arctic regions, as part of heath vegetation (Eidesen et al. 2007), while *Calluna* is known from nutrient-poor, bog-like habitats (Mai 1995). The macrofossil record of both genera is scarce and does not offer insight into their palaeoecological preferences: fossils of the subfamily Ericoideae (including *Calluna*) from pre-Quaternary deposits are doubtful (Mai 1995) and also the first fossil record of *Cassiope* deriving from the 3 myr old Beaufort Formation of Meighen Island in Canada still needs to be confirmed (Eidesen et al. 2007). Considering information of the extant ecology of *Cassiope* and *Calluna*, it is possible that ericoid taxa from Baltic amber inhabited open bog habitats whose presence is already indicated by conifers (see chapter 4.1.3) or/and open areas with heath-like vegetation.

Further key taxa are the highly diverse Fagaceae whose extant representatives (10 genera, 620-750 species; Kubitzki 1993, Manos et al. 2008, Grímsson et al. 2016) are deciduous or evergreen trees and shrubs, inhabiting temperate and 'subtropical' forests. Fagaceae mainly occur in the northern hemisphere, but cross the equator to the southern hemisphere in South-East Asia (Kubitzki 1993, Mai 1995). Fossil species of Palaeogene Fagaceae are also diverse [see Denk et al. (2012) for an extensive list of European fossil Fagaceae of the Eocene and Oligocene] and mostly based on fossil leaves (Mai 1995, Denk et al. 2012). Following Mai (1995), fossil species or sections of Quercoideae are good indicators for distinguishing between deciduous and laurel forests or sclerophyllous vegetation. Considering the evidence of a *Trigonobalanus* (Trigonobalanoideae) inclusion from Baltic amber, as well as the high abundance of *Quercus* species in the Baltic amber flora, Mai (1967) concluded that these taxa indicate a pine-oak-laurel forest (containing *Trigonobalanus* and *Quercus*) on nutrient-poor, acid soils of the Baltic amber source area. As already mentioned, the specimen of *Trigonobalanus* needs to be verified. Knowing that two more extant trigonobalanoid genera exist, their ecological preferences should also be considered when discussing palaeoecological implications of the presumed *Trigonobalanus* inclusion from Baltic amber. A mixture of Fagaceae and conifer taxa is also supported by current results of Sadowski et al. (2017a [5]) who showed that the Baltic amber source area harboured diverse warm-temperate conifer forests which were likely to have been inhabited by fagaceous taxa as well.

The above outlined preliminary research results and published studies from angiosperm inclusions from Baltic amber show that they are a helpful tool to assess the habitat types of the 'Baltic amber forest'. They support assumptions of a heterogeneous forest, as suggested by Sadowski et al. (2017a [5]), and highlight the openness and patchiness of the 'Baltic amber forest'. However, further research is needed, especially regarding the Fagaceae, to more precisely assess habitat types of the Baltic amber source area.

Climatic implications of Baltic amber angiosperms, as suggested by Czecczott (1961; Tab. 10) need further studies as well. Although she listed tropical angiosperm families within the category ‘tropical or subtropical’, she only refers to the listed taxa of this category as ‘tropical element’, emphasizing their high abundance. However, it is not clear which of the listed families are meant to indicate ‘subtropical’ or ‘tropical’ climate (Tab. 10; Czecczott 1961). Moreover, the categories that Czecczott (1961) used were not defined: it remains unclear what an ‘anomalous’ distribution means and how the other categories are distinguished from each other. This is especially the case for the term ‘subtropical’³, an arbitrary term which is often used differently in the scientific community (Corlett 2013). Furthermore, the categorization of families needs a critical revision as well; for instance, extant Lauraceae were listed within the tropical to subtropical category. However, Lauraceae also occur in temperate regions (Stevens 2001 onwards). This example shows that the categorization of Baltic amber plant families sensu Czecczott (1961) into ‘climatic categories’ is not specific enough and thus, not applicable to infer palaeoclimatic conditions of the ‘Baltic amber forest’. For future studies it is recommendable to exclusively use verified plant genera from Baltic amber to estimate palaeoclimatic conditions. A widely accepted concept of climate classification should be applied as well, such as the Köppen-Geiger system (Köppen 1900, Geiger 1952, Kottek et al. 2006, Peel et al. 2007) or the zoniobiome concept of Walter and Breckle (2002) which are both generally accepted among scientists.

Besides this inconsistent terminology, angiosperm indicators for tropical climates are still under debate. Mai (1995) discussed tropical indicator families of the European Palaeogene, stating that they are mostly not reliable for tropical climate estimations, as they contain ‘extratropical genera’ (taxa that do not exclusively occur within the tropics, but also in the ‘subtropics’ or mountainous regions of the tropics). For instance, palm fossils were often presumed as tropical indicators (Weitschat and Wichard 1998), but extant ‘tropical’ palms, such as *Trachycarpus*, also occur in temperate regions (Mai 1995). Therefore, it is likely that inclusions of palms from Baltic amber were often misinterpreted as tropical climate indicators of the ‘Baltic amber forest’. This example shows that angiosperm-based palaeoclimatic estimations for the Baltic amber flora are far from understood and still need revision.

³Due to the ambiguous meaning of the term ‘subtropical’, it is written in quote marks in the entire thesis. Please see Corlett (2013) for definitions of the ‘Subtropics’, and Sadowski et al. (2017a [5]) for an extensive discussion of the ‘Subtropics’ with reference to the ‘Baltic amber forest’.

4.3 Indicators for life forms and microhabitat complexity

According to Schaefer (2003), life forms are defined as organisms which show similar responses to specific environmental conditions (for instance in their morphological structures, developmental stages or behavior) and “having similar effects on the dominant ecosystem processes” (Díaz and Cabido 1997), such as hydrophytes, helophytes or xerophytes which are plants being adapted to different water contents of their habitat. Further kinds of life forms exhibit a specific adaptation to nutrition, for instance parasites, hemiparasites, saprophytes and carnivorous plants.

Previous studies about Baltic amber inclusions show that the ‘Baltic amber forest’ harboured various types of life forms, raising the complexity of this palaeoecosystem. The recent discovery of two Baltic amber leaf inclusions proved the presence of carnivorous plants within the Baltic amber flora (Sadowski et al. 2015). Both leaves, belonging to the family Roridulaceae, show the same specific morphology as their extant relatives *Roridula dentata* (Fig. 5D, I) and *R. gorgonias* (Fig. 5E-H). Both extant species excrete a terpenoid trapping glue through their glandular tentacles which trap all kinds of arthropods very effectively (Simoneit et al. 2008). But the trapping glue lacks specific enzymes and thus, the plant itself cannot digest the trapped prey. To solve this problem, extant Roridulaceae show a peculiar ecology: they live in a digestive mutualism with endemic hemipterans, which are able to walk on the tentacled leaves without getting trapped (Fig. 5D) (Anderson and Midgley 2003). These hemipterans feed on the entangled prey and defecate on the leaves of *Roridula* (Ellis and Midgley 1996). Their leaf surfaces possess nano-sized gaps to take up the hemipteran faeces compounds and the nutrients therein, ensuring the survival in a nutrient-poor habitat (Ellis and Midgley 1996, Anderson and Midgley 2002, Anderson 2005). Following the definition of plant carnivory, Roridulaceae fulfil all criteria: attraction and retention of the prey, prey digestion and nutrient uptake (Givnish et al. 1984, Adamec 1997, Anderson and Midgley 2003, Adamec 2013).

The question arises whether roridulid plants from Baltic amber were carnivorous as well or even had this digestive mutualism. Sadowski et al. (2015) argued that several morphological features of the inclusions allow the conclusion of a carnivorous nature. First of all, the morphology of the tentacles show signs for excretion, such as the singular pore at the glandular head of the tentacles (Fig. 5C). Fagaceous trichomes which are attached to the tentacles further indicate that the leaf surface was very suitable for entangling or even catching things (Sadowski et al. 2015). Moreover, the trap organization of extant *Roridula* is also present in the leaf inclusions: both show a hierarchical organization of the trap with different size classes of tentacles (long ones for the first contact and entanglement of prey; medium ones for the slowdown of prey, and short ones for final immobilization; Fig. 5B, F; (Voigt et al. 2009, Sadowski et al. 2015). Sadowski et al. (2015) concluded that the signs for excretion, entangled plant material, as well as the functional units of prey capture are good indicators for a carnivorous nature of the roridulid plants from Baltic amber. However, there was no evidence for a digestive mutualism so far (Sadowski et al. 2015).

Another life form reported from Baltic amber is indicated by inclusions of aerial parasites or mistletoes which are defined as hemiparasitic plants depending on a host plant, but also serving as important resource for various organisms (Calder 1983, Aukema 2003). Sadowski et al. (2017b [6]) described six species of dwarf mistletoes (*Arceuthobium* spp., Viscaceae) from Baltic amber. Their extant relatives (Fig. 8) exclusively parasitize conifers of the Pinaceae and Cupressaceae, causing extensive damage to the host tree, such as a decreased growth rate and reduced survival (Mathiasen 1996, Geils and Hawksworth 2002). Having numerous representatives of *Arceuthobium* in the ‘Baltic amber forest’ raises the question whether these ancient species were already parasitic and if so, how they influenced their palaeoenvironment on a micro- or even macrohabitat scale.

The morphology of the inclusions assigned to *Arceuthobium* is, except for a few features, in congruence with their extant relatives (Fig. 8D-G). Sadowski et al. (2017b [6]) particularly highlight the presence of squamate bracts, the characteristics of the fruits and the overall reduced morphology of the fossils which is interpreted as an adaptation to a parasitic life form. Also, phylogenetic analyses of the Santalales (sandalwood order; including Viscaceae) showed that parasitism developed within the Santalales (Nickrent 2011). Thus, except for three basal clades, all sandalwood families are parasitic (Nickrent 2011), supporting the assumption that the Baltic amber *Arceuthobium* species were parasitic. As shown by Sadowski et al. (2017a [5]), the ‘Baltic amber forest’ encompassed numerous conifer species of Pinaceae and Cupressaceae which could have served as potential dwarf mistletoe hosts. Interestingly, one of the *Arceuthobium* inclusions, *A. groehnii*, had clumps of pinaceous pollen attached to its base, indicating proximity to a tree of the Pinaceae (Sadowski et al. 2017b [6]).

Extant dwarf mistletoes are of great ecological significance and thus, are termed “ecological keystones”, since they have a disproportionately large influence on their environment compared to their relative abundance (Power et al. 1996). One reason for being termed an ecological keystone is that dwarf mistletoes increase the structural complexity of a forest by inducing malformations in their host trees. Dwarf mistletoe infected branches first show specific swellings (Fig. 8D) and then, excessively ramify into numerous distorted branches, forming dense clumps (= witches brooms) in the tree canopy (Fig. 8A-C) (Geils and Hawksworth 2002). These witches brooms change the canopy shape, decrease the crown density or even result into canopy gaps in case of host tree mortality (Mathiasen 1996). Besides structural impact, extant dwarf mistletoes increase the ecological complexity as well. Witches brooms serve as microhabitats that offer shelter and forage areas for many kind of arthropods, increasing the arthropod diversity of the forest (Hawksworth and Geils 1996, Halaj et al. 2000). Also, the avian and mammal diversity is positively influenced by dwarf mistletoes and their witches brooms: the densely branched witches brooms are a suitable nesting side for birds (Fig. 8H) and small mammals, while the dwarf mistletoe itself represents a food resource, especially during the



Fig. 8: Extant dwarf mistletoe species (*Arceuthobium* spp., Viscaceae) from the United States (A-C, G, H: Crater Lake National Park, southern Oregon; D, E, Siskiyou Mountains, Oregon-California border). (A, B) Stands of *Pinus albicaulis* and *P. monticola* with witches' brooms in the forest canopy (arrowheads). (C) Witches broom of *Pinus contorta* subsp. *latifolia*. (D) Male inflorescences of *Arceuthobium monticola* on *P. lambertiana*; note the swelling of the branch (white arrowhead). (E) Fruiting inflorescences of *A. campylopodum*, infecting *P. ponderosa*. (F) Fruiting inflorescence of *A. monticola* on *P. monticola*. (G) Fruiting inflorescence of *A. americanum* on *P. contorta* subsp. *latifolia*. (H) Bird nest in a witches broom of *P. contorta* subsp. *latifolia*. All photos E. M. Sadowski.

winter season when resources are generally scarce (Parks et al. 1999, Watson 2001, Hedwall and Mathiasen 2006, Watson and Herring 2012). Applying knowledge of extant *Arceuthobium* to ancient dwarf mistletoes of the ‘Baltic amber forest’, it is likely that they influenced the palaeoecosystem in a similar way as in extant forests (Sadowski et al. 2017b [6]). *Arceuthobium* from Baltic amber probably increased the structural complexity of the amber source forests by changing the canopy shape or affecting the tree survival, thus influencing the forest heterogeneity and habitat patchiness. According to Sadowski et al. (2017b [6]) potential interactions of the ancient dwarf mistletoes with the Baltic amber fauna are difficult to reconstruct, but however, should not be entirely ruled out, considering syninclusions of insects (e.g. Diptera, Aphids) closely located to the dwarf mistletoe inclusions. Last but not least, Sadowski et al. (2017b [6]) point out that extant *Arceuthobium* are known to induce high resin release in their hosts as a reaction to the infection or due to heavy witches brooms that may break off (Geils and Hawksworth 2002). Therefore, Baltic amber dwarf mistletoes should also be taken into account when discussing reasons for resin release in connection to the formation of the Baltic amber deposit (Sadowski et al. 2017b [6]).

Numerous Baltic amber inclusions of different liverwort and bryophyte species indicate the presence of epiphytic life forms within the ‘Baltic amber forest’. In their comprehensive study, Grolle and Meister (2004) identified about 22 liverwort species, and more species were discovered and revised in the following years (e.g. Heinrichs et al. 2015a, Heinrichs et al. 2016). According to Heinrichs et al. (2015b), these liverworts were likely epiphytic, growing in close proximity or even on trunks of resin-releasing trees within the ‘Baltic amber forest’. Also, Feldberg et al. (2014) points out that “the humidity maintained in forests is the most probable factor controlling the assembly of epiphytic liverwort diversity”, meaning that the highly diverse liverwort community is a good humidity indicator in the Baltic amber source area, at least at a microhabitat scale.

The same holds true for moss inclusions from Baltic amber, of which approximately 60 species have been described so far (Frahm 2010). Frahm (2010) mentions that extant analogues of Baltic amber moss species are epiphytes, occurring on trunks in oak-pine forests of mainly eastern and southern Asia. Besides epiphytic mosses, also terrestrial ones are known from Baltic amber. Heinrichs et al. (2014) reported a moss community, enclosed in a single piece of amber. Extant analogous species of these mosses are terrestrial, inhabiting shaded microhabitats, such as rocks and degraded wood. A syninclusion of a chilopod, a typical component of soil faunas, further supported the assumption of close vicinity to the forest floor and a likely terrestrial habitat of the mosses (Heinrichs et al. 2014). Besides mosses, also ferns of the Mationaceae were components of the terrestrial microhabitats within the ‘Baltic amber forest’, likely inhabiting rocks or the forest floor (Schmidt and Dörfelt 2007).

Further microhabitat constituents were lichens of which a high number of inclusions have just been reported recently (Kaasalainen et al. 2017). Lichens represent “stable mutualistic associations in which photoautotrophic algae and/or

cyanobacteria provide carbohydrates for heterotrophic fungi” (Kaasalainen et al. 2015). Those symbionts were even detected in several Baltic amber inclusions which exhibited sufficient preservation to differentiate between the lichen tissues, including the photobiont layer (Hartl et al. 2015, Kaasalainen et al. 2017). Lichen inclusions also serve as indicator taxa to estimate microhabitat conditions of the ‘Baltic amber forest’. For instance, Rikkinen and Poinar (2002) described a lichen inclusion as *Anzia electra*, with strong affinities to extant *Anzia* species of East Asia and eastern North America. According to the extant ecological preferences of *Anzia*, the fossil indicates a humid microclimate and a well-lit microhabitat, such as branches in an open canopy or sun-exposed trunks and rocks (Rikkinen and Poinar 2002). Similar microhabitat conditions (humid environment and illuminated areas) are as well estimated based on the presence of calicioid lichen inclusions which show affinities to extant *Calicium* and *Chaenotheca* (Rikkinen 2003). The most comprehensive work about lichens from Baltic amber was recently published by Kaasalainen et al. (2017) who discovered numerous, morphologically diverse lichen inclusions. Besides crustose and squamulose lichens, the authors highlighted the high amount of foliose and fructicose lichens, indicating that the majority of Baltic amber lichens were epiphytic. The morphological adaptations of the Baltic amber lichens gave insight into their ancient microenvironment which was “a humid and moderately well-illuminated temperate forest” (Kaasalainen et al. 2017).

Another important component of microhabitat communities of the ‘Baltic amber forest’ are fungi, such as *Metacapnodium succinum* (Ascomycota), an epiphytic sooty mould. It is a mat-forming fungus which abundantly occurs on Baltic amber plant inclusions, for instance on Cupressaceae twigs, oak leaves, but also on a foliose lichen (Schmidt et al. 2014). Another epiphytic fungus is *Casparytorula* which is another abundant constituent of Baltic amber microhabitats. According to Kettunen et al. (2015 [2]), inclusions of *Casparytorula* show that this fungus grew close or even on freshly excreted resin and thus, was likely epiphytic on the amber bearing tree (Kettunen et al. 2015 [2]). This is supported by syninclusions of flowers, spider webs and epiphytic lichens which indicate proximity to more elevated forest layers. *Casparytorula* was also reported to grow on a coniferous leaf with affinities to Pinaceae, ‘Taxodiaceae’ and Taxaceae (Kettunen et al. 2015 [2]). However, a more recent study of conifer leaves from Baltic amber (including this particular specimen), showed that this leaf is actually from an angiosperm with yet unclear affinities (*Dicotylophyllum* var. sp.; Sadowski et al. 2017a [5]).

Besides epiphytic fungi, parasitic fungi were also reported from Baltic amber, such as *Gonatobotryum*. Dörfelt and Schmidt (2007) found an inclusion of a coniferous seedling (possibly related to *Picea*) which was infected by *Gonatobotryum*. The well preserved nucleus remnant and cotyledons of the seedling indicated that it was still alive when the fungus infected it; thus, the authors supposed that the fungi attack caused the seedling’s death (Dörfelt and Schmidt 2007). A further fungus with affinities to either *Gonatobotryum* or to the related *Gonatobotrys* was found on a dwarf mistletoe inclusion (*Arceuthobium viscoides*; Sadowski et al. 2017b [6]). The dwarf mistletoe is partly entangled in a spider web and shows signs

of degradation, such as a shrunken surface (Sadowski et al. 2017b [6]). However, the dwarf mistletoe inclusion did not exhibit a clear morphological response to a parasitic attack, such as epidermal cells that block the fungal growth. Therefore, it is likely that in this case the fungus was an opportunistic saprotroph, starting to attack the dwarf mistletoe when it already had broken off the main plant and fallen into a spider web (pers. comm. Elina Kettunen, Helsinki). A very specific fungus in terms of nutrient supply is *Chaenothecopsis*, a further fungal taxon from Baltic amber. Many extant *Chaenothecopsis* species are resinicolous which means that they are able to grow on and even digest fresh or semisolidified coniferous resin (Tuovila et al. 2013). The same holds true for the ancient *Chaenothecopsis* from Baltic amber which shows similar morphological adaptations to the resinous habitat as its extant representative (Tuovila et al. 2013).

In summary, microhabitat communities of the ‘Baltic amber forest’ are very diverse in their taxonomical composition but also in the presence of different life forms, including saprophytes, parasites, symbionts, carnivorous plants and highly specialized resinicolous fungi. They also give insight into the environmental conditions of microhabitats, indicating that they were well-lit to shaded and humid.

5. What is new about the picture of the ‘Baltic amber forest’?

As explained in previous chapters, conifer and angiosperm inclusions from Baltic amber are useful tools to assess habitat types of the Baltic amber source area. In the following chapters, it is discussed how these current results change the traditional picture(s) of the ‘Baltic amber forest’ and how this new perspective differs from other interpretations of the Baltic amber source area.

5.1. Habitat heterogeneity and stratification of the ‘Baltic amber forest’

Based on several studies of plant inclusions from Baltic amber (chapters 4.1.3, 4.2.2 and 4.3), the following habitat types in the Baltic amber source area were reconstructed: coastal swamps, raised bogs, back swamps, riparian forests, mixed-mesophytic angiosperm-conifer forests, and open habitats (e.g. Sadowski et al. 2016a [3], b[4]; 2017a [5], b[6]).

Although several authors suggested a diverse landscape of the Baltic amber source area (e.g. Bachofen-Echt 1949) especially in terms of aquatic habitats (Ander 1942, Wichard et al. 2009, Alekseev and Alekseev 2016), the habitat types were not as specifically described and classified as by Sadowski et al. (2017a [5]). They confirmed the presence of riverine swamps in the Baltic amber source area which was just recently doubted by Alekseev and Alekseev (2016). The presence of swamps in the Baltic amber source area was already suggested by Kohlman-Adamska (2001) who, however, named *Glyptostrobus* as sole coniferous constituent of these swamps. The knowledge of the floristic composition of these swamps was further elaborated by Sadowski et al. (2017a [5]), since more plant taxa (especially conifers), which were unknown or unproven from Baltic amber before, were discovered (i.e. *Taxodium*, *Quasisequoia*; Sadowski et al. 2017a [5]). Another new aspect of Sadowski et al.’s (2017a [5]) picture of the ‘Baltic amber forest’ is the differentiation between coastal and back swamps, as well as tidal and freshwater inundations (Tab. 3). These different kinds of swampy habitats indicate that heterogeneous aquatic habitats, such as rivers, blind river arms, stagnant water bodies, alluvial meadows or tidal creeks were likely present in the Baltic amber source area.

The pine-oak steppe forest is a further habitat type of the Baltic amber source area which was reconstructed by Kohlman-Adamska (2001). According to Wendelberger (1989), this forest type is defined as “layered associations composed of forest and steppe layers in vertical superposition” (Wendelberger 1989, p. 185), meaning that the forest canopy of extant steppe forests is very open and numerous grasses occur in the herbaceous layer. Different types of pine steppe forests exist which either possess a rich shrubby layer (dwarf-shrubs such as *Calluna* and *Erica*) or a grassy layer, but lacking shrubs (Wendelberger 1989). Extant pine steppe forests mainly occur in regions with continental climates (Wendelberger 1989), but steppe-like elements may also occur in sub-continental to maritime climates. For instance, forests of *Pinus sylvestris* with dwarf shrubs and cryptogams in the understory

inhabit acidic and sandy soils, such as coastal dunes of today's Baltic Sea as well as inland dunes in north-eastern Germany (Heinken 2008).

On the one hand, several angiosperms (e.g. sedges, grasses, Ericaceae, Roridulaceae, *Arceuthobium*) and complex lichen communities indicate well-lit areas or even meadows within at least some parts of the 'Baltic amber forest'. This supports the assumption of an open canopy (as implied by steppe-forests; Kohlman-Adamska 2001) and rejects hypotheses of a dense forest (Ander 1942, Czacott 1961) or only rarely occurring meadows (Larsson 1978). On the other hand, the term 'pine-oak steppe forest' indicates that *Pinus* and *Quercus* were dominating the canopy of the 'Baltic amber forest' which was obviously not the case as many more conifer and fagaceous taxa were recently discovered from Baltic amber (Sadowski et al. 2017a [5]). However, it is likely that steppe-like elements were present in the Baltic amber source area; yet, they were not equivalent to vast extant continental steppes, but rather habitat patches that occurred due to local environmental conditions, such as acidic, nutrient-poor and dry soils.

Like Alekseev and Alekseev (2016), Sadowski et al. (2017a [5]) suggested a plain landscape for the Baltic amber source area which is different to the majority of theories interpreting the topography as mountainous (see Tab. 3 for references and chapter 5.3 for further discussion). On the contrary, Sadowski et al. (2017a [5]) saw evidence for a 'horizontal' stratification of the Baltic amber source area which encompassed a heterogeneous mixture of different habitat patches.

The coastal setting of the 'Baltic amber forest' as well as the presence of rivers, swamps and bogs could be indicative for an estuary-like setting. In extant estuaries, channel systems connect water bodies with each other. These channels can be stable, meandering, dendritic (irregular branches which lead to other channels) or braided (Simenstad 1983). In the last case, the channels are subdivided into smaller branches which divide the area into islands or bars, and then reunite downstream (Simenstad 1983). Further factors, such as regional climate, geological processes and the hydrology of the area create a diverse landscape (Obeysekera et al. 1999). This scenario could explain the large diversity of plant and animal taxa inclusions from different habitats of the 'Baltic amber forest': different habitat types existed in close proximity, such as swamps and bogs along inundated areas (tidal, brackish or freshwater) next to non-inundated habitats of elevated (terrace-like) areas, as well as blind river arms and oxbow lakes. Such a scenario would easily explain the large diversity of different habitat indicator inclusions (animals as well as plants) from Baltic amber. Grimaldi (1996) and Langenheim (2003) pointed out that an estuary locality of an amber forest is ideal for the deposition of amber: streams transport the buoyant resin from the forest into stillwater sediments of the estuary where they get buried by sediments and then turn into amber with time.

In contrast to this idea, Alekseev and Alekseev (2016) interpreted the Baltic amber source area as a climax community, highlighting it was "not a regularly disturbed cenosis of a river valley or delta", lacking "different succession stages" (Alekseev and Alekseev 2016, p. 78 and p. 85). However, the palaeobotanical evidence from Baltic amber indicates the presence of different successional stages in

the Baltic amber source area. For instance, *Taxodium* and *Quasisequoia couttsiae* are typical constituents of azonal vegetation, such as riparian forests (Kunzmann 1999, Sadowski et al. 2017a [5]). The theory of an undisturbed climax community by Alekseev and Alekseev (2016) is also in contrast to the coastal setting of the Baltic amber source area, where tidal changes influenced the water level and thus, ‘regularly disturbed’ the environment. In conclusion, a horizontal stratification of the Baltic amber source area into different plant communities can be expected, resulting into a heterogeneous mosaic of habitats which also included successional stages.

Besides this horizontal stratification, a vertical stratification into different vegetation layers can be assumed as well. The highest layer likely encompassed *Quasisequoia* trees whose fossil record show that they were large and massive, reaching up to 70 m height (Kunzmann 1999). They overtopped the medium-sized trees which encompassed several conifer and angiosperm taxa (including the Fagaceae). Shrubby layers may have been formed by fagaceous taxa as well, since growth habits of their extant representatives include shrub-like forms (Kubitzki 1993). More constituents of shrub and herbaceous layer were likely represented by Ericaceae; however, more studies are needed to clearly identify numerous ericaceous (e.g. *Calluna* and *Cassiope*-like leaves) and ericaceous-like inclusions from Baltic amber (e.g. *Dicotylophyllum* spp.). Further elements of the herbaceous layer were graminids, *Comptonia* and Roridulaceae; future studies will likely reveal even more plant taxa of each layer.

5.2. Palaeoclimatic estimations of the ‘Baltic amber forest’

As already described in chapter 4.2.2, presumed affinities of Baltic amber angiosperms to extant tropical or ‘subtropical’ families (Czeczott 1961) were used to argue for a subtropical to tropical climate of the ‘Baltic amber forest’. However, these interpretations are based on botanical inclusions which have not been revised and/or verified. Moreover, the presumed (sub)tropical affinities of Baltic amber plants are only based on families (Czeczott 1961) which is too imprecise, since most of the named families comprise non-tropical genera as well (see chapter 4.2.2 for further explanation). Therefore, the concept of (sub)tropical plants from Baltic amber, as it is represented by Czeczott (1961) is obsolete, but still, has often been cited as reference for a presumed tropical climate of the ‘Baltic amber forest’ (e.g. in Weitschat and Wichard 1998). Further evidence for a presumed tropical climate derives from arthropod inclusions from Baltic amber. Several taxa, for instance of Psocoptera and Diopsidae, were affiliated to extant tropical and subtropical faunas of South Asia, South America and Africa (Weitschat 1997). In contrast, Ander (1942) highlights the Holarctic affinities of the Diptera fauna from Baltic amber. In his opinion the Holarctic Dipterans represent a greater portion than those Dipteran taxa which are affiliated to extant Neotropical or Palaeotropical taxa (Ander 1942). Besides these examples, there are more arthropod inclusions from Baltic amber which have been interpreted differently regarding their palaeoclimatic implications (e.g. Weitschat and Wichard 1998, Serezhovskiy 2013, Alekseev and Alekseev 2016).

Moreover, studies on arthropods from Baltic amber only rarely include a comparison to fossil analogous taxa and their palaeoclimatic requirements. Therefore, it is unclear if the palaeoclimatic requirements of Baltic amber arthropods are really equivalent to these of extant taxa. Thus, there is a need for future studies which carefully discuss whether arthropod inclusions are reliable indicators for interpreting the palaeoclimate of the ‘Baltic amber forest’.

The newly discovered plant inclusions from Baltic amber, however, were related to fossil analogues or even represented fossil plant taxa that are known from other fossil assemblages of the European Palaeogene (e.g. *Cupressospermum saxonicum*, *Quasisequoia couttsiae*, and *Sciadopitys* cf. *tertiaria*; Sadowski et al. 2016a [3], 2017a [5]). Habitat requirements and palaeoclimatic preferences of the respective plant taxa are already known as well, based on numerous studies investigating these fossil assemblages (e.g. Kunzmann 1999; see Sadowski et al. 2017a [5] for further references); thus, in order to estimate the palaeoclimate of the ‘Baltic amber forest’, Sadowski et al. (2017a [5]) compared their results of Baltic amber plants to the vegetation and palaeoecology of ‘subtropical’ fossil floras of the European Eocene. According to the authors (Sadowski et al. 2017a [5]), the Kučlin flora and the Staré Sedlo Formation of North Bohemia (Czech Republic), both are late middle to late Eocene in age, exhibit a significantly lower conifer diversity and a different conifer composition to the Baltic amber flora. The same holds true for the Zeitz floristic complex of the Weißelster Basin which, as Kučlin, yields different conifer key taxa (*Dolistrobus* and *Tetraclinis*) that are not present in the Baltic amber flora. Following Sadowski et al. (2017a [5]), these striking differences between the Baltic amber flora and ‘subtropical’ Eocene floras show that ‘subtropical’ climates in the European Palaeogene resulted in another floristic composition and vegetation, compared to that of the Baltic amber source area.

Some authors mentioned similarities of the Baltic amber fauna to the fossil assemblage of the middle Eocene Eckfeld Maar (e.g. Wappler 2003, see chapter 1.6.1); a comparison of the Baltic amber flora to the named fossil assemblage however, revealed great differences. In Eckfeld Maar, conifers are rare: the only coniferous remains are fragments of a twig and a cone with presumed affinities to Taxodiaceae, and further fossils of *Cephalotaxus* and a cupressaceous twig (supposedly *Tetraclinis* (*Libocedrites*) *salicornioides*) (Wilde and Frankenhäuser 1998). Pollen of Pinaceae was found only in a moderate quantity (Wilde and Frankenhäuser 1998) and pollen of *Doliosstrobus taxiformis* (Doliosstrobaseae) indicates a further but rare coniferous constituent of the Eckfeld Maar flora (Nickel 1996). This is clearly different to the Baltic amber flora which is characterized by a high conifer diversity and abundance. Regarding angiosperms, Wilde and Frankenhäuser (1998) highlight the Juglandaceae as most important family of the Eckfeld Maar flora. A further common family in the Eckfeld fossil site is Theaceae (*Ternstroemites dentatus*), but also Rutaceae, Anacardiaceae and Mastixiaceae are present (Wilde and Frankenhäuser 1998). Except for Theaceae, none of the named families were reported from Baltic amber. However, inclusions with affinities to Theaceae, such as *Stewartia kowalewskii*, were doubtful (Mai 1971), not described

[one specimen of *S. kowalewskii* was listed by Pielińska (2001), but not further described or pictured] or not revised (*Pentaphylax oliveri*, Conwentz 1886). The floras of Eckfeld Maar and Baltic amber are also different in their habitat composition: while the ‘Baltic amber forest’ was situated in close proximity to the coast, the Eckfeld Maar was an isolated inland lake, far away from the coastal lowland (Wilde and Frankenhäuser 1998). In conclusion, this comparison shows that in terms of floristic composition and habitat types, both fossil assemblages of Eckfeld Maar and Baltic amber can be clearly distinguished from each other. Thus, presumed affinities or even a similar age of both fossil localities should be rejected.

Further comparison to extant floras which exhibit similar conifer diversity revealed affinities of the Baltic amber flora to East Asia, as well as to North America (Sadowski et al. 2017a [5]). The majority of extant conifer taxa, which are analogous to the conifers found in Baltic amber, prefer warm-temperate humid climates rather than ‘subtropical’ conditions (Sadowski et al. 2017a [5]). Combining the results of the comparisons of the Baltic amber flora to fossil and extant floras, Sadowski et al. (2017a [5]) saw strong evidence that the ‘Baltic amber forest’ was likely non-tropical, and thus, rejected former theories of a tropical to ‘subtropical’ forest, as suggested by Weitschat (1997, 2008) and Weitschat and Wichard (2010) (Tab. 3 for further references).

In summary, plant-based palaeoclimatic estimations are in congruence with climate reconstructions of Central Europe during the Eocene-Oligocene transition. This time period was characterized by an ongoing temperature decline and an overall increment of seasonality (Mosbrugger et al. 2005, Kvaček et al. 2014). Following Sadowski et al. (2017a [5]), the warm-temperate palaeoclimatic estimations for the ‘Baltic amber forest’ supports the late Eocene age of Baltic amber, as suggested by Standke (2008) who based her results on the evaluation of the geological setting.

5.3. Wheeler’s dilemma, the Eridanos river and the quest for mountains in the ‘Baltic amber forest’

One major factor which causes much confusion about the Baltic amber source vegetation is the occurrence of inclusions of plant and animal taxa which presumably show affinities to either (warm)-temperate or (sub)-tropical extant taxa. Most authors interpret this mixture as evidence for an altitudinal stratification of the Baltic amber source area (e.g. Larsson 1978 and Kohlman-Adamska 2001; see Tab. 3 for more references). The question of a mountainous source forest is also strongly connected to 1) the locality of the ‘Baltic amber forest’ (Fennoscandia vs. Baltic area, long-distance transport by the Eridanos river), 2) the interpretation of Baltic amber inclusions which are used as indicator taxa, and 3) the palaeoclimate of the forest.

A first explanation for the peculiar mixture of the Baltic amber flora and fauna was already given by Heer (1860) who supposed that the ‘Baltic amber forest’ covered vast areas from Germany, Poland and the Samland area up to Scandinavia. Heer (1860) further suggested that taxa with temperate affinities were located in the mountainous northern extents of the ‘Baltic amber forest’ while (sub)tropical plants

and animals inhabited forested areas in the South. Then, ambers with inclusions from the northern regions of Scandinavia were transported by a river system to the areas of Samland and Gdansk where they were contemporaneously deposited with tropical taxa. Thus, following Heer's (1860) theory, temperate taxa from Baltic amber represent an allochthonous deposition, while specimens of thermophilic taxa are autochthonous.

Wheeler (1910, 1915) discussed Heer's (1860) conjecture in studies about ant inclusions from Baltic amber. Wheeler pointed out that ant taxa with affinities to temperate climates outnumber those taxa with tropical affinities, which in his opinion, contradicts Heer's (1860) theory about a long distance transport (Wheeler 1910, 1915). Wheeler (1910) further supposed that the tropical ant taxa represented relicts which gradually became extinct.

Further scenarios, explaining the mixture of inclusions with presumed tropical and temperate affinities neglected Wheeler's (1910, 1915) ideas and instead suggested a similar scenario to Heer (1860). Kosmowska-Ceranowicz and Konart (1989), Kosmowska-Ceranowicz (1992), Schulz (1999), Weitschat (1997) and Weitschat and Wichard (1998) localized the entire 'Baltic amber forest' in the mountainous region of Fennoscandia. The amber from this forest was then transported by the hypothetical Eridanos river system to the Baltic region where it was deposited into late Eocene sediments (see chapter 1.6.1 for further references and explanations). However, this 'Eridanos hypothesis' is mainly driven by animal data from Baltic amber inclusions, while geological and palaeobotanical evidence is mostly ignored or misinterpreted.

From a geological perspective, previous results of Standke (2008) reject Heer's (1860) theory as well as the 'Eridanos hypothesis'. In both scenarios, the amber would have been transported over a very large distance of approximately 900 km from Fennoscandia to the Chłapowo-Samland-delta. However, outcrops along the Baltic coast do not provide evidence of the existence of such a river during the late Eocene (Standke 2008).

Contrastingly, a fluvio-deltaic system draining the southern North Sea Basin (including the Baltic area) was reported from the late Cenozoic (Sørensen et al. 1997, Overeem et al. 2001, Gibbard and Lewin 2016). This system persisted from the late Oligocene-Miocene to the Pleistocene and is also known as 'Baltic River System' (Bijlsma 1981). Overeem et al. (2001) suggested terming this fluvial drainage system 'the Eridanos river' with reference to Kosmowska-Ceranowicz (1992; 1997a) who introduced this term for the hypothetical river, transporting amber from Fennoscandia to the Baltic area during the Eocene (Kosmowska-Ceranowicz and Konart 1989). However, Overeem et al. (2001) did not mention that Kosmowska-Ceranowicz (1992; 1997a) and Kosmowska-Ceranowicz and Konart (1989) interpreted the Eridanos river as an Eocene river system. Even more confusion arose in a previous publication of Gibbard and Lewin (2016): the authors admit that there are contrasting theories about the Baltic River System, mentioning that Kosmowska-Ceranowicz dates this fluvial-deltaic system as Eocene in age, although other studies revealed that the Baltic River System is actually from the late Cenozoic (Gibbard and

Lewin 2016). However, in the same instance, Gibard and Lewin (2016) cite Kosmowska-Ceranowicz as reference for stating that deposition in the Baltic River System started during the Oligocene. Critically, checking the reference that Gibard and Lewin (2016) are citing (Kosmowska-Ceranowicz from 1988) it is clear that they actually meant a book chapter from ‘Tränen der Götter’ (here cited as Kosmowska-Ceranowicz 1997a). But in this particular chapter, Kosmowska-Ceranowicz (1997a) does not clearly mention any Oligocene deposition; however, she states that the term Eridanos river was introduced by her for describing the river that transported amber from Fennoscandia to the South (Kosmowska-Ceranowicz 1997a). Another publication (Kosmowska-Ceranowicz and Konart, 1989) contains a clear statement about the Eridanos river: “If we relate the myth [of Pytheas] to the Earth’s Eocene period and call the river Eridanus, the search for it [the amber river] could be finally over” (Kosmowska-Ceranowicz and Konart 1989, p. 205). But she does not present any geological data to prove the existence of the Eridanos river, so it seems that the Eridanos hypothesis is rather an idea, than a proven fact. Furthermore, studies of the Blue Earth layer clearly show that it had a marine origin and a low sediment input (Standke 1998; 2008), which is in contrast to the idea of a river transporting vast amounts of amber and sediment into a delta. Nonetheless, the idea of Eridanos became cited as realistic scenario by subsequent publications [e.g. Weitschat and Wichard 1998: the named authors did not term the river system ‘Eridanos’, but refer to Kosmowska-Ceranowicz (1997a) when describing the long-distance transport of Baltic amber].

In summary, it appears misleading to equalize a late Cenozoic fluvial-deltaic system whose existence has been proven by several studies (e.g. Bijlsma 1981, Sørensen et al. 1997, Overeem et al. 2001) with the hypothetical Eridanos river named by Kosmowska-Ceranowicz (1992; 1997a) and Kosmowska-Ceranowicz and Konart (1989). Following the primary definitions of the Baltic River System and the Eridanos river; both systems are related to different time periods. Therefore, it is strongly recommended to stick with the term ‘Baltic River System’ when talking about the late Cenozoic fluvio-deltatic system of the southern North Sea Basin. The Eridanos river as such should only be referred to when discussing theories about the geographical locality of the ‘Baltic amber forest’ and the redeposition of its amber.

The ‘Eridanos hypothesis’ is also connected to a presumed long-term persistence of the ‘Baltic amber forest’: since the main bearing layer of Baltic amber (Blue Earth) has been proven to be Priabonian in age (late Eocene), it was suggested that the ‘Baltic amber forest’ persisted for approximately 10 million years, so that amber was continuously redeposited from an early to middle Eocene forest in Fennoscandia to late Eocene sediments by the Eridanos river (Weitschat and Wichard 1998). Standke (2008) states that a continuous amber deposition over a great geographical distance resulting in mainly one sediment layer (Blue Earth) seems unlikely. Also, this theory of a long-distance amber transport neglects the transgression of the Palaeo-North Sea during the middle Ypresian (Eocene) where vast areas of Fennoscandia were covered (Standke 2008, Gibbard and Lewin 2016) and thus, could not have harboured the ‘Baltic amber forest’. Moreover, the

palaeobotanical record from Baltic amber does not reflect the early to middle Eocene age of Baltic amber, as suggested by (Weitschat 1997, Weitschat 2008). In contrast, conifer inclusions from Baltic amber support the late Eocene age of Baltic amber (Sadowski et al. 2017a [5]), as already proposed by Standke (1998, 2008). A further reason which argues against a long-term persistence of the ‘Baltic amber forest’ is its coastal setting, likely comparable to an estuary (chapter 5.1). Such a fluvial system changes over time and does not consistently exist for millions of years, as it would be expected for a 10 Ma old forest (Standke 2008). For all these reasons, a Fennoscandian origin of the ‘Baltic amber forest’ including long-distance transport of its amber is unlikely. A close proximity of Baltic amber formation and deposition is more probable, as already suggested by Standke (2008). Therefore, the provenance of the ‘Baltic amber forest’ must have been in the Baltic region (Sadowski et al. 2017a [5]).

Assuming a Baltic origin of Baltic amber, the question of a mountainous source area can be easily answered: the East European Craton (including the Baltic region) is a prime example of long-term geological stability (Nikishin et al. 1996). This precludes any orogenic events in the Baltic region during the Eocene and hence, there is no geological evidence for the presence of any mountains of any height in the Baltic amber source area.

The palaeobotanical record from Baltic amber also supports assumptions of a plain Baltic amber source area (Sadowski et al. 2017a [5]), but often has been misinterpreted as indicative for an altitudinal stratification of the Baltic amber source area (e.g. Larsson 1978, Kohlman-Adamska 2001, see Tab. 3 for more references). For instance, *Abies* inclusions from Baltic amber were often used as an example for mountain habitats in the ‘Baltic amber forest’ (Kohlman-Adamska 2001). However, in its extant distribution, *Abies* exhibits a broad ecological spectrum, occurring in lowland habitats as well as in alpine environments (Farjon 1990, Xiang et al. 2007). In its fossil record from Central Europe, *Abies* is a constituent of a non-mountainous mixed angiosperm forest, such as in the Miocene Wiesa flora (Kunzmann and Mai 2005) and therefore, *Abies* is not necessarily an indicator for mountain habitats (Sadowski et al. 2017a [5]). The same holds true for *Sciadopitys* which nowadays is restricted to rocky slopes of mountainous areas (Farjon 2005) and thus was used as an indicator for mountain habitats in the Baltic amber forest (Kohlman-Adamska 2001). However, during the Palaeogene *Sciadopitys* was a typical constituent of raised-bog habitats and therefore, is an indicator for the presence of coniferous bogs in the ‘Baltic amber forest’, rather than for mountain ranges (Sadowski et al. 2016a [3]). Further palaeobotanical evidence (discussed in chapter 5.2) rejects the altitudinal stratification of the Baltic amber source area into (sub)tropical lowland and temperate mountain forest, for the following reasons: 1) the Baltic amber flora is clearly different from other (sub)tropical Palaeogene floras; 2) the Baltic amber flora comprises mainly plant taxa of warm-temperate affinity; 3) presumed tropical indicator plants from Baltic amber are ambiguous and lack verification. Thus, the Baltic amber flora does not reflect a contrasting mixture of tropical and non-tropical

taxa and therefore, theories about lowland (sub)tropical and mountainous temperate ‘Baltic amber forests’ can be rejected.

In terms of animal inclusions from Baltic amber, Archibald and Farrell (2003) suggested a climatic explanation for the co-occurrence of tropical and temperate (animal) taxa which they termed ‘Wheeler’s dilemma’. As Wheeler (1910, 1915), Archibald and Farrell (2003) reject Heer’s (1860) theory of long distance transport, since syninclusions of presumed tropical and non-tropical taxa from Baltic amber prove the coexistence of these taxa on a small geographic scale. In their opinion, the reason for this coexistence is a “higher equability” of the climate, especially regarding the cold month mean (CMM): a reduced thermal seasonality and fewer frosts would enable tropical animal taxa to inhabit higher latitudes (Archibald and Farrell 2003). They conclude (Archibald and Farrell, 2003, p. 22): “The presence of fossil organisms with closely related modern representatives that have clear tropical affinities may be a consequence of raised CMM in cool climates (increased equability), not necessarily an indicator of raised MAT [mean annual temperature] (subtropical or tropical climates)”. With respect to the Baltic amber deposit, this raises the notion whether the presence of presumed tropical and non-tropical animal taxa in one deposit is a reliable indicator of tropical or subtropical climates and vegetation types or rather an expression of “more equable temperature seasonality” (Archibald and Farrell 2003).

In summary, geological and palaeobotanical evidence rejects a mountainous ‘Baltic amber forest’. The whole idea of a Fennoscandian origin of the ‘Baltic amber forest’ and a redeposition of amber from North to South by the putative Eocene Eridanos river lacks any geological evidence, and furthermore, has often been confused with the much younger Baltic River System of the late Oligocene-Miocene. Instead, the Baltic amber flora reflects many different kinds of habitats, rather than altitudinal zones. The diversity of inclusions could be explained by the heterogeneous mosaic-like landscape which allowed co-occurrences of many taxa in close proximity.

5.4. Geoflora concept – does it apply to the ‘Baltic amber forest’?

Based on the highly diverse Baltic amber flora with presumed tropical and temperate elements, Szwedó and Sontag (2009) rejected the theories of Wheeler (1910, 1915) and Archibald and Farrell (2003) (see chapter 5.3). As an explanation for the peculiar mixture of (sub)tropical and temperate taxa, Szwedó and Sontag (2009) followed Kohlman-Adamska (2001), who argued that the Baltic amber plant diversity not only indicated an altitudinal stratification of the source area, but mainly showed the convergence of a temperate and a ‘paratropical’ climatic zone, the latter being equivalent to a ‘subtropical’ climate (Szwedó and Sontag 2009). Thus, the ‘Baltic amber forest’ comprised two geofloras: the Arcto-Tertiary geoflora which is associated with temperate climate and the Palaeotropical geoflora which is indicated by thermophilous plant taxa (Szwedó and Sontag 2009).

The concept of geofloras dates back to Engler (1882) who studied Tertiary fossil floras from the Arctic. He observed that fossil plant taxa from Arctic assemblages are affiliated with extant floras of northern hemispheric temperate regions (North America, Europe and extratropical East Asia). For addressing this group of plant taxa, Engler (1882) introduced the term ‘Arcto-Tertiary element’. Plant taxa which are confined to extant Old World tropics were termed ‘Palaeotropical elements’. This concept was elaborated by Chaney (1959) who changed these terms to ‘Arcto-Tertiary/Palaeotropical geofloras’, stating that they all “must [...] have had a common area of origin”, meaning that for instance, all Arcto-Tertiary geofloras originated in northern latitudes, but alternated in their distribution according to environmental changes. Furthermore, geofloras “maintained [themselves] with only minor changes in composition for several epochs or periods of earth history...” (Chaney 1959). In the following years, the terms Arcto-Tertiary and Palaeotropical geoflora were widely used for taxa which were on the one hand deciduous and from temperate vegetation zones (Arcto-Tertiary geoflora) or on the other hand wintergreen and parts of (sub)tropical vegetation zones (Palaeotropical geoflora) (pers. comm. L. Kunzmann, Dresden).

This rather undifferentiated usage of the geoflora concept subsequently led to confusion and criticism. For instance, Wolfe (1972) and Graham (1972) rejected the geoflora concept, since to them, it was unlikely that a flora maintained stability for geological epochs. Such a concept would ignore physiological and genetic changes of plant lineages which can alter their ecological preferences through time (Wolfe 1972). Also, both authors criticized that the geoflora concept was too simple to reflect the rather complex history of Cenozoic floras (Graham 1972, Wolfe 1972). In contrast, Mai (1991) supports Engler’s (1882) and Chaney’s (1959) geoflora concept, stating that a classification of palaeofloristic units in geological time was possible.

A further revision of this concept was supplied by Kvaček (1994) who distinguished between ‘ancient’ and ‘modern’ Arcto-Tertiary elements. The first category contained extinct and extant taxa of angiosperms and gymnosperms which were mainly summergreen (e.g. *Metasequoia*, *Platanus schimperi*, *Corylites*, *Fagopsis*); the second category encompassed genera that migrated to Europe from eastern and north-eastern regions after the closure of the Turgai Strait (late Eocene-Oligocene). These genera either remained in Europe until recent time or became extinct after the Pliocene. Examples of these ‘modern’ Arcto-Tertiary elements are *Pseudolarix*, *Alnus* and *Acer*. Kvaček (1994) concluded that Arcto-Tertiary geofloras are heterogeneous, not only in terms of taxonomic diversity but also in their evolutionary and palaeoecological history.

A recent publication of Grímsson et al. (2015) raised doubts that the geoflora concept as such is reasonable. These authors studied fagaceous pollen floras of the middle Eocene of Western Greenland which should belong, according to the definitions presented above, to an Arcto-Tertiary geoflora. Grímsson et al. (2015) discovered a very diverse Fagaceae flora which, however, does not represent the oldest record so far. For instance, *Fagus* fossils were already found in early Eocene sediments of Washington and thus, predated the *Fagus* pollen of Western Greenland.

The same holds true for other genera of the Fagaceae which were found in the Western Greenland pollen record of the middle Eocene. This shows that the lineages of the Fagaceae were already diversified during the Eocene before they inhabited Greenland. Therefore, Grímsson et al. (2015) rejected the concept of Chaney (1959) and Mai (1991), since presumed Arcto-Tertiary elements, as the Fagaceae migrated into the Arctic, but certainly did not originate there.

Considering all these different perceptions of the geoflora concept, the question arises whether it is really suitable to apply to the Baltic amber flora. If applied in its strictest sense [sensu Engler (1882) and Chaney (1959)], do these geofloras really occur in the Baltic amber source area as it was suggested by Kohlman-Adamska (2001) and Szwedo and Sontag (2009)? First of all, it is not clear which kind of geoflora interpretation these authors used. Assuming that Kohlman-Adamska (2001) and Szwedo and Sontag (2009) applied the original concept of Engler (1882) and Chaney (1959), it initially seems that the Baltic amber flora indeed contained Arcto-Tertiary elements. For instance, Sadowski et al. (2017a [5]) highlighted that the ‘Baltic amber forest’ conifer diversity was comparable to temperate fossil floras of Spitzbergen. However, to be clearly Arcto-Tertiary (following Chaney’s definition), the Baltic amber conifers should be of an Arctic origin as well. This is for example not the case for *Pseudolarix* whose first fossil record was reported from the Early Cretaceous of southeastern Russia (Bureya Basin) and northeastern China (Fuxin Basins; LePage and Basinger 1995). If Kohlman-Adamska (2001) applied Kvaček’s (1994) revision of the Arcto-Tertiary element, then *Pseudolarix* would be assigned to ‘modern’ Arcto-Tertiary elements. ‘Ancient’ Arcto-Tertiary elements sensu Kvaček (i.e. *Metasequoia*), however, were not observed in the Baltic amber flora. Regarding palaeotropical elements, it should be taken into account that (as discussed in chapters 4.2.2 and 5.2) the validity of presumed tropical indicator plant taxa is doubtful. Thus, the presence of a Baltic amber palaeotropical geoflora lacks confirmation and should not be applied to the ‘Baltic amber forest’.

As outlined above, the geoflora concept is not generally accepted among scientists, as different interpretations and definitions of this concept exist. Also, as explained in the previous chapters (5.1, 5.3), the diverse flora from Baltic amber can be justified by its habitat heterogeneity. Thus, it does not appear reasonable to apply the rather uncertain geoflora concept for explaining the composition of the Baltic amber flora.

6. Conclusions and outlook

The presented new studies included in this thesis show the remarkable potential of plant inclusions from Baltic amber to reconstruct the vegetation of its source area. Based on these studies, a new picture of the ‘Baltic amber forest’ is emerging, showing that the ‘Baltic amber forest’ encompassed coastal swamps under brackish water influence, raised bogs, back swamps and riparian forests, as well as mixed-mesophytic angiosperm-conifer forests which were intermingled with open habitats (e.g. meadows and heaths). On a microhabitat scale, the communities are very complex as well, comprising a high diversity of taxa and life forms. The majority of plant taxa from Baltic amber involved in this thesis were previously unknown as inclusions (e.g. *Cathaya*, *Nothotsuga*, *Pseudolarix*, *Cupressospermum saxonicum*, and *Rhynchospora*) or not unambiguously proven (e.g. *Abies*, and *Sciadopitys*) from Baltic amber previously. Therefore, the list of conifer and angiosperm taxa from the Baltic amber flora was considerably revised and updated.

The new results of this study challenge previous notions about the (sub)tropical climatic conditions of the ‘Baltic amber forest’, its presumed Fennoscandian origin (including a long-distance transport of Baltic amber by the supposed Eridanos river), the often suggested early to middle Eocene age and the presence of mountains in its source area. Instead, the new palaeobotanical evidence enlightens some of the Baltic amber mysteries, supporting a late Eocene age of Baltic amber and a local, Baltic origin of a warm-temperate Baltic amber source ‘forest’. The latter was not a solely forest, but rather a mosaic of various habitat types in a very heterogeneous but plain landscape. However, this picture is still not complete, as more research is needed to revise and study further plant inclusions from Baltic amber. Preliminary results from inclusions of especially the Fagaceae, Ericaceae and Cupressaceae need to be progressed to further develop the new picture of the ‘Baltic amber forest’.

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8. References

- Adamec, L. 1997. Mineral nutrition of carnivorous plants: a review. *The Botanical Review* **63**:273-299.
- Adamec, L. 2013. Foliar mineral nutrient uptake in carnivorous plants: what do we know and what should we know? *Frontiers in Plant Science* **4**:10 doi: 10.338/fpls.2013.00010.
- Aleksandrova, G. N. and N. I. Zaporozhets. 2008a. Palynological characteristics of Upper Cretaceous and Paleogene deposits on the West of the Sambian Peninsula (Kaliningrad region), Part 1. *Stratigraphy and Geological Correlation* **16**:295-316.
- Aleksandrova, G. N. and N. I. Zaporozhets. 2008b. Palynological characteristics of Upper Cretaceous and Paleogene deposits on the West of the Sambian Peninsula (Kaliningrad region), Part 2. *Stratigraphy and Geological Correlation* **16**:528-539.
- Alekseev, V. I. and P. I. Alekseev. 2016. New approaches for reconstruction of the ecosystem of an Eocene amber forest. *Biology Bulletin* **43**:75-86.
- Ander, K. 1942. Die Insektenfauna des Baltischen Bernsteins nebst damit verknüpften zoogeographischen Problemen. *Kungl. Fysiografiska Sällskapets Handlingar* **53**:1-82.
- Anderberg, A. A., C. Rydin, and M. Källersjö. 2002. Phylogenetic relationships in the order Ericales s.l.: analyses of molecular data from five genes from the plastid and mitochondrial genomes. *American Journal of Botany* **89**:677-687.
- Anderson, B. 2005. Adaptations to foliar absorption of faeces: a pathway in plant carnivory. *Annals of Botany* **95**:757-761.
- Anderson, B. 2006. Inferring evolutionary patterns from the biogeographical distributions of mutualists and exploiters. *Biological Journal of the Linnean Society* **89**:541-549.
- Anderson, B. and J. Midgley. 2002. It takes two to tango but three is a tangle: mutualists and cheaters on the carnivorous plant *Roridula*. *Oecologia* **132**:369-373.
- Anderson, B. and J. Midgley. 2003. Digestive mutualism, an alternate pathway in plant carnivory. *Oikos* **102**:221-224.
- Anderson, K. B. 1994. New evidence concerning the structure, composition, and maturation of Class I (polylabdanoid) resinites. Pages 105-129 in K. B. Anderson and J. C. Crelling, editors. *Amber, resinite, and fossil resins*. ACS Symposium Series 617. American Chemical Society, Washington D.C.
- Anderson, K. B. 1996. The nature and fate of natural resins in the geosphere—VII. A radiocarbon (^{14}C) age scale for description of immature natural resins: an invitation to scientific debate. *Organic Geochemistry* **25**:251-253.
- Anderson, K. B. 2006. The nature and fate of natural resins in the geosphere. XII. Investigation of C-ring aromatic diterpenoids in Raritan amber by pyrolysis-

- GC-matrix isolation FTIR-MS. *Geochemical Transactions* 7: doi:10.1186/1467-4866-7-2.
- Anderson, K. B. and R. Botto. 1993. The nature and fate of natural resins in the geosphere—III. Re-evaluation of the structure and composition of Highgate Copalite and Glessite. *Organic Geochemistry* **20**:1027-1038.
- Anderson, K. B. and J. C. Crelling. 1995. Introduction. Pages xi-xvii in K. B. Anderson and J. C. Crelling, editors. *Amber, resinite, and fossil resins*. ACS Symposium Series 617. American Chemical Society, Washington D.C.
- Anderson, K. B. and B. A. LePage. 1995. Analysis of fossil resins from Axel Heiberg Island, Canadian Arctic. Pages 170-192 in K. B. Anderson and J. C. Crelling, editors. *Amber, resinite, and fossil resin*. ACS Symposium Series 617. American Chemical Society, Washington D.C.
- Anderson, K. B., R. Winans, and R. Botto. 1992. The nature and fate of natural resins in the geosphere—II. Identification, classification and nomenclature of resinites. *Organic Geochemistry* **18**:829-841.
- Antoine, P.-O., D. De Franceschi, J. J. Flynn, A. Nel, P. Baby, M. Benammi, Y. Calderón, N. Espurt, A. Goswami, and R. Salas-Gismondi. 2006. Amber from western Amazonia reveals Neotropical diversity during the middle Miocene. *Proceedings of the National Academy of Sciences of the United States of America* **103**:13595-13600.
- Archibald, B. and B. D. Farrell. 2003. Wheeler's dilemma. *Acta zoologica cracoviensia* **46** (suppl. – fossil Insects):17-23.
- Aukema, J. E. 2003. Vectors, viscin, and Viscaceae: mistletoes as parasites, mutualists, and resources. *Frontiers in Ecology and the Environment* **1**:212-219.
- Aycke, J. C. 1835. *Fragmente zur Naturgeschichte des Bernsteins*. Nicolai, Danzig.
- Azar, D., R. Gèze, and F. Acra. 2010. Lebanese Amber. Pages 271-298 in D. Penney, editor. *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific Press, Manchester.
- Bachofen-Echt, A. 1949. *Der Bernstein und seine Einschlüsse*. Springer, Wien.
- Barthel, M. and H. Hetzer. 1982. Bernstein-Inklusen aus dem Miozän des Bitterfelder Raumes. *Zeitschrift für angewandte Geologie* **28**:314-336 (In German with English summary).
- Beck, C. W., E. Wilbur, and S. Meret. 1964. Infra-red spectra and the origin of amber. *Nature* **201**:256-257.
- Beimforde, C., L. J. Seyfullah, V. Perrichot, K. Schmidt, J. Rikkinen, and A. R. Schmidt. 2016. Resin exudation and resinicolous communities on *Araucaria humboldtensis* in New Caledonia. *Arthropod-Plant Interactions*: doi:10.1007/s11829-016-9475-3.
- Bijlsma, S. 1981. Fluvial sedimentation from the Fennoscandian area into the North-West European Basin during the Late Cenozoic. *Geologie en Mijnbouw* **60**:337-345.

- Bisulca, C., P. C. Nascimbene, L. Elkin, and D. A. Grimaldi. 2012. Variation in the deterioration of fossil resins and implications for the conservation of fossils in amber. *American Museum Novitates* **3734**:1-19.
- Bogner, J., 1976. Die systematische Stellung von *Acoropsis* Conwentz, einer fossilen Aracee aus dem Bernstein. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie* **16**:95-98 (In German with English Abstract).
- Borgardt, S. J. and K. B. Pigg. 1999. Anatomical and developmental study of petrified *Quercus* (Fagaceae) fruits from the Middle Miocene, Yakima Canyon, Washington, USA. *American Journal of Botany* **86**:307-325.
- Bouchenak-Khelladi, Y., A. M. Muasya, and H. P. Linder. 2014. A revised evolutionary history of Poales: origins and diversification. *Botanical Journal of the Linnean Society* **175**:4-16.
- Bray, P. S. and K. B. Anderson. 2009. Identification of Carboniferous (320 million years old) Class Ic amber. *Science* **326**:132-134.
- Calder, D. M. 1983. Mistletoes in focus: an introduction. Pages 1-18 in D. M. Calder and P. Bernhardt, editors. *The biology of mistletoes*. Academic Press, Sydney, Australia.
- Caspary, R. 1872a. Pflanzliche Reste aus der Bernsteinbildung. Privatsitzung am 4. October. *Schriften der Königlichen physikalisch-ökonomischen Gesellschaft zu Königsberg* **13**:17-18.
- Caspary, R. 1872b. Pflanzliche Bernsteineinschlüsse. Privatsitzung am 1. November. *Schriften der Königlichen physikalisch-ökonomischen Gesellschaft zu Königsberg* **13**:20-21.
- Caspary, R. 1886. Einige neue Pflanzenreste aus dem samländischen Bernstein. *Schriften der Physikalisch-Ökonomischen Gesellschaft zu Königsberg* **27**:1-8.
- Caspary, R. and R. Klebs. 1907. *Die Flora des Bernsteins und anderer fossiler Harze des ostpreußischen Tertiärs, Band I. Königlich Preußische Geologische Landesanstalt Berlin.*
- Chaney, R. W. 1959. Miocene floras of the Columbia Plateau, I. Composition and interpretation. *Carnegie Institution of Washington Publication* **617**:1-134.
- Clauer, N., J. M. Huggett, and S. Hillier. 2005. How reliable is the K-Ar glauconite chronometer? A case study of Eocene sediments from the Isle of Wight. *Clay Minerals* **40**:167-176.
- Conwentz, H. 1886a. Die Bernsteinfichte. *Berichte der Deutschen Botanischen Gesellschaft* **4**:375-377.
- Conwentz, H. 1886b. Die Angiospermen des Bernsteins. — In H.R. Goepfert, and A. Menge, editors. *Die Flora des Bernsteins und ihre Beziehungen zur Flora der Tertiärformation und der Gegenwart, 2. Band*, Engelmann, Danzig.
- Conwentz, H. 1890. *Monographie der baltischen Bernsteinbäume: vergleichende Untersuchungen über die Vegetationsorgane und Blüten, sowie über das Harz und die Krankheiten der baltischen Bernsteinbäume*. Engelmann, Danzig.
- Corlett, R. T. 2013. Where are the Subtropics? *Biotropica* **45**:273-275.

- Czeczott, H. 1961. The flora of the Baltic amber and its age. *Prace Muzeum Ziemi* **4**:119-145 (In Polish with English summary).
- Daghlian, C. P. 1981. A review of the fossil record of monocotyledons. *The Botanical Review* **47**:517-555.
- Dell, B. and A. J. McComb. 1978. Plant resins—their formation, secretion and possible functions. *Advances in Botanical Research* **6**:277-316.
- Denk, T., F. Grímsson, and R. Zetter. 2012. Fagaceae from the early Oligocene of Central Europe: persisting new world and emerging old world biogeographic links. *Review of Palaeobotany and Palynology* **169**:7-20.
- Díaz, S. and M. Cabido. 1997. Plant functional types and ecosystem function in relation to global change. *Journal of Vegetation Science* **8**:463-474.
- Dolezych, M., T. Fischer, and A. Gröschke. 2011. *Pinuxylon succiniferum* (Goeppert) Kraeusel emend. Dolezych – amberized wood from Goeppert's type material restudied. *Mauritiana* **22**:43-60.
- Dolezych, M. and W. Schneider. 2007. Taxonomy and taphonomy of coniferous woods and cuticulae dispersae in the Second Lusatian coal seam (Miocene) of the Senftenberg area. *Palaeontographica B* **276**:1-95 (In German with English abstract).
- Dörfelt, H. and A. R. Schmidt. 2007. A conifer seedling with two herbicolous fungi from the Baltic amber forest. *Botanical Journal of the Linnean Society* **155**:449-456.
- Eckenwalder, J. E. 2009. *Conifers of the world: the complete reference*. Timber Press, Portland.
- Eidesen, P. B., T. Carlsen, U. Molau, and C. Brochmann. 2007. Repeatedly out of Beringia: *Cassiope tetragona* embraces the Arctic. *Journal of Biogeography* **34**:1559-1574.
- Ellis, A. G. and J. J. Midgley. 1996. A new plant-animal mutualism involving a plant with sticky leaves and a resident hemipteran insect. *Oecologia* **106**:478-481.
- Ellison, A. M., E. D. Butler, E. J. Hicks, R. F. C. Naczi, P. J. Calie, C. D. Bell, C. C. Davis. 2012. Phylogeny and biogeography of the carnivorous plant family Sarraceniaceae. *PloS ONE* **7**:e39291.
- Engler, A. 1882. Versuch einer Entwicklungsgeschichte der Pflanzenwelt, insbesondere der Florengebiete seit der Tertiärperiode. II. Theil. Die Extratropischen Gebiete der südlichen Hemisphäre und die Tropischen Gebiete. Wilhelm Engelmann, Leipzig.
- Farjon, A. 1990. Pinaceae. Drawings and descriptions of the genera *Abies*, *Cedrus*, *Pseudolarix*, *Keteleeria*, *Nothotsuga*, *Tsuga*, *Cathaya*, *Pseudotsuga*, *Larix* and *Picea*. Koeltz Scientific Books, Königstein.
- Farjon, A. 2005. A monograph of Cupressaceae and *Sciadopitys*. Royal Botanic Gardens Kew.
- Farjon, A., N. T. Hiep, D.K. Harder, P. K. Loc, and L. Averyanov. 2002. A new genus and species in Cupressaceae (Coniferales) from Northern Vietnam, *Xanthocyparis vietnamensis*. *Novon* **12**:179-189.

- Farr, E. R. and G. Zijlstra. 1996. Index Nominum Genericorum (Plantarum) [online]. Website <http://botany.si.edu/ing/> [accessed 06.04.2017].
- Farrell, B. D., D. E. Dussourd, and C. Mitter. 1991. Escalation of plant defense: do latex and resin canals spur plant diversification? *American Naturalist* **138**:881-900.
- Feldberg, K., H. Schneider, T. Stadler, A. Schäfer-Verwimp, A. R. Schmidt, and J. Heinrichs. 2014. Epiphytic leafy liverworts diversified in angiosperm-dominated forests. *Scientific Reports* **4**:5974, doi: 10.1038/srep05974.
- Florin, R. 1931. Untersuchungen zur Stammesgeschichte der Coniferales und Cordaitales. I. Morphologie und Epidermisstruktur der Assimilationsorgane bei den rezenten Koniferen. In *Kunglia Svenska Vetenskapsakademiens Handlingar*, Vol. 10, Almquist & Wiksells Boktryckeri-A.B., Stockholm.
- Forman, L. L. 1964. *Trigonobalanus*, a new genus of Fagaceae, with notes on the classification of the family. *Kew Bulletin* **17**:381-396.
- Frahm, J.-P. 2010. Die Laubmoosflora des Baltischen Bernsteinwaldes. Weissdorn-Verlag, Jena.
- Fu L., Y. Yongfu, and R. R. Mill. 1999. Taxodiaceae. In Wu Zheng-yi and P. H. Raven, editors. *Flora of China, Volume 4*. Beijing, Science Press; St. Louis, Missouri Botanical Garden.
- Geiger, K. 1952. Klassifikation der Klimate nach W. Köppen. Pages 603-607 in J. Bartels and P. Ten Bruggencate, editors. *Landolt-Börnstein, Zahlenwerte und Funktionen aus Physik, Chemie, Astronomie, Geophysik und Technik, III. Band: Astronomie und Geophysik*. Springer, Berlin.
- Geils, B. W. and F. G. Hawksworth. 2002. Damage, effects, and importance of dwarf mistletoes. Pages 57-65 in B. W. Geils, J. Cibrián Tovar, and B. Moody, tech. coords. *Mistletoes of North American Conifers*. General Technical Report RMRS-GTR-98. USDA Forest Service, Rocky Mountain Research Station, Ogden, Utah.
- Gibbard, P. L. and J. Lewin. 2016. Filling the North Sea Basin: Cenozoic sediment sources and river styles (André Dumont medallist lecture 2014). *Geologica Belgica* **19**:201-217.
- Girard, V., A. R. Schmidt, S. Struwe, V. Perrichot, G. Breton, and D. Néraudeau. 2009. Taphonomy and palaeoecology of mid-Cretaceous amber-preserved microorganisms from southwestern France. *Geodiversitas* **31**:153-162.
- Givnish, T. J., E. L. Burkhardt, R. E. Happel, and J. D. Weintraub. 1984. Carnivory in the bromeliad *Brocchinia reducta*, with a cost/benefit model for the general restriction of carnivorous plants to sunny, moist, nutrient-poor habitats. *The American Naturalist* **124**:479-497.
- Goeppert, H. R. 1836. Bemerkungen über die Abstammung des Bernsteins. Pages 624-625 In J. C. Poggendorf editor. *Annalen der Physik und Chemie*, 2. Reihe, 8. Band. Johann Ambrosius Barth, Leipzig.
- Goeppert, H. R. 1853. Über die Bernsteinflora. Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Königlich Preußischen Akademie der Wissenschaften zu Berlin:450-476.

- Goeppert, H. R. and G. C. Berendt. 1845. Der Bernstein und die in ihm befindlichen Pflanzenreste der Vorwelt. *In* G. C. Berendt, editor. Die im Bernstein befindlichen organischen Reste der Vorwelt, Band 1, 1. Abth. Nicolai, Berlin.
- Goeppert, H. R. 1883. Von den Bernstein-Coniferen, insbesondere auch in ihren Beziehungen zu den Coniferen der Gegenwart. *In* H. R. Goeppert and A. Menge, editors. Die Flora des Bernsteins und ihre Beziehungen zur Flora der Tertiärformation und der Gegenwart, Band 1. Engelmann, Danzig [in the majority of publications cited as Goeppert and Menge (1883)].
- Gothan, W. 1936. Nochmals die "Graskohle": Nadeln der Schirmtanne (*Sciadopitys*). *Zeitschrift für Gewinnung und Verwertung der Braunkohle* **40**:736-738.
- Gough, L. J., J. S. Mills. 1972. The composition of succinite (Baltic amber). *Nature* **239**:527-528.
- Graham, A. 1972. Outline of the origin and historical recognition of floristic affinities between Aisa and eastern North America. Pages 1-18 *in* A. Graham, editor. Floristics and palaeofloristics of Asia and eastern North America. Elsevier, Amsterdam.
- Grimaldi, D. A. 1996. Amber: window to the past. Harry N. Abrams in association with the American Museum of Natural History, New York.
- Grimaldi, D., E. Bonwich, M. Delannoy, and S. Doberstein. 1994. Electron microscopic studies of mummified tissues in amber fossils. *American Museum Novitates* **3097**:1-31.
- Grímsson, F., G. W. Grimm, R. Zetter, and T. Denk. 2016. Cretaceous and Paleogene Fagaceae from North America and Greenland: evidence for a Late Cretaceous split between *Fagus* and the remaining Fagaceae. *Acta Palaeobotanica* **56**:247-305.
- Grímsson, F., R. Zetter, G. W. Grimm, G. K. Pedersen, A. K. Pedersen, T. Denk. 2015. Fagaceae pollen from the early Cenozoic of West Greenland: revisiting Engler's and Chaney's Arcto-Tertiary hypotheses. *Plant Systematics and Evolution* **302**:809-832.
- Grolle, R. and K. Meister. 2004. The liverworts in Baltic and Bitterfeld amber. Weissdorn-Verlag, Jena.
- Haczewski, J. 1838. (Untitled). O bursztynie. *Sylwan* **14**:191-251.
- Hagerup, O. 1953. The morphology and systematics of the leaves in Ericales. *Phytomorphology* **3**:459-464.
- Halaj, J., D. W. Ross, and A. R. Moldenke. 2000. Importance of habitat structure to the arthropod food-web in Douglas-fir canopies. *Oikos* **90**:139-152.
- Hartl, C., A. R. Schmidt, J. Heinrichs, L. J. Seyfullah, N. Schäfer, C. Gröhn, J. Rikkinen, and U. Kaasalainen. 2015. Lichen preservation in amber: morphology, ultrastructure, chemofossils, and taphonomic alteration. *Fossil Record* **18**:127-135.
- Hawksworth, F. G. and B. W. Geils. 1996. Biotic associates. Pages 73-89 *in* F. G. Hawksworth and D. Wiens, editors. Dwarf Mistletoes: Biology, Pathology, and Systematics. USDA Forest Service Agriculture Handbook, Washington D.C.

- Hedwall, S. J. and R. L. Mathiasen. 2006. Wildlife use of douglas-fir dwarf mistletoe witches' brooms in the Southwest. *Western North American Naturalist* **66**:450-455.
- Heer, O. 1860. Untersuchungen über das Klima und die Vegetationsverhältnisse der Tertiärlandes. Wurster & Comp., Winterthur.
- Heinken, T. 2008. Natural Scots pine forests in Germany: habitats, distribution, and threat. Pages 19-41 *in* Nordwestdeutsche Forstliche Versuchsanstalt, editor. Die Waldkiefer - Fachtagung zum Baum des Jahres 2007. Beiträge aus der NW-FVA, Band 2. Universitätsverlag Göttingen (In German with English abstract).
- Heinrichs, J., L. Hedenäs, A. Schäfer-Verwimp, K. Feldberg, and A. R. Schmidt. 2014. An in situ preserved moss community in Eocene Baltic amber. *Review of Palaeobotany and Palynology* **210**:113-118.
- Heinrichs, J., M. E. Reiner-Drehwald, K. Feldberg, M. von Konrat, J. Hentschel, J. Váňa, D. A. Grimaldi, P. C. Nascimbene, and A. R. Schmidt. 2012. The leafy liverwort *Frullania* (Jungermanniopsida) in the Cretaceous amber forest of Myanmar. *Review of Palaeobotany and Palynology* **169**:21-28.
- Heinrichs, J., A. Scheben, G. E. Lee, J. Váňa, A. Schäfer-Verwimp, M. Krings, and A. R. Schmidt. 2015b. Molecular and morphological evidence challenges the records of the extant liverwort *Ptilidium pulcherrimum* in Eocene Baltic amber. *PloS ONE* **10**:e0140977, doi:10.1371/journal.pone.0140977.
- Heinrichs, J., A. R. Schmidt, A. Schäfer-Verwimp, L. Bauerschmidt, C. Neumann, C. Gröhn, M. Krings, and M. M. A. Renner. 2016. Revision of the leafy liverwort genus *Radula* (Porellales, Jungermanniopsida) in Baltic and Bitterfeld amber. *Review of Palaeobotany and Palynology* **235**:157-164.
- Heinrichs, J., A. R. Schmidt, A. Schäfer-Verwimp, C. Gröhn, and M. M. A. Renner. 2015a. The leafy liverwort *Notoscyphus balticus* sp. nov. (Jungermanniales) in Eocene Baltic amber. *Review of Palaeobotany and Palynology* **217**:39-44.
- Henwood, A. A. 1992. Soft-part preservation of beetles in tertiary amber from the Dominican Republic. *Palaeontology* **35**:901-912.
- Hermesen, E. J. 2013. A review of the fossil record of the genus *Itea* (Iteaceae, Saxifragales) with comments on its historical biogeography. *The Botanical Review* **79**:1-47.
- Hjelmquist, H. 1948. Studies on the floral morphology and phylogeny of the Amentiferae. *Botaniska Notiser Supplement* **2**:1-171.
- Hoffeins, C. and H. W. Hoffeins. 2003. On the frequency of inclusions in Baltic and Bitterfeld amber (Tertiary, Eocene) from unselected material, with special reference to the order Diptera. *Studia dipterologica* **10**:381-392 (In German with English abstract).
- Jähnichen, H. 1998. First record of *Taiwania*, *Cryptomeria* and *Liquidambar* from Bitterfeld and Baltic amber. *Mitteilungen aus dem Museum für Naturkunde Berlin, Geowissenschaften* **1**:167-178 (In German with English abstract).
- Janzen, D. H. 1975. Behavior of *Hymenaea courbaril* when its predispersal seed predator is absent. *Science* **189**:145-147.

- Kaasalainen, U., J. Heinrichs, M. Krings, L. Myllys, H. Grabenhorst, J. Rikkinen, and A. R. Schmidt. 2015. Alectorioid morphologies in Paleogene lichens: new evidence and re-evaluation of the fossil *Alectoria succini* Mägdefrau. *PLoS ONE* **10**:e0129526, doi:10.1371/journal.pone.0129526.
- Kaasalainen, U., A. R. Schmidt, and J. Rikkinen. 2017. Diversity and ecological adaptations in Palaeogene lichens. *Nature Plants* **3**:17049, doi:10.1038/nplants.2017.1049.
- Kasiński, J. R. and R. Kramarska. 2008. Sedimentary environment of amber-bearing association along the polish-russian baltic coastline. *Exkursionsführer und Veröffentlichungen der Deutschen Gesellschaft für Geowissenschaften* **236**:46-57.
- Kettunen, E., H. Grabenhorst, C. Gröhn, H. Dörfelt, E.-M. Sadowski, J. Rikkinen, and A. R. Schmidt. 2015. The enigmatic hyphomycete *Torula* sensu Caspary revisited. *Review of Palaeobotany and Palynology* **219**:183-193.
- King, R. J. 2006. Minerals explained 44, Amber (Part 1). *Geology Today* **22**:232-237.
- Kirchheimer, F. 1937. Beiträge zur Kenntnis der Flora des baltischen Bernsteins I. Beihefte zum Botanischen Centralblatt, Abteilung B **57**:441-482.
- Knobloch, E. 1971. Neue Pflanzenfunde aus dem böhmischen und mährischen Cenoman. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **139**:43-56.
- Kohlman-Adamska, A. 2001. A graphic reconstruction of an "amber" forest. Pages 15-18 in B. Kosmowska-Ceranowicz, editor. *The Amber Treasure Trove - The Tadeusz Giecowicz's Collection at the Museum of the Earth, Polish Academy of Sciences. Museum of the Earth Documentary Studies 18. Oficyna Wydawnicza Sadyba, Warsaw.*
- Köppen, W. 1900. Versuch einer Klassifikation der Klimate, vorzugsweise nach ihren Beziehungen zur Pflanzenwelt. *Geographische Zeitschrift* **6**:593-611.
- Kosmowska-Ceranowicz, B. 1990. The Scientific Importance of Museum Collections of Amber and other Fossil Resins. *Prace Muzeum Ziemi* **41**:141-148.
- Kosmowska-Ceranowicz, B. 1992. Spuren des Bernsteins. *Museum der Erde, Polnische Akademie der Wissenschaften, Warsaw.*
- Kosmowska-Ceranowicz, B. 1997a. Bernstein - die Lagerstätte und ihre Entstehung. Pages 161-168 in M. Ganzelewski and R. Slotta, editors. *Bernstein - Tränen der Götter. Glückauf GmbH, Essen.*
- Kosmowska-Ceranowicz, B. 1997b. Die tertiären und quartären Bernsteinvorkommen in Polen. Pages 299-310 in M. Ganzelewski and R. Slotta, editors. *Bernstein - Tränen der Götter. Glückauf GmbH, Essen.*
- Kosmowska-Ceranowicz, B. 1999. Succinite and some other fossil resins in Poland and Europe (deposits, finds, features and differences in IRS). *Estudios del Museo de Ciencias Naturales de Álava* **14** (Número especial 2):73-117.
- Kosmowska-Ceranowicz, B. 2015. Infrared spectra atlas of fossil resins, subfossil resins and selected imitations of amber. Pages 7-214 in B. Kosmowska-

- Ceranowicz, editor. Infrared spectra of the world's resin - Holotype characteristics. PAS Museum of the Earth, Warsaw.
- Kosmowska-Ceranowicz, B., A. Kohlman-Adamska, and I. Grabowska. 1997. Erste Ergebnisse zur Lithologie und Palynologie der bernsteinführenden Sedimente im Tagebau Primorskoje. *Metalla Sonderheft - Neue Erkenntnisse zum Bernstein* **66**:5-17.
- Kosmowska-Ceranowicz, B., T. Konart. 1989. *Secrets of amber*. Publishing House Sport i Turystyka, Warszawa (in Polish with English summary).
- Kosmowska-Ceranowicz, B., C. Kulicki, and M. Kuźniarski. 2008. Microcrystals in amber and microstructures in amber and its imitations. *Prace Muzeum Ziemi* **49**:109-132 (In Polish with English summary).
- Kottek, M., J. Grieser, C. Beck, B. Rudolf, and F. Rubel. 2006. World map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift* **15**:259-263.
- Kräusel, R. 1949. Die fossilen Koniferen-Hölzer (Unter Ausschluß von Araucarioxylon Kraus) II. Teil. Kritische Untersuchungen zur Diagnostik lebender und fossiler Koniferen-Hölzer. *Palaeontographica B* **89**: 83-203
- Krumbiegel, G., and B. Kosmowska-Ceranowicz. 2007. Die Arten des Bitterfelder Bernsteins. *Bitterfelder Heimatblätter – Sonderheft*:43-64.
- Krumbiegel, G., and B. Krumbiegel. 2005. *Bernstein - Fossile Harze aus aller Welt*. Quelle & Meyer Verlag, Wiebelsheim.
- Kubitzki, K. 1993. Fagaceae. Pages 301-309 in K. Kubitzki, J. G. Rohwer, and V. Bittrich, editors. *The Families and Genera of Vascular Plants, II. Flowering plants, Dicotyledons, Magnoliid, Hamamelid and Caryophyllid families*. Springer, Heidelberg.
- Kunzmann, L. 1999. Koniferen der Oberkreide und ihre Relikte im Tertiär Europas: ein Beitrag zur Kenntnis ausgestorbener Taxodiaceae und Geinitziaceae fam. nov. *Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden* **45**:1-191.
- Kunzmann, L., Z. Kvaček, D. H. Mai, and H. Walther. 2009. The genus *Taxodium* (Cupressaceae) in the Palaeogene and Neogene of Central Europe. *Review of Palaeobotany and Palynology* **153**:153-183.
- Kunzmann, L. and D. H. Mai. 2005. Conifers of the Mastixioideae-flora from Wiesa near Kamenz (Saxony, Miocene) with special consideration of leaves. *Palaeontographica B* **272**:67-135 (In German with English summary).
- Kunzmann, L. and W. Schneider. 2013. Stop 3.2: 'Tertiärwald' am Waldsee Lauer. Pages 124-136, in J. Rascher, C. Heinrich, U. Holz, L. Kunzmann, W. Schneider, G. Standke, R. Wimmer. *Exkursionsführer Bitterfelder Bernstein (Stop 1) und Geologie, Bergbaugeschichte sowie Entwicklung der Bergbaufolgelandschaft im Raum Profen/Cospuden (Stop 2 und Stop 3). Exkursionsführer und Veröffentlichungen der Deutschen Gesellschaft für Geowissenschaften* **249**:112-136.
- Kvaček, Z. 1994. Connecting links between the Arctic Palaeogene and European Tertiary floras. Pages 251-266 in M. C. Boulter and H. C. Fisher, editors.

- Cenozoic Plants and Climates of the Arctic. NATO ASI Series. Springer, Heidelberg.
- Kvaček, Z. 2010. Forest flora and vegetation of the European early Palaeogene - a review. *Bulletin of Geosciences* **85**:3-16.
- Kvaček, Z., V. Teodoridis, K. Mach, T. Přikryl, and Z. Dvořák. 2014. Tracing the Eocene-Oligocene transition: a case study from North Bohemia. *Bulletin of Geosciences* **89**:21-66.
- Labandeira, C. 2014. Amber. Pages 163-216 in M. Laflamme, J. D. Schiffbauer, and S. A. F. Darroch, editors. *Reading and Writing of the Fossil record: Preservational Pathways to Exceptional Fossilization*. The Paleontological Society Papers Vol. 20. The Paleontological Society Short Course, October 18, 2014.
- Lambert, J. B., J. A. Santiago-Blay, and K. B. Anderson. 2008. Chemical signatures of fossilized resins and recent plant exudates. *Angewandte Chemie International Edition* **47**:9608-9616.
- Langenheim, J. H. 1969. Amber: a botanical inquiry. *Science* **163**:1157-1169.
- Langenheim, J. H. 1994. Higher plant terpenoids: a phytocentric overview of their ecological roles. *Journal of Chemical Ecology* **20**:1223-1280.
- Langenheim, J. H. 1995. Biology of amber-producing trees: focus on case studies of *Hymenaea* and *Agathis*. Pages 1-31 in K. B. Anderson and J. C. Crelling, editors. *Amber, resinite, and fossil resin*. ACS Symposium Series 617. American Chemical Society, Washington D.C.
- Langenheim, J. H. 2003. *Plant resins - Chemistry, Evolution, Ecology, and Ethnobotany*. Timber Press, Portland.
- Langenheim, J. and C. W. Beck. 1965. Infrared spectra as a means of determining botanical sources of amber. *Science* **149**:52-54.
- Larsson, S. G. 1978. *Baltic Amber - a Palaeobiological Study*. Entomonograph Vo. 1. Scandinavian Science Press LTD., Klampenborg.
- Lenz, O. K., V. Wilde, D. F. Mertz, and W. Riegel. 2015. New palynology-based astronomical and revised $^{40}\text{Ar}/^{39}\text{Ar}$ ages for the Eocene maar lake of Messel (Germany). *International Journal of Earth Sciences* **104**:873-889.
- LePage, B. A. and J. F. Basinger. 1995. Evolutionary history of the genus *Pseudolarix* Gordon (Pinaceae). *International Journal of Plant Sciences* **156**:910-950.
- Linder, H. P. and P. J. Rudall. 2005. Evolutionary history of Poales. *Annual Review of Ecology, Evolution, and Systematics* **36**:107-124.
- Ma, Q.-W., S. V. Vikulin, C.-S. Li, and Y.-F. Wang. 2013. Details of compressions of *Glyptostrobus* (Cupressaceae s.l.) from the Eocene of Fushun, NE China. *Journal of Systematics and Evolution* **51**:601-608.
- Mai, D. H. 1967. Die tertiären Arten von *Trigonobalanus* Forman (Fagaceae) in Europa. *Jahrbuch für Geologie* **3**:381-409 (In German with English summary).
- Mai, D. H. 1971. Über fossile Lauraceae und Theaceae in Mitteleuropa. *Feddes Repertorium* **82**:313-341 (In German with English summary).

- Mai, D. H. 1995. Tertiäre Vegetationsgeschichte Europas. Gustav Fischer Verlag, Jena.
- Mai, D. H. and H. Walther. 1991. Die oligozänen und untermiozänen Floren Nordwest-Sachsens und des Bitterfelder Raumes. *Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden* **38**:1-230.
- Manos, P. S., C. H. Cannon, and S.-H. Oh. 2008. Phylogenetic relationships and taxonomic status of the paleoendemic Fagaceae of western North America: recognition of a new genus, *Notholithocarpus*. *Madroño* **55**:181-190.
- Martínez-Delclòs, X., D. E. G. Briggs, and E. Peñalver. 2004. Taphonomy of insects in carbonates and amber. *Palaeogeography, Palaeoclimatology, Palaeoecology* **203**:19-64.
- Mathiasen, R. L. 1996. Dwarf mistletoes in forest canopies. *Northwest Science* **70**:61-71.
- McKellar, R. C., A. P. Wolfe, K. Muehlenbachs, R. Tappert, M. S. Engel, T. Cheng, and G. A. Sánchez-Azofeifa. 2011. Insect outbreaks produce distinctive carbon isotope signatures in defensive resins and fossiliferous ambers. *Proceedings of the Royal Society of London B: Biological Sciences*: doi:10.1098/rspb.2011.0276
- Menge, A. 1858. Beitrag zur Bernsteinflora. *Neuste Schriften der naturforschenden Gesellschaft zu Danzig* **6**:1-18.
- Mertz, D. F. and P. R. Renne. 2005. A numerical age for the Messel fossil deposit (UNESCO World Heritage Site) derived from $^{40}\text{Ar}/^{39}\text{Ar}$ dating on a basaltic rock fragment. *Courier Forschungsinstitut Senckenberg* **255**:67-75.
- Mertz, D. F., C. C. Swisher, J. L. Franzen, F. O. Neuffer, and H. Lutz. 2000. Numerical dating of the Eckfeld maar fossil site, Eifel, Germany: a calibration mark for the Eocene time scale. *Naturwissenschaften* **87**:270-274.
- Mosbrugger, V., T. Utescher, and D. L. Dilcher. 2005. Cenozoic continental climatic evolution of Central Europe. *Proceedings of the National Academy of Science of the United States of America* **102**:14964-14969.
- Mosini, V. and R. Samperi. 1985. Correlations between Baltic amber and *Pinus* resins. *Phytochemistry* **24**:859-861.
- Nascimbene, P. and H. Silverstein. 2000. The preparation of fragile Cretaceous ambers for conservation and study of organismal inclusions. Pages 93-102 in D. A. Grimaldi, editor. *Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey*. Backhuys Publishers, Leiden.
- Neri, M., G. Roghi, E. Ragazzi, and C. A. Papazzoni. 2017. First record of Pliensbachian (Lower Jurassic) amber and associated palynoflora from the Monti Lessini (northern Italy). *Geobios* **50**:49-63.
- Nickel, B. 1996. Die mitteleozäne Mikroflora von Eckfeld bei Manderscheid/Eifel. *Mainzer Naturwissenschaftliches Archiv Beiheft* **18**:1-147.
- Nickrent, D. L. 2011. Santalales (including mistletoes). *In Encyclopedia of Life Sciences (ELS)*. John Wiley & Sons Ltd., Chichester, doi: 10.1002/9780470015902.a0003714.pub2.

- Nikishin, A. M., P. A. Ziegler, R. A. Stephenson, S. A. P. L. Cloetingh, A. V. Furne, P. A. Fokin, A. V. Ershov, S. N. Bolotov, M. V. Korotaev, A. S. Alekseev, V. I. Gorbachev, E. V. Shipilov, A. Lankreijer, E. Y. Bembinova, and I. V. Shalimov. 1996. Late Precambrian to Triassic history of the East European Craton: dynamics of sedimentary basin evolution. *Tectonophysics* **268**:23-63.
- Nixon, K. C. and W. L. Crepet. 1989. *Trigonobalanus* (Fagaceae): taxonomic status and phylogenetic relationships. *American Journal of Botany* **76**:828-841.
- Obeyssekera, J., J. Browder, L. Hornung, and M. A. Harwell. 1999. The natural South Florida system I: Climate, geology, and hydrology. *Urban Ecosystems* **3**:223-244.
- Oladele, F. A. 1983. Scanning electron microscope study of stomatal-complex configuration in Cupressaceae. *Canadian Journal of Botany* **61**:1232-1240.
- Overeem, I., G. J. Weltje, C. Bishop-Kay, and S. B. Kroonenberg. 2001. The Late Cenozoic Eridanos delta system in the Southern North Sea Basin: a climate signal in sediment supply? *Basin Research* **13**:293-312.
- Parks, C. G., E. L. Bull, R. O. Tinnin, J. F. Shepherd, and A. K. Blumton. 1999. Wildlife use of dwarf mistletoe brooms in Douglas-fir in Northeast Oregon. *Western Journal of Applied Forestry* **14**:100-105.
- Pastorelli, G. 2009. Archaeological Baltic amber: degradation mechanisms and conservation measures. Ph.D. dissertation. Università di Bologna, Bologna.
- Peel, M. C., B. L. Finlayson, and T. A. McMahon. 2007. Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences* **11**:1633-1644.
- Penney, D. 2010. Dominican Amber. Pages 22-41 in D. Penney, editor. Biodiversity of fossils in amber from the major world deposits. Siri Scientific Press, Manchester.
- Perrichot, V. 2004. Early Cretaceous amber from south-western France: insight into the Mesozoic litter fauna. *Geologica Acta* **2**:9-22.
- Perrichot, V., D. Néraudeau, A. Nel, and G. De Ploëg. 2007. A reassessment of the Cretaceous amber deposits from France and their palaeontological significance. *African Invertebrates* **48**:213-227.
- Pielińska, A. 1990. The list of plant inclusions in Baltic amber from collection of the Museum of the Earth in Warsaw (shortened version), Annex 3. Pages 147-148 in B. Kosmowska-Ceranowicz. The scientific importance of museum collections of amber and other fossil resins. *Prace Muzeum Ziemi* **41**:141-148.
- Pielińska, A. 2001. Plant inclusions in Baltic amber. Pages 5-14 in B. Kosmowska-Ceranowicz, editor. The Amber Treasure Trove - The Tadeusz Giecwicz's Collection at the Museum of the Earth, Polish Academy of Sciences. Museum of the Earth Documentary Studies 18. Oficyna Wydawnicza Sadyba, Warsaw.
- Pijut, P. M. 2004. *Comptonia peregrina*. Pages 237-239 in J. K. Francis, editor. Wildland shrubs of the United States and its territories. *Thamnic*. Vo. 1. Gen. Tech. Rep. IITF-26. U.S. Department of Agriculture, Forest Service, International Institute of Tropical Forestry, Rio Piedras.

- Poinar, G. O. Jr. 1992. *Life in Amber*. Standford University Press, Standford, California.
- Poinar, G. O. Jr. 2002. Fossil palm flowers in Dominican and Baltic amber. *Botanical Journal of the Linnean Society* **139**:361-367.
- Poinar, G. O. Jr., and J. Haverkamp. 1985. Use of pyrolysis mass spectrometry in the identficiation of amber samples. *Journal of Baltic studies* **16**:210-221.
- Poulin, J., and K. Helwig. 2012. Class Id resinite from Canada: A new sub-class containing succinic acid. *Organic Geochemistry* **44**:37-44.
- Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. *Bioscience* **46**:609-620.
- Ragazzi, E. and A. R. Schmidt. 2011. Amber. Pages 25-36 *in* J. Reitner and V. Thiel, editors. *Encyclopedia of Geobiology*. Springer, Dordrecht.
- Rascher, J., C. Heinrich, U. Holz, L. Kunzmann, W. Schneider, G. Standke, and R. Wimmer. 2013. Exkursionsführer Bitterfelder Bernstein (Stop 1) und Geologie, Bergbaugeschichte sowie Entwicklung der Bergbaufolgelandschaft im Raum Profen/Cospuden (Stop 2 und Stop 3). *Exkursionsführer und Veröffentlichungen der Deutschen Gesellschaft für Geowissenschaften* **249**:112-136.
- Rikkinen, J. 2003. Calicioid lichens from European Tertiary amber. *Mycologia* **95**:1032-1036.
- Rikkinen, J. and G. O. Poinar Jr. 2002. Fossilised *Anzia* (Lecanorales, lichen-forming Ascomycota) from European Tertiary amber. *Mycological Research* **106**:984-990.
- Ritzkowski, S. 1997. K-Ar-Altersbestimmungen der bernsteinführenden Sedimente des Samlands (Paläogen, Bezirk Kaliningrad). *Metalla Sonderheft - Neue Erkenntnisse zum Bernstein* **66**:19-23.
- Roghi, G., E. Ragazzi, and P. Gianolla. 2006. Triassic amber of the southern Alps (Italy). *Palaios* **21**:143-154.
- Ross, A. J., C. Mellish, P. York, and B. Crighton. 2010. Burmese Amber. Pages 208-235 *in* D. Penney, editor. *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific Press, Manchester.
- Rottländer, R. C. A. 1970. On the formation of amber from *Pinus* resin. *Archaeometry* **12**:35-52.
- Rüffle, L. and J. Helms. 1970. Waldsteppe und Insektenwelt im Bernstein, Beispiele aus der Bernsteinsammlung des Paläontologischen Museums. *Wissenschaftliche Zeitschrift der Humboldt-Universität zu Berlin, Mathematisch-Naturwissenschaftliche Reihe* **19**:243-249.
- Rust, J., H. Singh, R. Rana, T. McCann, L. Singh, K. Anderson, N. Sarker, P. C. Nascimbene, F. Stebner, J. C. Thomas, M. M. Solórzano Kraemer, C. J. Williams, M. S. Engel, A. Sahni, and D. A. Grimaldi. 2010. Biogeographic and evolutionary implications of a diverse paleobiota in amber from the early Eocene of India. *Proceedings of the National Academy of Science of the United States of America* **107**:18360-18365.

- Sadowski, E.-M., A. R. Schmidt, L. Kunzmann, C. Gröhn, and L. J. Seyfullah. 2016a. *Sciadopitys* cladodes from Eocene Baltic amber. *Botanical Journal of the Linnean Society* **180**:258-268.
- Sadowski, E.-M., A. R. Schmidt, P. J. Rudall, D. A. Simpson, C. Gröhn, J. Wunderlich, and L. J. Seyfullah. 2016b. Graminids from Eocene Baltic amber. *Review of Palaeobotany and Palynology* **233**:116-168.
- Sadowski, E.-M., A. R. Schmidt, L. J. Seyfullah, and L. Kunzmann. 2017a. Conifers of the 'Baltic amber forest' and their palaeoecological significance. *Stapfia* **in press**.
- Sadowski, E.-M., L. J. Seyfullah, F. Sadowski, A. Fleischmann, H. Behling, and A. R. Schmidt. 2015. Carnivorous leaves from Baltic amber. *Proceedings of the National Academy of Sciences of the United States of America* **112**:190-195.
- Sadowski, E.-M., L. J. Seyfullah, C. A. Wilson, C. L. Calvin, and A. R. Schmidt. 2017b. Diverse early dwarf mistletoes (*Arceuthobium*), ecological keystones of the Eocene Baltic amber biota. *American Journal of Botany* **104**:1-25.
- Schaefer, M. 2003. *Wörterbuch der Ökologie*. Spektrum Akademischer Verlag, Heidelberg.
- Schimper, W. P. 1870-72. *Traité de paléontologie végétale ou la flore du monde primitif dans ses rapports avec les formations géologiques et la flore du monde actuel*, Tome 2. J. B. Baillière et Fils, Paris.
- Schmidt, A. R., C. Beimforde, L. J. Seyfullah, S.-E. Wege, H. Dörfelt, V. Girard, H. Grabenhorst, M. Gube, J. Heinrichs, A. Nel, P. Nel, V. Perrichot, J. Reitner, J. Rikkinen. 2014. Amber fossils of sooty moulds. *Review of Palaeobotany and Palynology* **200**:53-64.
- Schmidt, A. R. and H. Dörfelt. 2007. Evidence of Cenozoic Matoniaceae from Baltic and Bitterfeld amber. *Review of Palaeobotany and Palynology* **144**:145-156.
- Schmidt, A. R., S. Jancke, E. E. Lindquist, E. Ragazzi, G. Roghi, P. C. Nascimbene, K. Schmidt, T. Wappler, and D. A. Grimaldi. 2012. Arthropods in amber from the Triassic Period. *Proceedings of the National Academy of Sciences of the United States of America* **109**:14796-14801.
- Schmidt, A. R., V. Perrichot, M. Svojtka, K. B. Anderson, K. H. Belete, R. Bussert, H. Dörfelt, S. Jancke, B. Mohr, E. Mohrmann, P. C. Nascimbene, A. Nel, P. Nel, E. Ragazzi, G. Roghi, E. E. Saupe, K. Schmidt, H. Schneider, P. A. Selden, and N. Vávra. 2010. Cretaceous African life captured in amber. *Proceedings of the National Academy of Sciences of the United States of America* **107**:7329-7334.
- Schönenberger, J., A. A. Anderberg, and K. J. Sytsma. 2005. Molecular phylogenetics and patterns of floral evolution in the Ericales. *International Journal of Plant Science* **166**:256-288.
- Schubert, K. 1953. Mikroskopische Untersuchung pflanzlicher Einschlüsse des Bernsteins - 2.Teil: Rinden und Borke. *Palaeontographica B* **93**:103-119.
- Schubert, K. 1961. Neue Untersuchungen über Bau und Leben der Bernsteinkiefern [*Pinus succinifera* (Conwentz) emend.] - Ein Beitrag zur Paläohistologie der

- Pflanzen. Beihefte zum Geologischen Jahrbuch **45**:1-149 (In German with English abstract).
- Schubert, K., F. Ritter, T. Sorkina, K.-H. Böhme, and C. Hörhold. 1969. Abbau von Steroiden—VIII: Bildung von [1,4-¹⁴C] Bernsteinsäure aus [1,3a-¹⁴C] 7a-methyl-5,6,7,7a-tetrahydroindan-1,5-dion-4-(3-Propionsäure) durch *Nocardia opaca*. Journal of Steroid Biochemistry **1**:1-7 (In German with English abstract).
- Schulz, C., K. V. Klaus, P. Knopf, M. Mundry, V. Dörken, and T. Stützel. 2014. Male cone evolution in conifers: not all that simple. American Journal of Plant Sciences **5**:2842-2857.
- Schulz, W. 1999. The Baltic Amber in Quaternary sediments, a review of its occurrence, the largest specimens and amber museums. Archiv für Geschichtskunde **2**:459-478 (In German with English abstract).
- Schuster, J. 1931. Über das Verhältnis der systematischen Gliederung, der geographischen Verbreitung und der paläontologischen Entwicklung der Cycadaceen. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie **64**:166-260.
- Seredszus, F. 2003. Wasserinsekten des Baltischen Bernsteins unter besonderer Berücksichtigung der Chironomiden. Grundlagen zum Verständnis von aquatischen Lebensräumen und Lebensgemeinschaften im eozänen Bernsteinwald. PhD. Dissertation. University of Cologne, Cologne.
- Seyfullah, L. J., E.-M. Sadowski, and A. R. Schmidt. 2015. Species-level determination of closely related araucarian resins using FTIR spectroscopy and its implications for the provenance of New Zealand amber. PeerJ **3**:e1067, doi: 10.7717/peerj.1067.
- Simenstad, C. A. 1983. The ecology of estuarine channels of the Pacific Northwest coast: a community profile. U.S. Fish Wildlife Service, FWS/OBS-83/05, Washington D.C.
- Simoneit, B. R. T., P. M. Medeiros, and E. Wollenweber. 2008. Triterpenoids as major components of the insect-trapping glue of *Roridula* species. Zeitschrift für Naturforschung **36c**:625-630.
- Skadell, L. E. 2016. Ferns from Baltic amber. Bsc. thesis, Georg-August-University of Göttingen, Göttingen.
- Solórzano Kraemer, M. M. 2010. Mexican Amber. Pages 42-56 in D. Penney, editor. Biodiversity of fossils in amber from the major world deposits. Siri Scientific Press, Manchester.
- Solórzano Kraemer, M. M., A. S. Kraemer, F. Stebner, D. J. Bickel, and J. Rust. 2015. Entrapment bias of arthropods in Miocene amber revealed by trapping experiments in a tropical forest in Chiapas, Mexico. PloS ONE **10**:e0118820, doi:10.1371/journal.pone.0118820.
- Sontag, E. 2003. Animal inclusions in a sample of unselected Baltic amber. Acta zoologica cracoviensia **46** (supp. – Fossil Insects):431-440.

- Sørensen, J. C., U. Gregersen, M. Breiner, and O. Michelsen. 1997. High-frequency sequence stratigraphy of Upper Cenozoic deposits in the central and southeastern North Sea areas. *Marine and Petroleum Geology* **14**:99-123.
- Spahr, U. 1993. Systematic catalogue and bibliography of flora in amber and copal. *Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie)* **195**:1-99 (In German with English abstract).
- Standke, G. 1998. Die Tertiärprofile der samländischen Bernsteinküste bei Rauschen. *Schriftenreihe für Geowissenschaften* **7**:93-133 (In German with English abstract).
- Standke, G. 2008. Bitterfelder Bernstein gleich Baltischer Bernstein? - Eine geologische Raum- Zeit- Betrachtung und genetische Schlussfolgerungen. *Exkursionsführer und Veröffentlichungen der Deutschen Gesellschaft für Geowissenschaften* **236**:11-33 (In German with English abstract).
- Stankiewicz, B. A., H. N. Poinar, D. E. G. Briggs, R. P. Evershed, and G. O. Poinar Jr. 1998. Chemical preservation of plants and insects in natural resins. *Proceedings of the Royal Society B: Biological Sciences* **265**:641-647.
- Sternberg, K. 1825. Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt. Regensburg.
- Stevens, P. F. 1970. *Calluna, Cassiope and Harrimanella*: a taxonomic and evolutionary problem. *New Phytologist* **69**:1131-1148.
- Stevens, P. F. 2001 onwards. Angiosperm Phylogeny Webservice [online], version 14, April 2015. Website <http://www.mobot.org/MOBOT/research/APweb/> (accessed 07.04.2017).
- Stevens, P. F., J. Luteyn, E. G. H. Oliver, T. L. Bell, E. A. Brown, R. K. Crowden, A. S. George, G. J. Jordan, P. Ladd, K. Lemson, C. B. McLean, Y. Menadue, J. S. Pate, H. M. Stace, and C. M. Weiller. 2004. Ericaceae. Pages 145-194 in K. Kubitzki, editor. *The Families and Genera of Vascular plants, VI. Flowering plants, Dicotyledons, Celastrales, Oxalidales, Rosales, Cornales, Ericales*. Springer, Heidelberg.
- Stout, E. C., C. W. Beck, and B. Kosmowska-Ceranowicz. 1995. Gedanite and Gedano-Succinite. Pages 130-148 in K. B. Anderson and J. C. Crelling, editors. *Amber, resinite, and fossil resins*. ACS Symposium Series 617. American Chemical Society, Washington D.C.
- Stroganov, Y. 1987. Tayne yantarya. *Pravat No. 304 (25291)*, Page 6, 31. Oktober 1987, Moscow.
- Szwedo, J. and E. Sontag. 2009. The traps of the “amber trap”. How inclusions could trap scientists with enigmas. *Denisia* **26**:155-169.
- Szykuła, J., C. Hebda, Orpizewski, R. Aichholz, and Szykiwicz. 1990. Studies on neutral fraction of Baltic amber. *Prace Muzeum Ziemi* **41**:15-20.
- Tappert, R., A. P. Wolfe, R. C. McKellar, M. C. Tappert, and K. Muehlenbachs. 2011. Characterizing modern and fossil gymnosperm exudates using micro-Fourier transform infrared spectroscopy. *International Journal of Plant Sciences* **172**:120-138.

- Thiergart, F. 1949. Die *Sciadopitys*zone und der *Sciadopitys*-Vorstoß in der niederrheinischen Braunkohle. *Braunkohle, Wärme und Energie* **1**:153-156.
- Tonidandel, L., E. Ragazzi, G. Roghi, and P. Traldi. 2008. Mass spectrometry in the characterization of ambers. I. Studies of amber samples of different origin and ages by laser desorption ionization, atmospheric pressure chemical ionization and atmospheric pressure photoionization mass spectrometry. *Rapid Communications in Mass Spectrometry* **22**:630-638.
- Tonidandel, L., E. Ragazzi, and P. Traldi. 2009. Mass spectrometry in the characterization of ambers. II. Free succinic acid in fossil resins of different origin. *Rapid Communications in Mass Spectrometry* **23**:403-408.
- Tropicos. 2017. Missouri Botanical Garden [online]. 10 May 2017. Website <http://www.tropicos.org> (accessed 07.04.2017).
- True, R. P. and A. G. Snow. 1949. Gum flow from turpentine pines inoculated with the pitch-canker *Fusarium*. *Journal of Forestry* **47**:894-899.
- Tuovila, H., A. R. Schmidt, C. Beimforde, H. Dörfelt, H. Grabenhorst, and J. Rikkinen. 2013. Stuck in time—a new *Chaenothecopsis* species with proliferating ascomata from *Cunninghamia* resin and its fossil ancestors in European amber. *Fungal Diversity* **58**:199-213.
- Vávra, N. 2009. The chemistry of amber – facts, findings and opinions. *Annalen des Naturhistorischen Museums in Wien* **111A**:445-474.
- Vávra, N. 2015. Mineral names used for fossil resins, subfossil resins and similar materials. Pages 215-280 in B. Kosmowska-Ceranowicz, editor. *Infrared Spectra of the World's Resins - Holotype Characteristics*. PAS Museum of the Earth in Warsaw, Warsaw.
- Voigt, D., E. Gorb, and S. Gorb. 2009. Hierarchical organisation of the trap in the protocarnivorous plant *Roridula gorgonias* (Roridulaceae). *The Journal of Experimental Biology* **212**:3184-3191.
- Walter, H. and S.-W. Breckle. 2002. *Walter's Vegetation of the earth: the ecological systems of the geo-biosphere*. Springer, Berlin.
- Wappler, T. 2003. How old is Baltic amber? – New evidence for a Middle Eocene age from limnic sediments. Page 82 in *Symposium on the Paleogene – Preparing for Modern Life and Climate*. 25-30 August 2003, Leuven, Belgium.
- Wappler, T. and M. S. Engel. 2003. The middle Eocene bee faunas of Eckfeld and Messel, Germany (Hymenoptera: Apoidea). *Journal of Paleontology* **77**:908-921.
- Wappler, T. and N. Møller Andersen. 2004. Fossil water striders from the Middle Eocene fossil sites of Eckfeld and Messel, Germany (Hemiptera, Gerromorpha). *Paläontologische Zeitschrift* **78**:41-52.
- Warren, B. H. and J. A. Hawkins. 2006. The distribution of species diversity across a flora's component lineages: dating the Cape's 'relicts'. *Proceedings of the Royal Society B: Biological Sciences* **273**:2149-2158.
- Watson, D. M. 2001. Mistletoe - a keystone resource in forests and woodlands worldwide. *Annual Review of Ecology and Systematics* **32**:219-249.

- Watson, D. M. and M. Herring. 2012. Mistletoe as a keystone resource: an experimental test. *Proceedings of the Royal Society B: Biological Sciences* **279**:3853-3860.
- Watson, L. 1964. The taxonomic significance of certain anatomical observations on Ericaceae. The Ericoideae, *Calluna* and *Cassiope*. *New Phytologist* **63**:274-280.
- Weitschat, W. 1997. Bitterfelder Bernstein - ein eozäner Bernstein auf miozäner Lagerstätte. *Metalla Sonderheft - Neue Erkenntnisse zum Bernstein* **66**:71-84 (In German with English summary).
- Weitschat, W. 2008. Bitterfelder und Baltischer Bernstein aus paläoklimatischer und paläontologischer Sicht. *Exkursionsführer und Veröffentlichungen der Deutschen Gesellschaft für Geowissenschaften* **236**:88-97 (In German with English abstract).
- Weitschat, W. and W. Wichard. 1998. *Atlas der Pflanzen und Tiere im Baltischen Bernstein*. Dr. Friedrich Pfeil, München.
- Weitschat, W. and W. Wichard. 2010. Baltic Amber. Pages 80-115 in D. Penney, editor. *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific Press, Manchester.
- Wendelberger, G. 1989. Clarifying the term "forest steppe". *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Österreich* **126**:185-195 (In German with English abstract).
- Wheeler, W. M. 1910. *Ants: their structure, development and behavior*. Columbia Biological Series Number 9. Columbia University Press, New York.
- Wheeler, W. M. 1915. The ants of the Baltic Amber. *Schriften der Physikalisch-Ökonomischen Gesellschaft zu Königsberg* **50**:1-142.
- Wichard, W., C. Gröhn, and F. Seredszus. 2009. *Aquatic Insects in Baltic Amber*. Verlag Kessel, Remagen-Oberwinter.
- Wilde, V. and H. Frankenhäuser. 1998. The Middle Eocene plant taphocoenosis from Eckfeld (Eifel, Germany). *Review of Palaeobotany and Palynology* **101**:7-28.
- Wolfe, A. P., R. C. McKellar, R. Tappert, R. N. S. Sodhi, and K. Muehlenbachs. 2016. Bitterfeld amber is not Baltic amber: Three geochemical tests and further constraints on the botanical affinities of succinite. *Review of Palaeobotany and Palynology* **225**:21-32.
- Wolfe, A. P., R. Tappert, K. Muehlenbachs, M. Boudreau, R. C. McKellar, J. F. Basinger, and A. Garrett. 2009. A new proposal concerning the botanical origin of Baltic amber. *Proceedings of the Royal Society B: Biological Sciences* **276**:3403-3412.
- Wolfe, J. A. 1972. An interpretation of Alaskan Tertiary Floras. Pages 201-234 in A. Graham, editor. *Floristics and palaeofloristics of Asia and eastern North America*. Elsevier, Amsterdam.
- Xiang, X., M. Cao, and Z. Zhou. 2007. Fossil history and modern distribution of the genus *Abies* (Pinaceae). *Frontiers of Forestry in China* **2**:355-365.

- Yamamoto, S., A. Otto, G. Krumbiegel, and B. R. T. Simoneit. 2006. The natural product biomarkers in succinite, glessite and stantienite ambers from Bitterfeld, Germany. *Review of Palaeobotany and Palynology* **140**:27-49.
- Zachos, J., M. Pagani, L. Sloan, E. Thomas, and K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* **292**:686-693.
- Zachos, J. C., G. R. Dickens, and R. E. Zeebe. 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* **451**:279-283.
- Zherikhin, V. V. 2002. Pattern of insect burial and conservation. Pages 17-64 *in* A. P. Rasnitsyn and D. L. J. Quicke, editors. *History of insects*. Kluwer Academic Publishers, Dordrecht.

Versicherung

Hiermit versichere ich an Eides statt, dass die vorliegende Dissertationsschrift
„Towards a new picture of the ‘Baltic amber forest’ - flora, habitat types, and
palaeoecology“ selbstständig und nur unter Verwendung der angegebenen Quellen
und Hilfsmittel angefertigt wurde.

Göttingen, den 14.05.2017



Eva-Maria Sadowski

Declaration about own contributions to the papers included in this thesis

[1] Seyfullah, L. J., E.-M. Sadowski, and A. R. Schmidt. 2015. Species-level determination of closely related araucarian resins using FTIR spectroscopy and its implications for the provenance of New Zealand amber. *PeerJ* 3:e1067, doi: 10.7717/peerj.1067.

Own contribution: ca. 20%. The paper was written by L. J. Seyfullah and A.R. Schmidt. I contributed to the experimental data acquisition and proofread the paper.

[2] Kettunen, E., H. Grabenhorst, C. Gröhn, H. Dörfelt, E.-M. Sadowski, J. Rikkinen, and A. R. Schmidt. 2015. The enigmatic hyphomycete *Torula sensu Caspary* revisited. *Review of Palaeobotany and Palynology* 219:183-193.

Own contribution: ca. 10%. The paper was written by E. Kettunen, J. Rikkinen and A.R. Schmidt. C. Gröhn and H. Dörfelt provided the specimens. I prepared, documented and identified a leaf inclusion, presented in this study.

[3] Sadowski, E.-M., A. R. Schmidt, L. Kunzmann, C. Gröhn, and L. J. Seyfullah. 2016a. *Sciadopitys cladodes* from Eocene Baltic amber. *Botanical Journal of the Linnean Society* 180:258-268.

Own contribution: ca. 70%. The paper was written by me, A.R. Schmidt and L. Kunzmann. I prepared and examined the inclusions of this study. I implemented the morphological studies and documentation of the specimens, their description and palaeoecological interpretations. A.R. Schmidt identified the specimen and L. Kunzmann contributed to the palaeoecological background of the study. A.R. Schmidt, L. Kunzmann and L.J. Seyfullah proofread the paper. C. Gröhn provided the amber specimen.

[4] Sadowski, E.-M., A. R. Schmidt, P. J. Rudall, D. A. Simpson, C. Gröhn, J. Wunderlich, and L. J. Seyfullah. 2016b. Graminids from Eocene Baltic amber. *Review of Palaeobotany and Palynology* 233:116-168.

Own contribution: ca. 70%. The paper was written by me, A.R. Schmidt and L.J. Seyfullah. I prepared and examined the inclusions of this study. I implemented the morphological studies and documentation of the specimens, their descriptions and palaeoecological interpretations. P. J. Rudall and D. A. Simpson contributed their long-term experience with graminids and helped identifying the specimens. L.J. Seyfullah helped developing the first draft. A.R. Schmidt, L.J. Seyfullah, P. J. Rudall and D. A. Simpson proofread the paper. C. Gröhn and J. Wunderlich provided the specimens.

[5] Sadowski, E.-M., A. R. Schmidt, L. J. Seyfullah, and L. Kunzmann. 2017a. Conifers of the 'Baltic amber forest' and their palaeoecological significance. *Stafia* in press.

Own contributions: ca. 70%. This paper is based on my and L. Kunzmann's research. I prepared and examined the inclusions of this study. I implemented the documentation of specimens, their descriptions, taxonomical identification and palaeoecological interpretations. L. Kunzmann contributed data on the taxonomic identity of specimens, the palaeoecological and geological background of specimens. The paper was written by me and amended by L. Kunzmann and A.R. Schmidt. L. J. Seyfullah checked the paper linguistically and proofread it.

[6] Sadowski, E.-M., L. J. Seyfullah, C. A. Wilson, C. L. Calvin, and A. R. Schmidt. 2017b. Diverse early dwarf mistletoes (*Arceuthobium*), ecological keystones of the Eocene Baltic amber biota. *American Journal of Botany* 104: 1-25. doi:10.3732/ajb.1600390:

Own contributions: ca. 80%. This paper is mainly written by me. I prepared and examined the inclusions of this study. I conducted morphological studies and documented the specimens. C. A. Wilson and C.L. Calvin contributed on morphological and evolutionary aspects of the specimens. A.R. Schmidt contributed to the systematic section and proofread the paper. L.J. Seyfullah helped developing the first draft and checked the paper linguistically.

Appendices

Appendix 1

Seyfullah, L. J., **E.-M. Sadowski**, and A. R. Schmidt. 2015. Species-level determination of closely related araucarian resins using FTIR spectroscopy and its implications for the provenance of New Zealand amber. PeerJ 3:e1067, doi: 10.7717/peerj.1067.

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Species-level determination of closely related araucarian resins using FTIR spectroscopy and its implications for the provenance of New Zealand amber

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Abstract

Some higher plants, both angiosperms and gymnosperms, can produce resins and some of these resins can polymerize and fossilize to form ambers. Various physical and chemical techniques have been used to identify and profile different plant resins and have then been applied to fossilized resins (ambers), to try to detect their parent plant affinities and understand the process of polymerisation, with varying levels of success. Here we focus on resins produced from today's most resinous conifer family, the Araucariaceae, which are thought to be the parent plants of some of the Southern Hemisphere's fossil resin deposits. Fourier transform infrared (FTIR) spectra of the resins of closed related Araucariaceae species were examined to test whether they could be distinguished at genus and species level and whether the results could then be used to infer the parent plant of a New Zealand amber. The resin FTIR spectra are distinguishable from each other, and the three *Araucaria* species sampled produced similar FTIR spectra, to which *Wollemia* resin is most similar. Interspecific variability of the FTIR spectra is greatest in the three *Agathis* species tested. The New Zealand amber sample is similar in key shared features with the resin samples, but it does differ from the extant resin samples in key distinguishing features, nonetheless it is most similar to the resin of *Agathis australis* in this dataset. However on comparison with previously published FTIR spectra of similar aged amber and older (Eocene) resinates both found in coals from New Zealand and fresh *Agathis australis* resin, our amber has some features that imply a relatively immature resin, which was not expected from an amber of the Miocene age.

Introduction

Resins are secondary metabolites produced in higher plants. Among the gymnosperms the most resinous plants today are found in the conifers, particularly the Pinaceae and the Araucariaceae, although some Cupressaceae can also produce some significant resin amounts (Langenheim, 2003). Tappert et al. (2011) showed that modern conifer resins fall into two broad categories: pinaceous resins and cupressaceous resins, depending on their terpenoid (isoprenoid) composition. Pinaceous resins, from the Pinaceae and *Torreya* (Taxaceae), are based on abietane or pimarane terpenes, whereas cupressaceous resins, which include the Araucariaceae, Cupressaceae, Podocarpaceae and Sciadopityaceae, are based on labdane terpenes. This indicates differences in the terpenoid synthases, which are genetically controlled, and so are of phylogenetic significance (Tappert et al., 2011).

Resins can become fossilized, although their potential to do so is directly linked to their terpene chemistry and this varies greatly across conifers. Resin chemistry analyses therefore allow correlations between living plant taxa and can indicate relationships with fossil resinous plants (Lambert, Santiago-Blay & Anderson, 2008).

Resins become fossilized through maturation; this includes their hardening and burial in sediment, where temperature, pressure and permeating fluids affect the rate of chemical transformation (Ragazzi & Schmidt, 2011). Resin maturation is age-related, but it also depends on the thermal history of the resin (Anderson, Winans & Botto, 1992), as well as its chemical structure and composition, since resins are a heterogeneous mixture of chemicals (Langenheim, 2003). Isotopic and chemical changes in amber composition through maturation are minor, except for polymerisation and the loss of volatile components (Nissenbaum & Yaker, 1995; Stout, 1995).

Fossil resins classified as Class I (polylabdanoid diterpenoids), based on the polymeric skeletons of their terpenes (Anderson, 1995; Lambert, Santiago-Blay & Anderson, 2008) comprise the majority of the world's major amber deposits, and thus can be thought to be most chemically similar to the cupressaceous conifer resin type of Tappert et al. (2011). However, the parent plants are still heavily disputed for the largest deposit ever discovered, the Baltic amber succinite deposit, despite being Class 1 (Class 1a: Anderson, 1995) ambers, and various pinaceous, araucarian and sciadopitoid affinities have been suggested (Schubert, 1961; Gough & Mills, 1972; Mosini & Samperi, 1985; Katinas, 1987; Beck, 1993; Langenheim, 1969, 2003; Wolfe et al., 2009) and as yet, none accepted.

Despite the problems of trying to identify the Baltic amber parent plant(s), advances are being made in identifying the parent plant(s) of other major world amber deposits (Penney, 2010). The important amber deposits in the Southern Hemisphere were thought to be mainly araucarian-derived (Lambert, Santiago-Blay & Anderson, 2008) fossil resins (Class 1b: Anderson, 1995). Southern Hemisphere amber has recently been recorded from Peru, South Africa, and Argentina in very

small amounts, with more significant amounts found in Australia (Hand et al., 2010) and New Zealand (Kaulfuss et al., 2011).

In Australia amber occurs in Miocene coals (Lyons, Masterlerz & Orem, 2009), and forms the Cape York deposit (post-Jurassic, pre-late Miocene in age: Hand et al., 2010). Amber that has been washed up on southern Australian beaches is not in situ as it has been transported across the ocean (Murray et al., 1994). Various sources for these ambers have been suggested, both an araucarian (Colchester, Webb & Emseis, 2006) and a dipterocarpacean (Sonibare et al., 2014) origin has been postulated. In New Zealand amber is found in Eocene, Oligocene and Miocene sediments and generally, an araucarian origin has been suggested (Thomas, 1969; Lambert et al., 1993; Lyons, Masterlerz & Orem, 2009).

Other Australian ambers tested by Lambert et al. (1993) and Lyons, Masterlerz & Orem (2009), both from southern Australia; and Sonibare et al. (2014, Cape York, northern Australia) appear to have a different botanical source, potentially among the Dipterocarpaceae (Sonibare et al., 2014), although the source area has not yet been identified (Lambert, Santiago-Blay & Anderson, 2008, Lambert et al., 2012; Lyons, Masterlerz & Orem, 2009). Members of the Dipterocarpaceae are some of the most resinous angiosperms (flowering plants) today and their resins can form amber, classified as Class II (polycadinene) fossil resins (Anderson, 1995; Rust et al., 2010).

No Dipterocarpaceae are known in today's Australian flora, but they are abundant in Southeast Asia, and are thought to have originated in Gondwana in the Late Cretaceous then rafted on the Indian plate and spread out into Asia, based on plant biogeography (Morley, 2000). The dipterocarps have a fossil resin and pollen record stretching back to the Eocene of India (Dutta et al., 2009), however, Australia's fossil record does not include Dipterocarpaceae, and so the source of the ambers with dipterocarpacean affinities is questionable. Sonibare et al. (2014) suggest transportation of amber from New Guinea despite amber not being known there, or from other Southeast Asian amber deposits. Murray et al. (1994) similarly suggested long distance oceanic transport of dipterocarp resin on to southern Australian beaches. Dipterocarpaceae is not present in the extant flora of New Zealand, nor in its fossil record.

A Podocarpaceae conifer origin for a sole mid-Eocene amber from New Zealand was suggested by Grimalt, Simoneit & Hatcher (1989). This amber was associated with unidentified coalified wood from the Brunner Coal Measures which had the Podocarpaceae pollen *Dacrydiiumites mawsonii* (now *Phyllocladidites mawsonii* Cookson 1947 ex Couper 1953) present. Lyons, Masterlerz & Orem (2009) also tested resins from the Eocene bituminous coals of the Brunner Coal Measures of the Reefton Coalfield, but inferred that this amber was more mature *Agathis* amber than younger New Zealand ambers.

Podocarpaceae are not highly resinous today and the family has not been analyzed chemically in detail. Resin only notably occurs in leaves but not from the stems of Podocarpaceae in quantities that would be commercially viable (Langenheim, 2003). There are representatives of Podocarpaceae in both the

Australian and New Zealand floras today, and there is a fossil record dating back to the Cretaceous in both Australia and New Zealand (Pole, 1995, 2000; Parrish, et al. 1998).

The majority of New Zealand ambers are thought to have been produced by *Agathis* (Lambert et al., 1993; Lyons, Masterlerz & Orem, 2009). The record of araucarian macrofossils in New Zealand may date back to the Cenomanian (Late Cretaceous, Pole, 2008). *Agathis* fossils are also known from the Eocene fossil record in Australia (Carpenter et al., 2004), and araucarian pollen is known from the Cretaceous of both New Zealand and Australia (Raine, Mildenhall & Kennedy, 2006). However, both Lambert et al. (1993), using NMR C¹³ spectroscopy, and Lyons, Masterlerz & Orem (2009) using FTIR spectroscopy, showed that some Australian ambers tested have a different, but related chemistry to those of New Zealand, potentially indicating a different parent plant species within *Agathis* or the Araucariaceae.

Araucarian conifers today have a Southern Hemisphere distribution and comprise three genera: *Agathis* Salisb., with 21 species, *Araucaria* Juss., with 19 species, and the monotypic *Wollemia nobilis* W.G. Jones, K. Hill & J.M. Allen. *Agathis* is the most resinous genus today. There have been some investigations of the resin chemistry of the Araucariaceae (Lyons, Masterlerz & Orem, 2009; Wolfe et al., 2009; Tappert et al., 2011), but to date the sampling within this family has focused on several species of *Araucaria*, the monospecific *Wollemia* and a few *Agathis* species (see Lyons, Masterlerz & Orem, 2009; Tappert et al., 2011).

Several different solid state spectroscopy methods have been used to analyse the bulk chemistry of both resins and ambers, including infrared (IR; e.g. Beck, Wilbur & Meret, 1964), Fourier transform infrared (FTIR Wolfe et al., 2009), Raman (Edwards, Farwell & Villar, 2007) and ¹³C nuclear magnetic resonance (¹³C NMR; Lambert et al., 1999; Martinez-Richa et al., 2000) spectroscopy. Interestingly, Wolfe et al. (2009) indicated that infra-specific variability in conifer resins was low, meaning that it could be possible to identify different species, perhaps despite quite different local ecological conditions.

Here we use Fourier transform infrared spectroscopy (FTIR) for studying the bulk chemistry of samples of resins across the Araucariaceae following Tappert et al. (2011) to investigate the resin chemistry variability between selected species of Araucariaceae (including some species that were not previously sampled), and to test subsequently whether some Miocene amber from New Zealand, thought to derive from *Agathis*, can be compared to or distinguished from the resins of these extant *Agathis* species that occur close to present day New Zealand.

Table 1. Modern Araucariaceae resins sampled.

Genus, species	Locality collected, date	Location of resin sampled
<i>Agathis australis</i> (D. Don) Loud.	Northland New Zealand, 2011	Trunk
<i>Agathis lanceolata</i> Warb.	Riviere Bleue, New Caledonia, 2011	Trunk
<i>Agathis ovata</i> (C. Moore ex Veill.) Warburg	west of Yaté, New Caledonia, 2011	Trunk
<i>Araucaria heterophylla</i> (Salisb.) Franco	cultivated tree, Göttingen, Germany, 2014	Trunk
<i>Araucaria humboldtensis</i> J.Buchholz	Mt Humboldt, New Caledonia, 2011	Branch tip
<i>Araucaria nemorosa</i> de Laub.	Port Boisé, New Caledonia, 2011	Trunk
<i>Wollemia nobilis</i> W.G. Jones, K.D. Hill & J.M. Allen	cultivated tree, Göttingen, Germany, 2014	Branch tip

Material & Methods

Seven resins from across the Araucariaceae were sampled from wild and cultivated specimens (Table 1). All except the *Araucaria heterophylla* and the *Wollemia nobilis* resins were collected in New Caledonia and New Zealand in 2011, with the two excepted resins collected in 2014. Fieldwork and collection in southern New Caledonia were kindly permitted by the Direction de l'Environnement (Province Sud), permit n° 17778/DENV/SCB delivered in November 2011. Samples were preferentially collected from trunks, if available, but exudates from branches were used if trunk exudates were not available (Table 1). Hardened resin was preferred, but in two cases (*W. nobilis* and *Ar. heterophylla*) semi-solidified resin was collected and prepared. A sample of amber from the early Miocene Idaburn locality in southern New Zealand (Figure 1) was also tested (see geological information for the amber specimen below). This single large piece of amber was collected in October 2011 and is housed at the Geology Museum of the University of Otago in Dunedin, collection number OU 33159.1. All samples without inclusions or any observable contaminants were chosen, freshly fractured and reduced to a fine powder for application to the central measuring point of the FTIR spectrometer, only tens of micrograms of samples are required per test. Pelletization with KBr was not necessary as the Attenuated Total Reflectance (ATR) technique was used. The absorption spectra were collected in the range 4000-650 cm^{-1} (wavenumbers), equivalent to 2.5-15 μm , using a Jasco 4100 Fourier transform infrared (FTIR) spectrometer. Spectral resolution was set at 4 cm^{-1} . Multiple replicate tests were run per sample until at least three spectra when overlaid were exactly the same, and each time new portions of the ground samples were used. The baseline was not corrected. Bands were identified by comparison with previous reports (e.g. Lyons, Masterlerz & Orem, 2009; Tappert et al., 2011).

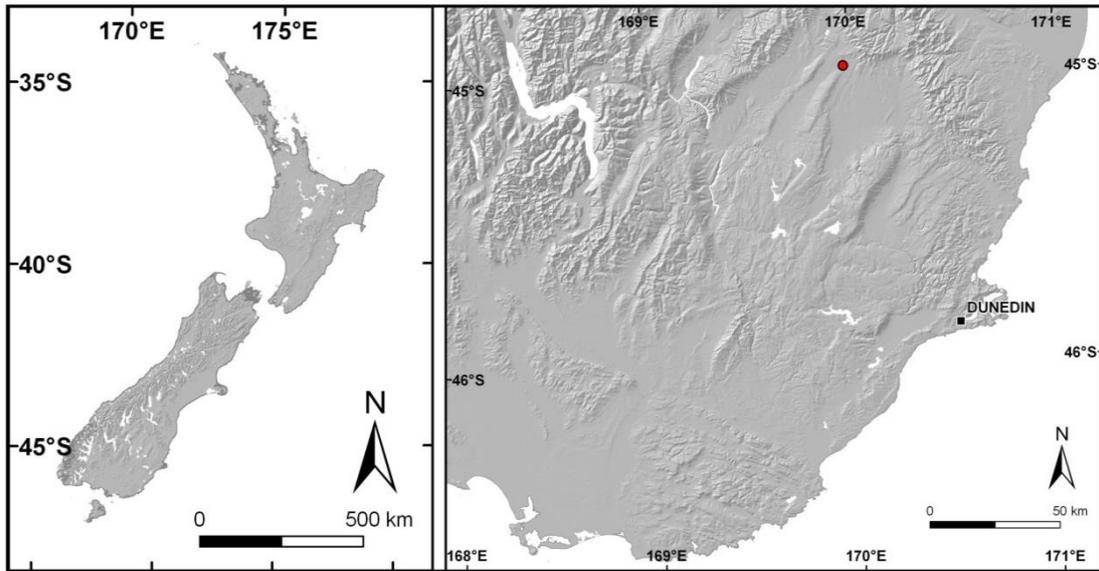


Figure 1: Map of New Zealand and close-up of Otago with Idaburn amber locality (red dot) indicated.

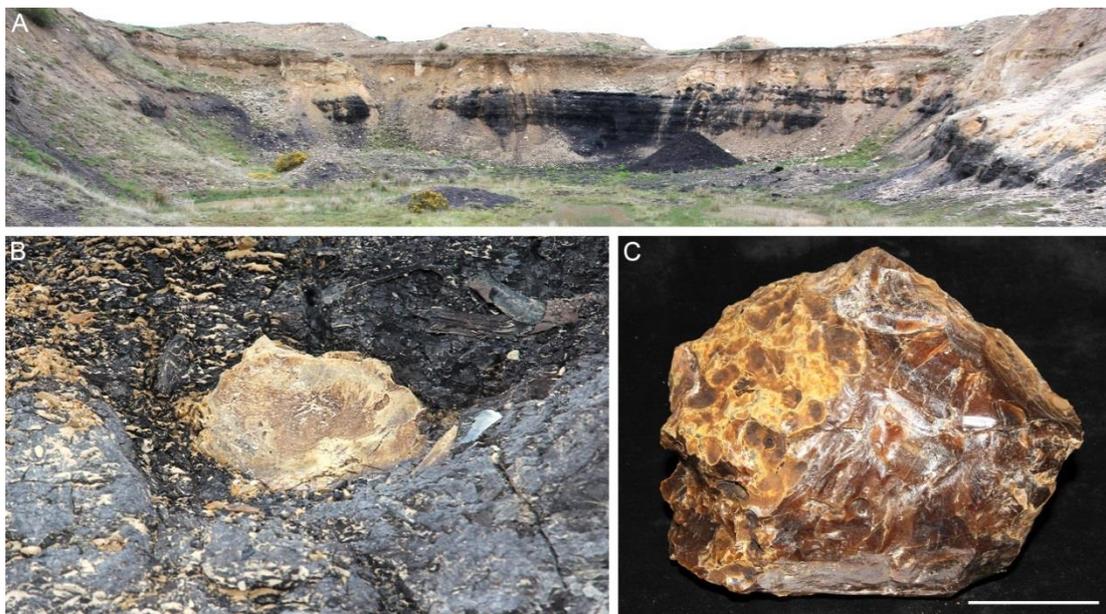


Figure 2: Amber from the former Idaburn Coal Mine, Otago, southern New Zealand. (A) Overview of the exposure of the Oturehua Seam in the Fiddlers Member, Dunstan Formation, from which the amber was collected. (B) In situ amber piece at the exposure of the lignite (Oturehua Seam). (C) Washed amber sample (shown in B) from the same site. Scale is 5 cm.

Geological information for the Idaburn amber sample

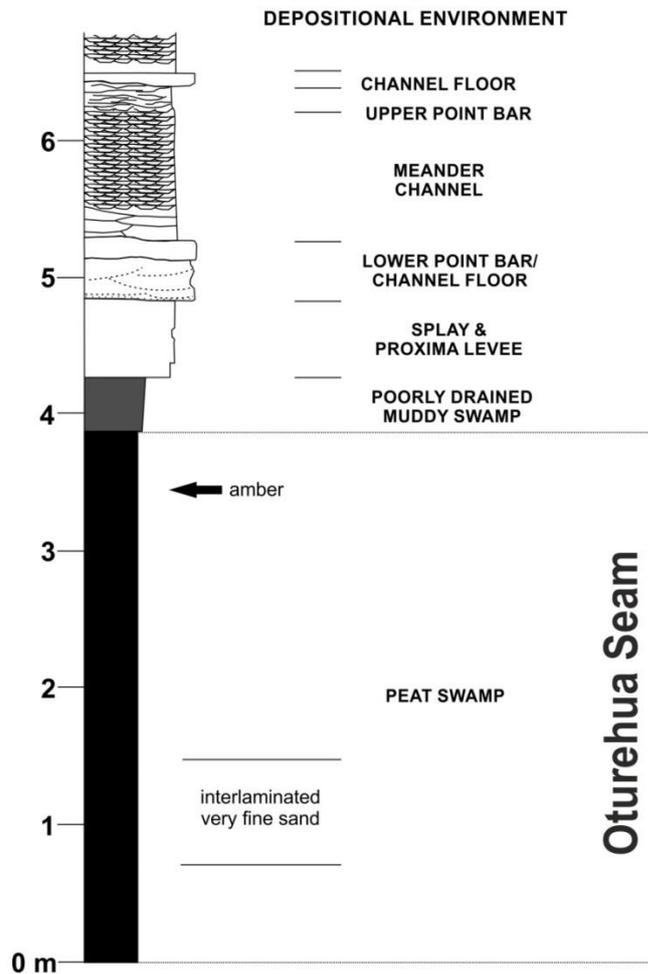


Figure 3: Diagrammatic representation of the exposure at the former Idaburn Coal Mine, Otago, southern New Zealand, showing where the amber was collected, with an interpretation of the depositional environment, redrawn from Lee et al. (2003) with permission

district and varies from a few metres to c. 150 m thick. It primarily consists of a fine-grained non-carbonaceous mud-dominated succession with occasional lignite beds. The Fiddlers Member is interpreted as a widespread low gradient flood-basin dominated plain, peripheral to an enlarging lake (Lake Manuherikia), with relatively few river channels (Lee et al., 2003).

The lignite of the Oturehua Seam (Fig. 3) was formed in a swamp forest and includes some beds with relatively high fusain content. There are some horizons with abundant woody remains (including tree trunks and stumps), and beds composed almost entirely of fern-like rachis litter. Very fine sand is found as discontinuous laminae in the lignite (Douglas, 1986; Lee et al., 2003). This means that the amber is considered in situ with no discernable transportation. Interestingly, the lignite has not been very deeply buried, in contrast to other lignites from elsewhere in New Zealand.

The amber sample was collected from the disused Idaburn Coal Mine (Fig. 2A), near Oturehua, Central Otago, New Zealand. The GPS coordinates of the site are 44°58'58.63'' S 169°58'52.65'' E. The sample (Fig. 2B-C) was taken from the 4 m thick Oturehua Seam (Fig. 3), Fiddlers Member, Dunstan Formation, Manuherikia Group (Douglas, 1986; Lee et al., 2003). The Manuherikia Group consists of fluvial lignite-bearing Dunstan Formation, and the overlying Bannockburn Formation that consists entirely of lacustrine sediments (Douglas, 1986; Lee et al., 2003).

The Fiddlers Member of the Dunstan Formation is widespread in the northern Idaburn

This is something that could be important in understanding diagenesis (particularly of this amber) and will be investigated further in future research (D.E. Lee pers comms).

The age of the lignite is early Miocene (Mildenhall, 1989). The amber sample (OU 33159.1, Geology Department collections, University of Otago) used for FTIR analyses was a single in situ piece (Fig. 2B) from near the top of the Oturehua Seam, which was sampled once removed and washed clean (Fig. 2C).

Results

Table 2: Distinctive features of FTIR spectra summarized allowing sample differentiation. Notes: p = peak, s = shoulder, - = no feature present, T = trough, wide = relatively wider peak, off = offset peak from measurement

Sample tested	Key distinguishing features (cm ⁻¹)											
	3400	1722	1460	1385	1365	1265	1234	1178	1150	1091	1030	791
Idaburn amber	s	s	-	s	s	-	-	-	-	-	off	s
<i>Agathis australis</i>	s	s	T	p	p	-	s	s	p	p	off	s
<i>Agathis lanceolata</i>	-	s	T	p	s	p	p	p	p	p	p	p
<i>Agathis ovata</i>	-	-	-	p	s	-	-	s	p	-	wide	p
<i>Araucaria heterophylla</i>	s	-	-	p	p	p	p	p	p	s	p	p
<i>Araucaria humboldtensis</i>	s	s	T	p	s	p	p	p	p	p	p	p
<i>Araucaria nemorosa</i>	s	-	T	p	s	p	p	p	p	p	p	p
<i>Wollemia nobilis</i>	-	s	-	p	s	p	p	p	p	p	p	p

The FTIR results (Fig. 4) show that the seven resins and the Miocene amber from New Zealand are clearly true plant resins, since they appear to have generally similar spectra, but they are distinguishable from each other. Analysis of the key features of the spectra helps to compare and distinguish the resins (Table 2). Moving from left to right across the spectra, key features are highlighted (Figs 4, 5). The first is a shoulder generally found around 3400 cm⁻¹ of variable amplitude caused by the stretching of O-H bonds, although it is absent in *Agathis lanceolata*, *Agathis ovata* and *Wollemia*. All samples share a small peak at 3076 cm⁻¹ caused by the asymmetric C-H stretching of monoalkyl groups and a more prominent peak at around 2935 cm⁻¹ represents a doublet produced by methylene groups, as well as two smaller peaks off the shoulder of the prominent (2935 cm⁻¹) peak at 2870 cm⁻¹ and 2848 cm⁻¹. These three peaks result from aliphatic stretching of single C-H bonds. The 2870 cm⁻¹ peak is associated with methyl groups and the 2848 cm⁻¹ one is a doublet produced by methylene groups.

The next peak shared by all taxa is at 1693 cm⁻¹, with a weak shoulder present at around 1722 cm⁻¹ for some taxa (amber sample, *Agathis australis*, *Wollemia*, *Araucaria humboldtensis* and *Agathis lanceolata*), both are related to the C=O bonds in the carboxyl groups of resin acids. A smaller peak shared by all taxa at 1460 cm⁻¹ is probably related to O-H bending bond (Tappert et al., 2011) or to exomethylene

(Lyons, Masterlerz & Orem, 2009). The next section (between 1550-650 cm^{-1}), known as the fingerprint region is shown in detail (Fig. 5), as there are many peaks and troughs here. At 1460 cm^{-1} *Agathis australis*, *Agathis lanceolata*, *Araucaria humboldtensis* and *Araucaria nemorosa* have a small trough on the shoulder of the peak at 1448 cm^{-1} , which is shared by all samples. These features are related to C-H bending motions of methyl and methylene functional groups.

The 1385 cm^{-1} peak is shared by all samples, except for the amber sample where this is a shoulder to a peak at around 1375 cm^{-1} , *Agathis australis* which also has a second equal peak at around 1365 cm^{-1} , and *Araucaria heterophylla*, which also has a slightly stronger second peak at around 1365 cm^{-1} , the other resins have a small shoulder at around 1365 cm^{-1} . The peaks between 1300-1100 cm^{-1} are features assignable to C-O single bonds, with the next peak occurring at 1265 cm^{-1} , except for *Agathis australis*, *Agathis ovata* and the amber sample. All samples except that of the amber, *Agathis australis* and *Agathis ovata* share a peak at 1234 cm^{-1} , and all samples except *Agathis australis*, *Agathis ovata* and the amber, have a peak at 1178 cm^{-1} , whereas both *Agathis australis* and *Agathis ovata* have a shoulder and the amber may be interpreted to have a shoulder to a very small peak. All samples, except for the amber share a peak at 1150 cm^{-1} . All samples then have a tiny peak at 1091 cm^{-1} , except the amber and a shoulder instead for *Araucaria heterophylla*. The next, larger peak is at 1030 cm^{-1} present in all samples except those of *Agathis ovata*, where it is a wider, shallower peak, and amber, where the peak appears offset, occurring at around 1012 cm^{-1} .

The next peak shared by all samples is at 887 cm^{-1} which is attributed to the out-of-plane C-H bending motions in terminal methylene groups. Both *Araucaria heterophylla* and *Araucaria nemorosa* have a smaller peak preceding this at around 930 cm^{-1} , on the shoulder of the peak at 887 cm^{-1} . The final feature of interest is a peak at 791 cm^{-1} , shared by all samples' spectra except those spectra for the amber and *Agathis australis* samples, which have a shoulder rising to a peak at around 780 cm^{-1} instead.

The overall picture in terms of spectra from the resins of extant araucarian trees is that the three *Araucaria* species are the most similar to each other as they each have nine distinguishing features in common.

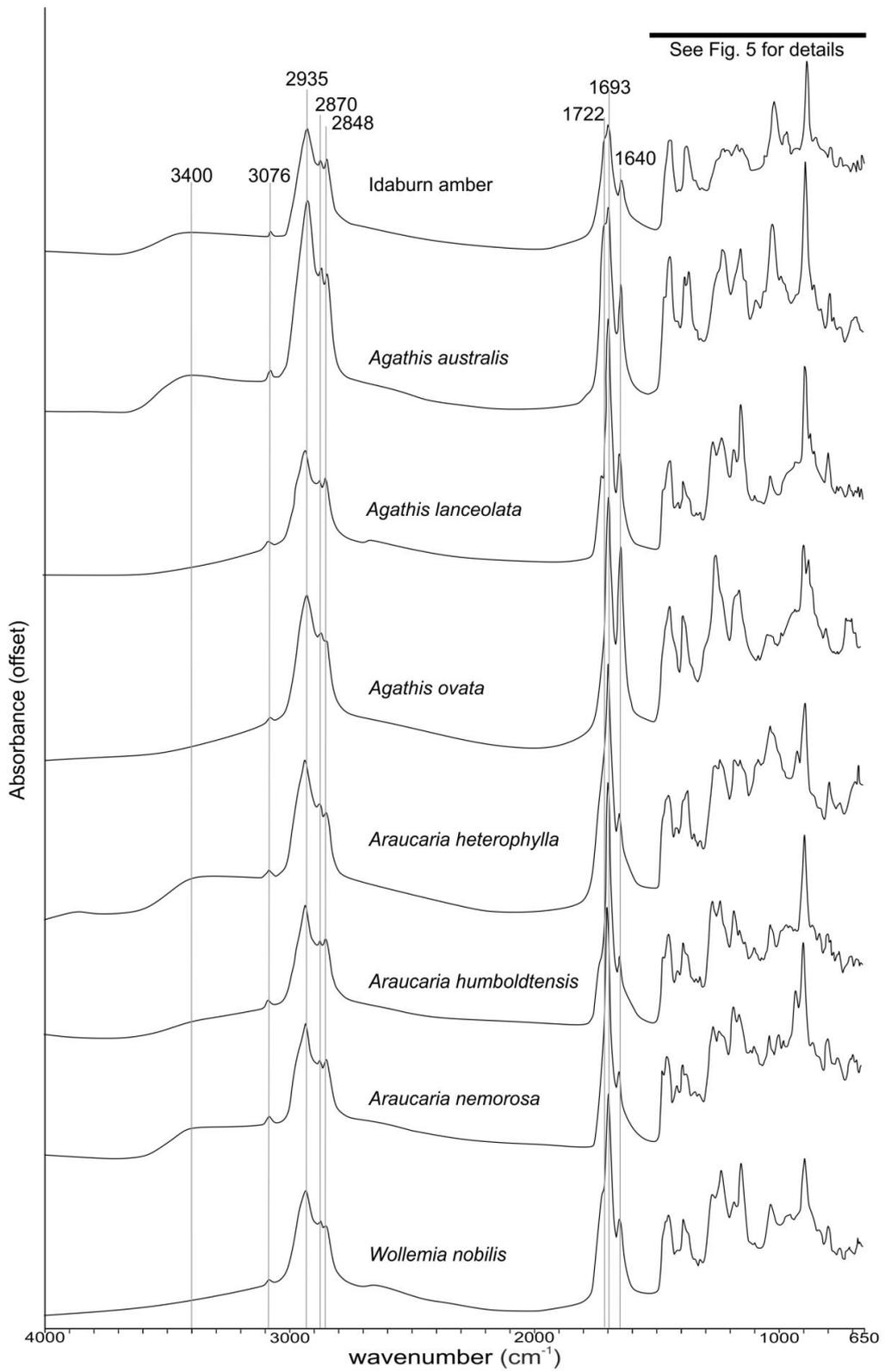


Figure 4: Fourier-Transform Infrared (FTIR) spectra of araucarian resins and a Miocene New Zealand amber.

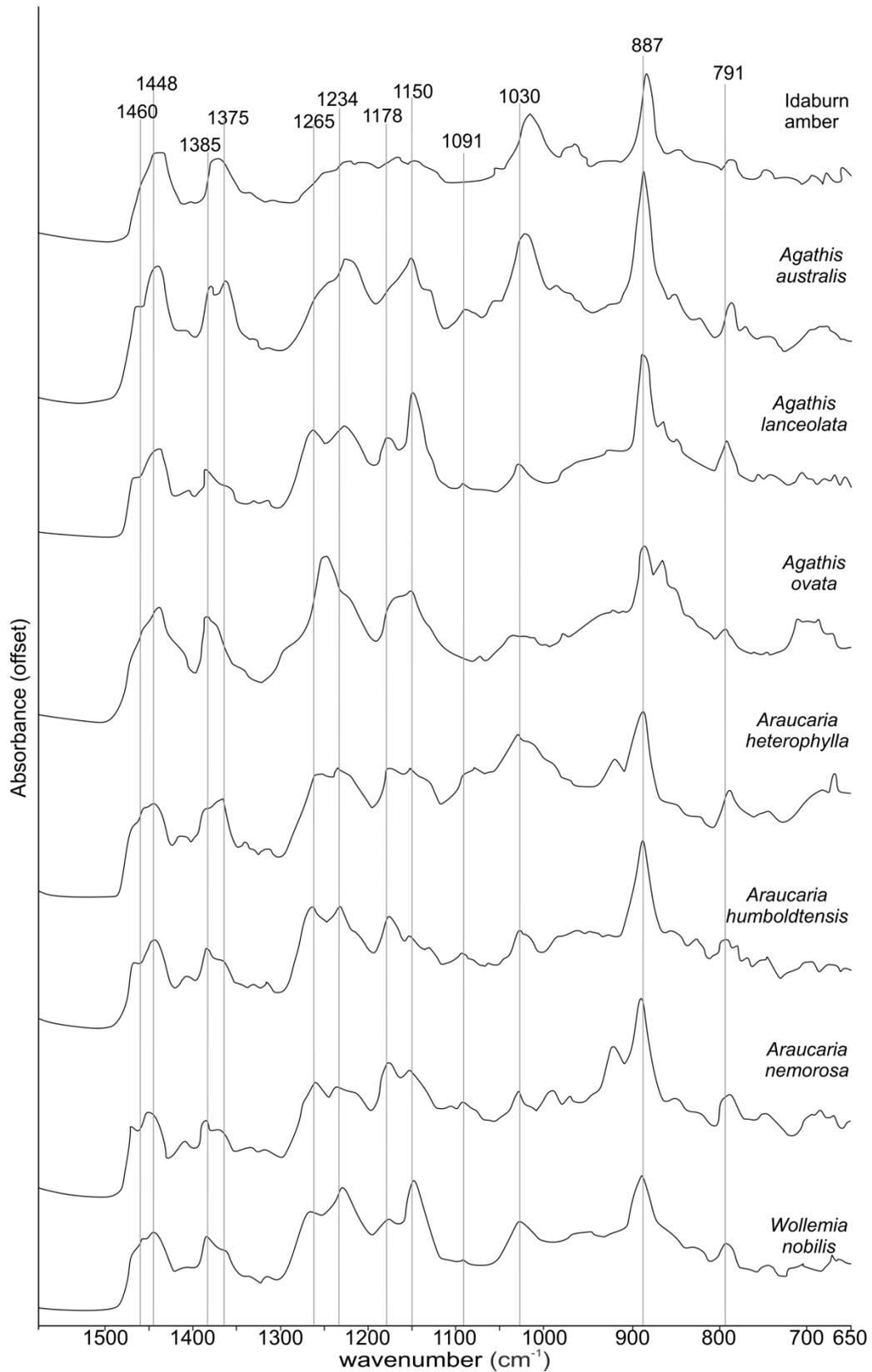


Figure 5: Close-up of the 1550-650 cm⁻¹ spectral region of the Fourier-Transform Infrared (FTIR) spectra of araucarian resins and a Miocene New Zealand amber shown in Fig. 4.

Wollemia and the three *Araucaria* species share eight distinguishing features, and the greatest variability in distinguishing features is seen within the three *Agathis* species (Table 2).

The Idaburn amber sample is similar in key (shared) features with the resin samples (Figs 4 and 5), but does differ from the extant resin samples in some of the distinguishing features (Table 2), particularly at 1385 cm^{-1} , with a shoulder instead of a peak, and having no distinctive peaks between $1265\text{-}1091\text{ cm}^{-1}$, unlike the resin spectra, which is most likely due to the different chemistry that has resulted from fossilization/polymerization. In terms of comparing the amber to the resins tested here, the amber shared most features with that of *Agathis australis* (Figs 4 and 5, Table 2).

Discussion

Comparing our results with that of Tappert et al. (2011) shows that our spectrum for *Agathis australis* is highly comparable to theirs, although there are some minor intensity differences. Our *Wollemia* spectrum is broadly similar, except that we do not have the shoulder at around 3400 cm^{-1} . This is most likely due to a difference in age or freshness between our sample and that of Tappert et al. (2011), and therefore the degree of polymerization, as suggested by Tappert et al. (2011). Mustoe (1985) states that while these hydroxyl groups may be structural components of the resin, they may also be from water vapour absorbed from the atmosphere. KBr pelletization saturates samples and can affect this signal, but the variation we see is unlikely to be due to sample preparation since both we and Tappert et al. (2011) did not need to use KBr pelletization. Diagenetic alteration can be excluded from our modern resin samples.

Wolfe et al. (2009) stated that the intensity of the C=O absorbance at $1600\text{-}1800\text{ cm}^{-1}$ and that of C-H at $1300\text{-}1500\text{ cm}^{-1}$ are related and modulated by the samples' oxidation history, but they also show that these spectral regions are still potentially useful in discriminating modern resin samples, where little oxidation would have occurred. Thus this potential alteration in the C=O absorbance at $1600\text{-}1800\text{ cm}^{-1}$ and of C-H at $1300\text{-}1500\text{ cm}^{-1}$ spectral regions must be taken in to account when comparing FTIR spectra of modern resins directly with fossilized ones. Polymerization reduces the number of hydroxyl (OH) groups, as well as having effects on other groups, and this can be seen to affect the intensity of the 3400 cm^{-1} region. The 3400 cm^{-1} region may also be affected by diagenetic alteration and by use of KBr pelletization (see below for the discussion about the Idaburn amber).

The differences could also possibly be due to differences in the environment surrounding the trees when they produced the resins, which could potentially affect the primary resin chemistry. The similarities of our spectra with those of Tappert et al. (2011) lead us to conclude that the spectra for our samples are comparable and expand our knowledge on araucarian resin FTIR spectra.

The relatively low variability of the *Araucaria* species' resins could be due to the low sample size across this genus of 19 species. Previous work by Tappert et al. (2011) sampled *Araucaria laubenfelsii*, and the published spectrum indicates potentially more variability across this genus. The greater variability of FTIR spectra within *Agathis* species shown here may also indicate that further sampling of araucarian species is needed to map the full FTIR spectral variation of both *Araucaria* and *Agathis* species. Additional samples from other parts of the plants should also be included to understand any potential variation in an individual of a species. Intraspecific variation of these species has not yet been tested, but Wolfe et al. (2009) showed that FTIR spectra of *Pinus* has greater interspecies variation than intraspecific variation across Canada.

Cupressaceous resins, which derive from Araucariaceae, Podocarpaceae, Sciadopityaceae and Cupressaceae, are mainly diterpenoid and have similar FTIR spectra, Tappert et al. (2011) state that they are not distinguishable, based on a very small sample number illustrated. This study has however shown that some bulk chemistry differences within the resins of the Araucariaceae are detectable and that there is much more variation between species than expected. This means that FTIR can be used as a first step to assess the similarity/differences of closely related resins and can be helpful in making an assessment of their interspecific variation.

A second application would be the detection of the first changes denoting polymerization of resins (Tappert et al., 2011). This means that resin FTIR spectra could be used to guide more intensive and expensive subsequent physical and chemical identification work (e.g. ^{13}C NMR, Pyrolysis gas chromatography mass spectrometry). Here we show that the New Zealand amber sample is quite distinct in our dataset, and our results support an *Agathis* affinity as there was most similarity to *Agathis australis* resin, which has been previously suspected of being the parent plant of New Zealand ambers (Lambert et al., 1993); but the sample size is too small to confirm this and a potentially extinct parent plant of the Araucariaceae cannot yet be ruled out. Pollen records show that *Araucariacites australis* Cookson has been present in Australia and New Zealand since the Cretaceous (Raine, Mildenhall & Kennedy, 2006), but this pollen could represent extinct species of both *Agathis* and *Araucaria*. Macrofossil evidence supports the presence of both *Agathis* and *Araucaria* in southern New Zealand in the late Oligocene to early Miocene (Lee, Bannister & Linqvist, 2007; Jordan et al., 2011). The third Araucariaceae genus, *Wollemia* may also have been present in New Zealand from the Jurassic to the early Miocene, based on distinctive pollen, although this pollen type could also have been produced by other *Agathis* species (Jordan et al., 2011; MacPhail & Carpenter, 2013).

Lyons, Masterlerz & Orem (2009) compared modern *Agathis australis* resin with various Southern Hemisphere resinates (amber fragments inside coals) of Eocene to Miocene age. Our amber spectrum has overall similarities to all of theirs, but ours lacks clear peaks between about $1265\text{-}1091\text{ cm}^{-1}$, and we suspect that this reflects an effect of maturation, a diagenetic alteration of the fossil resin.

Our spectrum of modern *Agathis australis* is more similar to the New Zealand resinite samples than to those Australian ones of Lyons, Masterlerz & Orem (2009). They considered the Australian resinites to have a different botanical origin from the *Agathis* source of the New Zealand resinites. Interestingly our amber spectrum has some further features that imply a relatively immature amber. Fossil resins undergo structural and compositional changes as a consequence of the effects of increasing degrees of maturation (e.g. Anderson, Winans & Botto, 1992). In Class 1b fossil resins, to which the Idaburn amber is thought to belong, this is most apparent by the loss of exomethylene through isomerization (Beck, Wibur & Meret, 1964, Beck et al., 1965; Beck, 1986; Anderson, Winans & Botto, 1992; Anderson, 1995; Clifford & Hatcher, 1995).

The presence of exomethylene groups are peaks at around 3082 cm^{-1} , 1644 cm^{-1} and 887 cm^{-1} (Anderson, Winans & Botto, 1992; Lyons, Masterlerz & Orem, 2009), seen in all samples tested here, although slightly less intense in the amber sample. Lyons, Masterlerz & Orem (2009) showed that exomethylene ($\text{C}=\text{CH}_2$) amounts in New Zealand fossil resinites decrease with maturation, with the exomethylene peaks becoming less distinct, eventually disappearing in more mature material. The Idaburn amber sample shows fairly strong exomethylene signals (particularly when compared to the Miocene amber FTIR spectra of Lyons, Masterlerz & Orem, 2009), indicating a relatively immature fossil resin, which is unexpected since the in situ Idaburn amber is Miocene in age (Mildenhall, 1989).

Other effects of maturation may be seen in FTIR spectra of the Idaburn amber sample when compared with the resin samples. Wolfe et al. (2009) stated that the absorbance of C-H at $1300\text{-}1500\text{ cm}^{-1}$ are related and modulated by the samples' oxidation history, possibly explaining why there is a shoulder at 1385 cm^{-1} rather than the peaks seen in all the resin samples. Absorbance peaks between 1265 cm^{-1} and 1091 cm^{-1} indicate C-O bonds, and these are subdued or absent in the amber, but various peaks are seen here in the resins.

It may be that the relatively shallow burial of the lignites of the Dunstan Formation (D.E. Lee, pers comms) is being at least partially reflected in the apparent low maturity of the Idaburn fossil resin, when compared to ambers from other localities in New Zealand where the lignites are known to have been more deeply buried.

Conclusions

This is the first study to apply FTIR spectroscopy to resins produced across closely related members of the Araucariaceae from *Agathis* and *Araucaria* plants growing in New Zealand and New Caledonia, and *Wollemia* from Australia (but grown in Germany). FTIR spectra of resins sampled across the Araucariaceae show unexpected variation, despite the small sample size: environmental variation could be a reason for the variability, but the spectra also show that the species' resins are similar in chemical composition. When the resin FTIR spectra are compared with a

Miocene New Zealand amber sample, a clear relationship is supported showing that the amber is indeed a fossilized Araucariaceae plant resin, but a contradiction appears since the amber has some features of a (relatively) immature fossil resin, particularly when compared to other fossil resins of the same age from New Zealand, perhaps indicating differences in diagenetic histories.

Further investigation is needed to better understand the chemistry of New Zealand amber. FTIR is a very simple, cheap and efficient method for detecting bulk chemistry of both resins and ambers, and needs very little preparation and sample size, making it an excellent first step in the physical and chemical analyses of resins.

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Additional information and declaration

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Competing Interests

The authors declare there are no competing interests.

Author Contributions

- Leyla J. Seyfullah conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.

- Eva-Maria Sadowski performed the experiments, wrote the paper, reviewed drafts of the paper.
- Alexander R. Schmidt conceived and designed the experiments, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.

Field Study Permissions

The following information was supplied relating to field study approvals (i.e., approving body and any reference numbers):

Fieldwork and collection in southern New Caledonia were kindly permitted by the Direction de l'Environnement (Province Sud), permit no 17778/DENV/SCB delivered in November 2011.

Supplemental Information

Supplemental information for this article can be found online at <http://dx.doi.org/10.7717/peerj.1067#supplemental-information>.

References

- Anderson KB, Winans RE, Botto RE. 1992. The nature and fate of natural resins in the Geosphere. II, *Organic Geochemistry* 18:829-841.
- Anderson KB. 1995. The Nature and Fate of Natural Resins in the Geosphere. Part V. New Evidence Concerning the Structure, Composition, and Maturation of Class I (Polylabdanoid) Resinites. In: Anderson KB & Crelling, JC, eds. *Amber, Resinite, and Fossil Resins*. Washington: American Chemical Society no. 617, 105-129; and errata thereto; *Organic Geochemistry* 1997, 25 (3/4), v-vi.
- Beck CW. 1986. Spectroscopic investigations of amber. *Applied Spectroscopy reviews* 22:57-110.
- Beck CW. 1993. Der Wissenstand über chemische Struktur und botanische Herkunft des Bernsteins. *Miscellanea Archeologica Thaddaea Malinowski Dedicata* 1993:27-38.
- Beck CW, Wilbur E, Meret, S. 1964. Infrared spectra and the origin of amber. *Nature* 201:256-257.
- Beck CW, Wilbur E, Meret S, Kossove D, Kermani K. 1965. The infrared spectra of amber and the identification of Baltic amber. *Archaeometry* 8:96-109.
- Carpenter RJ, Hill RS, Greenwood DR, Partridge AD, Banks MA. 2004. No snow in the mountains: Early Eocene plant fossils from Hotham Heights, Victoria, Australia. *Australian Journal of Botany* 52:685-718.
- Clifford DJ, Hatcher PG 1995. Maturation of Class Ib resinites. In: Anderson KB & Crelling, JC, eds. *Amber, Resinite, and Fossil Resins*. Washington: American Chemical Society no. 617, 92-104.

- Colchester DM, Webb G, Emseis P. 2006. Amber-like fossil resin from north Queensland, Australia. *Gemmologist* 22:378-834.
- Douglas, BJ. 1986. *Lignite Resources of Central Otago. Manuherikia Group of Central Otago, New Zealand: Stratigraphy, depositional systems, lignite resource assessment and exploration models*. NZ Energy Research and Development Committee Publication P104. 2 volumes.
- Dutta S, Mallick M, Bertram N, Greenwood PF, Mathews RP. 2009. Terpenoid composition and class of Tertiary resins from India. *International Journal of Coal Geology* 80:44-50.
- Edwards, HGM, Farwell, DW, Villar, SEJ. 2007. Raman microspectroscopic studies of amber resins with insect inclusions. *Spectrochimica Acta Part A* 68:1089-1095.
- Gough LJ, Mills JS. 1972. The composition of Succinite (Baltic amber). *Nature* 239:527-528.
- Grimalt JO, Simoneit BRT, Hatcher PG. 1989. The chemical affinities between the solvent extractable and the bulk organic matter of fossil resin associated with an extinct Podocarpaceae. *Phytochemistry* 28:1167-1171.
- Hand S, Archer M, Bickel D, Creaser P, Dettmann M, Godthelp H, Jones A, Norris B, Wicks D. 2010. Australian Cape York Amber. In: Penney D, ed, *Biodiversity of fossil in amber from the major world deposits*. Manchester: Siri Scientific Press, 69-79.
- Jordan GJ, Carpenter RJ, Bannister JM, Lee DE, Mildenhall DC, Hill RS. 2011. High conifer diversity in Oligo-Miocene New Zealand. *Australian Systematic Botany* 24:121-136.
- Katinas V. 1987. Über die Genese des Bernsteins. In: Stroganow I, (ed) *Zum Geheimnis des Bernsteins*. *Prawda* 31:10.
- Kaufuss U, Lee D, Bannister J, Lindqvist J, Mildenhall D, Perrichot V, Maraun M, Schmidt AR. 2011. Discovering the New Zealand amber forest biota. *Geoscience Society of New Zealand Newsletter* 5:20-25.
- Lambert JB, Johnson SC, Poinar GO, Frye JS. 1993. Recent and fossil resins from New Zealand and Australia. *Geoarchaeology* 8:141-155
- Lambert JB, Shawl CE, Poinar Jr GO, Santiago-Blay JA. 1999. Classification of modern resins by solid nuclear magnetic resonance spectroscopy. *Bioorganic Chemistry* 27:409-433.
- Lambert JB, Santiago-Blay JA, Anderson KA. 2008. Chemical signatures of fossilized resins and recent plant exudates. *Angewandte Chemie (International ed.)* 47:9608-9616.
- Lambert JB, Tsai CY-H, Shah MC, Hurlley AE, Santiago-Blay JA. 2012. Distinguishing amber classes by proton magnetic resonance spectroscopy. *Archaeometry* 54:332-348.
- Langenheim JH. 1969. Amber: a botanical inquiry. *Science* 163:1157-1169.
- Langenheim JH. 2003. *Plant resins. Chemistry, evolution, ecology and ethnobotany*. Portland, Cambridge: Timber Press.

- Lee DE, Lindqvist JK, Bannister JM, Cieraad E. 2003. Paleobotany and sedimentology of Late Cretaceous - Miocene nonmarine sequences in Otago and Southland. In: Cox S. & Smith Lyttle B (eds). *Geological Society of New Zealand Miscellaneous Publication 116B field trip guide*. 1-48.
- Lee DE, Bannister JM, Lindqvist JK. 2007. Late Oligocene-Early Miocene leaf macrofossils confirm a long history of *Agathis* in New Zealand. *New Zealand Journal of Botany* 45:565-578.
- Lyons PC, Masterlerz M, Orem WH. 2009. Organic geochemistry of resins from modern *Agathis australis* and Eocene resins from New Zealand: diagenetic and taxonomic implications. *International Journal of Coal Geology* 80:51-62.
- MacPhail M, Carpenter RJ, 2013. New potential nearest living relatives for Araucariaceae producing fossil Wollemi Pine-type pollen (*Dilwynites granulatus* W.K. Harris, 1965). *Alcheringa* 38:135-139.
- Martinez-Richa A, Vera-Graziano R, Rivera A, Joseph-Nathan P. 2000. A solid-state ¹³C NMR analysis of ambers. *Polymer* 41:743-750.
- Mildenhall DC. 1989. Summary of the age and paleoecology of the Miocene Manuherikia Group, Central Otago, New Zealand. *Journal of the Royal Society of New Zealand* 19:19-29.
- Morley RJ. 2000. *Origin and evolution of tropical rain forests*. Chichester: John Wiley and Sons.
- Mosini V, Samperi R. 1985. Correlations between Baltic amber and *Pinus* resins. *Phytochemistry* 24:859-861.
- Murray AP, Padley D, McKirdy DM, Booth WE, Summons RE. 1994. Oceanic transport of fossil dammar resin: The chemistry of coastal resinites from South Australia. *Geochimica et Cosmochimica Acta* 58:3049-3059.
- Mustoe GE. 1985. Eocene amber from the Pacific Coast of North America. *Bulletin of the Geological Society of America* 96:1530-1536.
- Nissenbaum A, Yaker D. 1995. Stable isotope composition of amber. In: Anderson KB & Crelling, JC, eds. *Amber, Resinite, and Fossil Resins*. Washington: American Chemical Society no. 617, 32-42.
- Parrish JT, Daniel IL, Kennedy EM, Spicer RA. 1998. Paleoclimatic significance of Mid-Cretaceous floras from the middle Clarence Valley, New Zealand. *Palaios* 13:149-159.
- Penney D. 2010. Dominican amber. In: Penney D, ed, *Biodiversity of fossils in amber from the major world deposits*. Manchester: Siri Scientific Press, 22-41.
- Pole MS. 1995. Late Cretaceous macrofloras of eastern Otago, New Zealand: Gymnosperms. *Australian Systematic Botany* 8:1067-1106.
- Pole MS. 2000. Mid-Cretaceous conifers from the Eromanga Basin, Australia. *Australian Systematic Botany* 13:153-197.
- Pole MS. 2008. The record of Araucariaceae macrofossils in New Zealand. *Alcheringa* 32: 409-430.
- Ragazzi E, Schmidt AR. 2011. Amber. In: Reitner J & Thiel V, eds. *Encyclopedia of Geobiology*. Berlin: Springer, 24-36.

- Raine JJ, Mildenhall DC, Kennedy EM. 2006. New Zealand fossil spores and pollen: an illustrated catalogue. 2nd ed. *GNS Science Miscellaneous Series* no. 4. http://www.gns.cri.nz/what/earthhist/fossils/spore_pollen/catalog/index.htm
- Rust J, Singh H, Rana RS, McCanna T, Singh L, Anderson K, Sarkare N, Nascimbene PC, Stebner F, Thomas JC, Solórzano Kraemer M, Williams CJ, Engel MS, Sahni A, Grimaldi D. 2010. Biogeographic and evolutionary implications of a diverse paleobiota in amber from the early Eocene of India. *Proceedings of the National Academy of Sciences of the United States of America* 107:18360-18365.
- Schubert K. 1961. Neue Untersuchungen ueber Bau und Leben der Bernsteinkiefern (*Pinus succinifera* (Conw.) emend.). Ein Beitrag zur Palaeohistologie der Pflanzen. *Geologisches Jahrbuch, Beihefte* 45:1-150.
- Sonibare OO, Agbaje OB, Jacob DE, Faithfull J, Hoffmann T, Foley SF. 2014. Terpenoid composition and origin of amber from the Cape York Peninsula, Australia. *Australian Journal of Earth Sciences* 61:979-985.
- Stout S. 1995. Resin-derived hydrocarbons in fresh and fossil Dammar resins and Miocene rocks and oils in the Mahakam delta, Indonesia. In: Anderson KB & Crelling, JC, eds. *Amber, Resinite, and Fossil Resins*. Washington: American Chemical Society no. 617, 43-75.
- Tappert R, Wolfe AP, McKellar RC, Tappert MC, Muehlenbachs K. 2011. Characterizing modern and fossil gymnosperm exudates using micro-Fourier transform infrared spectroscopy. *International Journal of Plant Sciences* 172:120-138.
- Thomas BR. 1969. Kauri resins – modern and fossil. In: Eglinton G & Murphy MTJ, eds, *Organic geochemistry*. Berlin: Springer, 599-618. .
- Wolfe AP, Tappert R, Muehlenbachs K, Boudreau M, McKellar MC, Basinger JC, Garrett A. 2009. A new proposal concerning the botanical origin of Baltic amber. *Proceedings of the Royal Society, B* 276:3403-3412.

Appendix 2

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

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The enigmatic hyphomycete *Torula sensu Caspary* revisited

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Abstract

About 130 years ago Robert Caspary described fossil fungi resembling the extant anamorphic genus *Torula* Persoon (Ascomycota, Pezizomycotina) from two pieces of Eocene Baltic amber. Despite being among the earliest fungi recognized from amber, these microfossils have received virtually no attention for the past 100 years. Our recent findings of similar fungal inclusions from Baltic and Bitterfeld amber have revealed that these fungi constituted an abundant, but poorly understood component of these Paleogene amber forests. Here we elucidate the morphology and growth mode of these enigmatic fungi and show that they are clearly distinguished from the moniliform hyphae of capnodialean sooty moulds (Ascomycota, Capnodiales), that they also do not correspond with the extant genus *Torula*, and cannot with confidence be assigned to any extant genus of dematiaceous hyphomycetes. The life cycle of the fungi involved transitions from vegetative hyphae to conidial states producing non-randomly disarticulating chains of multicellular phragmoconidia. We provide an emended description of these fungi and suggest a new fossil genus *Casparyotorula* that comprises three anamorphic species, *C. globulifera* (Caspary) comb. nov., *C. heteromorpha* (Caspary) comb. nov., and *C. arnoldii* sp. nov.

Key words: Amber; Ascomycota; *Casparyotorula*, conidiogenesis; dematiaceous hyphomycetes; fossil fungi

1. Introduction

Fungi from Baltic amber have been described since the mid-19th century (e.g., Berkeley, 1848; Menge, 1858; Caspary, 1886) and Caspary and Klebs (1907a, b) illustrated 14 morphologies of fossil fungi in their 'Flora of the Amber'. Most pieces of the famous Künow Collection of Baltic amber, to which the historic specimens of Caspary's collection now belong, are housed in the Museum of Natural History in Berlin. Among the fungal inclusions of this historic collection, we located the holotypes of *Torula globulifera* Caspary and *T. heteromorpha* Caspary. The original descriptions of these microfossils by Caspary (1886) were very brief and were not accompanied by any illustration, referring to filaments of globular cells that are sometimes connected to vegetative hyphae. Richard Klebs (in Caspary and Klebs, 1907a, b) extended the original descriptions and provided drawings of these fungi (Plate I). Their affiliation and life cycles, however, remained unclear based on the provided information. Caspary's holotypes are still so well preserved that hyphal growth and conidiogenesis are precisely traceable. While screening Baltic and Bitterfeld amber pieces for microinclusions, we recently discovered a plethora of further specimens of '*Torula*' sensu Caspary. Our reinvestigation of all these fossils revealed that they are clearly distinguished from the moniliform hyphae of capnodialean sooty moulds (Ascomycota, Capnodiales). Furthermore, based on preserved morphological features, an affiliation to the extant genus *Torula* (Pezizomycotina, Insertae sedis) as currently circumscribed (Crane, 2001) cannot be justified. We therefore suggest treating the amber fossils as a distinct fossil morphogenus, *Casparyotorula*. Their frequent and sometimes abundant occurrences suggest that these microfungi were common in the Baltic and Bitterfeld amber forests and that they often grew epiphytically on the resin-producing trees.

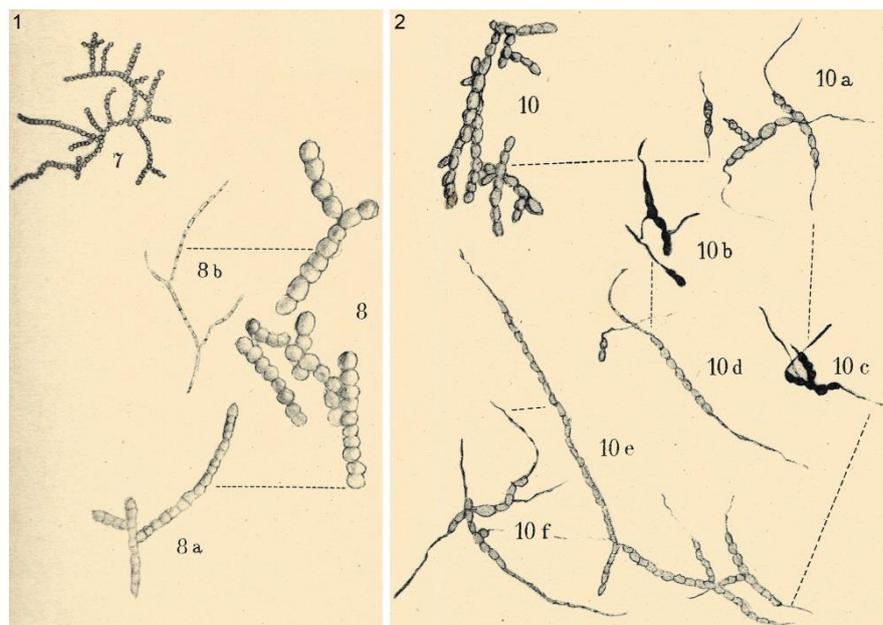


Plate I. Historic drawings of dematiaceous hyphomycetes in Baltic amber (from Caspary and Klebs, 1907b, Taf. 1). 1. *Torula globulifera* Caspary (1886). 2. *Torula heteromorpha* Caspary (1886).

2. Materials and methods

The amber pieces investigated originate from two major European Paleogene amber deposits, Baltic and Bitterfeld amber. The Eocene sediments containing the majority of Baltic amber in the Kaliningrad area (Russia) are 35–47 million years old (Standke, 1998). Bitterfeld amber originates from the Goitzsche mine near the city of Bitterfeld (central Germany) and was recovered from the Chattian 'Bernsteinschluff' Horizon in the upper part of the Cottbus Formation. The upper Oligocene amber-bearing sediment has an absolute age of 23.8–25.3 million years (Knuth et al., 2002; Blumenstengel, 2004). A previous notion that Bitterfeld amber represents re-deposited Eocene Baltic amber is based on the fact that there is a significant proportion of identical arthropod morphologies in amber from both localities (Weitschat, 1997). Redeposition of Baltic amber is unlikely based on the reconstruction of the sedimentary environment of this huge amber deposit (Standke, 2008). A local reworking of pre-Chattian amber, however, has not been dispelled so far (see Dunlop, 2010, for discussion).

The holotypes of *Torula globulifera* Caspary and *T. heteromorpha* Caspary are part of the Künow Amber Collection in the Museum of Natural History, Berlin. Amber piece Künow 153 (MB 1979/696) contains *T. globulifera* and the syntype of the moss *Dicranites casparyi* Klebs, and amber piece Künow 68 (MB 1979/636) contains *T. heteromorpha* along with the holotype of the liverwort *Radula sphaerocarpoidea* (Grolle, 1980), some bark remains, an ant and a spider. These historic amber preparations had been ashlar-shaped, polished from all sides. Due to deterioration the amber has darkened within the past decades and reticulate fissures have developed from the surface towards the centre of piece 153. Most inclusions, however, are still clearly visible. In order to prevent further degradation we embedded piece number 153 in a high-grade epoxy (Buehler Epoxicure) under vacuum (see Nascimbene and Silverstein, 2001, for protocols). After curing, the resultant epoxy plug surrounding the sample was cut and polished to create clear flat surfaces close to the amber and its inclusions. Piece number 68 is well-protected by glass slides and does currently not require further treatment.

Screening newly discovered Baltic and Bitterfeld amber specimens for fungal inclusions, we discovered 22 pieces containing a plethora of inclusions morphologically similar to Caspary's *Torula* species. Baltic amber piece number 3628 of the Carsten Gröhn Collection contains an undetermined lichen, four dipterans and several mites as syninclusions. Bitterfeld amber pieces Mi-19 to 32 and Mi-45 to 50 of the Heinrich Grabenhorst Collection also preserved nematodes, mites, minute faecal pellets of arthropods (likely of mites), dipterans, and an anther. Two pieces from the Heinrich Grabenhorst Collection (#collection number Mi-45 and 46) are now housed in the Geoscientific Collections of the Georg August University Göttingen (collection numbers GZG.BST.27302 and GZG.BST.27303, respectively). A further Bitterfeld amber piece (GZG.BST.27301) was provided by Volker Arnold for this study. Finally, an amber piece of the historic Königsberg Amber Collection (number GZG.BST 24340) that is housed in the Geoscience Collections of the

University of Göttingen, contains an entire conifer leaf overgrown by the fungi under study on both adaxial and abaxial leaf sides. The newly discovered amber pieces were ground and polished manually using a series of wet silicon carbide papers [grit from FEPA P 600–4000 (25.8 μm to 5 μm particle size), Struers]. A fraction of a millimetre of amber surface was gradually removed from each amber piece, while frequently checking the preparation under a stereoscope to ensure that the inclusions were not damaged. The flattened surface of the amber was brought to about 100 μm of the inclusions, if no valuable syninclusions were affected (see Schmidt et al., 2012, for protocols).

Prepared specimens were placed on a glass microscope slide with a drop of water applied to the upper surface of the amber and covered with a 0.06–0.08 mm thick glass coverslip (Menzel Inc., Braunschweig). This reduces light scattering from fine surface scratches and improves optical resolution.

The preparations were examined under a Carl Zeiss AxioScope A1 compound microscope equipped with a Canon 60D digital camera. Sometimes incident and transmitted light were used simultaneously. The images of Plates II to VI were obtained from several focal planes using the software package HeliconFocus 5.0 to enable a better illustration of the three-dimensional inclusions.

3. Results

Casparyotorula Rikkinen, A. R. Schmidt et Kettunen, gen. nov.

Type species: Casparyotorula globulifera (Caspary) Rikkinen, A. R. Schmidt et Kettunen

Mycobank number: MB 811953

Etymology: In honour of Johann Xaver Robert Caspary (1818 – 1887), who originally described these fungi from Baltic amber. The second part of the name refers to superficial similarities with the modern genus *Torula* Persoon.

Diagnosis: Fossil hyphomycetes with up to 7-septate phragmoconidia born in simple or sparingly branched chains, conidiogenous cells not distinguishable from other conidial cells, secession of mature conidia schizolytic or rhexolytic.

Description: Primary hyphae sparingly branched, hyaline to pale brown, thin-walled, smooth and not constricted at the septa. Secondary hyphae, more or less cylindrical, often with short lateral branches, at first thin-walled and pale but becoming progressively thicker-walled and pigmented in age and often developing a rough surface ornamentation. Secondary hyphae often transforming into conidiogenous hyphae. General and apical extension of conidium initials producing simple or sparingly branching chains of conidia. Conidia 0- to 7-septate, broadly ellipsoidal to cylindrical or obovoid, often constricted at the septa, becoming progressively thicker-walled and pigmented in age and sometimes developing a rough surface ornamentation, dehiscence by schizolysis or rhexolysis. Teleomorph unknown.

Commentary: The classification of anamorphic hyphomycetes is mostly based on the morphology of the conidia and the type of conidiogenesis. Despite superficially similar morphological characters, the *Casparyotorula* fossils lack the conidiogenous cells typical of extant species of *Torula*, and also the mode of conidiogenesis is different. Based on these differences we assign the fossil fungi to their own genus.

Casparyotorula globulifera (Caspary) Rikkinen, A. R. Schmidt et Kettunen, comb. nov.,

Plate II

Basionym: *Torula globulifera* Caspary (Caspary, R., 1886. *Schriften der physikalisch-ökonomischen Gesellschaft zu Königsberg* 27, p. 8.)

Holotype: MB 1979/696. Plate II, 11 is the validating illustration in fulfilment of Article 43.3 of the International Code of Nomenclature for algae, fungi, and plants (McNeill et al., 2012).

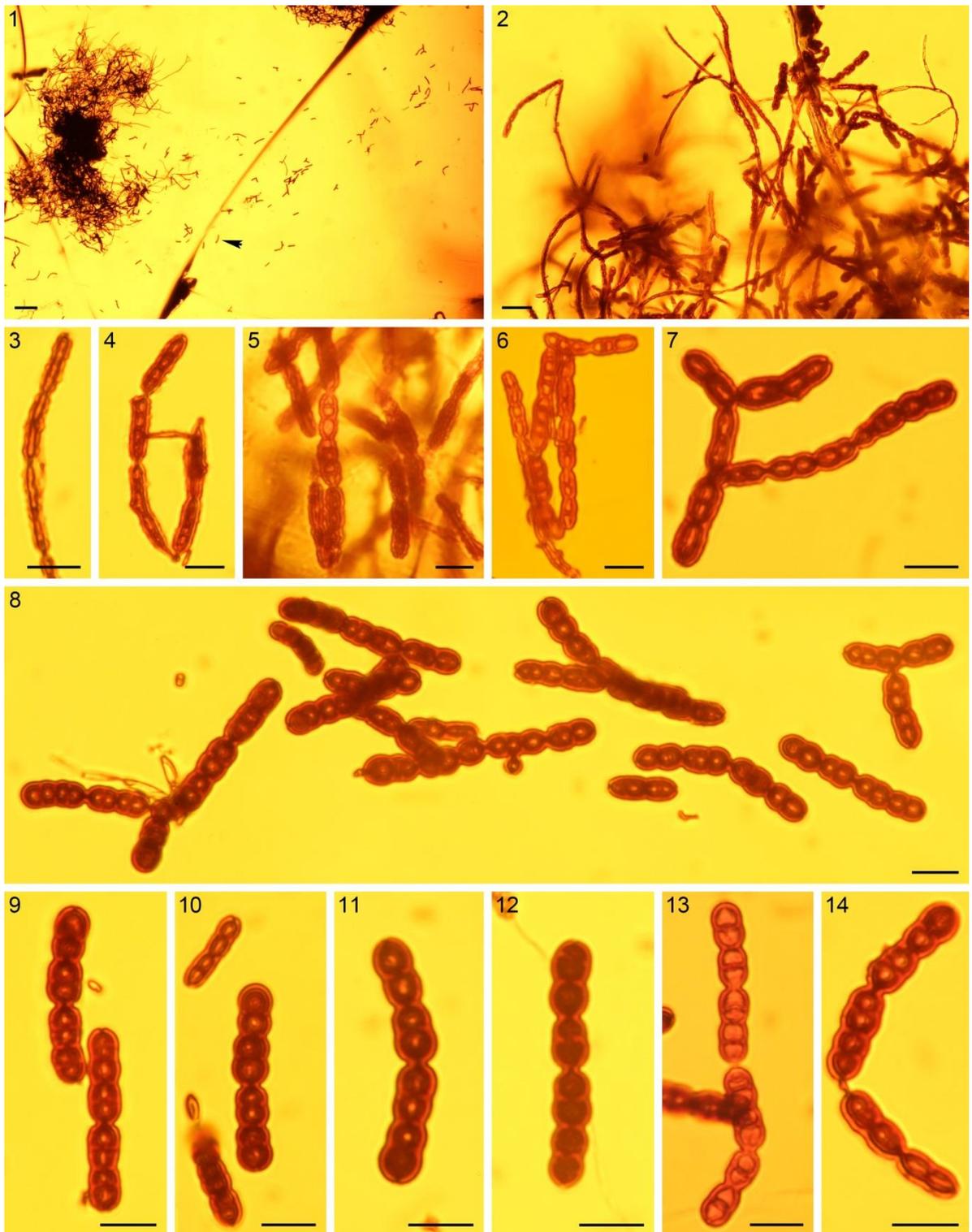


Plate II. *Casparyotorula globulifera* from Baltic amber (MB 1979/696; Künow Amber Collection 153). Scale bars 100 μm (1), 20 μm (2), and 10 μm (3–14). 1. Aerial mycelium and numerous detached conidia. The arrowhead points to the conidium representing the holotype. 2–7. Details of (1) showing delimitation of multiseptate conidia from pre-existing hyphae by successive constrictions at regular intervals with centrifugal septation. 8–14. Details of (1) showing mature, predominately 7-septate phragmoconidia in the amber matrix. Some phragmoconidia (8, 10) have further fragmented into 3-septate units. Figure 11 shows the conidium representing the holotype.

Mycobank number: MB 811954

Illustration: Caspary and Klebs (1907b) Taf. I, figs 7, 8 (Plate I, 1).

Diagnosis: Fossil hyphomycete with brown pluriseptate conidia born in simple or sparingly branched chains. Conidia moniliform, usually consisting of two 3-septate units, somewhat flattened at both ends. Secession of mature conidia schizolytic.

Emended description: Mycelium effuse, primary hyphae sparingly branched, 1.2 – 3.0 µm wide, with cells 4 – 20 µm long, hyaline to pale brown, thin-walled (wall < 1 µm wide), smooth and not constricted at the septa. Secondary hyphae superficial, up to 200 µm long or occasionally even longer, 1.6 – 3.2 µm wide, more or less cylindrical, often with short lateral branches, usually branched at a right angle, at first thin-walled but becoming progressively thicker-walled and more pigmented in age and developing a rough surface ornamentation, cell walls finally 0.8– 1.2 µm thick (Plate II, 1, 2). Secondary hyphae transforming into conidiogenous hyphae, which produce simple or sparingly branching chains of pluriseptate conidia (Plate II, 3–7). Conidiogenesis involves both general and apical extension of conidium initials. Conidia delimited by successive constrictions at regular intervals with centrifugal septation. As the septation of conidia starts to develop early, the cells in the conidia are of more or less the same length as in the hyphae that gave rise to them. Conidia at first narrow and pale brown to brown, becoming progressively thicker-walled and more pigmented in age. Centrifugal septation producing predominately 7-septate conidia (Plate II, 8–14); the formation of an initial septum in the middle is accompanied by an more or less concomitant formation of septa in the median of each of the two cells formed, and followed later with the formation of additional septa in the median of the four cells thus formed. Secession of mature conidia is schizolytic. Constrictions between adjacent conidia in intact conidial chains deep, clearly distinguishing one conidium from its neighbours. The central constrictions of conidia nearly as deep, dividing them into two 3-septate units, which frequently break off and act as independent propagules (Plate II, 9–14). Mature conidia dark brown, (23) 26 – 42 × (4.5) 5.3 – 6.2 (7.0) µm. The median septum of the conidium is typically lost during maturation and only seen as a deep constriction dividing it into two 3-septate units. The units are subcylindrical to ellipsoidal, somewhat flattened at both ends, with cell walls 0.5 – 0.9 µm thick. The median septum of the unit is structurally different and more deeply constricted than the two lateral septa. Occasionally shorter conidia with only one or a few septa occur mixed with 7-septate conidia in the same chain, especially near branching points. Any cell of a multiseptate conidium may initiate branching or bear a conidium scar.

Locality and age: Eocene Baltic amber, originating from the 35–47 million years old Blue Earth sediments at the east coast of Baltic Sea.

Material examined. Baltic amber: Museum für Naturkunde zu Berlin MB 1979/696 (Künow Amber Collection number 153) and Geoscientific Collections of the Georg August University Göttingen GZG.BST 24340 (Königsberg Amber Collection).

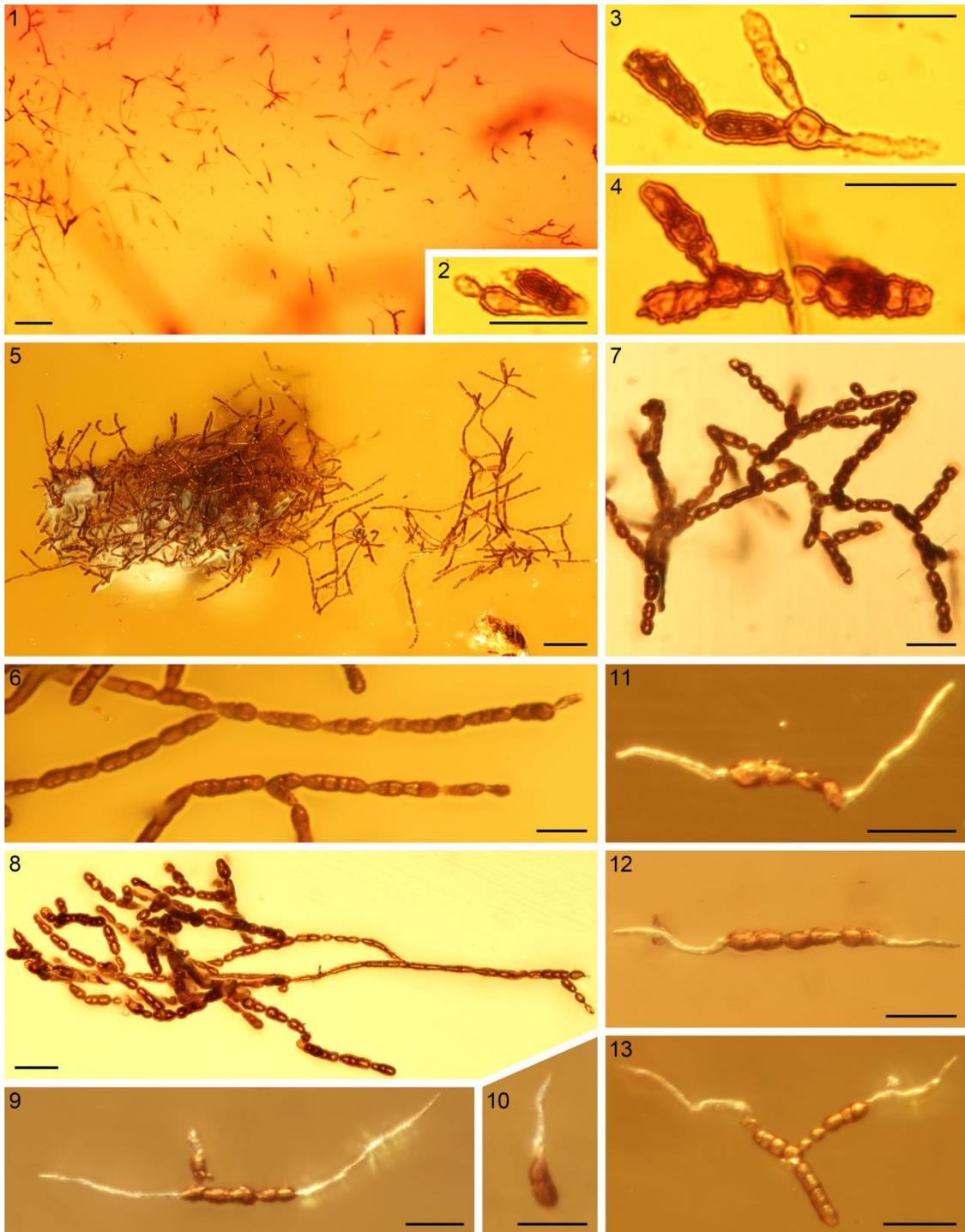


Plate III. *Casparyotorula heteromorpha* from Baltic and Bitterfeld amber. Scale bars 100 μm (1, 5), and 20 μm (2–4 and 6–13). 1. Detached hyphal fragments and multisepate conidia in Baltic amber (MB 1979/636; Künow Amber Collection 68). 2–4. Details of (1) showing acropetal production of multisepate conidia. Figure 3 shows the the holotype which is located very close to the polished amber surface on that side of the amber piece where the holotype of *Radula sphaerocaroides* is also located. 5–6. Fragments of an aerial mycelium with conidiophores producing simple and branching chains of multisepate conidia in Bitterfeld amber (GZG.BST.27302). 7–8. Conidiophores with branching chains of multisepate conidia in Bitterfeld amber (GZG.BST.27303). 9–13. Germinating multisepate conidia in Baltic amber (collection Gröhn 3628). Note the integrated delimitation of new conidial initials in some of the germinated hyphae (11, 13).

Commentary. Both *Casparyotorula globulifera* and *C. arnoldii* produce similar, structurally unique conidia. For distinguishing characteristics between the species, see commentary of *C. arnoldii*. Also present in the amber piece containing the holotype of *Casparyotorula globulifera* is a mycelium of another species of dematiaceous hyphomycetes with much larger, pluriseptate conidia (Plate V, 1). As no direct association between this fungus and *Casparyotorula* has been identified, it will not be discussed here.

Casparyotorula heteromorpha (Caspary) Rikkinen, A. R. Schmidt et Kettunen, comb. nov.,

Plate III

Basionym: *Torula heteromorpha* Caspary (Caspary, R., 1886. Schriften der physikalisch-ökonomischen Gesellschaft zu Königsberg 27, p. 8.)

Holotype: MB 1979/636. Plate III, 3 is the validating illustration in fulfilment of Article 43.3 of the International Code of Nomenclature for algae, fungi, and plants (McNeill et al., 2012).

Mycobank number: MB 811955

Illustration: Caspary and Klebs (1907b) Taf. I, Fig. 10 (Plate I, 2).

Diagnosis: Fossil hyphomycete with brown pluriseptate conidia born in simple or branching chains, intercalary conidia usually flattened at both ends, in terminal conidia the distal end usually rounded with narrower basal cells, usually 3-septate. Secession of mature conidia schizolytic.

Emended description: Mycelium effuse, primary hyphae sparingly branched, 1.5 – 3 µm wide, with cells 4 – 35 µm long, hyaline to pale brown, and not constricted at the septa. Secondary hyphae superficial, up to 35 µm long and 3.0 – 4.5 µm wide, more or less cylindrical, with lateral branches, usually branched at a right angle, at first thin-walled but becoming progressively thicker-walled and developing a rough surface ornamentation (Plate III, 1, 5). Conidiogenesis involving both general and apical extension of conidium initials, with the later predominating, producing simple or branching chains of conidia. Secondary hyphae developing into conidiogenous hyphae as they extend acropetally (Plate III, 6) or conidiophores arising as lateral branches from secondary hyphae (Plate III, 5, 7, 8). Conidia delimited by successive acropetal constrictions at rather irregular intervals with concomitant centrifugal septation to form simple or branching chains of up to 15 conidia. Conidia at first narrow and pale brown to brown, becoming progressively thicker-walled and more pigmented in age and sometimes developing a rather rough surface ornamentation. Apical conidial initials at first continuous then developing a median septum, usually followed by an additional septum in each cell, with the later two septa appearing more or less simultaneously. Sometimes additional faint septa are later added into the

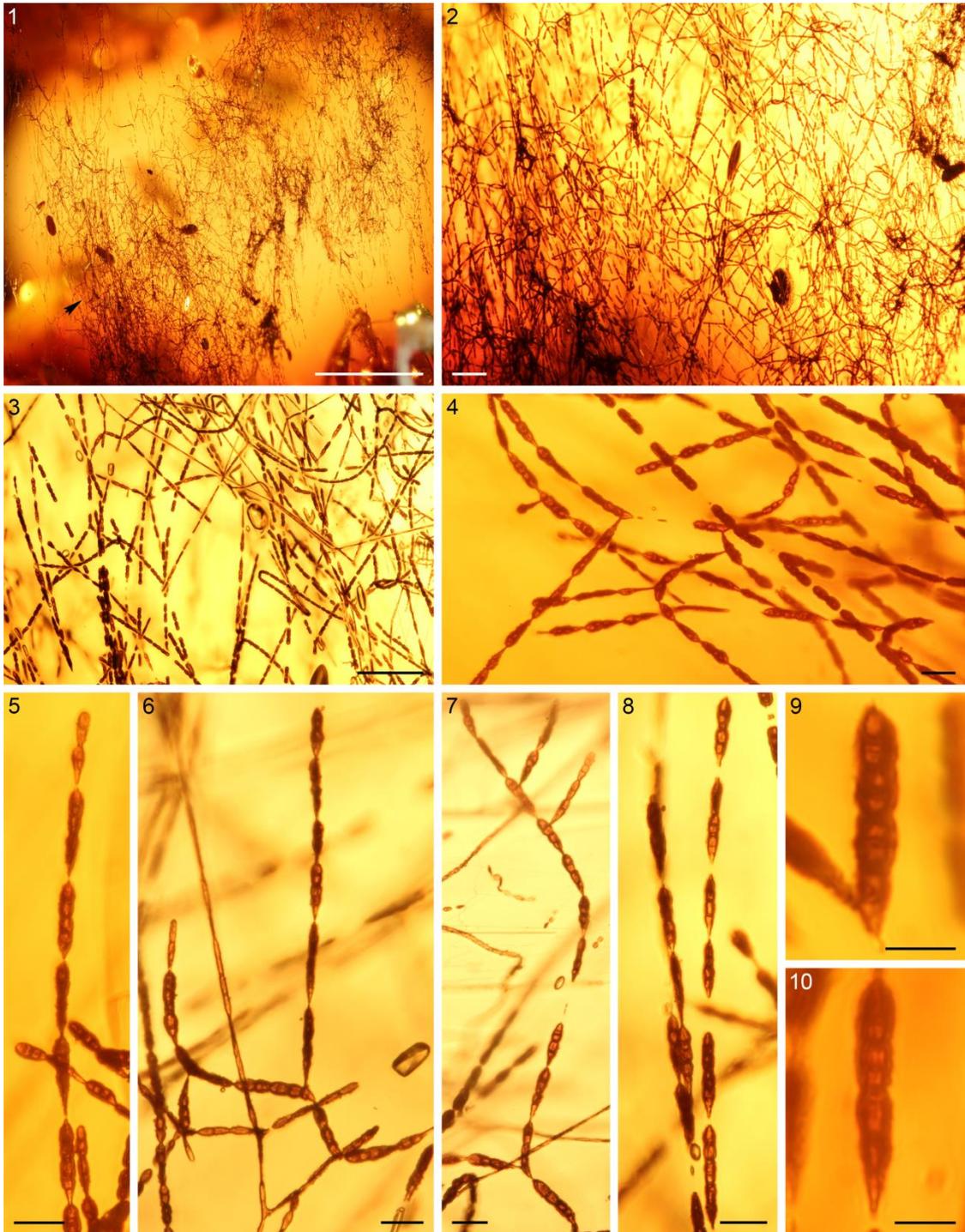


Plate IV. *Casparyotorula arnoldii* from Bitterfeld amber (GZG.BST.27301). Scale bars 1 mm (1), 100 μm (2, 3), 20 μm (4–8), and 10 μm (9, 10). 1. Extensive system of branched conidial chains. The arrowhead points to the conidial chain representing the holotype. 2–10. Details of (1) showing production of predominately 7-septate phragmoconidia through general and apical extension of conidium initials. Figure 5 shows the conidial chain representing the holotype.

basal part of the conidium. The different types of septa appear structurally different, with the median septum being the most conspicuous. Mature conidia narrowly ellipsoidal, subcylindrical or obovate, more or less flattened at both ends in intercalary conidia, but often with the distal end rounded in terminal conidia, dark brown, (6) 14–28 (40) × 4–8 µm, predominately 3-septate, slightly constricted at the septa. Shorter or longer conidia can occur mixed with typical conidia in the same chain in no particular order. Seccession of mature conidia schizolytic. Any cell of a multiseptate conidium may initiate branching or bear a conidium scar.

Locality and age: Eocene Baltic amber, originating from the 35–47 million years old Blue Earth sediments at the east coast of the Baltic Sea, and Bitterfeld amber from the upper Oligocene 23.8–25.3 million years old 'Bernsteinschluff' Horizon in the upper part of the Cottbus Formation near the city of Bitterfeld, Germany.

Material examined: Baltic amber: Museum für Naturkunde zu Berlin MB 1979/636 (Künow Amber Collection number 68) and Carsten Gröhn Collection 3628 (Glinde, Germany). Bitterfeld amber: Geoscientific Collections of the Georg August University Göttingen GZG.BST.27302 and GZG.BST.27303, Heinrich Grabenhorst Collection Mi-19 to 32 and Mi-47 to 50 (Wienhausen, Germany).

Commentary: The conidial production in *Casparyotorula heteromorpha* is more irregular than in the two other species which are both characterized by the production of structurally unique, predominately 7-septate conidia. It is probable that ambient conditions, particularly humidity, have played a role in the evolution of such irregularities. Many conidial fragments in the amber specimens MB 1979/636 and Gröhn 3628 had germinated prior to preservation, confirming their function as reproductive units (Plate III, 9–13). Their presence in the holotype of *C. heteromorpha* (MB 1979/636) was already illustrated in the classical drawing by Klebs (Plate I, 2). The germinating conidia show all stages of development from the initial production of peg-like germ tube initials through one or both terminal scars (Plate III, 10), elongation of slender germ tubes with gradually tapering apices (Plate III, 9, 12), branching of the young hyphae thus formed, and also the integrated delimitation of new conidia from these hyphae (Plate III, 11, 13).

***Casparyotorula arnoldii* Rikkinen, A. R. Schmidt et Kettunen, sp. nov., Plate IV**

Holotype: GZG.BST.27301. Plate IV, 5 is the validating illustration in fulfilment of Article 43.3 of the International Code of Nomenclature for algae, fungi, and plants (McNeill et al., 2012).

Mycobank number: MB 811956

Etymology: In honour of Dr. Volker Arnold (Heide, Germany), who has generously

supported research on fossil fungi over many years by screening amber pieces and donating them for study.

Diagnosis: Fossil hyphomycete with dark brown pluriseptate conidia born in simple or sparingly branched chains, conidia often 7-septate consisting of two 3-septate units. Secession of mature conidia rhexolytic.

Description: Mycelium effuse, sparingly branched, regularly forming parallel threads (Plate IV, 1–3). Hyaline hyphae turning into chains of conidia through general and apical extension of conidium initials (Plate IV, 4–8). Pluriseptate conidia delimited by successive constrictions at regular intervals (Plate IV, 3–8). As the septation of conidia starts to develop early, the cells in the conidia are of more or less the same length as in the hyphae that gave rise to them. Conidia at first narrow and pale brown to brown, becoming progressively thicker-walled and more pigmented in age and developing a rough surface ornamentation. Centrifugal septation producing predominately 7-septate conidia (Plate IV, 9, 10); the formation of an initial septum in the middle is accompanied by an more or less concomitant formation of septa in the median of each of the two cells formed, and followed later with the formation of additional septa in the median of the four cells thus formed. Secession of mature conidia is rhexolytic and mediated through narrow hyphal segments left between adjacent conidia. The constrictions between adjacent conidia are deep, clearly distinguishing each conidium from its neighbours. The constrictions in the median of conidia nearly as deep, clearly dividing them into two 3-septate units, which easily break apart and act as independent propagules. Mature conidia dark brown, $21 - 39 \times 3.5 - 6.3 \mu\text{m}$. The two types of lateral septa are structurally different, and are both more conspicuous than the median septum, which is typically lost during maturation and only seen as the deep constriction in the conidium. The two 3-septate parts of mature conidia are subcylindrical to ellipsoidal, somewhat flattened at both ends, with cell walls $0.8 - 1.2 \mu\text{m}$ thick. Occasionally shorter conidia with only one or a few septa occur mixed with 7-septate conidia in the same chain, especially near branching points. Any cell of a conidium may potentially initiate branching but most conidial chains are unbranched.

Locality and age: Bitterfeld amber from the upper Oligocene 23.8–25.3 million years old 'Bernsteinschluff' Horizon in the upper part of the Cottbus Formation near the city of Bitterfeld, Germany.

Material examined: Geoscientific Collections of the Georg August University Göttingen GZG.BST.27301.

Commentary: Both *Casparyotorula globulifera* and *C. arnoldii* produce similar, predominately 7-septate conidia. In the former species the chains of schizolytically dehiscing conidia develop from branches of secondary hyphae in morphologically more or less distinct conidiophores, whereas in the latter species the whole mycelium is transformed into rhexolytically dehiscing conidia. The holotype of *C. arnoldii* offers an exceptional view of conidiogenesis because of its unique mode of

preservation. Before the resin solidified, a slow unidirectional flow of the resin matrix gently moved the fungal mycelium and pulled many conidial units apart from each other (Plate IV, 2, 3). Several small air bubbles in the amber were also influenced by the movement and are now unidirectional and elongated indicating the direction and strength of the pull (Plate IV, 2, 3). This gentle pull broke the conidial chains into fragments of variable length. Even a casual count of the conidial fragments reveals that fragments of certain length, namely those consisting of either one or two 7-septate units, represent a disproportionately large fraction of all conidial fragments. This indicates that the anatomy in the contact points between two 7-septate conidia and those between the two 3-septate units of each conidium are fundamentally different. The “weak points” in the conidial chains indicate the positions of non-conidial segments in the hyphae that were transformed into conidial chains. Rhexolytic secession at these points combined with the very gentle pull of the viscous resin matrix broke the chains into single conidia or longer chains of several conidia. While the deep constrictions at the median of individual phragmoconidia (separating its two 3-septate units) are also highly susceptible to fragmentation, in this unique case the highly viscous resin matrix selectively preserved most of such contacts, providing compelling evidence for the primary structure of the phragmoconidia. The conspicuous septa at the median of the four 1-septate units of each phragmoconidium were clearly formed only after the outer cell wall of the conidium had already started to thicken. For this reason these sites are not susceptible to physical breakage, but may well dehisce by schizolysis during germination.

Also present in the amber specimen containing the holotype of *Casparyotorula arnoldii* are subhyaline to pale brown conidiophores borne on very narrow septate hyphae that have cells 7 – 16 μm long and 2 – 4 μm wide (Plate V, 2). The branching conidiophores are up to 42 μm long, terminating in acropetal chains of small conidia. Mature conidia are pale and non-septate, ellipsoid to fusiform, 3 – 6.2 \times 1.5 – 3 μm . No direct continuity between the hyphae bearing these *Chrysonilia*-like conidiophores and the hyphae of *Casparyotorula* has been identified, and the very different conidiophores and conidia serve to easily distinguish between the two species of fungi.

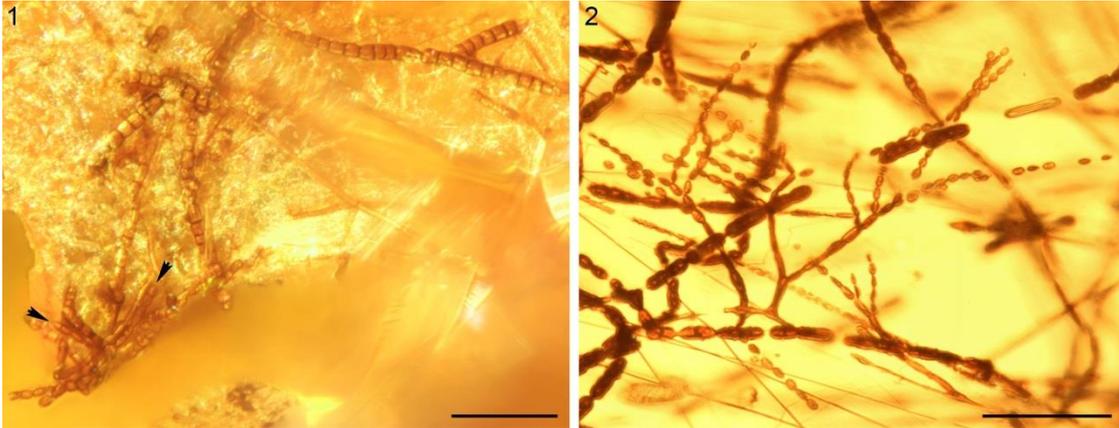


Plate V. Other fungi preserved as syninclusions in amber specimens containing *Casparyotorula* species. Scale bar 50 μm . 1. Unidentified dematiaceous hyphomycete preserved together with *Casparyotorula globulifera* in Baltic amber. The arrowheads indicate two conidial chains of *C. globulifera* (MB 1979/696; Künow Amber Collection 153). 2. Unidentified *Chrysonilia*-like hyphomycete preserved together with *Casparyotorula arnoldii* in Bitterfeld amber (GZG.BST.27301).

4. Discussion

In the revision of *Casparyotorula* species given above, we have given considerable emphasis to the different sequences of conidium septation that can rarely be documented for fossil fungi. As pointed out by Hughes (2007) such characters have been incorporated rarely even into descriptive accounts of extant filamentous fungi although there is evidence that many such differences are constant and merit recognition and documentation.

4.1. The modern genus *Torula*

The genus *Torula* Persoon (Pezizomycotina, Insertae sedis) was established by Persoon (1796) to encompass hyphomycetes with 1-celled, dark or subhyaline moniliform conidia. The type species of the genus is *Torula herbarum* (Persoon) Link. Over 400 species of filamentous microfungi have been described in *Torula*, but the vast majority of these are not closely related to *T. herbarum*. The fact that the name *Torula* has also been used for certain yeasts has added to the nomenclatural confusion (Crane, 2001; Seifert et al., 2011). The nomenclature and recent changes in the generic concept of *Torula* were summarised by Crane (2001). The extant number of species in *Torula* sensu stricto is unclear, but in addition to *T. herbarum* a couple of other species, like *T. caligans* (Batista et H.P. Upadhyay) M.B. Ellis and *T. terrestris* P.C. Misra have been recognized (Rao and de Hoog, 1975; Crane, 2001). The latest addition, *T. brunnea* Y. L. Jiang et T. Y. Zhang was recently described from China (Jiang and Zhang, 2008). According to Seifert et al. (2011) the genus would have seven or more species. *T. herbarum* grows usually on dead herbaceous stems, but occasionally on wood and leaves. It is cosmopolitan, but most often found in temperate regions, whereas *T. herbarum* f. *quarternella* Saccardo is more common in the tropics (Ellis, 1971).

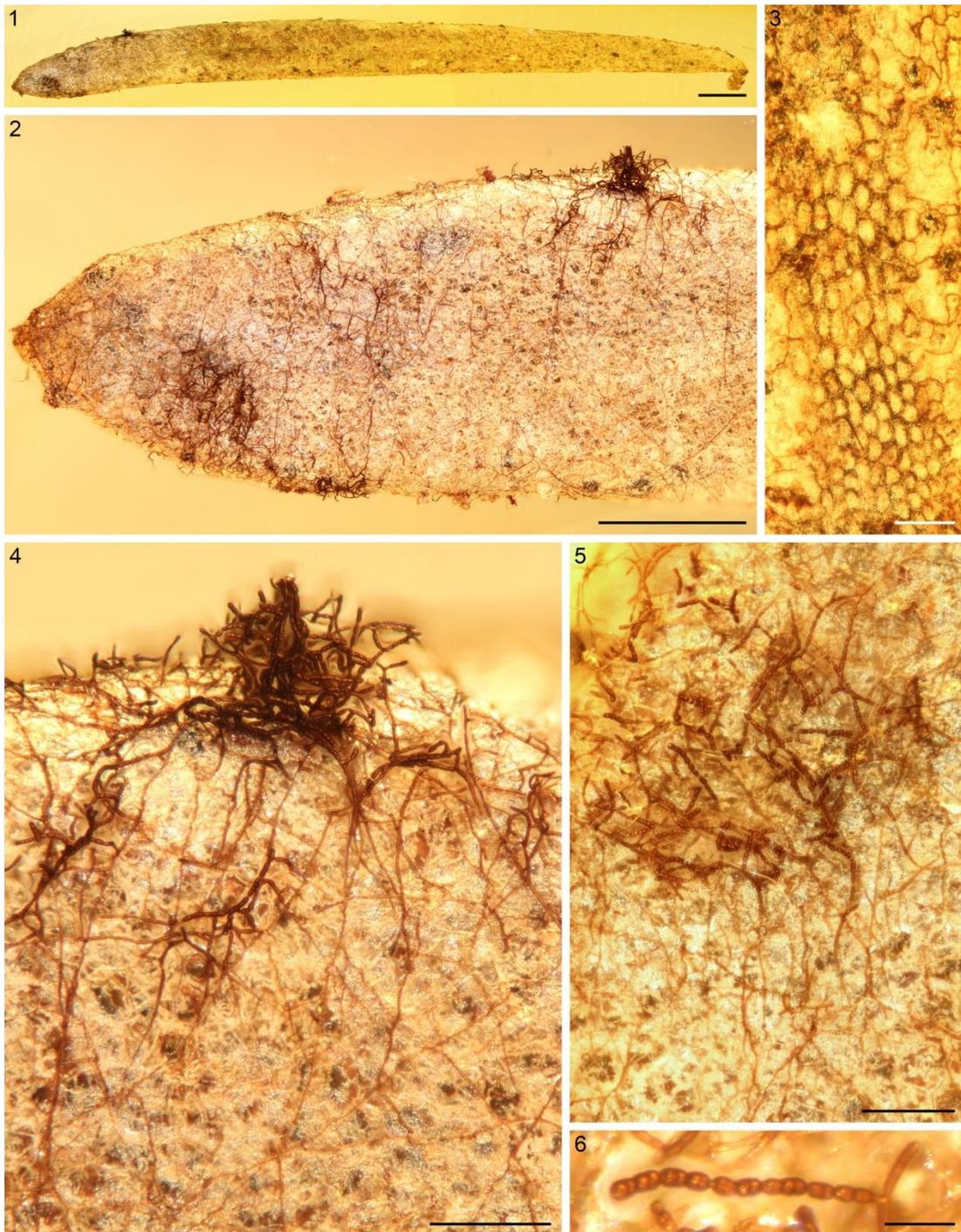


Plate VI. *Casparyotorula globulifera* on a conifer leaf in Baltic amber (GZG.BST 24340). Scale bar 1 mm (1), 500 µm (2), 100 µm (3-5), and 20 µm (6). 1. Conifer leaf, adaxial side. 2. Close-up of the leaf tip with scattered vegetative hyphae and prominent dark branching chains of conidia developing from upright conidiogenous hyphae. 3. Abaxial leaf side with vegetative hyphae along the borders of the epidermal cells, effectively outlining the faint plant cells. 4. Leaf margin with scattered vegetative hyphae and a particularly prominent cluster of branching chains of conidia. 5. Chains of conidia developing above the leaf surface from upright conidiogenous hyphae. 6. Close-up of a chain of conidia.

The distinguishing characters of the genus *Torula sensu stricto* are its unique sympodial, inflated and brown conidiogenous cells, the dark phragmoconidia borne in branched chains, and the ability of the apical cells of the conidia to become conidiogenous. Conidia of *T. herbarum* are formed in acropetal chains that can be simple or branched. Usually the conidia consist of four cells, but they can also comprise up to 10 cells. The conidia are typically verruculose or finely echinulate. The conidia of *T. herbarum* f. *quarternella* are usually three-celled consisting of two equal cells and a morphologically similar conidiogenous cell (Ellis and Griffiths, 1975). The conidia also have a smoother surface than those of *T. herbarum* (Ellis, 1971).

The conidiogenesis in *Torula* is monoblastic or polyblastic, and the distinctive conidiogenous cells have a thin-walled distal fertile part and a thick-walled, melanised proximal sterile part. Similar coronate conidiogenous cells are present also in the anamorphic genera *Dwayabeeja* Subramanian, *Bahusaganda* Subramanian, and *Bahuchashaka* Subramanian, which are considered to be related to *Torula*. The lack of coronate conidiogenous cells differentiates *Casparyotorula* from these genera, and the morphology of conidia is also distinguished. The precise systematic position of *Torula* is still unresolved, and it has not yet been assigned to any modern ascomycete family. However, Zang et al. (2009) suggested that it might belong in the Massariaceae (Pleosporales).

4.2. The fossil genus *Casparyotorula*

All *Casparyotorula* species lack the dark sympodial conidiogenous cells typical of extant species of *Torula*, and also their mode of conidiogenesis, often involving the integrated delimitation of pluriseptate conidia from pre-existing hyphae via successive constrictions and centrifugal septation, is quite different. Due to these differences it is necessary to establish a new genus to accommodate the fossil fungi. *Casparyotorula* species, when present in an amber piece, occur mostly as inclusions of numerous (up to several hundred) individual fragments of conidial chains and attached hyphae. Two amber pieces even contain dark lumps of conidia and vegetative hyphae of 1 – 7 mm size, indicating that these fungi grew in close proximity to the fresh resin flows and that parts of their colonies occasionally dropped onto liquid resin. The fungi were typically trapped in the resin together with aerial insects, epiphytic lichens and bryophytes, the remains of flowers and spider webs, but not with definite soil organisms, indicating the epiphytic growth of these fungi.

The evidence for the original substrate of *Casparyotorula* was not conclusive until we found a conifer leaf inclusion overgrown by *Casparyotorula globulifera* in the historic Königsberg Amber Collection (Plate VI). The conifer needle shows most similarities with some genera of the conifer families Pinaceae, ‘Taxodiaceae’, Taxaceae (including *Cephalotaxus*) and Podocarpaceae, based on the flat, linear leaf shape, the acute to obtuse leaf tip, the pronounced petiole, a single vein (midrib) and

the stomata confined to the abaxial lamina (Florin, 1931). The stomatal characters suggest monocyclic genera of Pinaceae such as *Larix* and *Pseudolarix*, and predominantly monocyclic genera of ‘Taxodiaceae’ such as *Cunninghamia*. On the abaxial leaf side, vegetative hyphae of *Casparyotorula* grew along the borders of the epidermal cells resulting in a growth pattern tracing the epidermal cell shape (Plate VI, 3). This specific growth in slight depressions along cell borders suggests an adaptation of the fungus to leaf surfaces, indicating that this leaf inclusion shows the typical microhabitat of *Casparyotorula*. Whereas these scattered nutrient hyphae are predominantly found on the lower leaf surface, conidiogenous hyphae developed on the adaxial leaf side (Plate VI, 2, 4–6). The conidiogenous hyphae are predominantly upright which supports the idea of elevated sporulation. We suspect that sporulation at a distance from the plant tissue is advantageous since conidia are less influenced by adhesion forces of the leaf surface. In addition, it permits rapid drying of spores after precipitation, which makes spore dispersal by wind and possibly insects more effective.

The amber piece containing the holotype of *Casparyotorula globulifera* contains a 0.7×0.3 mm sized fragment of solidified resin overgrown by at least two species of dematiaceous hyphomycetes, among them *C. globulifera* (Plate V, 1, arrowheads). The other fungus is a more robust dematiaceous hyphomycete forming moniliform conidial chains and hyphae. This hyphomycete is easily distinguished from *Casparyotorula* by its much larger cells that do not systematically form two-celled units (Plate V, 1). Caspary (1886) and Caspary and Klebs (1907a) did not mention the presence of two different fungi in that amber piece. The latter fungus, however, is hidden and hard to spot under transmitted light and we assume that it had remained unseen until now. Considering the frequent preservation, *Casparyotorula* probably grew as rather extensive epiphyllous and possibly corticolous colonies, and occasionally even grew onto solidified resin flows. The habitat and growth form of *Casparyotorula* may have resembled that of sooty moulds, with spongy subculta sometimes forming extensive mats on various plant surfaces (e.g. Schmidt et al., 2014). A similar morphology and ecology is also typical of extant *Torula* species and related fungi. Most Bitterfeld amber pieces containing *C. heteromorpha* also contain mites and abundant faecal pellets that were likely produced by mites. This taphonomic situation may suggest that abundant lumps of *Casparyotorula* were habitat and food source of mites and other microarthropods, similarly to sooty moulds that may be associated with thrips (Nel et al., 2013).

Many of the germinating conidia visible in the fossils seem to have germinated after being first trapped in liquid resin (Plate III, 1, 9–13). In some fossils also the apical cells of hyphae have started to produce new conidial initials (Plate III, 8). Often conidia and hyphae are arranged into belt-like patterns indicating that they had been moved and reorganized by the resin flow before it solidified (Plate II, 1).

A further fossil ‘*Torula*’ species from amber was established in Caspary and Klebs (1907). Klebs assigned the amber fossil *Sphaerophorus moniliformis* Menge (1858) and a newly discovered specimen with identical features to the genus *Torula* by establishing the species *Torula mengeanus*. Both specimens of this taxon are lost

without a trace. However, based on the original descriptions and drawings, Schmidt et al. (2014) identified them as metacapnodiaceous sooty moulds (Ascomycota, Capnodiiales, Metacapnodiaceae). Sooty moulds of this family have repeatedly been discovered as inclusions in Baltic and Bitterfeld amber (Rikkinen et al., 2003; Schmidt et al., 2014) and their tapering moniliform hyphae are clearly distinguishable from the conidial chains of *Casparyotorula*. However, the superficial similarities between sooty mould hyphae and toruloid fungi have also resulted in some modern sooty moulds being first assigned to ‘*Torula*’ (Crane, 2001).

5. Conclusions

The fossil fungi originally described by Caspary and here assigned to the new genus *Casparyotorula* are not with confidence assignable to any extant fungal lineage and cannot therefore be used as minimum age constraint for the occurrence of the genus *Torula* or other groups of filamentous ascomycetes. The common occurrence of these fossils in Baltic and Bitterfeld amber indicates the remarkable fossilization potential that is most likely due to epiphytic growth on resin-producing trees and their relative abundance in European Paleogene amber forests.

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References

- Berkeley, M.J., 1848. On three species of mould detected by Dr. Thomas in the amber of East Prussia. *Annals and Magazine of Natural History (series 2)* 2, 380–383.
- Blumenstengel, H., 2004. Zur Palynologie und Stratigraphie der Bitterfelder Bernsteinvorkommen (Tertiär). *Exkursionsführer und Veröffentlichungen der Deutschen Gesellschaft für Geowissenschaften* 224, 17.
- Caspary, R., 1886. Einige neue Pflanzenreste aus dem Samländischen Bernstein. *Schriften der physikalisch-ökonomischen Gesellschaft zu Königsberg* 27, 1–8.
- Caspary, R., Klebs, R., 1907a. Die Flora des Bernsteins und anderer fossiler Harze des ostpreußischen Tertiars. *Abhandlungen der Königlich Preußischen Geologischen Landesanstalt, Berlin, Neue Folge* 4, 1–181.

- Caspary, R., Klebs, R., 1907b. Atlas von dreissig Tafeln zu der Abhandlung: Die Flora des Bernsteins und anderer fossiler Harze des ostpreußischen Tertiärs. Abhandlungen der Königlich Preußischen Geologischen Landesanstalt, Berlin.
- Crane, J.L., 2001. A Nomenclator of *Torula* Pers.: Fr. and *Torula* Sensu Turpin. Mycotaxon 80, 109–162.
- Dunlop, J., 2010. Bitterfeld amber. In: Penney, D. (Ed.) Biodiversity of Fossils in Amber. Siri Scientific Press, Manchester, pp. 57–68.
- Ellis, M.B., 1971. Dematiaceous hyphomycetes. Commonwealth Mycological Institute, Kew, Surrey, England.
- Ellis, D.H., Griffiths, D.A., 1975. The fine structure of conidial development in the genus *Torula*. I. *T. herbarum* (Pers.) Link ex S. F. Gray and *T. herbarum* f. *quaternella* Sacc. Canadian Journal of Microbiology 20, 1661–1675.
- Florin, R., 1931. Untersuchungen zur Stammesgeschichte der Coniferales und Cordaitales, 1. Teil: Morphologie und Epidermisstruktur der Assimilationsorgane bei den rezenten Koniferen. Kungliga Svenska Vetenskapsakademiens Handlingar, ser. 3, 10, 1–88.
- Grolle, R., 1980. Lebermoose im Bernstein 2. Feddes Repertorium 91, 401–407.
- Hughes, S.J., 2007. *Heteroconium* and *Pirozynskiella* n. gen., with comments on conidium transeptation. Mycologia, 99, 628–638.
- Jiang, Y., Zhang, T., 2008. New species of *Bipolaris*, *Scolecobasidium* and *Torula* from soil. Mycotaxon 104, 135–140.
- Knuth, G., Koch, T., Rappsilber, I., Volland, L., 2002. Concerning amber in the Bitterfeld region - geologic and genetic aspects. Hallesches Jahrbuch für Geowissenschaften 24, 35–46.
- McNeill, J., Barrie, F.R., Buck, W.R., Demoulin, V., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Marhold, K., Prado, J., Prud'homme van Reine, W.F., Smith, G.F., Wiersema, J.H., Turland, N., 2012. International Code of Nomenclature for algae, fungi, and plants (Melbourne Code), adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011. Koeltz Scientific Books, Königstein.
- Menge, A., 1858. Beitrag zur Bernsteinflora. Schriften der Naturforschenden Gesellschaft in Danzig 5, 1–18.
- Nascimbene, P., Silverstein, H., 2000. The preparation of fragile Cretaceous ambers for conservation and study of organismal inclusions. In: Grimaldi, D. (Ed.), Studies on Fossils in Amber, with Particular Reference to the Cretaceous of New Jersey, Backhuys Publishers, Leiden, The Netherlands, pp. 93–102.
- Nel, P., Schmidt, A.R., Bässler, C., Nel, A., 2013. Fossil thrips of the Uzelothripidae family suggest 53 million years of morphological and ecological stability. Acta Palaeontologica Polonica 58, 609–614.
- Persoon, C.H., 1796. Observationes mycologicae. Seu descriptiones tam novorum, quam notabilium fungorum / exhibitae a C. H. Persoon. Pars prima cum tabulis VI aeneis pictis. Wolf, Lipsiae.
- Rao, V., de Hoog, G.S., 1975. Some notes on *Torula*. Persoonia. 8, 199–206.

- Rikkinen, J., Dörfelt, H., Schmidt, A.R., Wunderlich, J., 2003. Sooty moulds from European Tertiary amber, with notes on the systematic position of *Rosaria* (Cyanobacteria). *Mycological Research* 107, 251–256.
- Schmidt, A.R., Jancke, S., Lindquist, E.E., Ragazzi, E., Roghi, G., Nascimbene, P.C., Schmidt, K., Wappler, T., Grimaldi, D.A., 2012. Arthropods in amber from the Triassic Period. *Proceedings of the National Academy of Sciences of the United States of America* 109, 14796–14801.
- Schmidt, A.R., Beimforde, C., Seyfullah, L.J., Wege, S.-E., Dörfelt, H., Girard, V., Grabenhorst, H., Gube, M., Heinrichs, J., Nel, A., Nel, P., Perrichot, V., Reitner, J., Rikkinen, J., 2014. Amber fossils of sooty moulds. *Review of Palaeobotany and Palynology* 200, 53–64.
- Seifert, K.A., Morgan-Jones, G., Gams, W., Kendrick, B., 2011: The Genera of Hyphomycetes. CBS Biodiversity Series 9, CBS-KNAW Fungal Biodiversity Centre, Utrecht.
- Standke, G., 1998. Die Tertiärprofile der Samländischen Bernsteinküste bei Rauschen. *Schriftenreihe für Geowissenschaften* 7, 93–133.
- Standke, G., 2008. Bitterfelder Bernstein gleich Baltischer Bernstein? – Eine geologische Raum-Zeit-Betrachtung und genetische Schlußfolgerungen. In: Rascher, J., Wimmer, R., Krumbiegel, G., Schmiedel, S. (Eds.), *Bitterfelder Bernstein versus Baltischer Bernstein - Hypothesen, Fakten, Fragen. Exkursionsführer und Veröffentlichungen der Deutschen Gesellschaft für Geowissenschaften* 236, 11–33.
- Weitschat, W., 1997. Bitterfelder Bernstein - ein eozäner Bernstein auf miozäner Lagerstätte. *Metalla* 66, 71–84.
- Zhang, Y., Schoch, C.L., Fournier, J., Crous, P.W., de Gruyter, J., Woudenberg, J.H., Hirayama, K., Tanaka, K., Pointing, S.B., Spatafora, J.W., Hyde, K.D., 2009. Multi-locus phylogeny of Pleosporales: a taxonomic, ecological and evolutionary re-evaluation. *Studies in Mycology* 64, 85–100.

Appendix 3

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***Sciadopitys cladodes* from Eocene Baltic amber**

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Running title: *Sciadopitys* from Baltic amber

Abstract

The Baltic amber deposit represents the largest accumulation of any fossil resin worldwide and hundreds of thousands of entrapped arthropods have been recovered, so far. The source plants of Baltic amber, however, are still controversial, and the floristic composition of the ‘Baltic amber forest’ remains poorly studied. Here, we provide the first unequivocal Baltic amber inclusions of the umbrella pine *Sciadopitys* (Sciadopityaceae), a genus that has been suggested as the source of succinite, the main variety of Baltic amber, based on chemical analyses. Since previously suggested sciadopitoid inclusions must be reconsidered as being notional and rather representing angiosperm leaves, the new fossils are the first unambiguous macrofossil evidence of *Sciadopitys* from the ‘Baltic amber forest’, and the first pre-Oligocene macrofossil record of *Sciadopitys* from Europe. The fossil *Sciadopitys* cladodes provide new insights into the conifer diversity of the Baltic amber forest and broaden the picture of its palaeoecology, indicating the presence of humid swamp to raised bog habitats.

ADDITIONAL KEYWORDS: ‘Baltic amber forest’; palaeoecology; Sciadopityaceae; succinite; umbrella pine

INTRODUCTION

Eocene Baltic amber constitutes the largest amber deposit worldwide, with an annual mining production of several hundred tonnes from the Samland Peninsula (Kaliningrad district, Russia, Weitschat & Wichard, 2010). Despite the plethora of exquisitely preserved animal and plant inclusions, the botanical origin of the amber is still controversial, with conflicting evidence from botanical amber inclusions and chemical amber analyses (Langenheim & Beck, 1965; Langenheim, 1969; Poinar, 1992; Langenheim, 2003; Weitschat & Wichard, 2010). Several conifer genera have been proposed as possible amber sources, such as the extinct pine tree *Pinus succinifera* (Goepf.) Conw. (Pinaceae) (Conwentz, 1890), *Pseudolarix* Gordon (Pinaceae) (Grimaldi, 1996) or *Agathis* Salisb. (Araucariaceae) (Langenheim, 1969), but neither family fully complies with the chemical properties of succinite, the main type of Baltic amber, or the palaeobotanical record of its inclusions. Wolfe *et al.* (2009) shed new light on this 'Tertiary Baltic amber mystery' (Langenheim, 2003: 164), proposing the hitherto neglected conifer family Sciadopityaceae as the amber source, based on Fourier transform infrared (FTIR) examinations of Baltic amber and diverse extant plant resins. Unequivocal macrofossil evidence of Sciadopityaceae, however, has been absent from the 'Baltic amber forest' and from the entire pre-Oligocene of Europe, so far.

The extant Sciadopityaceae is a monotypic family, with *Sciadopitys verticillata* (Thunberg) Siebold and Zucc. being endemic to the temperate regions of central and western Japan (Eckenwalder, 2009). However, Sciadopityaceae representatives were once widespread across the Northern Hemisphere. In central Europe the extinct species *Sciadopitys tertiaria* Menzel occurred in the latest Oligocene to the Pliocene and it even formed fossilized masses of cladodes or roots in early to late Miocene brown coal seams of Germany (Gothan, 1936; Thiergart, 1949; Weyland, Kilpper & Berendt, 1967; Mai, 1999, 2000; Dolezych & Schneider, 2007).

Here, we present the first unambiguous inclusions of *Sciadopitys* cladodes, verifying the occurrence of this possible amber-source tree in the 'Baltic amber forest' and thus greatly extending the stratigraphic range of this taxon in central Europe. The occurrence of *Sciadopitys* as amber inclusions points to the palaeoecological and palaeoclimatic character of the 'amber forest' as well as on its putative palaeogeographical distribution.

MATERIAL AND METHODS

An entirely preserved *Sciadopitys* cladode is part of the historic Königsberg [Russian Kaliningrad] Amber Collection which is housed in the Geoscientific Collections of the University of Göttingen (coll. no. GZG.BST.24339). A fragment of a *Sciadopitys* cladode is part of the Carsten Gröhn Collection (Glinde, Germany), coll. no. P 6343. Both specimens originate from the Samland Peninsula (Kaliningrad district, Russia). The majority of the amber-bearing 'Blue Earth' layers in this area are Priabonian in age, with fewer amounts likely extending into Lutetian sediments, so that an age

range of 35 to 47 million years is estimated for the Baltic amber bearing strata (Standke, 2008).

Specimen GZG.BST.24339 was fully embedded in a high-grade epoxy (Buehler Epoxicure) under vacuum (see Nascimbene & Silverstein, 2000, for protocols). After curing, the specimen was ground and polished manually with wet silicon carbide papers (grit from 25.8 to 5 μm particle size, firm Struers).

Cladodes of extant *Sciadopitys verticillata* were obtained from cultivated specimens at the campus of the University of Göttingen.

Amber inclusions and extant cladodes of *S. verticillata* were examined under a Carl Zeiss AxioScope A1 compound microscope (Figs. 1, 2, 3C-E, 4C-H) and a Carl Zeiss Stereo Discovery.V8 dissection microscope (Figs. 3A-B, 4A-B), equipped with Canon EOS 5D digital cameras. In most instances, incident and transmitted light were used simultaneously. All figures are digitally stacked photomicrographic composites of up to 65 individual focal planes, obtained by using the software package HeliconFocus 5.0 (HeliconSoft, <http://www.heliconsoft.com>) for an enhanced illustration of three-dimensional structures. The overview images of Figs. 1A-B and 4A-B were obtained by merging up to four photomicrographic composites using the Adobe Photoshop CS6 software.

RESULTS

The entire cladode (GZG.BST.24339) is linear, straight, 1.7 cm long, and its margins are entire. The lamina narrows towards the slightly swollen base (0.14 cm wide) showing an elliptic to roundish attachment scar (Fig. 1A, B). Towards the tip, the lamina broadens (0.22 cm wide) and terminates in an emarginated or bifurcate apex with two lacerated tips (“double leaf tip”) (Fig. 1C). The upper (adaxial) side of the cladode possesses a glabrous median groove, proceeding longitudinally from the apex to the base (Fig. 1A). The longitudinal groove of the lower (abaxial) surface of the cladode is deeper than the adaxial one (Fig. 1B, D). It starts 0.2 cm above the base and terminates at the apex. The abaxial groove is 70 μm wide at the base, broadens at the distal part (up to 250 μm) and narrows at the tip (100 μm wide). The cladode fragment (Carsten Gröhn Collection, P 6343) is 0.54 cm long and 0.16 cm wide and its abaxial side possesses a longitudinal median groove which is 120 μm wide (Fig. 2A, B).

The abaxial groove of both specimens is lined with papillae which are short and knob-like (9 to 25 μm long and 10 to 20 μm wide) at the outer margin of the groove (Figs. 1E, 2B) and elongated rod-shaped towards the center of the groove (18 to 45 μm long and 9 to 15 μm wide) (Figs. 1F, 2B). The stomata are not visible. The epidermis of both sides of the cladodes is composed of rectangular cells which are arranged in regular lines, being orientated parallel to the longitudinal cladode axis. The lateral cells walls of the epidermis are straight; the polar cell walls are mostly perpendicular to the lateral cell walls, sometimes also slightly oblique (Figs. 1D, 2B). The epidermal cells are 42 to 155 μm long and 10 to 25 μm wide.

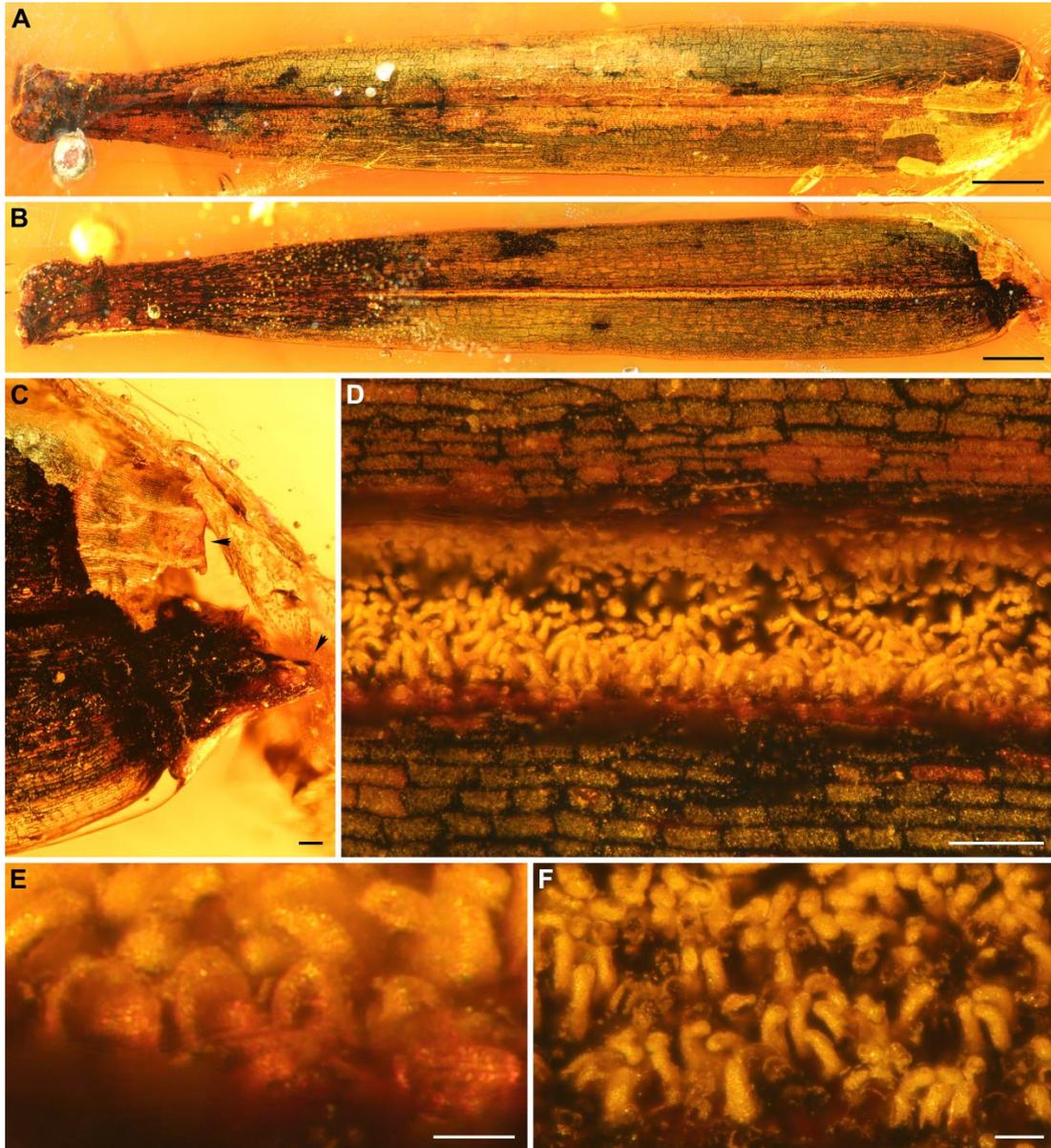


Figure 1. Complete *Sciadopitys* cladode from Baltic amber (GZG.BST.24339). A, Adaxial side. B, Abaxial side. C, Bifurcate tip, indicated by arrowheads. D, Abaxial papillate groove surrounded by rectangular epidermal cells. E, Short and knob-like papillae from the margin of the abaxial groove. F, Elongate rod-shaped papillae from the center of the abaxial groove. Scale bars: A, B, 1 mm; C, D, 100 μ m; D, E, 20 μ m.

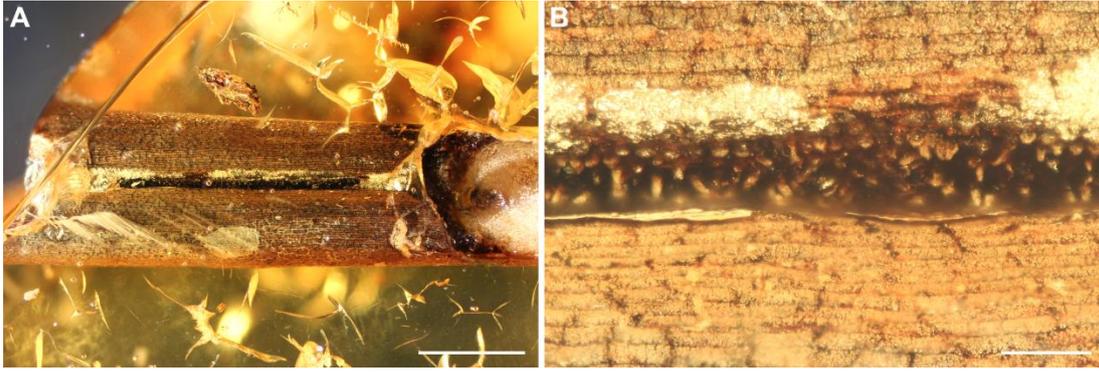


Figure 2. Fragment of a *Sciadopitys* cladode from Baltic amber (Carsten Gröhn Collection coll. no. P 6343). A, Abaxial side. B, Abaxial groove surrounded by rectangular rows of epidermal cells. Marginal knob-like papillae and rod-shaped papillae in the center of the groove are visible. Scale bars: A, 1 mm; B, 100 μ m.

DISCUSSION

COMPARISON OF THE AMBER INCLUSIONS TO EXTANT PINACEAE AND *SCIADOPITYS VERTICILLATA*

Regarding their gross-morphology, i.e. lamina shape, the amber inclusions resemble needles of several conifer taxa of the Pinaceae (*Abies* Miller, *Tsuga* (Endlicher) Carrière, *Pseudotsuga* Carrière) superficially since some species of these genera exhibit emarginated needle tips and a similar needle shape (Eckenwalder 2009). However, these taxa can clearly be distinguished from the amber inclusions by the absence of a median stomatal groove and long rod-shaped papillae on the abaxial side.

The sole extant *Sciadopitys* species possesses photosynthetic organs arranged in pseudowhorls that are termed ‘double needles’ and are regarded as cladodes, representing the main carbon-assimilating organs. The long, slender and linear cladodes are subtended by ‘true leaves’ which are, however, reduced to brown bracts (Florin, 1931; Farjon, 2005; Eckenwalder, 2009; Dörken & Stützel, 2011). The cladodes of *Sciadopitys verticillata* exhibit a unique morphology among extant conifers (Florin, 1922; Farjon, 2005; Eckenwalder, 2009). This specific morphology, which is also present in the amber specimens, comprises the glabrous shallow groove on the upper side of the cladode and the deep groove on the lower side, both proceeding longitudinally from the apex towards the base (Fig. 4A, B). As in extant *S. verticillata*, the groove on the underside of the fossil is lined with numerous papillae which typically overarch the stomata in fossil and extant *Sciadopitys* (Figs. 1D, 4F). The papillae of the amber inclusions are knob-like and short at the groove margins (Figs. 1E, 4G) and longer and rod-shaped towards the middle of the groove (Figs. 1F, 4H) like in other *Sciadopitys* species (Weyland *et al.*, 1967). The complete cladode inclusion possesses a linear, slender leaf shape, a broadened base and an emarginate apex (Fig. 1A-C) as in extant *Sciadopitys* (Fig. 4A-E) (Florin, 1931; Eckenwalder, 2009; Dörken & Stützel, 2011). Further specific features of extant

Sciadopitys cladodes are two vascular bundles proceeding longitudinally in each side of the cladode, separated by the median groove (Dörken & Stützel, 2011). Due to the poor preservation of the internal tissue in the amber fossils (as seen in the break surfaces of the Gröhn specimen, Fig. 2A), the presence of these two bundles could not be confirmed. However, the combination of characters of the amber fossils such as the bifurcate tip and shape of the cladode, the presence of a single papillate median groove on the underside, as well as the morphology of the papillae justify the assignment to the genus *Sciadopitys*.

THE FOSSIL RECORD OF THE SCIADOPITYACEAE AND PUTATIVELY RELATED TAXA

Fossil conifer needles possessing a deep papillate median groove on the underside were traditionally regarded as having close affinities to extant Sciadopityaceae. To accommodate such ‘*Sciadopitys*-like’ needles, the genus *Sciadopitytes* Goeppert et Menge 1883 was used by Halle (1915) and Florin (1922) and later replaced by the ‘fossil-genus’ *Sciadopityoides* Sveshnikova 1981, encompassing a heterogeneous complex of ‘*Sciadopitys*-like’ leaf types with epidermal characters similar to the extant *Sciadopitys* (Bose & Manum 1990). Four new genera with several species were introduced by Bose & Manum (1990) splitting up the form genus *Sciadopityoides* into *Mirovia* Reymanówna emend. Bose and Manum, *Oswaldheeria* Bose and Manum, *Holkopitys* Bose and Manum, and *Sciadopytoides* Sveshnikova emend. Bose and Manum. These genera were described from the Early Jurassic to Early Cretaceous of several circum-arctic localities (Bose, 1955; Bose & Manum, 1990; Bose & Manum, 1991), Northwestern Germany (Manum, Van Konijnenburg-Van Cittert & Wilde, 2000), Western Kazakhstan (Nosova & Kiritchkova, 2008) and from the Iberian Peninsula (Gomez, 2002). These sciadopitoid genera were transferred into the new family Miroviaceae, along with the genus *Tritaenia* Mägdefrau et Rudolf (Bose & Manum, 1991; Manum *et al.*, 2000). The Miroviaceae are distinguished from the extant Sciadopityaceae by the absence of the emarginate tip and two veins. The latter was discussed by Bose & Manum (1991) who postulated the presence of two vascular bundles in Miroviaceae leaves based on the stomata position, but without direct morphological evidence of two veins. Further features separating the Miroviaceae from *Sciadopitys* are missing evidence of scale leaves subtending the needles, the absence of the verticillate leaf arrangement, the stomata size and orientation as well as the position and morphology of the papillae (Manum, 1987; Bose & Manum, 1990). Hence, close affinities of the Miroviaceae to the extant *Sciadopitys verticillata* were doubted (Manum, 1987; Bose & Manum, 1990, 1991) and several authors discussed a relation of the Miroviaceae to the ‘Taxodiaceae’ (Manum *et al.*, 2000; Gordenko, 2007).

Besides the Miroviaceae, another sciadopitoid fossil was reported by Christophel (1973) from the Late Cretaceous to Paleogene from Western Alberta (Canada) who described shoots and leaf compression of *Sciadopitophyllum canadense*. Compared to the extant Sciadopityaceae he stated a close relationship due to similar gross morphology; however, *Sciadopitophyllum canadense* did not

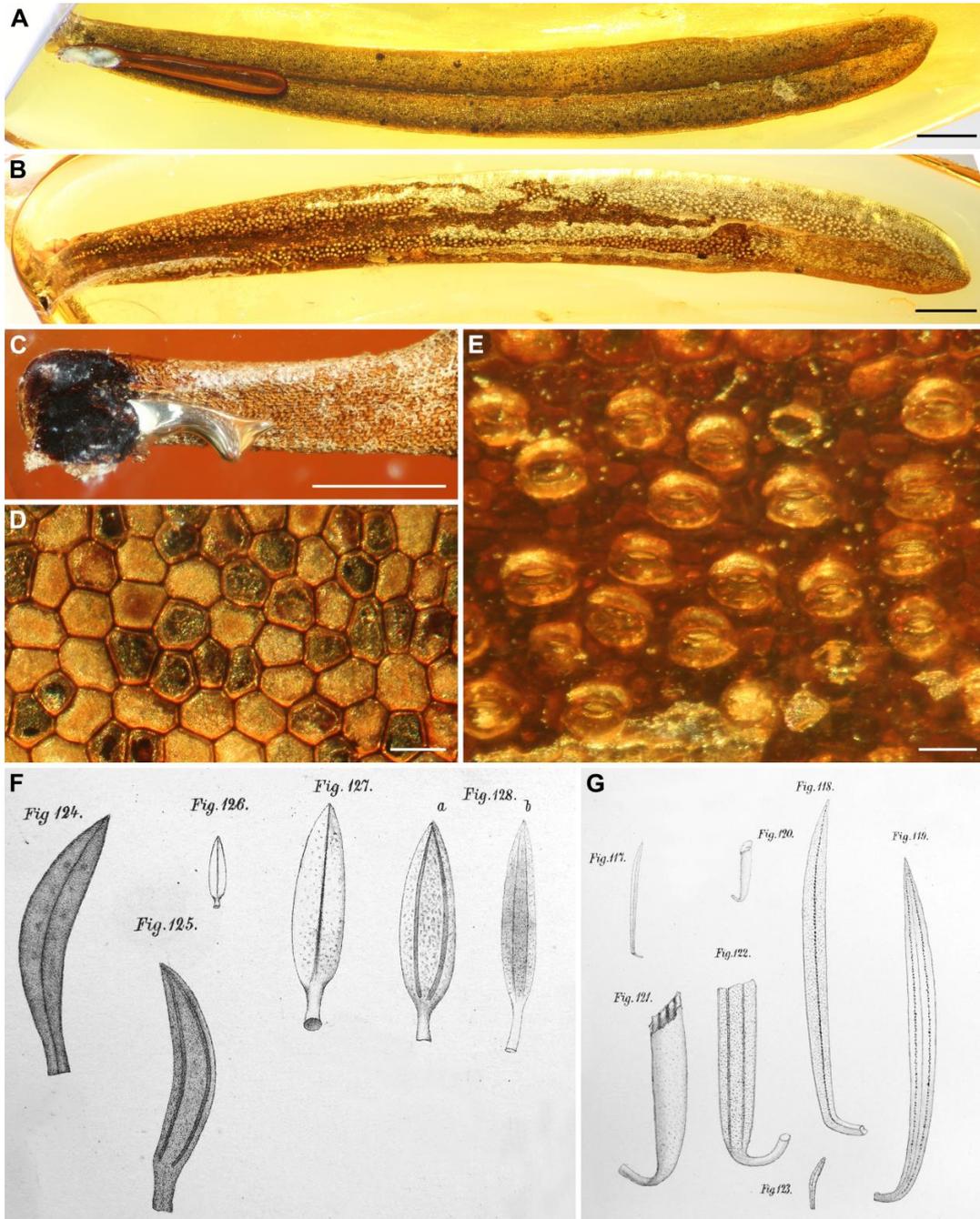


Figure 3. Putative sciadopitoid inclusions from Baltic amber (Max J. Kobbert Collection coll. no. P 134) (A-E) and historic drawings from Goeppert & Menge (1883) (F, G). A, Adaxial and B, Abaxial side of a needle-shaped angiosperm leaf. C, Curved pronounced petiole. D, Polygonal isodiametric epidermal cells of the adaxial leaf side. E, Non-sunken stomata with bean-shaped aperture cells. F, Historic drawings of *Sciadopitytes glaucescens* (from Goeppert & Menge, 1883, Taf. XIV, Figs. 124-128). G, Historic drawings of *Sciadopitytes linearis* (Fig. 117-119) and *S. glaucescens* (Fig. 120-123) (from Goeppert & Menge, 1883, Taf. XIII). Scale bars: A, B, 1 mm; C, 500 μ m; D, E, 50 μ m.

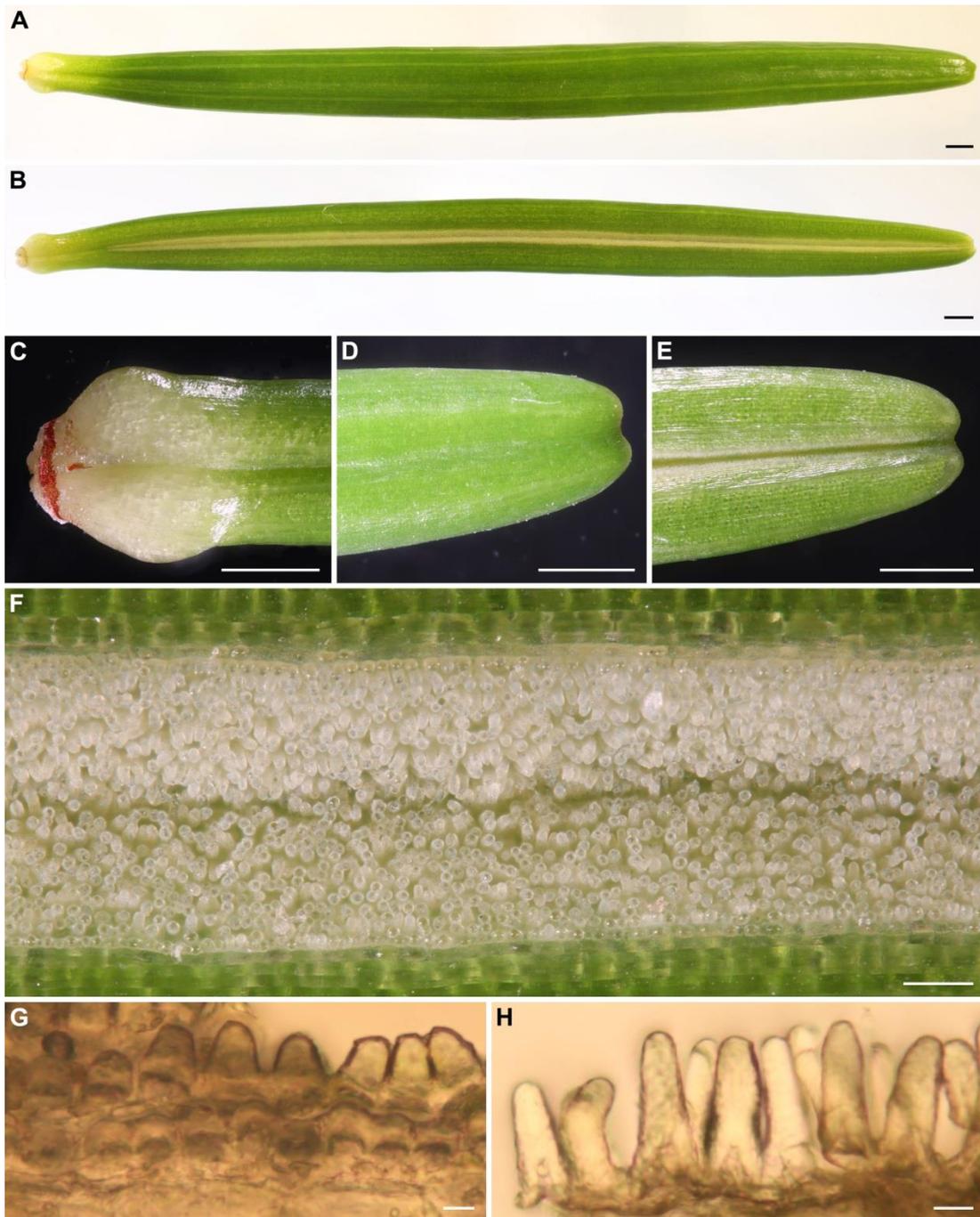


Figure 4. Cladode of the extant *Sciadopitys verticillata*. A, Adaxial side. B, Abaxial side. C, Broadened base. D, E, ‘Double leaf tip’ from the adaxial (D) and abaxial (E) side. F, Abaxial papillate groove. G, Knob-like short papillae from the margin of the abaxial groove. H, Elongate rod-shaped papillae from the center of the abaxial groove. Scale bars: A–E, 1 mm; F, 100 μ m; G, H, 10 μ m.

possess ‘double leaf tips’, and cuticular features such as the papillate groove, were not preserved (Christophel, 1973).

Sciadopityaceae or ‘*Sciadopitys*-like’ cladode fossils are very abundant in the European Neogene, with mass occurrences in the Miocene (Gothan, 1936; Thiergart, 1949; Dolezych & Schneider, 2007). The oldest European macrofossils that were assigned to the Sciadopityaceae extend to the late Paleogene. These are cladodes and cones of *Sciadopitys tertiaria* Menzel and wood of *Sciadopityoxylon wettsteini* from the late Oligocene to the late Pliocene of different locations in Germany (e. g. Herzogenrath, Aachen; Northeast Brandenburg and Southwestern Mecklenburg; Düren, Rhineland; Bitterfeld; Menzel, 1913; Florin, 1922; Jurasky, 1928; Weyland *et al.*, 1967; Mai, 2004; Dolezych, 2005; Schneider, 2008). A single record of *Sciadopitys tertiaria* cladodes from the early Oligocene of Seifhennersdorf (Jähnichen, 1969) is regarded as mis-determination (Walther & Kvaček, 2007; pers. communication with Zlatko Kvaček, Charles University Prague, 2015) whereby the earliest occurrence of this species in central Europe needs to be adjusted from the early Oligocene to the latest Oligocene (Schneider, 2008). *Sciadopitys* is also present in upper Oligocene-lower Miocene lacustrine sediments in the Li Basin, northern Thailand (Sawangchote, Grote & Dilcher, 2009).

The *Sciadopitys* pollen record of central Europe dates back to the Eocene (Kruttsch, 1971; Stuchlick, 2002), while further *Sciadopitys* pollen finds are known from high northern latitude localities of the Paleocene to early Eocene, including Iceland, Greenland and Ellesmere Island (Manum, 1962).

In conclusion, the fossil record of sciadopitoid plants is diverse, but in most cases the affinities of the Mesozoic sciadopitoid fossils to the extant Sciadopityaceae remain obscure. Exceptions are fossil cones, seeds and cladodes of the Sciadopityaceae recorded from the Late Cretaceous to the Pliocene of several localities of Japan (Ogura, 1932; Tsukada 1963; Saiki 1992; Ohsawa, 1994).

Fossil cladodes which clearly can be assigned to *Sciadopitys* have not been reported from any pre-late Oligocene sediment in Europe, so far. Thus, our amber inclusions represent the oldest unambiguous macrofossil of *Sciadopitys* in Europe.

AFFINITIES OF THE AMBER SPECIMENS TO SCIADOPITOID FOSSILS

As discussed above, several taxa of the Miroviaceae show sciadopitoid morphologies. Taxa of the Miroviaceae with a papillate groove on the needle underside (e.g. *Sciadopityoides* Sveshnikova, *Mirovia* Reymanówna emend. Bose & Manum) show features which are not present in the amber fossils, particularly the entire acute, obtuse or acuminate apices, but also different ‘needle’ shapes, a hole in the leaf bottom or tuberculate papillae (Bose & Manum 1990; Bose & Manum 1991; Gomez 2002). In addition, the known stratigraphic range of the Miroviaceae, extending from the Middle Jurassic to the Early Cretaceous (Bose & Manum, 1991), makes it rather unlikely that the late Eocene amber fossils are affiliated with this family.

Sciadopitoid fossils showing similarities to the amber specimens belong to *Sciadopitys tertiaria*, since they share the overall morphology of the cladode and the arrangement and morphology of the papillae. The leaves of *Sciadopitys tertiaria* are distinguished from the extant *S. verticillata* by fine and dense granulation of the epidermal cell walls and the absence of stellate sclerenchyma cells which are located inside of the mesophyll of extant *Sciadopitys* cladodes (Weyland *et al.*, 1967; Jähnichen, 1969). Both amber fossils lack granulated epidermal cells; sclerenchyma cells are, however, not visible using light microscopy and without destruction of the valuable fossils. We refrain from establishing a new species for the fossil cladodes from amber since relevant characters such as the detailed stomatal morphology, the phyllotaxis of the cladodes or the presence of scale-like ‘true leaves’ of *Sciadopitys* that discriminate the sole extant species from other fossil species are not preserved. Due to some similar features of the amber fossils to *Sciadopitys tertiaria* and its broad distribution in the European Oligocene to Pliocene, affinities to the amber specimens are likely. Thus, we suggest the following taxonomy:

FAMILY SCIADOPITYACEAE

GENUS *SCIADOPITYS* (Thunb.) Siebold and Zucc.

SCIADOPITYS CF. *TERTIARIA* Menzel emend. Weyland, Kilpper & Berendt

Synonymy

1913 *Sciadopitys tertiaria* Menzel, p. 23, pl. 3, fig. 21.

1967 *Sciadopitys marcodurensis* Weyland, Kilpper & Berendt, p. 159, pl. 30, figs 31-35 and pl. 31, figs 36-38.

1969 *Sciadopitys tertiaria* Menzel emend. Weyland, Kilpper & Berendt, Jähnichen, p. 90, pl. VIII, fig. 5, pl. IX.

PUTATIVE SCIADOPITOID INCLUSIONS FROM BALTIC AMBER

To our knowledge, there are no other inclusions from Baltic amber which show unequivocal affinities to the Sciadopityaceae. The first Sciadopityaceae-like inclusions reported from Baltic amber are needles of *Sciadopitytes* (Goeppert & Menge, 1883) which were questioned by several authors (Schimper & Schenk, 1890; Caspary & Klebs, 1907; Florin, 1922) and have even been supposed to have a dicotyledonous origin (Schimper & Schenk, 1890). The type specimens of *Sciadopitytes* are lost, precluding further reinvestigations. Drawings of these specimens in Goeppert & Menge (1883) show about 3 mm long lanceolate leaves with a pronounced curved petiole and an acute apex (Fig. 3F, G). According to Goeppert & Menge (1883: 36), the assignment to the Sciadopityaceae was based on “two veins” located on the needle underside, while the upper side only possesses ‘one vein’, without defining the real nature of these ‘veins’. Goeppert & Menge (1883: 36) admit that further structural details were not visible. Based on the available information a sciadopitoid origin of these specimens seems unlikely and

due to the long curved petioles and the leaf shape even an angiosperm origin cannot be completely excluded.

Goeppert & Menge (1883) assigned a wood inclusion to *Sciadopitys verticillata* based on the smooth ovate wood ray cells. Since detailed morphological descriptions and accurate images of the inclusions are not given, and since the original specimen is lost, it is impossible to confirm the sciadopitoid identity of this wood inclusion.

Wolfe *et al.* (2009) presented a needle-shaped inclusion from Baltic amber as being morphologically similar to the extant *Sciadopityaceae* cladodes. Our reinvestigation of this inclusion from the Max J. Kobbert Collection (Münster, Germany), coll. no. P134, revealed that none of the distinctive features of a sciadopitoid cladode as described above are present in this particular specimen (Fig. 3A-E). This specimen rather bears similarities to angiosperm leaves, such as the pronounced grooved petiole (Fig. 3C), the non-sunken stomata with bean-shaped guard cells (Fig. 3E) and the polygonal isodiametric epidermal cells which are irregularly arranged (Fig. 3D). Wolfe *et al.* (2009) also mention a putative sciadopitoid wood inclusion from Baltic amber. However, to confirm affinities to *Sciadopitys*, further data from the tangential section of the wood specimen are needed, proving typical sciadopitoid features such as the absence of wood parenchyma, the absent pitting on the transverse and tangential ray cell walls and the fenestriform cross field pits (Peirce, 1935; Dolezych, 2005).

PALAEOECOLOGICAL IMPLICATIONS OF THE SCIADOPITYS INCLUSIONS

The Eocene Baltic amber derives from a mixed conifer-angiosperm forest comprising Pinaceae such as *Pinus* and diverse Cupressaceae sensu lato as well as angiosperm families such as Fagaceae and Lauraceae (Kohlmann-Adamska, 2001; Jähnichen, 1998). However, the precise floristic composition of the ‘Baltic amber forest’ is still under debate, because the botanical inclusions from Baltic amber have not yet been thoroughly revised and reinvestigated since the most comprehensive studies of the 19th and early 20th century by Goeppert & Berendt (1845), Goeppert & Menge (1883), Conwentz (1886, 1890) and Caspary & Klebs (1907). The most recent synopsis by Czezzott (1961) points out that only 216 plant species of the 750 described botanical inclusions from Baltic amber are valid species, demonstrating the incompleteness of our knowledge about the floristic composition of its source forests (Langenheim, 2003). Thus, any determinable plant inclusion from Baltic amber, such as the *Sciadopitys* cladodes presented here, provide important knowledge about the floristic composition and habitat structure of the ‘Baltic amber forest’.

Today, *Sciadopitys verticillata* is endemic to the temperate regions of central Honshu, Shikoku and western Kyushu of Japan, growing on rocky, cool and moist localities at 600 to 1200 m altitudes with a mean annual precipitation between 1300 to 2600 mm/year (Mosbrugger *et al.*, 1994; Farjon, 2005; Eckenwalder, 2009). *S. verticillata* forms pure stands or inhabits mixed conifer-angiosperm forests, composed of different conifer species of *Chamaecyparis*, *Tsuga*, *Abies* and *Pinus* and

intermingled with angiosperm trees such as *Magnolia*, *Aesculus* or *Acer* (Farjon, 2005).

During the Neogene, *Sciadopitys* was a typical element of peat bog environments in central Europe. In several fossil localities from the Miocene to Pliocene of Germany and France, *Sciadopitys tertiaria* inhabited a specific plant community in peat bogs, namely the ‘*Sciadopitys* raised bog’ facies type (Schneider, 2004; Philippe *et al.*, 2002). This ombrogenous raised bog usually terminates a succession of paralic mires if precipitation is high enough to support a conifer-dominated peat swamp. This particular swamp vegetation is dominated by *Sciadopitys tertiaria* resulting in quite specific petrographic types of lignite, i.e. “Graskohle” (grassy lignite) mainly consisting of *Sciadopitys* cladodes, and “Marcoduria” lignite representing horizons with dense *Sciadopitys* roots (Schneider, 1992). Besides *Sciadopitys tertiaria* the conifer-dominated raised bog forest is formed by *Cathaya* (Pinaceae), and accessory elements such as Cupressaceae (cf. *Taxodium*), *Myrica* and cf. Sapotaceae (Dolezych & Schneider, 2007). The importance of the habitat humidity for *Sciadopitys* is also highlighted by Kawase *et al.* (2010) who illustrated the significance of summer monsoon effects for the distribution of extant *Sciadopitys*. The *Sciadopitys* cladodes from Baltic amber thus indicate high precipitation, at least locally high humidity, or even the presence of bogs within the ‘Baltic amber forest’ area.

High humidity in parts of the ‘Baltic amber forest’ area is also suggested by abundant amber inclusions of sooty moulds of the Metacapnodiaceae family (Capnariales, Ascomycota, Schmidt *et al.*, 2014) and diverse further epiphyllous fungi (Kettunen *et al.*, 2015) that also overgrew the base of the completely preserved cladode.

By floristic means the presence of *Sciadopitys* in the ‘Baltic amber forest’ distinguishes it from any hitherto known central European Eocene non-lignite flora (e.g. Messel, Geiseltal, Weißelster Basin in Germany; London Clay flora in UK; Kučlin, Staré Sedlo in Czech Republic) in which thermophilous and subtropical conifer taxa occur (Kvaček, 2010).

The new fossil discovery reported herein is in accordance with late Eocene *Sciadopitys* pollen records from central Germany which are interpreted as evidence for *Sciadopitys* raised bog facies type within late Eocene lignites, comparable to Miocene lignite seams in central Europe (Schneider, 2013).

Sciadopityaceae are an abundant constituent in the European vegetation from the latest Oligocene to the Pliocene. The characteristic morphology of extant *Sciadopitys* cladodes is congruent with both Baltic amber inclusions reported here. The fossils are the first case of unambiguous *Sciadopitys* cladodes from Baltic amber. Thus, our fossils provide macrofossil evidence for the presence of one of the possible source trees of succinite, the main resin type from the Baltic amber deposit, in addition to chemical evidence suggested by Wolfe *et al.* (2009). The occurrence of Sciadopityaceae in Baltic amber furthermore indicates humid source forests, or even raised bogs to swamp habitats, and thus broadens the picture of this Eocene palaeoecosystem.

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REFERENCES

- Bose MN. 1955. *Sciadopitytes variabilis* n. sp. from the Arctic of Canada. *Norsk Geologisk Tidsskrift* 35: 53-67.
- Bose MN, Manum SB. 1990. Mesozoic conifer leaves with ‘*Sciadopitys*-like’ stomatal distribution. A re-evaluation based on fossils from Spitsbergen, Greenland and Baffin Island. *Norsk Polarinstitutt Skrifter* 192: 5-80.
- Bose MN, Manum SB. 1991. Additions to the family Miroviaceae (Coniferae) from the Lower Cretaceous of West Greenland and Germany: *Mirovia groenlandica* n. sp., *Tritaenia crassa* (Seward) comb. nov., and *Tritaenia linkii* Mägdefrau et Rudolph emend. *Polar Research* 9: 9-20.
- Caspary R, Klebs R. 1907. *Die Flora des Bernsteins und anderer fossiler Harze des ostpreußischen Tertiärs*. Berlin: Abhandlungen der Königlich Preußischen Geologischen Landesanstalt, Neue Folge 4.
- Christophel DC. 1973. *Sciadopitophyllum canadense* gen. et sp. nov.: a new conifer from Western Alberta. *American Journal of Botany* 60: 61-66.
- Conwentz H. 1886. *Die Flora des Bernsteins, 2. Band: Die Angiospermen des Bernsteins*. Danzig: Engelmann.
- Conwentz H. 1890. *Monographie der Baltischen Bernsteinbäume: Vergleichende Untersuchungen über die Vegetationsorgane und Blüten, sowie über das Harz und die Krankheiten der Baltischen Bernsteinbäume*. Danzig: Engelmann.
- Czeczott H. 1961. The flora of the Baltic amber and its age. *Prace Muzeum Ziemi* 4: 119-145.
- Dolezych M. 2005. Coniferous wood from the Second Lusatian Seam (Brandenburg, Saxony) and their ecological significance. Ph.D Thesis, University of Utrecht.
- Dolezych M, Schneider W. 2007. Taxonomy and taphonomy of coniferous woods and cuticulae dispersae in the Second Lusatian coal seam (Miocene) of the Senftenberg area. *Palaeontographica Abt. B* 276: 1-95.
- Dörken VM, Stützel T. 2011. Morphology and anatomy of anomalous cladodes in *Sciadopitys verticillata* Siebold & Zucc. (Sciadopityaceae). *Trees* 25: 199-213.
- Eckenwalder JE. 2009. *Conifers of the world. The complete reference*. Portland: Timber Press.
- Farjon A. 2005. *A monograph of Cupressaceae and Sciadopitys*. Kew: Royal Botanic Gardens.
- Florin R. 1922. On the geological history of the Sciadopitineae. A preliminary note. *Svensk Botanisk Tidsskrift* 16: 260-270.

- Florin R. 1931. Untersuchungen zur Stammesgeschichte der Coniferales und Cordaitales, 1. Teil: Morphologie und Epidermisstruktur der Assimilationsorgane bei den rezenten Koniferen. *Kungliga Svenska Vetenskapsakademiens Handlingar* 10: 1-588.
- Goeppert HR, Berendt GC. 1845. *Die im Bernstein befindlichen organischen Reste der Vorwelt, 1. Abteilung: Der Bernstein und die in ihm befindlichen Pflanzenreste der Vorwelt*. Berlin: Nicolaische Buchhandlung.
- Goeppert HR, Menge A. 1883. *Die Flora des Bernsteins und ihre Beziehungen zur Flora der Tertiärformation und der Gegenwart, 1. Band: Von den Bernstein-Coniferen, insbesondere auch in ihren Beziehungen zu den Coniferen der Gegenwart*. Danzig: Engelmann.
- Gomez B. 2002. A new species of *Mirovia* (Coniferales, Miroviaceae) from the Lower Cretaceous of the Iberian Ranges (Spain). *Cretaceous Research* 23: 761-773.
- Gordenko NV. 2007. A new species of the conifer genus *Oswaldheeria* with well-preserved leaf anatomical elements from the Bathonian of the Kursk Region. *Paleontological Journal* 41: 319-326.
- Gothan W. 1936. Nochmals die „Graskohle“: Nadeln der Schirmtanne (*Sciadopitys*). *Zeitschrift für Gewinnung und Verwertung der Braunkohle* 35: 736-738.
- Grimaldi DA. 1996. *Amber window to the past*. New York: Harry N. Abrams.
- Halle TG. 1915. Some xerophytic leaf-structures in Mesozoic plants. *Geologiska Föreningens Förhandlingar* 37: 493-520.
- Jähnichen H. 1969. Revision zu Originalen strukturbietender Blätter aus der Lausitzer und Niederrheinischen Braunkohle. *Geologie* 18: 77-111.
- Jähnichen H. 1998. First record of *Taiwania*, *Cryptomeria* and *Liquidamber* from Bitterfeld and Baltic amber. *Mitteilungen aus dem Museum für Naturkunde in Berlin – Geowissenschaftliche Reihe* 1: 167-177.
- Jurasky KA. 1928. Paläobotanische Braunkohlen-Studien. Ein neuer Fund von *Sciadopitys* (Konif.) in der Braunkohle (*Sciadopityoxylon wettsteini* n. sp.). *Senckenbergiana* 10, 255-264.
- Kawase D, Tsumura Y, Tomaru N, Seo A, Yumoto T. 2010. Genetic structure of an endemic Japanese conifer, *Sciadopitys verticillata* (Sciadopityaceae), by using microsatellite markers. *Journal of Heredity* 101: 292-297.
- Kettunen E, Grabenhorst H, Gröhn C, Dörfelt H, Sadowski E-M, Rikkinen J, Schmidt AR. 2015. The enigmatic hyphomycete *Torula* sensu Caspary revisited. *Review of Palaeobotany and Palynology* 219: 183-193.
- Kohlman-Adamska A. 2001. A graphic reconstruction of an „amber“ forest. In: Kosmowska-Ceranowicz B, ed. *The amber treasure trove: The Tadeusz Giecwicz's Collection at the Museum of the Earth, Polish Academy of Sciences, Warsaw*. Warsaw: Oficyna Wydawnicza Sadyba, 15-18.
- Krutzsch W. 1971. *Atlas der mittel- und jungtertiären dispersen Sporen- und Pollen-sowie der Mikroplanktonformen des nördlichen Mitteleuropas. Lieferung VI: Coniferenpollen (Saccites und „Inaperturates“)*. Jena: Gustav Fischer Verlag.

- Kvaček Z. 2010. Forest flora and vegetation of the European early Palaeogene – a review. *Bulletin of Geosciences* 85: 63-76.
- Langenheim JH, Beck CW. 1965. Infrared spectra as a means of determining botanical sources of amber. *Science* 149: 52-54.
- Langenheim JH. 1969. Amber: a botanical inquiry. *Science* 163: 1157-1169.
- Langenheim JH. 2003. *Plant resins. Chemistry, evolution, ecology, and ethnobotany*. Portland: Timber Press.
- Mai DH. 1999. The Lower Miocene floras of the Spremberger sequence and the second browncoal horizon in the Lusatia region. Part I: Waterferns, conifers, and monocotyledons. *Palaeontographica B* 250: 1-76.
- Mai DH. 2000. The Middle and Upper Miocene floras of the Meuro and Rauno sequences in the Lusatia region. Part I: Waterferns, conifers, and monocotyledons. *Palaeontographica B* 256: 1-68.
- Mai DH. 2004. The Miocene and Pliocene floras from Northeast-Brandenburg and Southwest-Mecklenburg. *Palaeontographica B* 269: 1-130.
- Manum SB. 1962. Studies in the Tertiary flora of Spitsbergen, with notes on Tertiary floras of Ellesmere Island, Greenland and, Iceland. A palynological investigation. *Norsk Polarinstitutt Skrifter* 125: 1-131.
- Manum SB. 1987. Mesozoic *Sciadopitys*-like leaves with observations on four species from the Jurassic of Andøya, northern Norway, and emendation of *Sciadopityoides* Sveshnikova. *Review of Palaeobotany and Palynology* 51: 145-168.
- Manum SB, Van Konijnenburg-Van Cittert JHA, Wilde V. 2000. *Tritaenia* Maegdefrau et Rudolf, Mesozoic ‘*Sciadopitys*-like’ leaves in mass accumulations. *Review of Palaeobotany and Palynology* 109: 255-269.
- Menzel P. 1913. Beitrag zur Flora der Niederrheinischen Braunkohlenformation. *Jahrbuch der Königlich Preußischen Geologischen Landesanstalt zu Berlin* 34: 1-98.
- Mosbrugger V, Gee CT, Belz G, Ashraf AR. 1994. Three-dimensional reconstruction of an in-situ Miocene peat forest from the Lower Rhine Embayment, northwestern Germany – new methods in palaeovegetation analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 110: 295-317.
- Nascimbene P, Silverstein H. 2000. The preparation of fragile Cretaceous ambers for conservation and study of organismal inclusions. In: Grimaldi D, ed. *Studies on Fossils in amber with particular reference to the Cretaceous of New Jersey*. Leiden: Backhuys Publishers, 93-102.
- Nosova NV, Kiritchkova AI. 2008. First records of the genus *Mirovia* Reymanówna (Miroviaceae, Coniferales) from the Lower Jurassic of Western Kazakhstan (Mangyshlak). *Paleontological Journal* 42: 1383-1392.
- Ogura, Y. 1932. On the structure and affinities of some Cretaceous plants from Hokkaido, 2d contribution. *Journal of the Faculty of Science, Imperial University of Tokyo, Section III* 2: 455-483.

- Ohsawa, T. 1994. Anatomy and relationships of petrified seed cones of the Cupressaceae, Taxodiaceae, and Sciadopityaceae. *Journal of Plant Research* 107: 503-512.
- Peirce AS. 1935. Anatomy of the xylem of *Sciadopitys*. *American Journal of Botany* 22: 895-902.
- Philippe M, Méon H, Lambert G, Erdei B, Thevenard F, Gomez B. 2002. A palm-tree and *Sciadopitys* swamp-forest from the Neogene of Bresse (eastern France). *Comptes Rendus Palevol* 1: 221–225.
- Poinar Jr. GO. 1992. *Life in amber*. Stanford: Stanford University Press.
- Saiki, K. 1992. A new sciadopityaceous seed cone from the Upper Cretaceous of Hokkaido, Japan. *American Journal of Botany* 79: 989-995.
- Sawangchote P, Grote PJ, Dilcher DL. 2009. Tertiary leaf fossils of *Mangifera* (Anacardiaceae) from Li Basin, Thailand as examples of the utility of leaf marginal venation characters. *American Journal of Botany* 96: 2048-2061.
- Schimper WPh, Schenk A. 1890. Paläophytologie. In: Zittel KA, ed. *Handbuch der Paläontologie, II. Abteilung*. Leipzig: R. Oldenbourg, 293-346.
- Schmidt AR, Beimforde C, Seyfullah LJ, Wege S-E, Dörfelt H, Girard V, Grabenhorst H, Gube M, Heinrichs J, Nel A, Nel P, Perrichot V, Reitner J, Rikkinen J. 2014. Amber fossils of sooty moulds. *Review of Palaeobotany and Palynology* 200: 53-64.
- Schneider W. 1992. Floral successions in Miocene swamps and bogs in central Europe. *Zeitschrift für Geologische Wissenschaften* 20: 555-570.
- Schneider W. 2004: A leaf-bearing taphocoenosis in the 2nd Miocene seam from Nochten (Lusatia): taxonomy, taphonomy and phyt stratigraphy. *Palaeontographica B* 268: 1-74.
- Schneider W. 2008. Retinit und Bernstein als Komponenten phyto gener Taphocoenosen in Kohlenflözen und kohligen Begleitschichten. *Exkursionsführer und Veröffentlichungen der Deutschen Gesellschaft für Geowissenschaften* 236: 77-87.
- Schneider W. 2013. Zur Paläobotanik des Krantzites – Beiträge und Schlussfolgerungen zur Bernsteingenese. *Exkursionsführer und Veröffentlichungen der Deutschen Gesellschaft für Geowissenschaften* 249: 90-103.
- Standke G. 2008. Bitterfelder Bernstein gleich Baltischer Bernstein? – Eine geologische Raum- Zeit- Betrachtung und genetische Schlussfolgerungen. *Exkursionsführer und Veröffentlichungen der Deutschen Gesellschaft für Geowissenschaften* 236: 11-33.
- Stuchlick L. [ed.], 2002. *Atlas of Pollen and Spores of the Polish Neogene, vol. 2 – Gymnosperms*. Kraków: W. Szafer Institute of Botany.
- Thiergart F. 1949. Die *Sciadopitys*zone und der *Sciadopitys*-Vorstoß in der niederrheinischen Braunkohle. *Braunkohle, Wärme und Energie* 1: 153-156.
- Tsukada, M. 1963. Umbrella pine, *Sciadopitys verticillata*: past and present distribution in Japan. *Science* 142: 1680-1681.

- Walther H, Kvaček Z. 2007. Early Oligocene Flora of Seifhennersdorf (Saxony). *Acta Musei Nationalis Pragae, Series B, Historia Naturalis* 63: 85-174.
- Weitschat W, Wichard W. 2010. Baltic Amber. In: Penney D, ed. *Biodiversity of fossils in Amber from the major world deposits*. Manchester: Siri Scientific Press, 80-115.
- Weyland H, Kilpper K, Berendt W. 1967. Kritische Untersuchungen zur Kutikularanalyse tertiärer Blätter VII. Nachträge zu früheren Arbeiten über Epidermen aus der niederrheinischen Braunkohle und neue Arten. *Palaeontographica B* 120: 151-168.
- Wolfe AP, Tappert R, Muehlenbachs K, Boudreau M, McKellar RC, Basinger JF, Garrett A. 2009. A new proposal concerning the botanical origin of Baltic amber. *Proceedings of the Royal Society, B, Biological Sciences* 276: 3403-3412.

Appendix 4

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Graminids from Eocene Baltic amber

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ABSTRACT

We report the first bona fide graminid spikelet inclusions found in Eocene Baltic amber. The most informative anatomically preserved specimen is assigned to the genus *Rhynchospora* Vahl (Cyperaceae), whereas two others show affinities with sedges (Cyperaceae) or grasses (Poaceae). Examination of historic descriptions of putative graminid inclusions from Baltic amber suggest that one is of coniferous origin, while the affinities of other fragmentary specimens remain uncertain as they have been lost. The graminid inclusions described here challenge previous notions of the Baltic amber source area being a dark, close canopy forest and rather indicate at least some open and light habitats with swampy and wet areas within the ‘Baltic amber forest’, and thus enlighten its hitherto obscure palaeoenvironment and floristic composition.

Keywords: Cyperaceae; Palaeoecology; Poaceae; Rhynchosporae; *Zeites succineus*

1. Introduction

The commelinid monocot order Poales includes 17 families, of which three – Poaceae (grasses), Cyperaceae (sedges) and Juncaceae (rushes) – are here informally termed graminids because they share strong morphological similarities, notably a highly condensed inflorescence morphology. Graminids are of great ecological significance; they are globally distributed and represent common constituents of diverse habitats, including grasslands, heathlands and swamps. Grasses are also of considerable economic importance since they provide the basis for human agriculture (Watson, 1990; Bouchenak-Khelladi et al., 2014). Despite a relatively strong fossil record, there remain difficulties in interpreting graminid fossils (Crepet and Feldmann, 1991; Bouchenak-Khelladi et al., 2014). The earliest microfossil remains of Poales are pollen and phytoliths from the Maastrichtian of the late Cretaceous (Jacobs et al., 1999; Prasad et al., 2005). Macrofossils of grass spikelets first appear at the Paleocene–Eocene boundary (Thomasson, 1987; Crepet and Feldmann, 1991), whereas sedge fruits and endocarps are recorded from the Middle Paleocene onward in Eurasia (e.g. Chandler, 1963; Mai, 1987, 1997, 2000).

In amber, the only grass spikelets were reported from Miocene amber of the Dominican Republic (*Pharus* sp., Bambusoideae; Poinar and Columbus, 1992; *Alarista succina*, Bambusoideae; Poinar and Columbus, 2013) and a possible grass floret from mid-Cretaceous amber of Myanmar (Poinar et al., 2015). However, no graminid spikelet fossils have yet been recorded from Baltic amber. Here, we report new graminid inclusions from Baltic amber, comprising three inflorescences with poaceous and cyperaceous affinities. These specimens not only represent the first graminid inflorescences from Baltic amber, but also are important habitat indicators, giving new insights into the structure and composition of the ‘Baltic amber forest’.

2. Material and methods

The amber specimens derive from the “Blue Earth” layer of the Jantarny mine near Kaliningrad, Russia. The majority of the amber-bearing “Blue Earth” layers in this area is Priabonian in age, with some extending into Lutetian sediments; thus, an age range of 35 to 47 million years is estimated for Baltic amber (Standke, 2008). The Baltic amber plant inclusions were re-investigated from several major collections as part of a larger project to understand the Baltic amber flora; here we report the specimens that show graminid affinities. Amber specimen no. F939/BB/GR/CJW is part of the Jörg Wunderlich Amber Collection (Hirschberg an der Bergstraße, Germany); it will ultimately be deposited in the amber collection of the Senckenberg Forschungsinstitut und Naturmuseum (Frankfurt am Main, Germany). Specimen GPIH no. 4581 (= Carsten Gröhn Amber Collection no. 6533) is housed in the Geological-Palaeontological Institute and Museum of the University of Hamburg (GPIH) as part of the Carsten Gröhn Amber Collection. Amber specimen no. GZG.BST.27312, originally provided by Christel and Hans Werner Hoffeins

(Hamburg, Germany), is housed in the Geoscientific Collections of the University of Göttingen.

All specimens were ground and polished manually with wet silicon carbide papers (grit from FEPA P 600-4000, 25.8 -5 µm particle size, firm Struers) and examined under dissecting (Carl Zeiss Stereo Discovery V8) and compound (Carl Zeiss AxioScope A1) microscopes, using incident and transmitted light simultaneously in most instances. The images of Plates I to III, taken with a Canon 60D camera, are digitally stacked photomicrographic composites of up to 70 individual focal planes obtained using the software package HeliconFocus 5.0 to allow better illustration of the three-dimensional inclusions. The overview images of Plate II, 1 and 2 and Plate III, 3 were obtained by merging two photomicrographic composites, using Adobe Photoshop CS6 (Adobe Systems Inc., San Jose, California). For permanent preparation, the Gröhn specimen and the Hoffeins specimen were embedded in a high-grade epoxy resin (Buehler Epoxicure) under vacuum, following the protocols of Nascimbene and Silverstein (2000). After curing, the resultant epoxy plugs surrounding each sample were polished to create clear flat viewing surfaces to the amber and its inclusions. Epoxy treatment also resulted in considerable clearing of the amber specimen GPIH no. 4581, filling numerous fissures in the amber and thereby decreasing internal light scattering (see Plate III).

3. Results and Discussion

3.1. Systematic palaeontology

3.1.1. Specimens with cyperaceous affinities

Family Cyperaceae Juss.

Tribe Rhynchosporeae Nees

Genus *Rhynchospora* Vahl

Jörg Wunderlich Amber Collection, no. F939/BB/GR/CJW (Plate I).

Description: Vegetative organs – unknown. Inflorescence – in total approximately 1 cm long, composed of three pedicellate spikelets (S1 to S3) which arise from a single stem (3.0 mm × 0.24 mm) (Plate I, 1); Spikelets – lanceolate in shape, acute apices and laterally compressed, 5.0 to 5.44 mm × 0.84 to 0.96 mm, composed of six to eight alternate arranged bracts per spikelet (Plate I, 1). The apex of the first spikelet (S1) has broken off, the second spikelet (S2) is closed and the third spikelet (S3) exhibits two apical bracts that have opened at the spikelet tip (Plate I, 1). Bracts – Inflorescence subtended by single rectangular bract (0.92 mm × 0.36 mm), base ovate (Plate I, 2), trichomes acute, unicellular (6 to 66 µm × 12 to 18 µm), margin with small recurved hooks (42 to 45 µm × 15 to 24 µm) (Plate I, 3). Bracts of the spikelets ovate to lanceolate in outline, with entire margins. Lower bracts are 0.35 to 0.4 mm long, apical bracts increase in length (1.0 to 2.0 mm) terminating in an awn

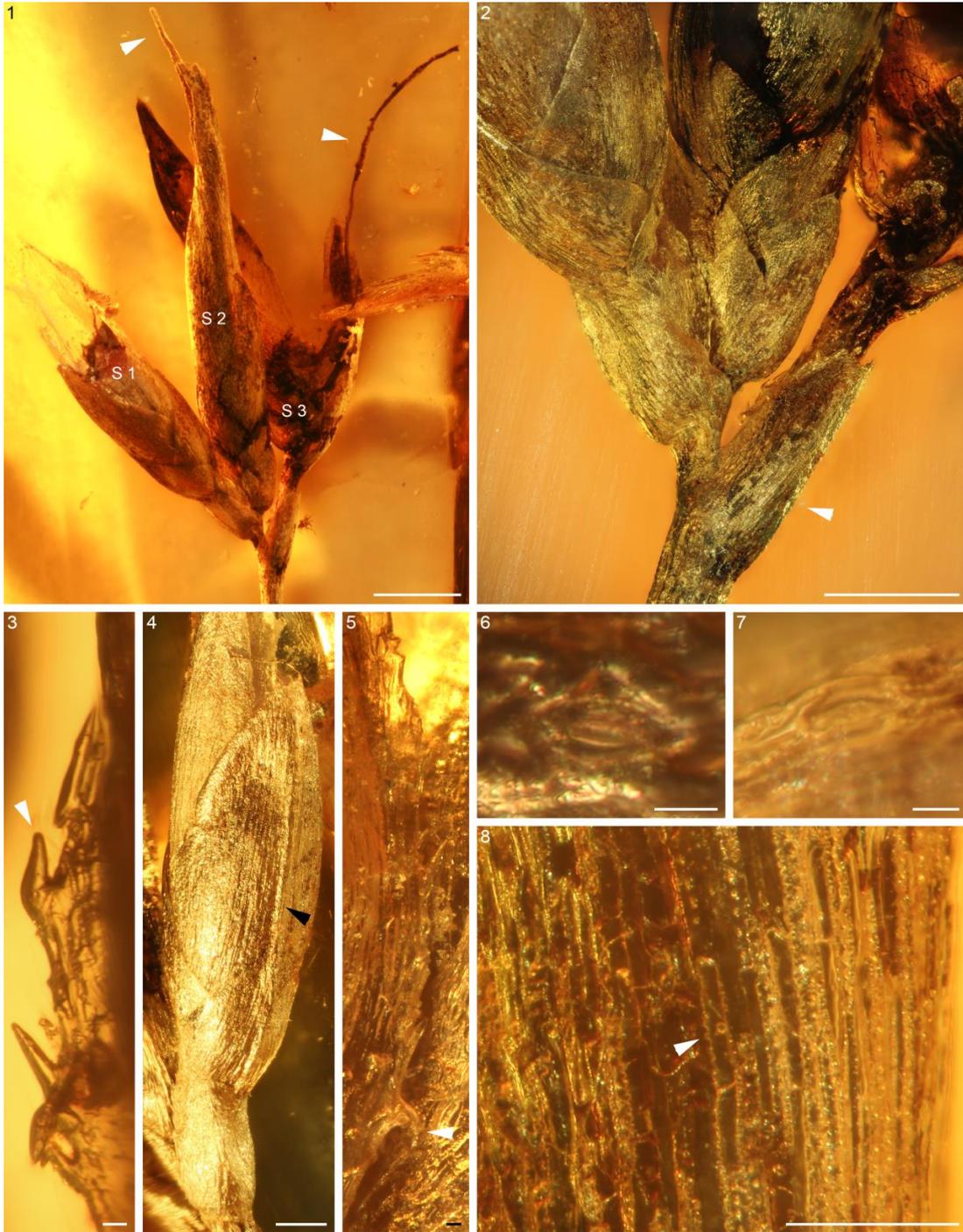


Plate I. *Rhynchospora* (Cyperaceae) spikelet from Baltic amber (Jörg Wunderlich Amber Collection F939/BB/GR/CJW). 1. Three pedicellate spikelets (S1 to S3). S2 and S3 terminate in an awn (arrowheads). Scale bar = 1 mm. 2. Base of the inflorescence subtended by a bract (arrowhead). Scale bar = 500 μm . 3. Margin of the subtending bract with hooks (arrowhead) and trichomes. Scale bar = 10 μm . 4. Lower bract with glabrous keel (arrowhead). Scale bar = 250 μm . 5. Serrated keel with a recurved hook (arrowhead) of the lower bract (S1). Scale bar = 10 μm . 6. and 7. Paracytic stomata from the stem of the inflorescence. Scale bars = 10 μm . 8. Bract epidermis with elongated cells possessing undulated cell walls (arrowhead). Scale bar = 100 μm .



Plate II. Immature cyperaceous spikelet from Baltic amber (GZG.BST.27312). 1. Three spikelets (S1 to S3), sheathed by a subtending bract (Sb). The arrowheads indicate the emarginate leaf tip of S1 and the hairy bract keel of S2. Scale bar = 1 mm. 2. Inflorescence seen from another angle showing S2, S3, and the ovate subtending bract (Sb). Scale bar = 1 mm. 3. and 4. Serrated and hairy bract keels. Scale bars = 100 μ m. 5. Serrated bract margin. Scale bar = 50 μ m. 6. Stem epidermis with short rectangular cells. Scale bar = 100 μ m. 7. Bract epidermis with elongated cells and undulate cell walls (arrowhead). Scale bar = 100 μ m. 8. Paracytic stoma of the stem with tall-dome shaped subsidiary cells. Scale bar = 30 μ m. 9. and 10. Paracytic stomata of the bracts with low-dome shaped subsidiary cells. Scale bars = 30 μ m.

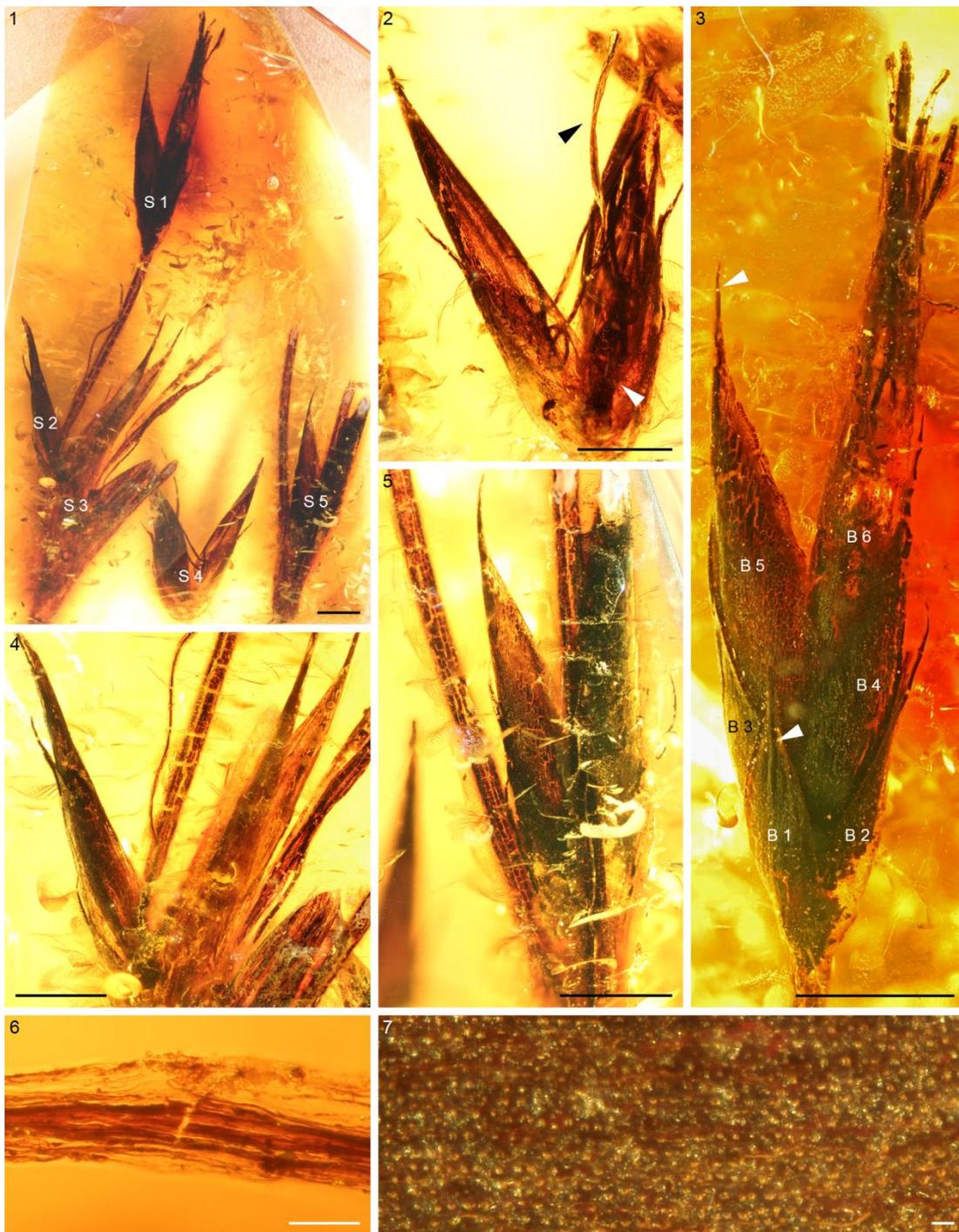


Plate III. Graminid spikelets from Baltic amber (GPIH 4581). 1. Overview of the five preserved spikelets (S1 to S5). Scale bar = 1 mm. 2. Spikelet exhibiting long filaments and the ovary (arrowheads). Scale bar = 1 mm. 3. Spikelet displaying all six bracts (B1 to B6), which end in a short awn (upper arrowhead). B1 is acentric and possesses a prominent midcosta (lower arrowhead). Scale bar = 1 mm. 4. and 5. Slightly opened spikelets. Scale bars = 1 mm. 6. Filament with a single vascular bundle. Scale bar = 50 μ m. 7. Epidermis of the bracts. Scale bar = 10 μ m.

(0.8 to 3.0 mm \times 0.05 to 0.08 mm). Keels of the more apical bracts glabrous and prominent (Plate I, 4), but one lower bract of S1 with irregularly dentate keel,

trichomes acute, simple, unicellular (18 to 45 $\mu\text{m} \times 6 \mu\text{m}$) and with hooks (39 $\mu\text{m} \times 15 \mu\text{m}$) (Plate I, 5). *Epidermis* – long rectangular cells (44 to 110 $\mu\text{m} \times 8$ to 12 μm) with sinuous cell walls (Plate I, 8). *Stomata* – present only on the stem and poorly preserved; elliptical, 21 to 24 $\mu\text{m} \times 12$ to 15 μm , with low-dome shaped paracytic subsidiary cells (Plate I, 6 to 7).

Discussion: The specimen is most likely a member of the sedge family, Cyperaceae. Two primary characters that clearly distinguish this spikelet fossil from the grass family, Poaceae, are (1) the presence of an involucre bract subtending the inflorescence (Poaceae inflorescences generally lack subtending bracts and leaves, though some bamboos have spathe-like structures located immediately below each inflorescence: Clayton, 1990; Malcomber et al., 2006), and (2) the absence of short-long cell alternations and silica bodies in the bract epidermis, which are invariably present in grass leaves (Rudall et al., 2014). Within Cyperaceae, the amber inclusion exhibits characters that are typical of extant *Rhynchospora* (Rhynchosporae): (i) an involucre bract subtending the inflorescence, (ii) lanceolate compressed spikelets composed of several spirally arranged bracts, (iii) increasing bract length from the spikelet base to the apex, and (iv) a slender keel on the bracts terminating in an awn (Strong, 2006). A new species is not erected here because the vegetative organs are unknown and although this sole specimen has clear affinities to *Rhynchospora*, details of the reproductive organs, especially the ovary, are not preserved.

Family Cyperaceae Juss.

Amber collection of the Geoscientific Collections of the Georg August University Göttingen, no. GZG.BST.27312 (Plate II).

Description: *Vegetative organs* – unknown. *Inflorescence* – composed of three closed spikelets (S1 to S3) that arise from a single stem (0.88 mm \times 0.84 mm) (Plate II, 1 and 2); *Spikelets* – elliptical in shape, obtuse apex and laterally compressed, 2.88 to 4.4 mm \times 1.36 to 2.88 mm, S1 is pedicellate whereas the others are basally sheathed by a subtending bract (Sb in Plate II); *Bracts* – subtending bract (2.84 mm \times 1.12 mm) ovate, dorsally rounded, with an obtuse tip, margins serrated (Plate II, 2), otherwise there are several bracts per spikelet (total number and arrangement not determinable, as the spikelets are closed), ovate to lanceolate in outline, obtuse to emarginated tip, midcosta and margins serrated, with teeth of different sizes (12 to 60 $\mu\text{m} \times 6$ to 24 μm , averaging 27.6 $\mu\text{m} \times 27.3 \mu\text{m}$) and with simple, unicellular, acute trichomes (24 to 126 $\mu\text{m} \times 12$ to 24 μm at the base, averaging 85.6 $\mu\text{m} \times 18 \mu\text{m}$) (Plate II, 3 to 5). *Epidermis* – long rectangular cells on the bracts (average 64 $\mu\text{m} \times 13 \mu\text{m}$) (Plate II, 7), shorter, wider rectangular cells on the stem (average 51 $\mu\text{m} \times 29 \mu\text{m}$) (Plate II, 6), epidermal cell walls moderately to deeply undulate with perpendicular to angled end walls (Plate II, 7). *Stomata* – 24 to 36 $\mu\text{m} \times 12$ to 30 μm , with paracytic subsidiary cells, which are tall dome-shaped on the stem (Plate II, 8) and low dome-shaped on the bracts (Plate II, 9 and 10).

Discussion: The spikelets of this specimen represent an immature inflorescence that is probably of sedge affinity. Features supporting an assignment to Cyperaceae are (i) the lateral compressed spikelets branching from the axil of a subtending bract, and (ii) stomata with pronounced subsidiary cells parallel to the aperture cells (Metcalf, 1971; Goetghebeur, 1998; Gaglioti et al., 2010). However, its immaturity precludes credible identification to genus level and thus we abstain from assigning the fossil to a new species.

3.1.2. Specimen with uncertain familial affinities

Family Cyperaceae Juss. *or* Poaceae Barnhart

Geological-Palaeontological Institute and Museum of the University of Hamburg, GPIH no. 4581 (= Carsten Gröhn Amber Collection, no. P 6533) (Plate III).

Description: *Vegetative organs* – unknown. *Inflorescence* – three spikelets (S1 – S3) are attached to the main stem and a further two are separate, probably broken off the same inflorescence (S4 and S5) (Plate III, 1); *Spikelets* – lanceolate in shape, acute apex, laterally compressed, 4.72 to 6.28 mm × 1.2 to 1.24 mm; six bracts per spikelet (B1 to B6, Plate III, 3). *Bracts* – distichously arranged, margins are entire, bract tips end in an acute short awn (Plate III, 3). Lower bracts ovate to elliptical in outline, apical bracts lanceolate. Lowermost bracts are the shortest (1.8 to 2.7 mm length); toward the apex, bract length increases from 2.8 to 3.7 mm length of the middle bracts to 4.6 to 6.3 mm length of the uppermost bracts. Lowermost bract (B1) of S1 possesses a prominent glabrous midcosta, terminating in an awn. The position of this lowermost bract is acentric compared with the other distichously arranged bracts, meaning that its distal part is not aligned with the subsequent bracts B2 to B6 (Plate III, 3). This location matches that of the other small lowermost bract of S4. *Androecium* – numerous stamens are exposed, 4.4 mm × 0.06 mm, anthers absent, filaments with single vascular strand (Plate III, 2 and 6); *Gynoecium* – S4 with elliptical ovary, 1.4 mm × 0.32 mm (Plate III, 2). *Epidermis* – glabrous, cells arranged in long linear rows (Plate III, 7). No further cell details or stomata are preserved.

Discussion: The conspicuous acentric position of the lowest bract B1 (Plate III, 3) could indicate B1 as a subtending bract, an arrangement that is typical of Cyperaceae. Furthermore, the spikelets lack a two-keeled palea, thus indicating a Cyperaceae affinity because Poaceae spikelets typically exhibit two-keeled paleas, though in some Poaceae the palea is minute or reduced (e.g. Dahlgren et al., 1985; Clayton, 1990; Kellogg, 2001). Assuming a Poaceae affinity for the fossil, the lowest acentric bract B1 must be interpreted as a glume that by definition subtends the florets. The arrangement of the spikelets inclines to a panicle, an architecture that is

abundant in Poaceae (Dahlgren et al., 1985), but also occurs in some Cyperaceae, such as the tribe Rhynchosporeae (Strong, 2006).

In conclusion, several characteristics of the spikelet inclusions indicate affinity with Cyperaceae, with similarities to the tribe Rhynchosporeae, though an affinity with Poaceae cannot be wholly rejected. Given the uncertain familial affinity and the minimal data available on both the androecium and the gynoecium of this specimen, we refrain from erecting a new species here.

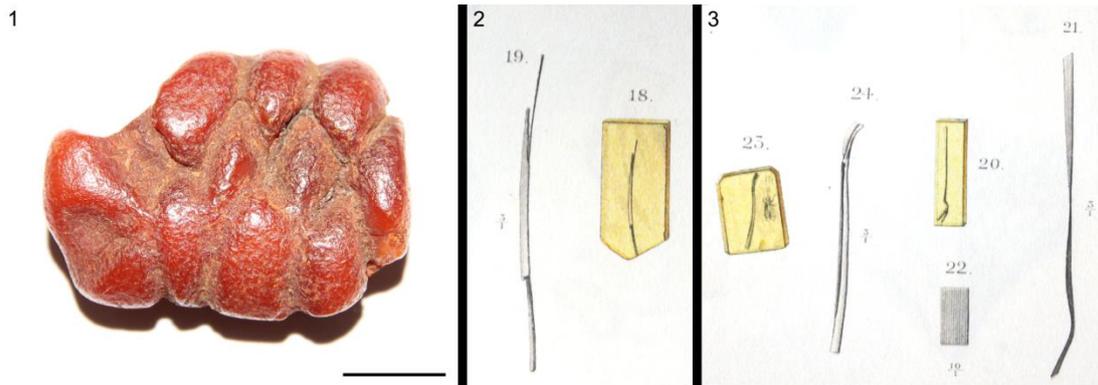


Plate IV. Putative graminid fossils from Baltic amber. 1. *Zeites succineus* Casp. from the Künow Amber Collection (MB.Pb.1979/604), likely representing an amber cast of a coniferous cone. Scale bar = 1 cm. 2 and 3. Historic drawings of *Graminophyllum succineum* Conw. (current whereabouts unknown) from Conwentz, 1886, Taf. I, Figs. 18–24.

3.2. Evaluation of putative graminid inclusions from Baltic amber

So far, no inclusions of graminid spikelets have been reported from Eocene Baltic amber. However, a few specimens of supposed graminid affinities were already described by Conwentz (1886) in the hitherto most comprehensive work about Baltic amber angiosperm inclusions.

The putative graminid inclusion *Zeites succineus* Casp. from the Künow Amber Collection was mentioned only briefly by Caspary (1872) and Conwentz (1886) as “some kind of corn crop with four rows of grains, preserved as amber cast” (Caspary, 1872, p. 17), without providing any illustrations or detailed descriptions. Kirchheimer (1937) stated that the specimen lacked sufficient detail to confirm affinities with either graminids or even plants in general, and suggested that it could instead represent a prehistoric artefact.

We located the original specimen of *Zeites succineus* in the Künow Amber Collection, housed in the Museum für Naturkunde Berlin (coll. no. MB.Pb.1979/604, Künow coll. no. 4; Plate IV, 1). The specimen is about 2.8 cm long x 2.1 cm wide and consists of 11 rhombic decussate segments, but typical graminid features as discussed above are absent. Given its size and general appearance, the specimen rather seems to be a peculiar preservation of a resinous female conifer cone. Sectioning this specimen was not possible. We hypothesize that the central cavities

between decomposed ovuliferous scales were filled with resin that later became amber. The rhombic-shaped segments would then represent casts of the ovuliferous scales, though the axial placements are not as regular as in extant conifers. Indeed, Schuster (1931) had already suggested that this putative graminid fossil actually represents a gymnosperm cone.

Further supposedly poaceous amber fossils were introduced by Conwentz (1886), who erected the species *Graminophyllum succineum* Conw. for three leaf fragments that are 5–19 mm long x 0.5–1 mm wide, with parallel rows of cells, a glabrous surface and entire margins (Plate IV, 2 and 3). However, the description and illustrations of the specimens provide insufficient information about detailed morphology, such as stomata shape or features of their subsidiary cells, to confirm this affinity. Moreover, as parallel cell rows and a glabrous surface are also present in some conifer needles of Pinaceae (Martin and Juniper, 1970), a gymnosperm origin cannot be excluded. We were unable to ascertain the current location of these specimens, so no further investigations were possible.

The sole sedge-like specimen, named *Acoropsis eximia* (Goeppert & Menge) Bogner was initially interpreted as an infructescence of a *Carex* representative by Goeppert and Menge (1853), but was later convincingly identified as the remains of an Araceae infructescence by Bogner (1976).

In addition to these macrofossils, ten pollen grains extracted from Baltic amber were placed in Poaceae (Willemstein, 1980), but no detailed description or illustrations are available, precluding re-investigation or confirmation of their affinity.

3.3. Palaeohabitats of the source area of the Baltic amber

The graminid amber inclusions described here represent part of the late Eocene ‘Baltic amber forest’ whose floristic composition and structure has been contentiously debated since the 19th century. Wichard et al. (2009) and Weitschat and Wichard (2010) subdivided this region into subtropical to tropical lowland rainforests and temperate montane forests, based on the high numbers of assumed tropical arthropod and plant species. Other interpretations led to the assumption of a dense and moist subtropical to warm-temperate forest (Ander, 1942; Kohlmann-Adamska, 2001), or comparison with mixed hardwood forests (termed “hammocks”) that today are typical of the Florida peninsula, composed of scattered patches of evergreen oaks and palms (Schubert, 1953; Vince et al., 1989). In any case, the source area of the Baltic amber likely contained several habitat types, as succession occurs in all forests, and small more open areas can even result from falling trees, allowing the graminids to grow. Therefore, we assume heterogeneity within the forest area at any given time, but overall species composition probably remained similar.

Our newly discovered graminid fossils from Baltic amber give fresh insight into the palaeoenvironment of the concept that is known as the ‘Baltic amber forest’. Extant graminids have a cosmopolitan distribution, dominating savannas, grasslands

and meadows, but are also present in woods and open forests. Some early-divergent grass lineages are relatively common in deeply shaded forest understorey (Linder and Rudall, 2005), but in general Poaceae prefer dry and sunny habitats, as in savannas and steppes. In contrast, Cyperaceae are most diverse in wet habitats containing many hygrophilous taxa (Ueno and Koyama, 1987; Bruhl, 1995; Bouchenak-Khelladi et al., 2014). Extant *Rhynchospora* species (Rhynchosporaceae, Cyperaceae) inhabit wet to dry savanna grasslands, peaty meadows, swamp forests and marshlands of both the lowlands and of mountainous regions (Kükenthal, 1949; Ueno and Koyama, 1987).

Hence, the cyperaceous inclusions hint at the presence of open, wet habitats within the ‘Baltic amber forest’ area, perhaps close to ponds, rivers and/or lakes. This assumption fits well with the evolutionary and ecological history of Cyperaceae, which are thought to have adapted to wetland habitats from the early Eocene to the late Oligocene (Linder and Rudall, 2005; Bouchenak-Khelladi et al., 2014), encompassing the same time frame as the origin of Baltic amber (35 – 47 Ma) (Standke, 2008).

The occurrence of wetland graminids in the ‘Baltic amber forest’ area is also congruent with the findings of Sadowski et al. (2016), who described the first confirmed Baltic amber inclusions of the umbrella pine *Sciadopitys*, a genus that serves as an indicator for swampy and humid habitats in the Paleogene and Miocene of central Europe. In addition, open habitats are indicated by the occurrence of Baltic amber inclusions of carnivorous plants belonging to the family Roridulaceae (Sadowski et al., 2015).

Many Baltic amber inclusions of insects with obligate aquatic larval stages further indicate a close proximity of resinous trees to aquatic habitats; these include Odonata (dragonflies), Ephemeroptera (mayflies) and Scirtidae (Coleoptera) and those of *Heleodromia* (aquatic dance flies, Diptera), Chironomidae (Diptera) as well as aquatic crustaceans (Wagner et al., 2000; Schmidt and Dilcher, 2007; Seredszus and Wichard, 2007; Heuss, 2008; Wichard et al., 2009).

Roháček (2012) examined Baltic amber inclusions of the Anthomyzidae (Diptera), which he proposed as indicators for humid and open graminid wetlands adjacent to the ‘Baltic amber forest’, acknowledging the habitat preferences of extant Anthomyzidae. Inclusions of the Pipunculidae (big-headed flies, Diptera) (Kehlmaier et al., 2014) also hint at open habitats, given that extant Pipunculidae predominantly appear in forest openings and wet environments where they are endoparasitoids on Auchenorrhyncha (Hemiptera) and Tipulidae (Diptera) (Koenig and Young, 2007; Rafael and Skevington, 2010; Kehlmeier et al., 2014).

Further arthropod inclusions potentially indicating the presence of open grass habitats in the ‘Baltic amber forest’ are the predatory flies Leptogastrinae (Asilidae, Diptera), which today are abundant in grasslands (Dikow, pers. comm., 2015 and Dikow, 2014) and shoot flies (Chloropidae, Diptera) whose extant relatives inhabit meadows where the immature stages mostly feed on and develop within Poaceae. Moreover, some Chloropidae are also gall inducers in sedges and grasses (Hennig, 1965; De Bruyn, 2005). Thus both the graminid, along with some other plant

inclusions and some faunal inclusions suggest some open, wet habitats within the ‘Baltic amber forest’.

4. Conclusions

The first unambiguous graminid spikelet inclusions found in Baltic amber show affinities with grasses or sedges; the best preserved of these fossils can be assigned to the extant genus *Rhynchospora* (Cyperaceae). Re-examination of *Zeites succineus*, an historic putative graminid fossil from Baltic amber, suggests a likely coniferous origin, whereas other previously reported graminid Baltic amber inclusions remain doubtful and were lost. Given our limited knowledge about the floral composition of the ‘Baltic amber forest’, these new graminid inclusions are welcome fossil indicator taxa, indicating the presence within the forest of open, wet habitats, such as swamps or peaty meadows. Together with other recent discoveries of arthropods and plants of humid and open wetlands, the graminid fossils challenge the traditional view of the ‘Baltic amber forest’ as a dense, dark and homogeneous place.

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References

- Ander, K., 1942. Die Insektenfauna des Baltischen Bernsteins nebst damit verknüpften zoogeographischen Problemen. Lunds Universitets Årsskrift 38(4),1–83.
- Bogner, J., 1976. Die systematische Stellung von *Acoropsis* Conwentz, einer fossilen Aracee aus dem Bernstein. Mitt. Bayer. Staatssamml. Paläont. hist. Geol. 16, 95–98 in German with English Abstr.
- Bouchenak-Khelladi, Y., Muasya, A.M., Linder, H.P., 2014. A revised evolutionary history of Poales: origins and diversification. Bot. J. Linn. Soc. 175, 4–16.
- Bruhl, J.J., 1995. Sedge genera of the world: relationships and a new classification of the Cyperaceae. Aust. Syst. Bot. 8, 125–305.

- Caspary, R., 1872. Pflanzliche Reste aus der Bernsteinbildung. Privatsitzung am 4. October. Schriften der Königlichen Physikalisch-Ökonomischen Gesellschaft zu Königsberg 13, 17–18.
- Chandler, M.E.J., 1963. The Lower Tertiary floras of southern England III. Flora of the Bournemouth Beds; the Boscombe, and the Highcliff Sands. British Museum (Natural History), London, UK.
- Clayton, W.D., 1990. The spikelet. In: Chapman, G.P. (Ed.), Reproductive versatility in the grasses. Cambridge Univ. Press, New York, pp. 32–51.
- Conwentz, H.W., 1886. Die Flora des Bernsteins. Vol. 2. Die Angiospermen des Bernsteins. Wilhelm Engelmann, Danzig.
- Crepet, W.L., Feldmann, G.D., 1991. The earliest remains of grasses in the fossil record. *Am. J. Bot.* 78(7), 1010–1014.
- Dahlgren, R.M.T., Clifford, H.T., Yeo, P.F., 1985. The families of the monocotyledons. Structure, evolution, and taxonomy. Springer, Berlin.
- De Bruyn, L. de, 2005. The biology, ecology, and evolution of shoot flies (Diptera: Chloropidae). In: Raman, A., Schaefer, C.W., Withers, T.M. (Eds.), Biology, ecology and evolution of gall-inducing Arthropods. Vol. 1. Science Publishers, Enfield, NH, pp. 373–405.
- Dikow, T., 2014. Review and phylogenetic placement of Asilidae (Diptera) in Tertiary: Ecoene ambers. figshare. <https://dx.doi.org/10.6084/m9.figshare.1243382.v1>. Retrieved Jun 08, 2015.
- Gaglioti, B.V., Severin, K., Wooller, M.J., 2010. Developing graminoid cuticle analysis for application to Beringian palaeoecology. *Rev. Palaeobot. Palynol.* 162, 95–110.
- Goeppert, H.R., Menge, A., 1853. Über die Bernsteinflora. Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Königlich Preussischen Akademie der Wissenschaften zu Berlin, 450-477.
- Goetghebeur, P., 1998. Cyperaceae. In: Kubitzki, K. (Ed.), The families and genera of vascular plants, Vol. IV Flowering plants - Monocotyledons Alismatanae and Commelinanae (except Gramineae), Springer, Berlin, Heidelberg, pp. 141–190.
- Jacobs, B.F., Kingston, J.D., Jacobs, L.L., 1999. The origin of grass-dominated ecosystem. *Ann. Mo. Bot. Gard.* 86(2), 590–643.
- Hennig, W., 1965. Die Acalyptratae des Baltischen Bernsteins und ihre Bedeutung für die Erforschung der phylogenetischen Entwicklung dieser Dipteren-Gruppe. *Stutt. Beitr. Naturkd.* 145, 1-213.
- Heuss, K., 2008. Zur Taxonomie und Ökologie der Schlammkäfer des Baltischen Bernsteins mit einem Gattungsschlüssel und der Beschreibung einer neuen Art (Coleoptera: Scirtidae). *Entomologische Zeitschrift* 118(3), 131–134.
- Kehlmeier, C., Dierick, M., Skevington, J.H., 2014. Micro-CT studies of amber inclusions reveal internal genitalic features of big-headed flies, enabling a systematic placement of *Metanephrocerus* Aczél, 1948 (Insecta: Diptera: Pipunculidae). *Arthropod Systematics & Phylogeny* 72(1), 23–36.

- Kellogg, E.A., 2001. Evolutionary history of the grasses. *Plant Physiol.* 125, 1198–1205.
- Kirchheimer, F., 1937. Beiträge zur Kenntnis der Flora des baltischen Bernsteins I. Beihefte zum Botanischen Centralblatt Abt. B 57, 441–482.
- Koenig, D.P., Young, C.W., 2007. First observation of parasitic relations between big-headed flies, *Nephrocerus* Zetterstedt (Diptera: Pipunculidae) and crane flies, *Tipula* Linnaeus (Diptera: Tipulidae: Tipulinae), with larval and puparial descriptions for the genus *Nephrocerus*. *Proc. Entomol. Soc. Wash.* 109(1), 52–65.
- Kohlman-Adamska, A. (Ed.), 2001. A graphic reconstruction of an ‘amber’ forest. In: The amber treasure trove: Part I. The Tadeusz Giecwicz’s Collection at the Museum of the Earth. Polish Academy of Sciences, Warsaw, Poland, pp. 15–18.
- Kükenthal, G., 1949. Vorarbeiten zu einer Monographie der Rhynchosporideae. *Bot. Jahrb. Syst.* 74(3), 375–509.
- Linder, H.P., Rudall, P.J., 2005. Evolutionary history of Poales. *Annu. Rev. Ecol. Evol. Syst.* 36, 107–124.
- Mai, D.H., 1987. Neue Früchte und Samen aus paläozänen Ablagerungen Mitteleuropas. *Feddes Repertorium* 98(3-4), 197–229 in German with English Abstr.
- Mai, D.H., 1997. Die oberoligozänen Floren am Nordrand der Sächsischen Lausitz. *Palaeontographica B* 244, 1–124 in German with English Abstr.
- Mai, D.H., 2000. Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil I. Farnpflanzen, Koniferen und Monokotyledonen. *Palaeontographica B* 256, 1–68 in German with English Abstr.
- Malcomber, S.T., Preston, J.C., Reinheimer, R., Kossuth, J., Kellogg, E.A., 2006. Developmental gene evolution and the origin of grass inflorescence diversity. *Adv. Bot. Res.* 44, 425–481.
- Martin, J.T., Juniper, B.E., 1970. *The cuticles of plants*. Edward Arnold Publishers, London.
- Metcalf, C.R., 1971. *Anatomy of the monocotyledons, V. Cyperaceae*. Clarendon Press, Oxford.
- Nascimbene, P.C., Silverstein, H., 2000. The preparation of fragile Cretaceous ambers for conservation and study of organismal inclusions. In: Grimaldi, D. (Ed.), *Studies on Fossils in amber, with particular reference to the Cretaceous of New Jersey*. Backhuys Publishers, Leiden, pp. 93–102.
- Poinar, G.O. Jr., Columbus, J.T., 1992. Adhesive grass spikelet with mammalian hair in Dominican amber: First fossil evidence of epizoochory. *Experientia* 48, 906–908.
- Poinar, G. Jr., Columbus, J.T., 2013. *Alarista succina* gen. et sp. nov. (Poaceae: Bambusoideae) in Dominican amber. *Historical Biology* 25, 691–696.
- Poinar, G. Jr., Alderman, S., Wunderlich, J., 2015. One hundred million year old ergot: psychotropic compounds in the Cretaceous? *Palaeodiversity* 8, 13–19.

- Prasad, V., Strömberg, C.A.E., Alimohammadian, H., Sahni, A., 2005. Dinosaur coprolites and the early evolution of grasses and grazers. *Science* 310, 1177–1180.
- Rafael, J.A., Skevington, J.H., 2010. Pipunculidae (big-headed flies). In: Brown, B.V., Borkent, A., Cumming, J.M., Wood, D.M., Woodley, N.E., Zumbado, M.A. (Eds.), *Manual of Central American Diptera*, NRC Research Press, Ottawa, pp. 793–803.
- Roháčec, J., 2012. New amber fossil Anthomyzidae (Diptera): an unexpected Eocene diversity. *J. Syst. Palaeontol.* 11(4), 1–43.
- Rudall, P.J., Prychid, C.J., Thomas, G., 2014. Epidermal patterning and silica phytoliths in grasses: an evolutionary history. *Bot. Rev.* 80, 59–71.
- Sadowski, E.-M., Schmidt, A.R., Kunzmann, L., Gröhn, C., Seyfullah, L.J. 2016. *Sciadopitys* cladodes from Baltic amber. *Bot. J. Linn. Soc.* 180, 258–268.
- Sadowski, E.-M., Seyfullah, L.J., Sadowski, F., Fleischmann, A., Behling, H., Schmidt, A.R., 2015. Carnivorous leaves from Baltic amber. *Proc. Natl. Acad. Sci. U.S.A.* 112(1), 190–195.
- Schmidt, A. R., Dilcher, D. L., 2007. Aquatic organisms as amber inclusions and examples from a modern swamp forest. *Proc. Natl. Acad. Sci. U.S.A.* 104, 16581–16585.
- Schubert, K., 1953. Mikroskopische Untersuchung pflanzlicher Einschlüsse des Bernsteins. 2. Teil: Rinden und Borken. *Palaeontographica B* 93, 103–119.
- Schuster, J., 1931. Über das Verhältnis der systematischen Gliederung, der geographischen Verbreitung und der paläontologischen Entwicklung der Cycadaceen. *Bot. Jahrb. Syst. Pflanzengesch. Pflanzengeogr.* 64, 165–260.
- Seredzus, F., Wichard, W., 2007. Fossil chironomids (Insecta, Diptera) in Baltic amber. *Palaeontographica A* 279, 49–91.
- Standke, G., 2008. Bitterfelder Bernstein gleich Baltischer Bernstein? Eine geologische Raum- Zeit- Betrachtung und genetische Schlussfolgerungen. *Exkurs.f. und Veröffentl. DGG* 236, 11–33 in German with English Abstr.
- Strong, M.T., 2006. Taxonomy and distribution of *Rhynchospora* (Cyperaceae) in the Guianas, South America. *Contributions from the United States National Herbarium* 53, 1–225.
- Thomasson, J.R., 1987. Fossil grasses: 1820–1986 and beyond. In: Soderstrom, T.R., Hilu, K.W., Campbell, C.S., Barkworth, M.E. (Eds.), *Grass systematics and evolution*. Smithsonian Institution Press, Washington D. C., pp. 159–167.
- Ueno, O., Koyama, T., 1987. Distribution and evolution of C₄ syndrome in *Rhynchospora* (Rhynchosporaceae-Cyperaceae). *Bot. Mag. Tokyo* 100, 63–85.
- Vince, S.W., Humphrey, S.R., Simons, R.W., 1989. The ecology of hydric hammocks: a community profile. *U.S. Fish Wildl. Serv. Biol. Rep.* 85 (7.26), 1–81.
- Wagner, R., Hoffeins, C., Hoffeins, H.W., 2000. Beschreibung einer weiteren Art der Gattung *Heledromia* (Diptera, Empididae, Hemerodromiinae) aus dem Bitterfelder Bernstein. *Studia dipterologica* 7(1), 19–23 in German with English Abstr.

- Watson, L., 1990. The grass family, Poaceae. In: Chapman, G.P. (Ed.), *Reproductive versatility in the grasses*. Cambridge Univ. Press, New York, pp. 1–31.
- Weitschat, W., Wichard, W., 2010. Baltic Amber. In: Penney, D., (Ed.), *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific Press, Manchester, UK, pp. 80–115.
- Wichard, W., Gröhn, C., Sereduszus, F., 2009. *Aquatic insects in Baltic amber*. Verlag Kessel, Remagen-Oberwinter, Germany.
- Willemstein, S.C., 1980. Pollen in tertiary insects. *Acta Bot. Neerla.* 29(1), 57–58.

Appendix 5

Sadowski, E.-M., A. R. Schmidt, L. J. Seyfullah, and L. Kunzmann. 2017a. Conifers of the 'Baltic amber forest' and their palaeoecological significance. *Stapfia*: in press.

Conifers of the ‘Baltic amber forest’ and their palaeoecological significance

Die Koniferen des ‚Baltischen Bernsteinwaldes‘ und ihre paläoökologische Bedeutung

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Abstract: Eocene Baltic amber constitutes the largest amber deposit on Earth, however, knowledge about the vegetation and habitat diversity of its source area is very fragmentary. We analysed coniferous foliage from several historic Baltic amber collections and from new material, and consequently verify the occurrence of *Calocedrus*, *Quasisequoia* and *Taxodium* (Cupressaceae), *Cupressospermum* (Geinitziaceae), *Abies*, *Cathaya*, *Nothotsuga*, *Pseudolarix* and *Pinus* (Pinaceae) in the ‘Baltic amber forest’. Except for *Pinus*, these taxa have not been unambiguously reported from Baltic amber. The historic descriptions of putative *Abies* inclusions from Baltic amber are revised as these specimens are angiosperm leaves, but we provide evidence for the presence of this genus based on a newly found fossil. The amber fossils of these nine conifer genera, along with recently described cladodes of *Sciadopitys* cf. *tertiaria* (Sciadopityaceae), indicate the presence of coastal swamps and mixed mesophytic conifer-angiosperm forests. Available data from extant and extinct analogues of these conifers suggest that Baltic amber derives from humid warm-temperate forests, with the closest modern analogues being the warm-temperate zoniobiome of East Asia and North America. Comparison of the conifer diversity from Baltic amber to other Eocene floras from Europe furthermore suggests a late Eocene age of the Baltic amber. Our results thus challenge previous notions that Baltic amber derives from early Eocene tropical or ‘subtropical’ forests.

Zusammenfassung: Der eozäne Baltische Bernstein bildet die weltweit größte Bernsteinlagerstätte, jedoch sind unsere Kenntnisse über die Vegetation und die Vielfalt der Lebensräume seines Herkunftsgebietes sehr fragmentarisch. Die Untersuchung von Koniferennadeln aus historischen Bernsteinsammlungen und von neuen Fundstücken bestätigt das Vorkommen von *Calocedrus*, *Quasisequoia* und *Taxodium* (Cupressaceae), *Cupressospermum* (Geinitziaceae), *Abies*, *Cathaya*, *Nothotsuga*, *Pseudolarix* und *Pinus* (Pinaceae) im ‚Baltischen Bernsteinwald‘. Mit der Ausnahme von *Pinus* sind diese Gattungen bisher noch nicht zweifelsfrei aus

Baltischen Bernstein nachgewiesen worden. Die bisher als *Abies* identifizierten Inkluden aus historischen Sammlungen wurden revidiert, da es sich bei ihnen um Angiospermenblätter handelt, jedoch konnte eine neu entdeckte Inkluse zweifelsfrei der Gattung *Abies* zugeordnet werden. Zusammen mit den kürzlich beschriebenen Kladodien von *Sciadopitys* cf. *tertiaria* (Sciadopityaceae) zeigen diese neun Koniferengattungen das Vorkommen von Küstensümpfen sowie gemischten mesophytischen Koniferen-Angiospermenwäldern an. Die verfügbaren ökologischen Daten der zu den Konifereneinschlüssen analogen rezenten und ausgestorbenen Taxa verweisen auf feuchte warm-temperate Waldgebiete, die denen des heutigen warm-temperaten Zonobioms Ostasiens und Nordamerikas ähneln. Der Vergleich der Koniferendiversität des Baltischen Bernsteins zu anderen eozänen Floren Europas deutet zudem auf ein späteozänes Alter des Bernsteins hin, was bisherigen Annahmen eines tropischen bis ‚subtropischen‘ früheozänen ‚Baltischen Bernsteinwaldes‘ widerspricht.

Key words

Baltic amber age, Baltic amber flora, fossil conifers, palaeoecology

INTRODUCTION

With estimated over 600,000 tons Baltic amber forms the largest deposit of any fossil resin on Earth. It is renowned for a vast diversity of organismic inclusions, predominantly arthropods (WEITSCHAT & WICHARD 2010). Although Baltic amber yields highly diverse and significant fossils, only little is known about the structure and composition of the amber-bearing forests, mainly because of the scarcity of determinable plant inclusions. In contrast to over 3,000 species of arthropods, only approximately 200 plant taxa have so far been described from Baltic amber (CZECZOTT 1961; WEITSCHAT & WICHARD 2010).

Although it is generally accepted that succinite, the main chemical variety (>90%) of Baltic amber (LANGENHEIM 2003), derives from a conifer, there is conflicting evidence from macrofossils and resin chemistry about its precise botanical source (WOLFE et al. 2009; DOLEZYCH et al. 2011). Comprehensive knowledge about the diversity of resinous trees is needed to solve the question of the botanical provenance of succinite, and to elucidate the so called Baltic amber forest as a habitat. Gymnosperm inclusions from Baltic amber had been intensively investigated from the mid-19th up to the early 20th century (GOEPPERT & BERENDT 1845; CONWENTZ 1886, 1890; GOEPPERT & MENGE 1883; CASPARY & KLEBS 1907; BACHOFEN-ECHT 1949). In these comprehensive studies a high number of different conifer taxa were described, with the Cupressaceae and Pinaceae being most abundant, and few species assigned to the former Taxodiaceae (now included in the Cupressaceae), Podocarpaceae and Sciadopityaceae (SPAHR 1993). The most recent review of these conifers (CZECZOTT 1961) suggested that some of the assignments are invalid, leading to two remaining families (Cupressaceae and Pinaceae) which comprise in total 33 species. However, the estimations by CZECZOTT (1961) are based on literature reviews only, and the holotypes had not been re-investigated. During World War II, numerous original specimens from Baltic amber collections were lost or destroyed, so the current whereabouts of many holotypes are unknown.

The lack of knowledge about the Baltic amber flora led to different interpretations of the 'Baltic amber forest' as an ecosystem, its floristic composition, and palaeoecology. GOEPPERT (1853) and CASPARY (1872) highlighted affinities of the Baltic amber vegetation to extant floras of northern latitudes which, according to these authors, indicated the presence of high mountain ranges. CASPARY (1872) furthermore suggested that subtropical species were located in the lowlands of the forest areas. GOEPPERT & MENGE (1883) regarded the Baltic amber vegetation as mixture of different habitats, ranging from forests and swamps to meadows. Contrarily, CONWENTZ (1890) emphasized the role of pine trees in the 'Baltic amber forest' as the dominant tree taxon, forming closed and almost pure stands which were only scarcely intermingled with deciduous tree species.

In his extensive survey of the Baltic amber fauna, ANDER (1942) found evidence that the majority of the examined animal species indicate a warm-temperate to subtropical climate. Considering the former knowledge of the Baltic amber flora,

he interpreted the presence of different climatic indicator taxa as a result of the vertical stratification of the forest into different altitudinal zones. ANDER (1942) further described the ‘Baltic amber forest’ as a warm-temperate, moist, dense, and cool ‘jungle’ mainly composed of conifer trees.

A similar picture of the ‘Baltic amber forest’ was suggested by BACHOFEN-ECHT (1949) and LARSSON (1978) who emphasized the various climatic implications of taxa from the Baltic amber flora and fauna. These taxa comprised elements which today occur in (sub)tropical to temperate zones, hinting to a diverse landscape which combined lowlands and mountain ranges covered by mixed forests, few meadows, as well as stagnant water bodies and arid areas (BACHOFEN-ECHT 1949, LARSSON 1978).

In a comprehensive paper about the Baltic amber flora, CZECZOTT (1961) summarized the described Baltic amber plants from the last decades and their extant analogous taxa. She highlighted the high proportion of tropical and subtropical plant taxa (23% of the total number of species) in the Baltic amber flora and confirmed ANDER’S (1942) suggestions of a moist dense amber forest. She further saw evidence that open glades existed which were inhabited by deciduous trees (CZECZOTT 1961).

Contrary to ANDER (1942) and CZECZOTT (1961), SCHUBERT (1953, 1961) and RÜFFLE & HELMS (1970) proposed drier conditions for the Baltic amber source area, similar to the ‘hammocks’ of Florida or mountain steppe forests of Cuba. Following the interpretation of the latter authors, the ‘Baltic amber forest’ was dominated by pines and palms with sclerophyllous vegetation along rivers and pine-oak forests in higher montane areas. In her re-evaluation of previous Baltic amber studies, KOHLMANN-ADAMSKA (2001) placed these pine-oak steppe-forests to lower mountainous areas and suggested that pure conifer forests were located at higher altitudes. Furthermore, she suggested the presence of humid swamp habitats along river valleys at lower elevations of the Baltic amber source area. She concluded that the 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 the high diversity of the flora, ranging from a warm-temperate to subtropical climate (KOHLMANN-ADAMSKA 2001).

In more recent publications, the ‘Baltic amber forest’ was often regarded as tropical, combined with mountainous subtropical rain forests (WEITSCHAT 1997; WEITSCHAT 2008; WICHARD et al. 2009; WEITSCHAT & WICHARD 2010). In contrast, coleopteran inclusions from Baltic amber studied by ALEKSEEV & ALEKSEEV (2016) hint to a plain landscape with a thermophilic, humid-mixed climax forest community.

It is the aim of this study to evaluate previously described and recently found inclusions of conifer needles from Baltic amber taxonomically and palaeoecologically, and to use these fossils along with data from their closest fossil and extant analogues for reconstructing habitats and climate of the source area of the Baltic amber. We provide evidence of nine conifer genera from Baltic amber and use them, along with the previously reported genus *Sciadopitys* SIEBOLD et ZUCC., to estimate habitat structure and climate of the Baltic amber source area. Our findings

indicate heterogeneous warm-temperate humid forests with swampy habitats, mesophytic forest patches and open light areas.

MATERIAL AND METHODS

Origin and age of the fossils

Baltic amber mainly derives from the amber-bearing marine ‘Blue Earth’ layers that are predominantly exposed in the Samland area of Kaliningrad (Russia), but Baltic amber is also frequently found washed ashore along the coast of the Baltic Sea and in adjacent areas.

The age of the Baltic amber is still under debate. Based on pollen and dinoflagellate data, the main Baltic amber source layer, the Blue Earth, was estimated to be upper Eocene (Priabonian) in age (34-38 Ma) (KOSMOWSKA-CERANOWICZ et al. 1997). Few amounts of amber also occur in older sediments (Lower Blue Earth, Lutetian) and even in younger horizons (Lower Gestreifter Sand, upper Oligocene), leading to an estimated age range of approximately 23 to 48 million years for all Baltic amber bearing strata (KOSMOWSKA-CERANOWICZ et al. 1997; STANDKE 1998; KASIŃSKI & KRAMARSKA 2008; STANDKE 2008).

The frequently cited Lutetian age of the Baltic amber from the Blue Earth was suggested by RITZKOWSKI (1997) who dated glauconites deriving from the Blue Earth layer. However, a study by CLAUER et al. (2005) showed that this dating method can lead to older age estimations if the glauconites have been reworked or if non-glauconized detrital mica ‘contaminated’ the glauconite splits.

Possible redeposition of the Baltic amber into the Blue Earth layer also has been discussed (WEITSCHAT & WICHARD 2010). However, amber from the Blue Earth layer does not show typical signs of erosion which normally occur if amber has been re-worked, such as ‘pebble-shaped’ amber pieces or a dark oxidised crust. In contrast, the majority of the Blue Earth amber is of a fresh lemon yellow colour and unoxidised (GRIMALDI & ROSS 2017). However, the pollen and dinoflagellate derived age estimation of Baltic amber still needs validation by an independent data set that is able to link the Baltic amber Lagerstätte to the global time scale. In short, a late Eocene age of both the ‘Baltic amber forest’ and the main amber Lagerstätte is commonly assumed but not unambiguously proven.

We searched through several historic amber collections which harbour botanical type material such as the collections of Carl Georg Berendt and Georg Künow at the Museum für Naturkunde Berlin, and the Königsberg Amber Collection at the University of Göttingen, and we also considered recently found amber pieces with conifer inclusions. Table 1 shows the repository of all taxa described in this study.

Tab. 1: Repository of conifer and angiosperm taxa described and examined in this study.

Fossil taxon	Name of collection	Institution	Current collection number	Former collection number	Figures
Cupressaceae					
<i>Calocedrus</i> sp.	Königsberg Amber Collection	University of Göttingen	GZG.BST.24645	G 3536	Fig. 3
<i>Calocedrus</i> sp.	Königsberg Amber Collection	University of Göttingen	GZG.BST.24632	G 3616	Fig. 2
<i>Quasisequoia couttsiae</i>	Königsberg Amber Collection	University of Göttingen	GZG.BST.24550	B 648	-
<i>Quasisequoia couttsiae</i>	Königsberg Amber Collection	University of Göttingen	GZG.BST.24606	G 3613	Fig. 5e-g
<i>Quasisequoia couttsiae</i>	Königsberg Amber Collection	University of Göttingen	GZG.BST.24633	G 3537	Fig. 5a-d
<i>Quasisequoia couttsiae</i>	Carsten Gröhn Amber Collection	University of Hamburg	GPIH 4583	Gröhn P 6380	Fig. 4
<i>Quasisequoia couttsiae</i>	Carsten Gröhn Amber Collection	Glinde	Gröhn P 25	-	-
<i>Widdringtonites oblongifolius</i>	Goepfert Collection	lost	-	-	Fig. 6a-d
<i>Sequoia couttsiae</i>	Caspary's private collection	lost	-	136	Fig. 7
<i>Taxodium</i> sp.	Königsberg Amber Collection	University of Göttingen	GZG.BST.24333	G 4397	Fig. 8
<i>Glyptostrobus europaeus</i>	Königsberg Amber Collection	University of Göttingen	GZG.BST.23520	S B 13	Fig. 10
Geinitziaceae					
<i>Cupressospermum saxonicum</i>	Hoffeins Collection	University of Göttingen	GZG.BST.21895	Hoffeins 186-1	Fig. 9
Pinaceae					
<i>Abies</i> sp.	Jürgen Velten Amber Collection	Idstein	IX 73	-	Fig. 11
<i>Cathaya</i> sp.	Königsberg Amber Collection	University of Göttingen	GZG.BST.23533	G 35	Fig. 12
<i>Nothotsuga protogaea</i>	Hoffeins Collection	University of Göttingen	GZG.BST.21896	Hoffeins 130-1	Fig. 13
<i>Nothotsuga protogaea</i>	Königsberg Amber Collection	University of Göttingen	GZG.BST.23535	G 1916	Fig. 14a-c
<i>Nothotsuga protogaea</i>	Königsberg Amber Collection	University of Göttingen	GZG.BST.24406	Casp. 159	Fig. 14d-g
<i>Pinus baltica</i>	Königsberg Amber Collection	University of Göttingen	GZG.BST.24652	G 3627	Fig. 15
<i>Pinus baltica</i>	Hoffeins Collection	University of Göttingen	GZG.BST.21899	Hoffeins 229	-
<i>Pinus baltica</i>	Hoffeins Collection	University of Göttingen	GZG.BST.21900	Hoffeins 1069/4	-
<i>Pinus banksianoides</i>	Menge Collection	lost	-	-	Fig. 16d-f
<i>Pinus silvatica</i>	Menge Collection	lost	-	-	Fig. 16g-i
<i>Pinus serrata</i>	Carsten Gröhn Amber Collection	University of Hamburg	GPIH 4584	Gröhn P 6357	Fig. 17
<i>Pinus serrata</i>	Künow Amber Collection	lost	-	42	Fig. 18
<i>Pinus künowii</i>	Künow's private collection	lost	-	-	Fig. 19a-f
<i>Pinus schiefferdeckeri</i>	Collection of the 'Physikalisch- ökonomische Gesellschaft Königsberg'	lost	-	5	Fig. 19g-j
<i>Pinus</i> aff. <i>schiefferdeckeri</i>	Königsberg Amber Collection	University of Göttingen	GZG.BST.24654	G 23	Fig. 22
<i>Pinus dolichophylla</i>	Caspary's private collection	lost	-	-	Fig. 20

Tab. 1 continued

<i>Pinites rigidus</i>	?	lost	-	-	Fig. 21a-d
<i>Pinites subrigida</i>	?	lost	-	-	Fig. 21e-i
<i>Pinus cembraefolia</i>	Hoffeins Collection	University of Göttingen	GZG.BST.21897	Hoffeins 1187-1	Fig. 23
<i>Pinus cembraefolia</i>	Westpreußisches Provinzialmuseum Danzig	lost	-	-	Fig. 24
<i>Pinus cembraefolia</i>	Klebs Amber Collection	lost	-	-	Fig. 25a-f
<i>Pinus cembraefolia</i>	Künow Amber Collection	lost	-	176	Fig. 25g-m
<i>Pseudolarix</i> sp.	Königsberg Amber Collection	University of Göttingen	GZG.BST.24338	G 4560	Fig. 26
<i>Pseudolarix</i> sp.	Hoffeins Collection	University of Göttingen	GZG.BST.21898	Hoffeins 997	Fig. 27
<i>Pseudolarix</i> sp.	Königsberg Amber Collection	University of Göttingen	GZG.BST.23536	Casp. 210	Fig. 28a-e
<i>Pseudolarix</i> sp.	Königsberg Amber Collection	University of Göttingen	GZG.BST.24334	B 14564	Fig. 28f-i
Angiosperms					
<i>Dicotylophyllum</i> sp. (' <i>Abies obtusifolius</i> ')	Berendt Amber Collection	Museum für Naturkunde Berlin	MB.Pb.1979/0591	-	Fig. 29
<i>Dicotylophyllum</i> sp. (' <i>Abies suckerii</i> ')	Königsberg Amber Collection	University of Göttingen	GZG.BST.23539	B 14645	Fig. 30
<i>Dicotylophyllum</i> sp. (' <i>Abies suckerii</i> ')	Königsberg Amber Collection	University of Göttingen	GZG.BST.24355	Casp. 52	Fig.31
<i>Dicotylophyllum</i> sp. (' <i>Dermatophyllites porosus</i> ')	Berendt Amber Collection	Museum für Naturkunde Berlin	MB.Pb.1979/0490	IB.C17	Fig. 32
<i>Dicotylophyllum</i> sp. (' <i>Abies linearis</i> ')	?	lost	-	-	Fig. 33
<i>Dicotylophyllum</i> sp. (' <i>Abies obtusifolia</i> ')	Künow Amber Collection	lost	-	-	Fig. 34
<i>Dicotylophyllum</i> sp.	Königsberg Amber Collection	University of Göttingen	GZG.BST 23540	G 3517	-
<i>Dicotylophyllum</i> sp.	Hoffeins Collection	University of Göttingen	GZG.BST.21901	Hoffeins 1045-2	-
<i>Dicotylophyllum</i> sp.	Königsberg Amber Collection	University of Göttingen	GZG.BST.24336	G 1956	-
<i>Dicotylophyllum</i> sp.	Königsberg Amber Collection	University of Göttingen	GZG.BST.24346	G 4507	-
<i>Dicotylophyllum</i> sp.	Königsberg Amber Collection	University of Göttingen	GZG.BST.24332	G 4508	-
<i>Dicotylophyllum</i> sp.	Königsberg Amber Collection	University of Göttingen	GZG.BST.24610	G 44	-
<i>Dicotylophyllum</i> sp.	Königsberg Amber Collection	University of Göttingen	GZG.BST.24651	G 3548	-
<i>Dicotylophyllum</i> sp.	Carsten Gröhn Amber Collection	Glinde	Gröhn P 3655	-	-
<i>Dicotylophyllum</i> sp.	Künow Amber Collection	Museum für Naturkunde Berlin	MB.Pb.1979/655	96	-
<i>Dicotylophyllum</i> sp.	Künow Amber Collection	Museum für Naturkunde Berlin	MB.Pb.1979/764	268	-
<i>Dicotylophyllum</i> sp.	Künow Amber Collection	Museum für Naturkunde Berlin	MB.Pb.1979/768l	283	-
<i>Dicotylophyllum</i> sp.	Künow Amber Collection	Museum für Naturkunde Berlin	MB.Pb.1979/768qu	288	-
<i>Dicotylophyllum</i> sp.	Künow Amber Collection	Museum für Naturkunde Berlin	MB.Pb.1979/768s	290	-

Preparation and imaging

In order to remove scratches and fissures, most amber specimens were slightly further ground and polished manually using wet silicon carbide papers (grit from 25.8 to 5 μm particle size, Struers company) for creating smooth and even surfaces parallel to the inclusions. This allows a better visualization of cellular details such as the stomata and cell morphology. The amber inclusions were examined under a Carl Zeiss AxioScope A1 compound microscope and a Carl Zeiss Stereo Discovery V8 dissecting microscope, each equipped with a Canon EOS 5D digital camera. In most instances incident and transmitted light were used simultaneously. All figures are digitally stacked photomicrographic composites of up to 120 individual focal planes, obtained by using the software package HeliconFocus 5.0. Some of the overview images result from merging up to four photomicrographic composites using the Adobe Photoshop CS6 software (Figs 2a; 3a; 4a; 5a and e; 10b; 13 and f; 14a, d, e; 17a, b; 23a; 26a, b; 30a; 32a, b). Using a micrometre eyepiece, the most important morphological features of the fossils were measured, comprising the total size of the inclusions, the leaf size, the size of the stomata complex and the stomatal pit (for details of the stomata morphology, see Fig. 1).

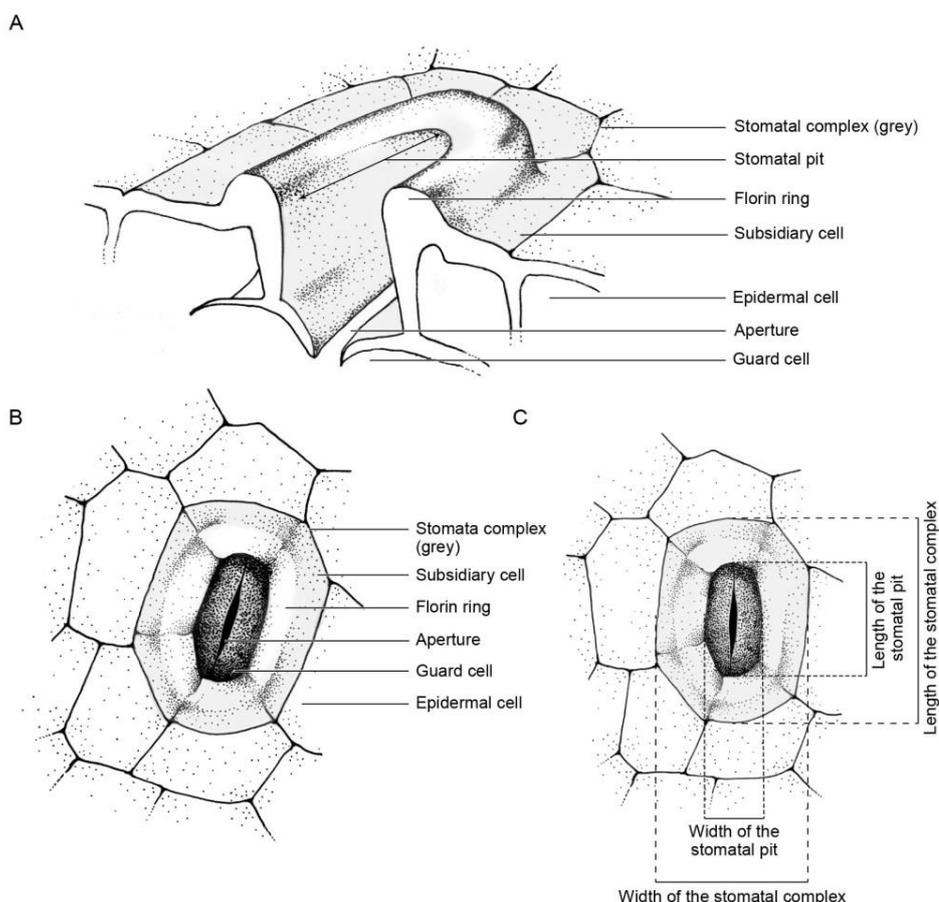


Fig. 1: Terminology of the stomata morphology used in this study (from FLORIN 1931 and EWIN 2004). (a) Cross section through a conifer stoma, adapted from EWIN (2004). (b) Surface view on a conifer stoma. (c) Stomata features which were measured in this study; the stomata complex is shaded in grey.

Where the holotypes and other previously described material were lost, we used the original illustration and descriptions from GOEPPERT & BERENDT (1845), GOEPPERT & MENGE (1883), CONWENTZ (1890) and CASPARY & KLEBS (1907) to evaluate the fossils (Figs 6; 7; 16; 18–21; 24; 25; 33; 34)

Terminology

In our study, as well as in the previous literature describing the ‘Baltic amber forest’, the terms ‘tropical’, ‘subtropical’ and ‘warm-temperate’ are used. Because these terms have been differently applied in the literature, their use could easily lead to misunderstandings. The definitions of these terms are therefore shortly discussed in this section.

The tropics extend to $\pm 23.4^\circ$ latitude which is mainly determined by the overhead sun (CORLETT 2013). This ‘solar definition’ is widely accepted, although more specific definitions exist which include temperature and vegetation (CORLETT 2013). As summarized by DOMROES (2003), the tropical climate is characterized by “homogeneous intra-annual temperature condition” (diurnal climate), lacking seasonality. For defining the northern and southern boundary of the tropics, the mean annual temperature of 18.3°C is used (DOMROES 2003). The so called tropical rainforest is an unspecific term, since many different forest types exist within the equatorial region and thus, a generalized picture is difficult to achieve. Very generally speaking, they share features such as a highly diverse tree stratum divided into storeys with trees of different heights, a dense canopy and only scarce light in the undergrowth. Further commonly used characteristics of a ‘tropical rainforest’ are a large leaf size of most plants, the dominance of phanerophytes (about 70% of all species) and the presence of lianas and epiphytes (WALTER & BRECKLE 2002c).

Following CORLETT (2013), the term ‘subtropical’ is arbitrary, since no unambiguous definition exists. From an etymological point of view, it describes a subdivision of the tropics, but commonly it is applied for regions bordering the tropics (CORLETT 2013). Physical geographers define the ‘subtropics’ climatically, extending to 35 to 40° latitude. The coldest month mean temperature is also frequently used to define the northern limits of the ‘subtropics’ and varies between 6°C or -3°C (CORLETT 2013). The most commonly used climate classification of Köppen-Geiger does not apply the term ‘subtropics’, but distinguishes between tropical, arid, temperate, cold and polar climates with several subdivisions (KÖPPEN 1900; GEIGER 1952; PEEL et al. 2007). Following PETERSEN et al. (2015), the Cfa climate sensu Köppen-Geiger (temperate, without dry season, hot summer), corresponds to a ‘humid subtropical’ climate, with high temperatures, convective precipitation during the summer season and colder temperatures with occasional frosts during winter.

Beside these examples, even more definitions exist (see CORLETT 2013 for details); hence, CORLETT reviewed the current usage of the term ‘subtropical’ in the scientific literature and summarized that in most instances the term is used to

describe the transitional zone between tropical and temperate regions. Thus, CORLETT (2013) suggested to define “the subtropics as a fixed latitudinal belt, as we do for the tropics”, located between 23.4° North and 30.0° South latitude.

Despite the unspecific meaning of the ‘subtropics’, this term is frequently used in the scientific literature about the ‘Baltic amber forest’. However, the particular authors did not clarify how they defined the ‘subtropics’.

When referring to the climate of the ‘Baltic amber forest’, the term ‘warm-temperate’ also occurs. In the updated world map of the Köppen-Geiger climate classification by KOTTEK et al. (2006) the warm-temperate climate type (C) is subdivided into seven sub-climates (Cfa, Cfb, Cfc, Csa, Csb, Csc, Cwa), encompassing fully humid climates to summer or winter dry climates with different temperature regimes (e.g. hot summer, warm summer, cool summer). In the most current update of this classification by PEEL et al. (2007), the main climate class C was termed ‘temperate’, although the subdivision stayed the same. In the climatic descriptions of the ‘Baltic amber forest’, no specific definition of the term ‘warm-temperate’ was given so far; thus, we assume that it was used following the main climate C sensu Köppen-Geiger, since this classification system is the most common climate map used among scientists (PEEL et al. 2007).

Since climate C (warm-temperate or temperate) sensu Köppen-Geiger encompasses several different sub-climates and regions, we decided to refer to the more specific zonobiome concept by WALTER & BRECKLE (2002a) which not only combines climatic data, but also vegetation and soil types to classify the world’s vegetation. They distinguish between nine ecological climatic zones and several ecotones. The warm-temperate zonobiome (zonobiome V = zonobiome of Laurel forests) sensu WALTER & BRECKLE is a transitional biome, “delimited from the subtropical/tropical rain forests which have more or less evenly distributed precipitation and temperatures, from sclerophyllic forests which have lower and sporadic precipitation ([predominantly in] winter) and regular fires, and from [deciduous] forests which have colder winters with late frosts and often drier summers” (WALTER & BRECKLE 2002b, p. 298). The mean annual temperature lies at around 15°C and rarely drops below 0°C during the cold season, but frost may occur. Precipitation during the winter period is abundant. The vegetation of the warm-temperate zonobiome is characterized by laurophyllous trees and pine forests, intermingled with Paleogene relict species. During winter, the vegetation is in a resting state; thermophilic, frost- and drought-sensitive trees are to some extent evergreen, but deciduous taxa also occur (mixed evergreen deciduous forests). Zonobiome V occurs on most continents, e.g. in the Southeastern USA (e.g. Florida), along the western coast of the USA and Canada and in east China (see WALTER & BRECKLE 2002a for detailed maps).

SYSTEMATIC PALAEOBOTANY

In this chapter, new specimens of conifer leaf inclusions from Baltic amber are described and historic descriptions of specific amber inclusions including type material are revised.

Family Cupressaceae GRAY, 1822

Genus *Calocedrus* KURZ, 1873

Calocedrus sp.

Figures 2 and 3

Specimens investigated

GZG.BST.24632; GZG.BST.24645

Description

Dorsiventral twig fragment (GZG.BST.24632) 12 mm long \times 3.5 mm wide, dimorphic, flattened, leaves decussate, imbricate and non-connate at the base (Fig. 2a-b). Lateral leaves 2.8 to 4.7 mm long (average 3.6 mm) \times 0.9 to 1.3 mm wide (average 1.1 mm), conduplicate, with free, incurved and apiculate leaf tips (Fig. 2f). Facial leaves 2.2 to 4.6 mm long (average 3.1 mm) \times 1.3 to 2.3 mm wide (average 1.9 mm), obtrullate in shape, with acute apices proceeding up to the base of the following facial leaf, slightly covering its base (Fig. 2a-c). Facials with prominent, broad adaxial keel, 0.2 to 0.4 mm wide and proceeding from the tip to the middle of the leaf (Fig. 2a-b). Margins of facials and laterals scariose, composed of obliquely arranged hyaline cells (Fig. 2c-d); every second cell of this margin terminates at the distal polar end in a short rounded papilla. One twig side with only a few stomata visible (Fig. 2b), other twig side with clear stomatal patches at the base of facials and laterals, proceeding to the upper third of the leaves (Fig. 2a). On lateral leaves, stomata arranged in more or less regular parallel rows, pores orientated towards the leaf tip (Fig. 2e). Stomata of facials clustered together in patches on either side of the longitudinal midline, partly orientated towards the leaf tip or variously orientated (Fig. 2d). Stomata complexes monocyclic, with steep lobed Florin rings and surrounded by a few round papillae on subsidiary cells (Fig. 2d). Stomatal pit irregular shaped, elongated, elliptic to rectangular; Stomatal pits are 18 to 30 μ m long (average 24 μ m) \times 6 to 12 μ m wide (average 10 μ m). Ordinary epidermal cells are 96 to 192 μ m long (average 140 μ m) \times 18 to 24 μ m wide (average 20 μ m), rectangular, arranged in regular rows. Rows of ordinary epidermal cells of lateral leaves proceed parallel to the longitudinal leaf axis (Fig. 2c); in facial leaves, ordinary epidermal cells are orientated towards the leaf tip; walls of ordinary

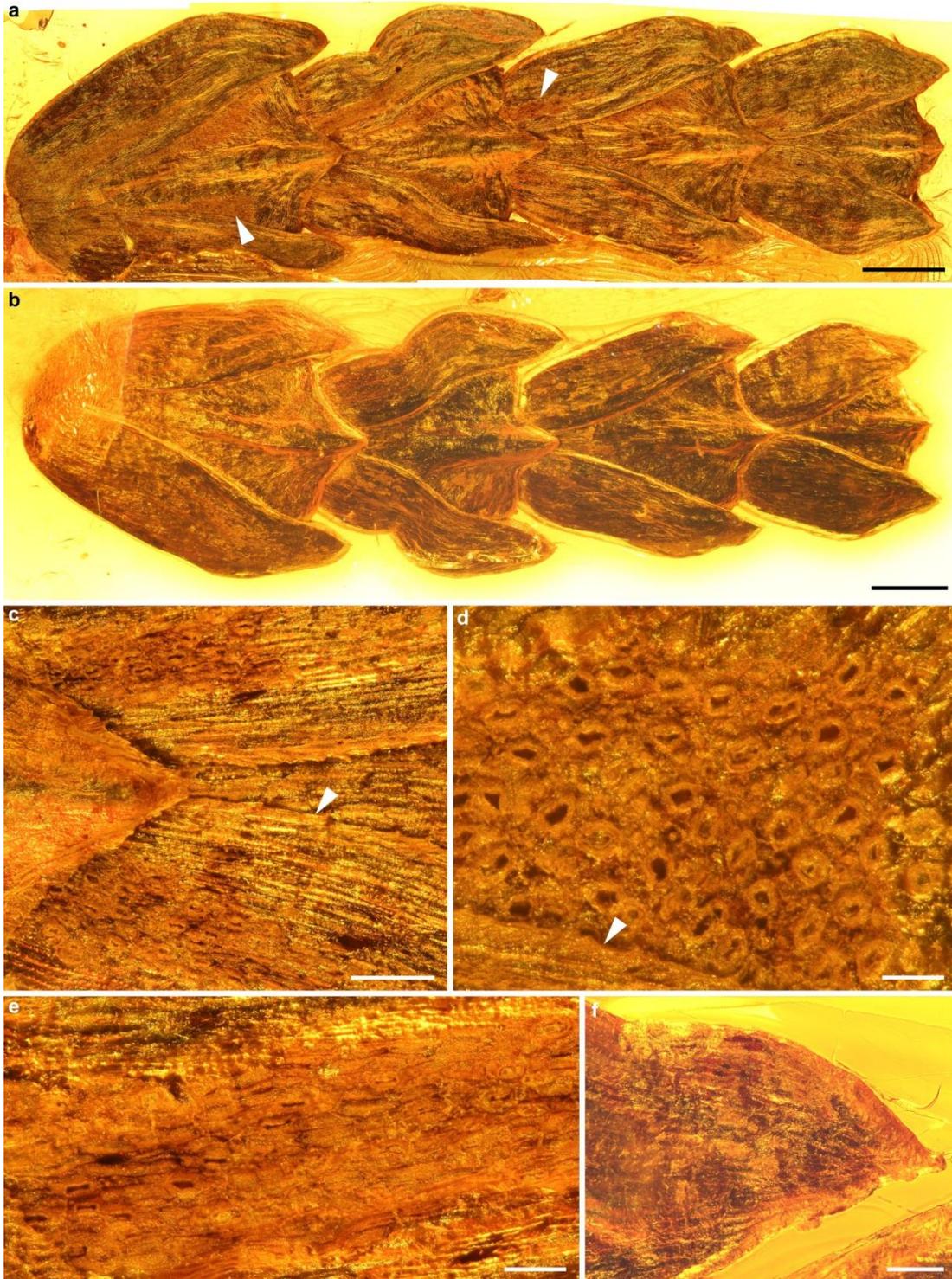


Fig. 2: Twig fragment of *Calocedrus* sp. from Baltic amber, GZG.BST.24632. **(a)** Lower side of the twig fragment with stomata patches (arrowheads). **(b)** Upper side of the twig without clear stomata patches. **(c)** Facial leaf tip covering the base of the lateral leaves showing scariose leaf margins (arrowhead). **(d)** Stomata patch of a facial leaf showing stomata with Florin rings and papillose subsidiary cells, arrowhead points to the scariose leaf margin. **(e)** Stomata patch of a lateral leaf. **(f)** Free incurved and apiculate tip of a lateral leaf. Scale bars = 1 mm (a, b), 100 μm (c, f), 50 μm (d, e).

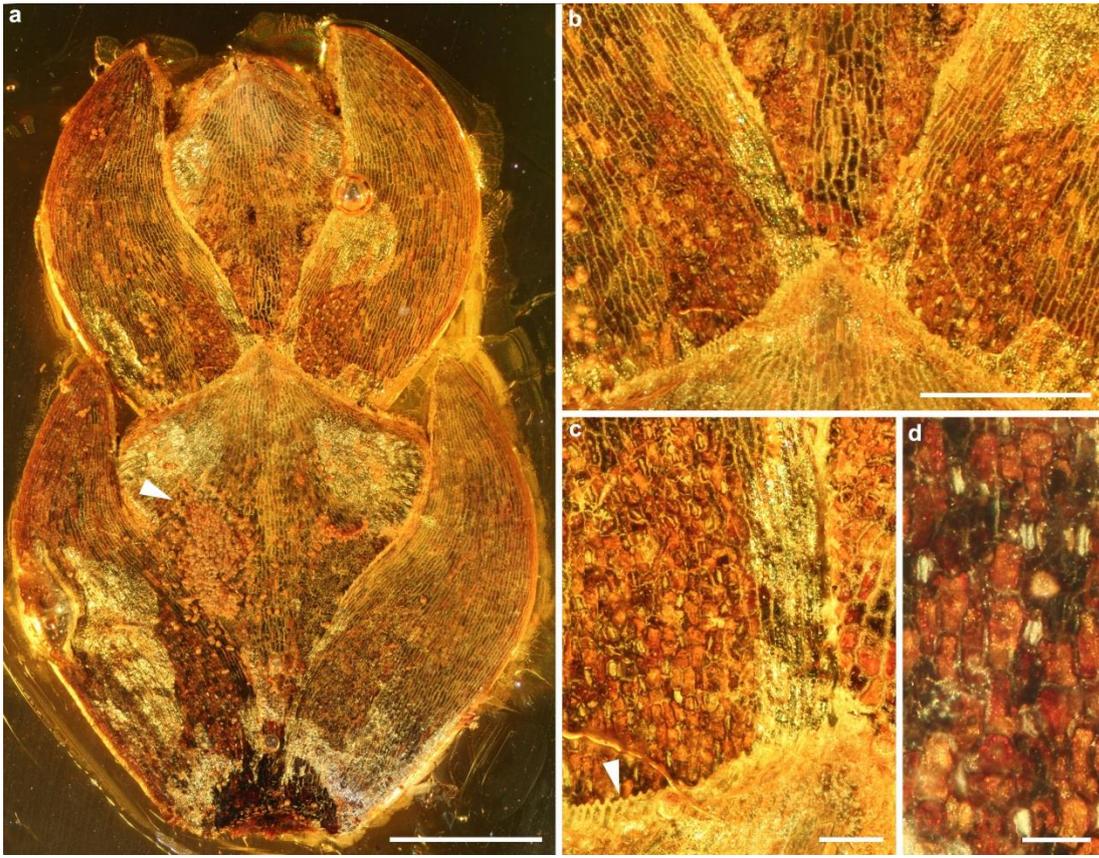


Fig. 3: Twig fragment of *Calocedrus* sp. from Baltic amber, GZG.BST.24645. **(a)** Underside of the twig fragment with stomata patches. Arrowhead indicates clumps of angiosperm pollen. **(b)** Facial leaf tip covering the base of the lateral leaves. **(c)** Stomata patch of one facial leaf showing the scariose margin (arrowhead). **(d)** Monocyclic stomata complexes of a lateral leaf. Scale bars = 1 mm (a), 500 µm (b), 100 µm (c), 50 µm (d).

epidermal cells straight, polar end walls perpendicular or oblique to the lateral walls (Fig. 2e).

Dorsiventral twig fragment (GZG.BST.24645) 5.4 mm long \times 3 mm wide, morphology very similar to GZG.BST.24632, except the more curved lateral leaves, probably due to the juvenile nature of this twig remnant (Fig. 3; for detailed measurements of each specimen see Table 2). Clustered angiosperm pollen is located on the basal facial leaf (Fig. 3a), possibly with affinities to Asteraceae (pers. comm. Hermann Behling, 2016).

Tab. 2: Measurements of *Calocedrus* specimens from Baltic amber. Centered numbers of the leaf and stomata sizes are average values; size ranges are provided in brackets. Features which were not measurable (due to poor preservation) are indicated by '-'.⁴

Collection number	GZG.BST.24632	GZG.BST.24645
Twig		
Length	12 mm	5.4 mm
Width	3.5 mm	3 mm
Lateral leaves		
Length	(2.8)-3.6-(4.7) mm	2.4-3.4 mm
Width	(0.9)-1.1-(1.3) mm	1-1.2 mm
Facial leaves		
Length	(2.2)-3.1-(4.6) mm	1.8-3.2 mm
Width	(1.3)-1.9-(2.3) mm	1.2-2.2 mm
Stomata complex		
Length	-	(60)-91-(120) µm
Width	-	(39)-55-(75) µm
Stomatal pit		
Length	(18)-24-(30) µm	(18)-21-(24) µm
Width	(6)-10-(12) µm	(6)-9-(12) µm
Ordinary epidermal cells		
Length	(96)-140-(192) µm	(80)-118-(150) µm
Width	(18)-20-(24) µm	(20)-23-(28) µm

Identification

The combination of the following features allow the assignment of the fossils to *Calocedrus*: the overall dimorphic twig morphology, the leaf shape, the sacriose papillate leaf margins, the absence of stomata or only few stomata present on one twig side, the stomata orientation and arrangement, the monocyclic stomatal complexes with Florin rings and only few papillae (KVAČEK 1999; FARJON 2005a; SHI et al. 2012). For an assignment at subgeneric level, the amber specimens do not provide sufficient information, such as the characteristics of the adaxial leaf side or the female cone morphology.

Comparison

Since the original specimens of Baltic amber Cupressaceae inclusions were not available, the *Calocedrus* specimens were compared to figures of fossil Cupressaceae taxa from Baltic amber pictured by GOEPPERT & BERENDT (1845), GOEPPERT & MENGE (1883) and CASPARY & KLEBS (1907). None of the previously described Cupressaceae taxa resembled the *Calocedrus* specimens in the most important features; hence the amber specimens illustrated in Figs 2 and 3 represent the first *Calocedrus* record from Baltic amber. These amber specimens can also be distinguished from fossil twig remains of *Calocedrus suleticensis* (BRABENEC) KVAČEK (early to late Oligocene of Suletice, North Bohemia, Czech Republic; KVAČEK 1999) by the presence of papillae on the subsidiary cells and in having stomata on the abaxial side of the facial leaves.

Genus *Quasisequoia* SRINIVASAN et E. M. FRIIS, 1989
Quasisequoia couttsiae (HEER, 1862) L. KUNZMANN, 1999
Figures 4 and 5

Synonymy

- 1853 *Widdringtonites oblongifolius* GOEPP. et MENGE, in GOEPPERT (1853), p. 460.
1862 *Sequoia couttsiae* HEER, pp. 369-377, pl. 18.
1883 *Widdringtonites oblongifolius* GOEPP. et MENGE, p. 40, pl. XIV, figs 165-172.
1907 *Widdringtonites oblongifolius* GOEPP. et MENGE, in CASPARY & KLEBS (1907), pp. 66-70, pl. IX, figs 52, 52a-d; 53, 53a-c; herein Fig. 6.
?1907 *Sequoia couttsiae* HEER, in CASPARY & KLEBS (1907), pp. 138-139, pl. XXIV, figs 111, 111a-111c; herein Fig. 7.
?1998 *Taiwania schaeferi* SCHLOEMER-JÄGER, in JÄHNICHEN (1998), p. 172, fig. 1A-C.
1999 *Quasisequoia couttsiae* (HEER) comb. nov. KUNZMANN, p. 57, text-figs 13, 14; pl. X, figs 5, 6; pl. XI, XII, XIII.

Specimens investigated

GPIH 4583, GZG.BST.24550, GZG.BST.24606, GZG.BST.24633, Carsten Gröhn Amber Collection P 25

Description

Several twig remains of *Quasisequoia couttsiae* are preserved, ranging in size between 6 mm to 27.5 mm length and 1.7 to 2.2 mm width (GPIH 4583, GZG.BST.24633, GZG.BST.24606; Figs 4-5; for detailed measurements of each specimen see Table 3). All twigs monomorphic with spirally arranged, decurrent awl-shaped leaves (1.8 to 3.5 mm long \times 0.5 to 0.8 mm wide; Fig. 4) or lanceolate-linear leaves (1.5 to 3.4 mm long \times 0.4 to 0.9 mm wide; Fig. 5). Leaf apices acute (Fig. 4f-g) or rounded (Fig. 5b), free, incurved to straight. Leaf margins entire and smooth (Fig. 5b) or with acute papillae which are arranged at an irregular distance to each other (Fig. 4g-h). Leaves amphistomatic; abaxially, stomata irregularly dispersed or arranged in short rows forming slender bands (Fig. 4b, c) or gappy patches (Fig. 5c, f), which are only basal or rarely proceeding up to the middle part of the leaves. Orientation of the stomatal pores within the patches or bands variable, mostly perpendicular or oblique to the longitudinal leaf axis (Figs 4c-e; 5c, d, f, g). Stomata complexes cyclocytic to amphicyclocytic, subsidiary cell ring narrow, forming an irregular roundish shape of the stomata complex (Figs 4d, e; 5d-g). Stomata complexes 48 to 72 μm long \times 45 to 63 μm wide. Stomatal pit elongated, elliptic in shape, size of the stomatal pit 18 to 39 μm long \times 6 to 27 μm wide. Ordinary epidermal cells 22 to 120 μm \times 12 to 30 μm wide, rectangular, elongated or almost squared, arranged in regular cell rows parallel to the longitudinal leaf axis.

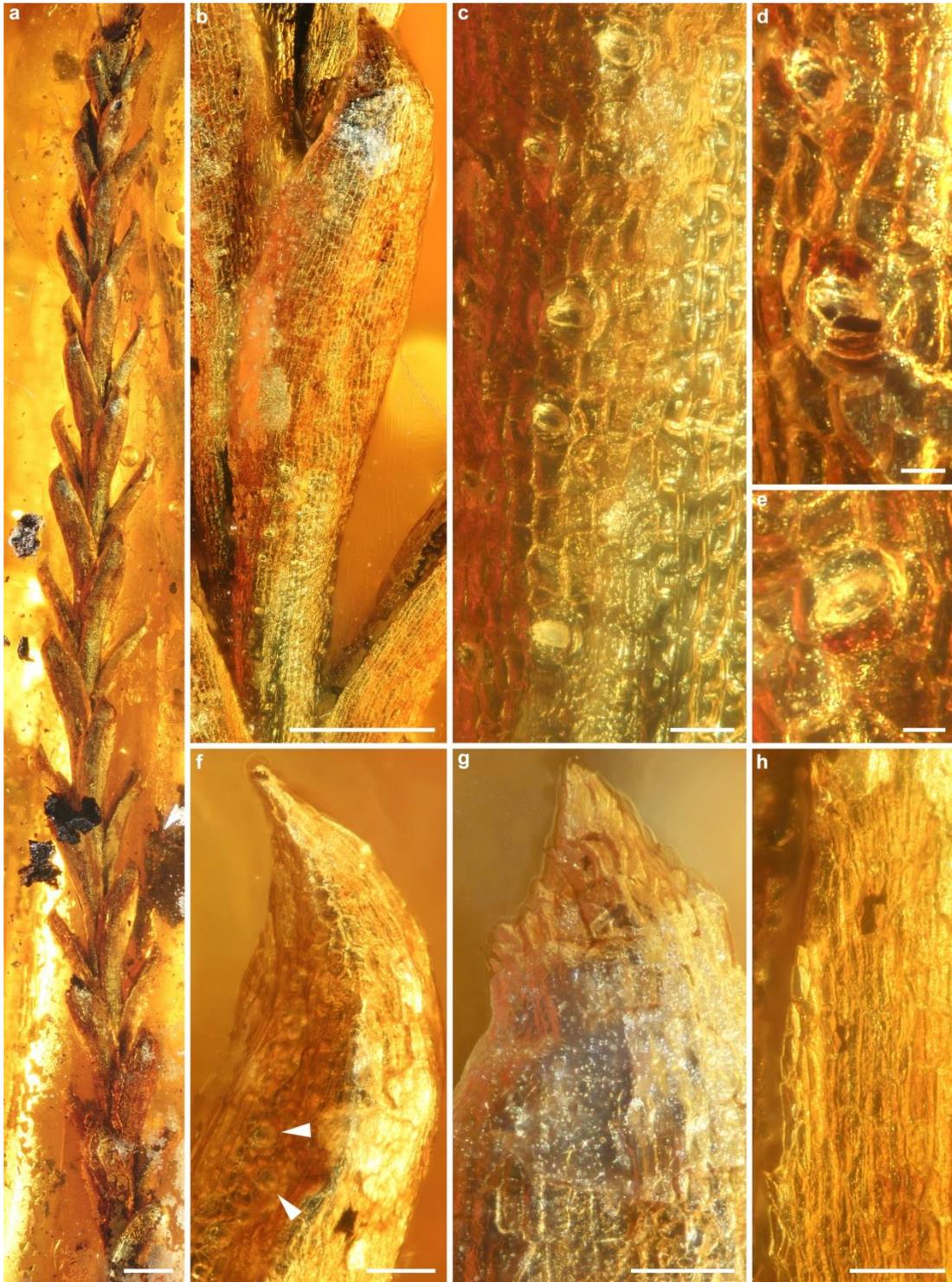


Fig. 4: Twig fragment of *Quasisequoia couttsiae* from Baltic amber, GPIH 4583. **(a)** Overview of the inclusion showing the spirally arranged awl-shaped leaves. **(b)** Abaxial leaf side showing the decurrent leaf base. **(c)** Short stomata row of the abaxial leaf side; note the rectangular to squared shape of ordinary epidermal cells. **(d)** Amphyccyctic stomata complex on the abaxial side of leaf. **(e)** Cyclocyctic stomata complex on the abaxial side of leaf. **(f)** Adaxial leaf side showing the adaxial stomata bands (arrowheads) and the incurved free leaf apex. **(g)** Leaf apex with acute papillae along the margin. **(h)** Irregularly arranged acute papillae along the leaf margin. Scale bars = 1 mm (a), 500 μ m (b), 50 μ m (c), 20 μ m (d, e), 100 μ m (f-h).

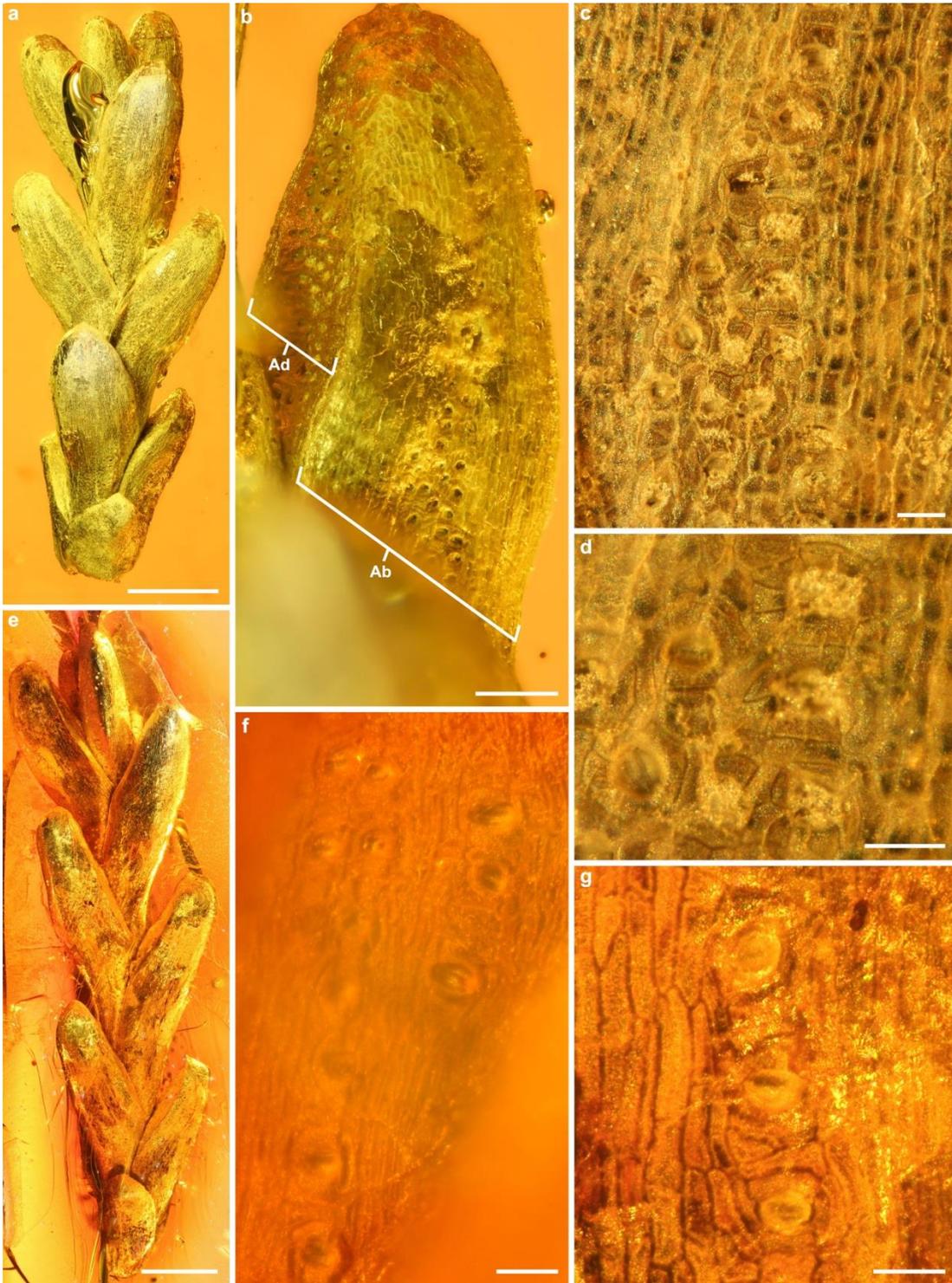


Fig. 5: Twig fragments of *Quasisequoia couttsiae* from Baltic amber with lanceolate-linear leaves; GZG.BST.24633 (a-d) and GZG.BST.24606 (e-g). **(a)** Overview of GZG.BST.24633. **(b)** Leaf showing gappy stomata patches on the adaxial (Ad) and abaxial (Ab) leaf sides. **(c)** Abaxial stomata patch. **(d)** Cyclocytic stomata complexes on the abaxial side of leaf. **(e)** Overview of GZG.BST.24606. **(f)** Stomata bands of the abaxial leaf side. **(g)** Amphicyclocytic stomata complexes, note the rectangular elongated shape of ordinary epidermal cells. Scale bars = 1 mm (a, e), 200 μ m (b), 50 μ m (c, d, f, g).

Walls of ordinary epidermal cells straight, polar end walls perpendicular or oblique to the lateral cell walls (Figs 4c; 5g). Adaxial leaf sides only partly preserved, showing two stomatal bands, composed of two stomata files which do not reach the leaf tip (Figs 4f; 5b).

Tab. 3. Measurements of *Quasisequoia couttsiae* specimens from Baltic amber. Centered numbers of the leaf and stomata sizes are average values; size ranges are provided in brackets.

Collection number	GPIH 4583	GZG.BST.24633	GZG.BST.24606
Twig			
Length	27.5 mm	6 mm	8.7 mm
Width	1.7 mm	2.2 mm	2.2 mm
Leaf			
Length	(1.8)-3-(3.5) mm	(1.8)-2-(2.4) mm	(1.5)-2.8-(3.4) mm
Width	(0.5)-0.7-(0.8) mm	(0.7)-0.7-(0.9) mm	(0.4)-0.8-(0.9) mm
Stomata complex			
Length	(51)-60-(69) μm	(48)-60-(72) μm	(48)-58-(69) μm
Width	(45)-51-(60) μm	(45)-53-(63) μm	(45)-53-(63) μm
Stomatal pit			
Length	(18)-30-(39) μm	(27)-32-(39) μm	(18)-25-(30) μm
Width	(15)-20-(27) μm	(12)-15-(18) μm	(6)-17-(24) μm
Ordinary epidermal cells			
Length	(30)-56-(120) μm	(22)-44-(72) μm	(48)-69-(120) μm
Width	(18)-22-(30) μm	(12)-16-(20) μm	(12)-16-(24) μm

Identification

The most important feature to distinguish *Quasisequoia couttsiae* from other monomorphic Cupressaceae is the combination of the leaf shape and the stomata micromorphology (especially the narrow subsidiary cell ring resulting an irregular roundish shape of the stomata complex) comprising the loose stomata arrangement at the leaf base and their irregular orientation to the midline. Scale-like and awl-shaped leaves of *Sequoia* ENDL., for instance on adult and fertile shoots, have a similar cuticle topography as *Quasisequoia couttsiae*, especially regarding the arrangement of stomata complexes. However, *Sequoia* is distinguished from *Quasisequoia couttsiae* in possessing cuticle swellings of outer anticlines of the subsidiary cell rings, located on the abaxial leaf side (see KUNZMANN 1999, pl. 1, fig. 8). Besides, leaves of *Sequoia* are dimorphic and heterophyllous, young short shoots have lanceolate flattened needles arranged in two files (KUNZMANN 1999; FARJON 2005a). Those short shoots usually exhibit few scale leaves in helical arrangement at their bases but are distinguished from *Quasisequoia* by the above mentioned cuticle swellings, the elliptic-polygonal shape of the subsidiary cell ring and the polygonal-isodiametric subsidiary cells.

Twigs of *Quasisequoia couttsiae* resemble monomorphic cupressoid twigs of extant *Glyptostrobus pensilis* (STAUNTON ex D. DON) K. KOCH, but in contrast to *Q. couttsiae* the latter species possesses broad stomatal patches on the abaxial leaf side which almost merge at the leaf base and narrow towards the leaf tip without reaching the leaf apex (FLORIN 1931). The specimens of *Q. couttsiae* with falcate spreading leaves also can be distinguished from cupressoid twigs of the fossil taxon

Glyptostrobus europaeus (BRONGNIART) UNGER which exhibit adpressed imbricate leaves (KUNZMANN 1999; HOLÝ et al. 2012; MA et al. 2013) (see Table 4 for a detailed comparison).

Comparison

CASPARY & KLEBS (1907) revised a monomorphic twig inclusion of *Widdringtonites oblongifolius* GOEPP. et MENGE from Baltic amber which was originally described by GOEPPERT (1853) and GOEPPERT & MENGE (1883). Figures of *W. oblongifolius* (CASPARY & KLEBS 1907, pl. IX, figs 52, 52a-d; herein Fig. 6) resemble our specimens of *Quasisequoia couttsiae*. Especially the branched twig of fig. 52 (Fig. 6a-d) shows similarities to the specimens GZG.BST.24633 (Fig. 5a-d) and GZG.BST.24606 (Fig. 5e-g), comprising the linear decurrent leaves with rounded apices and non-papillate margins; the amphistomatic stomata; the irregular orientation of the stomatal pores; the abaxial stomata arrangement in irregular patches in the lower leaf part; two stomata bands on the adaxial leaf side.

One specimen of *Widdringtonites oblongifolius* (Künow Collection No. 136, CASPARY & KLEBS 1907, pl. IX, fig. 53a-c; herein Fig. 6e-f) was identified as *Taiwania schaeferi* SCHLOEMER-JÄGER (JÄHNICHEN 1998) based on the drawings and descriptions of CASPARY & KLEBS (1907) and in comparison with a twig inclusion from Bitterfeld amber which was described as being analogous to the pictured twig of *W. oblongifolius* (JÄHNICHEN 1998). Scale-like cupressoid leaves of extant *Taiwania* HAYATA belong to adult twigs which exhibit a leaf size of 3 to 7 mm length \times 1.5 to 5 mm width (FLORIN 1931). However, the fossil is only 7 mm long in total, following the description of CASPARY & KLEBS (1907) and thus possibly represents a juvenile twig fragment. Juvenile twigs of extant *Taiwania* possess crescent-shaped acute leaves (FARJON 2005a) which is in contrast to the pictured fossil. Moreover, extant *Taiwania* exhibits large stomatal patches, proceeding from the base to the tip (FLORIN 1931), while the stomata patches of the described fossil are only located on the upper third of the leaves (Fig. 6e). The roundish cyclocytic stomata complexes and the irregular orientated stomatal pores of the pictured fossil (Fig. 6f) are rather similar to the stomata morphology of *Quasisequoia couttsiae*. Since the original specimen is lost, a definite assignment to a specific taxon is not possible. But based on the given information, it seems likely that this fossil is not affiliated to *Taiwania* and rather belongs to *Q. couttsiae*.

Two twig fragment inclusions of *Quasisequoia couttsiae* have already been described from one piece of Baltic amber as *Sequoia couttsiae* HEER (CASPARY & KLEBS 1907) which is the basionym for *Q. couttsiae* (KUNZMANN 1999). However, figures of this fossil show large triangular stomata patches on the abaxial leaf side which proceed from the base to the tip with densely arranged stomata complexes (CASPARY & KLEBS 1907, pl. XXIV, fig. 111a-c; herein Fig. 7a, b, d). Both features are rather untypical for *Q. couttsiae* where the stomata patches are mostly located on the lower third of the leaf and where stomata complexes are loosely dispersed within

the stomata patches. However, the leaf shape is similar to *Q. couttsiae* (KUNZMANN 1999). KLEBS himself stated that the inclusion was covered by fungi, hiding many

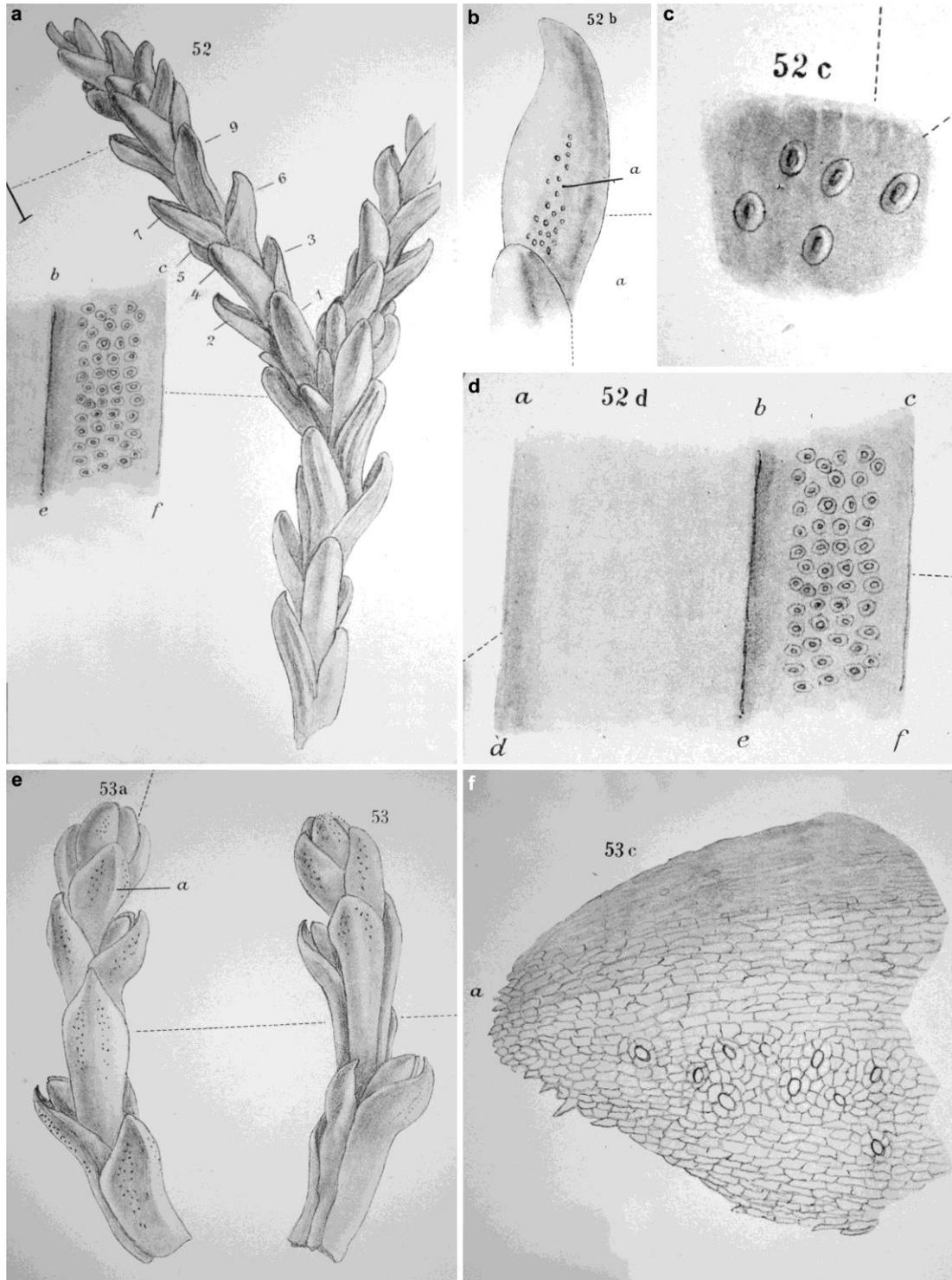


Fig. 6: Historic drawings of *Widdringtonites oblongifolius* (synonymous with *Quasisequoia couttsiae*) from Baltic amber (from the Goepfert Collection (a-d) and from the Künow Amber Collection (e, f), coll. No. 136, CASPARY & KLEBS 1907, pl. IX). (a) Overview of the twig. (b) Abaxial view of a singular leaf with stomata patch (indicated by a). (c) Stomata complexes. (d) Surface of leaf lamina (abaxial side indicated by a-b-d-e, adaxial side indicated by b-c-e-f). (e) Overview of the twig from two different angles; leaf indicated by a is magnified in (f). (f) Abaxial view of a singular leaf showing the stomata complexes and acute papillae along the leaf margin.

morphological details (CASPARY & KLEBS 1907, p. 139). Thus, the real identity of this particular specimen remains obscure since the type specimen is also lost.

Remarks

Quasisequoia couttsiae shows a great variability in the leaf shapes which is reflected in the present specimens. Generally, two leaf types can be distinguished: scale-like leaves and awl-shaped to lanceolate leaves (KUNZMANN 1999).

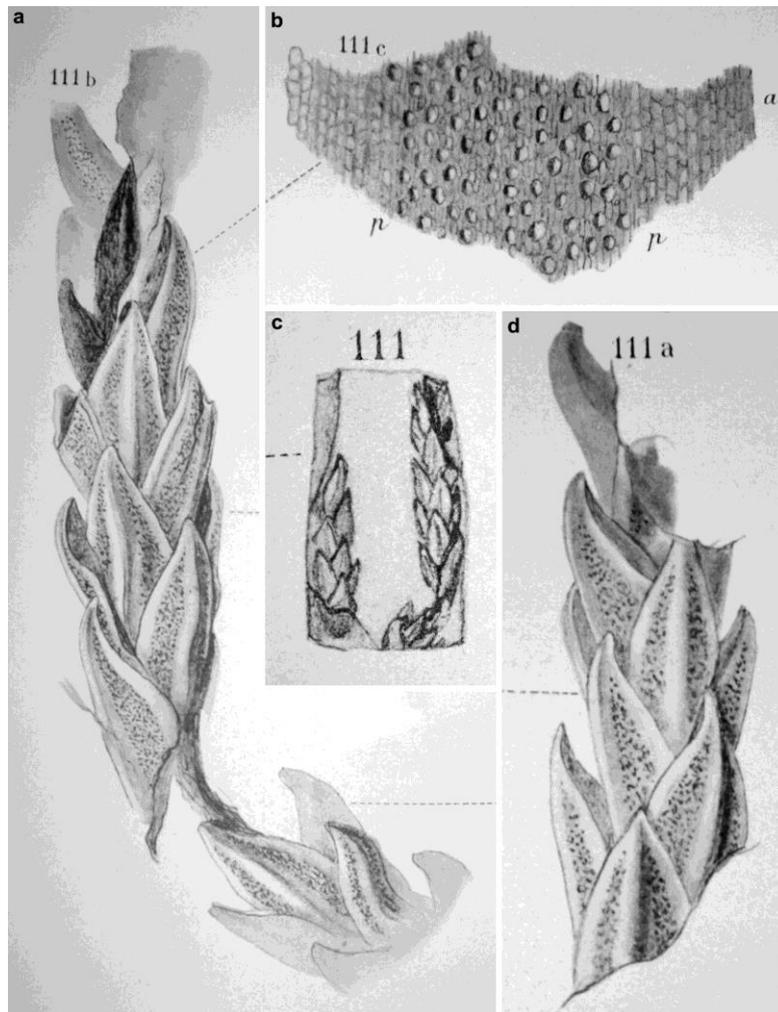


Fig. 7: Historic drawings of *Sequoia couttsiae* (synonymous with *Quasisequoia couttsiae*) from Baltic amber (from Caspary's private collection; CASPARY & KLEBS 1907, pl. XXIV). **(a)** Overview of one of the twigs. **(b)** Detail of the abaxial leaf surface of the twig shown in (a), stomata band indicated by *p-p*, and abaxial midrib indicated by *a*. **(c)** Overview of the amber specimen. **(d)** Overview of the other twig.

Genus *Taxodium* RICHARD, 1810*Taxodium* sp.

Figure 8

Specimen investigated

GZG.BST.24333

Description

Twig fragment 8 mm long (GZG.BST.24333), spirally arranged monomorphic lanceolate leaves (3.7 to 4.4 mm long \times 0.3 to 0.5 mm wide) with broad and long decurrent bases (Fig. 8). Leaves spreading from the twig at an angle of about 40° (Fig. 8a). Leaf apices acute and slightly incurved (Fig. 8c, f). Leaf margins with small teeth, arranged in long regular distances to each other (Fig. 8e). Leaves amphistomatic with more stomata on the adaxial side than abaxially. On adaxial side of lamina, stomata arranged in two stomatal bands separated by a longitudinal stomata-free zone (Fig. 8b). Stomatal bands composed of two to four stomata rows with stomata being closely arranged to each other (Fig. 8d). Abaxially, stomata are singular forming loose, gappy, short rows, located along the decurrent leaf base and on the lower third of the leaves. Stomata mainly perpendicularly orientated to the longitudinal leaf axis (Fig. 8d); only a few stomata oblique to parallel orientated. Subsidiary cells form a slender raised ring, surrounding the stomatal pit (Fig. 8g). More stomata details not preserved. Stomata complex 45 to 60 μm long \times 45 to 51 μm wide, roundish in shape. Stomatal pits are widely elliptic, 24 to 42 μm long (average 33 μm) \times 15 to 30 μm wide (average 22 μm). Ordinary epidermal cells arranged in regular rows parallel to the longitudinal leaf axis, 20 to 70 μm long (average 36 μm) \times 10 to 22 μm wide (average 18 μm), rectangular, elongated. Walls of ordinary epidermal cells straight, polar end walls mostly perpendicular to the lateral walls.

Identification

Due to the flat lanceolate leaf shape, the decurrent leaf bases and the amphistomatic stomatal distribution the genera *Taxodium* and *Sequoia* were considered. The stomatal distribution on the abaxial and adaxial surface of *Sequoia* lamina resembles the amber specimen, but in *Sequoia*, the stomata are mainly orientated parallel to the longitudinal leaf axis. In *Taxodium*, the leaves possess mostly perpendicular orientated stomata like in our amber specimen; that is why we assign the fossil to *Taxodium*. However, in extant and fossil *Taxodium* species, stomata are most abundant abaxially or equally distributed on both sides (KUNZMANN 1999; KUNZMANN et al. 2009), whereas the stomata are predominantly adaxially in the amber specimen. This could be an indicator for a hitherto unknown *Taxodium* species.

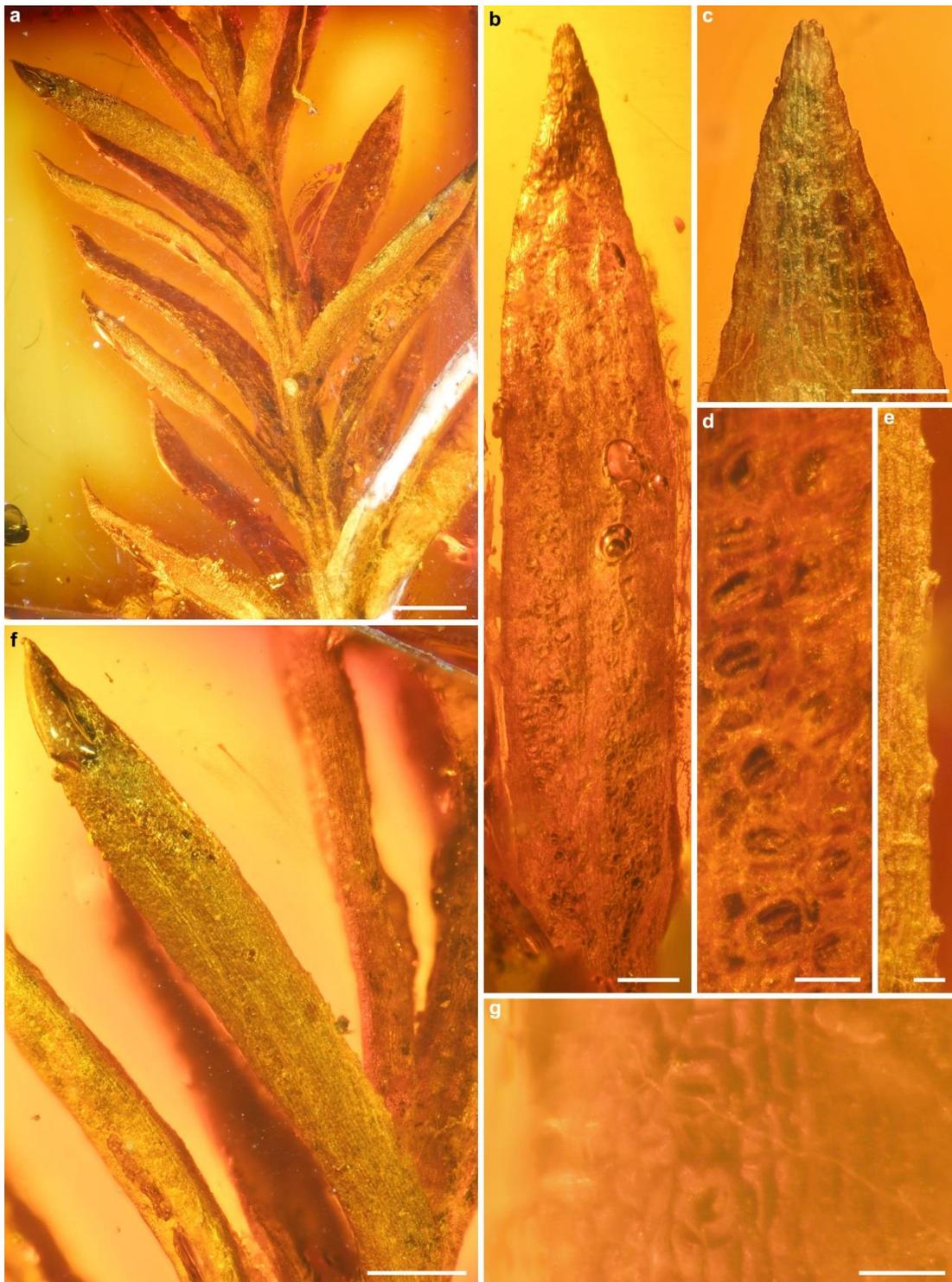


Fig. 8: Twig fragment of *Taxodium* sp., GZG.BST.24333. (a) Overview of the inclusion showing spirally arranged, lanceolate leaves. (b) Adaxial leaf side with two stomata bands on each side of the midline. (c) Acute leaf tip. (d) Enlargement of stomata rows shown in (b), stomatal pores perpendicular orientated towards the longitudinal midline. (e) Toothed leaf margin. (f) Abaxial leaf side. (g) Round stomata complexes on the abaxial side of leaf. Scale bars = 1 mm (a), 200 µm (b, c), 50 µm (d, e, g), 500 µm (f).

Comparison

Acute leaf inclusions with affinities to *Taxodium* were already described from Baltic amber (*Taxites affinis* GOEPP., GOEPPERT & BERENDT 1845; *Taxodium distichum* (L.) RICH., GOEPPERT & MENGE 1883), but the descriptions and figures of the *Taxodium* specimens do not reveal enough information to evaluate their affinities. A reevaluation of the putative *Taxodium* specimens was conducted by CASPARY & KLEBS (1907) who clearly expressed their doubts regarding the *Taxodium* affinities. The loss of the holotype precludes further investigations, whereby the *Taxodium* specimen presented herein becomes the first unambiguous *Taxodium* record in the Baltic amber flora.

Family Geinitziaceae L. KUNZMANN, 1999

Genus *Cupressospermum* MAI, 1960

Cupressospermum saxonicum MAI, 1960

Figure 9

Specimen investigated

GZG.BST.21895 (Hoffeins Amber Collection 186-1)

Selected synonymy

?1907 *Glyptostrobus europaeus* (BRONGNIART) UNGER, in CASPARY & KLEBS (1907, although misspelt *Glyptostrobus* herein), pp. 132-136, pl. XXII, figs 103, 103a-e; herein Fig. 10.

1960 *Cupressospermum saxonicum* MAI, p. 75, text-figs 1-2, pl. 3, figs 1-5.

1999 *Cupressospermum saxonicum* MAI, emend. KUNZMANN, p. 92, text-figs 18, 21:5, pl. XXI, XXII, XXIII.

Description

Twig fragment (GZG.BST.21895) 17 mm long × 2 mm wide, monomorphic, spirally arranged scale-like adpressed leaves with acute rounded tips, 1.6 to 3.2 mm long (average 2.4 mm) × 1 to 1.6 mm wide (average 1.4 mm) (Fig. 9a-b). Leaf margins entire, scariose, composed of slender rectangular cells, each terminating at their apical ends in a short round papilla (Fig. 9f). Abaxially, stomata located in two triangular shaped patches either side of the longitudinal broad midline; patches proceed from the leaf base towards the tip and terminate below the leaf apex (Fig. 9c). Stomata irregularly arranged within the patches and stomatal pores mostly perpendicularly but also obliquely orientated (Fig. 9d). Stomata complexes cyclocytic with 3 to 4 subsidiary cells (Fig. 9d-e). Stomata complexes are ovate to widely elliptic in shape, sometimes edged. Size of the stomata complexes 51 to 75

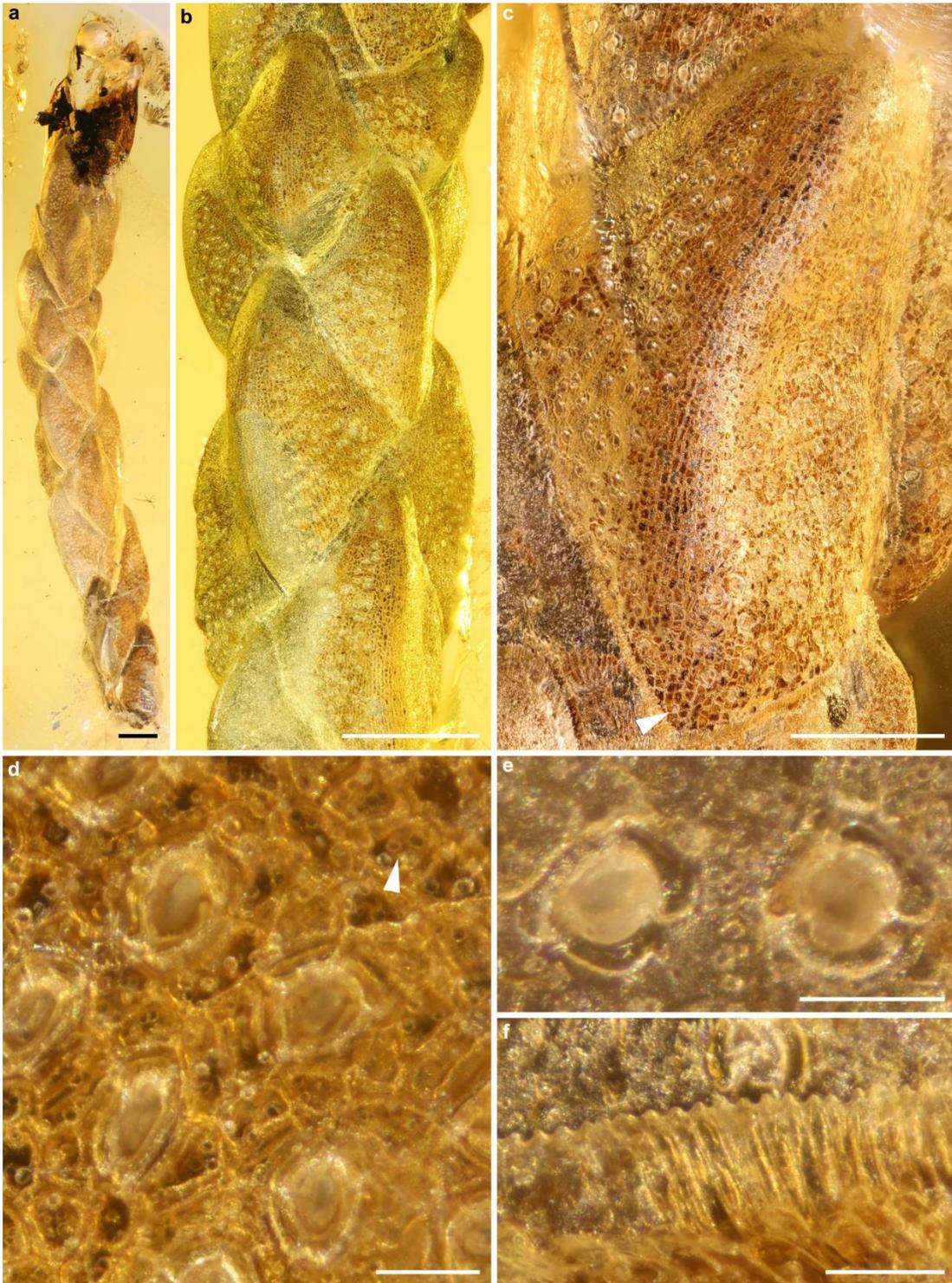


Fig. 9: Twig fragment of *Cupressospermum saxonicum*, GZG.BST.21895. **(a)** Overview of the inclusion. **(b)** Spirally arranged adpressed leaves. **(c)** Abaxial leaf surface showing two triangular stomata patches, arrowhead indicates the broadened ordinary epidermal cells at the basis. **(d)** Cyclocytic stomata complexes on the abaxial side of leaf, arrowhead indicates crystal bodies in ordinary epidermal cells. **(e)** Stomata complexes with three subsidiary cells. **(f)** Scariose leaf margin composed of papillate cells. Scale bars = 1 mm (a, b), 500 μm (c), 50 μm (d-f).

μm long (average $62 \mu\text{m}$) \times 33 to $58 \mu\text{m}$ wide (on average $46 \mu\text{m}$). The stomatal pits are roundish or widely elliptic, 24 to $42 \mu\text{m}$ long (average $31 \mu\text{m}$) \times 15 to $30 \mu\text{m}$ wide (average $21 \mu\text{m}$). Ordinary epidermal cells in stomata patches variously orientated with round crystal bodies (Fig. 9d). Ordinary epidermal cells of the stomata-free mid zone (middle and upper leaf part) composed of rectangular cells which are almost isodiametric (Fig. 9c), 21 to $45 \mu\text{m}$ long (average $32 \mu\text{m}$) \times 24 to $39 \mu\text{m}$ wide (average $30 \mu\text{m}$), with numerous crystal bodies. Ordinary epidermal cells of the basal stomata-free zones mostly broader than long, 15 to $30 \mu\text{m}$ long (average $24 \mu\text{m}$) \times 30 to $45 \mu\text{m}$ wide (average $38 \mu\text{m}$).

Identification

Among Cupressaceae, only few genera possess monomorphic twigs with a spiral phyllotaxis and rhombic-shaped scale leaves. Young shoots of *Sequoia* and mature shoots of *Quasisequoia* exhibit a similar leaf shape but have different stomata micromorphologies.

Cupressoid twigs of *Glyptostrobus pensilis* and *G. europaeus* are also similar to the specimen, but the *Cupressospermum* inclusion can be distinguished from *Glyptostrobus* by the following features: the leaf bases are not decurrent, the low number (three) of subsidiary cells which are cyclocytic or incomplete amphicyclic; the stomata complexes irregularly dispersed in triangular stomata patches proceeding below the leaf tip without reaching it; and the distinctive broadened ordinary epidermal cells of the basal stomata-free mid zone (see Table 4 as overview of the main morphological differences) (FLORIN 1931; KUNZMANN 1999).

Currently *Cupressospermum* is considered to be a monotypic genus with *C. saxonicum* known from the late Oligocene to the late Miocene of Europe (KUNZMANN 1999). As the Baltic amber twig does not differ from previously described material, neither by leaf gross-morphology nor by cuticle micromorphology, it is accommodated in *C. saxonicum* without any doubt. This implies a remarkable extension of the stratigraphic range of the genus and species towards the late Eocene.

Comparison

The presence of *Cupressospermum saxonicum* in Baltic amber was already suggested by KUNZMANN (1999) who noticed similarities between *C. saxonicum* and a Baltic amber inclusion of *Glyptostrobus europaeus* depicted by CASPARY & KLEBS (1907) (pl. XXII, figs 103, 103a-e, pl. XXIII, figs 104, 104a-b, 105, 105a-g). We found one of the original specimens of *G. europaeus* (CASPARY & KLEBS 1907, pl. XXII, figs 103, 103 a-e; herein Fig. 10) in the Königsberg Amber Collection (GZG.BST.23520). Regarding the leaf shape and leaf arrangement (Fig. 10a-c), the scariose papillate leaf margins (Fig. 10g) and the squared to rectangular ordinary epidermal cells (Fig. 10d, e), the *G. europaeus* specimen is similar to the



Fig. 10: Historic drawings of *Glyptostrobus europaeus* from Baltic amber and photos of this particular specimen. (a, d, f-h) from CASPARY & KLEBS 1907, pl. XXII; (b, c, e, i) GZG.BST.23520. (a, b) Overview of the twig. (c) Spirally arranged leaves, addressed to the twig. (d, e) Abaxial side of a singular leaf showing the stomata patch and the rectangular to squared ordinary epidermal cells. (f) Basal view of the twig, showing helical leaf arrangement. (g) Scariose leaf margin. (h, i) Stomata complexes on the abaxial side of leaf. Scale bars = 1 mm (a), 500 μm (b), 200 μm (e), 50 μm (i).

Cupressospermum inclusion. But the stomata patches of the *G. europaeus* specimen are smaller and only extend up to the middle part of the leaf (Fig. 10d). Due to the insufficient preservation of the cuticle of the *G. europaeus* specimen, important features of the stomata complexes (Fig. 10h-i) are not visible, thus it is impossible to confirm the suggested affinities to *C. saxonicum*.

Family Pinaceae SPRENG. ex F. RUDOLPHI, 1830

Genus *Abies* MILLER, 1754

Abies sp.

Figure 11

Specimen investigated

Jürgen Velten Amber Collection IX 73

Description

Two oblanceolate, pedicellate needles, 7.2 mm long \times 1.2 mm wide (widest part) (Fig. 11a). Margins entire. Leaf blade curved, resulting in slightly enrolled leaf margins towards the adaxial side (Fig. 11b). Adaxial and abaxial side without a pronounced longitudinal midrib. Leaf tip obtuse and thickened (Fig. 11b, c). Pedicel shrunken with disk-shaped round base, still attached to plant tissue remains (Fig. 11d-e). These tissue remains are lined with clavate multicellular trichomes (Fig. 11d, e). Needles are hypostomatic with two stomatal bands on the abaxial side (Fig. 11c). Within the bands, stomata are arranged in short to long irregular rows (Fig. 11f). At the widest needle part, there are 7 to 8 stomata rows in each band, number of rows decreases within both bands towards the needle base and tip. Stomata sunken, no Florin rings, stomata pits orientated parallel to the longitudinal midline (Fig. 11f). Stomata complexes 75 to 110 μm long (average 91 μm) \times 50 to 75 μm wide (average 58 μm). Stomata complexes irregular in shape, mostly roundish to elliptic or sometimes slightly edged, cyclocytic, composed of 6 to 7 subsidiary cells of which two are polar and the remaining ones laterally arranged (Fig. 11g). Polar subsidiary cells are unshared between adjacent stomata complexes, lateral subsidiary cells only rarely shared between neighbouring stomata complexes (Fig. 11g). Stomatal pits 35 to 50 μm long (average 45 μm) \times 20 to 35 μm wide (average 28 μm), round to elliptic in shape. Ordinary epidermal cells 54 to 114 μm long (average 89 μm) \times 14 to 20 μm (average 19 μm) wide, rectangular, elongated, with numerous crystal gaps in each cell (Fig. 11h). Lateral end walls more or less irregular, slightly undulate (Fig. 11h). Polar end walls of the ordinary epidermal cells straight, mostly oblique to the lateral cell walls, and sometimes perpendicular.



Fig. 11: Two needles of *Abies* sp. from Baltic amber (no. IX 73). **(a)** Overview of the needle inclusions. **(b)** Adaxial needle surface showing the slightly enrolled needle margins and the acute-obtuse apex of needle 1. **(c)** Abaxial surface of needle 1 with two stomata bands on each side of the longitudinal midline. **(d)** Base of both needles, left arrowhead points to the papillae on the plant tissue remains, middle arrowhead indicates the shrunken disc shaped needle base, right arrowhead shows ripped-off plant tissue remains from the twig. **(e)** Needle 1 from another angle showing the round shape of the base and the papillae (arrowhead) on the tissue remains. **(f)** Stomata band on abaxial surface of needle 1. **(g)** Stomata complexes. **(h)** Ordinary epidermal cells on abaxial side of needle 1 with slightly undulate lateral walls and numerous crystal gaps (arrowhead). Scale bars = 1 mm (a), 500 μ m (b, c), 200 μ m (d, e), 50 μ m (f, g), 10 μ m (h).

Identification

The cuticular features, as well as the shape of the needle inclusions appear similar to *Picea*. However, most *Picea* species are four-angled in cross section and only rarely dorsiventrally flattened. Furthermore, *Picea* differs from the amber specimen in the following features: needles are epistomatic or amphistomatic; crystal gaps are only rarely found; needle base with short petiole, attached to a pulvinus (thickened peg, protruding from the twig) (FLORIN 1931; FARJON 1999; ECKENWALDER 2009).

In living needles of extant *Picea*, the pulvinus breaks off with the needle attached; only if dead, the pulvinus remains on the twig, while the needle is dropped (FARJON 1999). Both needle inclusions show papillate ripped up plant material at their bases which is, however, not peg shaped, indicating that both needles were directly ripped off the twig. Moreover, the bases of both needles are disc-shaped which is an indicative feature of *Abies* (FLORIN 1931; ECKENWALDER 2009). Further similarities to *Abies* are the needle shape, the obtuse apex, the indistinct abaxial midrib, the entire margins and the hypostomatic stomata distribution (FLORIN 1931). Besides the gross morphology, the micromorphology of the stomata and the ordinary epidermal cells are similar to *Abies*, especially the stomata arrangement in short to long rows, the unshared polar subsidiary cells, the indistinct undulate walls of the ordinary epidermal cells and the crystal gaps of the epidermis (FLORIN 1931). However, the amber specimens differ from extant *Abies* in some aspects. In *Abies*, the stomata complexes are arranged at a more regular distance to each other than in the amber specimens. Following FLORIN (1931), *Abies* possesses amphicyclocytic stomata with 4 to 6 subsidiary cells which is also different to the amber inclusions. However, ECKENWALDER (2009) mentioned 1 to 3 cycles of subsidiary cells which shows that there is a variability of the cellular structure of stomata complexes in *Abies*.

Due to the distinctive disc-shaped needle base as well as the above mentioned similarities, we assign the fossils to the genus *Abies*. The identification of *Abies* species that is only based on fossil or extant needle cuticles is generally difficult (MAI 1997; KUNZMANN & MAI 2005; ECKENWALDER 2009). Hence, it is impossible to evaluate the amber inclusions at infrageneric level.

Comparison

Abies taxa are common constituents of the Central European Paleogene floras, often represented by the fossil-species *A. resinosa* MAI, which is recorded since the late Oligocene of Lusatia (Germany), up to the Pliocene of Thuringia (Germany) (MAI 1997, 2000; KUNZMANN & MAI 2005). *A. resinosa* is based on dispersed seeds, but associated dispersed leaves are also accommodated in this fossil-species. However, *A. resinosa* leaves can be distinguished from the amber specimen by the emarginated leaf tip and the stomata micromorphology (KUNZMANN & MAI 2005).

A further common fossil-taxon of *Abies* is *A. albula* (LUDWIG) MÜLLER-STOLL from the Pliocene of Dernbach (Rhineland-Palatinate, Germany) (MÜLLER-

STOLL 1938) which shares the needle gross morphology with the amber specimens, but is different in the stomata micromorphology. *Abies* taxa were also described from Baltic amber (e.g. in CASPARY & KLEBS 1907), but are of angiosperm origin (see *Dicotylophyllum* sp. below, for details).

Except for *Abies* pollen from the European Eocene, no further *Abies* fossils have been recorded so far from Eocene sediments of Europe (XIANG et al. 2007). Consequently, the amber specimen presented herein is the first macrofossil record of *Abies* from the Eocene of Europe and the first undisputed one from Baltic amber.

Genus *Cathaya* CHUN et KUANG, 1962

Cathaya sp.

Figure 12

Specimen investigated

GZG.BST.23533

Description

Needle narrow oblong, petiolate, flattened, 15 mm long \times 4 mm wide (widest part), tapering towards the leaf base (0.1 cm wide) (Fig. 12a-b). Apex rounded, margins entire, petiole 2 mm long with slightly discoidal broadened leaf base (Fig. 12b). Adaxial side flattened with a slightly sunken longitudinal midline in the lower third of the leaf (Fig. 12a). Stomata sunken, only located on the abaxial side (hypostomatic) in two narrow bands, separated by the longitudinal midline (Fig. 12b). Each stomatal band composed of 6 to 7 stomata rows which are very closely spaced to each other or rarely separated by a single longitudinal row of ordinary epidermal cells (Fig. 12c). Stomata pores uniformly longitudinally orientated (Fig. 12c). Stomata complexes almost rectangular to box shaped with cyclocytic stout subsidiary cells (Fig. 12d). Polar subsidiary cells rectangular, straight to slightly convex sided and not shared between adjacent stomata complexes (Fig. 12d). Stomata complexes 33 to 54 μm long (average 43 μm) \times 30 to 45 μm wide (average 36 μm). Stomatal pit rectangular to elliptic, 12 to 24 μm long (average 18 μm) \times 12 to 24 μm wide (average 15 μm). Ordinary epidermal cells of the abaxial midline slender and narrow, 180 to 390 μm long (average 279 μm) \times 13 to 20 μm wide (average 18 μm); ordinary epidermal cells of the abaxial stomata-free bands along the margins are 120 to 230 μm long (average 167 μm) \times 20 to 40 μm wide (average 58 μm) and thus, wider and shorter than ordinary cells of the midline. All ordinary cells are elongated and rectangular with straight cell walls (Fig. 12c); polar end walls of ordinary cells are perpendicular or oblique to lateral walls.

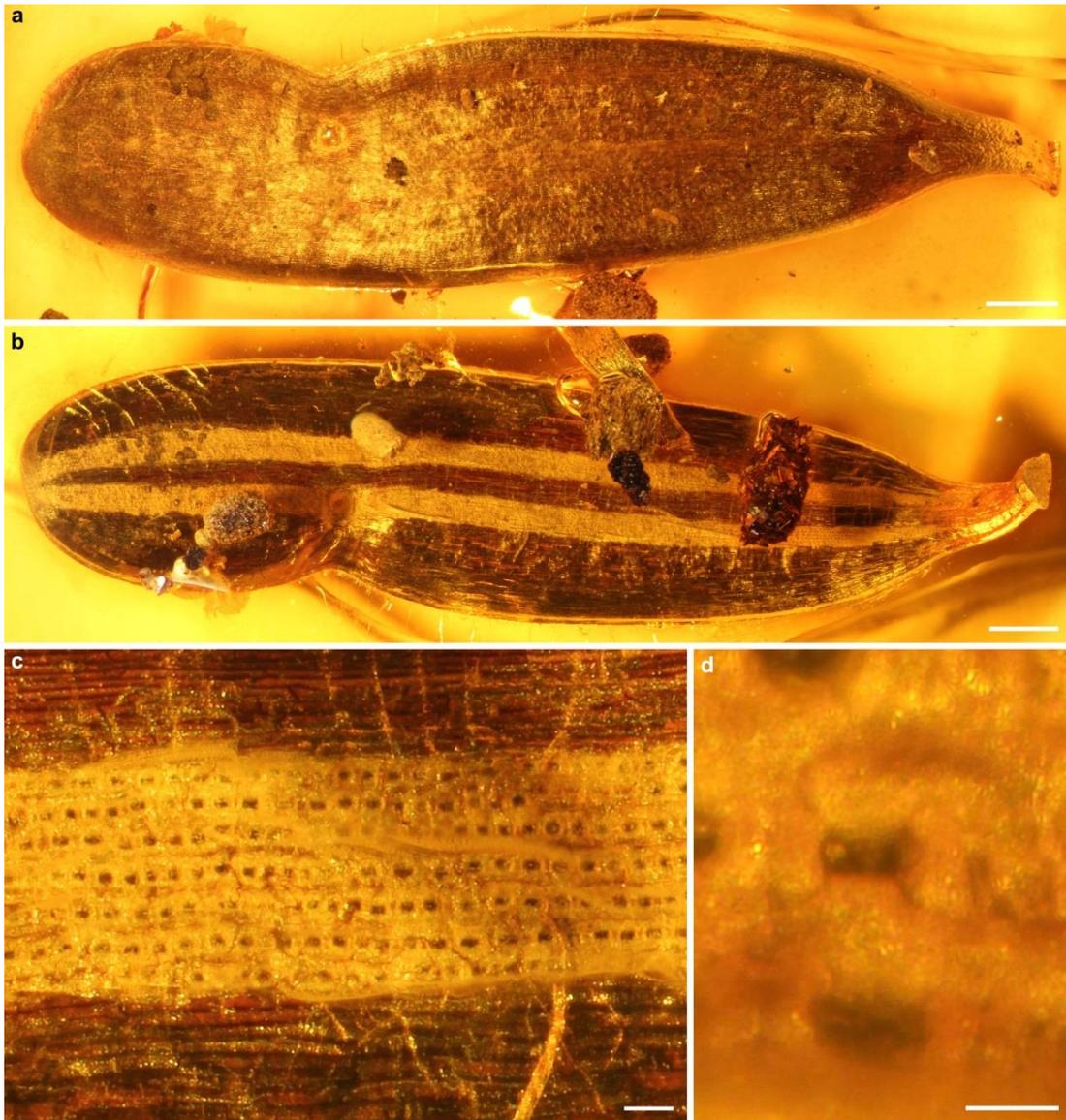


Fig. 12: Needle of *Cathaya* sp. from Baltic amber, GZG.BST.23533. **(a)** Adaxial needle side. **(b)** Abaxial needle side with two stomata bands. **(c)** Middle portion of the lower stomatal band, shown in **(b)** with closely arranged stomata rows. Note the narrow ordinary cells of the midline in comparison to the broader ordinary cells of the stomata-free margin. **(d)** Box-shaped stomata complex with four subsidiary cells. Scale bars = 1 mm (a, b), 100 μm (c), 20 μm (d).

Identification

The most striking feature of this specimen is the very closely spaced, strict and continuous stomata rows, which are typical of *Cathaya* (KUNZMANN & MAI 2005). *Pseudotsuga* CARRIÈRE has similar leaf morphology and stomata arrangement but the leaves can be distinguished from *Cathaya* by several rows of ordinary epidermal cells that separate the individual stomata files from each other within a stomatal band (KUNZMANN & MAI 2005). However, a determination to species level is not possible since it requires morphological information about the female cone and seed morphology.

Genus *Nothotsuga* H. H. HU ex C.N. PAGE, 1989

Nothotsuga protogaea L. KUNZMANN et MAI, 2005

Figures 13 and 14

Specimens investigated

GZB.BST.21896 (Hoffeins Amber Collection 130-1), GZG.BST.23535, GZG.BST.24406

Synonymy

2005 *Nothotsuga protogaea* L. KUNZMANN et MAI, pp. 89-95, text-fig. 6, pl. 8, 9.

Description

Linear petiolate needles, 5.5 to 9.7 mm long \times 0.9 to 1.1 mm wide (for detailed measurements of each specimen see Table 5), apices obtuse, margins entire (Figs 13a-b, e-f; 14a, d, e). Petiole pronounced, not twisted, 0.6 to 1 mm long \times 0.3 to 0.4 mm wide. Amphistomatic. Adaxial side with only 4 to 5 gappy stomata rows (in one case only one short row, Fig. 13a). Abaxial side with two stomatal bands, each of them composed of 3 to 6 stomata rows and separated by a broad stomata-free midline (Fig. 13b, f; 14b). Stomata pores are orientated parallel to the longitudinal needle axis, stomata sunken and amphicylocytic (Figs 13c, g; 14c, f). Stomata complexes 60 to 249 μm long \times 42 to 96 μm wide, elliptic in shape. Polar subsidiary cells elongated and often shared between the stomata of one row (Figs 13c; 14f). Lateral subsidiary cells arch-shaped, and not shared (Fig. 13d, h). Stomatal pit elliptic elongated or roundish, 21 to 45 μm long \times 9 to 35 μm wide. Ordinary epidermal cells elongated, rectangular, 35 to 229 μm long \times 10 to 36 μm wide. Walls of ordinary epidermal cells straight, sometimes curved, but not undulate (Figs 13g, 14f), polar end walls mostly slightly inclined or oblique to the lateral cell walls

Identification

The amber inclusions match the diagnosis of *Nothotsuga protogaea*, (given by KUNZMANN & MAI 2005) which is the only known fossil species of this genus in Europe.

At first sight, the pronounced petiole, the linear leaf shape and the obtuse leaf tip of the amber specimens appear similar to *Abies* and *Tsuga* (ENDL.) CARRIÈRE. However, *Abies* needles have a broadened suction-cup shaped leaf base, undulate cell walls and strict continuous stomata rows. The micromorphology of the stomata complexes of *Abies* is also different to the fossils: in *Abies*, stomata complexes possess short, often squarish polar subsidiary cells that are only rarely shared between adjacent stomata complexes of the same row (ECKENWALDER 2009; FLORIN 1931). In contrast, polar subsidiaries of *Nothotsuga* are rather elongated and often shared between adjacent stomata complexes (KUNZMANN & MAI 2005). *Tsuga*

needles have a similar stomata type as in the presented amber specimens but they are hypostomatic, have a twisted petiole and thus, can be excluded (Kunzmann & Mai 2005).

Comparing the leaf inclusions to the only known fossils of *Nothotsuga* from the European Neogene (*Nothotsuga protogaea*, KUNZMANN & MAI 2005), many similarities can be found, comprising the gross morphology (needles petiolate, linear-lanceolate with entire margins, acute-obtuse apex, dorsoventrally flattened), as well as the amphistomatic stomata (adaxial 1-3 gappy stomata rows, mostly not reaching the leaf base; abaxial 4-11 stomata rows; stomata rows separated by rows of ordinary epidermal cells) and the micromorphology of the stomata complexes (amphicyclocytic, polar subsidiary cells often shared between adjacent stomata complexes, lateral subsidiary cells unshared, walls of subsidiary and ordinary cells straight or arch-shaped, and not sculptured). Thus, there is sufficient evidence to assign the amber specimens to *Nothotsuga protogaea*, which is the first record of this particular taxon from Baltic amber.

Tab. 5: Measurements of the *Nothotsuga protogaea* specimens from Baltic amber. Centered numbers of the leaf and stomata sizes are average values; the size ranges are provided in brackets.

Collection number	GZG.BST.21896 Needle 1	GZG.BST.21896 Needle 2	GZG.BST.23535	GZG.BST.24406
Leaf				
Length	5.5 mm	6.5 mm	9.7 mm	6.5 mm
Width (middle)	1 mm	1.1 mm	0.9 mm	0.9 mm
Petiole				
Length	1 mm	0.9 mm	0.7 mm	0.6 mm
Width	0.3 mm	0.3 mm	0.4 mm	0.3 mm
Stomata complex				
Length	(78)-120-(249) μm	(105)-131.4-(156) μm	(90)-107-(132) μm	(60)-82-(111) μm
Width	(45)-61-(84) μm	(60)-78-(93) μm	(51)-71-(96) μm	(42)-51-(60) μm
Stomatal pit				
Length	(24)-34-(45) μm	(21)-24-(27)	(27)-35-(45) μm	(21)-27-(35) μm
Width	(15)-20-(27) μm	(9)-13-(15) μm	(12)-15-(21) μm	(18)-31-(35) μm
Ordinary epidermal cells				
Length	(86)-157-(229) μm	(77)-123-(187) μm	(39)-74-(165) μm	(35)-77-(115) μm
Width	(16)-18-(20) μm	(20)-25-(27) μm	(18)-25-(36) μm	(10)-16-(20) μm

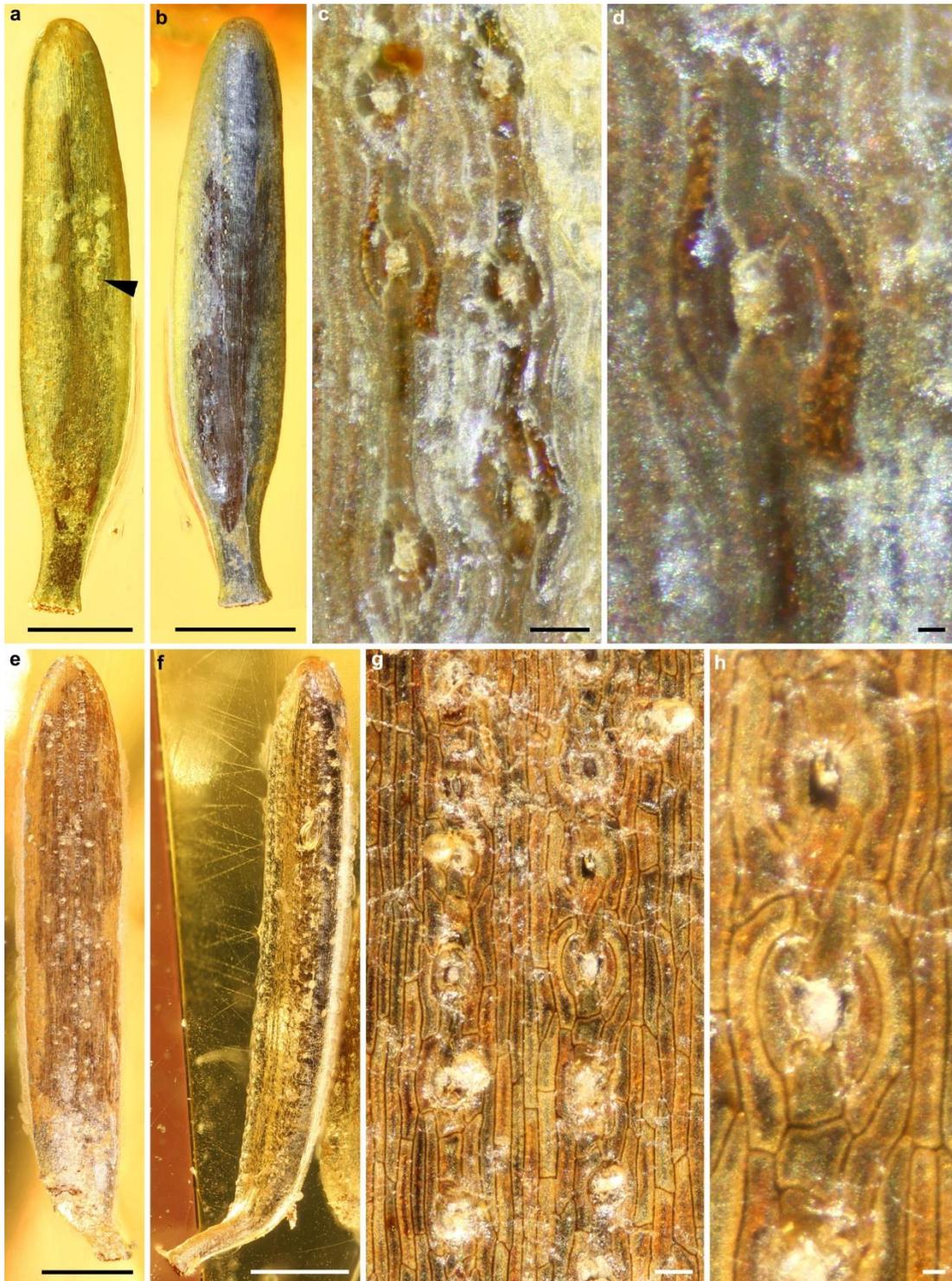


Fig. 13: Two needles of *Nothotsuga protogaea* from Baltic amber, situated in a single piece of amber, GZG.BST.21896. **(a, e)** Adaxial needle side; arrowhead in (a) indicates short stomata row. **(b, f)** Abaxial needle side. **(c)** Abaxial stomata row; note the elongated polar subsidiary cells. **(d, h)** Amphicyclocytic stomata complexes from the abaxial (d) and adaxial (h) needle side. **(g)** Adaxial stomata row. Scale bars = 1 mm (a, b, e, f), 50 μm (c, g), 10 μm (d, h).

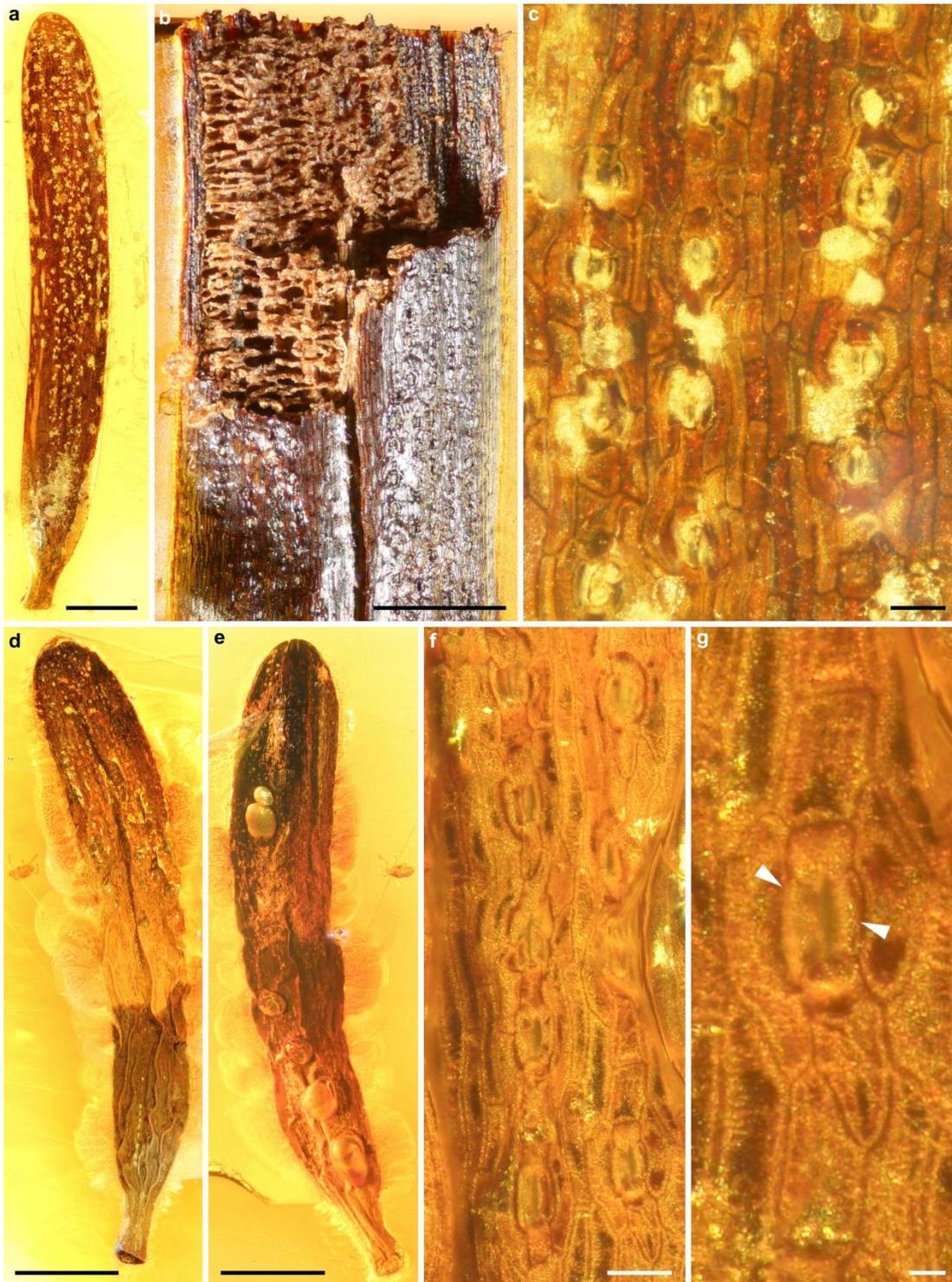


Fig. 14: Needles of *Nothotsuga protogaea* from Baltic amber, (a-c) GZG.BST.23535, (d-g) GZG.BST.24406. (a) Adaxial needle side. (b) Abaxial surface of lamina showing stomata rows and a sunken midline; internal tissue is exposed at the amber surface. (c) Adaxial stomata rows, showing amphicyclic stomata complexes. (d) Adaxial and (e) abaxial needle side, both with very shrunken surfaces. (f) Adaxial stomata rows. (g) Stomata complex with visible guard cells (arrowheads) which are normally sunken, but probably were pressed upwards to the outer epidermal surface during the fossilization process. Scale bars = 1 mm (a, d, e), 500 μ m (b), 50 μ m (c, f), 10 μ m (g).

Genus *Pinus* L., 1753

Needles of the genus *Pinus* are easily distinguishable from other conifers due to the grouping of the needles in bundles (fascicles) sheathed by scales at the base; the shape and size of the needle and the strict, continuous and monotonous stomata rows, proceeding parallel to the longitudinal leaf axis (FARJON 2005b).

We have discovered additional specimens of *Pinus* needle inclusions from Baltic amber in historic and recent amber collections. Based on needle cuticle micromorphology only, species assignments of the needle inclusions to extant *Pinus* taxa are difficult to achieve without further information regarding the cone and seed morphology as well as the number of vascular bundles in the leaf.

GOEPPERT & BERENDT (1845), GOEPPERT & MENGE (1883), CONWENTZ (1890) and CASPARY & KLEBS (1907) described several new species of *Pinus*, based on needle inclusions from Baltic amber. The whereabouts of the holotypes of these specimens are unknown. Thus, we compared *Pinus* needle inclusions to illustrations and descriptions of the lost holotypes, published by the named authors. Based on this comparison, one specimen is tentatively accommodated into a fossil *Pinus* species from Baltic amber; further specimens can be assigned with certainty to three fossil species of *Pinus*, exclusively described from Baltic amber. Since the holotypes of *Pinus* species from Baltic amber are lost, newly discovered *Pinus* inclusions were erected as neotypes and their diagnoses were accommodated to the new findings. All specimens can be distinguished from each other by the needle shape, the needle number per fascicle as well as the stomata position. To facilitate the identification of *Pinus* needle inclusions from Baltic amber, we assigned the specimens to four morphotypes which can be easily distinguished from each other:

Identification key

- | | |
|--|---|
| 1a. needles amphistomatic..... | 2 |
| 1b. needles epistomatic..... | 3 |
| 2a. cross section semi-circular shaped, fascicle of two needles..... | |
| | Morphotype 1: <i>Pinus baltica</i> |
| 2b. cross section broadly triangular, abaxially rounded, fascicle of three needles | |
| | Morphotype 2: <i>Pinus serrata</i> |
| 3a. cross section broadly triangular, abaxially rounded, fascicle of three needles | |
| | Morphotype 3: <i>Pinus</i> aff. <i>schiefferdeckeri</i> |
| 3b. cross section triangular, adaxial side flat, abaxial side slightly convex, fascicle of five needles..... | Morphotype 4: <i>Pinus cembraefolia</i> |

The well-known *Pinus succinifera* (GOEPP.) CONW. which has been discussed as the source tree of Baltic amber is not treated here, since this species is based on wood and root fragment inclusions (CONWENTZ 1890).

Pinus baltica CONW., 1890 emend.

Figure 15

Neotype

GZG.BST.24652, selected herein, Fig. 15.

Synonymy

1890 *Pinus baltica* CONWENTZ, p. 68, pl. XVI, figs. 10, 11; pl. XVII, fig. 2; herein Fig. 16a-c.

Additional specimens investigated

GZG.BST.21899 (Hoffeins Amber Collection 229), GZG.BST.21900 (Hoffeins Amber Collection 1069/4)

Emended diagnosis

Fascicle of two needles; needles > 5 mm long, linear, elongated, slightly curved; needle 1-2 mm wide, cross section semi-circular shaped; needle tip acute, pointed; short, rounded lobes in regular distances along needle margins; amphistomatic, 10-12 stomata rows abaxially and adaxially, stomata rows singular; stomata complexes cyclocytic, 6 subsidiary cells, polar subsidiary cells elongated, shared between adjacent stomata complexes, lateral subsidiary cells rectangular, unshared; stomatal pits round to elliptic; lateral walls of ordinary epidermal cells undulate.

Description

Needle fragment (GZG.BST.24652), 48 mm long × 22 mm wide, tapering towards a pointed acute tip (Fig. 15a). Needle base not preserved. One side flattened (adaxial, Fig. 15b), the other side rounded (abaxial, Fig. 15c), indicating that the specimen was originally grouped in a fascicle of two needles. Needle margins regularly dentate with short, rounded lobes (Fig. 15d). Strict, continuous stomata rows singular, separated by numerous rows of ordinary epidermal cells (Fig. 15b). Stomata rows are located on both leaf sides (amphistomatic) with about 11 stomata rows on the flat (adaxial) side and 10 to 12 stomata rows on the rounded (abaxial) side. Stomata complexes cyclocytic, 33 to 54 µm wide (average 46 µm). Elongated polar subsidiary cells are mostly shared between adjacent stomata (Fig. 15e), separating the stomata complexes at a distance of 36 to 78 µm from each other. Lateral subsidiary cells unshared, rectangular (Fig. 15e). Stomatal pits are round to elliptic, size of the stomatal pits 27 to 36 µm long (average 32 µm) × 18 to 27 µm wide (average 23 µm). Ordinary epidermal cells rectangular with undulate lateral cell walls (Fig. 15f); Width of ordinary cells 15 to 21 µm (average 17 µm; cell length not measurable, since polar cell walls not preserved).

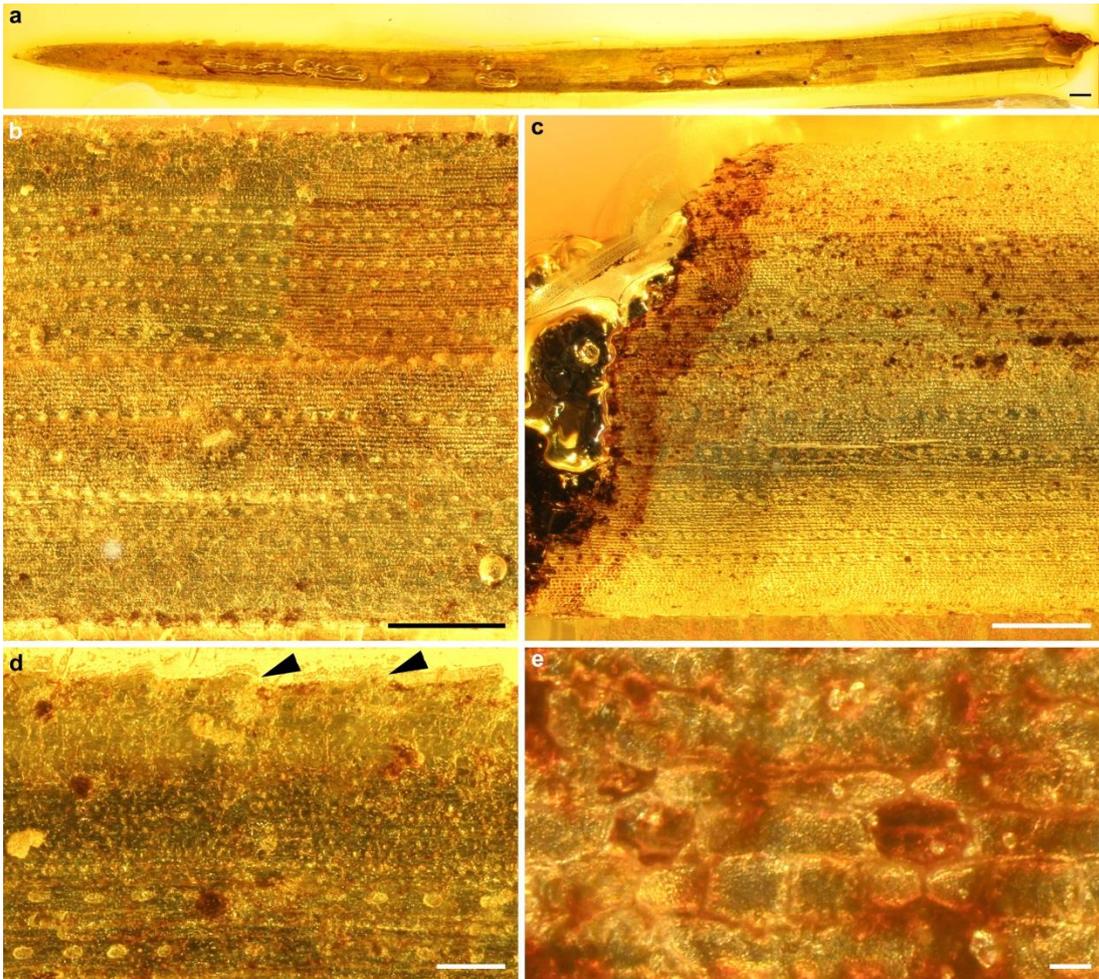


Fig. 15: Needle fragment of *Pinus baltica* (Neotype, morphotype 1, GZG.BST.24652). (a) Overview of the needle fragment. (b) Flattened adaxial side showing regular stomata rows. (c) Rounded abaxial side close to the degraded needle base, surface of lamina with regular stomata rows. (d) Needle margin with short rounded lobes (arrowheads). (e) Stomata complexes, note the undulate lateral walls of ordinary epidermal cells. Scale bars = 1 mm (a), 500 µm (b, c), 100 µm (d), 10 µm (e).

Identification

CONWENTZ (1890) described three *Pinus* species from Baltic amber which are characterized by a fascicle of two amphistomatic needles (*Pinus baltica* CONW., Fig. 16a-c; *P. banksianoides* GOEPP. et MENGE, Fig. 16d-f and *P. silvatica* GOEPP. et MENGE, Fig. 16g-i; see Table 6 for comparison). *P. baltica* and GZG.BST.24652 share relevant morphological features comprising the semi-circular cross sections (Fig. 16a, c); amphistomatic stomata distribution; and stomata arranged in single rows which are separated by several rows of ordinary epidermal cells (Fig. 16c). The walls of ordinary epidermal cells of *P. baltica* are straight; moreover, the needle of *P. baltica* seems to possess teeth along the leaf margins which succeed at a broad distance to each other (Fig. 16c). In the amber specimen GZG.BST.24652, the distance between the teeth is smaller. Besides this difference, however, we see enough similarities to assign specimen GZG.BST.24652 to the fossil species *Pinus baltica*.

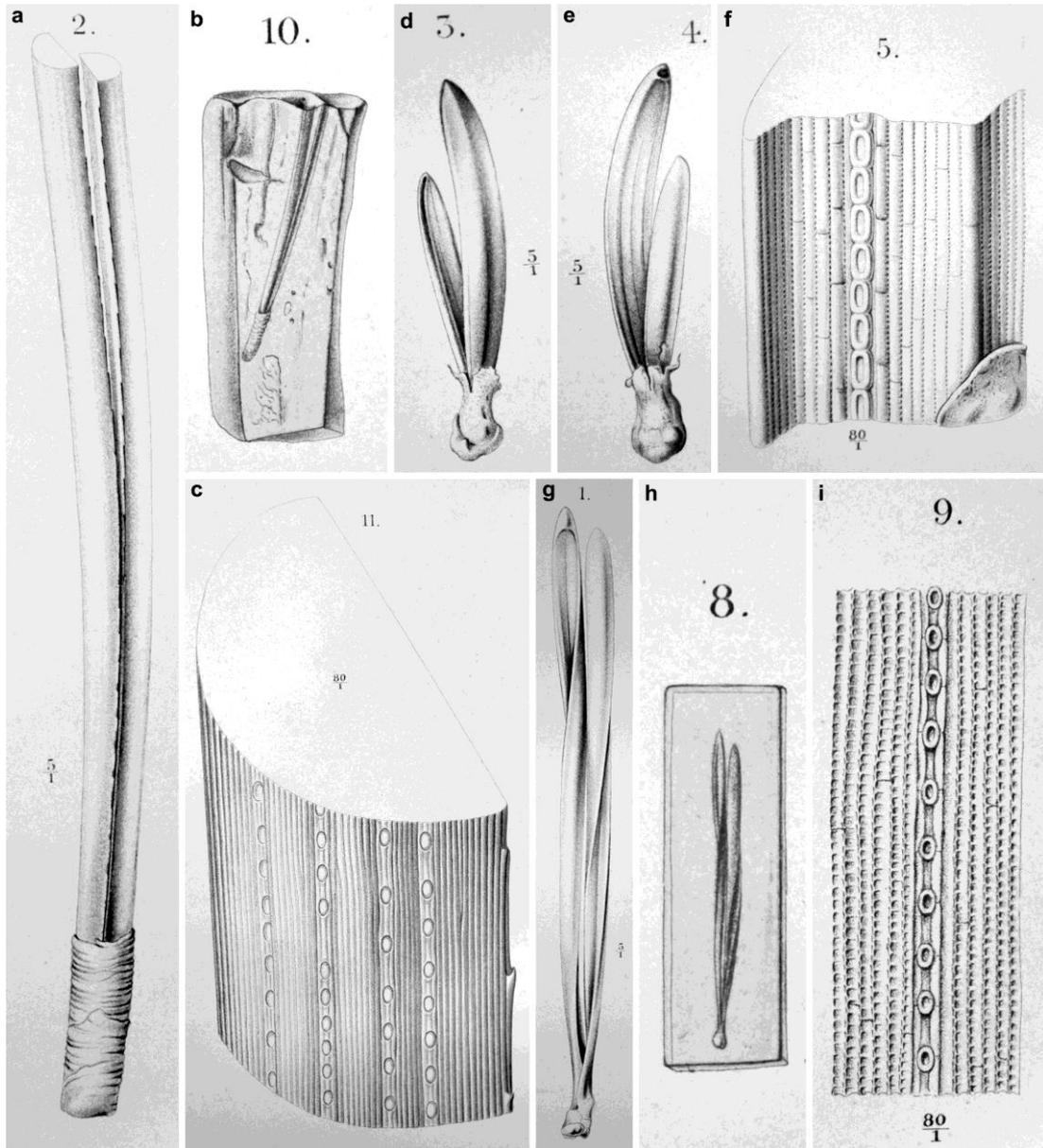


Fig. 16: Historic drawings of needle inclusions of *Pinus baltica* (a-c), *P. banksianoides* (d-f) and *P. silvatica* (g-i) from Baltic amber (Menge Collection; from CONWENTZ 1890, pl. XVI and XVII). **(a)** Fascicle of two needles. **(b)** Amber specimen with the needle fascicle shown in (a). **(c)** Abaxial needle side with regular stomata rows and toothed margin. **(d, e)** Fascicle of two needles from two different angles. **(f)** View on the adaxial needle side, showing a single row of densely arranged stomata complexes. **(g)** Fascicle of two needles which both are helically twisted. **(h)** Amber specimen with the needle fascicle shown in (g). **(i)** Single row of widely arranged stomata complexes from the needle surface.

Comparison

The needle inclusion GZG.BST.24652 can be distinguished from *Pinus banksianoides* in several aspects: the needle margins are entire (Fig. 16f) and the needle shape of *P. banksianoides* is oblong-linear with a crescent-shaped needle cross section (Fig. 16d-e). The stomata of *P. banksianoides* are only poorly preserved (Fig. 16f) but the very short polar subsidiary cells were highlighted by CONWENTZ (1890). *Pinus silvatica* and GZG.BST.24652 are similar in the stomata arrangement and morphology (Fig. 16i). However, the needles of *P. silvatica* are helically twisted and exhibit entire margins (Fig. 16g).

Tab. 6: Morphological features of the needle inclusion *Pinus baltica* (Neotype, morphotype 1, GZG.BST.24652), compared to historic descriptions of *Pinus* needle inclusions from Baltic amber. Information about the historic specimens is taken from descriptions and figures of the indicated references. Certain features which were not visible or absent are indicated by '-'

Taxon	<i>Pinus baltica</i> GZG.BST.24652, Neotype	<i>Pinus baltica</i>	<i>Pinus banksianoides</i>	<i>Pinus silvatica</i>
Preservation	fragment of the upper part of the needle	needle fragments of the lower part of the fascicle	entire needle fascicle	entire needle fascicle
Needle				
No./fascicle	2	2	2	2
Cross section	semicircular	semicircular	crescent-shaped	abaxially convex; needles helically twisted
Size (singular needle)				
Length	48 mm	24 mm	7 mm	22.5-23 mm
Width	2.2 mm	1.15 mm	0.5-0.8 mm	1 mm
Margin	regularly dentate	regularly dentate	entire, glandular hairs	entire
Stomata				
Distribution	amphistomatic	amphistomatic	-	amphistomatic
Stomata rows	singular; separated by numerous epidermal cell rows	singular; separated by numerous epidermal cell rows	singular	singular; along each needle margin 2 rows
Adaxial	10 to 12	-	-	7
Abaxial	Ca. 11	10	-	4
Subsidiary cells				
Polar cells	shared, elongated	shared, elongated	shared, very short	shared, elongated
Lateral cells	unshared, rectangular	unshared, narrow	-	unshared, narrow
Size of stomatal pit				
Length	(27)-32-(36) µm	43.7 µm	37 µm	15.6 µm
Width	(18)-23-(27) µm	-	-	-
Shape	round to elliptic	elongated elliptic	oblong elliptic	elliptic
Ordinary epidermal cells				
Length	-	-	-	-
Width	(15)-17-(21) µm	-	-	-
Lateral cell walls	undulate	straight	undulate	undulate
Polar cell walls	-	-	perpendicular	-
References				
	this paper	CONWENTZ 1890	CONWENTZ 1890	CONWENTZ 1890

Pinus serrata CASP., 1907 emend.

Figure 17

Neotype

GPIH 4584, selected herein, Fig. 17.

Synonymy

1907 *Pinus serrata* CASP., pp. 167-169, pl. XXX, figs 129, 129a-129f. herein Fig. 18.

Emended diagnosis

Fascicle of three needles, needle > 28 mm long, linear; needle cross section broadly triangular, 1.2-2.5 mm wide, abaxially rounded; needle margins and adaxial keel regularly serrated with multicellular papillae; amphistomatic, abaxially 8-15 rows, adaxially 6-9 rows on each side of keel; stomata in single or rarely double rows; stomata complexes cyclocytic, rectangular shape, 6 subsidiary cells (two polar, four lateral), polar subsidiary cells shared between adjacent stomata complexes; stomatal pit round to elliptic; lateral walls of ordinary epidermal cells undulate.

Description

Needle fragment (GPIH 4584), 28 mm long × 2.5 mm wide (width of the abaxial side) (Fig. 17a-b). Cross section broad-triangular with two flat sides (adaxial) and one rounded side (abaxial) (Fig. 17g), indicating that the needle was originally grouped in a bundle of three needles. Leaf margins and adaxial keel with multicellular papillae, arranged at regular distance to each other (Fig. 17f). Amphistomatic stomata distribution, with single (rarely double), strict, continuous stomata rows, separated by several rows of ordinary epidermal cells (Fig. 17e). Abaxially about 11 to 15 stomata rows (Fig. 17c), adaxially on each side with about 6 to 9 rows (Fig. 17d). Stomata complexes 42 to 51 µm wide (average 45 µm), rectangular shaped. Six subsidiary cells, two polar subsidiaries and four lateral subsidiaries (Fig. 17h). Elongated polar subsidiary cells are shared between adjacent stomata complexes, widely separating the stomata from each other at distances of 60 to 120 µm. Lateral subsidiary cells short, unshared, rectangular. Stomatal pits round to elliptic, 24 to 36 µm long (on average 30 µm) × 12 to 24 µm wide (average 19 µm). Ordinary epidermal cells rectangular, elongated, 96 to 258 µm long (average 173 µm) × 12 to 24 µm wide (average 17 µm). Lateral walls of ordinary epidermal cells undulate (Fig. 17h), polar end walls straight and oblique or perpendicular to lateral walls.

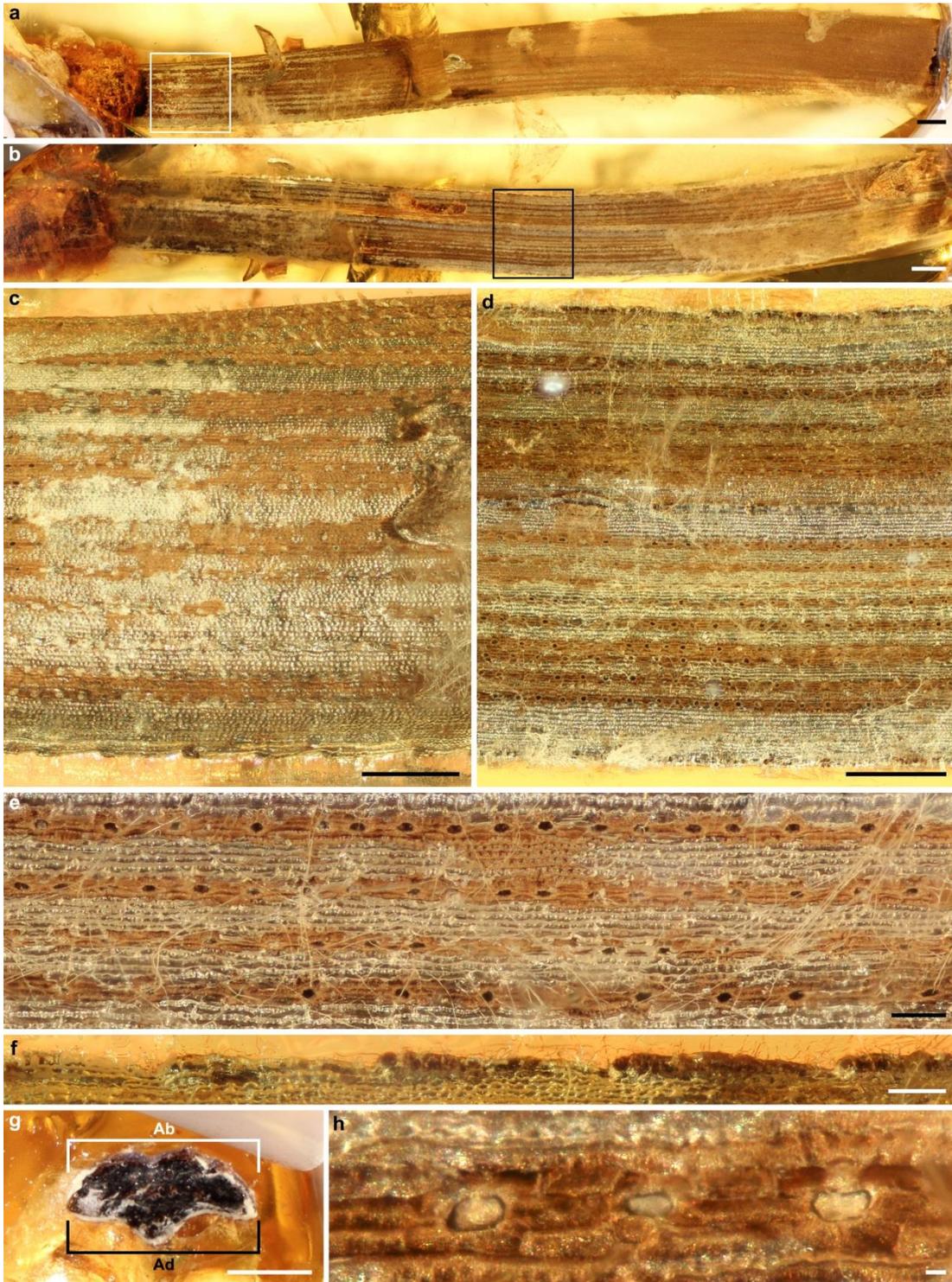


Fig. 17: Needle fragment of *Pinus serrata* (Neotype, morphotype 2, GPIH 4584). **(a)** Overview of the needle fragment from the abaxial side; white solid-line inset is magnified in **(c)**. **(b)** Overview of the needle fragment from the adaxial side; black solid-line inset is magnified in **(d)**. **(c, d)** Abaxial **(c)** and abaxial needle side **(d)** showing the regular distributed stomata rows. **(e)** Abaxial stomata rows. **(f)** Needle margin with papillae. **(g)** Needle cross section; needle surfaces are indicated with Ab (abaxial) and Ad (adaxial). **(h)** Stomata complexes in a row on an abaxial needle side. Scale bars = 1 mm (a, b), 500 µm (c, d), 100 µm (e, f), 10 µm (h).

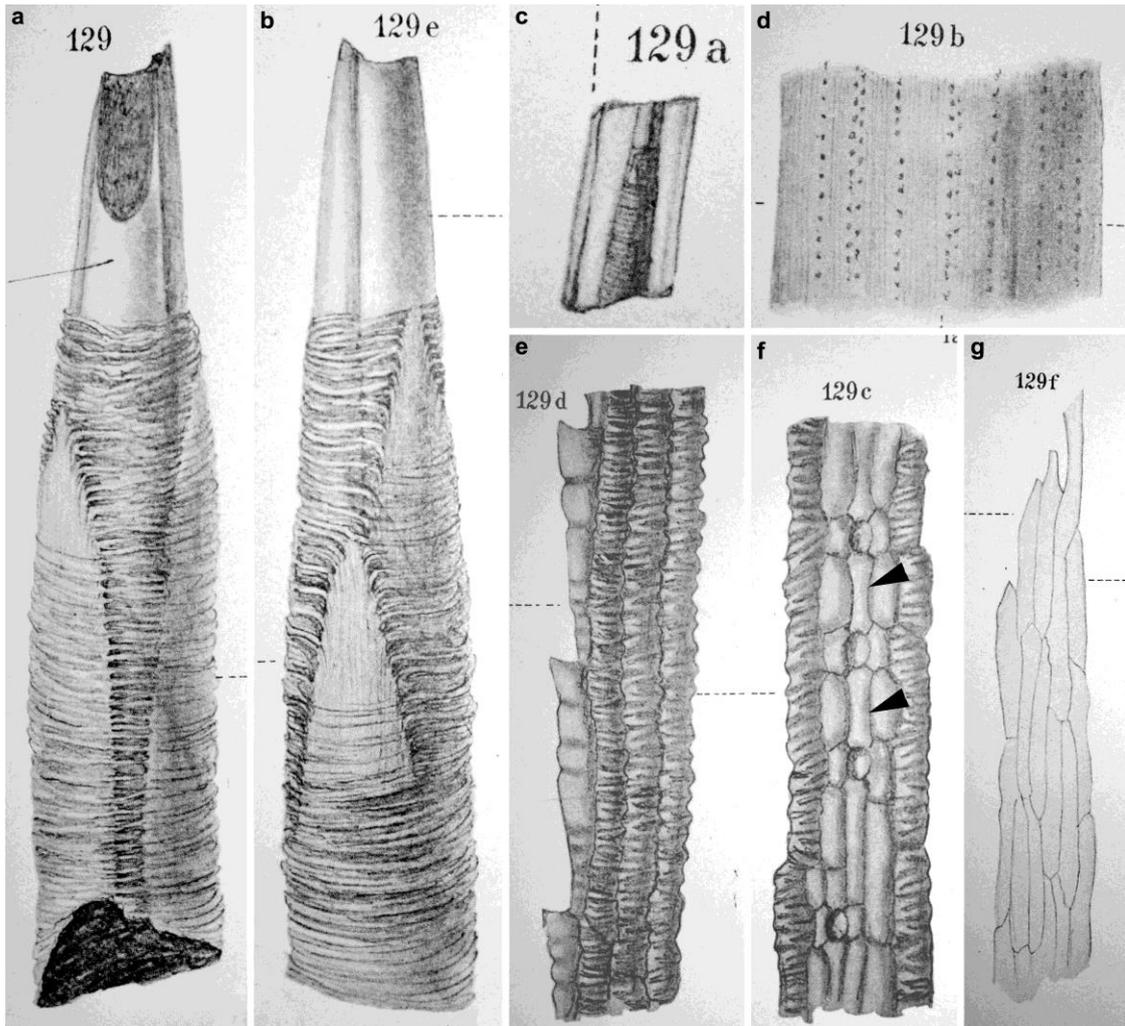


Fig. 18: Historic drawings of a lost three needled fascicle inclusion of *Pinus serrata* (Künow Amber Collection, coll. no. 42; from CASPARY & KLEBS 1907, pl. XXX). (a, b) Inclusion shown from different angles, base of the needle fascicle is covered by scales. (c) Amber specimen with the inclusion shown in (a, b). (d) Abaxial needle surface with numerous stomata rows. (e) Needle margin with multicellular teeth and epidermal cells with perpendicular wedged-shaped cell wall thickenings. (f) Stomata row composed of several stomata complexes, showing the elongated polar subsidiary cells (arrowheads). (g) Ordinary epidermal cells of a scale, sheathing the fascicle base.

Identification and comparison

Several *Pinus* species with fascicles of three needles were described from Baltic amber by GOEPPERT & BERENDT (1845), GOEPPERT & MENGE (1883) and CASPARY & KLEBS (1907): *P. serrata* CASP. (Fig. 18), *Pinus künowii* CASP. (Fig. 19a-f), *P. schiefferdeckeri* CASP. et R. KLEBS (Fig. 19g-j), *P. dolichophylla* CASP. (Fig. 20), *Pinites rigidus* GOEPP. et BER., (Fig. 21a-d), a synonym of *P. subrigida* GOEPP. et MENGE (Fig. 21e-i;) and (see Table 7 for comparison). Only *P. künowii* is clearly amphistomatic, while the stomata distribution of the remaining *Pinus* species mentioned above has not been verified.

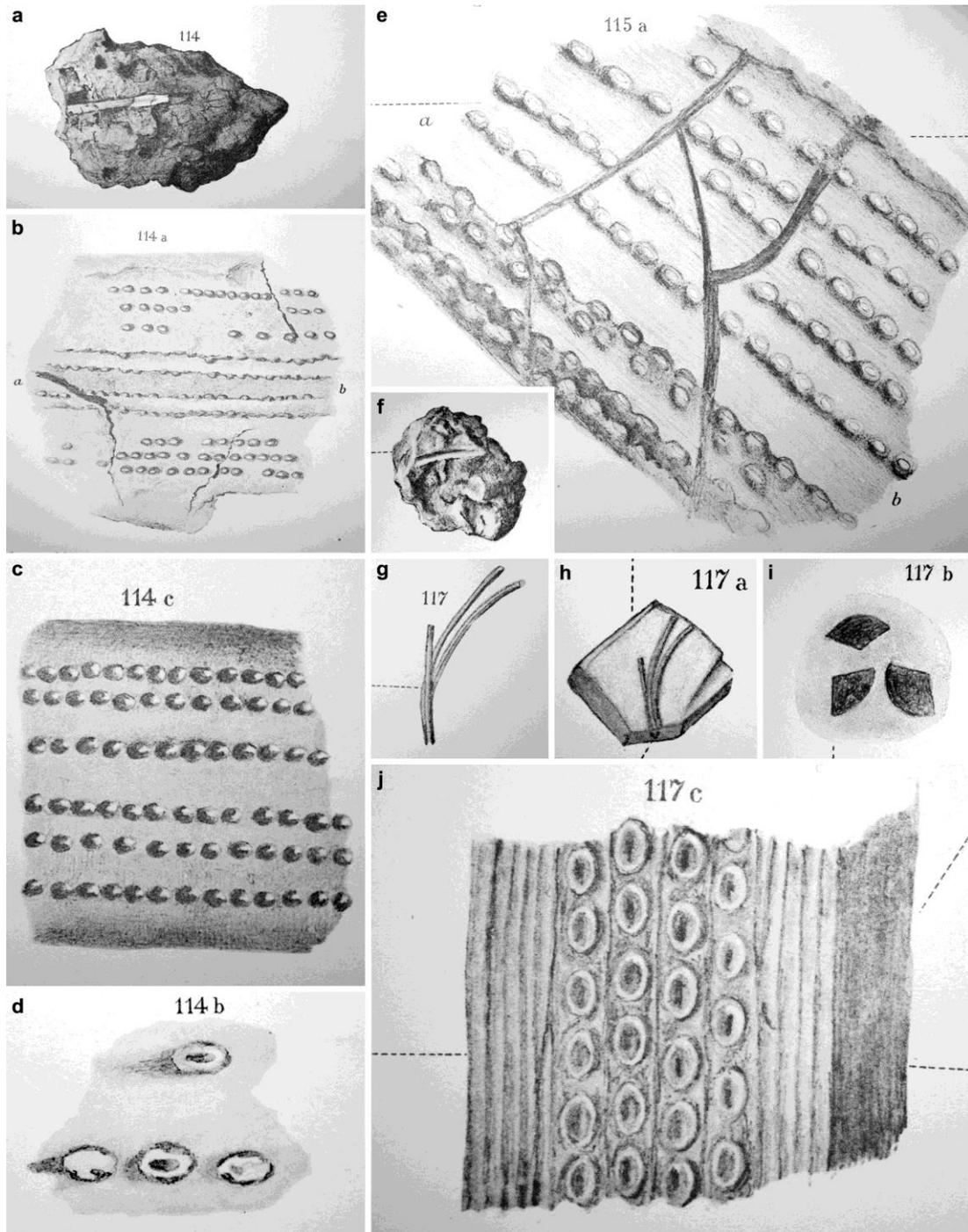


Fig. 19: Historic drawings of lost needle inclusions; two specimens of *Pinus künowii* (a-f, Künow's private collection) and one specimen of *P. schiefferdeckeri* (g-j, Physikalisch-ökonomische Gesellschaft Königsberg) from Baltic amber (from CASPARY & KLEBS 1907, pl. XXV and pl. XXVI). **(a)** Impression and coalificated remains of the needle in Stantenite. **(b)** Adaxial needle side. **(c)** Abaxial needle side. **(d)** Stomata. **(e)** Adaxial needle side of the specimen pictured in (f). **(f)** Needle impression in a piece of Stantenite. **(g, h)** Needle fascicle inclusion of the amber specimen figured in (h). **(i)** Triangular cross sections through the needle fascicle. **(j)** Needle surface with stomata complexes, arranged in rows.

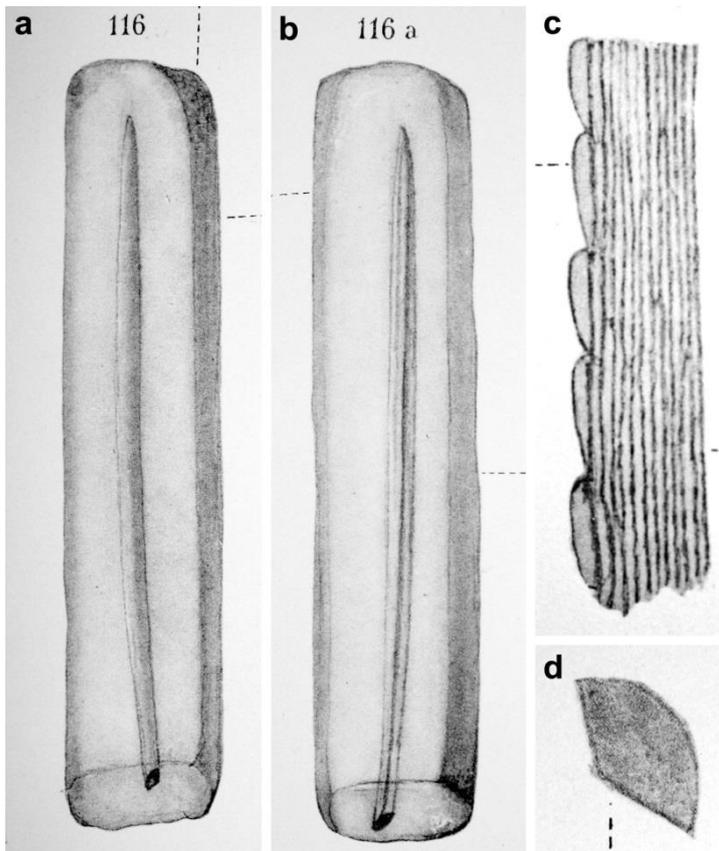


Fig. 20: Historic drawing of a lost needle inclusion of *Pinus dolichophylla* (Caspary's private collection; from CASPARY & KLEBS 1907, pl. XXVI). (a, b) Needle inclusion shown from different angles. (c) Dentate needle margin. (d) Needle cross section.

The stomata rows of *Pinus künowii* and *P. schiefferdeckeri* are arranged very close to each other and not separated by rows of ordinary epidermal cells (Fig. 19e, j). In addition, the stomata complexes of these species seem to be densely arranged to each other (Fig. 19c, e, j). Both species possess entire needle margins too; hence they are very different to GPIH 4584. Regarding *P. dolichophylla*, the amber inclusion GPIH 4584 shows a similar cell morphology with the dentate needle margin (Fig. 20c) and also undulate cell walls (mentioned in the description of CASPARY & KLEBS 1907), but details

of the stomata were not preserved and are therefore lacking in the illustration by CASPARY & KLEBS (1907). Thus, it is not possible to confidently assign GPIH 4584 to *P. dolichophylla*.

Pinus subrigida was first described as *Pinites rigidus* (Fig. 21a-d; GOEPPERT & BERENDT 1845) and later revised and transferred to *Pinus subrigida* (Fig. 21e-i; GOEPPERT & MENGE 1883), partly based on the same amber specimens. *P. subrigida* has a strongly keeled adaxial side and dentate needle margins (Fig. 21b, f). The stomata of *P. subrigida* are arranged in singular rows which are separated by several rows of ordinary epidermal cells, as in the amber specimen (Fig. 21b, f). It is not clear if these needles were amphistomatic or epistomatic, but the authors (GOEPPERT & BERENDT 1845; GOEPPERT & MENGE 1883) only describe stomata rows from the flat sides of the needles which could suggest that stomata were absent from the rounded (abaxial) side. CONWENTZ (1890, p. 65) stated that the inclusions of *P. subrigida* were too poorly preserved to allow an infrageneric assignment. Since the

holotype of *P. subrigida* is lost and due to the imprecise descriptions and pictures of *P. subrigida*, a reevaluation of its affinities is not possible.

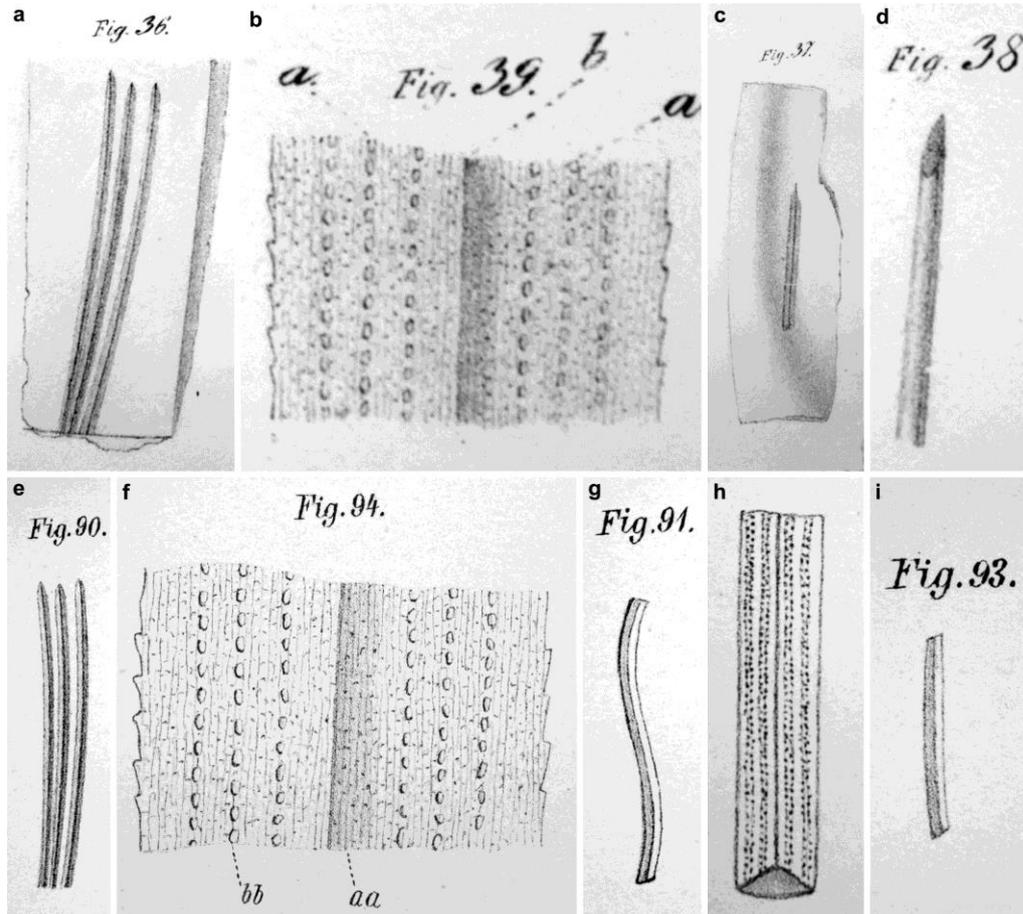


Fig. 21: Historic drawings of lost needle inclusions showing two specimens of *Pinites rigidus* (a-d, from GOEPPERT & BERENDT 1845, pl. V), a taxon which was later revised as *Pinus subrigida* (e-i; from GOEPPERT & MENGE 1883, pl. XIII). (a, e) Drawings of the same specimen, showing a three needle fascicle from different angles which was first described as *Pinites rigidus* (a, b) and later revised and newly figured as *Pinus subrigida* (e, f). (b, f) Adaxial needle side of the specimen figured in (a, e) with toothed margins, *a* and *bb* indicate the stomata rows, *b* and *aa* indicate the longitudinal midrib. (c) A further amber piece with a single needle of *Pinites rigidus*. (d) Needle inclusion of (c), magnified. (g) Specimen of *Pinus subrigida* with only one needle fragment inclusion. (h) Needle fragment of (g), magnified, showing the triangular needle cross section. (i) Needle fragment; the third specimen of *Pinus subrigida*, possibly the same specimen as shown in (c, d).

The only species similar to GPIH 4584 is *P. serrata* (Fig. 18), a closed juvenile fascicle inclusion of three needles (CASPARY & KLEBS 1907). GPIH 4584 conforms to *Pinus serrata* as this fossil species possesses a rounded abaxial side (Fig. 18a, b); the arrangement of the stomata in single rows and only rarely in double rows on the abaxial side (Fig. 18d); the pronounced teeth along the leaf margins (Fig. 18e); the stomata complexes being far apart from each other due to elongated polar subsidiary cells which are shared between adjacent stomata complexes (Fig. 18f); the rectangular lateral subsidiary cells (Fig. 18f; undulate cell walls of the epidermis, Fig. 18e). Since the needle fascicle of *P. serrata* is closed, CASPARY & KLEBS (1907)

Tab. 7: Morphological features of needle inclusions of *Pinus serrata* (Neotype, morphotype 2, GPIH 4584) and *Pinus* aff. *schiefferdeckeri* (morphotype 3, GZG.BST.24654), compared to historic descriptions of *Pinus* needle inclusions from Baltic amber. Information about the historic specimens is taken from descriptions and figures of the indicated references. Features which were not visible or absent are indicated by '-'.

Taxon	<i>Pinus serrata</i> GPIH 4584, Neotype	<i>P. serrata</i>	<i>P. künowii</i>	<i>Pinus</i> aff. <i>schiefferdeckeri</i> GZG.BST.24654	<i>P. schiefferdeckeri</i>	<i>P. dolichophylla</i>	<i>P. subrigida</i>
Preservation	needle fragment of the middle part	juvenile fascicle, needle apices not preserved	impression of a needle fragment	fascicle fragment of the middle part	fascicle fragment of the middle part	fascicle fragment of the upper part	fascicle fragment of the upper part
Needle							
No./fascicle	3	3	3	3	3	3	3
Cross section	broadly triangular, abaxial rounded, adaxial flattened	broadly triangular, abaxial rounded, adaxial flattened	broadly triangular, abaxial rounded, adaxial flattened	broadly triangular, abaxial rounded, adaxial flattened	broadly triangular, abaxial rounded, adaxial flattened	broadly triangular, abaxial rounded, adaxial flattened	broadly triangular, abaxial rounded, adaxial flattened
Size (singular needle)							
Length	28 mm	13 mm	15-23 mm	42 mm	9-14 mm	105 mm	-
Width	2.5 mm	1.25-2.5 mm	2 mm	1 mm	0.5 mm	2.5 mm	-
Margin	multicellular teeth	multicellular teeth	-	small papillae	entire	dentate, small teeth	dentate
Stomata							
Distribution	amphistomatic	-	amphistomatic	epistomatic	epistomatic?	-	epistomatic?
Stomata rows	singular; rows separated by epidermal cell rows	singular, rarely in double rows; rows separated by epidermal cell rows	singular or in bands; rows separated by ≥ 1 epidermal cell rows	single to double rows; double rows separated by one epidermal cell row	in bands; rows closely together	-	singular; rows separated by epidermal cell rows
Adaxial	ca. 6-9 rows on each side	-	5 rows on each side	ca. 3-4 rows on each side	4 rows on each side	-	-
Abaxial	11-15	8 rows	2 bands with 3 rows each	-	-	-	-
Subsidiary cells							
Polar cells	shared, elongated	shared, elongated	-	shared, short	shared, small	-	-
Lateral cells	unshared, rectangular	unshared, rectangular	-	-	unshared	-	-
Size of stomatal pit							
Length	(24)-30-(36) μm	24.8 μm	59.6-73.8 μm	(24)-29-(36) μm	39.9-46.6 μm	-	-
Width	(12)-19-(24) μm	20.7 μm	28.4-39.7 μm	(9)-12-(15) μm	23.3-33.3 μm	-	-
Shape	round to elliptic	elliptic	elliptic	elliptic	round to elliptic	-	-
Ordinary epidermal cells							
Length	(96)-173-(258) μm	132.5 μm	-	(175)-243-(485) μm	-	-	-
Width	(12)-17-(24) μm	24.8-29.0 μm	-	(15)-19-(25) μm	16.6 μm	-	-
Lateral cell walls	undulate	undulate	-	straight	straight	undulate	-
Polar cell walls	perpendicular to oblique	perpendicular to oblique	-	perpendicular, rarely oblique	oblique	oblique	-
References							
	this paper	CASPARY & KLEBS 1907	CASPARY & KLEBS 1907	this paper	CASPARY & KLEBS 1907	CASPARY & KLEBS 1907	GOEPPERT & BERENDT 1845; GOEPPERT & MENGE 1883

could not describe the adaxial side. They also mention perpendicular wedged-shaped cell wall thickenings of the epidermis which we cannot see in the amber specimen GPIH 4584 (Fig. 18e). However, we interpret these thickenings as a result of the fossilization process and thus are not indicative morphological features. Based on the strong similarities we accommodate GPIH 4584 in *P. serrata*.

Pinus aff. schiefferdeckeri CASP. et R. KLEBS, 1907

Figure 22

Specimen investigated

GZG.BST.24654

Compare

1907 *Pinus schiefferdeckeri* CASP. et R. KLEBS, pp. 150-151, pl. XXVI, figs 117, 117a-c; herein Fig. 19g-j.

Synonymy

? 1845 *Pinites rigidus* GOEPP. et BER., pp. 91-92, pl. V, figs 36-39; herein Fig. 21a-d.

? 1853 *Pinus subrigida* GOEPP., p. 463.

? 1870-72 *Pinus rigida* (GOEPP.) SCHIMPER, p. 291.

? 1883 *Pinus subrigida* GOEPP. et MENGE, p. 33, pl. XIII, figs 90-94; herein Fig. 21e-i.

? 1907 *Pinus schiefferdeckeri* CASP. et R. KLEBS, pp. 150-151, pl. XXVI, figs 117, 117a-c; herein Fig. 19g-j.

Description

Fascicle with three needles (base and tip not preserved) clustered together, 42 mm long × 1 mm wide (each needle) (GZG.BST.24654, Fig. 22a). Cross section broadly triangular with two flat sides (adaxial) and one rounded side (abaxial) (Fig. 22b). Needle margins with small papillae, which are arranged at a long distance to each other (Fig. 22c). Adaxial side with prominent longitudinal keel (Fig. 22b). Needles epistomatic, about 3 to 4 stomata rows on each flat side (Fig. 22b, d). Stomata rows are singular or double. Double stomata rows are separated from each other by a single line of ordinary epidermal cells (Fig. 22d). Stomata complexes are arranged closely to each other at a distance of 9 to 27 µm (average 20 µm). Polar subsidiary cells are shared between adjacent stomata complexes. More details of the stomata complexes are not preserved. Stomatal pits are elliptic, 24 to 36 µm long (average 29 µm) × 9 to 15 µm wide (average 12 µm). Ordinary epidermal cells elongated, rectangular with straight lateral cell walls (Fig. 22d); 175 to 485 long (average 243

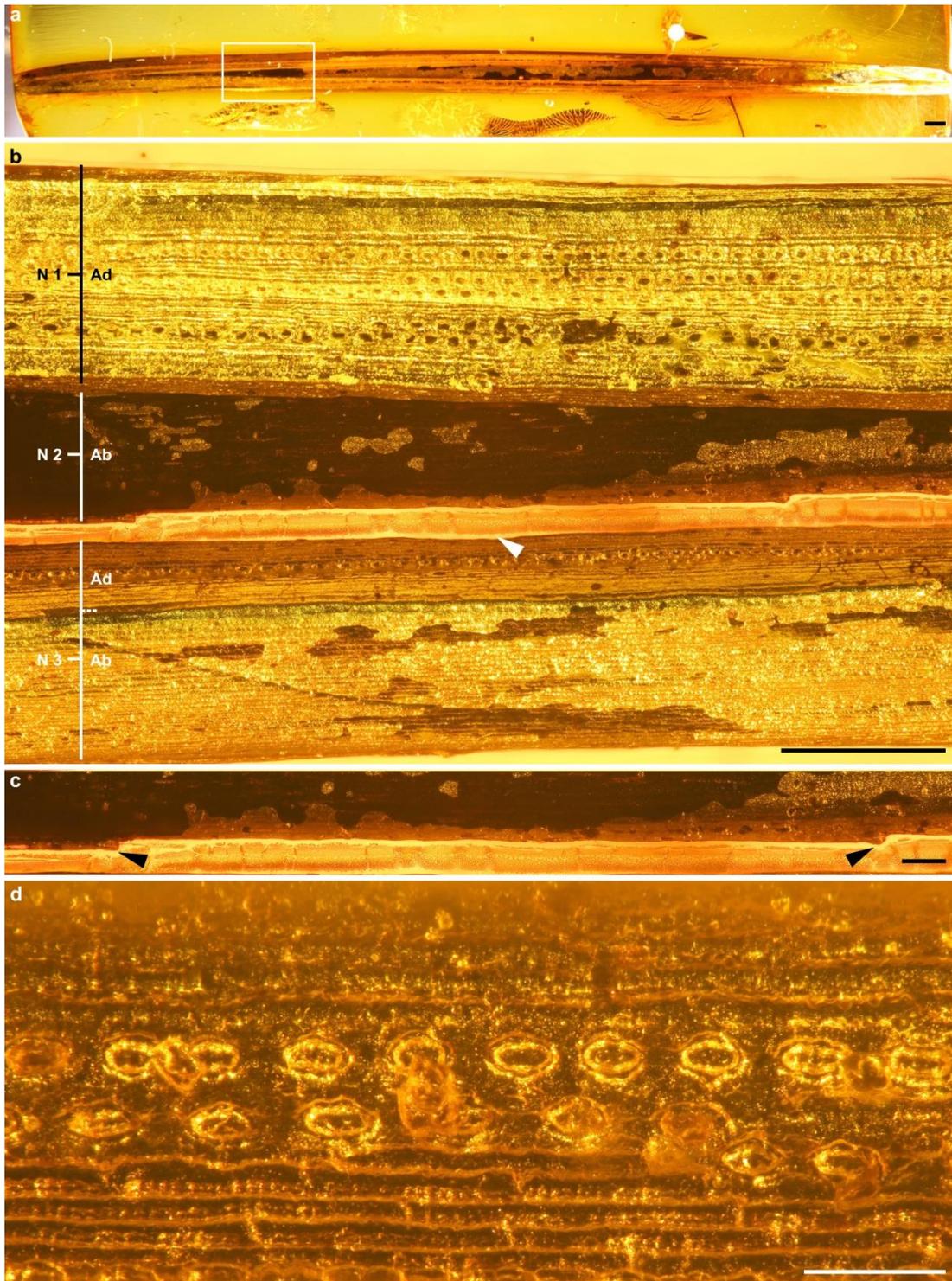


Fig. 22: Fragment of a three needled fascicle inclusion of *Pinus* aff. *schiefferdeckeri* (morphotype 3, GZG.BST.24654). **(a)** Overview of the needle fascicle; portion framed with a rectangle is magnified in **(b)**. **(b)** Detail of the needle fascicle showing the three needles (N 1 to N 3) and the different needle surfaces, indicated with Ad (adaxial) and Ab (abaxial); note the adaxial longitudinal keel (arrowhead). **(c)** Needle margin with papillae (arrowheads), located in a long distance to each other. **(d)** Double stomata rows and ordinary epidermal cells on an adaxial side of needle. Scale bars = 1 mm (a), 500 μ m (b), 100 μ m (c, d).

μm) \times 15 to 25 μm wide (average 19 μm). Polar cell walls mostly perpendicular, rarely oblique to lateral cell walls.

Identification and comparison

The only *Pinus* species from Baltic amber with needles in fascicles of three which might be epistomatic are *P. schiefferdeckeri* and probably *P. subrigida* (see Table 7 for comparison).

Following the descriptions and illustrations by Caspary & Klebs (1907) *Pinus schiefferdeckeri* has needles with entire margins, in contrast to the amber specimen GZG.BST.24654 which has fine papillae far apart from each other along the margins. Despite this, the stomata drawings of *P. schiefferdeckeri* (Caspary & Klebs 1907; herein Fig. 19j) look similar to the stomata of GZG.BST.24654 (Fig. 22d); both specimens share the elliptic shape of the stomatal pits; stomata complexes closely arranged to each other, sharing polar subsidiary cells; about 4 stomata rows on each adaxial side; straight walls of ordinary epidermal cells (Tab. 7). It remains unclear if needles of *P. schiefferdeckeri* were epistomatic: Caspary & Klebs (1907) only described stomata of *P. schiefferdeckeri* from the flat (adaxial) sides, but without clearly stating that the rounded (abaxial) side was stomata free (CASPARY & KLEBS 1907). Thus, we cannot to confirm affinities between both specimens, but certain similarities are present.

Baltic amber inclusions of needles of *Pinus subrigida* (synonymous for *P. rigidus*; please see comparison and identification chapter of *P. serrata* for more details), were only poorly preserved (Conwentz 1890, p. 65). Based on descriptions and drawings of *P. subrigida* (Goeppert & Berendt 1845; Goeppert & Menge 1883; herein Fig. 21), it is impossible to confirm an epistomatic stomata distribution for *P. subrigida*. Following the descriptions of the named authors, *P. subrigida* possesses dentate margins and singular stomata rows which are separated by rows of ordinary epidermal cells (Fig. 21b, f). These features are also present in the amber specimen GZG.BST.24654; however, more morphological characteristics of *P. subrigida* are necessary to definitely confirm affinities to the amber specimen. Thus, the definite affinity of *P. subrigida* remains obscure, but it is possible that this taxon is most likely morphotype 3.

Pinus cembraefolia CASP., 1886 emend.

Fig. 23

Neotype

GZG.BST.21897 (Hoffeins Amber Collection 1187-1), selected herein, Fig. 23.

Synonymy

1883 *Pinus silvatica* GOEPP. et MENGE, p. 34, pl. XIII, figs 97-101.

1886 *Pinus cembraefolia* CASP., p. 6.

? 1890 *Pinus cembraefolia* CASP., in CONWENTZ (1890), pp. 69-71, pl. XVI, fig. 14, pl. XVII, figs 8-10; herein Fig. 24d-g.

1890 *Pinus cembraefolia* CASP., in CONWENTZ (1890), pp. 69-71, pl. XVI, fig. 13, pl. XVII, figs 6-7; herein Fig. 24a-c.

1907 *Pinus cembraefolia* CASP., in CASPARY & KLEBS (1907), pp. 151-153, pl. XXVI, fig. 118, 118a-e, pl. XXVII, fig. 119, 119a-f; herein Fig. 25.

Emended diagnosis

Fascicle of 5 needles, singular needle 23-55 mm long \times 0.8 mm wide, slender, elongated, linear, tapering towards the apex; needle tip acute; needle cross section triangular, adaxial side flat, abaxial side slightly convex; needle margins regularly serrated, short acute teeth at 1 mm intervals; round flat papillae on abaxial surface; epistomatic, stomata rows singular or double, 3-5 rows per adaxial side; adjacent stomata complexes closely together, polar subsidiary cells shared, short, lateral subsidiary cells unshared, narrow; stomatal pit elongated, elliptic; walls of ordinary epidermal cells straight.

Description

Fascicle of five needles (GZG.BST.21897), in total 55 mm long, each needle is about 0.8 mm wide (width of the abaxial side); needles elongated, very slender, tapering gradually towards the acute needle tips which are partly degraded (Fig. 23a). Needle cross section triangular with two flat sides (adaxial) and one slightly convex side (abaxial) (Fig. 23b). Teeth along the margins arranged at a regular distance of about 1 mm to each other (Fig. 23c-d); on abaxial side, roundish flat elongated papillae clustered together or singular (Fig. 23d). Needles epistomatic, 3 to 5 stomata rows on each adaxial side, stomata either in single or double rows, separated by one or several rows of ordinary epidermal cells. Adjacent stomata complexes in one row close together (Fig. 23e), separated by a singular polar subsidiary cell, 9 to 30 μ m

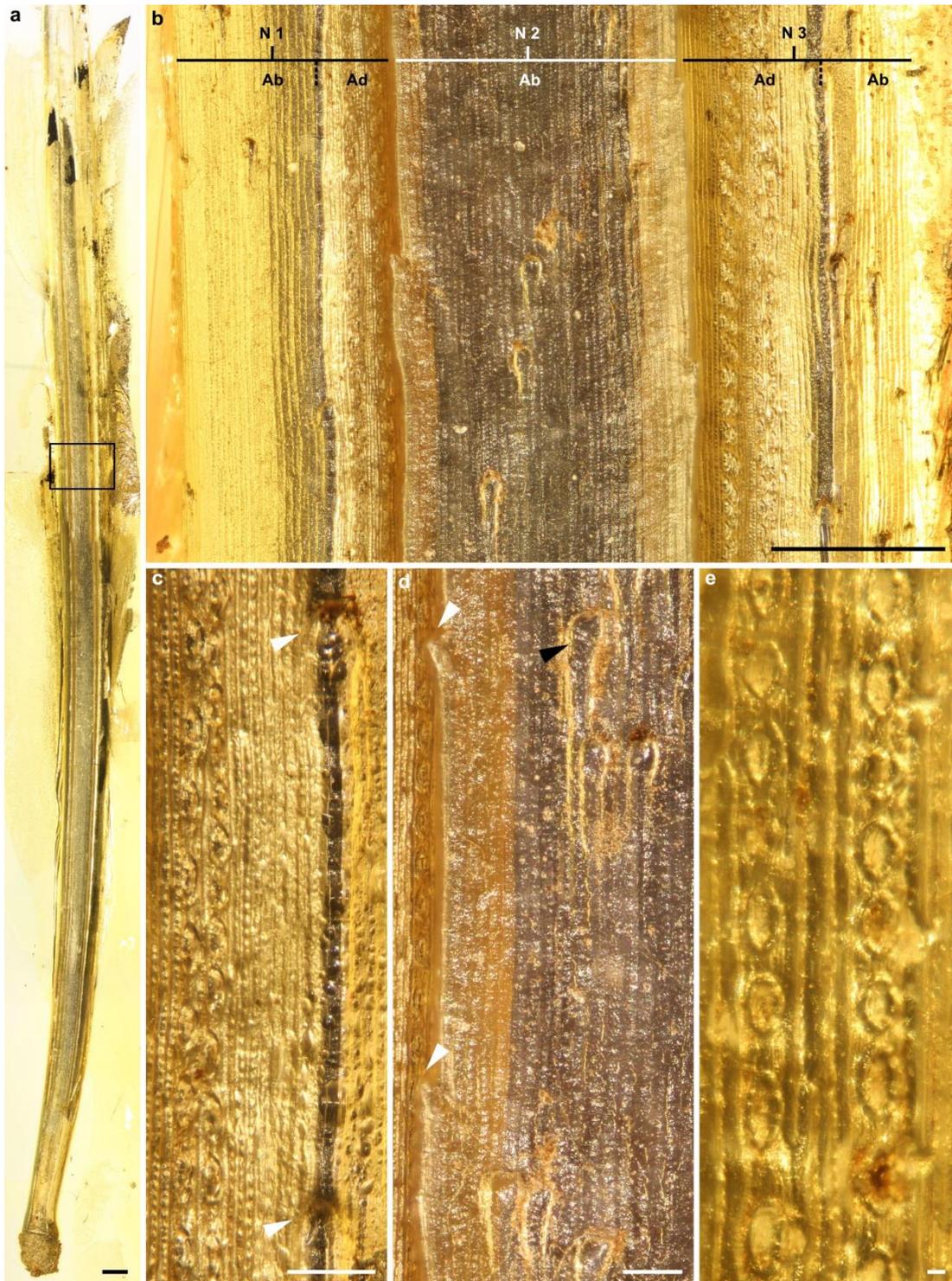


Fig. 23: Entire five needled fascicle of *Pinus cembra* (Neotype, morphotype 4, GZG.BST.21897. (a) Overview of the needle fascicle; black-lined inset is magnified in (b) (b) Detail of (a) showing three needles (N1 to N3) and the different needle surfaces, indicated with Ad (adaxial) and Ab (abaxial). (c, d) Toothed margins of needles N1 (c) and N 2 (d) (indicated with white arrowheads) and round flattened papillae on the abaxial surface of needle N2 (d), indicated by a black arrowhead. (e) Singular stomata rows, separated by several rows of ordinary epidermal cells. Scale bars = 1 mm (a), 500 μ m (b), 100 μ m (c, d), 10 μ m (e).

long (on average 17 μm). Lateral subsidiary cells unshared, narrow (Fig. 23e). Size of the stomata complexes is not measurable due to preservation. Stomatal pit is elongated elliptic, 27 to 45 μm long (on average 35 μm) \times 12 to 21 μm wide (on average 17 μm). Ordinary epidermal cells 15 to 30 μm wide (average 23 μm ; cell length not measurable, since polar cell walls not preserved). Lateral walls of ordinary epidermal cells straight to slightly undulate.

Tab. 8: Morphological features of the needle inclusion *Pinus cembra* (Neotype, morphotype 4, GZG.BST.21897), compared to historic descriptions of *Pinus cembra* needle inclusions from Baltic amber. Information about the historic specimens is taken from descriptions and figures of the indicated references. Certain features which were not visible or absent are indicated by '–'.

Taxon	<i>Pinus cembra</i> GZG.BST.21897, Neotype	<i>Pinus cembra</i>
Preservation	needle fascicle; apices partly not preserved	needle fascicle; apices partly not preserved
Needle		
No./fascicle	5	5
Cross section	triangular; adaxial side flat, abaxial side slightly convex	triangular; abaxial side convex
Size (singular needle)		
Length	55 mm	23-25-30-52.5 mm
Width	0.8 mm	0.82 mm
Margin	teeth in a long regular distance	teeth in a long regular distance
Stomata		
Distribution	epistomatic	epistomatic
Stomata rows	single or double rows, separated by ≥ 1 epidermal cell rows	single or double rows, separated by 2-8 epidermal cell rows
Adaxial	3 to 5 rows on each side	3 to 4 rows on each side
Abaxial	-	-
Subsidiary cells		
Polar cells	shared, short	shared, short
Lateral cells	unshared, narrow	-
Size of stomatal pit		
Length	(27)-35-(45) μm	37.5 μm
Width	(12)-17-(21) μm	-
Shape	elongated, elliptic	elliptic
Ordinary epidermal cells		
Length	-	-
Width	(15)-23-(30) μm	22.7-28.4 μm
Lateral cell walls	straight to slightly undulate	straight to slightly undulate
Polar cell walls	-	perpendicular to oblique
References		
	this paper	CASPARY 1886; CONWENTZ 1890; CASPARY & KLEBS 1907

Identification and comparison

CASPARY (1886) described a *Pinus* fascicle composed of five needles from Baltic amber as *P. cembra* CASP. Later, CONWENTZ (1890) assigned two further Baltic amber inclusions to *P. cembra* CASP. (Fig. 24), revising one specimen which GOEPPERT & MENGE (1883) originally published as *P. silvatica* since the latter authors interpreted the inclusion inadvertently as a three-needled fascicle. CASPARY & KLEBS (1907) published two further Baltic amber inclusion of *Pinus cembra* (Fig. 25), highlighting similarities to needles of the extant *Pinus cembra* L.

Based on the given descriptions and pictures of *Pinus cembra* by CASPARY & KLEBS (1907; herein Fig. 25) and CONWENTZ (1890; herein Fig. 24a-c) many similarities to the amber inclusion GZG.BST.21897 can be found (see Table 8 for comparison): the slender elongated shape of the needle (Figs 23a; 24a, c); small teeth along the needle margins in a long regular distance to each other (Figs 23d; 24a; 25f); epistomatic stomata distribution; stomata rows separated by one or more rows of ordinary epidermal cells (Figs 23e; 24b; 25f, j, k-l); stomata complexes with a narrow subsidiary cell ring, polar subsidiary cells are short, rectangular and shared between adjacent stomata (Figs 23e; 24b; 25e, j); lateral walls of ordinary epidermal cells straight to slightly undulate (Figs 23d; 24b).

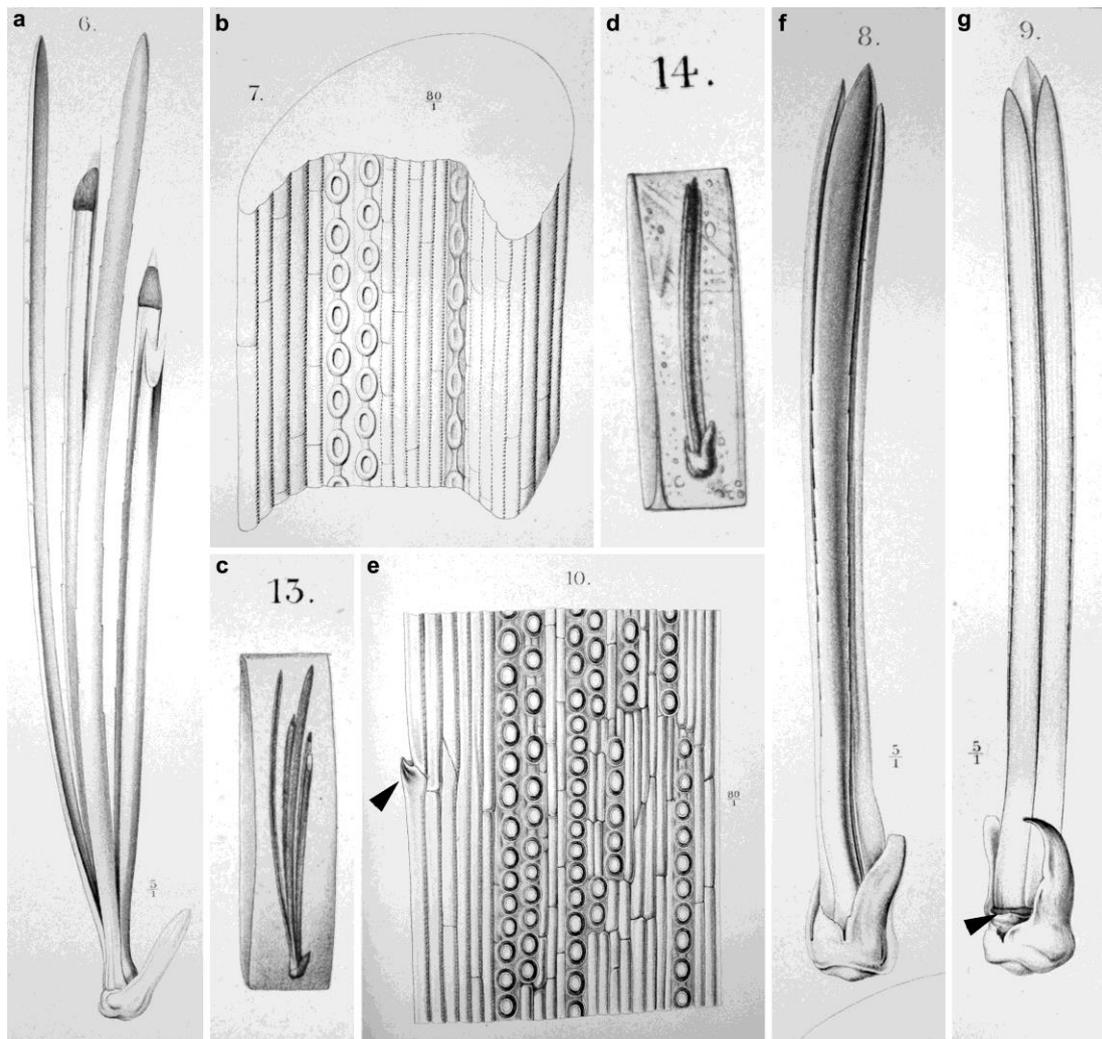


Fig. 24: Historic drawings of two lost Baltic amber specimens with five needled fascicle inclusions of *Pinus cembra* (from CONWENTZ 1890, pl. XVI and pl. XVII). (a) Overview of the five needled fascicle inclusion. (b) Detail of the adaxial leaf side, showing the stomata rows and the shape of the needle cross section. (c) Amber specimen with the needle fascicle inclusion of (a). (d) Overview of another amber specimen with *P. cembra* needles. (e) Detail of the adaxial needle surface with several stomata rows and the dentate needle margin. (f, g) Overview of the needle fascicle with only three remaining needles, the fascicle base in (g) shows the abscission scar of two further needles (arrowhead).

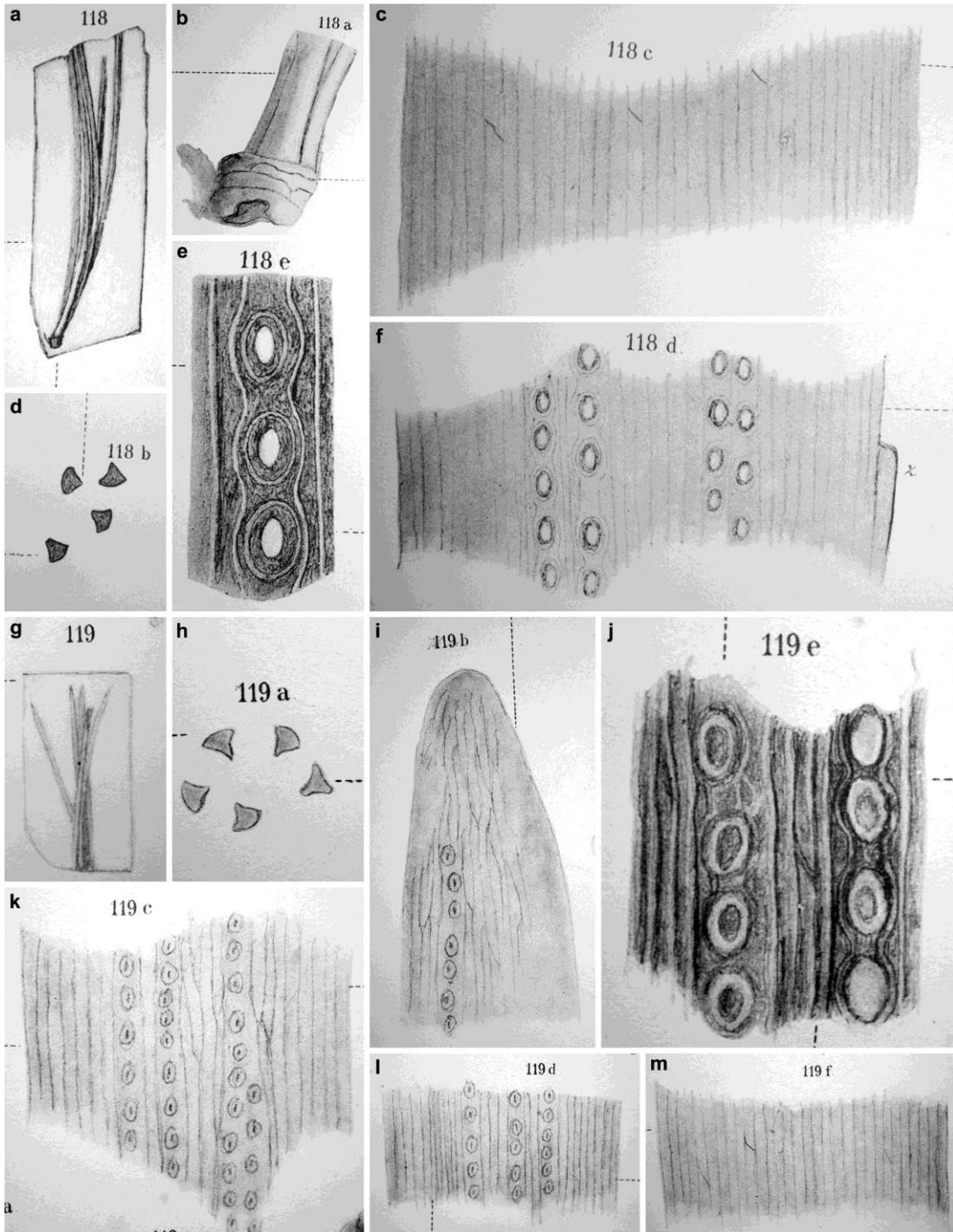


Fig. 25: Historic drawings of two lost Baltic amber specimens with a five needled fascicle inclusion of *Pinus cembra* (a-f, specimen of *P. cembra* from the Klebs Collection; g-m, specimen of *P. cembra* from the Künow Amber Collection, coll. no. 176; from CASPARY & KLEBS 1907, pl. XXVI and pl. XXVII). (a) Overview of the amber piece with the five needled fascicle inclusion. (b) Base of the needle fascicle. (c) Ordinary epidermal cells of the abaxial needle side. (d) Cross sections of four needles of (a). (e) Stomata complexes in a row. (f) Stomata rows on the adaxial needle side. (g) Overview of another amber specimen with *P. cembra* needles. (h) Cross sections of the needles figured in (g). (i) Needle apex. (j) Stomata complexes in a row. (k, l) Adaxial needle surfaces with stomata rows. (m) Ordinary epidermal cells of the abaxial needle surface.

CASPARY & KLEBS (1907) evaluated the affinities of the two specimens of *Pinus cembraefolia* which were described by CONWENTZ (1890). One of the specimens (Fig. 24d-g) was doubted to be *P. cembraefolia*, since this particular specimen exhibited a more lanceolate needle shape (Fig. 24f-g); the leaf margin was irregularly dentate with a higher number of teeth along the middle needle part (Fig. 24f); the higher stomata number; stomata rows were arranged in a different pattern (Fig. 24e). Based on the pictures from CONWENTZ (1890; herein Fig. 24d-g), we also see these differences, but without the holotype we cannot confidently reevaluate the assumptions of CASPARY & KLEBS (1907).

Genus *Pseudolarix* GORDON, 1858

Pseudolarix sp.

Figures 26-28

Specimens investigated

GZG.BST.21898 (Hoffeins Amber Collection 997), GZG.BST.23536, GZG.BST.24334, GZG.BST.24338

Description

Linear to oblanceolate needles (Figs 26a, b; 27a, b; 28a, b, f, g), 17 to 21 mm long \times 1 to 2 mm wide, tapering towards a slender flattened to triangular base (Figs 26e; 27d; 28c-i), 0.4 to 0.6 mm wide (for detailed measurement values of all *Pseudolarix* specimens see Table 9). Apices acute to obtuse (Figs 26a; 27c; 28b, f). Surface of needle lamina flat or with an adaxial longitudinal shallow groove and an abaxial longitudinal keel (Fig. 26a, b). Needle margins entire and glabrous. Hypostomatic, with two stomata bands separated by the prominent midrib (Figs 26c; 27e). Per band, 3 to 6 irregular stomata rows, parallel to the longitudinal axis. Stomata complexes monocyclic, 111 to 210 μm long \times 36 to 84 μm wide, no Florin rings and with 4 to 6 subsidiary cells of which two are polar and the remaining ones lateral. Polar cells somewhat rectangular, elongated and often shared between adjacent stomata in the same row. Lateral subsidiary cells rectangular to convex and curved, rarely shared between the stomatal complexes of adjacent rows (Figs 26d; 27f; 28d, h). Stomata sunken, stomatal pit elongated rectangular, 10 to 40 μm long \times 5 to 15 μm wide. Ordinary cells of the epidermis are mainly rectangular, sometimes elongated, 80 to 310 μm long \times 20 to 50 μm wide, arranged in regular rows (Figs 26f; 28e). Walls of ordinary cells are straight, polar end walls are perpendicular or oblique to the lateral walls.

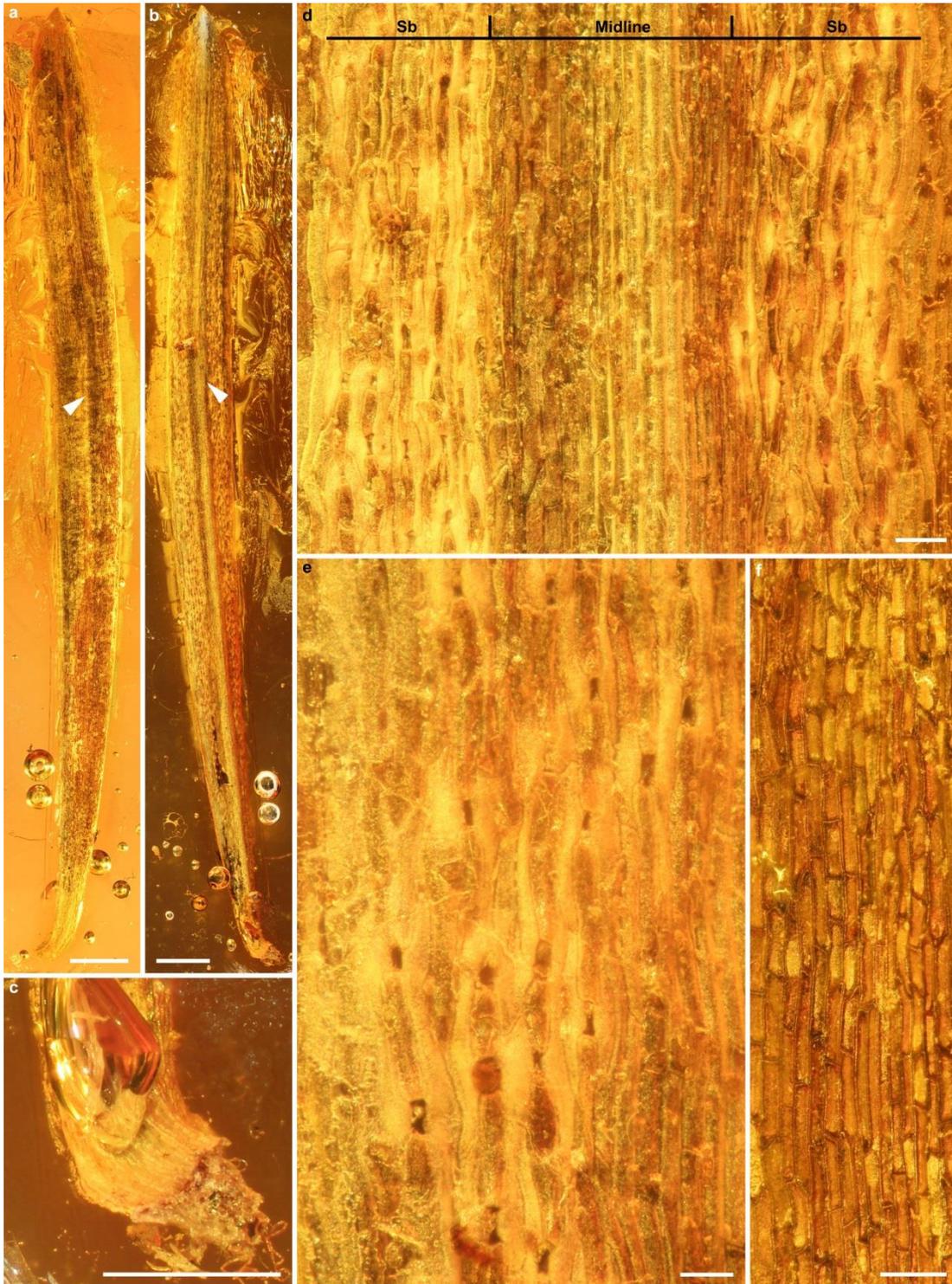


Fig. 26: Needle of *Pseudolarix* sp. from Baltic amber, GZG.BST.24338. **(a, b)** Overview of the needle from the adaxial (a) and abaxial (b) side; arrowheads indicate the adaxial longitudinal groove (a) and the abaxial longitudinal keel (b). **(c)** Triangular needle base. **(d)** Abaxial surface showing two stomata bands (indicated with Sb) on each side of the midline. **(e)** Monocyclic stomata complexes in irregular rows. **(f)** Ordinary epidermal cells on the adaxial needle side. Scale bars = 1 mm (a, b), 100 μ m (d, f), 50 μ m (e), 500 μ m (c).

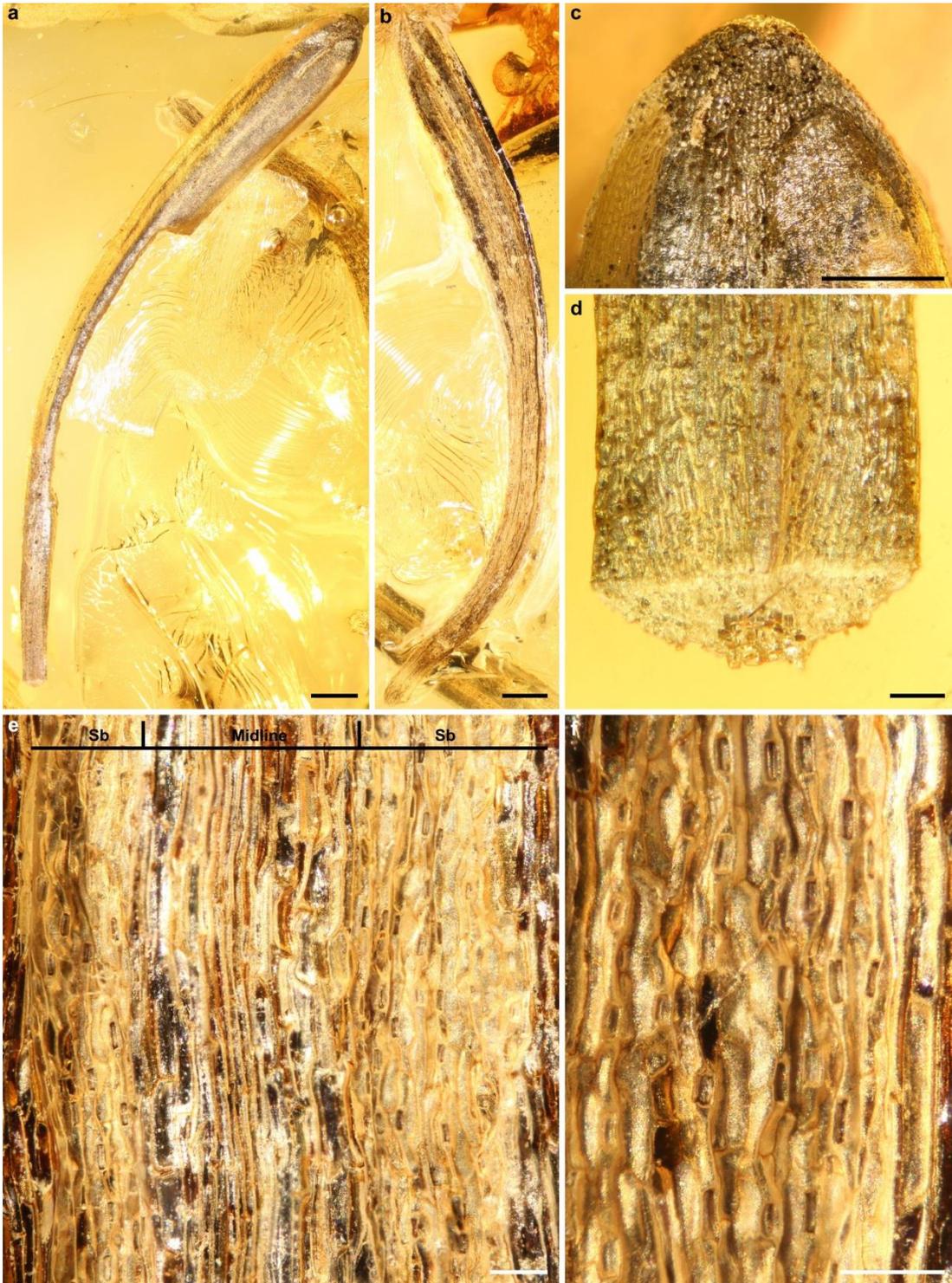


Fig. 27: Needle of *Pseudolarix* sp. from Baltic amber, GZG.BST.21898. **(a, b)** Overview of the needle from the adaxial (a) and abaxial (b) side. **(c)** Acute-obtuse needle tip. **(d)** Triangular needle base. **(e)** Abaxial surface showing two stomata bands (indicated by Sb) on each side of the midline. **(f)** Monocyclic stomata complexes in irregular rows (abaxial side). Scale bars = 1 mm (a, b), 500 μm (c), 100 μm (d-f).

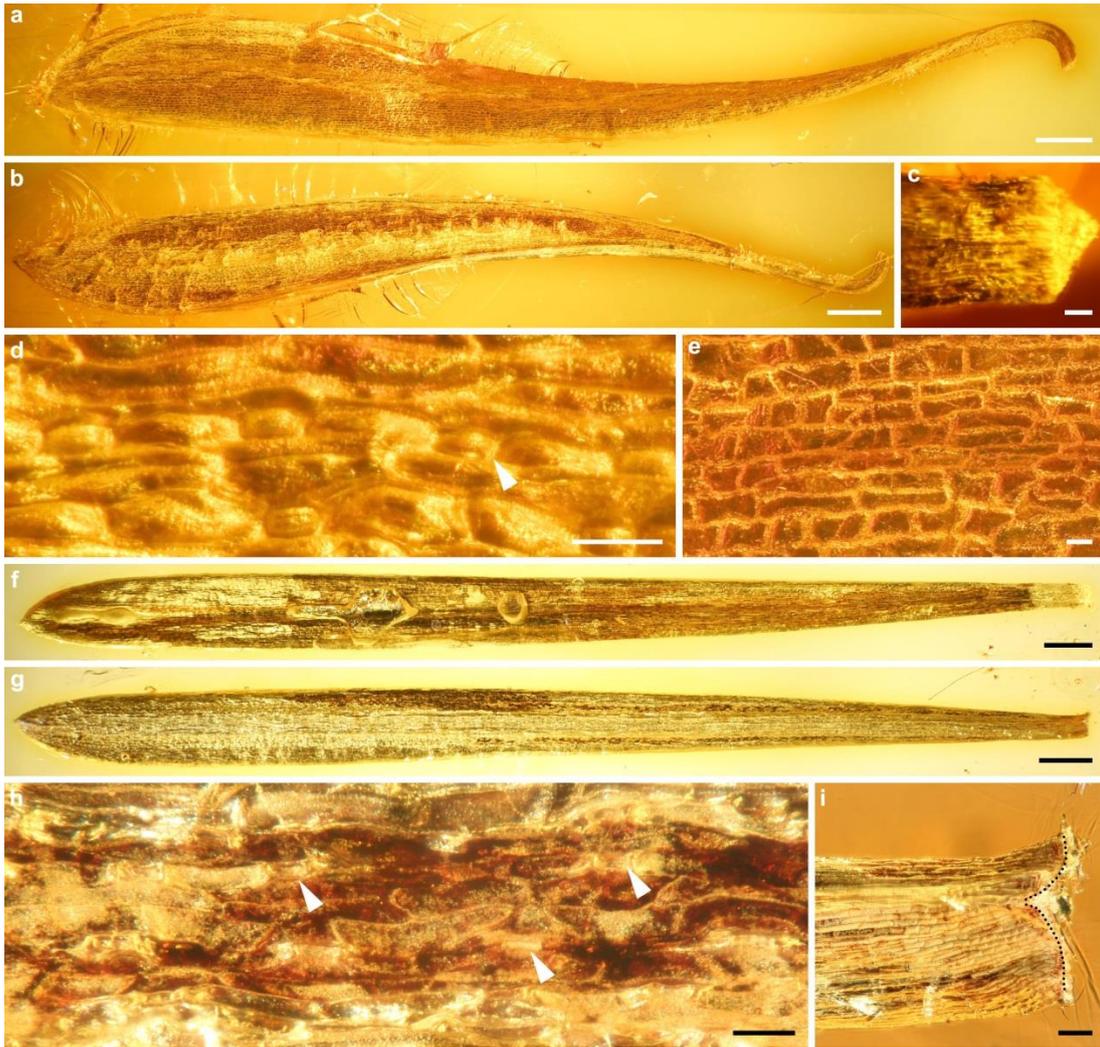


Fig. 28: Needles of *Pseudolarix* sp. from Baltic amber, (a-e) GZG.BST.23536, (f-i) GZG.BST.24334. (a, f) Overview of the needle from the adaxial side. (b, g) Overview of the needle from the abaxial side. (c, i) Triangular needle base; dotted black line indicates the triangular shape. (d, h) Monocyclic stomata complexes in irregular rows (abaxial side), arrowheads indicate the rectangular stomatal pit. (e) Ordinary epidermal cells of the adaxial needle side. Scale bars = 1 mm (a, b, f, g), 100 μ m (c, i), 50 μ m (d, e, h).

Tab. 9: Measurements of the *Pseudolarix* specimens from Baltic amber. Centered numbers of the stomata sizes are average values; size ranges are provided in brackets.

Collection number	GZG.BST.24338	GZG.BST.21898	GZG.BST.23536	GZG.BST.24334
Leaf				
Length	17 mm	17 mm	19 mm	21 mm
Width (widest)	1.1 mm	1.6 mm	2 mm	1.5 mm
Width (base)	0.4 mm	0.6 mm	0.6 mm	0.5 mm
Stomata complex				
Length	(135)-168-(210) μm	(117)-138-(165) μm	(111)-142-(186) μm	(135)-155-(175) μm
Width	(39)-46-(54) μm	(39)-46-(51) μm	(45)-63-(84) μm	(36)-43-(51) μm
Stomatal pit				
Length	(10)-28-(40) μm	(24)-29-(33) μm	(24)-32-(39) μm	(27)-32-(36) μm
Width	(5)-10-(15) μm	(6)-13-(15) μm	(12)-15-(15) μm	(6)-10-(15) μm
Ordinary epidermal cells				
Length	(80)-196-(310) μm	(80)-156-(240) μm	(80)-159-(300) μm	(140)-219-(310) μm
Width	(20)-26-(35) μm	(20)-29-(50) μm	(20)-34-(47) μm	(20)-28-(35) μm

Identification

The needle shape, the abaxial keel, the hypostomatic stomata distribution and their arrangement in irregular longitudinal rows in combination with the monocyclic stomata type, the shape of the outer stomatal aperture and shape of the subsidiary cells are typical of *Pseudolarix* (FLORIN 1931; FARJON 1990; LEPAGE & BASINGER 1995; ECKENWALDER 2009). A similar stomata type is also found in *Larix* MILL., but needles of this genus exhibit a triangular to rhombic transection, and are mostly amphistomatic and keeled on both leaf surfaces (FARJON 1990).

None of the descriptions and figures of conifer needle inclusions from Baltic amber by GOEPPERT & BERENDT (1845), GOEPPERT & MENGE (1883), CONWENTZ (1890) and CASPARY & KLEBS (1907) show any similarity to the fossils presented in Figs 26-28. Hence, our fossils represent the first record of *Pseudolarix* from Baltic amber.

Remarks

The specimens show variation in the needle shape, which we interpret as infraspecific to infrageneric morphological variations, since the micromorphological features such as the stomata characteristics are the same in all the specimens.

Revision of angiosperm leaves initially assigned to conifers

We evaluated previous descriptions of conifer foliage assigned to different *Abies* species (GOEPPERT & BERENDT 1845; GOEPPERT 1853; GOEPPERT & MENGE 1883; CASPARY & KLEBS 1907) and show that these specimens are of unknown angiosperm origin.

Magnoliopsida

Order and family unknown

Genus *Dicotylophyllum* SAPORTA, 1892

Dicotylophyllum var. sp.

Figs 29-32

Specimens investigated

MB.Pb.1979/0490, MB.Pb.1979/0591, MB.Pb.1979/655, MB.Pb.1979/764,
 MB.Pb.1979/768l, MB.Pb.1979/768qu, MB.Pb.1979/768s, GZG.BST.21901
 (Hoffeins Amber Collection 1045-2), GZG.BST.23539, GZG.BST 23540,
 GZG.BST.24336, GZG.BST.24346, GZG.BST.24355, GZG.BST.24610,
 GZG.BST.24651, Carsten Gröhn Amber Collection P 3655

List of rejected citations of conifers from Baltic amber

- 1845 *Abietites obtusifolius* GOEPP. et BER., p. 96, pl. V, figs 41-45; herein Fig. 29.
 1845 *Dermatophyllites porosus* GOEPP. et BER., p. 77, pl. V, figs 58, 59; herein Fig. 32.
 1847 *Pinites obtusifolius* ENDLICHER, p. 283.
 1853 *Abietites claveolatus* MENGE et GOEPP., in GOEPPERT (1853), p. 462.
 1870-72 *Abies obtusifolia* (GOEPP.) SCHIMPER, p. 303.
 1883 *Abies obtusifolia* (GOEPP. et BER.) GOEPP. et MENGE, p. 35, pl. XIII, figs 107-110; herein Fig. 33.
 1907 *Abies linearis* CASP. et R. KLEBS, pp. 175-176, pl. XXX, figs 134, 134a-f; herein Fig. 34.
 1907 *Abies suckerii* CASP. et R. KLEBS, pp. 171-175, pl. XXX, figs 131-133f; herein Figs 30-31.

Description

Oblanceolate-linear dorsoventrally flattened needle-shaped leaves (MB.Pb.1979/0591, MB.Pb.1979/0490, GZG.BST.23539, GZG.BST.24355; Figs 29a, b; 30a, b; 31a; 32a, b) 6.5 to 16 mm long × 0.8 to 1.8 mm wide (for detailed measurement values see Table 10), apices obtuse (Figs 29d; 30b; 32a), margins

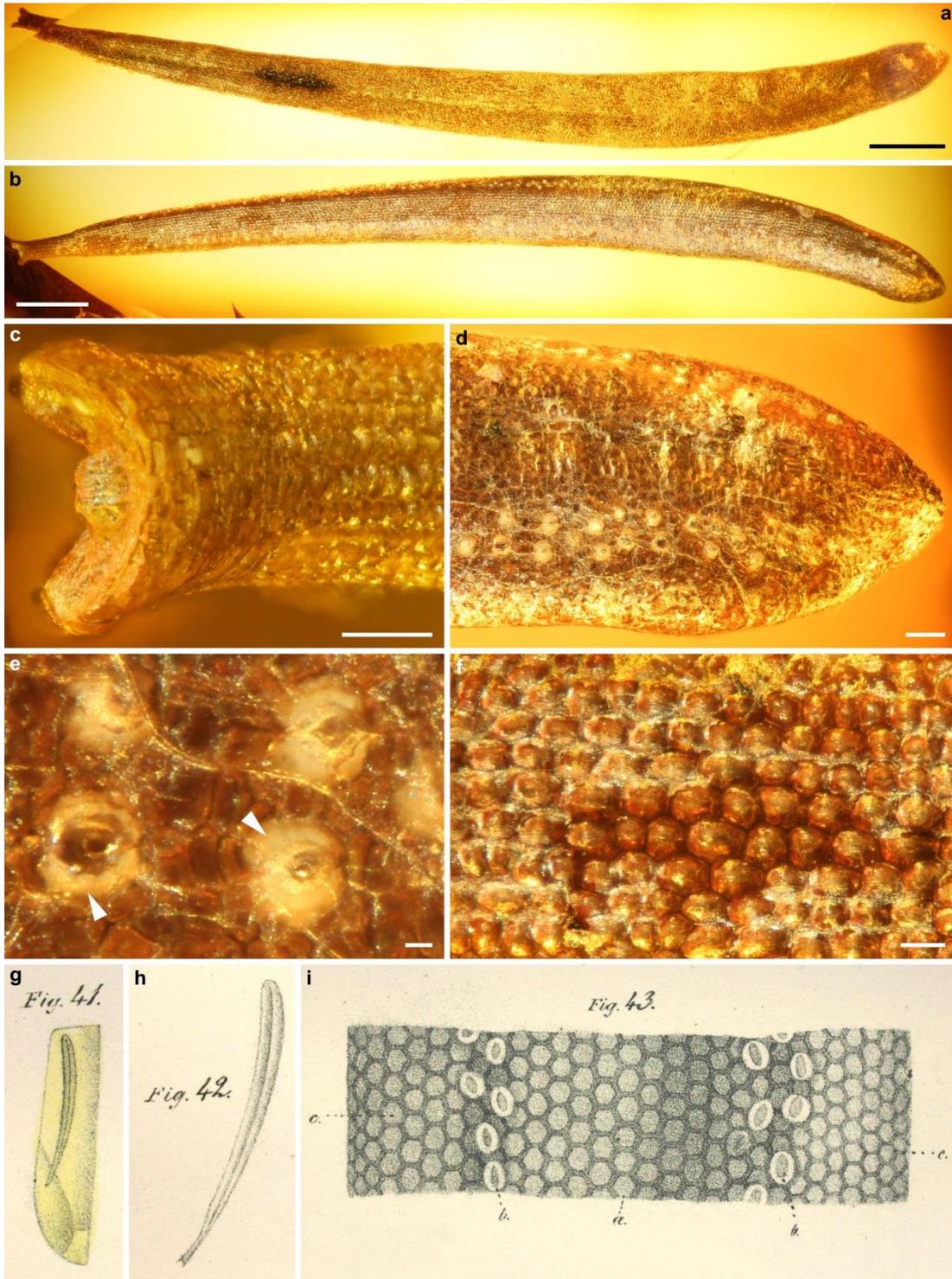


Fig. 29: Holotype of the ‘needle’ of *Abietites obtusifolius* from Baltic amber (a-f, MB.Pb.1979/0591) and the historic drawings of this particular specimen (g-i, from GOEPPERT & BERENDT 1845, pl. V). (a, b) Overview of the leaf from the adaxial (a) and abaxial (b) side. (c) Incurved petiole. (d) Obtuse leaf apex and the abaxial lamina with two stomata bands on each side of the longitudinal midline. (e) Stomata complexes, arrowheads indicate the non-sunken bean-shaped guard cells; fungal hyphae cover the leaf surface. (f) Papillose epidermal cells of the abaxial midline. (g, h) Overview of the specimen. (i) Abaxial surface of leaf lamina, a midline, b stomata, c cells of the leaf margin. Scale bars = 1 mm (a, b), 100 μm (c, d), 10 μm (e), 50 μm (f).

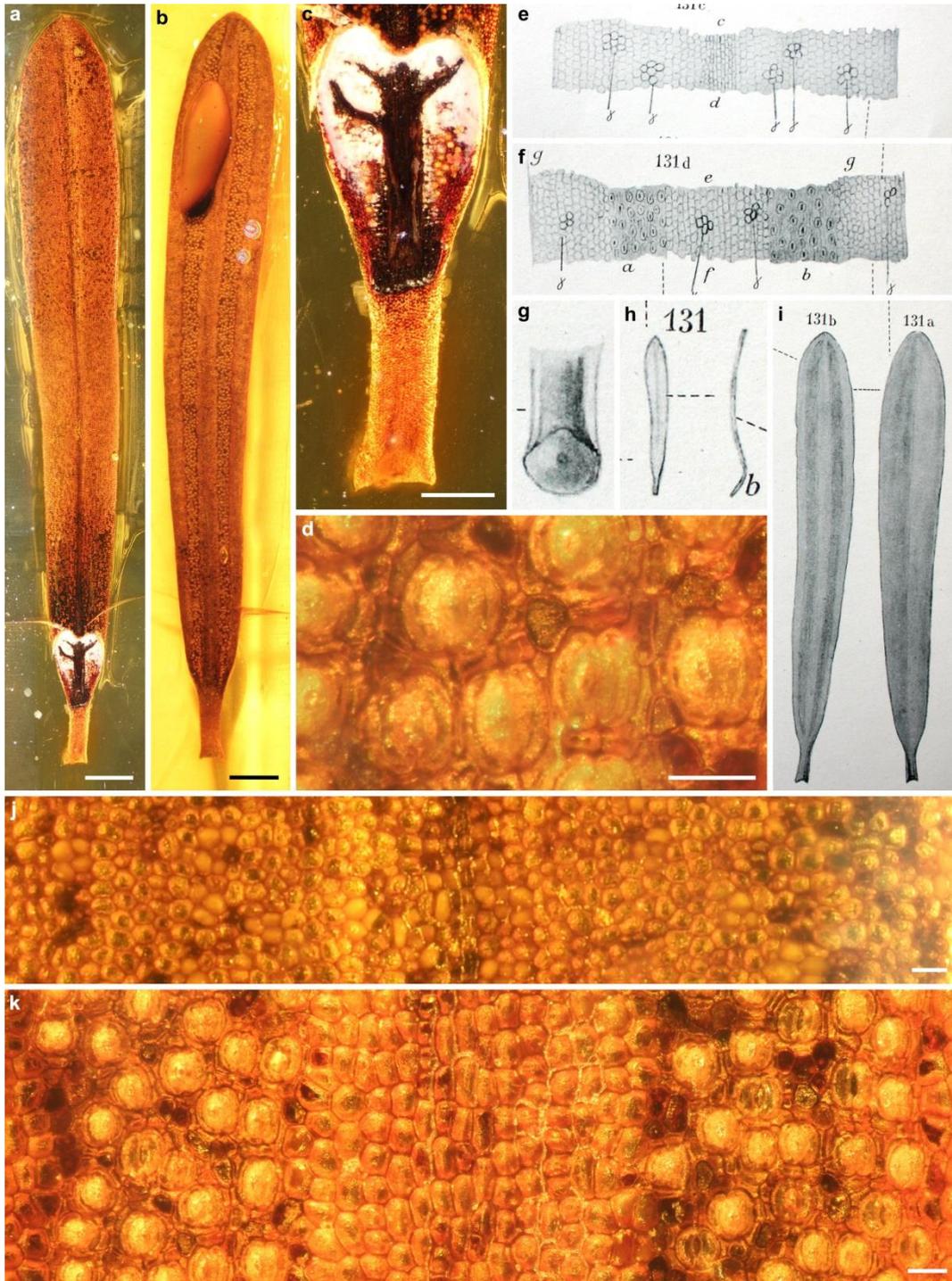


Fig. 30: ‘Needle’ of *Abies suckerii* from Baltic amber (a-d and i-j, GZG.BST.23539) and the historic drawings of this particular specimen (e-i, from CASPARY & KLEBS 1907, pl. XXX). (a, b, i) Overview of the leaf inclusion from the adaxial (a, i: 131a) and abaxial side (b, i: 131b). (c) Abaxial view of the leaf base showing the long grooved petiole and the interior venation exposed at the amber surface. (d) Cyclocytic stomata complexes with numerous subsidiary cells and non-sunken guard cells. (e) Adaxial surface of leaf lamina; *cd*: midline; Υ : ordinary epidermal cells of light yellow colour. (f) Abaxial surface of the leaf lamina; *ef*: midline; *ab*: stomata bands; *gg*: bands of ordinary epidermal cells along both margins; Υ : ordinary epidermal cells of light yellow colour. (g) The grooved petiole. (h) Overview of the needle inclusion from above and the side (indicated by *b*). (j) Adaxial side, ordinary epidermal cells are polygonal isodiametric. (k) Abaxial side showing the stomata bands on each side of the longitudinal midline; note the rectangular epidermal cells of the midline. Scale bars = 1 mm (a, b), 500 μ m (c), 50 μ m (d-k).

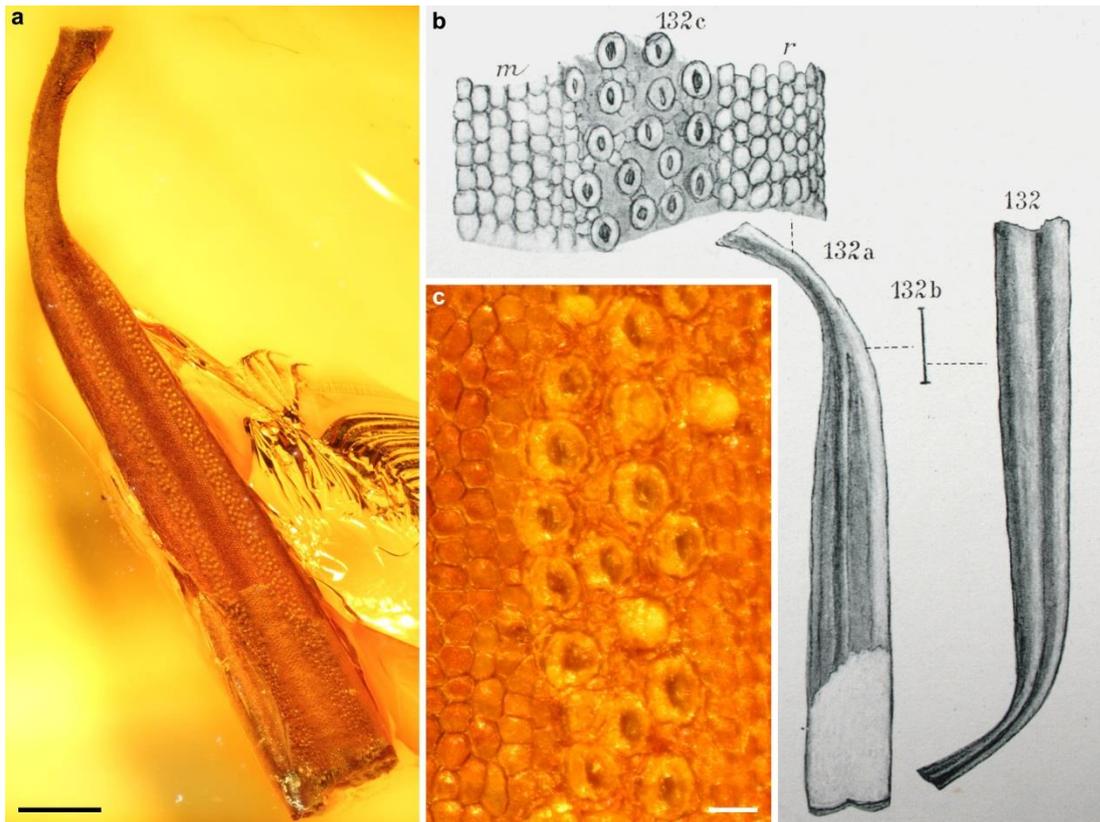


Fig. 31: ‘Needle’ of *Abies suckerii* from Baltic amber (a, c, GZG.BST.24355) and the historic drawings of this particular specimen (b, from CASPARY & KLEBS 1907, pl. XXX). **(a)** Overview of the leaf inclusion from the abaxial side showing two stomata bands on each side of the longitudinal midline and a very pronounced petiole. **(b)** Overview of the leaf inclusion from the abaxial (132 a) and abaxial side (132) and detail of the stomata (132 c). **(c)** Non-sunken stomata complexes with bean-shaped guard cells on the abaxial side, note the polygonal ordinary epidermal cells on each side of the stomata band. Scale bars = 1 mm (a), 50 µm (c).

entire, petiolate. Petioles 0.8 to 2.5 mm long \times 0.3 to 0.5 mm wide, grooved to incurved on the adaxial side (Figs 29c; 30c; 31a; 32a).

Hypostomatic, stomata irregularly clustered together in two bands (no stomata rows), bands separated by the midrib (Figs 29d; 30k; 31a; 32c). Stomata pits parallel orientated towards the longitudinal midrib, 42 to 66 µm long \times 39 to 60 µm wide, non-sunken with two bean-shaped guard cells (Figs 29e; 32d). Stomata complexes round, cyclocytic with a slender ring of 6 to 10 subsidiary cells (Figs 30d; 31c; 32d), stomata complexes 66 to 125 µm long \times 54 to 105 µm wide. Ordinary epidermal cells with straight cell walls; ordinary epidermal cells of abaxial midline rectangular or polygonal, papillous, 30 to 85 µm long \times 52 to 85 µm wide (Figs 29f; 30k; 31c; 32c). The abaxial stomata free zones along both leaf margins and the entire adaxial leaf side composed of mostly isodiametric polygonal cells (Figs 30j; 32e); 25 to 60 µm long \times 20 to 65 µm wide.

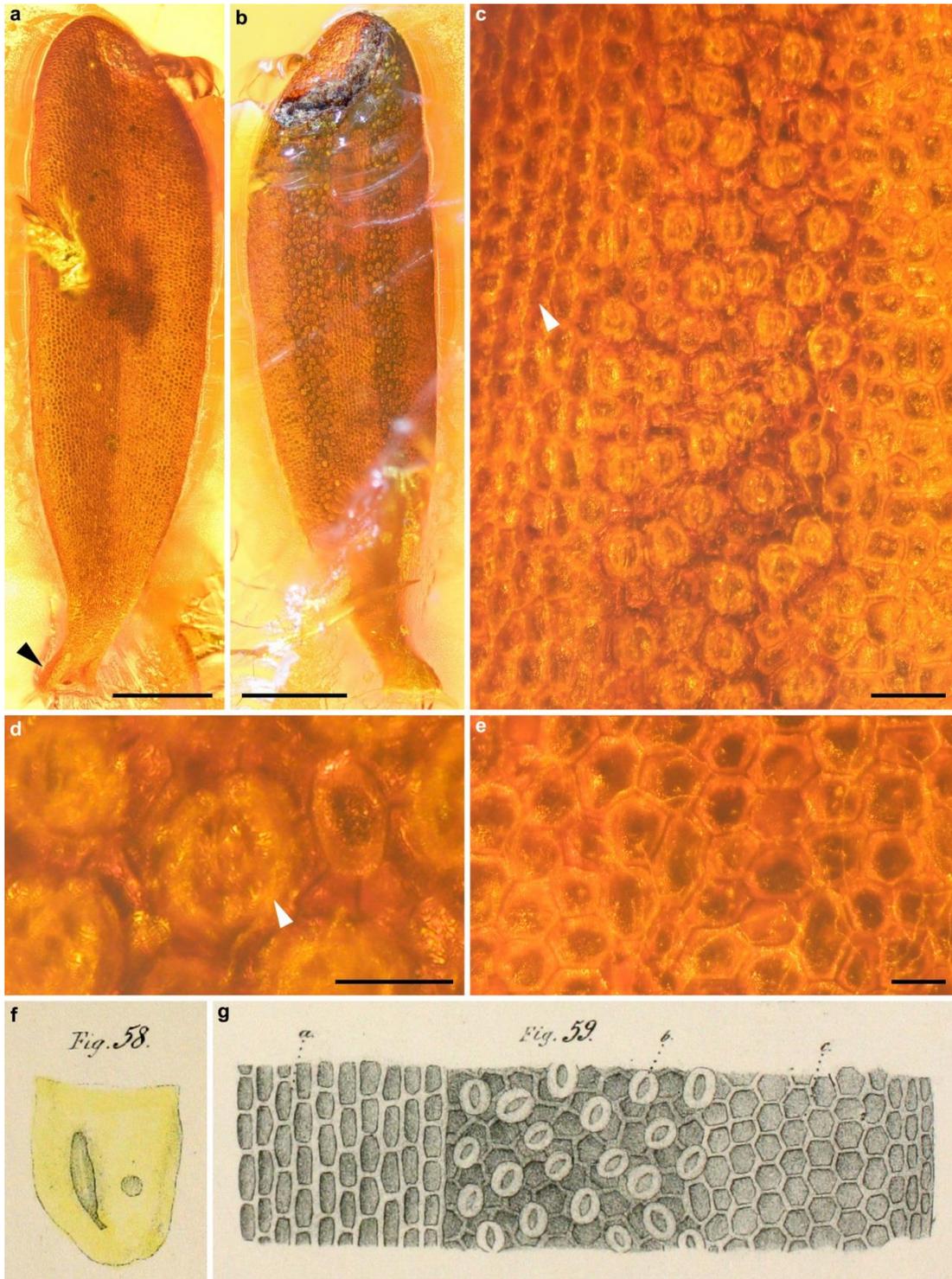


Fig. 32: Leaf inclusion of *Dermatophyllites porosus* from Baltic amber (a-e, MB.Pb.1979/0490) and the historic drawings of this particular specimen (f-g, from GOEPPERT & BERENDT 1845, pl. V). (a, b) Overview of the leaf inclusion from the adaxial (a) and abaxial (b) side, arrowhead indicates the grooved petiole (a). (c) Stomata band of the abaxial leaf side, arrowhead indicates the rectangular cell of the longitudinal midline. (d) Stomata complex on the abaxial side, with narrow ring of cyclocytic subsidiary cells and non-sunken guard cells (arrowhead). (e) Polygonal isodiametric cells of the abaxial epidermis. (f) Overview of the amber specimen with the inclusion of *D. porosus*. (g) Abaxial surface of lamina, showing the midrib with ordinary epidermal cells of rectangular shape (a), the stomata band (b) and the ordinary epidermal cells of polygonal shape, located along the leaf margin (c). Scale bars = 1 mm (a, b), 100 μ m (c), 50 μ m (d, e).

Tab. 10: Measurements of the *Dicotylophyllum* specimens from Baltic amber. Centered numbers of the leaf and stomata sizes are average values; size ranges are provided in brackets. Information about ‘*Abies linearis*’ is taken from descriptions and figures of the indicated reference. Certain features which were not available are indicated by ‘-’.

Specimen	<i>Abietes obtusifolius</i>	<i>Abies suckerii</i>	<i>Abies suckerii</i>	<i>Abies linearis</i>	<i>Dermatophyllites porosus</i>
Collection number	MB.Pb.1979/0591	GZG.BST.23539	GZG.BST.24355	lost	MB.Pb.1979/0490
Preservation	entire leaf	entire leaf	leaf fragment	entire leaf	entire leaf
Leaf					
Length	12 mm	15 mm	10 mm	16 mm	6.5 mm
Width (widest part)	1 mm	1.7 mm	1.5 mm	0.8 mm	1.8 mm
Petiole					
Length	0.8 mm	1.3 mm	2.5 mm	1 mm	1 mm
Width	0.3 mm	0.4 mm	0.4 mm	-	0.5 mm
Stomata complex					
Length	(66)-84-(105) μm	(75)-85-(102) μm	(66)-80-(90) μm	-	(85)-108-(125) μm
Width	(54)-69-(81) μm	(54)-66-(75) μm	(60)-68-(78) μm	-	(65)-82-(105) μm
Stomatal pit					
Length	(45)-53-(60) μm	(42)-51-(60) μm	(51)-55-(60) μm	-	(48)-60-(66) μm
Width	(45)-49-(60) μm	(42)-48-(54) μm	(39)-46-(54) μm	-	(42)-50-(60) μm
Ordinary epidermal cells (midline)					
Length	(39)-49-(60) μm	(30)-42-(52) μm	(35)-50-(80) μm	-	(45)-61-(85) μm
Width	(25)-35-(45) μm	(24)-29-(36) μm	(25)-31-(40) μm	-	(30)-37-(55) μm
Ordinary epidermal cells (margins)					
Length	(30)-41-(50) μm	(27)-42-(57) μm	(25)-36-(50) μm	-	(35)-48-(60) μm
Width	(35)-49-(60) μm	(27)-38-(54) μm	(20)-34-(45) μm	-	(45)-54-(65) μm
References					
	this paper	this paper	this paper	CASPARY & KLEBS 1907	this paper

Identification

Several complete leaves, leaf fragments and a twig fragment were described as *Abietes obtusifolius* GOEPP. et BER. (Fig. 29) and *Abies obtusifolia* (GOEPP. et BER.) GOEPP. et MENGE (Fig. 33) due to a similar needle shape and whitish stomata bands as in extant *Abies* species (GOEPPERT & BERENDT 1845, GOEPPERT & MENGE 1883). Our reinvestigation of the original specimen of *Abietes obtusifolius* from GOEPPERT & BERENDT (1845; MB.Pb.1979/0591; pl. V, figs 41-45; herein Fig. 29), revealed that this putative *Abies* inclusion does not show the typical *Abies* features [broadened disc-shaped needle base; stomata in regular dense files, sunken, amphicyclocytic with two polar subsidiary cells and 2 to 4 lateral subsidiaries; walls of ordinary epidermal cells mostly undulate; FLORIN (1931)]. Instead, an angiosperm origin is very likely, due to the non-sunken stomata with broad bean-shaped guard cells (Fig. 29e), the irregular distribution of the stomata within the stomata bands (Fig. 29d, i), the polygonal isodiametric shape of ordinary epidermal cells (Fig. 29f, i) and the incurved grooved long petiole (Fig. 29c).

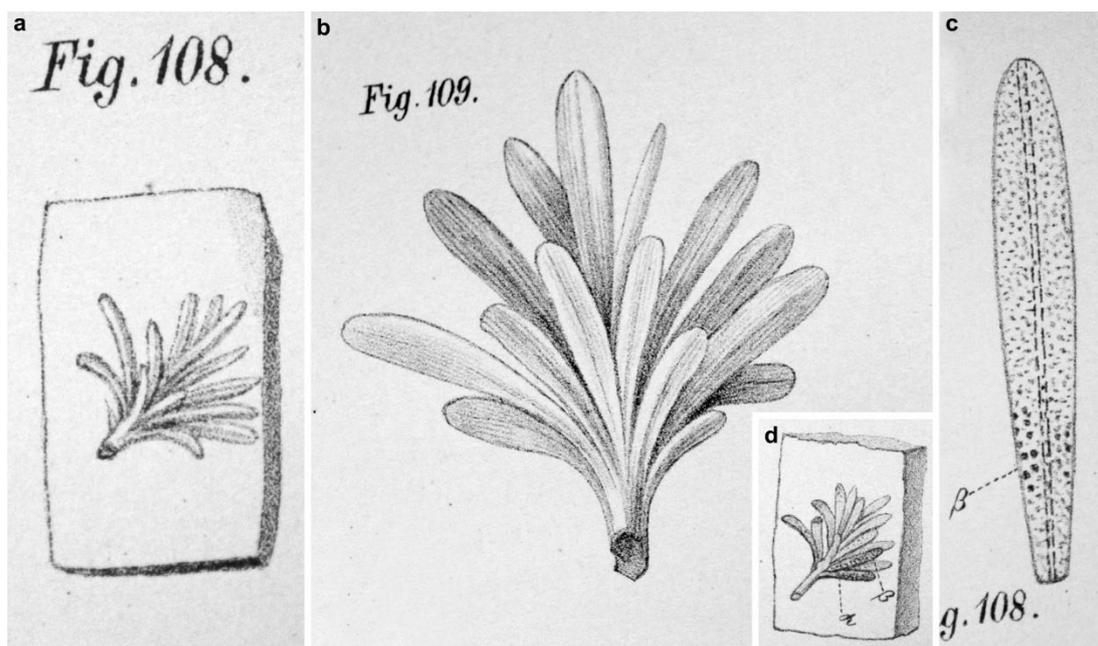


Fig. 33: Historic drawings of two lost amber specimens of *Abies obtusifolia* from Baltic amber (from GOEPPERT & MENGE 1883, pl. XIII). (a) Twig fragment in a piece of amber. (b) Twig fragment shown in (a), magnified. (c) Needle of the twig fragment shown in (a, b); β indicates the stomata. (d) Another amber specimen of *A. obtusifolia*.

Further *Abies* specimens assigned to *Abies suckerii* CASP. et R. KLEBS (CASPARY & KLEBS 1907, pl. XXX, figs 131, 131a-d, 132, 132a-c; herein Fig. 30 and Fig. 31 respectively) show similar stomata and epidermis morphology and the pronounced grooved petiole as in the putative *Abietites obtusifolius* specimen. However, these specimens are slightly broader and flatter. Specimen GZG.BST.23539 exhibits the interior venation on the adaxial leaf side (Fig. 30c), showing the branching of the central vessel which is untypical for conifers with needle-shaped leaves.

Another putative *Abies* specimen, described as *Abies linearis* CASP. et R. KLEBS (CASPARY & KLEBS 1907, pl. XXX, figs 134, 134a-f; herein Fig. 34) is also very similar to the leaves described above. Although CASPARY & KLEBS (1907) mentioned that the specimen of *A. linearis* can be distinguished from *A. obtusifolia* by its size, width and enrolled margins, drawings of *A. linearis* are very similar to those of *A. suckerii* and *A. obtusifolia*. Thus, we conclude, that *A. linearis* is analogous to these taxa, at least at genus level.

CASPARY & KLEBS (1907) mentioned morphological similarities between *Abies suckerii* and leaf inclusions of *Dermatophyllites porosus* (Ericaceae) GOEPP. et BER. from Baltic amber (GOEPPERT & BERENDT 1845, pl. V, figs 58-59; herein Fig. 32). *Dermatophyllites* was introduced by GOEPPERT & BERENDT (1845) for coriaceous leaf inclusions. They described nine species which were partly revised by CONWENTZ (1886) but he did not mention *D. porosus*. When comparing the original specimen of *D. porosus* (MB.Pb.1979/0490) from GOEPPERT & BERENDT (1845) to *A. suckerii*, we confirm that both specimens are very alike, sharing the same gross

morphology and the micromorphology of the stomata and the epidermis. Thus, we conclude that they both derive at least from the same genus.

The general appearance of the ‘*Abies*’-assigned leaf inclusions is similar to some extant Ericaceae leaves, but in contrast to the leaf inclusions, most Ericaceae possess anomocytic or paracytic stomata although exceptions may occur (METCALFE & CHALK 1950).

Hence, these specimens originally described as *Abies* are clearly of angiosperm origin. A similar needle-shaped leaf specimen but with putative *Sciadopitys* affinities has already been revised by SADOWSKI et al. (2016a). However, the identity of these angiosperm leaves is not fully resolved yet and not under the scope of the present paper.

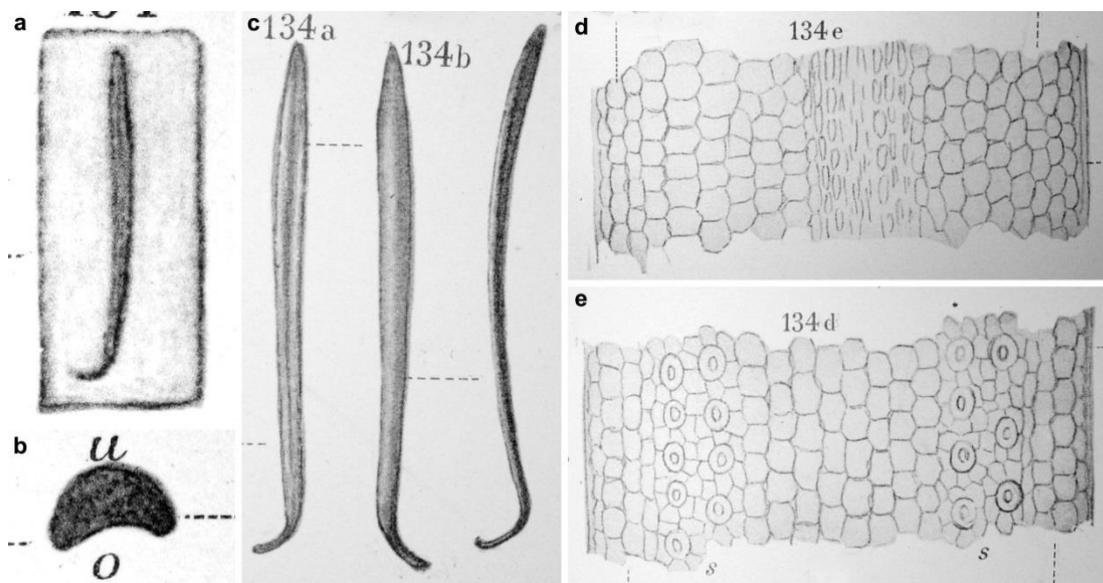


Fig. 34: Historic drawings of the ‘needle’ inclusion of *Abies linearis* from Baltic amber (from CASPARY & KLEBS 1907, pl. XXX, Künow Amber Collection). (a) Overview of the amber specimen with a ‘needle’ inclusion of *A. linearis*. (b) Outline of the petiole base showing the groove; *u* indicates abaxial and *o* indicates adaxial. (c) Overview of the leaf from different angles, note the pronounced petiole. (d) Adaxial leaf side with rectangular ordinary epidermal cells along the midline and polygonal ordinary epidermal cells on each side of the midline. (e) Abaxial leaf side with two stomata bands on each side of the midline; *s* indicates stomata band.

Remarks

The original labels of the amber specimens GZG.BST.23539 and GZG.BST.24355 are lost, but due to their strong similarities to the figures of CASPARY & KLEBS (1907) and to their descriptions and measurements, we conclude that these specimens are the holotypes for CASPARY & KLEBS’ (1907) ‘*Abies suckeri*’. The exposure of the interior of the leaf (GZG.BST.23539) probably dates back to preparations which were conducted sometime after the publication of CASPARY & KLEBS (1907).

DISCUSSION

The fossil record of conifers from Baltic amber

The amber inclusions of *Calocedrus*, *Cathaya*, *Nothotsuga*, *Pseudolarix* and *Cupressospermum* described here represent the first records of these genera from Baltic amber. These new findings broaden the stratigraphic occurrence of all named taxa in Europe extensively, from the Miocene and Oligocene to the late Eocene (see Table 11). Specimens of *Taxodium*, *Quasisequoia couttsiae* and *Abies* have been described from Baltic amber before, but with ambiguous specimens which did not sufficiently confirm their presumed identity. The new amber inclusions presented here definitely prove the occurrence of *Taxodium*, *Quasisequoia couttsiae* and *Abies* in the ‘Baltic amber forest’ and their late Eocene age is in congruence with the stratigraphic range of these taxa across Europe (see Table 11).

The reconstruction of the palaeobiogeographic history of *Pseudolarix* is mostly based on macrofossils, since *Pseudolarix* pollen strongly resemble other Pinaceae taxa in size and morphology, making “reliable identifications [...] problematic and past reports questionable” (LEPAGE & BASINGER 1995). The earliest macrofossil record of *Pseudolarix* derives from the Early Cretaceous of the Bureya and Fuxin Basins of Southeast Russia and Northeast China. The fossil record of *Pseudolarix* extends to the Plio-Pleistocene of Asia (e.g. SE Russia, NE China, E Mongolia), North America (e.g. Canada: Ellesmere Island, Axel Heiberg Island; Washington State), and Europe (e.g. eastern Germany) (LEPAGE & BASINGER 1995). Up to now, the fossil record of *Pseudolarix* indicates that it first occurred in Europe in the latest Oligocene or early Miocene. This was assumed to be a result of the closure of the epicontinental Turgai Strait seaway at the Eocene-Oligocene boundary, which previously separated eastern Asia from West Asia and Europe, preventing the westwards migration of East Asian flora (LEPAGE & BASINGER 1995). Alternatively, a floristic exchange between North America, Asia and Europe might also have taken place via the Beringian Corridor (LEPAGE & BASINGER 1991; LIU & BASINGER 2000) and the North Atlantic Land Bridge (DENK et al. 2010). Having this in mind, the global cooling trend, i.e. in Central Europe from ‘subtropical’-tropical to warm-temperate at the end of the Eocene, may have induced the migration of *Pseudolarix* from northern temperate regions to Central Europe (LEPAGE & BASINGER 1995).

Considering the assumed Priabonian age of Baltic amber, the findings of four *Pseudolarix* leaf inclusions from Baltic amber show that this genus arrived much earlier in Europe than originally thought. Thus, we suggest a circumarctic distribution of *Pseudolarix* during the early Paleogene with subsequent migration to the southern continents and to Central Europe during the Eocene. This is supported by the wide distribution of *Pseudolarix* in Russia and North America during the early Paleogene, as well as by the land bridges both the DeGeer Route and Thulian Route, which connected North America with Fennoscandia and Europe up to the Eocene, facilitating the distribution of *Pseudolarix* to the European land mass (LEPAGE & BASINGER 1995).

Tab. 11: Palaeoecological information about the described conifer taxa from Baltic amber.

Taxon	Stratigraphic range	Habitat	Selected associated plant taxa	References
Cupressaceae				
<i>Calocedrus</i>	early Oligocene (Czech Republic, Hungary), Oligocene (S China), early Miocene (Greece), middle Miocene, Pliocene	thermophilous subhumid; 'subtropical' humid conditions (S China) or temperate-warm or cooler climate (North America)	Flora of Suletice (early to late Oligocene, Czech Republic): <i>Tetraclinis</i> , <i>Cephalotaxus</i> , <i>Engelhardia</i> , <i>Sloanea</i> , <i>Platanus</i> , <i>Acer</i> , <i>Carpinus</i> , <i>Carya</i> , <i>Craigia</i> , Fabaceae, Lauraceae	KVAČEK 1999; SHI et al. 2012
<i>Quasisequoia couttsiae</i>	upper Paleocene to upper Miocene of Central, western and southeastern Europe	laurel forest, coastal plains, swamps, riparian forests, lake shores	Flora of Schleenhain, Saxony (Flora complex Zeitz, late Eocene, Germany): <i>Taxodium</i> , <i>Eotrigonobalanus</i> , <i>Rhodomyrthophyllum</i> , <i>Actinodaphne</i> , <i>Vaccinioides</i> , palms	KUNZMANN 1999; HENNIG & KUNZMANN 2013
<i>Taxodium</i>	since late Cretaceous of Europe and North America	near-shore to lowland riparian or gallery forests, waterlogged back swamps, tidal plains in brackish environments, flooded back levee	Flora of North Bohemian Basin (<i>Taxodium-Nyssa haidingeri</i> association; early Miocene, Czech Republic): <i>Glyptostrobus europaeus</i> , <i>Quasisequoia couttsiae</i> , <i>Myrica</i> , <i>Betula</i> , <i>Nyssa</i> , <i>Rubus</i> , <i>Spondiaecarpum</i>	BOULTER et al. 1993; KUNZMANN et al. 2009
Geinitziaceae				
<i>Cupressospermum saxonicum</i>	upper Oligocene of Central to eastern Germany and Czech Republic; lower Miocene of eastern and western Germany to upper Miocene of western Germany	eutrophic swamps, coastal environments	Flora of Mockrehna, Saxony (Flora complex Mockrehna-Witznitz, early Miocene, Germany): <i>Cephalotaxus</i> , <i>Pinus</i> , <i>Sequoia</i> , <i>Tetraclinis</i> , <i>Taxodium</i> , <i>Limnocarpus</i> , <i>Comptonia</i> , <i>Potamogeton</i> , <i>Ficus</i> , <i>Fagus</i>	MAI & WALTHER 1991; KUNZMANN 1999
Pinaceae				
<i>Abies</i>	late Cretaceous (Siberia), Eocene to Pleistocene (Central Asia, China, Japan, Europe, Russia, USA)	diverse	Flora of Dernbach (upper Pliocene, Germany): <i>Picea</i> , <i>Pinus</i> , <i>Sequoia</i> , <i>Populus</i> , <i>Juglans</i> , <i>Carpinus</i> , <i>Betula</i> , <i>Corylus</i> , <i>Fagus</i> , <i>Quercus</i> , <i>Ulmus</i> , <i>Magnolia</i> , <i>Acer</i>	MÜLLER-STOLL 1938; FLORIN 1963; FARJON 1990; XIANG et al. 2007
<i>Cathaya</i>	Eocene Buchanan Lake Formation, Axel Heiberg Island (Canadian Arctic), Oligocene to Pliocene of Eurasia (primarily Central and South Europe)	mixed mesophytic forest with 'subtropical' and evergreen elements, warm-temperate to 'subtropical' humid climate (Cfa, Köppen-Geiger)	Flora of Wiesa-Kamenz, Saxony (Flora complex Wiesa; lower Miocene, Germany): <i>Keteleeria</i> , <i>Nothotsuga</i> , <i>Sequoia</i> , <i>Pinus</i> , <i>Pseudolarix</i> , <i>Torreya</i> , <i>Tsuga</i> , <i>Tetraclinis</i> , <i>Quasisequoia</i> , <i>Symplocos</i> , <i>Laurocarpum</i> , <i>Mastixia</i> , Fagaceae spp.	LIU & BASINGER 2000; KUNZMANN & MAI 2005
<i>Nothotsuga protogaea</i>	Paleogene of North Siberia, lower Miocene to lower middle Miocene, Neogene of Wiesa (near Kamenz, Saxony, Germany)	20-23 °C mean annual temperature, 800-2000 mm precipitation (Wiesa flora)		FARJON 1990; KUNZMANN & MAI 2005
<i>Pseudolarix</i>	early Cretaceous to Pliocene (North America, Eurasia, Europe)	cool-temperate, warm-temperate, 'subtropical' mesophytic forests of middle latitudes; high precipitations	Flora of Niederheide, Saxonian Lusatia (Flora complex Thierbach to Mockrehna-Witznitz; upper Oligocene, Germany): <i>Pinus</i> , <i>Abies</i> , <i>Pseudotsuga</i> , <i>Tetraclinis</i> , <i>Laurocarpum</i> , <i>Liquidambar</i> , <i>Fagus</i> , <i>Salix</i> , <i>Rubus</i> , <i>Eurya</i> , <i>Symplocos</i>	FARJON 1990; LEPAGE & BASINGER 1995; MAI 1997; BUDANTSEV & GOLOVNEVA 2009
<i>Pinus</i>	since Triassic? (Siberian formations), Jurassic (Europe), Cretaceous; fanning out since the Paleogene	diverse	diverse	FARJON 2005b; ECKENWALDER 2009
Sciadopityaceae				
<i>Sciadopitys cf. tertiaria</i>	since late Eocene (Baltic amber), lower Oligocene (eastern Germany) to upper Pliocene (eastern Germany; East France)	raised bogs, swamp forest, high precipitation, humid	Flora of Northeast Brandenburg (Flora complex Wiesa-Eichelskopf, Miocene, Germany): <i>Cathaya</i> , <i>Pinus</i> , <i>Quasisequoia</i> , <i>Ilex</i> , <i>Nyssa</i> , <i>Magnolia</i> , <i>Palmoxyton</i> , <i>Rubus</i> , <i>Scirpus</i>	MENZEL 1913; VON DER BRELIE & WOLF 1981; PHILIPPE et al. 2002; MAI 2004; SADOWSKI et al. 2016a

Macrofossils of *Cathaya* are generally rare worldwide, while pollen is more frequently found (LIU & BASINGER 2000). The fossil record of *Cathaya* possibly goes back to the Early Cretaceous (Aptian to Albian) of Canada (Northwest Territories) which is indicated by *Cathaya*-like pollen. *Cathaya* spread in Europe during the Paleogene with distribution patterns similar to *Pseudolarix*, possibly being blocked by the Turgai Strait and migrating over the DeGeer Route and the Thulian Route to Europe. There, it was mainly distributed in Central Europe with several fossil localities (including macrofossil and pollen finds of *Cathaya*) in Germany (THIELE-PFEIFFER 1988; ASHRAF & MOSBRUGGER 1996; KNOBLOCH et al. 1996; NICKEL 1996; LIU & BASINGER 2000).

The earliest fossils of *Abies* are pollen from the Late Cretaceous of Siberia (see XIANG et al. 2007 and reference therein for a comprehensive list of the fossil record of *Abies*); leaves, cone scales and further pollen of *Abies* are recorded from throughout Eocene of the Northern Hemisphere (e.g. Shandong, China; Idaho, Nevada and Colorado, USA; Europe) until the Pleistocene (e.g. Poland, Japan) (FARJON 1990; XIANG et al. 2007). Following XIANG et al. (2007), the distribution pattern of *Abies* is similar to the migration routes of *Cathaya* and *Pseudolarix*, originating on the Eurasian continent and gradually distributing via land bridges, such as the Thulian Route to Europe.

Pinus fossils are numerous and have been recorded from many different localities worldwide. The first fossil record of *Pinus* is under debate with unverified *Pinus* pollen from the Upper Triassic of Siberia (MIROV 1967). Unambiguous *Pinus* fossils have been reported from Jurassic up to Quaternary sediments worldwide, except for the Southern Hemisphere (MIROV 1967). Via land bridges, *Pinus* spread from North-East Asia to North America and then from the Paleogene on, fanning out across the entire Northern Hemisphere (FARJON 2005b; MIROV 1967). Remains of pines also have been reported from Baltic amber and based on wood inclusions, the taxon *Pinus succinifera* was described and supposed to be one of the major Baltic amber producing trees (CONWENTZ 1890). A reinvestigation of the holotype of *P. succinifera* by DOLEZYCH et al. (2011) proved its affinity to *Pinus* with similarities to the extant sections *Parrya* MAYR and *Strobus* LITTLE et CRITCHFIELD. However, resins of extant Pinaceae do not comply with the geochemical requirements of Baltic amber, and instead the Sciadopityaceae were recently suggested as one of the source plants (WOLFE et al. 2009).

The fossil record of *Nothotsuga* is very scarce and up to now there are only two known records, i.e. from the Paleogene of northern Siberia (GAUSSEN 1966; KUNZMANN & MAI 2005) and from the lower Miocene Wiesa flora of Saxony (Germany) (KUNZMANN & MAI 2005). Our record further substantiates the presence of this rare extant genus in the European Paleogene and is its oldest record from Central Europe.

Calocedrus fossils are known from the Oligocene to the Pliocene of North America (Alaska, Idaho, Nevada), Central Europe (Poland, Czech Republic, Germany, Hungary, Greece) and East Asia (southeastern China, Japan, Korea),

proposing a circumboreal distribution for *Calocedrus* (SHI et al. 2012). The occurrence in the Oligocene to Pliocene of Central Europe is thought to go back to migrations via land bridges, connecting North America, Asia and Europe, as already described for *Cathaya* and *Pseudolarix*. Due to morphological differences between the European *Calocedrus* fossils to Asian and North American fossil specimens, SHI et al. (2012) suggested that the transpacific distribution pattern of *Calocedrus* was already established in the Eocene which fits well with the occurrence of *Calocedrus* in Eocene Baltic amber.

Taxodium fossils are known since the Late Cretaceous (Cenomanian and Maastrichtian) of Europe and North America (AULENBACK & LEPAGE 1998; KNOBLOCH & MAI 1986). From the Paleogene to the Neogene they were widely distributed across Eurasia and North America, with high abundances in Oligocene and Miocene swamps of Central Europe (KUNZMANN et al. 2009). The occurrence in Baltic amber therefore fits well within this picture.

Quasisequoia couttsiae occurred from the late Paleocene (France) to the late Miocene (Germany) and then became extinct (KUNZMANN 1999). Interestingly, it was also reported from the Oligocene of Otradnoje (Russia) which is located in the Kalinigrad area (KUNZMANN 1999) and thus supports the presence of *Q. couttsiae* in the Baltic amber flora.

The presence of the monotypic genus *Cupressospermum saxonicum* in Baltic amber predates all previous occurrences as it was only recorded from the late Oligocene (Central to eastern Germany and Czech Republic) to the late Miocene so far (western Germany) (KUNZMANN 1999).

In conclusion, our evaluation of conifer taxa from historic and recent collections of Baltic amber extends the stratigraphic range for certain conifer genera in Europe, namely *Calocedrus*, *Cupressospermum*, *Pseudolarix*, *Cathaya* and *Nothotsuga* into the Eocene, according to the Priabonian age of the Blue Earth layer. Also for *Sciadopitys* cf. *tertiaria* MENZEL emend. WEYLAND, KLIPPER et BERENDT, the stratigraphic range was extended with its oldest macrofossil occurrence from Baltic amber (SADOWSKI et al. 2016a).

Habitat types of the ‘Baltic amber forest’

Based on autecological characteristics of the described conifer taxa from other fossil localities, we are able to infer the presence of different habitat types in the source area of Baltic amber (see Table 11 for further information). We suggest the presence of lowland nearshore swamps which were mostly influenced by brackish water, back swamps in floodplains and mixed mesophytic forests and meadows which were not affected by periodic flooding and waterlogging (Fig. 35).

Coastal swamp communities are indicated by the extinct conifer *Cupressospermum saxonicum* which was reported from eutrophic swamps in coastal environments of the Miocene brown coal mires of Lusatia (Saxony and Brandenburg, Germany) and of the earliest Miocene Mockrehna floras [Saxony, Germany; MAI &

WALTHER (1991)]. In tidal-influenced parts of those coastal plains, *Cupressospermum* replaced *Glyptostrobus europaeus* (KUNZMANN et al. 2012) and was associated with angiosperms such as the Lauraceae, *Liquidambar* L., *Magnolia* L. and palms, but also with different conifer genera that usually occur in lowland swamp forests, for instance *Cunninghamia* R. BR. ex A. RICH., *Sciadopitys*, and *Tetraclinis* MASTERS (KUNZMANN 1999; KUNZMANN et al. 2012; KUNZMANN & SCHNEIDER 2013). *Sciadopitys* foliage has been recently described from the Baltic amber (SADOWSKI et al. 2016a) and these fossils are the first unequivocal proof of the presence of this conifer from Baltic amber. According to KUNZMANN & SCHNEIDER (2013: fig. 19) only *Cupressospermum saxonicum* was located within parts of coastal swamps which were affected by tidal or brackish waters, whereas the other conifers grew above this zone, *Cunninghamia* and *Tetraclinis* on air-ventilated peat, and *Sciadopitys* on water-saturated peat. Compared to *Cupressospermum* remains from non-tidal influenced parts of coastal mires in Lusatia, *Cupressospermum* shows remarkable resin segregation in brackish influenced stands (pers. comm. Wilfrid Schneider, 2016). The occurrence of both *Cupressospermum* and *Sciadopitys* in the Baltic amber is a good hint for a coastal swamp forest in the Baltic amber source vegetation. *Sciadopitys* today does not occur in lowland swamp habitats as it is restricted to mountainous areas of Japan with high levels of rainfall (ECKENWALDER 2009). Anyhow, SADOWSKI et al. (2016a) argue for a potential swamp habit of *Sciadopitys* from Baltic amber, based on its fossil record in the European Paleogene where mass occurrences of *Sciadopitys* cladodes and roots formed specific lignite seams, showing that it was a dominant constituent of raised bog habitats (GOTHAN 1936; THIERGART 1949; DOLEZYCH & SCHNEIDER 2007). The autochthony of these cladode mass occurrences has been evidently shown by the co-occurrence of numbers of upright (autochthonous) *Sciadopitys* stems in the same horizons (DOLEZYCH & SCHNEIDER 2007).

Interestingly, *Cupressospermum saxonicum* is also known from the late Oligocene Bitterfeld flora (Germany) where fossil twig and cone remains with in situ amber were found (BARTHEL & HETZER 1982). This particular amber sample was identified as Gedanite, a rare amber variety occurring in the Baltic region, Bitterfeld and in the district of Chatanga (Russia) (MAI & SCHNEIDER 1988; FUHRMANN 2010; VÁVRA 2015). The IR (infrared) spectroscopic examination of Gedanite, as well as the small amount of free succinic acid distinguishes it from succinite, the most abundant Baltic amber variety (STOUT et al. 1995). However, the botanical affinities of Gedanite are still unresolved, since similarities of the Gedanite IR-spectrum to resin from *Agathis australis* (D. DON) LOUDON, (Araucariaceae) were found (VÁVRA 2015).

A further constituent of a late Oligocene coastal swamp community in central Germany is the extinct *Quasisequoia couttsiae* (KUNZMANN 1999). During the Paleogene this giant tree was a typical component of brown coal mires, occurring in mixed swamp associations together with laurels and evergreen Fagaceae such as *Eotrigonobalanus furcinervis* (ROSSMÄSSLER) WALTHER et KVAČEK [e.g. late Eocene

flora of Schleenhain, KUNZMANN & WALTHER (2002); early Oligocene flora of Haselbach, KUNZMANN & WALTHER (2012)]. In middle to late Eocene assemblages of central Europe *Quasisequoia couttsiae* also occurred in swamp habitats, riparian forests and nearshore lacustrine environments far from the sea [e.g. KUNZMANN (1999), KUNZMANN et al. (2015)]. Thus, *Q. couttsiae* indicates lowland swamps and riparian sites in the Baltic amber source area. Other Eocene Central Europe localities revealed that these habitats were not influenced by brackish waters.

These swamp communities were further inhabited by *Taxodium* whose fossil representatives were typical for riparian habitats and swamps of the European Oligocene and Miocene (KUNZMANN et al. 2008). But also extant *Taxodium* species inhabit inundated areas along rivers, shallow waters and swamps (FARJON 2005).

Cathaya possibly grew along the swamp margins, as it is known from multiple fossil records from the lower and middle Miocene Lusatian brown coal seams where it was situated along the edges of *Sciadopitys* dominated raised bogs (DOLEZYCH & SCHNEIDER 2007). These swamp edges also might have been inhabited by *Pinus* which is ecologically very broad in its habitat preferences, but *Pinus* is also known from swamp margins today (ECKENWALDER 2009). In contrast, the *Cathaya bergeri* (F. KIRCHHEIMER) W. SCHNEIDER/*C. roseltii* W. SCHNEIDER whole-plant, recorded by a mass occurrence of seed cones and leaves in the Wiesa site (Saxony, Germany) is interpreted to be an element in a conifer-rich lowland mixed mesophytic forest associated with *Keteleeria* CARRIÈRE, *Nothotsuga*, and *Tsuga* (KUNZMANN & MAI 2005). A similar forest type including the same conifer components is known from modern vegetation in central and southern China. The *Cathaya* record from the Baltic amber thus does not necessarily suggest that this genus belonged to swamp vegetation.

The presence of mixed mesophytic conifer-angiosperm forests in the Baltic amber source habitat is further supported by the amber inclusions of *Pseudolarix*, *Nothotsuga*, and *Calocedrus*. All these conifer taxa are described from Paleogene and Neogene mixed mesophytic forests with high humidity and warm-temperate climate (LEPAGE & BASINGER 1995; KVAČEK 1999; LIU & BASINGER 2000; KUNZMANN & MAI 2005; SHI et al. 2012). This corresponds with the extant distribution of these taxa, mostly in warm-temperate climates with approximately 1000 to 2000 mm precipitation/year (Table 12). Today, these genera occur with a wide range of other conifer taxa such as *Pinus*, *Abies*, *Pseudotsuga*, *Tsuga* or *Chamaecyparis* SPACH, but also with many different angiosperms, especially those belonging to the Fagaceae (e.g. *Quercus* L., *Castanopsis* (D. DON) SPACH, *Lithocarpus* BLUME, *Fagus* L., and *Cyclobalanopsis* OERST.) at different elevations (Table 12 for references). This association is also reflected in the Baltic amber flora which shows a very high number of inclusions with affinities to Fagaceae (*Quercus* spp., *Trigonobalanus succinea* (GOEPP. et MENGE) D. H. MAI, such as stellate trichomes, flowers, fruits and buds (CONWENTZ 1886; CZECZOTT 1961; FORMAN 1964; MAI 1967).

Tab. 12: Sociobiological and ecological features of the nearest living relatives of the conifers from Baltic amber.

Fossil	Analogous extant taxon	Distribution	Vegetation	Climate	Associated taxa	References
Cupressaceae						
<i>Calocedrus</i>	<i>Calocedrus</i> spp.	West Coast USA to Mexico (Oregon to Baja California); Taiwan, SW China, SE Asia	mixed conifer broad-leaved forests to montane mixed evergreen conifer-broad-leaved forests	tropical to 'subtropical' montane regions	<i>Pinus, Abies, Pseudotsuga, Sequoiadendron, Chamaecyparis, Arctostaphylos, Ceanothus, Castanopsis, Quercus, Lithocarpus</i>	FARJON 2005a; SHI et al. 2012
<i>Taxodium</i>	<i>Taxodium</i> spp.	SE USA, Mexico, Guatemala	peat bogs, swamps, alluvial or coastal plains, riparian forests, stagnant pools, gallery woodlands	warm-temperate to 'subtropical', humid	<i>Pinus, Nyssa, Acer, Magnolia, Fraxinus, Quercus, Liquidambar, Ilex, Viburnum, Platanus, Populus, Salix, Ficus, Inga</i>	FARJON 2005a; KUNZMANN et al. 2009
Pinaceae						
<i>Abies</i>	<i>Abies</i> spp.	worldwide (Northern Hemisphere)	from low elevations to montane subalpine forests; mixed conifer-deciduous-broad-leaved forests	temperate, high mountains of 'subtropical' and warm-temperate regions	<i>Picea, Tsuga, Thuja, Pinus, Chamaecyparis, Pseudotsuga, Larix, Cryptomeria, Fagus sylvatica</i>	FARJON 1990; XIANG et al. 2007; ECKENWALDER 2009
<i>Cathaya</i>	<i>Cathaya argyrophylla</i>	South Central China	sclerophyllous broad-leaved forests to deciduous broad-leaved forests	warm-temperate to 'subtropical', humid (1000-2000 mm/a)	<i>Pinus, Tsuga, Nothotsuga, Quercus, Castanopsis, Lithocarpus, Fagus, Cyclobalanopsis, Theaceae, Clethra, Vaccinium, Prunus, Blastus, Carrierea, Sorbus, bamboo</i>	FARJON 1990; LIU & BASINGER 2000; KUNZMANN & MAI 2005
<i>Nothotsuga protogaea</i>	<i>Nothotsuga longibracteata</i>	SE China	evergreen sclerophyllous broad-leaved forests to mixed mesophytic broad-leaved forests	warm-temperate to temperate, humid (1000-2000 mm/a)	<i>Pinus, Cephalotaxus, Cunninghamia, Chamaecyparis, Ginkgo, Podocarpus, Pseudotsuga, Tsuga, Taxus, Castanopsis, Lithocarpus, Quercus, Fagus, Tetracentron, Schima, Michelia, Magnolia, Cinnamomum, Altingia, Nyssa</i>	KUNZMANN & MAI 2005; FARJON 1990
<i>Pinus</i>	<i>Pinus</i> spp.	worldwide (Northern Hemisphere)	boreal forests and alpine shrubberies to lowland tropical savannas, swamp margins to desert slopes	diverse	diverse	FARJON 2005b; ECKENWALDER 2009
<i>Pseudolarix</i>	<i>Pseudolarix amabilis</i>	SE China	mixed-mesophytic and evergreen sclerophyllous broad-leaved forest; hills and alluvial plains	warm-temperate to temperate, humid (1500-2000 mm/a)	<i>Ginkgo, Pinus, Torreya, Liquidambar, Nyssa, Acer, Quercus, Pterocarya, Platycarya, Rhus, Magnolia</i>	LEPAGE & BASINGER 1995; FARJON 1990; KUNZMANN & MAI 2005
Sciadopityaceae						
<i>Sciadopitys</i> cf. <i>tertiaria</i>	<i>Sciadopitys verticillata</i>	Japan	mixed conifer-angiosperm forests	temperate, humid	<i>Chamaecyparis, Tsuga, Abies, Pinus, Aesculus, Magnolia, Acanthopanax, Cercidiphyllum, Acer</i>	TSUKADA 1963; FARJON 2005a

A further constituent of the mixed forest was possibly *Abies*, which today inhabits forests of sea level altitudes to very high mountain ranges (up to 4700 m elevation) and is adapted to cold temperatures and both low to high annual precipitations (FARJON 1990; XIANG et al. 2007). In general, *Abies* is less drought resistant than other Pinaceae genera and always requires a certain amount of moisture (FARJON 1990). Extant species are (sub) climax trees and have a limited competitive ability against many other tree species (FARJON 1990). Since extant *Abies* is very abundant in montane regions, its fossils are often interpreted as indicators for high altitudinal belts (KUNZMANN & MAI 2005). However, the East European Craton is a prime example of long-term geologic stability (NIKISHIN et al. 1996), and there were no orogenic events in the Baltic region during the late Eocene when Baltic amber likely originated, precluding the *Abies* inclusion as altitudinal indicator. The occurrence of *Abies* in mixed angiosperm forests of different European fossil floras [e.g. Wiesa flora, Miocene (KUNZMANN & MAI 2005) or the Dernbach flora, late Pliocene (MÜLLER-STOLL 1938), see Table 11] suggests that it was part of mixed mesophytic conifer-angiosperm forests within the Baltic amber vegetation.

Besides swampy habitats and habitats with mixed mesophytic communities, light and comparatively drier areas opened up within the ‘Baltic amber forest’ area. They were inhabited by graminids [sedges and grasses, SADOWSKI et al. (2016b)] and by carnivorous plants of the Roridulaceae (SADOWSKI et al. 2015), but very likely

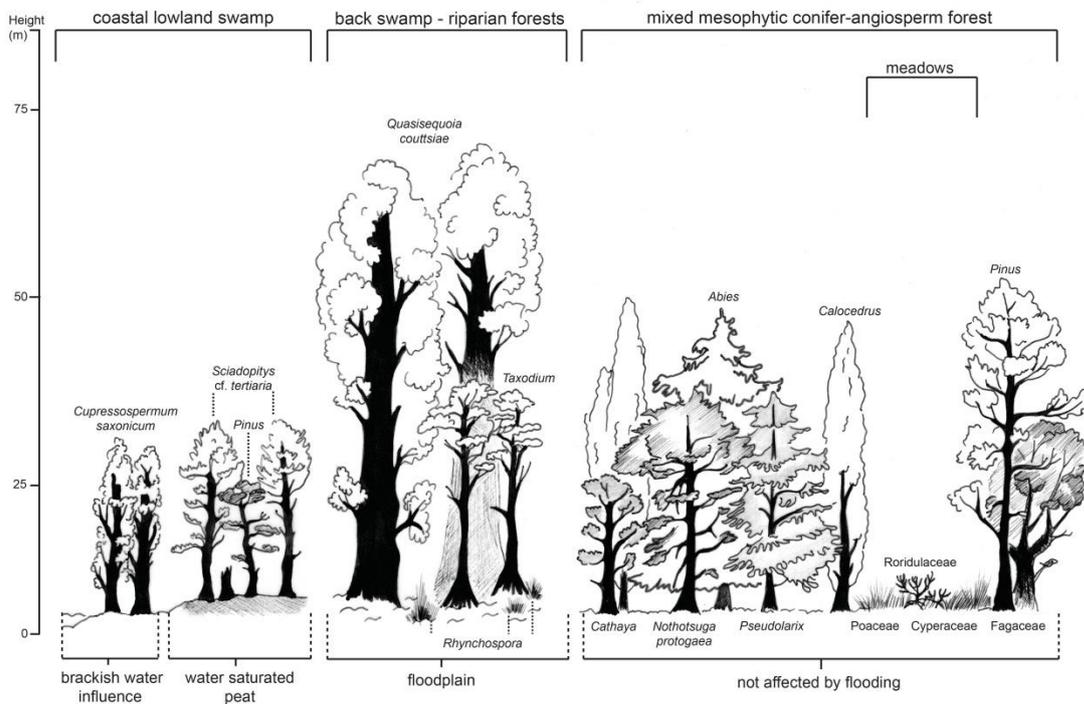


Fig. 35: Reconstruction of the habitat types of the Eocene ‘Baltic amber forest’ based on conifer taxa inclusions: coastal lowland swamps, back swamps to riparian forests and mixed mesophytic conifer-angiosperm forests with meadows. Tree height was estimated from fossil and extant analogous taxa, taken from ECKENWALDER (2009), FARJON (1990, 2005a, b) and KUNZMANN (1999).

also by different *Pinus* species. *Pinus* today and in the past had a very wide ecological range, adapting to numerous habitat types such as boreal and alpine forests to savannas, desert slopes and ‘subtropical’ forests (ECKENWALDER 2009; FARJON 2005b). Although *Pinus* is an indicator for various habitat types, it is known as a pioneer plant requiring much light and open conditions (ECKENWALDER 2009), which supports the assumption of its presence in open habitat patches within the ‘Baltic amber forest’, but also in the swamp communities, like the extant slash pine *P. elliottii* ENGELM., occurring in extensive swamps of Florida and Georgia (USA) where palmetto palms and various grasses are associated undergrowth (FARJON 2005b).

Summarizing, the conifer taxa that are proven from inclusions herein, along with fossils indicating open habitats, suggest heterogeneous vegetation with forests in diverse habitat types. They comprise coastal swamps and bogs, lowland swamps separated from the coastline, humid mixed conifer-angiosperm forest with mesophytic elements, as well as open, drier and light patches which intermingled with the forest (Fig. 35). Overall, a warm-temperate but not ‘subtropical’ climate may be assumed.

Comparison of the conifer diversity of Baltic amber to European fossil floras

Because Baltic amber has been considered to be of Eocene age, (KOSMOWSKA-CERANOWICZ et al. 1997; STANDKE 1998; KASIŃSKI & KRAMARSKA 2008; STANDKE 2008), we compare the taxonomic diversity of its conifer inclusions with those of other important European assemblages of fossil plants (Table 13). We also consider Oligocene sites and early Miocene Wiesa floristic assemblages because their conifer diversity is rather similar to the Baltic amber conifers described herein (Table 13).

A high conifer diversity with at least ten conifer genera distinguishes the Baltic amber flora from any other ‘subtropical’ middle-late Eocene flora of Central Europe, such as the zonal Kučlin flora and the Staré Sedlo Formation of North Bohemia (Czech Republic).

The radiometric age of the Kučlin site ranges from the late middle to early late Eocene (about 38 myr). The sediments of Kučlin are diatomites from a freshwater maar lake, which was surrounded by a heterogeneous broad-leaved evergreen forest (KVAČEK 2002; KVAČEK & TEODORIDIS 2011). The conifer diversity in the Kučlin flora is low; the macrofossil record only indicates two taxa, *Doliosstrobos* MARION (Doliosstrobaceae) and *Tetraclinis* (Cupressaceae) which are both not recorded from Baltic amber. *Doliosstrobos*, an extinct conifer, was fairly abundant in the Kučlin flora and the only hygrophilic conifer taxon, while *Tetraclinis* was extremely rare (KVAČEK & TEODORIDIS 2011). Also Pinaceous pollen with similarities to *Cathaya*, and unidentified Cupressaceae pollen were found (KVAČEK & TEODORIDIS 2011). In contrast to the Baltic amber vegetation, extensive deep swamps did not exist for the vegetation of Kučlin.

Tab. 13: Comparison of the conifer diversity of Baltic amber to European fossil floras. Conifer taxa from Baltic amber which also occur in other European fossil floras are printed in bold.

Fossil site	Age	Vegetation belt	Climate	Cupressaceae	Doliosrobacae	Geinitziacae	Sciadopityacae	Taxaceae	Pinaceae	Reference
Baltic amber										
	late Eocene?	mixed mesophytic	warm-temperate	<i>Calocedrus</i> sp. <i>Quasisequoia couttsiae</i> <i>Taxodium</i> sp.	-	<i>Cupressospermum saxonicum</i>	<i>Sciadopitys</i> cf. <i>tertiaria</i>	-	<i>Abies</i> sp. <i>Cathaya</i> sp. <i>Nothotsuga protogaea</i> <i>Pinus baltica</i> , <i>P. serrata</i> , <i>P. aff. schiefferdeckeri</i> , <i>P. cembraefolia</i> <i>Pseudolarix</i> sp.	this paper, SADOWSKI et al. 2016a
Spitsbergen										
	early Paleocene-early Eocene	polar deciduous to mixed mesophytic	arctic cool temperate	<i>Fokieniopsis catenulate</i> <i>Glyptostrobus nordenskiöldii</i> <i>Mesocyparis sabiniana</i> <i>Metasequoia</i> spp. <i>Sequoia brevifolia</i> <i>Taiwania schaeferi</i> <i>Taxodium olrikii</i> <i>Thuja ehrenswaerdii</i>	-	-	-	-	<i>Picea</i> sp. <i>Pseudolarix septentrionalis</i> <i>Pityolepis</i> spp.	BUDANTSEV & GOLOVNEVA 2009; KVAČEK 2010
Messel										
	latest early Eocene	notophyllous broad-leaved evergreen	warm humid paratropical	-	<i>Doliosrobis taxiformis</i>	-	<i>Sciadopitys</i> pollen	<i>Cephalotaxus messelensis</i>	pollen	WILDE 2004
Zeitl, Weibelster Basin										
	latest middle-late Eocene	notophyllous broad-leaved evergreen	'subtropical'	<i>Chamaecyparites hardtii</i> <i>Cupressoconus rhenanus</i> <i>Glyptostrobus europaeus</i> <i>Quasisequoia couttsiae</i> <i>Sequoia abietina</i> <i>Taxodium dubium</i> <i>Tetraclinis salicornioides</i>	<i>Doliosrobis taxiformis</i>	-	<i>Sciadopitys</i> pollen	<i>Cephalotaxus saxonica</i>	<i>Pinus dixonii</i> , <i>P. eophylla</i> , <i>P. cf. hepios</i> , <i>P. cf. robustifolia</i> , <i>P. stroboides</i> , <i>P. thomasiiana</i>	MAI & WALTHER 1985; MORAWECK et al. 2015
Staré Sedlo										
	late Eocene	notophyllous broad-leaved evergreen	'subtropical'	<i>Quasisequoia couttsiae</i> <i>Sequoia abietina</i> <i>Taxodium balticum</i>	? <i>Doliosrobis taxiformis</i>	-	<i>Sciadopitys</i> pollen	? <i>Cephalotaxus</i> sp.	<i>Cathaya</i> pollen <i>Pinus</i> pollen, <i>Pinus ornata</i> , <i>P. stroboides</i> , <i>P. cf. thomasiiana</i>	KNOBLOCH et al. 1996
Kučlín										
	late middle Eocene-early late Eocene	notophyllous broad-leaved evergreen	'subtropical'	<i>Tetraclinis salicornioides</i>	<i>Doliosrobis taxiformis</i>	-	-	-	-	KVAČEK & TEODORIDS 2011
Haselbach, Weibelster Basin										
	early Oligocene	mixed mesophytic	temperate	<i>Glyptostrobus europaeus</i> <i>Quasisequoia couttsiae</i> <i>Sequoia abietina</i> <i>Taxodium dubium</i> <i>Tetraclinis salicornioides</i>	-	-	-	<i>Cephalotaxus</i> ex. gr. <i>harringtonia</i>	<i>Pinus eophylla</i> , <i>P. palaeostrobus</i> , <i>P. cf. robustifolia</i> <i>Tsuga plicata</i>	KUNZMANN & WALTHER 2012

Tab. 13 continued

Thierbach, Weißelster Basin										
	early late Oligocene	mixed mesophytic	warm- temperate, humid	<i>Glyptostrobus europaeus</i> <i>Sequoia abietina</i> <i>Taxodium dubium</i> <i>Tetraclinis salicornioides</i>	-	<i>Cupressospermum saxonicum</i>	-	-	<i>Tsuga schneideriana</i>	MAI & WALTHER 1991; unpubl.
Wiesa										
	late early Micoene	mixed mesophytic to evergreen broad-leaved	warm- temperate	<i>Quasisequoia couttsiae</i> <i>Sequoia abietina</i> <i>Tetraclinis salicornioides</i>	-	-	-	<i>Taxus engelhardtii</i> <i>Torreya bilinica</i>	<i>Abies resinosa</i> <i>Cathaya bergeri</i> <i>Keteleeria hoehnei</i> <i>Nothotsuga protogaea</i> <i>Pseudolarix schmidtgenii</i> <i>Pseudotsuga jechorekiae</i> <i>Tsuga schneideriana, T. moenana</i> <i>Pinus grossana, P. hampeana, P. palaeostrobus, P. cf. heptos</i> <i>Pityophyllum wiesaensis</i>	KUNZMANN & MAI 2005; KUNZMANN 2014

Regarding the angiosperms, fagaceous macrofossils and pollen are very rare in the fossil record of Kučlin. This is also different from the Baltic amber flora which is characterized by its high abundance of Fagaceae inclusions; stellate trichomes with affinities to *Quercus* even constitute the most abundant plant inclusions in Baltic amber (CONWENTZ 1886; KIRCHHEIMER 1937; CZECHOTT 1961).

Another well studied late Eocene fossil flora of North Bohemia was recovered from the Staré Sedlo Formation which derives from fluvial sedimentation processes. In contrast to the Kučlin flora, the vegetation of Staré Sedlo is intrazonal, comprising broad-leaved evergreen gallery forests with palms, located in the ‘subtropical’ zone of mid-latitudinal Europe (KNOBLOCH et al. 1996; KVAČEK 2010). As with the Kučlin flora, the vegetation of Staré Sedlo is characterized by the low abundance of conifers, including *Pinus*, *Quasisequoia couttsiae*, *Sequoia abietina* (BRONGNIART) KNOBLOCH, *Taxodium balticum* SVEŠNIKOVA et BUDANTSEV and putative findings of *Doliosrobis* and *Cephalotaxus* SIEBOLD et ZUCC. ex ENDL. The pollen record indicates the presence of *Sciadopitys*, *Cathaya* and Cupressaceae in this locality (KNOBLOCH et al. 1996). Although Staré Sedlo has a higher conifer diversity than Kučlin, it is distinguished from the Baltic amber flora in its conifer composition, since taxa such as *Cupressospermum*, *Calocedrus*, *Nothotsuga* and *Pseudolarix* are absent from Staré Sedlo. A further difference to the Baltic amber flora is the lack of extensive swamp communities in Staré Sedlo; however, both floras share the high abundance of Fagaceae taxa (KNOBLOCH et al. 1996). The palaeoclimate of Kučlin is described as ‘subtropical’ with mean annual temperatures of 16.5-18.0 °C, mean warmest month temperature of 24.7- 27.1°C , and 7.7-10.0°C mean temperature of the coldest month (estimations derived from the Coexistence Approach, KVAČEK & TEODORIDIS 2011).

Palaeotemperature estimations for the Staré Sedlo floristic assemblage resulted in similar ranges, i.e. mean annual temperatures of 15.7-23.9 °C, mean warmest month temperature of 25.6-28.1 °C, and 5.0-13.6°C mean temperature of the coldest month (estimations derived from the Coexistence Approach, TEODORIDIS et al. 2012). Although the mean annual precipitation was generally high for both fossil floras (1003-1613 mm for Kučlin, and 1122-1613 mm for Staré Sedlo; KVAČEK & TEODORIDIS 2011, TEODORIDIS et al. 2012), seasonality in precipitation characterized the palaeoenvironment of Kučlin (KNOBLOCH et al. 1996; KVAČEK & TEODORIDIS 2011).

Extensive middle and late Eocene lignite swamp communities in coastal plains are known from central Germany, e.g. from the late middle to late Eocene Zeitz floristic complex of the Weißeelster Basin (KUNZMANN et al. 2016). However, the Zeitz floristic complex shares only *Quasisequoia couttsiae*, *Taxodium*, *Pinus* and *Sciadopitys* (Table 13) with the Baltic amber assemblage, indicating that these ‘subtropical’ lignite swamps differ from the swampy vegetation in the ‘Baltic amber forest’. Besides *Quasisequoia couttsiae* the ‘subtropical’ conifer *Doliosrobis taxiformis* (STERNBERG) KVAČEK emend. is common in the riparian environments of the Weißeelster Basin (KUNZMANN 1999).

Doliosstrobos taxiformis is considered as a key element of the ‘subtropical’ vegetation in the Eocene of Germany and the Czech Republic (KUNZMANN et al. 2016; Table 13) and thus nicely illustrates an important difference to the vegetation preserved in Baltic amber.

The comparison of the Baltic amber flora to North Bohemian and German floras highlights the obvious differences between them, especially in terms of conifer and habitat diversity. In summary, there are three distinct habitat types known from Central European floras of the late Eocene: (1) fluvial, estuarine and swamp deposits in coastal plains (e.g. Weißelster Basin; KUNZMANN et al. 2016); (2) lacustrine deposits in volcanic settings in the hinterland (e.g. Kučlin; KVAČEK 2002; KVAČEK & TEODORIDIS 2011); and (3) fluvial settings of the hinterland (e.g. Staré Sedlo; KNOBLOCH et al. 1996). All these depositional facies types rather share similar conifer components, such as *Doliosstrobos* and *Tetraclinis* and thus, do not exhibit the same conifer diversity as the ‘Baltic amber forest’. In its habitat diversity, the ‘Baltic amber forest’ is also more heterogeneous as the named floras.

These main differences show that the ‘subtropical’ climate of late Eocene floras of Central Europe led to vegetation types different to that of the ‘Baltic amber forest’. This strongly suggests that the source vegetation of Baltic amber grew under a non-tropical climate.

Unlike the North Bohemian and German fossil floras, the northern fossil floras of Spitsbergen are conifer rich. In general, the flora of Spitsbergen can be divided into three different assemblages, the Barendsburg flora (Early Paleocene), the Storvola flora (late Paleocene to early Eocene) and the Renardodden flora (late Eocene) (BUDANTSEV & GOLOVNEVA 2009). All these floras are dominated by conifers, such as *Picea* A. DEITR., *Pseudolarix*, *Glyptostrobos*, *Metasequoia* H. H. HU et W.C. CHENG, *Sequoia*, *Taiwania*, *Taxodium* and *Thuja* L., but also angiosperms were present, such as *Platanus* L., *Quercus*, *Carpinus* L., *Acer* L. and *Nyssa* L. (BUDANTSEV & GOLOVNEVA 2009). The conifer biodiversity of the Spitsbergen floras is similar to the Baltic amber flora in sharing taxa such as *Taxodium* and *Pseudolarix*; however, the Spitsbergen flora possesses also many gymnospermous taxa which are not present in Baltic amber, such as *Ginkgo* L., as well as also *Sequoia*, *Metasequoia* and *Picea*. The palaeoclimate for the early Paleocene to early Eocene of the Spitsbergen flora was warm-temperate, with decreasing temperatures up to the late Eocene (cool-temperate). Precipitation was high without dry seasons (BUDANTSEV & GOLOVNEVA 2009). Although the Spitsbergen floras show some differences to the Baltic amber flora, it becomes clear that a temperate to cool climate and a high humidity favoured the biodiversity of conifers during the early Paleocene up to the Eocene, supporting the suggested warm-temperate climate for the ‘Baltic amber forest’. However, more knowledge, especially about the angiosperm diversity of Baltic amber is needed to further specify the climatic estimations.

Comparing our results to the different previous notions about the Baltic amber flora mentioned in the introduction, we can now confirm that the Baltic amber

source area was a diverse landscape as suggested by many authors (e.g. ANDER 1942, BACHOFEN-ECHT 1949, LARSSON 1978). However, we did not find evidence for a vertical stratification of the ‘forest’ into different altitudinal zones. Instead, the conifer inclusions 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. Thus, neither the proposed absence of swamps and dominance of very dry steppe-forests (ANDER 1942; SCHUBERT 1953; CZECZOTT 1961; SCHUBERT 1961; RÜFFLE & HELMS 1970) were confirmed, nor did we find evidence of a purely moist and dense ‘Baltic amber forest’ (ANDER 1942; CZECZOTT 1961) or pure pine stands which are only rarely mixed with other tree species (CONWENTZ 1890).

Our results confirm the presence of swamp habitats as suggested by GOEPPERT & MENGE (1883) or KOHLMANN-ADAMSKA (2001); however, the new findings of conifer taxa such as *Quasisequoia*, *Taxodium* or *Cupressospermum* indicate a more complex picture of the floristic composition and location of these swamps. Moreover, this is in contrast to the forest reconstruction of ALEKSEEV & ALEKSEEV (2016), describing the Baltic amber vegetation as a non-disturbed and non-inundated climax community.

As discussed before, the entirety of the Baltic amber conifer diversity hints to a warm-temperate climate which partly corresponds to the proposed reconstructions of the ‘Baltic amber forest’ by ANDER (1942) and KOHLMANN-ADAMSKA (2001). However, this is in contrast to the assumptions of SCHUBERT (1961), WEITSCHAT (1997; 2008), WICHARD et al. (2009) and WEITSCHAT & WICHARD (2010), since these authors suggested a tropical climate, and an early to middle Eocene age for Baltic amber. During this interval of time the Eocene thermal maximum led to the global spread of megathermal vegetation such as rain forests and mangroves, including the European continent (ZACHOS et al. 2001; COLLINSON 2004; ZACHOS et al. 2008) and reaching palaeolatitudes of 55° to 65° North and South (WOLFE 1980, 1985; COLLINSON 1990; POLE & MACPHAIL 1996; COLLINSON 2004).

The long term global temperature decline started during the Eocene Climatic Optimum and proceeded to the late Eocene and early Oligocene (MOSBRUGGER et al. 2005). As mentioned before, the interpretation of the newly found conifer taxa and their comparison to other Eocene fossil floras indicate non-tropical conditions which fits to the climate estimations of the Eocene-Oligocene transition in Central Europe where temperatures decreased, while the seasonality increased (KVAČEK et al. 2014; MOSBRUGGER et al. 2005). The global cooling of this time period led to the broad occurrence of deciduous to semi-evergreen forests with open canopies and an increasing abundance of the Pinaceae up to the northern latitudes (BASINGER et al. 1994; COLLINSON 1992, 2004). This is in congruence with the high Pinaceae diversity of the ‘Baltic amber forest’ and its habitat composition as well as with the estimations of a warm-temperate climate for the Baltic amber source vegetation, indicating a late Eocene age of Baltic amber.

A late Eocene origin of Baltic amber is supported by the studies of STANDKE (1998; 2008), KOSMOWSKA-CERANOWICZ et al. (1997) and KASIŃSKI & KRAMARSKA (2008) who estimated a Priabonian age of the main amber bearing Blue Earth layer. In contrast to studies supposing a redeposition of Baltic amber into the Blue Earth layer (WEITSCHAT 1997), STANDKE (2008) concluded that there was no major hiatus between the Baltic amber formation and its deposition in marine sediments, and our inferred climate range for the ‘Baltic amber forest’ appears to lend support this latter idea.

Comparison to extant floras

The majority of the newly described conifers from Baltic amber show affinities to extant floras of East Asia, especially southeastern China, but also to North American floras (see Table 12). Species such as *Cathaya argyrophylla* CHUN et KUANG, *Nothotsuga longibracteata* (W. C. CHENG) H. H. HU ex C. N. PAGE and *Pseudolarix amabilis* (J. NELSON) REHDER are today monotypic and endemic to a few localities in South Central and South eastern China (FARJON 1990). Extant *Sciadopitys* is endemic to a few localities of Japan (FARJON 2005a). *Calocedrus* shows a disjunct distribution with *C. macrolepis* KURZ occurring in southwestern China, Vietnam, Thailand and Myanmar, *C. formosana* (FLORIN) FLORIN being endemic to Taiwan, and *C. decurrens* (TORR.) FLORIN being restricted to western North America (SHI et al. 2012). A further taxon with affinities to North American floras is *Taxodium*.

Although rare as a Baltic amber inclusion, *Abies* is widely distributed in the Northern Hemisphere and it is particularly diverse in East Asian and North American floras which are both considered to represent the main diversity centres of *Abies*, due to the high number of endemic species [East Asia (China, Japan, Korea and Vietnam), 22 endemic *Abies* spp.; North America (USA, Mexico), 9 endemic *Abies* spp.; XIANG et al. 2007].

Only *Pinus* is not restricted to a specific locality but shows a worldwide predominantly Northern Hemisphere distribution in diverse habitats and climatic zones (FARJON 2005b; ECKENWALDER 2009).

Regarding the sociobiological and ecological features of the extant relatives of the described fossil conifer taxa from Baltic amber, it is striking that all the extant analogous conifer taxa prefer warm-temperate rather than ‘subtropical’ humid climates (see Table 12 for references).

As already mentioned in the terminology chapter, we use the term warm-temperate in reference to the zonobiome concept of WALTER & BRECKLE (2002b). In Asia, zonobiome V comprises the southern parts of South Korea and Japan and southern China [Zhejiang, Jiangxi, Hunan, Guizhou and Yunnan, compare HÄMET-AHTI et al. (1974)], although the southern border of the warm-temperate zone of southern China is not well defined (WALTER & BRECKLE 2002b). In North America, forests proceeding along the West Coast of North America up to southern Canada with conifers such as *Sequoia sempervirens* (D. DON) ENDL., *Tsuga heterophylla*

(RAF.) SARG., *Thuja plicata* DONN ex D. DON and *Pseudotsuga menziesii* (MIRB.) FRANCO also belong to the zonobiome of warm-temperate humid climates (WALTER & BRECKLE 2002b). The eastern coast of the United States encompass further areas assigned to zonobiome V, which are termed ‘temperate broad-leaved evergreen forests’, located in North Florida, Southeast Georgia and along the northern Atlantic coast up to North Carolina (GRELLER 2003).

In reference to the ‘Baltic amber forest’, our study shows that the Baltic amber flora comprises elements of both extant northern American and East Asian warm-temperate floras. It further reveals that the ‘Baltic amber forest’ was warm-temperate and humid, being in contrast to the traditional perception of the ‘Baltic amber forest’ as a dense tropical rainforest.

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REFERENCES

- ALEKSEEV, V.I. & ALEKSEEV, P.I. (2016): New approaches for reconstruction of the ecosystem of an Eocene amber forest. — *Biology Bulletin* **43**: 75-86.
- ANDER, K. (1942): Die Insektenfauna des Baltischen Bernsteins nebst damit verknüpften zoogeographischen Problemen. — *Lunds Universitets Årsskrift* **38**: 1-82.
- ASHRAF, A.R. & MOSBRUGGER, V. (1996): Palynologie und Palynostratigraphie des Neogens der Niederrheinischen Bucht. Teil 2: Pollen. — *Palaeontographica Abteilung B* **241**: 1-98.
- AULENBACK, K.R. & LEPAGE, B.A. (1998): *Taxodium wallissii* sp. nov.: first occurrence of *Taxodium* from the Upper Cretaceous. — *International Journal of Plant Sciences* **159**: 367-390.
- BACHOFEN-ECHT, A. (1949): Der Bernstein und seine Einschlüsse. — Springer, Wien.
- BARTHEL, M. & HETZER, H. (1982): Bernstein-Inklusen aus dem Miozän des Bitterfelder Raumes. — *Zeitschrift für angewandte Geologie* **28**: 314-336.

- BASINGER, J.F., GREENWOOD, D.R. & SWEDA, T. (1994): Early Tertiary vegetation of Arctic Canada and its relevance to paleoclimatic interpretation. — *In* BOULTER, M.C. & FISHER, H.C. [eds.], *Cenozoic plants and climates of the Arctic*, Springer, Berlin: 175-198.
- BOULTER, M.C., HUBBARD, R.N.L.B. & KVAČEK, Z. (1993): A comparison of intuitive and objective interpretations of Miocene plant assemblages from north Bohemia. — *Palaeogeography, Palaeoclimatology, Palaeoecology* **101**: 81-96.
- BUDANTSEV, L.Y. & GOLOVNEVA, L.B. (2009): Fossil Flora of Arctic II - Paleogene Flora of Spitsbergen — Russian Academy of Sciences, Komarov Botanical Institute, St. Petersburg: 1-399 (In Russian, English summary).
- CASPARY, R. (1872): Privatsitzung am 4. October. — *Schriften der Königlichen physikalisch-ökonomischen Gesellschaft zu Königsberg* **13**: 15-19.
- CASPARY, R. (1886): Einige neue Pflanzenreste aus dem samländischen Bernstein. — *Schriften der Physikalisch-Ökonomischen Gesellschaft zu Königsberg* **27**: 1-8.
- CASPARY, R. & KLEBS, R. (1907): Die Flora des Bernsteins und anderer fossiler Harze des ostpreußischen Tertiärs, Band I. — Königlich Preußische Geologische Landesanstalt Berlin: 1-181.
- CHRISTOPHEL, D.C. (1976): Fossil floras of the Smoky Tower locality, Alberta, Canada. — *Palaeontographica, Abteilung B* **157**: 1-43.
- CLAUER, N., HUGGETT, J.M. & HILLIER, S. (2005): How reliable is the K-Ar glauconite chronometer? A case study of Eocene sediments from the Isle of Wight. — *Clay Minerals* **40**: 167-176.
- COLLINSON, M.E. (1990): Plant evolution and ecology during the early Cainozoic diversification. — *Advances in Botanical Research* **17**: 1-98.
- COLLINSON, M.E. (1992): Vegetational and floristic changes around the Eocene/Oligocene boundary in western and Central Europe. — *In* PROTHERO, D.R. & BERGGREN, W.A. [eds.], *Eocene-Oligocene Climatic and Biotic Evolution*, Princeton University Press, Princeton: 437-450.
- COLLINSON, M.E. (2004): Cenozoic evolution of modern plant communities and vegetation. — *In* CULVER, S.J. & RAWSON, P.F. [eds.], *Biotic response to Global Change - the last 145 million years*, Cambridge University Press, Cambridge: 223-243.
- CONWENTZ, H. (1886): Die Angiospermen des Bernsteins. — *In* GOEPPERT, H.R. & MENGE, A. [eds.], *Die Flora des Bernsteins und ihre Beziehungen zur Flora der Tertiärformation und der Gegenwart*, 2. Band, Engelmann, Gdansk: 1-140.
- CONWENTZ, H. (1890): Monographie der baltischen Bernsteinbäume: vergleichende Untersuchungen über die Vegetationsorgane und Blüten, sowie über das Harz und die Krankheiten der baltischen Bernsteinbäume. — Engelmann, Gdansk: 1-151.
- CORLETT, R.T. (2013): Where are the Subtropics? — *Biotropica* **45**: 273-275.

- CZECZOTT, H. (1961): The flora of the Baltic amber and its age. — *Prace Muzeum Ziemi* **4**: 119-145
- DENK, T., GRÍMSSON, F. & ZETTER, R. (2010): Episodic migration of oaks to Iceland: evidence for a North Atlantic “land bridge” in the latest Miocene. — *American Journal of Botany* **97**: 276-287.
- DOLEZYCH, M., FISCHER, T. & GRÖSCHKE, A. (2011): *Pinuxylon succiniferum* (Goeppert) Kraeusel emend. Dolezych – amberized wood from Goeppert’s type material restudied. — *Mauritiana* **22**: 43-60.
- DOLEZYCH, M. & SCHNEIDER, W. (2007): Taxonomy and taphonomy of coniferous woods and cuticulae dispersae in the Second Lusatian coal seam (Miocene) of the Senftenberg area. — *Palaeontographica, Abteilung B* **276**: 1-95 (In German, English abstract).
- DOMROES, M. (2003): Climatological characteristics of the tropics in China: climate classification schemes between German scientists and Huang Bingwei. — *Journal of Geographical Sciences* **13**: 271-285.
- ECKENWALDER, J.E. (2009): *Conifers of the world: the complete reference*. — Timber Press, Portland: 1-720.
- ENDLICHER, S. (1847): *Synopsis Coniferarum*. — Apud Scheitlin & Zollikofer, San Galli: 283.
- EWIN, T.A.M. (2004): Identification of conifer families using SEM analysis of fossil and extant conifer leaf cuticles Vol. I. — Ph.D., University of Manchester, Manchester: 37-38.
- FARJON, A. (1990): Pinaceae. Drawings and descriptions of the genera *Abies*, *Cedrus*, *Pseudolarix*, *Keteleeria*, *Nothotsuga*, *Tsuga*, *Cathaya*, *Pseudotsuga*, *Larix* and *Picea*. — Koeltz Scientific Books, Königstein: 1-330.
- FARJON, A. (2005a): A monograph of Cupressaceae and *Sciadopitys*. — Royal Botanic Gardens, Kew: 1-643.
- FARJON, A. (2005b): *Pines: drawings and descriptions of the genus Pinus*, 2nd ed. — Brill, Leiden: 1-235.
- FLORIN, R. (1931): Untersuchungen zur Stammesgeschichte der Coniferales und Cordaitales. I. Morphologie und Epidermisstruktur der Assimilationsorgane bei den rezenten Koniferen. — *Kunglia Svenska Vetenskapsakademiens Handlingar* **10**: 1-588.
- FLORIN, R. (1963): The distribution of conifer and taxad genera in time and space. — *Acta Hort. Bergiani* **20**: 121-312.
- FORMAN, L.L. (1964): *Trigonobalanus*, a new genus of Fagaceae, with notes on the classification of the family. — *Kew Bulletin* **17**: 381-396.
- FUHRMANN, R. (2010): Bitterfeld amber species. — *Mauritiana* **21**: 13-58 (In German, English abstract).
- GAUSSEN, H. (1966): Les Gymnospermes actuelles et fossiles, fascicule 8. Travaux du Laboratoire Forestier de Toulouse, Tome 2, sect. 1, vol. 1, chap. 11. — Université Paul Sabatier, Toulouse.
- GEIGER, R. (1952): Klassifikation der Klimate nach W. Köppen. — In BARTELS, J. & TEN BRUGGENCATE, P. [eds.], *Landolt-Börnstein, Zahlenwerte und*

- Funktionen aus Physik, Chemie, Astronomie, Geophysik und Technik, alte Serie, 3. Band, Springer, Berlin: 603-607.
- GOEPPERT, H.R. (1853): Über die Bernsteinflora. — Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Königlich Preußischen Akademie der Wissenschaften zu Berlin: 450-477.
- GOEPPERT, H.R. & BERENDT, G.C. (1845): Der Bernstein und die in ihm befindlichen Pflanzenreste der Vorwelt. — In BERENDT, G.C. [ed.], Die im Bernstein befindlichen organischen Reste der Vorwelt, Nicolai, Berlin, Germany: 1-125.
- GOEPPERT, H.R. & MENGE, A. (1883): Von den Bernstein-Coniferen, insbesondere auch in ihren Beziehungen zu den Coniferen der Gegenwart. — In GOEPPERT, H.R. & MENGE, A. [eds.], Die Flora des Bernsteins und ihre Beziehung zur Flora der Tertiärformation und der Gegenwart, 1. Band, Engelmann, Gdansk: 1-63.
- GOTHAN, W. (1936): Nochmals die "Graskohle": Nadeln der Schirmtanne (*Sciadopitys*). — Zeitschrift für Gewinnung und Verwertung der Braunkohle **35**: 736-738.
- GRELLER, A.M. (2003): A review of the temperate broad-leaved evergreen forest zone of southeastern North America: floristic affinities and arborescent vegetation types. — The Botanical Review **69**: 269-299.
- GRIMALDI, D.A. & ROSS, A.J. (2017): Extraordinary Lagerstätten in Amber, with particular reference to the Cretaceous of Burma. — In FRASER, N.C. & SUES, H.-D. [eds.], Terrestrial Conservation Lagerstätten: Windows into the Evolution of Life on Land, Dunedin Academic Press Ltd, Edinburgh: in press.
- HÄMET-AHTI, L., AHTI, T. & KOPONEN, T. (1974): A scheme of vegetation zones for Japan and adjacent regions. — Annales Botanici Fennici **11**: 59-88.
- HEER, O. (1862): On certain fossil plants from the Hempstead Beds of the Isle of Wight. Quarterly Journal of the Geological Society of London **18**: 369-377.
- HENNIG, D. & KUNZMANN, L. (2013): Taphonomy and vegetational analysis of a late Eocene flora from Schleenhain (Saxony, Germany). — Geologica Saxonica - Journal of Central European Geology **59**: 75-87.
- HOLÝ, F., KVAČEK, Z. & TEODORIDIS, V. (2012): A review of the early Miocene mastixioid flora of the Kristina Mine at Hrádek nad Nisou in North Bohemia (the Czech Republic). — Acta Musei Nationalis Pragae, Series B, Historia Naturalis **68**: 53-118.
- JÄHNICHEN, H. (1998): First record of *Taiwania*, *Cryptomeria* and *Liquidambar* from Bitterfeld and Baltic amber. — Mitteilungen aus dem Museum für Naturkunde Berlin, Geowissenschaften **1**: 167-178 (In German, English abstract).
- KASIŃSKI, J.R. & KRAMARSKA, R. (2008): Sedimentary environment of amber-bearing association along the Polish-Russian Baltic coastline. — Exkursionsführer und Veröffentlichungen der Deutschen Gesellschaft für Geowissenschaften **236**: 46-57.

- KIRCHHEIMER, F. (1937): Beiträge zur Kenntnis der Flora des baltischen Bernsteins I. — Beihefte zum Botanischen Centralblatt, Abteilung B **57**: 441-482.
- KNOBLOCH, E., KONZALOVÁ, M. & KVAČEK, Z. (1996): Late Eocene flora of the Staré Sedlo Formation in Bohemia. — Rozpravy Českého Geologického Ústavu **49**: 1-260 (In German, English summary).
- KNOBLOCH, E. & MAI, D.H. (1986): Monographie der Früchte und Samen in der Kreide von Mitteleuropa. — Rozpravy ústředního ústavu geologického **47**: 1-219.
- KOHLMAN-ADAMSKA, A. (2001): A graphic reconstruction of an "amber" forest. — In KOSMOWSKA-CERANOWICZ, B. [ed.], The Amber Treasure Trove - The Tadeusz Giecwicz's Collection at the Museum of the Earth, Polish Academy of Sciences, Oficyna Wydawnicza Sadyba, Warsaw: 15-18.
- KÖPPEN, W. (1900): Versuch einer Klassifikation der Klimate, vorzugsweise nach ihren Beziehungen zur Pflanzenwelt. — Geographische Zeitschrift **6**: 593-611.
- KOSMOWSKA-CERANOWICZ, B., KOHLMANN-ADAMSKA, A. & GRABOWSKA, I. (1997): Erste Ergebnisse zur Lithologie und Palynologie der bernsteinführenden Sedimente im Tagebau Primorskoje. — Metalla Sonderheft - Neue Erkenntnisse zum Bernstein **66**: 5-17.
- KOTTEK, M., GRIESER, J., BECK, C., RUDOLF, B. & RUBEL, F. (2006): World map of the Köppen-Geiger climate classification updated. — Meteorologische Zeitschrift **15**: 259-263.
- KUNZMANN, L. (1999): Koniferen der Oberkreide und ihre Relikte im Tertiär Europas: ein Beitrag zur Kenntnis ausgestorbener Taxodiaceae und Geinitziaceae fam. nov. — Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden **45**: 1-190
- KUNZMANN, L. (2014): On the fossil history of *Pseudotsuga* Carr. (Pinaceae) in Europe. — Palaeobiodiversity and Palaeoenvironments **94**: 393-409.
- KUNZMANN, L. & WALTHER, H. (2002): A leaf flora from the Upper Eocene of the Weisselster Basin, Central Germany. — Paläontologische Zeitschrift **76**: 261-282 (In German, English abstract).
- KUNZMANN, L. & MAI, D.H. (2005): Conifers of the Mastixioideae-flora from Wiesa near Kamenz (Saxony, Miocene) with special consideration of leaves. — Palaeontographica, Abteilung B **272**: 67-135 (In German, English summary).
- KUNZMANN, L., KVAČEK, Z., MAI, D.H. & WALTHER, H. (2009): The genus *Taxodium* (Cupressaceae) in the Palaeogene and Neogene of Central Europe. — Review of Palaeobotany and Palynology **153**: 153-183.
- KUNZMANN, L., SCHNEIDER, W., DOLEZYCH, M. & MAI, D.H. (2012): Palaeoecology of extinct conifer genera in the European Cenozoic. — Japanese Journal of Palynology (Special Issue) **58**: 118.
- KUNZMANN, L. & WALTHER, H. (2012): Early Oligocene plant taphocoenoses of the Haselbach megafloral complex and the reconstruction of palaeovegetation. — Palaeobiodiversity and Palaeoenvironments **92**: 295-307.

- KUNZMANN, L. & SCHNEIDER, W. (2013): Stop 3.2: 'Tertiärwald' am Waldsee Lauer. — In RASCHER J., HEINRICH, C., HOLZ, U., KUNZMANN, L., SCHNEIDER, W., STANDKE, G., WIMMER, R., Exkursionsführer Bitterfelder Bernstein (Stop 1) und Geologie, Berbaugeschichte sowie Entwicklung der Berbaufolgerlandschaft im Raum Profen/Cospuden (Stob 2 und Stop 3), Exkursionsführer und Veröffentlichungen der Deutschen Gesellschaft für Geowissenschaften **249**: 124-136.
- KUNZMANN, L., KVAČEK, Z., TEODORIDIS, V., MÜLLER, C. & MORAWECK, K. (2015): Vegetation dynamics of riparian forest in Central Europe during the late Eocene. — *Palaeontographica, Abteilung B* **295**: 67-88.
- KVAČEK, Z. (1999): An ancient *Calocedrus* (Cupressaceae) from the European Tertiary. — *Flora* **194**: 237-248.
- KVAČEK, Z. (2002): Late Eocene landscape, ecosystems and climate in northern Bohemia with particular reference to the locality of Kučlín near Bílina. — *Bulletin of the Czech Geological Survey* **77**: 217-236.
- KVAČEK, Z. (2010): Forest flora and vegetation of the European early Paleogene - a review. — *Bulletin of Geosciences* **85**: 63-76.
- KVAČEK, Z. & TEODORIDIS, V. (2011): The late Eocene flora of Kučlín near Bílina in North Bohemia revisited. — *Acta Musei Nationalis Pragae, Series B, Historia Naturalis* **67**: 83-144.
- KVAČEK, Z., TEODORIDIS, V., MACH, K., PŘIKRYL, T. & DVOŘÁK, Z. (2014): Tracing the Eocene-Oligocene transition: a case study from north Bohemia. — *Bulletin of Geosciences* **89**: 21-66.
- LANGENHEIM, J.H. (2003): *Plant resins - Chemistry, Evolution, Ecology, and Ethnobotany* — Timber Press, Portland: 1-586.
- LARRSON, S.G. (1978): *Baltic Amber – a paleobiological study*. Scandinavian Science Press, Klampenborg: 26-59.
- LEPAGE, B.A. & BASINGER, J.F. (1991): A new species of *Larix* (Pinaceae) from the early Tertiary of Axel Heiberg Island, Arctic Canada. — *Review of Palaeobotany and Palynology* **70**: 89-111.
- LEPAGE, B.A. & BASINGER, J.F. (1995): Evolutionary history of the genus *Pseudolarix* Gordon (Pinaceae). — *International Journal of Plant Sciences* **156**: 910-950.
- LIU, Y.-S. & BASINGER, J.F. (2000): Fossil *Cathaya* (Pinaceae) pollen from the Canadian High Arctic. — *International Journal of Plant Sciences* **161**: 829-847.
- MA, Q.-W., VIKULIN, S.V., LI, C.-S. & WANG, Y.-F. (2013): Details of compressions of *Glyptostrobus* (Cupressaceae s.l.) from the Eocene of Fushun, NE China. — *Journal of Systematics and Evolution* **51**: 601-608.
- MAI, D.H. (1960): Über neue Früchte und Samen aus dem deutschen Tertiär. — *Paläontologische Zeitschrift* **34**: 73-90.
- MAI, D.H. (1967): Die tertiären Arten von *Trigonobalanus* Forman (Fagaceae) in Europa. — *Jahrbuch für Geologie* **3**: 381-409.

- MAI, D.H. (1997): Floras from the Upper Oligocene at the northern margin of Lausitz, Saxony. — *Palaeontographica, Abteilung B* **244**: 1-124 (In German, English abstract).
- MAI, D.H. (2000): The Middle and Upper Miocene floras of the Meuro and Rauno sequences in the Lusatica region: Part I: Waterferns, conifers, and monocotyledons. — *Palaeontographica, Abteilung B* **256**: 1-68 (In German, English abstract).
- MAI, D.H. (2004): The Miocene and Pliocene floras from Northeast-Brandenburg and Southwest-Mecklenburg. — *Palaeontographica, Abteilung B* **269**: 1-130 (In German, English abstract).
- MAI, D.H. & WALTHER, H. (1985): Die obereozänen Floren des Weißelster-Beckens und seiner Randgebiete. — *Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden* **33**: 1-176.
- MAI, D.H. & SCHNEIDER, W. (1988): Über eine alttertümliche Konifere im Jungtertiär und deren Bedeutung für Braunkohlen- und Bernsteinbildung. — *Feddes Repertorium* **99**: 101-112 (In German, English summary).
- MAI, D.H. & WALTHER, H. (1991): Die oligozänen und untermiozänen Floren Nordwest-Sachsens und des Bitterfelder Raumes. — *Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden* **38**: 1-230.
- MENZEL, P. (1913): Beitrag zur Flora der niederrheinischen Braunkohlenformation. — *Jahrbuch der Königlich Preußischen Geologischen Landesanstalt zu Berlin* **34**: 1-98.
- METCALFE, C.R. & CHALK, L. (1950): Anatomy of the dicotyledons - leaves, stem, and wood in relation to taxonomy with notes on economic uses, Vol. 2 — Oxford University Press, London: 827-836.
- MIROV, N.T. (1967): The genus *Pinus*. — The Ronald Press Company, New York: 1-602.
- MORAWECK, K., UHL, D. & KUNZMANN, L. (2015): Estimation of late Eocene (Bartonian–Priabonian) terrestrial palaeoclimate: Contributions from megafloral assemblages from central Germany. — *Palaeogeography, Palaeoclimatology, Palaeoecology* **433**: 247-258.
- MOSBRUGGER, V., UTESCHER, T. & DILCHER, D.L. (2005): Cenozoic continental climatic evolution of Central Europe. — *Proceedings of the National Academy of Science of the United States of America* **102**: 14964-14969.
- MÜLLER-STOLL, W.R. (1938): Die jüngsttertiäre Flora des Eisensteins von Dernbach (Westerwald). — *Beihefte zum Botanischen Centralblatt, Abteilung B* **58**: 376-434.
- NICKEL, B. (1996): Palynofazies und Palynostratigraphie der Pechelbronn Schichten im nördlichen Oberrheintalgraben. — *Palaeontographica Abteilung B* **240**: 1-151 (In German, English summary).
- NIKISHIN, A.M., ZIEGLER, P.A., STEPHENSON, R.A., CLOETINGH, S.A.P.L., FURNE, A.V., FOKIN, P.A., ERSHOV, A.V., BOLOTOV, S.N., KOROTAEV, M.V., ALEKSEEV, A.S., GORBACHEV, V.I., SHIPILOV, E.V., LANKREIJER, A., BEMBINOVA, E.Y. & SHALIMOV, I.V. (1996): Late Precambrian to Triassic

- history of the East European Craton: dynamics of sedimentary basin evolution. — *Tectonophysics* **268**: 23-63.
- PEEL, M.C., FINLAYSON, B.L. & MCMAHON, T.A. (2007): Updated world map of the Köppen-Geiger climate classification. — *Hydrology and Earth System Sciences* **11**: 1633-1644.
- PETERSEN, J.F., SACK, D. & GABLER, R.E. (2015): Climate classification: tropical, arid and mesothermal climate regions. — *In* *Fundamentals of physical geography*, Cengage Learning, Stamford: 153-190.
- PHILIPPE, M., MÉON, H., LAMBERT, G., ERDEI, B., THEVENARD, F. & GOMEZ, B. (2002): A palm-tree and *Sciadopitys* swamp-forest from the Neogene of Bresse (eastern France). — *Comptes Rendus Palevol* **1**: 221-225.
- POLE, M.S. & MACPHAIL, M.K. (1996): Eocene *Nypa* from Regatta Point, Tasmania. — *Review of Palaeobotany and Palynology* **92**: 55-67.
- RITZKOWSKI, S. (1997): K-Ar - Altersbestimmungen der bernsteinführenden Sedimente des Samlands (Paläogen, Bezirk Kaliningrad). — *Metalla Sonderheft - Neue Erkenntnisse zum Bernstein* **66**: 19-23.
- RÜFFLE, L. & HELMS, J. (1970): Waldsteppe und Insektenwelt im Bernstein, Beispiele aus der Bernsteinsammlung des Paläontologischen Museums. — *Wissenschaftliche Zeitschrift der Humboldt-Universität zu Berlin, Mathematisch-Naturwissenschaftliche Reihe* **19**: 243-249.
- SADOWSKI, E.-M., SEYFULLAH, L.J., SADOWSKI, F., FLEISCHMANN, A., BEHLING, H. & SCHMIDT, A.R. (2015): Carnivorous leaves from Baltic amber. — *Proceedings of the National Academy of Sciences of the United States of America* **112**: 190-195.
- SADOWSKI, E.-M., SCHMIDT, A.R., KUNZMANN, L., GRÖHN, C. & SEYFULLAH, L.J. (2016a): *Sciadopitys* cladodes from Eocene Baltic amber. — *Botanical Journal of the Linnean Society* **180**: 258-268.
- SADOWSKI, E.-M., SCHMIDT, A.R., RUDALL, P.J., SIMPSON, D.A., GRÖHN, C., WUNDERLICH, J. & SEYFULLAH, L.J. (2016b): Graminids from Eocene Baltic amber. — *Review of Palaeobotany and Palynology* **233**: 116-168.
- SCHIMPER, W.P. (1870-72): *Traité de paléontologie végétale ou la flore du monde primitif dans ses rapports avec les formations géologiques et la flore du monde actuel*, Tome 2. — J. B. Baillièrre et Fils, Paris: 301-304.
- SCHUBERT, K. (1953): Mikroskopische Untersuchung pflanzlicher Einschlüsse des Bernsteins - 2.Teil: Rinden und Borke. — *Palaeontographica Abteilung B* **93**: 103-119.
- SCHUBERT, K. (1961): Neue Untersuchungen über Bau und Leben der Bernsteinkiefer [*Pinus succinifera* (Conwentz) emend.] - Ein Beitrag zur Paläohistologie der Pflanzen. — Beihefte zum Geologischen Jahrbuch **45**: 1-149 (In German, English abstract).
- SHI, G., ZHOU, Z. & XIE, Z. (2012): A new Oligocene *Calocedrus* from South China and its implications for transpacific floristic exchanges. — *American Journal of Botany* **99**: 108-120.

- SPAHR, U. (1993): Systematic catalogue and bibliography of flora in amber and copal. — Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie) **195**: 1-99 (In German, English abstract).
- STANDKE, G. (1998): Die Tertiärprofile der samländischen Bernsteinküste bei Rauschen —Schriftenreihe für Geowissenschaften **7**: 93-133 (In German, English abstract).
- STANDKE, G. (2008): Bitterfelder Bernstein gleich Baltischer Bernstein? - Eine geologische Raum- Zeit- Betrachtung und genetische Schlussfolgerungen. — Exkursionsführer und Veröffentlichungen der Deutschen Gesellschaft für Geowissenschaften **236**: 11-33 (In German, English abstract).
- STOUT, E. C., BECK, C. W., KOSMOWSKA-CERANOWICZ, B. (1995). Gedanite and Gedano-Succinite. — In ANDERSON, K. B. & CRELLING, J. C. [eds.], Amber, resinite, and fossil resins, ACS Symposium Series 617, Washington D.C.: 130-148.
- TEODORIDIS, V., KVAČEK, Z., ZHU, H. & MAZOUCH, P. (2012): Environmental analysis of the mid-latitude European Eocene sites of plant macrofossils and their possible analogues in East Asia. — Palaeogeography, Palaeoclimatology, Palaeoecology **333-334**: 40-58.
- THIELE-PFEIFFER, H. (1988): The microflora from the middle Eocene oil shale of Messel near Darmstadt. — Palaeontographica Abteilung B **211**: 1-86.
- THIERGART, F. (1949): Die *Sciadopitys*-zone und der *Sciadopitys*-Vorstoß in der niederrheinischen Braunkohle. — Braunkohle, Wärme und Energie **1**: 153-156.
- TSUKADA, M. (1963): Umbrella pine, *Sciadopitys verticillata*: past and present distribution in Japan. — Science **142**: 1680-1681.
- VÁVRA, N. (2015): Mineral names used for fossil resins, subfossil resins and similar materials. — In KOSMOWSKA-CERANOWICZ, B. [ed.], Infrared Spectra of the World's Resins - Holotype Characteristics, PAS Museum of the Earth in Warsaw, Warsaw: 215-280.
- VICKULIN, S.V., LEPAGE, B.A. & SHALISKO, V.Y. (2003): Palaeogene leaf compressions of *Taxodium mucronatum* Ten. affinity from Pasekovo, middle Russian upland, southern European Russia. — Scientia CUCBA **5**: 63-87.
- VON DER BRELIE, G. & WOLF, M. (1981): *Sequoia* and *Sciadopitys* in the brown coal swamps of the Lower Rhine Basin. — Fortschritte in der Geologie von Rheinland und Westfalen **29**: 177-191 (In German, English abstract).
- WALTER, H. & BRECKLE, S.-W. (2002a): Ecological systems and biology of ecosystems. — In Walter's Vegetation of the earth: the ecological systems of the geo-biosphere, Springer, Berlin: 75-111.
- WALTER, H. & BRECKLE, S.-W. (2002b): Zonobiome of laurel forests (zonobiome of the warm-temperate humid climate). — In Walter's Vegetation of the earth: the ecological systems of the geo-biosphere, Springer, Berlin: 295-307.
- WALTER, H. & BRECKLE, S.-W. (2002c): Zonobiome of the evergreen tropical rain forest (Zonobiome of the equatorial humid diurnal climate). — In Walter's

- Vegetation of the earth: the ecological systems of the geo-biosphere, Springer, Berlin: 115-162.
- WEITSCHAT, W. (1997): Bitterfelder Bernstein - ein eozäner Bernstein auf miozäner Lagerstätte. — *Metalla Sonderheft - Neue Erkenntnisse zum Bernstein* **66**: 71-84 (In German, English summary).
- WEITSCHAT, W. (2008): Bitterfelder und Baltischer Bernstein aus paläoklimatischer und paläontologischer Sicht. — *Exkursionsführer und Veröffentlichungen der Deutschen Gesellschaft für Geowissenschaften* **236**: 88-97 (In German, English abstract).
- WEITSCHAT, W. & WICHARD, W. (2010): Baltic Amber. — *In* PENNEY, D. [ed.], *Biodiversity of fossils in amber from the major world deposits*, Siri Scientific Press, Manchester: 80-115.
- WICHARD, W., GRÖHN, C. & SEREDSZUS, F. (2009): *Aquatic Insects in Baltic Amber*. — Verlag Kessel, Remagen-Oberwinter: 1-336.
- WILDE, V. (2004): Aktuelle Übersicht zur Flora aus dem mitteleozänen "Ölschiefer" der Grube Messel bei Darmstadt (Hessen, Deutschland). — *Courier Forschungsinstitut Senckenberg* **252**: 109-114.
- WOLFE, A.P., TAPPERT, R., MUEHLENBACHS, K., BOUDREAU, M., MCKELLAR, R.C., BASINGER, J.F. & GARRETT, A. (2009): A new proposal concerning the botanical origin of Baltic amber. — *Proceedings of the Royal Society B: Biological Sciences* **276**: 3403-3412.
- WOLFE, J.A. (1980): Tertiary climates and floristic relationships at high latitudes in the Northern Hemisphere. — *Palaeogeography, Palaeoclimatology, Palaeoecology* **30**: 313-323.
- WOLFE, J.A. (1985): Distribution of major vegetational types during the Tertiary. — *In* SUNDQUIST, E.T. & BROECKER, W.S. [eds.], *The Carbon Cycle and Atmospheric CO₂: Natural Variations Archean to Present*, American Geophysical Union, Washington D.C.: 357-375.
- XIANG, X., CAO, M. & ZHOU, Z. (2007): Fossil history and modern distribution of the genus *Abies* (Pinaceae). — *Frontiers of Forestry in China* **2**: 355-365.
- ZACHOS, J., PAGANI, M., SLOAN, L., THOMAS, E. & BILLUPS, K. (2001): Trends, rhythms, and aberrations in global climate 65 Ma to present. — *Science* **292**: 686-693.
- ZACHOS, J.C., DICKENS, G.R. & ZEEBE, R.E. (2008): An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. — *Nature* **451**: 279-283.

Appendix 6

Sadowski, E.-M., L. J. Seyfullah, C. A. Wilson, C. L. Calvin, and A. R. Schmidt. 2017b. Diverse early dwarf mistletoes (*Arceuthobium*), ecological keystones of the Eocene Baltic amber biota. *American Journal of Botany* 104:1-25, doi:10.3732/ajb.1600390.

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DIVERSE EARLY DWARF MISTLETOES (*ARCEUTHOBIMUM*), ECOLOGICAL KEYSTONES OF THE EOCENE BALTIC AMBER BIOTA¹

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Premise of the study: Extant dwarf mistletoes (*Arceuthobium* M. Bieb., Viscaceae) are hemiparasites with complex roles in nature. They are one of the most severe pests in Northern Hemisphere conifer forests, but they also enhance the structural complexity and species diversity of the forests. Here, we describe the first pre-Miocene macrofossils of dwarf mistletoes. The fossils from Eocene Baltic amber provide new insights into the morphological evolution of the *Arceuthobium* lineage and its paleobiogeography.

Methods: The amber inclusions were investigated with light microscopy and compared to extant Viscaceae and to historic descriptions of lost Baltic amber fossils with affinities to Viscaceae.

Key results: Six fossil species of the *Arceuthobium* lineage, *A. johnianum* comb. nov., *A. mengeanum* comb. nov., *A. conwentzii* sp. nov., *A. groehnii* sp. nov., *A. viscoides* comb. nov., and *A. obovatum* sp. nov. occurred in source forests of Baltic amber, representing the oldest macrofossil evidence of dwarf mistletoes. They share morphological features of their bracts, internodes, fruits, and stomata with extant *Arceuthobium*. Differences from extant dwarf mistletoes, such as the perianth merosity, the non-fusion of squamate bracts and presence of oblanceolate expanded leaves, indicate their affiliation to an ancient lineage of the genus.

Conclusions: The occurrence of six species of dwarf mistletoes in a single amber deposit suggests *Arceuthobium* was a keystone taxon of the Baltic amber source area. As in extant conifer forests, they probably influenced the structural complexity of the forest, not only leading to more open woodlands but also increasing species diversity, at least at a microhabitat scale.

Key words: Baltic amber forest; *Enantioblastos*; paleoecology; *Patzsea*; succinite; Viscaceae

INTRODUCTION

Extant dwarf mistletoes mainly occur in the northern hemisphere with the greatest distribution and diversity in Canada, the United States and Mexico, with only a few species inhabiting eastern Africa, Central to East Asia and the Mediterranean region (Barlow, 1983; Hawksworth and Wiens, 1996a; Kuijt, 2015). Based on morphological, physiological and phenological features, the number of dwarf mistletoe species was first estimated at 42 (Hawksworth and Wiens, 1996b), but this estimate was recently reduced to 26, based on phylogenetic studies using ITS sequences (Nickrent et al., 2004).

Especially in North American forests, dwarf mistletoes can be one of the most severe plant pests, infecting economically important trees of the Pinaceae and Cupressaceae, and causing conifer growth losses that are estimated to be 11.8 million m³/year (418 million cubic feet/year) in the United States alone (Drummond, 1982). Effects of dwarf mistletoes on their host trees are numerous, comprising a decrease of the growth rate in height and diameter and a reduction in reproductive success and survival (Mathiasen, 1996; Geils and Hawksworth, 2002). Although dwarf mistletoes cause economic damage, they variously affect the ecology of infested stands by changing the forest structure and by serving as forage, nesting sites and microhabitats for numerous different organisms such as birds, squirrels and Arthropoda (Mathiasen, 1996). Despite their extant ecological significance, the evolutionary history of dwarf mistletoes is far from understood, because macrofossils of *Arceuthobium* M. Bieb. are scarce. Previous to this study, the oldest unambiguous macrofossils of dwarf mistletoes are described from the Miocene of Poland (Łańcucka-Środoniowa, 1980) with a few additional fossils from the Pleistocene and younger sediments of the United States (e.g. California, Nevada, and Texas) (Chaney and Mason, 1927, 1930, 1933; Spaulding, 1977).

Further but uncertain reports of fossils with similarities to extant dwarf mistletoes derive from Eocene Baltic amber. Conwentz (1886a) assigned several amber inclusions of foliage stems and fruiting stages of inflorescences to *Patzea* Casp. recognizing two species, *P. johniana* Conw. and *P. mengeana* Conw. He highlighted morphological similarities of these two extinct species to several extant taxa of the Loranthaceae and Viscaceae, such as *Loranthus* Jacq., *Phthirusa* Mart. or *Arceuthobium*; however, Conwentz (1886a) also noted differences between these extant taxa and *Patzea*; thus, he refrained from assigning the fossils to an extant lineage of Santalales. The current whereabouts of these amber specimens of *Patzea* are unknown, but based on Conwentz's detailed descriptions and drawings of the specimens, several authors briefly commented on *Patzea*, doubting its affinity to *Arceuthobium* (Kirchheimer, 1957; Łańcucka-Środoniowa, 1980; Hawksworth and Wiens, 1996a). Here, we report new amber inclusions of the *Arceuthobium* lineage, comprising fragments of shoots and fruiting inflorescences from the late Eocene of the Baltic. We revise the systematic assignment of previously described fossils of

Patzea from Baltic amber and propose to accommodate all dwarf mistletoe fossils known from Baltic amber in the extant genus *Arceuthobium*.

MATERIAL AND METHODS

Geological setting—Baltic amber from the Baltic Sea region represents the most famous amber deposit worldwide and has been known for many centuries. Today, most Baltic amber is mined in the Samland area near Kaliningrad, Russia, where it predominantly occurs in “Blue Earth” layers. These amber-bearing strata are Priabonian in age, but small amounts of amber also occur in Lutetian and Oligocene sediments, leading to a possible age range of ca. 25 to 43 million years for all strata bearing Baltic amber (Kosmowska-Ceranowicz et al., 1997; Standke, 1998; Kasiński and Kramarska, 2008; Standke, 2008). It is unclear whether the Oligocene amber represents redeposited Eocene material (Standke, 2008); thus, we currently consider a Lutetian to Priabonian age for Baltic amber. Baltic amber that eroded from these sediments is often found washed ashore along the coast of the Baltic Sea, and a large proportion of historic and new amber collections contain this “sea amber”. A precise locality of origin can therefore not be provided for Baltic amber pieces from historic collections that were developed in the Königsberg (Kaliningrad) and Danzig (Gdansk) areas during the 19th and early 20th centuries. This fact, however, does not affect the age estimate given above since the vast majority was initially embedded in these Eocene sediments (Standke, 2008).

Specimen preparations—Of all the specimens in this study, only specimen GZG.BST.21950 (Hoffeins 1422-2) was fully embedded in high-grade epoxy (Epo-Tek 301-2, Epoxy Technology, Billerica, Massachusetts, USA) under vacuum (for protocols, see Nascimbene and Silverstein, 2000). All specimens were carefully ground and polished manually with wet silicon carbide papers (grit from 25.8 to 5.0 µm particle size, Struers, Sarasota, Florida, USA) to remove scratches and to create smooth surfaces parallel to inclusions.

All amber inclusions were examined with a Stereo Discovery V8 dissection microscope (Carl Zeiss, Oberkochen, Germany) and an AxioScope A1 compound microscope (Carl Zeiss, Oberkochen, Germany) using incident and transmitted light simultaneously. Images were taken with Canon EOS 5D digital cameras (Canon Inc., Tokyo, Japan) attached to these microscopes. For enhanced illustration of three-dimensional structures, all figures are photomicrographic composites which were digitally stacked from up to 103 focal planes, using the software package HeliconFocus 5.0 (Helicon Software, Kharkov, Ukraine). The overview images of Figs. 4A and 5D were obtained by merging up to three photomicrographic composites using Adobe Photoshop CS6 (San Jose, California, USA). Illustrations of specimen GZG.BST.21950 (Figs. 7, 9) were established using a drawing tube, attached to the dissection microscope. The halftone elements of Figs. 7 and 9 were processed in Photoshop CS6; line elements were added with Adobe Illustrator CS6.

Repository—The amber specimens investigated are housed in the public paleontological collections shown in Table 1.

Specimen descriptions and identification—The morphology and measurement data of new amber fossils were compared to morphological descriptions of extant *Arceuthobium* (see Table 2 for references and detailed information). Since current whereabouts of the amber inclusions of *Patzea* are unknown, the detailed descriptions and figures of Conwentz (1886a; Fig. 1) were used for descriptions and emended diagnoses in the following sections and subsections, including Table 2. The newly discovered amber inclusions of the *Arceuthobium* lineage facilitated the interpretation of illustrations of *Patzea* and thus, opened up a new perspective on their morphology.

Tab. 1: Overview of the fossil *Arceuthobium* specimens from Baltic amber and their repository.

Fossil	Collection number	Collection	Institution	Figures
<i>Arceuthobium johinianum</i>	lost	Goeppert Amber Collection	Mineralogical Museum of the University of Berlin	Fig. 1A, C, E–G
		Amber collection	Westpreußisches Provinzial-Museum Danzig	Fig. 1B, D
		Sommerfeld Amber Collection	Königsberg	-
		Amber collection	Naturforschende Gesellschaft Emden	-
<i>Arceuthobium mengeanum</i>	lost	Menge Amber Collection	Westpreußisches Provinzial-Museum Danzig	Fig. 1H–M
<i>Arceuthobium conwentzii</i>	GZG.BST.24548	Königsberg Amber Collection, no. G 1	University of Göttingen	Fig. 2, Fig. 3A, B
<i>Arceuthobium groehnii</i>	GPIH 4582	Carsten Gröhn Amber Collection, no. P 6551	University of Hamburg	Fig. 4
<i>Arceuthobium viscoides</i>	MB.Pb.1981-2	Berendt Amber Collection, no. 3551	Museum für Naturkunde zu Berlin	Fig. 5
	GZG.BST.21950	Hoffeins Amber Collection, no. 1422-2	University of Göttingen	Figs 6–9
	GZG.BST.21951	Hoffeins Amber Collection, no. 1156-3	University of Göttingen	-
<i>Arceuthobium obovatum</i>	GZG.BST.24359	Königsberg Amber Collection, no. Casp. G 4639	University of Göttingen	Fig. 10, Fig. 3 C, D

SYSTEMATICS

The following subsections provide diagnoses and short descriptions for each inclusion of *Arceuthobium* from Baltic amber, including an identification key for fossil species. Species based on the missing *Patzea* specimens have been revised, and emended diagnoses are given.

Key to Eocene species of *Arceuthobium*

- 1a.** Perianth 4-merous; stigma non-lobed or 5-lobed; internodes in cross section terete; bracts squamate, broadly-ovate**2**
1b. Perianth less than 4-merous; stigma 2–3-lobed; internodes in cross section angular; bracts squamate and differently shaped**3**
2a. Fruits widely obovate, distal portion $\geq 50\%$ of total fruit length; stigma nonlobed and minute*A. johnianum*
2b. Fruits elongated-elliptic, distal portion 25–50% of total fruit length; stigma 5-lobed*A. mengeanum*
3a. Fruits with 3-merous perianth; fruits longer than 1.4 mm*A. conwentzii*
3b. Perianth merosity indistinct; fruits shorter than 1.4 mm**4**
4a. Fruits widely obovate, distal fruit portion $> 70\%$ of total fruit length.....
.....*A. obovatum*
4b. Fruits elliptic, distal fruit portion $< 70\%$ **5**
5a. Expanded oblanceolate leaves present; stigma 2-lobed..... *A. viscoides*
5b. No expanded leaves present; stigma 2–3-lobed..... *A. groehnii*

Order —Santalales

Family —Viscaceae Batsch.

Genus —*Arceuthobium* M. Bieb.

Species —*Arceuthobium johnianum* comb. nov. (Fig. 1A–G)

Basionym—*Patzea johniana* Conw., Conwentz 1886a, pp. 135–138, pl. XIII, figs 8–14.

Synonyms

1845 *Ephedrites johnianus* Goep. et Berendt, Goepfert and Berendt (1845): p. 105, pl. IV, figs 8–10, pl. V, fig. 1

1853 *Ephedra johniana* Goep. et Berendt, Goepfert (1853): p. 463

1872 *Patzea gentoides* Casp., Caspary (1872): p. 20.

1883 *Ephedra johniana* Goep. et Berendt, Goepfert and Menge (1883): pp. 47–48, pl. XVI, figs. 243, 247.

Emended diagnosis—Shoots decussately branched, internodes roundish in cross section. Expanded leaves present: linear-oblanceolate leaves, entire, decussate.

Inflorescence bracts squamate, widely-ovate, entire, decussate. Fruits more than three per node, widely obovate, divided, distal zone with adnate 4-merous perianth; stigma non-lobed.

Holotype—lost.

Repository—unknown; Conwentz (1886a) listed four specimens of *Patzea johniana* of which he only illustrated two. The latter two derived from the Goepfert Amber Collection in the Mineralogical Museum of the University of Berlin (specimen of fruiting inflorescence, Fig. 1A, C, E–G) and from the Westpreußisches Provinzial-Museum Danzig (foliage stem, Fig. 1B, D), respectively. He described the third *P. johniana* (= *Patzea gnetoides* Casp.) specimen of a fruiting inflorescence and a foliage stem which was found by R. Caspary in the Sommerfeld Amber Collection (Königsberg) and mentioned the fourth specimen from the collection of the Naturforschende Gesellschaft Emden. Current locations of these four specimens are unknown.

Type locality—Baltic Sea coast.

Stratigraphy—Baltic amber derives from Priabonian to Lutetian sediments.

Description—Conwentz (1886a) originally described *Patzea johniana* on the basis of two specimens: one amber piece with a fruiting inflorescence (1.5 mm long; Fig. 1A, C) and another amber specimen containing a foliage stem (2.5 cm long; Fig 1B, D) with a degraded fruiting inflorescence, morphologically similar to the former.

Conwentz (1886a) describes stems as terete in cross-section with internodes (Fig. 1C, D). As shown by his illustration (Fig. 1C) and mentioned in his text (Conwentz, 1886a), each node of the fruiting inflorescence is covered by squamate bracts that are broadly-ovate with entire margins, not fused together at their bases and decussately arranged. Following Conwentz (1886a), each squamate bract pair subtends numerous pedicellate fruits (at least three, Fig. 1C). In his illustrations, these fruits are widely obovate and divided into a proximal conical-shaped and a distal ($\geq 50\%$) globular-shaped portion (Fig. 1F, G). Conwentz (1886a) mentions that the distal portion of the fruit is composed of segments, which we interpret as four sepals that are fused together and adnate with the fruit (Fig. 1E). In his descriptions, Conwentz indicates that each fruit apex possesses a minute protuberance that he construed as stigma; indeed, his illustrations (Fig. 1E–G) show a non-lobed stigma at fruit apices.

Conwentz (1886a) also described a foliage stem with linear-oblong leaves that are curved, flat, and glabrous with entire margins and rounded apices. He mentions that they are decussately arranged and free from the stem except at the base (Fig. 1D). The branching type of the foliage stem is visible in his illustration of the inclusion (Fig. 1D), but not mentioned in the description (Conwentz, 1886a). The base of the illustrated foliage stem clearly shows three branches that are decussately arranged (Fig. 1D).

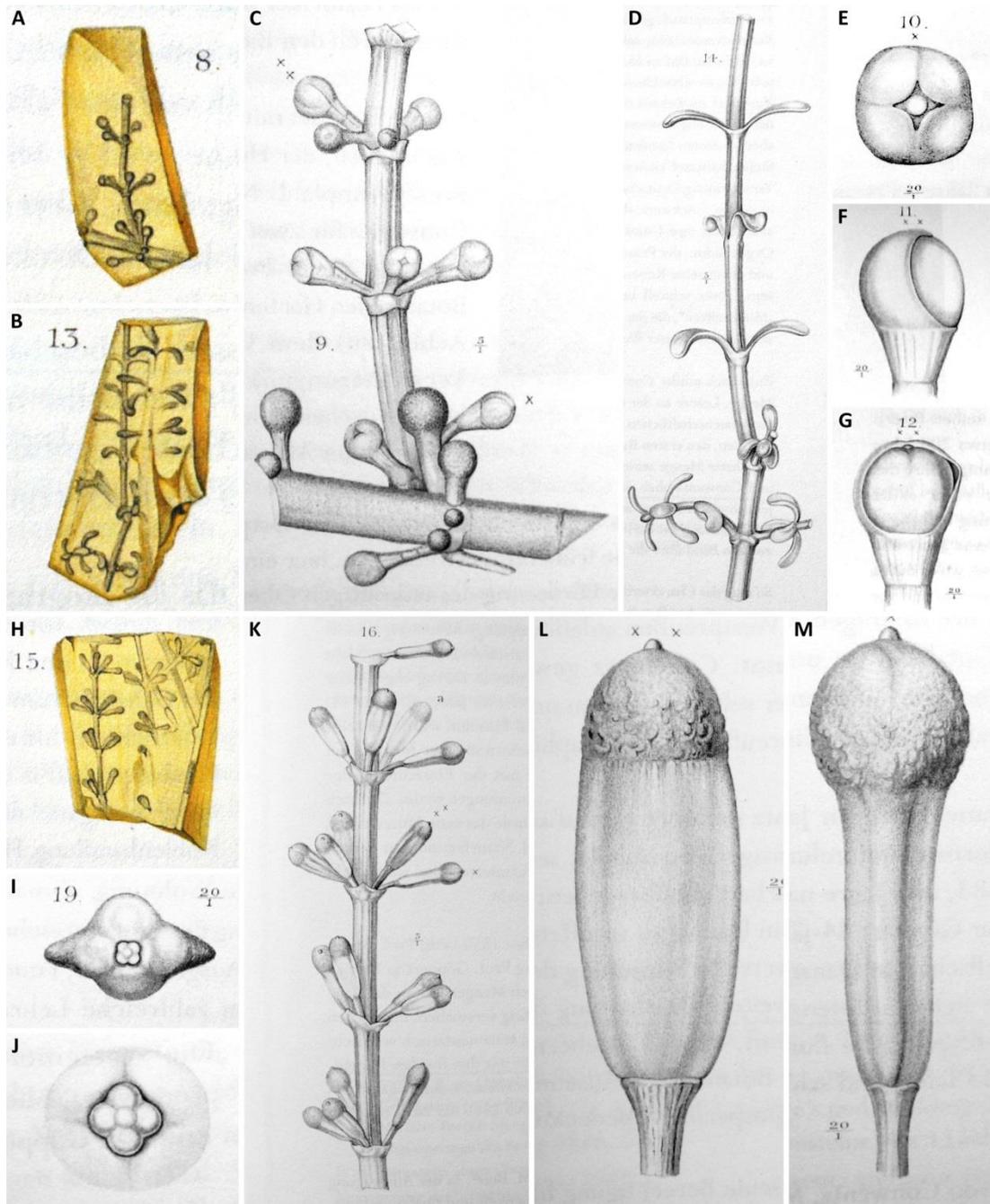


Fig. 1. Historic figures of Baltic amber inclusions of *Patzea johniana* (A–G) and *P. mengeana* (H–M) (Loranthaceae), taken from Conwentz (1886a, plate XIII, figs. 8–20), now redescribed as *Arceuthobium johnianum* comb. nov. and *A. mengeanum* comb. nov. (Viscaceae). (A) Amber specimen with inclusion of fruiting inflorescence of *A. johnianum*. (B) Amber specimen with a foliage stem and a degraded fruiting inflorescence of *A. johnianum*. (C) Magnified fruiting inflorescence of the specimen shown in (A); *x* marks the fruits which are figured in (E–G). (D) Stem with oblanceolate leaves, of the amber piece shown in (B). (E) Fruit from above, showing the minute central stigma and 4-merous perianth. (F, G) Fruit from the side with a junction line, dividing the fruit into two parts; the surface of the distal part is partly degraded. (H) Amber specimen of *A. mengeanum* with several fragments of fruiting inflorescences. (I, J) Fruits from above with 4-merous perianth (I) and a five-lobed stigma (J). (K) Fruiting inflorescence of the amber specimen shown in (H); *x* marks the fruits which are figured in (L, M). (L, M) Fruits from the side, exhibiting a clear division into two parts.

Remarks—Based on Conwentz’s descriptions and illustrations, *Arceuthobium johnianum* can clearly be distinguished from extant and fossil *Arceuthobium* species by the combination of the following features: internode terete in cross section; the presence of expanded leaves; widely obovate fruits, broadly-ovate squamate bracts; the 4-merous perianth and the minute non-lobed stigma (see Table 2 for comparison).

Species—*Arceuthobium mengeanum* comb. nov. (Fig. 1H–M)

Basionym—*Patzea mengeana* Conw., Conwentz 1886a, p. 138, pl. XIII, figs 15–20.

Synonyms

1883 *Ephedra mengeana* Goepp., Goeppert and Menge (1883): p. 48, pl. XVI, figs 248–250.

Emended diagnosis—Internode cross section terete to angular. Bracts two-paired, decussate, squamate, broadly-ovate, entire, apex acute. At least four fruits per node, 3.4–4 mm long, elongated-elliptic, divided, distal portion 25–50% of total fruit, distal zone with adnate 4-merous perianth; stigma 5-lobed.

Holotype—lost.

Repository—unknown; originally from the Amber Collection of Menge, West-Preußisches Provinzial-Museum Danzig.

Type locality—Baltic Sea coast.

Stratigraphy—Baltic amber derives from Priabonian to Lutetian sediments.

Description—Conwentz (1886a) described *Patzea mengeana* on the basis of one specimen that contained several fragments of fruiting inflorescences that are 2.1 cm long (Fig. 1H) and that possess internodes with terete to angular cross sections (Fig. 1K). As found by Conwentz (1886a), each node is covered by a pair of squamate bracts that are broadly ovate with entire margins and acute apices (Fig. 1K). Furthermore, Conwentz (1886a) described the bracts as non-fused at their bases and decussately arranged. As shown in his illustrations (Fig. 1K) but also mentioned in his text (Conwentz, 1886a), each bract pair subtends a whorl of pedicellate fruits (at least four) that are 3.4–4 mm long and elongated-elliptic. The illustrations (Fig. 1L, M) of Conwentz (1886a) clearly show that all fruits are divided into a dark, wrinkled distal part and a light proximal part. Based on his illustrations, the distal portion is estimated to comprise approximately 25–50% of the total fruit. Conwentz (1886a) observed four apical “lobes” that we interpret as four perianth segments adnate to the distal part of the fruit body (Fig. 1I). Conwentz (1886a) described a five-lobed stigma of which four lobes encircle the centrally located elongated fifth lobe (Fig. 1J).

Remarks—Based on Conwentz’s descriptions and illustrations, *A. mengeanum* exhibits a combination of several features that is not present in extant *Arceuthobium*

species, namely, nonfused squamate bracts, the presence of four perianth segments and the five-lobed stigma. *Arceuthobium mengeanum* is different from other fossil *Arceuthobium* species in its stigma morphology, the relatively large fruit length of 3–4 mm, and the small distal fruit portion of 25–50% of the total fruit length (see Table 2 for comparison). Conwentz mentioned that he dissected the original specimen of *Patzea mengeana* in two pieces, which is not shown in his figures.

Species—*Arceuthobium conwentzii* sp. nov. (Fig. 2).

Diagnosis—Internode cross section angular, internodes 2.8–3.7 mm long \times 0.5–0.7 mm wide, unbranched. Bracts two-paired, decussate, entire, rhombic, not fused, 0.8–1.2 mm long \times 1.2–1.6 mm wide. Fruits seven or eight per node, elliptic, 1.4–2.2 mm long \times 0.6–1.1 mm wide, divided, distal part deeply furrowed, proximal part finely ribbed; distal portion 45–68% of total fruit. Perianth 3-merous, adnate to distal part of the fruit body.

Holotype—GZG.BST.24548 (Fig. 2), Fig. 2A (arrowhead) represents the holotype.

Repository—Königsberg Amber Collection, Geoscientific Collections of the University of Göttingen, Germany.

Type locality—Samland, Kaliningrad.

Stratigraphy—Baltic amber derives from Priabonian to Lutetian sediments.

Etymology—The species is named after the botanist and amber researcher Hugo Wilhelm Conwentz (1855–1922) who examined and described numerous plant inclusions from Baltic amber.

Description—The inclusion consists of two stems, each is approximately 1.5 cm long (Fig. 2A). Both stems are unbranched with angled internodes that are 2.8–3.7 mm long \times 0.5–0.7 mm wide. Each node is enclosed by a pair of squamate, entire bracts that are 0.8–1.2 mm long \times 1.2–1.6 mm wide. They are decussately arranged and rhombic in shape. They are not fused at their bases and form a cup-like structure (Fig. 2B). At each node, the squamate bracts subtend a whorl of seven or eight pedicellate, elliptic fruits (Fig. 2A–C) that are 1.4–2.2 mm long \times 0.6–1.1 mm wide. The majority of fruits are divided into two zones; the upper (distal) part of the fruit is deeply wrinkled and dark, while the lower (proximal) part is smooth, finely ribbed, and light (Fig. 2D, E). The distal portion comprises 45–68% of the total fruit length. Only a few fruits are undivided and due to their small size (0.4–0.7 mm long \times 0.4–0.6 mm wide) they were probably immature (Fig. 2C arrowhead, F). The distal part of each fruit exhibits three perianth segments that are adnate to the fruit body. The perianth segments slightly overarch the base of the style in some fruits (Fig. 2G).

Protruding from the distal end of each fruit is a broad style with a 2 to 4-lobed stigma that is covered with round papillae (Fig. 2G, H). The base of the proximal fruit portion exhibits the rounded receptacle of the pedicel (Fig. 2D, E). The pedicels are 0.6–1.28 mm long \times 0.24–0.4 mm wide, straight, or slightly curved, but sometimes bent at an angle of about 90° to the longitudinal axis of the stem.

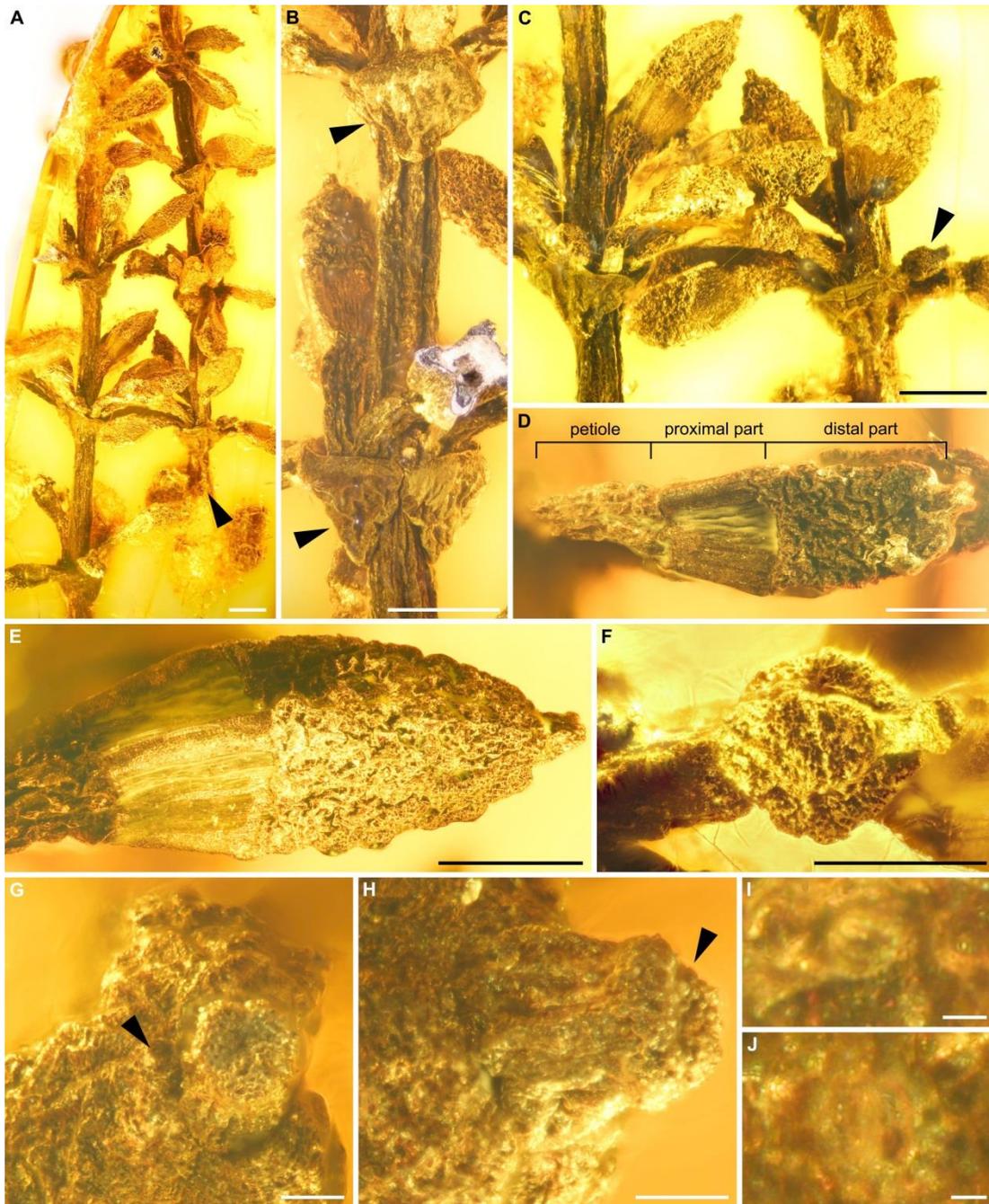


Fig. 2. *Arceuthobium conwentzii* sp. nov. from Baltic amber (GZG.BST.24548). (A) Fruiting inflorescences; arrowhead points to the holotype of *A. conwentzii*. (B) Stem with decussate, non-fused squamate bract pairs (arrowheads) at each node. (C) Petiolate fruits arising from the nodes; arrowhead indicates an immature fruit. (D, E) Fruits being clearly divided into a finely ribbed proximal and deeply furrowed distal part. (F) Non-divided immature fruit. (G) Fruit from above showing a 3-lobed stigma and 3-merous perianth, which slightly covers the base of the style (arrowhead). (H) Style with 2-lobed stigma, covered with round papillae (arrowhead). (I, J) Paracytic stomata from the distal fruit part. Bars = 1 mm (A–C), 500 μ m (D–F), 100 μ m (G–H), 10 μ m (I–J).

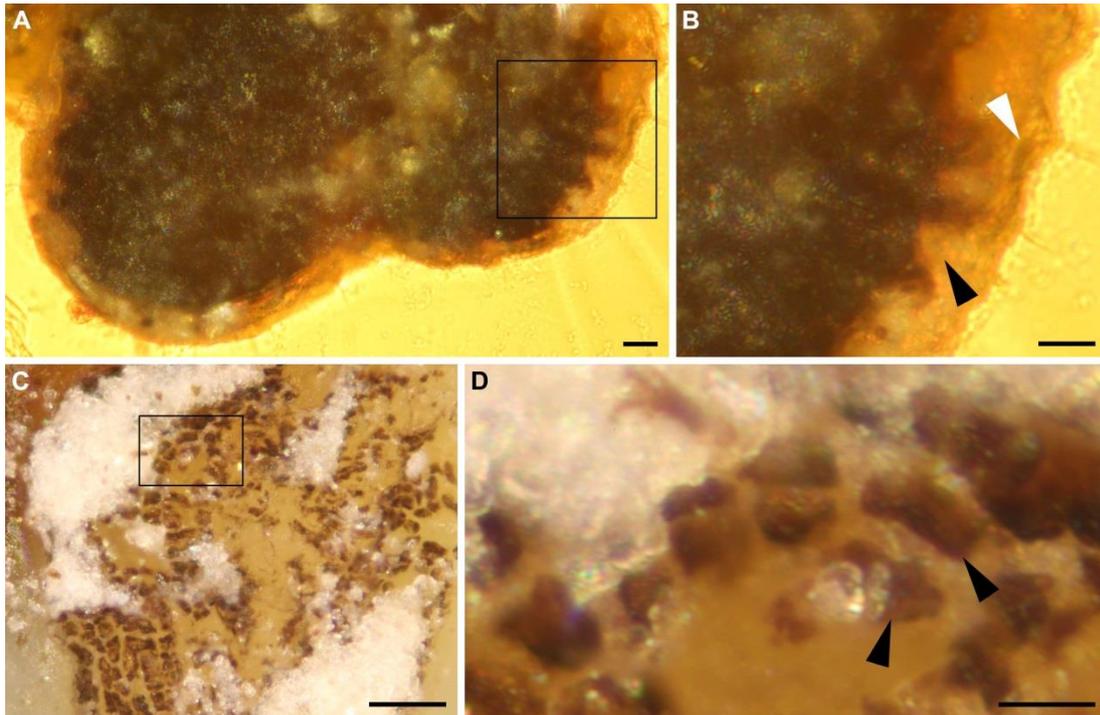


Fig. 3. Cuticular epithelium preserved in *Arceuthobium conwentzii* (GZG.BST.24548; A, B) and *A. obovatum* (GZG.BST.24359; C, D). (A) Transverse view of a fruit of *A. conwentzii*, showing a thickened cuticular layer. (B) Solid-line inset from (A) showing pegs of the cuticular epithelium (black arrowhead) and an elongate cell embedded in the cuticular layer (white arrowhead). (C) Remains of the shoot epidermis of *A. obovatum* (paradermal view). (D) Solid-line inset from (C), showing an arc of cells; arrowheads indicate two sister cells that have moved apart from each other. Bars = 10 μm (A, B, D), 50 μm (C).

One fruit located at the amber surface reveals a cross section through the fruit epidermis. The cuticular layer is very prominent (6.5–20 μm wide) and forms “pegs” which extend into the subepidermal cell layer, separating cells from each other (Fig. 3A, B, black arrowhead). Also seen is a cell that is isolated in the cuticular layer (Fig. 3A, B, white arrowhead).

Stomata are only located on distal portions of fruits, while proximal portions are devoid of stomata. Stomata are perpendicularly oriented to the longitudinal plant axis (Fig. 2I, J). Due to the insufficient surface preservation, further stomatal details cannot be observed. Stomata on bracts and internodes are not preserved.

Remarks—The fossil species *Arceuthobium conwentzii* is distinct from extant species because it has non-fused squamate bracts, a 3-merous perianth, fruits with a large distal portion (45–68%), and overall small fruit size. *Arceuthobium conwentzii* can be distinguished from other fossil *Arceuthobium* species through a combination of the following features: the large dimensions of fruits, the distinct fruit division, the 3-merous perianth and the greater number of fruits per node (see Table 2 for comparison).

Species—*Arceuthobium groehnii* sp. nov. (Fig. 4).

Diagnosis—Shoots unbranched, internode cross section angled, 1–1.7 mm long \times 0.7–0.8 mm wide. Bracts squamate, widely obtrullate, dentate margins, acuminate apices, decussate, rounded non-fused bases, 0.7–0.9 mm long \times 1.1–1.3 mm wide. Fruits 5–7 per node, elliptic, 0.3–0.8 mm wide, two distinct zones absent, surface smooth.

Holotype—GPIH 4582 (Gröhn coll. no. P 6551) (Fig. 4).

Repository—Geological-Paleontological Institute and Museum of the University of Hamburg (GPIH), as part of the Carsten Gröhn Amber Collection.

Type locality—Samland, Kaliningrad.

Stratigraphy—Blue Earth layer, late Eocene.

Etymology—The specific epithet honors Carsten Gröhn (Glinde, Germany) who provided the fossil for study.

Description—The inclusion is an unbranched stem that is about 1.3 cm length (Fig. 4A). The stem has internodes 1–1.7 mm long and 0.7–0.8 mm wide, that are longitudinally furrowed and angular in cross section (Fig. 4A). Each node is enclosed by a pair of squamate bracts that are 0.7–0.9 mm long \times 1.1–1.3 mm wide. Bracts are decussately arranged, widely obtrullate with irregular dentate margins distally and acuminate apices (Fig. 4A–C). They form a cup-like structure and are not fused at their bases. At each node, the bracts subtend a whorl of 5–7 pedicellate, elliptical fruits whose bases are mostly covered by the two bracts (except the two fruits at the base of the stem) (Fig. 4A, B). The visible part of the fruits is 0.5–0.9 mm long (measured from the fruit apex to the bract margin) \times 0.3–0.8 mm wide. The distal end of each fruit terminates in a massive broad style with a 2- or 3-lobed stigma that is covered by numerous round papillae (Fig 4C, E). Proximal and distal portions of fruits are not distinct and fruits do not show remains of the perianth. The fruit surface is smooth and composed of regular rectangular to polygonal cells that form short rows or are irregularly arranged (Fig. 4D).

The apex of the shoot exhibits a globular bud that is 0.7 mm long \times 0.9 mm wide and composed of four visible bracts (Fig. 4A).

Stomata are regularly distributed on the fruit surface (Fig. 4D), the abaxial bract surface (Fig. 4G), and the stem (Fig. 4H). They are elliptic in shape and paracytic with two slender subsidiary cells (Fig. 4F–H). On fruits, the stomata are not sunken and are obliquely to perpendicularly arranged relative to the longitudinal plant axis (Fig. 4D, F); on stems (Fig. 4H) and bracts (Fig. 4G), the sunken stomata are oriented only perpendicularly. In some cases, stomata are also present on the style.

The epidermis of the stem consists of rectangular cells that are arranged in rows (Fig. 4H). Pinaceous pollen is attached to the base of the stem (Fig. 4I).



Fig. 4. *Arceuthobium groehnii* sp. nov. from Baltic amber (GPIH 4582). (A) Overview of the fruiting inflorescence; arrowhead indicates pollen shown in (I). (B) Cup-shaped non-fused squamate bract pair subtending a whorl of fruits. (C) Fruit with 2-lobed papillous stigma; arrowhead indicates acuminate bract apex. (D) Fruit epidermis, composed of polygonal to rectangular cells; arrowheads indicate stomata complexes. (E) 3-lobed stigma with round papillae. (F–H) Paracytic non-sunken stomata of the fruits (F) and squamate bracts (G), as well as sunken stomata of the stem (H). (I) Pinaceous pollen attached to the lowest part of the stem. Bars = 1 mm (A), 500 µm (B), 200 µm (C), 100 µm (D), 50 µm (E, I), 10 µm (F–H).

Remarks—*Arceuthobium groehnii* is distinguished from extant *Arceuthobium* species and from the other Eocene fossil taxa by a combination of the following features: non-fused squamate bracts with dentate margins and acuminate apices, the elliptic fruit shape, the indistinct perianth merosity and the absence of expanded leaves (see Table 2 for comparison).

Species —*Arceuthobium viscoides* comb. nov. (Figs. 5–9).

Basionym—*Enantioblastos viscoides* (Goepf. et Ber.) Conwentz 1886a: pp. 127–128, pl. XII, figs 20–22.

Synonyms

1845 *Enantioblastos viscoides* Goepf. et Berendt, Goepfert and Berendt: p. 76, pl. VI, figs. 6–7.

1853 *Enantioblastos viscoides* Goepf. et Berendt, Goepfert (1853): p. 467.

Diagnosis—Shoots verticillately branched, internodes 1.2–5.2 mm long \times 0.2–0.4 mm wide. Expanded leaves oblanceolate, margins entire, decussate, 1.2–2.3 mm long \times 0.2–0.4 mm wide, leaving a convex abscission scar; axillary buds, decussate, two-paired, with four decussate scale pairs, one scale pair comparatively minute at the bud side. Squamate bracts: only at nodes of fruiting inflorescence, two-paired, decussate, rhombic, entire margins, subtending a whorl of pedicellate fruits. Mature fruits elliptic, 0.6–0.7 mm long \times 0.3 mm wide, divided, distal part deeply furrowed, proximal part finely ribbed.

Holotype—MB.Pb.1981-2 (Fig. 5).

Repository—Berendt Amber Collection; Museum für Naturkunde zu Berlin.

Paratype—Hoffeins Amber Collection, GZG.BST.21950 (Hoffeins 1422-2), Geoscientific Collections of the University of Göttingen, Germany (Figs 6–9).

Further specimen investigated—GZG.BST.21951 (Hoffeins 1156-3), Geoscientific Collections of the University of Göttingen, Germany (not figured).

Type locality—Samland, Kaliningrad.

Stratigraphy—Blue Earth layer, late Eocene.

Etymology—The specific epithet was chosen by Goepfert and Berendt (1845) to refer to the similarity of the fossil to the extant genus *Viscum*.

Description—The holotype of *Arceuthobium viscoides* (MB.Pb.1981-2) is a foliage stem inclusion (Fig. 5A, C, D) about 6.7 mm long that has two internodes (1.1–3.1 mm long \times 0.4–0.5 mm wide). The internode segments are angular in cross section and longitudinally furrowed (Fig. 5C, D). One leaf pair is located at the apex of the stem segment. The leaves are 2 mm long \times 0.4–0.6 mm wide, oblanceolate, with entire margins and rounded apices. On the adaxial leaf surface, a pair of widely ovate scales is located at the leaf base (Fig. 5E). One pair of axillary buds arises from the

middle part of the stem inclusion, decussate to the leaves with each bud subtended by a convex leaf abscission scar (Fig. 5B, F, G). The buds are roundish, consisting of three pairs of visible decussate round scales, with entire margins and acute apices. The fourth minute scale pair is located at the side of the bud (Fig. 5B, F).

The paratype of *A. viscoides* (GZG.BST.21950) contains two branch fragments; one branch fragment is 1.5 cm long, with its main axis ramifying into 3 branches (Figs. 6A, 6B, 7A, 7D). The other branch fragment is about 1.7 cm long, with two main axes ramifying into five smaller branches (Figs. 8A, 9A, 9D). Further short branch fragments and leaves are entangled in these two branch fragments. The branching type is verticillate.

Each branch has internodes, 1.4–5.2 mm long \times 0.24–0.4 mm wide. Each node is covered by one pair of oblanceolate decussate leaves (Figs. 6E, 6G, 7A, 7D, 8D, 9A, 9D), 1.2–2.3 mm long \times 0.2–0.4 mm wide. The leaves are rather fleshy, with entire margins and rounded apices.

Stomata are located on both sides (amphistomatic) of the oblanceolate leaves and show an undefined orientation pattern towards the longitudinal leaf axis (Fig. 6I), while on the stem, stomata are perpendicularly arranged (Fig. 6H). However, due to preservation, no further stomatal details (e.g. on squamate bracts) could be observed. The epidermis of the leaf base is composed of rectangular cells that become more polygonal towards the apex (Fig. 8H). The epidermal cells of the stem are rectangular, forming regular rows (Fig. 6H).

Each leaf pair exhibits one pair of axillary buds (Figs. 6D; 7B; 8C), composed of eight visible scales which are decussately arranged (Figs. 6C, 6D, 7B, 7C); the first scale pair is minute, inconspicuous and located at the side of the bud (Figs. 6D, 7B, 7C). The scales are widely ovate with obtuse to acute apices and entire margins. In cases where the subtending leaf had abscised, axillary buds are subtended by convex abscission scars (Fig. 6C).

The main axes of both branches exhibit four axillary buds at the lowermost node with two buds on each side (Figs. 6F, 7E, 7F, 8I, 9B).

One branch bears a fruiting inflorescence (Figs. 8B, 9A, 9C) and a further fragment of a fruiting inflorescence is entangled within the two main branches (Fig. 8F, 8G). The fruiting inflorescences are divided into internodes similar to foliar branches. At each node, a pair of squamate rhombic bracts forms a cup-like structure (0.7 mm wide \times 0.4–0.5 mm long), enclosing several petiolate fruits (Figs. 8B, 9A, 9C). The fruits are elliptic and elongate with a broad 2-lobed stigma at their apices (Fig. 8E–G). One fruit exhibits a clear division into a proximal finely ribbed part and a distal deeply furrowed part (Fig. 8F, G). The distal portion of this fruit encompasses 59 % of the total fruit length. However, most of the fruits are only poorly preserved; thus, further details regarding their epidermal structure are not visible.

The inclusions are partly degraded and covered by sporulating fungi (Figs. 8D; 9D) with affinities to *Gonatobotrys* Corda and *Gonatobotryum* Sacc. (Ascomycota) (E. Kettunen, Helsinki, personal communication). A syninclusion of a

potential Psychodidae (Trichomoyiinae) is closely located to one of the branches (F. Stebner, Bonn, personal communication).

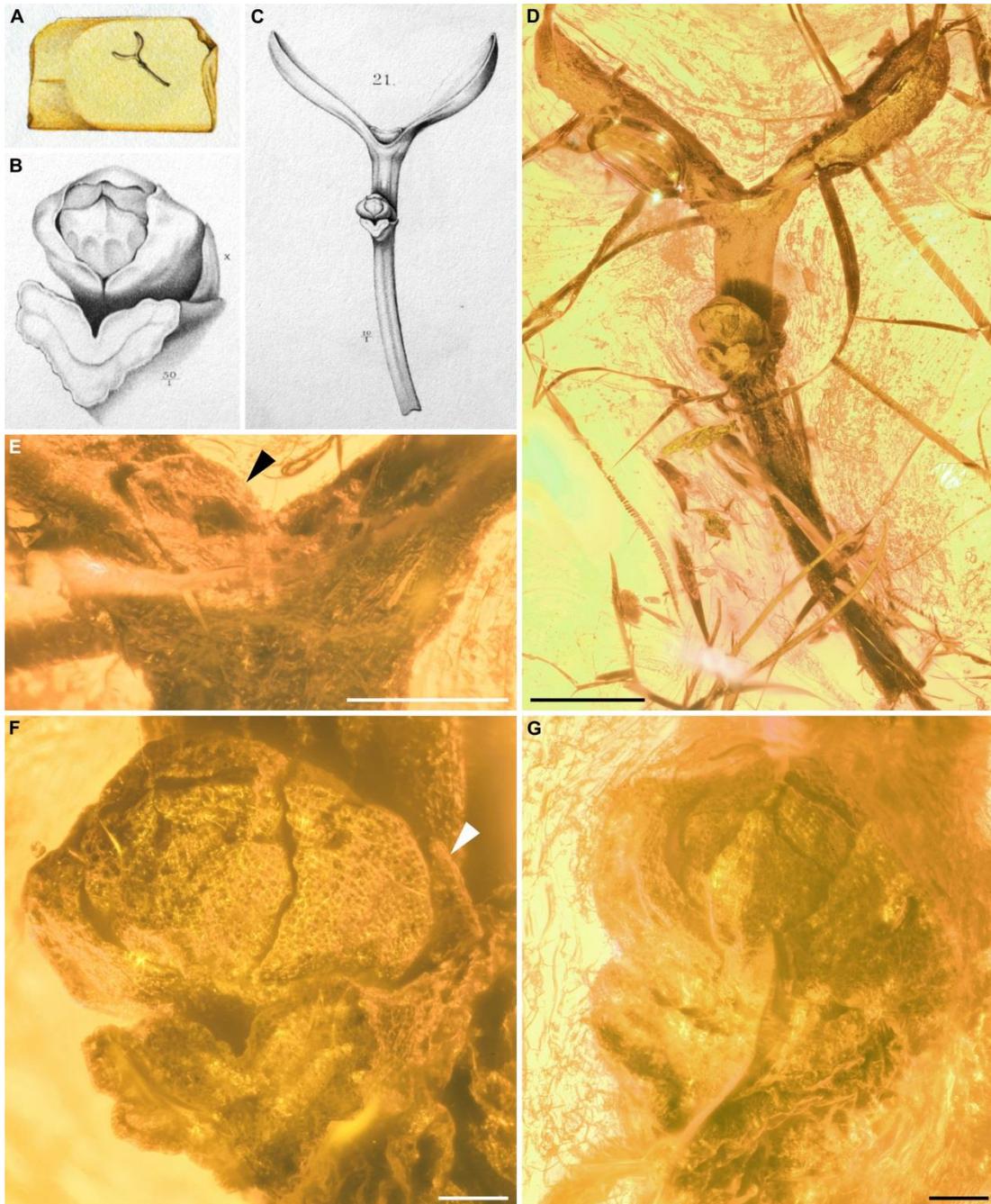


Fig. 5. Historic figures of *Enantioblastos viscoides* (Rubiaceae) (A–C) (taken from Conwentz 1886a, plate XII, figs 20–22) and photos of this particular specimen (D–G), representing the holotype of *Arceuthobium viscoides* comb. nov. (Viscaceae) (MB.Pb.1981-2) from Baltic amber. (A) Overview of the amber specimen, containing a foliage stem fragment, magnified in (C) and (D). (B) Axillary bud, subtended by a leaf abscission scar; *x* marks a minute scale at the side of the bud. (E) Axil of the oblanceolate leaf pair with two scales (arrowhead). (F) Axillary bud pictured in (B), arrowhead indicates the minute bract. (G) Axillary bud from the opposite side of the stem. Bars = 1 mm (D), 300 μ m (E), 100 μ m (F, G).



Fig. 6. Paratype of *Arceuthobium viscoides* (GZG.BST.21950) from Baltic amber. (A, B) Amber piece with branch fragments of *A. viscoides* from two different perspectives; photos of this plate derive from the branch at the side (arrowheads). (C) Axillary bud composed of four scale pairs and subtended by a leaf abscission scar (arrowhead). (D) Axillary bud of (C) from the side; arrowhead indicates minute scale at the side. (E) Oblanceolate leaf with fungal infection. (F) Axillary buds from the side, located at the lowermost node of the main stem. (G) Oblanceolate leaf pair with axillary buds. (H, I) Perpendicular stomata on the stem (H, arrowheads) and on the adaxial leaf side (I). Bars = 1 mm (A, B), 100 μ m (C, D, F), 500 μ m (E, G), 10 μ m (H, I).

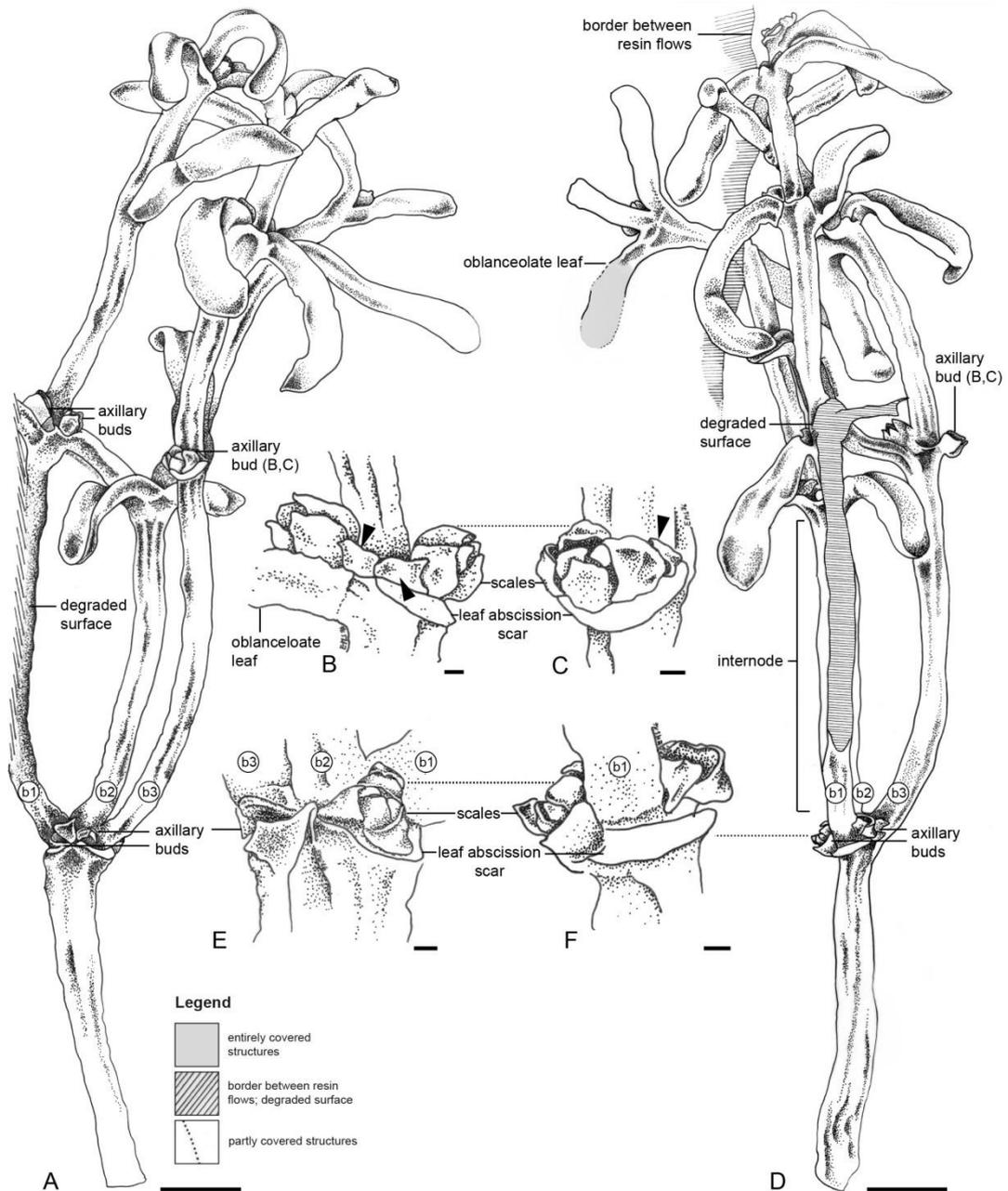


Fig. 7. Illustration of one branch of *Arceuthobium viscoides* (GZG.BST.21950) from Baltic amber, shown in Fig. 6A–B (arrowheads). (A, D) Overview of the same branch fragment from two different angles. The main stem ramifies into three smaller branches (b1–b3); the surface of b1 is strongly degraded from one side (dashed surface). (B) Axillary bud pair from the side (same as Fig. 6D), arrowheads indicate minute scales at the side of each bud. (C) Axillary bud of (B) from another angle (same as Fig. 6C), arrowhead indicates the small scale at the side. (E) Two of four axillary buds located at the lowermost node of the main stem. (F) Axillary bud shown in (E) from the side (same as Fig. 6F); the identical buds are indicated by the dotted line; the opposite side of this node possesses another pair of axillary buds, resulting into four buds in total at the lower most node. Bars = 1 mm (A, D), 100 µm (B, C, E, F).

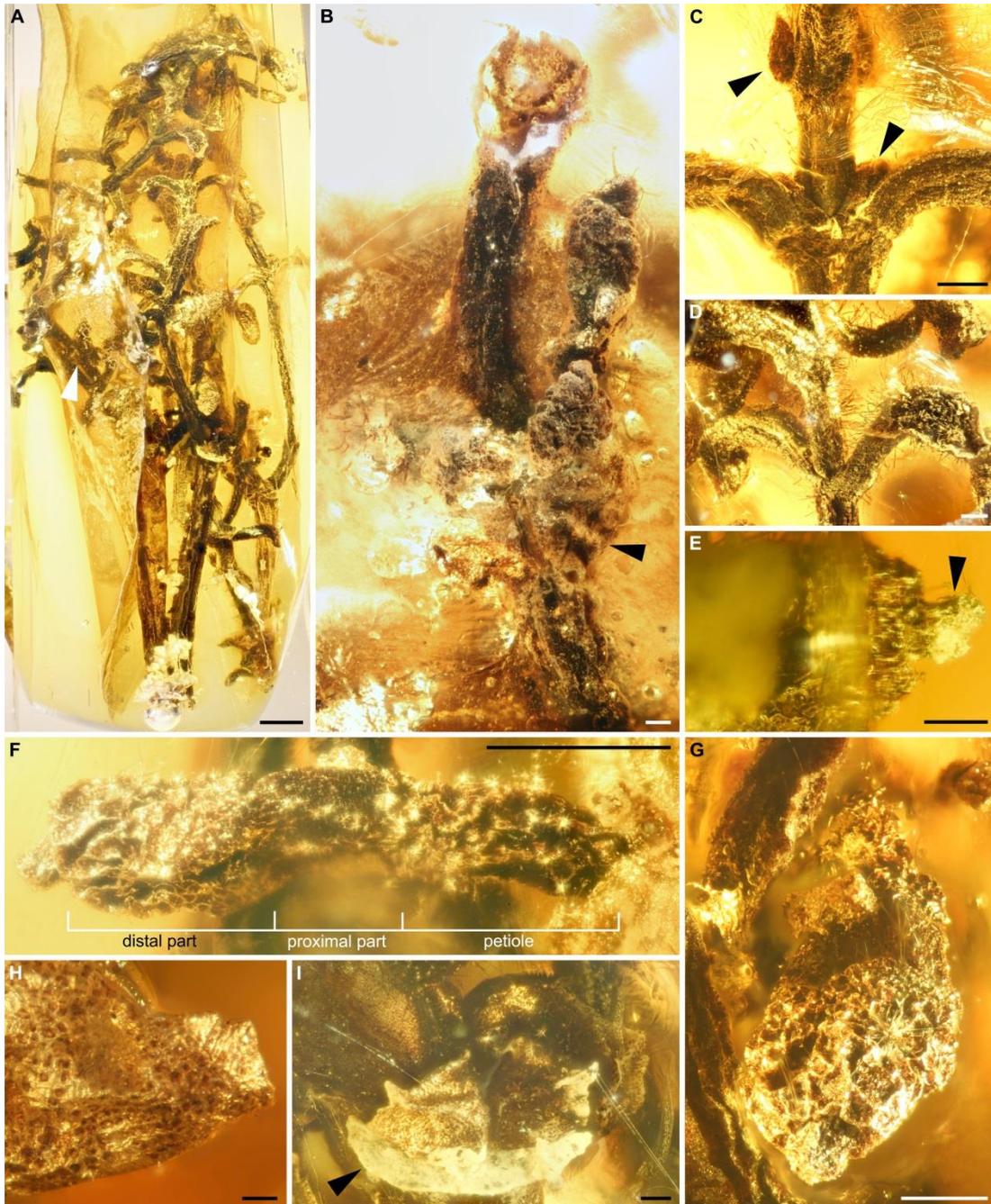


Fig. 8. Paratype of *Arceuthobium viscoides* (GZG.BST.21950) from Baltic amber. (A) Amber piece (shown from another perspective than in Fig. 6A, B) with branch fragments of *A. viscoides* bearing a fruiting inflorescence (arrowhead). (B) Fruiting inflorescence indicated in (A) with squamate bracts (arrowhead) subtending petiolate fruits. (C) Nodes with decussately arranged leaf pairs, each with an axillary bud (arrowheads). (D) Oblanceolate leaves covered with fungi. (E) Style (arrowhead) and a 2-lobed papillous stigma from a fruit. (F, G) Fruit divided into a distal and proximal part, emerging from another fruiting inflorescence which is entangled within the main branches. (H) Epidermis of abaxial leaf side, showing polygonal cells. (I) Scales of axillary buds, arrowhead indicates the abscission scar of an ob lanceolate leaf (see branch on the right, Fig. 9D). Bars = 1 mm (A), 100 μm (B, E, I), 200 μm (C, D, G), 50 μm (H), 500 μm (F).

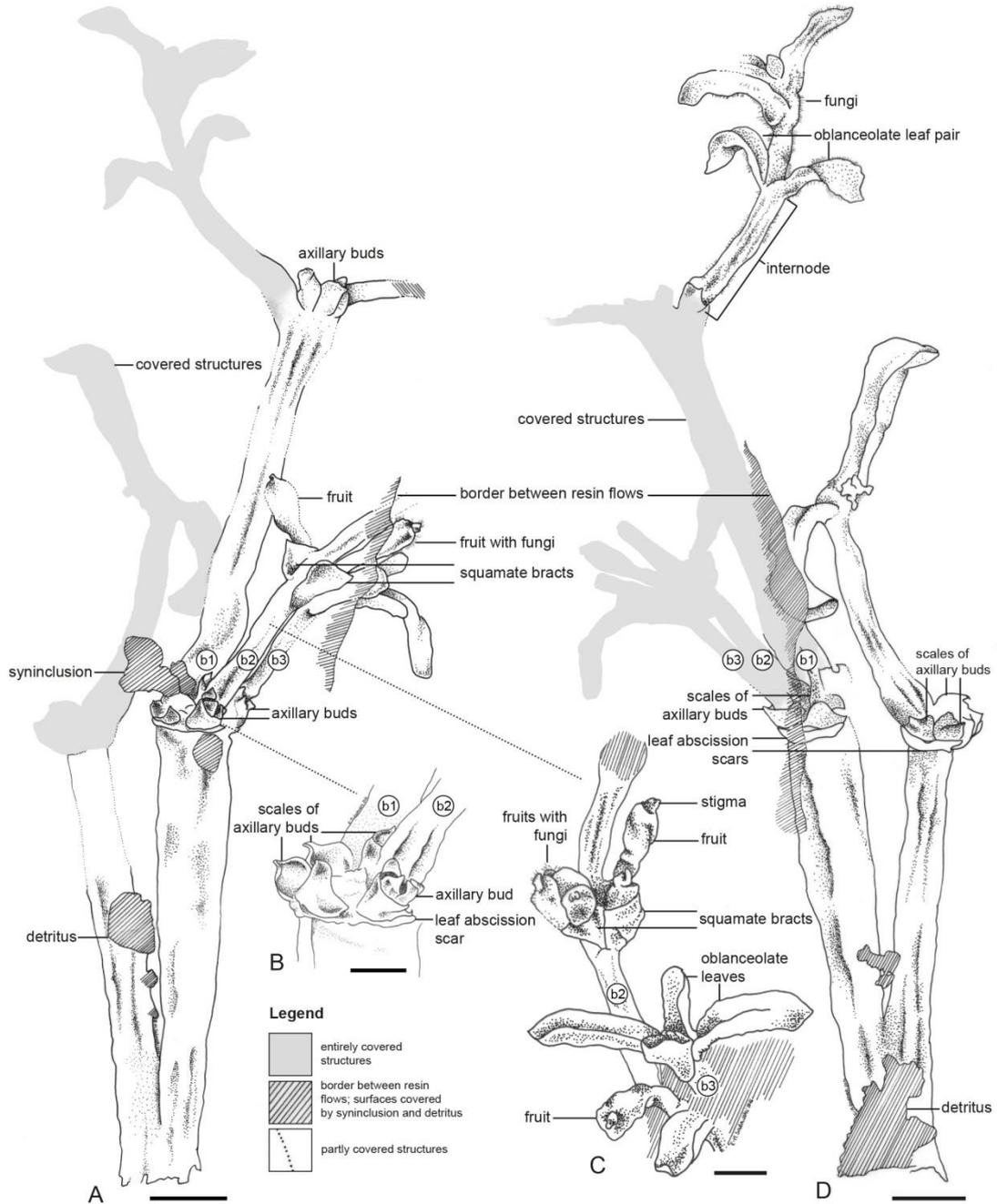


Fig. 9. Illustration of a further branch of *Arceuthobium viscoides* (GZG.BST.21950), bearing the fruiting inflorescence, shown in Fig. 8A and B. (A, D) Overview of the same branch fragment from two different angles. Structures which were entirely covered from one side were colored in grey. One main stem ramifies into three branches (b1–b3) of which b2 is the fruiting inflorescence. (B) Axillary bud pair of the lowermost node. (C) Fruiting inflorescence (b2) and branch (b3) shown in (A) from another angle (same as Fig. 8B). Bars = 1 mm (A, D), 500 µm (B, C).

Remarks—*Arceuthobium viscoides* (specimen MB.Pb.1981-2) was first described as *Enantioblastos viscoides* (Loranthaceae) due to its similarities to extant *Viscum* (Goepfert and Berendt, 1845), a genus now considered within the Viscaceae. Later, Conwentz (1886a) assigned the specimen to the Rubiaceae based on its “hollow leaves” and the presence of intrapetiolar stipules, located on the adaxial side of its leaf bases (Fig. 5E) and at both sides of the axillary bud (Fig. 5B, F, G). According to the author, both were atypical features of the Loranthaceae, but rather common to the Rubiaceae (Conwentz, 1886a). Similar to Conwentz (1886a), we observed two scales on the adaxial side of the foliage leaves (Fig. 5E), but we interpret these scales as remains of the axillary buds, rather than stipules.

The assignment of the *Enantioblastos viscoides* specimen and the amber specimen GZG.BST.21950 to the same taxon is mainly based on the shared distinct morphology of axillary buds, including the scale shape, scale number, their decussate arrangement, and the presence of a very small scale pair at the bud side. Furthermore, both specimens share leaf and internode sizes, as well as the shape of the internode cross section (see Table 2 for comparison).

Based on the morphology of the fruiting inflorescence of the amber fossil GZG.BST.21950, the assignment to *Arceuthobium* is justified, since typical dwarf mistletoe features such as squamate bracts and the arrangement and morphology of fruits are present. *Arceuthobium viscoides* is different from extant *Arceuthobium* species by the presence of expanded leaves and the non-fused squamate bracts. Although some of the fossil *Arceuthobium* species of this paper show at least one of the morphological features described above, the combination of them is unique for *A. viscoides* (see Table 2 for comparison).

Species —*Arceuthobium obovatum* sp. nov. (Fig. 10).

Diagnosis—Internodes 0.7–2 mm long × 0.7 mm wide, angular in cross section, branched. Squamate bracts entire to dentate, widely obtrullate, non-fused base, decussate, 0.7 mm long × 1 mm wide; expanded leaves oblanceolate, 1.8–2.2 mm long × 0.5–0.9 mm wide. Fruits five or six per node, widely obovate in shape, 0.6–1 mm long × 0.5–0.9 mm wide, occasionally divided, distal part shallow furrowed, proximal part finely ribbed.

Holotype—GZG.BST.24359 (Fig. 10).

Repository—Königsberg Amber Collection, Geoscientific Collections of the University of Göttingen, Germany.

Type locality—Baltic Sea coast.

Stratigraphy—Baltic amber derives from Priabonian to Lutetian sediments.

Etymology—The specific epithet refers to the widely obovate shape of the fruits.

Description—The inclusion consists of a branched stem (Fig. 10A); the main stem is about 1 cm long, ramifying at its base into one smaller branch (0.6 cm long). Each

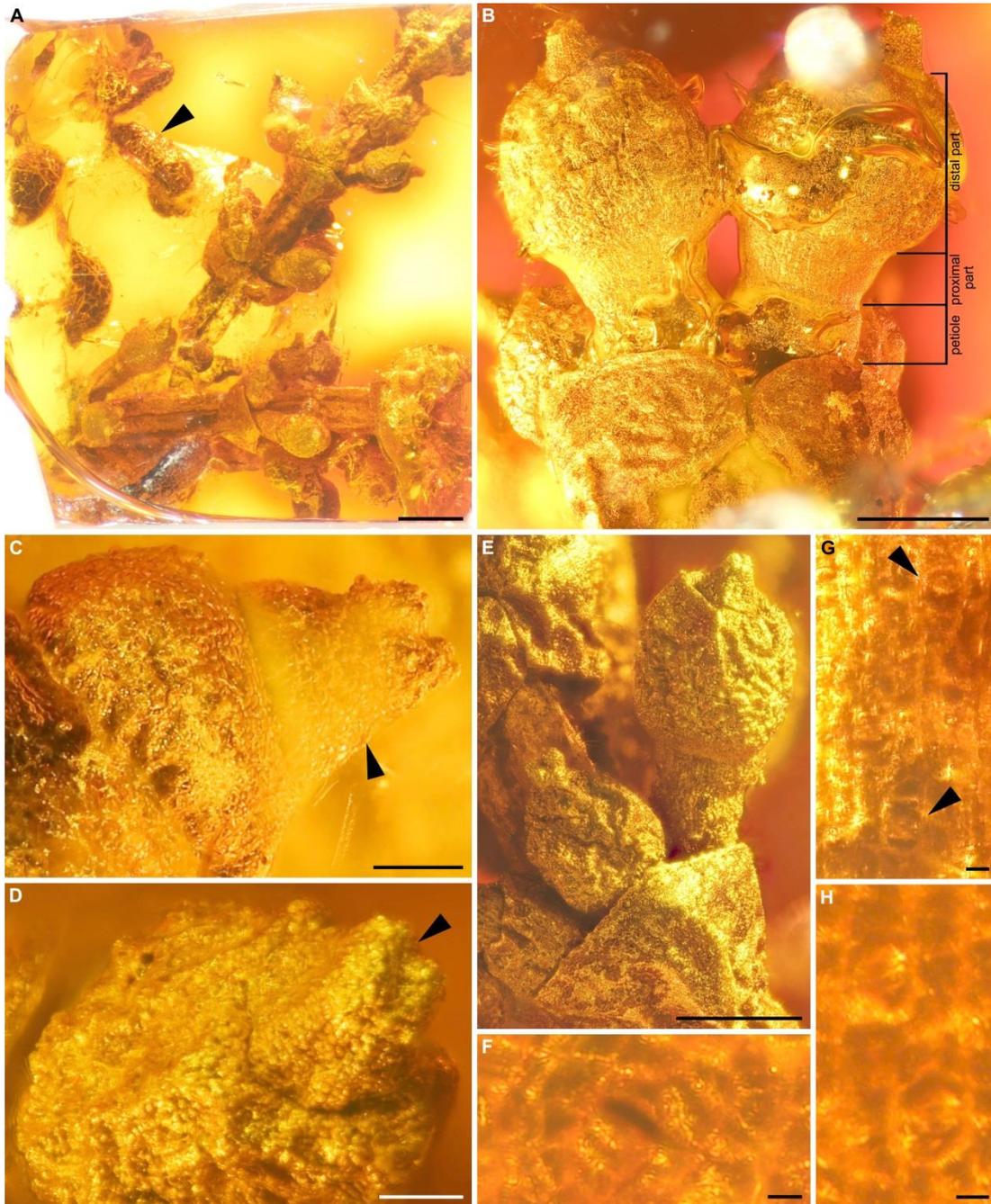


Fig. 10. *Arceuthobium obovatum* sp. nov. from Baltic amber (GZG.BST.24359). (A) Overview of the specimen showing a branched fruiting inflorescence and remains of oblanceolate leaves (arrowhead). (B) Widely obovate fruits, divided into a proximal and distal part; non-fused squamate bracts subtend the fruits. (C, D) Fruits with massive styles, terminating each in a 3-lobed papillous stigma (arrowheads). (E) Fruits subtended by a squamate bract with dentate margin. (F-H) Paracytic stomata of the distal fruit part (F) and the stem (G, H). Bars = 1 mm (A), 500 μ m (B), 100 μ m (C, D), 500 μ m (E), 10 μ m (G, F, H).

stem has internodes that are 0.6–2 mm long \times 0.7 mm wide, angular in cross section with a deep furrow on each side (Fig. 10A). Each node is enclosed by a pair of squamate bracts (Fig. 10A, B, E) that are 0.7 mm long \times 1 mm wide. The bracts are decussately arranged and widely obtrullate. Towards the bract apex, the margin is slightly irregular and dentate. The bracts are not fused at their bases (Fig. 10B) and form a cup-like structure. Remains of expanded, oblanceolate, curved leaves are spreading from the base of the branch (Fig. 10A). Due to its insufficient preservation, more details of these leaves and a clear connection to the main stem could not be observed.

At each node, the squamate bracts subtend a whorl of five or six pedicellate, widely obovate fruits (Fig. 10B, E) that are 0.6–1 mm long \times 0.5–0.9 mm wide. Some fruits exhibit a division into a finely ribbed proximal part and a more deeply folded distal part (Fig. 10B). The distal portion is about 74–88 % of the entire fruit length. However, this division is not clearly visible in all fruits. The perianth merosity is indistinct. Each fruit apex terminates in a massive broad style with a 2–3-lobed stigma that is covered by numerous round papillae (Fig. 10C, D). The fruit pedicels are broad and erect, so that most fruits point upward (Fig. 10B, E); some fruit pedicels are short and covered by the bracts. At the fruit base, the pedicel forms a rounded receptacle (Fig. 10B).

Parts of the stem were broken off from the amber, leaving remains of the stem epidermis attached to the amber. Some of the cells seemed to have moved apart from their sister cells, appearing as an arc of cells and forming pegs between the cells (Fig. 3C, D). Stomata are located on the abaxial leaf surface, the distal portion of the fruit surface (Fig. 10F) and on the stem (Fig. 10G, H). They are 9–21 μ m long \times 9–18 μ m wide, elliptical, arranged perpendicularly to the longitudinal plant axis and paracytic with two slender subsidiary cells (Fig. 10F–H). The epidermis of the stem consists of rectangular cells mostly arranged in rows and with straight cell walls (Fig. 10G).

Closely located to the inclusion of *A. obovatum* and on its surface, syninclusions of aphids were detected, possibly belonging to Aphididae, Thelaxidae or Callaphididae (T. Wappler, Bonn, personal communication).

Remarks—Despite the insufficient preservation of the oblanceolate leaves, we think it is likely that they derive from the main stem of *A. obovatum*. This is supported by the proximity of the leaves to the main stem, but also by the presence of expanded leaves in *A. viscoides* and *A. johnianum*, indicating that this kind of foliage occurred in the fossil lineage of *Arceuthobium*.

A. obovatum is distinct from extant *Arceuthobium* species in the presence of expanded leaves, the large distal portion of the total fruit length (74–88%), the non-fused squamate bracts and the small size of fruits. *A. obovatum* can be distinguished from other fossil *Arceuthobium* species in the fruit shape, the shallow furrowed distal fruit part, the large distal portion (74–88%) of the total fruit length and the indistinct perianth merosity (see Table 2 for comparison).

DISCUSSION

Generic assignment—The Angiosperm Phylogeny Group III (2009) embedded Viscaceae (including *Arceuthobium*) in Santalaceae s.l.; however, we follow Kuijt (2015) and Nickrent et al. (2010) in treating Viscaceae as a distinct family, which is justified by its monophyly and its morphology (e.g. unisexual flowers, paired phyllotaxy; Kuijt, 2015), that distinguishes Viscaceae from all other clades of Santalaceae s.l.

Viscaceae encompass seven genera: *Arceuthobium*, *Dendrophthora* Eichler, *Ginalloa* Korth., *Korthalsella* Tiegh., *Notothixos* Oliv., *Phoradendron* Nutt. and *Viscum* L. (Kuijt, 2015). Except for *Arceuthobium*, all genera of Viscaceae can be distinguished from the Baltic amber inclusions of this paper in the following features: the internode morphology (compressed, flattened in *Korthalsella*; flattened, terete or succulent in squamate leaved *Viscum* species; tomentose in *Notothixos*), the morphology of fruits and inflorescences (sunken, sessile flowers and fruits in *Dendrophthora* and *Phoradendron*; terminal monoecious inflorescences with fan-shaped pedunculate flower units in *Notothixos*; inflorescence that is a flabellate dichasium and non-petiolate fruits in *Viscum*; monoecious flower triads or single flowers in *Ginalloa*) and the sympodial branching in most *Viscum* species (Heide-Jørgensen, 2008; Kuijt, 2015).

The extant genus *Arceuthobium* comprises shrubs and herbs, ranging in height from 0.5–70 cm. The stems have secondary growth and decussate or flabellate branching. Side branches derive from axillary buds that occur in pairs at nodes below where flowers arise. The entire stem is composed of internode segments whose cross sections are four-angled basipetally and angular throughout the entire segment. Rarely, the internode cross section may be terete towards the upper part of the internode. The leaves are reduced to minute entire bract-like leaves which are fused into a cup-like structure, surrounding the stem at each node. The decussate phyllotaxis of these reduced leaves distinguishes *Arceuthobium* from all other genera/lineages of mistletoes. The pistillate flowers are epigynous with only one style. The persistent perianth segments are 2-merous and enclose the style, so that only the stigma is exposed. Sepals are adnate to the 1-chambered ovary and persist at the distal end of the fruit during maturation. The proximal portion of the fruit is light and finely ribbed, while the distal portion with its adnate sepals is dark and folded. This results in a division of the entire structure into proximal and distal portions separated by a so-called junction line. The distal portion comprises between 21–45 % of the total fruit length. The pedicellate fruits are ovoid, oblong or elliptic in shape and decussately arranged (rarely whorled) (Gill, 1935; Kuijt, 1955; Hawksworth and Wiens, 1972, 1996c, d; Wilson and Calvin, 1996; Ziegler and Ross Friedman, 2017).

Due to the extreme morphological reduction in *Arceuthobium*, the distinction among species is challenging and is mostly based on quantitative features, such as plant size, dimensions of the third internode and relative sizes of the proximal and distal fruit portions (Hawksworth and Wiens, 1972; Nickrent et al., 2004). Also the shoot and fruit color, as well as the staminate and pistillate flower morphology,

phenology and host plant can help to distinguish among species (Hawksworth and Wiens, 1996b). Some of these characters are not detectable in amber fossils; however, the comparison of vegetative features and fruit morphologies to extant *Arceuthobium* is possible (see Table 2).

Specimens from Baltic amber and extant dwarf mistletoes share a shoot structure that is comprised of angular and rarely terete internode segments. The branching pattern is only preserved in *Arceuthobium johnianum* (decussate branching, Fig. 1D) and in *A. viscoides* (verticillate branching, Figs. 7A, D; 9A, D). In extant dwarf mistletoes, primary branching is decussate, while secondary branching is either verticillate or flabellate (Hawksworth and Wiens, 1996d). Thus, the branching pattern of the named fossils is consistent with extant dwarf mistletoes, although it is impossible to assert if the fossils show primary or secondary branching. The pairwise arrangement of axillary buds in *A. viscoides* (Figs. 5D; 6D; 7B; 8C) is also in congruence with extant dwarf mistletoes, as this was observed by Wilson and Calvin (1996) in extant *Arceuthobium* (Table 2).

The squamate, cuspidate bracts, which are decussately arranged, are present in extant dwarf mistletoes and amber fossils (Figs. 1C, K; 2B; 4A; 8B; 9A; 10A). However, contrary to fossil *Arceuthobium* species, squamate bracts of extant dwarf mistletoes are fused at the base and extend along the internode, resulting in a broadening of the upper internode (Wilson and Calvin, 1996). The presence of expanded leaves (e.g. Figs. 7A; 9A) is also unknown in extant *Arceuthobium* species.

The fruits of both Eocene and extant *Arceuthobium* species are ovoid, oblong or elliptic (e.g. Figs. 2E, 4B, 8F, 10B) and terminate at their distal end in the adnate perianth which surrounds a short style with a single, lobed and papillous stigma (Figs. 1J; 2G, H; 4C, E; 8E; 10D). As already mentioned, extant *Arceuthobium* fruits show a clear division into an upper (distal) and lower (proximal) part (Wilson and Calvin, 1996; Ziegler and Ross Friedman, 2017). This clear division is also present in fruits of fossil species *A. johnianum* (Fig. 1F, G), *A. mengeanum* (Fig. 1L, M), *A. viscoides* (only in specimen GZG.BST.21950, Fig. 8F, G) and *A. conwentzii* (Fig. 2D, E), although the distal portion of the total fruit in fossil *Arceuthobium* species is larger (45–88 %) when compared to extant dwarf mistletoes (21–45 %) (Table 2; Hawksworth and Wiens, 1972). Fruits of *A. obovatum* also exhibit a fruit division, however, it is not as distinct as in the other four species (Fig. 10B). Also, the distal portion of the fruits in *A. obovatum* is quite large, encompassing 74–88% of the total fruit length. We suggest that the partly indistinct fruit division as well as the large distal portion observed in *A. obovatum* is due to the immaturity of these fruits, which is also indicated by their straight pedicels. In extant dwarf mistletoes, the fruit pedicel is erect and the junction line is still indistinct during the first year of fruit maturation, while only ripe fruits possess an elongated recurved pedicel whereby the distal fruit end points downwards (Gill, 1935; Kuijt, 1955; Hinds et al., 1963; Ziegler and Ross Friedman, 2017).

Tab. 2: Comparison of extant *Arceuthobium* to the dwarf mistletoe inclusions from Baltic amber. Certain features that were not visible or absent are indicated by -, the presence of features is indicated by +. Information about extant *Arceuthobium* were taken from Gill (1935), Kuijt (1955, 2015), Hawksworth and Wiens (1972, 1996b, c, d) and Wilson and Calvin (1996). Information about *A. johnianum* and *A. mengeanum* derives from Conwentz (1886a).

Morphology	Extant <i>Arceuthobium</i>	<i>A. johnianum</i>	<i>A. mengeanum</i>	<i>A. conwentzii</i>	<i>A. groehnii</i>	<i>A. viscoides</i>	<i>A. viscoides</i>	<i>A. obovatum</i>			
Collection number	-	-	-	GZG.BST.24548	GPIH 4582	MB.Pb.1981-2	GZG.BST.21950	GZG.BST.24359			
Stem											
Internodes	angular, rarely terete	terete	terete-angular	angular, furrowed	angular, furrowed	angular, furrowed	angular, furrowed	angular, furrowed			
Length (mm)	1-≥17 (third)	-	-	2.8-3.7	1-1.7	1.1-3.1	1.4-5.2	0.6-2			
Width (mm)	≤1-6 (third internode)	-	-	0.5-0.7	0.7-0.8	0.4-0.5	0.2-0.4	0.7			
Branching type	primary: decussate secondary: flabellate to verticillate	decussate	-	-	-	-	verticillate	-			
Leaf and bract anatomy											
Expanded leaves	-	+	-	-	-	+	+	+			
Shape	squamate, cuspidate	squamate, broadly-ovate	linear-oblongate	squamate, broadly-ovate	squamate, rhombic	squamate, widely obtusulate	oblongate	squamate, widely trullate	oblongate	squamate, widely trullate	oblongate
Margin	entire	entire	entire	entire	entire	dentate	entire	dentate	entire	dentate	-
Phyllotaxis	decussate	decussate	decussate	decussate	decussate	decussate	decussate	decussate	decussate	decussate	-
Fused base	+	-	-	-	-	-	-	-	-	-	-
Size											
Length (mm)	-	-	-	-	0.8-1.2	0.7-0.9	2.2-2.3	0.7	1.2-2.3	0.7	1.8-2.2
Width (mm)	-	-	-	-	1.1-1.6	1.1-1.3	0.4-0.6	1	0.2-0.6	1	0.5-0.9
Fruit anatomy											
Shape	ovoid, oblong, elliptic	widely obovate	elongated-elliptic	elliptic	elliptic	-	-	elliptic	-	widely obovate	-
Perianth	2-merous	4-merous	4-merous	3-merous	3-merous	-	-	-	-	-	-
No. of fruits/node	-	> 3	> 4	7-8	6	-	-	> 3	-	6	-
Fruit arrangement	decussate, rarely	whorled	whorled	whorled	whorled	whorled	-	whorled	-	whorled	-
Size											
Length (mm)	2-15	-	3.4-4	1.4-2.2	> 0.5-0.9, base covered	-	-	0.6-0.9	-	0.6-1	-
Width (mm)	-	-	-	0.6-1.1	0.3-0.8	-	-	0.3	-	0.5-0.9	-
Pedicellate	+	+	+	+	+	-	-	+	-	+	-
Division	+	+	+	+	+	-	-	+	-	+	-
Distal portion % of total fruit	21-45	≥ 50	25-50	45-68	-	-	-	59	-	74-88	-
Epidermis											
Distal portion	dark, folded	-	dark, folded	deeply wrinkled	rectangular to polygonal cells, smooth	-	-	deeply wrinkled	-	shallow furrowed	-
Proximal	light, finely ribbed	-	light	finely ribbed	-	-	-	finely ribbed	-	finely ribbed	-
Stigma											
Papillae	entire or 2-4-lobed	nonlobed	5-lobed	2-4-lobed	2-3-lobed	-	-	2-lobed	-	2-3-lobed	-
Papillae	+	-	-	+	+	-	-	+	-	+	-
Stomata											
Distribution											
Stem	highest density on distal	-	-	-	regularly distributed	-	-	regularly distributed	-	regularly distributed	-

Tab. 2 continued

Bracts/expanded leaves										
Abaxial	abundant	-	-	-	+	-	-	+	+	+
Adaxial	sparse to absent	-	-	-	-	-	-	-	-	-
Fruits	distal	-	-	distal	regularly distributed	-	-	-	-	distal
Longitudinal orientation										
Fruits and	perpendicular	-	-	perpendicular	perpendicular-oblique	-	-	perpendicular	-	perpendicular
Bracts/expanded leaves	perpendicular	-	-	-	perpendicular	-	-	undefined	-	perpendicular
Sunken	+	-	-	-	only on the stem	-	-	-	-	-
Subsidiary cells	paracytic	-	-	paracytic	paracytic	-	-	-	-	paracytic

The absence of two distinct zones in the fruits of *A. groehnii* (Fig. 4B) is possibly due to immaturity as well. As already described, the majority of the fruits observed in *A. groehnii* (Fig. 4B) are still covered by squamate bracts that conceal more than half of the fruit and thus further morphological features such as a possible junction line. All fruits of *A. groehnii* are erect, indicating an early stage of fruit maturation as already described above. Thus we interpret the absent fruit division as well as the erect fruit orientation as a sign of immaturity in this species as well. This view is also supported by preservation of the *A. conwentzii* fossil, which has besides divided large fruits, a few very small fruits (0.4–0.7 mm long \times 0.4–0.6 mm wide; see Fig. 2C, F). The smaller fruits do not exhibit a division into two distinct zones, and are likely immature or were even not fertilized.

Generally, the fruits of the fossil dwarf mistletoes are shorter (0.5–4 mm) than modern *Arceuthobium* taxa (2–15 mm; Table 2). This may be related to the immaturity of the fossils, but also can be due to shrinkage processes during fossilization.

Although none of the amber specimens possesses pistillate flowers, the adnate perianth is preserved in *A. conwentzii* and is visible at the distal end of the fruit. The perianth has three sepal lobes (3-merous) that slightly overarch the base of the style in some fruits (Fig. 2G). Conwentz (1886a) observed 4-merous perianths for *A. mengeanum* and *A. johnianum* (Fig. 1E, I). The perianth segments of extant *Arceuthobium* species are also persistent on the fruit body, but are usually 2-merous (Hawksworth and Wiens, 1996c). However, 3-merous perianths occur, but very rarely, in some extant *Arceuthobium* species, such as *A. vaginatum* (Humb. & Bonpl. ex Willd.) J. Presl and *A. pusillum* Peck (Gill, 1935; Kuijt, 1955); 4-merous pistillate perianths are not reported from any extant dwarf mistletoe.

The perianth merosity in the remaining amber specimens is either not visible due to the poor preservation (*A. viscoides*) or is indistinct, as in *A. obovatum* and *A. groehnii*, likely due to immaturity (as discussed above).

Some extant *Arceuthobium* species exhibit a rounded receptacle at the distal end of the pedicel that forms a ring-like structure at the fruit base (Hawksworth and Wiens, 1972). This is also visible in amber specimens (Figs. 1F, L, M; 2D, E; 8F; 10B), except *A. groehnii* where the basal portion of fruits is concealed by bracts.

The stomatal distribution in combination with their distinctive morphology characterizes extant *Arceuthobium* species. Stomata are orientated perpendicular to the longitudinal plant axis and are overarched by the paracytic subsidiary cells which project above the sunken guard cells (Metcalf and Chalk, 1950; Wilson and Calvin, 1996). The stomatal distribution in extant dwarf mistletoes is unique, since on fruits, only the distal portion, with its adnate sepals, has stomata. For extant *Arceuthobium* species, stomatal concentration is highest on the distal third of internodes, which is adjacent to and below the node with its squamate bract or bract-like leaf pair. This area of high stomatal abundance corresponds to the extended bract or leaf base that is fused with the stem. The extension of the base along the internode is likely the reason for the different distributional densities, since the lower internode segments only possess few stomata (Wilson and Calvin, 1996).

In cases of sufficient cuticle preservation in amber specimens, the same stomatal morphology as in extant dwarf mistletoes was observed (e.g. Figs. 2I, 4H, 6H, 10F–H; Table 2), although stomata on the fruits appear to be relatively shallow and not deeply sunken as in extant *Arceuthobium* species (e.g. in *A. groehnii*, Fig. 4D, F, G).

Regarding the stomatal distribution, *Arceuthobium conwentzii* and *A. obovatum* are similar to extant *Arceuthobium* in having the proximal fruit portion devoid of stomata, while the distal part possesses stomata. However, the internodes of all fossil *Arceuthobium* specimens (inflorescences) do not show a stomatal concentration in the upper third of the internode as in the extant species (Wilson and Calvin, 1996), but rather a regular distribution along the whole internode (Table 2). The reason for the regular stomata distribution on the internodes may be the absence of a fused and extended bract base.

A specific feature of Viscaceae is the cuticular epithelium, a thick layer that is formed by epidermal and subepidermal cells. So-called cuticular pegs develop between epidermal cells, shifting them apart from each other. The epidermal cells become isolated within the cuticular epithelium, but continue to expand with the increase in stem circumference. These elongate, isolated cells embedded in the cuticular material are a typical feature of a cuticular epithelium (Wilson and Calvin, 1996, 2003). Fruits of *Arceuthobium conwentzii* show structures similar to cuticular pegs, as well as elongate isolated cells within the cuticular layer (Fig. 3A, B), indicating that a cuticular epithelium eventually covered the fruit body.

In *Arceuthobium obovatum*, epidermal cells of the shoots form a conspicuous arc-like pattern (Fig. 3C, D). The arc of cells suggests that these sets of cells were shifting apart from each other and from other adjacent set of sister cells. This arc-like pattern could be explained by the formation of pegs of the cuticular epithelium, which would assist this process.

Summarizing, all amber specimens and extant *Arceuthobium* share at least four of the following relevant features (Table 2): (1) decussate phyllotaxis, (2) squamate bracts, (3) branching type (either decussate or verticillate), (4) angular internode cross section, (5) pedicellate fruits and their whorled arrangement at each node, (6) fruit shape, (7) fruit division into two portions, (8) stigma morphology, (9) cuticular epithelium, and/or (10) stomata characteristics, including their perpendicular orientation and their distinct distribution on fruits.

Differences between extant dwarf mistletoes and *Arceuthobium* fossils include at least the first two of the following features (Table 2): (1) squamate bracts are not fused and their bases do not extend along internodes, (2) regular stomatal distribution along internodes, (3) presence of expanded leaves, (4) 4-merous perianth, and (5) shorter length of fruits.

Fossil record of *Arceuthobium*—The fossils of *Arceuthobium johniana* and *A. mengeana* were already discovered in the 19th century; however, their affinities to extant dwarf mistletoes were not recognized ab initio. *A. johniana* was first described as *Ephedrites johniana* Goepf. et Berendt with affinities to the Ephedraceae

(Gnetales, Gymnospermae) (Goeppert and Berendt, 1845). This specimen was later definitely assigned to the gnetalean *Ephedra* L., and a further species *Ephedra mengeana* Goepp. was discovered (Goeppert, 1853; Goeppert and Menge, 1883).

Caspary (1872) reported another Baltic amber inclusion with affinities to the Gnetales; he introduced the new fossil genus *Patzea* and named the specimen *P. gnetoides* Casp.

Conwentz (1886a) restudied the specimens of *Ephedra johniana*, *E. mengeana* and *Patzea gnetoides*, discovering their strong similarities to extant *Loranthus*, *Arceuthobium* and *Phthirusa*. According to former taxonomic treatments, he assigned all three taxa to the Loranthaceae, using Caspary's genus name *Patzea* (Conwentz, 1886a). The location of the type specimens of *Patzea mengeana*, and *P. johniana* are unknown, precluding a re-investigation of these fossils. Contrarily, Kirchheimer (1957) doubted affinities to extant *Arceuthobium*, criticizing that the position of the gynoeceum in relation to the receptacle in *Patzea* is different from extant dwarf mistletoes. Also other authors questioned the affinities of *Patzea*, as being congeneric with *Arceuthobium*, but without clarifying the precise reasons for their concerns (Łańcucka-Środoniowa, 1980; Hawksworth and Wiens, 1996a). We propose to accommodate these two fossil species in *Arceuthobium* due to the presence of squamate bracts that surround the nodes, decussate phyllotaxis, pedicellate fruits that arise from each inflorescence node, fruit shape, and, division of the fruit into a proximal and distal portion.

The oldest previously known macrofossils of *Arceuthobium* were twig remains with fruits as well as pistillate and staminate flowers that were discovered in late Miocene strata of Lower Silesia in Poland and have affinities to extant *A. oxycedri* (DC.) M. Bieb. (Łańcucka-Środoniowa, 1980). Further macrofossils belonging to extant *A. campylopodium* Engelm. are known from the Pleistocene of California (Santa Cruz Island, Carpinteria, Tomales Bay) (Chaney and Mason, 1927, 1930, 1933; Hawksworth and Wiens, 1996a). Fossils of *Arceuthobium* shoots with fruits and flowers, assigned to extant *A. abietinum* (Engelm.) Hawksw. & Wiens, *A. cyanocarpum* (A. Nelson ex Rydb.) J.M. Coult. & A. Nelson and *A. divaricatum* Engelm. were reported from Pleistocene and Holocene sediments of the southwestern United States and adjacent Mexico (Sheep Mountains, Nevada; Chaco Canyon, New Mexico; Heuco and Chisos Mountains, Texas) (Spaulding, 1977; Van Devender and Hawksworth, 1986; Hawksworth and Wiens, 1996a).

The oldest fossil pollen with affinities to *Arceuthobium* is *Spinulaepollis arceuthobioides* W. Krutzsch from the middle Eocene up to the Pliocene strata of eastern Germany, with main occurrence in the late Eocene to Miocene (Krutzsch, 1962). Further fossil pollen finds that were assigned to the same species are *S. arceuthobioides* subsp. *major* Stuchlik from the Miocene of Poland. Other European fossil pollen has been assigned to *Arceuthobium oxycedri* and derives from the Pliocene of Germany, and the Pleistocene of Spain and Greece, as well as from several Holocene localities in Greece, Poland, Spain and the former Yugoslavia (see the detailed table 5.8 of Hawksworth and Wiens, 1996a).

There are only three Miocene sites in North America with fossil pollen of *Arceuthobium*, the Alaska Range, Wyoming, and North-Central Colorado. Quaternary pollen of different *Arceuthobium* species is more abundant in several locations from western North America and Mexico (e.g. Sierra Nevada, California; Yellowstone, Wyoming; Tlaxcala and Michoacán, Mexico; see the detailed table 5.9 of Hawksworth and Wiens, 1996a).

To the best of our knowledge, the new fossil findings of dwarf mistletoes from Eocene Baltic amber represent the oldest macrofossil record of the *Arceuthobium* lineage worldwide. The Eocene occurrence of *Arceuthobium* is not only supported by the pollen finds described above, but also by phylogenetic analyses, dating the divergence of *Arceuthobium* from other Viscaceae lineages to the middle Eocene (Lutetian) (Vidal-Russell and Nickrent, 2008).

Evolutionary trends within *Arceuthobium*—Hypotheses of evolutionary tendencies of the dwarf mistletoe morphology have been developed by Gill (1935), such as reduction of shoot size, general to specific host associations and an extended fruit maturation period. Hawksworth and Wiens (1972, 1996e) corresponded these features to ancestral (= plesiomorphic) and derived (= apomorphic) species groups of *Arceuthobium* and added further evolutionary tendencies, such as the secondary branching type which they considered verticillate in ancestral and flabellate in derived dwarf mistletoe species.

However, recent phylogenetic studies of *Arceuthobium* revealed that not all of these hypothesized evolutionary trends are likely. Nickrent et al. (2004) showed that secondary verticillate branching is a symplesiomorphic character, as it occurs in the clade of Old World *Arceuthobium* species, as well as in some representatives of the genetically distinct New World species.

As the amber inclusions in our study represent the earliest macrofossils of *Arceuthobium*, they provide new insights into the morphology of the early-diverging *Arceuthobium* lineage and their ancestral traits. The presence of squamate bracts and expanded leaves is only found in the fossil *Arceuthobium* taxa. The foliage stems with oblanceolate leaves (which are absent in all extant taxa) were likely reduced during the post-Eocene evolutionary history of *Arceuthobium*, which would fit the general trend of reduction based on the parasitic life style. This was already mentioned by Vidal-Russell and Nickrent (2008) who explained that a “squamate habit” was typical for mistletoes such as *Arceuthobium*. The reduction of leaves to scale-like bracts is due to the decreased photosynthetic activity (Vidal-Russell and Nickrent, 2008), which would also explain why foliage stems with expanded leaves are no longer present in extant dwarf mistletoes.

Interestingly, presence of distinct leaf types has been described for the closest extant relatives of *Arceuthobium*: *Dendrophthora* and *Phoradendron*, Viscaceae (Kuijt, 1959; Mathiasen et al., 2008).

In early dwarf mistletoes, squamate bracts were already present but lacked fusion at their bases and to the stem internode. Reduction of expanded leaves was possibly restricted to the inflorescence, with squamate bract-like vegetative leaves

developing later. Further reductions took place resulting in the merging of squamate bract bases to a cup-like structure adnate to the internode, the concentration of stomata on the fused bract bases, and in reductions of the perianth from 4-merous to 2-merous. Another ancestral trait that is not present in living dwarf mistletoes but does occur in the amber fossils is the clear differentiation between the foliage shoot and the inflorescence, as in *Arceuthobium viscoides* and *A. johnianum*. In contrast, extant *Arceuthobium* do not exhibit specified flower-bearing shoots; in fact, they are “so expressly modified for reproductive purposes that [the shoot] might very well be regarded as an inflorescence” (Gill, 1935, p. 121).

In conclusion, the amber fossils of dwarf mistletoes clearly show features that can be interpreted as plesiomorphic characters, as they are not present in extant *Arceuthobium* taxa. These ancestral features are the lack of fusion of squamate bracts at their bases and to the internode, differences in the stomatal distribution along the internode, presence of expanded leaves and the 4-merous perianth (Table 3). Some of the morphological characters that are shared between fossil and extant dwarf mistletoes are defining features of the *Arceuthobium* clade: the decussate arrangement of bracts and divided fruits. The presence of these features justifies placing the fossils into the extant genus *Arceuthobium*. The combination of shared characters with extant Viscaceae (expanded leaves, perianth merosity, orientation of the stomata; Table 3) along with unique characters exclusively found in the *Arceuthobium* fossils argue for their position within the stem group of *Arceuthobium*. However, pre- and post-Eocene fossils would be necessary to clearly determine the position of our dwarf mistletoe fossils within their phylogenetic context.

Tab. 3: Key morphological features present in extant Viscaceae, *Arceuthobium* and in the Baltic amber fossils. Information about extant Viscaceae and *Arceuthobium* were taken from Gill (1935), Kuijt (1955, 2015), Hawksworth and Wiens (1972, 1996b) and Wilson and Calvin (1996).

Morphology	Present in most Viscaceae	Present in extant <i>Arceuthobium</i>	Found in Baltic amber fossils
Expanded leaves	yes	no	yes
Fused leaf and/or bract bases	yes	yes	no
Fruit arrangement	dichasial (2–3 flowers)	mostly decussate – rarely whorled	whorled
Perianth merosity	3–4	2	3–4
Equatorial line between distal and proximal portions of fruit	no	yes	yes
Distal portion of fruits	-	≤45%	mostly > 45%
Stomatal orientation	perpendicular	perpendicular	perpendicular (mostly)

Biogeographic implications—Extant *Arceuthobium* species are largely restricted to the Northern Hemisphere. In the Old World, this distribution encompasses the entire Mediterranean region from the Azores, Morocco, Algeria to southern Europe and the Middle East, but also Central and East Asia (Afghanistan, Pakistan, India, Nepal, Bhutan and Xizang, Yunnan and Sichuan of China) with a few disjunct populations in Eritrea, Ethiopia and Kenya. The greatest distribution and diversity however, is in the New World, especially in Mexico (Sierra Madre Occidental, Durango) and northern California (United States) with other regions from Northern to Central America (Canada, Belize, Honduras, Guatemala and San Salvador) having fewer species (Barlow, 1983; Hawksworth and Wiens, 1996a; Kuijt, 2015).

Following the study of Kuijt (1970) on branching patterns of *Arceuthobium* and based on own observations, Hawksworth and Wiens (1972) distinguished between two subgenera: *Arceuthobium* and *Vaginata*. The former mostly occurs in the Old World and is characterized by verticillate secondary branching, while the strictly American subgenus *Vaginata* is defined by flabellate secondary branching. They also regarded the genus *Korthalsella* (Viscaceae) as the closest extant taxon to *Arceuthobium*. Extant *Korthalsella* is widespread from East and South Asia to Australia and New Zealand, but also occurs in Ethiopia, Madagascar, the Comores and Mascarenes islands. Based on the idea of an arceuthoboid-korthalselloid ancestor, it was hypothesized that *Arceuthobium* originated in Northeast Asia during the late Paleogene and then migrated via the Bering land bridge to the North American continent. Hence, the western USA and Mexico would represent centers of secondary species radiation (Hawksworth and Wiens, 1972; Barlow, 1983). Nickrent (1996) suggested *Notothixos* (Viscaceae) as sister to *Arceuthobium*; since *Notothixos* has its origin and highest diversity in Asia, the migration scenario was assumed to be as described above, with *Arceuthobium* originating on the Asian continent (Hawksworth and Wiens, 1996e).

Recent phylogenetic analyses of all *Arceuthobium* taxa reduced the species number from 42 to 26 and supported the suggestion by Hawksworth and Wiens (1972) that Old and New World species are genetically distant. Based on this phylogeny and on plastome analyses, it was postulated that dwarf mistletoes originated in the New World (Nickrent et al., 2004; Nickrent and García, 2009). This second hypothesis is supported by further phylogenetic analyses of the Santalaceae that resolved *Arceuthobium* as closely related to the New World taxa *Dendrophthera* and *Phoradendron* (Viscaceae) (Nickrent et al., 2010); thus, their common ancestor possibly first occurred in North America, and then spread to other Northern Hemisphere regions (Nickrent et al., 2010).

Considering the estimated divergence time of the *Arceuthobium* lineage of 42 Ma and its occurrence in the late Eocene of Central Europe, a Laurasian origin during the Eocene seems more likely, meaning that the first scenario fits better with our new fossil evidence. However, the new fossil evidence does not exclude the second hypothesis either because the *Arceuthobium* lineage could have originated in

the New World approximately 42 million years ago and from the New World spread across Laurasia.

Ecology and paleoecology of Arceuthobium species—Mistletoes (including *Arceuthobium* subspecies) are stem hemiparasites which depend in different degrees on a host plant (Calder, 1983; Aukema, 2003). With a specialized endophytic structure, the haustorium, mistletoes invade the host xylem in order to extract nutrients, and water, and in the case of *Arceuthobium*, photosynthates also (Hull and Leonard, 1964; Calder, 1983). However, the term “mistletoe” only refers to the life style and not to a particular evolutionary lineage (Aukema, 2003; Nickrent, 2011). In extant *Arceuthobium*, hosts exclusively encompass conifer taxa of the Pinaceae [*Pinus* L., *Abies* Miller, *Picea* A. Deitr, *Larix* Mill., *Tsuga* (Endl.) Carrière, *Pseudotsuga* Carrière, *Keteleeria* Carrière] and Cupressaceae (*Juniperus* L. and *Cupressus* L.) (Hawksworth and Wiens, 1972; Geils and Hawksworth, 2002; Kuijt, 2015). This raises the questions whether the ancient *Arceuthobium* taxa from Baltic amber were also parasitic, and how they influenced their ecosystem. Remains of an endophytic system, which would be direct evidence for parasitism, are not preserved in the amber specimens. However, the small size and reduced morphology of amber fossils are in congruence with extant *Arceuthobium* species and can be interpreted as morphological adaptation to a parasitic life style.

A very specific ecological trait of extant *Arceuthobium* is their seed dispersal, a hydrostatically controlled and thermogenetically triggered explosive mechanism (Hinds et al., 1963; Hinds and Hawksworth, 1965; DeBruyn et al., 2015). A viscous layer surrounding the seed accumulates hydrostatic pressure, when the surface temperature increases. On reaching the greatest pressure and temperature, the exocarp contracts and the seed discharges in a maximal velocity of 2600 cm/s, reaching distances of up to 16 m (Hinds et al., 1963; Hinds and Hawksworth, 1965; Hawksworth and Wiens, 1996d; Ross Friedman and Sumner, 2009; DeBruyn et al., 2015).

This specific seed release mechanism is reflected in the morphology of their fruits and pedicels. Besides the viscous cell layer surrounding the seed, the stomatal density on the distal fruit part is of great significance for releasing the seed. The density of the stomata declines with fruit maturation and thus, minimizes water loss of the fruit, contributing indirectly to an increasing hydrostatic pressure of the entire fruit (Ziegler and Ross Friedman, 2017). The repositioning of the pedicel from erect to recurve improves the height and distance for the final explosive seed discharge (Hinds et al., 1963).

We could not detect a viscin layer in any of the fossils. Although the stomata morphology of the fossils is identical to extant dwarf mistletoes, it is impossible to reconstruct the stomata density of the fossils in reference to fruit maturation. Thus, there is no direct evidence in the fossils for an explosive seed discharge mechanism. However, these fossils show very specific features to prevent water loss, such as the cuticular epithelium on the fruit body and the stomata restriction to the distal fruit

part. In extant dwarf mistletoes, all the features mentioned indirectly facilitate an increased hydrostatic pressure, which is necessary for seed discharge.

Probable host trees were definitely present in the Baltic amber source vegetation as confirmed by needle and twig fragment inclusions of Pinaceae and Cupressaceae (Conwentz, 1886b, 1890; Caspary and Klebs, 1907; Czecczott, 1961; Sadowski et al., in press). On a specimen of *A. groehnii* we found pinaceous pollen attached to the internode (Fig. 4I) that indicates a certain proximity to conifers of the Pinaceae.

Further evidence for the parasitism of the ancient *Arceuthobium* taxa is given by Nickrent (2011) and Nickrent et al. (2010), who showed that except for three early-diverging groups, all clades of the Santalales are parasitic and all Viscaceae are branch hemiparasites (mistletoes). Thus, it is very likely that these *Arceuthobium* taxa from Baltic amber were also mistletoes, and hence represent the first unambiguous evidence for plant hemiparasitism in the Baltic amber flora.

The presence of diverse dwarf mistletoes in the Baltic amber source vegetation must have had a major impact on the habitat, as in modern forests when Viscaceae are present. Mathiasen (1996) pointed out that dwarf mistletoes variously influence their environment. For instance, *Arceuthobium* infections induce “witches brooms” in the host which are malformations of the branches, resulting in excessive branching (Tinnin et al., 1982; Geils and Hawksworth, 2002). These brooms influence the growth of the host, as well as its crown shape, especially when very large brooms and their host branches break off. *Arceuthobium* infections also raise the mortality rate of the host trees, resulting in dead trees, snags and tree gaps that contribute to changes in the canopy structure (Mathiasen, 1996; Geils and Hawksworth, 2002; Godfree et al., 2003). It is likely that fossil *Arceuthobium* taxa had similar effects on their host trees, raising the complexity of the Baltic amber vegetation structure. Extant host branches with dwarf mistletoe infections induce excess resin exudation (Geils and Hawksworth, 2002), which also should be considered when discussing the reasons for the formation of the Baltic amber deposit.

Although dwarf mistletoes are often considered destructive, they also serve as an important constituent of their present ecosystem, and on a longer term they increase species diversity of forests. Hence, they are considered to be ecological keystones, “whose effect is large, and disproportionately large relative to its abundance” (Power et al., 1996, p. 609).

Dwarf mistletoes increase the structural diversity of the canopy and thus, positively influence arthropod abundance and diversity because they serve as forage sites for several arthropod groups, such as mites and spiders (Hawksworth and Geils, 1996; Mathiasen, 1996; Halaj et al., 2000). Numerous insect taxa are specific to dwarf mistletoes and feed on their shoots. Examples are larvae of the lepidopteran *Filatima natalis* Heinrich, but also bugs (*Neoborella tumida* Knight) and several species of Coleoptera and Thysanoptera (Hawksworth and Geils, 1996; Mathiasen, 1996; Halaj et al., 2000; Shaw et al., 2004). Therefore, it is very likely that the numerous fossil *Arceuthobium* species may have had a comparable influence on the

high number of arthropod taxa that are known from Baltic amber (Weitschat and Wichard, 2010).

The dwarf mistletoe brooms are used as nests for numerous birds and small mammals, and their fruits, flowers and foliage also serve as important nutritional sources, especially in winter when many other resources are unavailable (Mathiasen, 1996; Parks et al., 1999; Watson, 2001; Hedwall and Mathiasen, 2006; Watson and Herring, 2012). Several studies demonstrated that dwarf mistletoes increase avian diversity (Bennetts et al., 1996; Watson, 2001) and that of mammals, such as red squirrels (*Tamiasciurus hudsonicus* Erxleben), the American marten (*Martes americana* Turton) and woodrats (*Neotoma cinerea* Ord) are associated with these parasitic plants (see Shaw et al., 2004 for an exhaustive list of wildlife interactions). We cannot specify possible interactions of the fossil *Arceuthobium* species with mammals; however, it is probable that the high diversity of dwarf mistletoes in the source area of the Baltic amber significantly influenced the ecosystem complexity. Thus, the presence of at least six species of dwarf mistletoes in the Baltic amber source vegetation very likely had similar effects as in modern forests, resulting in increased small-scale to large-scale habitat heterogeneity.

In the most recent studies by Sadowski et al. (2016a, in press), this habitat heterogeneity was already suggested based on plant inclusions from Baltic amber which served as “key-taxa”, showing the presence of coastal and back swamps, riparian forests and mixed-mesophytic conifer-angiosperm forests. Open areas likely intermingled with the “Baltic amber forest”, indicated by inclusions of graminids and carnivorous plants (Sadowski et al., 2015, 2016b). Due to their strong influence on the canopy structure, dwarf mistletoes from Baltic amber support this evidence of the presence of light and open areas within the “Baltic amber forest”.

Conclusions—Baltic amber inclusions of dwarf mistletoes represent the oldest fossils of *Arceuthobium* so far and give valuable insight into their evolutionary history. The fossils share the following key features with extant *Arceuthobium*: (1) decussate phyllotaxis, (2) squamate bracts, (3) branching type (either decussate or verticillate), (4) angular internode cross section, (5) pedicellate fruits and their whorled arrangement at each node, (6) fruit shape, (7) fruit division into two portions, (8) stigma morphology, (9) cuticular epithelium, and/or (10) stomata characteristic, including their perpendicular orientation and their distinct distribution on fruits.

Morphological differences between the fossils and extant representatives are interpreted as ancestral traits (plesiomorphies) of the *Arceuthobium* lineage, comprising (1) presence of expanded leaves, as well as bracts, (2) the differentiation between the foliage shoot and the inflorescence, (3) the lack of fusion of squamate bracts at their bases and to the internode, and (4) a 4-merous perianth. These ancestral morphologies changed over time, possibly as further adaptations to the parasitic life style, leading to the disappearance of shoots with expanded leaves, to merged cup-like bracts in the inflorescence and to a 2-merous perianth in extant *Arceuthobium* taxa.

This study of fossil dwarf mistletoes from Baltic amber clearly enhances the picture of the “Baltic amber forest”, indicating the presence of aerial parasites which served as habitat structure modifiers. The presence of dwarf mistletoes highlights the paleoecological complexity of the “Baltic amber forest”, but also raise the question about dwarf mistletoes being possible triggers for enhanced resin exudation.

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LITERATURE CITED

- ANGIOSPERM PHYLOGENY GROUP III. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society* 161: 105-121.
- AUKEMA, J. E. 2003. Vectors, viscin, and Viscaceae: mistletoes as parasites, mutualists, and resources. *Frontiers in Ecology and the Environment* 1: 212-219.
- BARLOW, B. A. 1983. Biogeography of Loranthaceae and Viscaceae. In D. M. Calder AND P. Bernhardt [eds.], *The biology of mistletoes*, 19-46. Academic Press, Sydney, Australia.
- BENNETTS, R. E., G. C. WHITE, F. G. HAWKSWORTH, AND S. E. SEVERS. 1996. The influence of dwarf mistletoe on bird communities in Colorado ponderosa pine forests. *Ecological Applications* 6: 899-909.
- CALDER, D. M. 1983. Mistletoes in focus: an introduction. In D. M. Calder AND P. Bernhardt [eds.], *The biology of mistletoes*, 1-18. Academic Press, Sydney, Australia.
- CASPARY, R. 1872. Pflanzliche Bernsteineinschlüsse, Privatsitzung am 1. November. *Schriften der Königlichen Physikalisch-Ökonomischen Gesellschaft zu Königsberg*, XIII. Jahrgang, Sitzungsberichte, p. 20. Commission, Königsberg.
- CASPARY, R., AND R. KLEBS. 1907. *Die Flora des Bernsteins und anderer fossiler Harze des ostpreußischen Tertiärs*, Band I, 1-181. Königlich Preußische Geologische Landesanstalt Berlin, Germany.

- CHANEY, R. W., AND H. L. MASON. 1927. Fossil plants. *Science* 66: 156-157.
- CHANEY, R. W., AND H. L. MASON. 1930. A Pleistocene flora from Santa Cruz Island, California. Studies of the Pleistocene Palaeobotany of California, Publication 415, 1-24, Contributions to Palaeontology, Carnegie Institution of Washington, Washington D.C., USA.
- CHANEY, R. W., AND H. L. MASON. 1933. A Pleistocene flora from the asphalt deposits at Carpinteria, California. Studies of the Pleistocene Palaeobotany of California, Publication 415, 45-79. Contributions to Palaeontology, Carnegie Institution of Washington, Washington D.C., USA.
- CONWENTZ, H. 1886a. Die Angiospermen des Bernsteins. In H. R. Goepfert AND A. Menge [eds.], Die Flora des Bernsteins und ihre Beziehungen zur Flora der Tertiärformation und der Gegenwart, vol. 2, 1-140. Engelmann, Danzig.
- CONWENTZ, H. 1886b. Die Bernsteinfichte. *Berichte der Deutschen Botanischen Gesellschaft* 4: 375-377.
- CONWENTZ, H. 1890. Monographie der baltischen Bernsteinbäume: vergleichende Untersuchungen über die Vegetationsorgane und Blüten, sowie über das Harz und die Krankheiten der baltischen Bernsteinbäume, 1-151. Engelmann, Danzig.
- CZECZOTT, H. 1961. The flora of the Baltic amber and its age. *Prace Muzeum Ziemi* 4: 119-145.
- DEBRUYN, R. A. J., M. PAETKAU, K. A. ROSS, D. V. GODFREY, AND C. ROSS FRIEDMAN. 2015. Thermogenesis-triggered seed dispersal in dwarf mistletoe. *Nature Communications* 6: 6262.
- DRUMMOND, D. B. 1982. Timber loss estimates for the coniferous forests of the United States due to dwarf mistletoes. Forest Pest Management Methods Application Group, Rpt. 83-2, 1-24. USDA Forest Service, Fort Collins, Colorado, USA.
- GEILS, B. W., AND F. G. HAWKSWORTH. 2002. Damage, effects, and importance of dwarf mistletoes. In B. W. Geils, J. Cibrián Tovar, AND B. Moody [tech. coords.], Mistletoes of North American Conifers. General Technical Report RMRS-GTR-98, 57-65. USDA Forest Service, Rocky Mountain Research Station, Ogden, Utah, USA.
- GILL, L. S. 1935. *Arceuthobium* in the United States. *Transactions of the Connecticut Academy of Arts and Science* 32: 117-245.
- GODFREE, R. C., R. O. TINNIN, AND R. B. FORBES. 2003. Relationships between dwarf mistletoe and the canopy structure of an old-growth lodgepole pine forest in central Oregon. *Canadian Journal of Forest Research* 33: 997-1009.
- GOEPPERT, H. R., AND G. C. BERENDT. 1845. Der Bernstein und die in ihm befindlichen Pflanzenreste der Vorwelt. In G. C. Berendt [ed.], Die im Bernstein befindlichen organischen Reste der Vorwelt, vol. 1, 1-125. Nicolai, Berlin, Germany.
- GOEPPERT, H. R. 1853. Über die Bernsteinflora. Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Königlich Preußischen

- Akademie der Wissenschaften zu Berlin, 450-476. Königliche Akademie der Wissenschaften, Berlin, Germany.
- GOEPPERT, H. R., AND A. MENGE. 1883. Von den Bernstein-Coniferen, insbesondere auch in ihren Beziehungen zu den Coniferen der Gegenwart. *In* H. R. Goepfert AND A. Menge [eds.], *Die Flora des Bernsteins und ihre Beziehungen zur Flora der Tertiärformation und der Gegenwart*, vol. 1, 1-63. Engelmann, Danzig.
- HALAJ, J., D. W. ROSS, AND A. R. MOLDENKE. 2000. Importance of habitat structure to the arthropod food-web in Douglas-fir canopies. *Oikos* 90: 139-152.
- HAWKSWORTH, F. G., AND B. W. GEILS. 1996. Biotic associates. *In* F. G. Hawksworth AND D. Wiens [eds.], *Dwarf Mistletoes: Biology, Pathology, and Systematics*, 73-89. USDA Forest Service Agriculture Handbook 709, Washington D.C., USA.
- HAWKSWORTH, F. G., AND D. WIENS. 1972. Biology and classification of dwarf mistletoes (*Arceuthobium*). USDA Forest Service Agriculture Handbook 401, 1-234, Washington D.C., USA.
- HAWKSWORTH, F. G., AND D. WIENS. 1996a. Biogeography and paleogeographic history. *In* F. G. Hawksworth AND D. Wiens [eds.], *Dwarf mistletoes: Biology, pathology, and systematics*, 27-41. USDA Forest Service Agriculture Handbook 709, Washington D.C., USA.
- HAWKSWORTH, F. G., AND D. WIENS. 1996b. Systematics: philosophy, problems, and criteria for classification. *In* F. G. Hawksworth AND D. Wiens [eds.], *Dwarf mistletoes: biology, pathology, and systematics*, 141-153. USDA Forest Service Agriculture Handbook 709, Washington D.C., USA.
- HAWKSWORTH, F. G., AND D. WIENS. 1996c. Formal taxonomy. *In* F. G. Hawksworth AND D. Wiens [eds.], *Dwarf Mistletoes: Biology, Pathology, and Systematics*, 173-270. USDA Forest Service Agriculture Handbook 709, Washington D.C., USA.
- HAWKSWORTH, F. G., AND D. WIENS. 1996d. Generalized life cycle. *In* F. G. Hawksworth AND D. Wiens [eds.], *Dwarf Mistletoes: Biology, Pathology, and Systematics*, 7-14. USDA Forest Service Agriculture Handbook 709, Washington D.C., USA.
- HAWKSWORTH, F. G., AND D. WIENS. 1996e. Mechanism and trends of evolution. *In* F. G. Hawksworth AND D. Wiens [eds.], *Dwarf Mistletoes: Biology, Pathology, and Systematics*, 23-26. USDA Forest Service Agriculture Handbook 709, Washington D.C., USA.
- HEDWALL, S. J., AND R. L. MATHIASSEN. 2006. Wildlife use of douglas-fir dwarf mistletoe witches' brooms in the Southwest. *Western North American Naturalist* 66: 450-455.
- HEIDE-JØRGENSEN, H. S. 2008. Parasitic Flowering Plants, 25-144. Brill, Leiden, Netherlands.
- HINDS, T. E., F. G. HAWKSWORTH, AND W. J. MCGINNIES. 1963. Seed discharge in *Arceuthobium*: a photographic study. *Science* 140: 1236-1238.

- HINDS, T. E., AND F. G. HAWKSWORTH. 1965. Seed dispersal velocity in four dwarf mistletoes. *Science* 148: 517-519.
- HULL, R. J., AND O. A. LEONARD. 1964. Physiological aspects of parasitism in mistletoes (*Arceuthobium* and *Phoradendron*). I. The carbohydrate nutrition of mistletoe. *Plant Physiology* 39: 996-1007.
- KASIŃSKI, J. R., AND R. KRAMARSKA. 2008. Sedimentary environment of amber-bearing association along the Polish-Russian Baltic coastline. *Exkursionsführer und Veröffentlichungen der Deutschen Gesellschaft für Geowissenschaften* 236: 46-57.
- KIRCHHEIMER, F. 1957. Die Laubgewächse der Braunkohlenzeit, 388-389. Wilhelm Knapp Verlag, Halle (Saale), Germany.
- KOSMOWSKA-CERANOWICZ, B., A. KOHLMAN-ADAMSKA, AND I. GRABOWSKA. 1997. Erste Ergebnisse zur Lithologie und Palynologie der bernsteinführenden Sedimente im Tagebau Primorskoje. *Metalla Sonderheft - Neue Erkenntnisse zum Bernstein* 66: 5-17.
- KRUTZSCH, W. 1962. Stratigraphically and botanically important new forms of spores and pollen from the German Tertiary. *Geologie* 11: 265-307 (in German with English summary).
- KUIJT, J. 1955. Dwarf mistletoes. *Botanical Review* 21: 569-627.
- KUIJT, J. 1959. A study of heterophylly and inflorescence structure in *Dendrophthora* and *Phoradendron* (Loranthaceae). *Acta Botanica Neerlandica* 8: 506-546.
- KUIJT, J. 1970. A systematic study of branching patterns in dwarf mistletoes (*Arceuthobium*). *Memoirs of the Torrey Botanical Club* 22: 1-38.
- KUIJT, J. 2015. Viscaceae. In K. Kubitzki [ed.], Flowering Plants. Eudicots. Santalales, Balanophorales, vol. 12, The Families and Genera of Vascular Plants 169-185. Springer, Heidelberg, Germany.
- ŁAŃCUCKA-ŚRODONIOWA, M. 1980. Macroscopic remains of the dwarf mistletoe *Arceuthobium* Bieb. (Loranthaceae) in the Neogene of Poland - Preliminary report. *Acta Palaeobotanica* 21: 61-66.
- MATHIASSEN, R. L. 1996. Dwarf mistletoes in forest canopies. *Northwest Science* 70: 61-71.
- MATHIASSEN, R. L., D. L. NICKRENT, D. C. SHAW, AND D. M. WATSON. 2008. Mistletoes: Pathology, systematics, ecology, and management. *Plant Disease* 92: 988-1006.
- METCALFE, C. R., AND L. CHALK. 1950. Anatomy of the dicotyledons - leaves, stem, and wood in relation to taxonomy with notes on economic uses, 1188-1194. Oxford University Press, London, UK.
- NASCIMBENE, P., AND H. SILVERSTEIN. 2000. The preparation of fragile Cretaceous ambers for conservation and study of organismal inclusions. In D. A. Grimaldi [ed.], Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey, 93-102. Backhuys, Leiden, Netherlands.
- NICKRENT, D. L. 1996. Molecular systematics. In F. G. Hawksworth AND D. Wiens [eds.], Dwarf Mistletoes: Biology, Pathology, and Systematics, 155-172. USDA Forest Service Agriculture Handbook 709, Washington D.C., USA.

- NICKRENT, D. L. 2011. Santalales (including mistletoes), *In* Encyclopedia of Life Sciences (ELS). John Wiley, Chichester, UK. DOI: 10.1002/9780470015902.a0003714.pub2.
- NICKRENT, D. L., AND M. A. GARCÍA. 2009. On the brink of holoparasitism: plastome evolution in dwarf mistletoes (*Arceuthobium*, Viscaceae). *Journal of Molecular Evolution* 68: 603-615.
- NICKRENT, D. L., M. A. GARCÍA, M. P. MARTÍN, AND R. L. MATHIASSEN. 2004. A phylogeny of all species of *Arceuthobium* (Viscaceae) using nuclear and chloroplast DNA sequences. *American Journal of Botany* 91: 125-138.
- NICKRENT, D. L., V. MALÉCOT, R. VIDAL-RUSSELL, AND J. P. DER. 2010. A revised classification of Santalales. *Taxon* 59: 538-558.
- PARKS, C. G., E. L. BULL, R. O. TINNIN, J. F. SHEPHERD, AND A. K. BLUMTON. 1999. Wildlife use of dwarf mistletoe brooms in Douglas-fir in Northeast Oregon. *Western Journal of Applied Forestry* 14: 100-105.
- POWER, M. E., D. TILMAN, J. A. ESTES, B. A. MENGE, W. J. BOND, L. S. MILLS, G. DAILY, et al. 1996. Challenges in the quest for keystones. *BioScience* 46: 609-620.
- ROSS FRIEDMAN, C. M., AND M. J. SUMNER. 2009. Maturation of the embryo, endosperm, and fruit of the dwarf mistletoe *Arceuthobium americanum* (Viscaceae). *International Journal of Plant Sciences* 170: 290-300.
- SADOWSKI, E.-M., L. J. SEYFULLAH, F. SADOWSKI, A. FLEISCHMANN, H. BEHLING, AND A. R. SCHMIDT. 2015. Carnivorous leaves from Baltic amber. *Proceedings of the National Academy of Sciences, USA* 112: 190-195.
- SADOWSKI, E.-M., A. R. SCHMIDT, L. KUNZMANN, C. GRÖHN, AND L. J. SEYFULLAH. 2016a. *Sciadopitys* cladodes from Eocene Baltic amber. *Botanical Journal of the Linnean Society* 180: 258-268.
- SADOWSKI, E.-M., A. R. SCHMIDT, P. J. RUDALL, D. A. SIMPSON, C. GRÖHN, J. WUNDERLICH, AND L. J. SEYFULLAH. 2016b. Graminids from Eocene Baltic amber. *Review of Palaeobotany and Palynology* 233: 161-168.
- SADOWSKI, E.-M., A. R. SCHMIDT, L. J. SEYFULLAH, AND L. KUNZMANN. In press. Conifers of the 'Baltic amber forest' and their palaeoecological significance. *Stapfia*.
- SHAW, D. C., D. M. WATSON, AND R. L. MATHIASSEN. 2004. Comparison of dwarf mistletoes (*Arceuthobium* spp., Viscaceae) in the western United States with mistletoes (*Amyema* spp., Loranthaceae) in Australia—ecological analogs and reciprocal models for ecosystem management. *Australian Journal of Botany* 52: 481-498.
- SPAULDING, W. G. 1977. Late Quaternary vegetational change in the Sheep Range, Southern Nevada. *Journal of the Arizona Academy of Science* 12: 3-8.
- STANDKE, G. 1998. Die Tertiärprofile der samländischen Bernsteinküste bei Rauschen *Schriftenreihe für Geowissenschaften* 7: 93-133 [in German with English abstract].

- STANDKE, G. 2008. Bitterfelder Bernstein gleich Baltischer Bernstein? - Eine geologische Raum- Zeit- Betrachtung und genetische Schlussfolgerungen. *Exkursionsführer und Veröffentlichungen der Deutschen Gesellschaft für Geowissenschaften* 236: 11-33 [in German with English abstract].
- TINNIN, R. O., F. G. HAWKSWORTH, AND D. M. KNUTSON. 1982. Witches' broom formation in conifers infected by *Arceuthobium* spp.: an example of parasitic impact upon community dynamics. *American Midland Naturalist* 107: 351-359.
- VAN DEVENDER, T. R., AND F. G. HAWKSWORTH. 1986. Fossil mistletoes in packrat middens from the southwestern United States. *Madroño* 33: 85-99.
- VIDAL-RUSSELL, R., AND D. L. NICKRENT. 2008. The first mistletoes: origins of aerial parasitism in Santalales. *Molecular Phylogenetics and Evolution* 47: 523-537.
- WATSON, D. M. 2001. Mistletoe - a keystone resource in forests and woodlands worldwide. *Annual Review of Ecology and Systematics* 32: 219-249.
- WATSON, D. M., AND M. HERRING. 2012. Mistletoe as a keystone resource: an experimental test. *Proceedings of the Royal Society B, Biological Sciences* 279: 3853-3860.
- WEITSCHAT, W., AND W. WICHARD. 2010. Baltic Amber. In D. Penney [ed.], *Biodiversity of fossils in amber from the major world deposits*, 80-115. Siri Scientific Press, Manchester, UK.
- WILSON, C. A., AND C. L. CALVIN. 1996. Anatomy of the dwarf mistletoe shoot system. In F. G. Hawksworth AND D. Wiens [eds.], *Dwarf Mistletoes: Biology, Pathology, and Systematics*, 95-111. USDA Forest Service Agriculture Handbook 709, Washington D.C., USA.
- WILSON, C. A., AND C. L. CALVIN. 2003. Development, taxonomic significance and ecological role of the cuticular epithelium in the Santalales. *International Association of Wood Anatomists Journal* 24: 129-138.
- ZIEGLER, D. J., AND C. M. ROSS FRIEDMAN. 2017. Morphology and stomatal density of developing *Arceuthobium americanum* (lodgepole pine dwarf mistletoe) fruit: a qualitative and quantitative analysis using “environmental” scanning electron microscopy. *Botany* 95: 347-356.