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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 zonobiome 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.

Keywords: Baltic amber age, Baltic amber flora, fossil conifers, palaeoecology.

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Die Koniferen des ‚Baltischen Bernsteinwaldes' und ihre paläoökologische Bedeutung

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 zeigt 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* waren diese Gattungen bisher noch nicht zweifelsfrei aus Baltischem Bernstein nachgewiesen worden. Die bisher als *Abies* identifizierten Inklusen 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 mit anderen eozänen Floren Europas deutet zudem auf ein späteozänes Alter des Bernsteins hin, was bisherigen Annahmen eines tropischen bis ‚subtropischen' früheozänen ‚Baltischen Bernsteinwaldes' widerspricht.

Keywords: Alter des Baltischen Bernsteins, Baltische Bernstein Flora, Fossile Koniferen, Paläoökologie.

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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, Kohlman-Adamska (2001) placed these pine-oak steppe-forests in 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 (Kohlman-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.

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; 13e 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).

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 ± 23.4° 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

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

Tab. 1: continued

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

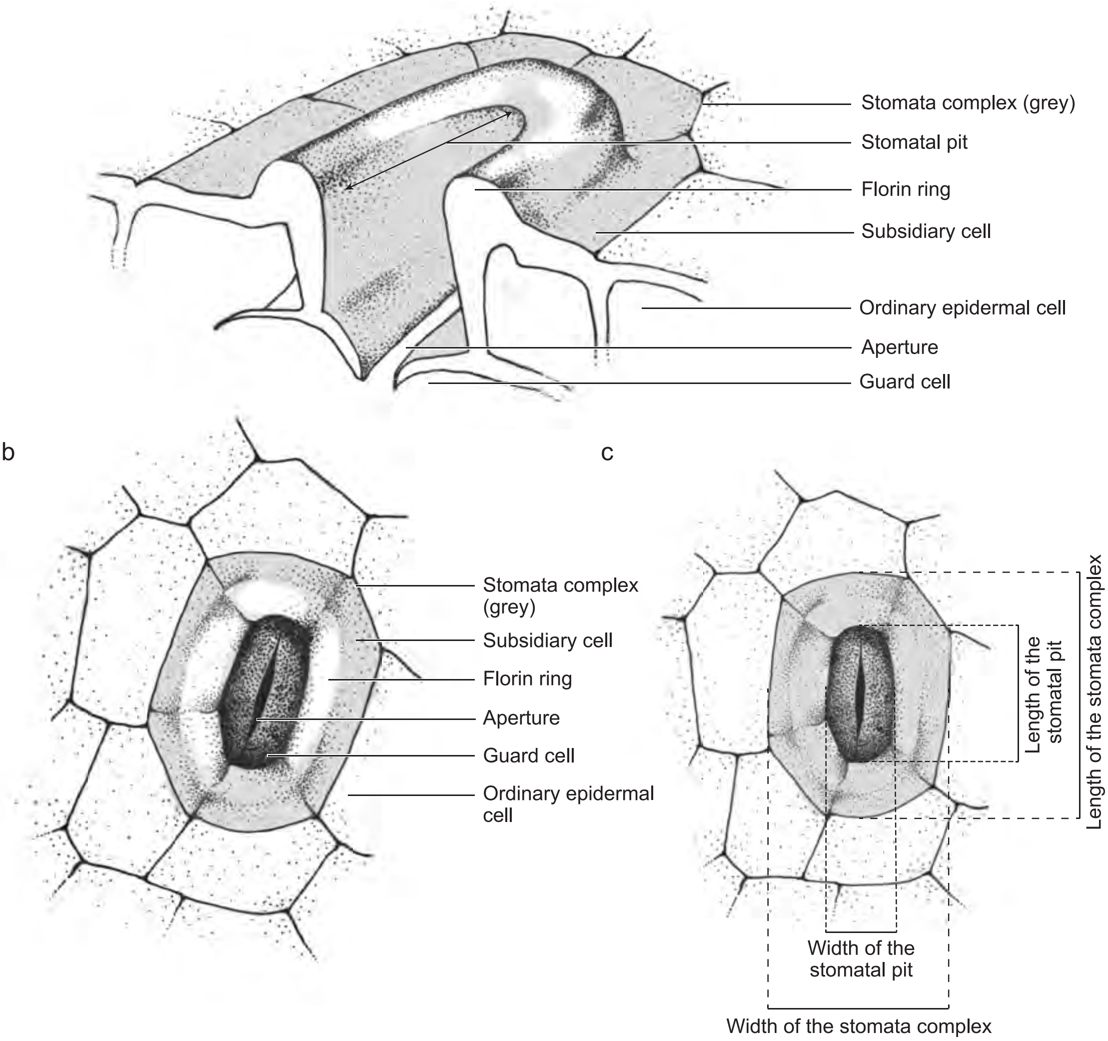

Fig. 1: Terminology of the stomata morphology used in this study (from Florin 1931 and Ewin 2004). (a) Cross section through a conifer stoma, adapted from Ewin (2004). (b) Surface view on a conifer stoma. (c) Stomata features which were measured in this study; the stomata complex is shaded in grey.

high temperatures, convectional 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° and 30.0°.

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 (2002b) 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 Palaeogene 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 × 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) × 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) × 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 µm long (average 24 µm) × 6 to 12 µm wide (average 10 µm). Ordinary epidermal cells are 96 to 192 µm long (average 140 µm) × 18 to 24 µm wide (average 20 µm), 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 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 × 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).

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.

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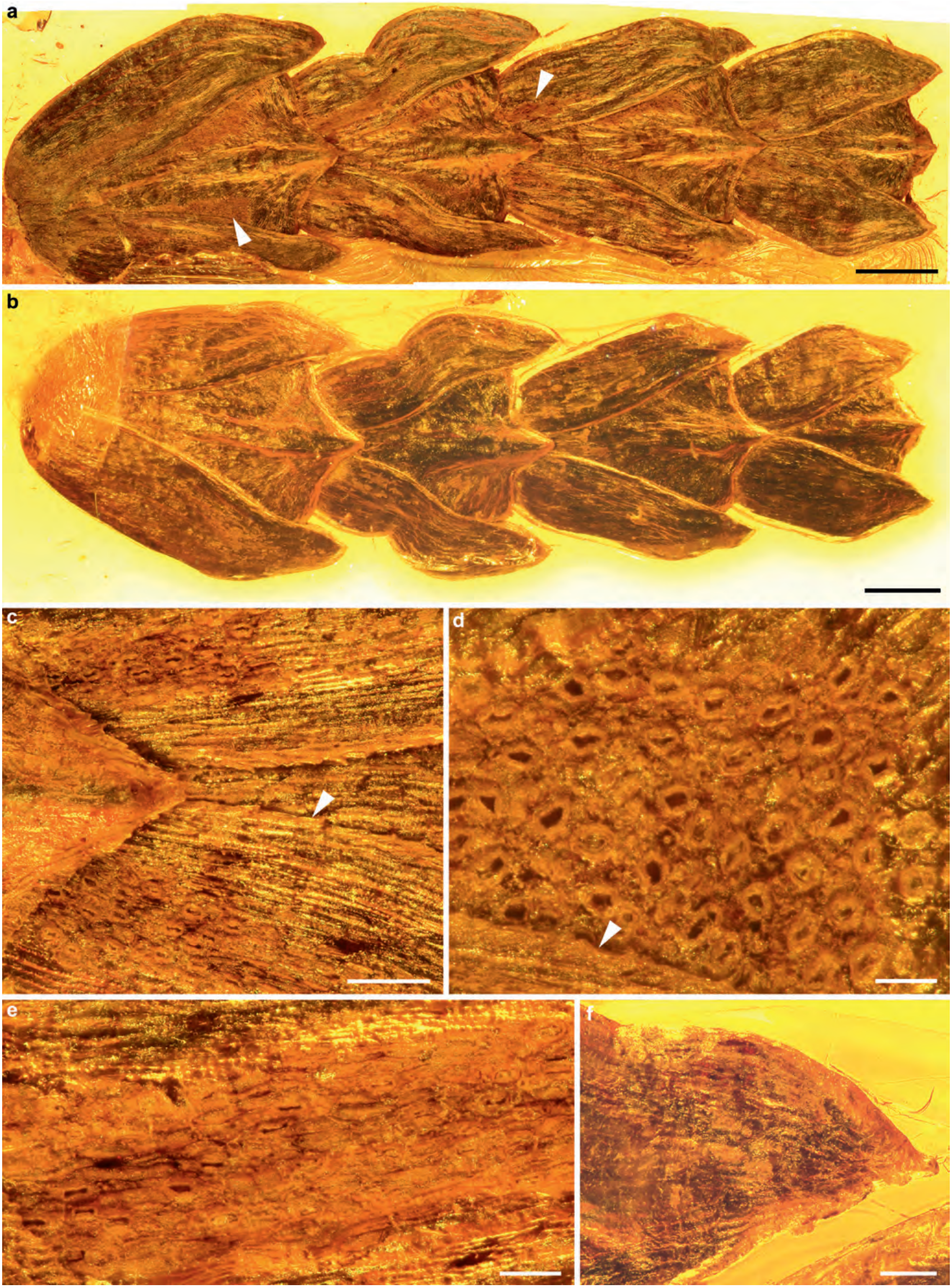
Fig. 2: Twig fragment of *Calocedrus* sp. from Baltic amber, GZG.BST.24632. (a) Lower side of the twig fragment with stomata patches (arrowheads). (b) Upper side of the twig without clear stomata patches. (c) Facial leaf tip covering the base of the lateral leaves showing scariose leaf margins (arrowhead). (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).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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 measureable (due to poor preservation) are indicated by -.

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

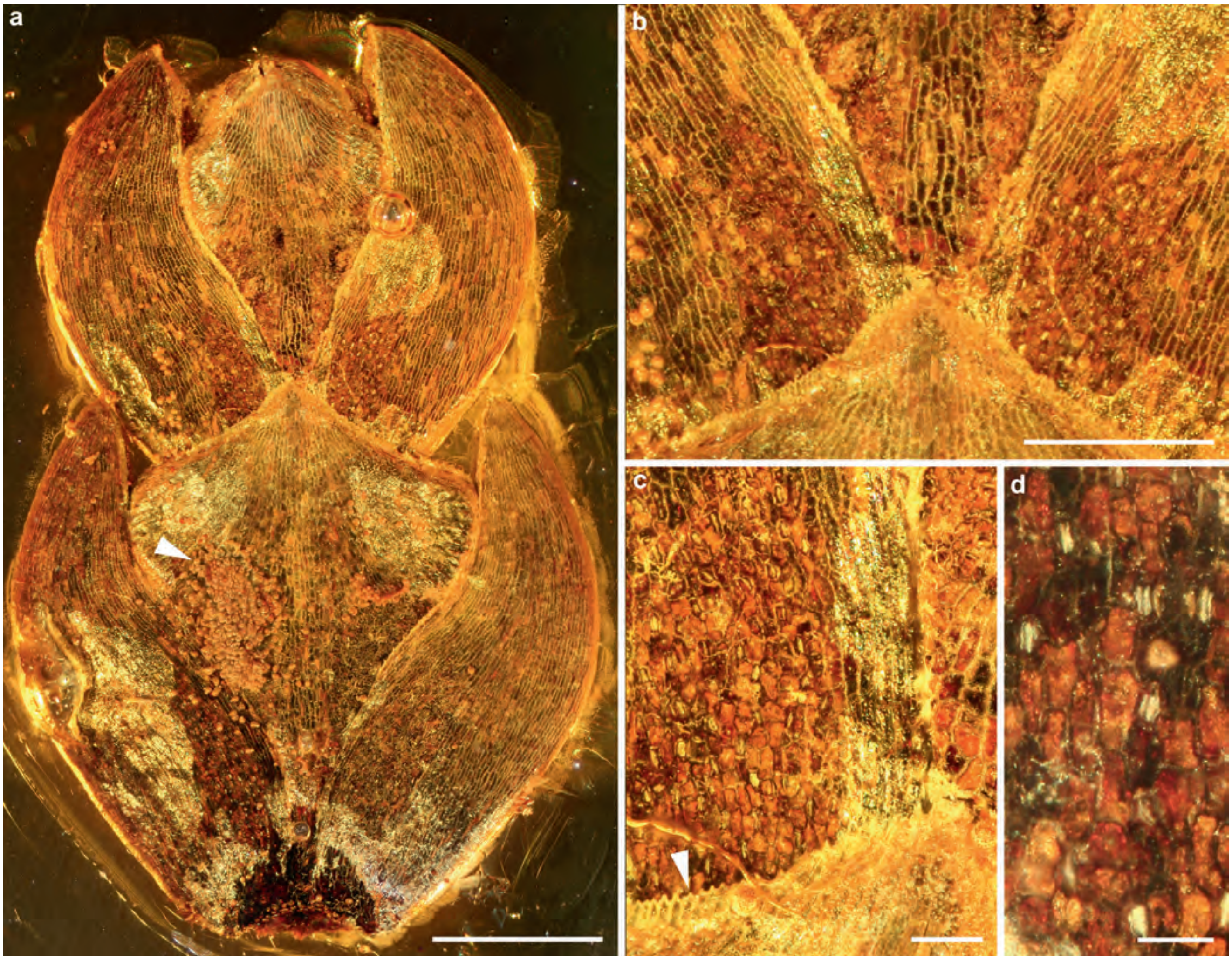

Fig. 3: Twig fragment of *Calocedrus* sp. from Baltic amber, GZG.BST.24645. (a) Underside of the twig fragment with stomata patches. Arrowhead indicates clumps of angiosperm pollen. (b) Facial leaf tip covering the base of the lateral leaves. (c) Stomata patch of one facial leaf showing the scariose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

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

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*** Sriniv. 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. L.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 × 0.5 to 0.8 mm wide; Fig. 4) or lanceolate-linear leaves (1.5 to 3.4 mm long × 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

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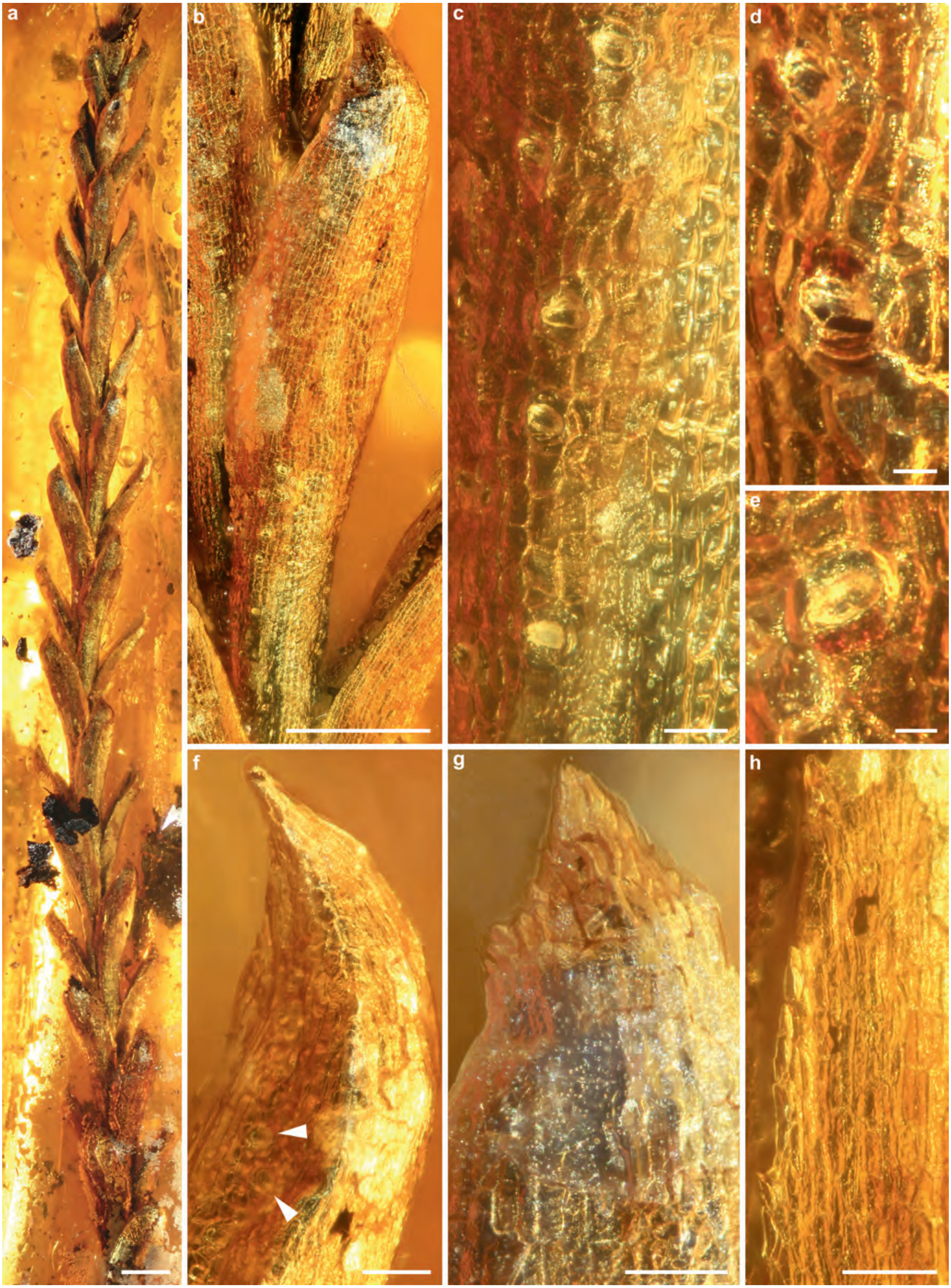
Fig. 4: Twig fragment of *Quasisequoia couttsiae* from Baltic amber, GPIH 4583. (a) Overview of the inclusion showing the spirally arranged awl-shaped leaves. (b) Abaxial leaf side showing the decurrent leaf base. (c) Short stomata row of the abaxial leaf side; note the rectangular to squared shape of ordinary epidermal cells. (d) Amphicyclocytic stomata complex on the abaxial side of leaf. (e) Cyclocytic 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) Irregular arranged acute papillae along the leaf margin. Scale bars = 1 mm (a), 500 µm (b), 50 µm (c), 20 µm (d, e), 100 µm (f-h).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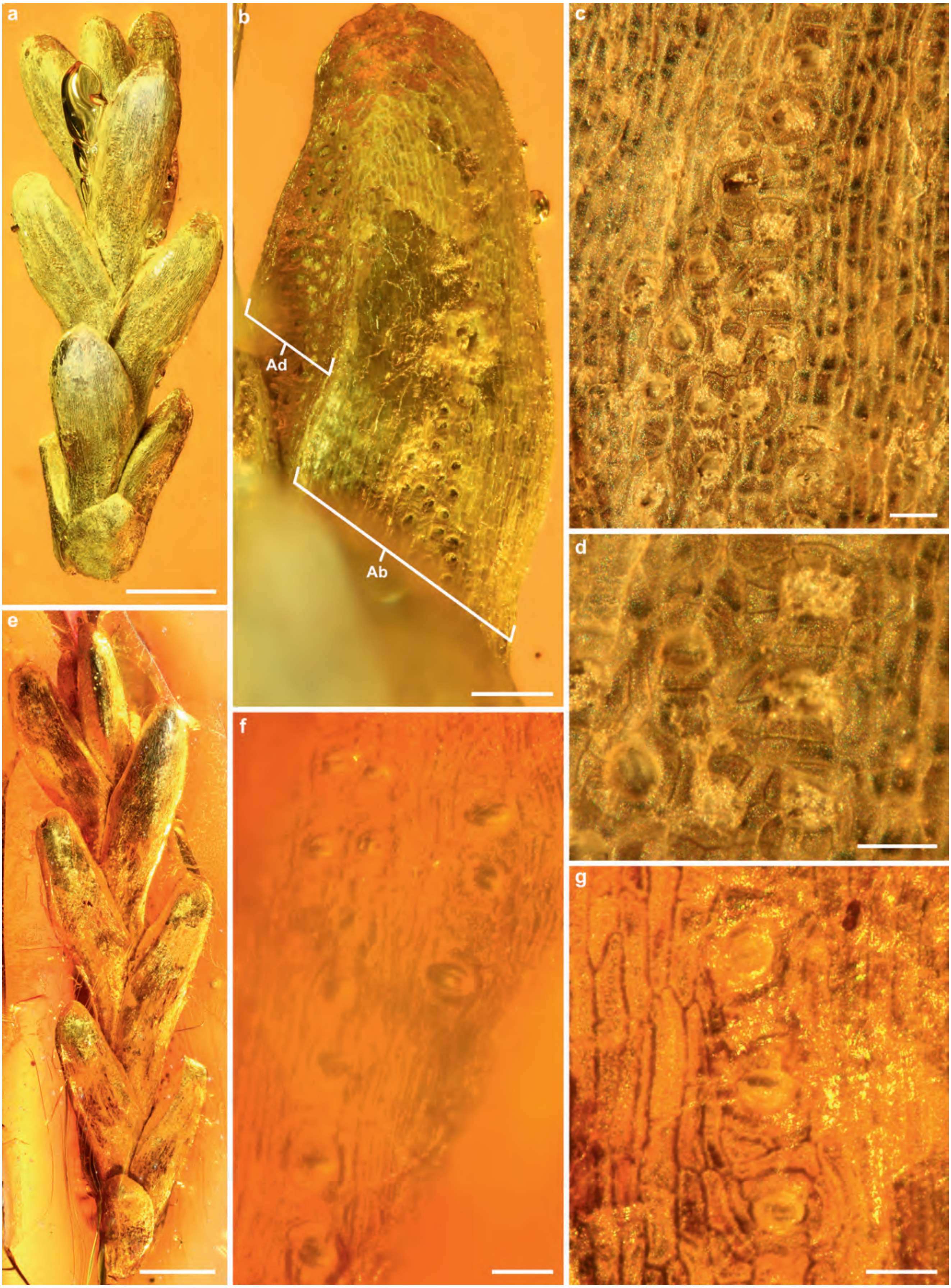
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(Fig. 5c, f), which are only basal or rarely proceeding up to the middle part of the leaves. Orientation of the stomatal pores within the patches or bands variable, mostly perpendicular or oblique to the longitudinal leaf axis (Figs 4c-e; 5c, d, f, g). Stomata complexes cyclocytic to amphicyclocytic, subsidiary cell ring narrow, forming an irregular roundish shape of the stomata complex (Figs 4d, e; 5d, f, g). Stomata complexes 48 to 72 µm long × 45 to 63 µm wide. Stomatal pit elongated, elliptic in shape, size of the stomatal pit 18 to 39 µm long × 6 to 27 µm wide. Ordinary epidermal cells 22 to 120 µm × 12 to 30 µm wide, rectangular, elongated or almost squared, arranged in regular cell rows parallel to the longitudinal leaf axis. 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).

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 in 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 × 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

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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 µm (b), 50 µm (c, d, f, g).

Tab. 4: Leaf morphology and cuticular features of extant *Glyptostrobus pensilis* and the fossil taxa *G. europaeus*, *Cupressospermum saxonicum* and *Quasisequoia couttsiae*. Unavailable information is marked with -.

Taxon	***Glyptostrobus pensilis***			***Glyptostrobus europaeus***			***Cupressospermum saxonicum***	***Quasisequoia couttsiae***	
Leaf types	3			3			1	2	
	taxoid	cryptomerioid	cupressoid	taxoid	cryptomerioid	cupressoid	cupressoid	immature needles	mature needles
Leaf morphology									
Shape	linear	linear-subulate, awl-shaped	scale-like	linear	linear-subulate	scale-like, almost triangular	scale-like, rhombic	awl-shaped-lanceolate	scale-like, rhombic
Base	decurrent			decurrent			non-decurrent	decurrent	
Apex	acute	acute-acuminate incurved	free, incurved	acute	slightly incurved-straight	bluntly pointed	acute with rounded apex, adpressed, incurved	free, falcate, adpressed, acute, rounded	
Margin	entire	entire	scariose	-	-	-	rectangular narrow cells with papillose apices	only apical free needle part with papillose margin	entire margin with isodiametric cells and roundish papillae
Phyllotaxis	spirally, spreading from the twig or two-ranked	spirally, spreading from the twig	spirally, adpressed to the twig, rarely spreading, imbricate	spirally, spreading from the twig	spirally	spirally, adpressed to the twig, imbricate	spirally, slightly imbricate	spirally, adpressed-spreading	
Stomata									
Distribution	amphistomatic			amphistomatic rarely hypostomatic	amphistomatic		amphistomatic	amphistomatic	
Stomata arrangement									
Adaxial	2 bands	2 bands, stomata in short rows or irregular	2 bands, loosely irregular arranged stomata	densely arranged; in bands			two stomata rows	2 bands, start below the apex, reach the base; stomata in short rows	2 bands, stomata irregular distributed, bands do not reach the base or the apex
Abaxial	2 bands	2 bands, 1 row/band; stomata in short rows or irregular	2 bands, merged at the base, proceeding to tip; rows far apart from each other				2 triangular stomata patches, covering almost the whole leaf lamina, not reaching the leaf tip; stomata in groups of 2 to 3, irregular distributed	2 bands, only on needle part which is merged with the twig; stomata in groups or rows	2 triangular patches, only on needle part which is merged with the twig; stomata in groups of 2 to 3, irregular distributed
Stomata complex									
Type	cyclocytic - amphicyclocytic	amphicyclocytic	amphicyclocytic	amphicyclocytic			cyclocytic - incomplete amphicyclocytic	cyclocytic - amphicyclocytic	amphicyclocytic
Subsidiary cells	4 to 7			mostly 5, rarely 4 or 6			mostly 3, up to 5	4 to 6, rarely 7	
Stomatal pit									
Orientation (longitudinal)	parallel	parallel	irregular, oblique, perpendicular (adaxial leaf base)	parallel	mostly oblique, rarely perpendicular		irregular	irregular	
Epidermis (abaxial stomata free midzone)									
Cell shape	-		rectangular	elongated, longer than broad			leaf base: rectangular, broader than long midline: polygonal, isodiametric	narrow rectangular, irregular	rectangular to squared
References	Florin 1931; Farjon 2005a; Ma et al. 2013			Christophel 1976; Vickulin et al. 2003; Holy et al. 2012; Ma et al. 2013			Kunzmann 1999		

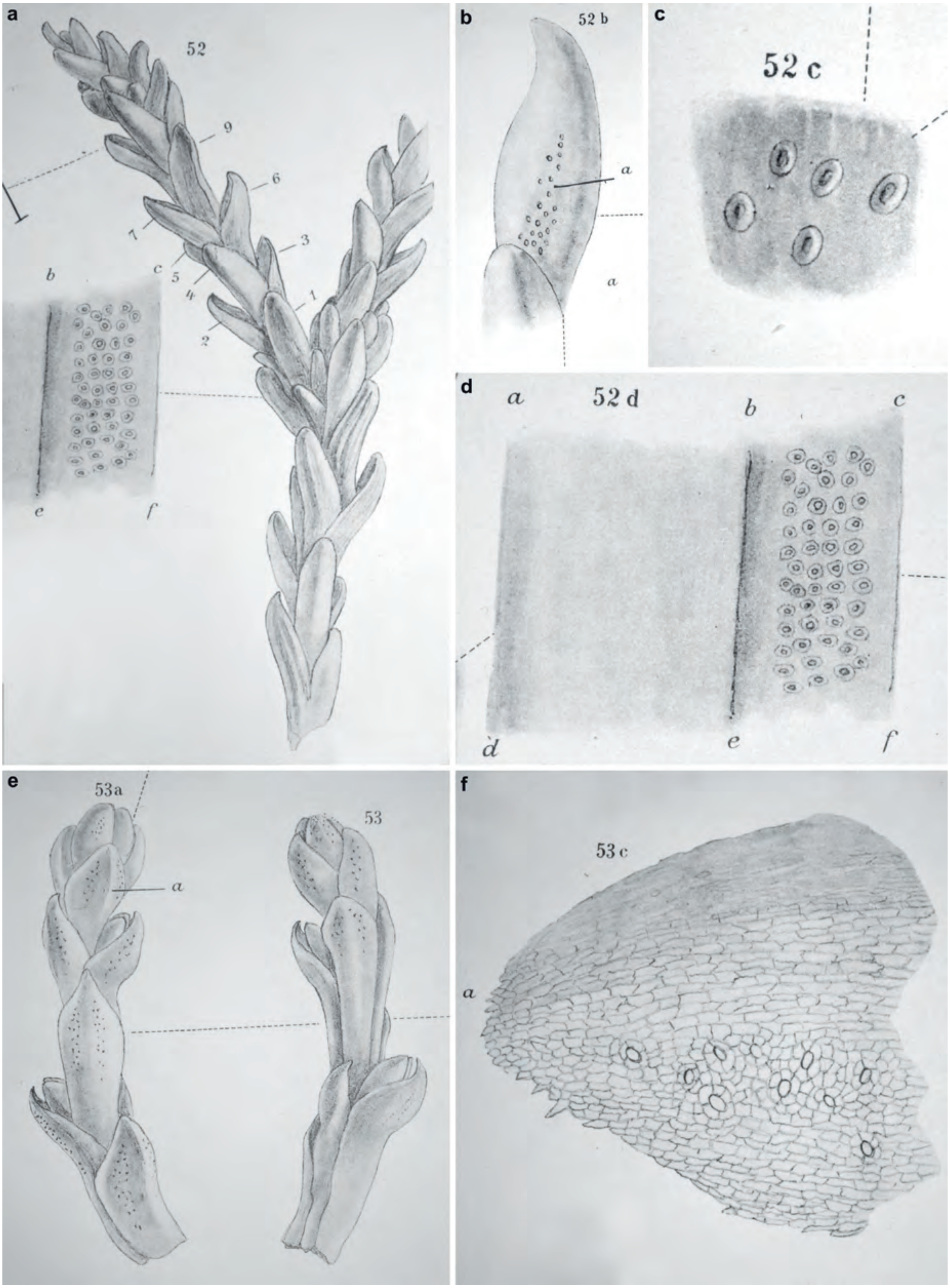


Fig. 6: Historic drawings of *Widdringtonites oblongifolius* (synonymous with *Quasisequoia couttsiae)* from Baltic amber (from the Goeppert Collection (a-d) and from the Künow Amber Collection (e, f), coll. No. 136, Caspary & Klebs 1907, pl. IX). (a) Overview of the twig. (b) Abaxial view of a singular 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.

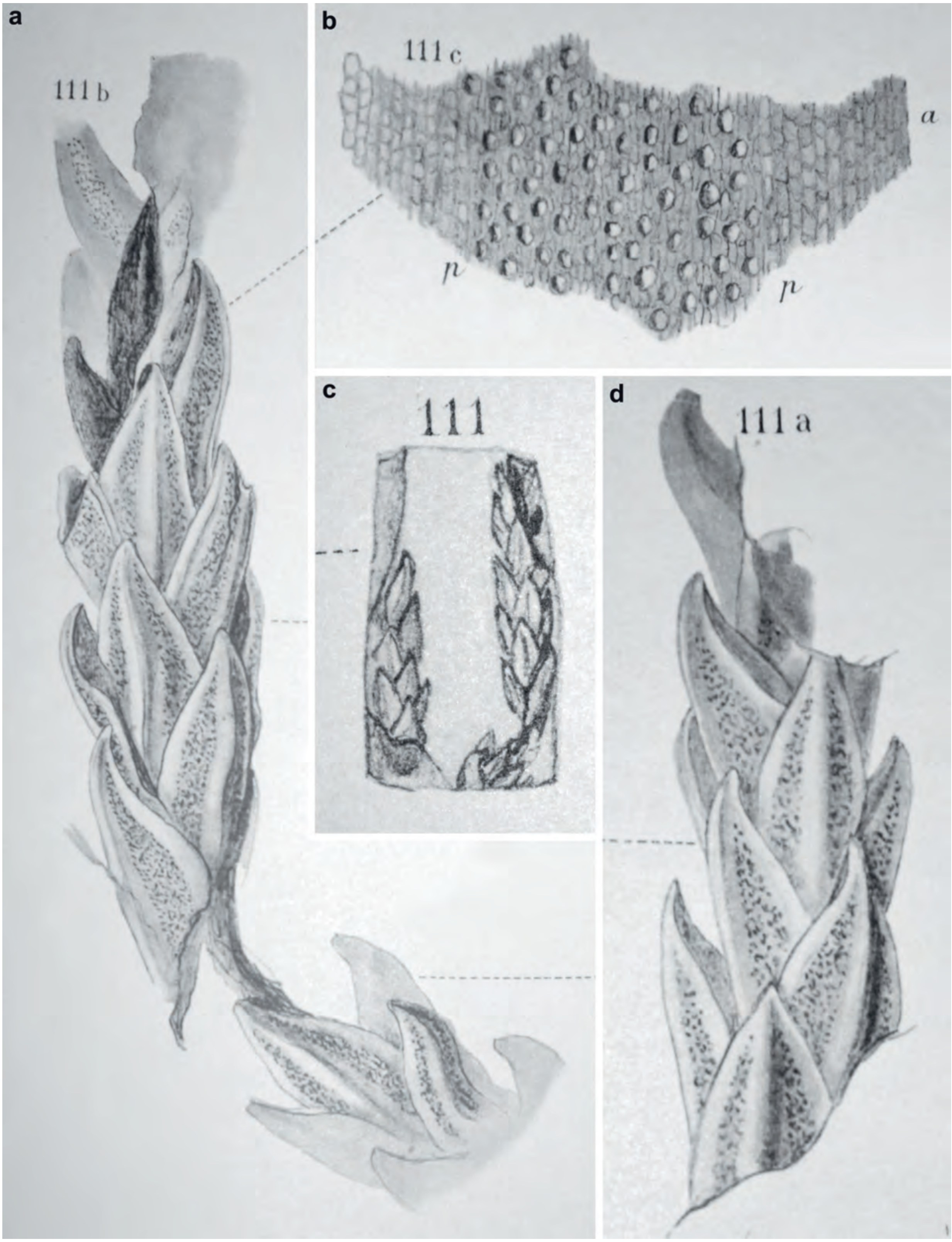
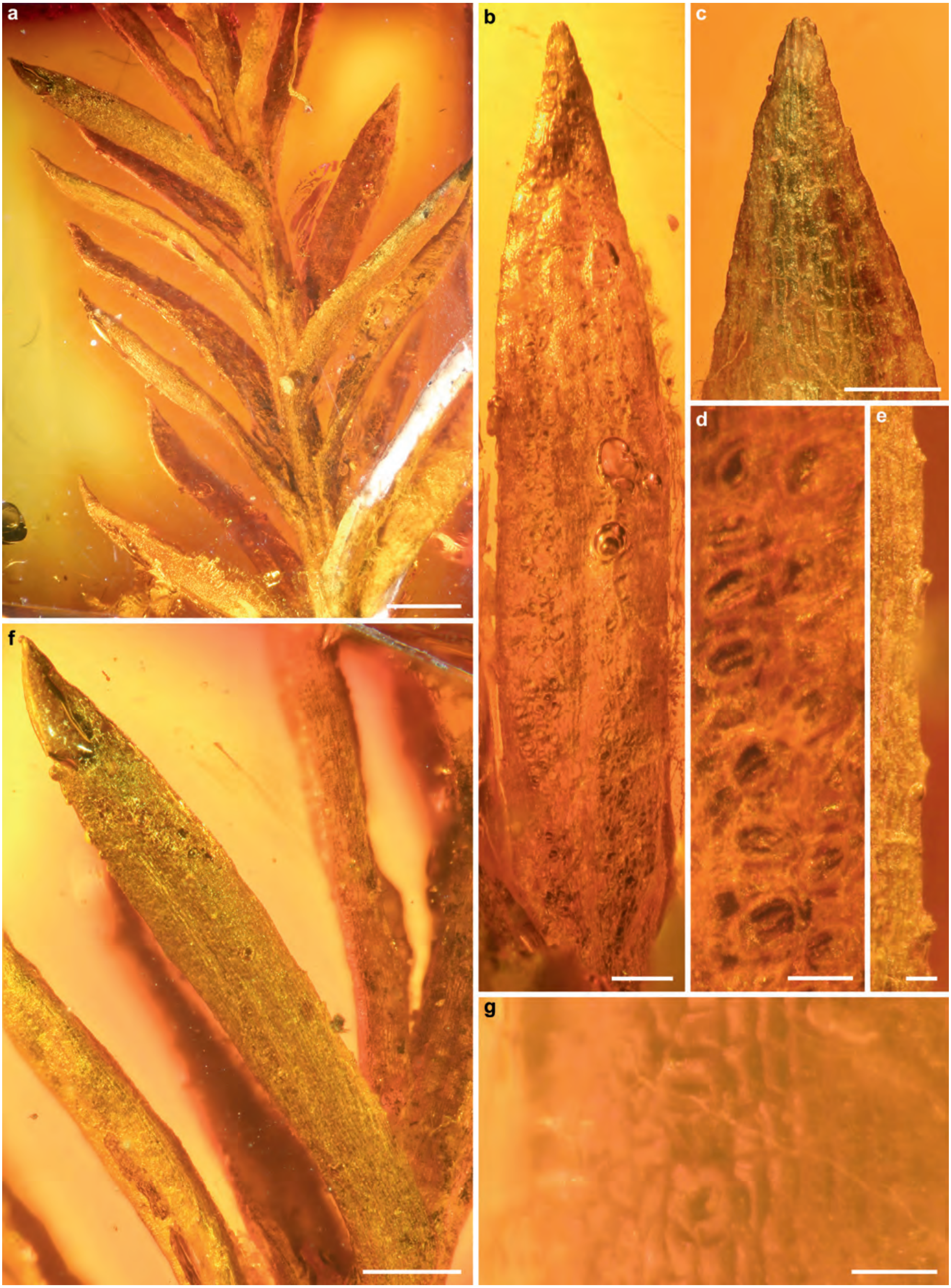


Fig. 7: Historic drawings of *Sequoia couttsiae* (synonymous with *Quasisequoia couttsiae*) from Baltic amber (from Caspary's private collection; Caspary & Klebs 1907, pl. XXIV). (a) Overview of one of the twigs. (b) Detail of the abaxial leaf surface of the twig shown in (a), stomata band indicated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

Genus ***Taxodium*** Rich., 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 × 0.3 to 0.5 mm wide) with broad and long decurrent bases (Fig. 8a, f). 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 × 45 to 51 µm wide, roundish in shape. Stomatal pits are widely elliptic, 24 to 42 µm long (average 33 µm) × 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) × 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.

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.

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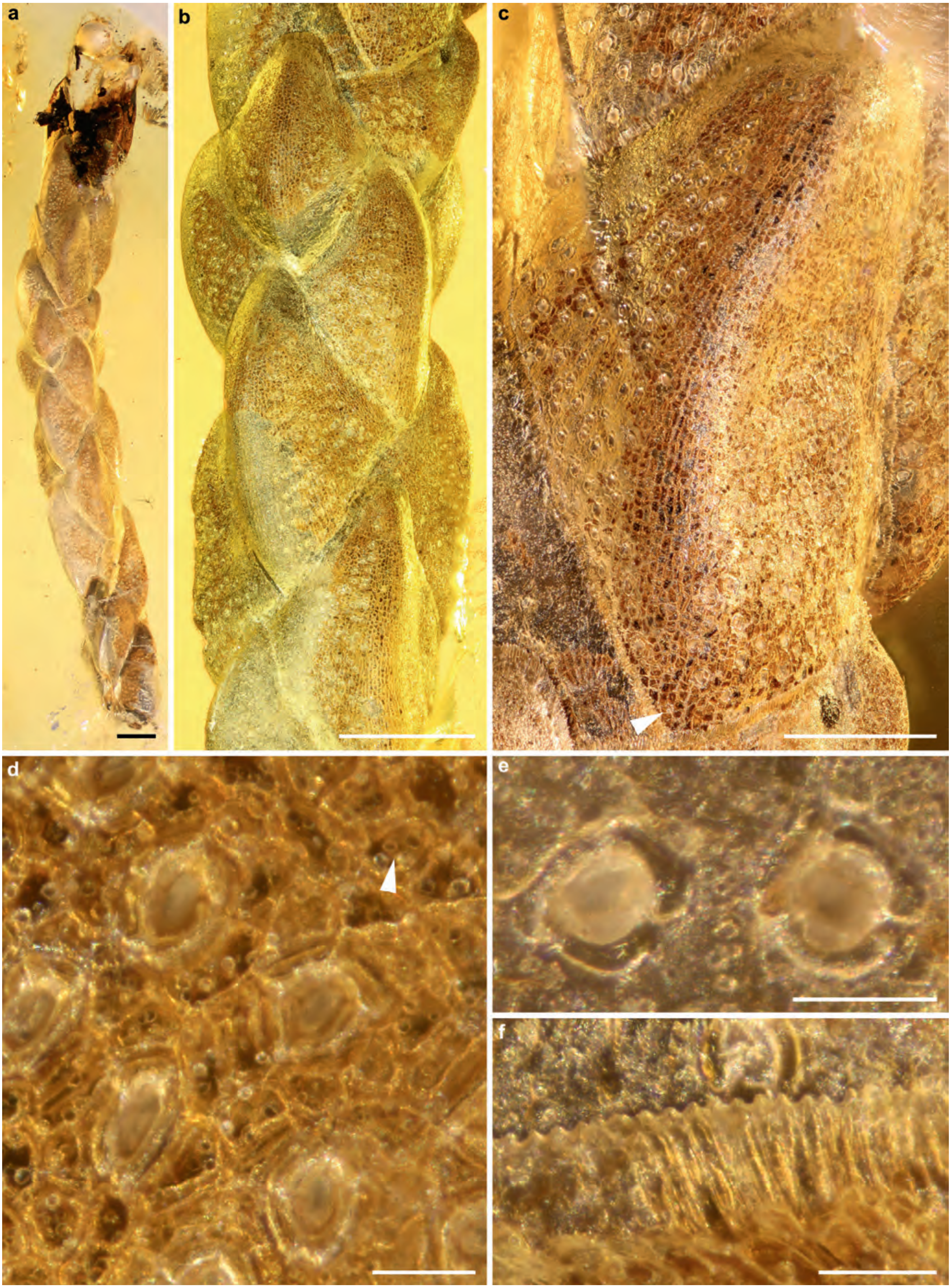
Fig. 8: Twig fragment of *Taxodium* sp., GZG.BST.24333. (a) Overview of the inclusion showing spirally arranged, lanceolate leaves. (b) Adaxial leaf side with two stomata bands on each side of the midline. (c) Acute leaf tip. (d) Enlargement of stomata rows shown in (b), stomatal pores perpendicular 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).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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* (Brongn.) Unger, in Caspary & Klebs (1907, although misspelt *Glytostrobus* 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. L.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 µm long (average 62 µm) × 33 to 58 µm wide (on average 46 µm). The stomatal pits are roundish or widely elliptic, 24 to 42 µm long (average 31 µm) × 15 to 30 µm wide (average 21 µm). 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 µm long (average 32 µm) × 24 to 39 µm wide (average 30 µm), with numerous crystal bodies. Ordinary epidermal cells of the basal stomata-free zones mostly broader than long, 15 to 30 µm long (average 24 µm) × 30 to 45 µm wide (average 38 µm).

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 amphicyclocytic; 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, 1041-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 Coll-

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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).

▶

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, adpressed 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).


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7
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b
d
e
103 c
103 b
3 a
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103 b
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103 e
h
103 d
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a
Needle 1
Needle 2
b
c
d
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ection (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 *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*** Mill., 1754

***Abies* sp.**

(Figure 11)

Specimen investigated

Jürgen Velten Amber Collection IX 73

Description

Two oblanceolate, pedicellate needles, 7.2 mm long × 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) × 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) × 20 to 35 µm wide (average 28 µm), round to elliptic in shape. Ordinary epidermal cells 54 to 114 µm long (average 89 µm) × 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.

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 1990; 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 1990). 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*.

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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 µm (b, c), 200 µm (d, e), 50 µm (f, g), 10 µm (h).

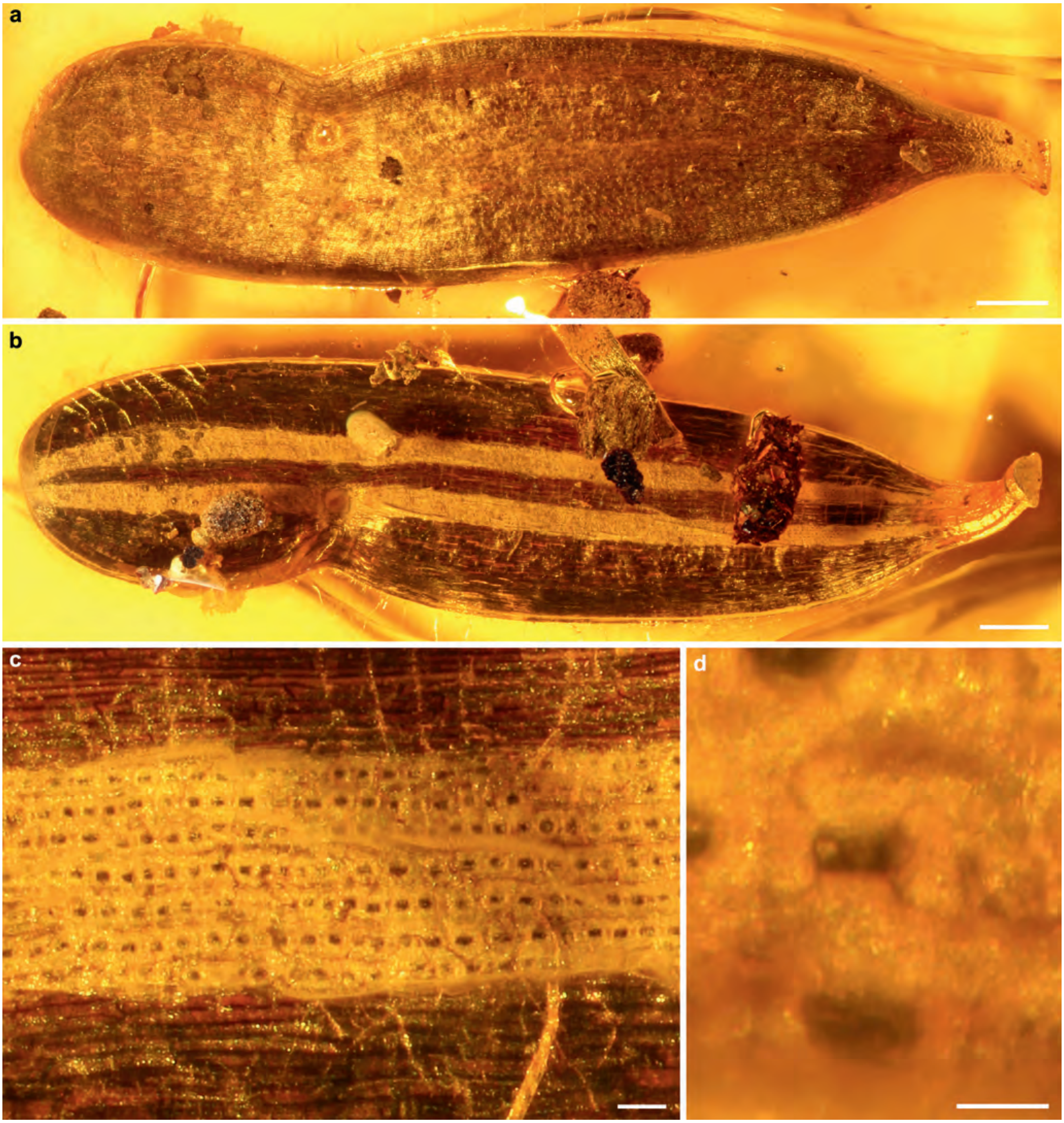


Fig. 12: Needle of *Cathaya* sp. from Baltic amber, GZG.BST.23533. (a) Adaxial needle side. (b) Abaxial needle side with two stomata bands. (c) Middle portion of the lower stomatal band, shown in (b) with closely arranged stomata rows. Note the narrow ordinary cells of the midline in comparison to the 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).

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 Palaeogene floras, often represented by the fossil-species *Abies 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 × 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) × 30 to 45 µm wide (average 36 µm). Stomatal pit rectangular to elliptic, 12 to 24 µm long (average 18 µm) × 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) × 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) × 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.

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*** 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

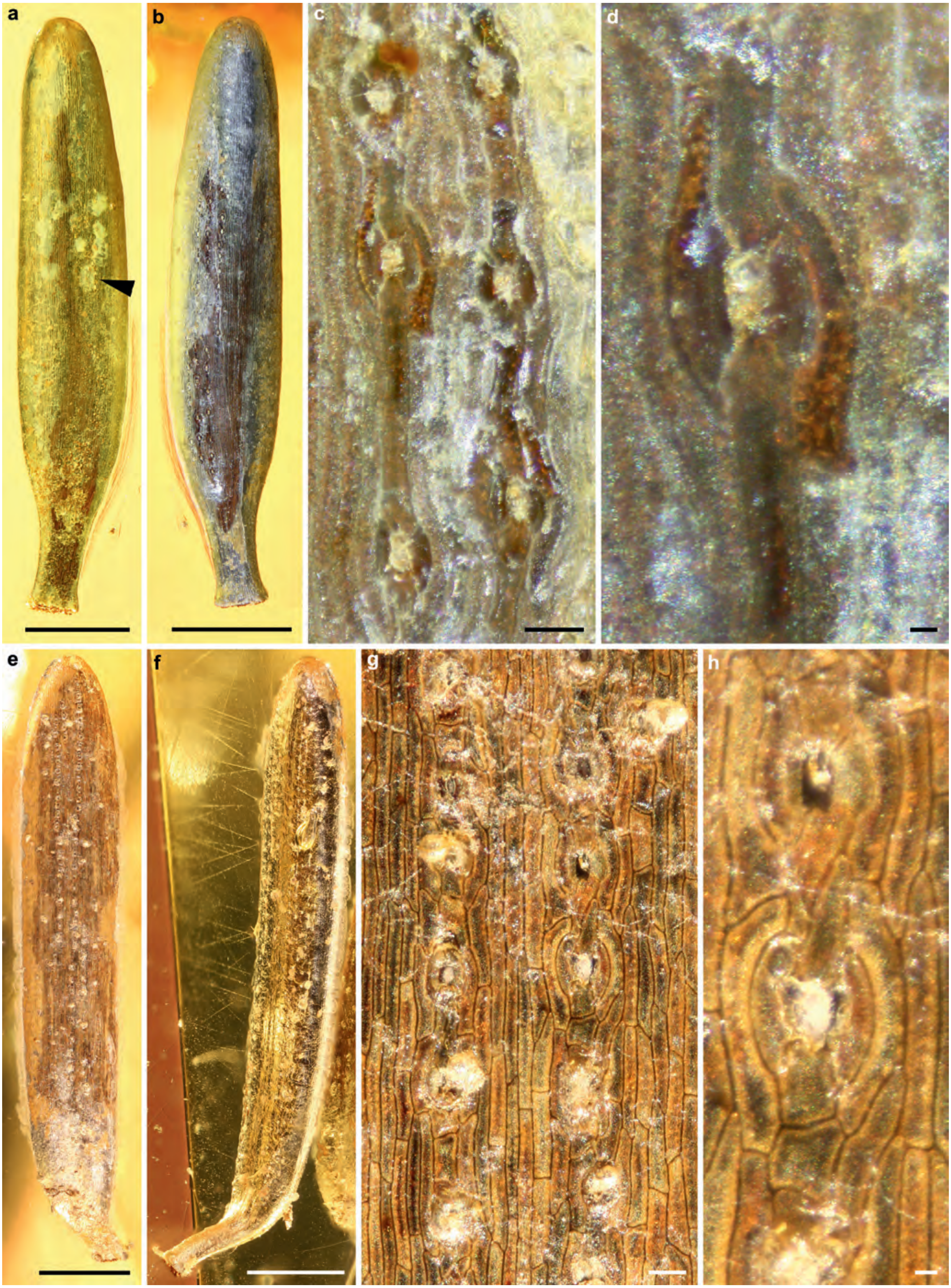
2005 *Nothotsuga protogaea* L.Kunzmann et Mai, pp. 89-95, text-fig. 6, pl. 8, 9.

Description

Linear petiolate needles, 5.5 to 9.7 mm long × 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

▶

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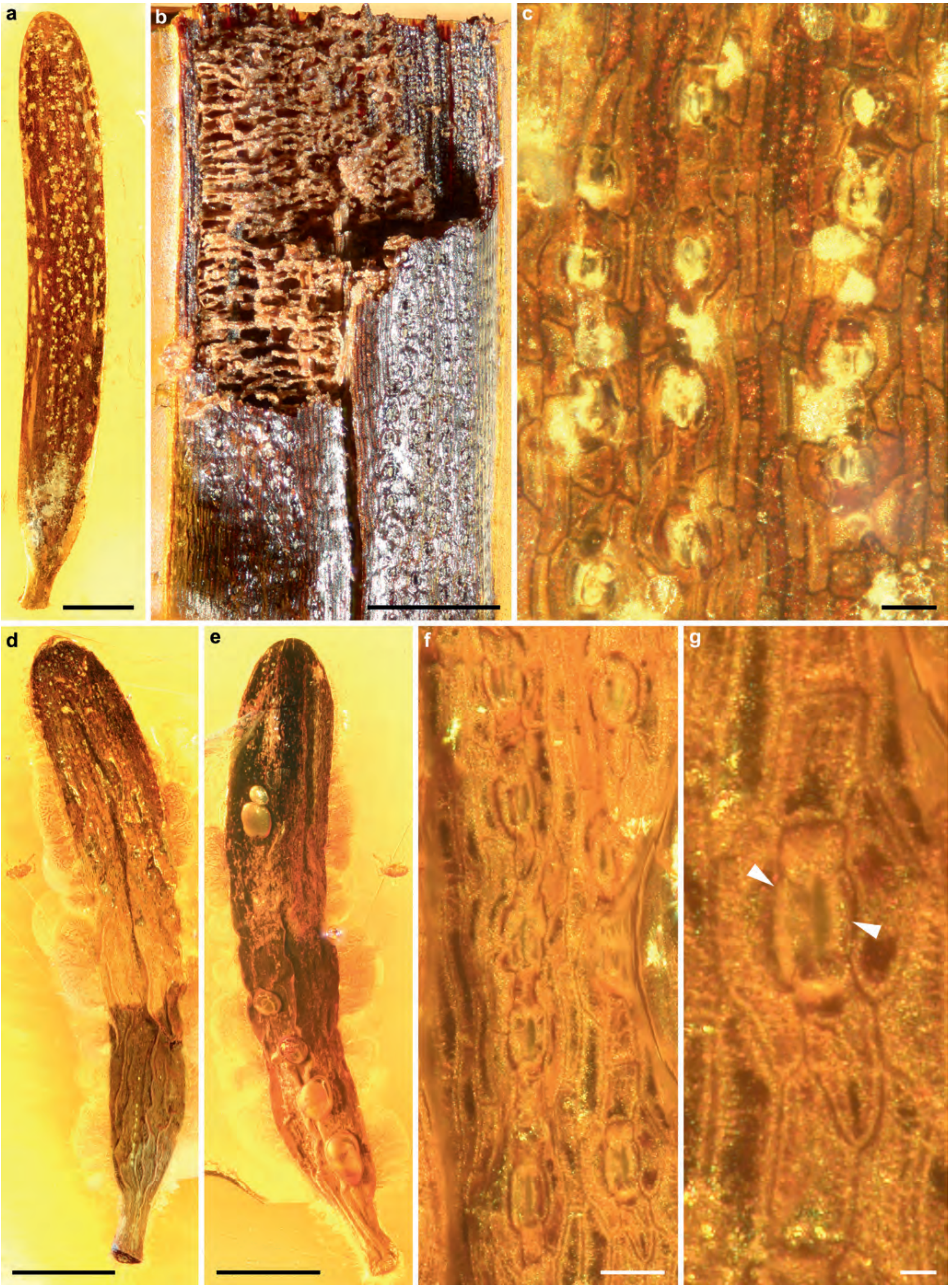
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Tab. 5: Measurements of the *Nothotsuga protogaea* specimens from Baltic amber. Centered numbers of the leaf and stomata sizes are average values; the size ranges are provided in brackets.

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

pronounced, not twisted, 0.6 to 1 mm long × 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 × 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 × 9 to 35 µm wide. Ordinary epidermal cells elongated, rectangular, 35 to 229 µm long × 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 (Kunzmann & Mai 2005) and thus, can be excluded.

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.

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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 amphicyclocytic 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 µm (b), 50 µm (c, f), 10 µm (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 accomodated 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 according to the Identification key shown below.

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* Conw., 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

Identification key for *Pinus* needle inclusions from Baltic amber

1a needles amphistomatic **2**
1b needles epistomatic. **3**

2a cross section semi-circular shaped, fascicle of two needles. . . . . Morphotype 1: ***Pinus baltica***
2b cross section broadly triangular, abaxially rounded, fascicle of three needles . . . . . . .Morphotype 2: ***Pinus serrata***

3a cross section broadly triangular, abaxially rounded, fascicle of three needles . . . . Morphotype 3: ***Pinus*** aff. ***schiefferdeckeri***
3b cross section triangular, adaxial side flat, abaxial side slightly convex, fascicle of five needles . . . . Morphotype 4: ***Pinus cembrifolia***

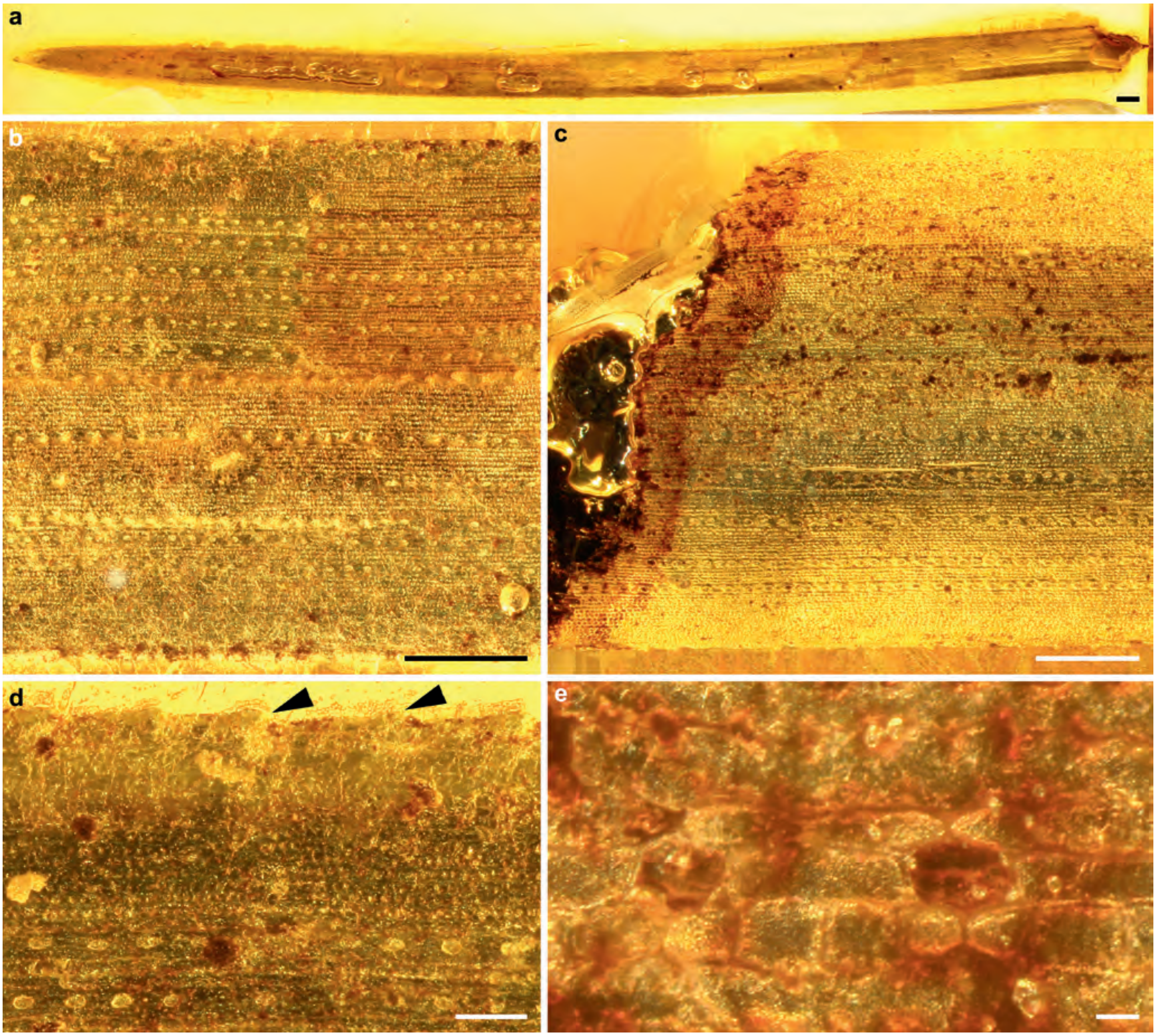


Fig. 15: Needle fragment of *Pinus baltica* (Neotype, morphotype 1, GZG.BST.24652). (a) Overview of the needle fragment. (b) Flattened adaxial side showing regular stomata rows. (c) Rounded abaxial side close to the degraded needle base, surface of lamina with regular stomata rows. (d) Needle margin 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).

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. 15e); Width of ordinary cells 15 to 21 µm (average 17 µm; cell length not measurable, since polar cell walls not preserved).

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	***Pinus baltica*** GZG.BST.24652, Neotype	***Pinus baltica***	***Pinus banksianoides***	***Pinus silvatica***
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

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*.

Comparison

The needle inclusion GZG.BST.24652 can be distinguished from *Pinus banksianoides* in several aspects (Tab. 6): 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).

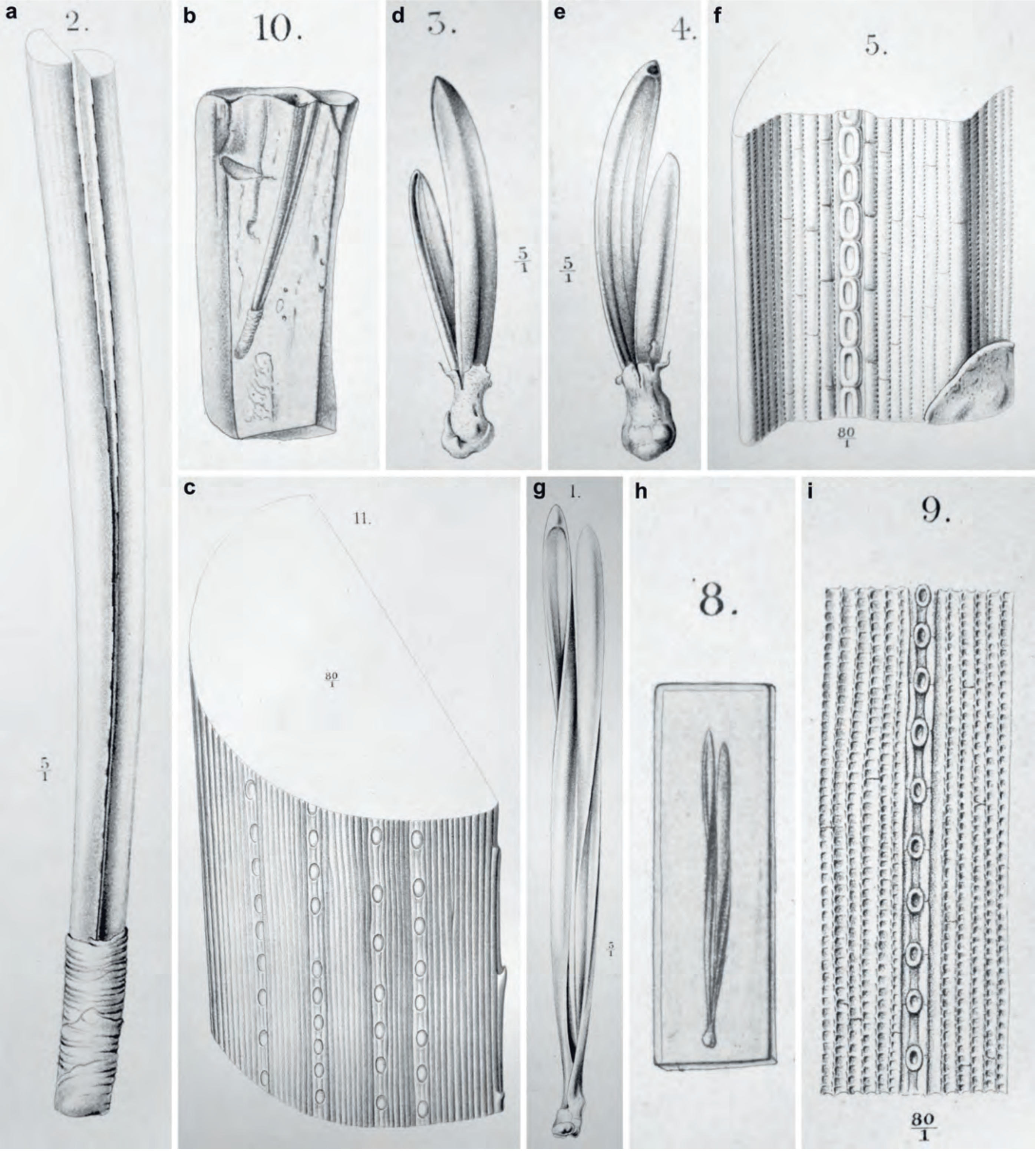
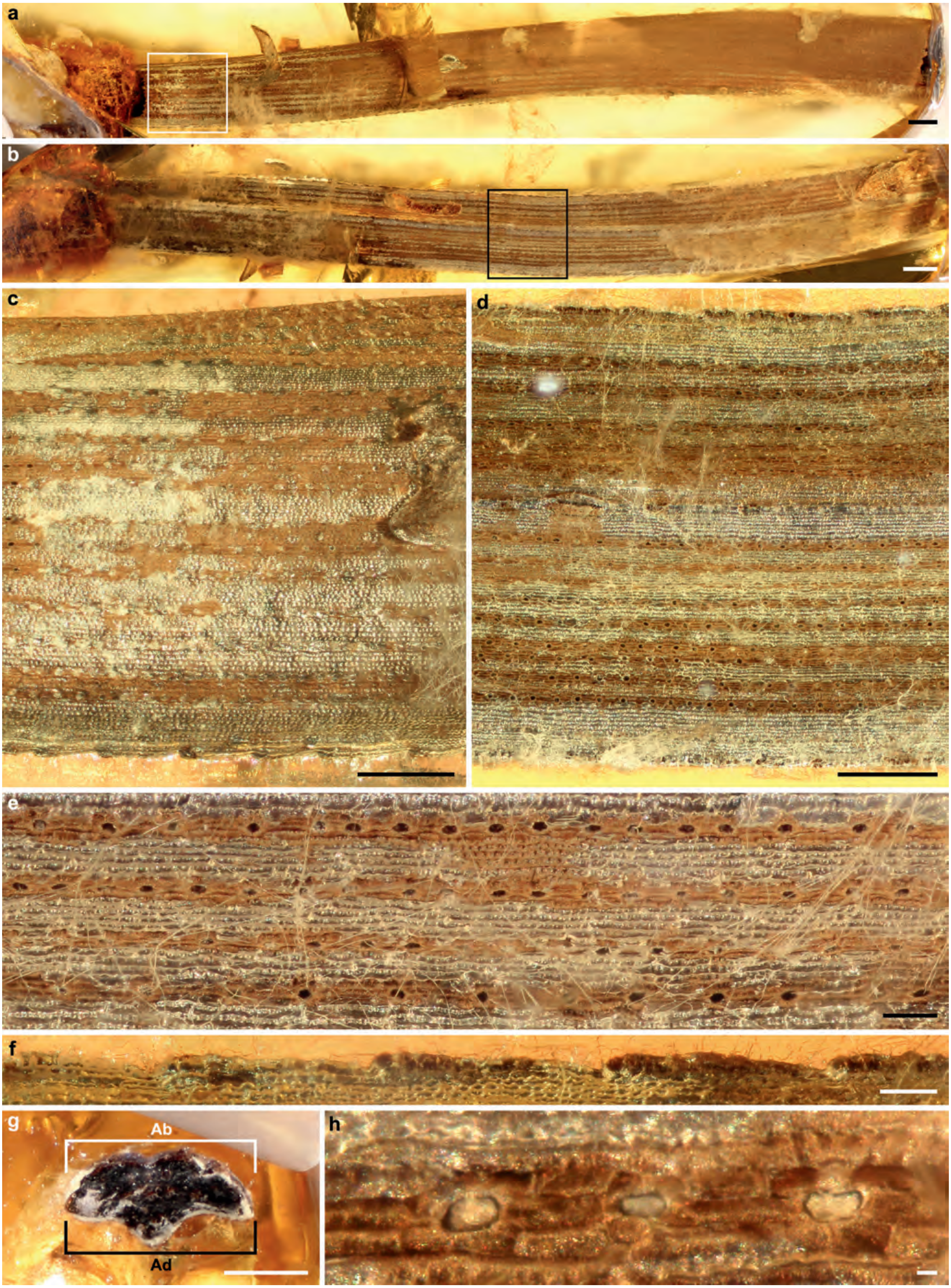


Fig. 16: Historic drawings of needle inclusions of *Pinus baltica* (a-c), *P. banksianoides* (d-f) and *P. silvatica* (g-i) from Baltic amber (Menge Collection; from Conwentz 1890, pl. XVI and XVII). (a) Fascicle of two needles. (b) Amber specimen with the needle fascicle shown in (a). (c) Abaxial needle 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.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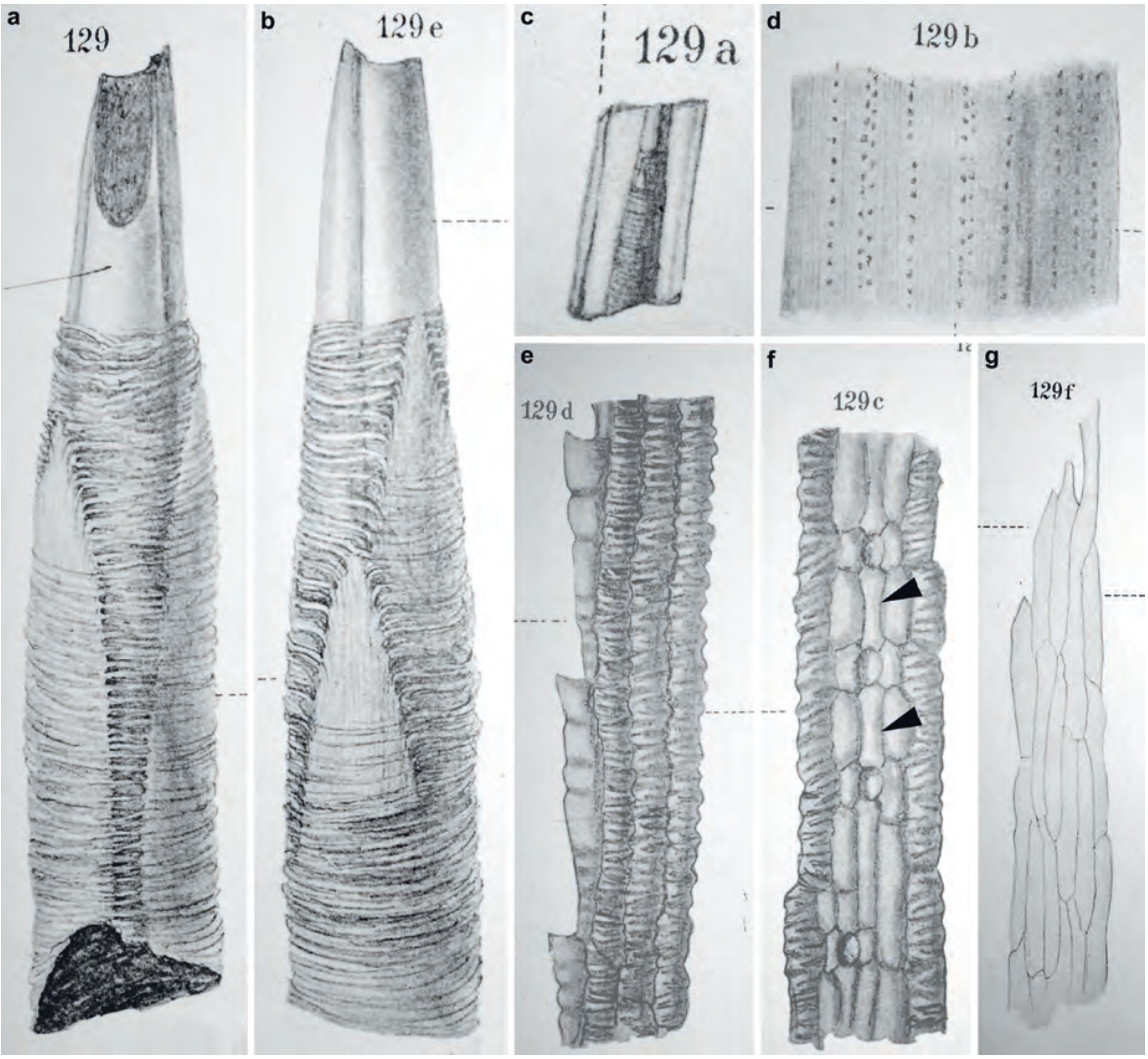


Fig. 18: Historic drawings of a lost three needled fascicle inclusion of *Pinus serrata* (Künow Amber Collection, coll. no. 42; from Caspary & Klebs 1907, pl. XXX). (a, b) Inclusion shown from different angles, base of the needle fascicle is covered by scales. (c) Amber specimen with the inclusion shown 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.

◀

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 adaxial 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, g), 500 µm (c, d), 100 µm (e, f), 10 µm (h).

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 stomata rows, ad-axially 6-9 stomata 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.

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), *P. künowii* Casp. (Fig. 19a-f), *P. schiefferdeckeri* Casp. et R. Klebs (Fig. 19g-j), *P. dolichophylla* Casp. (Fig. 20), and *Pinites rigidus* Goepp. et Ber., (Fig. 21a-d), a synonym of *Pinus subrigida* Goepp. et Menge (Fig. 21e-i; 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.

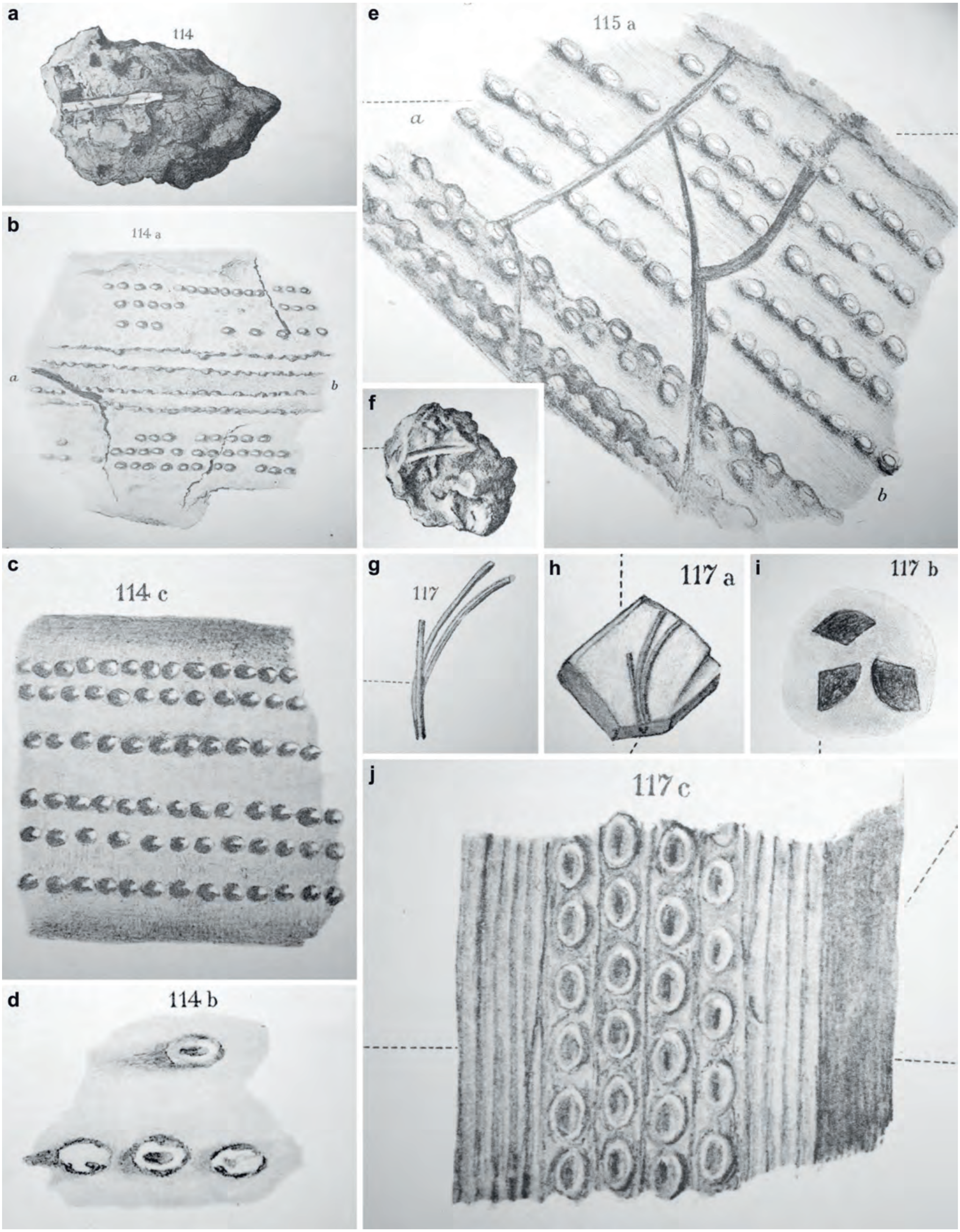
The stomata rows of *Pinus künowii* and *P. schiefferdeckeri* are arranged very close to each other and not separated by rows of ordinary epidermal cells (Fig. 19e, j). In addition, the stomata complexes of these species seem to be densely arranged to each other (Fig. 19c, e, j). Both species possess 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 revaluation of its affinities is not possible.

▶

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 stantienite. (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 Stantinite. (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.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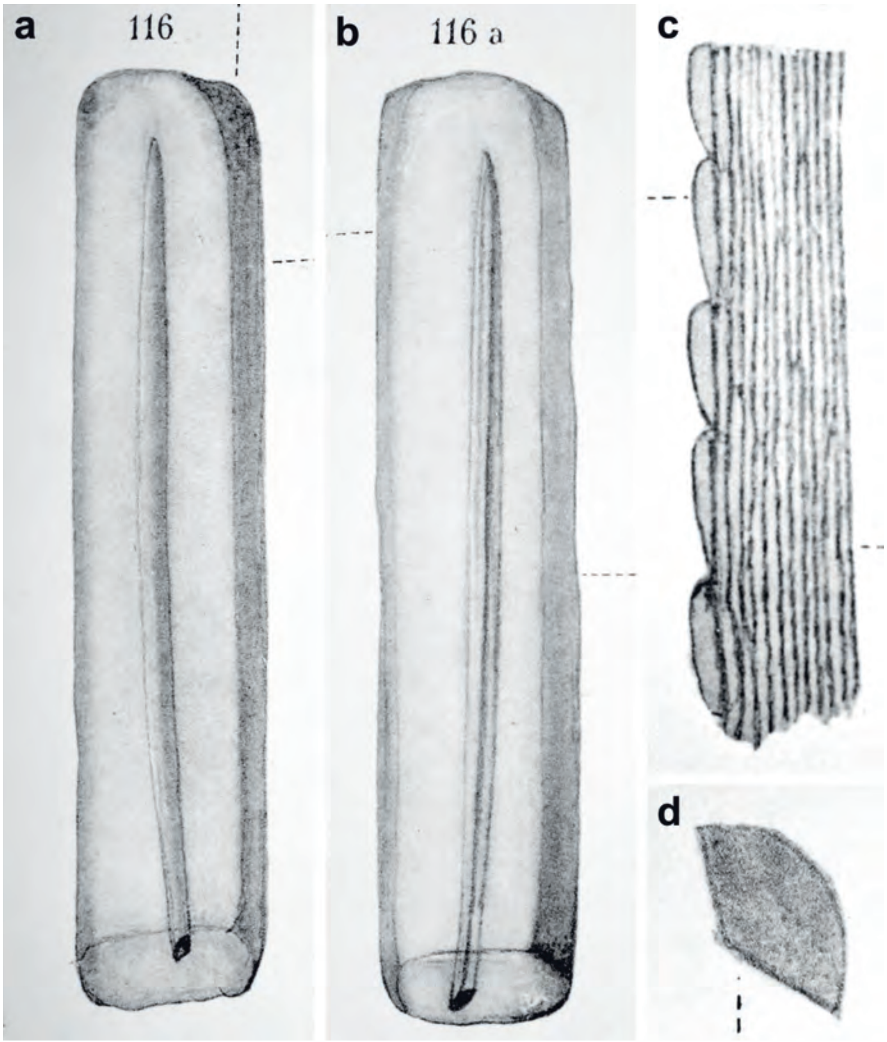


Fig. 20: Historic drawing of a lost needle inclusion of *Pinus dolichophylla* (Caspary's private collection; from Caspary & Klebs 1907, pl. XXVI). (a, b) Needle inclusion shown from different angles. (c) Dentate needle margin. (d) Needle cross section.

Tab. 7: Morphological features of needle inclusions of *Pinus serrata* (Neotpye, 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	***Pinus serrata*** GPIH 4584, Neotype	***P. serrata***	***P. künowii***	***Pinus* aff. *schiefferdeckeri*** GZG.BST.24654	***P. schiefferdeckeri***	***P. dolichophylla***	***P. subrigida***
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	-	-	-	-
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

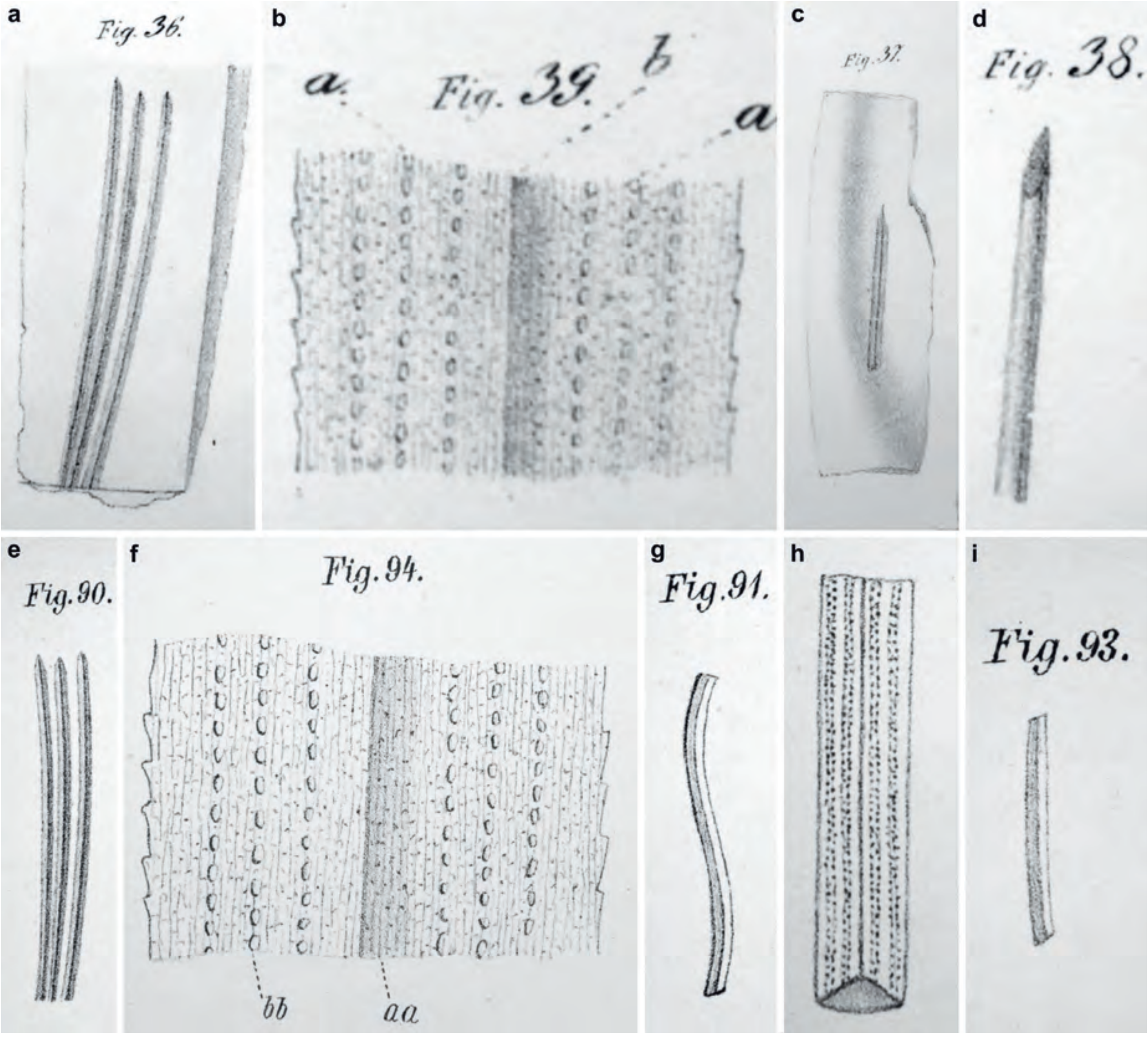
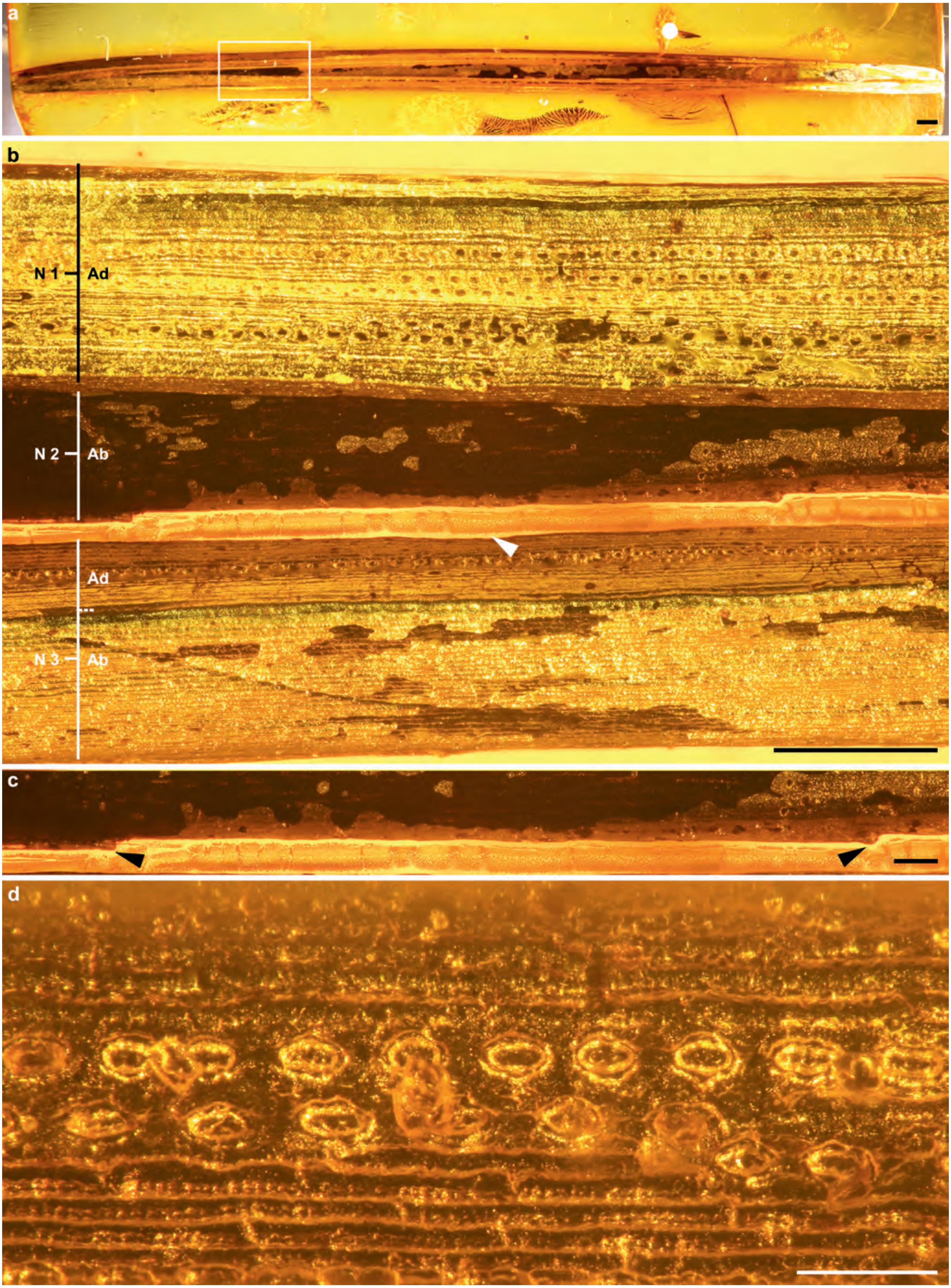


Fig. 21: Historic drawings of lost needle inclusions showing two specimens of *Pinites rigidus (*a-d, from Goeppert & Berendt 1845, pl. V), a taxon which was later revised as *Pinus subrigida* (e-i; from Goeppert & Menge 1883, pl. XIII). (a, e) Drawings of the same specimen, showing a three needle fascicle 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) 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*.


a
b
N 1
Ad
N 2
Ab
Ad
N 3
Ab
c
d

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 Berendt, pp. 91-92, pl. V, figs 36-39; herein Fig. 21a-d.

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

?1870-72 *Pinus rigida* (Goepp.) Schimp., 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 µm) × 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 *Pinites rigidus*; please see comparison and identification chapter of *Pinus serrata* and Tab. 7 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.

◄

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 µm (b), 100 µm (c, d).

Pinus cembrifolia Casp., 1886 emend.

(Figure 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 cembrifolia* Casp., p. 6.

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

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

1907 *Pinus cembrifolia* 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 × 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 µm 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) × 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.

Identification and comparison

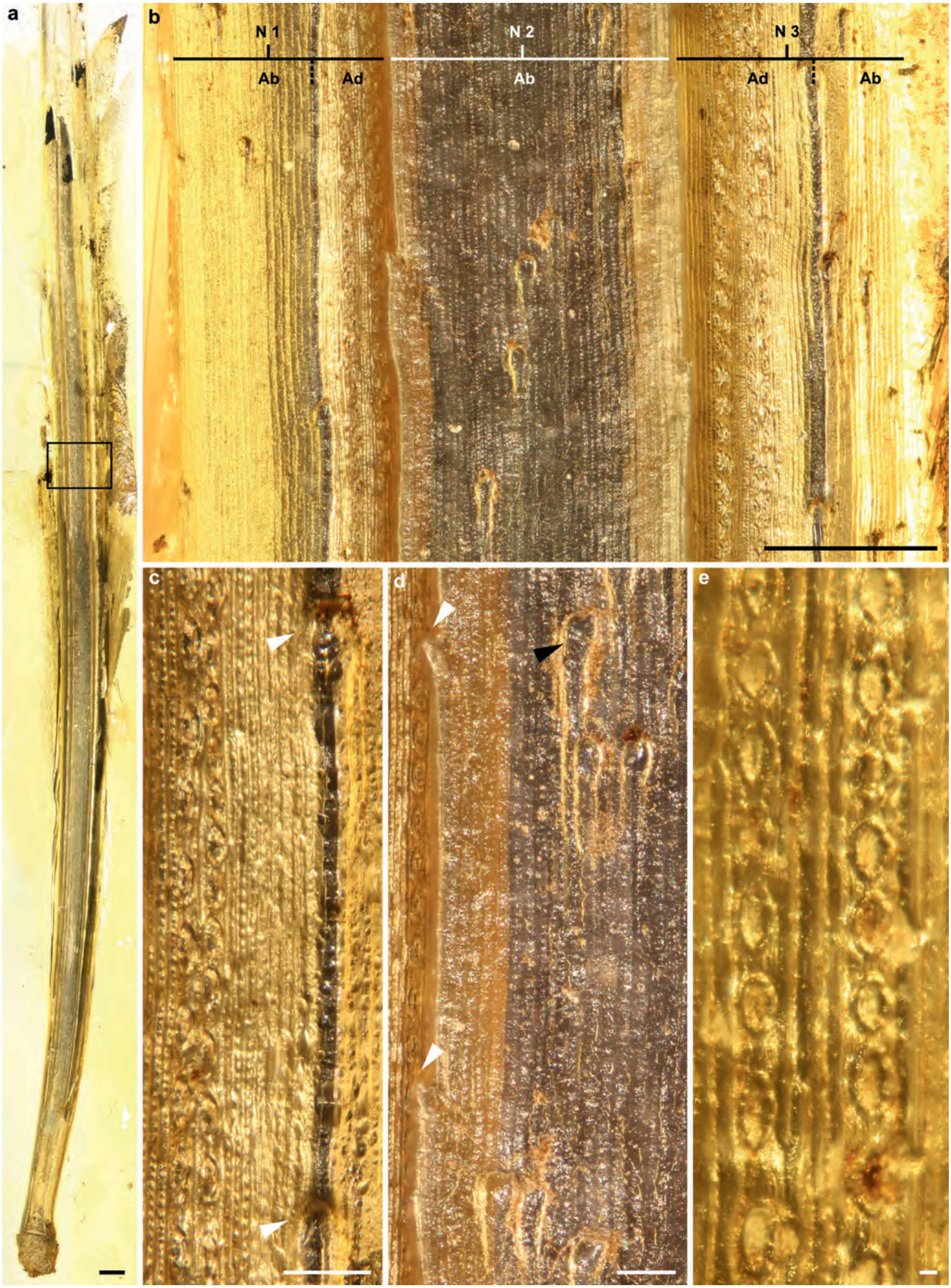
Caspary (1886) described a *Pinus* fascicle composed of five needles from Baltic amber as *P. cembrifolia* Casp. Later, Conwentz (1890) assigned two further Baltic amber inclusions to *P. cembrifolia* Casp. (Fig. 24), revising one specimen which Goeppert & Menge (1883) originally published as *P. silvatica*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

Based on the given descriptions and pictures of *Pinus cembrifolia* 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-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).

Caspary & Klebs (1907) evaluated the affinities of the two specimens of *Pinus cembrifolia* which were described by Conwentz (1890). One of the specimens (Fig. 24d-g) was doubted to be *P. cembrifolia*, 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).

▶

Fig. 23: Entire five needled fascicle of Pinus cembrifolia (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 µm (b), 100 µm (c, d), 10 µm (e).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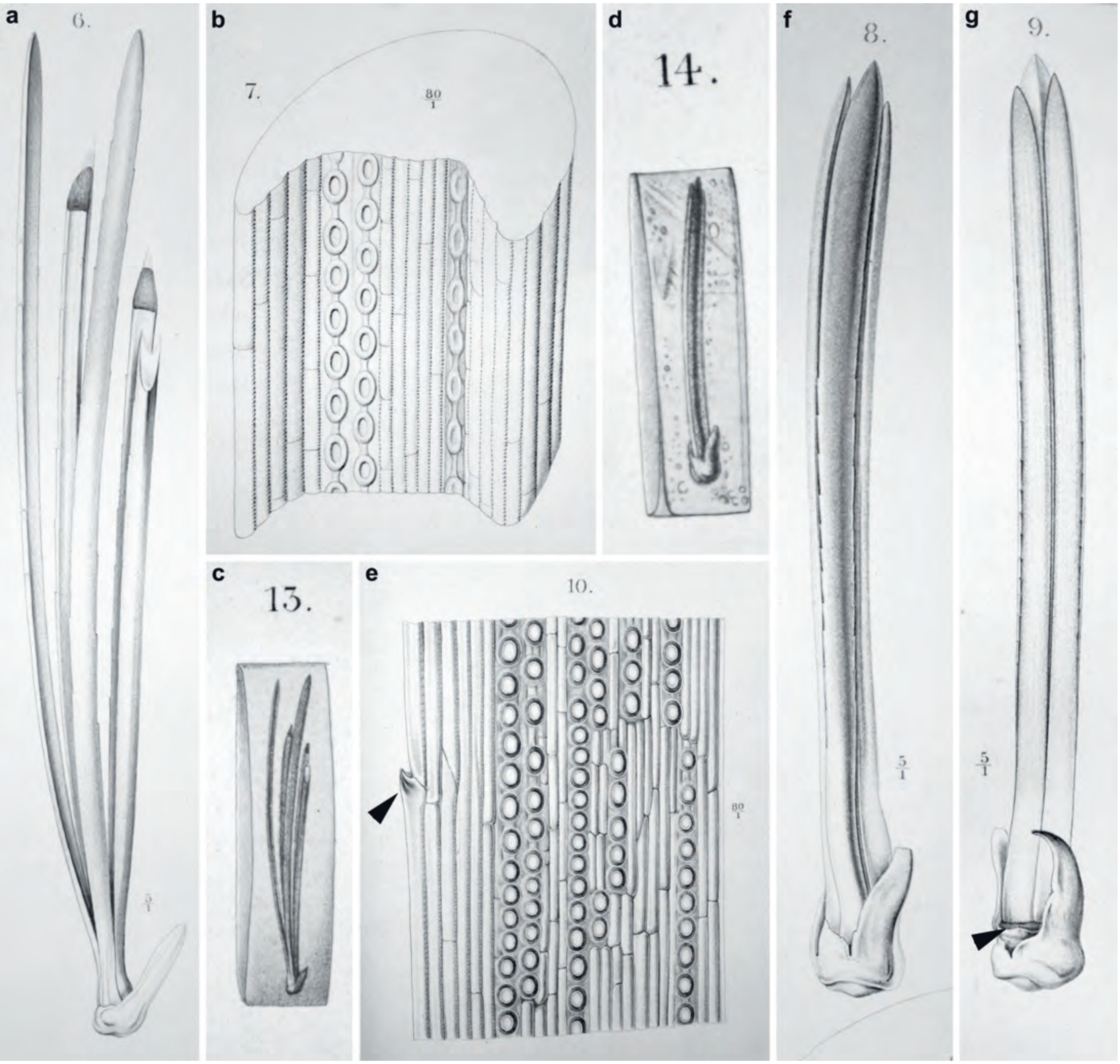
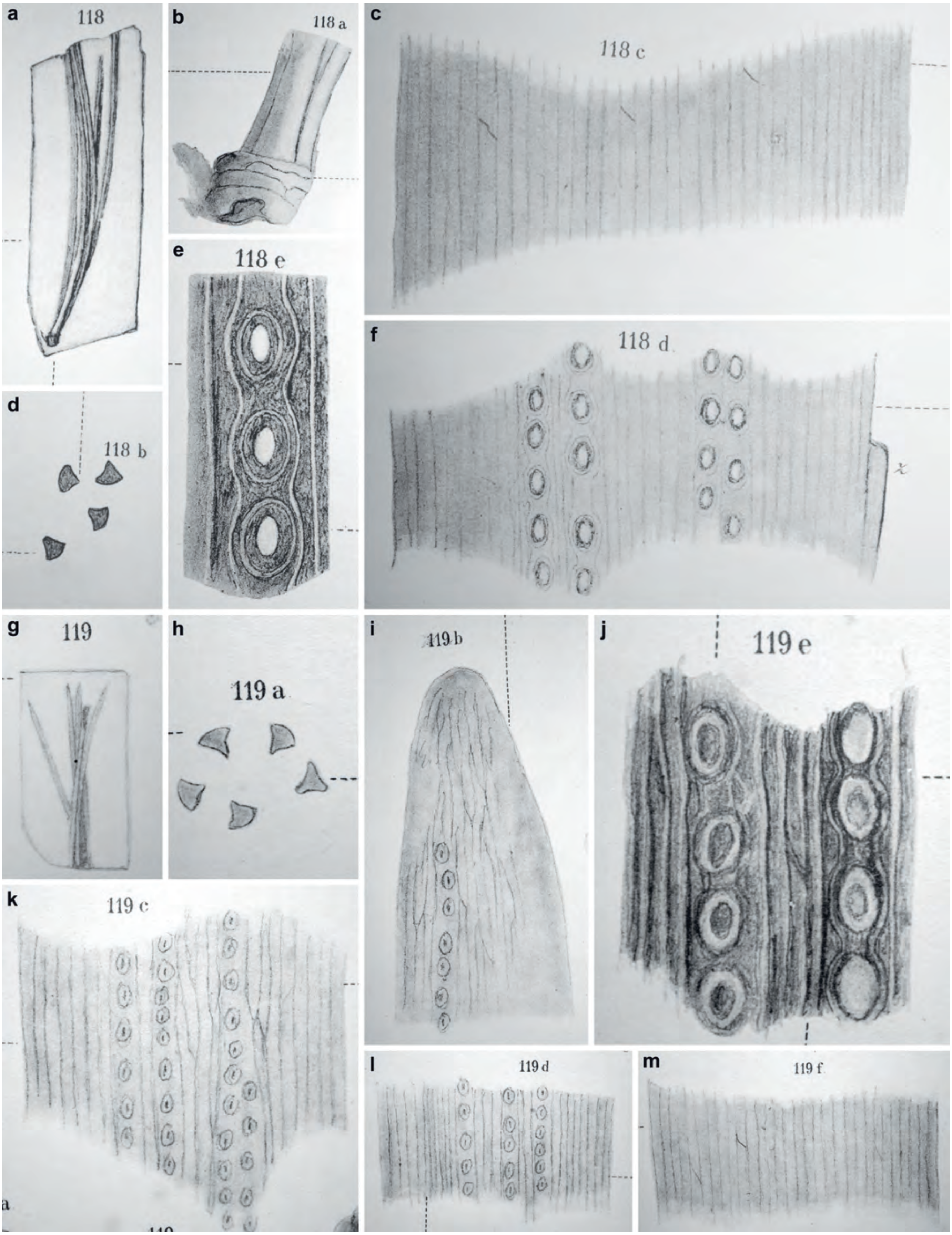


Fig. 24: Historic drawings of two lost Baltic amber specimens with five needled fascicle inclusions of *Pinus cembrifolia* (from Conwentz 1890, pl. XVI and pl. XVII). (a) Overview of the five needled fascicle inclusion. (b) Detail of the adaxial leaf side, showing the stomata rows and the shape of the needle cross section. (c) Amber specimen with the needle fascicle inclusion of (a). (d) Overview of another amber specimen with *P. cembrifolia* needles. (e) Detail of the adaxial needle surface with several stomata rows and the dentate needle margin (arrowhead). (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 cembrifolia* (a-f, specimen of *P. cembrifolia* from the Klebs Amber Collection; g-m, specimen of *P. cembrifolia* 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. cembrifolia* 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.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Tab. 8: Morphological features of the needle inclusion *Pinus cembrifolia* (Neotype, morphotype 4, GZG.BST.21897 [Hoffeins 1187-1]), compared to historic descriptions of *P. cembrifolia* 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	***Pinus cembrifolia*** GZG.BST.21897, Neotype	***Pinus cembrifolia***
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

Genus ***Pseudolarix*** Gordon, 1858

***Pseudolarix* sp.**

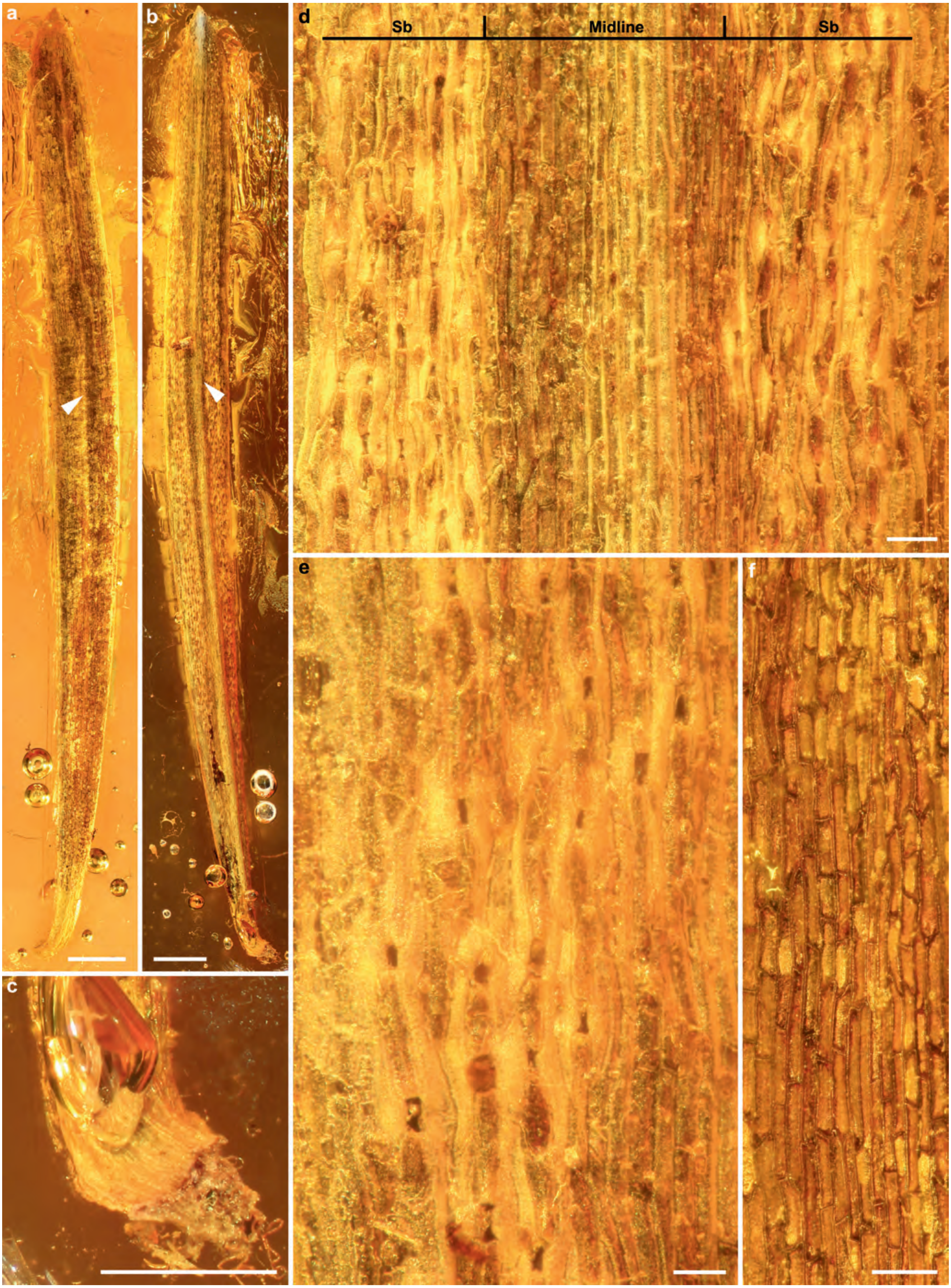
(Figures 26-28)

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 × 1 to 2 mm wide, tapering towards a slender flattened to triangular base (Figs 26c; 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 midline (Figs 26d; 27e). Per band, 3 to 6 irregular stomata rows, parallel to the longitudinal axis. Stomata complexes monocyclic, 111 to 210 µm long × 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, e; 27f; 28d, h). Stomata sunken, stomatal pit elongated rectangular, 10 to 40 µm long × 5 to 15 µm wide. Ordinary cells of the epidermis are mainly rectangular, sometimes elongated, 80 to 310 µm long × 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.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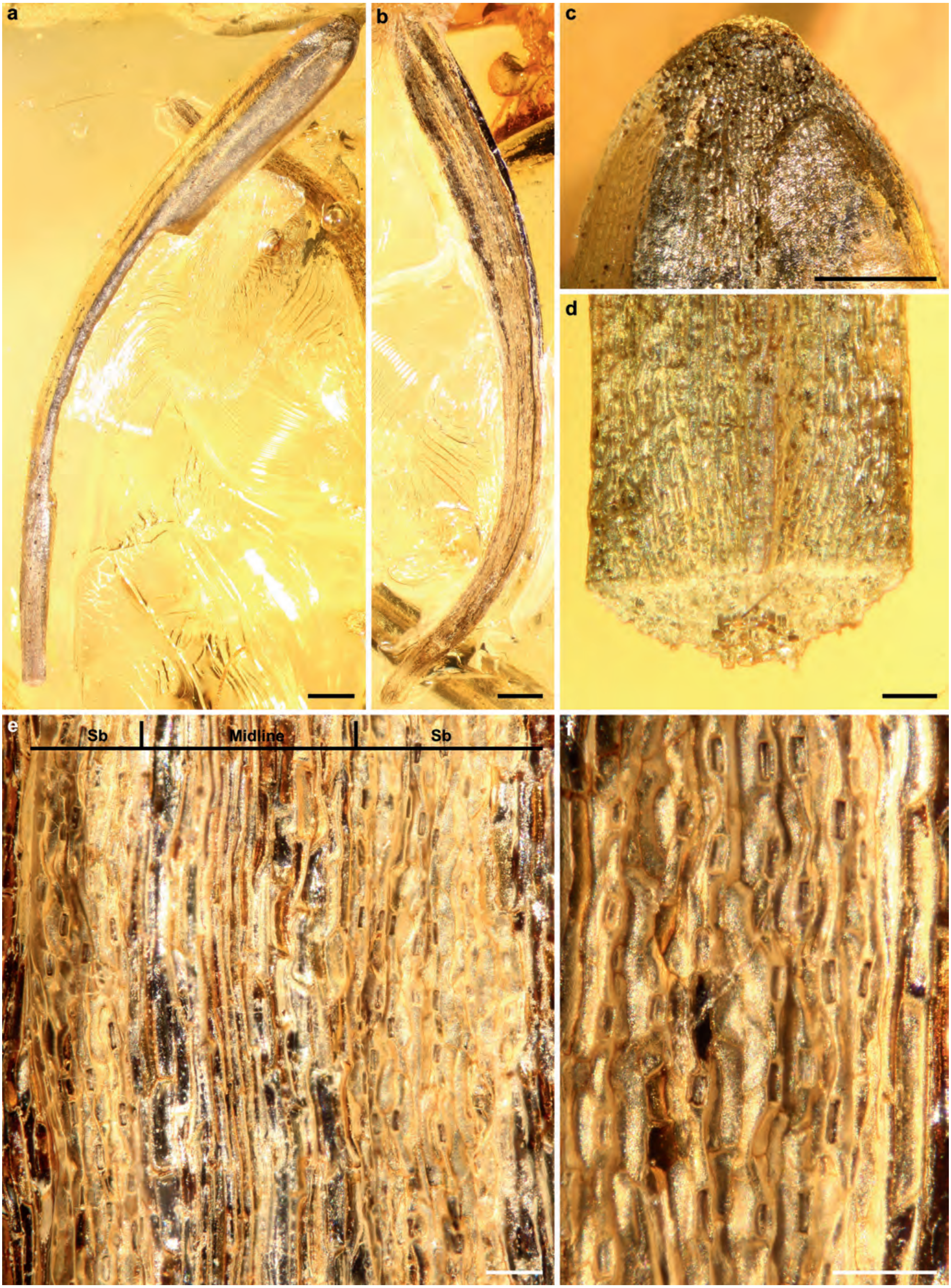
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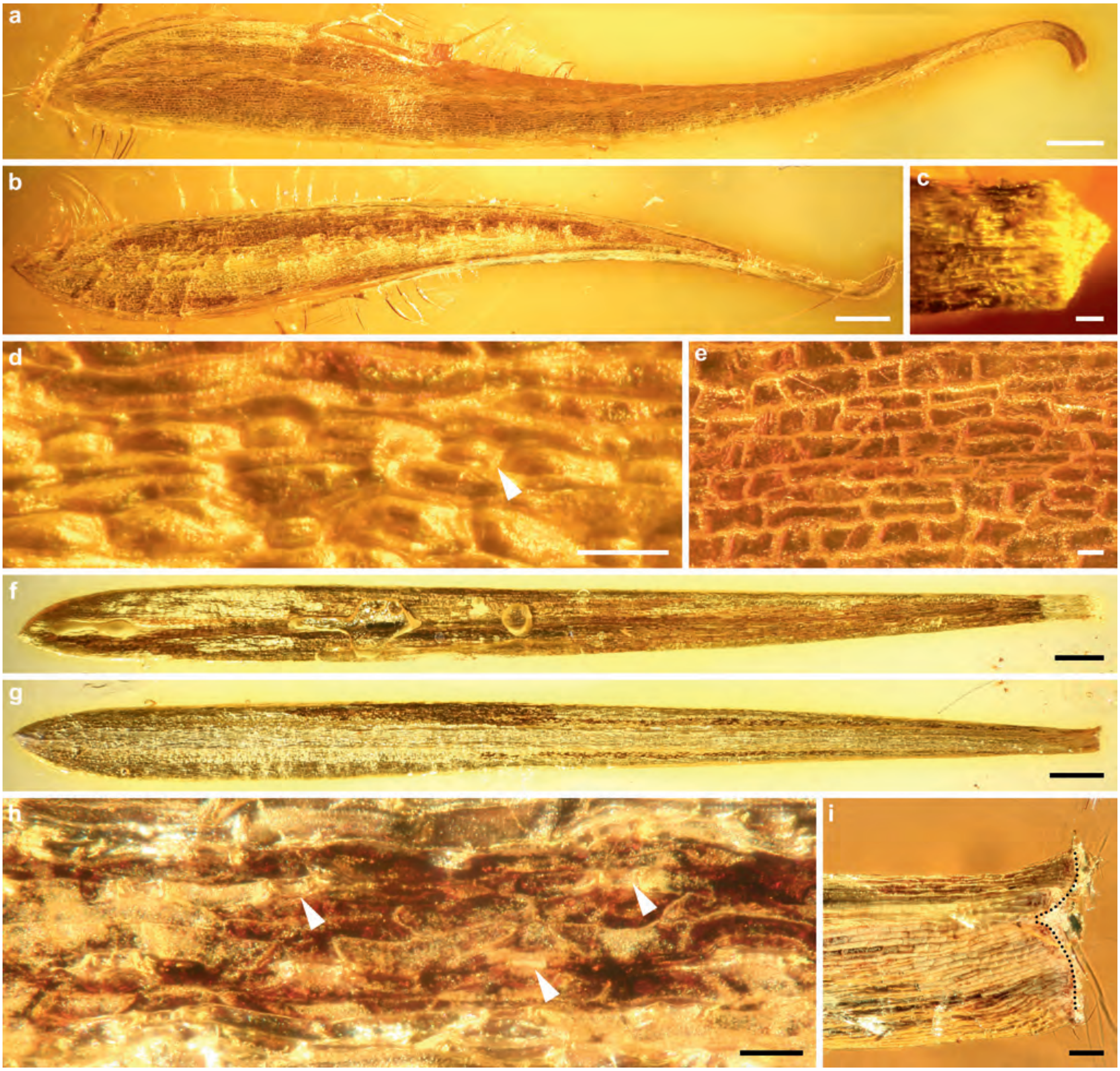

Fig. 28: Needles of *Pseudolarix* sp. from Baltic amber, (a-e) GZG.BST.23536, (f-i) GZG.BST.24334. (a, f) Overview of the needle from the adaxial side. (b, g) Overview of the needle from the abaxial side. (c, i) Triangular needle base; dotted black line indicates the triangular shape. (d, h) Monocyclic 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 µm (c, i), 50 µm (d, e, h).

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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 µm (d, f), 50 µm (e), 500 µm (c).

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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 with 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).

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 part)	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 cross section, 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.

(Figures 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 Berendt, p. 96, pl. V, figs 41-45; herein Fig. 29.

1845 *Dermatophyllites porosus* Goepp. et Berendt, 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.) Schimp., p. 303.

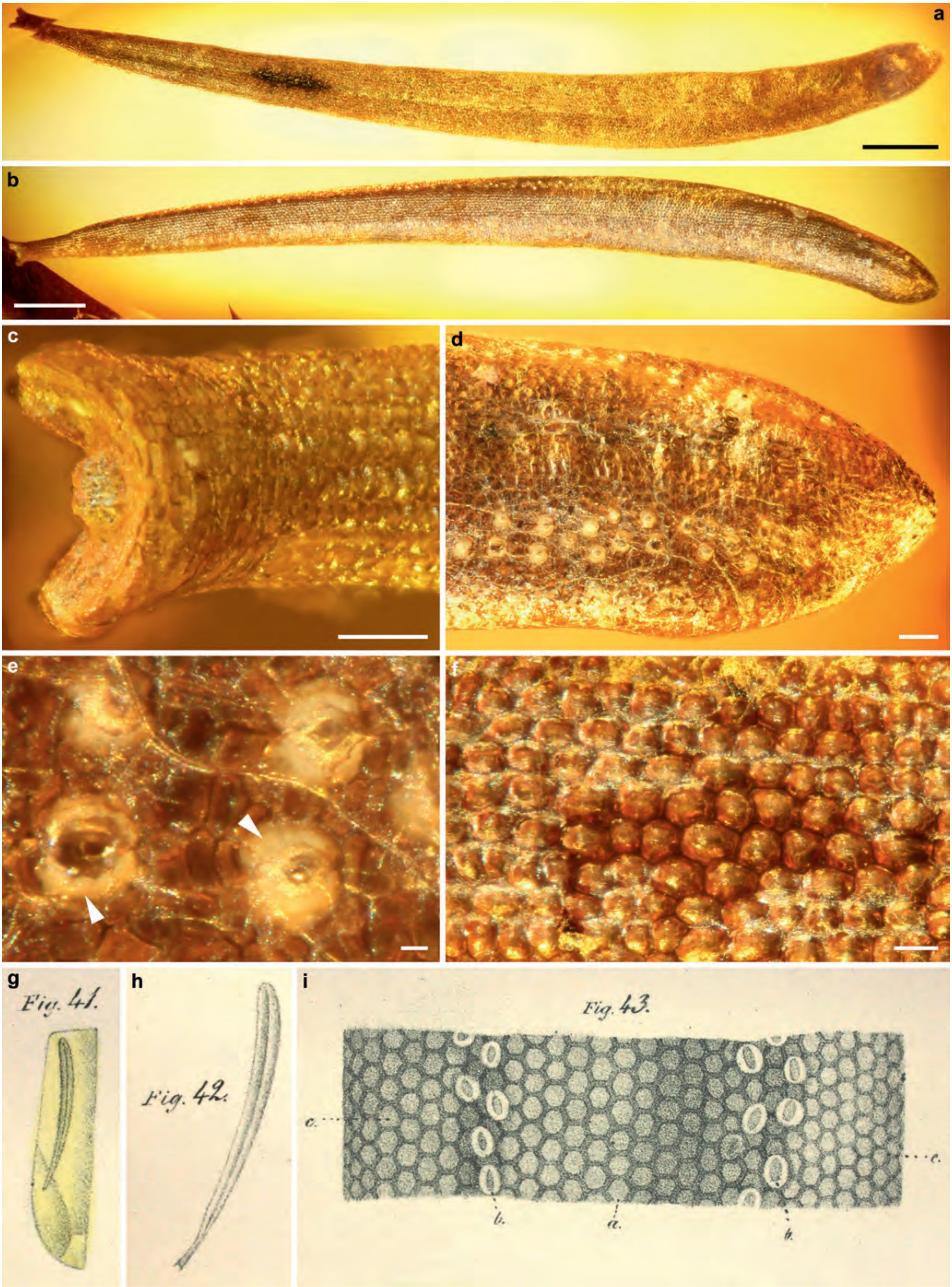
1883 *Abies obtusifolia* (Goepp. et Berendt) Goepp. et Menge, p. 35, pl. XIII, figs 107-110; herein Fig. 33.

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.

▶

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).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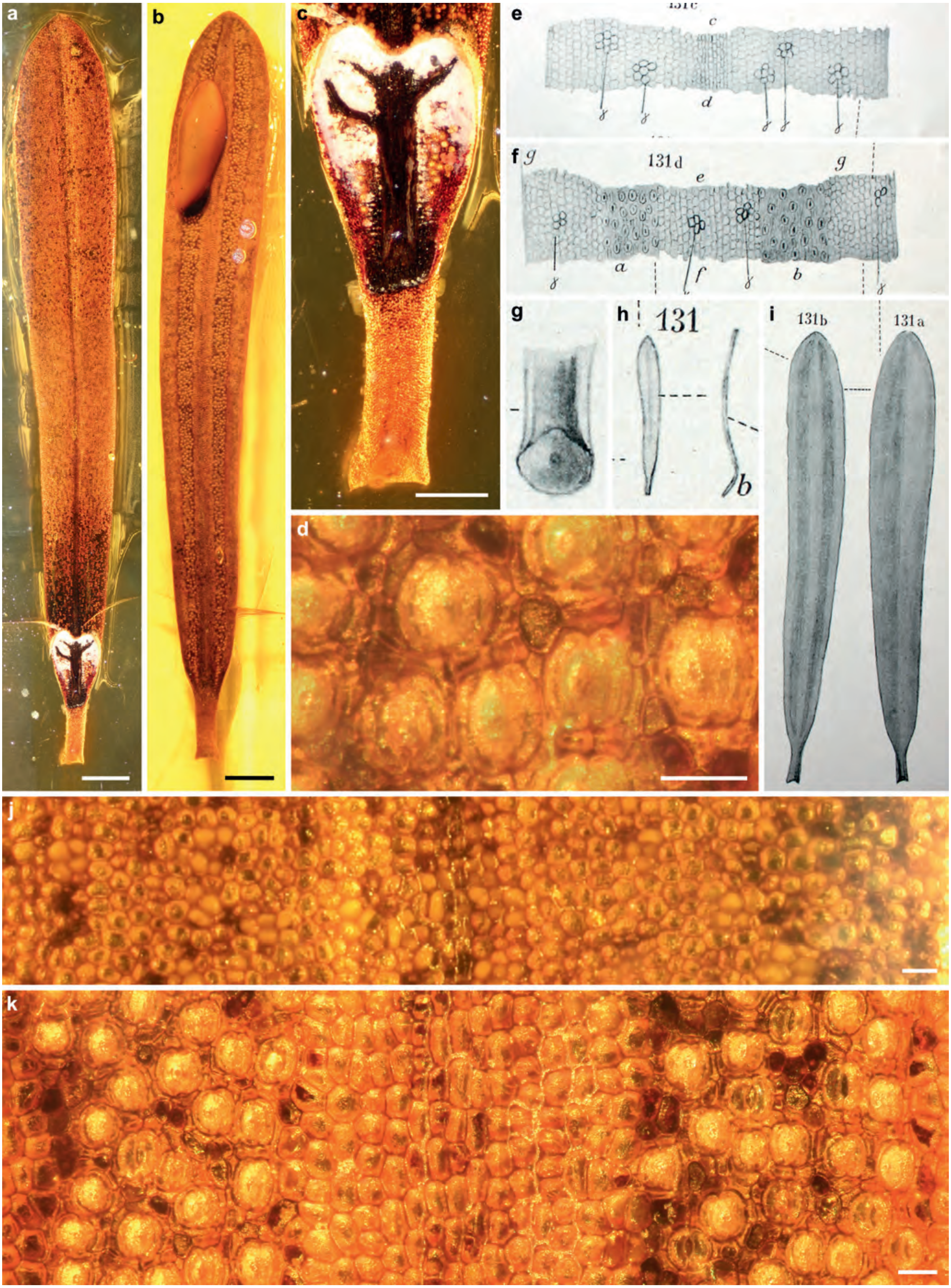
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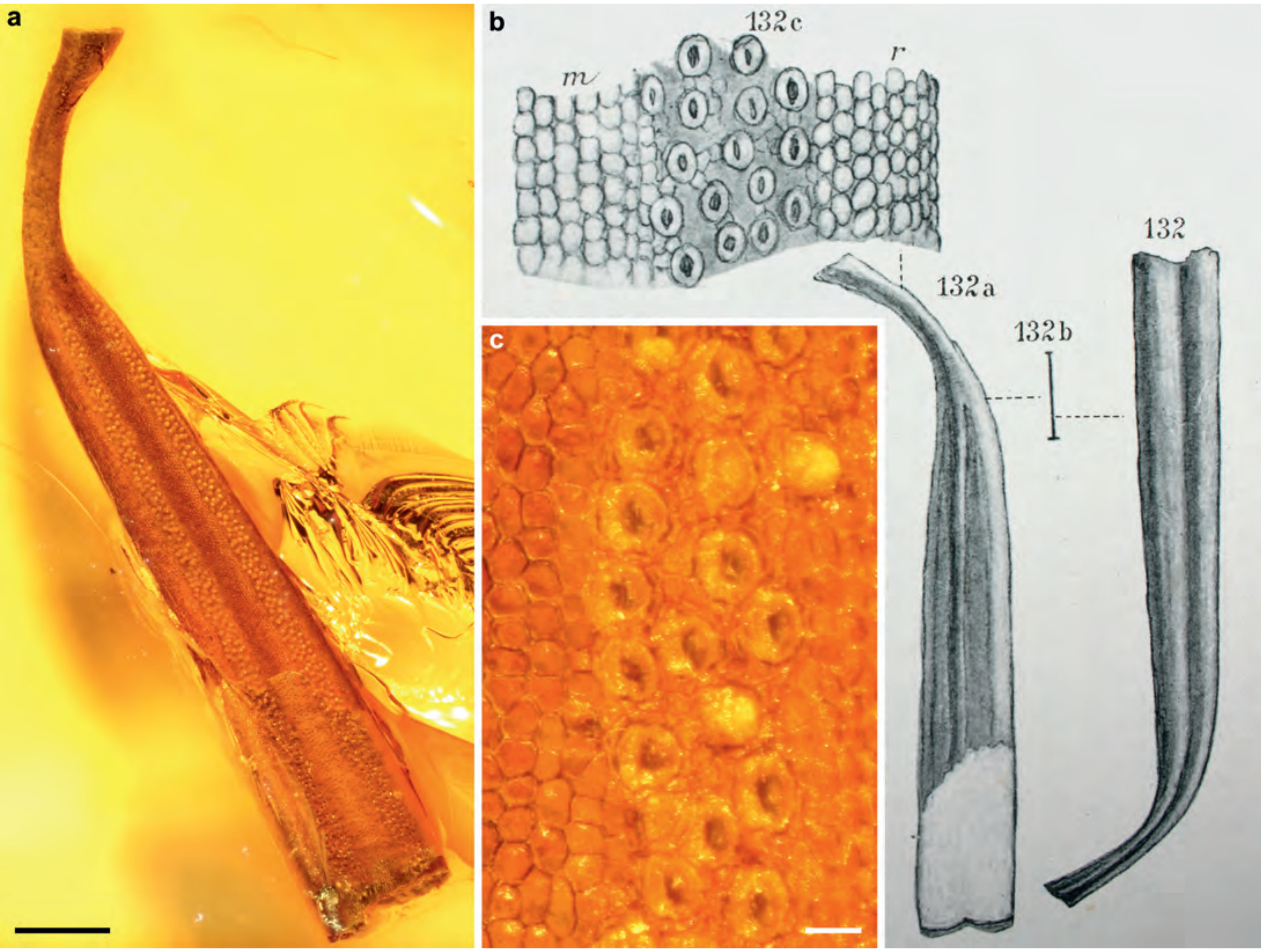

Fig. 31: 'Needle' of *Abies suckerii* from Baltic amber (a, c, GZG.BST.24355) and the historic drawings of this particular specimen (b, from Caspary & Klebs 1907, pl. XXX). (a) Overview of the leaf inclusion from the abaxial side showing two stomata bands on each side of the longitudinal midline and a very pronounced petiole. (b) Overview of the leaf inclusion from the abaxial (*132a*) and abaxial side (*132*) and detail of the stomata (*132c*). (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).

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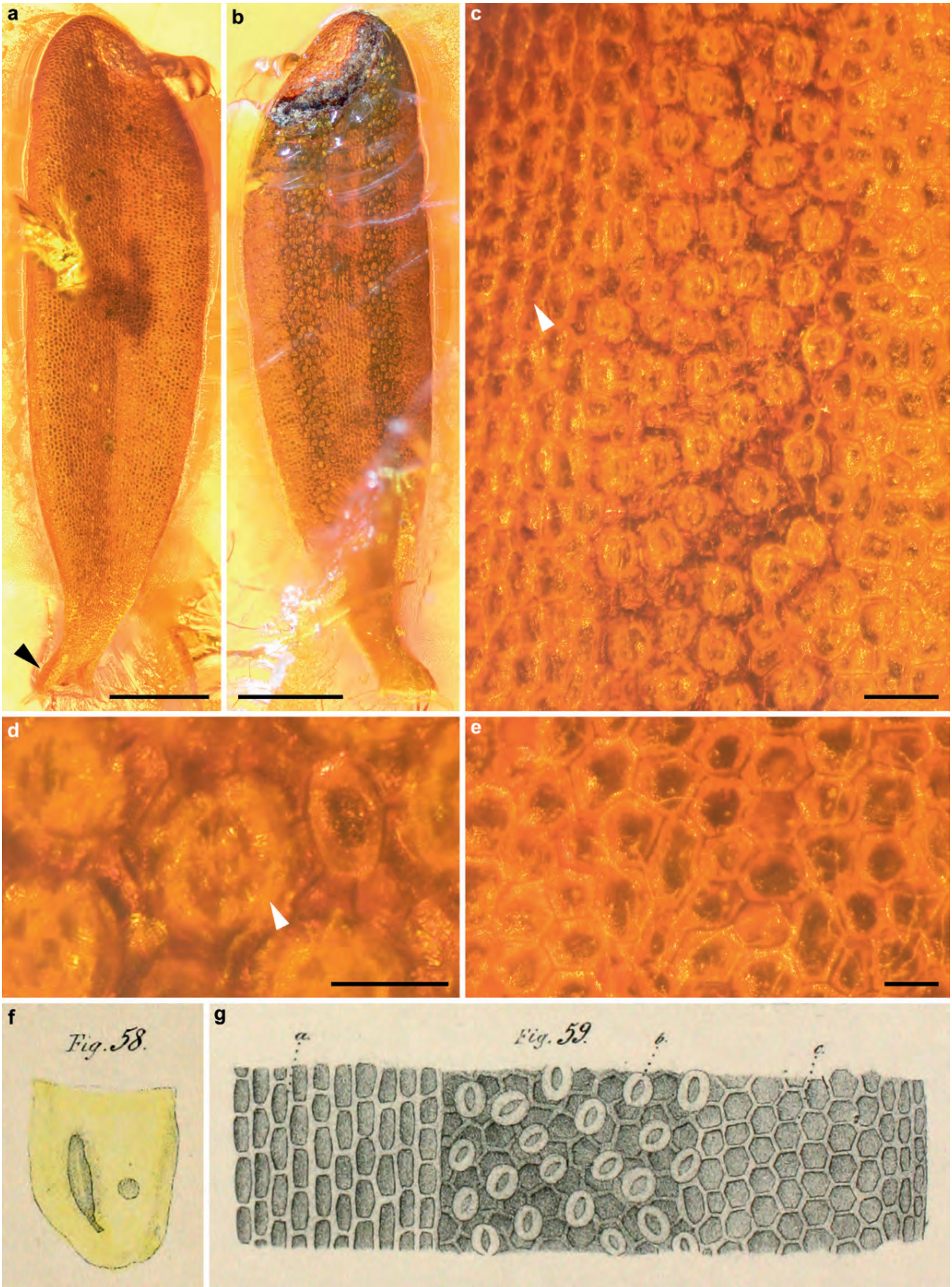
Fig. 30: 'Needle' of *Abies suckerii* from Baltic amber (a-d and i-j, GZG.BST.23539) and the historic drawings of this particular specimen (e-i, from Caspary & Klebs 1907, pl. XXX). (a, b, i) Overview of the leaf inclusion from the adaxial (a, i: *131a*) and abaxial side (b, i: *131b*). (c) Abaxial view 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; Ɣ: 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; Ɣ: 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 µm (c), 50 µm (d-k).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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	***Abietites obtusifolius***	***Abies suckerii***	***Abies suckerii***	***Abies linearis***	***Dermatophyllites porosus***
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

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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 µm (c), 50 µm (d, e).

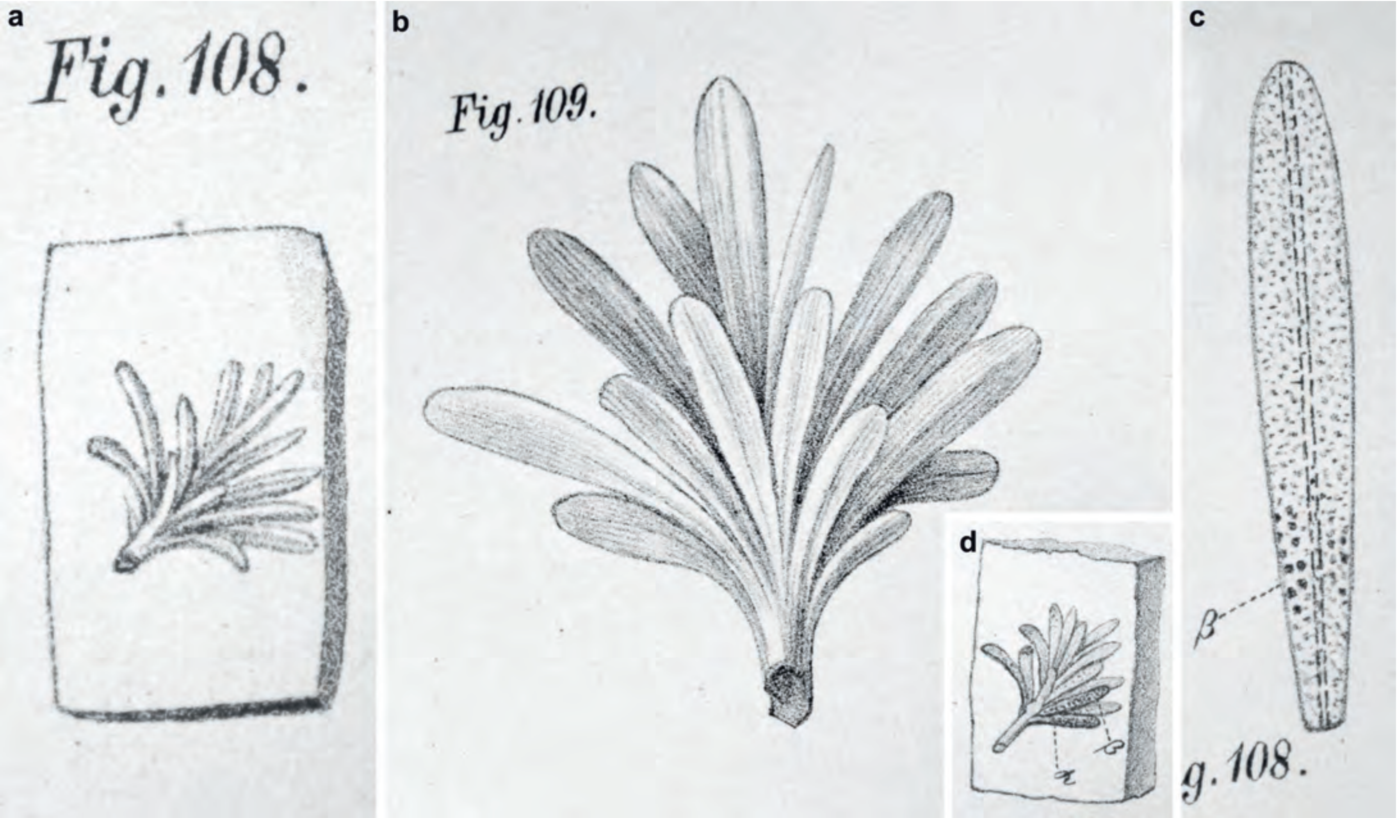

Fig. 33: Historic drawings of two lost amber specimens of *Abies obtusifolia* from Baltic amber (from Goeppert & Menge 1883, pl. XIII). (a) Twig fragment in a piece of amber. (b) Twig fragment shown in (a), magnified. (c) Needle of the twig fragment shown in (a, b); ß indicates the stomata. (d) Another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

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 entire, petiolate. Petioles 0.8 to 2.5 mm long × 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; 32b). Stomata pits parallel orientated towards the longitudinal midrib, 42 to 66 µm long × 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 × 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 × 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 × 20 to 65 µm wide.

Identification

Several complete leaves, leaf fragments and a twig fragment were described as *Abietites obtusifolius* Goepp. et Berendt (Fig. 29) and *Abies obtusifolia* (Goepp. et Berendt) 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 *Abietites 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),

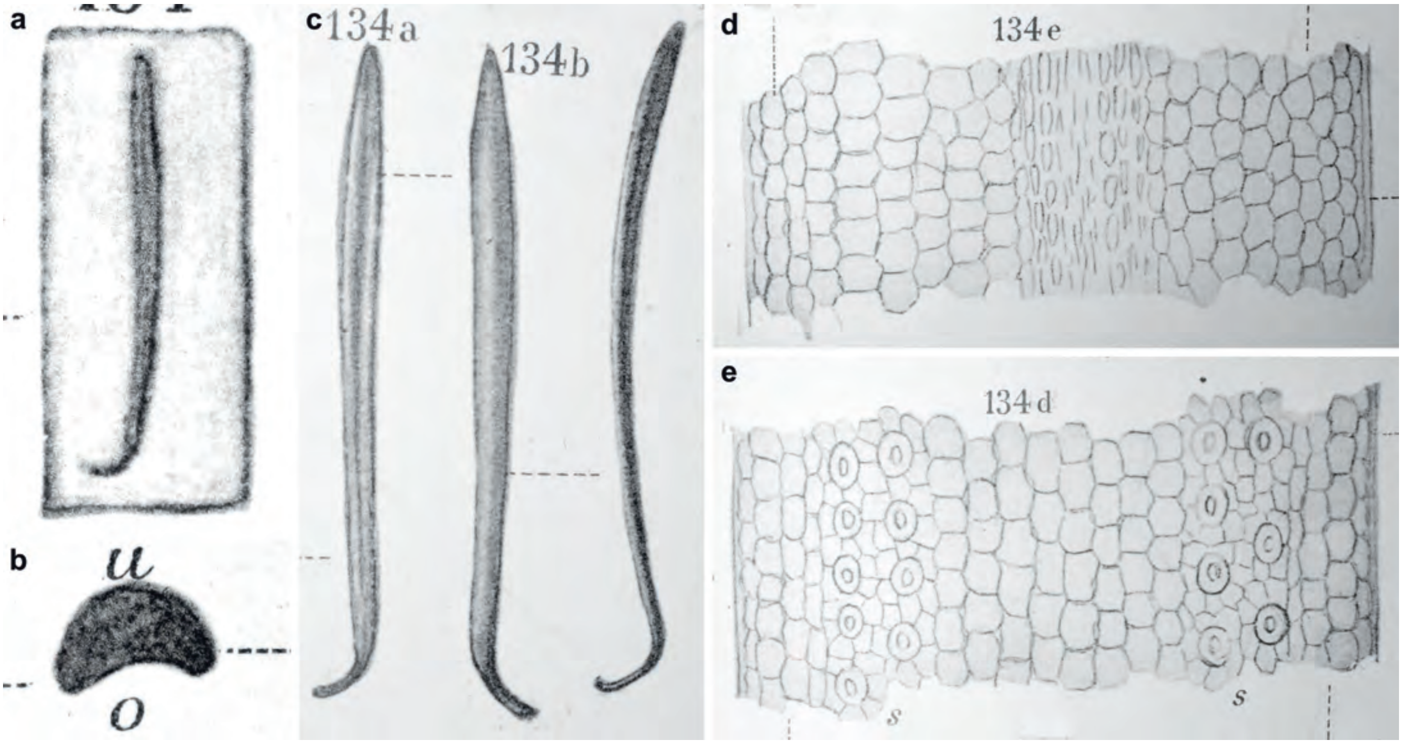

Fig. 34: Historic drawings of the 'needle' inclusion of *Abies linearis* from Baltic amber (from Caspary & Klebs 1907, pl. XXX, Künow Amber Collection). (a) Overview of the amber specimen with a 'needle' inclusion of *A. linearis.* (b) Outline of the petiole base showing the groove; *u* indicates abaxial 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.

the polygonal isodiametric shape of ordinary epidermal cells (Fig. 29f, i) and the incurved grooved long petiole (Fig. 29c).

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 Berendt 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 re-

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

Taxon	Stratigraphic range	Habitat	Selected associated plant taxa	References
Cupressaceae				
Calocedrus	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): *Tetraclinis, Cephalotaxus, Engelhardia, Sloanea, Platanus, Acer, Carpinus, Carya, Craigia*, Fabaceae, Lauraceae	Kvaček 1999; Shi et al. 2012
Quasisequoia couttsiae	upper Palaeocene 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): *Taxodium, Eotrigonobalanus, Rhodomyrthophyllum, Actinodaphne, Vaccinioides*, palms	Kunzmann 1999; Hennig & Kunzmann 2013
Taxodium	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** (*Taxodium-Nyssa haidingeri* association; early Miocene, Czech Republic): *Glyptostrobus europaeus, Quasisequoia couttsiae, Myrica, Betula, Nyssa, Rubus, Spondiaecarpum*	Boulter et al. 1993; Kunzmann et al. 2009
Geinitziaceae				
Cupressospermum saxonicum	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): *Cephalotaxus, Pinus, Sequoia, Tetraclinis, Taxodium, Limnocarpus, Comptonia, Potamogeton, Ficus, Fagus*	Mai & Walther 1991; Kunzmann 1999
Pinaceae				
Abies	late Cretaceous (Siberia), Eocene to Pleistocene (Central Asia, China, Japan, Europe, Russia, USA)	diverse	**Flora of Dernbach** (upper Pliocene, Germany): *Picea, Pinus, Sequoia, Populus, Juglans, Carpinus, Betula, Corylus, Fagus, Quercus, Ulmus, Magnolia, Acer*	Müller-Stoll 1938; Florin 1963; Farjon 1990; Xiang et al. 2007
Cathaya	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) 20-23 °C mean annual temperature, 800-2000 mm precipitation (Wiesa flora)	**Flora of Wiesa-Kamenz, Saxony** (Flora complex Wiesa; lower Miocene, Germany): *Keteleeria, Nothotsuga, Sequoia, Pinus, Pseudolarix, Torreya, Tsuga, Tetraclinis, Quasisequoia, Symplocos, Laurocarpum, Mastixia*, Fagaceae spp.	Liu & Basinger 2000; Kunzmann & Mai 2005
Nothotsuga protogaea	Palaeogene of North Siberia, lower Miocene to lower middle Miocene, Neogene of Wiesa (near Kamenz, Saxony, Germany)			Farjon 1990; Kunzmann & Mai 2005
Pseudolarix	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): *Pinus, Abies, Pseudotsuga, Tetraclinis, Laurocarpum, Liquidambar, Fagus, Salix, Rubus, Eurya, Symplocos*	Farjon 1990; LePage & Basinger 1995; Mai 1997; Budantsev & Golovneva 2009
Pinus	since Triassic? (Siberian formations), Jurassic (Europe), Cretaceous; fanning out since the Palaeogene	diverse	diverse	Farjon 2005b; Eckenwalder 2009
Sciadopityaceae				
Sciadopitys cf. *tertiaria*	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): *Cathaya, Pinus, Quasisequoia, Ilex, Nyssa, Magnolia, Palmoxylon, Rubus, Scirpus*	Menzel 1913; von der Brelie & Wolf 1981; Philippe et al. 2002; Mai 2004; Sadowski et al. 2016a

vised 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.

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 palaeobiogegraphic 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 Palaeogene 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 Palaeogene, 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).

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 Palaeogene 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 Palaeogene 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 Palaeogene of northern Siberia (Gaussen 1966; Kunzmann & Mai 2005) and from the lower Miocene Wiesa flora of Saxony (Germany)

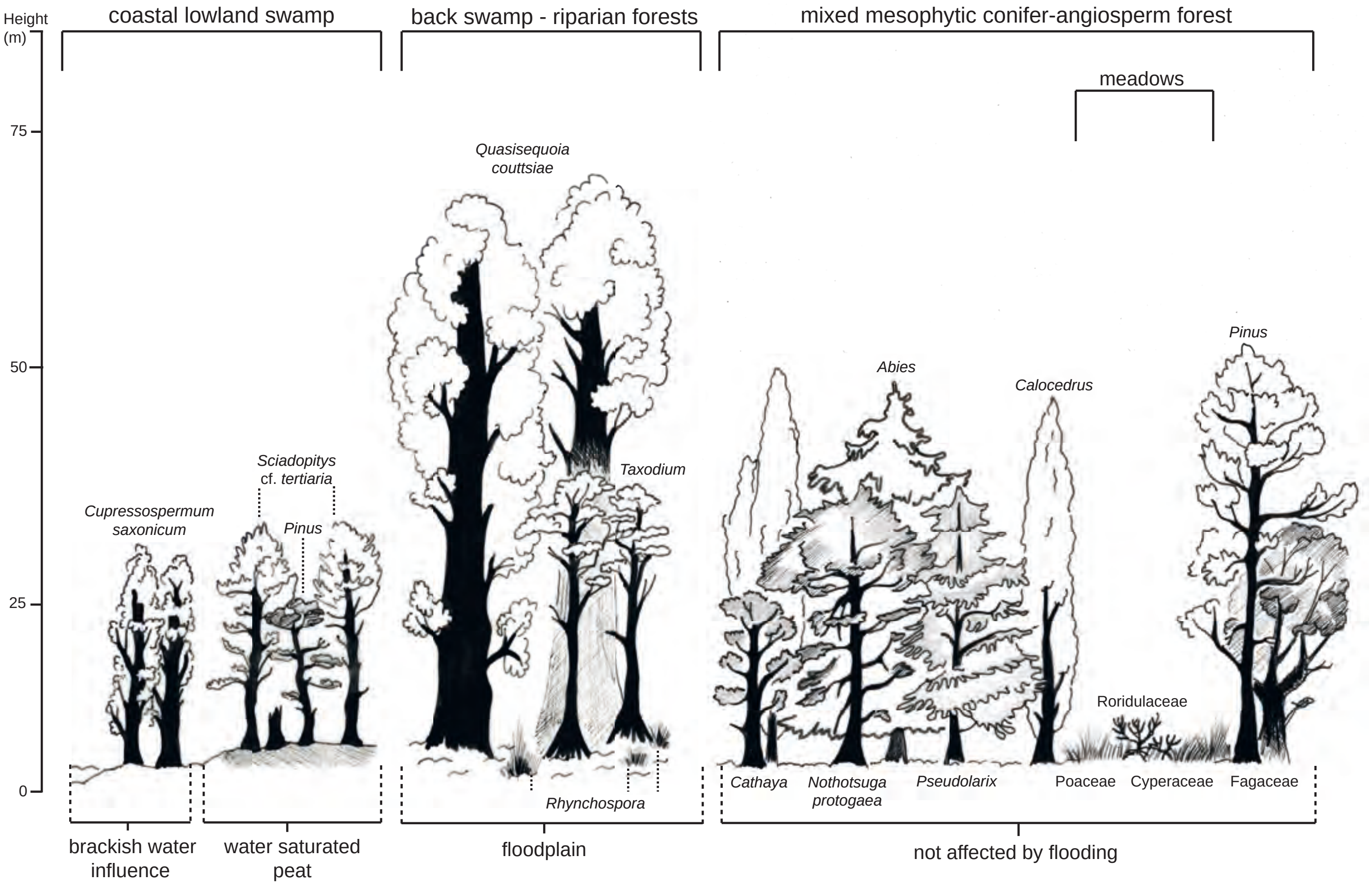

Fig. 35: Reconstruction of the habitat types of the Eocene 'Baltic amber forest' based on conifer taxa inclusions: coastal lowland swamps, back swamps to riparian forests and mixed mesophytic conifer-angiosperm forests with meadows. Tree height was estimated from fossil and extant analogous taxa, taken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

(Kunzmann & Mai 2005). Our record further substantiates the presence of this rare extant genus in the European Palaeogene 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 Palaeogene 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 Palaeocene (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* Mast. (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 Palaeogene 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) Loud., (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 Palaeogene 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* (Rossm.) 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 European localities revealed that these habitats were not influenced by brackish waters.

These swamp communities were further inhabited by *Taxoidum* whose fossil representatives were typical for riparian habitats and swamps of the European Oligocene and Miocene (Kunzmann et al. 2009). But also extant *Taxodium* species inhabit inundated areas along rivers, shallow waters and swamps (Farjon 2005a).

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* (Kirchh.) 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*.

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

Fossil	Analogous extant taxon	Distribution	Vegetation	Climate	Selected associated taxa	References
Cupressaceae						
Calocedrus	*Calocedrus* 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	*Pinus, Abies, Pseudotsuga, Sequoiadendron, Chamaecyparis, Arctostaphylos, Ceanothus, Castanopsis, Quercus, Lithocarpus*	Farjon 2005a; Shi et al. 2012
Taxodium	*Taxodium* spp.	SE USA, Mexico, Guatemala	peat bogs, swamps, alluvial or coastal plains, riparian forests, stagnant pools, gallery woodlands	warm-temperate to ‘subtropical’, humid	*Pinus, Nyssa, Acer, Magnolia, Fraxinus, Quercus, Liquidambar, Ilex, Viburnum, Platanus, Populus, Salix, Ficus, Inga*	Farjon 2005a; Kunzmann et al. 2009
Pinaceae						
Abies	*Abies* 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	*Picea, Tsuga, Thuja, Pinus, Chamaecyparis, Pseudotsuga, Larix, Cryptomeria, Fagus sylvatica*	Farjon 1990; Xiang et al. 2007; Eckenwalder 2009
Cathaya	*Cathaya argyrophylla*	South Central China	sclerophyllous broad-leaved forests to deciduous broad-leaved forests	warm-temperate to ‘subtropical’, humid (1000-2000 mm/a)	*Pinus, Tsuga, Nothotsuga, Quercus, Castanopsis, Lithocarpus, Fagus, Quercus* group *Cyclobalanopsis,* Theaceae, *Clethra, Vaccinium, Prunus, Blastus, Carrierea, Sorbus,* bamboo	Farjon 1990; Liu & Basinger 2000; Kunzmann & Mai 2005
Nothotsuga protogaea	*Nothotsuga longibracteata*	SE China	evergreen sclerophyllous broad-leaved forests to mixed mesophytic broad-leaved forests	warm-temperate to temperate, humid (1000-2000 mm/a)	*Pinus, Cephalotaxus, Cunninghamia, Chamaecyparis, Ginkgo, Podocarpus, Pseudotsuga, Tsuga, Taxus, Castanopsis, Lithocarpus, Quercus, Fagus, Tetracentron, Schima, Michelia, Magnolia, Cinnamomum, Altingia, Nyssa*	Kunzmann & Mai 2005; Farjon 1990
Pinus	*Pinus* spp.	worldwide (Northern Hemisphere)	boreal forests and alpine shrubberies to lowland tropical savannas, swamp margins to desert slopes	diverse	diverse	Farjon 2005b; Eckenwalder 2009
Pseudolarix	*Pseudolarix amabilis*	SE China	mixed-mesophytic and evergreen sclerophyllous broad-leaved forest; hills and alluvial plains	warm-temperate to temperate, humid (1500-2000 mm/a)	*Ginkgo, Pinus, Torreya, Liquidambar, Nyssa, Acer, Quercus, Pterocarya, Platycarya, Rhus, Magnolia*	Farjon 1990; LePage & Basinger 1995; Kunzmann & Mai 2005
Sciadopityaceae						
Sciadopitys cf. *tertiaria*	*Sciadopitys verticillata*	Japan	mixed conifer-angiosperm forests	temperate, humid	*Chamaecyparis, Tsuga, Abies, Pinus, Aesculus, Magnolia, Acanthopanax, Cercidiphyllum, Acer*	Tsukada 1963; Farjon 2005a

All these conifer taxa are described from Palaeogene 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 *Quercus* group *Cyclobalanopsis* (Oerst.) Schneid.) 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) Forman), such as stellate trichomes, flowers, fruits and buds (Conwentz 1886; Czeczott 1961; Forman 1964; Mai 1967).

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 orogenetic 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 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, *Doliostrobus* Marion (Doliostrobaceae) and *Tetraclinis* (Cupressaceae) which are both not recorded from Baltic amber. *Doliostrobus*, 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 un-identified 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.

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; Czeczott 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 *Doliostrobus* 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,

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	Doliostrobaceae	Geinitziaceae	Sciadopityaceae	Taxaceae	Pinaceae	Reference
Baltic amber										
	late Eocene?	mixed mesophytic	warm-temperate	*Calocedrus* sp. *Quasisequoia couttsiae* *Taxodium* sp.	-	*Cupressospermum saxonicum*	*Sciadopitys* cf. *tertiaria*	-	*Abies* sp. *Cathaya* sp. *Nothotsuga protogaea* *Pinus baltica, P. serrata, P.* aff. *schiefferdeckeri, P. cembrifolia* *Pseudolarix* sp.	this paper, Sadowski et al. 2016a
Spitsbergen										
	early Palaeocene-early Eocene	polar deciduous to mixed mesophytic	arctic cool temperate	*Fokieniopsis catenulate* *Glyptostrobus nordenskioldii* *Mesocyparis sabiniana* *Metasequoia* spp. *Sequoia brevifolia* *Taiwania schaeferi* ***Taxodium*** *olrikii* *Thuja ehrenswaerdii*	-	-	-	-	*Picea* sp. ***Pseudolarix*** *septentrionalis* *Pityolepis* spp.	Budantsev & Golovneva 2009; Kvaček 2010
Messel										
	latest early Eocene	notophyllous broad-leaved evergreen	warm humid paratropical	-	*Doliostrobus taxiformis*	-	***Sciadopitys*** pollen	*Cephalotaxus messelensis*	pollen	Wilde 2004
Zeitz, Weißelster Basin										
	latest middle-late Eocene	notophyllous broad-leaved evergreen	'subtropical'	*Chamaecyparites hardtii* *Cupressoconus rhenanus* *Glyptostrobus europaeus* ***Quasisequoia couttsiae*** *Sequoia abietina* ***Taxodium*** *dubium* *Tetraclinis salicornioides*	*Doliostrobus taxiformis*	-	***Sciadopitys*** pollen	*Cephalotaxus saxonica*	***Pinus*** *dixoni, P. eophylla, P.* cf. *hepios, P.* cf. *robustifolia, P. stroboides, P. thomasiana*	Mai & Walther 1985; Moraweck et al. 2015
Staré Sedlo										
	late Eocene	notophyllous broad-leaved evergreen	'subtropical'	***Quasisequoia couttsiae*** *Sequoia abietina* ***Taxodium*** *balticum*	*?Doliostrobus taxiformis*	-	***Sciadopitys*** pollen	*?Cephalotaxus* sp.	***Cathaya*** pollen ***Pinus*** pollen, *Pinus ornata, P. stroboides, P.* cf. *thomasiana*	Knobloch et al. 1996
Kučlin										
	late middle Eocene-early late Eocene	notophyllous broad-leaved evergreen	'subtropical'	*Tetraclinis salicornioides*	*Doliostrobus taxiformis*	-	-	-	-	Kvaček & Teodoridis 2011
Haselbach, Weißelster Basin										
	early Oligocene	mixed mesophytic	temperate	*Glyptostrobus europaeus* ***Quasisequoia couttsiae*** *Sequoia abietina* ***Taxodium*** *dubium* *Tetraclinis salicornioides*	-	-	-	*Cephalotaxus* ex. gr. *harringtonia*	***Pinus*** *eophylla, P. palaeostrobus, P.* cf. *robustifolia* *Tsuga plicata*	Kunzmann & Walther 2012
Thierbach, Weißelster Basin										
	early late Oligocene	mixed mesophytic	warm-temperate, humid	*Glyptostrobus europaeus* *Sequoia abietina* ***Taxodium*** *dubium* *Tetraclinis salicornioides*	-	***Cupressospermum saxonicum***	-	-	*Tsuga schneideriana*	Mai & Walther 1991; unpubl.
Wiesa										
	late early Micoene	mixed mesophytic to evergreen broad-leaved	warm-temperate	***Quasisequoia couttsiae*** *Sequoia abietina* *Tetraclinis salicornioides*	-	-	-	*Taxus engelhardtii* *Torreya bilinica*	***Abies*** *resinosa* ***Cathaya*** *bergeri* *Keteleeria hoehnei* ***Nothotsuga protogaea*** ***Pseudolarix*** *schmidtgenii* *Pseudotsuga jechorekiae* *Tsuga schneideriana, T. moenana* ***Pinus*** *grossana, P. hampeana, P. palaeostrobus, P.* cf. *hepios* *Pityophyllum wiesaensis*	Kunzmann & Mai 2005; Kunzmann 2014

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 Weißelster 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 *Doliostrobus taxiformis* (Sternberg) Kvaček is common in the riparian environments of the Weißelster Basin (Kunzmann 1999).

Doliostrobus 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 *Doliostrobus* 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 Barensburg flora (Early Palaeocene), the Storvola flora (late Palaeocene to early Eocene) and the Renardodden flora (late Eocene) (Budantsev & Golovneva 2009). All these floras are dominated by conifers, such as *Picea* A. Dietr., *Pseudolarix, Glyptostrobus, Metasequoia* 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 *Sequoia*, *Metasequoia* and *Picea*. The palaeoclimate for the early Palaeocene 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 Palaeocene 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 Kohlman-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 Kohlman-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) Hu ex C. N. Page and *Pseudolarix amabilis* (J. Nelson) Rehder are today mono-typic 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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