Staminate inflorescences with *in situ* pollen from Eocene Baltic amber reveal high diversity in *Fagaceae* (oak family)

Abstract: Eocene Baltic amber forms the largest amber deposit worldwide; however, its source vegetation and climate are much debated. Representatives of the oak family (*Fagaceae*) were abundant in the Baltic amber source area based on numerous inclusions of staminate inflorescences or individual florets, previously assigned to *Castanea* and *Quercus*. However, the actual generic and infrageneric diversity of *Fagaceae* from Baltic amber remained unknown. Using flower characteristics and section-diagnostic *in situ* pollen of staminate inflorescences and detached floret inclusions, we describe 18 fossil-species of *Fagaceae* making this family by far the most diverse plant family preserved in Baltic amber. We substantiate the occurrence of the *Castaneoideae*, *Quercoideae* (*Quercus* sect. *Cyclobalanopsis*/*Lobatae*, *Q.* sect. *Lobatae*, *Q.* sect. *Protobalanus*), Trigonobalanoideae and the extinct genus *Eotrigonobalanus*. Among the 18 fossil-species, six are described as new: *Q. aimeeana*, *Q. casparyi*, *Q. multipilosa*, *E. campanulata*, *E. conwentzii*, *E. longianthera*; and one new combination is published: *Q. brachyandra* (≡ *Castanea brachyandra*). In addition, a lectotype is designated for the name *Quercites meyerianus* and neotypes are designated for the names *Castanea inclusa* and *Quercus longistaminea* (≡ *C. longistaminea*). Members of the *Fagaceae* probably inhabited azonal and zonal vegetation types of the amber source area, including bottomland flood-plains and stream banks (*Q.* sect. *Lobatae*), dry habitats (*Q.* sect. *Lobatae*, *Q.* sect. *Protobalanus*), peaty soils, riparian and swamp forests (*Castanopsis*, *Eotrigonobalanus*), as well as mixed mesophytic forests (*castaneoids*, *Quercoideae*, trigonobalanoids). Affinities to extant North American and E to SE Asian floras support the recent notion that late Eocene Baltic amber (38–34 Ma) was formed in a warm-temperate climate.

Key words: Baltic amber forest, *Castaneoideae*, *Eotrigonobalanus*, *Fagaceae*, *Formanodendron doichangensis*, *Quercus* sect. *Lobatae*, *Quercus* sect. *Protobalanus*, palaeobotany, palaeoecology, palynology, *Trigonobalanus verticillata*

Article history: Received 12 February 2020; peer-review completed 25 May 2020; received in revised form 29 July 2020; accepted for publication 20 August 2020.

Citation: Sadowski E.-M., Schmidt A. R. & Denk T. 2020: Staminate inflorescences with *in situ* pollen from Eocene Baltic amber reveal high diversity in *Fagaceae* (oak family). – Willdenowia 50: 405–517. doi: https://doi.org/10.3372/wi.50.50303

1. Introduction

The *Fagaceae* (oak family) are the most diverse extant N temperate woody plant family, comprising ten genera (*Castanea* Mill., *Castanopsis* (D. Don) Spach, *Chrysolepis* Hjelmq., *Colombobalanus* Nixon & Crepet, *Fagus* L., *Formanodendron* Nixon & Crepet, *Lithocarpus* Blume, *Notholithocarpus* Manos & al., *Quercus* L., *Trigonobalanus* Forman) and more than 900 species. They are chiefly distributed in the N hemisphere, occurring from Canada to Colombia, across temperate Eurasia and extending into tropical forests of SE Asia (Soepadmo 1972; Kremer & al. 2012). *Quercus* and *Colombobalanus* occur as far south as equatorial Colombia in the Americas and *Castanopsis* and *Lithocarpus* cross the equator in Malesia (New Guinea, New Britain; Govaerts & Frodin

---

1 Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Invalidenstraße 43, 10115 Berlin, Germany; *e-mail: eva-maria.sadowski@mfn.berlin (author for correspondence).
2 Department of Geobiology, University of Göttingen, Goldschmidtstraße 3, 37077 Göttingen, Germany.
3 Department of Palaeobiology, Swedish Museum of Natural History, Box 50007, 10405 Stockholm, Sweden.
1998). *Quercus* is by far the most diverse genus of the family; its main diversity centre is Mexico (161 accepted species; Valencia-A. 2004) followed by China with more than 100 accepted species (Huang & al. 1999). Further diversity hotspots of the *Fagaceae* are subtropical-temperate forests of E and SE Asia (*Castanopsis*, *Lithocarpus*, *Quercus* sect. *Cyclobalanopsis* (Oerst.) Benth. & Hook. f.; Wu & Raven 1999; Menitsky 2005). *Fagaceae* of SE Asia are most diverse in mid-montane forests and are (co-)dominant trees with *Altingia* Noronha (*Altingiaceae*), *Engelhardia* Lesch. ex Blume (*Juglandaceae*), *Laureaceae* and *Schima* Reinn. ex Blume (*Theaceae*), as well as with conifers (*Araucariaceae*, *Podocarpaceae*; Soepadmo 1972).

All genera of the *Fagaceae* are important constituents of deciduous and evergreen forests, but are also major components of Mediterranean chaparral and woodlands (Nixon 1997). In addition, many species of *Quercus* sect. *Quercus* and *Q*. sect. *Lobatae* Loudon (white and red oaks) are important elements of riparian and swamp forests (Flora of North America Editorial Committee 1993). As nut-bearing plants, *Fagaceae* represent an important food source for vertebrates, which feed on the nuts, such as European jays, acorn woodpeckers, squirrels and pigs. These animals also play significant roles in the dispersal of *Fagaceae* (Vander Wall 2001).

As in extant forests, *Fagaceae* were important in Cenozoic palaeoecosystems of the N hemisphere. Extant genera of the *Fagaceae* mainly diversified during the Eocene, as shown for the genera *Fagus* (Manchester & Dillhoff 2004; Denk & Grimm 2009; Hofmann & al. 2019), *Quercus* and *Castanopsis* (Mai 1976; Manchester 1999; Grimsson & al. 2016) as well as *Castanea* (Crepet & Daghlian 1980; Manchester 1999). In Europe, *Fagaceae* were more diverse during the Paleogene than today, comprising several extinct genera, such as *Castaneophyllum* J. H. Jones & Dilcher, *Eotrigonobalanus* H. Walther & Kvaček and *Trigonobalanus* Kvaček & H. Walther (Walther & Zetter 1993; Kvaček & Walther 2012). The majority of fagaceous fossils are leaves and pollen, and occasionally fossil acorns and nuts (Denk & al. 2012; Barrón & al. 2017). In general, fossils of fagaceous stamine inflorescences are rare, because they are probably too delicate for preservation in the rock record. Up to now, impression fossils of stamine catkins of the *Fagaceae* include only few records, for instance from the middle Eocene Claiborne group (W Tennessee, U.S.A.; Wang & al. 2013), from the Eocene of Buchanan clay pit (Tennessee; Daghlian & Crepet 1983; Crepet 1989; Crepet & Nixon 1989a) and the late Oligocene of Texas ( Catahoula formation; Crepet & Nixon 1989b). In contrast, stamine inflorescences of the *Fagaceae* abundantly occur as inclusions in late Eocene Baltic amber (Conwentz 1886).

It is widely recognized that *Fagaceae* are recorded from Baltic amber, which is due to the presence of stellite trichomes, which are presumed to derive from oaks in nearly every fossiliferous specimen of Baltic amber. The Baltic amber deposit is also famous for the exquisite and three-dimensional preservation of plant organs, which are otherwise rare in the fossil record, including *Fagaceae* (Weitschat & Wichard 2010). For instance, Sadowski & al. (2018) recently reported a partial pistillate inflorescence of *Castanopsis*, which showed a life-like preservation of all internal structures. Stamine catkins of *Fagaceae* are also preserved in high fidelity, showing delicate structures such as petals, anthers and trichomes, which are significant for identification. The taxonomic affinities of these catkins in the Baltic amber flora were differently interpreted in the past. Caspary (1880, 1881, 1886a, 1886b) described 13 species of *Fagaceae* (12 species of *Quercus* and one species of *Castanea*), whereas Conwentz (1886) reported four castaneoid and 10 *Quercus* species. Kirchheimer (1937) reviewed the *Fagaceae* catkins from Baltic amber and placed them into three species of *Quercus* and one species of *Castanea*. The latest review by Iljinška (1982) accepted two species of *Castanea* and four species of *Quercus*, which significantly reduced the number of *Fagaceae* species from Baltic amber. All previous studies referred amber inclusions of stamine catkins to modern European genera.

Our recent survey of historic collections of Baltic amber and newly found material indicated that *Fagaceae* were more diverse in the source area of Baltic amber than previously suggested and that previous records need revision. Therefore, the aim of this study was to clarify the generic and infrageneric diversity of *Fagaceae* preserved in Baltic amber and to use the three-dimensionally preserved fossils to investigate their evolutionary and palaeogeographic implications.

This study focuses on the stamine inflorescences of Baltic amber *Fagaceae*. Evaluation of the amber fossils required a thorough assessment of the morphology of extant fagaceous stamine catkins, as comprehensive comparative studies on stamine inflorescences of the *Fagaceae* are still not available. Up to now, there are only few studies that mention or briefly describe the morphology of fagaceous catkins (e.g. Trelease 1924; Hjelmqvist 1948). Therefore, we studied herbarium specimens of the *Fagaceae* to investigate the morphology of extant stamine inflorescences and to assess whether they exhibit genus-diagnostic features. We then provide a comprehensive revision of fagaceous inclusions from Baltic amber, including type material of museum collections as well as newly discovered specimens. For assignment of these inclusions we also used in situ pollen extracted from the anthers of the stamine catkin inclusions. Numerous previous studies of *Fagaceae* pollen (fossil and extant; Solomon 1983a, 1983b; Denk & Grimm 2009; Makino & al. 2009; Denk & al. 2010, 2012; Grimsson & al. 2015, 2016a, 2016b) have shown that pollen provides sufficient information for distinguishing genera and subgroups of the *Fagaceae*. Our investigation of extant
herbarium material, amber specimens and their in situ pollen revealed a highly diverse fagaceous flora of the Baltic amber source area, encompassing Quercus sect. Lobatae, Q. sect. Protobalanus (Trel.) O. Schwarz, trigonobalanoid and castanoid taxa, as well as the extinct genus Eotrigonobalanus. For the latter, we report the first known fossil record of its staminate inflorescences.

2. Material and methods

2.1. Origin and age of the fossils

The majority of Baltic amber derives from opencast mines of the Sambian Peninsula (Samland, Kaliningrad Oblast, Russia) where up to several hundred tons of amber are currently mined every year. Baltic amber mainly originates from the so-called Blue Earth layer, which was dated as late Eocene (Priabonian; 37.8 – 33.9 Ma) on the basis of lithological and biostratigraphic studies, including pollen, spores and phytoplankton (Kosmowska-Ceranowicz 1997; Kasinski & Kramarska 2008; Standke 2017). Based on K-Ar age estimates of glauconites from the Blue Earth, a Lutetian (47.8 – 41.2 Ma) age of Baltic amber was suggested (Ritzkowsi 1997). However, a study by Clauser & al. (2005) questioned the reliability of glauconite-based chronometers, because contamination of the glauconite splits or reworking processes of the glauconites can lead to older age estimations (Clauser & al. 2005; Grimaldi & Ross 2017). The Lower Blue Earth (Lutetian) and the Lower Gestreifte Sande (upper Oligocene) also yield Baltic amber, but in smaller quantities. Hence, all amber-bearing strata possibly cover an age range of 48 to 23 million years (Kosmowska-Ceranowicz & al. 1997; Kasinski & Kramarska 2008; Standke 1998, 2008; see Sadowski & al. 2017a for further age discussion). However, the amber concentrations of the Lower Blue Earth and the Lower Gestreifte Sande are low. Therefore, the Lower Gestreifte Sande are treated as overburden in the opencast mines and is not further processed (pers. comm. with Dr. Gerda Standke, Freiberg). In the lithological section, the Lower Lutetian Blue Earth layer is located about 20 m beneath the Blue Earth and has been reported only from a single drilling core (Standke 2008: fig. 5; Störr & al. 1998, cited from Standke 2008). Due to the great depth of this layer and its low amber concentration, the Lower Blue Earth layer is not mined either (Standke 2017; pers. comm. with Dr. Gerda Standke, Freiberg). Baltic amber that eroded from the amber-bearing sediments can be found along the Baltic and North Sea coasts, where it is occasionally washed ashore (Weitschat & Wichard 2010). It is not documented whether historic Baltic amber collections contain these “sea ambers”, but because the layers of the Blue Earth are exposed on the coast of the Samland Peninsula (Usaityte 2000), they are likely the source layers of these “sea ambers”. All in all, it is most likely that the vast majority of Baltic amber collections derive from the Priabonian Blue Earth and are therefore 33.9 to 37.8 million years old.

2.2. Examination, preparation and imaging of specimens

For reviewing historic publications of fagaceous inclusions from Baltic amber, the type specimens described by Göppert & Berendt (1845), Caspary (1881, 1886) and Conwentz (1886) were required. However, due to losses in World War II, the location of many specimens is unknown (Kosmowska-Ceranowicz 1990). Therefore, we screened historic amber collections of the Museum für Naturkunde Berlin and of the Geoscientific Collection of the University of Göttingen (Germany) for type material. Furthermore, we studied recently collected amber specimens from the Hoffeins Amber Collection housed at the University of Göttingen. All amber specimens used in this study, including repository information, are listed in Table S1 (see Supplemental content online). If type material could not be found, we reviewed specimens by using original descriptions and illustrations.

Most specimens did not require preparation because they were already ground into shape and polished by previous preparators, curators and/or collectors. Therefore, in most cases, inclusions were located close to the amber surface with their anthers exposed (e.g. Fig. 16L; J; 23F, G; 49I–K). If available, pollen was carefully removed from the anthers using a scalpel and placed on carbon-covered SEM mounts, sputtered with gold/palladium (11 – 14 nm coat thickness), using an Automatic Sputter Coater (Canemco Inc.). The samples were then examined with a field emission scanning electron microscope (Carl Zeiss LEO 1530).

Two specimens from the Hoffeins Amber Collection (GZG.BST.21992 and GZG.BST.21991) needed further preparation. In both cases, wet silicon carbide paper was used (manufacturer Struers) to grind the specimens in stages (grit sizes FEPA 800, 1200, 2400, 4000) for creating even and parallel facets closely located to the inclusions. In a final step, the specimens were polished using a tooth-paste suspension, which was applied on a leather cloth (for more details on amber embedding and preparation see Nascimbene & Silverstein 2000 and Schmidt & al. 2018).

All amber specimens and the extant herbarium material were examined with a Carl Zeiss AxioScope A1 compound microscope, a Carl Zeiss Discovery V8 dissecting microscope and a Carl Zeiss Stemi 508 Microscope. We used incident and transmitted light simultaneously and photographed each specimen with digital Cameras (Canon EOS 5D), which were installed on both microscopes. We took up to 170 images from numerous focal planes, which were then merged to photomicrographic composites using the software package Helicon Focus 6.3.3 Pro for enhanced illustration of the three-dimensional inclusions. A micrometre eyepiece was used for measuring morphological features.
We examined extant herbarium material of staminate inflorescences of Castaneoideae, Quercoidae and Trigonobalanoidae representatives (Table S2, see Supplemental content online). Morphological features investigated are listed in Table 1 and explained in the Terminology section (see below); if available, we also used data on the flower morphology from previous studies (for references, see Table 1, 2).

Suitable herbarium specimens of the Trigonobalanoidae were only available for Formanodendron doichangensis (A. Camus) Nixon & Crepet and Trigonobalanus verticillata Forman. Information on Colombobalanus excelsa (Lozano & al.) Nixon & Crepet was obtained from previous studies (Hjelmqvist 1948; Forman 1964; Soepadmo 1972; Abbe 1974; Lozano-C. & al. 1979; Nixon & Crepet 1989; Kubitzki 1993). Within Quercus, we examined staminate inflorescences of most Quercus sections (Q. sect. Cerris Loudon, Q. sect. Cyclobalanopsis, Q. sect. Ilex Loudon, Q. sect. Lobatae, Q. sect. Protopalanus and Q. sect. Quercus; see Table 2, Fig. 7–13) with special focus on Q. sect. Lobatae, because their pollen was most abundant in the studied amber samples. We also sampled staminate inflorescences of all genera of the Castaneoideae.

2.3. Terminology

In the descriptions of fossil and extant fagaceous staminate inflorescences, we followed Simpson (2010).

2.3.1. Perianth morphology

The perianth of staminate florets differs among species of the Fagaceae. In the present study, we distinguished between different shapes of the perianth and the degree of its incision. We further described the shape of the perianth lobes, and whether their margins were entire, serrate or irregularly incised.

**Top-shaped** — The perianth is shaped like a cone, but with the apex pointing downward. The base of the perianth is narrow and then expands upward (Fig. 1A).

**Campanulate** — Bell-shaped; the perianth is more or less tube-shaped, basally rounded and flaring toward the apex. The upper margin is incised (mostly to the upper third) and forms triangular lobes (Fig. 1B, C). Campanulate perianths commonly occur in extant red oaks, such as Quercus agrifolia Née (Fig. 9F).

**Cyathiform** — The perianth is shaped like a cup and shorter and wider than a campanulate perianth. The perianth is incised to the upper third or the middle, forming lanceolate or triangular lobes (Fig. 1D, E).

**Deeply lobed** — In perianths where the incision extends to the base, the shape is difficult to assess, as the perianth lobes are diverting from each other (Fig. 1F, G; e.g. Quercus robur L., Fig. 12A, F). In this case, we did not mention a specific shape of perianth.

![Fig. 1. Perianth shapes of staminate inflorescences of Fagaceae. – A: top-shaped; B, C: campanulate; D, E: cyathiform; F, G: deeply lobed.](image-url)
There is a large variation of these shapes among extant and fossil Fagaceae, and sometimes transitions between these shapes were observed, such as in Quercus imbricaria Michx. (Fig. 10E, J).

2.3.2. Anther morphology

Anthers of Fagaceae differ in the shape of their apices and in the way they are attached to the filament. To distinguish between the different morphologies, we applied the following terms:

Mucronate — The anther is apically pointed (Fig. 2A; e.g. Quercus agrifolia, Q. sect. Lobatae, Fig. 9A, F; Quercus australis Jaub. & Spach, Q. sect. Ilex, Fig. 8G, H). This “peak” can be very acute or obtuse. However, we do not differentiate between different types of apical “peaks”.

Acute — The anther tapers gradually toward the apex and ends in an acute tip (Fig. 2B; e.g. Quercus chrysolepis Liebm., Q. sect. Protobalanus, Fig. 7A, B).

Notched — The anther is apically emarginate. This is a typical feature of the Castaneoideae (Fig. 2C; e.g. Castanopsis cuspidata (Thunb.) Schottky, Fig. 4O).

Obtuse — The anther is apically rounded (Fig. 2D; e.g. Quercus suber L., Q. sect. Cerris, Fig. 8C, D).

The attachment of the anthers to the apex of the filament differs among Fagaceae. Quercoideae possess anthers that are basifixed (Hjelmqvist 1948), meaning that the distal end of the filament connects to the base of the anther connective (Fig. 2E). In contrast, all Castaneoideae possess stamens where the anthers are dorsifixed (Hjelmqvist 1948). In this case, the filament apex is attached dorsally or medially to the anther (Fig. 2F). In Trigonobalanaloideae, anthers are basifixed with a pronounced heart-shaped (cordate) base (Fig. 2G; e.g. Trigonobalanus verticillata, Fig. 6C).

2.3.3. Trichomes

The trichomes of fagaceous leaves were intensely...
Table 1. Morphology of staminate inflorescences of extant Fagaceae, including Quercoidae, Castaneoideae and Trigonobalanoideae. Certain features that were not visible or absent are indicated by −, presence of features is indicated by +.

| Genus                | Quercoidae | Castaneoideae | Chrysolepis chrysophylla | Lithocarpus densiflorus | Notholithocarpus densiflorus | Trigonobalanus verticillata | Formanendron doichangensis | Colombobalanus excelsa |
|----------------------|------------|---------------|--------------------------|-------------------------|-----------------------------|-----------------------------|---------------------------|------------------------|
| **Rachis**           |            |               |                          |                         |                             |                             |                           |                        |
| Shape                |            |               |                          |                         |                             |                             |                           |                        |
| Rachis Shape         | pendulous catkin; sometimes branched | spike, erect, cylindrical with female flowers at base numerous; rarely glandular | spike, erect, cylindrical, rigid; sometimes panicles like numerous or glabrous | spike, elongate, stiff, sometimes branched or panicle-like densely pubescent, peltate trichomes | spike, erect, stiff, sometimes branched or panicle pubescent, rarely glabrous | spike, erect, stiff, androgy nous or only staminate | spike, erect, stiff, usually branched | pendulous catkin, lax, unbranched |
| Trichomes            | numerous or glabrous | numerous or glabrous | densely pubescent, peltate trichomes | densely pubescent; densely pubescent | densely pubescent; finely pubescent to glabrous | finely pubescent, "glandular"-peltate trichomes | stellate |                        |
| **Floret**           |            |               |                          |                         |                             |                             |                           |                        |
| Singular             | −/+        | −; helically arranged 3–7 | −/+; loosely arranged 1 or 3–7 | −/+; loosely arranged 1 or 3–7; normally 1 | 3–7(–11) | 1 or 3–7; normally 1 | 3–7; normally 3; rarely 30 | −/+ |
| No./dichasium        | 1(–4) | 3–7 | 3–7(–11) | 1(–)3–7(–12) | 1–3 | 2–7 |                        |                        |
| **Perianth**         |            |               |                          |                         |                             |                             |                           |                        |
| Shape                | campanulate to cyathiform | campanulate; deeply lobed | cyathiform, campanulate | cyathiform, campanulate | deeply lobed | top-shaped, connate in lower part | top-shaped, connate at base, apically rounded, margin in parts irregularly incised | deeply incised, connate at base |
| Lobes                | (4–)6(–9); obtuse, ovate, short, rounded, incised, connate at base | (5 or)6(or 7); oval to rounded, arranged in 2 rows (3 outer and 3 inner leaves) | 5 or 6; oval-rounded, regular, connate, in 2 well-defined cycles | (4–)6(or 7); merged at base, often divided into 3 internal and 3 external lobes | 5 or 6; ovate, elliptic, triangular, obtuse to slightly acute | 5 or 6; ovate, imbricate | 5–7; apex acute |
| Trichomes            | densely tomentose, pubescent to glabrous | finely pubescent or glabrous | tomentose | glabrous or with trichomes | pubescent | ciliate at margin | ciliate at margin, few trichomes on outer side of perianth |
| Central trichome tuft | −/+ | + (dense) | +, rudimentary pistillode | +, rudimentary pistillode | + | + | + |                        |
| **Stamens**          |            |               |                          |                         |                             |                             |                           |                        |
| No./floret           | (3–)5 or 6 (typically 6–12, rarely 9–15) | 6–20 | 10–15 | (6–10) or 12 | (8–)10–12(–15) | 10–12 | 6 | 6 | 6 |
| Filament | slender, curved, short in proportion to perianth | free, curved, far projecting | free, filiform, glabrous, far projecting | far projecting | relatively long, filiform, glabrous | elongated, overtopping perianth | overtopping perianth | overtopping perianth |
|----------|-----------------------------------------------|-------------------------------|------------------------------------------|----------------|-----------------------------------|-------------------------------|-------------------|-------------------|
| **Anthers** | | | | | | | | |
| Length (mm) | 0.5–1 | ≥ 0.5 (rarely longer) | 0.25–0.35 | ≥ 0.5 (rarely longer) | 0.2–0.5 | 0.25 | 0.5–1 | 0.5–0.6 | 0.5–1 |
| Shape | ovoid-oblong, elliptic, sub-globose, glabrous, pubescent | ovado to subglobose | subglobose or ovado, reniform | as broad as long | reniform or subglobose | broadly ovate | broadly ovate | oblong |
| Base | cordate to broadly rounded | notched | notched | notched | slightly notched | strongly cordate | strongly cordate | strongly cordate |
| Apex | notched, obtuse or mucronate | notched | notched | notched | slightly notched | muconate | muconate | notched |
| Attachment | basifixed | dorsifixed | dorsifixed | dorsifixed | dorsifixed | basifixed | basifixed | sub dorsifixed or basifixed | +/- |
| Subtending bract | +/- | + | + | + | + | + | + | + | +/- |
| Shape | 1 bract/floret; small, lanceolate, acute, caducous | rhombic, subtending each dichasium | small | large, ovate, mucronate; 1 bract per floret/ dichasium | middle bract ovate, rounded, pubescent; laterally very small bracts | 1 primary bract, 2 secondary bracts: middle bract broadly oblate; 2 lateral smaller bracts | basal: 1 broadly triangular bract; lateral: 2 smaller bracts, membranous, persistent or caducous | 3 bracts, ovate-lanceolate, pubescent, caducous |

**References**
Camus 1929, 1936–1938; Hjelmqvist 1948; Camus 1952–1954a, 1952–1954b; Forman 1964; Soepadmo 1970, 1972; Abbe 1974; Lonzano-C. & al. 1979; Manchester & Crane 1983; Kaul 1985; Nixon & Crepet 1989; Kubitzki 1993; Borgardt & Pigg 1999; this study
Table 2. Morphology of staminate inflorescences of extant sections of *Quercus*. Certain features that were not visible or absent are indicated by −, presence of features is indicated by +. Additional information of *Quercus* sect. *Cyclobalanopsis* and *Q.* sect. *Quercus* was taken from Hjelmqvist (1984), Kaul (1985) and Nixon (1993).

| Quercus | Q. sect. Cyclobalanopsis | Q. sect. Protobalanus | Q. sect. Cerris | Q. sect. Ilex | Q. sect. Lobatae | Q. sect. Quercus |
|---------|-------------------------|----------------------|----------------|--------------|----------------|----------------|
| Figures | Fig. 7C–J               | Fig. 7A, B           | Fig. 8A–F      | Fig. 8G–L    | Fig. 9–11, 13A, B, D, E | Fig. 12, 13C, F, G, H |
| Rachis  |                         |                      |                |              |                |                |
| Shape   | pendulous catkin        | pendulous catkin     | pendulous catkin | pendulous catkin | pendulous catkin | pendulous catkin |
| Trichomes | numerous to pubescent | pubescent           | numeros to pubescent | numeros to pubescent | pubescent or only few trichomes | few to pubescent |
| Floret  |                         |                      |                |              |                |                |
| No./dichasium | 3               | 1                   | 1              | 1            | 1              | 1              |
| Perianth |                         |                      |                |              |                |                |
| Shape   | deeply lobed            | cyathiform, widely open; incised to upper third and base | cyathiform to campanulate, incised to lower third | cyathiform, incised to upper or lower third, closed | campanulate, cyathiform, or deeply lobed | campanulate; deeply incised to base, widely open |
| Lobes   | 5 or 6; large ovate to lanceolate or not discernible | acute apex, triangular | ovate to lanceolate | acute apex, triangular | 2–6; acute or rounded apex; triangular or lanceolate | narrow, linear; triangular |
| Trichomes | numerous: outer surface, margin, flower centre (tuft) | along margin and on outer surface; bulbous | perianth surface | mainly along margin; few on perianth | glabrous or trichomes along margin and/or upper third | margin, outer surface |
| Central trichome tuft | +               | –                   | only few trichomes | +            | −/+             | −/+            |
| Stamens |                         |                      |                |              |                |                |
| No./floret | 5(–17)                 | 6–8                 | 6              | 3–6         | 5 or 6         | 7 or 8         |
| Filament | short in proportion to perianth | short; entirely covered by perianth | short; reaching perianth margin | short; entirely covered by perianth | short; covered by perianth | short; as long as perianth or even shorter |
| Anthers |                         |                      |                |              |                |                |
| Shape   | elliptic to widely elliptic, round | elliptic | elliptic to widely elliptic; trichomes on anthers (or glabrous) | elliptic, mostly covered by perianth; trichomes on anthers (or glabrous) | elliptic, elongated | elliptic |
| Apex    | notched or mucronate | acute | notched or obtuse | mucronate | notched or mucronate | notched |
| Attachment | basifixed             | basifixed          | basifixed     | basifixed  | basifixed     | basifixed     |
| Subtending bract |                         |                      |                |              |                |                |
| Shape   | ovate, large bract per floret or dichasium; mostly singular, exceeding perianth, caducous or persistent | linear, elongated (longer than perianth) or absent | as long as perianth, as long as perianth; or lanceolate; or absent | as long as perianth, as long as perianth; or absent | lanceolate, slender, long |
studied by Camus (1929, 1936–1938, 1952–1954a, 1952–1954b), Jones (1986) and Deng & al. (2013, 2014), but using different terminologies. A consistent classification of trichomes of the Fagaceae was proposed by Deng & al. (2014), who also incorporated observations of Jones (1986) and Camus (1929, 1936–1938, 1952–1954a, 1952–1954b). In most instances, we followed Deng & al. (2014) and applied her terminology. In cases of trichome types not covered by Deng & al. (2014), such as the peltate type, we followed Jones (1986). In this study, we mainly observed the following trichome types:

**Solitary** — Simple, acute and singular trichomes, which differ in length (Fig. 3A, B). In some specimens, these trichomes were helically curled or “wavy” (Fig. 3B); however, in most cases they were rather stiff and straight (Fig. 3A).

**Bifurcate** — The trichome consists of two rays, which are fused at their base. Both rays possess an acute apex (Fig. 3C). Deng & al. (2014) suggested that bifurcate trichomes were reduced stellate trichomes and should therefore be incorporated into the category “simplified stellate”. However, “simplified stellate” also comprises trichomes with up to eight arms and is therefore a category too unspecific for our study. For this reason, we kept the category “bifurcate”.

**Stellate** — In stellate trichomes, unicellular, apically acute rays radiate from a fused base. The number of rays varies (about ≥ 7 rays per trichome; Fig. 3D).

**Uniseriate** — Singular trichomes, consisting of numerous cells, which are arranged in a simple row. They vary in length and terminate in an acute apex or a rounded, enlarged cell (Fig. 3E). The basal cells are similar to the terminal ones and are often bulbous (Type 15, “simple uniseriate” sensu Jones 1986).

**Branched uniseriate** — A basal cell branches into numerous multicellular arms. In each arm, the cells are arranged in a simple row (Fig. 3F). In our study, the basal cell was not as large, as observed by Deng & al. (2014). However, we consider this difference to be a variation of this trichome type, which was previously observed by Jones (1986; Type 18, “branched uniseriate”).

**Peltate** — For this trichome type we follow Jones (1986). This trichome type consists of a short stalk, which apically terminates into a round, flat cap. This cap is composed of numerous cells, which radiate from the centre (Fig. 3G, H). Jones (1986) distinguished between “thick-walled” and “thin-walled” peltate trichomes. This is, however, not discernible in our fossils.

### 2.4. Phylogenetic framework

We used the molecular phylogeny by Oh & Manos (2008) as a phylogenetic framework for subgroups within Fagaceae. Four groups corresponding to morphologically based subfamilies comprise the monophyletic Trigonobalanidae (a single extant genus *Fagus*), the monophyletic *Trigonobalanus* (comprising the extant genera *Colobobalanus, Formanodendron* and *Trigonobalanus*), the paraphyletic *Castaneoidae* (*Castanea, Castanopsis, Chrysolepis, Lithocarpus, Notholithocarpus*), and the monophyletic *Quercoideae* (a single extant genus *Quercus*). For the infrageneric classification of *Quercus*, we follow Denk & al. (2017).

### 3. Results

#### 3.1. Staminate inflorescences of extant Fagaceae

In previous studies on staminate inflorescences of the Fagaceae from Baltic amber, Caspary (1880, 1881, 1886a, 1886b), Conwentz (1886), Kirchheimer (1937) and Iljinskaja (1982) used different morphological features of the florets to distinguish between species and genera. The taxonomic value of these characteristics in extant Fagaceae has not been comprehensively studied.

Although several studies provide information on staminate inflorescences of modern taxa (e.g. Camus 1929, 1936–1938; Hjelmqvist 1948; Soepadmo 1972), they did not picture the florets and entire catkins of all genera or sections of *Castaneoidae, Trigonobalanidae* and *Quercus*. In the following, we describe and compare the different morphological characters of staminate inflorescences of the Fagaceae, mainly based on our own observations (see Table 1, 2).

In *Castaneoidae*, the staminate inflorescences are spikes, which are ascending, rigid and sometimes branched (Fig. 4A, E, I, K; 5A–F, I, L). They can be exclusively staminate and androgynous with pistillate flowers at their bases, such as in *Castanea* (Camus 1929) or *Notholithocarpus densiflorus* (Hook. & Arn.) Manos & al. (Camus 1952–1954b). In contrast, staminate inflorescences of *Quercus* are always a pendulous catkin with a lax rachis, which may be branched (e.g. Fig. 12A–D), but which is never androgynous. The staminate florets of the *Castaneoidae* are mostly clustered together in dichasia of three to 11 florets (Fig. 4I, K, M; 5B, E), whereas in *Quercus*, the florets are mainly arranged singularly along the rachis (e.g. Fig. 9A–D; except for *Q*. sect. *Cyclobalanopsis*, Fig. 7C–J). Another major difference between both groups is the morphology of stamens. In the *Castaneoidae*, the filaments project far beyond the perianth and are about twice as long (or more) as the perianth (Fig. 4A, B, F, H, M–Q; 5D, K). In contrast, most staminate florets of *Quercus* exhibit stamens with short filaments, which are mostly covered by the perianth (Fig. 8F, G, H, J). Anthers of *Castaneoidae* are round and dorsifixed (Fig. 4B, H, N,
Fig 4. Staminate inflorescences of extant *Castanea* (A–F) and *Castanopsis* (G–Q) (*Castaneoideae*), sampled from herbarium specimens (see Table S2 [Supplemental content online] for affiliations). – A, B: staminate catkin (A) and florets (B) of *Castanea sativa* with elongated stamens, projecting far beyond perianth; note dense arrangement of florets along rachis; C, D: densely pubescent staminate catkin of *Castanea pumila* (L.) Mill.; E, F: *Castanea dentata* (Marshall) Borkh.; G, H: *Castanopsis indica* (Roxb. ex Lindl.) A. DC.; note pronounced trichome tuft in floret centre (H); I, J: *Castanopsis argentea* (Blume) A. DC.; K, L: *Castanopsis tribuloides* (Sm.) A. DC.; note loose arrangement of florets along rachis; M, N: *Castanopsis fissa* (Champ. ex Benth.) Rehder & E. H. Wilson; O, P: *Castanopsis cuspidata*; note small, dorsifixed anthers (O); Q: *Castanopsis orthacantha* Franch. – Scale bars: A, C, E, G, I, K, M, P, Q = 1 mm; B, D, F, H, J, L, N, O = 500 µm.
Fig. 5. Staminate inflorescences of extant Chrysolepis (A, B), Notholithocarpus (C, D) and Lithocarpus (E–K) (Castaneoideae), sampled from herbarium specimens (see Table S2 [Supplemental content online] for affiliations). – A, B: staminate catkin of Chrysolepis chrysophylla with very densely arranged, pubescent florets; C, D: pubescent staminate catkin of Notholithocarpus densiflorus; E, F: Lithocarpus dealbatus (Hook. f. & Thomson ex Miq.) Rehder; note large bract (arrowhead) subtending floret cluster; G, H: Lithocarpus corneus (Lour.) Rehder; I, J: Lithocarpus craibianus Barnett; note pronounced central trichome tuft (J); K, L: Lithocarpus polystachyus (Wall. ex A. DC.) Rehder; note densely pubescent rachis and central trichome tuft (K). – Scale bars: A, C, F, G, I, L = 1 mm; B, D, E, H, J, K = 500 µm.
Fig. 6. Staminate inflorescences of extant *Trigonobalanus verticillata* (A–D) and *Formanodendron doichangensis* (E–K) (*Trigonobalanaceae*), sampled from herbarium specimens (see Table S2 [Supplemental content online] for affiliations). – A: overview of staminate catkin of *Trigonobalanus*; rachis is rigid; B, D: dichasia of florets; note central trichome tuft (B, arrowhead); C: anthers with mucronate apex and cordate base; E: overview of staminate catkin of *Formanodendron*; rachis is lax; F: dichasium of numerous florets; G: rachis with different trichome types; H: detached floret; arrowhead indicates dense, central trichome tuft; I: anthers with mucronate apex (arrowhead) and cordate base; J, K: “glandular” peltate trichomes of rachis. – Scale bars: A, E = 1 mm; B, D, F, H = 500 µm; C, G, I = 300 µm; J, K = 50 µm.
Fig. 7. Staminate inflorescences and florets of extant Quercus sect. Protobalanus (A, B) and Q. sect. Cyclobalanopsis (C–J), sampled from herbarium specimens (see Table S2 [Supplemental content online] for affiliations). – A, B: Quercus chrysolepis; note acute anthers (B); C–E: Quercus glauca; note elongated linear bract subtending dichasium (C) and large ovate subtending bracts (D, E); F, G: pubescent, staminate catkin (F) and dichasium (G) of Quercus salicina Blume; H–J: Quercus kerrii Craib; note short filaments and dense arrangement of florets in dichasium. – Scale bars: A, C, D, F, H = 1 mm; B, E, G, I, J = 500 µm.
Table 3. Species list of fagaceous staminate inflorescences and detached floret inclusions from Baltic amber, including synonyms and publications where the respective name was mentioned or differently interpreted. The total species number for each publication is summarized at the end of this table, excluding taxa that are dubious or of uncertain affinity.

| Collection number | Göppert & Berendt 1845 | Bronniart 1849; Unger 1850 | Göppert 1853 | Caspary 1880 | Caspary 1881 | Caspary 1886a, 1886b | Conwentz 1886 | Kirchheimer 1937 | Iljinskaja 1982 | This study |
|-------------------|------------------------|-----------------------------|--------------|-------------|-------------|-------------------|---------------|----------------|---------------|-----------|
| GZG.BST.21989     | —                      | —                           | —            | —           | —           | Castanea inclusa   | Castanea longistaminea | Castanea inclusa | ? Castanea inclusa (Castaneoideae) |
| GZG.BST.21991     | —                      | —                           | —            | —           | —           | —                 | Castanea longistaminea | —              | Castanea longistaminea (Castaneoideae) |
| MB.Pb.1979/0817   | Quercites meyerianus   | Quercus meyeriana           | —            | Quercus subglabra | —           | —                 | Quercus subglabra | Quercus subglabra | Quercus subglabra | Quercus caspary (Q. sect. Cyclobalanopsis or Q. sect. Lobatae) |
| GZG.BST.24389     | —                      | —                           | —            | —           | —           | —                 | Quercus subglabra | —              | Quercus subglabra (Q. sect. Lobatae) |
| GZG.BST.24414     | —                      | —                           | —            | —           | —           | —                 | —              | —              | Quercus multi-pilosa (Q. sect. Lobatae) |
| GZG.BST.24402     | —                      | —                           | —            | —           | —           | —                 | —              | —              | —              |
| MB.Pb.1979/0660   | —                      | —                           | —            | —           | —           | Castanea brachyandra | Castanea brachyandra | —              | Quercus brachyandra (Q. sect. Protobalanus) |
| MB.Pb.1979/0813   | Quercites meyerianus   | Quercus meyeriana           | —            | Quercus meyeriana | —           | —                 | Quercus subglabra | Quercus subglabra | Quercus subglabra | Quercus meyeriana (section undetermined) |
| MB.Pb.1979/0868   | —                      | —                           | —            | Quercus mucronata | —           | Quercus mucronata | Quercus mucronata | Quercus mucronata | Quercus mucronata (section undetermined) |
| MB.Pb.1979/0814   | —                      | —                           | —            | Quercus trichota | —           | Quercus trichota | Quercus trichota | Quercus trichota | Quercus trichota (section undetermined) |
| MB.Pb.1979/0656   | —                      | —                           | —            | Quercus nuda | —           | Quercus nuda | Quercus nuda | Quercus subglabra | Quercus subglabra | Quercus nuda (section undetermined) |
| MB.Pb.1979/0521   | —                      | —                           | —            | Quercus limbata | —           | Quercus limbata | Quercus limbata | Quercus subglabra | Quercus subglabra | Quercus limbata (section undetermined) |
| Code            | Quercus trichota var. macranthera | Quercus mucronata | Quercus meyeriana var. denticulata | Quercus subglabra | Quercus subglabra | Quercus subvillosa | Quercus capitato-pilosa | Castanea subvillosa | Castanea longistaminea | In total |
|-----------------|-----------------------------------|-------------------|-----------------------------------|-------------------|-------------------|-------------------|-----------------------|-------------------|-----------------------|----------|
| GZG.BST.21995   | —                                 | —                 | —                                 | —                 | —                 | —                 | —                     | —                 | —                     | 11       |
| GZG.BST.21996   | —                                 | —                 | —                                 | —                 | —                 | —                 | —                     | —                 | —                     | 11       |
| GZG.BST.6895    | —                                 | —                 | —                                 | —                 | —                 | —                 | —                     | —                 | —                     | 11       |
| GZG.BST.24568   | —                                 | —                 | —                                 | —                 | —                 | —                 | —                     | —                 | —                     | 11       |
| GZG.BST.24419   | —                                 | —                 | —                                 | —                 | —                 | —                 | —                     | —                 | —                     | 11       |
| MB.Pb.1979/0815 | Quercites meyerianus              | Quercus meyeriana | Quercus meyeriana                 | —                 | —                 | —                 | —                     | —                 | —                     | 11       |
| MB.Pb.1979/0816 | —                                 | —                 | —                                 | —                 | —                 | —                 | —                     | —                 | —                     | 11       |
| MB.Pb.1979/0644 | —                                 | —                 | Quercus ciliata                   | —                 | —                 | —                 | Quercus meyeriana    | —                 | —                     | 11       |
| lost            | —                                 | —                 | —                                 | —                 | —                 | —                 | —                     | —                 | —                     | 11       |
| lost            | —                                 | —                 | —                                 | —                 | —                 | —                 | Quercus klebsii       | —                 | —                     | 11       |
| lost            | —                                 | —                 | —                                 | —                 | —                 | —                 | Quercus klebsii       | —                 | —                     | 11       |
| lost            | —                                 | —                 | —                                 | —                 | —                 | —                 | Quercus meyeriana    | —                 | —                     | 11       |
| lost            | —                                 | —                 | —                                 | —                 | —                 | —                 | —                     | —                 | —                     | 11       |
| lost            | —                                 | —                 | —                                 | —                 | —                 | —                 | —                     | —                 | —                     | 11       |
| lost            | —                                 | —                 | —                                 | —                 | —                 | —                 | —                     | —                 | —                     | 11       |
| lost            | —                                 | —                 | —                                 | —                 | —                 | —                 | —                     | —                 | —                     | 11       |
| lost            | —                                 | —                 | —                                 | —                 | —                 | —                 | —                     | —                 | —                     | 11       |
| In total        | 1                                 | 1                 | 2                                 | 2                 | 11                | 1                 | 14                    | 4                 | 6                     | 18       |
Table 4. Morphological features of staminate inflorescences of *Castaneoideae* from Baltic amber. In case of missing type material, information on morphology was taken from descriptions of Caspary (1881) and Conwentz (1886). Features that were absent or not discernible/described are indicated by −; presence of features is indicated by +.

| Taxon | ? Castanea inclusa | ? Castanea inclusa | ? Castanea longistaminea | ? Castanea longistaminea | Castaneoid, genus indet. |
|-------|-------------------|-------------------|--------------------------|--------------------------|--------------------------|
| Figures | GZG.BST.21989 (neotype) | holotype lost | GZG.BST.24371 (neotype) | holotype lost | GZG.BST.21991 |
| Inflorescence | detached florets | detached florets | detached florets | detached florets | rigid, erect |
| Length (cm) | − | − | − | − | 2.4 |
| Rachis | Width (μm) | − | − | − | 620–800 |
| Floret | Trichomes | − | − | − | peltate |
| No./dichasium | − | − | − | − | ≥ 6 |
| Perianth | Length (mm) | 0.7 | 0.2 | 1.3–1.7 | 0.2–0.23 |
| Width (mm) | 0.8 | − | − | 1.2–2.2 | − |
| Shape | campanulate to top-shaped, deeply incised | campanulate to top-shaped, deeply incised | campanulate to top-shaped, deeply incised | campanulate to top-shaped, deeply incised | incised up to middle |
| Lobes | 6; linear to lanceolate, apex acute-obtuse, margin ciliate | 6; oblanceolate-lanceolate, apex acute, margin ciliate | 6; linear to lanceolate, apex acute-obtuse, glabrous | 6; linear to lanceolate, apex acute, margin ciliate | 5; apex rounded to slightly acute, margin ciliate |
| Trichomes (on floret) | Morphology | uniseriate; solitary | solitary | − | solitary |
| Location | only central trichome tuft on perianth | − | − | − | margin extremely hairy |
| Central trichome tuft | + | − | − | − | + |
| Stamens | No./floret | > 4–6 | 10 | 9 | 9–12 |
| Filament | elongated, projecting far beyond perianth | 2–2.5 × as long as perianth | elongated, projecting far beyond perianth | elongated, projecting far beyond perianth | elongated, projecting far beyond perianth |
| Length (μm) | 1220–1640 | − | (1800–)2180(–2520) | − | (840–)1600(–1480) |
| Width (μm) | 40–70 | − | (60–)63(–70) | − | (50–)67(–80) |
| Anthers | Length (μm) | 200–250 | − | (390–)444(–470) | − | (240–)258(–300) |
| Width (μm) | 160–250 | − | (200–)270(–330) | − | (150–)190(–220) |
| Shape | elliptic to round | almost round | elliptic | ovate | elliptic to circular |
| Apex | notched | notched | notched | notched | notched |
| Attachment | dorsifixed | dorsifixed | dorsifixed | dorsifixed | dorsifixed |
| Subtending bract | Length (mm) | − | − | − | up to 3 |
| Width (mm) | − | − | − | − | 0.4–0.7 |
| Shape | − | − | − | − | 0.64–1.2 |
| Trichomes | − | − | − | − | broadly ovate |

Sadowski, P. et al.: Staminate inflorescences of Fagaceae from Eocene Baltic amber.
O), whereas in *Quercus*, anthers are often quite large and elliptic with a basified attachment to the filament apex (e.g. Fig. 9F, G, I). As far as we observed in the herbarium specimens, none of the Castaneoideae possessed staminate florets with mucronate anther apices; however, this often occurs in *Quercus* (Q. sect. *Ilex* and Q. sect. *Lobatae*, Fig. 8H, 9F). Most staminate florets of *Quercus* are subtended by narrow and acute bracts (Fig. 8E, L; 12D), which differ from the large and ovate bracts subtending staminate florets of the Castaneoideae (Fig. 5E). Due to these differences between staminate inflorescences of Castaneoideae and *Quercus*, it is possible to distinguish staminate inflorescences of both groups from another.

Among the Trigonobalanoidae, only Trigonobalanus verticillatus possesses staminate inflorescences that are spike-like and ascending (Fig. 6A). However, *Pseudobalanus verticillata* possesses staminate inflorescences that are more spaced out and ascending (Fig. 6A). However, *T. verticillata* is distinct from the Castaneoideae in the morphology of the stamens: anthers are basified, the anther base is distinctly cordate and the anther apex is mucronate (Fig. 6C), anthers are larger, and filaments are not as elongated as in the Castaneoideae.

The bigger challenge is to differentiate between staminate inflorescences of genera and species within the Castaneoideae, because the staminate inflorescences of castaneoids share many features, such as the morphology of stamens (Table 1). However, among the studied species, we found a few distinct characteristics of each genus. Staminate florets of *Castanea* are more densely clustered and helically arranged along the rachis (Fig. 4A–F). In *Castanopsis*, the florets are more loosely arranged (Fig. 4I–Q, except for *Castanopsis indica* (Roxb. ex Lindl.) A. DC., Fig. 4G). In addition, *Castanopsis* and Lithocarpus exhibit a dense trichome tuft in the floret centre (Fig. 4H, L, N, O; 5K) or a pistillode, which is rudimentary in *Castanopsis* and more pronounced in *Lithocarpus* (Fig. 5I, Table 1 for references). Staminate inflorescences of Chrysopleis and Notholithocarpus are the most pubescent spikes of all Castaneoideae observed in this study (Fig. 5A–D). In contrast, staminate inflorescences of the remaining genera possessed trichomes (Fig. 4C, D, I, J; 5G, H), but never in such a dense cover as in these two genera. Despite the named features, it remains difficult to distinguish between castaneoid staminate inflorescences. Pollen of *Castanea* is uniform and therefore cannot be used for identification to genus level (Praglowski 1984; Grímsson & al. 2015).

Within the Trigonobalanoidae, genera can be differentiated by their pollen ornamentation as well as by the morphology of the staminate catkins (Table 1). As already mentioned, staminate inflorescences of Trigonobalanus are rigid spikes (Fig. 6A); in contrast, Formanodendron (Fig. 6E, G) and Colobobalanus possess pendulous catkins with a lax rachis (Lozano-C. & al. 1979). Formanodendron exhibits “glandular” peltate trichomes on the rachis (type 19 sensu Jones 1986; Fig. 6J, K), which only occur in this particular genus of the Fagaceae (Jones 1986). Staminate florets of all three species are arranged in clusters from two to seven (Fig. 6D, F) or may be singular in Colobobalanus and Trigonobalanus (Lozano-C. & al. 1979). All three species possess trichome tufts in the floret centre (Fig. 6B, H) and six stamens per floret, but in Formanodendron and Trigonobalanus the anthers are mucronate (Fig. 6C, I), while anthers in Colobobalanus are apically notched (Lozano-C. & al. 1979). All three species also differ in their pollen morphology: pollen of Trigonobalanus is rod-like vertical (Denk & Grimm 2009) with fine granular exine ornamentation (Nixon & Crepet 1989). In Colobobalanus and Formanodendron, pollen is microverrate (Denk & Grimm 2009) with tightly arranged, agglomerated tufts and well-defined rugae (Nixon & Crepet 1989; Denk & Grimm 2009). Both species differ from each other in the pollen shape (prolate in Colobobalanus and peroblate in Formanodendron) and in the arrangement of rugae, which is denser in Formanodendron (Nixon & Crepet 1989). Staminate inflorescences of Trigonobalanus differ from *Quercus* by the rigid rachis (pendulous in *Quercus*). Staminate catkins from Colobobalanus and Formanodendron are also distinct from *Quercus* in the following features: stamens overtop the perianth (Fig. 6F), the strongly cordate base of the anthers (Fig. 6C, I), florets arranged in dichasia (Fig. 6D, F) and the presence of one to numerous ovate bracts, which subtend the floret dichasia (Hjelmqvist 1948; Forman 1964; Soepadmo 1972; Abbe 1974; Lozano-C. & al. 1979; Nixon & Crepet 1989).

Although sections of *Quercus* can be differentiated by their distinct pollen morphology (Denk & Grimm 2009), the distinction between sections of *Quercus* based on the morphology of their staminate catkins is difficult (Table 2). Staminate catkins of *Q. sect. Cyclobalpinus* are most distinct from all other *Quercus* sections. The staminate florets are arranged in dichasia of three (Fig. 7C–J; florets are singular in all other sections) and possess up to 17 stamens per floret (which is the highest stamen number within quercoids). Due to the very dense arrangement of the florets, the perianth is almost invisible (Fig. 7C, G), but according to Hjelmqvist (1948) and Kaul (1985) it is deeply incised, forming ovate to lanceolate lobes. The anthers are apically notched and round in shape (Fig. 7G, J), whereas in all other quercoids they are mostly elliptic. Another striking feature of *Q. sect. Cyclobalpinus* is the large bract subtending the dichasia (Fig. 7C, D, I, J; Hjelmqvist 1948; Kaul 1985). In addition, we observed a very slender and elongated bract located beneath the flower dichiasium of *Q. glauca Thunb.* (Fig. 7C).
Quercus sect. Cerris possesses staminate florets with campanulate to cyathiform perianths that are incised to the lower third or partly to the base, forming ovate to lanceolate lobes (Fig. 8B, D, F). Trichomes are very abundant and are located on the rachis, on the perianth surface and on the anthers (Fig. 8A–C, E, F). Hairy anthers are a distinct feature shared with Q. sect. Ilex (Fig. 8H). However, unlike the mucronate anthers in Q. sect. Ilex (Fig. 8H, J), anthers in Q. sect. Cerris are apically notched (Fig. 8A–F). Another difference between these
Fig. 9. Staminate inflorescences and florets of extant *Quercus* sect. *Lobatae*, sampled from herbarium specimens (see Table S2 [Supplemental content online] for affiliations). Note short filaments, large anthers and cyathiform perianth, which are typical features of *Q.* sect. *Lobatae*. – A, F: *Quercus agrifolia*; B, G: *Quercus coccinea* Münchh.; C, H: *Quercus depressa* Bonpl.; D, I: *Quercus crassifolia* Bonpl.; note trichome tuft in floret centre and basifixed anthers; E, J: *Quercus crassipes* Bonpl. – Scale bars: A–E = 1 mm; F–J = 500 µm.
Fig. 10. Staminate inflorescences and florets of extant Quercus sect. Lobatae, sampled from herbarium specimens (see Table S2 [Supplemental content online] for affiliations). Note short filaments, large anthers and cyathiform perianth, which are typical features of Q. sect. Lobatae. – A: Quercus falcata Michx.; B, G: Quercus georgiana M. A. Curtis; C, H: Quercus grahamii Benth.; D, I: Quercus hypoleucoides A. Camus; E, F: Quercus imbricaria. – Scale bars: A–D, E = 1 mm; F–I, J = 500 µm.
two sections is the cyathiform perianth in *Q.* sect. *Ilex* (Fig. 8H–L), which is more closed than in *Q.* sect. *Cerris* (Fig. 8D–F).

The perianth in staminate catkins of *Quercus* sect. *Lobatae* is campanulate (Fig. 9F) to cyathiform (Fig. 10F). Sometimes the perianth has only two incisions, forming two lobes (Fig. 10J, 11E), whereas other species exhibit up to six lobes (Fig. 10H, I; 11D, F). Trichomes are sparser than in *Q.* sect. *Cerris* and *Q.* sect. *Cyclobalanopsis* and are mostly located along the margin of the perianth or on the outer perianth surface (Fig. 9G, H; 10H, I; 11F). The rachis, however, can be pubescent (Fig. 9A, C–E; 10A, C–E; 11A, C) or more or less glabrous (Fig. 9B; 10B; 11B). The anthers are notched (Fig. 9H; 10F, H; 11C) to mucronate (Fig. 9F; 11D), elliptic in shape and mostly basally covered by the perianth (Fig. 11A–F), because the filaments never overtop the perianth (Fig. 9A–C, E). Subtending bracts are caducous and shed early and were observed in only one specimen.

*Quercus* sect. *Quercus* differs from the other sections by the deeply incised perianths, forming linear slender lobes (Fig. 12F–J). However, some species of *Q.* sect. *Quercus* also possess campanulate perianths with triangular lobes (Fig. 12D, I). Some species possess catkins with few trichomes (Fig. 12A–C), whereas other species are more pubescent (Fig. 12D, E). The anthers of all species of *Q.* sect. *Quercus* examined in this study are notched (Fig. 12F–J).
Table 5. Morphology of staminate inflorescences of *Quercus subglabra* (*Q. sect. Lobatae*) and *Q. meyeriana* from Baltic amber. Features that were absent or not discernible are indicated by −; presence of features is indicated by +.

| Taxon | *Quercus subglabra* | *Quercus subglabra* | *Quercus subglabra* | *Quercus meyeriana* |
|-------|---------------------|---------------------|---------------------|---------------------|
| Collection number | GZG.BST.24535 | GZG.BST.24418 | MB.Pb.1979/0817 (holotype) | MB.Pb.1979/0813 (lectotype) |
| Figures | Fig. 21, 22 | Fig. 23, 24 | Fig. 20 | Fig. 36 |
| Inflorescence | pendulous catkin | pendulous catkin | pendulous catkin | pendulous catkin |
| Length (cm) | 3.2 | 4.4 | 0.48 | 1.9 |
| Rachis | | | | |
| Width (µm) | 280–400 | 300–500 | 400 | 280 |
| Trichomes | stellate, loosely distributed | stellate, loosely distributed | stellate, loosely distributed | stellate below each floret |
| Floret | | | | |
| No./dichasium | 1 | 1 | 1 | 1 |
| Perianth | | | | |
| Length (mm) | (1.4–1.7)(−2) | (1–1.5)(−2) | 1.4–2 | 1.4–2.6 |
| Width (mm) | (1.6–1.9)(−2.3) | (1.4–1.7)(−2.2) | 1.3−1.4 | 0.9–1.2 |
| Shape | campanulate, incised up to middle | campanulate, incised up to middle | campanulate, incised up to middle | cyathiform |
| Lobes | triangular, short, acute apex, irregularly serrate margin | triangular, short, acute apex, irregularly serrate margin | triangular, short, acute apex, irregularly serrate margin | 5 or 6; triangular-ovate, acute or obtuse apex, entire to irregularly incised margin |
| Surface | glabrous | glabrous | glabrous | glabrous |
| Pedicel | + | + | +/- | +/- |
| Length (µm) | (120–1296)(–480) | 400–480 | 150 | — |
| Width (µm) | (240–304)(–360) | 280–320 | 400 | — |
| Trichomes (on floret) | + (scarce) | + (scarce) | + (scarce) | + |
| Morphology | solitary; uniseriate | solitary | solitary | solitary |
| Location | margin | pedicel | margin | margin (solitary), pedicel (stellate) |
| Central trichome tuft | + | + | + | (not visible) |
| Stamens | | | | |
| No./flower | 7–9 | 6–9 | 8 | 6–8 |
| Filament | short; covered by perianth | short; covered by perianth | short; covered by perianth | covered by perianth |
| Length (µm) | — | — | — | — |
| Width (µm) | — | — | — | — |
| Anthers | | | | |
| Length (µm) | (800–1988)(–1160) | (1000–1096)(–1300) | (1000–1253)(–1440) | (1200–1350)(–1500) |
| Width (µm) | (340–398)(–460) | (460–544)(–660) | (360–493)(–600) | (500–595)(–660) |
| Shape | narrowly elliptic | elliptic to narrowly elliptic | elliptic to narrowly elliptic | narrowly elliptic |
| Apex | notched | notched | notched | obtuse |
| Attachment | basified | basified | basified | basified |
| Subtending bract | + | + | + | + |
|-----------------|---|---|---|---|
| No./ flower | 1 | 1 | 1 | 1 |
| Length (mm) | (2–)3(–3.8) | (1.8–)3.5(–5.2) | 1–1.5 | 0.7–1.7 |
| Width (mm) | (0.08–)0.11(–0.12) | (0.12–)0.19(–0.24) | 0.9–1.7 | 0.06–0.1 |
| Shape | linear, acute, very slender | linear, acute, very slender | linear, acute, very slender | elongated-linear, acute |
| Trichomes | scarce | scarce | scarce | – |
| Morphology | solitary; bifurcate | solitary | solitary | – |
| Location | margin, apex | surface, apex | margin | – |

**Pollen**

**LM**

| Polar axis (μm) | (18–)22.5(–24) | 25–30 | – | – |
| Equatorial axis (μm) | (12–)14(–15) | 17–21 | – | – |

**SEM**

| Polar axis (μm) | (17–)20(–23) | 17 | – | – |
| Equatorial axis (μm) | (11–)13(–14) | (19–)23(–25) | – | – |
| Equatorial outline | elliptic | elliptic | – | – |
| Sculpturing (SEM) | tectum microverrucate, perforate; microverrucae weakly developed in polar area, more distinct in mesocolpium | – | – | – |

**Affinity**

| Quercus sect. Lobatae | Quercus sect. Lobatae | Quercus sect. Lobatae | – |
Table 6. Morphology and affinities of staminate inflorescence and floret inclusions of *Quercus meyeriana*, *Q. meyerina var. denticulata* and *Q. subglabra* from Baltic amber. Information was taken from Göppert & Berendt (1845), Caspary (1881), Conwentz (1886) and from reinvestigations of the specimens in the present study. When no specimens of the named taxa were described by the respective author, this is indicated by −.

| Taxon                      | Göppert & Berendt 1845                        | Caspary 1881                               | Conwentz 1886                        | This study                        |
|----------------------------|-----------------------------------------------|--------------------------------------------|--------------------------------------|-----------------------------------|
| *Quercus meyeriana*        | Specimens MB.Pb.1979/0813, MB.Pb.1979/0817, MB.Pb.1979/0815 | information not available                  | new type; lost                       | MB.Pb.1979/0813 (lectotype)       |
| **Affinities**             | *Quercus*                                     | *Quercus*                                  | *Quercus* (our interpretation: eotrigonobalanoid) | *Quercus*                        |
| Perianth                   | cyathiform, irregularly lobed; lobes 6–8, elongated lanceolate | divided, smooth                           | campanulate, divided, smooth, margin ciliate | cyathiform; lobes 5 or 6, triangular-ovate, acute or obtuse along perianth margin (solitary trichomes), stellate trichomes on pedicel |
| Trichomes                  | along margin of lobes stellate, with 4 to 5 arms | along margin of lobes                      | along margin of lobes simple trichomes | 6–8; filaments covered by perianth; anthers apically obtuse, narrowly elliptic |
| Stamens                    | 6–10; filaments as long as perianth            | 6–10; 2.5 × as long as perianth; anthers apically notched | 6–8; filaments covered by perianth; anthers apically notched, elongated cordate | 6–8; filaments covered by perianth; anthers apically notched, narrowly elliptic |
| *Quercus meyeriana*        | Specimen −                                     | −                                          | MB.Pb.1979/0815                       | MB.Pb.1979/0815 (holotype)         |
| **var. denticulata**       | **Affinities**                                | *Quercus*                                  | trigonobalanoid or castaneoid         | solitary trichomes (central tuft), uniseriate trichomes rarely along perianth margin and subtending bract |
| Perianth                   | **Affinities**                                | *Quercus*                                  | top-shaped, glabrous; lobes lanceolate, apex acute, margin irregularly dentate and incised | 6; filaments projecting slightly beyond perianth; anthers round, apically notched |
| Trichomes                  | central trichome tuft                         | central trichome tuft                      | central trichome tuft                | 6; filaments projecting slightly beyond perianth; anthers round, apically notched |
| Stamens                    | 5–7; stamen 2 × longer as perianth; anthers elliptic, obtuse, cordate | 5–7; stamen 2 × longer as perianth; anthers elliptic, obtuse, cordate | 5–7; stamen 2 × longer as perianth; anthers elliptic, obtuse, cordate | 5–7; stamen 2 × longer as perianth; anthers elliptic, obtuse, cordate |
| *Quercus subglabra*        | Specimens −                                   | MB.Pb.1979/0817                            | MB.Pb.1979/0813, MB.Pb.1979/0817      | MB.Pb.1979/0817 (holotype)         |
| **Affinities**             | *Quercus*                                     | *Quercus*                                  | *Quercus* sect. Lobatae              | *Quercus* sect. Lobatae            |
| Perianth                   | dentate, (almost) smooth, domed               | urceolate, almost smooth; lobes 5–7, triangular, ovate, acute, margin entire | campanulate, incised; lobes triangular, acute, margin irregularly serrate | campanulate, incised; lobes triangular, acute, margin irregularly serrate |
| Trichomes                  | information not available                      | simple trichomes on rachis and pedicel of florets, bracts, floret centre; stellate | solitary and sometimes uniseriate trichomes along perianth margin (scarce) | solitary and sometimes uniseriate trichomes along perianth margin (scarce) |
| Stamens                    | 5–7                                          | 7; stamen 2 × as long as perianth; anthers cordate at base | 8; filaments covered by perianth; anthers narrowly elliptic, apically notched | 8; filaments covered by perianth; anthers narrowly elliptic, apically notched |
Fig. 12. Staminate inflorescences of extant *Quercus* sect. *Quercus*, sampled from herbarium specimens (see Table S2 [Supplemental content online] for affiliations). – A, F: *Quercus robur*; note deeply incised perianth forming linear lobes; B, G: *Quercus pubescens* Willd.; C, H: *Quercus alba* L.; D, I: *Quercus magnolifolia* Née; E, J: *Quercus microphylla* Née. – Scale bars: A–E = 1 mm; F–J = 500 μm.
Table 7. Morphology of staminate inflorescences from Baltic amber assigned to Quercus sect. Lobatae and Q. sect. Cyclobalanopsis/Lobatae. Features that were absent or not discernible are indicated by −; presence of features is indicated by +.

| Taxon | Collection number | Figure(s) | Inflorescence | Length (cm) | Rachis Width (µm) | Trichomes (on floret) Location | Floret | No./dichasium | Perianth, length × width (mm) | Lobe Shape | Stamina No./flower | Filament Length (µm) | Width (µm) | Anthers Length (µm) | Width (µm) |
|-------|-------------------|-----------|---------------|-------------|------------------|-------------------------------|--------|-------------|--------------------------|------------|-----------------|----------------------|------------|------------------|------------|
| Q. casparyi | GZG.BST.24402 (holotype) | Fig. 18, 19 | pendulous catkin | 2.6 | 250–370 | stellate; solitary | 1–3 | 1 | (1.6–2.2) × (1.1–1.9–2.6) | triangular, acute apex, margin incised to lower third; widely open | 7–9 | 200–300 | 120–1359 | 680–772 |
| Q. multipilosa | GZG.BST.24414 (holotype) | Fig. 25, 26 | pendulous catkin | 4.5 | 360–640 | stellate, densely distributed | 1 | 1 | (4.8–2.3) × (1.9–2.6) | campanulate to cyathiform, incised to middle | 9–11 | 400–500 | 1000 × 280 | 1080–1576 |
| | | | | | | | | | | | | | |
| Q. multipilosa | GZG.BST.24490 (holotype) | Fig. 27, 28 | detached flower | 2.3 | 240–280 | stellate | 1 | 1 | 0.8–1.7 × 1.8–2.6 | campanulate, mainly cyathiform; incised to middle of lower third; widely open | 9–11 | 200–300 | 320–400 | 1000–230 |
| | GZG.BST.24491 | | pendulous catkin | 2.6 | 450–600 | stellate | 1 | 1 | (1–1.7–2.2) × (1.9–2.4–2.7) | campanulate to triangular, acute apex, margin irregularly serrate | 9–11 | 200–300 | 320–400 | 1000–230 |
| Q. aimeeana | GZG.BST.24389 (holotype) | Fig. 29, 30 | pendulous catkin | 2.3 | 240–280 | stellate | 1 | 1 | 0.8–1.7 × 1.8–2.6 | campanulate, mainly cyathiform; incised to middle of lower third; widely open | 10–12 | 200–300 | 320–400 | 1000–230 |
| | GZG.BST.24388 | | pendulous catkin | 2.3 | 240–280 | stellate | 1 | 1 | (1–1.7–2.2) × (1.9–2.4–2.7) | campanulate to triangular, acute apex, margin irregularly serrate | 10–12 | 200–300 | 320–400 | 1000–230 |
| Q. sect. Lobatae | | | | | | | | | | | | | | |
| Q. sect. Cyclobalanopsis/Lobatae | | | | | | | | | | | | | | |

Features that were absent or not discernible are indicated by −; presence of features is indicated by +.
| Shape       | elliptic | narrowly elliptic | elliptic to narrowly elliptic | elliptic | elliptic to narrowly elliptic |
|-------------|----------|--------------------|-----------------------------|----------|-------------------------------|
| Apex        | mucronate| notched            | notched                     | obtuse   | obtuse                         |
| Attachment  | basifixed| basifixed          | basifixed                   | basifixed| basifixed                     |
| Subtending bract | +/-     | +                  | -                           | +        | +                             |
| No./flower  | 1        | 1                  | -                           | 1        | 1                             |
| Length (mm) | 0.9–4.8  | (3.3–)5.3(–8)      | –                           | (1.6–)1.9(–2.8) | –                     |
| Width (mm)  | 0.12–0.4 | (80–)0.14(–0.24)   | –                           | (0.2–)0.27(–0.32) | –                 |
| Shape       | linear, acute, short to elongated | – | – | linear, acute, very slender, elongated | – |
| Trichomes   | –        | –                  | –                           | –        | scarce; solitary; located on surface |

**Pollens**

**LM**

| Polar axis (μm) | (21–)27(–33) | 30–48 | (34–)46(–52) | (18–)25(–30) | (24–)27(–30) |
|-----------------|--------------|-------|--------------|--------------|--------------|
| Equatorial axis (μm) | (18–)20(–24) | 18–30 | (23–)31(–37) | (9–)17(–21) | (12–)16(–21) |

**SEM**

| Polar axis (μm) | (19–)23(–27) | (22–)26(–28) | (27–)30(–31) | 19 | – |
|-----------------|--------------|--------------|--------------|----|---|
| Equatorial axis (μm) | 15–19 | (13–)17(–19) | (19–)20(–22) | 16 | – |
| Equatorial outline | elliptic | elliptic | elliptic | elliptic | elliptic |
| Sculpturing (SEM) | monad, tricolpate, scabrate, verrucate; rod-like masked | microverrucate, perforate, microverrucae weakly developed; footlayer thin and discontinuous | weakly microverrucate,perforate, secondary sporopollenin commonly covering perforations | |
| Affinity | *Quercus* sect. *Cyclobalanopsis* or *Q.* sect. *Lobatae* | *Quercus* sect. *Lobatae* | *Quercus* sect. *Lobatae* | *Quercus* sect. *Lobatae* | *Quercus* sect. *Lobatae* |
Fig. 13. Different developmental stages in extant staminate inflorescences of \textit{Quercus} (see Table S2 [Supplemental content online] for affiliations). – A, D: staminate inflorescence of \textit{Quercus candeicans} (\textit{Q. sect. Lobatae}); “immature”, as shown by closed anthers and short stamens still covered by perianth; B, E: staminate inflorescence of \textit{Q. candeicans} (\textit{Q. sect. Lobatae}); “mature”, as indicated by open anthers and elongated stamens; note that perianth shape and indumentum are the same in both maturity stages (A, D and B, E); C, F: staminate inflorescence of \textit{Quercus grisea} (\textit{Q. sect. Quercus}); “immature”, as indicated by closed anthers and short filaments covered by perianth; G, H: staminate catkin of \textit{Q. grisea}; “mature”, as indicated by open anthers and long filaments. – Scale bars: A–C, G = 1 mm; D–F, H = 500 µm.
Fig. 14. Floret inclusion of ? Castanea inclusa (Castaneoideae; neotype, GZG.BST.21989) from Baltic amber and historic illustrations of the original specimen of C. inclusa, which is currently lost (from Conwentz 1886: t. IV, fig. 5–7). – A: overview of detached floret showing elongated filaments, projecting far beyond perianth; B: perianth with numerous trichomes along margin of lobes; C: dorsifixed anthers; D, E: uniseriate and simple trichomes (E, arrowhead) along perianth margin; F, G: overview of neotype specimen from above (F) and from side (G); note pubescent perianth margin; H: overview of amber piece with detached floret shown in F and G. – Scale bars: A = 500 µm; B = 200 µm; C = 100 µm; D, E = 50 µm.
Fig. 15. Two floret inclusions of *? Castanea longistaminea* (Castaneoideae; neotype, GZG.BST.24371) from Baltic amber and historic illustrations of the original specimen of *C. longistaminea*, which is currently lost (from Conwentz 1886: t. IV, fig. 3, 4). Floret shown in B, E and G represents the neotype. – A–C: overview of detached florets showing elongated stamens, which project beyond perianth; D: amber specimen with floret inclusion of C; E: trichome tuft (arrowhead) in floret centre; F, G: dorsifixixed anthers, which are round to slightly elliptic; H: glabrous perianth incised to lower third. – Scale bars: A, B = 500 µm; E, H = 300 µm; G, F = 200 µm.
Fig. 16. Inclusion of staminate inflorescence with affinities to *Castanopsis* and *Lithocarpus* (Castaneoideae, genus indet.; GZG. BST.21991) from Baltic amber. – A: overview of staminate catkin with florets helically arranged along rigid rachis; B, C: dichasia with numerous florets densely clustered together; arrowhead (C) indicates large bracts subtending dichasium; D: floret shown from above; arrowheads indicate trichome tuft in floret centre (right arrowhead) and ciliate perianth margin (left arrowhead); E, F: dorsifixed, round anthers; G: peltate trichome on rachis; H: bifurcate and solitary trichomes located on subtending bract; I: anther with *in situ* pollen (arrowhead) located at amber surface; J: tricolporate pollen magnified from I. – Scale bars: A = 1 mm; B, C = 500 µm; D = 300 µm; E–H = 100 µm; I = 50 µm; J = 10 µm.
In summary, some sections of *Quercus* exhibit distinct features in their staminate inflorescences, such as the high number of stamens per floret in *Q.* sect. *Cyclobalanopsis*. However, many features, for instance the campanulate perianth shape, are not exclusive for one section and are shared between sections (Table 2). Therefore, to distinguish staminate inflorescences of *Quercus* sections, additional information from pollen ornamentation is needed.

Conwentz (1886) chose the perianth shape and trichomes to distinguish between species of *Quercus*. When Kirchheimer (1937) reinvestigated Baltic amber inclusions of staminate inflorescences of the *Fagaceae*, he stated that these features were not reliable because they depended on the maturity of the inflorescence and, therefore, may differ within one individual inflorescence.

When examining extant herbarium specimens of the *Fagaceae*, we noticed that staminate florets of a catkin mostly looked similar. However, in a specimen of *Quercus grisea* Liebm. (*Q.* sect. *Quercus*; Fig. 13C, F, G, H), some florets had elongated filaments (Fig. 13G, H), whereas others of the same specimen had short filaments (Fig. 13C, F). Because the anthers of the short filaments were mostly closed (Fig. 13C, F), we interpreted this particular catkin as “immature” (before anthesis), whereas the other catkin with elongated sta-

| Taxon                  | *Quercus brachyandra* | *Quercus brachyandra* |
|------------------------|------------------------|------------------------|
| Collection number      | MB Pb 1979/0660 (holotype) | GZG BST 24385         |
| Figures                | Fig. 33                | Fig. 34, 35            |
| Inflorescence          | flower dichasium       | flower dichasium       |
| Diameter (distal view, in mm) | 4–5                     | 5–7                    |
| Floret                 |                         |                        |
| No./dichasium         | 6                      | 4                      |
| Perianth, length × width (mm) | –                       | 2.6–3.2 × 2.8–3.1      |
| Shape                  | incised, lobes only fused at base | incised, lobes only fused at base |
| Lobes                  | 6                      | 5–7; linear, acute or rounded apex, margin irregularly incised |
| Trichomes (on floret)  | solitary, very long and helically curled | solitary, very long and helically curled |
| Location               | margin densely hairy    | margin densely hairy    |
| Central trichome tuft  | –                      | +                      |
| Stamens                |                         |                        |
| No./flower             | 7                      | 7–9                    |
| Filament               | projecting beyond perianth | projecting beyond perianth |
| Length (μm)            | (90–)111(–150)         | (1680–)2000(–2200)     |
| Width (μm)             | (900–)994(–1140)       | (1240–)1488(–1920)     |
| Anthers                |                         |                        |
| Shape                  | elliptic               | elliptic               |
| Apex                   | mucronate              | mucronate              |
| Fixation               | basifixed              | basifixed              |
| Subtending bract       | +                      | +                      |
| No./flower             | 2                      | 2                      |
| Length × width (mm)    | 1.5–1.8 × 0.8–2        | (1.1–)1.9(–3) × (0.4–)0.8(–1.3) |
| Shape                  | ovate-lanceolate       | linear, lanceolate, slightly ovate, rounded apex |
| Trichomes              | solitary               | solitary, very long and helically curled |
| Location               | margin                 | margin                 |
| Pollen                 |                         |                        |
| LM                     |                         |                        |
| Polar axis (μm)        | –                      | (24–)26(–30)           |
| Equatorial axis (μm)   | –                      | (18–)20(–24)           |
| Equatorial outline     | –                      | elliptic               |
| Sculpturing (SEM)      | –                      | smooth, verrucate, microechinate, apical parts of rodlets appearing nubby, rodlke masked; markedly thick footlayer in mesocolpium |
| Affinity               | *Quercus sect. Protobalanus* | *Quercus sect. Protobalanus* |
mens had widely open anthers (Fig. 13G, H) and therefore was likely more “mature” (at or after anthesis). Despite the different maturities of florets, their morphology was alike and we did not observe differences in the perianth shape or trichome distribution. We further compared two herbarium sheets of *Q. candicans* Née (*Q.* sect. *Lobatae*) from Mexico to test whether different morphologies of staminate inflorescences occurred within one species of *Quercus*. We further compared two herbarium sheets of *Q. candicans* Née (*Q.* sect. *Lobatae*) from Mexico to test whether different morphologies of staminate inflorescences occurred within one species of *Quercus* (Fig. 13A, B, D, E). We again observed that the staminate inflorescences of both specimens possessed filaments of different length (Fig. 13A vs. 13B), which is likely related to the immaturity of the catkin, because the shorter filaments possessed closed anthers (Fig. 13D). Besides the differences in filament length, all other features, such as the perianth shape, were alike. Based on this observation, we concluded that different stages of maturity of staminate catkins not necessarily lead to a marked morphological change. However, the maturity of anthers needs to be considered when discussing the length of filaments as a distinguishing feature.

Our comparative study of extant *Fagaceae* showed that it is possible to distinguish between the staminate inflorescences of *Quercus*, *Castaneoideae* and *Trigonobalanoideae*. To differentiate between sections of *Quercus*, additional information from pollen morphology is needed, because morphological features of the staminate catkins are not always distinct enough within each section (Table 2). Based on staminate inflorescences only, it is difficult to distinguish between genera of the *Castaneoideae*; however, the density of pubescence and the arrangement of florets along the rachis are indicative for some genera (Table 1). Within *Trigonobalanoideae*, the morphology of the staminate inflorescence in combination with the pollen sculpturing are very helpful to differentiate between species/genera (Table 1).

Based on this comparison, we considered the following features to be reliable for distinguishing between staminate inflorescences of *Quercus*, *Castaneoideae* and *Trigonobalanoideae*: rachis (pendulous or rigid), shape and degree of incision of the perianth, trichome morphology and their presence or absence, length of filaments

Table 9. Morphology of staminate florets of *Quercus* from Baltic and Bitterfeld amber with section undetermined. Features that were absent or not discernible are indicated by −; presence of features is indicated by +.

| Taxon                                | *Quercus mucronata* | *Quercus emanuelii* | *Quercus trichota* |
|--------------------------------------|---------------------|---------------------|--------------------|
| **Collection number**                | MB.Pb.1979/0868 (holotype) | MB.Pb.2009/0261 (holotype) | MB.Pb.1979/0814 (holotype) |
| **Figures**                          | Fig. 37            | Fig. 38             | Fig. 39            |
| **Perianth**                         |                     |                     |                   |
| Length (mm)                          | 1.6                 | 1.4                 | 1.8               |
| Width (mm)                           | 0.5 (difficult to measure) | 3                  | 1.64              |
| Shape                                | widely open, top-shaped, incised to base | cyathiform, incised to base, widely open | campanulate, incised to up to middle |
| Lobes                                | linear, fused only at base, acute apex | linear to lanceolate, acute apex | triangular, acute apex |
| Surface                              | glabrous            | with trichomes      | upper third densely hairy |
| **Trichomes**                        |                     |                     |                   |
| Morphology                           | solitary            | solitary            | solitary           |
| Location                             | along entire margin of perianth lobes | perianth margin, on entire outer surface of perianth | perianth margin, mainly on upper third of perianth surface |
| Central trichome tuft                | +                   | +                   | −                  |
| Pedicel                              | −                   | −                   | −                  |
| Subtending bract                      | −                   | −                   | −                  |
| **Stamens**                          |                     |                     |                   |
| Number                               | 6                   | 6                   | 6                  |
| Filament                             | projecting slightly beyond perianth | projecting beyond perianth | projecting beyond perianth |
| Length (µm)                          | (1400–1600(–1800)   | −                   | −                  |
| Width (µm)                           | (70–78(–80)         | −                   | −                  |
| **Anthers**                          |                     |                     |                   |
| Length (µm)                          | (600–777(–920)      | (880–920(–1000)     | 900–1000           |
| Width (µm)                           | (380–450(–560)      | (560–648(–760)      | 540–640            |
| Shape                                | rounded to elliptic | slightly elliptic   | slightly elliptic  |
| Apex                                 | mucronate           | mucronate           | mucronate          |
| Attachment                           | basifix            | basifix             | basifix           |
Fig. 17. Pollen extracted from anthers of GZG.BST.21991 (Castaneoideae, genus indet.); a = endoaperture, t = tectum, c = columellae, f = footlayer, ed = endexine, co = colpus. – A: overview of pollen grain, partly enclosed in amber; B: sculpturing of polar area; C: sculpturing of mesocolpium with elongated, fused rods and smooth striation; D, E: cross-section through pollen; white-framed area in E is magnified in D showing that tectum, columellae and footlayer are of same thickness in mesocolpium; F: endoaperture (a) and colpus (arrowhead) magnified in G; note parallel-running rodlets along endoporus; G: colpus membrane; H, I: cross-section through pollen grain, white-framed area in H is magnified in I; note footlayer (f) and tectum (t), which narrow toward colpus. – Scale bars: A = 2 µm; B, C, I = 200 nm; D = 500 nm; E–H = 1 µm.
Fig. 18. Inclusion of staminate inflorescence of *Quercus casparyi* from Baltic amber (holotype, GZG.BST.24402) with affinities to *Q.* sect. *Lobatae* or *Q.* sect. *Cyclobalanopsis*. – A: overview of staminate catkin with lax rachis; B: dichasium with three florets; C: single floret; note cyathiform shape of perianth and elongated stamens projecting beyond perianth; D: mucronate, basifixed anther; E: elongated, slender bract subtending florets; F: rachis with stellate trichomes; G: perianth lobe with uniseriate trichomes along margin; H: bifurcate trichome on outer perianth surface; I: uniseriate and branched uniseriate trichomes on perianth margin; J, K: *in situ* pollen of anthers in cross-section (J) and in polar view (K). – Scale bars: A–C, E = 1 mm; D = 500 µm; F = 300 µm; G–I = 100 µm; J, K = 10 µm.
440 Sadowski & al.: Staminate inflorescences of *Fagaceae* from Eocene Baltic amber

(overtopping the perianth or covered by it; considered when anthers were open, meaning they were “mature”), anther shape and apex (notched, mucronate, obtuse or acute), fixation of anthers (dorsifixed or basifixed), and shape of the subtending bract. If available, we further included pollen morphology in the study of the Baltic amber fossils.

3.2. Systematic palaeobotany

Order: *Fagales*
Family: *Fagaceae*
Subfamily: *Castaneoideae*

Inclusions of staminate inflorescences and singular florets of *Castaneoideae* are easily distinguishable from other fagaceous taxa, because castaneoids possess elongated filaments that project far beyond the perianth; dorsifixed, small and almost round anthers; and pollen (if available) with striate ornamentation (see section 3.1 above).

Göppert & Berendt (1945) and Caspary (1881) reported staminate inflorescence inclusions from Baltic amber, which they assigned to *Castanea*. Conwentz (1886) studied further amber specimens and described in total four species of staminate inflorescence inclusions from Baltic amber, all of which he assigned to *Castanea*.

Fig. 19. Pollen extracted from anthers of *Quercus casparyi* (holotype, GZG.BST.24402) with affinities to *Q*. sect. *Lobatae* or *Q*. sect. *Cyclobalanopsis*; *t* = tectum, *c* = columellae, *f* = footlayer, *ed* = endexine. – A: overview of pollen showing microrugulate-arareolate sculpturing; distal ends of microrugulae form microechini, typical for *Q*. sect. *Cyclobalanopsis*; B: cross-section through pollen; white-framed area is magnified in C; C: cross-section through pollen wall showing different layers; note thin footlayer, which is typical for *Q*. sect. *Lobatae*; amber enclosing pollen penetrated into pores forming cast of pollen surface. – Scale bars: A = 2 µm; B, C = 500 nm.
Fig. 20. Inclusion of staminate inflorescence of *Quercus subglabra* (*Q.* sect. Lobatae; holotype, MB.Pb.1979/0817) from Baltic amber and historic drawing of this particular specimen (H, I; taken from Göppert & Berendt 1845: t. IV, fig. 36, 37) with its handwritten label. – A, H: overview of staminate inflorescence; arrowheads indicate linear subtending bracts; B: singular floret with short stamens; C: campanulate perianth; D: rachis with stellate trichomes; E: basifixed and apically notched anther; F: stellate trichome of rachis; G: perianth margin with bases of uniseriate trichomes, which have broken off; I: overview of amber specimen with inclusion shown in A and H; J: original label of amber specimen, handwritten and signed by Caspary “*Quercus sub-glabra* Casp. ex parte *Q. meyeriana* … Caspary”. – Scale bars: A = 1 mm; B, C = 500 µm; D, E = 200 µm; F = 100 µm; G = 50 µm.
Fig. 21. Inclusion of staminate inflorescence of *Quercus subglabra* (Q. sect. Lobatae; GZG.BST.24535) from Baltic amber. – A, B: florets with campanulate perianth and irregular serrate margin (B, arrowhead); florets are subtended by linear bract (A, arrowhead); C: overview of staminate catkin with singularly arranged florets along lax rachis; D: cross-section through floret; note central trichome tuft (arrowhead) and short filaments covered by perianth; black-framed area is magnified in I; E: basifixed and apically notched anthers; F: stellate trichomes on rachis; G, H: uniseriate (H) and simple trichomes (G) along perianth margin; I: pollen cluster located in anthers (black-framed area in D). – Scale bars: A, B, D = 500 μm; C = 1 mm; E = 200 μm; F, G = 100 μm; H, I = 50 μm.
(C. brachyandra Casp., C. inclusa Conv., C. longistaminea (Casp.) Conv., C. subvillosa Casp.). Kirchheimer (1937) and Iljinskaja (1982) re-evaluated the affinities of these specimens and reduced the number of species to one (C. longistaminea; Kirchheimer 1937) and two (C. inclusa, C. longistaminea; Iljinskaja 1982; Table 3).

The locations of the holotypes of these species names (except for C. brachyandra) are unknown. Therefore, we compared stamine inflorescence and floret inclusions to illustrations and descriptions of the lost holotypes, published by Conwentz (1886), Kirchheimer (1937) and Iljinskaja (1982). Based on this comparison, we accommodated several specimens into the fossil-species Castanea inclusa and C. longistaminea (although their placement in the genus Castanea could not be determined; see under these two species below). Because the type specimens of these names of species from Baltic amber are lost, newly discovered inclusions were used to designate neotypes and to emend the diagnoses. Castanea brachyandra was accommodated into Quercus (see Q. sect. Protovalnus), while the true generic identity of C. subvillosa remains unresolved, because neither detailed descriptions nor illustrations of this species exist. Besides these neotypes, we found further amber inclusions of castaneoid affinities that have not been reported from Baltic amber before.

Genus: **not determined**

? **Castanea inclusa** Conv., Die Angiospermen des Bernsteins: 37–38, t. IV, fig. 5–7 [herein Fig. 14F–H]. 1886, **emended here**. – Type: lost. – **Neotype (designated here):** GZG.BST.21989 (Hoffeins 66-1) [Fig. 14A–E]. Geoscientific Collection of the University of Göttingen. – **Fig. 14.**

**Additional references**

Castanea longistaminea (Casp.) Conv.: Kirchheimer in Beih. Bot. Centrallbl., Abt. B, 57: 465–466 [no figure]. 1937.

Castanea inclusa Conv.: Iljinskaja, Fossil Fl. Pl. USSR 2: 77, text-fig. 60: 3–5. 1982.

**Emended diagnosis.** — Stamine florets with campanulate to top-shaped perianth, incised to lower third forming 6 lanceolate to linear lobes. Apex of lobes obtuse, margins of lobes slightly curved inward, densely ciliate with 2 trichome types (uniseriate; solitary). Outer surface of perianth with few trichomes of both types. Stamens up to 10 per floret, projecting far beyond perianth, filiform. Anthers almost round, dorsifixed, apically notched. Centre of floret with dense trichome tuft, composed of solitary trichomes.

**Description.** — Detached florets. **Perianth:** campanulate to top-shaped, 700 µm long × 800 µm wide, surface almost glabrous, incised to lower third, connate at base, lobes linear to lanceolate with obtuse apex, margin entire and ciliate (Fig. 14A, B, F, G). **Stamens:** 4–6 stamens per floret (likely more because filaments are partly broken-off); filaments elongated, longer than perianth, 1220–1640 µm long × 40–70 µm wide (Fig. 14A, F, G); anthers elliptic to round with notched apex, dorsifixed (Fig. 14C), 200–250 µm long × 160–250 µm wide. **Trichomes:** 2 types: uniseriate and solitary; both types along perianth margin (Fig. 14D, E) and rarely on perianth surface (Fig. 14B); solitary trichomes forming very dense tuft in floret centre.

**Remarks.** — From all fagaceous inflorescences from Baltic amber described and pictured by Conwentz (1886), specimen GZG.BST.21989 most closely resembles Castanea inclusa in the following aspects: campanulate glabrous perianth, ciliate perianth margin, deeply incised with elongated lanceolate lobes, filaments longer than perianth (2–2.5 × as long as the perianth), small and round anthers (Table 4). However, Conwentz (1886) did not mention the central trichome tuft and the different trichome types.

Castanea inclusa was first described by Conwentz (1886), but later Kirchheimer (1937) included C. inclusa within C. longistaminea, arguing that the absence or presence of trichomes was not a valuable morphological feature to distinguish species of Castanea (Table 3). However, in extant castaneoid genera, species clearly differ by their indumentum (compare Fig. 4A–F). Furthermore, Jones (1986) showed that trichome types are diverse and distinct among certain genera of Fagaceae.

Hence, we followed Iljinskaja (1982) and distinguished two species of Castanea from Baltic amber. The floret inclusion shares some features with a castaneoid stamine inflorescence (see below; specimen GZG.BST.21991, subfamily Castaneoideae, genus indet.), such as the elongated stamens, the small anthers and the dense trichome tuft; however, GZG.BST.21991 does not show uniseriate trichomes along the perianth margin, but has solitary and bifurcate trichomes (Table 4). Therefore, it remains unclear if C. inclusa and GZG.BST.21991 belong to the same genus. Comparing the floret inclusion with extant genera of Castaneoideae, the following similarities occur: elongated filaments, dorsifixed and roundish anthers, presence of trichomes, and perianth shape are found in all modern genera (Table 1). Uniseriate trichomes mainly occur in Castanea and Lithocarpus (Jones 1986); however, Lithocarpus may exhibit a pronounced pistilode in the floret centre (Soepadmo 1970; Fig. 5J), which is missing in C. inclusa. At this point, it is impossible to definitely assign C. inclusa to a particular genus of the Castaneoideae.

**Additional specimens investigated** — GZG.BST.24395, GZG.BST.24396.

? **Castanea longistaminea** (Casp.) Conv., Die Angiospermen des Bernsteins: 36–37, t. IV, fig. 3, 4 [herein Fig. 15C, D]. 1886, **emended here** = Quercus longistaminea Casp.
Fig. 22. Pollen extracted from anthers of *Quercus subglabra* (*Q.* sect. *Lobatae*; GZG.BST.24535); t = tectum, c = columellae, f = footlayer, ed = endexine. – A: overview of pollen partly enclosed in amber; B: tricolpate pollen; C: polar view of pollen; note distinctly developed microverrucae in mesocolpium; D: polar view, magnified in E; microverrucae only weakly developed; E: microverrucate, perforate tectum; F: cross-section of pollen wall; endexine and footlayer are not distinguishable. – Scale bars: A, B = 2 µm; C, D = 1 µm; E = 200 nm; F = 500 nm.
Fig. 23. Inclusion of staminate inflorescence of *Quercus subglabra* (*Q.* sect. *Lobatae*; GZG.BST.24418) from Baltic amber. – A: overview of staminate catkin with singularly arranged florets along lax rachis; B: singular florets, each with elongated, linear subtending bract; C: floret with basifixed, short stamens; D: rachis; note trichome cover; E: stellate trichomes on rachis; F: anther in cross-section, exposed at amber surface and containing numerous pollen grains; G: *in situ* pollen in anthers. – Scale bars: A, B = 1 mm; C = 500 µm; D = 200 µm; E, F = 100 µm; G = 20 µm.
Table 10. Morphology of staminate florets of *Quercus* from Baltic amber with section undetermined. In case of missing type material, information on morphology was taken from descriptions and illustration of Conwentz (1886) and Caspary (1880, 1881). Features that were absent or not described are indicated by −.

| Taxon                  | *Quercus limbata* | *Quercus piligera* | *Quercus taeniato-pilosa* | *Quercus nuda* | *Quercus nuda* |
|------------------------|-------------------|--------------------|---------------------------|----------------|----------------|
| **Collection number**  | MB.Pb.1979/0521 (holotype) | holotype lost | holotype lost | MB.Pb.1979/0656 (holotype) | specimen lost |
| **Figures**            | Fig. 40           | Fig. 41A–D        | Fig. 41E–G               | Fig. 42D–I     | Fig. 42A–C    |
| **Type**               | detached floret with rachis remain | detached floret; inflorescence | detached floret | detached floret | detached floret; inflorescence |
| **Rachis**             | only fragmentary  | pendulous, filiform, densely tomentose | −                  | −              | filiform, pendulous, glabrous |
| **Floret**             |                   |                    |                          |                |                |
| **No./dichasium**      | 1                 | 1–3               | −                        | 1              | 2 or 3        |
| **Length × width (mm)**| 3.9 × 2           | −                 | −                        | 3.2 × 1.9      | 1.5–2         |
| **Perianth**           |                   |                    |                          |                |                |
| **Length × width (mm)**| 2.2 × 2           | −                 | 3                        | 2.2 × 1.8      | −             |
| **Shape**              | campanulate; margin incised | campanulate | top-shaped campanulate; deeply incised | campanulate; deeply incised on one side | campanulate to cyathiform; between lobes |
| **Lobes**              | 5; triangular; margin ciliate | triangular-ovate; margin entire or dentate | 6; elongated ovate, acute; margin entire, ciliate | triangular | widely ovate to triangular, longitudinal median folded and with keel; margin dentate |
| **Surface**            | sparsely with solitary trichomes | with trichomes | glabrous | uniseriate, solitary trichomes | glabrous |
| **Trichomes**          |                   |                    |                          |                |                |
| **Morphology**         | solitary, bifurcate | simple, acute trichomes; stellate with 10–12 rays | − | uniseriate, solitary | − |
| **Location**           | subtending bracteole (abaxial), perianth margin, very few on perianth surface | stellate trichomes on rachis and pedicels; simple trichomes on perianth surface | on perianth base and pedicel; inconspicuous trichome rows along perianth margin and between perianth lobes | only on perianth surface, very sparsely arranged | − |
| **Pedicel**            | −                 | roundish, short, densely tomentose | short, hairy, round | − | glabrous |
| **Subtending bract**   | 2 bracts present; elongated, ovate, obtuse, margin entire, abaxial surface and margin tomentose; linear, acute, with solitary trichomes | lancelolate, ovate, elongated acute, tomentose | − | − | linear |
Emended diagnosis — Staminate florets with campanulate to top-shaped perianth, incised to lower third forming 6 lanceolate to linear lobes. Apex of lobes acute-obtuse, margins of lobe and outer surface of perianth glabrous. Stamens 9–12 per floret, longer than perianth, filiform. Anthers round to slightly elliptic, dorsifixed, apically notched. Centre of floret with dense trichome tuft, composed of solitary trichomes.

Description — Four detached florets in one specimen (neotype is Fig. 15B, E, G). Perianth: campanulate, 1280–1680 µm long × 1200–2200 µm wide, glabrous, incised to lower third, connate at base, lobes linear to lanceolate, each with acute-obtuse apex, margins entire and glabrous (Fig. 15A–C, H). Stamens: 9 per floret; filaments elongated, longer than perianth (Fig. 15A–C), (1200–)1266(–1360) µm long × (560–)644(–800) µm wide; anthers elliptic with notched apex, dorsifixed (Fig. 15F, G), (390–)444(–470) long × (200–)270(–330) µm wide. Trichomes: solitary, forming very dense trichome tuft in floret centre (Fig. 15E); otherwise all surfaces glabrous (Fig. 15H).

Remarks — From all fagaceous inflorescences from Baltic amber described and pictured by Conwentz (1886), specimen GZG.BST.24371 most closely resembles *Castanea longistaminea* in the following aspects: campanulate glabrous perianth, perianth deeply incised with elongated lanceolate lobes, up to 9 stamens per floret, filaments much longer than perianth. In the original description, Conwentz (1886) did not illustrate or mention a central trichome tuft, but he observed few trichomes on the perianth surface, which we did not find. *Castanea longistaminea* differs from *C. inclusa* in the glabrous perianth margin, the longer anthers and the larger perianth size (Table 4).

In Caspary’s (1881) original description, *Castanea longistaminea* was described as a species of *Quercus*. Later, Conwentz (1886) transferred the species to *Castanea* due to the elongated filaments and elliptic-round anthers; this was accepted by Kirchheimer (1937) and Iljinskaja (1982; Table 3). Comparing the inclusion with extant *Castaneoideae*, *Chrysolepis* and *Notholithocarpus* differ by a densely pubescent perianth. The perianth of *Castanea* is pubescent as well, especially along the margin and the upper third of the lobes, which is dissimilar to

### Additional references

*Castanea longistaminea* (Casp.) Conv.: Kirchheimer in Beih. Bot. Centrbl., Abt. B, 57: 456–466 [no figure]. 1937.

*Castanea longistaminea* (Casp.) Conv.: Iljinskaja, Fossil Fl. Pl. USSR 2: 76–77, text-fig. 60: 1–2. 1982.

### Table 1

| Stamens Number | Filament length (µm) | Perianth length (µm) | Perianth width (µm) | Anthers length (µm) | Anthers width (µm) | Anthers shape | Anthers attachment |
|----------------|----------------------|----------------------|---------------------|---------------------|-------------------|--------------|-------------------|
| 7–10           | 1200–1520            | 105–150              | 1020–1400           | 1120–1266           | 560–964           | elliptic      | basifixed         |
| 10             | 1200–1520            | 105–150              | 1020–1400           | 1120–1266           | 560–964           | elliptic      | basifixed         |
| 7–9            | 1100–1240            | 500–800              | 560–644            | 1100–1240           | 500–700           | elliptic      | basifixed         |
the inclusion. Only Castanopsis and Lithocarpus exhibit perianths that can be glabrous on the outside, but possess a dense trichome tuft in the floret centre. In our opinion this is not sufficient morphological evidence for assigning the amber specimen to one of the mentioned castaneoid genera. Therefore, we retain the name C. longistaminea with the question mark highlighting its general castaneoid affinities.

Additional specimens investigated — GZG.BST.24361, GZG.BST.24392, GZG.BST.24397, GZG.BST.21990 (Hoffeins 477-2), MB.Pb.1979/0669.

Castaneoid – Fig. 16, 17.
Affinities: Castanopsis (D. Don) Spach, Hist. Nat. Vég. Phan. 11: 142, 185. 1841; Lithocarpus Blume, Bijdr.: 526. 1825–1826.

Specimen investigated — GZG.BST.21991 (Hoffeins 1145-2), Geoscientific Collection of the University of Göttingen.
Fig. 24. Pollen extracted from anthers of *Quercus subglaًbra* (*Q.* sect. *Lobatae*; GZG.BST.24418); t = tectum, c = columnellae, f = footlayer, ed = endexine. – A: overview of inner side of pollen fragment enclosed in amber; B: amber imprint of pollen wall; C: pollen wall showing perforate, microverrucate tectum; D, E: cross-sections through pollen wall; note thin footlayer (f) and microverrucae of tectum (t). – Scale bars: A, C = 1 µm; B = 2 µm; D, E = 500 nm.
Table 12. Morphology of staminate inflorescences of *Eotrigonobalanus* species from Baltic amber. Features that were absent or not discernible are indicated by −; presence of features is indicated by +.

| Species | *Eotrigonobalanus conwentzii* | *Eotrigonobalanus cf. conwentzii* | *Eotrigonobalanus longianthera* | *Eotrigonobalanus campanulata* |
|---------|-------------------------------|-----------------------------------|---------------------------------|---------------------------------|
| **Collection number** | GZG.BST.6895 (holotype) | GZG.BST.24577 | GZG.BST.24568 (holotype) | GZG.BST.24419 (holotype) |
| **Figures** | Fig. 45, 46 | Fig. 47, 48 | Fig. 49, 50 | Fig. 51 |
| **Inflorescence** | pendulous catkin | pendulous catkin | pendulous catkin | pendulous catkin |
| **Length (cm)** | 3.5 | 2.4 | 3 | 2.8 |
| **Rachis** | | | | |
| **Width (µm)** | 320–600 | 520–720 | 140–460 | 200–400 |
| **Trichomes** | − | scarce: stellate, solitary | stellate; uniseriate | scarce: solitary; stellate |
| **Floret** | | | | |
| **No./dichasium** | 1–3 | 1 or 2 | 1 | 1 or 3 |
| **Perianth** | | | | |
| **Length (mm)** | (1.2–)1.5(–2) | 1.4–2.2 | (1.8–)2.2(–2.6) | (0.8–)1.1(–1.8) |
| **Width (mm)** | (1.7–)2(–2.7) | 1.7–2.2 | (2–)2.1(–2.4) | (1.2–)1.6(–1.9) |
| **Shape** | cyathiform, incised to lower third | cyathiform, incised to middle or lower third | campanulate to cyathiform, incised to lower third/middle | campanulate, incised to lower third |
| **Lobes** | triangular, acute apex, irregular margin | triangular, acute apex | triangular, acute apex, irregular margin | triangular, acute apex, irregular margin |
| **Pedicel** | − | + | − | − |
| **Length (µm)** | − | 800 | − | − |
| **Width (µm)** | − | 420 | − | − |
| **Trichomes (on floret)** | scarce | +/− | scarce | scarce |
| **Morphology** | solitary | uniseriate; stellate; solitary | solitary; uniseriate; bifurcate | solitary; uniseriate |
| **Location** | margin, outer surface of perianth | margin, scarcely on perianth surface; stellate only on pedicel | margin, outer surface and base of perianth | scarcely on margin and outer surface of perianth |
| **Central trichome tuft** | + | + | + | + |
| **Stamens** | | | | |
| **No./floret** | 6–11 | 4 or 5 | 8 or 9 | 6 or 7 |
| **Filament** | elongated, projecting beyond perianth | covered by perianth | elongated; projecting far beyond perianth | elongated; projecting far beyond perianth |
| **Length (µm)** | (1240–)1580(–1880) | − | (1520–)1920(–2520) | (1300–)1488(–1740) |
| **Width (µm)** | (80–)92(–120) | − | (60–)76(–80) | (80–)92(–100) |
| **Anthers** | | | | |
| **Length (µm)** | (880–)1184(–1360) | (1000–)1100(–1280) | (1600–)1795(–2200) | (860–)1116(–1300) |
| **Width (µm)** | (400–)432(–480) | (480–)637(–800) | (500–)664(–900) | (340–)467(–560) |
| Shape         | narrowly elliptic | narrowly elliptic | narrowly elliptic | narrowly elliptic |
|--------------|-------------------|-------------------|-------------------|-------------------|
| Apex         | notched           | notched           | microneate        | notched           |
| Attachment   | basifixed         | basifixed         | basifixed         | basifixed         |
| Subtending bract | +                | +                 | +                 | +                 |
| No./ floret  | 1                 | 1                 | 1                 | 1                 |
| Length (mm)  | (0.9–)1.4(–2.4)   | 0.9–1.6           | 2.5–2.7           | 1–1.5             |
| Width (mm)   | (0.1–)0.3(–0.6)   | 0.2–0.4           | 0.2–0.6           | 0.3               |
| Shape        | lanceolate to linear | linear, acute | triangular to lanceolate | lanceolate |
| Trichomes    | solitary          | uniseriate        | solitary; bifurcate | –                 |
| Location     | margin, surface   | margin, surface   | margin, surface   | –                 |
| Pollen       |                   |                   |                   |                   |
| LM           |                   |                   |                   |                   |
| Polar axis (μm) | (20–)26(–32)   | (16–)19(–24)     | (15–)23(–27)     | –                 |
| Equatorial axis (μm) | (12–)15(–20) | (10–)12(–14)    | (12–)16(–21)    | –                 |
| SEM          |                   |                   |                   |                   |
| Polar axis (μm) | (20–)22.5(–26) | 21                | 19–26             | –                 |
| Equatorial axis (μm) | (10–)14(–16) | 15                | (15–)16(–21)    | –                 |
| Equatorial outline | elliptic    | elliptic          | elliptic          | –                 |
| Rugulae width (μm) | (0.3–)0.4(–0.5) | (0.2–)0.4(–0.7) | (0.3–)0.5(–0.8) | –                 |
| Sculpturing (SEM) | microrugulate, perforate, microrugulae twisted and interwoven, forming aggregates; footlayer moderately thick in mesocolpium | microrugulate, microrugulae twisted and interwoven forming rugulae; rugulae separated by deep furrows or perforations | – | – |
Fig. 25. Inclusion of staminate inflorescence of *Quercus multipilosa* (*Q.* sect. *Lobatae*; holotype, GZG.BST.24414) from Baltic amber. – A: overview of staminate catkin with lax rachis and singularly arranged florets; B, C: florets with campanulate to cyathiform perianths and short stamens; D: cross-section through floret; arrowhead indicates central trichome tuft; E: basifixed anther (arrowhead); F: stellate trichomes on rachis; G, H: lobe (G) and margin (H) of perianth with uniseriate trichomes (G, right arrowhead) and branched uniseriate trichomes (G, left arrowhead; H). – Scale bars: A–D = 1 mm; E, F = 300 µm; G, H = 100 µm.
Fig. 26. Pollen extracted from anthers of *Quercus multipilosa* (*Q.* sect. *Lobatae*; holotype, GZG.BST.24414); c = columellae, f = footlayer, ed = endexine. – *A*: cluster of tricolpate pollen attached to amber; *B*: polar view of pollen; *C*, *D*: mesocolpium; note weakly developed microverrucae and perforate tectum (*D*); *E*: cross-section through pollen partly enclosed in amber; white-framed area is magnified in *F*; *F*: cross-section through pollen wall with thin, discontinuous footlayer (*f*; indicated by dotted lines). – Scale bars: *A* = 10 µm; *B*, *D*, *F* = 1 µm; *C* = 2 µm; *E* = 3 µm.
Table 13. Morphology of staminate florets of fagaceous species from Baltic amber with unresolved affinities. Information of *Quercus trichota var. macroanthera*, *Q. meyeriana* (sensu Conwentz), *Q. klebsii* and *Q. capitato-pilosa* derives from descriptions of Conwentz (1886) and Caspary (1880, 1881). Features that were absent or not discernible are indicated by −; presence of features is indicated by +.

| Taxon | *? Eotrigonobalanoid sp. 1* | *? Eotrigonobalanoid sp. 2* | *Quercus ciliata* |
|-------|-----------------------------|-----------------------------|------------------|
|       | (Quercus trichota var. macroanthera) | (Quercus meyeriana sensu Conwentz 1886) |               |
| Collection number | holotype lost | holotype lost | MB.Pb.1979/0644 |
| Figures | Fig. 52A, B | Fig. 52C, D | Fig. 53 |
| Type | detached floret | detached floret | two detached florets |
| **Perianth** | | | |
| Length × width (mm) | 2.2 × 2.65 | 2–3.5 (size of entire floret) | 1.5–1.6 × 1–1.4 |
| Shape | campanulate to top-shaped | campanulate to top-shaped | campanulate to deeply lobed |
| Lobes | 5 or 6; lanceolate-oblong or lanceolate, apex acute, margin entire | 6; oblong or elongated or lanceolate, margin entire, ciliate | lanceolate-triangular, apex acute, margin irregularly incised |
| Surface | densely covered with short trichomes | glabrous | margin ciliate; perianth with few trichomes |
| **Trichomes** | | | |
| Morphology | short | simple, long | solitary |
| Location | on entire perianth surface | margins of lobes, rarely on perianth surface | margins of lobes, few on perianth surface |
| Central trichome tuft | − | − | + (densely pubescent) |
| Pedicel | − | − | − |
| Subtending bract | − | − | − |
| **Stamens** | | | |
| Number/floret | 9 | 6–10 | 6 |
| **Filament** | entire stamens 2–3 × as long as perianth | entire stamens 2–3 × as long as perianth | projecting beyond perianth |
| Length (µm) | | | 1000–2000 |
| Width (µm) | | | 80–100 |
| **Anthers** | | | |
| Length (µm) | − | − | 820–1040 |
| Width (µm) | − | − | 500–800 |
| Shape | large; oblong, base heart-shaped | elongated, almost heart-shaped | elliptic |
| Apex | obtuse | slightly notched or obtuse | notched to mucronate |
| Attachment | basifixed | basifixed | basifixed |

continued on next page
Table 13 (continued from previous page)

| Taxon | Castaneoid or trigonobalanoid (Quercus meyeriana var. denticulata) | ? Quercus (Quercus nuda var. serrulata) | ? Quercus klebsii | ? Quercus capitato-pilosa |
|-------|---------------------------------------------------------------|----------------------------------------|-----------------|------------------------|
| Collection number | MB.Pb.1979/0815 (holotype) | MB.Pb.1979/0816 (holotype) | holotype lost | holotype lost |
| Figures | Fig. 54 | Fig. 55 | – | – |
| Type | detached floret | detached floret | inflorescence, rachis densely pubescent | detached floret |
| **Perianth** | | | | |
| Length × width (mm) | 1.8 × 1.8 | 2 × 1 | 2.5–3 × 1.75 | – |
| Shape | top-shaped | bell-shaped, incised up to middle | top-shaped | – |
| Lobes | lanceolate, fused only at base, apex acute, margin irregularly dentate and incised | triangular to linear, apex acute or emarginate, margin incised | 5; triangular, as long as wide, apex acute | triangular |
| Surface | glabrous | glabrous | glabrous | with trichomes |
| **Trichomes** | | | | |
| Morphology | uniseriate; solitary (only as trichome tuft) | solitary; bifurcate | stellate | glandular |
| Location | rarely along perianth margin and subtending leaf; solitary trichomes only as central tuft | irregularly distributed along perianth margin, rarely on perianth surface | rachis | glandular trichomes on perianth margin; further trichomes on perigon surface and margin |
| Central trichome tuft | + | – | – | – |
| Pedicel | – | – | – | – |
| Subtending bract | linear, acute | – | linear-lanceolate, as long as perianth | – |
| **Stamens** | | | | |
| Number/floret | 6 | 7 | 9 or 10 | 10 |
| Filament | projecting slightly beyond perianth | short, not projecting beyond perianth | stamens projecting slightly beyond perianth | – |
| Length (µm) | (1200–)1330(– 1400) | – | – | – |
| Width (µm) | (60–)76(– 110) | – | – | – |
| **Anthers** | | | | |
| Length (µm) | (600–)635(– 680) | (1360–)1592(– 1860) | – | – |
| Width (µm) | (540–)570(– 600) | (600–)696(– 820) | – | – |
| Shape | round | elongated, elliptic | elliptic, base emarginate | – |
| Apex | obtuse to slightly notched | acute-obtuse | slightly mucronate | – |
| Attachment | – | busifixed | – | – |
Fig. 27. Inclusion of detached staminate floret of *Quercus multipilosa* (Q. sect. Lobatae; GZG.BST.21992) from Baltic amber. – A: overview of floret; arrowhead indicates pollen discharged from anthers; B: triangular perianth lobe; C: apically notched anther releasing pollen (arrowhead); D: trichomes on perianth margin: bifurcate, uniseriate and simple (left to right); E: bifurcate trichome on perianth margin; F, G: tricolpate pollen released from anthers. – Scale bars: A = 1 mm; B, C = 500 µm; D, E = 100 µm; F = 50 µm; G = 30 µm.
Fig. 28. Pollen extracted from anthers of *Quercus multipilosa* (Q. sect. *Lobatae*; GZG.BST.21992); t = tectum, c = columellae, f = footlayer, ed = endexine. – A: group of tricolpate pollen partly attached to amber; B: tricolpate pollen; C: microverrucate, perforate sculpturing of mesocolpium; D: pollen with partly removed pollen wall showing inner structure of colpus; white-framed area is magnified in E; E: cross-section through pollen wall with thin footlayer and endexine. – Scale bars: A = 10 µm; B = 2 µm; C, E = 1 µm; D = 3 µm.
Fig. 29. Inclusion of staminate inflorescence of *Quercus aimeeana* (*Q. sect. Lobatae*; holotype, GZG.BST.24389) from Baltic amber. – A: overview of staminate catkin; B, C: singular, stalked florets with campanulate to cyathiform perianths and up to 12 stamens per floret; D: bract subtending floret (highlighted with dotted line; r = rachis, f = floret); E: basifixed, apically obtuse anther; F: stellate trichomes on rachis; G: bifurcate trichome scarcely located on perianth surface; H: tricolpate pollen in anthers. – Scale bars: A–D = 1 mm; E = 500 µm; F = 200 µm; G = 100 µm; H = 30 µm.
lular centre; on rachis (Fig. 16G); each floret with very dense, central trichome tuft (solitary trichome type; Fig. 16D). Pollen: monad, tricolporate (Fig. 17E, H), equatorial outline elliptic (Fig. 16J), polar axis (11–14(–17) µm in LM, 11–13 µm in SEM, equatorial axis (6–)8(–9) µm in LM, 6–8 µm in SEM, sculpturing (micro)rugulate-fossulate, surface formed by elongated fused rods (rugulae), striation smooth (Fig. 17A–C); individual rugulae running parallel to polar axis (longitudinal) or obliquely and thereby forming triangular configuration (Fig. 17A–C). Close to endoaperture, 2 or 3 pairs of parallel rugulae framing apertural area (Fig. 17F, G). Footlayer, tectum, and columellae of same thickness in mesocolpium (Fig. 17D, I).

Remarks — The pollen sculpturing of GZG.BST.21991 suggests affinities to Castaneoideae, because the smooth striation is typical for all genera of the Castaneoideae. However, based on pollen morphology only, genera of Castaneoideae are nearly indistinguishable, because pollen size and shape of Castanopsis, Chrysolepis, Lithocarpus and Notholithocarpus are very similar (Grimsson & al. 2015; Praglowski 1984). As possible exceptions, pollen of Castanea can be distinguished from other castaneoids by its smaller size (Grimsson & al. 2015) and by the smooth tectum in the polar region (Bouchal & al. 2014); however, the preservation of pollen of GZG.BST.21991 does not allow evaluating the sculpturing of the polar region.

Besides pollen morphology, features of staminate inflorescences of the Castaneoideae are similar to specimen GZG.BST.21991 in that they are all rigid, spike-like and erect; thus they can be clearly distinguished from Colombobalanus, Formanodendron and Quercus, which all possess pendulous and lax catkins (see Table 1 for references). Only Trigonobalanus exhibits spike-like and erect staminate inflorescences as well (Forman 1964),
Fig. 31. Inclusion of staminate inflorescence of *Quercus aimeeana* (*Q.* sect. *Lobatae*; GZG.BST.24388) from Baltic amber. – A: overview of staminate catkin; florets are densely arranged along rachis; B: singular, stalked floret; arrowhead indicates remains of caducous subtending bract (magnified in G); perianth is widely open and cyathiform; C: apically obtuse, basifixed anther; D, E: campanulate perianth (D) and triangular perianth lobe (E), mostly glabrous; F: stellate trichomes on rachis; G: remains of subtending bract; H, I: tricolpate in situ pollen. – Scale bars: A, B, D = 1 mm; C, E = 300 µm; F, G = 200 µm; H = 50 µm; I = 10 µm.
but shows a fine granular and rugulate pollen sculpturing (Denk & Grimm 2009; Nixon & Crepet 1989), which is different from the rugulate-fossulate pollen of specimen GZG.BST.21991.

Specimen GZG.BST.21991 is not as densely pubescent as staminate inflorescences of Notholithocarpus and the tomentose perianth of Chrysolepis. Species of Castanea, Castanopsis and Lithocarpus, however, vary in the morphology of their staminate inflorescences, all combining features that occur in specimen GZG.BST.21991, such as the number of florets per dichasium, the shape and number of lobes, the glabrous perianth with ciliate margins, the central, dense trichome tuft and the protruding stamens (Table 1). Within castaneoid Fagaceae, peltate trichomes occur only in Chrysolepis, Castanopsis and Lithocarpus (Jones 1986). Among these taxa, peltate trichomes of GZG.BST.21991 are most similar to thin-walled peltate trichomes sensu Jones (1986) of Castanopsis and Lithocarpus, because these exhibit multicellular centres with stellate to discoidal caps (unlike Chrysolepis, which possesses radially fused peltate trichomes; Jones 1986).

These shared synapomorphies support the assignment of specimen GZG.BST.21991 to the Castanoeidae. Based on the presence and morphology of peltate trichomes, and the absence of a dense indumentum covering the entire inflorescence (as it is present in Chrysolepis and Notholithocarpus and described species of the Castaneoideae pertyarensis Crepet & Daghlian (1886) and Conwentz (1886)). The pollen sculpturing of specimen GZG.BST.21991 further resembles some species of Castanopsis by the rugulate-fossulate pattern in the mesocolpium and the parallel running rodots along the endoporus and proximal colpus (cf. Praglowski 1984; Castanopsis mollifyana King, C. paucispina Soepadmo, Chrysolepis sempervirens [Kellogg] Hjelmq. [as Castanopsis sempervirens (Kellogg) Dudley]).

In the 19th century, Caspary (1881), and Conwentz (1886) described species of the Castanoeidae from Baltic amber: Castanea brachyandra, C. inclusa, C. longistaminea and C. subvillosa. Except for C. brachyandra, these fossil-species represent floret inclusions, detached from the inflorescence axis. Because all specimens (except for C. brachyandra) are currently missing, we use descriptions and figures by Conwentz (1886), as well as the neotypes, for comparison (Table 4). Castanea inclusa has an almost glabrous perianth with uniseriate trichomes along the margin, different from the solitary trichomes along the margin of specimen GZG.BST.21991.

Castanea longistaminea has an almost glabrous perianth with sparse trichomes on its outer surface (Conwentz 1886), but does not possess a ciliate perianth margin. Castanea brachyandra and C. subvillosa were not illustrated by Caspary (1881) and Conwentz (1886). Caspary (1881) and Conwentz (1886) distinguished C. subvillosa from other fagaceous species by the strongly tomentose perianth surface and glabrous apices of the lobes. Further morphological details were not given; also, Conwentz (1886) mentioned that the specimen of C. subvillosa was rather poorly preserved and therefore C. subvillosa still needs verification. Anyhow, the indumentum described for C. subvillosa does not match specimen GZG.BST.21991, which has a glabrous perianth and hairy margins. Following Conwentz’s (1886) description, C. brachyandra is a dichasium of seven florets with elliptic, short to elongated, mucronate anthers dissimilar to the round, emarginate anthers of specimen GZG.BST.21991 (see text below for more discussion on C. brachyandra).

Based on these differences, we do not assign specimen GZG.BST.21991 to one of the previously described Castanea species from Baltic amber.

Crepet & Daghlian (1980) described fossil staminate inflorescences of Castanoeidea purpareaensis Crepet & Daghlian (Castanoeidae, Fagaceae) from the middle Eocene Claiborne Formation (Tennessee, U.S.A.). This species differs from the amber fossil in the presence of dichasia of three florets and in the absence of peltate trichomes and ciliate perianth margins.

Subfamily: Quercoidae

Inclusions of staminate inflorescences and singular florets of Quercus are easily distinguishable from other genera of the Fagaceae due to the combination of the following characters: rachis pendulous, florets mostly singular, short filaments (covered by the perianth) and basifixed anthers (see Table 1 for references). If available, pollen sculpturing supports the assignment to the Quercoidae (Denk & Grimm 2009).

The majority of Quercus holotypes from Baltic amber are lost, except for eight holotypes (of Q. brachyandra (Casp.) Sadowski & al. [≡ Castanea brachyandra], Q. limbata Casp., Q. meyeriana var. denticulata Conw., Q. mucronata Casp., Q. nuda Casp., Q. nuda var. serrulata Conw., Q. subglabra Casp., Q. trichota Casp.), which are located in the Kühnow Amber Collection and Berendt Amber Collection of the Museum für Naturkunde Berlin. We compared amber specimens from several amber collections (listed in Table S1, see Supplemental content online) with the holotypes found in the Museum für Naturkunde Berlin, but also with descriptions and illustrations of lost specimens, published by Göppert & Berendt (1845), Caspary (1880, 1881, 1886a, 1886b) and Conwentz (1886) for revising the Quercoidae from Baltic amber. Based on the comparison, we assigned two specimens to one fossil-species of Quercus (Q. subglabra, Q. sect. Lobatae); we revised another species originally assigned to Castanea and accommodated it within Quercus (Q. brachyandra, Q. sect. Protobalanus; Table 3). Additionally, we found three new species of Quercus that we assigned to either Q. sect. Lobatae or Q. sect. Cylobalanopsis/Lobatae based on pollen morphology. We also restudied the holotypes and emended their diagnoses with new information.
Genus: **Quercus** L., Sp. Pl. 2: 994. 1753.

**Quercus** sect. *Cyclobalanopsis* (Oerst.) Benth. & Hook. f., Gen. Pl. 3: 408, 1880 or *Q.* sect. *Lobatae* Loudon, Hort. Brit. 385. 1830.

**Quercus casparyi** Sadowski, A. R. Schmidt & Denk, sp. nov. – Holotype: GZG.BST.24402 [Fig. 18], Geoscientific Collection of the University of Göttingen. – Fig. 18, 19.

**Diagnosis** — Staminate catkin, pendulous with lax rachis. Rachis covered with stellate and bifurcate trichomes. Florets petiolate, singular or arranged in dichasia of 2 or 3 florets. Perianth campanulate to cyathiform, incised to dichasia of 2 or 3 florets. Perianth lobes apically acute, margin irregularly incised or dentate with uniseriate and branched uniseriate trichomes, outer surface of lobes almost glabrous, rarely with bifurcate or solitary trichomes. Stamens 7–9 per floret, filaments projecting beyond perianth. Anthers elliptic, mucronate, basifixed. Each floret subtended by glabrous bract, short to elongated, linear with acute apex. Pollen monad, tricolpate, scabrate (LM), tectum microrugulate-areolate, microechinate, fossulate (SEM); footlayer thin.

**Description** — Staminate inflorescence: pendulous (Fig. 18A), 2.6 cm long; rachis 250–370 µm wide. **Florets**: petiolate, singular or in dichasia of 2 or 3 florets (Fig. 18A, B). **Perianth**: (1–)1.6(–2) mm long × (1.4–)1.9(–2.6) mm wide, widely open, campanulate to cyathiform, incised to dichasia of 2 or 3 florets (Fig. 18C); perianth lobes triangular, each with acute apex, margin irregular incised to dentate (Fig. 18B, G); surface of lobes glabrous or very rarely with singular simple trichomes, margins with irregularly distributed trichomes (Fig. 18G). **Stamens**: 7–9 stamens per floret; filaments projecting beyond perianth (Fig. 18C), 1320–2160 µm long × (50–)72(–90) µm wide; anthers elliptic with mucronate apex, basifixed (Fig. 18D), (1140–)1466(–1560) µm long × (680–)772(–900) µm wide. **Subtending bract**: each floret subtended by 1 linear, acute, elongated or short bract (Fig. 18E), 0.9–4.8 mm long × 0.12–0.4 mm wide, glabrous on both surfaces. **Trichomes**: 5 types: stellate, bifurcate, solitary, branched uniseriate and uniseriate. Stellate and bifurcate trichomes located on rachis (Fig. 18F); bifurcate and solitary trichomes rarely on outer perianth (Fig. 18H); branched uniseriate and uniseriate trichomes on perianth margin and pedicel (Fig. 18G, I). **Pollen**: monad, tricolpate, polar outline trilobate, equatorial outline elliptic (Fig. 18J, K), polar axis (21–)27(–33) µm in LM, (19–)23(–27) µm in SEM, equatorial axis (18–)20(–24) µm in LM, 15–19 µm in SEM; in SEM: sculpturing microrugulate-areolate (Fig. 19A), fossulate, microrugulae partly masked by sporopollenin in distal ends forming microechini (Fig. 19B, C).

**Remarks** — *Quercus casparyi* is different from the other amber specimens of *Quercus* in the elongated filaments, which project beyond the perianth, the mucronate anthers and the arrangement of 2 or 3 florets in dichasia. The fossil catkin therefore combines characteristics found in *Q.* sect. *Cyclobalanopsis* (high number of stamens per florets, 2 or 3 florets per dichasium, elongated subtending bract exceeding the perianth, mucronate anthers) and *Q.* sect. *Lobatae* (campanulate perianth; Table 2).

Likewise, the pollen sculpturing of *Quercus casparyi* shares features with pollen of *Q.* sect. *Cyclobalanopsis*, e.g. *Q. acuta* Thunb. and *Q. glauca* (Denk & Grimm 2009; Makino & al. 2009), with virtually identical pollen sculpturing. At the same time, the relatively thin footlayer as seen in the fossil specimen (Fig. 19C) appears to be more typical of *Q.* sect. *Lobatae* (Denk & Tekleva 2014). Also, the relatively large size of the pollen fits better with *Q.* sect. *Lobatae* than with *Q.* sect. *Cyclobalanopsis*.

**Etymology** — *Quercus casparyi* is named in honour of Johann Xaver Robert Caspary (1818–1887), who described numerous *Quercus* species from Baltic amber.

**Quercus** sect. *Lobatae* Loudon, Hort. Brit. 385. 1830.

**Quercus subglabra** Casp. in Schriften Phys.-Ökon. Ges. Königscburg 22: 22. [no figure]. 1881, **emended here**. – Holotype: MB.Pb.1979/0817 [Fig. 20], Museum für Naturkunde Berlin. – Fig. 20–24.

– **Quercites meyerianus** Göpp. & Berendt, Der Bernstein und die in ihm befindlichen Pflanzenreste der Vorwelt: 84–85, t. IV, fig. 36–37 [herein Fig. 20H, I]. 1845, pro parte, excuslo lectotypy. – Note: one of the three syntypes of *Q. meyerianus*, MB.Pb.1979/0817, was designated as the holotype of *Quercus subglabra*.

**Emended diagnosis** — Staminate catkins, pendulous with lax rachis. Rachis with stellate trichomes randomly arranged, but not forming dense cover. Florets sessile or petiolate, singular. Perianth campanulate, incised to middle forming triangular lobes. Perianth lobes apically...
acute, margin irregularly incised or dentate, with few solitary and uniseriate trichomes; outer surface of lobes almost glabrous, rarely with solitary trichomes. Centre of perianth with solitary trichome tuft. Stamens 7–9 per florets, filaments as long as perianth. Anthers elliptic, notched, basifixed. Each floret subtended by glabrous bract, short to elongated, linear with acute apex.

Description — Three staminate inflorescences (for detailed measurements see Table 5). Rachis: pendulous, 3.2–4.4 cm long × 240–400 µm wide, loosely covered with stellate trichomes (Fig. 20A, D; 21C, F; 23A, D). Florets: singular; stalked, pedicel 120–480 µm long × 240–360 µm wide. Perianth: 1–2 mm long × 1.4–2.2 mm wide, campanulate, incised to middle; perianth lobes triangular, short, each with acute (partly elongated) apex, margin irregular serrate; outer surface and margin of lobes mostly glabrous, central trichome tuft present (Fig. 20B, C; 21B, D; 23C). Stamens: 7–9 stamens per floret; filaments covered by perianth (not measurable); anthers elliptic to narrowly elliptic with notched apex, basifixed (Fig. 20E; 21E; 23C); 800–1300 µm long × 340–660 µm wide. Subtending bract: present; linear, acute, very slender (Fig. 20A; 23B), 1.8–5.2 mm long × 0.08–0.24 mm wide, mostly glabrous on both surfaces, rarely with trichomes along margin or on bract surface. Trichomes: 3 types: solitary, uniseriate and stellate; location of trichomes: solitary trichomes as central trichome tuft (Fig. 21D), few on perianth margin and margin and surface of subtending bracts (Fig. 21G); few uniseriate trichomes on perianth margin (Fig. 21H); stellate trichomes loosely distributed on rachis and stalk of florets (Fig. 20D, F; 21F; 23D, E). Pollen: monad, tricolpate, polar outline trilobate, equatorial outline elliptic (Fig. 21I; 22A–C; 23F, G; 24A), polar axis 18–30 µm in LM, 17–23 µm in SEM, equatorial axis 12–21 µm in LM, 11–14 µm in SEM (due to preservation of pollen of GZG.BST.24414, only pollen diameter was measurable: [19–]23[–25] µm); tectum microverrucate, perforate (Fig. 22D, E; 24B, C); microverrucae weakly developed in polar area, more distinct in mesocolpium (Fig. 22C).
Fig. 33. Inclusion of staminate floret dichasium of *Quercus brachyandra* (*Q. sect. Protobalanus*; holotype, MB.Pb.1979/0660) from Baltic amber. – A: distal view of dichasium showing six florets (f1–f6, indicated by dashed lines) densely clustered together; B: proximal view of dichasium subtended by seven bracts (b1–b7); C: lateral view of dichasium showing florets f1–f3 and f6 as well as corresponding subtending bracts (b1–b5); D: lateral view of dichasium from other side; note elongated stamens projecting beyond perianths; E: singular floret (f3) showing deeply lobed perianth; F: stamens with mucronate anther apices (right arrowhead); left arrowhead indicates malformed, fused filaments; G: perianth margin with elongated, solitary trichomes; H: historic, handwritten label of specimen indicating it as “*Castanea brachyandra* Casp., Coll. Künow 105”. – Scale bars: A–D = 1 mm; E = 500 µm; F = 300 µm; G = 200 µm.
Fig. 34. Inclusion of staminate floret dichasium of *Quercus brachyandra* (*Q.* sect. *Protobalanus*; GZG.BST.24385) from Baltic amber. – A: distal view of dichasium showing four florets (f1–f4, indicated by dashed lines) densely clustered together; B: proximal view of dichasium subtended by seven bracts (b1–b7); C: lateral view of dichasium showing florets f1, f3 and f4 as well as corresponding subtending bracts (b1–b5); note linear perianth lobes (p); D: floret from side; note deeply lobed perianth and dense, central trichome tuft; E: elongated, solitary trichomes along perianth margin; F, G: basifix (F), apically mucronate (G, arrowhead) anthers; H, I: cluster of tricolpate pollen located in anther (H) and single pollen grain (I). – Scale bars: A–D = 1 mm; E = 200 µm; F, G = 500 µm; H, I = 10 µm.
Fig. 35. Pollen extracted from anthers of Quercus brachyandra (Q. sect. Protobalanus; GZG.BST.24385); t = tectum, c = columnellae, f = footlayer. – A: tricolpate pollen partly enclosed in amber; B: rod-like masked sculpturing; apical parts of rodlets appear nubby; C: imprint of pollen; arrowhead indicates roundish imprints of rodlets; D: cross-section through pollen wall showing thick footlayer; E, F: cross-section through pollen (E); white-framed area is magnified in F; note markedly thick footlayer in mesocolpium. – Scale bars: A = 2 µm; B, D, E = 1 µm; C = 300 nm; F = 500 nm.
Remarks — The holotype specimen of *Quercus subglabra* is also a syntype, but not the lectotype, of *Quercites meyerianus* Göpp. & Berendt (1845). However, *Quercites* Göpp. (1844) is an illegitimate later homonym of *Quercites* H. Berger (1832), as well as an illegitimate renaming of *Kloeodinia* Göpp. (Doweld 2018). Consequently, *Quercites* Göpp. cannot be used to name staminate inflorescence inclusions from Baltic amber.

Göppert & Berendt (1845) described three amber specimens with two catkins and one detached floret as *Quercites meyerianus*, but they did not designate a holotype (Table 6). *Quercites meyerianus* was later renamed as *Quercus meyeriana* (Göpp. & Berendt) Brongn. (Brongniart 1849, Unger 1850). Caspary (1881) included *Quercites meyeriana* in an identification key, but he assigned one of the original specimens to a new species, *Quercus subglabra* Casp. (Table 3, 6). Caspary (1881) did not mention a collection number for this particular specimen. We found all three specimens of *Quercites meyerianus* of Göppert & Berendt (1845; MB.Pb.1979/0813, MB.Pb.1979/0817 and MB.Pb.1979/0815) in the amber collection of the Museum für Naturkunde Berlin. A handwritten, historic label of MB.Pb.1979/0817 reads “Quercus sub-glabra Casp. ex parte Q. meyeriana”, signed by Caspary (Fig. 20J). Therefore, we think that this particular specimen was renamed as *Quercus subglabra* by Caspary himself in 1881 and is therefore the holotype of *Q. subglabra*.

Conwentz (1886) re-evaluated *Quercus meyeriana* and assigned all three original specimens of *Quercites meyerianus* from Göppert & Berendt (1845; MB.Pb.1979/0813, MB.Pb.1979/0817 and MB.Pb.1979/0815) to different species, partly following Caspary (1881). Conwentz (1886) assigned MB.Pb.1979/0813 and MB.Pb.1979/0817 to *Quercus subglabra* and MB.Pb.1979/0815 to *Quercus meyeriana* var. denticulata, a variety that was described by Conwentz (1886; see a discussion on *Q. meyeriana* var. denticulata in Unresolved affinities).

However, the two specimens of *Quercus subglabra* sensu Conwentz MB.Pb.1979/0813 and MB.Pb.1979/0817 are clearly distinct (Table 6): MB.Pb.1979/0813 has a widely open, cyathiform perianth, which is dissimilar to the closed, campanulate perianth of MB.Pb.1979/0817 (Fig. 20B). Furthermore, the rachis of MB.Pb.1979/0813 is rather glabrous, except for the trichome tufts at the base and pedicel of each floret. The perianth margin of MB.Pb.1979/0813 is entire with few solitary trichomes, whereas the other specimens possess irregularly serrate perianth margins. Anther apices in MB.Pb.1979/0813 are obtuse, whereas they are clearly notched in MB.Pb.1979/0817 (Fig. 20E). Based on these differences, we treat both specimens as distinct species and follow Caspary’s (1881) definition of *Q. subglabra* with MB.Pb.1979/0817 as its holotype, while we designate MB.Pb.1979/0813 as the lectotype of *Quercites meyerianus* (see explanation and discussion on *Quercus meyeriana* below).

The amber specimens we studied, GZG.BST.24535 and GZG.BST.24418, are similar to specimen MB.Pb.1979/0817 (= *Quercus subglabra*, Fig. 20) in the following features (Table 5): small size of anthers and perianth; campanulate perianth; number of stamens per floret (7–9); glabrous perianth surface; anthers apically notched; linear subending bracts; stellate trichomes on rachis; and presence of acute, simple and singular trichomes (preserved as trichome bases in GZG.BST.24418 and MB.Pb.1979/0817). However, Conwentz (1886) did not mention uniseriate trichomes along the perianth margin.

Comparing MB.Pb.1979/0817, GZG.BST.24535 and GZG.BST.24418 to other inclusions of *Quercus* inflorescences, specimens of *Q. subglabra* differ in the following features: perianth short, narrow, campanulate, not as deeply incised or widely open as in *Q. aimeeana* Sadowski & al.; low number of stamens per floret (e.g. 9–11 in *Q. multipilosa* Sadowski & al.; 8–13 in *Q. aimeeana*); small size of apically notched anthers (e.g. in *Q. casparyi* [1140–14661–1560] µm long × [680–1772–900] µm wide); and small pollen size. Among *Quercus* species described by Conwentz (1886) and Caspary (1880, 1881, 1886a, 1886b), *Q. limbata*, *Q. nuda*, *Q. piligera* Casp. and *Q. taeniato-pilosa* Conw. exhibit a perianth that is not incised to the base. However, they differ from specimens of *Q. subglabra* in the following aspects: *Q. limbata* has a ciliate margin, elongated filaments overarching the perianth and densely pubescent subending bracts; *Q. nuda* has a widely open perianth and a glabrous rachis; *Q. piligera* has broadly ovate subending bracts and a pubescent perianth surface; and *Q. taeniato-pilosa* has six stamens and trichomes on the outer surface of the perianth.

Based on the pollen morphology of GZG.BST.24535 and GZG.BST.24418 (weakly microverrucate perforate tectum, thin footlayer; Fig. 22F; 24D, E) both specimens are assigned to *Quercus* sect. *Lobatae*. Among modern species, pollen very similar to *Q. subglabra* occurs, for instance, in *Q. imbricaria* (see Solomon 1983b: fig. 10a).

Additional specimens investigated — GZG.BST.24535 (Fig. 21, 22), GZG.BST.24418 (Fig. 23, 24).

*Quercus multipilosa* Sadowski, A. R. Schmidt & Denk, sp. nov. — Holotype: GZG.BST.24414 [Fig. 25, 26], Geoscientific Collection of the University of Göttingen. — Fig. 25–28.

Diagnosis — Pendulous staminate inflorescence, rachis densely covered by stellate trichomes. Florets singular and stalked. Perianth campanulate to cyathiform, incised to middle, forming triangular lobes. Lobes with acute apex, margin of lobes irregularly dentate, with trichomes of four different types sparsely distributed along margin: bifurcate, uniseriate, branched uniseriate and solitary. Outer surface of lobes glabrous. Each floret with sparse central trichome tuft composed of solitary trichomes. Stamens 9–11 per floret, filaments short and in most cases entirely covered by perianth. Anthers
large, elliptic to narrowly elliptic with notched apex, basified. Each floret subtended by glabrous bract, linear, slender with acute apex. Pollen microverrucate, perforate, large, with thin footlayer.

**Description** — Detached floret (GZG.BST.21992; Fig. 27) and staminate inflorescence (GZG.BST.24414, Fig. 25; for detailed measurements see Table 7). *Rachis*: pendulous, 4.5 cm long × 360–640 µm wide (Fig. 25A). *Florets*: singular; stalked, pedicel 400–1000 µm long × 200–300 µm wide. *Perianth*: 1.4–2.6 mm long × 1.9–4.5 mm wide, campanulate to cyathiform, incised to middle or less (Fig. 25B, C; 27A); lobes triangular with acute apex, margin irregularly dentate, margin with different trichome types (Fig. 25G; 27D); surface of lobes glabrous, central trichome tuft scarce (Fig. 25D). Perianth margin (Fig. 25G, H; 27D, E) and stellate trichomes on the rachis; however, the anthers of *Q. klebsii* are mucronate (Conwentz 1886).

**Remarks** — The distinct and numerous trichome types, as well as 9–11 anthers per floret, the notched apex of anthers and the large pollen size distinguish *Quercus multi­pliosa* from all other staminate inflorescence inclusions of *Quercus* (Table 7). Although *Q. multi­pliosa* resembles *Q. nuda* and *Q. subglabra* in the shape of the perianth and in the notched anthers, *Q. nuda* lacks trichomes (Conwentz 1886) and *Q. subglabra* possesses only two trichome types. *Quercus klebsii* Casp. also possesses 9 or 10 anthers per floret and stellate trichomes on the rachis; however, the anthers of *Q. klebsii* are mucronate (Conwentz 1886).

Both specimens belong to *Quercus* sect. *Lobatae*, because they share the following pollen morphological features: tectum microverrucate-perforate, footlayer-endexine thin and discontinuous.

**Etymology** — The specific epithet refers to the high number and morphological diversity of trichomes located on the perianth margin.

**Additional specimen investigated** — GZG.BST.21992 (Hoffeins 623; Fig. 27, 28).

**Quercus aimeeana** Sadowski, A. R. Schmidt & Denk, sp. nov. — Holotype: GZG.BST.24389 [Fig. 29, 30], Geoscientific Collection of the University of Göttingen. — Fig. 29–32.

**Diagnosis** — Pendulous staminate inflorescences, rachis with stellate trichomes. Florets singular, stalked. Perianth cyathiform, short and widely open, sometimes campanulate; incised to middle or lower third, forming triangular to lanceolate lobes with irregular serrate margins. Outer perianth surface and margin glabrous, only very rarely with 1 solitary trichome. Each floret with a central trichome tuft, composed of solitary trichomes. Stamens numerous, 8–13 per floret, filaments short and mostly covered by perianth. Anthers elliptic to narrowly elliptic with obtuse apex, basified. Some florets subtended by singular, linear, slender bract terminating in acute apex; bracts mostly glabrous, with sparse solitary trichomes. Pollen weakly microverrucate, perforate.

**Description** — Two staminate inflorescences (for detailed measurements see Table 7). *Rachis*: pendulous (Fig. 29A; 31A), 2–2.3 cm long × 240–600 µm wide. *Florets*: singular; stalked (Fig. 31B), pedicel 320–1080 µm long × 200–600 µm wide. *Perianth*: 0.8–2.2 mm long × 1.8–2.7 mm wide; occasionally campanulate, mainly cyathiform; incised to middle or occasionally to lower third; perianth widely open, lobes triangular to lanceolate, each with acute apex, margin irregular serrate (Fig. 29C; 31B, D); outer surface and margin of lobes mostly glabrous (Fig. 31E), only rarely with very few trichomes, central trichome tuft present. *Stamens*: 8–13 stamens per floret; filaments covered by perianth (Fig. 29B, C), only rarely measurable: 588–823 µm long × 47–71 µm wide; anthers elliptic to narrowly elliptic with obtuse apex, basified (Fig. 29E; 31C), 1120–1480 µm long × 520–800 µm wide. *Subtending bract*: present to absent (caducous; Fig. 31B, G); some florets subtended by 1 linear, acute, slender bract (Fig. 29D), (1.6–)1.9(–2.8) mm long × (0.2–)0.27(–0.32) mm wide, glabrous on both surfaces. *Trichomes*: 3 types: solitary, bifurcate and stellate; location of trichomes: solitary trichomes as central trichome tuft (Fig. 25D), solitary, bifurcate, uniseriate, and stellate trichomes on perianth margin (Fig. 25G, H; 27D, E) and stellate trichomes on rachis (Fig. 25F). *Pollen*: monad, tricolpate, polar outline trilobate, equatorial outline elliptic (Fig. 26A, B, E; 27F, G; 28A, B), polar axis 30–52 µm in LM, 22–31 µm in SEM, equatorial axis 18–37 µm in LM, 13–22 µm in SEM; in SEM: sculpturing microverruccate, perforate, microverrucae weakly developed (Fig. 26B–D; 28B, C); footlayer thin and discontinuous (Fig. 26E, F; 28D, E).

**Remarks** — The specific epithet refers to the high number and morphological diversity of trichomes located on the perianth margin.

**Additional specimen investigated** — GZG.BST.21992 (Hoffeins 623; Fig. 27, 28).
Fig. 36. Inclusion of staminate inflorescence of *Quercus meyeriana* (lectotype, MB.Pb.1979/0813) from Baltic amber and historic drawing of this particular specimen (A, B, E, K; from Conwentz 1886: t. III, fig. 3–6). – A, C: overview of staminate catkin with singularly arranged florets; B: amber specimen with catkin inclusion shown in A and C; D, E: singular floret; arrowhead indicates linear, elongated bract subtending floret; note widely open, cyathiform perianth; F: short stamens with apically rounded anthers; G: apical part of catkin showing pubescent rachis and widely open perianths; H: indumentum of rachis (arrowhead); I: long, solitary trichomes located on perianth margin; J: basifixed, apically rounded anther; K: stellate trichome of rachis. – Scale bars: C, D, F, G = 1 mm; H = 500 µm; I = 300 µm.
cally obtuse, and only few stellate trichomes on its ra-
chis (in contrast to the dense stellate trichome cover of Q.
aimeeana).

Some Quercus species from Baltic amber differ from Q. aimeeana by possessing mucronate to acute anthers (Q. mucronata, Q. nuda var. serrulata, Q. trichota), cili-
ate perianth margins and/or pubescent perianth surface (Q. limbata, Q. meyeriana, Q. meyeriana var. denticu-
lata, Q. mucronata, Q. taeniato-pilosa, Q. trichota, Q. trichota var. macranthera Conw.), a glabrous rachis (Q. nuda) and different perianth shapes (e.g. campanulate in Q. limbata, Q. nuda var. serrulata, Q. piligera). In summary, Q. aimeeana is distinct from other species of Quercus in the combination of the following features: short and wide perianth, presence of three trichome types, high number of stamens per floret (8–13), comparatively short and wide anthers, obtuse anther apex and smaller pollen size (Table 7).

Fig. 37. Detached staminate floret inclusion of Quercus mucronata (holotype, MB.Pb.1979/0868) from Baltic amber and historic drawing of specimen (from Conwentz 1886: t. II, fig. 15, 16). – A–C: overview of floret from different sides; note deeply lobed perianth; D: amber piece with floret inclusion shown in A–C; E: trichomes singular, elongated and partly helically twisted located along perianth margin; F, G: anthers apically mucronate (F, arrowhead) and basifixed (G, arrowhead); H, I: linear perianth lobes with glabrous surface and trichomes along margins. – Scale bars: A, B = 1 mm; E–G = 300 µm; H, I = 200 µm.
Based on the pollen morphology (weakly microverru
cate, perforate), both specimens are assigned to Quercus
sect. Lobatae.

Etymology — The species is named to honour Aimée An-
toinette Camus (1879–1965) and her outstanding mag-
um opus on extant Fagaceae.

Additional specimen investigated — GZG.BST.24388
(Fig. 31, 32).

Quercus sect. Protobalanus (Trel.) O. Schwarz in Notizbl. Bot. Gart. Berlin-Dahlem 13: 21. 1936.

Quercus brachyandra (Casp.) Sadowski, A. R. Schmidt & Denk, comb. nov. = Castanea brachyandra Casp. in Schriften Phys.-Ökon. Ges. Königsberg 22: 23. 1881 [no
figure]; Conwentz, Die Angiospermen des Bernsteins: 38
[no figure]. 1886. – Holotype: MB.Pb.1979/0660 [Fig.
33], Museum für Naturkunde Berlin. – Fig. 33–35.

Emended diagnosis — Florets in dichasia of up to 6; flo-
rets sessile, clustered. Perianth widely open and incised
to base, forming 5–7 linear lobes, connate at base and
acute to rounded at apex. Surface of lobes glabrous, mar-
gin of lobes irregular incised and ciliate with solitary,
elongated and helically curled trichomes. Each floret
with a central, dense trichome tuft. Stamens 7–9 per flo-
ret with filaments projecting beyond perianth. Anthers el-
liptic, apically mucronate, basifixed. Dichasia subtended
by up to 7 bracts, linear, lanceolate or ovate, glabrous on
abaxial and adaxial side, but ciliate along margin. Pollen
with elliptic equatorial outline, sculpturing smooth,
verrucate, microechinate, apical parts of rodlets appear-

Fig. 38. Inclusion of detached staminate floret of Quercus emanuelii (holotype, MB.Pb.2009/0261) from Bitterfeld amber. – A:
overview of floret with deeply lobed perianth; B: perianth lobe with solitary trichomes on outer surface and along margin; C: peri-
anth lobe; arrowhead indicates solitary helically curled trichomes located in floret centre and along perianth margin; D: basifixed,
apically mucronate (arrowhead) anther. – Scale bars: A = 1 mm; B = 200 µm; C = 300 µm; D = 500 µm.
Fig. 39. Inclusion of detached staminate floret of *Quercus trichota* (A–E; holotype, MB.Pb.1979/0814) from Baltic amber, historic drawing of this specimen (H, I) and additional specimen (F, G) of same species (from Conwentz 1886: t. II, fig. 17–20). – A, B, I: overview of specimen with campanulate perianth and dense indumentum in upper third of perianth; note short stamens; C: basi-fixed, mucronate anther (arrowhead); D, E: solitary trichomes located on outer surface of perianth (D) and along perianth margin (E); F: additional floret inclusion of *Q. trichota*, which is currently lost; G: amber specimen with inclusion shown in F; H: amber specimen with inclusion shown in A–E and I. – Scale bars: A, B = 500 µm; C–E = 200 µm.
Description — Staminate dichasium: dichasium consisting of 4–6 florets (Fig. 33A–D; 34A–C), 5–7 mm × 4–5 mm across. Florets: non-petiolate, densely arranged (Fig. 33A; 34A). Perianth: 2.6–3.2 mm long × 2.8–3.1 mm wide, widely open, deeply incised almost to base, connate at base (Fig. 33E; 34C, D); perianth lobes 5–7, (1.4–)1.7(–2.4) mm long (likely longer because base is covered) × (0.3–)0.5(–0.7) mm wide, linear, each with acute or rounded apex, margin irregularly incised; surface of lobes glabrous, margins densely hairy (Fig. 33G; 34D, E). Stamens: 7–9 stamens per floret; filaments projecting beyond perianth (Fig. 33D; 34D), (1680–)2000–2200 μm long × (70–)1000–130 μm wide; anthers elliptic with mucronate apex, basifixated (Fig. 33F; 34F, G), 900–1920 μm long × 420–620 μm wide. Subtending bract: up to 7; each floret subtended by 1 or 2 linear, lanceolate or slightly ovate bracts (Fig. 33B; 34B, C), 1.1–3 mm long × 0.4–2.3 mm wide, glabrous on both surfaces, trichomes along margin. Trichomes: solitary, elongated, helically curled (Fig. 33G; 34E); distributed along margins of bracts and perianth and inside each floret, forming dense, central trichome tuft (Fig. 34C, D). Pollen: monad, tricolpate, polar outline trilobate, equatorial outline elliptic (Fig. 34H, I), polar axis (24–)26–30 μm in LM, equatorial axis (18–)20–24 μm in LM; in SEM: sculpturing perforate (Fig. 35B), verrucate (Fig. 35B–F), microechinate (Fig. 35A, B), only apical parts of rod-shaped structures visible, rod-like masked sensu Denk & Grimm (2009).

Remarks — The only inclusion of a fagaceous staminate dichasium with more than three florets is Castanea brachyandra, described by Caspary (1881) as follows: dichasium with seven florets; perianth with six lobes; dichasium with six ovate-lanceolate subtending bracts; long trichomes along the margin of perianth lobes and subtending bracts; stamens numerous, in total 31 (likely more because some stamens are broken-off); anthers elliptic with heart-shaped base and mucronate apex. However, Caspary (1881) did not publish a figure showing the inclusion of Castanea brachyandra. Conwentz (1886) repeated Caspary’s description from 1881, but without illustrating the inclusion. We found a specimen with a handwritten label of Castanea brachyandra in the Künow Amber Collection of the Museum für Naturkunde Berlin, specimen MB.Pb.1979/0660 (Fig. 33H), which resembles Caspary’s description in most aspects, except for the number of florets with six instead of seven singular florets. However, Caspary mentioned that Castanea brachyandra derived from the Künow Amber Collection, as specimen MB.Pb.1979/0660. Therefore, it is very likely that this specimen is actually the holotype of Castanea brachyandra.

Comparing the type specimen MB.Pb.1979/0660 (Fig. 33) with GZG.BST.24385 (Table 8, Fig. 34), similarities occur, including: numerous florets clustered in one dichasium, which is subtended by large bracts (Fig. 34B); perianth divided into distinct lobes, which have ciliate margins (Fig. 34C–E); stamens overarching the florets (Fig. 34B); anthers mucronate and elongated (Fig. 34F, G). However, florets in GZG.BST.24385 are more open and wider (Fig. 34A), which is probably due to maturity. Specimen MB.Pb.1979/0660 has only up to seven stamens per floret, but we observed several malformations of stamens, because filaments of neighbouring stamens were fused (Fig. 33F). Therefore, it is difficult to determine the exact number of stamens per floret. Also, anthers of MB.Pb.1979/0660 are shorter than in GZG. BST.24385, which might be related to the deformed filaments as well. The holotype did not contain any pollen; however, based on the very distinct morphology shared between MB.Pb.1979/0660 and GZG.BST.24385, we think that they represent the same taxon.

Conwentz (1886) stated that Castanea brachyandra is likely not affiliated with Castanea, because the anthers were too elongated and the filaments too short. In his revision of plant inclusions from Baltic amber, Kirchheimer (1937) also had difficulty assigning this specimen of Castanea brachyandra. The pollen morphology of GZG.BST.24385 supports affinities with Quercus. The rod-like masked, microechinate sculpturing of pollen grains was reported by Denk & Grimm (2009) and Bouchal & al. (2014) and assigned to Q. sect. Protobalanus. In addition to the pollen morphology, several other features of Castanea brachyandra justify assignment to Quercus: basifixated, elliptic, large (1.2–2 mm long) and mucronate anthers; perianth deeply incised and connate at the base. Because of these morphological similarities, we propose the new combination Quercus brachyandra. Although the pollen morphology of Quercus brachyandra unambiguously proves its affinities to Q. sect. Protobalanus, extant Q. sect. Protobalanus examined in this study (Table 2, Fig. 7A, B) is different from the amber fossils in the singular florets, the indumentum, short filaments and acute anther apex. However, we studied only Q. chrysolepis of Q. sect. Protobalanus, which may not reflect the overall morphology of staminate inflorescences within this section.

Up to now, there was no staminate catkin of Quercus from Baltic amber that exhibited a dichasium with at least four florets, as in Q. brachyandra. However, a singular floret of Quercus with a deeply incised perianth and lanceolate-linear lobes was described as Q. mucronata (Conwentz 1886). The holotype of Q. mucronata (MB.Pb.1979/0868; Fig. 37) resembles Q. brachyandra in the following features: the shape and size of the perianth; the presence and distribution of long, simple, acute trichomes along the perianth margin; the central trichome tuft; the mucronate anthers. However, Q. mucronata can be clearly distinguished from Q. brachyandra in the shorter length of filaments and in the significantly smaller anther size (600–920 μm long × 380–560 μm wide).
Quercus meyeriana is another species with singular florets that resemble Q. brachyandra, with specimens of both species sharing the following features: perianth deeply incised with obovate, elongated or lanceolate lobes; perianth glabrous with ciliate margins; stamen number 6–10; filaments elongated; size of entire floret 2–3.5 mm long (Conwentz 1886). The only distinguishing feature is the apically emarginate anthers in Q. meyeriana, which are mucronate in Q. brachyandra. Hence, in view of the different anther morphology, we refrain from assigning Q. brachyandra to Q. meyeriana.

The singular floret of Quercus trichota (MB.Pb.1979/0814; Fig. 39) also possesses mucronate anthers, but differs from Q. brachyandra by its triangular perianth lobes, the pubescent outer surface of the perianth, but differs from MB.Pb.1979/0814; Fig. 39) also possesses mucronate anthers in Q. meyeriana, which are mucronate in Q. brachyandra. Hence, in view of the different anther morphology, we refrain from assigning Q. brachyandra to Q. meyeriana.

Hence, in view of the different anther morphology, we refrain from assigning Q. brachyandra to Q. meyeriana.

Quercus meyeriana (Göpp. & Berendt) Brongn., Dict. Univ. Hist. Nat. 13: 165 [no figure, no description]. 1849 ['meyeri anus']. emended here = Quercites meyerianus Göpp. & Berendt. Die im Bernstein befindlichen Pflanzenreste der Vorwelt: 84, 85, t. IV, fig. 33, 34. 1845. – Lectotype (designated here): MB.Pb.1979/0813 [Fig. 36], Museum für Naturkunde Berlin. – Fig. 36.

Additional specimens investigated — GZG.BST.24385 (Fig. 34, 35), GZG.BST.21993 (Oe 201).

Quercus meyeriana section not determined

Quercus meyeriana (Göpp. & Berendt) Brongn., Dic t. Univ. Hist. Nat. 13: 165 [no figure, no description]. 1849 ['meyeri anus']. emended here = Quercites meyerianus Göpp. & Berendt. Die im Bernstein befindlichen Pflan zenreste der Vorwelt: 84, 85, t. IV, fig. 33, 34. 1845. – Lectotype (designated here): MB.Pb.1979/0813 [Fig. 36], Museum für Naturkunde Berlin. – Fig. 36.

Additional references

Quercus meyeriana (Göpp. & Berendt) Brongn.: Unger, Gen. Sp. Pl. Foss.: 404 [no figure]. 1850.

Quercus meyeriana (Göpp. & Berendt) Brongn.: Caspar in Schriften Phys.-Ökon. Ges. Königsberg 22: 22 [no figure]. 1881.

Quercus meyeriana (Göpp. & Berendt) Brongn.: Kirchheimer in Beih. Bot. Centralbl., Abt. B, 57: 465 [no figure]. 1937.

Quercus subglabra Casp.: Conwentz, Die Angiospermen des Bernstein: 29, t. III, fig. 3–6 [herein Fig. 36A, B, E, K]. 1886.

Quercus subglabra Casp.: Iljinskaja, Fossil Fl. Pl. USSR 2: 113, text-fig. 83: 1–4. 1982.

Emended diagnosis — Staminate catkins, pendulous with lax rachis. Rachis with stellate trichomes below each floret. Florets sessile or petiolate, singular. Perianth cyathiform with 5 or 6 triangular-ovate lobes with acute or obtuse apices. Perianth margin entire to irregularly incised with few solitary trichomes; outer surface of lobes glabrous. Centre of perianth with solitary trichome tuft. Stamens 6–8 per floret, filaments as long as perianth. Anthers elliptic, obtuse, basifix ed. Each floret subtended by glabrous bract, short to elongated, linear with acute apex.

Description — Staminate inflorescence: 1.9 cm long; rachis pendulous, 280 µm wide, covered with stellate trichomes below each floret (Fig. 36E, H). Florets: singular; stalked. Perianth: 1.4–2.6 mm long × 0.9–1.2 mm wide, cyathiform, widely open; perianth lobes triangular-ovate, each with acute or obtuse apex, margin irregular incised, but mostly entire (Fig. 36D, E, G); outer surface glabrous, margin of lobes with few solitary trichomes, central trichome tuft present. Stamens: 6–8 stamens per floret; filaments covered by perianth (not measurable, Fig. 36F); anthers narrowly elliptic with obtuse apex, basifixed (Fig. 36D), (1200–1350)–1500) µm long × (500–5595)–660) µm wide. Subtending bract: present; linear, acute, very slender (Fig. 36D), 0.7–1.7 mm long × 0.06–0.1 mm wide, mostly glabrous on both surfaces. Trichomes: 2 types: solitary and stellate; location of trichomes: solitary trichomes as central trichome tuft, few on perianth margin (Fig. 36D); stellate trichomes distributed on rachis, mainly below each floret (Fig. 36E, G, H, K).

Remarks — Quercus meyeriana was first published as Quercites meyerianus (Göppert & Berendt 1845). Bron niart (1849) mentioned Quercus “meyeri anus” in a list of fossil plants (where the spelling of the epithet is correctable to meyeriana) and hence was the first to publish the new combination Quercus meyeriana. Unger (1850) was unaware of Bronniart’s publication and independently published the combination Quercus meyeriana, including the diagnosis of Göppert & Berendt (1845), but without further illustrations of the specimens (Table 3).

Göppert & Berendt (1845) described three amber specimens with two catkins and one detached floret as Quercites meyerianus, but they did not designate a holotype. We found all three specimens (MB.Pb.1979/0813, MB.Pb.1979/0817 and MB.Pb.1979/0815; Table 6) in the amber collection of the Museum für Naturkunde Berlin. Of these specimens, which are syntypes, MB.Pb.1979/0817 was subsequently designated as the holotype of Quercus subglabra (Caspar 1881), based on the morphology of the perianth. MB.Pb.1979/0813 was also transferred to Q. subglabra (Conwentz 1886), although we noted that MB.Pb.1979/0813 is clearly different from MB.Pb.1979/0817, e.g. in the open cyathiform perianth.

Conwentz (1886) retained the species Quercus meyeriana, but he changed the diagnosis, assigned two of the three syntypes of Göppert & Berendt (1845; MB.Pb.1979/0813, MB.Pb.1979/0817; Table 6) to a different species and chose a different specimen apparently to serve as a type for Q. meyeriana. According to the International Code of Nomenclature for algae, fungi, and plants (Turland & al. 2018), a later homonym is published if the type of an existing name is definitely excluded (Art. 48.1); however, in 1886 Quercus meyeriana did not have a type, so that all three syntypes would have had to be excluded (Art. 48.2), which Conwentz (1886) did not do; he retained one syntype in Q.
Fig. 40. Inclusion of detached staminate floret of Quercus limbata (B, C, E–I; holotype, MB Pb.1979/0521) and historic drawing of this specimen (A, B; from Conwentz 1886: t. III, fig. 12, 13). – A–C: overview of floret from different sides; note large subtending bract (arrowheads); D: amber specimen is a disc-shaped bead containing floret shown in A–C; E: base of floret with remains of rachis (arrowhead); F: basifix, apically notched anther; G: second linear bract subtending floret; numerous solitary trichomes are located along margin; H: solitary, helically curled trichomes along perianth margin; I: bifurcate and solitary trichomes on abaxial side of large bract. – Scale bars: B, C = 1 mm; E = 500 μm; F = 300 μm; G–I = 200 μm.
meyeriana, as the type of *Q. meyeriana var. denticulata* (see below).

Unfortunately, the specimen that Conwentz intended to serve as the type of his *Quercus meyeriana* is lost. The illustration of this specimen shows features that are rather typical for *Eotrigonobalanus* (such as the projecting filaments; for further discussion see *Eotrigonobalanus*). Moreover, Conwentz’s (1886) description of his *Q. meyeriana* differs greatly from the diagnosis of *Quercites meyerianus* given by Göppert & Berendt (1845; see Table 6), for instance in the campanulate perianth (cyathiform in Göppert & Berendt 1845), the elongated filaments more than twice as long as the perianth (filaments as long as the perianth in Göppert & Berendt 1845) and in the presence of simple trichomes (stellate in Göppert & Berendt 1845) and in the presence of simple trichomes (stellate in Göppert & Berendt 1845).

MB.Pb.1979/0815, one of the syntypes of *Quercites meyerianus* (Göppert & Berendt 1845), was later renamed *Quercus meyeriana var. denticulata* (Conwentz 1886). However, MB.Pb.1979/0815 differs from the diagnosis of *Q. meyerianus* in its top-shaped, glabrous perianth, round anthers and longer filaments, which to some extent resembles castaneoids or trigonobalanoids (for further discussion on *Q. meyeriana var. denticulata* see Unresolved affinities).

In summary, all original specimens of *Quercites meyerianus* (MB.Pb.1979/0813, MB.Pb.1979/0817, MB.Pb.1979/0815) are morphologically distinct and are recognized here as separate taxa. Only MB.Pb.1979/0813 corresponds to the original diagnosis of *Q. meyerianus* and is therefore designated as lectotype of that name.

As explained above, MB.Pb.1979/0817 was previously designated as the holotype of *Quercus subglabra*, and MB.Pb.1979/0815, the holotype of *Q. meyeriana var. denticulata*, is also excluded from *Q. meyeriana* because its affinities to *Quercus* are unresolved.

*Quercus meyeriana* (MB.Pb.1979/0813) is distinct from *Q. subglabra* in the open cyathiform perianth, the entire perianth margin, the obtuse anthers and densely arranged, stellate trichomes at the base of each floret. Although *Q. meyeriana* shares features with *Q. casparyi* (e.g. the number of stamens per floret) and *Q. aimeeana* (e.g. perianth shape and size of anthers), it is different from both species in the obtuse anthers (mucronate in *Q. casparyi*) and the number of stamens (10–12 in *Q. aimeeana*).

*Quercus mucronata* Casp. in Schriften Phys.-Ökon. Ges. Königsberg 22: 22 [no figure]. 1881, emended here; Conwentz, Die Angiospermen des Bernsteines: 27–28, t. II. fig. 15, 16 [herein Fig. 37C, D]. 1886. – Holotype: MB.Pb.1979/0868 [Fig. 37], Museum für Naturkunde Berlin. – Fig. 37.
Emended diagnosis — Staminate florets top-shaped to deeply lobed, widely open, incised to base, forming six linear lobes. Apex of lobes acute, margins of lobes entire with solitary trichomes, long, helically curled to straight. Outer and inner surface of perianth glabrous. Stamens 6 per floret, projecting slightly beyond perianth, filiform. Anthers rounded to elliptic, basifixed, apically mucronate. Centre of floret with tuft of solitary trichomes.

Description — Detached florets. Perianth: top-shaped to deeply lobed (Fig. 37A–C), 1.6 mm long × 0.5 mm wide, glabrous, incised to base, lobes linear to lanceo-
Fig. 43. Inclusion of staminate inflorescence with affinities to *Trigonobalanus* (Trigonobalanoid sp. 1, *Trigonobalanoideae*, GZG. BST.21995) from Baltic amber. – A: overview of stamine catkin with pubescent, rigid rachis; floret dichasia subtended by bracts (b); B: overview of dichasium with numerous florets subtended by large bract (b); C: basifixed, apically mucronate (arrowhead) anther; D: floret from side with elongated stamens projecting beyond perianth; arrowhead indicates cordate anther base; E: cross-section through floret showing dense trichome tuft in floret centre (arrowhead); F: perianth lobe with ciliate margin; G: subtending bract; note pubescent abaxial surface; H: solitary trichomes on rachis. – Scale bars: A, B = 1 mm; C, F, H = 100 µm; D, E = 500 µm; G = 200 µm.
late with acute apex, margins entire and with long trichomes (Fig. 37H, I). Stamens: 6 stamens per floret; filaments projecting slightly beyond perianth (Fig. 37B), (1400–)1600(–1800) µm long × (70–)78(–80) µm wide; anthers elliptic to round with mucronate apex, basifixed (Fig. 37F, G), (600–)777(–920) µm long × (380–)450(–560) µm wide. Trichomes: 1 type: solitary, helically curled or straight, located along perianth margin (Fig. 37E) and forming a trichome tuft in floret centre (Fig. 37B).

Remarks — Quercus mucronata was first described by Caspary (1881) and later illustrated by Conwentz (1886, t. II, fig. 15, 16; herein Fig. 37C, D).

Quercus mucronata differs from other Quercoideae from Baltic amber in the deeply incised perianth with linear lobes and long, solitary trichomes along the lobe margins (Table 9). Only Q. brachyandra possesses a deeply incised perianth, but differs from Q. mucronata by its larger anthers (up to 1920 µm long in Q. brachyandra, up to 920 µm in Q. mucronata), the dense, central trichome tuft, the higher number of stamens per floret, and the longer filaments (2000 µm in Q. brachyandra, 1600 µm in Q. mucronata).

Quercus emanuelii, which was described based on a single floret inclusion from Bitterfeld amber (May 2003; holotype MB.Pb.2009/0261; Fig. 38), also possesses mucronate anthers (Fig. 38A, D); however, Q. mucronata differs from Q. emanuelii in its perianth being more deeply incised and glabrous, whereas Q. emanuelii exhibits trichomes on its perianth (Fig. 38B, C).

The remaining species of Quercus from Baltic amber do not share the combination of features of Q. mucronata (perianth incised to the base, linear lobes, long trichomes along lobe margins, stamens not projecting beyond perianth, anthers mucronate and round-elliptic). Therefore, we treat Q. mucronata as a separate fossil-species.

In extant Quercoideae, mainly Quercus sect. Quercus exhibits staminate florets with deeply incised perianths and linear lobes (Fig. 12). However, from the studied extant species of Q. sect. Quercus, none exhibited mucronate anthers. Therefore, affinities of Q. mucronata to extant groups of the Quercoideae cannot be resolved.

Additional specimens investigated — GZG.BST.24478, GZG.BST.24408, GZG.BST.24399, GZG.BST.24382.

Quercus trichota Cesp. in Schriften Phys.-Okon. Ges. Königsberg 22: 22 [no figure]. 1881. emended here; Conwentz, Die Angiospermen des Bernstein’s, 28, t. II, fig. 17–20 [herein Fig. 39F–I]. 1886. – Holotype: MB.Pb.1979/0814 [Fig. 39A–E], Museum für Naturkunde Berlin. – Fig. 39.

Additional references

Quercus mucronata Cesp.: Kirchheimer in Beih. Bot. Centalbl., Abt. B, 57: 465 [no figure]. 1937.
thers (herein Fig. 39H, I), whereas the other specimen (Fig. 39F, G) had rounded anthers. Because this particular specimen is lost, we cannot confirm this observation. However, we found further inclusions of detached florets (not figured) that exhibited a dense trichome cover (restricted to the upper third of the perianth) and mucronate anthers. Therefore, the mentioned characteristics are considered key features of *Q. trichota*.

Conwentz (1886) also described a variety of *Quercus trichota*, *Q. trichota* var. *macranthera*. However, illustrations of this specimen clearly differ from the type of *Q. trichota* (MB.Pb.1979/0814, i.e. in the larger, apically rounded anthers), which is why we excluded *Q. trichota* var. *macranthera* from *Q. trichota* (for a detailed discussion see Unresolved affinities).

**Quercus limbata** Casp. in Schriften Phys.-Ökon. Ges. Königsberg 22: 23 [no figure]. 1881. **Emended here:** Conwentz, Angiospermen des Bernsteins: 33, t. III, fig. 12, 13 [herein Fig. 40A, D]. 1886. – *Holotype:* MB.Pb.1979/0521 [Fig. 40], Museum für Naturkunde Berlin. – Fig. 40.

?= *Quercus piligera* Casp. in Schriften Phys.-Ökon. Ges. Königsberg 22: 23 [no figure]. 1881; Conwentz, Die Angiospermen des Bernsteins: 34–35, t. III, fig. 17–20 [herein Fig. 41A–D]. 1886. – Type: lost.

?= *Quercus taeniato-pilosa* Conv., Die Angiospermen des Bernsteins: 33–34, t. III, fig. 14–16 [herein Fig. 41E–G]. 1886. – Type: lost.

**Additional references**

*Quercus subglabra* Casp.: Kirchheimer in Beih. Bot. Centabl., Abt. B, 57: 465 [no figure]. 1937.

*Quercus subglabra* Casp.: Iljinskaja, Fossil Fl. Pl. USSR 2: 113, text-fig. 83: 10–13. 1982.

*Quercus piligera* Casp.: Iljinskaja, Fossil Fl. Pl. USSR 2: 113, text-fig. 84: 1–4. 1982.

**Emended diagnosis** — Staminate floret, campanulate perianth with 5 triangular lobes. Apex of lobes acute, perianth margin entire and densely covered with long, solitary trichomes, perianth surface almost glabrous. Stamens 5 per floret, filaments only slightly overtopping perianth. Anthers basifixed, elliptic, apex obtuse. Floret subtended by ovate, obtuse, partially pubescent bract and by linear, apically acute bract.

**Description** — Detached floret with glabrous Rachis remains at base (Fig. 40E). *Floret:* singular, 3.9 mm long × 2 mm wide. *Perianth:* campanulate, 2.2 mm long × 2 mm wide; 5 perianth lobes, triangular, margin densely pubescent (Fig. 40A–C, H), perianth surface sparsely covered with trichomes (Fig. 40E). *Stamens:* 5, filaments mainly covered by perianth (length not measurable), only slightly overtopping perianth (Fig. 40B); anthers basifixed, elongated, 1100–1240 µm long × 560–600 µm wide, apex obtuse (Fig. 40F). *Subtending bracts:* 2 bracts present, both subtending floret (Fig. 40E); 1 bract as long as perianth, 2.2 mm long × 0.6 mm wide, ovate, apex obtuse, margins entire, upper half of abaxial surface and margin tomentose, adaxial side glabrous (Fig. 40E); other bract 920 µm long × 120 µm wide, linear, acute, slightly enrolled and twisted, with few trichomes (Fig. 40G). *Trichomes:* 2 types: solitary and bifurcate. Solitary trichomes often helically curled, located at base of floret, along perianth margin (Fig. 40H), rarely on perianth surface, on bracts (Fig. 40I); bifurcate trichomes located along margin of perianth and bract, as well as on abaxial surface (mainly upper half) of ovate bract (Fig. 40I).

**Remarks** — *Quercus limbata* (MB.Pb.1979/0521; Fig. 40) was first described by Caspary (1881), who included this species in an identification key of fagaceous inflorescence inclusions from Baltic amber. Conwentz (1886) published illustrations of *Q. limbata* (MB.Pb.1979/0521, Fig. 40A, D) and gave a more detailed description. Kirchheimer (1937) and Iljinskaja (1982) lumped *Q. limbata* into *Q. subglabra*, because they did not accept the perianth shape and indumentum as diagnostic features (Table 3). However, our study of extant inflorescences of Fagaceae showed that the indumentum and the perianth shape indeed differ between taxa.

Comparing *Quercus limbata* to other fagaceous inflorescences from Baltic amber, similarities to *Q. piligera* occur (Table 10). The latter species was also first introduced by Caspary (1881) and further described and illustrated by Conwentz (1886). However, the holotype of *Q. piligera* is not available. Comparing Conwentz’s (1886) illustrations of *Q. piligera* (Fig. 41A–D) with MB.Pb.1979/0521 of *Q. limbata*, the following features are shared between both species: subtending bract elongated, ovate (Fig. 40A–C; 41C); abaxial side of bract pubescent (Fig. 40C, E, I; Fig. 41C); shape of perianth campanulate (Fig. 40A); elongated anthers with round apex (Fig. 40F); stamens about twice as long as perianth (Fig. 40A, B, 41A, C); trichomes on perianth margin (Fig. 40A, B, H; 41C). As opposed to *Q. piligera*, *Q. limbata* possesses an additional small, linear subtending bract (Fig. 40A–C, G), which Conwentz (1886) interpreted as remains of the rachis. These linear bracts are often caducous, so it is possible that they were already shed in *Q. piligera*. The perianth of *Q. limbata* is sparsely covered with trichomes (Fig. 40C) and seems not as densely hairy as the perianth of *Q. piligera*. Furthermore, *Q. limbata* possesses only five stamens (seven to nine in *Q. piligera*; Fig. 41A, C).

An additional species similar to *Quercus limbata* is *Q. taeniato-pilosa* (Fig. 41E–G), which also possesses a similar perianth shape (Fig. 41F, G), trichomes on the perianth surface and along the margin, as well as six stamens with similar length and morphology (Fig. 41F, G; Table 10). However, in *Q. taeniato-pilosa* the trichomes are arranged in rows that proceed only along the margin and between the perianth lobes (Conwentz 1886; Fig.
This specific arrangement was considered diagnostic of *Q. taeniato-pilosa*, distinguishing it from other *Quercus* species from Baltic amber (Conwentz 1886). According to Conwentz (1886), Caspary suggested that this particular specimen might belong to *Q. piligera*. Because the type specimens of *Q. piligera* and *Q. taeniato-pilosa* are lost, it is impossible to clarify their definite affinities with *Q. limbata*. However, certain similarities are present (Table 10), which is why we tentatively accommodate them into one species.

Comparing *Quercus limbata* with other *Quercus* species from Baltic amber, *Q. aimeeana*, *Q. casparyi*, *Q. multipilosa* and *Q. subglabra* resemble *Q. limbata* in the shape of the perianth. However, *Q. limbata* differs from the aforementioned species by the tomentose, ovate bracts (which are linear, elongated, very narrow and glabrous in those species), the tomentose perianth (which is glabrous in all those species), the rounded elongated anthers (mucronate in *Q. casparyi*), and the number of stamens (more than nine stamens in *Q. aimeeana* and *Q. multipilosa*).

Fig. 44. Inclusion of staminate inflorescence with affinities to *Trigonobalanus* (Trigonobalanoid sp. 2, *Trigonobalanoidae*: GZG. BST.21996) from Baltic amber. – A: overview of staminate catkin; arrowheads indicate floret dichasia, which are magnified in B, C and F (upper arrowhead) and D (lower arrowhead); B: floret dichasium magnified from A (upper arrowhead) with two florets (f1, f2, indicated by dotted line) subtended by large, central bract (b1); C: floret magnified from B (f1) from side; note glabrous adaxial surface and pubescent abaxial side of subtending bract (b1); D: floret dichasium magnified from A (lower arrowhead) with large subtending bracts (b1–b4) and one visible floret (f); E: basifixed, mucronate (arrowhead) anther; F: floret magnified from A (upper arrowhead) and B (f2) showing stamens projecting beyond perianth; G: indumentum of rachis. – Scale bars: A, B = 1 mm; C, D = 500 µm; E–G = 200 µm.
Fig. 45. Inclusion of staminate inflorescence of *Eotrigonobalanus conwentzii* (holotype, GZG.BST.6895) from Baltic amber. – A: overview of staminate catkin; B: floret with cyathiform perianth subtended by bract (arrowhead); note glabrous rachis; C: distal view of floret showing central loose trichome tuft (arrowhead); note elongated stamens; D: two fused anthers; E: basifixed, apically notched anther; F: three stamens with fused filaments (arrowhead); G, H: subtending bract with few solitary trichomes (G, arrowheads) along margin; I: pollen located in anthers; J: tricolporate pollen. – Scale bars: A–C = 1 mm; D–F = 200 µm; G, H = 100 µm; I = 30 µm; J = 20 µm.
Fig. 46. Pollen extracted from anthers of Eotrigonobalanus conventzii (holotype, GZG.BST.6895); t = tectum, c = columellae, f = footlayer, ed = endexine. – A: pollen attached to amber; B: pollen partly enclosed by amber with microrugulate, perforate sculpturing; C, D: sculpturing with twisted, interwoven microrugulae forming aggregates; E, F: cross-sections of pollen wall with moderately thick footlayer. – Scale bars = A = 10 µm; B, C, F = 1 µm; D, E = 200 nm.
**Quercus nuda** Casp. in Schriften Phys.-Ökon. Ges. Königsberg 21: 28 [no figure]. 1880, *emended here*; Caspary in Schriften Phys.-Ökon. Ges. Königsberg 22: 22 [no figure]. 1881. – Holotype: MB.Pb.1979/0656 [Fig. 42D–I], Museum für Naturkunde Berlin. – Fig. 42.

Additional references

Quercus nuda Casp.: Conwentz, Angiospermen des Bernstein: 31, t. III, fig. 7–9 [herein Fig. 42A–C]. 1886.

Quercus subgabra Casp.: Kirchheimer in Beih. Bot. Centbl., Abt. B, 57: 465 [no figure]. 1937.

Quercus subgabra Casp.: Iljinskaja, Fossil Fl. Pl. USSR 2: 111–113, text-fig. 83: 5–7. 1982.

Emended diagnosis — Staminate florets campanulate, incised to upper third (rarely to middle), forming triangular lobes. Apex of lobes acute, margin entire. Margin of lobes and outer perianth surface almost glabrous, only scarcely with inconspicuous small, solitary trichomes. Stamens up to 10 per floret, filaments projecting only slightly beyond perianth. Anthers elliptic, overtopping perianth, basifixed, apex acute.

Description — According to Conwentz (1886) and Caspary (1880), *Quercus nuda* is described as follows: *Staminate inflorescence:* pendulous, 1.5 cm long; *rachis* filiform, glabrous (Fig. 42A, B). *Florets:* 1.5–2 mm in size, shortly petiolate, in dichasia of 2 or 3 florets (Fig. 42A). *Perianth:* widely open, campanulate to cyathiform (Fig. 42C, D, E); margin dentate; perianth lobes widely ovate to triangular (Fig. 42E, H), longitudinal median with “keel” (Fig. 42C). *Stamens:* 7–10 stamens per floret, entire stamens twice as long as perianth, anthers basifixed, elongated with slightly acute apex (Fig. 42C, E, G). *Subtending bract:* not preserved. *Trichomes:* in MB.Pb.1979/0656, few, scarcely distributed trichomes were observed on surface and at base of perianth (Fig. 42H, I). Caspary (1880, 1881) and Conwentz (1886) described *Q. nuda* as glabrous.

Remarks — A handwritten label of specimen MB.Pb.1979/0656 assigns it to *Quercus nuda* Casp. (Fig. 42F). Because Caspary (1880) did not illustrate *Q. nuda* in his first description and did not mention a particular specimen, we do not know the original material. However, Caspary (1880) mentioned that there were two detached florets, which belonged to the amber preparator Künow, but it is unclear whether they were two distinct specimens or two florets in one amber piece. Conwentz (1886) stated that *Q. nuda* is based on a detached floret, which belonged to Künow. As MB.Pb.1979/0656 derives from the Künow Amber Collection, it could represent this particular specimen. Moreover, specimen MB.Pb.1979/0656 shares all features with the diagnosis of *Q. nuda* by Caspary (1880), including a detached floret with ten stamens, a campanulate perianth that appears “keeled”, and acute anthers overarching the perianth. Therefore, it is likely that MB.Pb.1979/0656 is the type of *Q. nuda*. In contrast to Caspary (1880, 1881), we observed several trichomes on the surface of the perianth and at the base (Fig. 42H, I); because they are very inconspicuous, they might have been overlooked by Caspary (1880, 1881), who mentioned that the perianth surface was entirely devoid of hairs.

Conwentz (1886) assigned an additional specimen to *Quercus nuda*, a catkin with numerous florets, arranged in dichasia of two to three (Fig. 42A–C). Conwentz (1886) also described the anthers as acute, although this is not clearly visible in his illustration. Because the specimen illustrated in Conwentz (1886) is lost, it is impossible to compare it in detail to MB.Pb.1979/0656 (Table 10). However, based on the mentioned similarities, it is likely that they both represent *Q. nuda*.

Of all species of *Quercus* from Baltic amber, there is no specimen that is as glabrous as MB.Pb.1979/0656 and that possesses ten stamens per floret. Conwentz (1886) mentioned strong similarities of *Q. nuda* with *Q. subgabra*, noting that the main distinguishing feature between both species is the absence of trichomes in *Q. nuda*. Kirchheimer (1937) considered this feature to be irrelevant because, in extant *Quercus*, trichomes may be dropped with increasing maturity of the inflorescence. We observed that the presence or absence of trichomes, as well as their morphology, helps in distinguishing species of *Quercus*. Therefore, the glabrous perianth of *Q. nuda* can be used to discriminate this species from *Q. subgabra*. Furthermore, *Q. nuda* differs from *Q. subgabra* in the acute anthers and in the higher number of stamens per floret. Hence, both species should be treated as distinct taxa.

Subfamily: *Trigonobalanoidae*

Genus: not determined

**Trigonobalanoid sp. 1** — Fig. 43.

**Trigonobalanoid sp. 1**

**Trigonobalanoid** sp. 1 — Fig. 43.

Affinities: *Trigonobalanus* Forman in Taxon 11: 140. 1962.

Specimen investigated — GZG.BST.21995 (Hoffeins 1145-4), Geoscientific Collection of the University of Göttingen.

Description — *Staminate catkin:* rigid, 2 cm long: *rachis* 1–1.2 mm wide, with solitary and stellate trichomes, densely pubescent (Fig. 43A, H). *Florets:* in dichasia of 7 or 8, densely arranged around rachis (Fig. 43A). *Perianth:* campanulate to top-shaped (number of lobes not determinable due to dense arrangement; Fig. 43B) with incised to connate base, lobes ob lanceolate with obtuse apex, outer surface almost glabrous (occasionally with solitary trichomes), margins entire and ciliate (Fig. 43F). *Stamens:* about 5 or 6 stamens per floret (difficult to count due to dense arrangement of florets); filaments elongated, projecting...
Fig. 47. Baltic amber inclusion of staminate inflorescence of *Eotrigonobalanus cf. conwentzii* (GZG.BST.24577), which is deformed and likely immature. – A: floret subtended by bract (b); arrowhead indicates closed floret at base; B: basifixed, apically notched anther with fungi (arrowhead); C: overview of staminate inflorescence; arrowheads indicate deformed florets; D: floret, covered with fungi (arrowhead); E: rachis with few stellate trichomes (arrowhead); F: subtending bract (b) with uniseriate trichomes along margin (arrowhead); G: perianth margin showing few trichomes; H: base of floret with trichome tuft; I, J: tricolporate *in situ* pollen. – Scale bars: A, C, D = 1 mm; B = 500 µm; E = 200 µm; F–H = 100 µm; I, J = 20 µm.
Fig. 48. Pollen extracted from anthers of *Eotrigonobalanus* cf. *conwentzii* (GZG.BST.24577); *t* = tectum, *c* = columellae, *f* = footlayer, *ed* = endexine. A: polar view of pollen partly enclosed in amber; B, C: perforate sculpturing of pollen with twisted, interwoven microrugula forming aggregates; D–F: cross-sections through pollen (E), and pollen wall (D, F) showing moderately thick footlayer (*f*). Scale bars: A = 2 µm; B, E = 1 µm; C, D = 200 nm; F = 500 nm.
Fig. 49. Inclusion of staminate inflorescence of *Eotrigonobalanus longianthera* (holotype, GZG.BST.24568) from Baltic amber. – A: overview of staminate catkin; note large anthers and lax rachis; B: floret with elongated filaments projecting beyond perianth; C: cross-section through floret; arrowhead indicates trichome tuft; D: basifixed, mucronate (arrowhead) anther; E: uniseriate trichomes along perianth margin; F: solitary and bifurcate trichomes on subtending bract; G, H: uniseriate (G) and stellate (H) trichomes loosely distributed on rachis; I: pollen cluster located in anther; J, K: *in situ* pollen. – Scale bars: A = 1 mm; B, C = 500 µm; D = 300 µm; E = 100 µm; F–I = 50 µm; J, K = 20 µm.
far beyond perianth (Fig. 43D), > (1080 –)1240(– 1600) µm long × (40–)64(– 80) µm wide (basal part of filaments not discernible); anthers elliptic to round with mucronate apex, base markedly cordate, basifix (Fig. 43C, D); (600–)694(– 780) µm long × (480 –)568(– 780) µm wide. 

Subtending bracts: broadly ovate to lanceolate, abaxially densely pubescent (Fig. 43G); at least 1 bract per floret (total number not discernible). Trichomes: 2 types: solitary (varying in length and stellate); location of trichomes: solitary trichomes on subtending bract (Fig. 43G), located along perianth margin (Fig. 43F) and rarely on perianth surface, forming very dense and large trichome tuft (Fig. 43E) completely filling each floret from inside; stellate trichomes on rachis (Fig. 43H).

Remarks — This specimen is unique among all fagaceous inflorescences from Baltic amber described and depicted by Convenc (1886). It differs from Quercus by its stiff rachis with florets arranged in dense dichasia. This morphology occurs only in the Castaneoideae and Trigonobalanoideae. However, in contrast to the castaneoideans, the specimen possesses basifix, mucronate anthers, which are also larger than in castaneoid florets (anthers are 0.2 – 0.5 mm long in all extant genera of Castaneoideae; see Table 1 for references). This anther type is known from extant Trigonobalanoideae, of which only Trigonobalanus verticillata has a spike-like, rigid staminate inflorescence (Forman 1964; Table 1). Additional features shared between the amber specimen and T. verticillata (Fig. 6A–D) are: florets arranged in dense dichasia; perianth deeply incised with oblanceolate, ciliate lobes; stamens projecting beyond perianth; anthers elliptic to round, basifix; anthers with mucronate apex and cordate base.

Unlike Trigonobalanus, the amber specimen possesses a broad, densely pubescent rachis, which is thinner and almost glabrous or only puberulous in extant T. verticillata (Forman 1964). Furthermore, we could not observe three subtending bracts as described by Forman (1964) for extant T. verticillata (one central bract is broadly oblale, the lateral ones are smaller). Nevertheless, subtending bracts are present in the fossil. Because the pollen extraction from the amber specimen failed, we could not compare the pollen ornamentation to extant Trigonobalanoideae. In summary, most morphological features of the amber specimen correspond with T. verticillata. However, due to the mentioned differences, we refrain from assigning the specimen to Trigonobalanus, but suggest general affinities to the Trigonobalanoideae.

**Trigonobalanoid sp. 2** — Fig. 44.

**Affinities:** Trigonobalanus Forman in Taxon 11: 140. 1962.

**Specimen investigated** — GZG.BST.21996 (Hoffeins 1037-2), Geoscientific Collection of the University of Göttingen.

**Description — Staminate catkin:** rigid (Fig. 44A), 1.9 cm long; rachis 1.2 – 1.6 mm wide, with solitary and stellate trichomes, densely pubescent (Fig. 44A, G). Florets: in dichasia of 2 or singular (Fig. 44B, D). Perianth: cyathiform, 800 – 1120 µm long × 1200 – 1520 µm wide (only 2 florets measurable due to dense trichome cover) with incised to connate base, lobes lanceolate to linear each with acute to obtuse apex (Fig. 44C, F), outer surface almost glabrous (Fig. 44C; occasionally with solitary and bifurcate trichomes), margins entire and ciliate. Stamens: about 4 – 7 stamens per floret (in 2 florets stamens broken off or not visible); filaments projecting only slightly beyond perianth (Fig. 44F), >495 – 675 µm long × 60 – 75 µm wide (filaments longer, but base concealed and therefore not measurable); anthers elliptic to round with mucronate apex, base markedly cordate, basifix (Fig. 44E), 460 – 640 µm long × 380 – 480 µm wide. Subtending bracts: obovate, curved, apices acute, rounded or incised, abaxially pubescent (Fig. 44B–D); 4 bracts per dichasia: 1 large bract subtending dichasia centrally, 1 or 2 bracts located laterally (Fig. 44D); singular florets subtended by 2 – 4 bracts. Trichomes: 3 types: solitary (varying in length and thickness), stellate and bifurcate; location of trichomes: solitary trichomes along perianth margin and rarely on perianth surface, forming dense, central trichome tuft in each floret; stellate trichomes: on rachis (Fig. 44G); bifurcate trichomes: rarely on outer surface of perianth (Fig. 44C).

Remarks — Among all staminate inflorescences investigated here, specimen GZG.BST.21996 resembles only the trigonobalanoid sp. 1 in the densely pubescent and rigid rachis, the mucronate, basifix anthers with a cordate base and the deeply lobed perianth (Table 1). Both specimens differ from each other in the number of florets per dichasia, the arrangement of florets on the rachis, the filament length, the shape and number of subtending bracts and the size of the anthers (Table 1).

Several features of specimen GZG.BST.21996 resemble extant Trigonobalanus verticillata: the rigid rachis, the arrangement of florets in dichasia, the deeply lobed perianth with ciliate margins, the central trichome tuft and the presence of several subtending bracts (Fig. 6A–D, see Table 1 for references). However, extant T. verticillata possesses longer stamens and its rachis is not as densely pubescent and not as broad (Forman 1964) as in the amber specimen. Formanodontrod doichangensis exhibits mucronate anthers (Fig. 61), a deeply incised perianth (Fig. 6H) and a pubescent rachis (Fig. 6E, G); but the rachis of F. doichangensis is not as broad as in the amber specimen, is rather lax and exhibits peltate trichomes (Fig. 6J, K), which are absent in GZG.BST.21996. In the absence of in situ pollen information, we therefore assign the specimen to the Trigonobalanoideae, highlighting its similarities with T. verticillata.
Fig. 50. Pollen extracted from anthers of *Eotrigonobalanus longianthera* (holotype, GZG.BST.24568); t = tectum, c = columellae, f = footlayer, ed = endexine. – A: polar view of pollen partly enclosed in amber; B: cross-section through pollen showing tricolporate shape and thick pollen wall; C: regulate, perforate sculpturing; microrugulae form twisted and interwoven rugulae separated by deep furrows and perforations; D, E: cross-sections through pollen wall; note thick footlayer. – Scale bars: A, B = 2 µm; C = 200 nm; D, E = 500 nm.
Fig. 51. Inclusion of staminate inflorescence of *Eotrigonobalanus campanulata* (holotype, GZG.BST.24419) from Baltic amber. – A: overview of staminate catkin; B: dichasium of three florets, each with elongated filaments projecting far beyond perianth; C: floret; note campanulate shape of perianth and large bract (b) subtending floret; D: basifixed, apically notched anthers; E: loose trichome tuft in floret centre (arrowhead); F, G: rachis with only few stellate trichomes (arrowhead), magnified in G; H, I: perianth margin with few solitary trichomes (H) and uniseriate trichomes (I). – Scale bars: A, B = 1 mm; C, D = 500 µm; E = 200 µm; F–H = 100 µm; I = 50 µm.
Subfamily: not determined

Extinct genus: *Eotrigonobalanus* H. Walther & Kvaček in Feddes Repert. 100: 578. 1989.

*Eotrigonobalanus conwentzii* Sadowski, A. R. Schmidt & Denk, sp. nov. – Holotype: GZG.BST.6895 [Fig. 45, 46], Geoscientific Collection of the University of Göttingen. – Fig. 45–48.

**Diagnosis** — Pendulous staminate inflorescence, rachis glabrous. Florets singular or in clusters of 2 or 3, sessile. Perianth cyathiform, incised to lower third, forming triangular, acute lobes with irregular serrate margin. Outer perianth surface and margin only rarely with solitary trichomes. Each floret with central, loose trichome tuft composed of solitary trichomes. Stamens numerous, 6–11 stamens per floret; filaments elongated, projecting beyond perianth. Anthers narrowly elliptic, apically notched, basifixed. Florets subtended by single bract, lanceolate to linear, terminating in acute apex; bracts mostly glabrous, scarcely with few solitary trichomes on margin and abaxial lamina. Pollen tricolporate, elliptic, microrugulate, perforate, microrugulae twisted and interwoven, forming aggregates; footlayer moderately thick in mesocolpium.

**Description** — Staminate catkin: pendulous, 3.5 cm long; rachis 320–600 µm wide, glabrous (Fig. 45A, B). Florets: singular or in dichasia of 2 or 3 florets, sessile (Fig. 45B), floret dichasia irregularly distributed along rachis (Fig. 45A). Perianth: (1.2–)1.5(–2) mm long × (1.7–)2(2.7) mm wide, cyathiform, incised to lower third and connate at base, more or less glabrous; perianth lobes triangular, each with acute apex, margin irregular serrate (Fig. 45B). Stamens: 6–11 stamens per floret; filaments elongated, projecting beyond perianth (Fig. 45C), (1240–)1580(–1880) µm long × (80–)92(–120) µm wide; anthers narrowly elliptic with notched apex, basifixed (Fig. 45C–F), (880–)1184(–1360) µm long × (400–)432(–480) µm wide; with malformations, occasionally anthers or filaments fused (Fig. 45D, F). Subtending bract: each floret subtended by lanceolate to linear bract (Fig. 45H), (0.9–)1.4(–2.4) mm long × (0.1–)0.3(–0.6) mm wide, almost glabrous. Trichomes: 1 type: solitary, very scarcely distributed on outer surface and margin of perianth and subtending bracts (Fig. 45G), forming loose, central trichome tuft in each floret (Fig. 45C). Pollen: monad, tricolporate, equatorial outline elliptic (Fig. 45I, J; 46A), polar axis (20–)26(–32) µm in LM, (20–)22.5(–26) µm in SEM, equatorial axis (12–)15(–20) µm in LM, (10–)14(–16) µm in SEM, sculpturing perforate and rugulate in SEM (Fig. 46B–D); rugulae (0.3–)0.4(–0.5) µm wide, twisted and interwoven, flattened, forming aggregates (Fig. 46C, D); footlayer moderately thick (≤ 1 µm) in mesocolpium (Fig. 46E, F).

**Remarks** — The features of the *in situ* pollen grains corre-
492 Sadowski & al.: Staminate inflorescences of Fagaceae from Eocene Baltic amber

spond to pollen of *Eotrigonobalanus* sp. from the Eocene of W Greenland, especially by the interwoven and twisted rugulae (compared to Grimsson & al. 2015: plate 6, fig. a–c) and the Oligocene of C Europe (Denk & al. 2012). For this reason, we assign GZG.BST.6895 to *Eotrigonobalanus*. Dispersed pollen of *Eotrigonobalanus* has been assigned to the fossil-species *E. eiszmannii* H. Walther & Zetter (Walther & Zetter 1993) and corresponds in most features to pollen of GZG.BST.6895 (one exception is the thinner pollen wall in *E. conwentzii*; Fig. 46E, F). According to Kohlman-Adamska & Ziembín’ska-Tworzydło (2000), the correct name for such dispersed pollen grains is *Tricolporopollenites villensis* (Thomson) Thomson & Pflug. Here we follow a whole-plant concept (Kvaček 2008) and do not treat in situ pollen as distinct fossil-species.

*Eotrigonobalanus conwentzii* is distinguished from other *Eotrigonobalanus* species (*E. campanulata* Sadowski & al., *E. longianthera* Sadowski & al.; see below) in the following features (Table 12): rachis wider and glabrous (with trichomes in *E. campanulata* and *E. longianthera*); florets arranged in dichasia of 2 or 3; perianth cyathiform (campanulate in *E. campanulata*); filaments shorter but wider; anthers smaller than and not as wide as in *E. longianthera*, with a notched apex (mucronate in *E. longianthera*). Moreover, *E. conwentzii* lacks multicellular and flattened trichomes, which are present on the perianth of *E. longianthera*. Both specimens also differ in the pollen morphology: in *E. conwentzii*, the twisted rugulae form short (< 1 µm) aggregates with little relief (Fig. 46D), whereas in *E. longianthera* they form longer rugulae (> 1 µm) and have a stronger relief (Fig. 50C). Furthermore, the pollen wall is thinner in *E. conwentzii* (Fig. 46E, F) than in *E. longianthera* (Fig. 50D, E).

Malformations of stamens, as observed in GZG.
BST.6895, were mentioned by Hjelmqvist (1948) as an eventual result of stamen reduction in *Quercus* and *Cyclobalanopsis* Oerst. (now *Q.* sect. *Cyclobalanopsis*).

A further inclusion of a staminate inflorescence that possesses similar pollen to that of *E. conventzii* is specimen GZG.BST.24577 (Fig. 47). However, GZG.BST.24577 differs from the other *Eotritonobalanus* species from the Baltic amber (Table 12) by the short filaments (Fig. 47A, C, D), fewer anthers per floret (Fig. 47D) and the presence of three different trichome types (maybe due to fungi; Fig. 47D), by the immaturity of the inflorescence (anthers are closed; Fig. 47B–D) or if they are of taxonomic value. Comparing the pollen of the three specimens, pollen of GZG.BST.24577 is the smallest (Fig. 47I, J). The sculpturing of the pollen (Fig. 48) resembles *E. conventzii* and would support inclusion of this specimen within *E. conventzii,* however, based on the morphological differences of the inflorescences, we only tentatively assign GZG.BST.24577 to *E. conventzii* (E. cf. *conventzii*).

Specimen GZG.BST.24577 (*Eotritonobalanus cf. conventzii*) is labelled with its original collection number SB6 of the Stantien and Becker Amber Collection from Königsberg, which was later incorporated into the Königsberg Amber Collection (now housed at the University of Göttingen, Germany). In the catalogue of the Stantien and Becker Amber Collection, specimen SB6 is listed as “inflorescence of *Quercus subglabra* Casp. original” (Klebs 1889), meaning that this particular specimen was studied and possibly also published by Caspany. Caspary (1881) did not describe this particular specimen and only included *Q. subglabra* in an identification key for staminate inflorescences from Baltic amber. Conwentz (1886) described *Q. subglabra* in detail, but illustrated a specimen (MB.Pb.1979/0813, Fig. 36; here *Q. meyeriana*, see also text above) other than SB6 (= GZG.BST.24577). However, he mentioned that in total ten specimens of *Q. subglabra* existed, and it is not documented which of these specimens was later transferred to the Stantien and Becker Amber Collection.

Etymology — The specific epithet refers to Hugo Wilhelm Conwentz (1855–1922), a botanist and amber researcher, who comprehensively studied plant inclusions from Baltic amber, including the *Fagaceae*.

Additional specimen investigated — GZG.BST.24577 (Fig. 47, 48).

*Eotritonobalanus longianthera* Sadowski, A. R. Schmidt & Denk, sp. nov. – Holotype: GZG.BST.24568 [Fig. 49, 50], Geoscientific Collection of the University of Göttingen. – Fig. 49, 50.

Diagnosis — Pendulous staminate inflorescence, rachis occasionally with uniseriate and stellate trichomes. Florets singular, sessile. Perianth campanulate to cyathiform, incised to lower third or to middle, forming triangular, acute lobes with irregular serrate margins. Outer perianth surface and margin only rarely with trichomes (3 types: solitary, uniseriate and bifurcate). Each floret with central trichome tuft composed of solitary trichomes. Stamens numerous, 8 or 9 stamens per floret, filaments elongated and projecting far beyond perianth. Anthers narrowly elliptic, very long, apically mucronate, basifixid. Florets subtended by singular bract, triangular to lanceolate with acute apex; bracts almost glabrous, scarcely with few solitary or bifurcate trichomes on margin and abaxial surface. Pollen elliptic, tricolporate, microrugulate, microrugulae twisted and interwoven forming rugulae; rugulae separated by deep furrows or perforations.

Description — Staminate catkin: pendulous, 3 cm long; rachis 140–460 µm wide, with trichomes (Fig. 49A, G, H). Florets: singular, non-petiolate, irregularly distributed along rachis (Fig. 49A, B). Perianth: (1.8–)2.2–(2.6) mm × (2–)2.1–(2.4) mm wide, campanulate to cyathiform, incised to lower third and connate at base; perianth lobes triangular, each with acute apex, margin irregular serrate (Fig. 49B, C). Stamens: 8 or 9 stamens per floret; filaments elongated, projecting far beyond perianth, (1520–)1920–(2520) µm long × (60–)76(–80) µm wide; anthers narrowly elliptic with mucronate apex, basifixid (Fig. 49D), (1600–)1795–(2200) µm long × (500–)664(–900) µm wide. Subtending bract: each floret subtended by triangular to lanceolate bract, 2.5–2.7 mm long × 0.2–0.6 mm wide, almost glabrous (Fig. 49B).

Trichomes: 4 types: solitary, bifurcate, uniseriate and stellate; location of trichomes: solitary, bifurcate and uniseriate trichomes on outer surface and on margin of perianth (Fig. 49E); solitary and bifurcate trichomes on abaxial surface and along margin of subtending bract (Fig. 49F), solitary trichomes forming loose, central trichome tuft in each floret (Fig. 49C); uniseriate and stellate trichomes loosely distributed along rachis (Fig. 49G, H). Pollen: monad, tricolporate, equatorial outline elliptic (Fig. 49I–K), polar axis (15–)23–(27) µm in LM, 19–26 µm in SEM, equatorial axis (12–)16–(21) µm in LM, (15–)16(–21) µm in SEM, sculpturing regulate, perforate in SEM (Fig. 50A, C); microrugulae forming rugulae (0.3–)0.5(–0.7) µm wide, twisted and interwoven, with distinct relief (Fig. 50C); rugulae separated by deep furrows and perforations (Fig. 50C); pollen wall thick (Fig. 50B, D, E), > 1 µm, with thick footlayer (Fig. 50D).

Remarks — *Eotritonobalanus longianthera* differs from *E. campanulata* and *E. conventzii* in the following features (Table 12): rachis with stellate and simple acute trichomes; florets singular; filaments and anthers longer; anthers wider; apex of anthers mucronate; four trichome types present. The pollen ornamentation of *E. longianthera* differs from *E. conventzii* in the wider rugulae, the stronger relief and the thicker pollen wall.
**Etymology** — The specific epithet refers to the long anthers of this species.

*Eotrigonobalanus campanulata* Sadowski, A. R. Schmidt & Denk, sp. nov. — Holotype: GZG.BST.24419 [Fig. 51], Geoscientific Collections of the University of Göttingen. — Fig. 51.

**Diagnosis** — Pendulous staminate inflorescence, rachis occasionally with solitary and stellate trichomes. Florets singular or in dichasia of 3 florets, sessile. Perianth campanulate, mostly incised to upper third, sometimes also to lower third, forming triangular, acute lobes with irregular serratate margin. Outer perianth surface only rarely with solitary trichomes. Each floret with loose, central trichome tuft composed of solitary trichomes. Stamens numerous, 6 or 7 stamens per floret, filaments elongated, projecting far beyond perianth. Anthers narrowly elliptic, apically notched, basifixed. Dichasia subtended by singular, glabrous bract, sometimes lacking (caducous), lanceolate, terminating in acute apex.

**Description** — Staminate catkin: pendulous, 2.8 cm long; rachis 200–400 μm wide, with few stellate and solitary trichomes (Fig. 51A, F). Florets: singular or in dichasia of 3 florets, sessile (Fig. 51A–C). Perianth: (0.8–)1.1–(– 1.8) mm long × (1.2–)1.6–(– 1.9) mm wide, campanulate, mostly glabrous, margin irregular serratate, mainly incised to upper third; perianth lobes triangular, with elongated acute apex (Fig. 51B, C). Stamens: 6 or 7 stamens per floret; filaments elongated, projecting far beyond perianth (Fig. 51B, C), (1300–)1488(– 1740) μm long × (80–)92(–100) μm wide; anthers narrow-ly elliptic with notched apex, basifixed (Fig. 51D), (860–)1116(– 1300) μm long × (340–)467(–560) μm wide; with malformations: occasionally filaments fused. Subtending bract: present or absent; dichasium or singular floret subtended by lanceolate bract (Fig. 51B), 1–1.5 mm long × 0.3 mm wide, glabrous. Trichomes: 3 types: solitary, stellate and uniseriate; location of trichomes: solitary trichomes very scarcely located on outer perianth surface and margin (Fig. 51H, I); solitary trichomes forming loose, central trichome tuft in each floret (Fig. 51E); stellate trichomes loosely distributed on rachis (Fig. 51F, G).

**Remarks** — The combination of the following features supports the assignment of GZG.BST.24419 to *Eotrigonobalanus* (Table 12): rachis pendulous; filaments projecting far beyond the perianth; anthers basifixed and large; florets singular or in dichasia; subtending bracts present; trichomes generally scarce; loose, central trichome tuft present. However, *E. campanulata* differs from *E. convenzii* and *E. longianthera* by the smaller, campanulate perianth, the lower number of notched anthers and from *E. longianthera* by the florets arranged in dichasia of three (Table 12).

**Remarks** — The specific epithet refers to the campanulate perianth shape.

*Comparison of Eotrigonobalanus species from Baltic amber* — Among staminate inflorescences and singular florets of the *Fagaceae* from Baltic amber, *Quercus meyeriana* sensu Conwentz (here treated as ? *Eotrigonobalanoid sp.* 2) and *Q. trichota* var. *macranthera* (here treated as ? *Eotrigonobalanoid sp.* 1; see below) resemble the three *Eotrigonobalanus* species in their high number of stamens, the projecting filaments and the elliptic, elongated, large anthers. However, the perianth of *E. convenzii* and *E. longianthera* is more cyathiform with triangular lobes, whereas *Q. meyeriana* sensu Conwentz and *Q. trichota* var. *macranthera* possess a slender, top-shaped perianth with lanceolate to oblanceolate lobes. *Quercus meyeriana* sensu Conwentz has a ciliate perianth margin (Conwentz 1886), which is not the case in the *Eotrigonobalanus* specimens. Moreover, *E. longianthera* has mucronate anther apices, in contrast to the rounded anthers of *Q. meyeriana* and *Q. trichota* var. *macranthera*. The latter taxon is also distinct by its pubescent perianth surface, which is almost glabrous in specimens of *Eotrigonobalanus*.

Grönsson & al. (2015) compared the fossil-taxon *Amentoplexipollenites catahoulaensis* Crepet & Nixon from a staminate catkin of the middle to late Oligocene (Texas, U.S.A.; Crepet & Nixon 1989b) to pollen of *Eotrigonobalanus* based on some similarities of the sculpturing of the pollen grains. However, the staminate inflorescence of *A. catahoulaensis* differs from *E. campanulata, E. convenzii* and *E. longianthera* by its robust, erect rachis and in the case of *E. campanulata* and *E. convenzii* by its mucronate anthers. This suggests that superficial similarities of pollen ornamentation in *Amentoplexipollenites* and *Eotrigonobalanus* do not indicate a close relationship between these taxa. *Amentoplexipollenites* has a pollen sculpturing consisting of loosely braided (micro)rugulae lacking the regular perforations and furrows (Crepet & Nixon 1989b: fig. 16, 18). Therefore, the staminate catkins of *Eotrigonobalanus* reported in this study add previously unknown information to the morphology of the extinct fagaceous genus *Eotrigonobalanus*.

**Unresolved affinities**

Subfamily: not determined
Genus: not determined

**? Eotrigonobalanoid sp. 1** — Fig. 52A, B. = *Quercus trichota* var. *macranthera* Conw., Die Angiospermen des Bernsteins: 28–29, t. III, fig. 1, 2 [herein Fig. 52A, B]. 1886. — Type: lost.

**Affinities**: *Eotrigonobalanus* H. Walther & Kvaček.

**Additional references**

*Quercus mucronata* Conw.; Kirchheimer in Beih. Bot. Centralbl., Abt. B, 57: 465 [no figure]. 1937.
Fig. 54. Inclusion of *Quercus meyeriana* var. *denticulata* (A–I; holotype, MB.Pb.1979/0815) from Baltic amber; one of the original specimens (H, I) published by Conwentz (1886: t. II, fig. 11, 12) and currently lost. Second specimen (J, K) from Conwentz (1886: t. II, fig. 13, 14). Both specimens show affinities to *Castaneoideae* and *Trigonobalanoideae*. – A–C: overview of detached floret from different sides showing top-shaped perianth; outward-bent perianth lobe (A–C, arrowheads; I, a), which Conwentz (1886) interpreted as a subtending bract; D: dense, central trichome tuft, which overtops perianth lobes; E: perianth from below; white lines indicate basally merged perianth lobes; linear, slender bract subtends floret (arrowhead); F: perianth lobe with few trichomes along margin (white arrowhead) and subtending bract (black arrowhead); G: apically notched anthers (arrowhead); H: overview of amber specimen with inclusion shown in A–G and I; J, K: further amber specimen with detached floret (J) and proximal overview of respective floret (K); apex (a) of anther that is flipped over, creating acute shape; however, Conwentz (1886) mentioned that all anthers were not mucronate. – Scale bars: A–C = 1 mm; D, F, G = 200 µm; E = 500 µm.
**Quercus mucronata** Conw.: Iljinskaja, Fossil Fl. Pl. USSR 2: 111, text-fig. 82: 9, 10. 1982.

**Description** — Conwentz (1886) described the species as follows: detached floret (Fig. 52A, B), *Perianth*: campanulate to top-shaped, 2.2 mm long × 2.65 mm wide, incised to lower third, lobes 5 or 6, lanceolate-oblancoolate, each with acute apex, margins entire, outer surface of perianth pubescent (Fig. 52A). *Stamens*: 9 stamens per floret; filaments projecting beyond perianth, 2–3 × as long as perianth; anthers elliptic, large, with rounded apex (Fig. 52A). *Trichomes*: on entire outer surface of perianth (Fig. 52A).

**Remarks** — Although the original specimen of *Quercus trichota* var. *macranthera* is lost, Conwentz’s (1886) illustration and description clearly show that this particular specimen differs from *Q. trichota* in the larger size of the perianth, the greater number of stamens (nine in *Q. trichota* var. *macranthera*, six in *Q. trichota*), the elongated...
filaments, which are two to three times as long as the perianth, and the rounded apex of anthers (mucronate in *Q. trichota*). According to Conwentz (1886), *Q. trichota* var. *macranthera* and *Q. trichota* shared the pubescent outer surface of the perianth, which, however, was not restricted to the upper third. Due to these differences, we exclude *Q. trichota* var. *macranthera* from *Q. trichota*.

We disagree with the assignment of *Quercus trichota* var. *macranthera* to *Q. mucronata*, as suggested by Kirchheimer (1937) and Iljinška (1982; Table 3). The holotype of *Q. mucronata* (Fig. 37) clearly differs from *Q. trichota* var. *macranthera* by its mucronate anthers. However, the anthers in *Q. trichota* var. *macranthera* are basifixed (Fig. 52A) and elliptic, which is different to the round, dorsifixed anthers of the castaneoids. The long filaments also occur in the *Eotrigonobalanus* species recogised in the present study, the perianth margins are not as ciliate as shown in Conwentz’s illustration. Therefore, we suggest affinities to *Eotrigonobalanus*, but we cannot unambiguously resolve the true affinities of *Q. meyeriana* sensu Conwentz, because the type specimen is lost.

Conwentz (1886) listed *Quercus ciliata* as a synonym of *Q. meyeriana*. Caspary (1880) published a diagnosis and description of florets of *Q. ciliata* without an illustration. We found an amber specimen with inclusions of two detached florets (Fig. 52A, D), accompanied by a handwritten label of *Q. ciliata* (MB.Pb.1979/0644; Fig. 53H). One of these florets is similar to Caspary’s (1880) description (Fig. 53A–C; campanulate perianth, six-lobed, six stamens), but is different to Conwentz’s (1886) illustration of *Q. meyeriana*, for instance in the apically acute perianth lobes. The second detached floret of MB.Pb.1979/0644 (Fig. 53D–G) is different to *Q. meyeriana* sensu Conwentz in having mucronate anthers. The very long stamens with large, elliptic anthers and the long filaments resemble *Eotrigonobalanus*. However, in other *Eotrigonobalanus* species recognized in the present study, the perianth margins are not as ciliate as shown in Conwentz’s illustration. Therefore, we suggest affinities to *Eotrigonobalanus*, but we cannot unambiguously resolve the true affinities of *Q. meyeriana* sensu Conwentz, because the type specimen is lost.

Conwentz (1886) listed *Quercus ciliata* sensu Conwentz as inadmissible, because Conwentz (1886) chose a new specimen to serve as the type. For the distinction of Conwentz’s taxon from *Q. meyeriana* (Göpp. & Berendt) Brongn. and *Q. subglabra*, see under those species above (and Table 6).

*Quercus meyeriana* sensu Conwentz also differs from other *Quercus* species in Baltic amber by having 6–10 stamens that project beyond the perianth, notched anthers, and a deeply incised perianth with ciliate margins (Table 13). Although *Q. brachyandra* exhibits elongated stamens and trichomes along the margin of the perianth lobes, it clearly differs from *Q. meyeriana* sensu Conwentz in having mucronate anthers. The very long stamens with large, elliptic anthers, the basifixed anthers and the deeply incised perianth resemble *Eotrigonobalanus*. In other *Eotrigonobalanus* species recognized in the present study, the perianth margins are not as ciliate as shown in Conwentz’s illustration. Therefore, we suggest affinities to *Eotrigonobalanus*, but we cannot unambiguously resolve the true affinities of *Q. meyeriana* sensu Conwentz, because the type specimen is lost.

*Remarks* — As discussed above, *Quercus meyeriana* sensu Conwentz is inadmissible, because Conwentz (1886) chose a new specimen to serve as the type. For the distinction of Conwentz’s taxon from *Q. meyeriana* (Göpp. & Berendt) Brongn. and *Q. subglabra*, see under those species above (and Table 6).

*Quercus meyeriana* sensu Conwentz also differs from other *Quercus* species in Baltic amber by having 6–10 stamens that project beyond the perianth, notched anthers, and a deeply incised perianth with ciliate margins (Table 13). Although *Q. brachyandra* exhibits elongated stamens and trichomes along the margin of the perianth lobes, it clearly differs from *Q. meyeriana* sensu Conwentz in having mucronate anthers. The very long stamens with large, elliptic anthers, the basifixed anthers and the deeply incised perianth resemble *Eotrigonobalanus*. However, in other *Eotrigonobalanus* species recognized in the present study, the perianth margins are not as ciliate as shown in Conwentz’s illustration. Therefore, we suggest affinities to *Eotrigonobalanus*, but we cannot unambiguously resolve the true affinities of *Q. meyeriana* sensu Conwentz, because the type specimen is lost.

Conwentz (1886) listed *Quercus ciliata* as a synonym of *Q. meyeriana*. Caspary (1880) published a diagnosis and description of florets of *Q. ciliata* without an illustration. We found an amber specimen with inclusions of two detached florets (Fig. 52A, D), accompanied by a handwritten label of *Q. ciliata* (MB.Pb.1979/0644; Fig. 53H). One of these florets is similar to Caspary’s (1880) description (Fig. 53A–C; campanulate perianth, six-lobed, six stamens), but is different to Conwentz’s (1886) illustration of *Q. meyeriana*, for instance in the apically acute perianth lobes. The second detached floret of MB.Pb.1979/0644 (Fig. 53D–G) is different to *Q. meyeriana* sensu Conwentz in having mucronate anthers (Fig. 53G) and short filaments (Fig. 53D; Table 13).

Based on these differences, it seems doubtful that the floret inclusions of *Quercus ciliata* (MB.Pb.1979/0644) are conspecific with *Q. meyeriana* sensu Conwentz. Furthermore, the morphology of *Q. ciliata* (MB.Pb.1979/0644) is quite similar to *Q. emanuelii* from Bitterfeld amber and to *Q. mucronata* and *Q. trichota* from Baltic amber. Therefore, *Q. ciliata* (MB.Pb.1979/0644) is too indistinct in its morphology to be kept as a separate species or to be incorporated into one of the existing *Quercus* species from Baltic amber.
Quercus meyeriana (Göpp. & Berendt) Brongn.: Kirchheimer in Beih. Bot. Centralbl., Abt. B, 57: 465 [no figure]. 1937.

Quercus meyeriana (Göpp. & Berendt) Brongn.: Iljinskaja, Fossil Fl. Pl. USSR 2: 110–111, text-fig. 82: 1, 2. 1982.

Description — Detached floret. Perianth: top-shaped (Fig. 54A–C, I), 1.8 mm long × 1.8 mm wide, glabrous surface, incised to base (Fig. 54E), lobes lanceolate each with acute apex, margins irregularly dentate and incised (Fig. 54A–C, I). Stamens: 6 stamens per floret; filaments projecting slightly beyond perianth (Fig. 54A–C, I), (1200–)1330(– 1400) µm long × (60 –)76(– 110) µm wide; anthers round with notchched apex (Fig. 54G), (600–)635(– 680) µm long × (540–)570(– 600) µm wide. Subtending bract: linear with acute apex, glabrous surface, occasionally with a trichome along margin (Fig. 54E, F). Trichomes: 2 types: solitary (helically curled or straight) and uniseriate; location of trichomes: solitary trichomes forming tuft in floret centre (Fig. 54D); uniseriate trichomes few, rarely located along margin of perianth lobes and subtending leaf (Fig. 54F).

Remarks — MB.Pb.1979/0815 is one of the syntype specimens of Quercites meyerianus (= Quercus meyeriana) from Göppert & Berendt (1845). Conwentz (1886) restudied MB.Pb.1979/0815 and observed a dentate perianth margin. Due to this feature, he introduced the variety Q. meyeriana var. denticulata. Kirchheimer (1937) and Iljinskaja (1982) regarded these differences as irrelevant and did not accept Conwentz’s variety (1886; Table 3).

Conwentz (1886) illustrated two species of Quercus meyeriana var. denticulata (Fig. 54H–K), of which only one (MB.Pb.1979/0815; Fig. 54A–I) was available for reinvestigation. Quercus meyeriana var. denticulata (MB.Pb.1979/0815) differs from the holotype of Quercites meyerianus (MB.Pb.1979/0813) in the following features: perianth top-shaped, deeply lobed (cyathiform in MB.Pb.1979/0813), perianth lobes lanceolate (triangular in MB.Pb.1979/0813) and anthers round, apically notched (narrowly elliptic, apically obtuse in MB.Pb.1979/0813). Therefore, MB.Pb.1979/0815 should be excluded from Quercus meyeriana.

Currently, there are no other species of Quercus from Baltic amber that resemble MB.Pb.1979/0815 in all aspects (Table 13). Additional staminate florets of Quercus from Baltic amber that exhibit a deeply lobed perianth as in MB.Pb.1979/0815 are Q. brachyandra and Q. mucronata. MB.Pb.1979/0815 is distinct from these species, because it has round and notched anthers (anthers elliptic and mucronate in Q. brachyandra and Q. mucronata) and lacks long, simple trichomes along the perianth margin (perianth margin ciliate in Q. brachyandra and Q. mucronata).

The top-shaped perianth, elongated filaments and round, comparatively small anthers are atypical features for Quercus, but partly occur in the castaneoids and trigonobalanoids from Baltic amber. The fixation of anthers in MB.Pb.1979/0815 would be a helpful indicator to confirm affinities to either Castaneoideae or Trigonobalanoidae, but the anthers cannot be assessed in this particular amber specimen. Therefore, definite affinities of MB.Pb.1979/0815 remain unresolved.

Affinities: Quercus L.

Additional references
Quercus subglabra Casp.: Kirchheimer in Beih. Bot. Centralbl., Abt. B: 57: 465 [no figure]. 1937.

Quercus subglabra Casp.: Iljinskaja, Fossil Fl. Pl. USSR 2: 111–112, text-fig. 83: 8, 9. 1982.

Description — Detached floret, pedicellate (Fig. 55A, B, G, H). Perianth: campanulate, 2 mm long × 1 mm wide, incised to middle, lobes triangular (Fig. 55A, B), longitudinally keeled, each with acute or emarginate apex, margins serrate (Fig. 55D). Stamens: 7 stamens per floret; filaments concealed by perianth. Anthers basifixed, elongated, elliptic, apex acute (Fig. 55C), (1360–)1592(– 1860) µm long × (600–)696(–820) µm wide. Trichomes: 2 types: solitary and bifurcate; both types irregularly distributed along perianth margin (Fig. 55F), rarely located on perianth surface (Fig. 55E).

Remarks — The holotype of Quercus nuda var. serrulata (MB.Pb.1979/0816) was labelled as “Quercus subglabra var. denticulata” by Caspary (Fig. 55I). Conwentz (1886) was aware of this label but disagreed with Caspary, because the keeled perianth of the holotype is similar to Q. nuda. There is no diagnosis or description of Q. subglabra var. denticulata, and this varietal name is not validly published.
Conwentz (1886) assigned MB.Pb.1979/0816 to *Quercus nuda*, because he could not observe any trichomes. Based on the serrat perianth margin, he established the new variety *Q. nuda var. serrulata*. Conwentz (1886) mentioned that MB.Pb.1979/0816 likely represents the type specimen of *Q. serrata* from Baltic amber (Göppert 1853), but that species name was not validly published because Göppert (1853) did not provide a description. Furthermore, the epithet “serrata” was already validly published for the extant species *Q. serrata* Murray (Murray 1784) and therefore cannot be applied to the amber inclusion. Reinvestigation of the holotype of *Q. nuda var. serrulata* (MB.Pb.1979/0816; Fig. 55) and of the type of *Q. nuda* (MB.Pb.1979/0656; Fig. 42) revealed the presence of trichomes on the perianth in both specimens (Fig. 42H, I: 55D–F). *Quercus nuda* has acute anthers and the same perianth shape as MB.Pb.1979/0816. However, anthers in *Q. nuda* are smaller ([1120–]1236–[1369] µm long × [560–]644–[800] µm wide) than in MB.Pb.1979/0816. Therefore, affinities of MB.Pb.1979/0816 (*Q. nuda var. serrulata*) to *Q. nuda* seem unlikely.

Kirchheimer (1937) and Iljinskaja (1982) did not see enough evidence to treat MB.Pb.1979/0816 as a variety of *Quercus nuda* and included it in *Q. subglabra* (Table 3). Comparing the holotype MB.Pb.1979/0816 of *Q. nuda var. serrulata* with *Q. subglabra*, they share the following features: the perianth shape and irregular perianth margin; the anther number and length of filaments; solitary trichomes scarcely distributed along perianth margin; more or less glabrous perianth surface. However, all specimens of *Q. subglabra* possess significantly smaller anthers with notched apices. Therefore, we disagree with Kirchheimer (1937) and Iljinskaja (1989) and would not include MB.Pb.1979/0816 in *Q. subglabra*.

*Quercus multipilosa* has anthers and stamens of similar size as in the holotype MB.Pb.1979/0816 of *Q. nuda var. serrulata*, a similar perianth shape and bifurcate trichomes; however, they are distinct from each other, in that *Q. multipilosa* possesses 9–11 notched anthers per floret and five distinct trichome types. Because the morphology of MB.Pb.1979/0816 is intermediate between specimens of *Q. multipilosa* and *Q. subglabra*, it is impossible to assign it unambiguously to one of these taxa. No other specimens of staminate florets from Baltic amber resemble MB.Pb.1979/0816 and its morphology is not distinct enough to justify a new species name (Table 13). The overall morphology of MB.Pb.1979/0816 resembles *Quercus*, especially in the campanulate perianth, the large, basifixated anthers and short filaments. However, we observed in MB.Pb.1979/0816 that not all anthers are completely open, which may be a sign of immaturity of the floret. This may affect stamen length, which is a significant feature for the generic assignment. Based on the ambiguous morphology of MB.Pb.1979/0816, we cannot definitely assign this specimen to any fagaceous genus.
**Description** — Following Conwentz (1886), the specimen is described as follows: Staminate floret. **Perianth**: dentate, entirely covered with trichomes, margin with capitate trichomes. **Stamens**: 10.

**Remarks** — The distinguishing feature of *Quercus capitato-pilosa* is the presence of capitate trichomes along the perianth (Caspari 1881; Conwentz 1886; Table 13). This trichome type was not observed in any of the specimens investigated during this study. Based on the incomplete description and missing illustration of *Q. capitato-pilosa* it is impossible to evaluate its affinities (Table 13).

### Key to staminate inflorescences of *Fagaceae* from Baltic and Bitterfeld amber

1. Rachis pendulous and lax, inflorescence catkin-like; anthers basifixed, filaments concealed by perianth or projecting (far) beyond perianth ........................................ 2
   - Rachis rigid and erect, inflorescence spike-like; anthers dorsifixed or basifixed, filaments projecting (far) beyond perianth; perianth deeply incised ........ 3
2. Filaments elongated, projecting far beyond perianth; florets mostly arranged in dichasia of 2 or 3 or singular; pollen microrugulate, perforate, microrugulae twisted and interwoven, forming aggregates ....... *Eotrigonobalanus*
   - Filaments concealed by perianth or overtopping it slightly; florets mostly singular or rarely in dichasia; pollen ornamentation not as above ...... *Quercus*
3. Stamens ≥ 9 per floret, anthers round and small, 0.2–0.5 mm long × 0.2–0.3 mm wide, dorsifixed, base and apex notched .................. *Castaneoideae*
   - Stamens ≤ 7 per floret, anthers elliptic-roundish, 0.4–0.8 mm long × 0.4–0.8 mm wide, basifixed, base strongly cordate, apex mucronate .................. *Trigonobalanoideae*

#### Eotrigonobalanus

1. Anthers apically mucronate; florets singular .......... *E. longianthera*
   - Anthers apically notched; florets in dichasia of 2 or 3, rarely singular .......................... 2
2. Perianth cyathiform; stamens 6–11 per floret; perianth almost glabrous, very scarcely with solitary trichomes on surface and margin ........ *E. conwentzii*
   - Perianth campanulate; stamens 6 or 7 per floret; perianth scarcely with solitary and uniseriate trichomes on surface and margin ........ *E. campanulata*

#### Quercus

1. Anthers apically mucronate .......................... 2
   - Anthers not mucronate ........................... 6

2. Stamens 7–9 per floret, filaments overtopping perianth ........................................ 3
   - Stamens 6 per floret, filaments as long as perianth ............................................. 4
3. Dichasia with up to 6 florets; perianth incised to base, lobes linear, margin densely hairy, surface glabrous; pollen verrucate, microteichine, apical parts of rodlets appearing nubby, rod-like masked; footlayer thick ........................................ *Q. brachyandra*
   - Dichasia with 2 or 3 florets, or florets singular; perianth campanulate to cyathiform, incised to middle, margin and surface with solitary, bifurcate, uniseriate and branched uniseriate trichomes; pollen microrugulate-areolate, microteichine, fossulate; footlayer thin ........................................ *Q. casparyi*
4. Perianth campanulate, incised to middle, lobes triangular, perianth margin and upper third of perianth surface densely covered with solitary trichomes .................. *Q. emanuelii*
   - Perianth top-shaped or cyathiform, incised to base, lobes linear to lanceolate, perianth margin with loosely arranged solitary trichomes, indumentum on perianth surface not as above ....................... 5
5. Perianth cyathiform, lobes linear to lanceolate, solitary trichomes along perianth margin and on surface ........................................ *Q. multipilosa*
   - Perianth top-shaped, lobes linear, solitary trichomes only along perianth margin, surface glabrous ........................................ *Q. mucronata*
6. Anthers apically notched ................................ 7
   - Anthers apically obtuse or acute ................... 8
7. Stamens 6–9 per floret; perianth margin with 2 trichome types: solitary and uniseriate or bifurcate .......... *Q. subglabra*
   - Stamens 9–11 per floret; perianth margin with 4 trichome types: solitary, bifurcate, uniseriate and branched uniseriate .................. *Q. multipilosa*
8. Anthers apically acute; rachis glabrous .......... *Q. nuda*
   - Anthers apically obtuse; rachis with trichomes .......... 9
9. Perianth margin densely pubescent with long, solitary trichomes; stamens 5; floret subtended by an ovate bract and a linear bract; perianth campanulate .......... *Q. limbata*
   - Perianth margin glabrous or with only few solitary trichomes; stamens more than 5; floret subtended by only a linear bract; perianth mainly cyathiform .......... 10
10. Stamens 8–13 per floret; perianth margin glabrous; rachis entirely covered with stellate trichomes .......... *Q. aimeeana*
   - Stamens 6–8 per floret; perianth margin with only few solitary trichomes; stellate trichomes of rachis mainly located below each floret .......... *Q. meyeriana*

#### Castaneoideae

1. Perianth 5-lobed, incised to middle, margin densely
ciliate with simple trichomes

- Perianth margin glabrous; filaments 2–3 mm long. **Castaneoid, genus indet.**

- Perianth 6-lobed, deeply incised, margin glabrous or with uniseriate trichomes; filaments 1–2 mm long. **? Castanea inclusa**

- Perianth margin glabrous; filaments 2–3 mm long. **? Castanea longistaminea**

**Trigonobalanoideae**

1. Florets in dichasia of 7 or 8; filaments projecting far beyond perianth. **Trigonobalanooid sp. 1**

- Florets singular or in dichasia of 2; filaments projecting only slightly beyond perianth. **Trigonobalanooid sp. 2**

4. Discussion

4.1. Diversity and biogeographic patterns of Fagaceae in the Baltic amber flora

In the present study, we reveal a remarkably high diversity of Fagaceae in Baltic amber (Table 3). In total, we distinguish 18 Fagaceae fossil-species, which derive from the Quercoideae (two sections of Quercus: Q. sect. Lobatae and Q. sect. Protobalanus and ten Quercus species), Castaneoideae (three species) and Trigonobalanoideae (two species) and the extinct genus Eotrigonobalanus (three species). Eight species that were originally assigned to Quercus were dubious or their affinities could not be entirely resolved (Table 3). Still, the number of species greatly exceeds the numbers recognized in the most recent revisions of Baltic amber Fagaceae by Kirchheimer (1937) and Ilijinskaja (1982). It is noteworthy that in all previous accounts on staminate catkins from Baltic amber, only two genera (Castanea, Quercus) were recognized, whereas our study provides unambiguous evidence for the presence of two sections of Quercus (Q. sect. Lobatae, Q. sect. Protobalanus), at least one member of the subfamily Castaneoideae (Castanopsis/Lithocarpus) and one member of the subfamily Trigonobalanoideae (with affinity to Trigonobalanus). Further, we note some diversity in the extinct genus Eotrigonobalanus, which up to now has been described from fossil leaves (E. fusciclavus (Rossm.)), H. Walthier & Kvaček; Kvaček & Walthier 1989), fruits and cupules (E. andreanszkyi (Mai) Kvaček & H. Walthier; Mai 1970; Walthier & Zetter 1993) and pollen (E. eizmannii; Denk & al. 2012). The fagaceous flora from Baltic amber shows strong affinities to extinct warm-temperate floras of E and SE Asia, as well as North America (SW and SE U.S.A. and Mexico). In the following, implications of Baltic amber Fagaceae for the (palaeo)biogeography of this family will be discussed.

Fagaceae from Baltic amber include sections of Quercus that are today endemic to the Americas (Q. sect. Lobatae, Q. sect. Protobalanus). The main extant diversity centre of Quercus is Mexico, which harbours about 161 Quercus species, of which 76 species are red oaks (Q. sect. Lobatae; Valencia-A. 2004). A high number of Quercus species is also found in the U.S.A., with about 89 species (Nixon 2002). Although the extent range of Q. sect. Lobatae is confined to North and Central America, this section had a wider N hemisphere distribution during the Paleogene and Neogene. The oldest fossil record is pollen from the middle Eocene of W Greenland (Grimsson & al. 2015); fossils of leaves, cupules and acorns of Q. sect. Lobatae were described from Oligocene deposits of Texas (Catahoula formation; Daghlil & Crepet 1983) and NE Asia (see Denk & al. 2017a for references) and from the Oligocene and Neogene of Europe (Denk & al. 2017a; Barrón & al. 2017 and references therein). The broad N hemisphere distribution of Q. sect. Lobatae from the Paleogene onward fits with the presence of this section in the Eocene Baltic amber forest.

Quercus sect. Protobalanus is also endemic to North America but contains far fewer species than Q. sect. Lobatae; five species occur in the SW U.S.A. and NW Mexico (Manos 1997). It was recently suggested that Q. sect. “Protobalanus appeared in the Eocene of North America and seems to be always limited to this continent” (Barrón & al. 2017: 86). In contrast, the presence of Q. sect. Protobalanus or a precursor of this lineage in Eocene strata of Greenland (Grimsson & al. 2015) and in latest Eocene strata of W North America (Bouchal & al. 2014) already indicated that Q. sect. Protobalanus had a wider distribution than previously thought. Therefore, inclusions of Q. sect. Lobatae and Q. sect. Protobalanus from the Eocene Baltic amber further demonstrate a wide Paleogene distribution of these sections including Europe and the North Atlantic land bridges, which connected Greenland, the landmasses of Fennoscandia and North America (Tiffney 1985; Tiffney & Manchester 2001).

In contrast to Quercus sect. Lobatae and Q. sect. Protobalanus, extant Q. sect. Cycllobalanopsis is restricted to Himalayan to SE and E Asian broad-leaved evergreen forests, where it is a dominant and diverse section (90–122 species; Deng 2007, cited from Deng & al. 2014). However, its oldest records are suggested to be cupule fossils from the Lutetian (48 Ma) of W North America (Manchester 1994), “but without preserved stigmas the assignment of these fruits remains ambiguous” (Denk & al. 2017a: 31). More reliable records of Q. sect. Cycllobalanopsis are known from middle Eocene and early Oligocene strata of S China (leaves and pollen; Hofmann 2010; Liu & al. 2019) and from the Eocene/Oligocene boundary in SE Tibet (leaves; Su & al. 2018). So far, there are no unambiguous fossils of Q. sect. Cycllobalanopsis from Europe (Denk & al. 2017a). Oligocene leaf fossils from Hungary referred to Cycllobalanopsis (Andreánszky 1966) and Pliocene leaf fossils from Bulgaria, which were described as C. stojanovitii Palam. & G.
Table 14. Palaeoecological information about Fagaceae taxa from other fossil localities.

| Taxon                  | Stratigraphic range                                                                 | Habitat                                                                 | Selected associated plant taxa                                                                 | References                                      |
|------------------------|-------------------------------------------------------------------------------------|-------------------------------------------------------------------------|------------------------------------------------------------------------------------------------|------------------------------------------------|
| **Castaneoideae**      |                                                                                     |                                                                         |                                                                                                |                                                |
| Castanopsis            | middle Eocene to Miocene of C Europe (Geiseltal flora, Lower Rhine embayment near Cologne, Germany); middle Eocene (Oregon, U.S.A.), late Eocene (Samland, Russia), Pliocene (W Yunnan, China) | acidic and oligotrophic soils, peat-like habitats, river sands and dunes | Frielendorf, Germany: *Pinus, Quercus* sect. *Erythrobalanus, Sequoia, Taxodium* lower Miocene, Osieczów, Poland: *Carya, Dorypymys, Engelhardtia, Juglans, Laurus, Magnolia, Mastixia, Myrica, palms, Persea, Pinus, Quercus* sect. *Erythrobalanus, Sequoia* | Mai 1976, 1989; Manchester 1994; Gee & al. 2003; Wu & al. 2014; Sadowski & al. 2018 |
| Lithocarpus saxonicus  | Oligocene (Lausitia, Germany)                                                          |                                                                         | Kleinensaubernitz (Oligocene, Bautzen, E Germany): *Acer, Alnus, Betula, Carpinus, Carya, Lauraceae, Quercus, Trigonobalanopsis* | Kvaček & Walther 1987 |
| Castaneophyllum        |                                                                                     |                                                                         |                                                                                                |                                                |
| venosum                | late Eocene (Staré Sedlo, North Bohemia, Czech Republic), Oligocene (České středohoří mts volcanic complex, North Bohemia, Czech Republic) | mixed mesophytic forests, intrazonal to azonal; *Castaneophyllum lonchitiforme*: arboreal element, warm temperate climate, thermophilous; *C. venosum*: riparian evergreen forests | late Eocene of North Bohemia (Castaneophyllum lonchitiforme): *Engelhardtia, Icacinaceae, Lauraceae, Platanus neptuni, Sloanea* | Kvaček & Walther 2012 |
| puryearensis           | middle Eocene (Clairborne formation, Tennessee, U.S.A.)                             | warm-temperate to cool-subtropical with dry to moist seasons            |                                                                                                 |                                                |
| **Quercoideae**        |                                                                                     |                                                                         |                                                                                                |                                                |
| Quercus sect.          |                                                                                     |                                                                         |                                                                                                |                                                |
| Cyclobalanopsis        | middle Eocene (Clarno formation, Oregon, U.S.A.); late Eocene (Florissant fossil beds, Colorado, U.S.A.) | moisture-loving, thermophilic                                           | Nut beds flora (middle Eocene, Clarno Formation, Oregon, U.S.A.): *Anacardiaceae, Amonacaceae, Arecaceae, Castanopsis, Flacourtiaceae, Lauraceae, Magnolia, Musaceae, Pinus, Taxus* | Manchester 1994; Bouchal & al. 2014; Barrón & al. 2017 |
| Quercus sect.          |                                                                                     |                                                                         |                                                                                                |                                                |
| Lobatae                | middle Eocene (Clairborne formation, U.S.A.; W Greenland), late Eocene (Florissant fossil beds, Colorado, U.S.A.), Oligocene (Catahoula formation, Texas, U.S.A.), Oligocene to Miocene (C Europe) | Quercus rhena (Q. sect. Lobatae), early Miocene of Austria: river banks, swamps, lignite-forming; warm climate; *Quercus* sect. *Lobatae*, Florissant, late Eocene; sclerophyllous forests to nemoral coniferous forests | Florissant (late Eocene of Colorado, U.S.A.): *Anacardiaceae, Castaneoideae, Cercidiphyllaceae, Cretaegus, Daphne, Ephedra, Lonicera, Malus, Pinus, Quercus* sect. *Cyclobalanopsis, Q. sect. Lobatae, Q. sect. Quercus, Ribes, Torreya, Viburnum* | Daghdian & Crepet 1983; Kovar-Eder & Meller 2003; Wang & al. 2013; Bouchal & al. 2014; Grímssson & al. 2015; Denk & al. 2017a |
| Protobalanus           | middle Eocene (W Greenland); late Eocene (Florissant fossil beds, Colorado, U.S.A.) | sclerophyllous forests to nemoral coniferous forests                    |                                                                                                 | Bouchal & al. 2014; Grímssson & al. 2015      |
**Trigonobalanoideae**

**Trigonobalanoida americana**
- Late Paleocene (near Buchanan, Tennessee, U.S.A.)
- Warm-temperate to cool-subtropical, slightly moist to seasonally dry

**Trigonobalanopsis exacantha**
- Upper Oligocene (Linz, Austria), Lower Miocene (Wiesa, Hartau, Spremberg, Wackersdorf, Germany; Hřídek, Cheb basin, Czech Republic), Upper Miocene (Düren, Germany)
- Accessory element of riparian forests on eutrophic soils, mesophilic; avoids oligotrophic habitats; dominant element of Lauraceae forests on eutrophic soils; warm-humid conditions; warm-temperate, mixed mesophytic forests

**Trigonobalanopsis rhamnoides**
- Late Eocene (Staré Sedlo, Czech Republic), Late Oligocene (Siebengebirge, Bonn, Germany), Early Miocene (Adendorf, Germany), Late Miocene (Val d’Arno, Italy)
- Late Eocene: evergreen laurel forests; Oligocene: mixed mesophytic forests; Riparian forests

**Eotrigonobalanus**

**Eotrigonobalanus** spp.
- Middle Eocene to Lower Miocene of C Europe (Sokolov basin, Nove Sedlo, Cheb basin, Czech Republic; Kleinsaubernitz, Profen, Altenrath, Haselbach, Germany; Bovey Tracey, U.K.)
- Middle to upper Eocene: swamps, riparian forests, mires; Broadleaved evergreen riparian gallery forests with palms; Laurel-conifer forests; Early Oligocene: Peat-forming swamps, floodplain, mixed mesophytic forests; Middle Oligocene: oligotrophic, warm and humid habitats; Accessory element of mixed mesophytic forests; Upper Oligocene: azonal, coal-forming vegetation

| Location                                      | Time Period                      | Habitat Description                                                                 | References                                      |
|-----------------------------------------------|----------------------------------|-------------------------------------------------------------------------------------|------------------------------------------------|
| Buchanan (Paleocene/Eocene, W Tennessee, U.S.A.)    | Euphorbiaceae, Faboideae, Juglandaceae, Mimosoideae, Poaceae | Accessory element of riparian forests on eutrophic soils, mesophilic; avoids oligotrophic habitats; dominant element of Lauraceae forests on eutrophic soils; warm-humid conditions; warm-temperate, mixed mesophytic forests | Dilcher 1971; Crepet & Taylor 1985; Crepet & Nixon 1989a; Crepet & Feldman 1991 |
| Flora of Wiesa (middle Miocene, Kamenz, E Germany)   | Castanopsis toscana, Cinnamomum spp., Eurya stigmosa, Laurophyllum, Leucothoe saportae, Mastixia lusatica, Sapium germanicum, Symposcos spp., Tectocarya lusatica, Tetrastigma chandleri | | Mai 1970 (and references therein); Kvaček & Walther 1988; Kovar-Eder & al. 1998 |
| Flora of Wiesa (middle Miocene, Kamenz, E Germany)   | Castanopsis toscana, Cinnamomum spp., Eurya stigmosa, Laurophyllum, Leucothoe saportae, Mastixia lusatica, Sapium germanicum, Symposcos spp., Tectocarya lusatica, Tetrastigma chandleri | | Mai 1970 (and references therein); Kvaček & Walther 1988; Kovar-Eder & al. 1998 |
| Flora of Wiesa (middle Miocene, Kamenz, E Germany)   | Castanopsis toscana, Cinnamomum spp., Eurya stigmosa, Laurophyllum, Leucothoe saportae, Mastixia lusatica, Sapium germanicum, Symposcos spp., Tectocarya lusatica, Tetrastigma chandleri | | Mai 1970 (and references therein); Kvaček & Walther 1988; Kovar-Eder & al. 1998 |
| Flora of Wiesa (middle Miocene, Kamenz, E Germany)   | Castanopsis toscana, Cinnamomum spp., Eurya stigmosa, Laurophyllum, Leucothoe saportae, Mastixia lusatica, Sapium germanicum, Symposcos spp., Tectocarya lusatica, Tetrastigma chandleri | | Mai 1970 (and references therein); Kvaček & Walther 1988; Kovar-Eder & al. 1998 |
| Flora of Wiesa (middle Miocene, Kamenz, E Germany)   | Castanopsis toscana, Cinnamomum spp., Eurya stigmosa, Laurophyllum, Leucothoe saportae, Mastixia lusatica, Sapium germanicum, Symposcos spp., Tectocarya lusatica, Tetrastigma chandleri | | Mai 1970 (and references therein); Kvaček & Walther 1988; Kovar-Eder & al. 1998 |
| Flora of Wiesa (middle Miocene, Kamenz, E Germany)   | Castanopsis toscana, Cinnamomum spp., Eurya stigmosa, Laurophyllum, Leucothoe saportae, Mastixia lusatica, Sapium germanicum, Symposcos spp., Tectocarya lusatica, Tetrastigma chandleri | | Mai 1970 (and references therein); Kvaček & Walther 1988; Kovar-Eder & al. 1998 |
| Flora of Wiesa (middle Miocene, Kamenz, E Germany)   | Castanopsis toscana, Cinnamomum spp., Eurya stigmosa, Laurophyllum, Leucothoe saportae, Mastixia lusatica, Sapium germanicum, Symposcos spp., Tectocarya lusatica, Tetrastigma chandleri | | Mai 1970 (and references therein); Kvaček & Walther 1988; Kovar-Eder & al. 1998 |
Kitan. (Palamarev & Kitanov 1988; Palamarev & Ivanov 2003; cited from Barrón & al. 2017) may belong to Q. sect. *Cyclobalanopsis*, but leaf morphological and anatomical characteristics found in this fossil-species also occur in Q. sect. *Ipomoea* and in other *Fagaceae*. Dispersed pollen from the Sarmatian of Austria (Grímsson & al. 2016b) superficially resembles Q. sect. *Cyclobalanopsis*, but probably belong to Q. sect. *Lobatae*. Likewise, *Q. casparyi* (GZG.BST.24402) from Baltic amber and referred in the present study to Q. sect. *Cyclobalanopsis* or Q. sect. *Lobatae* closely resembles modern species of Q. sect. *Cyclobalanopsis* in terms of pollen sculpturing, while the thin and discontinuous footlayer in this specimen fits better with Q. sect. *Lobatae*.

All in all, *Quercus* inclusions from Baltic amber suggest wider amphiatlantic distributions of sections today confined to America and support notions of transatlantic migration patterns.

Extant *Castaneoideae* occur in North America, S and SE Asia until New Guinea, as well as in Europe (Kubitzki 1993). *Castanopsis* and *Lithocarpus* are major constituents of mid-montane SE Asian forests (Soepadmo 1972; Boer & al. 1995; Sunarno & al. 1995). In contrast, *Casta­nea* does not extend to the tropics (Kubitzki 1993); about six species of *Casta­nea* occur in E Asia and E North America. The original distribution of the economically important *C. sativa* Mill. is difficult to assess, because it “has been masked by strong human impact” (Krebs & al. 2004: 145); however, it is the only native species of *Casta­nea* in Europe (Conedera & al. 2004). *Chrysolepis* (C. *chrysophylla* (Douglas ex Hook.) Hjelmq. and C. *serrata* and *Notholithocarpus densiflorus* are endemic to W North America and restricted to warm-temperate forests of California, Oregon and Washington (Flora of North America 2008a, 2008b; Manos & al. 2008).

Corresponding to their extant distribution, fossils of the *Castaneoideae* are known from America, Europe and Asia (e.g. Crepet and Daghlian 1980; Kvaček & Walther 1987; Mai 1989; Kvaček & Walther 2012; Wu & al. 2014). In C Europe, several genera of the *Castaneoideae* (*Castanopsis*, *Lithocarpus*, extinct *Castanephyllum*) occurred from the middle Eocene onward (see Table 14 for an overview). However, the definite assignments of their leaf and wood fossils to extant lineages is often challenging; therefore, so far only *Castanopsis* and *Lithocarpus* have been unambiguously proven from the fossil record of C Europe (Mai 1995). The recently discovered Baltic amber inclusion of a cupule of *Castanopsis kaulii* Sadowski & al. already proved the presence of this particular genus in the Baltic amber flora (Sadowski & al. 2018). Although we cannot unambiguously assign the castaneoid inflorescences from amber to an extant genus, it is likely that at least one of them belongs to *Castanopsis*. The presence of several species of castaneoids in late Eocene Baltic amber further supports the wide distribution of *Castaneoideae* in the Paleogene of C Europe and reflects their high diversity.

Extant *Trigonobalanus verticillata* occurs in montane broad-leaved forests of S China (Hainan), Malaysia and Indonesia (Sulawesi, Sumatra; Nixon & Crepet 1989; Ng & Lin 2008). In contrast, *Formanodendron doichangensis* is restricted to a few localities of evergreen broad-leaved forests in SW China (Yunnan) and N Thailand (Sun & al. 2007). The endemic South American *Colombobalanus excelsa* occurs solely in montane tropical forests of Colombia (Lozano-C. & al. 1979; Nixon & Crepet 1989). The fossil history of these three taxa is still unresolved. It was suggested that the extinct *Trigonobalanopsis exacantha* (Mai) Kvaček & H. Walther of the late Eocene to Pliocene of Europe and Asia shows similarities to *Colombobalanus* and may therefore be affiliated with this particular taxon (Kvaček & Walther 1988). However, pollen of *T. exacantha* shows closer affinities to *Lithocarpus* (Denk & al. 2012). Another fossil-taxon with affinities to the trigonobalanoids is *Trigonobalanoides* Crepet & Nixon, which was described from the Eocene Buchanan formation of Tennessee (Crepet & Nixon 1989a). Infructescences and dispersed fruits of this taxon showed more similarities to *Colombobalanus* and *Formanodendron* than to *Trigonobalanus*, while fossil catkins of *Trigono­balanoides* were morphologically transitional between *Colombobalanus*, *Fagus*, *Formanodendron* and *Quercus* (Crepet & Nixon 1989a). A trigonobalanoid fruit inclusion from Baltic amber was initially described as *Fagus succinea* Goeppe, & Menge (Göppert 1853; Conwentz 1886) and later Forman (1964) and Mai (1970) discussed affinities of this inclusion to *Trigonobalanus*. The type specimen is lost, which impede further investigation. However, illustrations of the specimen (Conwentz 1886) show typical features of *Trigonobalanus*, as such the trigonous shape, triangular abscission scar and capitate stigmas (Forman 1964), but future studies are needed to confirm the affinities of this fruit. Yet, considering the trigonobalanoid staminate inflorescences of the present study, it seems likely that *Trigonobalanus* or a precursor of the lineage existed in the Baltic amber flora. This indicates that the trigonobalanoids were already present in the late Eocene of C Europe, supporting assumptions of an “Euro-American distribution” in the early Paleogene (Crepet & Nixon 1989a).

*Eostrigonobalanus* is an extinct genus, which was established by Kvaček and Walther (1989) for fossils of leaves, female infructescences, cupules and fruits deriving from middle Eocene to early Miocene strata of C Europe (Kvaček & Walther 1989; see Denk & al. 2012: table 2 for a summary and references of the fossil record of *Eostrigonobalanus*). Pollen clumps that were found on *Eostrigonobalanus* leaf fossils were described as *E. eiszmannii* (Walther and Zetter 1993). However, fossils of staminate catkins of *Eostrigonobalanus* from the European Paleogene have not been discovered so far. Therefore, the amber specimens reported here represent the first fossil records of staminate inflorescences of *Eostrigonobalanus*. *Eostrigonobalanus* was a widely
distributed, abundant component of azonal associations in Paleogene and early Neogene forests of C Europe and was even a lignite-forming taxon (Mai 1995), extending to arctic regions in Greenland (Grímsson & al. 2016a). Its occurrence in Eocene Baltic amber therefore fits with the general distribution of the genus during the Paleogene.

Although Baltic amber Fagaceae are very diverse, certain fagaceous taxa have not been found there so far, including Fagus, Quercus sect. Cerris, Q. sect. Cyclobalanopsis, Q. sect. Ilex (all Q. subg. Cerris) and Q. sect. Quercus. The oldest fossil record of Q. sect. Ilex in Europe is pollen of early Oligocene age (Saxony, Germany; Denk & al. 2012; Denk & al. 2017b) and Q. sect. Cerris had not yet evolved by the Eocene (Hipp & al. 2019). Quercus sect. Cyclobalanopsis has never been reported from W Eurasia (in particular the characteristic cycle cups) and could be an example of a taxon that migrated from North America to Asia via the Bering land bridge or indeed never occurred outside E Asia (see above). In contrast, Q. sect. Quercus had a wide N hemisphere distribution during the Neogene (Borgardt & Pigg 1999). Denk & al. (2017a) mentioned that one Baltic amber inclusion of a singular staminate flower might be affiliated with Q. sect. Quercus, based on pollen extracted from this particular fossil (Crepet 1989: 61, fig. 4.9A, B). Therefore, it is likely that future studies of male inflorescences from Baltic amber will reveal even more taxa of Quercus and other Fagaceae.

Notably, the Baltic amber flora encompasses numerous taxa that are today most diverse and/or endemic in evergreen broad-leaved forests of mid-montane regions in SE Asia, as well as typical of warm-temperate forests of the U.S.A. and Mexico. A similar pattern was previously observed for the conifer diversity in Baltic amber, which also showed a peculiar mixture of Asian and North American taxa, including genera that are rare today, such as Cathaya Chun & Kuang, Nothotsuga Hu ex C. N. Page, Pseudolarix Gordon and Sciadopitys Siebold & Zucc. (Sadowski & al. 2016a, 2017a). The occurrence of Asian Fagaceae in the Baltic amber flora is in congruence with the evolutionary history of numerous endemic plants from Asia. It has been shown that several extant endemic taxa of Asia, including conifers such as Cathaya and Nothotsuga, occurred in North America and Europe during their fossil history (Manchester & al. 2009). The extant distribution of these plants in Asia is mainly relictual, resulting from the cooling climate and glaciation during the Pliocene and Pleistocene (Manchester & al. 2009). The extent distribution of these plants in Asia is mainly relictual, resulting from the cooling climate and glaciation during the Pliocene and Pleistocene (Manchester & al. 2009). The extant distribution of these plants in Asia is mainly relictual, resulting from the cooling climate and glaciation during the Pliocene and Pleistocene (Manchester & al. 2009). Furthermore, the hyperdiverse Fagaceae from Baltic amber indicate that modern lineages of the Fagaceae “were already diversified by the Eocene” (Grímsson & al. 2015: 830), as it was shown by the middle Eocene Fagaceae flora of W Greenland (Grímsson

Fig. 56. Suggested habitat types of the Baltic amber source area accommodating the diverse Fagaceae (indicated in grey boxes) from Baltic amber (modified after Sadowski & al. 2017a).
& al. 2015). As in a previous study reassessing the conifer diversity in Baltic amber (Sadowski & al. 2017a), the present re-evaluation of amber inclusions of Fagaceae resulted in a highly refined picture of fagaceous diversity in the Paleogene of N Europe.

4.2. Palaeoecology of hyperdiverse Fagaceae from Baltic amber

The Baltic amber source area was composed of a variety of habitats, which were previously reconstructed mainly using inclusions of conifers (Sadowski & al. 2016a, 2017a), as well as graminids, dwarf mistletoes and calicioid lichens and fungi (Kaasalainen & al. 2017; Sadowski & al. 2016a, 2016b; 2017a, 2017b; Rikkinen & Schmidt 2018). These habitat types encompass azonial vegetation, including coastal lowland swamps with areas of brackish water influence and water-saturated peat, as well as back swamps and riparian forests. Areas not affected by flooding are mixed mesophytic conifer-angiosperm forests including open areas.

When Mai (1970) discussed the diversity of Fagaceae in the Baltic amber flora, he concluded that Castanea, Quercus and Trigonobalanus were the most abundant taxa of the Fagaceae. He interpreted them as constituents of Lauraceae-oak-pine-Trigonobalanus forests that grew on oligotrophic, acidic soils (Mai 1970). We partly agree with this reconstruction, but suggest that the fagaceous taxa occurred in different habitats within the Baltic amber source area and were not restricted to one singular forest type. Furthermore, we suggest that Fagaceae from Baltic amber support assumptions of a warm-temperate, humid source area.

Among castaneoid inclusions from Baltic amber, the staminate catkins showed closest affinities to Castanopsis and/or Lithocarpus, which is why we focus on these two taxa when analysing the (palaeo)ecological requirements of the Castaneoideae from Baltic amber (Table 14). Baltic amber castaneoids (excluding Castanopsis, see below) most likely grew within the mixed mesophytic angiosperm-conifer forest (Fig. 56). This is supported by the extant distribution of Castaneoideae, which mainly occur in mixed angiosperm-conifer forests with a warm-temperate, humid climate. For instance, Lithocarpus grows in mid-montane forests of Malaysia, where it is a dominant or co-dominant tree, associated with taxa such as Castanopsis, Engelhardia, Lauraceae, Quercus and conifers such as Araucariaceae and Podocarpaceae (Agathis Salis., Phyllocladus Rich. ex Mirb., Podocarpus Labill.; Soepadmo 1972). Furthermore, Lithocarpus (L. saxonicus H. Walther & Kvaček) of the European Paleogene grew in evergreen Engelhardia-Fagaceae-Lauraceae associations of mixed mesophytic angiosperm forests (Oligocene, Kleinsaubermitz, E Germany; Kvaček & Walther 1987; Table 14). The Paleogene castaneoid Castanophyllum lonchitiforme Kvaček & H. Walther of C Europe is a typical constituent of mixed mesophytic forests as well (Kvaček & Walther 2012; Table 14). North American Chrysopelis and Notholithocarpus also occur in mixed forests with coniferous and broad-leaved evergreen angiosperm trees (“mixed evergreen forests”, see Wainwright & Barbour 1984 for discussion) as well as in conifer forests of the W U.S.A. (California, Oregon, Washington; Flora of North America 2008a, 2008b; Manos & al. 2008). Chrysopelis chrysophylla also occurs in broad-leaved evergreen forests of NW North America, where it grows in dense, moist forests (pers. comm. with Paul S. Manos, Duke University).

Extant evergreen Castanopsis is a major constituent of mid-montane forests, e.g. in Thailand and W Java, and even forms pure stands (Soepadmo 1972; Sunarno & al. 1995). Its highest diversity is reached in SW China, where the tropical and temperate regions overlap (Ma-sahiko 1993). In contrast, Paleogene Castanopsis from C Europe was typically associated with Lauraceae and various conifer taxa forming the so-called “Castanop-sietum oligo-miocenicum taphocoenosis” (Mai 1970 and references therein; Mai 1989; Table 14) resembling more closely extant forests along the S foothills of the Himalaya (e.g. Mentisky 2005). This particular taphocoenosis of the Oligocene-Miocene occurred on acidic soils, oligotrophic dunes and on river sands. According to Mai (1989), this plant association differed from such ones containing Eotrigonobalanus, various extinct Castaneoideae (such as Dryophyllum Debev) and Trigonobalanopsis and from plant associations including roburoid Quercus species. As already mentioned, a pistillate inflorescence inclusion of Castanopsis kaulii was previously reported from Baltic amber, a likely constituent of riparian forests as well as raised bogs within the Baltic amber source area (Sadowski & al. 2018). Therefore, it is likely that one of the staminate florets and/or the inflorescence from this study belonged to Castanopsis and were part of the flood-plain habitats (Fig. 56).

The few surviving Trigonobalanoidae occur in montane evergreen broad-leaved forests of SE Asia (Formanodendron, Trigonobalanus) and Colombia (Colombobalanus) (Lozano-C. & al. 1979; Nixon & Crepet 1989; Sun & al. 2007; Ng & Lin 2008). Trigonobalanus verticillata inhabits broad-leaved forests of S China, Malaysia and Indonesia and is accompanied by angiosperms (e.g. Al-tingia, Castanopsis, Lithocarpus) and conifers (e.g. Agra-this, Araucariaceae; Dacrydium Lamb., Podocarpus, Podocarpaceae; Forman 1964; Forman & Cutler 1967). Forest communities with Formanodendron doichangensis of SW China and Thailand also include Castanopsis and Lithocarpus, as well as diverse angiosperms, such as An-neslea fragrans Wall. (Pentaphylacaceae), Apostrova villosa (Lindl.) Baill. (Phyllanthaceae), Schima wallichii (DC.) Korth. (Theaceae), Vaccinium L. spp. (Ericaceae) and Wendlandia tinctoria (Roxb.) DC. (Rubiaceae) (Li 1994).

In contrast to extant trigonobalanoids, fossils with affinities to the Trigonobalanoidae inhabited forests with
a warm-temperate to cool subtropical temperature regime (Trigonobalanoideae americana Crepet & Nixon, Eocene, Buchanen formation; Dilcher 1971, Crepet & Nixon 1989a; Table 14) and evergreen laurel forests (Trigono-balanoideae rosmanoides (Rossm.) Kvaček & H. Walther; late Eocene, Staré Sedlo; Kvaček & Walther 1988; T. exacantha; middle Miocene, Wiesa; Mai 1970; Table 14). However, T. exacantha also occurred as an accessory element in Miocene riparian forests on eutrophic soils (Mai 1970; see Table 14 for more references), avoiding oligotrophic habitats completely (Mai 1970). Yet, we suggest that trigonobalanoids from Baltic amber likely grew in the mixed mesophytic angiosperm-conifer forest of the Baltic amber source area (Fig. 56), because Trigonobalanoideae of the European Paleogene and Neogene mainly inhabited mixed mesophytic and laurel forests as well (Table 14).

Habitat preferences of extant Quercus are very diverse. Quercus is most diverse in seasonally dry forests and in mild temperate seasonal forests of Mexico and Pacific Central America (Nixon 2006). In North America, Quercus can be a dominant constituent of the canopy or is shrub-like or medium-sized, especially in the chaparral vegetation (Nixon 2006). Some North American Quercus species also grow in extreme habitats, such as in swamps or on serpentine rocks (Nixon 2006). In the U.S.A., Quercus dominates open to closed Mediterranean woodlands (mainly Q. sect. Quercus and Q. sect. Protobalanus, less commonly Q. sect. Lobatae), partly with a pronounced understory of annual grasses (Allen-Diaz & al. 2007), as well as humid temperate forests and flood-plains (Q. sect. Lobatae and Q. sect. Quercus; Jensen 1997). In California oak woodlands, several species of Q. sect. Lobatae and Q. sect. Quercus co-occur with other angiosperm trees, e.g. Aesculus californica (Spach) Nutt., Arbutus menziesii Pursh, Notholithocarpus densiflorus and Umbellularia californica (Hook. & Arn.) Nutt., as well as conifers, e.g. Pinus L. (Allen-Diaz & al. 2007).

In Florida, oak diversity is very high (26 species in total); for instance, forest communities of N Florida comprise up to 17 species of Quercus sect. Lobatae, Q. sect. Quercus and Q. sect. Virentes Loudon, which are able to co-exist within one forest region, comprising sandhill, hammock and scrub communities (Cavender-Bares & al. 2004). The high number of locally occurring oak species is the result of phylogenetic overdispersal. This means that the three main habitats are inhabited by phylogenetically unrelated oak species, while at the same time oaks within the same clade show less niche overlap than expected (Cavender-Bares & al. 2004; Cavender-Bares 2019).

Baltic amber species of Quercus sect. Lobatae might have occurred in woodlands, as well as on flood-plains and stream banks of the Baltic amber source area, as it is the case in extant forest communities in Florida (Jensen 1997; Cavender-Bares & al. 2004). This is also indicated by the fossil record of Q. sect. Lobatae, which is known as a constituent of coniferous forests (e.g. from the late Eocene Florissant fossil beds; Bouchal & al. 2014) and from river banks and swamps (e.g. Q. rhenana (Kräusel, Weyl.) Erw. Knobloch & Kvaček, Miocene of Austria; Kvar-Eder & Mellor 2003; Table 14).

Quercus sect. Protobalanus is restricted to the seasonally dry climates of Pacific North America (Bouchal & al. 2014) and inhabits chaparral vegetation, rocky and steep slopes of montane forests, ranging from dry to moist locations (Manos 1997). It forms dense thickets (Q. palmeri Engelm., Q. vaccinifolia Kellogg), inhabits narrow canyons (Q. tomentella Engelm.) or occurs in crevices, growing on rocky or sandy substrate along slopes or in valleys (Q. chrysolepis; Camus 1952–1954a). In the fossil record, Q. sect. Protobalanus was recorded from selcrophyllous forests to nemoral coniferous forests in the middle Eocene of Greenland (Grímsøn & al., 2015), in the latest Eocene of Colorado (MacGinitie 1953; Bouchal & al. 2014), in the Oligocene of New Jersey (Prader & al. 2020) and probably in the Miocene Macall flora of Oregon and the Pliocene Sonoma flora of California (references in Barrón & al. 2017), co-existing with species of Q. sect. Lobatae (Bouchal & al. 2014; Grímsøn & al. 2015; Prader & al. 2020; Table 14). Therefore, it would be likely that Q. sect. Lobatae and Q. sect. Protobalanus were also associated in the Baltic amber source area. A diverse fagaceous pollen flora of the late Eocene Florissant beds of Colorado showed that Q. sect. Lobatae and Q. sect. Protobalanus were already adapted to seasonally dry climate during the late Eocene (Bouchal & al. 2014; Table 14). The Baltic amber source area also encompassed drier habitats (Sadowski & al. 2016b) that could have harboured thermophilic Quercus taxa, such as Q. sect. Lobatae and Q. sect. Protobalanus.

The extant and fossil examples of habitat types and conditions show that numerous Quercus species are able to co-occur in the same habitat and that Quercus has a large range in habitat requirements. Based on the high diversity of Quercus from Baltic amber, they likely formed mixed stands. As today, they were probably associated with other angiosperm and conifer taxa, being part of the canopy as well as the understorey.

Eotrigonobalanus was an abundant constituent of European florals from the middle Eocene to the late Miocene. During this time span, Eotrigonobalanus occurred in different habitats (Table 14). In the middle Eocene floristic complex Schepplitz of the Geiselatal section (C Germany), Eotrigonobalanus was associated with taxa such as Areceae (e.g. Phoenix L., Sabal Adans.), Lauraceae (Actinodaphne Nees, Daphnogene Unger, Laurophyllum Goeppe.), Myricaceae (Comptonia L’Hér. ex Aiton, Myrica L.), Myrtaeae (Rhodomyrtophyllum Rüffle & Jahnichen) and Theaceae (e.g. Schima) (Mai & Walther 2000). In the late Eocene, Eotrigonobalanus occurred in coal-forming azonal vegetation, such as coastal lowland peat bogs (C German Leipzig embayment, Kunzmann &
al. 2018), and riparian forests (Kvaček & Walther 1989; Table 14). *Eotrigonobalanus* was also part of zonal evergreen pine- and oak-*Lauraceae* forests (Weißelber ser., floristic complex *Zeitiz*), which were characterized as evergreen notophyllous vegetation (Mai & Walther 2000). In contrast, Kvaček (2010) defined this unit as intrazonal broad-leaved evergreen riparian gallery forest with palms as a dominant Eocene vegetation type of C Europe. A further vegetation type of the Eocene that included *Eotrigonobalanus* was the *Doliostrobus* Marion / *Quasisequoia* V. Sriniv. & E. M. Friis mixed evergreen broad-leaved swamp forest (Kvaček 2010).

From the middle Oligocene, *Eotrigonobalanus* was an accessory element in the mixed mesophytic forests that encompassed numerous E Asian plant taxa (Mai & al. 2018), and riparian forests (Kvaček & Walther 1989; Table 14). *Eotrigonobalanus* was also part of zonal evergreen pine- and oak-*Lauraceae* forests (Weißelber ser., floristic complex *Zeitiz*), which were characterized as evergreen notophyllous vegetation (Mai & Walther 2000). In contrast, Kvaček (2010) defined this unit as intrazonal broad-leaved evergreen riparian gallery forest with palms as a dominant Eocene vegetation type of C Europe. A further vegetation type of the Eocene that included *Eotrigonobalanus* was the *Doliostrobus* Marion / *Quasisequoia* V. Sriniv. & E. M. Friis mixed evergreen broad-leaved swamp forest (Kvaček 2010).

From the middle Oligocene, *Eotrigonobalanus* was an accessory element in the mixed mesophytic forests that encompassed numerous E Asian plant taxa (Mai & Walther 2000). In contrast, Kvaček (2010) defined this unit as intrazonal broad-leaved evergreen riparian gallery forest with palms as a dominant Eocene vegetation type of C Europe. A further vegetation type of the Eocene that included *Eotrigonobalanus* was the *Doliostrobus* Marion / *Quasisequoia* V. Sriniv. & E. M. Friis mixed evergreen broad-leaved swamp forest (Kvaček 2010).

From the middle Oligocene, *Eotrigonobalanus* was an accessory element in the mixed mesophytic forests that encompassed numerous E Asian plant taxa (Mai & Walther 2000). In contrast, Kvaček (2010) defined this unit as intrazonal broad-leaved evergreen riparian gallery forest with palms as a dominant Eocene vegetation type of C Europe. A further vegetation type of the Eocene that included *Eotrigonobalanus* was the *Doliostrobus* Marion / *Quasisequoia* V. Sriniv. & E. M. Friis mixed evergreen broad-leaved swamp forest (Kvaček 2010).

From the middle Oligocene, *Eotrigonobalanus* was an accessory element in the mixed mesophytic forests that encompassed numerous E Asian plant taxa (Mai & Walther 2000). In contrast, Kvaček (2010) defined this unit as intrazonal broad-leaved evergreen riparian gallery forest with palms as a dominant Eocene vegetation type of C Europe. A further vegetation type of the Eocene that included *Eotrigonobalanus* was the *Doliostrobus* Marion / *Quasisequoia* V. Sriniv. & E. M. Friis mixed evergreen broad-leaved swamp forest (Kvaček 2010).

From the middle Oligocene, *Eotrigonobalanus* was an accessory element in the mixed mesophytic forests that encompassed numerous E Asian plant taxa (Mai & Walther 2000). In contrast, Kvaček (2010) defined this unit as intrazonal broad-leaved evergreen riparian gallery forest with palms as a dominant Eocene vegetation type of C Europe. A further vegetation type of the Eocene that included *Eotrigonobalanus* was the *Doliostrobus* Marion / *Quasisequoia* V. Sriniv. & E. M. Friis mixed evergreen broad-leaved swamp forest (Kvaček 2010).

From the middle Oligocene, *Eotrigonobalanus* was an accessory element in the mixed mesophytic forests that encompassed numerous E Asian plant taxa (Mai & Walther 2000). In contrast, Kvaček (2010) defined this unit as intrazonal broad-leaved evergreen riparian gallery forest with palms as a dominant Eocene vegetation type of C Europe. A further vegetation type of the Eocene that included *Eotrigonobalanus* was the *Doliostrobus* Marion / *Quasisequoia* V. Sriniv. & E. M. Friis mixed evergreen broad-leaved swamp forest (Kvaček 2010).

From the middle Oligocene, *Eotrigonobalanus* was an accessory element in the mixed mesophytic forests that encompassed numerous E Asian plant taxa (Mai & Walther 2000). In contrast, Kvaček (2010) defined this unit as intrazonal broad-leaved evergreen riparian gallery forest with palms as a dominant Eocene vegetation type of C Europe. A further vegetation type of the Eocene that included *Eotrigonobalanus* was the *Doliostrobus* Marion / *Quasisequoia* V. Sriniv. & E. M. Friis mixed evergreen broad-leaved swamp forest (Kvaček 2010).
age of the Blue Earth (Standke 2017), together with the absence of signs of reworking of amber in the marine sediment (Grimaldi & Ross 2017), strongly suggest that Baltic amber was produced in the late Eocene under a more temperate climate (cf. Zachos & al. 2001).

The highly diverse Fagaceae from Baltic amber further substantiates pronounced differences between the late Eocene Baltic amber flora and the subtropical to tropical middle Eocene fossil assemblages of Eckfeld and Messel. In the Eckfeld flora, no macrofossils of the Fagaceae have been discovered so far (Wilde & Frankenhaus 1998), whereas Fagaceae are taxonomically diverse in the rich record of dispersed pollen (Nickel 1996), indicating that the local Eckfeld flora was probably poor in Fagaceae. Likewise, macrofossils of Fagaceae are also entirely absent in the Messel flora (Wilde 1989, 2004; Collinson & al. 2012). In contrast, the dispersed pollen record from Messel (Thiele-Pfieffer 1988) documents abundant pollen of Tricolporopollenites cingulum (R. Potonié) Thomson & Pfug that corresponds to either Castaneoideae or Eotrigonobalanus, while in situ pollen from insect fossils from Messel and Eckfeld (Grimsson & al. 2017) comprises pollen of Castaneoideae with affinities to Castanopsis and Lithocarpus. Yet, several pollen taxa from Messel and Eckfeld (e.g. Tricolporopollenites liblaren sis (Thomson & Pfug) Hochuli / T. quisquisalis (Potonié) Krutzsch) are difficult to assign to modern genera of Fagaceae and would need to be studied using SEM in order to be comparable to particular pollen types found in Baltic amber. At present, it appears that the Messel and Eckfeld assemblages are dominated by extinct groups of Fagaceae, entirely lacking the high diversity of modern types of Quercus pollen. This further distinguishes the warmer middle Eocene from the more temperate late Eocene floras.

The absence of Fagaceae in the well-studied leaf and carpological record from Messel suggests that they were not common near the area of deposition or that they grew distantly from the lake as part of the hinterland vegetation (Collinson & al. 2012). Both the Messel and Eckfeld plant assemblages contain a great number of paratropical to subtropical evergreen broad-leaved elements (such as Arecaceae, Juglandaceae, Moraceae and Zingiberaeae; Wilde 1989; Grein & al. 2011; Collinson & al. 2012) and, taken the leaf, carpological and palynological records together, are conspicuously more diverse than what is currently known from the Baltic amber. It should be kept in mind, however, that the taphonomic filter acting on Baltic amber plant fossils is only poorly understood and that the Baltic amber flora is not as comprehensively studied as the fossil floras of Messel and Eckfeld.

In any case, the diversity of Fagaceae from Baltic amber supports the presence of diverse azonal vegetation types in accordance with previous interpretations based on inclusions of conifers (Sadowski & al. 2017a). This contrasts with the Eckfeld and Messel floras, both of which represent zonal vegetation of isolated maar lakes at some distance to the coast (Mai & Walther 2000). Ten genera of conifers of the Cupressaceae, Geinitziaceae, Pinaceae and Sciadopityaceae recorded as Baltic amber inclusions witness a highly diverse conifer flora (Sadowski & al. 2016a, 2017a), which is fundamentally different from the middle Eocene floras of Eckfeld and Messel. The latter two fossil assemblages yield only few macrofossils of conifers, including Tetraclinis Mast. (Cupressaceae) and Cephalotaxus (with affinities to, Cathaya, Cephalotaxus, Ephedra L., Cupressaceae, papillate Cupressaceae [former Taxodiaceae], Pinus and Tetraclinis). Therefore, both maar floras are very distinct in terms of taxonomic composition, species richness and depositional setting from the flora of the Baltic amber source area. Diverse Fagaceae with many modern taxa and hyperdiverse conifers underscores the warm-temperate character of the Baltic amber plant assemblage, although much of the plant diversity of Baltic amber remains to be described.

In general, a warm-temperate climate is defined by humid conditions, warm summers and mild winters (Bo x & Fuj i wara 2015), with only short periods of frost (Brown & al. 1995). The zonal vegetation type of warm-temperate regions is evergreen broad-leaved forests or “laurel forests”, which today occur in E Asia, in the montane belts of tropical Asia and S of the Himalaya, in the SE U.S.A., S Brazil, N New Zealand, and in parts of E Australia as well as the Azores, Madeira and the Canary Islands. Where winters are too cold for evergreen tree species in the forest canopy, warm-temperate deciduous forests occur, such as in Japan, mainland E Asia and the SE U.S.A. (Box & Fujiwara 2015). Following Walther & Breckle (2002), warm-temperate biomes encompass the W coast of North America as well, while Brown & al. (2007) also included forests and woodlands of Mexico and Guatemala. Warm-temperate forests of North America show a great diversity of Fagaceae; for instance, the Sierra Madre Oriental in the E part of Mexico harbours humid montane oak forests that comprise numerous species Quercus sect. Lobatae and Q. sect. Quercus (Luna-Vega & al. 2006). Interestingly, the thermophilous Q. subg. Cerris (including Q. sect. Cyclobalanopsis and Q. sect. Ilex) is not recorded from the Baltic amber flora so far. In contrast, Q. sect. Lobatae and Q. sect. Protobalanus prevailed in the Baltic amber flora, and these are both typical taxa of warm-temperate climates (Barrón & al. 2017). Apart from the extant distribution of Fagaceae, the predominance of fagaceous taxa in Paleogene and Neogene warm-temperate, mixed mesophytic forests (e.g. Trigonobalanopsis exacantha, Trigonobalanoidae americana; see Table 14 for references) support the assumption of a warm-temperate Baltic amber source area.
5. Conclusions

Eocene Baltic amber is considered the largest amber deposit on Earth and reconstruction of the source forests and climate is crucial for evaluation of hundreds of thousands of fossil organisms preserved as inclusions. It has been widely accepted that representatives of the oak family (Fagaceae) were abundant in the source area of Baltic amber, which is due to the presence of numerous staminate inflorescences, detached florets and individual florets. However, the actual generic and infrageneric diversity of staminate inflorescences or individual florets. However, the actual generic and infrageneric diversity of Fagaceae from Baltic amber remained unknown.

In our study, we revealed 18 fossil-taxa from Baltic amber, including the Castaneoideae (affinities with Castanopsis, Lithocarpus), Quercoideae (Quercus sect. Lobatae and Q. sect. Protobalanus), Trigonobalanoidae (affinity with Trigonobalanus verticillata) and the extinct Eotrigonobalanus. We studied inclusions of staminate inflorescences, detached florets and in situ pollen with affinities to the Fagaceae, including historic type material and newly discovered amber inclusions. Staminate inflorescences of extant taxa were examined to identify diagnostic features distinguishing fagaceous genera and sections in order to facilitate the identification of the inclusions. Morphological features of fagaceous staminate inflorescences, such as the habit of the rachis (flexuous or stiff), stamen length and number, anther size and apex (notched, acute, mucronate, obtuse), trichomes (type, distribution), and the perianth shape constitute valuable characteristics to distinguish families of the Fagaceae. In combination with in situ pollen, it is possible to differentiate between subfamilies and genera of the Fagaceae as well as sections of Quercus. For the extinct Eotrigonobalanus, staminate inflorescences are reported for the first time. The occurrence of North American endemic Q. sect. Lobatae and Q. sect. Protobalanus show a wider N hemisphere distribution of these taxa during the Paleogene, which involved the North Atlantic land bridges to the European continent. Furthermore, the extraordinarily diverse Baltic amber Fagaceae support affinities to modern North American, E Asian, and SE Asian floras.

Comparisons of Baltic amber Fagaceae with extant and fossil analogous Fagaceae taxa further substantiates our notion of the habitat heterogeneity of the amber source area, which comprised azonal and zonal vegetation types. Castanoids (affinity Castanopsis) and Eotrigonobalanus grew in oligotrophic flood-plain habitats (riparian forests, swamps, peat bogs). Quercus inhabited riverine habitats (Q. sect. Lobatae), as well as drier habitat patches (Q. sect. Lobatae and Q. sect. Protobalanus) within the Baltic amber source area, while trigonobalanoids and further castanoids occurred in the mixed mesophytic angiosperm-conifer forest (Fig. 56). No additional habitat types / forest types are necessary to accommodate the various Fagaceae representatives reported in this study other than those reconstructed by Sadowski & al. (2017a) based on available conifer inclusions from Baltic amber. The hyperdiverse Fagaceae from Baltic amber further indicate a warm-temperate climate for the Baltic amber forest.

Acknowledgements

We thank Christel and Hans Werner Hoffeins (Hamburg) for providing amber specimens. Many thanks to Marc Appelhans (Göttingen) for kindly providing access to herbarium specimens. We are grateful to Jinjin Hu and Jian Huang (Xishuangbanna Tropical Botanical Garden, Yunnan) for collecting and providing extant specimens of Fagaceae. Many thanks to Andreas Abele (Berlin), Hermann Behling (Göttingen), Alexander Gehler (Göttingen), Dorothea House-Reitner (Göttingen), Victoria Hentschke (Heidelberg), Lutz Kunzmann (Dresden), Lothar Maitas (Berlin), Christian Neumann (Berlin), Gerda Standke (Freiberg) and Manuela Tilling (Berlin) for discussion and support. We thank Patrick S. Herendeen (Chicago Botanic Garden), Paul S. Manos (Duke University), one anonymous reviewer and the editor Nicholas Turland (Berlin) for constructive comments that helped to improve the manuscript.

References

Abbe E. C. 1974: Flowers and inflowerences of the “Amentiferae”. – Bot. Rev. 40: 159–261.
Allen-Diaz B., Standiford R. & Jackson R. D. 2007: Oak woodlands and forests. – Pp. 313–338 in: Barbour M. G., Keeler-Wolf T. & Schoenherr A. A. (ed.), Terrestrial vegetation of California, ed. 3. – Berkeley: University of California Press.
Ander K. 1942: Die Insektenfauna des Baltischen Bernsteins nebst damit verkniipften zoogeographischen Problemen. – Kungl. Fysiografiska Sällskapets Handlingar 53: 1–82.
Baranov V. A., Schädel M. & Haug J. T. 2019: Fly palaeo-ovo-devo: immature stages of bibionomorph dipterans in Baltic and Bitterfeld amber. – PeerJ 7: e7843.
Barrón E., Averyanova A., Kvaček Z., Momohara A., Pigg K. B., Popova S., Postigo-Mijarra J. M., Tiffany B. H., Utescher T. & Zhou Z. K. 2017: The fossil history of Quercus. – Pp. 39–106 in: Gil-Pelegrín E., Pegoero-Pina J. I. & Sancho-Knapik D. (ed.), Oaks physiological ecology – exploring the functional diversity of the genus Quercus. – Cham: Springer.
Boer E., Sosef M. S. M., Wong W. C. & Vu-Cong Q. 1995: Lithocarpus Blume. – Pp. 284–306 in: Lemmens R. H. M. J., Soerianegara I. & Wong W. C. (ed.), Plant
resources of South-East Asia 5(2), Timber trees: minor commercial timbers. – Leiden: Backhuys Publishers.

Borgardt S. J. & Pigg K. B. 1999: Anatomical and developmental study of petrified Quercus (Fagaceae) fruits from the middle Miocene, Yakima Canyon, Washington, USA. – Amer. J. Bot. 86: 307–325.

Bouchal J., Zetter R., Grimsson F. & Denk T. 2014: Evolutionary trends and ecological differentiation in early Cenozoic Fagaceae of western North America. – Amer. J. Bot. 101: 1332–1349.

Box E. O. & Fujiwara K. 2015: Introduction: why warm-temperate deciduous forests? – Pp. 1–5 in: Box E. O. & Fuj iwara K. (ed.), Warm-temperate deciduous forests around the northern hemisphere. Geobotany Studies. – Cham, Heidelberg: Springer.

Bronnignart A. T. 1849: Végétaux, plantes, Flore de l’époque de Sylviculture. – Paris: Paul Lechevalier.

Brown D. E., Reichenbacher F. & Franson S. E. 1995: A classification system and map of the biotic communities of North America. – Gen. Techn. Rep. R. M., U.S. Forest Serv. 264: 109–123.

Brown D. E., Unmack P. R. & Brennan T. C. 2007: Digitized map of biotic communities for plotting and comparing distributions of North American animals. – S. W. Naturalist 52: 610–616.

Camus A. 1929: Les chataigniers – monographie des genres Castanea et Castanopsis. Encyclopédie Économique de Sylviculture III. – Paris: Paul Lechevalier.

Camus A. 1936–1938: Les chênes – monographie du genre Quercus, tome I, genre Quercus sous-genre Cyclobalanmus, sous-genre Euquerus (sections Ceris et Mesobalanus). Encyclopédie Économique de Sylviculture VI. – Paris: Paul Lechevalier.

Camus A. 1952–1954a: Les chênes – monographie du genre Quercus, tome III (1er partie), genre Quercus sous-genre Euquerus (sections Protobalanus et Erythrobalanus) et monographie du genre Lithocarpus. Encyclopédie Économique de Sylviculture VIII. – Paris: Paul Lechevalier.

Camus A. 1952–1954b: Les chênes – monographie du genre Quercus, tome III (2me partie), genre Quercus sous-genre Euquerus (sections Protobalanus et Erythrobalanus) et monographie du genre Lithocarpus. Encyclopédie Économique de Sylviculture VIII. – Paris: Paul Lechevalier.

Caspary R. 1886a: Ueber neue Bernsteinpflanzen. Sitzung am 4. März 1886. – Schriften Phys.-Ökon. Ges. Königsberg (Sitzungsberichte) 27: 18–19.

Caspary R. 1886b: Einige neue Pflanzenreste aus dem sammländischen Bernstein. – Schriften Phys.-Ökon. Ges. Königsberg (Abhandlungen) 27: 1–8.

Cavender-Bares J. 2019: Diversification, adaptation, and community assembly of the American oaks (Quercus), a model clade for integrating ecology and evolution. – New Phytol. 221: 669–692.

Cavender-Bares J., Acerly D. D., Baum D. A. & Bazzaz F. A. 2004: Phylogenetic dispersal in Floridian oak communities. – Amer. Naturalist 163: 823–843.

Clauer N., Huggett J. M. & Hillier S. 2005: How reliable is the K-Ar glauconite chronometer? A case study of Eocene sediments from the Isle of Wight. – Clay Miner. 40: 167–176.

Collinson M. E., Manchester S. R. & Wilde V. 2012: Fossil fruits and seeds of the middle Eocene Messel biota, Germany. – Abh. Senckenberg. Naturf. Ges. 570: 1–251.

Conedera M., Manetti M. C., Giudici F. & Amorini E. 2004: Distribution and economic potential of the sweet chestnut (Castanea sativa Mill.) in Europe. – Ecol. Medit. 30: 179–193.

Conwentz H. 1886: Die Angiospermen des Bernsteins. – Pp. 1–140 in: H. R. Göppert & Menge A. (ed.), Die Flora des Bernsteins und ihre Beziehungen zur Flora der Tertiärformation und der Gegenwart 2. – Danzig: Engelmann.

Crepet W. L. 1989: History and implications of the early North American fossil record of Fagaceae. – Pp. 45–66 in: Crane P. R. & Blackmore S. (ed.), Evolution, systematics, and fossil history of the Hamamelidae, vol. 2 ‘Higher’ Hamamelidae. The Systematics Association Special Volume No. 40B. – Oxford: Clarendon Press.

Crepet W. L. & Daghlian C. P. 1980: Castaneoid inflorescences from the middle Eocene of Tennessee and the diagnostic value of pollen (at the subfamily level) in the Fagaceae. – Amer. J. Bot. 67: 739–754.

Crepet W. L. & Feldman G. D. 1991: The earliest remains of grasses in the fossil record. – Amer. J. Bot. 78: 1010–1014.

Crepet W. L. & Nixon K. C. 1989a: Earliest megafossil evidence of Fagaceae: phylogenetic and biogeographic implications. – Amer. J. Bot. 76: 842–855.

Crepet W. L. & Nixon K. C. 1989b: Extinct transitional Fagaceae from the Oligocene and their phylogenetic implications. – Amer. J. Bot. 76: 1493–1505.

Crepet W. L. & Taylor D. W. 1985: The diversification of the Leguminosae: first fossil evidence of the Mimosaoidae and Papilionoidae. – Science 228: 1087–1089.

Culley T. M., Weller S. G. & Sakai A. K. 2002: The evolution of wind pollination in angiosperms. – Trends Ecol. Evol. 17: 361–369.
Czeczott H. 1961: The flora of the Baltic amber and its age. – Prace Muz. Ziemi 4: 119–145.

Daghlian C. P. & Crepet W. 1983: Oak catkins, leaves and fruits from the Oligocene Catalhaua formation and their evolutionary significance. – Amer. J. Bot. 70: 639–649.

Deng M. 2007: Anatomy, taxonomy, distribution & phylogeny of Quercus subg. Cyclobalanopsis (Oersted) Schneid. (Fagaceae). – Kunming: D. Phil. Thesis, Kunming Institute of Botany, Chinese Academy of Sciences.

Deng M., Hipp A., Song Y.-G., Li Q.-S., Coombes A. & Cotton A. 2014: Leaf epidermal features of Quercus subgenus Cyclobalanopsis (Fagaceae) and their systematic significance. – Bot. J. Linn. Soc. 176: 224–259.

Deng M., Li Q.-S., Yang S.-T., Liu Y.-C. & Xu J. 2013: Comparative morphology of leaf epidermis in the genus Lithocarpus and its implication in leaf epidermal feature evolution in Fagaceae. – Pl. Syst. Evol. 299: 659–681.

Denk T. & Grimm G. W. 2009: Significance of pollen characteristics for infrageneric classification and phylogeny in Quercus (Fagaceae). – Int. J. Pl. Sci. 170: 926–940.

Denk T. & Grimm G. W. 2010: The oaks of western Eurasia: traditional classifications and evidence from two nuclear markers. – Taxon 59: 351–366.

Denk T., Grímsson F. & Zetter R. 2010: Episodic migration of oaks to Iceland: evidence for a North Atlantic “land bridge” in the latest Miocene. – Amer. J. Bot. 97: 276–287.

Denk T., Grímsson F. & Zetter R. 2012: Fagaceae from the early Oligocene of Central Europe: persisting new world and emerging old world biogeographic links. – Rev. Palaeobot. Palynol. 169: 7–20.

Denk T., Grimm G. W., Manos P. S., Deng M. & Hipp A. L. 2017a: An updated infrageneric classification of the oaks: review of previous taxonomic schemes and synthesis of evolutionary patterns. – Pp. 13–38 in: Gil-Pelegrín E., Pego-Ptero-Pina J. J. & Sancho-Knapik D. (ed.), Oaks physiological ecology – exploring the functional diversity of the genus Quercus L. – Cham: Springer.

Denk T. & Tekleva M. V. 2014: Pollen morphology and ultrastructure of Quercus with focus on Group Ilex (= Quercus subgenus Heterobalanus (Oerst.) Menitsky): implications for oak systematics and evolution. – Grana 53: 255–282.

Denk T., Velízselos D., Güner T. H., Bouchal J. M., Grímsson F. & Grimm G. W. 2017b: Taxonomy and palaeoecology of two widespread western Eurasian Neogene sclerophyllous oak species: Quercus drymeja Unger and Q. mediterranea Unger. – Rev. Palaeobot. Palynol. 241: 98–128.

Dilcher D. L. 1971: A revision of the Eocene flora of southeastern North America. – Palaeobotanist 20: 7–18.

Doweld A. B. 2018: (2606) Proposal to conserve the name Dictyophyllum against Quercites (fossil Pteridophyta: Matoniopsida). – Taxon 67: 455–456.

Flora of North America Editorial Committee (ed.) 1993+: Flora of North America north of Mexico. 20+ vols. – New York and Oxford: Oxford University Press.

Flora of North America 2008a: Chrysolepis chrysophylla. – In: Flora of North America North of Mexico. Missouri Botanical Garden & Harvard University Herbaria. – Published at http://www.efloras.org/florataxon.aspx?flora_id=1&taxon_id=220002877 [accessed 5 Apr 2019].

Flora of North America 2008b: Chrysolepis sempervirens. In: Flora of North America North of Mexico. Missouri Botanical Garden & Harvard University Herbaria. – Published at http://www.efloras.org/florataxon.aspx?flora_id=1&taxon_id=233500374 [accessed 5 Apr 2019].

Forman L. L. 1962: A new genus in the Fagaceae. – Taxon 11: 139–140.

Forman L. L. 1964: Trigonobalanus, a new genus of Fagaceae, with notes on the classification of the family. – Kew Bull. 17: 381–396.

Forman L. L. & Cutler D. F. 1967: Additional notes on Trigonobalanus Forman (Fagaceae). – Kew Bull. 21: 331–334.

Gee C. T., Sander P. M. & Petzelberger B. E. M. 2003: A Miocene rodent nut cache in coastal dunes of the lower Rhine embayment, Germany. – Palaeontology 46: 1133–1149.

Göppert H. R. 1853: Über die Bernsteinflora. – Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin. 1853: 450–477.

Göppert H. R. & Berendt G. C. 1845: Der Bernstein und die in ihm befindlichen Pflanzenreste der Vorwelt. – Pp. 1–125 in: Berendt G. C. (ed.), Die im Bernstein befindlichen organischen Reste der Vorwelt, Erster Band, I. Abtheil. – Berlin: Nicolai.

Govaerts R. & Frodin D. G. 1998: World checklist and bibliography of Fagales (Betulaceae, Corylaceae, Fagaceae and Ticodendraceae). – Kew: Royal Botanic Gardens.

Grein M., Utescher T., Wilde V. & Roth-Nebsack A. 2011: Reconstruction of the middle Eocene climate of Messel using palaeobotanical data. – Neues Jahrb. Geol. Päliontol., Abh. 260: 305–318.

Grimaldi D. & Ross A. J. 2017: Extraordinary Lagerstätten in amber, with particular reference to the Cretaceous of Burma. – Pp. 287–342 in: Fraser N. C. & Sues H.-D. (ed.), Terrestrial conservation Lagerstätten: windows into the evolution of life on land. – Edinburgh: Dunedin Academic Press.

Grímsson F., Grimm G. W., Meller B., Bouchal J. M. & Zetter R. 2016b: Combined LM and SEM study of the middle Miocene (Sarmatian) palynoflora from the Lavanttal basin, Austria: part IV. Magnoliophyta 2 – Fagales to Rosales. – Grana 55: 101–163.
Kunzmann L. & Walther H. 2012: Early Oligocene plant taphocoenoses of the Haselbach megafossil complex and the reconstruction of palaeovegetation. – Palaeobiodivers. Palaeoenviron. 92: 295–307.

Kunzmann L., Uhl D. & Krüger P. S. 2018: Withish leaves in Eocene lignites in central Germany – a brief survey from the viewpoint of palaeobotany. – Freiberger Forschungsh., C 554: 213–223.

Kvaček Z. 2008: Whole-plant reconstructions in fossil angiosperm research. – Int. J. Pl. Sci. 169: 918–927.

Kvaček Z. 2010: Forest flora and vegetation of the European early Palaeogene – a review. – Bull. Geosci 85: 3–16.

Kvaček Z. & Walther H. 1987: Revision der mittel- und weisbürtigen tertiären Fagaceen nach blatterpidermalen Charakteristiken I. Teil Lithocarpus Blume. – Feddes Repert. 98: 637–652.

Kvaček Z. & Walther H. 1988: Revision der mittel- und weisbürtigen tertiären Fagaceen nach blatterpidermalen Charakteristiken. II. Teil Castanopsis (D. Don) Spach, Trigonobalanus Forman, Trigonobalanops Kvaček & Walther. – Feddes Repert. 99: 395–418.

Kvaček Z. & Walther H. 1989: Revision der mittel- und weisbürtigen tertiären Fagaceen nach blatterpidermalen Charakteristiken. III. Teil Dryophyllum Debev ex Saporta und Eorigonobalanus Walther & Kvaček gen. nov. – Feddes Repert. 100: 575–601.

Kvaček Z. & Walther H. 2012: European Tertiary Fagaceae with chinquapin-like foliage and leaf epidermal characteristics. – Feddes Repert. 121: 248–267.

Liu X.-Y., Xu S.-L., Han M. & Jin J.-H. 2019: An early Oligocene fossil acorn, associated leaves and pollen of the ring-cupped oaks (Quercus subg. Cyclobalanopsis) from Maoming Basin, South China. – J. Syst. Evol. 57: 153–168.

Lozano-C. G., Hernández-Camacho J. & Henao-S. J. E. 1979: Hallazgo del genero Trigonobalanus Forman, 1962 (Fagaceae) en el neotropico – I. – Caldasia 12: 517–537.

Luna-Vega I., Alcántara-Ayala O., Ruiz-Jiménez C. A. & Contreras-Medina R. 2006: Composition and structure of humid montane oak forests at different sites in central and eastern Mexico. – Pp. 101–112 in: Kapelle M. (ed.), Ecology and conservation of neotropical montane oak forests. Ecological Studies 185. – Heidelberg: Springer.

MacGinitie H. D. 1953: Fossil plants of the Florissant beds, Colorado. – Carnegie Institute of Washington Publication 599.

Mai D. H. 1970: Die tertiären Arten von Trigonobalanus Forman (Fagaceae) in Europa. – Jahrb. Geol. 3: 381–409.

Mai D. H. 1976: Fossile Früchte und Samen aus dem Mitteleozän des Geiseltales. – Abh. Zentr. Geol. Inst., Palaontol. Abh. 26: 93–149.

Mai D. H. 1989: Fossil remains of Castanopsis (D. Don) Spach (Fagaceae) and their importance to the European laurel-oak-forests. – Flora 182: 269–286.

Mai D. H. 1995: Tertiäre Vegetationsgeschichte Europas. – Jena: Gustav Fischer.

Mai D. H. 2003: A flower of Quercus (Fagaceae) included in the Bitterfeld amber. – Phytol. Balcan. 9: 157–164.

Mai D. H. & Walther H. 1978: Die Floren der Haselbacher Serie im Weiβelstecken (Bezirk Leipzig, DDR). – Abh. Staatl. Mus. Mineral. Geol. Dresden 28: 1–200.

Mai D. H. & Walther H.: 1985: Die obereozänen Floren des Weiβelstecken-Bereichs und seiner Randgebiete. – Abh. Staatl. Mus. Mineral. Geol. Dresden 33: 1–176.

Mai D. H. & Walther H. 2000: Die Fundstellen eozäner Floren des Weiβelstecken-Bereichs und seiner Randgebiete. – Altenburg. Naturwiss. Forsch. 13: 1–59.

Makino M., Hayashi R. & Takahra H. 2009: Pollen morphology of the genus Quercus by scanning electron microscope. – Sci. Rep. Kyoto Pref. Univ., Life Environ. Sci. 61: 53–81.

Manchester S. R. 1994: Fruits and seeds of the middle Eocene Nut Beds Flora, Clarno Formation, Oregon. – Palaeontogr. Amer. 58: 1–205.

Manchester S. R. 1999: Biogeographical relationships of North American Tertiary floras. – Ann. Missouri Bot. Gard. 86: 472–522.

Manchester S. R., Chen Z.-D., Lu A.-M. & Uemura K. 2009: Eastern Asian endemic seed plant genera and their paleogeographic history throughout the northern hemisphere. – J. Syst. Evol. 47: 1–47.
Manchester S. R. & Crane P. R. 1983: Attached leaves, inflorescences, and fruits of Fagopsis, an extinct genus of fagaceous affinity from the Oligocene Flora of Colorado, U.S.A. – Amer. J. Bot. 70: 1147–1164.

Manchester S. R. & Dillhoff R. M. 2004: Fagus (Fagaceae) fruits, foliage, and pollen from the middle Eocene of Pacific northwestern North America. – Canad. J. Bot. 82: 1509–1517.

Manos P. S. 1997: Quercus sect. Protobalanus. – P. 468 in: Flora of North America Editorial Committee (ed.), Flora of North America north of Mexico 3, – New York & Oxford: Oxford University Press.

Manos P. S., Cannon C. H. & Oh S.-H. 2008: Phylogenetic relationships and taxonomic status of the paleoendemic Fagaceae of western North America: recognition of a new genus, Notholithocarpus. – Madroño 55: 181–190.

Manos P. S., Doyle J. J. & Nixon K. C. 1999: Phylogeography, biogeography, and processes of molecular differentiation in Quercus subgenus Quercus (Fagaceae). – Molec. Phylogen. Evol. 12: 333–349.

Masahiko O. 1993: Latitudinal pattern of mountain vegetation zonation in southern and eastern Asia. – Plant Sci. 4: 13–18.

Menitisky Y. L. 2005: Oaks of Asia. – New Hampshire: Science Publishers.

Mertz D. F. & Renne P. R. 2005: A numerical age for the Menitsky Y. L. 2005: Oaks of Asia. – New Hampshire: Science Publishers.

Nixon K. C. 1997: Fagaceae. – Pp. 436–506 in: Flora of North America Editorial Committee (ed.), Flora of North America: north of Mexico 3, Magnoliophyta: Magnoliidae and Hamamelidae, – Oxford: Oxford University Press.

Nixon K. C. 2006: Global and neotropical distribution and diversity of oak (genus Quercus) and oak forests. – Pp. 3–13 in: Kapelle M. (ed.), Ecology and conservation of neotropical montane oak forests. Ecological Studies 185. – Heidelberg: Springer.

Nixon K. C. & Crepet W. L. 1989: Trigonobalanus (Fagaceae): taxonomic status and phylogenetic relationships. – Amer. J. Bot. 76: 828–844.

Oh S.-H. & Manos P. S. 2008: Molecular phylogenetics and cupule evolution in Fagaceae as inferred from nuclear CRABS CLAW sequences. – Taxon 57: 434–451.

Palamarev E. & Ivanov D. 2003: A contribution to the Neogene history of Fagaceae in the central Balkan area. – Acta Palaeobot. 43: 51–59.

Palamarev E. & Kitanov G. 1988: Fossil macroflora of the Beli Brjag coal basin. – Pp. 183–206 in: Velchev, V., Markova M., Palamarev E. & Vanev S. (ed.), 100th anniversary of the National Academy A. Stojanov. – Sofia: Bulgarian Academy of Sciences.

Pragowski J. 1984: Fagaceae Dumort., Castaneoideae Oerst. – Pp. 1–21 in: Nilsson S. (ed.), World pollen and spore flora. – Stockholm: Almquist & Wiksell.

Rikkjnen J. & Schmidt A. R. 2018: Morphological convergence in forest microfungi provides a proxy for Paleogene forest structure. – Pp. 527–549 in: Krings M., Harper C. J., Cúneo N. R. & Rothwell G. W. (ed.), Transformative paleobotany. – London: Academic Press.

Ritzkowski S. 1997: K-Ar-Altersbestimmungen der Messel fossil deposit (UNESCO World Heritage Site) derived from 40Ar/39Ar dating on a basaltic rock fragment. – Courier Forschungsinst. Senckenberg 255: 67–75.

Moore B. R., Dilcher D. L. & Gibson M. A. 2003: Paleoenvironmental setting, depositional setting, and plant fossil diversity found in the Claiborne formation (middle Eocene) of Tennessee. – Pp. 187–198 in: Cox R. T. (comp.), Field trip guidebook, joint meeting, Paleogene forest structure. – Pp. 527–549 in: Krings M., Harper C. J., Cúneo N. R. & Rothwell G. W. (ed.), Transformative paleobotany. – London: Academic Press.
Sadowski E.-M., Seyfullah L. J., Schmidt A. R. & Kunzmann L. 2017a: Conifers of the ‘Baltic amber forest’ and their palaeoecological significance. – Stapfia 106: 1–73.

Sadowski E.-M., Seyfullah L. J., Wilson C. A., Calvin C. L. & Schmidt A. R. 2017b: Diverse early dwarf mistletoes (Arceuthobium), ecological keystones of the Eocene Baltic amber biota. – Amer. J. Bot. 104: 694–718.

Schmidt A. R., Kauffuss U., Bannister J. M., Baranov V., Beimfoerde G., Bleile N., Borkent A., Busch A., Conran J. G., Engel S. M., Harvey M., Kennedy E. M., Kerr P. H., Kettunen E., Kiecksee A. P., Lengeling F., Lindqvist J. K., Maran M., Mildenhall D. C., Perriçot V., Rikkinen J., Sadowski E.-M., Seyfullah L. J., Stebner F., Szweido J., Ulbrich P. & Lee D. E. 2018: Amber inclusions from New Zealand. – Gondwana Res. 56: 135–146.

Simpson M. G. 2010: Plant morphology. – Pp. 451–514 in: Plant systematics. – Amsterdam: Elsevier.

Soepadmo E. 1972: Florae malesianae praecursores – Pp. 451 – 514 in: Lemmens R. H. M. J., Soerianegara I. & Wong Timmerman R. (eds.), Plant resources of South-East Asia in: Plant systematics. – Amsterdam: Elsevier.

Soepadmo E. 1970: Florae malesianae praecursores – Pp. 265 – 403 in: Van Steenis C. G. G. J. (ed.), Flora malesiana, series I Fagaceae. – Pp. 108 – 118 in: Plant systematics. – Amsterdam: Elsevier.

Solomon A. M. 1983a: Pollen morphology and plant taxonomy of white oaks in eastern North America. – Amer. J. Bot. 70: 481–494.

Solomon A. M. 1983b: Pollen morphology and plant taxonomy of red oaks in eastern North America. – Amer. J. Bot. 70: 495–507.

Standke G. 1998: Die Tertiärrprofile der Samländischen Bernsteinküste bei Rauschen. – Schriftenreihe Geowiss. 7: 93–133.

Standke G. 2008: Bitterfelder Bernstein gleich Baltischer Bernstein? – Eine geologische Raum- Zeit- Betrachtung und genetische Schlußfolgerungen. – Exkursionsführer und Veröffentlichungen der Deutschen Gesellschaft für Geowissenschaften 236: 11–33.

Standke G. 2017: Significance and results of palynological research using the example of vertical sections of Tertiary sediments on the “Sambian amber coast” (Russia). – Mauritiana 31: 23–34.

Sun W.-B., Han C.-Y., Gao L.-M. & Wilson C. A. 2007: Genetic diversity of the rare Asian plant, Trigonobalanus doichangensis (Fagaceae). – Austral. J. Bot. 55: 10–17.

Thiele-Pfieffer H. 1988: The microflora from the middle Eocene oil shale of Messel near Darmstadt. – Palaeontographica, Abt. B, Paläophytol. 211: 1–86.

Thunberg C. P. 1784: Flora japonica […] – Lipsiae: in bibliopilo I. G. Müllieriano.

Tiffney B. H. 1985: The Eocene North Atlantic land bridge: its importance in Tertiary and modern phytogeography of the northern hemisphere. – J. Arnold Arbor. 66: 243–273.

Tiffney B. H. & Manchester S. R. 2001: The use of geological and palaeontological evidence in evaluating plant phyleogeographic hypotheses in the northern hemisphere Tertiary. – Int. J. Pl. Sci. 162: 3–17.

Trelease W. 1924: The American oaks. – Mem. Natl. Acad. Sci. 20: 1–255.

Tropicos.org 2019+ [continuously updated]: Tropicos.org. – Published at https://www.tropicos.org/ [accessed 11 Oct 2019].

Vander Wall S. B. 2001: The evolutionary ecology of nut dispersal. – Bot. Rev. 67: 74–117.

Valencia-A. S. 2004: Diversidad del género Quercus (Fagaceae) en México. – Bol. Soc. Bot. México 75: 53–53.

Vaidyanathan K. 1999: The taphonomy of a Miocene lake in southern India. – Palaeontol. Electronica 2: 1–255.

Vander Wall S. B. 2001: The evolutionary ecology of nut dispersal. – Bot. Rev. 67: 74–117.

Vandenberg C. P. 1784: Flora japonica […] – Lipsiae: in bibliopilo I. G. Müllieriano.

Wappler T. 2003: How old is Baltic amber? – New evidence for a middle Eocene age from limnic sediments. – P. 82 in: Symposium on the Paleogene – preparing
for modern life and climate, 25–30 August 2003. – Leuven: ISPS.

Wappler T. & Engel S. M. 2003: The middle Eocene bee faunas of Eckfeld and Messel, Germany (Hymenoptera: Apoidea). – J. Paleontol. 77: 908–921.

Weitschat W. 1997: Bitterfelder Bernstein – ein eozäner Bernstein auf miozäner Lagerstätte. – Metalla Sonderh. 1: 71–84.

Weitschat W. 2008: Bitterfelder und Baltischer Bernstein aus paläoklimatischer und paläontologischer Sicht. – Exkursionsführer und Veröffentlichungen der Deutschen Gesellschaft für Geowissenschaften 236: 88–97.

Weitschat W. & Wichard W. 1998: Atlas der Pflanzen und Tiere im Baltischen Bernstein. – München: Dr. Friedrich Pfeil.

Weitschat W. & Wichard W. 2010: Baltic amber. – Pp. 80–115 in: Penney D. (ed.), Biodiversity of fossils in amber from the major world deposits. – Manchester: Siri Scientific Press.

Wichard W., Gröhn C. & Seredszus F. 2009: Aquatic insects in Baltic amber. – Remagen-Oberwinter: Verlag Kessel.

Wilde V. 1989: A systematic study of leaf remains from the middle Eocene of Gruppe Messel near Darmstadt (Hessen, Federal Republic of Germany). – Courier Forschungsinst. Senckenberg 115: 1–213.

Wilde V. 2004: Aktuelle Übersicht zur Flora aus dem mitteleozänen „Ölschiefer” der Grube Messel bei Darmstadt (Hessen, Deutschland). – Courier Forschungsinst. Senckenberg 252: 109–114.

Wilde V. & Frankenhäuser H. 1998: The middle Eocene plant taphocoenosis from Eckfeld (Eifel, Germany). – Rev. Palaeobot. Palynol. 101: 7–28.

Winterscheid H. 2018: Revision of a late Oligocene florule from the south-western edge of the Lower Rhine Basin (western Germany). – Acta Palaeobot 58: 49–60.

Wu J.-Y., Ding S.-T., Li Q.-J., Zhao Z.-R., Dong C. & Sun B.-N. 2014: A new species of Castanopsis (Fagaceae) from the upper Pliocene of west Yunnan, China and its biogeographical implications. – Palaeoworld 23: 370–382.

Wu Z.-Y. & Raven P. H. (ed.), 1999: Flora of China 4. Cycadaceae through Fagaceae. – Beijing: Science Press; St. Louis: Missouri Botanical Garden Press.