

A NEW FOSSIL GENUS OF ALTINGIACEAE BASED ON UNLOBED LEAVES FROM EOCENE SUBTROPICAL EVERGREEN BROAD-LEAVED FOREST IN EUROPE

Mengxiao Wu,^{1,*} Jian Huang,[†] Zhekun Zhou,[†] and Lutz Kunzmann*

*Senckenberg Natural History Collections Dresden, Königsbrücker Landstraße 159, 01109 Dresden, Germany; and [†]CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla 666303, Yunnan, China

Editor: Kathleen B. Pigg

Premise of research. Abundant fossil records of Altingiaceae have been discovered from all Northern Hemisphere continents and suggest its widespread occurrence during the Paleogene, shedding light on its evolutionary history. However, records of unlobed Altingiaceae leaf fossils are rare and discovered only in East Asia to date.

Methodology. Plant fossils were collected from the lignite opencast mine Profen-Süd in central Germany from late Eocene sediments of an alluvial coastal plain. From a total of 140 compressed leaves, cuticles were obtained from 52 specimens for studying epidermal characters. Leaf architecture and cuticle micromorphology were described and compared with fossil and extant species sharing similar characteristics.

Pivotal results. The new material belongs to a rare and incompletely known fossil species from the same region and age. For taxonomic reasons, a new fossil genus—*Zlatkophyllum* gen. nov.—associated with Altingiaceae is established. *Zlatkophyllum fischkandelii* sp. nov. et comb. nov. is redescribed and reconsidered on the basis of the simple dentate, almost circular leaves with semicraspedodromous secondary vein framework; Ω -shaped anticlinal walls of epidermal cells; and brachyparacytic stomata.

Conclusions. The new fossil genus is the first representative of Altingiaceae from the European Cenozoic with exclusively unlobed leaves, thus providing important implications for the evolutionary history of the family. In the fossil assemblage, *Z. fischkandelii* co-occurs with abundant *Steinhauera subglobosa* infructescences from the same family, and thus the new fossil taxon is hypothetically the previously unknown foliage of the *S. subglobosa*-producing fossil plant.

Keywords: leaf architectures, cuticle micromorphology, *Steinhauera*, *Liquidambar*, paleobiogeography.

Online enhancements: appendix tables.

Introduction

Altingiaceae Horan. [nom. cons.] includes only one extant genus, *Liquidambar* L., which contains 15 evergreen or deciduous tree species. This genus is characterized by spherical pistillate and staminate inflorescence and distributed from the Mediterranean and East Asia to Malesia, Central America (Stevens 2001–; Ickert-Bond and Wen 2013). Historically, *Liquidambar*, *Altingia* Noronha, and *Semiliquidambar* H.T.Chang were distinguished and comprised a subfamily within the Hamamelidaceae (s.l.), namely, Liquidambaroideae or Altingioideae (Chang 1973,

1979; Bogle 1986; Endress 1989). The three genera are remarkably similar in reproductive organs but differ from the other genera of Hamamelidaceae by both morphological and molecular characters (Li and Hickey 1988; Shi et al. 2001). In particular, the marginal teeth of leaves of Altingiaceae are asymmetrical, with glands at the apices, while teeth of Hamamelidaceae are symmetrical and glandless (Li and Hickey 1988).

Molecular studies strongly supported recognizing Altingiaceae and Hamamelidaceae (s.str.) as separate families within the order Saxifragales (Stevens 2001–). While morphological phylogenies suggest the existence of at least two genera, *Altingia* and *Liquidambar* (e.g., Ickert-Bond et al. 2007), molecular phylogenies have recognized only a single genus *Liquidambar* (e.g., Shi et al. 2001; Ickert-Bond and Wen 2013).

In former classifications, *Liquidambar* (s.str.) comprised four to five species with a disjunct distribution in Asia, the Mediterranean, and in North to Central America (Wen 1999). *Altingia* included

¹ Author for correspondence; email: mengxiao.wu@senckenberg.de.

Manuscript received March 2024; revised manuscript received July 2024; electronically published September 25, 2024.

five to 15 species that are distributed in tropical and subtropical Asia (Ickert-Bond et al. 2007). *Semiliquidambar*, encompassing three to five species, is considered natural hybrid transient individuals between *Altingia* and *Liquidambar* endemic to South and eastern China (Chang 1962; Ickert-Bond and Wen 2006; Xu et al. 2024). Ickert-Bond and Wen (2013) listed all taxa (15 species) of Altingiaceae in *Liquidambar* in their monographic revision of the family. The family's crown group age is the Paleogene to the early Neogene (between 54 and 19.5 Ma; Ickert-Bond and Wen 2006) and the divergence of the extant clades occurring during the Paleocene to Eocene, which is important data for the interpretation of fossil record.

The fossil records of *Liquidambar* (s.l.; herein we follow the concept of the monotypic family) and the presumably extinct relatives within Altingiaceae suggest a widespread occurrence in the Northern Hemisphere during the Paleogene and Neogene. Indeed, abundant fossil records of Altingiaceae have been discovered across the Northern Hemisphere (e.g., Mai 1968; Mai and Walther 1978, 1991; Wolfe and Tanai 1980; Maslova 1995, 2003; Pigg et al. 2004; Collinson et al. 2012; Lai et al. 2018, 2021; Scharfstein et al. 2020). One of the earliest records is from the mid-Cretaceous of the Russian Far East, *Anadyricarpa altingiosimila* N.Maslova & Herman, which was described from the Anadyr River Basin in Siberia (Maslova and Herman 2004). From Late Cretaceous deposits, three fossil genera of Altingiaceae—namely, *Microaltingia* Z.K.Zhou, *Protoaltingia* Scharfstein, Stockey & Rothwell, and *Paleoaltingia* Y.J.Lai—were described, and an inflorescence similar to those of Altingiaceae was reported from North America (Herendeen et al. 1999; Zhou et al. 2001; Scharfstein et al. 2020; Lai et al. 2021). *Liquidambar fontanella* Brown, a fossil species considered belonging to the extant genus, was reported from the Late Cretaceous of North America too (Brown 1933) but is in need of revision.

Steinhauera Presl, an extinct genus of Altingiaceae, is known from only the European Paleogene (Mai 1968; Knobloch et al. 1996; Collinson et al. 2012). It is based on the isolated infructescences (fruiting heads). Other organs of this fossil plant are not found to date. Mai (1968) synonymized the Eocene European fossil genera *Eoliquidambar* E.Reid & M.Chandler and *Protaltingia* E.Reid & M.Chandler with *Steinhauera*, which was accepted in all later publications (e.g., Collinson et al. 2012).

Macrofossils (leaves, inflorescences, wood) and pollen recognized as Altingiaceae were recovered from the Paleocene and younger deposits of North America, Europe, and Asia (e.g., Chandler 1961; Mai and Walther 1978, 1991; Wolfe and Tanai 1980; Muller 1981; Maslova 1995; Maslova and Krassilov 1997; Huang and Song 2002; Pigg et al. 2004). In North America and Asia, the fossil history dates back to the Cretaceous (Maslova and Herman 2004; Lai et al. 2021), while the family did not appear in Europe before the Paleocene (Chandler 1961). Fossils ascribed to modern *Liquidambar* appeared during the early Oligocene (Mai 1995). The stratigraphic range of the European fossil record extends to the Pleistocene (Martinetto 1998), but the genus has persisted in the eastern Mediterranean bioprovince until today, namely, *Liquidambar orientalis* Mill. in western Turkey and Rhodes (Endress 1993; Palamarev et al. 2005; Ickert-Bond and Wen 2006).

Although fossil and phylogenetic evidences support that unlobed leaves were not present in the earliest diverging clades of *Liquidambar* (Ickert-Bond et al. 2007; Lai et al. 2018), both

palmately lobed and unlobed leaves have been reported from *Liquidambar maomingensis* from the late Eocene of south China. The European fossil leaf record encompasses only lobed leaves of *Liquidambar* and is recorded from only the early Oligocene and younger deposits to date (Mai 1995).

In this paper, rich new leaf material of the rare Priabonian fossil species *Laurophyllum fischkandelii* L.Kunzmann & Walther 2002—sampled from a new Eocene locality in Profen-Süd, federal state of Sachsen-Anhalt, Germany—has been investigated. In reconsideration of the unique Ω -shaped anticlinal walls of the cuticles of the simple and dentate leaves, a new fossil genus and a new combination—*Zlatkophyllum fischkandelii* gen. nov. et comb. nov.—were established. It is the first fossil representative of Altingiaceae from the European Cenozoic, which has exclusively unlobed leaves.

Material and Methods

Material

The new specimens were collected from the opencast mine Profen-Süd near Zeitz in the federal state of Sachsen-Anhalt, Germany (site Universal Transverse Mercator coordinates: 33U 56.68875 N, 30.12500 E; 108–110 m asl). The fossil site is situated in the Weißelster lignite mining area south of the city of Leipzig (fig. 1A, 1B). The depositional area is known as Leipzig Embayment, which was a marginal part of the Northwest German-Polish Basin in the Cenozoic. During the Paleogene, central Germany was situated in close proximity to the coast of the Paleo-North Sea because of the global sea level highstand (Standke 2008; Standke et al. 2010). Regional middle Eocene to lower Oligocene sedimentary sequences in the southern part of the Leipzig Embayment are characterized by siliciclastic unconsolidated terrestrial and marginal marine sediments intercalated by lignite seam complexes. The fossil-bearing Luckenau Clay complex (LC; fig. 1C), which represents sediments of an alluvial-lacustrine braid plain in a coastal lowland, is the uppermost part of the Zeitz Member of the Borna Formation on the basis of modern regional lithostratigraphic concepts (fig. 1D; Standke et al. 2010). According to the regional spore-pollen-paleogene (SPP) zonation, LC can be placed into the regional SPP zone 17/18 (latest Bartonian) or could even belong to the basalmost SPP zone 18 (Kruttsch 2011). Therefore, an upper Bartonian to lower Priabonian age of the fossils can be assumed (Kruttsch 2011). The fossils are preserved as compressions, that is, coalified organic matter with preserved cuticles.

The type material of *Laurophyllum fischkandelii*, which is reconsidered here, came from the upper Priabonian Domsen Member of the Borna Formation of the Leipzig Embayment, placed into SPP zone 19 by Kruttsch (2011). The type locality is the opencast mine Vereinigtes Schleenhain in Saxony, Germany, from the same lignite mining area (fig. 1B, 1D; Kunzmann and Walther 2002). The macroflora was described by Kunzmann and Walther (2002) and reconsidered by Kunzmann et al. (2016).

Macrofloras from the Borna Formation belong to the late Eocene Zeitz floristic complex, and those from LC are the most typical ones (Mai and Walther 1985, 2000; Kunzmann et al. 2019). The Profen-Süd LC flora was preliminarily described by Kunzmann et al. (2019) as a fossil assemblage derived from an evergreen broad-leaved forest growing under subtropical humid paleoclimate conditions. The fossil assemblage,

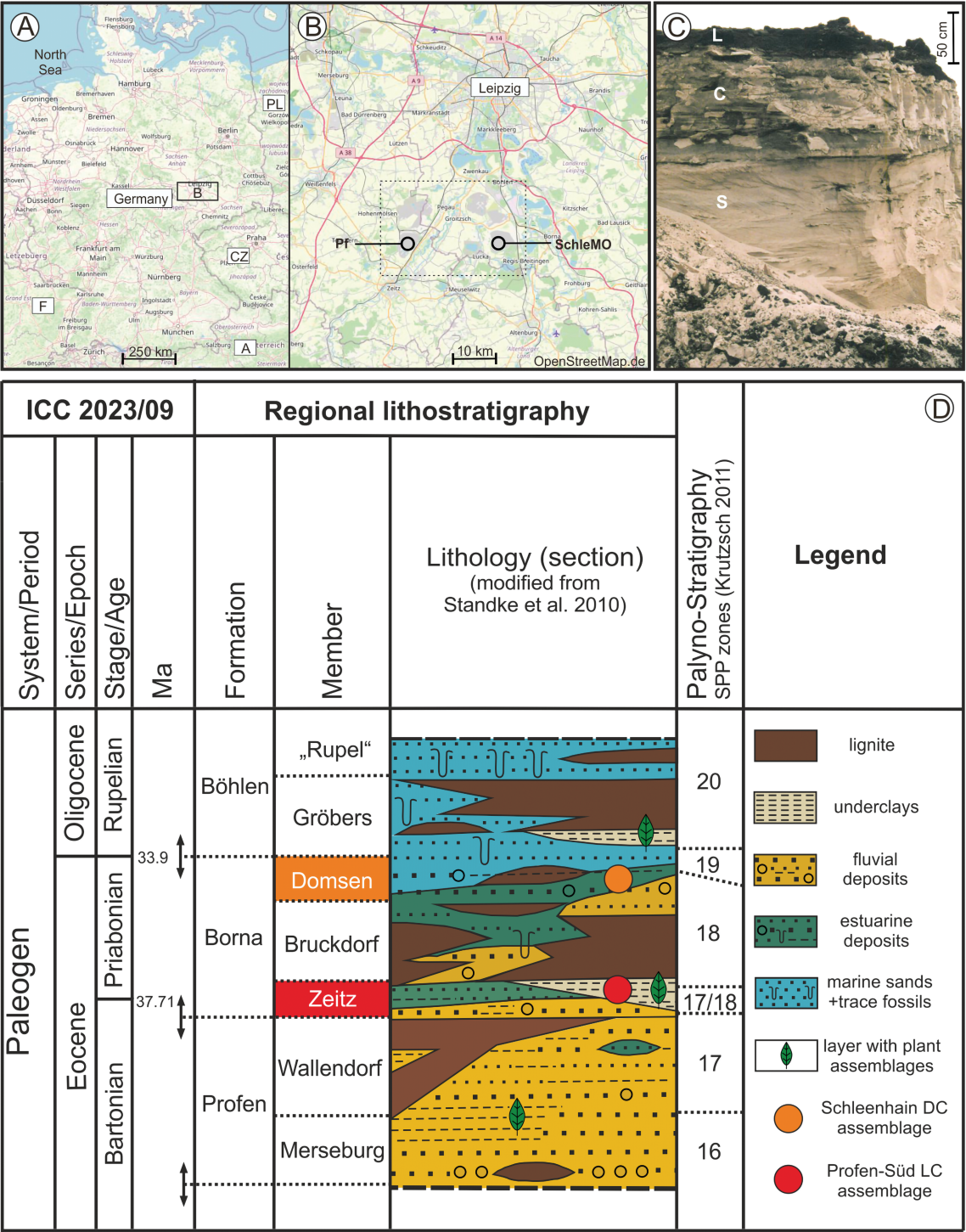


Fig. 1 Location of fossil site Profen-Süd and outcrop details. A, Map of Germany. Box indicates location of map section in B. Data are from OpenStreetMap.de (<http://opendatacommons.org>). B, Map with area south of city Leipzig. Dashed lines indicate Weißelster lignite mining area. Pf = Profen-Süd opencast mine, federal state of Sachsen-Anhalt, Germany; SchleMO = Vereinigtes Schleenhain opencast mine, federal state of Sachsen, Germany. C, High wall in Profen-Süd opencast mine. L = lignite; C = thin-bedded silty clay, fossil-bearing horizon (Luckenau Clay complex, Zeitz Member, Borna Formation). Image was taken in September 1999 by Lutz Kunzmann. For occupational safety and health standards, the high wall was not directly accessible for sampling; fossiliferous sediment blocks were removed by a shovel excavator. D, Litho- and chronostratigraphic age of fossils: general lithostratigraphic section of Paleogene sediments in southern part of Leipzig Embayment, central Germany. Lithostratigraphie: Standke et al. (2010); palynostratigraphy: Krutzsch (2011); correlation to global scale according to Standke et al. (2010); International Chronostratigraphic Chart (ICC), version 2023/09: International Commission on Stratigraphy (<https://www.stratigraphy.org>). Modified after Standke et al. (2010) and Kunzmann et al. (2017).

as far as known, mainly represents azonal communities and is characterized by a *Rhodomorphophyllum-Steinhauera* riparian association typical for the middle to late Eocene in this region (Kunzmann et al. 2019).

Methods

The morphological studies were undertaken using a stereomicroscope Leica MZ APO equipped with a camera lucida for line drawings. Photos were taken with a Canon PowerShot G1 X Mark III camera. The preparation of leaf cuticles for light microscopy (LM) and scanning electron microscopy (SEM) followed common procedures; that is, samples of coalified fossil leaves were treated with Schulze solution (for more details, see, e.g., Kunzmann et al. 2009). For LM preparations, clean cuticles were stained with safranin and mounted on glass slides with glycerol jelly; for SEM preparations, clean cuticles were mounted on stubs, coated with an approximately 4- μ m-thick Au/Pd covering on a Polaron SC7640 sputter-coater. Preparations were examined with a Leica DM 5500B light microscope equipped with a Leica DFC 480 digital camera and with a Zeiss EVO 50 SEM at 20 kV. For measurements of the micromorphological features, a Keyence VHX 7000 digital microscope was additionally used. Digital images were adjusted (contrast, brightness) with Adobe Photoshop CC 2019.

For the description of leaf morphology, the Manual of Leaf Architecture (Ellis et al. 2009) was used. The terminology of cuticular micromorphology followed Dilcher (1974) and Schneider (2004). Specimen data of extant species of *Liquidambar* used for comparison were obtained from JSTOR (<https://plants.jstor.org/>), National Cleared Leaf Collection (NCLC; <https://collections.peabody.yale.edu/pb/nclc/>), Chinese Virtual Herbarium Data Portal (<http://www.cvh.ac.cn/>), and herbarium at the Kunming Institute of Botany (China). Multiple images of the same cuticular area taken under the same magnification at different focal levels were merged into stacked images using Adobe Photoshop CC 2019. The dimensions of stomatal complexes and epidermal cells were measured and their frequencies were counted using ImageJ 1.54d. Stomatal frequencies, including stomatal index (proportion of stoma to all epidermal cells) and stomatal density (number of stomata per unit leaf area), were calculated. An undulation index was calculated on the basis of Kürschner (1997) to describe the pattern of anticlinal walls of epidermal cells.

Systematic Description

Family—*Altingiaceae* Horan. 1841

Fossil genus—*Zlatkophyllum* M.Xiao Wu & L.Kunzmann *gen. nov.*

Etymology. The name *Zlatkophyllum* is a combination of the first name of the late Czech paleobotanist Zlatko Kvaček (1934–2020) and the Latin word “phyllum,” derived from the ancient Greek word φύλλον (phúllon), meaning leaf. The name Zlatko is chosen in honor of the former doyen of Cenozoic paleobotany and the specialist in leaf architecture and leaf cuticle micromorphology.

Type species—*Zlatkophyllum fischkandelii* (L.Kunzmann & Walther 2002) M.Xiao Wu & L.Kunzmann *sp. nov.*
et comb. nov.

Generic diagnosis. Leaves distinguished by unlobed, obovate, or broadly elliptic shapes; semicraspedodromous simply toothed margin, rarely with spherulate tooth apices; anticlinal epidermal walls with regular Ω -shaped undulations with deep amplitude.

Taxonomic and nomenclatural remarks. Our material is identical to *Laurophyllum fischkandelii* L.Kunzmann & Walther 2002. This fossil species was erected because of the unique Ω -shaped undulations of the anticlinal cell walls. Provisional accommodation into *Laurophyllum* was based on insufficiently preserved leaf margins of the two type specimens in combination with the brachyparacytic type of the stomatal complexes. Here, we demonstrate that only basal portions of leaf margin may be entire, while the major parts of the margins are dentate. Thus, affiliation with *Laurophyllum* cannot be maintained. Instead, in order for us to highlight the unique combination of morphological and micromorphological characters, a new fossil genus is established and *L. fischkandelii* is recombined with it. For inclusion of the leaf margin character into the specific diagnosis, an epitype is selected from the Profen-Süd LC material.

Fossil species—*Zlatkophyllum fischkandelii* (L.Kunzmann & Walther 2002) M.Xiao Wu & L. Kunzmann *comb. nov.*

Basionym. *Laurophyllum fischkandelii* L.Kunzmann & Walther 2002. Palaeontol Z 76(2), 268–272, figs. 4k, v, 6, 7a–c, 8a–d; holotype: MMG PB SchleMO 146:2a; paratype: MMG PB SchleMO 145:1a.

Epitype, selected herein. MMG PB Pf 0409 (fig. 2F); open-cast mine Profen-Süd, federal state of Sachsen-Anhalt, Germany; Luckenau Clay Complex, Zeitz Member, Borna Formation, Leipzig Embayment; upper Bartonian to lower Priabonian, Eocene.

Emended specific diagnosis. Leaf bases truncate or rounded, apices obtuse to rounded or acuminate to shortly acuminate. Epimedial tertiaries anastomose, forming a net; exterior tertiaries looped. Epidermises glabrous; anticlinal walls of epidermal cells strongly undulate with knobbed ornamentation on undulations; periclinal walls nearly smooth; stomatal complexes brachyparacytic.

Occurrences. Opencast mines Vereinigtes Schleenhain near Borna, federal state of Sachsen (Kunzmann and Walther 2002), and Profen-Süd near Zeitz, federal state of Sachsen-Anhalt (this paper), Germany.

Litho- and chronostratigraphic ranges. Southern Leipzig Embayment, Borna Formation, upper Bartonian to upper Priabonian, Eocene (Kunzmann et al. 2019; Kunzmann and Walther 2002).

Material. Opencast mine Vereinigtes Schleenhain: MMG PB SchleMO 145:1a (paratype) with slide 175/94, SchleMO 146:2a (holotype) with slides 176/94, 1/00–3/00 (Kunzmann and Walther 2002).

Opencast mine Profen-Süd. For specimen numbers, see table S1 (tables S1 and S2 are available online).

Description. Leaves simple, marginally attached, unlobed, symmetric, obovate or broadly elliptic, rarely elliptic (fig. 2A). Leaf sizes notophyll, rarely mesophyll, preserved laminae parts 4.71–9.25 cm in length and 3.12–8.98 cm in width, length to width ratio varies between 1.27 and 1.56. Bases truncate or rounded, apices obtuse to rounded or acuminate (fig. 2A) to shortly acuminate (fig. 2G). Primary vein framework pinnate,

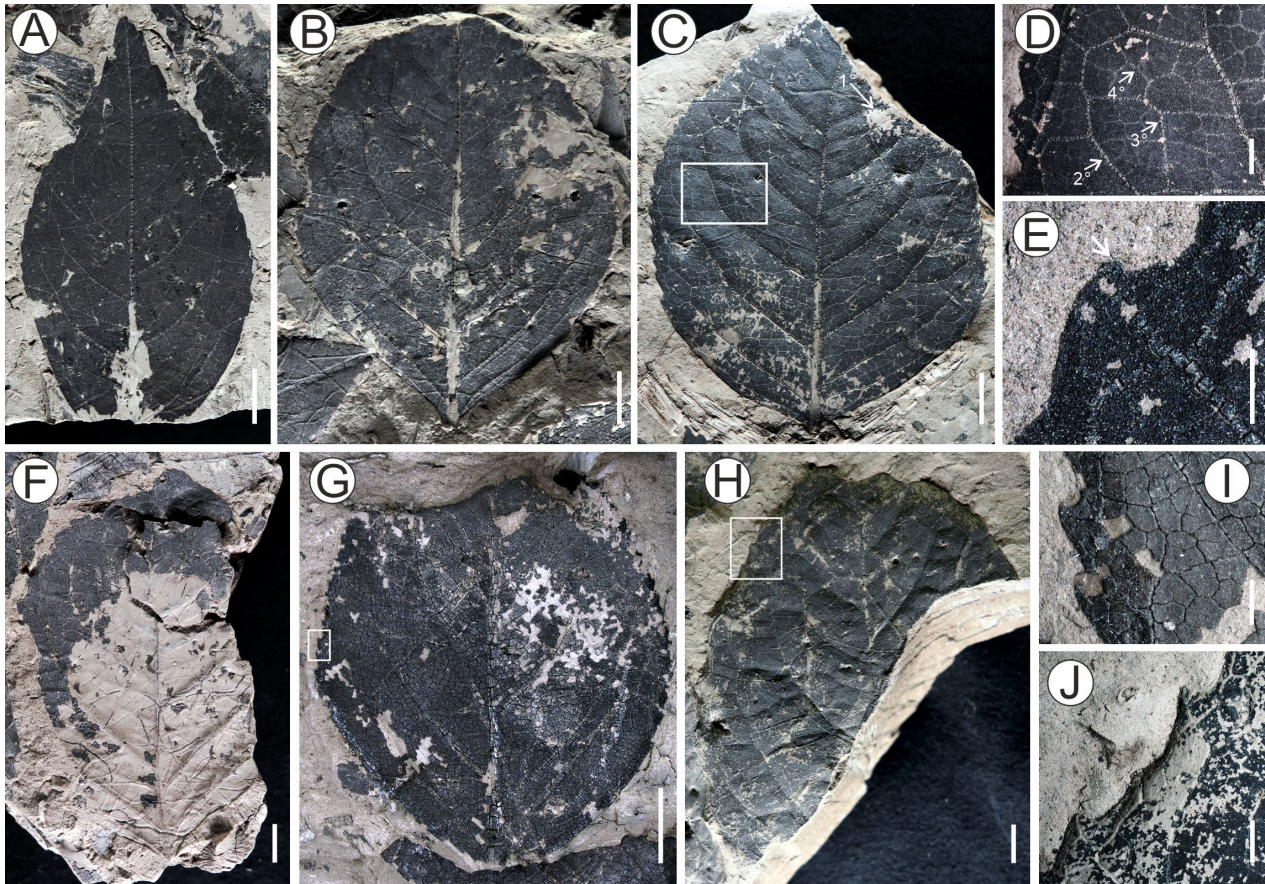


Fig. 2 Leaf fossils of *Zlatkophyllum fischkandelii* gen. nov. et comb. nov. A–C, F–H, Gross morphology. A, MMG PB Pf 1466. B, MMG PB Pf 1379. C, MMG PB Pf 1727. F, MMG PB Pf 0735. G, MMG PB Pf 0405. H, MMG PB Pf 0400. D, E, Details of C, showing secondary and higher-order venation (2°, 3°, 4°); E shows spherulate tooth apex. I, J, Details of G and H, respectively, showing serrations. Scale bars = 1 cm (A–C, F–H, K–N), 2 mm (D, J), 1 mm (E), 4 mm (J).

major secondary vein framework semicraspedodromous, five to eight pairs of secondaries, spacing regular, angles of major secondary to midvein uniform, 32°–60°, decurrently or excurrently attached to the midvein. Intercoastal tertiary vein fabric anastomosing with other tertiary veins or secondary veins, forming an irregular reticulate pattern (fig. 2A). Epimedial tertiaries anastomose with other tertiary veins to form a net. Exterior tertiaries looped. Quaternary veins anastomose with other veins, forming an irregular reticulate pattern (fig. 2D). Areolation well developed. Margins toothed, except for the basal parts in some leaves (e.g., Pf 405a, 408a, 409a, 411:1a; fig. 3B, 3C), one order of teeth, tooth space regular, two to four teeth per centimeter. Sinus rounded. Tooth shape CC/CV or CC/RT (figs. 2I, 2J, 3A). Teeth principal vein present, terminating in the apex of tooth (fig. 3A₁), rarely with spherulate tooth apex (fig. 2E).

Leaf cuticles thin but abaxial cuticle more delicate than the adaxial; sometimes cuticles obtainable only in smaller fragments. Cuticles of both sides show segmentation into coastal and intercoastal areas. Leaves hypostomatic and glabrous (fig. 4A). Adaxially, ordinary epidermal cells polygonal and isodiametric (fig. 4C, 4E), cells of coastal areas (above veins) are four sided and rectangular, 50–56 μm in length, 30–37 μm in width, anticlinal walls strongly undulate, Ω -shaped undulation with deep am-

plitude, undulation index 2.2–2.6, knobbed ornamentation on undulations. Periclinal wall nearly smooth. Shape of abaxial epidermal cell similar to that of adaxial epidermal cell (fig. 4C, 4E), 30–58 μm in length, 16–31 μm in width, undulation index 2.2–2.9. Abaxial anticlinal walls of intercoastal areas often very flat (fig. 4A) and sometimes only faintly visible. Stomatal complexes brachyparacytic; stomata elliptic or suborbicular in outline, narrow elliptic pori randomly oriented. Guard cells 11–17 μm in length, 4–8 μm in width. Pori 8–10 μm in length, around 1 μm in width, two marked stomatal ledges (fig. 5F). Two wing-shaped, often asymmetrically developed subsidiary cells of variable polygonal outlines, 17–23 μm in length, 8–12 μm in width. Anticlinal walls of subsidiaries vary from simply curved to wavy and undulated. Stomatal density around 400/mm², stomatal index around 17.4.

Discussion

Comparisons and Justification of Taxonomic Concept

This fossil leaf type is remarkably distinct from others in the regional fossil floras in central Germany (e.g., Kunzmann et al.

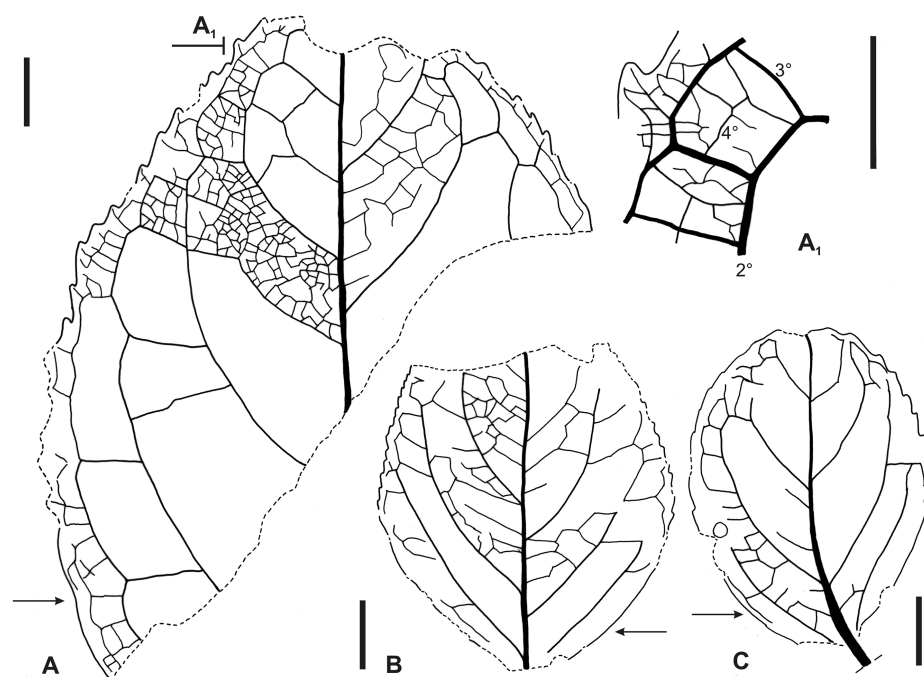


Fig. 3 Camera lucida drawings of selected specimens of *Zlatkophyllum fischkandelii* gen. nov. et comb. nov. exhibiting gross morphological characters. Arrows indicate entire-margined leaf bases. For clarity, not all visible higher-order veins are shown. A, MMG PB Pf 400:1a. Higher-order veins are shown only in selected loops of secondary veins. A₁, Close-up of a tooth and venation; venation order indicated by 2°, 3°, 4°. B, MMG PB Pf 405a. C, Epitype MMG PB Pf 409a with partly preserved petiole. Scale bars = 10 mm (A–C), 5 mm (A₁).

2016, 2019; Kunzmann and Walther 2002) and in the adjacent northern part of the Czech Republic (Knobloch et al. 1996; personal communication with the late Zlatko Kvaček) both in leaf architecture and in cuticle micromorphology. A survey of the literature dealing with Paleogene fossil floras from other parts of midlatitudinal Europe also revealed no similar leaf type described so far. Simple dentate, more or less circular leaves with a semicraspedodromous secondary vein framework are quite rare in the predominantly evergreen subtropical paleovegetation in midlatitudinal Europe during the Eocene.

However, similar leaf architectures are not very rare in living species. Ericales, Celastrales, and Saxifragales include several genera with similar elliptic leaf shapes, looped secondary venation, and one order of teeth. We compared *Zlatkophyllum fischkandelii* with representatives of these families sharing similar characteristics (table S2). Celastraceae, Pentaphylacaceae, and Theaceae are different from *Z. fischkandelii* in stoma type and framework of secondary and intersecondary veins. Salicaceae and Styrcaceae share the same vein characters with *Z. fischkandelii* but can be distinguished by tooth type, stoma type, and other epidermal characters. Ericaceae has subparallel oriented stomata and a festooned semicraspedodromous secondary vein framework that is different from that of *Z. fischkandelii*. On the basis of the combination of main characteristics, *Z. fischkandelii* has almost the same characteristics as living Altingiaceae except for the micromorphology of anticlinal cell walls and position of the teeth (table S2). Regardless of whether the leaf lamina is lobed, brachyparacytic stomata, the structures of the secondary, tertiary, and quaternary veins are

consistent within the Altingiaceae (fig. 6C, 6D, 6H, 6I) and present within our leaf fossils (fig. 2D).

Undulated anticlinal epidermal cell walls are known from several fossil and extant species, but the quite regular uniform outline on both leaf surfaces and the conspicuous Ω shape are unique among known fossils (Kunzmann and Walter 2002). The undulation index of epidermal cell walls in extant leaves of *Liquidambar* ranges from 1.1 to 1.6, and the index of shade leaves is higher than that of sun leaves (Xiao et al. 2011; Maslova et al. 2018). On the basis of the undulation index of the leaves, we cannot recognize a micromorphological variability in this undulation pattern as usually known from sun and shade leaves of the same species, that is, shade leaves with pronounced undulation and sun leaves with less pronounced to absent undulation. Taphonomic processes tend to preserve the commonly more robust sun leaves, and thus fossil leaf assemblages are usually characterized by a higher abundance of sun leaves (Kürschner 1997; Wang et al. 2018). However, all cuticles obtained in this study (52 fossil leaves) showed pronounced undulated anticlinal cell walls. Simultaneously, a marked variation in leaf size is documented. Thus, we are convinced to conclude that the Ω -shaped undulation of the epidermal cell walls is the consistent character of the fossil species independent from the potential influence of exposition to the sun. It is the most distinctive character of *Zlatkophyllum* gen. nov.

Hence, the uniform anticlinal cell wall undulation is a diagnostic character of the fossil taxon, as already stated by Kunzmann and Walther (2002) in their diagnosis. However, the type material

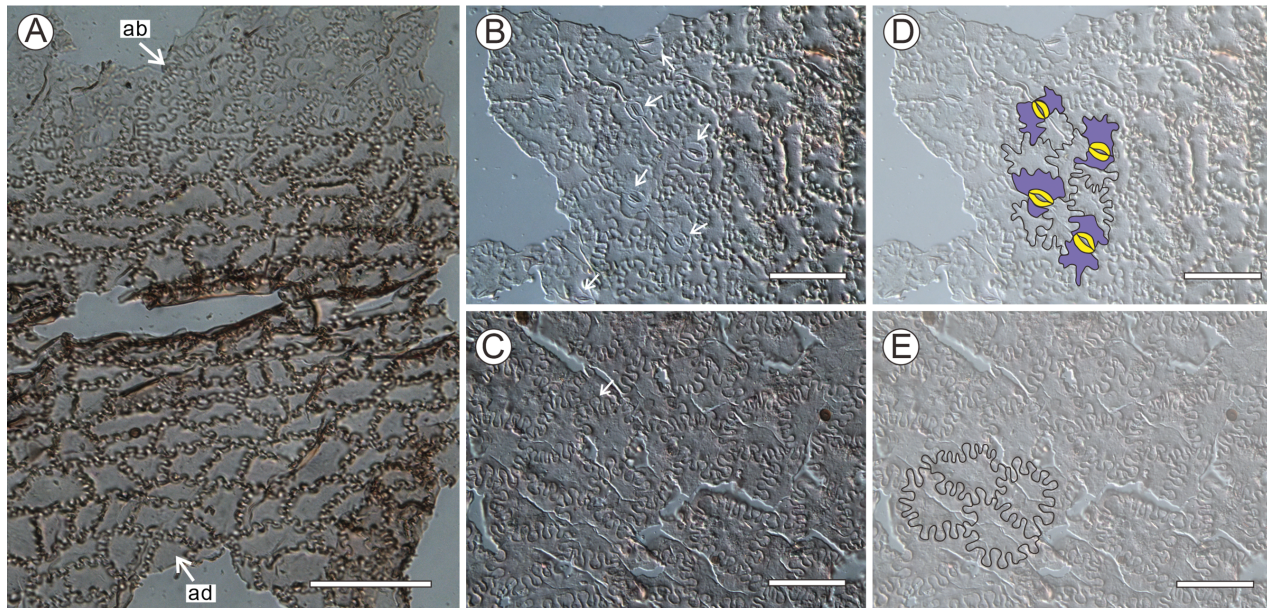


Fig. 4 Transmitted light microscopic images of *Zlatkophyllum fischkandelii* gen. nov. et comb. nov. A, Cuticular membranes. B, D, Slide Pf 22/22 from specimen MMG PB Pf 934l. C, E, Slide Pf 419/12 from specimen MMG PB Pf 315r. A, Part of abaxial cuticle (ab; with stomata) and part of adaxial cuticle (ad; without stomata) near leaf margin. B, Enlargement of abaxial cuticle. Arrows refer to stomatal complexes. C, Drawing of outlines of ordinary epidermal cells and stomatal complexes on abaxial cuticle. Periclinal areas of guard cells are colored in yellow and subsidiary cells in purple. D, Enlargement of adaxial cuticle. Arrow refers to epidermal cell. E, Drawing of outlines of ordinary epidermal cells on adaxial cuticle. Scale bars = 100 μm (A), 50 μm (B–E).

encompassed only two specimens; that is, the holotype is an incomplete leaf specimen represented by the basal-middle fragment of the lamina, and the paratype is a small basal fragment of the lamina (Kunzmann and Walther 2002, figs. 7a, 7c). Only the holotype shows a part of the leaf margin that is entire. Furthermore, the cuticles of the type material are a bit more robust than in the Profen-Süd material, and the outlines of the stomatal complexes are predominantly broad-elliptic and less asymmetrical compared with the Profen-Süd material. A single micromorphological feature from the type material is not recognized from the Profen-Süd material, which is the rare occurrence of gland-like apertures on the adaxial cuticle. These gland-like apertures consist of an almost circular cell with central roundish opening surrounded by four to five distinct, small epidermal cells. The absence of such micromorphological structures from the Profen-Süd material could be explained by its rareness in combination with the fact that the rather thin cuticles can be obtained only in smaller portions. The latter prevent an overview of the complete leaf surfaces and their micromorphological patterns.

The following characters—(1) supposed entire leaf margin, (2) pinnate-camptodromous venation pattern, (3) broadly elliptic outline of brachyparacytic stomatal complexes, and (4) rare gland-like elements in the adaxial cuticle—led Kunzmann and Walther (2002) to the definition of a new fossil species that could be provisionally accommodated into the broadly defined fossil genus *Laurophyllum* Göpp. They assumed that *Laurophyllum fischkandelii* has micromorphological similarities to extant species of *Laurus* L. but refrained from affiliation with *Laurus* because in *Laurus* the overall outline of the stomatal complexes is rhomboidal (diamond shaped).

Herein, we can state that our material is nearly identical to the type material in cuticle micromorphology but shows better preservation of leaf architectural elements. The leaf margin is entire in only the basal leaf portions but regular dentate for most of the leaf (figs. 2A–2C, 2F–2H, 2K–2M, 3). Thus, the secondary vein framework is not camptodromous as described in the original diagnosis but semicamptodromous. It has to be mentioned that only the holotype exhibits a complete secondary vein course seemingly intermediate between camptodromous and brochidodromous. Consequently, the fossil species cannot be longer affiliated with *Laurophyllum* but needs to be recombined to another (fossil)-genus. An emended diagnosis is needed to clarify distinguishing characters.

Putative Relationship to *Steinhauera* Presl

During the Paleocene and Eocene, the extinct genus *Steinhauera* was present in European fossil floras. According to Mai (1968), who revised this fossil and related fossil genera, *Steinhauera* was monotypic and endemic to Europe. In his analysis, he stated that whether *Steinhauera subglobosa* should be accommodated within an extant genus or kept separate was a matter of taxonomic philosophy, but in his opinion *Steinhauera* was more closely related to *Altingia* and could potentially be affiliated as fossil subgenus within *Altingia* (Mai 1995). Nevertheless, Mai (1968) maintained the generic concept for *Steinhauera* because not all important structural characters for infructescences of Altingiaceae were preserved in the fossil material available at that time. Furthermore, Mai (1968) placed the two monotypic Eocene fossil genera *Eoliquidambar* E.Reid et M.Chandler and *Protoaltingia*

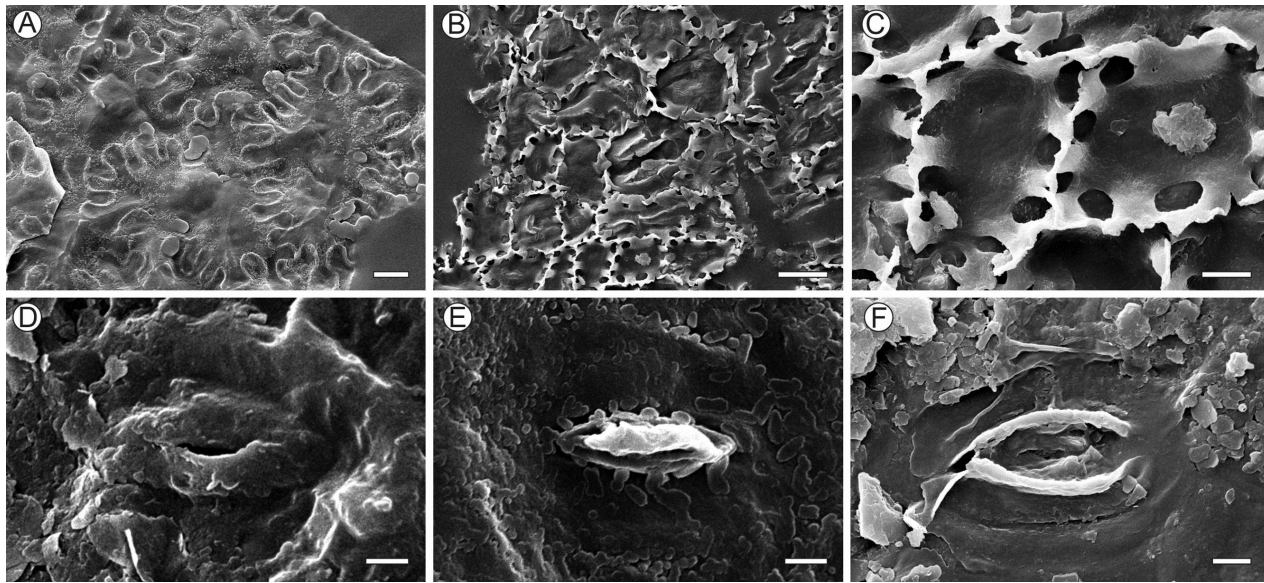


Fig. 5 SEM images of *Zlatkophyllum fischkandelii* gen. nov. et comb. nov. cuticles. A, D, Stub S 43/11 from specimen MMG PB Pf 406a. B, C, E, F, Stub S 37/11 from specimen MMG PB Pf 405a. A, Inner side of abaxial cuticle. B, Inner side of abaxial cuticle. C, Enlargement of B, showing anticlinal cell walls. D, Outer side of adaxial cuticle, showing stomatal complex. E, Outer side of abaxial cuticle, showing closed stomatal aperture. F, Inner side of abaxial cuticle, showing open stomatal aperture. Scale bars = 10 μ m (A), 20 μ m (B), 5 μ m (C), 2 μ m (D–F).

E.Reid & M.Chandler into synonymy with *Steinhauera*. Although several authors had excluded *Steinhauera* from Altingiaceae (Brown 1962; Wehr 1995), *Steinhauera* is septically and loculicidally identical with fruits of Altingiaceae (Pigg et al. 2004; Ickert-Bond et al. 2005, 2007). The genus concept was reconfirmed by Knobloch et al. (1996) and Collinson et al. (2012). During their investigation of early Eocene material from Messel in Germany, Collinson et al. (2012) referred again to morphological similarities of *Steinhauera* infructescences to *Liquidambar* and *Altingia* but stated the following differences: (1) lack of persistent styles compared with *Liquidambar* and (2) presence of both loculicidal and septicidal dehiscences in *Altingia*. However, the Messel material seems to be more similar to extant *Liquidambar*—that is, *Liquidambar orientalis*—than to *Altingia* because of surface ornamentation features (Collinson et al. 2012). All in all, it has to be noted that both Mai (1968) and Collinson et al. (2012) used the concept of two (three) genera within Altingiaceae. All their arguments should be reconsidered under the concept of the monotypic extant Altingiaceae, testing whether *Steinhauera* is evidently distinct from *Liquidambar* (s.l.). Recent micro-computed tomography scanning results additionally confirmed that these fossils belong to Altingiaceae but still lack sufficiently detailed information on the seeds (Strullu-Derrien et al. 2022).

Steinhauera is known from more than 25 localities in Europe (see lists in Mai 1968; Mai and Walther 1985, 2000; Kunzmann et al. 2016). In none of these fossil assemblages were *S. subglobosa* fruiting heads associated with leaf types whose architecture points to Altingiaceae. We have rechecked this conclusion with available literature. The Profen-Süd LC assemblage is the first fossil flora in which an altingiacean leaf type, *Z. fischkandelii* gen. nov. et comb. nov., co-occurs with abundant *S. subglobosa* infructescences (preliminary counting: >100 specimens). Thus,

the leaves are the first candidate for being the foliage of a fossil plant that produces *S. subglobosa* infructescences. However, *S. subglobosa* was not found in the assemblage of the type locality of *Z. fischkandelii* gen. nov. et comb. nov. (Kunzmann and Walther 2002). Moreover, a reevaluation of the compositions of macrofloras from the late Eocene of the Leipzig Embayment led to the assumption that the regionally stratigraphically important elements *Rhodomyrtophyllum reticulosum* (Myrtaceae) and *S. subglobosa* were already extirpated in the late Priabonian assemblages, such as the Schleenhain Domsen Complex flora, the type assemblages of *Z. fischkandelii* gen. nov. et comb. nov. In short, it remains an open question whether *S. subglobosa* and *Z. fischkandelii* belonged to the same fossil plant, although assembling appears very plausible.

Lobed versus Unlobed Leaves within Modern Altingiaceae

Although our study material consists of only unlobed leaves, being one of the diagnostic characters of the new fossil genus, it needs to be stated that leaf lobation is not a consistent feature of all members of Altingiaceae. In former classifications within the family, the predominantly lobed leaf type of *Liquidambar* was distinguished from the predominantly unlobed leaves of *Altingia* (e.g., Endress 1993); the hybrid genus *Semiliquidambar* is not taken into account in the present discussion. However, neither the lobed leaf laminae nor the unlobed leaf laminae are autapomorphies of the genera. *Liquidambar chingii* (Metcalf) Ickert-Bond & J.Wen can develop three- and two-lobed leaves as well as simple leaves on the same branch (Ickert-Bond and Wen 2013). In the eastern Mediterranean species *L. orientalis* Mill., two varieties—*L. orientalis* var. *orientalis* and *L. orientalis* var. *integriloba* Fiori—are distinguished by the presence of lobed and unlobed leaves, respectively. But Yüzer et al. (2024) could

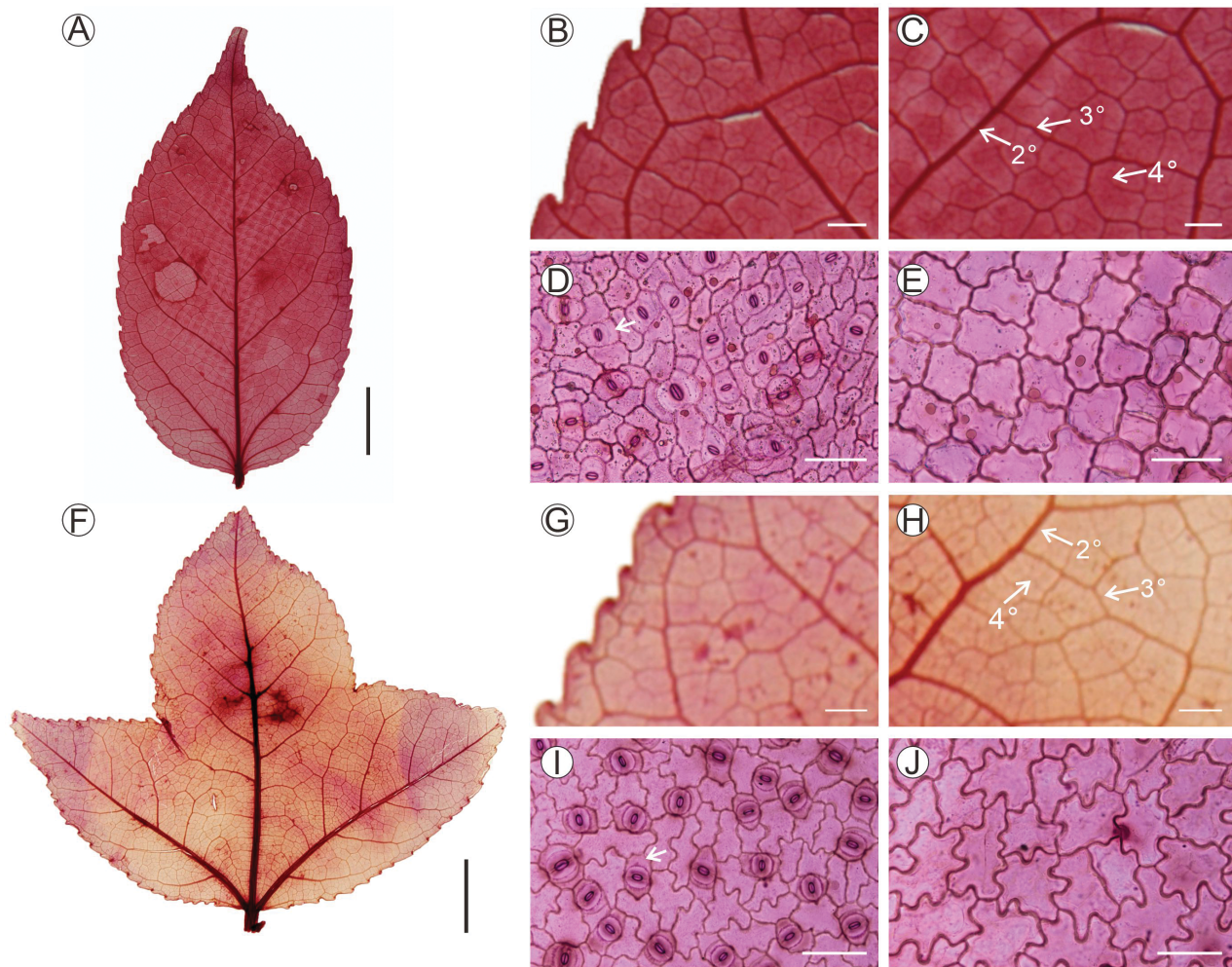


Fig. 6 Leaflet architecture and cuticles of living Altingiaceae. A, Cleared leaf of *Liquidambar excelsa* (specimens NCLC-USNH1332767). B, C, Close-up of teeth and venation in A. D, E, Abaxial cuticle and adaxial cuticle of *L. excelsa* (specimens HJ-L00351). Arrow in D refers to subsidiary cell of brachyparacytic stomatal complex. F, *Liquidambar formosana* (specimens NCLC-USNH1700185). G, H, Close-up of teeth and venation in F. I, J, Abaxial cuticle and adaxial cuticle of *L. formosana* (specimens HJ-L00521). Arrow in I refers to subsidiary cell of brachyparacytic stomatal complex. Scale bars = 1 cm (A, F), 1 mm (B, C, G, H), 50 μ m (D, E, I, J).

demonstrate that a separation into two varieties is not supported by molecular data.

It can only be speculated whether unlobed leaves are a consistent character of *Zlatkophyllum* gen. nov. The presence of unlobed leaves could hypothetically support separation of extinct *Steinhauera* from *Liquidambar* (s.l.). However, any evidence can only come from new and well-preserved fossil material that needs to be utilized in a phylogenetic analysis.

Paleobiogeographic Aspects

The lobed-leaved lineages of extant Altingiaceae are found in North America to Central America, the Mediterranean, and East Asia, whereas the unlobed-leaved lineages are almost limited to tropical and subtropical Asia (Lai et al. 2018), except for the Mediterranean *L. orientalis* var. *integriloba* (see above). Fossils with palmately lobed leaves—such as elements of *Acer*, *Gossypium*,

Platanus, *Sterculia*, *Vitis*, and others—were sometimes erroneously misidentified as *Liquidambar* (Lesquereux 1878; Berry 1937), and *Liquidambar* was sometimes misidentified and determined as representative of another genus with lobed leaf architecture (Tanai 1983).

In Europe, *Liquidambar europaea* A. Braun—which has three to five, sometimes two additional minor lobes—is a common fossil species in the Oligocene and Neogene temperate forests (Mai 1995; Mai and Walther 1978, 1991; Kohlman-Adamska et al. 2004; Kova-Eder et al. 2004; Martinetto et al. 2020). Moreover, the fossil species *Liquidambar formosana* Hance and *Liquidambar protensa* Ung. are mentioned from the Miocene localities, but they should be synonymized with *L. europaea*, according to Mai (1995). Interestingly, Mai (1995) refers to a predominance of three-lobed leaves in fossil *Liquidambar* during the Oligocene and Early Miocene and a predominance of five-lobed leaves during the Late Miocene and Pliocene. Paleobiogeographically, *L. europaea* is present only in midlatitudinal Europe during the Oligocene

to Early Miocene but absent in the Tethyan and Paratethyan regions (Handtke 1966; Mai 1995). It is also not evidenced from hinterland floras in volcanic-shaped regions during this time interval, likely because of paleoecological limitations (Akhmetiev et al. 2009). Later, *Liquidambar* extended its distribution area toward the Mediterranean, where it was present, for example, in the Pliocene and Pleistocene of Italy (e.g., Sadori et al. 2010).

Records of unlobed Altingiaceae leaf fossils are rare and discovered only in East Asia to date. The first unlobed leaf assigned to Altingiaceae appeared in the late Paleocene to the early Eocene strata in western Kamchatka, Russia—namely, *Evacarpa polysperma* N. Maslova et Krassilov (Maslova and Krassilov 1997). The major secondaries of this species are craspedodromous and thus different from the semicraspedodromous ones of our fossils. Remarkably, in several fossil species of *Liquidambar* in Asia, both lobed and unlobed leaf types are identified. *Liquidambar maomingensis* N. Maslova, Kodrul, Song & Jin—which includes three-lobed, unlobed, and intermediate leaf types with semicraspedodromous major secondaries—was reported from the late Eocene of China (Maslova et al. 2015). It was considered the ancestor of modern East Asian endemic lineages, which are characterized by unlobed leaves and pinnate venation framework (Lai et al. 2018). In the same basin, *Liquidambar bella* N. Maslova & Kodrul was reported, whose characters were interpreted as evidence for the merging of the three extant genera into one (Maslova et al. 2019). In the Miocene, another fossil species—*Liquidambar fujianensis* J.L. Dong & B.N. Sun, with three-lobed and unlobed leaves—was reported from China (Dong et al. 2018). The leaf shape and major secondaries of unlobed types of *L. fujianensis* are similar to our fossils, and spherulate tooth apices could be observed in several teeth. Similar to extant Mediterranean *L. orientalis* (see above), ex-

tant Asian *L. formosana* also exhibits morphological variations from lobed to unlobed leaves, and major secondaries could be also craspedodromous. All in all, it seems that in fossil *Liquidambar* (s.str.), the occurrence of both lobed and unlobed leaves in the same species is a common feature in Asian clades. This is in contrast to the European record of *L. europaea*, whose leaves seem to be exclusively lobed, according to our literature survey.

The European record of unlobed Altingiaceae leaves is currently restricted to *Z. fischkandelii* gen. nov. et comb. nov. If this fossil species really belongs to the same fossil plant as *S. subglobosa*, its stratigraphic range could encompass the Paleocene and Eocene, putatively coinciding with the appearances of unlobed altingiacean leaves in Asia.

Acknowledgments

We are indebted to the Mitteldeutsche Braunkohlengesellschaft (MIBRAG) lignite mining company (Zeitz) for permission to access the Profen-Süd opencast mine in 1998 and technical support for sampling; in particular, we thank former company geologist Thomas Fischkandl. We thank members of Lutz Kunzmann's working group at Senckenberg Dresden: freelancer Dorothea Bräutigam for careful macroscopic preparation of the fossils and paleobotanical preparator Carola Kunzmann for high quality and quantity of cuticle preparations (light microscopy, scanning electron microscopy). We also thank the late Zlatko Kvaček (Prague) and the late Wilfried Schneider (Hoyerswerda) for scientific discussions. Mengxiao Wu kindly acknowledges financial support from the Sino-German (China Scholarship Council–Deutscher Akademischer Austauschdienst [CSC-DAAD]) Postdoc Scholarship Program (grant 57607866).

Literature Cited

- Akhmetiev M, H Walther, Z Kvaček 2009 Mid-latitude Palaeogene floras of Eurasia bound to volcanic settings and palaeoclimatic events—experience obtained from the Far East of Russia (Sikhote-Alin') and Central Europe (Bohemian Massif). *Acta Mus Natl Pragae Ser B* 65:61–129.
- Berry EW 1937 Upper Cretaceous plants from Patagonia. *Science* 86:221–222.
- Bogle AL 1986 The floral morphology and vascular anatomy of the Hamamelidaceae: subfamily Liquidambaroideae. *Ann Mo Bot Gard* 73:325–347.
- Brown RW 1933 A Cretaceous sweet gum. *Geology* 94:611–615.
- 1962 Paleocene floras of the Rocky Mountains and Great Plains. US Geological Survey Professional Paper 375. US Government Printing Office, Washington, DC.
- Chandler MEJ 1961 The lower Tertiary floras of southern England. Vol. 1. Palaeocene Floras, London Clay Flora (supplement). British Museum (Natural History), London.
- Chang HT 1962 *Semiliquidambar*, Novum Hamamelidacearum genus sinicum. *Bull Sun-Yatsen Univ* 7:35–44.
- 1973 A revision of the Hamamelidaceae Xora of China. *Bull Sun-Yatsen Univ* 1:54–71.
- 1979 Hamamelidaceae. Pages 36–116 in HT Chang, ed. *Flora Reipublicae Popularis Sinicae*. Science, Beijing.
- Collinson ME, SR Manchester, V Wilde 2012 Fossil fruits and seeds of the Middle Eocene Messel biota, Germany. *Abh Senckenb Naturforsch Ges* 570:1–249.
- Dilcher D 1974 Approaches to the identification of angiosperm leaf remains. *Bot Rev* 40:1–157.
- Dong JL, BN Sun, T Mao, DF Yan, CH Liu, ZX Wang, PH Jin 2018 *Liquidambar* (Altingiaceae) and associated insect herbivory from the Miocene of southeastern China. *Palaeogeogr Palaeoclimatol Palaeoecol* 497:11–24.
- Ellis B, DD Douglas, JH Leo, RJ Kirk, DM Jhon, W Peter, SL Wing 2009 *Manual of leaf architecture*. Cornell University Press, Ithaca, NY.
- Endress PK 1989 A suprageneric taxonomic classification of the Hamamelidaceae. *Taxon* 38:371–376.
- 1993 Hamamelidaceae. Pages 322–330 in K Kubitzki, JG Rohwer, B Bittrich, eds. *The families and genera of vascular plants. II. Flowering plants: dicotyledons, Magnoliid, Hamamelid and Caryophyllid families*. Springer, Berlin.
- Handtke R 1966 Die fossilen *Liquidambar*-Reste (Amberbaum) aus der Molasse der Schweiz und von Oehningen (Südbaden). *Ber Schweiz Pal Ges Basel* 59:981–988. (In German.)
- Herendeen PS, S Magallon-Puebla, R Lupia, PR Crane, J Kobylinska 1999 A preliminary conspectus of the Allon flora from the Late Cretaceous (late Santonian) of central Georgia, USA. *Ann Mo Bot Gard* 86:407–471.
- Huang F, ZC Song 2002 Tertiary flora and climate in China inferred from fossil records of Altingiaceae and Juglandaceae. *Acta Palaeontol Pol* 41:232–240. (In Chinese with English abstract.)
- Ickert-Bond SM, KB Pigg, J Wen 2005 Comparative infructescence morphology in *Liquidambar* (Altingiaceae) and its evolutionary significance. *Am J Bot* 92:1234–1255.
- 2007 Comparative infructescence morphology in *Altingia* (Altingiaceae) and discordance between morphological and molecular phylogenies. *Am J Bot* 94:1094–1115.

- Ickert-Bond SM, J Wen 2006 Phylogeny and biogeography of Altingiaceae: evidence from combined analysis of five non-coding chloroplast regions. *Mol Phylogenet Evol* 39:512–528.
- 2013 A taxonomic synopsis of Altingiaceae with nine new combinations. *PhytoKeys* 31:21–61.
- Knobloch E, M Konzalova, Z Kvaček 1996 Die obereozäne Flora der Staré Sedlo-Schichtenfolge in Böhmen (Mitteleuropa). *Rozpr Česk Geol Ust* 49:1–260. (In German.)
- Kohlman-Adamska A, M Ziemińska-Tworzydło, E Zastawniak 2004 In situ pollen in some flowers and inflorescences in the Late Miocene flora of Sośnica (SW Poland). *Rev Palaeobot Palynol* 132:261–280.
- Kova-Eder J, Z Kvaček, M Ströbitzer-Hermann 2004 The Miocene flora of Parschlug (Styria, Austria)—revision and synthesis. *Ann Nathist Mus Wien* 105:45–159.
- Krutzsch W 2011 Stratigraphy and climate of the Palaeogene in the Central German estuary and related marine environment. *J Appl Reg Geol* 162:19–46.
- Kunzmann L, Z Kvaček, DH Mai, H Walther 2009 The genus *Taxodium* (Cupressaceae) in the Palaeogene and Neogene of Central Europe. *Rev Palaeobot Palynol* 153:153–183.
- Kunzmann L, Z Kvaček, V Teodoridis, C Müller, K Moraweck 2016 Vegetation dynamics of riparian forest in central Europe during the late Eocene. *Acta Mus Natl Pragae Ser B* 295:69–89.
- Kunzmann L, K Moraweck, C Müller, L Schröder, T Wappler, M Grein, A Roth-Nebelsick 2019 A Paleogene leaf flora (Profen, Sachsen-Anhalt, Germany) and its potentials for palaeoecological and palaeoclimate reconstructions. *Flora* 254:71–87.
- Kunzmann L, C Müller, K Moraweck, D Bräutigam, T Wappler, A Nel 2017 First record of insects in lignite-bearing formations (upper Eocene) of the central German Leipzig Embayment. *Palaeontol Z* 91:315–326.
- Kunzmann L, H Walther 2002 A leaf flora from the Upper Eocene of the Weissester Basin, Central Germany. *Palaeontol Z* 76:261–282. (In German with English abstract.)
- Kürschner WM 1997 The anatomical diversity of recent and fossil leaves of the durmast oak (*Quercus petraea* Lieblein/Q. *pseudocastanea* Goepfert)—implications for their use as biosensors of palaeoatmospheric CO₂ levels. *Rev Palaeobot Palynol* 96:1–30.
- Lai YJ, MA Gandolfo, WL Crepet, KC Nixon 2021 *Paleoaltingia* gen. nov., a new genus of Altingiaceae from the Late Cretaceous of New Jersey. *Am J Bot* 108:461–471.
- Lai YJ, SJ Li, WM Wang 2018 Evolutionary trends in leaf morphology and biogeography of Altingiaceae based on fossil evidence. *Palaeoworld* 27:415–422.
- Lesquereux L 1878 Contributions to the fossil flora of the Western Territories. Pt 2. The Tertiary flora. *U S Geol Surv Territ* 7:1–343.
- Li HM, LJ Hickey 1988 Leaf architecture and systematics of the Hamamelidaceae sensu lato. *J Syst Evol* 26:96–110. (In Chinese with English abstract.)
- Mai DH 1995 Tertiäre Vegetationsgeschichte Europas: Methoden und Ergebnisse. Fischer, Jena.
- 1968 Zwei ausgestorbene Gattungen im Tertiär Europas und ihre Florengeschichtliche Bedeutung. *Palaeontogr Abt B* 123:184–199.
- Mai DH, H Walther 1978 Die Floren der Haselbacher Serie im Weissester-Becken (Bezirk Leipzig, DDR). *Abh Staatl Mus Mineral Geol Dresden* 28:1–200.
- 1985 Die obereozänen Floren des Weissester-Beckens (Bezirk Leipzig, DDR). *Abh Staatl Mus Mineral Geol Dresden* 33:1–260. (In German with English abstract.)
- 1991 Die oligozänen und untermiozänen Floren Nordwest-Sachsens und des Bitterfelder Raumes. *Abh Staatl Mus Mineral Geol Dresden* 38:1–230.
- 2000 The locations of Eocene floras in the Weissester Basin and its peripheral areas. Altenburg Scientific Research, Altenburg. (In German.)
- Martinetto E 1998 East Asian elements in the Plio-Pleistocene floras of Italy. Pages 71–87 in A Zhang, W Sugong. eds. *Proceedings of the International Symposium on Floristic Characteristics and Diversity of East Asian Plants*. Springer, Berlin.
- Martinetto E, N Boonchai, F Grímsson, P Grote, G Jordan, M Kováčová, L Kunzmann, et al 2020 Triumph and fall of the wet, warm, and never-more-diverse temperate forests (Oligocene-Pliocene). Pages 55–81 in E Martinetto, E Tschopp, RA Gastald, eds. *Nature through time: virtual field trips through the nature of the past*. Springer, Cham.
- Maslova NP 1995 *Liquidambar* L. from the Cenozoic of eastern Asia. *Paleontol J* 29:145–158.
- 2003 Extinct and modern Platanaceae and Hamamelidaceae: morphology, systematics, and phylogeny. *J Paleontol* 37:467–589.
- Maslova NP, AB Herman 2004 New finds of fossil hamamelids and data on the phylogenetic relationships between the Platanaceae and Hamamelidaceae. *J Paleontol* 38:563–575.
- Maslova NP, EV Karasev, TM Kodrul, RA Spicer, LD Volkova, TE Spicer, JH Jin, X Liu 2018 Sun and shade leaf variability in *Liquidambar chinensis* and *Liquidambar formosana* (Altingiaceae): implications for palaeobotany. *Bot J Linn Soc* 188:296–315.
- Maslova NP, TM Kodrul, AB Herman, M Tu, XY Liu, JH Jin 2019 A new species of *Liquidambar* (Altingiaceae) from the late Eocene of South China. *J Plant Res* 132:223–236.
- Maslova NP, TM Kodrul, Y Song, LD Volkova, JH Jin 2015 *Liquidambar maomingensis* sp. nov. (Altingiaceae) from the late Eocene of South China. *Am J Bot* 102:1356–1370.
- Maslova NP, VA Krassilov 1997 New Hamamelid infructescences from the Palaeocene of western Kamchatka. Russia *Rev Palaeobot Palynol* 97:67–78.
- Muller J 1981 Fossil pollen records of extant angiosperms. *Bot Rev* 47:1–140.
- Palamarev E, V Bozukov, K Uzunova, A Petkova, G Kitanov 2005 Catalogue of the Cenozoic plants of Bulgaria (Eocene to Pliocene). *Phytol Balc* 11:215–346.
- Pigg KB, SM Ickert-Bond, J Wen 2004 Anatomically preserved *Liquidambar* Altingiaceae from the middle Miocene of Yakima Canyon, Washington state, USA, and its biogeographic implications. *Am J Bot* 91:499–509.
- Sadori L, M Giardini, E Chiarini, M Mattei, F Papasodaro, M Porreca 2010 Pollen and macrofossil analyses of Pliocene lacustrine sediments (Salto river valley, central Italy). *Quat Int* 225:44–57.
- Scharfstein AR, RA Stockey, GW Rothwell 2020 Evolution and phylogeny of Altingiaceae: anatomically preserved infructescences from Late Cretaceous deposits of Vancouver Island, British Columbia, Canada. *Int J Plant Sci* 181:452–463.
- Schneider W 2004 Eine blätterführende Taphocenose im 2. Miozänen Flöz von Nochten (Lausitz): Taxonomie, Taphonomie und Phytostatigraphie. *Palaeontogr Abt B* 268:1–74.
- Shi S, Y Huang, Y Zhong, Y Du, Q Zhang, H Chang, DE Boufford 2001 Phylogeny of the Altingiaceae based on cpDNA matK, PY-IGS and nrDNA ITS sequences. *Plant Syst Evol* 230:13–24.
- Standke G 2008 The paleogeographic situation of the older Tertiary (Paleocene to Lower Miocene) in central Germany. *J App Reg Geol* 159:81–103. (In German with English abstract.)
- Standke G, D Escher, J Fischer, J Rascher 2010 The Tertiary of North-west Saxony. Saxon State Office for the Environment, Agriculture, and Geology, Freiberg. (In German with English abstract.)
- Stevens PF 2001– Angiosperm Phylogeny Website. Version 14, July 2017. <http://www.mobot.org/MOBOT/research/APweb/>.
- Strullu-Derrien C, ART Spencer, P Kenrick, WS Judd, D De Franceschi, SR Manchester 2022 Revisions to the Eocene carpoiflora of Anjou, western France, with new data from X-ray tomography. *Bot Lett* 169:454–465.
- Tanai T 1983 Revisions of Tertiary *Acer* from East Asia. *J Fac Sci Hokkaido Univ* 20:291–390.

- Wang YQ, A Ito, YJ Huang, T Fukushima, N Wakamatsu, A Momohara 2018 Reconstruction of altitudinal transportation range of leaves based on stomatal evidence: An example of the Early Pleistocene *Fagus* leaf fossils from central Japan. *Palaeogeogr Palaeoclimatol Palaeoecol* 505:317–325.
- Wehr WC 1995 Early Tertiary flowers, fruits and seeds of Washington State and adjacent areas. *Wash Geol* 23:3–16.
- Wen J 1999 Evolution of Eastern Asian and Eastern North American disjunct distributions in flowering plants. *Annu Rev Ecol Syst* 30:421–455.
- Wolfe JA, T Tanai 1980 The Miocene Seldovia Point flora from the Kenai Group, Alaska. US Geological Survey Professional Paper 1105. US Government Printing Office, Washington, DC.
- Xiao L, BN Sun, XC Li, WX Ren, H Jia 2011 Anatomical variations of living and fossil *Liquidambar* leaves: a proxy for paleoenvironmental reconstruction. *Sci China Earth Sci* 54:493–508.
- Xu WQ, CQ Ren, XY Zhang, HP Comes, XH Liu, YG Li, CJ Kettle, et al 2024 Genome sequences and population genomics reveal climatic adaptation and genomic divergence between two closely related sweetgum species. *Plant J* 118:1372–1387.
- Yüzer Ö, A Tonguç, E Doğaç 2024 Genetic characterization of relic endemic *Liquidambar orientalis* (Altingiaceae) populations. *Mugla J Sci Technol* 10:42–50.
- Zhou ZK, WL Crepet, KC Nixon 2001 The earliest fossil evidence of the Hamamelidaceae: Late Cretaceous (Turonian) inflorescences and fruits of Altingioideae. *Am J Bot* 88:753–766.