Evidence for the evolutionary history and diversity of fossil sweetgums: leaves and associated capitate reproductive structures of *Liquidambar* from the Eocene of Hainan Island, South China

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Abstract: Extant species of *Liquidambar* L. exhibit a disjunct distribution between western and eastern Asia and eastern North America to Central America, with the highest species diversity being in China. In this study, two new species of *Liquidambar* are described from the Eocene of Hainan Island, South China: *L. hainanensis* on basis of the leaf fossils, and *L. ovoidea* based on compressions of infructescences. The co-occurrences of *L. hainanensis* leaves, associated infructescences of *L. ovoidea* and dispersed pantoporate pollen grains have the combination of morphological features peculiar to the genera *Liquidambar* and former *Semiliquidambar* and *Altingia*. This is considered further palaeobotanical justification for the placement of these three genera into a single genus, *Liquidambar*, proposed earlier based on molecular markers. Our data provide evidence for the occurrence of an ancestral polymorphic group of *Liquidambar* species (*L. maomingensis* with associated capitate infructescences, *L. bella*, *L. hainanensis* and *L. ovoidea*) during the Eocene in South China, and corroborate the view that South China could have been a centre of *Liquidambar* speciation during the Eocene. The morphological similarity of *L. hainanensis* leaves to those of the extant species *L. orientalis* from Western Asia and the North American *L. styraciflua* may support the importance of both the North Atlantic Land Bridge and the Bering Land Bridge for the dispersal of *Liquidambar*. Analysis of fossil species of *Liquidambar* from eastern Asia also contributes to further understanding of patterns in the taxonomic diversity and evolutionary history of this genus.

Key words: *Liquidambar*, Eocene, leaf fossil, infructescence, pantoporate pollen grain, Hainan Island.

THE extant family Altingiaceae (Saxifragales) consists of a single genus *Liquidambar* L. with 15 species (Ickert-Bond & Wen 2013). This family is a classic example of an intercontinental disjunct distribution with modern occurrences in western and eastern Asia and eastern North America to Central America, with the highest species richness in Asia (Ickert-Bond & Wen 2006).

The fossil records of Altingiaceae including leaves, infructescences and inflorescences, pollen and woods have been widely reported from the Upper Cretaceous to Neogene of the northern hemisphere. The most extensive occurrences of Altingiaceae fossils are known from the Cenozoic of middle to low latitudes in Asia (e.g. Endo & Morita 1932; Makarova 1957; Kuprianova 1960; Suzuki 1961; Huzioka 1972; Onoe 1974; Huzioka & Uemura 1979; Uemura 1983; Ozaki 1991; Maslova 1995, 2003; Ina et al. 2007; Xiao et al. 2011; Oskolski et al. 2012; Maslova et al. 2015, 2019; Dong et al. 2018; Huang et al. 2021). In Europe, reliable fossils of this family have been recorded from the Paleocene to Pliocene (e.g. Kirchheimer 1943; Mai 1968; Ferguson 1971, 1989; Koch et al. 1973; Martinetto 1998; Teodoridis 2003; Worobiec et al. 2012; Strullu-Derrien et al. 2022). In North America, the earliest leaf fossils assigned to *Liquidambar fontanella* Brown

date back to the Late Cretaceous (Brown 1933), however, the altingioid identity of these fossils is uncertain (Ferguson 1989; Pigg *et al.* 2004). Other fossils of Altingiaceae in North America have been reported mainly from the Palaeocene to Pliocene (e.g. Knowlton 1902; MacGinitie 1941; Graham 1965; Smiley *et al.* 1975; Wolfe & Tanai 1980; Melchior 1998; Pigg *et al.* 2004; Wheeler *et al.* 2010; Stults & Axsmith 2011). Still older occurrences, based on reproductive structures, similar in some aspects to those of Altingiaceae, have been described from the upper Turonian of New Jersey, USA (Zhou *et al.* 2001; Lai *et al.* 2021) and lower Coniacian of Vancouver Island, British Columbia, Canada (Scharfstein *et al.* 2020), while anatomically preserved reliable infructescences of *Liquidambar* are currently known only from the Miocene of Washington, USA and Fujian Province, southeastern China (Pigg *et al.* 2004; Dong *et al.* 2018). Pantoporate *Liquidambar*-like pollen grains (= *Periporopollenites sakhaensis* Hofmann, Spicer, Ahlberg & Herman) are recognized as early as the Campanian–Maastrichtian (Hofmann *et al.* 2011).

The majority of fossil *Liquidambar* species have been described based on leaves, whereas fossil reproductive structures are generally a far less common phenomenon. Leaves of *Liquidambar* may be identified confidently by their semicraspedodromous to festooned semicraspedodromous secondary venation and evenly spaced concave/retroflexed teeth that have more prominent proximal flanks and glandular apices. To date, several *Liquidambar* fossil taxa have been described from China based on leaves and/or reproductive structures. Some *Liquidambar* leaves, being fragmentarily preserved from the Yilan flora, Dalianhe Formation, Heilongjiang Province and the Huadian flora, Jilin Province, have been identified only to the genus level (He & Tao 1997; Manchester *et al.* 2005). Two Eocene species, *L. maomingensis* N. Maslova, Kodrul, Song & Jin (Maslova *et al.* 2015) and *L. bella* N. Maslova & Kodrul (Maslova *et al.* 2019), have been recognized from the Huangniuling Formation, Guangdong Province, South China. Two other species, *L. fujianensis* J.L. Dong & B.N. Sun from the Fotan Group in Fujian Province (Dong *et al.* 2018) and *L. miosinica* Hu & Chaney from the Shanwang Formation in Shandong Province (Hu & Chaney 1940) and the Shengxian Formation in Zhejiang Province (Xiao *et al.* 2011, 2013, 2015), have been described from the Miocene of China.

In this study we describe two new species of *Liquidambar* based on leaves and capitate infructescences from the middle–upper Eocene of Hainan Island, South China. The co-occurrence of apparently sun and shade leaves of *Liquidambar*, associated infructescences with affinities to extant Altingiaceae and *ex situ* pantoporate pollen grains expand our understanding of patterns in the evolutionary history of this genus and its taxonomic diversity, and also support recent taxonomic changes merging the formerly recognized extant genera *Altingia* and *Semiliquidambar* into the single genus *Liquidambar* (Ickert-Bond & Wen 2013).

MATERIAL AND METHOD

Geological setting

The Changchang Basin, northeast Hainan Island, South China (Fig. 1), contains a succession of Palaeogene terrestrial deposits subdivided into three formations: the lowermost Paleocene Changtou Formation, overlain sequentially by the Eocene Changchang and the Wayao formations (Zhou & Chen 1988; Lei *et al.* 1992; Spicer *et al.* 2014). The lower part of the plant-bearing Changchang Formation consists of clastic terrigenous and coaliferous deposits probably formed in lacustrine and paludal environments, while the upper part of the formation is composed of predominantly lacustrine and fluvial mudstones, siltstones and sandstones. The Changchang Formation contains well-preserved plant megafossils including leaves, fruits, seeds and fossil wood (Spicer *et al.* 2014, 2017), as well as diverse palynomorph assemblages (Zhang 1980; Lei *et al.* 1992; Yao *et al.* 2009; Hofmann *et al.* 2019). The Changchang flora of Hainan Island shares numerous characteristic taxa with the Youganwo flora of the nearby Maoming Basin on the Chinese mainland, and therefore the Changchang Formation is taken to be contemporaneous with the Youganwo Formation (Spicer *et al.* 2014). Based on magnetostratigraphic data (Wang *et al.* 1994), palynomorphs and vertebrate fossils, the age of the Youganwo Formation has recently been confined to the middle to early late Eocene (Spicer *et al.* 2014; Aleksandrova *et al.* 2015; Hofmann *et al.* 2019).

Specimen preparation

A total of 74 leaf impressions and compressions, seven compressed infructescences, and many dispersed pollen grains were examined from the Changchang Formation. Images of the plant fossils were taken using an Olympus E-500 digital camera. Leaf teeth and fine venation details were photographed using a Leica M165 stereomicroscope equipped with a Leica DFC420 digital camera. For leaf description terminology, we follow Ellis *et al.* (2009). The length to width (L/W) ratio for fragmentary leaves was calculated using reconstructed laminae. Plant megafossils are curated in the Museum of Biology, Sun Yat-sen University, Guangzhou, China, with specimen numbers prefixed by CC.

Pollen preparation followed standard wet chemical procedures described by Klaus (1987). The samples were crushed by hand in a mortar with a pestle, then
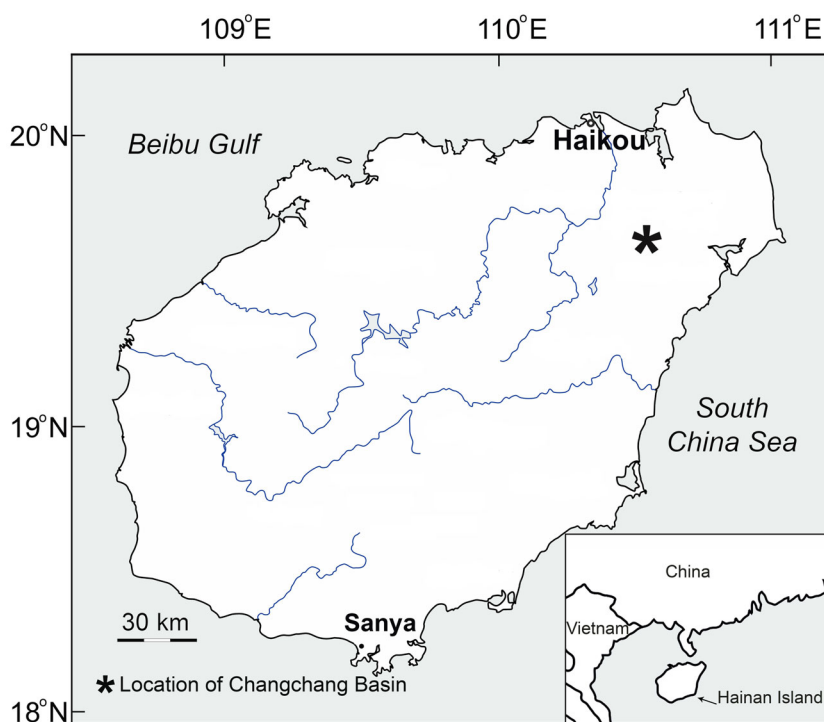
FIG. 1. Geographical map showing the location of Changchang Basin on Hainan Island, South China (base map from d-maps: https://d-maps.com).

transferred into a glass beaker and boiled in concentrated HCl until the carbonate part was dissolved. After settling, the acid was decanted, the residue washed three times, and the sediment transferred into polyethylene beakers and then treated with 33% HF to dissolve the silicates (cold processing over 4 days). After the residue settled, the acid was decanted, the residue washed three times, and the organic residue boiled in concentrated HCl for 5 min. After settling the acid was decanted and the residue was washed three times with distilled water. Then the residue was mixed with *c.* 10 mL of a solution of sodium chlorate (cold saturated) and 4 drops of HCl and boiled in a water bath for *c.* 4 min (bleaching). After this process the residue was washed three times with water and once with concentrated acetic acid. No sieving occurred, so as to retain palynomorphs <10 μm in size. Next, the organic residue was mixed with 10 mL of acetolysis fluid (10 parts acetic anhydride mixed with one part concentrated sulphuric acid) and boiled in a water bath for *c.* 4 min. After that, the sample was washed three times with distilled water and transferred with glycerol into small sample vials. For light microscopy (LM) investigation, the residues in glycerol were evenly smeared onto a glass slide and the investigated pollen isolated with a micro-manipulator (a hair mounted on a needle) from the sample smears into a small clean drop of glycerol on a new slide and photographed with an Olympus camera equipped with the ProGres digital image system. The photographed pollen grains were transferred with a micro-manipulator to scanning electron microscope (SEM) stubs and washed with a small drop of 100% alcohol to wash off the glycerol. The stubs were immediately sputtered with gold and examined with an SEM (FEI InspectS 500). Stubs and photographs are stored in the Department of Paleontology, University of Vienna, under inventory numbers IPUW 7836_Hai_Liqu.

SYSTEMATIC PALAEONTOLOGY

By Vasilisa Kachkina, Natalia Maslova, Tatiana Kodrul *and* Jian-Hua Jin

Order SAXIFRAGALES Berchtold & J. Presl, 1820
Family ALTINGIACEAE Horaninow, 1841
Genus LIQUIDAMBAR Linnaeus, 1753
Liquidambar hainanensis sp. nov.
Figures 2A, C, 3–7

Derivation of name. The specific name refers to the source area, Hainan Island.

Holotype. CC-769-1, leaf, designated here (Fig. 2A, C).

Specimens examined. CC-11; CC-13; CC-234; CC-260a, b–CC-262a, b; CC-263; CC-264a, b–CC-268a, b; CC-269; CC-271; CC-324; CC-769-1; CC-769-2; CC-770a, b; CC-771; CC-880-1; CC-880-2; CC-942; CC-1101; CC-1122; CC-1221a, b; CC-1222; CC-1223a, b; CC-1224; CC-1225; CC-1227–CC-1229; CC-1230a, b; CC-1232; CC-1233; CC-1246a, b; CC-1288a, b; CC-1289–CC-1296; CC-1680; CC-1681a, b; CC-1682a, b-1; CC-1682a, b-2; CC-1682a, b-3; CC-1683a, b; CC-1684a-1; CC-1684a-2; CC-1684b; CC-1685a, b; CC-1686–CC-1688; CC-1754a, b; CC-1755–CC-1757; CC-1758-1, 1758-2, 1758-3, 1758-4, 1758-5; CC-1759; CC-1760; CC-1761a, b; CC-1762; CC-2618-2; CC-2646; CC-2678; CC-3248-1.

Diagnosis. Leaves simple, palmately lobed. Lamina symmetrical or asymmetrical with medial or base width asymmetry. Petiole long, slender. Base angle of lamina obtuse, base shape convex, cuneate, rounded or slightly cordate. Apices of lateral lobes directed upwards or horizontally; apex angle of lobes acute, apex shape straight. Deep sinuses between lobes angular or rounded in shape, untoothed. Leaf margin serrate from the base, frequently leaf base partly untoothed. Teeth irregularly spaced, concave/retroflexed, sinus shape rounded, tooth apex non-specific. Venation basal or suprabasal actinodromous, with three to four primary veins; lateral primary veins extend outward or upward. Secondaries up to 6–10 pairs, alternate to sub-opposite, rarely opposite, often irregular, semicraspedodromous or festooned semicraspedodromous, arching upward near the margin; intersecondaries weak. Tertiary veins alternate percurrent or mixed opposite–alternate percurrent. Fourth-order veins alternate percurrent.

Description. Leaves are simple, polymorphic, palmately lobed, petiolate. Leaves predominantly three-lobed (Figs 2A, C, 3B–E, 4A–E, 5A–C, E, F, 6A, C–G, 7B–Q), although one leaf possesses
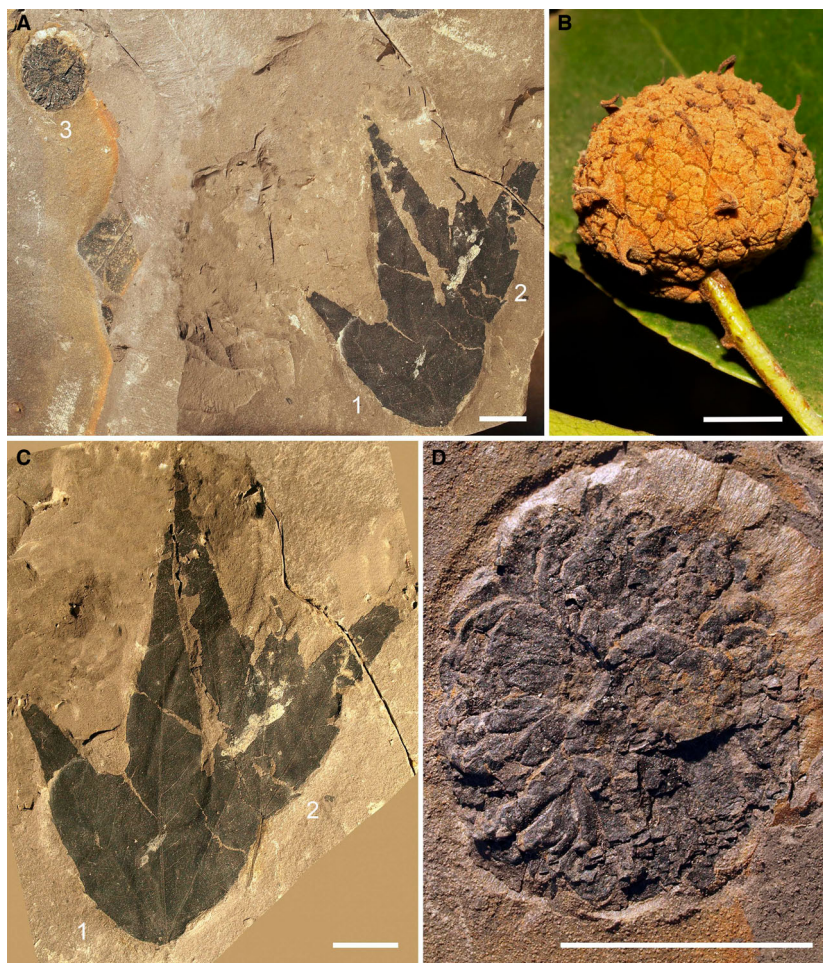

FIG. 2. Leaves of *Liquidambar hainanensis* sp. nov. (A, C), associated infructescence of *Liquidambar ovoidea* sp. nov. (A, D) from the middle–upper Eocene Changchang Formation of the Changchang Basin, and an extant infructescence for comparison (B). A, leaf with narrowly triangular lobes, CC-769-1 (holotype), a similar leaf, CC-769-2, and an associated infructescence, CC-769-3. B, infructescence of the extant species *Liquidambar obovata*. C, enlargement of leaves in A, CC-769-1 (holotype), CC-769-2. D, enlargement of infructescence in A, CC-769-3. Scale bars represent 1 cm.

four lobes with a small fifth lobe (Figs 3A, 7A), developed on the lowermost agrophic veins of the lateral primary vein. The longest preserved fragment of petiole reaches 34 mm in length and 1.5 mm in width. Base angle of the lamina is obtuse; base shape is convex (Figs 2A, C, 4F, 6F, 7E, K, P, Q), cuneate (Figs 3D, 5E, 7J), rounded (Figs 5A, 6B, C, 7B, G, H) or slightly cordate (Figs 5F, 6A, 7C, I), symmetrical (Figs 5A, E, 6B, 7B, J, G) or asymmetrical (Figs 3A, D, 6E, 7A). Estimated lamina length varies between 52 and 140 mm, lamina width varies between 34 and 134 mm; the length of the central lobe varies from 30 to 80 mm, with its width between 10 and 27 mm. Length/width (L/W) ratio of the lamina varies from 0.71 to 1.64 (average, 1.30). Leaves are predominantly symmetrical or rarely asymmetrical with a different depth of sinuses between the lobes (Figs 3A, D, 4A, 5C, 7A, D, E, N) or/and medial asymmetry (Figs 2A, C, 3A, D, 6E, 7A, E, P). The shape of the central lobe is triangular (Figs 5A, F, 6E, 7B, H, I), but more frequently narrowly triangular with nearly parallel leaf margins at the lobe base (Figs 3C, 4A–D, 5B, C, E, 6D, G, 7D, E, L–O, Q) or narrowing towards the base (Figs 3A, E, 4E, 7A).

Apex angle of the lobes is acute. The shape of the lobe apices is straight (Figs 2A, C, 3E, 7A, P). Lateral lobes extend upwards, reaching the length of the central lobe (Figs 4A, D, E, 5B, 7F, M, N), rarely they extend obliquely upward, reaching approximately half of the lamina length, and then curve to the horizontal direction (Figs 3E, 5A, C, F, 6E, 7B, D, I). Deep sinuses between lobes are angular, rarely rounded in shape, untoothed (Figs 2A, C, 3A, C–E, 4A–E, 5A–C, E, F, 6C, D, E, 7A–F, I–K, M–Q).

The leaf margin is serrate from the leaf base (Figs 2C, 3A, D, 5A, B, 6A, 7A–C, F, P), frequently the leaf base is partly untoothed (Figs 4C, F, 5E, 6F, 7H, J, K). Teeth are somewhat irregularly spaced, numerous, 3–6 per 1 cm of leaf margin, mostly 4 per 1 cm. Teeth are appressed, concave/retroflexed, with more prominent proximal flanks and rounded sinuses (Figs 3D, E, 4A, C–E, 5A–E, G, 6B, 7B, D, F, G, J, M, N). Teeth vary slightly in size, some larger teeth are beak shaped. Tooth apices are non-specific.

Venation is basal (Figs 2A, C, 3A, D, 5A, B, E, F, 6A, C, F, 7A–C, F, I–K, P) or suprabasal (Figs 4B, C, 6B, E, 7E, G, H)

FIG. 3. Leaves of *Liquidambar hainanensis* sp. nov. from the middle–upper Eocene Changchang Formation of the Changchang Basin. A, four-lobed leaf with small fifth lobe developed on the lowermost agrophic veins of the lateral primary vein, CC-1229. B, leaf with a triangular central lobe, CC-262a. C, leaf with narrowly triangular lobes, CC-266b. D, asymmetrical leaf showing basal venation, cuneate base, and irregularly spaced large marginal teeth, CC-1758-1. E, leaf with a central lobe narrowing towards the base, CC-1228. Scale bars represent 1 cm.
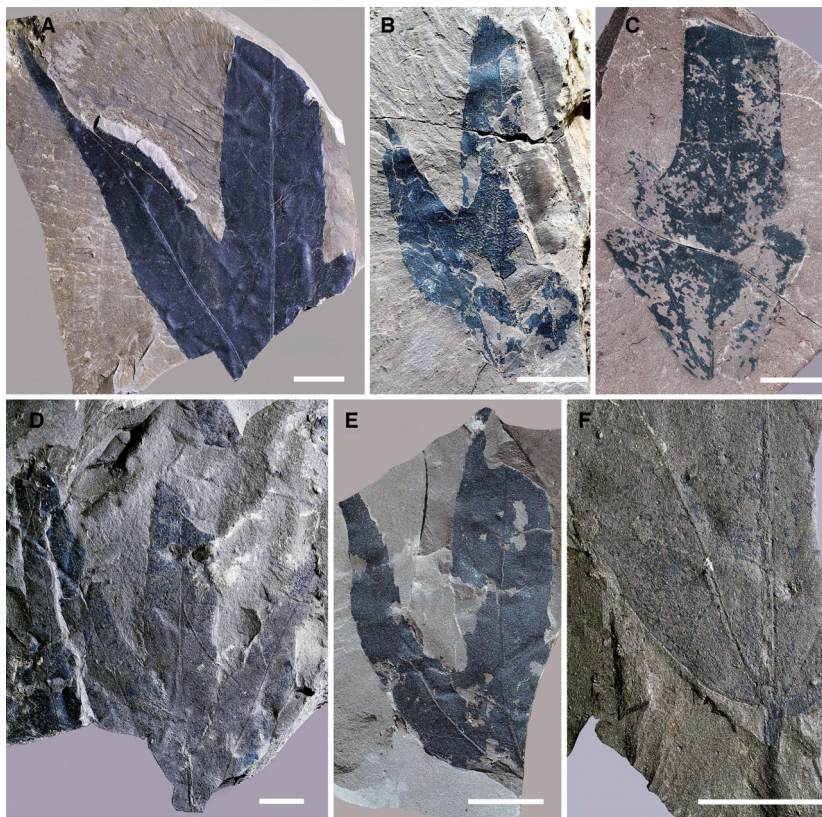
FIG. 4. Possible shade morphotypes of *Liquidambar hainanensis* sp. nov. from the middle–upper Eocene Changchang Formation of the Changchang Basin showing elongate leaves with relatively inconspicuous venation. A, leaf with lateral lobes extending upwards and reaching the central lobe length, CC-260a. B–C, leaves with suprabasal venation, convex base and relatively small marginal teeth, CC-1224, CC-1755, respectively. D, leaf showing lateral lobes oriented upwards and reaching the length of the central lobe, CC-1682b-2. E, leaf with a central lobe narrowing towards the base, CC-1230a. F, leaf with a convex asymmetrical base, partly untoothed, CC-1683b. Scale bars represent 1 cm.

actinodromous, with three, occasionally four, primary veins. The midvein is straight. Lateral primary veins are equal in thickness to the midvein, diverging from the midvein at 30–55°. They are straight (Figs 2A, C, 3A, 4A, D, 5B, 7A, F, K, M, N, P), slightly curved outward (Figs 5A, C, F, 6E, 7B, D, I) or upward (Fig. 4E). Secondary veins are thin, 6–10 pairs, alternate to subopposite, rarely opposite, often irregularly spaced, semicraspedodromous or festooned semicraspedodromous. Intersecondary veins are weak, extend about one-half of the distance between leaf margin and midvein, usually one or two per intercostal area. Tertiary veins are alternate percurrent or mixed opposite–alternate percurrent; fourth-order veins are alternate percurrent (Figs 5D, 6G).

Locality. Changchang Basin, Jiazi Town, Hainan Island, South China.

Stratigraphical position. Changchang Formation, middle–upper Eocene.

Repository. The Museum of Biology, Sun Yat-sen University, Guangzhou, Guangdong Province, China.

Liquidambar ovoidea sp. nov.
Figures 2A, D, 8

Derivation of name. The specific name refers to the ovoid shape of infructescences.

Holotype. CC-1866a, CC-1866b (part and counterpart), infructescence, designated here (Fig. 8A, B).

Specimens examined. CC-769-3; CC-1866a, b; CC-1867; CC-1869–CC-1872.

Diagnosis. Capitate infructescences (heads) ovoid to sub-globose, pedunculate. Peduncles more than 8.5 mm long and up to 2.5 mm wide. Heads 13–16 × 13–18.5 mm in size, composed of 12–16 individual fruits. Fruits bilocular, with styles. Extrafloral structures between fruits prominent, broad and smooth. Outer fruit wall layer composed of elongate polygonal or rectangular cells.

Description. The capitate infructescences are ovoid, occasionally sub-globose and somewhat flattened transversally, 13–16 × 13–18.5 mm in size, pedunculate (Figs 2A, D, 8A–D). Incompletely
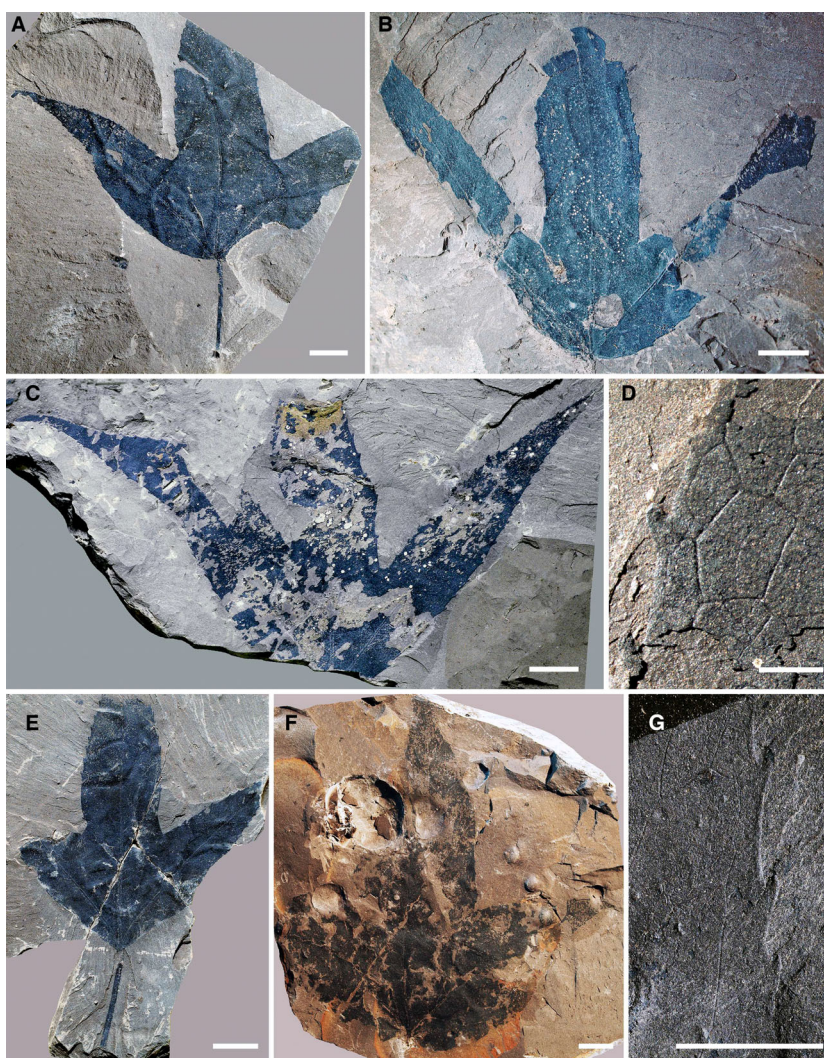
FIG. 5. Leaves of *Liquidambar hainanensis* sp. nov. from the middle–upper Eocene Changchang Formation of the Changchang Basin. A, symmetrical leaf showing a fragmentary preserved slender petiole, rounded base and lateral lobes extended obliquely upwards and then curved horizontally, CC-1223a. B–C, leaves with narrow lateral lobes extended obliquely upwards, CC-1295, CC-1222, respectively. D, G, marginal teeth, CC-1873, CC-1682b-2, respectively. E, leaf with a fragmentary preserved petiole and cuneate base, CC-1221a. F, leaf with a cordate base and wide triangular lobes, CC-264a. Scale bars represent: 1 cm (A–C, E, F); 1 mm (D); 5 mm (G).

preserved peduncles are up to 8.5 mm long and up to 2.5 mm wide. Infructescences are composed of *c.* 12–16 individual bilocular fruits measuring typically 3.5–4.5 × 5–7 mm. Bilocular fruits are separated from each other by a broad rim of relatively smooth extrafloral structures. Remnants of styles are represented only by style bases (Fig. 8A, B). The outer fruit wall layer is composed of elongate polygonal or rectangular cells, *c.* 10 × 10 μm or 10 × 20 μm in size (Fig. 8E, F).

Locality. Changchang Basin, Jiazi Town, Hainan Island, South China.

Stratigraphical position. Changchang Formation, middle–upper Eocene.

Repository. The Museum of Biology, Sun Yat-sen University, Guangzhou, Guangdong Province, China.

DISCUSSION

Morphological comparison of Liquidambar hainanensis *with the extant and fossil* Liquidambar *species*

The extant flora of Hainan Island includes three *Liquidambar* species, *L. chinensis* Champ. (formerly *Altingia chinensis* (Champ.) Oliver ex Hance), *L. obovata* (Merrill & Chun) Ickert-Bond & J. Wen (formerly *Altingia obovata*
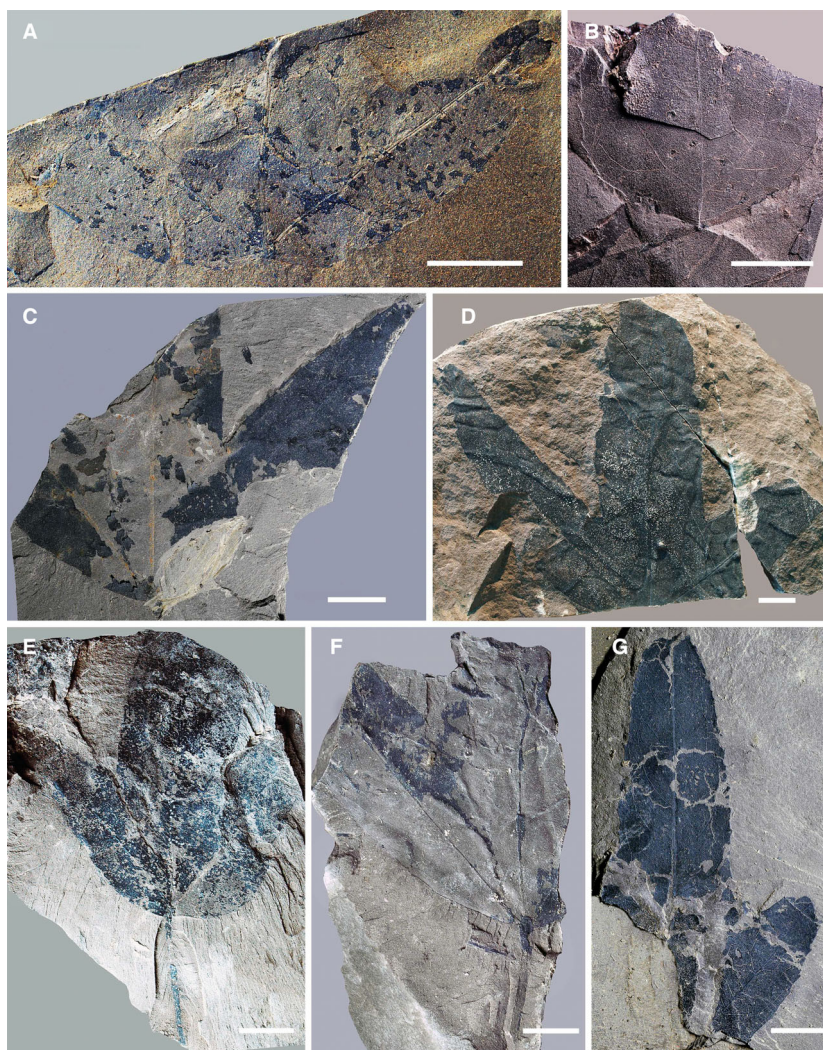
FIG. 6. Leaves of *Liquidambar hainanensis* sp. nov. from the middle–upper Eocene Changchang Formation of the Changchang Basin. A, leaf showing prominent venation and a cordate base, CC-263. B, leaf with suprabasal venation and a rounded base, CC-1758-2. C, leaf with a rounded base and an angular sinus between lobes, CC-13. D, symmetrical leaf with lateral lobes extended obliquely upwards, CC-261a. E, asymmetrical leaf with a fragmentary preserved petiole, suprabasal venation and a widely triangular central lobe, CC-1289. F, petiolate leaf with a convex base, CC-1292. G, leaf showing prominent venation, CC-1101. Scale bars represent 1 cm.

Merrill & Chun), and *L. formosana* Hance (Ickert-Bond & Wen 2013). *Liquidambar chinensis* and *L. obovata* are characterized by unlobed leaves, whereas *L. formosana* possesses three-lobed leaves. In *L. hainanensis*, only lobate leaf morphotypes have been identified with a pre-dominance of three-lobed leaves (Fig. 7). Leaves of *L. hainanensis* are morphologically more similar to those of the extant *L. chingii* (Metcalf) Ickert-Bond & J. Wen (formerly *Altingia chingii* Metcalf) from Fujian, Guangdong, Guangxi, Guizhou and Jiangxi provinces and *L. caudata* (H.T. Chang) Ickert-Bond & J. Wen (formerly *Semiliquidambar caudata* H. T. Chang) from Fujian and Zhejiang provinces of mainland China in having some

leaves with the suprabasal venation, but differ in the absence of unlobed morphotypes. All extant *Liquidambar* species and the overwhelming majority of fossil species with lobed leaves differ from those of *L. hainanensis* in terms of their exclusively basal venation type. Currently, the only known fossil species having suprabasal lateral primary veins is *L. bella* (Maslova *et al.* 2019).

The leaves of all extant *Liquidambar* species have horizontally extended lateral lobes. In *L. hainanensis*, lateral lobes generally extend upwards, reaching nearly the length of the central lobe or then curve to the horizontal direction. Another mode, in which lateral lobes develop horizontally, is less common. Among fossil *Liquidambar*, such
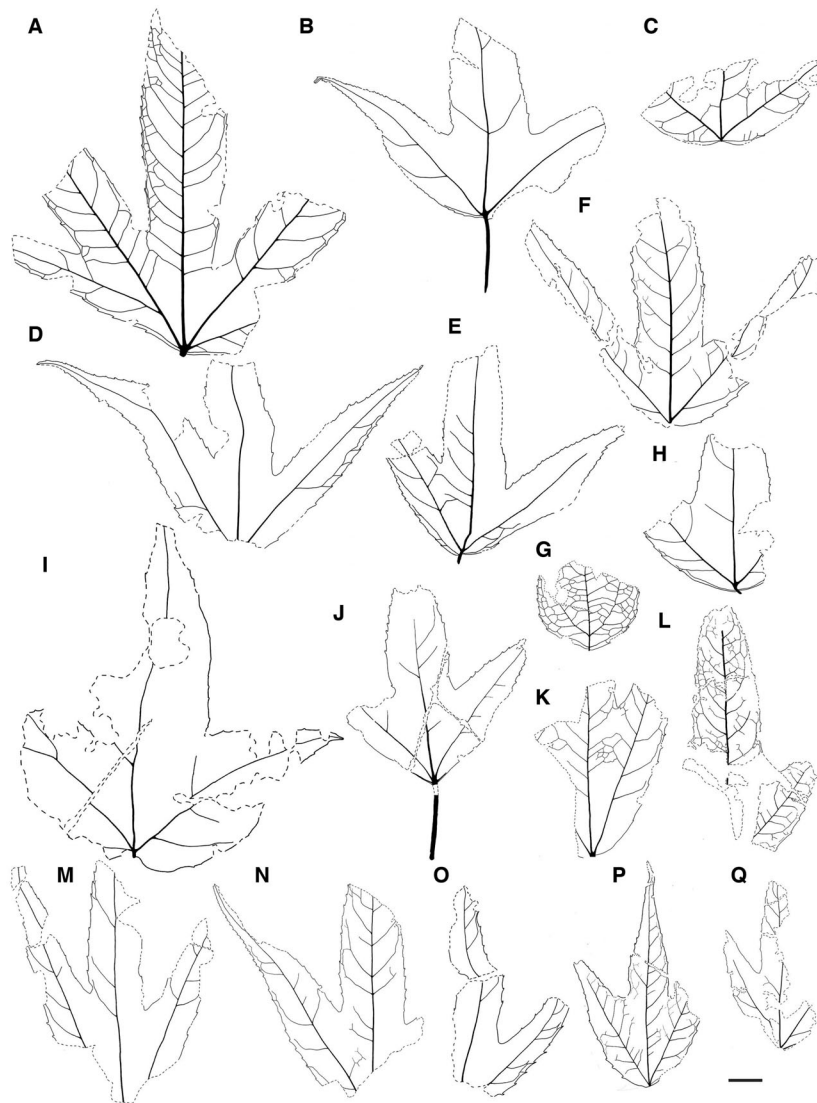
FIG. 7. The range of leaf morphology variation seen in *Liquidambar hainanensis* sp. nov. from the middle–upper Eocene Changchang Formation of the Changchang Basin. A, CC-1229. B, CC-1223a. C, CC-263. D, CC-1222. E, CC-265b. F, CC-1295. G, CC-1758-2. H, CC-1290. I, CC-264a. J, CC-1221a. K, CC-1683a. L, CC-1101. M, CC-1682b-2. N, CC-260a. O, CC-266b. P, holotype CC-769-1. Q, CC-1224. Scale bar for all figures represents 1 cm.

leaf dimorphism with both types of the lateral lobe orientation (upward or horizontal) is typical for the Eocene *L. maomingensis* (Maslova *et al.* 2015) and *L. bella* (Maslova *et al.* 2019), the Miocene *L. fujianensis* (Dong *et al.* 2018) (Table 1), and the Miocene–Pliocene *L. europaea* A. Braun (Givulescu 1986). Leaves of *L. hainanensis* possess three types of central lobe shape: (1) triangular; (2) triangular with narrowing towards the base; and (3) narrowly triangular with nearly parallel lobe edges at the base. *Liquidambar hainanensis* shares this morphological feature with the fossil species *L. bella* and two extant species, *L. orientalis* Mill. from western Asia

(Fig. 9), as well as the North American *L. styraciflua* L. These two species differ from other extant species by having more dissected leaves with very narrow long lobes. Among fossil *Liquidambar*, similar characteristics are observed in some morphotypes of the polymorphic Miocene–Pliocene species *L. europaea* (Makarova 1957; Ferguson 1971; Knobloch & Kvaček 1976), *L. miosinica* Hu & Chaney (Hu & Chaney 1940; Tanai 1967, 1970, 1976; Ishida 1970; Ablaev *et al.* 1990; Ozaki 1991; Ina *et al.* 2007), *L. yabei* (Morita) Huzioka (Huzioka 1974), and *L. mioformosana* Tanai (Tanai 1961), as well as the Eocene *L. maomingensis* (Maslova *et al.* 2015) and species
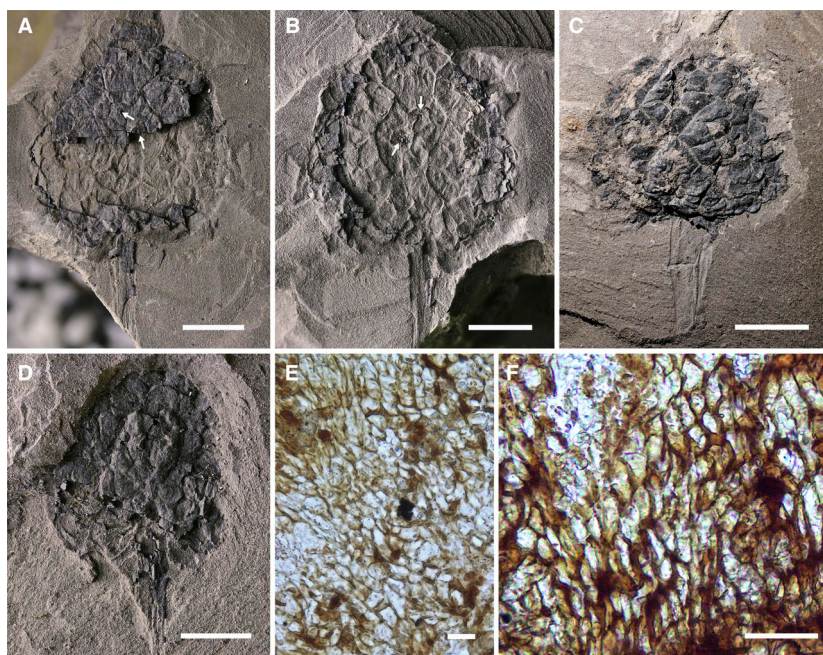
FIG. 8. Infructescences of *Liquidambar ovoidea* sp. nov. associated with *Liquidambar hainanensis* sp. nov. from the middle–upper Eocene Changchang Formation of the Changchang Basin. A–B, an ovoid pedunculate infructescence composed of bilocular fruits, note the bases of the styles (arrows), holotype CC-1866a, CC-1866b, part and counterpart. C, sub-globose pedunculate infructescence showing a broad rim of smooth extrafloral structures between adjacent bilocular fruits, CC-1867. D, ovoid infructescence, CC-1870. E–F, cells of the outer layer of the fruit wall. Scale bars represent: 5 mm (A–D); 25 μm (F); 20 μm (E).

from the Oligocene of Japan assigned to the extant species *L. formosana* (Matsuo 1970).

Liquidambar hainanensis differs from all extant and fossil species in having irregularly spaced teeth, fairly often with a partly untoothed lamina base margin and lobe base margin. It should be noted that the regularly toothed leaf margin is a diagnostic feature for extant species of *Liquidambar* (Fig. 9). A further distinctive feature of *L. hainanensis* leaves is a low number of teeth per centimetre (3–6 teeth per cm). For comparison, an average value of 5–7 teeth per cm was observed in extant *L. formosana* (Endo 1968) and fossil *L. maomingensis* (Maslova *et al.* 2015) and *L. bella* (Maslova *et al.* 2019), whereas the maximum value known in extant *L. styraciflua* is 7–9 teeth per cm (Endo 1968). Romanova (1971) mentioned a partly untoothed lamina base in *L. kazachstanica* Romanova from the upper Eocene of the Zaysan depression (Eastern Kazakhstan).

Thus, *L. hainanensis* is most similar to the Eocene *L. bella* from the nearby region of mainland China in terms of it having lobed leaves with basal and suprabasal venation and a similar L/W ratio, but it differs in having lobed morphotypes with long narrow lobes and different tooth spacing (Table 1). The leaves of *L. hainanensis* are also similar to those of *L. yabei* (Morita) Huzioka from the Late Miocene Daibo flora, Japan (Huzioka 1974) and

L. pachyphyllum Knowlton from the upper Eocene Lyukama Formation, Eastern Sakhalin (Maslova 1995, 2003), the Miocene Mascall Formation, Oregon, west of North America (Knowlton 1902) and the Seldovia Point flora, Alaska, North America (Wolfe & Tanai 1980), but differ in having suprabasal venation.

Shade and sun leaves of Liquidambar hainanensis

Previous studies of shade and sun leaves in extant *Liquidambar* have shown the importance of their morphological and epidermal features for more reliable identification of foliar polymorphisms and, accordingly, more accurate systematic determinations of fossil species (Maslova *et al.* 2018, 2019). The principal morphological characters distinguishing sun and shade leaves are the L/W ratio, the degree of venation network development, and the tooth size and shape. In sun leaves, compared with shade leaves, the L/W ratio is lower, venation is more conspicuous (secondary and tertiary veins are more prominent), the laminae are more dissected with longer lobes, and teeth are rather large. By contrast, shade morphotypes include leaves with higher L/W ratios, less pronounced venation and smaller, widely spaced teeth.

TABLE 1. Morphological comparison of leaves of *Liquidambar hainanensis* sp. nov. and fossil species of *Liquidambar* from South China.

Species	*Liquidambar maomingensis* (Maslova et al., 2015)	*Liquidambar bella* (Maslova et al., 2019)	*Liquidambar fujianensis* (Dong et al. 2018)	*Liquidambar hainanensis* sp. nov.
Location/Age	South China, Maoming Basin/late Eocene	South China, Maoming Basin/late Eocene	Southeastern China, Fotan Group/middle Miocene	China, Hainan Island, Changchang Basin/ middle–late Eocene
Leaves	Palmately 3-lobed and unlobed	Palmately 3-lobed	Palmately 3–5-lobed	Palmately 3–4-lobed
Leaf symmetry	Symmetric	Symmetric or asymmetric	Symmetric or asymmetric	Symmetric or asymmetric
Petiole	Length up to 50 mm, width 1 mm	Longest fragment 20 mm	Length up to 52 mm, width 2 mm	Longest fragment 34 mm, width up to 1.5 mm
Apices of the lobes	Acute, straight or acuminate	Acute and frequently strongly acuminate	Acuminate or convex	Acute to acuminate
Lateral lobes	Reaching half of the lamina length	Reaching the length of the central lobe	Reaching half of the lamina length	Reaching the length of the central lobe or half of the lamina length
Lamina length (mm)	46–125	37–80	52–122	52–140
Lamina width (mm)	45–150	19–140	78–165	34–134
Central lobe length (mm)	22–75	15–50	37–50	30–80
Central lobe width (mm)	14–35	10–28	21–33	10–27
Shape of the central lobe	Triangular	Triangular or frequently narrowly triangular	Triangular or elongate and parallel-margined	Triangular or frequently narrowly triangular
L/W ratio of the lamina	0.66–1.22 (average, 0.86)	0.69–2.07 (average, 1.15)	0.65–0.84 (average, 0.73)	0.71–1.64 (average, 1.30)
Base shape of the lamina	Rounded, slightly cordate	Rounded or truncate, sometimes slightly cordate	Cuneate or cordate	Convex, cuneate, rounded or slightly cordate
Venation	Basal actinodromous	Basal or suprabasal actinodromous	Basal actinodromous	Basal or suprabasal actinodromous
Midvein	Straight	Straight	Straight	Straight
Lateral primary veins (LPV)	Equal in thickness to the midvein	Equal in thickness to the midvein	Equal in thickness to the midvein	Equal in thickness to the midvein or slightly thinner
LPV diverging from the midvein	35–60°	20–50°	30–80°	30–55°
LPV shape	Straight, slightly curved	Frequently slightly arch shaped, curved, rarely straight	Straight, slightly curved	Straight, slightly curved
Secondary veins (SV)	Thin, semicraspedodromous (festooned semicraspedodromous)	Thin, festooned semicraspedodromous	Thin, semicraspedodromous or festooned semicraspedodromous	Thin, semicraspedodromous
Pairs of SV	8–10	6–10		6–10
Intersecondaries	Weak	Weak	Weak	Weak

(continued)

TABLE 1. (Continued)

| Species	Liquidambar maomingensis (Maslova et al., 2015)	Liquidambar bella (Maslova et al., 2019)	Liquidambar fujianensis (Dong et al. 2018)	Liquidambar hainanensis sp. nov.
Tertiaries veins	Percurrent and opposite–alternate percurrent	Percurrent	Alternate percurrent to opposite–alternate percurrent	Alternate percurrent and opposite–alternate percurrent
Leaf margin	Serrate	Serrate	Serrate	Serrate
Marginal teeth	Starting from petiole insertion point or rarely just above, 5–7 per cm	Starting from petiole insertion point, 5–8 per cm	Starting at the basal part	Starting frequently above petiole insertion point, 3–6 per cm
Tooth shape	Concave/retroflexed, with a more prominent proximal flank	Concave/retroflexed, with a more prominent proximal flank	Proximal flank concave (teeth small, appressed) or retroflexed (teeth large, pronounced)	Concave/retroflexed, with a more prominent proximal flank
Tooth apices	Inconspicuous or prominent non-specific	Glandular or without any pronounced glands, beak shaped	Inconspicuous and glandular	Non-specific, some larger teeth are beak shaped
Sinuses between teeth	Rounded	Rounded	Rounded	Rounded
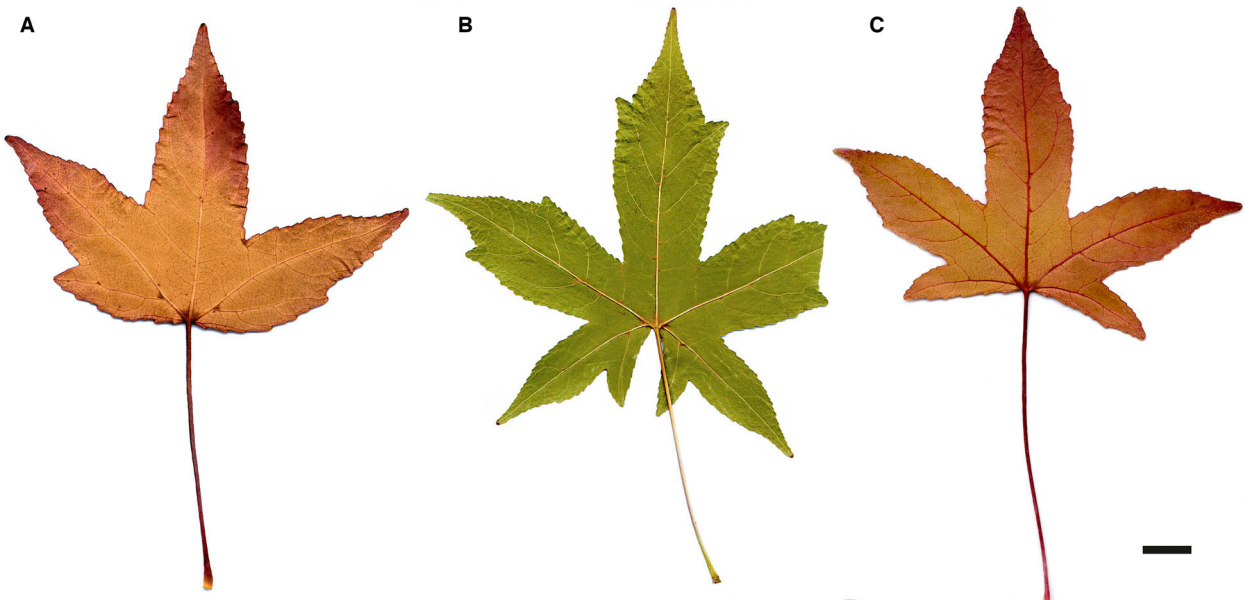
FIG. 9. A–C, leaves of extant species *Liquidambar orientalis* from the Sukhumi Botanical Garden, South Caucasus. Scale bar represents 1 cm.

The available number of completely preserved leaves of *L. hainanensis* is insufficient for the reliable division of all specimens into sun/shade morphotypes. However, based on their different features it is possible to identify some sun and shade leaves. Shade leaves of *L. hainanensis* tend to be more elongate with a higher L/W ratio, a less pronounced venation network and relatively small sparse teeth (e.g. Fig. 4). By contrast, sun leaves exhibit a lower L/W ratio, conspicuous venation network and larger teeth (e.g. Figs 3D, E, 5C, 6A).

Comparison of the reproductive structures of Liquidambar ovoidea *and extant and fossil* Liquidambar *species*

Reproductive structures of *Liquidambar ovoidea* are characterized by a combination of diagnostic features

confirming their affinity to Altingiaceae: capitate infructescences (heads), bilocular fruits lacking perianth elements, and prominent rims of the extrafloral structures around the fruits. Compared with typically globose infructescences of extant *Liquidambar s.s.*, those formerly ascribed to *Altingia* (Fig. 2B) are sub-globose or occasionally elongate (Ickert-Bond *et al.* 2007). Fossil capitate reproductive structures from Hainan are similar to those of the extant species *L. gracilipes* (Hemsl.) Ickert-Bond & J. Wen (formerly *Altingia gracilipes* Hemsl.), *L. siamensis* (Craib) Ickert-Bond & J. Wen (formerly *Altingia siamensis* Craib), and *L. yunnanensis* (Rehder & E.H. Wilson) Ickert-Bond & J. Wen (formerly *Altingia yunnanensis* Rehder & Wilson) in that they have sub-globose or ovoid (elongate) head shapes and a low fruit number per infructescence, whereas infructescences of other extant *Liquidambar* species differ in their large numbers (up to 40) of fruits per head. These three extant species, previously considered within the genus *Altingia*, are also characterized by relatively short deciduous styles often represented on mature infructescences only by style bases (Ickert-Bond *et al.* 2007), as in *L. ovoidea*. In contrast, in *Liquidambar s.s.* styles are elongate, curved, with broad stigmatic surfaces that are sclerified on mature infructescences (Ickert-Bond *et al.* 2005). The cells of the outer fruit wall in *L. ovoidea* are polygonal, whereas they are elongate with oblique end walls in the various species of *Liquidambar s.s.* (Ickert-Bond *et al.* 2005). While extrafloral structures of most species of *Liquidambar s.s.* are spine-like, those of *Altingia* are typically non-spiny, mammilate or knoblike (Ickert-Bond *et al.* 2005), similar to the extrafloral structures of *L. ovoidea*. It should be noted that spine-like extrafloral processes are also lacking in two extant species of *Liquidambar s.s.*: *L. styraciflua* and *L. orientalis* (Ickert-Bond *et al.* 2005), which share morphologically similar leaves with the new fossil species *L. hainanensis*. However, in contrast to *L. ovoidea*, extant species *L. styraciflua* and *L. orientalis* possess a larger number of fruits per head: *c.* 37 and *c.* 48 bilocular fruits, respectively (Ickert-Bond *et al.* 2005).

The earliest reproductive structures assigned to Altingiaceae are known from the upper Turonian of New Jersey, USA (Zhou *et al.* 2001; Lai *et al.* 2021) and the lower Coniacian of Vancouver Island, British Columbia, Canada (Scharfstein *et al.* 2020). Capitate infructescences of *Liquidambar ovoidea* differ from pistillate inflorescences of *Microaltingia* Zhou, Crepet & Nixon from the Turonian of New Jersey and infructescences of *Paleoaltingia* Y.J. Lai, Gandolfo, Crepet & Nixon from the same deposits in their much larger size (up to 16 × 18.5 mm in *L. ovoidea* vs 7 mm in diameter in *Microaltingia* and up to 3 mm in diameter in *Paleoaltingia*), but are comparable to these Cretaceous reproductive structures in the number of florets or fruitlets (12–16 in *L. ovoidea* vs 8–12 in *Microaltingia* and 10–15 in *Paleoaltingia*). Moreover, *Microaltingia* differs from other known fossil and extant Altingiaceae in having up to three whorls of sterile phyllomes around the gynoecium and in producing tricolpate, perprolate and small (9–10 μm) pollen grains. Conversely, infructescences of *L. ovoidea* are rather similar to those of *Protoaltingia* Scharfstein, Stockey & Rothwell from the Coniacian of British Columbia in size (up to 16 × 18.5 mm in *L. ovoidea* vs *c.* 10 mm in *Protoaltingia*), however, the number of bilocular fruits per infructescence is almost half that seen in fruiting heads of *Protoaltingia* (12–16 in *L. ovoidea* vs *c.* 24 in *Protoaltingia*). Additionally, *L. ovoidea* possesses non-spiny extrafloral structures similar to those in the Turonian–Coniacian genera of Altingiaceae.

As compared with Cenozoic infructescences of Altingiaceae, *L. ovoidea* heads are morphologically very similar to those associated with leaves of the Eocene *L. maomingensis* from the Maoming Basin, South China (Maslova *et al.* 2015). They resemble each other by having the same size of heads, bilocular fruits, and a prominent rim of extrafloral structures dividing adjacent fruits. However, the infructescences from the Changchang Basin differ in having a larger number of fruits per head (12–16 in *L. ovoidea* vs ≤10 in *L. maomingensis*), an ovoid head shape, slightly smaller sizes of individual fruits, and an almost complete lack of visible style fragments. Very small persistent styles are known in *L. changii* Pigg, Ickert-Bond & Wen from the Middle Miocene of Yakima Canyon, Washington, USA (Pigg *et al.* 2004), whereas other fossil *Liquidambar*-like infructescences have relatively long persistent styles. The Eocene genus *Steinhauera* C. Presl, which has capitate infructescences, 1.8–3.0 cm in diameter with bilocular fruits lacking persistent styles, was suggested to be related to members of Altingiaceae (Kirchheimer 1943; Mai 1968), but its assignment to this family has been questioned for a long time (Pigg *et al.* 2004). Recently, micro-computed tomography scanning showed that the affinity of a globose head from the Eocene of western France aligns clearly with the Altingiaceae. This fossil infructescence assigned to *Steinhauera* consists of an aggregation of paired locules (Strullu-Derrien *et al.* 2022).

Dispersed pantoporate pollen grains

Investigation of the palynomorph assemblages from the Changchang Formation found pantoporate pollen types (with *c.* 16–18 pores), which may be affiliated with *Liquidambar*. These pollen grains are circular to elliptical in outline, and of medium size with dimensions ranging from 20.3 × 21.9 μm to 32.3 × 35.5 μm. The exine is regularly perforate to foveolate and covered with more-or-less

regularly distributed supratectal micro-echini. The tectum surface often has fine fossulae connecting the perforations, eventually mimicking a 'crotonoid' pattern. The pores are elliptical to circular in shape and generally have smooth margins, and are rarely irregular or cracked. The pore membranes are either covered with densely or loosely arranged angular micro-verrucae, covered with micro-echini or sometimes lost (Fig. 10). Using the SEM, it is easy to distinguish *Liquidambar* pollen from other panto-porate pollen such as the much smaller *Plantago* grains with few circular pores, the much smaller Chenopodiaceae grains with much smaller and more abundant pores, and Caryophyllaceae grains with much larger pores in relation to pollen size and echinate pore membranes. *Juglans* grains have annulate pores and regular micro-echini, but lack fossulae and perforations.

As is already known (Chang 1958, 1959, 1964; Kupria-nova 1960; Ickert-Bond *et al.* 2007), pollen morphology appears approximately uniform throughout *Liquidambar*. Extant *Liquidambar* species are distinguished by the pore shape (circular or elliptical), the type of pore margin (smooth or irregular), and the character of the pore membrane ornamentation (size and shape of micro-verrucae). The pollen grains of *L. orientalis* have elliptical pores with smooth margins; the pores of *L. styraciflua*

pollen grains are circular and have irregular margins with numerous small cracks, and the pollen grains of *L. formosana* have round pores with smooth margins (Kuprianova 1960). These morphological features may vary in some extant species (Chang 1958; Bogle & Phil-brick 1980). Thus, Chang (1958) identified two types of pollen grains in *L. formosana*. One grain type has pores with smooth margins whereas the other type is character-ized by pores with irregular margins bearing numerous small cracks. Plants with the first pollen type grow in Southern China (Guangdong and Hainan provinces), and the second pollen type is common in plants growing in Japan and Central China. Based on pollen morphology, Chang (1958) considered *L. formosana* an intermediate species between *L. orientalis* and *L. styraciflua*. Variability of pollen morphology was also observed in different populations of *L. styraciflua*. Plants from New Jersey were characterized by pollen grains with elongated (elliptical) pores resembling the pollen of *L. orientalis* (Kuprianova 1960).

Overall, studied pollen grains from the Changchang Basin are closely related to those of extant *L. orientalis*. Fossil pollen grains similar to those of *L. orientalis* were also described from the lower Oligocene of Karsakpai in western Kazakhstan (Kuprianova 1960). The
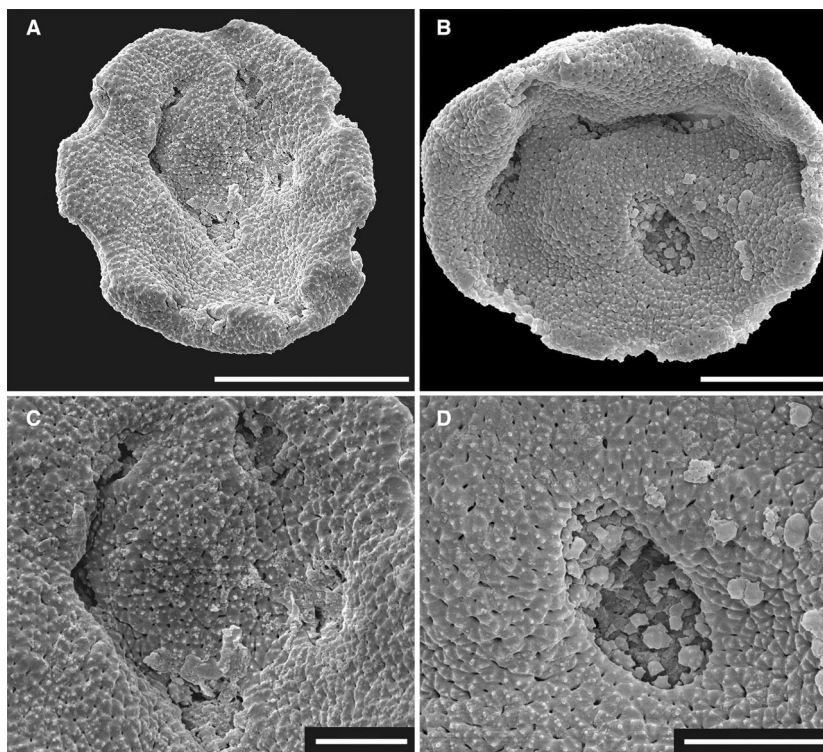

FIG. 10. Dispersed pantoporate pollen grains associated with leaves of *Liquidambar hainanensis* sp. nov., IPUW 7836_Hai_Liqu. Scale bars represent: 20 μm (A); 10 μm (B); 5 μm (C, D).

palynomorph assemblage from Karsakpai has some taxonomic similarity to the palynoflora from the Changchang Basin, sharing a number of common subtropical and tropical taxa, including representatives of Lauraceae, Fagaceae (mostly evergreen oaks), Altingiaceae, Myricaceae and Sterculiaceae (Kuprianova 1960; Spicer *et al.* 2014, Hofmann *et al.* 2019).

Our data support the idea of Kryshtofovich *et al.* (1956) that the appearance of the *L. orientalis*-type pollen was ancient. Both Asian and North American extant *Liquidambar* species show the same pattern of pollen morphological variability as plants from the Changchang Basin, which produced the pollen reported here.

Palaeoenvironmental conditions

Extant *Liquidambar* species are a common component of broad-leaved forests occupying mainly middle–low altitude areas with humid temperate, subtropical and tropical climates. Similar warm and wet climate conditions were inferred for late Eocene and Miocene *Liquidambar* species from South China (Maslova *et al.* 2015, 2019; Dong *et al.* 2018). Quantitative palaeoclimate estimates obtained using a CLAMP analysis (Yang *et al.* 2011) indicate a subtropical to tropical temperature regime for the Changchang flora (Spicer *et al.* 2014, 2017). The Changchang flora mean annual temperature (MAT) was estimated to have been 21.3°C with an uncertainty of ±4.7°C (2 SD), and a growing season precipitation of 2020 mm ± 122 mm (2 SD). Overall, the climate was humid, and the length of the plant growing season was nearly 12 months.

Significance for plant taxonomy, phylogeny and phytogeography

Traditionally, the family Altingiaceae has been considered to consist of three genera: *Liquidambar* with four species, *Altingia* with eight species, and *Semiliquidambar* with three species. Early morphological research suggested the possibility of combining *Altingia* and *Liquidambar* (the genus *Semiliquidambar* was established later) into one genus (Blume 1828; Lindley 1836; Oken 1841; Bentham & Hooker 1865). Later, this idea was explored using cladistic analysis of morphological and molecular data and has received significant support in a number of studies (Shi *et al.* 2001; Ickert-Bond *et al.* 2005, 2007; Ickert-Bond & Wen 2006). Recently, *Altingia*, *Liquidambar* and *Semiliquidambar* were combined into one genus, *Liquidambar* with 15 species, based on analysis of fruit anatomy, pollen morphology and molecular data (Ickert-Bond & Wen 2013), but the discussion regarding this taxonomic

decision is still ongoing. Morphological phylogenetic studies combining extant and fossil species provide grounds to recognize *Altingia* and *Liquidambar* as separate sister clades (Scharfstein *et al.* 2020).

Several current lines of research provide palaeobotanical evidence that justifies the combining of *Altingia*, *Semiliquidambar* and *Liquidambar* into a single genus, *Liquidambar*. Leaves of *L. maomingensis* described from the Eocene Huangniuling Formation of the Maoming Basin, Guangdong Province, South China are similar to those of extant species previously considered within the genera *Liquidambar s.s.* and former *Altingia* and *Semiliquidambar*, while the associated fossil infructescences are close to those of former *Altingia* (Maslova *et al.* 2015). Additionally, the combination of leaf morphological features characteristic of *Liquidambar s.s.* and former *Semiliquidambar* were observed in *L. bella* from the stratigraphically lower beds of the Huangniuling Formation (Maslova *et al.* 2019). The co-occurrence of *L. hainanensis* leaves, associated infructescences of *L. ovoidea* and *ex situ Liquidambar* pollen provide additional data on the diversity of Palaeogene *Liquidambar* species, which share this combination of morphological features with extant species formerly treated within *Semiliquidambar* and *Altingia* as well as *Liquidambar s.s.* Moreover, a new species of altingioid wood, *Altingioxylon hainanensis* Oskolski & Jin, described earlier from the Changchang Formation is close to extant species previously assigned to former genera *Altingia* and *Semiliquidambar*, in part due to its possession of prismatic crystals in ray cells (Oskolski *et al.* 2012).

Leaves of *Liquidambar hainanensis* and associated reproductive structures of *L. ovoidea* are also important for understanding the evolutionary history and diversification of the genus. Based on the whole plant concept proposed by Kvaček (2008), we assume that leaves and reproductive structures studied and reported here probably belong to the same plants. *Liquidambar hainanensis* is most closely related to extant *L. orientalis* from western Asia in terms of their distinctive leaf morphology (possessing oblong narrow lobes with parallel, or narrowing towards the base, margins) and pollen (with elliptical pores). In turn, *L. orientalis* is very similar in leaf morphology to *L. styraciflua* from North America, which may suggest their conspecific status (Ferguson 1989) despite the high level of molecular divergence (Wen 1998, 1999, 2001). Based on the leaf similarity of Eocene *L. hainanensis* and extant *L. orientalis* and *L. styraciflua*, we assume that the morphological characters of these types of leaves were formed as late as the middle–late Eocene and remained essentially invariable to the present time. This demonstrates leaf morphological stasis along with only minor morphological variations. Infructescences of *L. ovoidea* are similar to those

of extant *Liquidambar* species previously considered within former genus *Altingia*, whereas infructescences of *L. orientalis* and *L. styraciflua* differ from those of former *Altingia* in morphology (Ickert-Bond *et al.* 2005, 2007). The association of one type of *Liquidambar* leaves with morphologically different reproductive structures may indicate a greater evolutionary conservatism of leaves compared with more labile reproductive structures. A similar pattern was shown earlier for fossil *Platanus*-like leaves and associated infructescences and inflorescences (Maslova 2008, 2010).

The biogeographic history of Altingiaceae is complex. Hoey & Parks (1994) have speculated that western Asian *L. orientalis* and North American *L. styraciflua* appear to be the most closely related intercontinental species, providing evidence for the North Atlantic Land Bridge as late as the Miocene. Based on isozyme (Hoey & Parks 1994) and molecular (Ickert-Bond *et al.* 2007) studies, these two species diverged in the Middle Miocene. On the basis of molecular genetic analysis, Bobrov *et al.* (2020) showed that two clades are clearly distinguishable within Altingiaceae: a 'western' clade (North American *L. styraciflua* and *L. macrophylla* Oerst. and western Asian *L. orientalis*) and an 'eastern' clade (all other species of this family). Tiffney & Manchester (2001) suggested that *L. orientalis* may have diverged from relatives of *L. styraciflua* prior to the disruption of the North Atlantic Land Bridge. A difference between *L. changii* from the Middle Miocene of North America and extant North American *L. styraciflua* and other species, and the close relationship of *L. changii* with the eastern Asian extant species *L. acalycina* are considered by Pigg *et al.* (2004) as evidence of *Liquidambar* migration across the Bering Land Bridge. A close resemblance of the wood anatomy of Eocene *Altingioxylon hainanensis* and Miocene–Pliocene *Altingia hisauchii* (Watari) Wheeler, Baas & Lee from eastern Asia and *Liquidambar* sp. from the Middle Miocene of Washington, USA provides an additional indication of the Beringian biogeographic connection between eastern Asia and western North America (Oskolski *et al.* 2012).

As hypothesized previously (Maslova *et al.* 2019), South China may have been a centre of *Liquidambar* speciation during the Eocene. Our data provide evidence of the occurrence of an ancestral polymorphic group of *Liquidambar* species (*L. maomingensis* with associated capitate infructescences, *L. bella*, *L. hainanensis* and *L. ovoidea*) during the Eocene in South China (including Hainan Island). It seems plausible that a hypothetical plant with *L. hainanensis* leaves and *L. ovoidea* infructescences could have been a common ancestor of the similar extant species *L. orientalis* and *L. styraciflua*, the separation of which arose from different dispersal routes. Phylogenetic analyses of molecular data indicate that North American *L. styraciflua* and western Asian *L. orientalis*

form a monophyletic group, which is sister to a clade that includes all of the Asian extant species in the Altingiaceae (Shi *et al.* 2001). Ancestral individuals of *L. orientalis* may have dispersed westward to western Asia and Europe through central Asia, whereas those of North American *L. styraciflua* may have migrated from South China to North America via the Bering Land Bridge. *Liquidambar kazachstanica* from the upper Eocene of Eastern Kazakhstan that is very similar to *L. orientalis* in leaf morphology (Romanova 1971), and dispersed *Liquidambar* pollen with oblong pores from the lower Oligocene of western Kazakhstan (Kuprianova 1960) are indirect evidence that supports this assumption. Furthermore, *L. yabei* from the Upper Miocene of Japan with leaves deeply dissected into three narrow lobes (Huzioka 1974) and *L. pachyphyllum* from the upper Eocene Lyukama Formation (Eastern Sakhalin) (Maslova 1995, 2003), the Miocene Mascall Formation (Oregon, western coast of North America) (Knowlton 1902), and the Miocene Seldovia Point flora (Alaska, North America) (Wolfe & Tanai 1980) possessing leaves with five narrow lobes, are similar to the extant North American *L. styraciflua*. Wolfe & Tanai (1980) suggested that *L. pachyphyllum* and *L. styraciflua* may belong to lineages that were derived from a common ancestor in the Palaeogene.

Fossil species similar to the extant Asian species *L. formosana* are known in East Asia since the Eocene. In Japan, leaves and infructescences of *L. protoformosana* Endo var. *eocenica* Endo were described from the Eocene of Hokkaido (Endo 1968), three-lobed leaves of *L. cordata* (K. Suzuki) Uemura were reported from the Lower Miocene and Pliocene of Honshu (Uemura 1983), and some fossil leaves have been assigned to *L. formosana* (Matsuo 1970). The infructescences and associated leaves of *L. fujianensis* J.L. Dong & B.N. Sun that are closely related to those of *L. formosana* have also been described from the Middle Miocene of southeastern China (Dong *et al.* 2018). Numerous leaves from the Neogene of East Asia, similar to those of *L. formosana*, have been assigned to *L. miosinica* (Hu & Chaney 1940; Tanai & Suzuki 1965; Ishida 1970; Onoe 1974; Ozaki 1991; Ina *et al.* 2007). Overall, Tanai (1967, 1970, 1976) proposed that all *Liquidambar* species from the Palaeogene and Neogene of East Asia be assigned to the single species *L. miosinica*. To date, the range of *L. formosana* is restricted to China, Laos and Vietnam (Ickert-Bond & Wen 2013).

Currently, the highest number of naturally growing species of *Liquidambar* exists in South China. Apparently, the diversification of a Chinese ancestral group of *Liquidambar* species was facilitated in the Eocene by an availability of diverse habitats in temperate, subtropical and tropical regions (Maslova *et al.* 2019) and seasonal climate variations (Herman *et al.* 2017; Spicer 2017; Spicer *et al.* 2017).

CONCLUSION

Liquidambar from the middle–upper Eocene of the Changchang Basin on Hainan Island comprises leaves assigned to the new species *L. hainanensis*, which are morphologically close to those of extant species previously considered within *Liquidambar s.s.* and former *Semiliquidambar*, as well as associated infructescences of *L. ovoidea* similar to those of former *Altingia*, and *ex situ* pollen grains that closely resemble those of *L. orientalis*. These fossils provide palaeobotanical evidence justifying the integration of three genera, *Liquidambar s.s.* and former *Altingia* and *Semiliquidambar*, into a single genus, *Liquidambar*. A polymorphic group of *Liquidambar* species (Maslova *et al*. 2015, 2019, this paper) that evolved during the Eocene in South China gave rise to the extant species that are widely distributed in China, as well as to specific diversity of this genus in the modern floras of North America and the Mediterranean region. Our results support the importance of both the North Atlantic Land Bridge and the Bering Land Bridge for the dispersal of *Liquidambar*. This genus is a useful model for studying the evolution of species that are closely related but which form allopatric populations. The evolutionary history and diversification of species within *Liquidambar* seem to result from complex processes such as migration, speciation and extinction, accompanied by a degree of morphological stasis. Further analysis of fossil (with special emphasis on Late Cretaceous fossils) and extant members of Altingiaceae from eastern Asia, Europe and North America would be of a great interest for understanding the evolution of this family and biogeographic history of the northern hemisphere. In particular, a comprehensive search for such fossil taxa in the Cenozoic sediments of northeastern Russia and Alaska is needed to confidently document migrations via the Bearing Land Bridge.

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