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A new species of *Liquidambar* (Altingiaceae) from the late Eocene of South China

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Abstract
A new fossil leaf species, *Liquidambar bella* (Altingiaceae), is described from the lower part of the Eocene Huangniuling Formation, Maoming Basin, South China. Suprabasal venation in the fossil lobed *Liquidambar* leaves is reported for the first time. The new species provides additional palaeobotanical evidence on the morphological variability of this genus supporting the idea of combining the genera *Liquidambar, Semiliquidambar* and *Altingia* into the single genus *Liquidambar* as proposed based on molecular markers.

Keywords Altingiaceae · Eocene · Huangniuling Formation · *Liquidambar* · Maoming Basin · South China

Introduction

Extant species of the genus *Liquidambar* L. (Altingiaceae) possess a disjunctive pan-continental natural distribution in eastern and western Asia, Europe and North and Central America (e.g., Wen 1998, 1999). Study of related fossil taxa, which can provide evidence about the diversification and evolutionary history of the genus, are therefore of particular interest. Fossils of Altingiaceae have been reported from the Cretaceous, Paleogene and Neogene of Asia, Europe and North America. The earliest fossil record of reproductive structures similar to those typical of this family is known from the upper Turonian (Zhou et al. 2001). Permineralized female reproductive structures unequivocally assigned to *Liquidambar* were described from the Miocene (Pigg et al. 2004). The first appearance of the *Liquidambar* foliar morphological type (Maslova 1995), wood of the Altingiaceae

type (Melchior 1998; Wheeler et al. 2010) and *Liquidambar* pollen grains (Graham 1965; Kuprianova 1960; Muller 1981) are dated as Paleocene. *Liquidambar*-type leaves are well represented in the Cenozoic of Asia (e.g., Dong et al. 2018; Endo and Morita 1932; Huzioka 1972; Huzioka and Uemura 1979; Maslova 1995, 2003; Maslova et al. 2015; Onoe 1974; Ozaki 1991; Suzuki 1961; Uemura 1983), Europe (e.g., Ferguson 1971, 1989; Koch et al. 1973; Martinetto 1998; Worobiec et al. 2012), and North America (e.g., Brown 1933; Knowlton 1902; MacGinitie 1941; Smiley et al. 1975; Stults and Axsmith 2011; Wolfe and Tanai 1980).

In China, several fossil occurrences of *Liquidambar* have been recognized based on leaves and/or reproductive structures: Eocene *L. maomingensis* N. Maslova, Kodrul, Song et Jin from the Huangniuling Formation, Guangdong Province (Maslova et al. 2015) and two Miocene species *L. miosinica* Hu et Chaney from the Shanwang Formation in Shandong Province (Hu and Chaney 1940) and the Shengxian Formation in Zhejiang Province (Xiao et al. 2011, 2013, 2015) as well as *L. fujianensis* J.L. Dong et B.N. Sun from the Fotan Group in Fujian Province (Dong et al. 2018). Apart from these, several Eocene fossil leaves have been ascribed to genus level only (Dalianhe Formation, Heilongjiang Province, He and Tao 1997; Huadian flora, Jilin Province; Manchester et al. 2005).

Taxonomic revision of the modern *Liquidambar* (Ickert-Bond and Wen 2013), adopting a broad circumscription of the genus and subsuming the previously recognized genera

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Altingia Noronha and *Semiliquidambar* H.-T. Chang, shows that the genus includes 15 species, 11 of which grow in China. They are: *L. acalycina* H. T. Chang (Anhui, Guangdong, Guangxi, Guizhou, Hubei, Hunan, Jiangsu, Jiangxi, Sichuan and Zhejiang provinces), *L. caudata* (H. T. Chang) Ickert-Bond et J. Wen (Fujian and Zhejiang provinces), *L. chinensis* Champ. (Guangdong, Guangxi, Guizhou, Hainan provinces and Hong Kong), *L. chingii* (Metcalf) Ickert-Bond et J. Wen (Fujian, Guangdong, Guangxi, Guizhou and Jiangxi provinces), *L. excelsa* (Noronha) Oken (Yunnan Province), *L. formosana* Hance (Anhui, Chongqing, Fujian, Gansu, Guangdong, Guangxi, Guizhou, Hainan, Hunan, Hubei, Jiangsu, Jiangxi, Shanxi, Sichuan, Zhejiang provinces, Taiwan and Hong Kong), *L. gracilipes* (Hemsl.) Ickert-Bond et J. Wen (Fujian, Guangdong, Zhejiang provinces and Hong Kong), *L. multinervis* (Cheng) Ickert-Bond et J. Wen (Guizhou Province), *L. obovata* (Merrill et Chun) Ickert-Bond et J. Wen (Hainan Province), *L. siamensis* (Craib) Ickert-Bond et J. Wen (Guangdong and Yunnan provinces), *L. yunnanensis* (Rehder et Wilson) Ickert-Bond et J. Wen (Yunnan Province) (Ickert-Bond and Wen 2013). Hence, China should be the place where the maximal number of naturally growing representatives of the *Liquidambar* occur today.

Here we introduce new species of *Liquidambar* from the Eocene Huangniuling Formation (Maoming Basin, Guangdong Province) with brief discussion on its palaeoecology and habitat conditions. These fossils are from stratigraphically lower beds than the previously described species, *L. maomingensis* which also occurs in the Huangniuling Formation. We demonstrate similarities in leaf form of the new species to the species of the former genus *Semiliquidambar*.

New finds of fossil *Liquidambar* species in China are therefore of an exceptional importance for a reconstructing the phylogeny of the genus, particularly in view of recent taxonomic changes (Ickert-Bond and Wen 2013).

Materials and methods

The plant fossils examined were collected in the Jintang opencast mine (21°42′50″N, 110°52′35″E) of the Maoming Basin located northwest of Maoming City in southwestern Guangdong Province, China (Fig. 1). The stratigraphic succession of this locality is composed of the Youganwo and Huangniuling formations. The Youganwo Formation consists of terrigenous coal-bearing deposits in its lower part and oil shales in the upper part. The overlying Huangniuling Formation is composed mainly of fluvial sandstones, siltstones, and conglomerates with extended lenses of mudstones. Details of the Jintang opencast mine section are given in Aleksandrova et al. (2015). The upper part of the Youganwo Formation has been dated as late Eocene on the basis of the vertebrate fossils (Averianov et al. 2017; Jin 2008). In a recent palynological study the Youganwo and Huangniuling formations are considered to be Lutetian-Bartonian and Priabonian in age, respectively (Aleksandrova et al. 2015). Therefore, the new species of *Liquidambar* is supposed to be of a late Eocene age.

About 145 fossil leaf impressions of the new species were recovered from a lens of mudstone in the lower part of the Huangniuling Formation (locality MMJ2-2) which is approximately 20 m below the occurrence of previously reported *Liquidambar maomingensis* from the Upper

Fig. 1 Outline map showing the fossil locality
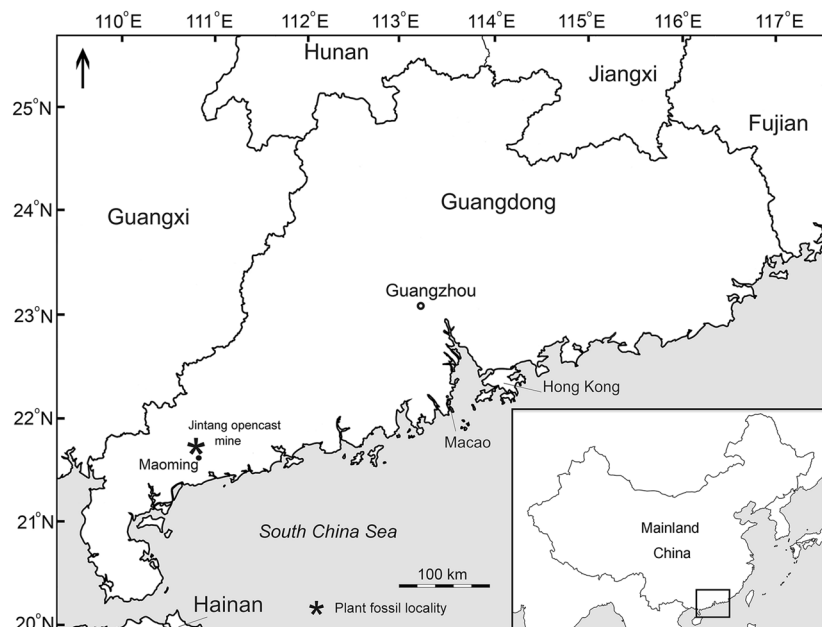
Huangniuling flora (Maslova et al. 2015). Plant megafossil assemblage of the Lower Huangniuling flora contains a few taxa of conifers (Pinaceae, Podocarpaceae) but is dominated by angiosperms of the Lauraceae, Fagaceae, Hamamelidaceae, Altingiaceae, Myrtaceae, Juglandaceae, Aceraceae, Dipterocarpaceae, Rhamnaceae, Fabaceae, and Celastraceae families. Fagaceae, along with Altingiaceae, are the most common components of this flora (Spicer et al. 2016, 2017).

The specimens are housed at the Museum of Biology of Sun Yat-sen University, Guangzhou, China. Images of the leaves were taken using digital cameras: an Olympus E-500 and a Panasonic GX7 with a Leica DG MacroElmarit 1:2.8/45 mm macro lens. For the leaf descriptions, we used terms from the Manual of Leaf Architecture (Ellis et al. 2009). The length to width (L/W) ratio of the lamina was calculated using the maximum lamina length and width. The L/W ratio for incompletely preserved leaves was calculated using the reconstructed lamina. Biotic damage types on the *Liquidambar* leaves were considered using the "Guide to Insect (and Other) Damage Types on Compressed Fossil Plants" (Labandeira et al. 2007).

Comparative material of extant *Liquidambar caudata* was obtained from the South China Botanical Garden, Guangzhou.

Systematics

Family: Altingiaceae Horan. 1841

Genus: *Liquidambar* L. 1753

Species: *Liquidambar bella* N. Maslova et Kodrul, sp. nov.

Holotype: MMJ2-2-161a-1, MMJ2-2-161b-1, designated here, a leaf part and counterpart (Fig. 2d, g).

Locality: northwest of Maoming City, southwestern Guangdong, Maoming Basin, China.

Geological horizon and age: lower part of the Huangniuling Formation, late Eocene.

Etymology: from *bellus* (lat.)—beautiful.

Repository: The Museum of Biology, Sun Yat-sen University, Guangzhou, P. R. China.

Diagnosis

Leaves simple, palmately three-lobed. Lamina symmetric or asymmetric with medial asymmetry and base asymmetry in insertion and/or width. Leaves serrate from the base. Teeth regularly spaced, small, concave/retroflexed, with more prominent basal side, sinus shape rounded, tooth apex glandular. Apices of lateral lobes directed upwards or horizontally; apex angle of lobes acute, apex shape straight or acuminate. Base angle of lamina obtuse or rarely acute, base shape rounded or truncate, rarely slightly cordate. Venation

suprabasal or basal actinodromous, with three primary veins; lateral primary veins straight or curved, extending outward or upward, often diverging from midvein suboppositely at various angles. Secondaries up to 6–10 pairs, alternate to subopposite, often irregular, semicraspedodromous or festooned semicraspedodromous, arching upward near the margin; branches from loops terminating in teeth; intersecondaries weak. Tertiary veins alternate percurrent to mixed opposite–alternate percurrent. Fourth order veins alternate percurrent.

Description

Leaves are simple, palmately three-lobed, with petioles. The longest preserved fragment of petiole is 20 mm. Leaves are symmetric or asymmetric with different depths of sinuses between the lobes (Figs. 2c, 4e, f) and medial asymmetry (Figs. 3a, 4e, f). Laminar bases are also symmetrical or asymmetrical in insertion and/or width (Figs. 3a, d, 4g). Insertion points of lamina base on either side of the petiole are occasionally separated by 1–2 mm (Figs. 3a, b, 4g). The lamina length varies from 37 to 80 mm, lamina width—from 19 to 140 mm. The length of the central lobe varies from 15 to 50 mm, width—from 10 to 28 mm. The shape of the central lobe is triangular (Figs. 2h, 4a, b, d, h) or frequently narrowly triangular (Figs. 2a–e, 3a, 4c), with nearly parallel margins at the lobe base (Figs. 2a, 3a, 4c) or narrowing towards the base (Figs. 2c, d, 3f). Lobe apices are acute (Figs. 3g, 4d, h) and frequently strongly acuminate (Figs. 2a, c, d, 4a, b). In some leaves lateral lobes extend obliquely upwards (Figs. 2a–e, 3a, d, g, 4c–h), reaching the length of the central lobe (Figs. 2c, d, 4d, g). In other leaves the lateral lobes extend obliquely upward and then curve to the horizontal direction (Fig. 3a, b). Length/width (L/W) ratio of the lamina varies from 0.60 to 2.07 (1.15 in average). Leaf base is rounded (Figs. 2a–e, g, 3d, g, 4c–h) or truncate (Figs. 2f, 3b, c), sometimes slightly cordate (Fig. 3e, f). Leaf margin is serrate from the leaf base (Fig. 2a–h, 3a–g, 4c–h). Marginal teeth vary in shape and size (Fig. 5a, b, d, e). Teeth are regularly spaced, small, appressed, concave/retroflexed, with more prominent basal side. Tooth apices are glandular or sometimes without any pronounced glands (Fig. 2a, 3a, c, e, g,). Some larger teeth are beak-shaped (Figs. 2b, e, 4a, b, 5e). Sinuses between teeth are rounded. Venation is suprabasal or basal actinodromous, with three primaries. The midvein is straight. Lateral primary veins are equal in their thicknesses to the midvein, suboppositely diverging from the midvein at the angle between 20° and 50° (usually 40°) (Fig. 2f, 3a–d, 4e, f–h). Frequently they are slightly arch-shaped, curved outward or upward. More rarely the lateral primary veins are straight over the most part of their length, exceeding the length of a half of the lamina length, sometimes reaching the length of the central lobe (Fig. 2d). Secondary veins are
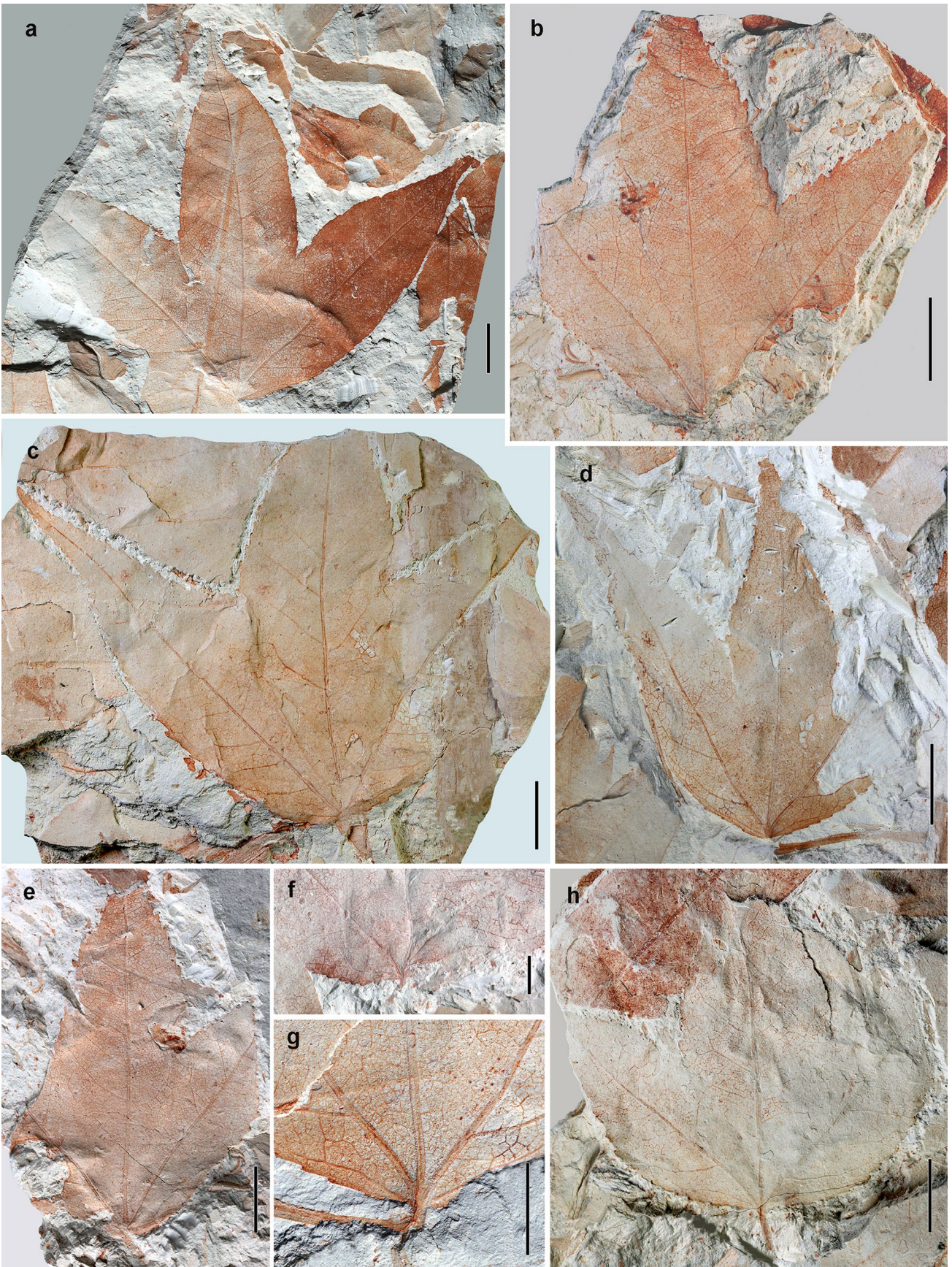
◄**Fig. 2** Three-lobed leaves of *Liquidambar bella* sp. nov. from the lower part of the Eocene Huangniuling Formation, Maoming Basin, Jintang opencast mine. Fossil leaves with lateral lobes oriented obliquely upward, reaching more than two-thirds of the lamina length (**a–e**). **a** Leaf with narrowly triangular lobes and acuminate apex of the central lobe. MMJ2-2-037a-1. **b, e** Leaf showing large marginal teeth with glandular apex. Note the margin feeding with a distinct reaction rim (DT14), MMJ2-2-114a, MMJ2-2-114b, part and counterpart, respectively (**b**, Maslova et al. 2018, Fig. 13D). **c** Leaf showing skeletonized areas with poorly developed reaction rims (DT16). MMJ2-2-011. **d, g** Holotype, part and counterpart, MMJ2-2-161b-1, MMJ2-2-161a-1, respectively. Note suprabasal actinodromous venation and on the leaf in **d** margin feeding (DT13) and skeletonization (DT16). **f** Truncate leaf base showing lateral primary veins, diverging from the midvein suboppositely. MMJ2-2-354-1. **h** Leaf with triangular central lobe and basal actinodromous venation. MMJ2-2-359. Scale bars are 10 mm in **a–e, h**, 5 mm in **f, g**

thin, consisting of 6–10 pairs, alternate to subopposite, often irregular, forming a series of loops along the leaf margin. Short branches diverge from the last order loops and terminate in the marginal teeth (festooned semicraspedodromous venation) (Fig. 2a, b, 4a, b, f, 5a, b, d). Intersecondary veins are weak (Fig. 5a). Tertiary veins are weakly percurrent, sinuous or random reticulate (Figs. 2a, b, 3g, 4a, b, f, 5a, c, d). Higher order venation is represented by a net consisting of square, rectangular and polygonal cells (Fig. 5a–d, f). Freely ending veinlets are mostly two branched (Fig. 5b, c).

Discussion

Morphological comparison

Liquidambar bella differs from all previously described fossil species of *Liquidambar*, first of all, in having leaves with suprabasal venation. Such suprabasal venation is known in extant species of *Liquidambar chingii* (previously attributed to *Semiliquidambar cathayensis* H. T. Chang) and *L. caudata* (previously belonged to *Semiliquidambar caudata* H. T. Chang) (Fig. 6). All other *Liquidambar* species with lobed laminae, both extant and fossil, have a basal origin of the lateral primary veins.

Three-lobed leaves of the recently described *L. maomingensis* from the Eocene of South China (Maslova et al. 2015) and *L. fujianensis* from the middle Miocene of Southeastern China (Dong et al. 2018) are most similar to the new species. *L. maomingensis*, however, is characterised by displaying a higher variability of leaf form: the species possesses three-lobed leaves together with forms with additional small lobes and even unlobed morphotypes. Apart from having three-lobed leaves with suprabasal venation, the new species differs from *L. maomingensis* in having smaller laminae: their length vary from 37 to 80 mm in *L. bella* and from 46 to 125 mm in *L. maomingensis*, their width – from 19 to 140 mm in *L. bella* and from 45 to 150 mm

in *L. maomingensis*. Also, the new species has smaller central lobes: in *L. bella* they are 15–50 mm in length and 10–28 mm in width, while in *L. maomingensis* – 22–75 mm in length and 14–35 mm in width. The average L/W ratio is higher in the new species (1.15) than in *L. maomingensis* (0.86), which means that in *L. bella*, unlike *L. maomingensis*, leaves where the length exceeds the width predominate. Other distinctive features of the new species are asymmetry of the lamina and leaf base, as well as a variable angle between the midvein and lateral primary veins.

A variable lamina shape is also a characteristic feature of *L. fujianensis*: three-lobed leaves predominate, but five-lobed and unlobed leaves are also present. Three-lobed leaves of this species differ from *L. bella* leaves in displaying a more variable angle between the lateral primary veins and the midvein. Moreover, the lateral lobes in *L. fujianensis* occupy a lower position, whereas in *L. bella* they extend upwards reaching the upper half of the lamina and sometimes even the apex of the central lobe. Besides, in *L. fujianensis* the lateral primary veins always diverge from the midvein basally. Unfortunately, Dong et al. (2018) did not provide measurements of this species, which makes comparison with *L. bella* difficult.

Sun and shade leaves of *Liquidambar bella*

Recently, we released a study of morphological and epidermal character variability for distinguishing shade and sun leaves in two extant species of *Liquidambar* with different lamina types, unlobed with pinnate venation in *L. chinensis* and palmately lobate with actinodromous venation in *L. formosana* (Maslova et al. 2018). We focused on those leaf characters that are often available for study in fossil material. Such features include L/W ratio, the degree of development of venation networks, tooth size and shape, size of epidermal ordinary cells, and their anticlinal wall outlines. Shade leaves are narrower in comparison to sun leaves, having a finer leaf texture, less pronounced venation and smaller marginal teeth, whereas sun leaves in general have more extended lobe tips, a coarser texture, a prominent venation and larger teeth. Shade leaves differ from sun leaves in possessing sinuous anticlinal walls of ordinary epidermal cells (especially on the upper lamina surface) and relatively larger ordinary cells on both lamina surfaces. Earlier, by analogy with leaf morphology of extant *L. formosana*, fossil leaves of *L. maomingensis* from the Eocene of southern China, preserved only as impressions, were categorized into sun and shade morphotypes (Maslova et al. 2015).

Our collection of *L. bella* fossil leaves is also representative enough to distinguish sun and shade morphotypes. Leaves with a minimal L/W ratio of 0.60 are characterised by more prominent secondary and tertiary veins, more dissected laminae with deeper sinuses between lobes and
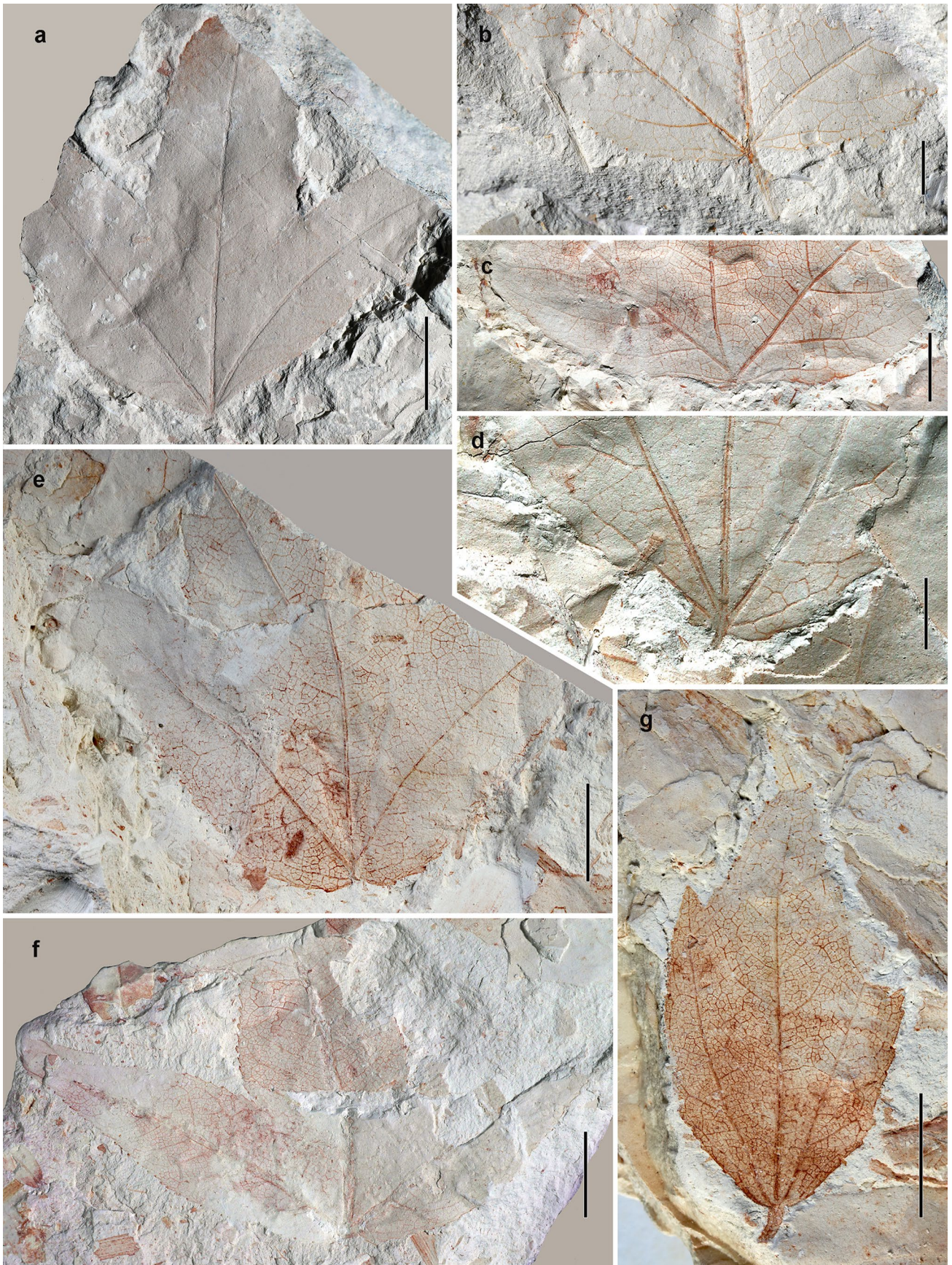
◄**Fig. 3** Fossil leaves of *Liquidambar bella* sp. nov. from the lower part of the Eocene Huangniuling Formation, Maoming Basin, Jintang opencast mine. **a** Leaf showing asymmetrical width of lamina base and nearly parallel lobe edges at the base. MMJ2-2-135-1. Leaf bases showing lateral primary veins, diverging from the midvein subopposi-tely (**b**–**d**). **b** Truncate leaf base with slightly asymmetrical lamina insertion. MMJ2-2-027-2. **c** Truncate leaf base. MMJ2-2-221-1. **d** Rounded leaf base showing asymmetrical width. MMJ2-2-333-4. **e** Leaf showing slightly cordate base and suprabasal venation with lat-eral veins diverging suboppositely. MMJ-2-2-031. **f** Leaf with slightly cordate base and lateral lobes arching downwards. MMJ2-2-391-1. **g** Leaf with small lateral lobes and acuminate apex. MMJ2-2-029a (Maslova et al. 2018, Fig. 13B). Scale bars are 10 mm in **a, c, e**–**g**, 5 mm in **b, d**

relatively larger marginal teeth (Figs. 2b, e, 3a). This leaf morphotype we interpret to have been sun leaves. On the other hand, leaves with a maximal L/W ratio of 2.07 possess poorly developed and less prominent venation, less dissected laminae and small appressed teeth (Figs. 3g, 4e) and are likely to have been shade leaves. It should be noted that the complete sets of the features mentioned above are character-istic only for typical sun (growing in the crown periphery) and shade (located in the very inner parts of a tree crown) leaf morphotypes. Between these extreme morphotypes there are transitional forms belonging to leaves growing in the middle part of a tree crown. Among these transitional forms leaf morphotypes in which leaf length exceeds leaf width predominate; this feature also distinguishes the new species from *L. maomingensis*.

Fossil *Liquidambar* species in Asia

Most Asian fossil *Liquidambar* species described in the mid-dle of the last century used very limited fossil leaf mate-rial and without any analysis of intraspecific variability. We therefore believe that a large number of these fossil species will require reappraisal of the diagnostic value of individual morphological features. Tanai (1967, 1970, 1976) attempted to merge several Asian species into one *L. miosinica* due to their small differences and general similarity with the extant *L. formosana*. *Liquidambar miosinica*, which includes both three-lobed and five-lobed leaves, has been described from the Paleogene (Eocene) and Neogene of Japan (e.g., Matsuo 1970; Ozaki 1991; Tanai 1967, 1970, 1976), China (e.g., Hu and Chaney 1940), Korea (e.g., Ablaev et al. 1990; Huzioka 1972) and the Russian Far East (e.g., Ablaev 1974, 1978; Maslova 1995). The new species differs from *L. miosinica* in lacking five-lobed leaves and in having forms with supra-basal venation.

Matsuo (1970) attributed leaves from the Oligocene Sakito Flora (Japan) to the extant species *L. formosana* because he did not find any macromorphological differences between their leaves. We, however, believe that it is incor-rect to name fossil leaves as an extant species if there is

no information on reproductive structures belonging to the same plant as the fossil leaves. Also, in the Cenozoic floras of Japan the following species were identified: *L. cordata* (K. Suzuki) Uemura (Uemura 1983), *L. protoformosana* Endo var. *eocenica* Endo (Endo 1968), *L. protopalmata* (K. Suzuki) Uemura (Uemura 1983), *L. yabei* (Morita) Huzioka (Huzioka 1974). Among them, *L. protopalmata*, unlike all other species including *L. bella*, has a large number of lobes (5–7), and *L. yabei* possesses a strongly dissected lamina and narrow lobes with almost parallel margins. All other fea-tures (a lobed lamina, basal type of the lateral primary veins divergence, semicraspedodromous venation, and marginal teeth morphology) are common for all previously described Asian fossil species and fit the variability of the extant *L. formosana*.

Palaeoecological and palaeoclimatic conditions

Natural populations of extant *Liquidambar* species exist in humid warm temperate, subtropical and tropical climates and are mainly distributed in middle-low latitude areas. They are a common component of broad-leaved evergreen forests and grow at an elevation up to 1500 m.

Fossil *Liquidambar* species are inferred to have inhabited areas with warm and wet climatic conditions as well (Dong et al. 2018; Maslova et al. 2015). The use of the new *Liquidambar* species alone for the palaeoclimate reconstruction is limited. Earlier, we estimated the palaeoclimate variables using the CLAMP (Climate Leaf Analysis Multivariate Pro-gram: Wolfe 1993; Yang et al. 2011; http://clamp.ibcas.ac.cn/) technique based on 46 woody dicot leaf morphotypes (species) of the Lower Huangniuling flora (Spicer et al. 2016, 2017). Our data showed that this flora experienced a humid subtropical climate with hot summers, warm winters and relatively low seasonal rainfall variations (climate Cfa according to the Köppen's classification of global climates: Köppen 1936; Peel et al. 2007).

A progressive warming and increase in climate season-ality over the middle–late Eocene interval in South China (Spicer et al. 2017) could influence significantly interactions within plants and other organisms and affect the diversity and frequency of damage types (DTs) in the palaeofloras. A recent study (Kodrul et al. 2018) of the DTs in the Eocene *Liquidambar* taxa from the Maoming and Changchang basins revealed that most of them could be assigned to arthropod functional feeding groups. The fossil leaves of these taxa exhibit mostly external foliage feeding, which includes margin feeding, skeletonization, and hole feeding. Skeletonization and margin feeding are two dominating types of arthropod damage in *L. bella*. Skeletonized areas are usually exemplified by large or small polygonal patches of completely or partly removed interveinal tissue, with or without reaction rims (Figs. 2c, d, 4e, g, 5d). Margin feeding
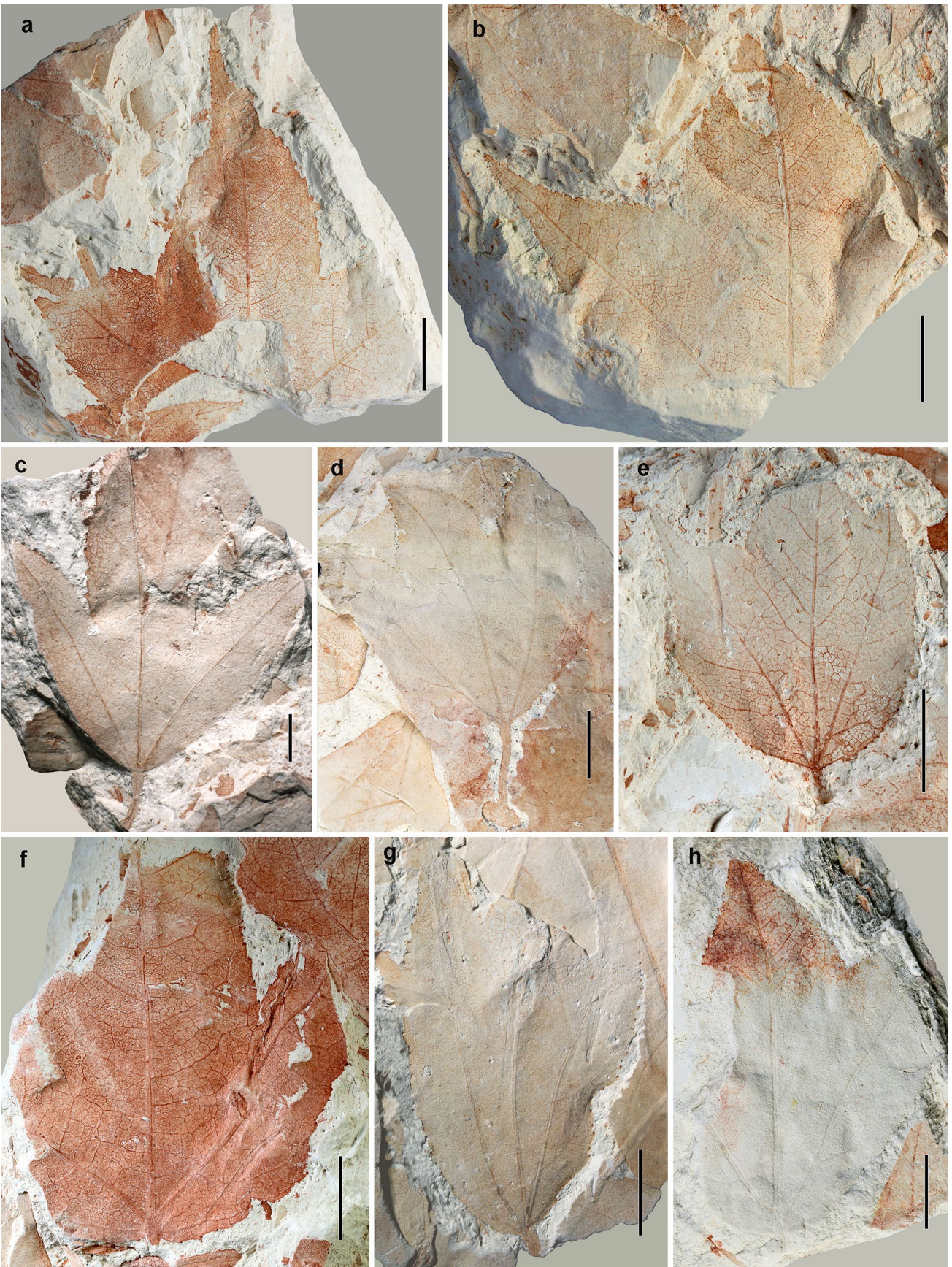
◀**Fig. 4** Fossil leaves of *Liquidambar bella* sp. nov. from the lower part of the Eocene Huangniuling Formation, Maoming Basin, Jintang opencast mine. **a, b** Leaves with triangular lobes and acuminate apices. MMJ2-2-173b, MMJ2-2-342-3, respectively. **c** Small leaf showing narrowly triangular lobes with nearly parallel lobe edges at the base. MMJ2-2-358. **d** Leaf showing triangular lobes with acute apices and shallow sinuses. MMJ2-2-378-2. **e** Leaf with asymmetrical lamina and small lobes. Note the skeletonized areas with poorly developed reaction rims (DT16). MMJ2-2-045-3. **f** Leaf showing suprabasal venation and different depth of the sinuses between the lobes. MMJ2-2-013-1. **g** Narrow leaf with lateral lobes oriented sharply upward, asymmetrical lamina basal width, and lateral veins diverging suboppositely. MMJ2-2-374-1. **h** Leaf showing triangular lobes with acute apices, suprabasal venation and suboppositely diverging lateral veins. MMJ2-2-028. Scale bars are 10 mm in **a, b, d**–**h**, 5 mm in **c**

differs in morphology and size of leaf margin excisions, and could be caused by different arthropods (Figs. 2b, d, e, 3b, d, 4b). The proportion of arthropod endophytic feeding damage types (galls) is low (Fig. 5g, i). Only three fossil leaves of *L. bella* exhibit damage traces resembling a consequence of fungal activity (Fig. 5b, f, h).

Several recent studies of plant-insect interaction (Endara and Coley 2011; Lemoine et al. 2017) revealed a high herbivory level on early successional, fast-growing pioneer species that correspond well with the data obtained from our study. Some extant species of *Liquidambar* are generally dominants or companion species during early successional stages (Brewer 2001; Chen et al. 2017). Fossil *Liquidambar* species from the Maoming Basin may have possessed similar life-history strategies with the extant ones because early successional riparian forests are assumed to be widespread on the nutrient-rich alluvial soils during deposition of the Huangniuling Formation (Kodrul et al. 2018). Significant damages by leaf-chewing insects on both *L. bella* and *L. maomingensis* may support this assumption.

The systematic importance of *Liquidambar bella*

A recent study (Ickert-Bond and Wen 2013) significantly changed the classification of species within the Altingiaceae, by sinking *Semiliquidambar* and *Altingia* into *Liquidambar*. Before this publication, three extant genera *Liquidambar, Altingia* and *Semiliquidambar* were supposed to be the members of this family (e.g., Chase et al. 1993; Ickert-Bond et al. 2005, 2007; Li et al. 1999; Takhtajan 2009) or the members of the subfamily Altingioideae belonging to family Hamamelidaceae (e.g., Endress 1989a, b; Endress and Igersheim 1999; Fang and Fan 1993; Hoey and Parks 1994; Hufford and Crane 1989; Maslova 2010; Zhang and Lu 1995). Molecular-genetic study together with cladistic analysis of morphological features (Ickert-Bond et al. 2005, 2007; Ickert-Bond and Wen 2006; Shi et al. 2001) allowed Ickert-Bond and Wen (2013) to merge these three genera into one with a priority generic name *Liquidambar*. Also,

Ickert-Bond and Wen (2013) published a key for the species determination and taxonomic synopsis.

Morphological similarities and differences of the extant representatives of Altingiaceae are well-studied (e.g., Bogle 1986; Ickert-Bond et al. 2005, 2007). The plants of this family commonly have capitate infructescences with bicarpellate polyspermous fruits with styles of different length divided by sclerenchymatous tissue, and capitate staminate inflorescences with tetrasporangiate stamens and polyporate pollen. The former genera *Liquidambar, Altingia* and *Semiliquidambar* were well-differentiated by leaf morphology: *Liquidambar* possesses only palmately-lobed leaves with 3–7 lobes, *Altingia*—only unlobed leaves, and *Semiliquidambar*—both palmately-lobed and unlobed leaves.

The new species *L. bella* helps elucidate the history of Altingiaceae. This species combines a mosaic of leaf features characteristic of genera *Liquidambar* and former *Semiliquidambar*. Apart from having leaf morphology distinctive for these two taxa like lobed leaves, semicraspedodromous venation, intersecondary veins and characteristic marginal teeth, the new *Liquidambar* species possesses a suprabasal type of the lateral primary veins characteristic of former *Semiliquidambar* leaves only. At the same time the *Semiliquidambar* lobed leaf morphotype differs from that of *Liquidambar* in having less dissected laminae (*Semiliquidambar* leaves have small lobes without attenuate apices). The new species differs from former *Semiliquidambar* in having more dissected leaves and irregular suprabasal venation, as well as in the lack of unlobed laminae.

Earlier we examined the significance of fossil *L. maomingensis* for the systematics of the genus (Maslova et al. 2015). We showed that polymorphic leaves of this species, lobed and unlobed morphotypes of which are similar to those previously ascribed to the *Liquidambar, Altingia* and *Semiliquidambar*, and associated capitate infructescences similar to those of former *Altingia*, possibly belonged to a single plant species. Our study of two Eocene species from the Maoming Basin therefore provides palaeobotanical evidence for the merging of three extant genera *Liquidambar, Altingia* and *Semiliquidambar* into one.

In the geological past a group of polymorphic *Liquidambar* species existed in South China. Although taxonomical diversity of the *Liquidambar* fossil species so far identified in this region is not considerable (*L. miosinica, L. fujianensis, L. maomingensis*, and *L. bella*), significant variety of morphological characters of leaves and associated reproductive structures are recorded for these species. We hypothesize that there was a center of *Liquidambar* speciation in South China during the Eocene. *L. bella* and *L. maomingensis* probably gave rise to the extant species *L. caudata* which is widespread in China and *L. formosana* which is a typical resident of modern floras of Central and South China as well as several other regions in East Asia. A revision of
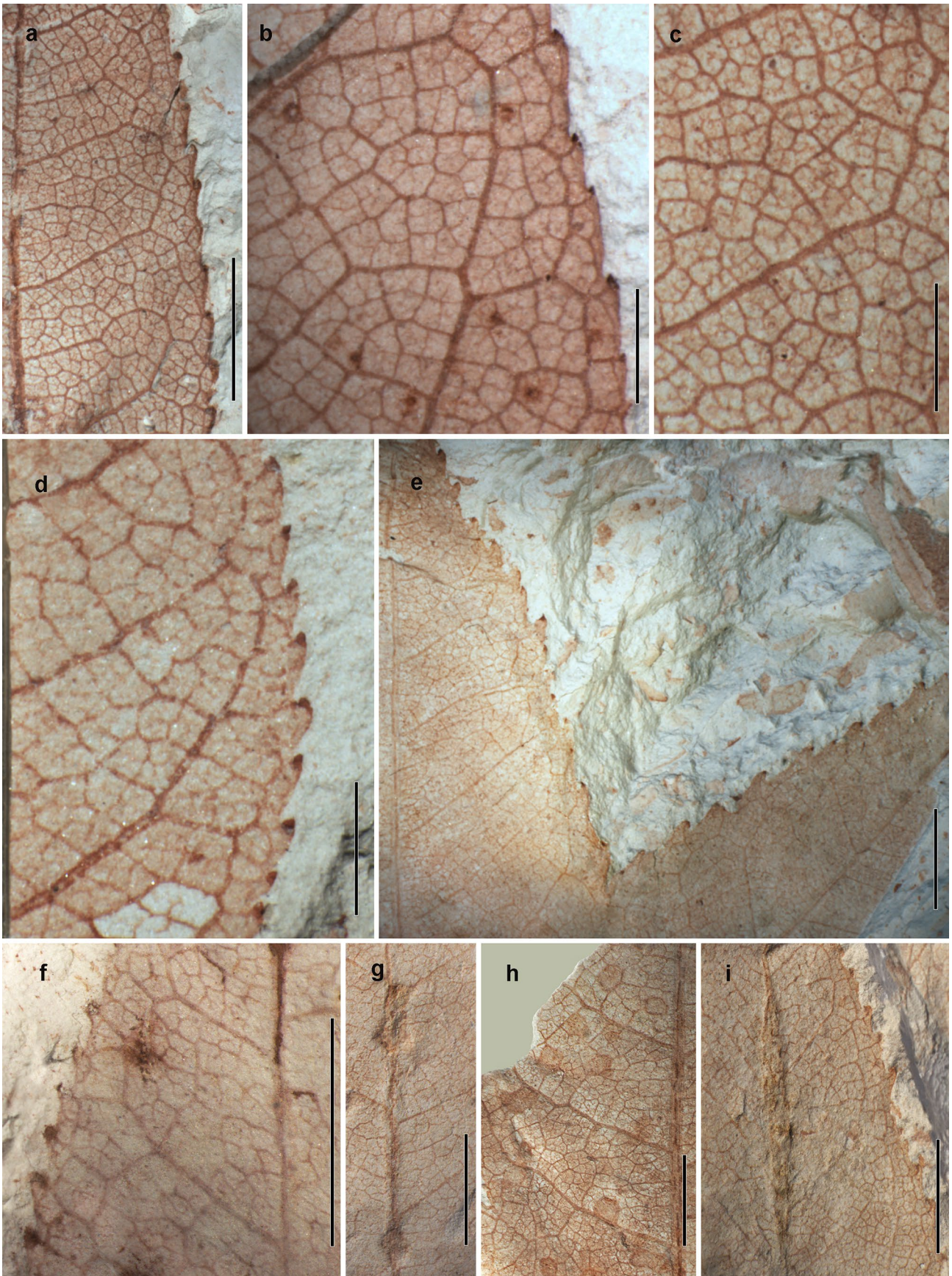
◄**Fig. 5** Venation patterns and teeth characters of fossil leaves of *Liquidambar bella* sp. nov. from the lower part of the Eocene Huangniuling Formation, Maoming Basin, Jintang opencast mine. **a** Venation pattern of leaf lateral lobe. Note the relatively small teeth with nonspecific apices. MMJ2-2-030. **b** Detail of marginal venation and teeth characters of leaf lateral lobe. Note small rounded damage probably caused by fungi. MMJ2-2-034a-1. **c** Detail of tertiary and higher-order leaf venation. MMJ2-2-030. **d** Venation of leaf lateral lobe showing prominent marginal teeth with glandular apices. Note the skeletonized area with poorly developed reaction rims (DT16). MMJ2-2-032b-1. **e** Leaf lobes with large beak-shaped marginal teeth. MMJ2-2-114a. **f, h** Possible fungal infection on the leaf surface. MMJ2-2-390-6, MMJ2-2-036b, respectively. **g, i** Galls positioned on the primary veins (DT33). MMJ2-2-023, MMJ2-2-361-1, respectively. Scale bars are 5 mm in **a, e–i**, 2 mm in **b–d**

the leaf fossil species of Altingiaceae, including taxa from Asia, for revealing an evolutionary trends in leaf morphology has been carried out by Lai et al. (2018). These authors also have suggested that southeast Asia is a diversity center of Altingiaceae species. Of note is that a molecular-genetic study of simple sequence repeats in individuals from geographically separated populations of the extant *L. formosana* in China (Sun et al. 2016) shows maximal genetic variability of this species located in southwestern China. Based on this, these authors speculated that southwestern China may be
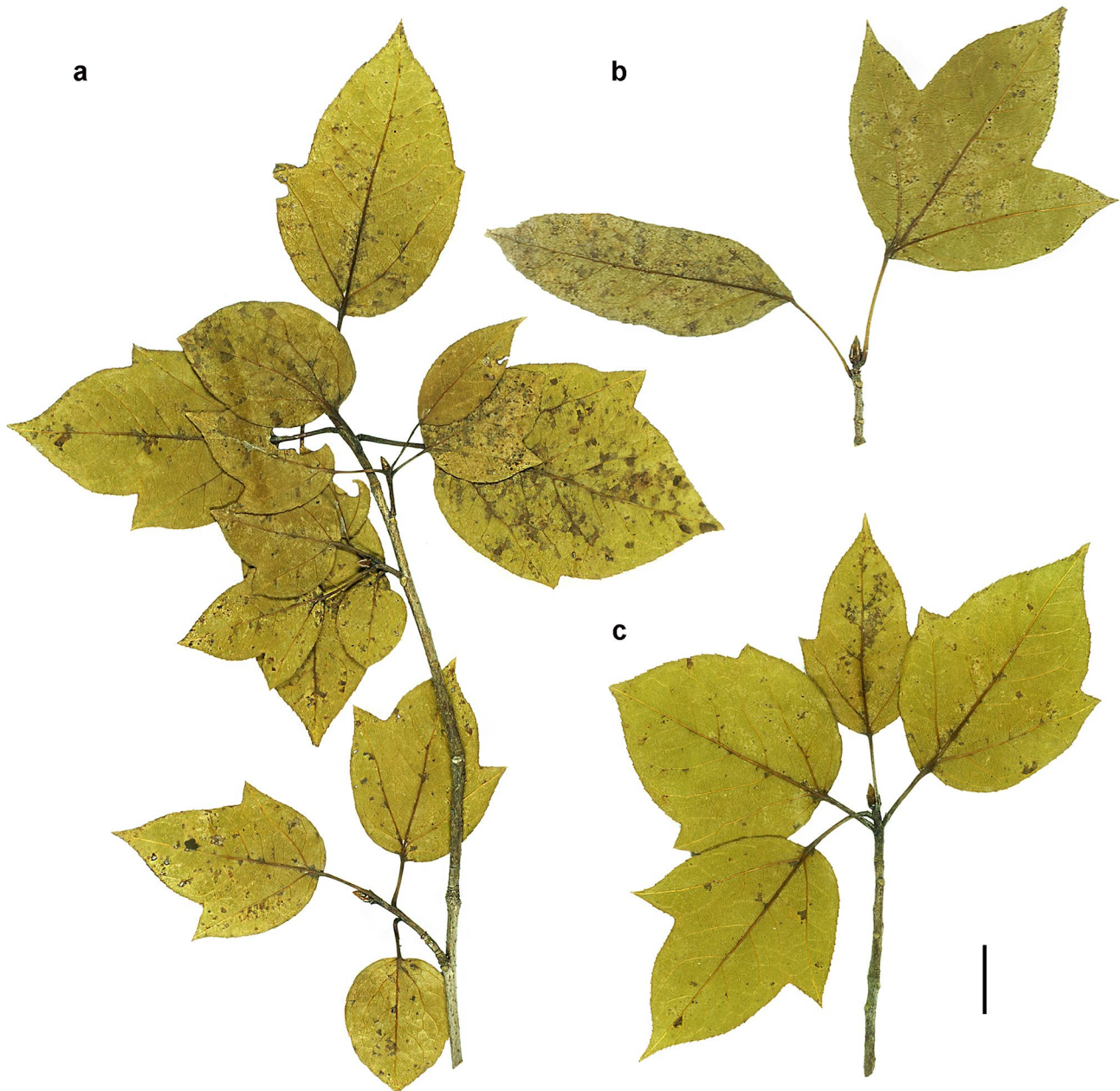

Fig. 6 Leaves of extant species *Liquidambar caudata* (H. T. Chang) Ickert-Bond et J. Wen, South China Botanical Garden, Guangzhou (**a–c**). Note the lobed and unlobed leaves with suprabasal venation, suboppositely diverging lateral veins, and occasionally asymmetrical lamina basal insertion. Scale bar is 10 mm

the centre of genetic diversity for this species. This radiation might have been enhanced by a strong abiotic natural selection due to an existence of a mosaic of different topographic habitats and seasonal climate variations: in South China rainfall seasonality increased progressively achieving modern monsoon-like wet season/dry season precipitation ratios by the early Oligocene (Herman et al. 2017; Spicer 2017; Spicer et al. 2017). We believe that future palaeobotanical studies could provide us with valuable information on even greater diversity of the Eocene and Miocene species of the Altingiaceae, the adaptive radiation of which gave rise to high specific diversity within the Altingiaceae in the modern flora of China.

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