

Liquidambar maomingensis sp. nov. (Altingiaceae) from the late Eocene of South China¹

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PREMISE OF THE STUDY: Phylogenetic analysis of DNA sequence data has changed our view on the evolution and systematics of plant taxa. Based on the phylogenetic analysis of several molecular markers, fruit anatomy, and pollen morphology, the genera *Altingia* and *Semiliquidambar* were formally transferred to the genus *Liquidambar*. The new species of *Liquidambar* from the Eocene of South China significantly extends our knowledge of the variability of the morphological characters of this genus in the geological past. Fossil leaves in conjunction with data on the associated reproductive structures allow us to make inferences about patterns in the evolutionary history of *Liquidambar*.

METHODS: Fossil leaves and associated reproductive structures preserved as impressions were described and compared with the corresponding organs of extant and fossil relatives. The morphological variation of numerous leaves was examined by stereomicroscopy.

KEY RESULTS: *Liquidambar maomingensis* sp. nov. is characterized by polymorphic leaves including both palmately lobed and unlobed leaves. This study presents the first observations of such dimorphism in the fossil record of *Liquidambar* leaves. Two distinct leaf groups are interpreted as sun and shade leaves.

CONCLUSIONS: The fossil leaves and associated infructescences from Maoming probably belong to the same plant. The occurrence of fossil leaves similar to those of extant species previously considered within *Semiliquidambar* and *Liquidambar* with the associated infructescences close to those of *Altingia* provide paleobotanical evidence that justifies combining the genera *Liquidambar*, *Altingia*, and *Semiliquidambar* into the single genus *Liquidambar* as recently proposed based on molecular markers.

KEY WORDS Altingiaceae; late Eocene; leaves; *Liquidambar*; Maoming; reproductive structures; South China

The genus *Liquidambar*, along with *Altingia* Noronha and *Semiliquidambar* H.-T.Chang, was traditionally recognized within the subfamilies Liquidambaroideae or Altingioideae of the family Hamamelidaceae (e.g., Endress, 1989a, b; Hufford and Crane, 1989; Fang and Fan, 1993; Hoey and Parks, 1994; Zhang and Lu, 1995; Endress and Igersheim, 1999; Maslova, 2010). More recently, however, these taxa have been considered to represent a distinct saxifragalean family, Altingiaceae Horan. (e.g., Chase et al., 1993; Li et al., 1999; Ickert-Bond et al., 2005, 2007; Takhtajan, 2009).

Traditionally, *Liquidambar* has been circumscribed to include four species growing in the temperate zone of the northern

hemisphere: *L. acalycina* H.-T.Chang and *L. formosana* Hance in East Asia, *L. orientalis* Mill. in West Asia, and *L. styraciflua* L. in North America. The genus *Altingia* has been considered to include 5–15 species, mainly occurring in the tropical zone or rarely in the subtropical areas of Asia. *Semiliquidambar*, comprising three species with restricted habitat in southern China has been hypothesized to have originated via an intergeneric hybridization between *Altingia* and *Liquidambar* (Bogle, 1986; Ickert-Bond et al., 2005). Recently, *Altingia*, *Liquidambar*, and *Semiliquidambar* were combined into one genus *Liquidambar* (*Liquidambar* has a nomenclatural priority) on the basis of phylogenetic analysis and a detailed examination of the fruit anatomy and pollen morphology (Ickert-Bond and Wen, 2013). Ickert-Bond and Wen (2013) provided a taxonomic revision of the Altingiaceae to include one genus *Liquidambar* with 15 species and a key for the specific identification. This idea was already discussed in a series of papers based on results of cladistic analysis of the morphological and molecular data (Shi et al., 2001; Ickert-Bond et al., 2005, 2007; Ickert-Bond and Wen, 2006). It should be noted here that the previous classic morphological studies also suggested the possibility of combining *Altingia* and

¹ Manuscript received 17 January 2015; revision accepted 6 July 2015.

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doi:10.3732/ajb.1500019

Liquidambar (genus *Semiliquidambar* had not yet been known) into one genus (e.g., Blume, 1828; Lindley, 1836; Oken, 1841; Benthams and Hooker, 1865). The effect of these changes in taxonomic concepts has not yet been considered in the context of paleobotanical record.

Liquidambar is widespread in the Cenozoic floras of the northern hemisphere. The most common macrofossils of this genus are leaves, although reproductive organs and wood are also known. *Liquidambar*-like leaves are known from the late Paleocene (Maslova, 1995, 2007), and the earliest remains of the reproductive structures are dated to the Eocene (Maslova, 2003; as *Steinhauera* in Collinson et al., 2012). The first anatomical data for fossil *Liquidambar* infructescences were obtained from the middle Miocene (Pigg et al., 2004). The earliest fossil wood assigned to the genus was described from the Paleocene (Melchior, 1998). Fossil pollen grains of the *Liquidambar-Altingia* type are also known from the Paleocene (Kuprianova, 1960; Graham, 1965; Muller, 1981).

Numerous fossil representatives of *Liquidambar* plus a few other taxa related to the family Altingiaceae have been reported (Kirchheimer,

1943; Mai, 1968; Krassilov, 1976; Friis, 1985; Ferguson, 1989; Agarwal, 1991; Gottwald, 1992; Maslova and Krassilov, 1997; Maslova and Golovneva, 2000; Maslova, 2009; Oskolski et al., 2012). The earliest-known fossil reproductive structures with altingioid affinities are from the late Turonian (Zhou et al., 2001). Most of the *Liquidambar* leaves were described from the Eocene, Miocene, and Pliocene floras of Asia (Endo and Morita, 1932; Suzuki, 1961; Huzioka, 1972; Onoe, 1974; Huzioka and Uemura, 1979; Uemura, 1983; Ozaki, 1991; Maslova, 1995; Xiao et al., 2011), Europe (e.g., Koch et al., 1973; Ferguson, 1989), and North America (e.g., Knowlton, 1902; Brown, 1933; MacGinitie, 1941; Wolfe and Tanai, 1980; Stults and Axsmith, 2011). Most of the studies are based on one or a few specimens, without much attention to morphological variation within the population.

We present here a new fossil species, *Liquidambar maomingensis* sp. nov. based on a large number of specimens, which significantly extends our knowledge of the variability of the morphological characters of fossil *Liquidambar*. In conjunction with data on the associated capitate reproductive structures, it allows us to make

inferences about patterns in the evolutionary history of this genus.

MATERIALS AND METHODS

The material studied here was collected from the small, oil-shale-bearing Maoming Basin, located in southwest Guangdong Province, South China (Fig. 1). The Upper Cretaceous to Neogene sedimentary sequence of the Maoming Basin is subdivided into eight formations (Fm.) in ascending stratigraphic order: Sanyajiang Fm., Tongguling Fm., Shangdong Fm., Youganwo Fm., Huangniuling Fm., Shangcun Fm., Laohuling Fm., and Gaopengling Fm. (Nan and Zhou, 1996). The Paleogene fluvial and lacustrine deposits of the Youganwo and Huangniuling Formations have been studied in detail from three sites: Zhenjiang, Shigu, and Jintang opencast mines.

The Youganwo Formation consists of interbedded mudstones, siltstones, and sandstones with thin coal seams in the lower part of the formation. The upper part of this formation consists of dark-brown oil shales. Coal-bearing sediments in the lower part of the Youganwo Formation contain abundant plant megafossils (tree trunks, leaves, fruits, rhizomes, and seeds). This flora, known as the Youganwo flora, yields the horsetails, ferns (*Osmunda*-ceae, *Polypodiaceae*, *Salviniaceae*), conifers (*Podocarpaceae*), and angiosperms (*Nelumbonaceae*, *Lauraceae*, *Platanaceae*, *Altingiaceae*, *Fagaceae*,

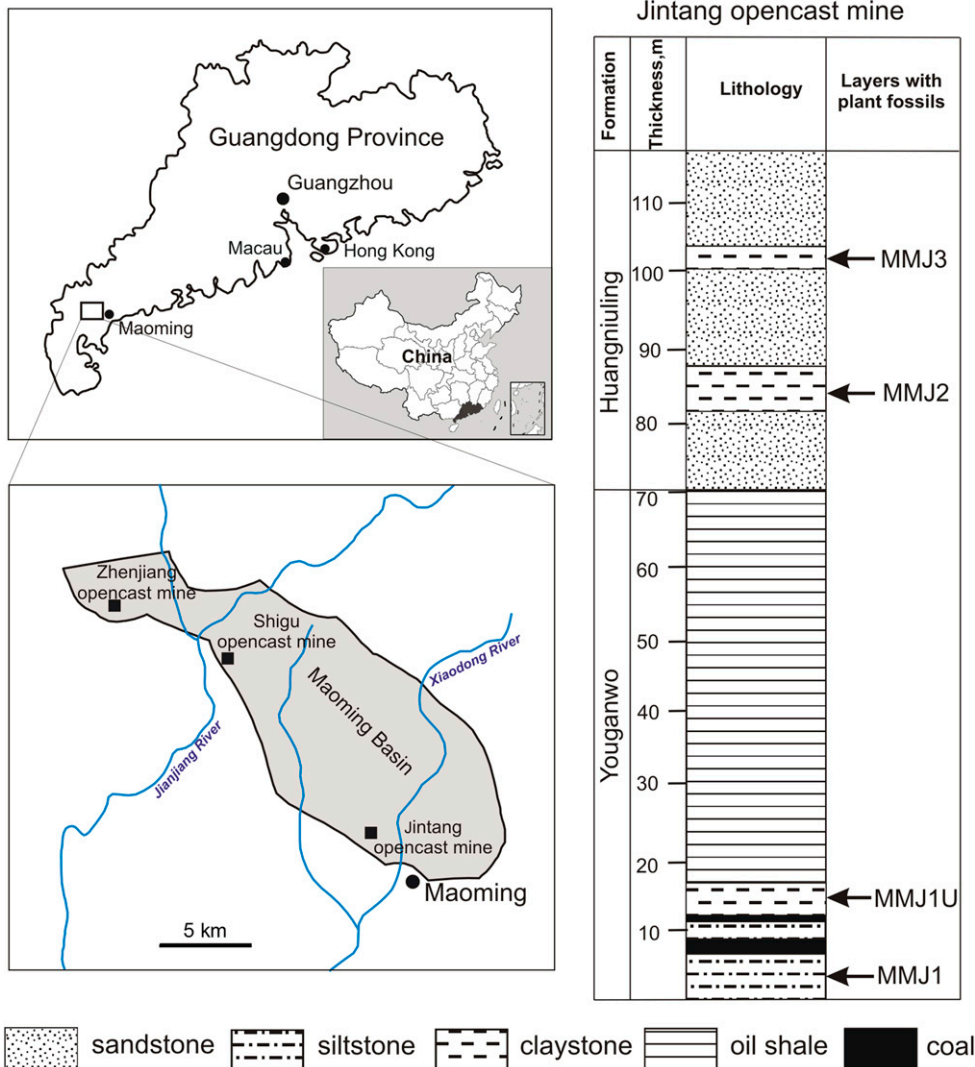


FIGURE 1 Map showing location of the Maoming Basin, Guangdong Province, China, and stratigraphic column of the Youganwo and Huangniuling Formations in the Jintang opencast mine. Layers with plant fossils are indicated by arrows.

Fabaceae, Anacardiaceae, Rhamnaceae, Ulmaceae, and Arecaceae). Numerous vertebrate fossils found within dark-brown oil shales in the upper part of the Youganwo Formation include reptiles, fishes, and mammals (see references in Danilov et al., 2013). The overlying Huangniuling Formation is composed mainly of gray, yellow to white sandstones, siltstones, and conglomerates with beds and lenses of various colored mudstones and claystones. Plant megafossils are well preserved in several horizons of mudstones and claystones. The Huangniuling flora contains ferns (Lygodiaceae), conifers (Pinaceae, Podocarpaceae, and Taxaceae), and angiosperms (Lauraceae, Fagaceae, Hamamelidaceae, Altingiaceae, Fabaceae, Juglandaceae, Myricaceae, Myrtaceae, Dipterocarpaceae, Rhamnaceae, Celastraceae, Nyssaceae, and Ulmaceae). Both the Youganwo and the Huangniuling Formations contain dispersed pollen and spores.

The Youganwo Formation has been dated as late Eocene on the basis of the vertebrate fossils and palynomorph assemblages (Jin, 2008). Based on the recent palynological study, the Youganwo Formation and Huangniuling Formation are considered to be Lutetian-Bartonian and Priabonian in age, respectively (Aleksandrova et al., 2015).

The plant fossils described in this paper were collected from the Huangniuling Formation in the Jintang opencast mine (the locality MMJ3). The leaves (92 specimens) and reproductive structures (9 specimens) are preserved as impressions. No cuticle could be obtained from the plant remains. Collections MMJ3 are housed at the Museum of Biology of Sun Yat-sen University, Guangzhou, China.

Images of the leaves and infructescences were taken using a digital camera Olympus E-500. Photos of fine venation details were made with Leica M165 stereomicroscope equipped with a Leica DFC420 digital camera. 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 leaf lamina was calculated on the basis of the maximum lamina length and width, no matter what part of the lamina was used in the calculations. The L/W ratio for fragmentary remains was calculated using the reconstructed leaf lamina.

SYSTEMATICS AND RESULTS

Family—Altingiaceae Horan. 1841.

Genus—*Liquidambar* L. 1753.

Species—*Liquidambar maomingensis* N. Maslova, Kodrul, Song et Jin sp. nov.

Etymology—From the Maoming locality.

Holotype—MMJ3-134a-1, MMJ3-134b-1, designated here (Figs. 2, 3, 52C), a leaf part and counterpart.

Specific diagnosis—Leaves simple, polymorphic, palmately lobed, rarely unlobed, wide elliptic to elliptic. In lobate leaves, apices of lateral lobes directed upward or horizontally; apex angle of lobes acute, apex shape straight or acuminate; apex of unlobed leaves acute, straight, or convex. Base angle of lamina obtuse or reflex, rarely acute; base shape rounded or slightly cordate, rarely cuneate. Venation basally actinodromous, with three primaries; lateral primary veins straight, occasionally slightly curved, extending outward or upward; venation of unlobed leaves pinnate. Secondaries

up to 8–10 pairs, alternate to subopposite, often irregular, semicraspedodromous or festooned semicraspedodromous, arching upward near the margin; branches from loops terminating in teeth; intersecondaries weak. Tertiaries alternate percurrent to mixed opposite–alternate percurrent. Fourth order veins alternate percurrent. Lamina serrate from base or slightly above. Teeth mostly regularly spaced, small, concave/retroflexed, with more prominent basal side, sinus shape rounded, tooth apex nonspecific.

Locality—Jintang opencast mine, Maoming Basin, Guangdong Province, China.

Stratigraphic position and age—Huangniuling Formation, late Eocene.

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

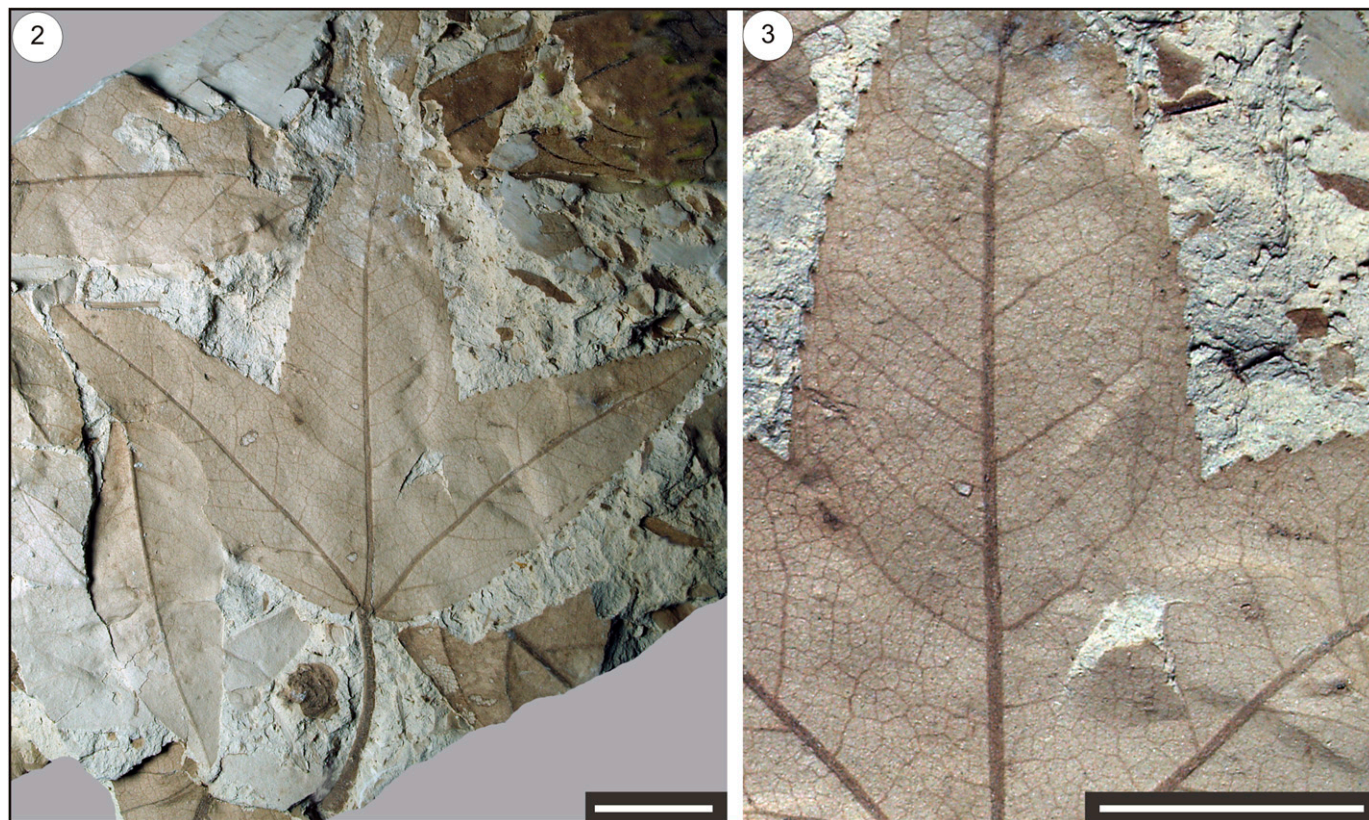
Description—Leaves are simple, polymorphic, palmately lobed (Figs. 2–34, 36, 59 [A–S]), rarely unlobed (Figs. 35, 37, 59 [T, U]), petiolate. Petioles are long (up to 50 mm), ca. 1 mm wide, slightly widened at base. Leaves with three lobes are dominant, but there are a few leaves with an extra small lobe, developed on the lowermost agrophic vein of the lateral primary vein (Figs. 34, 36). The laminae of three-lobed leaves predominantly have symmetrical lobes; however, some leaves reveal a different depth of the sinuses between the lobes (Figs. 16, 18, 19, 26, 32); lamina length varies between 46 and 125 mm, width between 45 and 150 mm; the central lobe length varies between 22 and 75 mm, with its width between 14 and 35 mm. The shape of the central lobe is triangular (Figs. 13, 21, 22, 25–33, 59 [N–S]), more often narrowly triangular (Figs. 5–8, 12, 14–19, 59 [B, C, E, J–M]) or with the nearly parallel lobe edges at the base (Figs. 4, 9–11, 23, 59 [D, F–I]).

Apices of the lobes are acute, straight, or acuminate (Figs. 2, 7, 9, 10, 33, 36, 59 [A, C, D, G, K, P]). Lateral lobes extend obliquely upward or horizontally, reaching approximately half of the leaf lamina length (Figs. 2, 8, 25, 27, 59 [B, C, R]) or sometimes more than two-thirds the length of the lamina (Figs. 4, 5, 9, 12–15, 20–22, 29, 33, 59 [E–G, J, L, N–P]). The L/W ratio of the lamina is 0.60–1.22 (average 0.86). Base shape of the lamina is rounded or slightly cordate (Figs. 59 [A–D]).

Venation of the lobate leaves is basally actinodromous. The midvein is straight. Lateral primary veins are equal in their thickness to the midvein, diverging from the midvein at 35° to 60°; they are either mostly straight or occasionally slightly curved, extending outward or upward. Secondary veins are thin, consisting of 8–10 pairs, alternate to subopposite, often irregular relative to one another, semicraspedodromous or festooned semicraspedodromous, intersecondaries weak (Figs. 3, 30); vein angles to midvein are 45°–80°. Tertiaries are alternate percurrent to mixed opposite–alternate percurrent (Figs. 3, 30). Fourth order veins are alternate percurrent (Figs. 3, 24).

The leaf margin is serrate. The teeth start at the very base of the lamina (Figs. 59 A–D, K, M) or just above the base (Figs. 59 E, F). Tooth spacing is mostly regular, 5–7 teeth/cm. Tooth shape is concave/retroflexed, with more prominent basal side and rounded sinuses. Teeth vary in size and apex shape: they are small, appressed, with inconspicuous tooth apex (e.g., Figs. 13, 29–31) or slightly larger with prominent nonspecific apex (e.g., Figs. 2, 3, 7, 8, 12, 17, 23).

The size of unlobed leaves varies between 42–80 mm long and 12–42 mm wide. The lamina of these leaves is elliptic, the apex is



FIGURES 2, 3 Holotype of *Liquidambar maomingensis* sp. nov., MMJ3-134-1, from the Eocene Huangniuling Formation of the Maoming Basin, Jintang opencast mine. **2.** Complete three-lobed leaf with curved petiole and marginal teeth with nonspecific apex. MMJ3-134a-1 (part). **3.** Detail of venation and teeth characters from the part of holotype in Fig. 2. Scale bars = 10 mm.

acute, straight, or convex; base shapes range from rounded with an obtuse angle to cuneate with an acute angle (Figs. 35, 37). The L/W ratio of the lamina is 2.0–3.5. Primary venation is pinnate, with straight midrib. Secondaries are semicraspedodromous to festooned semicraspedodromous, with irregular spacing and inconsistent vein angles. The lowest pair of secondary veins is occasionally strongly developed; the pair diverges from midvein at more acute angle than the pairs above, nearly equal in thickness to midvein; simple agrophic veins are present. Tertiaries are alternate percurrent to mixed opposite–alternate percurrent (Figs. 35, 37). The margins are serrate, with mostly regular tooth spacing, rounded sinuses, and 5–7 teeth/cm. Tooth shape is concave/retroflexed, with more prominent basal side. Teeth are very similar to those in the lobate leaves: they vary from small with inconspicuous tooth apex (Fig. 37) to more pronounced, with prominent nonspecific apex (Fig. 35).

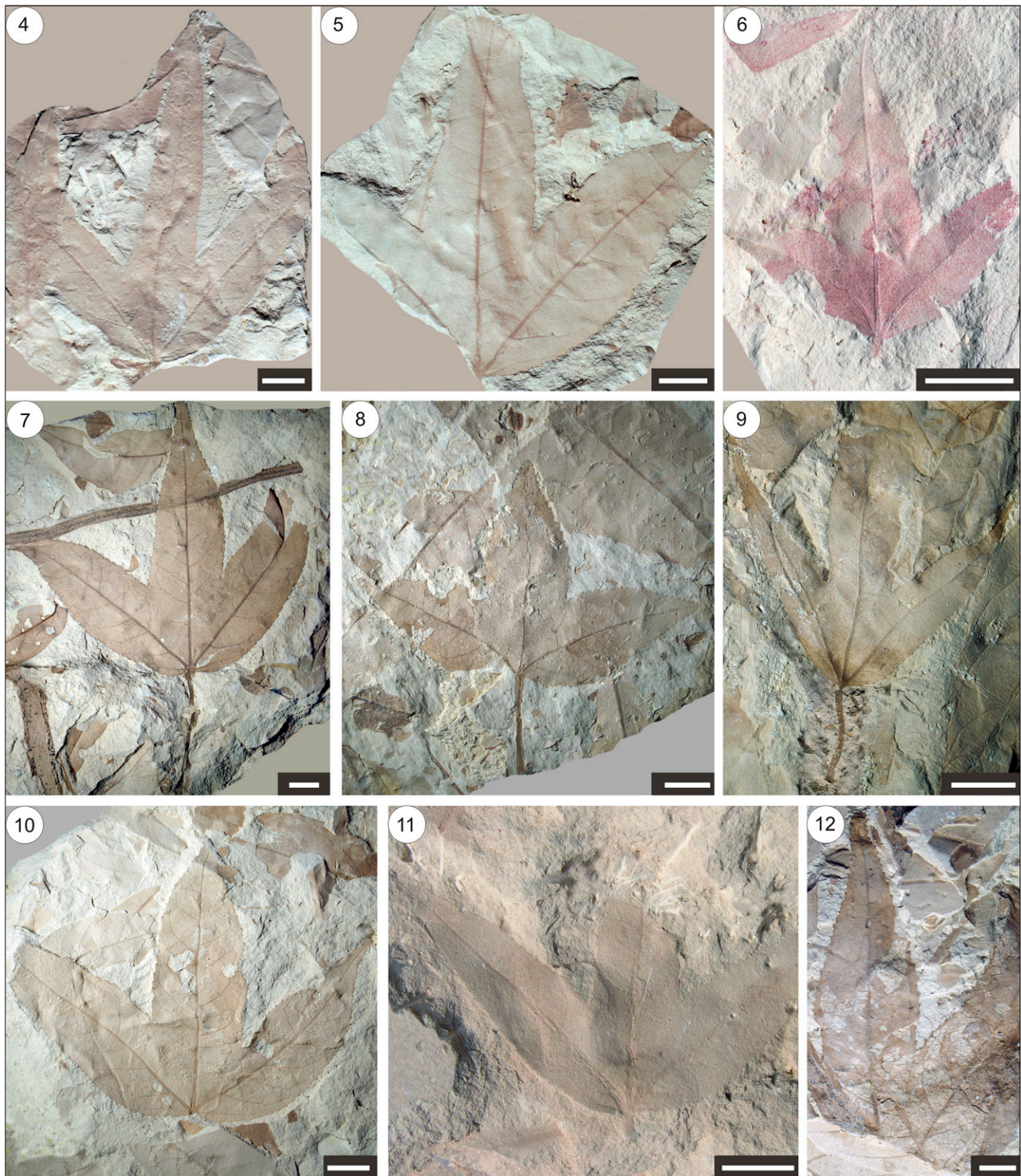
COMPARISONS AND DISCUSSION

Variability of the *L. maomingensis* leaves and comparison with the modern species of *Liquidambar*—Leaves of *L. maomingensis* are polymorphic. Because of the large number (92) of specimens studied, we could analyze the variability of the morphological characters of the leaves. In *L. maomingensis*, such characters as shape (palmately lobed and unlobed), length, width, and L/W ratio of the lamina; size and shape of the lobes; size and shape of the teeth; and

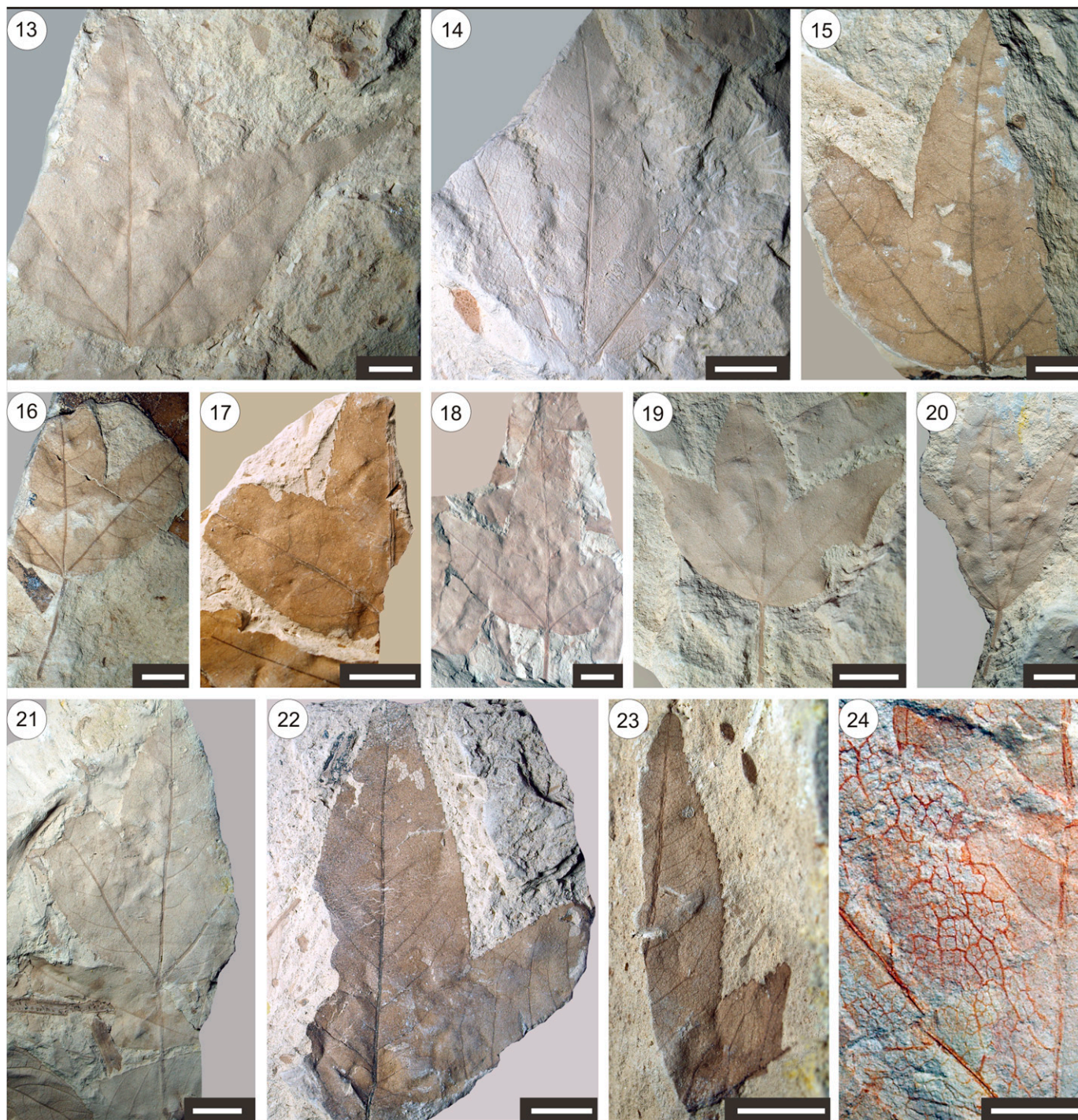
thickness of the secondary and tertiary veins are very variable. There are two distinct leaf morphotypes in the *L. maomingensis*—3-lobed and unlobed. Despite the large range of morphological variations, the leaves of both morphotypes are considered to fall within the same species because transitional forms are observed between these two main morphotypes (Fig. 59T).

The lobate morphotype can be divided into two groups depending on the L/W ratio of the leaf laminae. In Group 1, the L/W ratio is approximately 0.60, which indicates that the width substantially exceeds the length (Figs. 2, 8, 10, 27). The analysis of other morphological characters in this group showed that the leaves of Group 1 possess more pronounced venation (both secondary and tertiary veins are more prominent in this group), their laminae are palmately lobed with deep sinuses between the lobes; the relatively large marginal teeth have prominent nonspecific apices. In Group 2, L/W ratio is typically about 1.22, so the length exceeds the width of the lamina (Figs. 9, 20, 29–32). The leaves of Group 2 are characterized by weak venation (secondary and especially tertiary veins are inconspicuous), their laminae are generally less dissected, marginal teeth are small, appressed, without the prominent nonspecific apices.

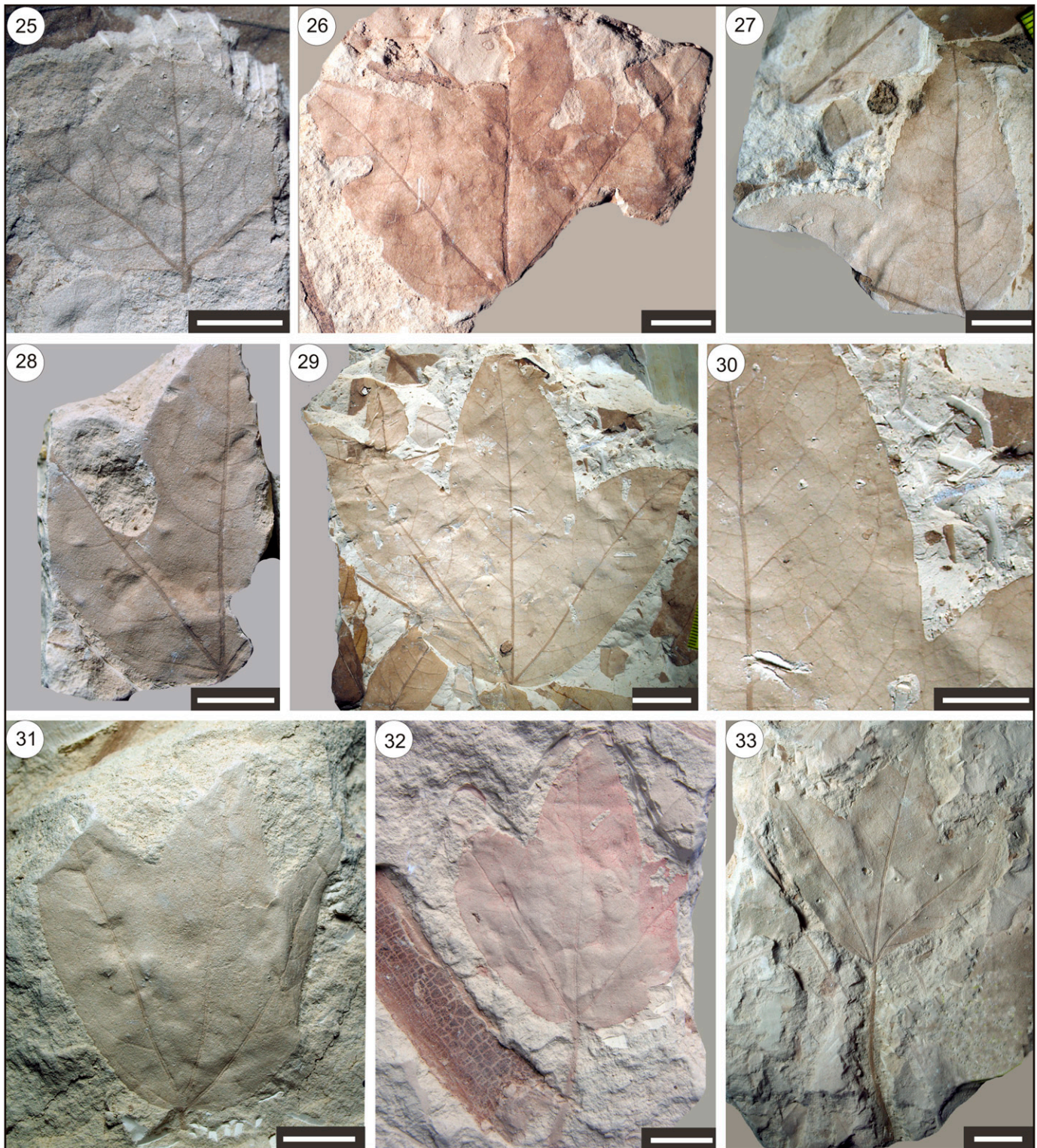
By analogy with the extant *L. formosana*, it seems plausible to assume that the leaves of Group 1 developed on the periphery of the crown (sun morphotype), whereas leaves of Group 2 grew inside the crown closer to the stem (shade morphotype). Preliminary studies have shown that *L. formosana* leaves, developing inside the crown, possess an L/W ratio of more than 1 (Fig. 41). These leaves



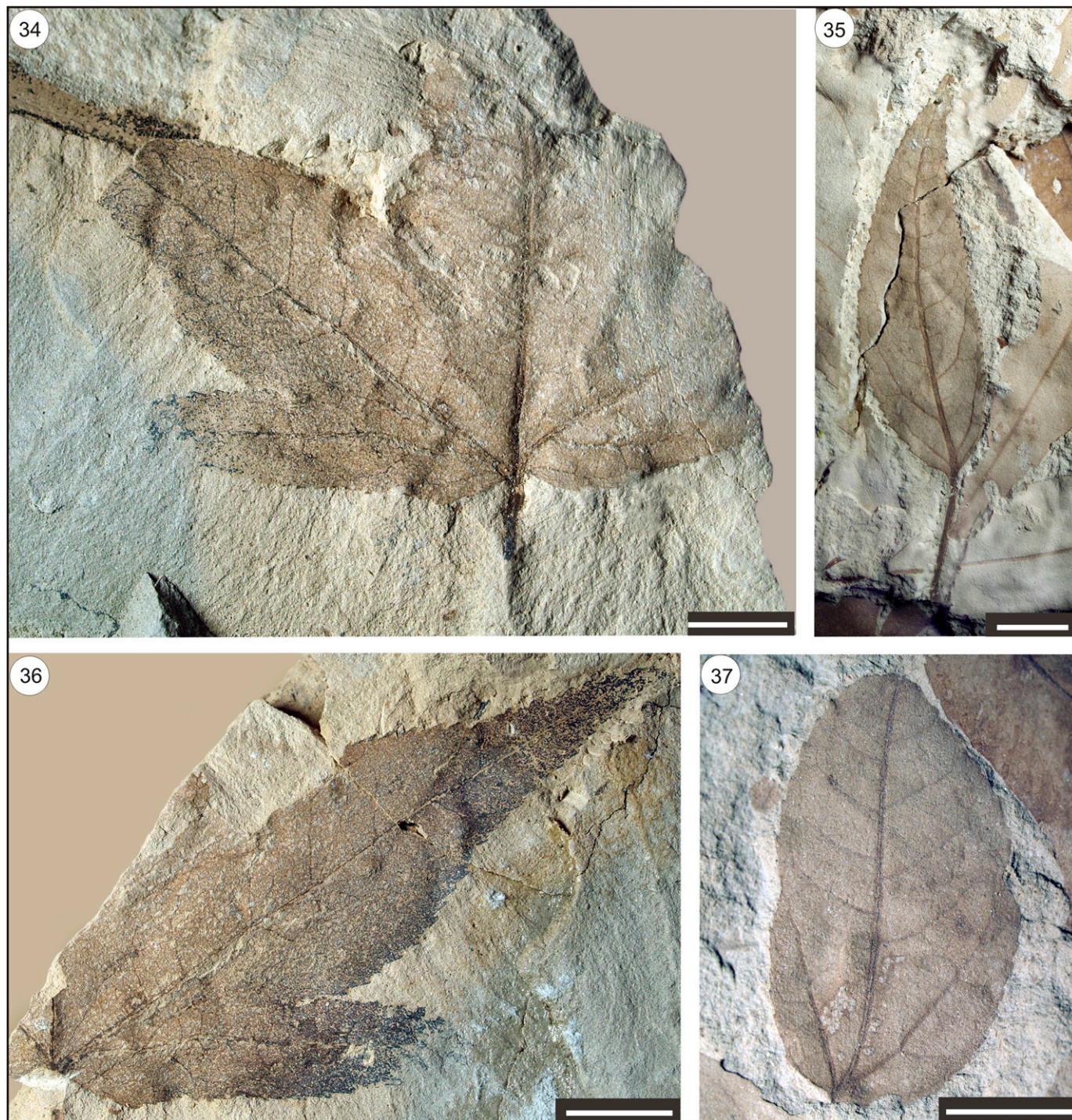
FIGURES 4–12 Three-lobed leaves of *Liquidambar maomingensis* sp. nov. from the Eocene Huangniuling Formation of the Maoming Basin, Jintang opencast mine. **4.** Leaf with deep sinuses and nearly parallel lobe edges. MMJ3-026. **5, 6.** Leaves with narrowly triangular lobes and lateral primary veins, extending upward and outward. MMJ3-020-3, MMJ3-025, respectively. **7, 10.** Sun leaves with L/W ratio < 1, pronounced venation, and relatively large marginal teeth with well-developed nonspecific apex. Note damage from insect feeding. MMJ3-142b-1, MMJ3-129a-1, respectively. **8.** Leaf with horizontally oriented lateral lobes. MMJ3-018a-1. **9, 12.** Leaves with lateral lobes oriented obliquely upward, reaching more than two-thirds of the lamina length. Note leaf damage caused by leaf-skeletonizing insects (Fig. 12). MMJ3-141-1, MMJ3-127-1, respectively. **11.** Leaf with nearly parallel lobe edges at the base. MMJ3-060. Scale bars = 10 mm (Figs. 4–11), 5 mm (Fig. 12).



FIGURES 13–24 Three-lobed leaves of *Liquidambar maomingensis* sp. nov. from the Eocene Huangniuling Formation of the Maoming Basin, Jintang opencast mine. **13.** Leaf with acuminate apex of the lateral lobe. MMJ3-053. **14.** Leaf with narrowly triangular central lobe and lateral lobes oriented obliquely upward. MMJ3-066-1. **15.** Leaf with distinct venation and relatively large marginal teeth. MMJ3-123. **16.** Leaf with slightly cordate base, revealing different depth of the sinuses between the lobes. MMJ3-068b. **17.** Leaf showing relatively large marginal teeth with well-developed nonspecific apices. MMJ3-160-1. **18, 19.** Leaves with slightly asymmetric base and different depth of the sinuses between the lobes. MMJ3-028-1, MMJ3-126-1, respectively. **20.** Leaf with lateral lobes oriented obliquely upward and small marginal teeth. MMJ3-133-1. **21.** Leaf with slightly asymmetrical base and irregularly spaced teeth. MMJ3-150-1. **22.** Leaf with triangular central lobe and densely spaced, small teeth. Note insect damage (skeletonization) at the apex of central lobe. MMJ3-158. **23.** Leaf with distinct venation and prominent teeth. MMJ3-139-1. **24.** Detail of tertiary and quaternary venation. MMJ3-166b-1. Scale bars = 10 mm.



FIGURES 25–33 Three-lobed leaves of *Liquidambar maomingensis* sp. nov. from the Eocene Huangniuling Formation of the Maoming Basin, Jintang opencast mine, shade leaf morphotypes. **25**. The smallest leaf. MMJ3-159a-3. **26, 28**. Leaves with triangular lobes and shallow sinuses. MMJ3-022-2, MMJ3-071, respectively. **27**. Leaf with horizontally oriented lateral lobes. MMJ3-124-1. **29**. Large leaf with tiny, appressed marginal teeth and shallow sinuses. MMJ3-151a-1. **30**. Detail of marginal and intercostal venation and teeth characters from specimen in Fig. 29. **31, 32**. Leaves with inconspicuous secondary and tertiary venation and small marginal teeth. MMJ3-016-1, MMJ3-072a-1, respectively. **33**. Leaf with small marginal teeth and long petiole. MMJ3-054-1. Scale bars = 10 mm.

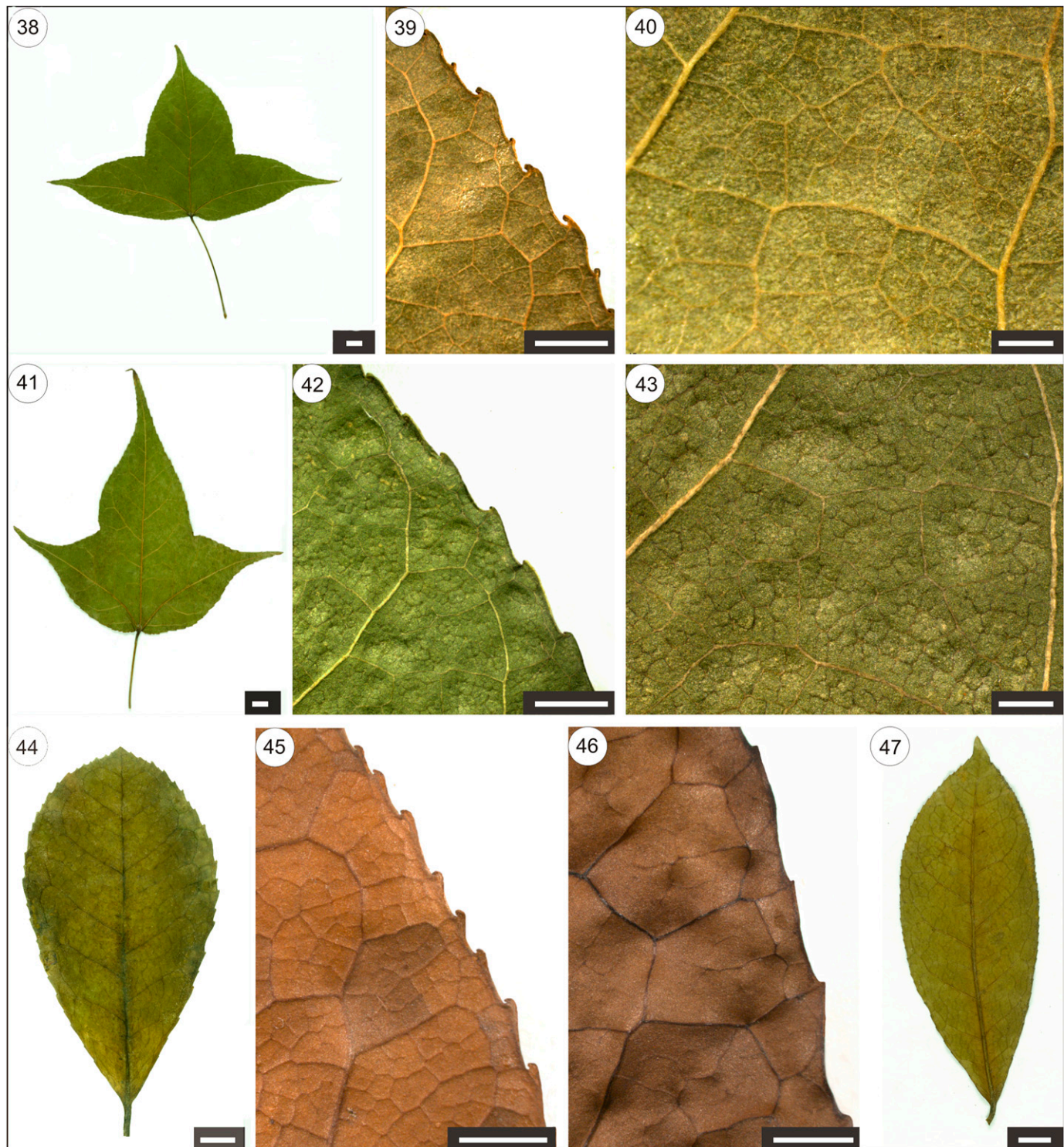


FIGURES 34–37 Three-lobed and unlobed leaves of *Liquidambar maomingensis* sp. nov. from the Eocene Huangniuling Formation of the Maoming Basin, Jintang opencast mine. **34.** Three-lobed asymmetric leaf with additional small lobe on one side of lamina. MMJ3-144a-1. **35.** Unlobed leaf with distinct secondary veins and pronounced, densely spaced teeth with nonspecific apex. MMJ3-162-1. **36.** Incomplete counterpart of specimen in Fig. 34. MMJ3-144b-1. **37.** Unlobed leaf with the lowest pair of secondary veins strongly developed; it can be considered as a transitional morphotype between the unlobed and lobed leaves. MMJ3-159a-1. Scale bars = 10 mm.

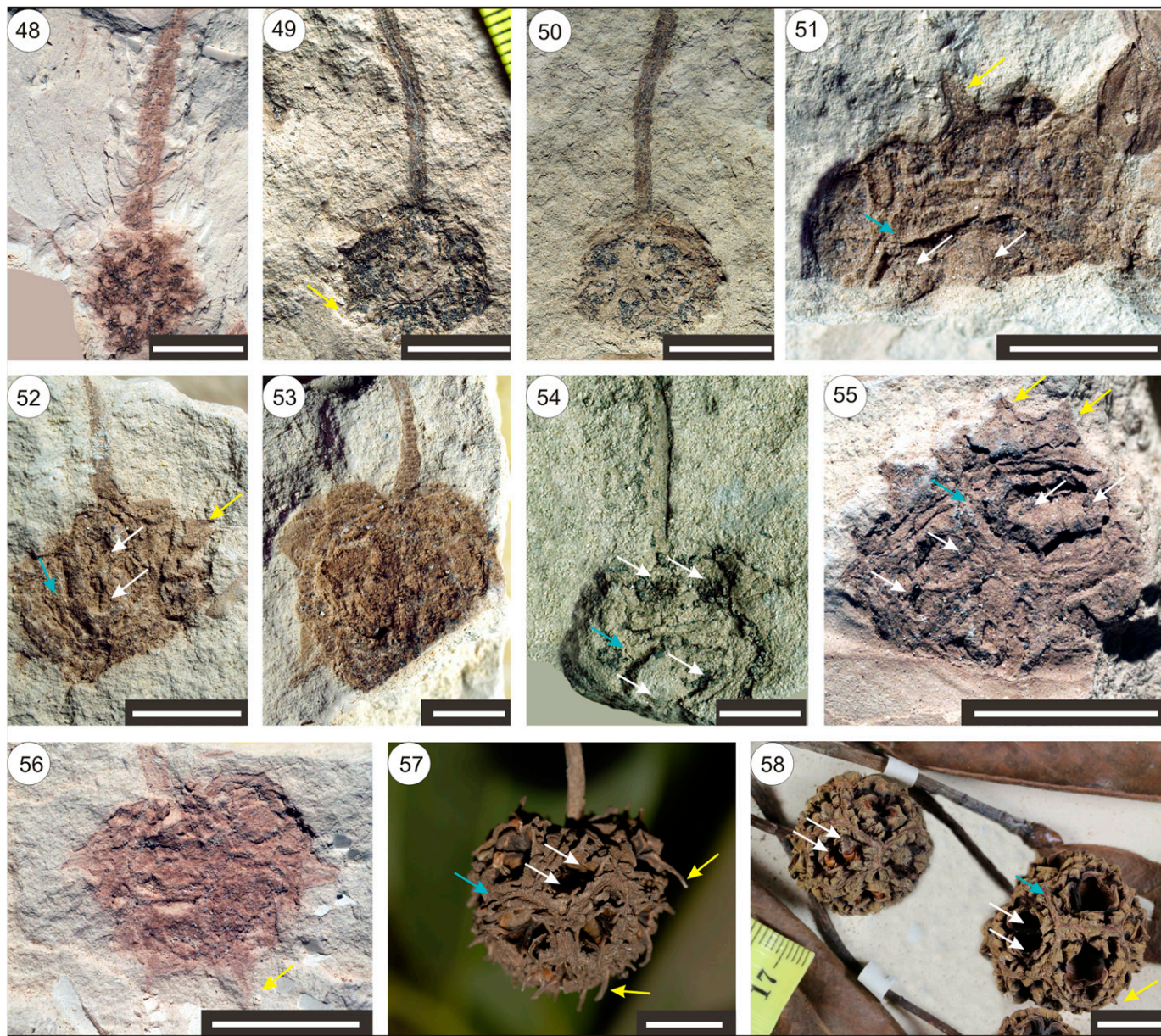
are characterized by less-prominent venation and small, appressed teeth (Figs. 42, 43). In contrast, the leaves from the periphery of the crown of the same trees have an L/W ratio of less than 1 (Fig. 38). They are characterized by more prominent venation,

and their teeth are relatively large, with distinct glandular apices (Figs. 39, 40).

According to Zalsky's law (Zalsky, 1904), the leaves of woody plants that develop on the top region of the crown, where



FIGURES 38–47 Leaves of the extant species *Liquidambar formosana* Hance (38–43) and *Liquidambar chinensis* Champion (44–47). **38.** Sun leaf with L/W ratio of lamina less than 1. **39.** Detail of the sun leaf margin; the relatively large teeth with glands are seen. **40.** Detail of the sun leaf lamina with prominent tertiary veins. **41.** Shade leaf with L/W ratio of lamina greater than 1. **42.** Detail of the shade leaf margin with small teeth without glands. **43.** Detail of the shade leaf lamina with weak tertiary veins. **44.** Sun leaf. **45.** Detail of the sun leaf margin with relatively large glandular teeth and prominent veins. **46.** Detail of the shade leaf margin with relatively weak tertiary veins and small teeth. **47.** Shade leaf. Scale bars = 10 mm (Figs. 38, 41, 44, 47), 3 mm (Figs. 39, 42, 45, 46), 1 mm (Figs. 40, 43).



FIGURES 48–58 Infructescences associated with *Liquidambar maomingensis* sp. nov. leaves (48–56) in the same plant assemblages from the Eocene Huangniuling Formation of the Maoming Basin, Jintang opencast mine, and infructescences of the extant *Liquidambar yunnanensis* (Rehder et E.H.Wilson) Ickert-Bond et J.Wen (57) and *Liquidambar siamensis* Craib (58). **48.** Rounded infructescence with thick, long peduncle. MMJ3-29. **49, 50.** Slightly flattened, globose infructescence (part and counterpart) showing a small number of bilocular fruits with style bases (yellow arrow) and complete peduncle. MMJ3-152a-1, MMJ3-152b-1, respectively. **51.** Infructescence detail showing several bilocular fruits (white arrow marks one locule), slightly raised smooth tissue between fruits (blue arrow) and style base (yellow arrow). MMJ3-156-1. **52.** Infructescence with clearly visible, large, bilocular fruit (white arrow marks one locule) surrounded by slightly raised, smooth tissue (blue arrow), style base (yellow arrow). MMJ3-032b-1. **53.** Globose pedunculate infructescence. MMJ3-153-1. **54.** Slightly flattened, rounded infructescence with long peduncle and bilocular fruits (white arrow shows one locule) surrounded by slightly raised, smooth tissue (blue arrow). MMJ3-130. **55.** Fragment of globose infructescence with style bases (yellow arrow); note broad rims of tissue (blue arrow) between adjacent fruits and bilocular fruits (white arrow marks one locule). MMJ3-031a. **56.** Spherical infructescence with numerous style bases (yellow arrow); the borders of individual fruits are visible. MMJ3-30a. **57.** Spherical infructescence of *Liquidambar yunnanensis* with bilocular fruits (white arrow marks one locule) surrounded by prominent tissue (blue arrow); long styles (yellow arrow) are visible. **58.** Spherical infructescence of the *Liquidambar siamensis* with bilocular fruits (white arrow marks one locule), broad rims of tissue (blue arrow), and style bases (yellow arrow). Scale bars = 10 mm (Figs. 48–50, 52, 55–58), 5 mm (Figs. 51, 53, 54).

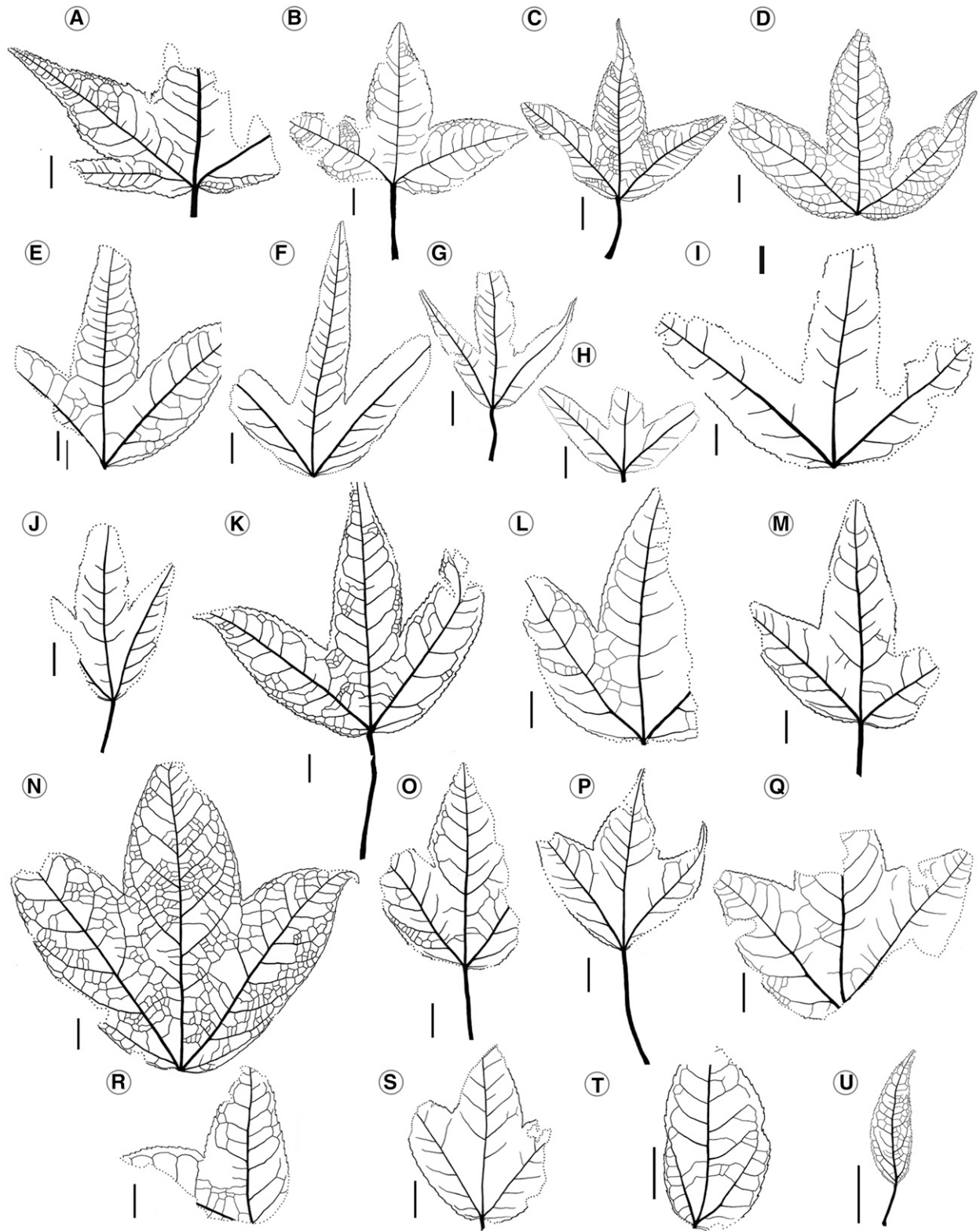


FIGURE 59 The range of leaf morphology variation of *Liquidambar maomingensis* sp. nov. from the Eocene Huangniuling Formation of the Maoming Basin, Jintang opencast mine. (A) MMJ3-144a-1, MMJ3-144b-1 (composite drawing prepared using both incomplete counterparts). (B) MMJ3-018a-1. (C) Holotype. MMJ3-134a-1. (D) MMJ3-129a-1. (E) MMJ3-020-3. (F) MMJ3-26. (G) MMJ3-141-1. (H) MMJ3-060. (I) MMJ3-131-1. (J) MMJ3-133-1. (K) MMJ3-142b-1. (L) MMJ3-123. (M) MMJ3-028-1. (N) MMJ3-151a-1. (O) MMJ3-150-1. (P) MMJ3-054-1. (Q) MMJ3-022-2. (R) MMJ3-124-1. (S) MMJ3-072a-1. (T) MMJ3-159a-1. (U) MMJ3-162-1. Scale bars = 10 mm.

they are more exposed to sunlight, have generally more xeromorphic characters than those that are sunlight deficient. Xeromorphic characters are reflected in the size of the lamina (smaller in sun leaves), in the texture of the leaf lamina (more dense in sun leaves), in the degree of pubescence (more pronounced in sun leaves), in the frequency and thickness of the secondary and tertiary veins (they are more prominent in sun leaves), and also in cuticular-epidermal characters. Earlier (Maslova et al., 2008) studies of the extant species *Platanus acerifolia* Willd., which is characterized by a similar modus of leaf variation (lobate and unlobed morphotypes) have shown that the leaves that develop inside the crown are generally oblong ($L/W > 1$), as opposed to the leaves from the periphery of the crown ($L/W < 1$). It should be noted that *L. maomingensis* morphotypes with the more elongated leaf lamina are also characterized by shade leaf characters such as less-pronounced venation and small teeth without noticeable nonspecific apices.

The lobate leaves with different types of lateral lobe orientation (upward or horizontally) are also connected with the same species, *L. maomingensis*, by a series of the transitional forms. As have been shown earlier (Givulescu, 1986), this kind of leaf dimorphism is typical of the leaves of *L. europaea* A. Braun from the lower-upper Miocene and Pliocene of Europe since the early Miocene. All modern species of *Liquidambar* are characterized only by lateral lobes with horizontal direction.

Despite the fact that unlobed leaves of *L. maomingensis* are not so numerous, they can also be divided into two groups. Group 1 consists of the leaves with less prominent venation and small teeth (Fig. 37). Group 2 includes leaves with distinct veins and teeth with prominent nonspecific apices (Fig. 35). By analogy with the lobed *L. maomingensis* leaves, as well as with the modus of variability in the extant *L. chinensis* Champion (Figs. 44–47), we suppose that the unlobed leaves of Group 1 are the shade leaves, whereas the unlobed leaves of Group 2 are the sun ones.

The validity of combining lobed and unlobed leaves studied here into the single species *L. maomingensis* is supported by the shared complex of the characters: the same type of secondary (semicraspedodromous) and tertiary (alternate percurrent to mixed opposite-alternate percurrent) venations, and the characteristic leaf margin with frequent small teeth having two types of apices, either inconspicuous or prominent nonspecific. The unlobed leaves with the lowest pair of secondary veins well developed can be considered as a transitional morphotype between the unlobed and lobed leaves (Fig. 37). An indirect confirmation of this conclusion is the same leaf damage caused by insect skeletonization (Figs. 2, 12, 22, 37).

Thus, in the Eocene deposits of the Maoming Basin both lobed and unlobed leaves of *L. maomingensis* are recognized. Marginal morphotypes in *L. maomingensis* are combined in a single range of variability by the transitional forms reflecting probably a well-developed mosaic leaf arrangement on the shoots.

Similar variability of the lamina shape is observed in the extant *Liquidambar* species: *L. caudata* (H.-T.Chang) Ickert-Bond et J. Wen and *L. chingii* (previously they belonged to the genus *Semiliquidambar*). However, lobate morphotypes of these species differ from those of *L. maomingensis* by their short lobes without acuminate apices, by lamina L/W ratio usually exceeding 1, and by the suprabasal actinodromous venation (other extant species of the genus and the lobate morphotypes of *L. maomingensis* are characterized by the basal actinodromous venation). The unlobed leaves in *L. chingii* and *L. caudata* are also generally characterized by higher values of the L/W ratio than *L. maomingensis*.

In addition, the range of leaf shape variability in these modern species includes a large portion of the asymmetric morphotypes (with a lobe on one leaf side only). The lobate morphotypes of *L. maomingensis* are most similar to those of the modern *L. formosana* in the 3-lobed lamina with the acuminate apex of the lateral lobes.

Comparison with the fossil species of *Liquidambar*—The actual diversity of the genus *Liquidambar* in the geological past is controversial and requires special analysis. The most important points are that many fossil species (as well as their varieties) were described on the basis of a very limited material (one or several samples) and that morphological variability was not taken into consideration. Some insignificant characters (such as, e.g., the angle of a divergence of the basal veins, the shape of the leaf lamina base, and the frequency of the teeth) were used as the main diagnostic features, and on such basis, numerous new species were identified.

For example, the fossil species *L. cordata* (K. Suzuki) Uemura from the lower Miocene and Pliocene of Japan (Uemura, 1983) and *L. protoformosana* Endo var. *eocenica* Endo from the Eocene of Japan (Endo, 1968) should be noted among the known Asian species. The first was compared with extant *L. formosana*, differing by the larger angle between the central and lateral lobes. As Endo (1968) has mentioned, the second species is also similar to *L. formosana*, but differs from the modern species in more rare teeth.

Mostly 5-, rarely 7-lobed leaves from the upper Miocene of Japan have been assigned to *L. protopalmata* (K. Suzuki) Uemura (Uemura, 1983). According to Uemura (1983), this species differs from all fossil and modern species in the smaller and more frequent teeth. The main differences of *L. protopalmata* from *L. cordata* and *L. formosana* are the larger number of lobes and the lack of the prominent teeth glands. *Liquidambar maomingensis* and *L. protopalmata* are similar in their teeth characters (except for the presence of marginal teeth with nonspecific apex in the Eocene new species), differing in the prevalence of the 3-lobed leaves in *L. maomingensis*.

The range in leaf lamina shape in *L. maomingensis* also includes deeply lobate leaves with three narrow oblong lobes that are similar to the leaves of *L. yabei* (Morita) Huzioka from the late Miocene Daibo flora, Japan (Huzioka, 1974).

Some fossil species from Asia were assigned to the extant *L. formosana* (e.g., from the Oligocene Sakito flora, Matsuo, 1970) due to their morphological similarity. However, the assignment of the fossil plants to the extant species only on the basis of macromorphology is a questionable approach. As was shown earlier for the fossil platanoids (Maslova, 2007, 2010), a morphological type of the leaf, which is typical for the modern *Platanus*, appears in the geological past much earlier than the modern kind of reproductive structures. The fossil leaves showing morphological features typical of the modern genus could be associated with the inflorescences and infructescences that are macromorphologically close to those of *Platanus*, but different significantly in the microstructure. There are no reproductive structures of the modern genus in association with the fossil *L. formosana* leaves.

Most of the Asian fossil leaves of *Liquidambar* that were younger than Eocene were assigned to *L. miosinica* Hu et Chaney (Hu and Chaney, 1940). Originally, this species was characterized exclusively by 3-lobed leaves, and later 5-lobed morphotypes were included (e.g., Ozaki, 1991). In general, *L. miosinica* is similar to extant *L. formosana*. Tanai (1967, 1970, 1976) proposed to assign

all *Liquidambar* species from the Paleogene and Neogene of East Asia to the single species *L. miosinica*, referring to their similarity with *L. formosana* and insignificant differences between them.

The lobate leaves of *L. maomingensis* with some transitional morphotypes are also similar to *L. miosinica*. Based on the previous criteria, these transitional forms, taken individually, could be attributed to different species. Moreover, *L. maomingensis* is characterized by unlobed and asymmetric (with the additional small lobe on one side) morphotypes. Distinct leaf dimorphism is the main difference between new species and other known fossil species. A different number of lobes (3–5–7) in the fossil *Liquidambar* species is known (e.g., Makarova, 1957; Wolfe and Tanai, 1980; Uemura, 1983; Ozaki, 1991), whereas unlobed morphotypes together with lobed ones appear in the fossil record for the first time.

Reproductive structures associated with *L. maomingensis* sp. nov. leaves

The capitate infructescences are rounded, slightly flattened, from 13 to 16 mm in diameter (excluding the style protrusions). Style fragments are up to 3 mm. Fruit number per head, according to the fruit scars, apparently does not exceed 10. Maximum diameter of the individual fruit is 8–10 mm; the fruit scars are oval (Figs. 51–56); the fruits are distinctly separated from each other by the slightly raised, smooth tissue (Figs. 49–51, 54, 55). Perianth elements are lacking. Fruits are bilocular (Figs. 51, 52, 54, 55).

Although these heads were not found in an organic connection with *L. maomingensis* leaves, they presumably belong to the same plant. No other leaf morphotypes with obvious affinity to Altingiaceae have been found at the fossil locality. The preservation of the fossils (impressions without phytolite marks) does not allow us to obtain information on the micromorphology of the infructescences and fruits. Thus, we do not consider it possible to describe these reproductive structures under the same specific name as the leaves.

The fossil reproductive structures from the Eocene of the Maoming Basin have a combination of significant diagnostic features confirming their affinity to Altingiaceae: capitate infructescences, bilocular fruits without any perianth elements, and prominent, slightly raised tissue between fruits. As described by Ickert-Bond et al. (2005, 2007), pistillate reproductive structures of *Liquidambar* and *Altingia* are characterized by a spherical inflorescence that develops into a woody infructescence (head). The main morphological differences between these two genera are the number of fruits per head, development of areas between individual fruits, absence/presence of a cuplike bract at the base of the infructescence, style length and shape, and type of extrafloral structures. Additional differences between species of those two genera are based on variation in the anatomy of the outer fruit tissues, carpel wall, and seeds (Ickert-Bond et al., 2005, 2007). In the number of fruits per head and the degree of style development the Eocene infructescences associated with *L. maomingensis* leaves are similar to the infructescences of extant species of *Liquidambar* previously considered within the genus *Altingia* (Figs. 57, 58; see also in Ickert-Bond et al., 2007: figs. 1, 26, 35, 66). For example, the infructescences from the Maoming Basin are comparable in fruit number with the modern *L. gracilipes* (Hemsl.) Ickert-Bond et J.Wen (previously *Altingia gracilipes* Hemsl.), *L. siamensis* (Craib) Ickert-Bond et J.Wen (previously *A. siamensis* Craib), and *L. yunnanensis* (Rehder et E.H.Wilson) Ickert-Bond et J.Wen (previously *A. yunnanensis* Rehder et E.H.Wilson)

differing in the absence of the bracts at the infructescence base (Figs. 57, 58). In addition, these extant species are characterized by exclusively unlobed leaves, while in *L. maomingensis* leaves are mostly lobate. All other extant *Liquidambar* species are characterized by a large number (up to 40) of fruits per head.

Among previously described fossil plants, the capitate infructescences associated with *L. maomingensis* are most similar in morphology to those with long persistent styles, occurring with *L. protopalmata* (Uemura, 1983), but they differ in being smaller and having fewer fruits.

CONCLUSION

The new species *L. maomingensis* from the late Eocene of South China (Maoming Basin) differs from previously described fossil species in the range of the lamina shape from 3-lobed to unlobed and in the recognition of distinctions between sun and shade leaf types. The sun and shade leaves can be distinguished based on analysis of morphological features of the lamina (L/W ratio, peculiarities of the venation, and the type of teeth). The extant species, *L. chingii* and *L. caudata* (previously placed in the genus *Semiliquidambar*), possess a similar range of leaf morphological variation. However, they differ in the lobe shape and suprabasal arrangement of the basal veins as well as in different lamina L/W ratio (typically more than 1 in the modern species).

The female reproductive organs (heads) of altingiaceae affinity were also found in this locality. These heads resemble those of extant *L. gracilipes* (previously *Altingia gracilipes*) and *L. siamensis* (formerly *A. siamensis*) but differ in the absence of bracts at the base of the head.

The fossil plant record from the Eocene of the Maoming Basin including *L. maomingensis* leaves similar to those of extant species previously considered within the genera *Semiliquidambar* (comparable range of morphotypes) and *Liquidambar* (similar lobate morphotypes), as well as fossil infructescences close to those of *Altingia*, is the paleobotanical evidence that justifies combining genera *Liquidambar*, *Altingia*, and *Semiliquidambar* into a single genus, *Liquidambar*, as proposed recently based on phylogenetic analysis, fruit anatomy, and pollen morphology (Ickert-Bond, Wen, 2013).

ACKNOWLEDGEMENTS

This study was supported by the National Natural Science Foundation of China (Grant nos. 41210001, 40972011), the Russian Foundation for Basic Research (Grant no. 14-04-00800), the joint Project of the National Natural Science Foundation of China and the Russian Foundation for Basic Research (Grant nos. 413111040, 14-05-91163), State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, CAS) (Grant no. 123110), the Fundamental Research Funds for the Central Universities (Grant no. 12lgjc04), and the Key Project of Sun Yat-sen University for inviting foreign teachers. The authors are grateful to Prof. S. R. Manchester (Florida Museum of Natural History, Gainesville, FL, USA) for valuable advice and comments, Dr. M. Romanov (Department of Dendrology, N. V. Tsitin Main Botanical Garden RAS, Moscow) for providing a digital image of *Altingia yunnanensis* Rehder et E.H.Wilson infructescence, and Prof. A. Reznikov (Black Hills State University, Spearfish, SD, USA)

for correcting the English of the manuscript. The authors thank the editor and two anonymous reviewers for their constructive and helpful comments.

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