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A preliminary assessment of plant–biotic interactions in the Eocene of South China: Evidence from *Liquidambar* L. (Saxifragales: Altingiaceae)

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A R T I C L E I N F O

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A B S T R A C T

The study of fossil plant–biotic (mainly arthropod) interactions offers an opportunity to understand the evolutionary process in palaeoecosystems and their response to climate fluctuation. Despite the importance of such investigations, not much is known about plant–arthropod associations from the Cenozoic floras of Asia. Exceptionally diverse Eocene floras from adjacent Maoming and Changchang sedimentary basins of southern China provide valuable insights into low-latitude palaeoecosystems. These floras indicate different intensities of plant–arthropod interactions and probably viral, bacterial or fungal infection. Two upper Eocene floras from the Maoming Basin are markedly distinct from two approximately contemporaneous middle Eocene floras of the Changchang and Maoming basins in exhibiting much more abundant and diverse plant damage types (DTs). For equivalent comparisons we focus on well-sampled fossil leaves of *Liquidambar* L. (Altingiaceae) present and relatively abundant in both basins. *L. maomingensis* and *Liquidambar* sp. 1 from both upper Eocene Maoming floras exhibit mainly external foliage feeding. In contrast, almost only galling occurs on *Liquidambar* sp. 2 leaves from the middle Eocene Changchang flora. The differences in the diversity and frequency of DTs in the studied palaeofloras could have been affected by a progressive warming and increase in climate seasonality over the middle–late Eocene interval as well as by habitat conditions and plant successional status. We hypothesize that *L. maomingensis* and *Liquidambar* sp. 1 from the Maoming Basin inhabited the early successional riparian forests on an alluvial plain, whereas *Liquidambar* sp. 2 from the Changchang Basin was a component of more mature plant communities.

1. Introduction

Different types of plant interactions with other members of their ecological communities not only affect population dynamics, diversity and evolutionary changes of interacting organisms, but can have wide-ranging impact on ecological variations. On the other hand, environmental conditions influence significantly interactions within plant associations and other biota, including arthropods, nematodes, fungi, bacteria, and viruses (e.g., Agrawal et al., 2012; Fussmann et al., 2007; Futuyma and Agrawal, 2009; Johnson, 2011; Johnson et al., 2009). The study of fossil plant–biotic (mainly arthropod) interactions offers an opportunity to understand better on palaeoecosystem responsing to environmental changes.

The plant fossil damage types resulting from the insects and, to considerably lesser degree, from plant pathogens (fungi, bacteria) have been well documented in the recent years using Cenozoic floras of North America (e.g., Currano et al., 2008, 2010, 2016; Donovan et al., 2014; Ellis et al., 2003; Labandeira and Currano, 2013; Labandeira et al., 2002a, b, 2007; Smith, 2008; Wilf and Labandeira, 1999; Wilf et al., 2001, 2006), Central and South America (Carvalho et al., 2014; Wilf et al., 2005a, b; Wing et al., 2009), and Europe (Gunkel and Wappler, 2015; Knor et al., 2012, 2013; Prokop et al., 2010; Wappler, 2010; Wappler and Denk, 2011; Wappler et al., 2009, 2010, 2012). These studies have focused on different aspects of plant–insect interactions, including the influence of climate fluctuations (e.g., Currano et al., 2008, 2010; Wappler et al., 2012; Wilf and Labandeira, 1999; Wilf et al., 2001) or mass extinctions (Labandeira et al., 2002a, b; Wilf et al., 2006). By contrast, limited evidence of plant–insect interactions,

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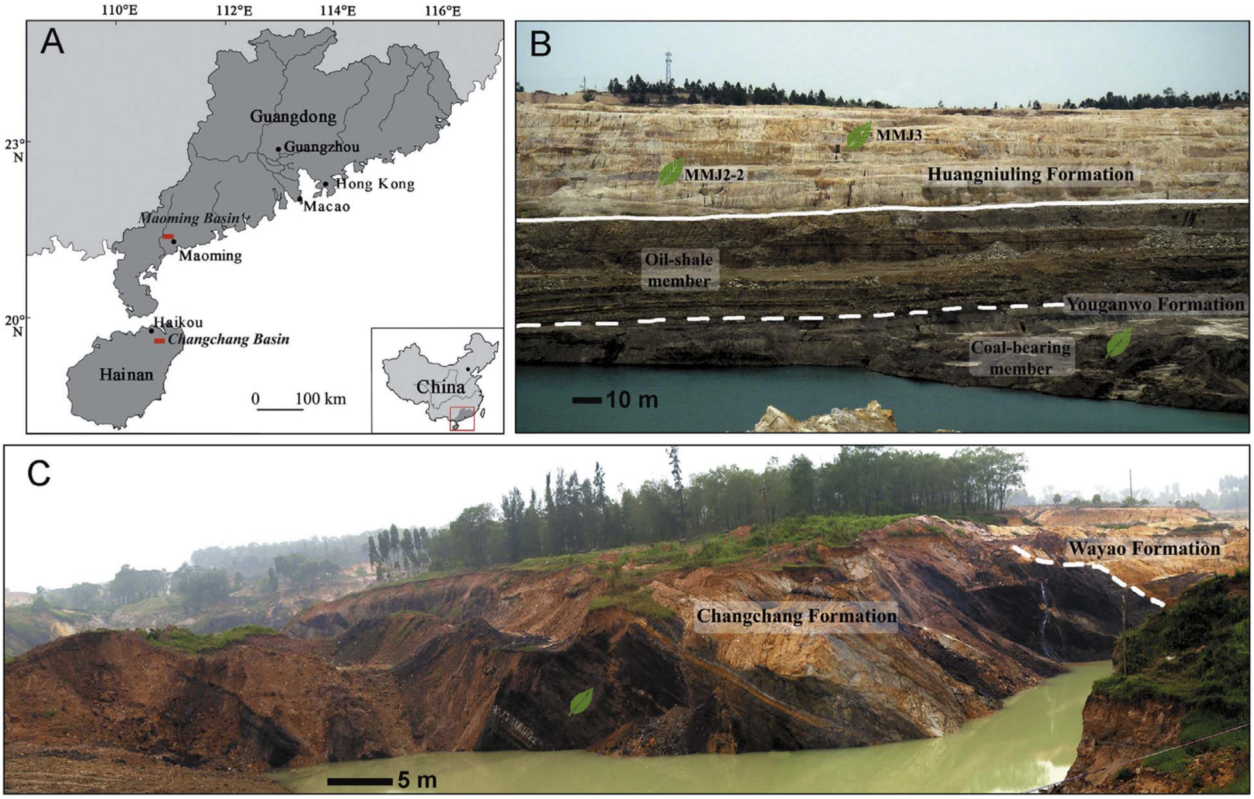

Fig. 1. Geographical and geological setting of the studied sedimentary basins of southern China. A, Location of the Maoming and Changchang basins. B, Geological section of the Maoming Basin. C, Geological section of the Changchang Basin (modified from Spicer et al., 2014). MMJ2-2, MMJ3, and a leaf symbol designate the plant fossil localities.

specifically foliar damage, has been documented from the Cenozoic floras of Asia. Special attention has been paid to the degree and types of insect damage traces on the leaves of fossil plants of the lower Miocene flora of Korea (Paik et al., 2012) and the Cenozoic floras of India (Khan et al., 2014, 2015; Srivastava and Srivastava, 1998; Srivastava et al., 2000), while the effect of Quaternary climate change on plant–insect interactions has been investigated by examination of insect damage on leaves of the genus *Quercus* from the upper Pliocene flora and eight living forests in southwestern China (Su et al., 2015).

Eocene terrestrial biotas from the Cenozoic sedimentary basins of southern China and their associated palaeoclimate have been studied extensively in the last decade (e.g. Aleksandrova et al., 2015; Averianov et al., 2016; Danilov et al., 2013; Jin et al., 2009; Herman et al., 2017; Spicer et al., 2014, 2016, 2017; Wang et al., 2007b; and references therein). The Maoming Basin (Guangdong Province) and the neighboring Changchang Basin (Hainan Island) located about 250 km to the south, provide continuous successions of Paleogene lacustrine and fluvial deposits and yield abundant vertebrate and invertebrate fossils as well as plant remains. Preliminary observations from the exceptionally diverse Eocene floras of these two basins indicate a different rate of plant–arthropod interactions and probably viral, bacterial or fungal infection. Two upper Eocene floras from the Maoming Basin are markedly distinct from the two approximately contemporaneous middle Eocene floras of Changchang and Maoming basins in exhibiting extremely abundant and diverse plant damage types (DTs).

Numerous studies of fossil plant–insect interactions have in general documented positive correlations between temperature and atmospheric pCO_2 concentration and diversity and frequency of insect herbivore damage (Currano et al., 2008, 2010; Wappler et al., 2012; Wilf and Labandeira, 1999; Wilf et al., 2001), which is supported by the observation that in extant tropical and subtropical habitats strong correlations exist between plant diversity and that of herbivorous insects (Haddad et al., 2011; Lewinsohn and Roslin, 2008; Siemann et al., 1998). The purpose of this study was to examine leaf damage types in the Eocene floras of the Maoming and Changchang basins and to reveal possible relationships between frequency and diversity of different damage types and climate. For consistency we focus on well-sampled fossil leaves of *Liquidambar* L. (Altingiaceae) that are present and relatively abundant in both basins throughout the middle to upper Eocene. Studies of long-term changes in insect damage for single plant taxa can help to differentiate changes of damage diversity, frequency, and composition caused by changes in floral composition from those induced by climatic fluctuations (Wappler and Denk, 2011).

Fossil records of *Liquidambar* leaves, more rarely reproductive structures and woods, are widely distributed in the Cenozoic deposits of the Northern hemisphere. Plant fossils similar to the modern genus *Liquidambar* and related to the family Altingiaceae are known from the late Paleocene (Agarwal, 1991; Ferguson, 1989; Friis, 1985; Gottwald, 1992; Graham, 1965; Kirchheimer, 1943; Krassilov, 1976; Mai, 1968; Makarova, 1957; Maslova, 1995, 2003, 2009; Maslova and Krassilov, 1997; Melchior, 1998; Muller, 1981; Pigg et al., 2004). A large number of the *Liquidambar* leaves, and rarely Altingiaceae wood, have been described from the Eocene, Miocene and Pliocene floras of Asia (Endo and Morita, 1932; Huzioka, 1972; Huzioka and Uemura, 1979; Maslova, 1995; Maslova et al., 2015; Onoe, 1974; Oskolski et al., 2012; Ozaki, 1991; Suzuki, 1961; Uemura, 1983; Xiao et al., 2011), Europe (Ferguson, 1989; Koch et al., 1973; Worobiec et al., 2012) and North America (Brown, 1933; Knowlton, 1902; MacGinitie, 1941; Stults and Axsmith, 2011; Wolfe and Tanai, 1980).

The genus *Liquidambar*, along with *Altingia* Noronha and *Semiliquidambar* H.-T.Chang, was considered to represent the family Altingiaceae Horan. (Takhtajan, 2009). Recently, based on the phylogenetic analysis of several molecular markers, fruit anatomy, and pollen morphology (Ickert-Bond and Wen, 2013), all *Altingia* and *Semiliquidambar* species were formally transferred to one genus, *Liquidambar*, consisting of 15 species. The palaeobotanical evidence that

Table 1
Occurrences of damage types on the leaves of fossil *Liquidambar* from South China.

Taxa	No leaves	No leaves with DTs (%)	No DTs occurrences	HF (n)	MF (n)	S (n)	SF (n)	G (n)	BF (n)	No DTs
L. maomingensis	125	49 (39)	79	17	20	23	9	4	6	18
Liquidambar sp. 1	41	20 (49)	31	4	12	8		4	3	11
Liquidambar sp. 2	56	10 (18)	10	2		1		5	2	6

DTs — damage types, HF — hole feeding, MF — margin feeding, S — skeletonization, SF — surface feeding, G — galling, BF — bacterial or fungal infection.

justifies combining the genera *Liquidambar*, *Altingia*, and *Semiliquidambar* into a single genus is the new species *Liquidambar maomingensis* N. Maslova, Kodrul, Song et Jin recently described from the Eocene of the Maoming Basin. Polymorphic leaves of *L. maomingensis* similar to those of extant species previously considered within the genera *Semiliquidambar* and *Liquidambar* are associated with reproductive structures close to those of *Altingia* (Maslova et al., 2015).

2. Geological setting, material and methods

The plant fossils examined were collected from the Maoming and Changchang sedimentary basins of South China (Fig. 1A). The stratigraphic succession of the Maoming Basin located northwest of Maoming City, southwestern Guangdong, comprises upper Cretaceous to Neogene deposits (Nan and Zhou, 1996). The fluvial and lacustrine succession of the Jintang opencast mine (21°43′ N., 110°53′ E) is composed of the Eocene Youganwo and Huangniuling formations (Fig. 1B). The Youganwo Formation consists of interbedded mudstones, siltstones and sandstones with thin coal seams in its lower part and dark brown oil shales in the upper part. Coal-bearing and oil-shale units of the Youganwo Formation contain abundant plant and vertebrate fossils, respectively (see references in Aleksandrova et al., 2015 and Averianov et al., 2016). The overlying Huangniuling Formation is composed mainly of fluvial sandstones, siltstones, and conglomerates with beds and lenses of mudstones and claystones. Well-preserved plant megafossils occur at two horizons of mudstones and claystones near the base of the Huangniuling Formation and in its upper part. Plant megafossil assemblage from the lower horizon consists of at least 139 fossil taxa, including conifers (Pinaceae, Podocarpaceae, and Taxaceae), and angiosperms (Lauraceae, Hamamelidaceae, Altingiaceae, Fagaceae, Fabaceae, Juglandaceae, Myrtaceae, Aceraceae, Dipterocarpaceae, Rhamnaceae, Celastraceae). Taxonomic composition of the megafossil flora from the upper fossiliferous horizon has yet to be completed, but 158 fossil taxa so far identified include ferns (Lygodiaceae), conifers (Pinaceae, Podocarpaceae, and Taxaceae), and angiosperms (Lauraceae, Hamamelidaceae, Altingiaceae, Fagaceae, Fabaceae, Juglandaceae, Myricaceae, Dipterocarpaceae, Rhamnaceae).

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 and Huangniuling formations are considered to be Lutetian-Bartonian and Priabonian in age, respectively (Aleksandrova et al., 2015).

The Paleogene deposits of the Changchang Basin (19°38′ N., 110°27′ E) located northwest of Jiazi Town, Qiongshan County, in the northeastern part of Hainan Island, are subdivided into the Paleocene Changtou Formation and the Eocene Changchang and Wayao formations (Lei et al., 1992; Zhou and Chen, 1988) (Fig. 1C). The fossiliferous Changchang Formation formed in lacustrine, fluvial, and paludal environments and is represented by mudstones, coaly shales and thin coal seams with a few layers of siltstones and sandstones in the lower part of the succession. The upper part of the formation consists mainly of mudstones with several fluvial sandstone units and minor layers of oil shales in the uppermost unit of the formation. Numerous well-preserved plant megafossils, as well as gastropod and bivalve mollusc remains and fish bones, teeth and scales were collected mainly from the lower part of the Changchang Formation. Changchang Flora contains horsetails (Equisetaceae), ferns (Osmundaceae, Blechnaceae, Polypodiaceae, Thelypteridaceae, Salviniaceae), conifers (Podocarpaceae), and angiosperms (Nelumbonaceae, Lauraceae, Fagaceae, Platanaceae, Altingiaceae, Myricaceae, Rubiaceae, Aceraceae, Fabaceae, Moraceae, Juglandaceae, Rhamnaceae, Simaroubaceae, Celastraceae, Arecaceae) belonging to over 200 fossil taxa (Spicer et al., 2014). Based on palynological data the Changchang Formation was dated as late early Eocene to early late Eocene (Lei et al., 1992) or as early–middle Eocene (Yao et al., 2009). The Changchang flora of Hainan Island reveals a notable taxonomic similarity to the Youganwo flora of the Maoming Basin sharing a number of common taxa (Spicer et al., 2014). Due to this similarity, corroborated by a palynological data, these two floras are assumed to be of the same age (Aleksandrova et al., 2015).

The *Liquidambar* fossil leaf impressions and compressions that form the basis of this study were collected from the Huangniuling Formation in the Jintang opencast mine of the Maoming Basin and from the Changchang Formation of the Changchang Basin, Hainan Island. A total of 125 leaves (including 49 leaves with damage traces) of *Liquidambar maomingensis* recovered from the upper part of the Huangniuling Formation, 41 leaves (including 20 specimens with damage) of *Liquidambar* sp.1 from the base of the Huangniuling Formation, and 56 leaves (with 10 damaged leaves) from the Changchang Formation were analyzed (Table. 1). All specimens are housed at the Museum of Biology, Sun Yat-sen University, Guangzhou, China, with collection numbers beginning MMJ2-2 and MMJ3 (collections from the Maoming Basin) and CC (collections from the Changchang Basin).

The modern leaves of *Liquidambar formosana* Hanse have been collected in the Zhongshan Arboretum of Zhongshan City, Guangdong Province. Plant collections in the arboretum are grouped taxonomically by genus. Sampling was carried out in *Liquidambar* area along small tracks. *Liquidambar* trees grow here in semi-natural settings and it seems without pest control. The specimens were collected in December from the outer crowns of five trees located about 10 m from each other. Two small branches per tree with four to nine leaves were randomly selected at around 2 m above the ground.

Damage types (DTs) were assigned using the “Guide to Insect (and Other) Damage Types on Compressed Fossil Plants” (Labandeira et al., 2007); formal morphological classification was used for the description of a fossil columnar gall (Vasilenko, 2005; Vasilenko and Maslova, 2015; Vyalov, 1975).

Fossil leaves were photographed using an Olympus E-500 digital camera and a Panasonic GX7 digital camera with a Leica DG Macro-Elmarit 1:2.8/45 mm macro lens. Microphotography of the leaf damage was performed using Leica M165 and Olympus SZX10 stereo microscopes and a Tescan scanning electron microscope (SEM) under low vacuum conditions without gold coating. All photographs were optimized for size, color and contrast using Adobe Photoshop CS2.

3. Results

3.1. Damage on the leaves of Liquidambar maomingensis (plant fossil locality MMJ3, upper part of the Huangniuling Formation)

The majority of DTs recognized on *Liquidambar maomingensis* leaves

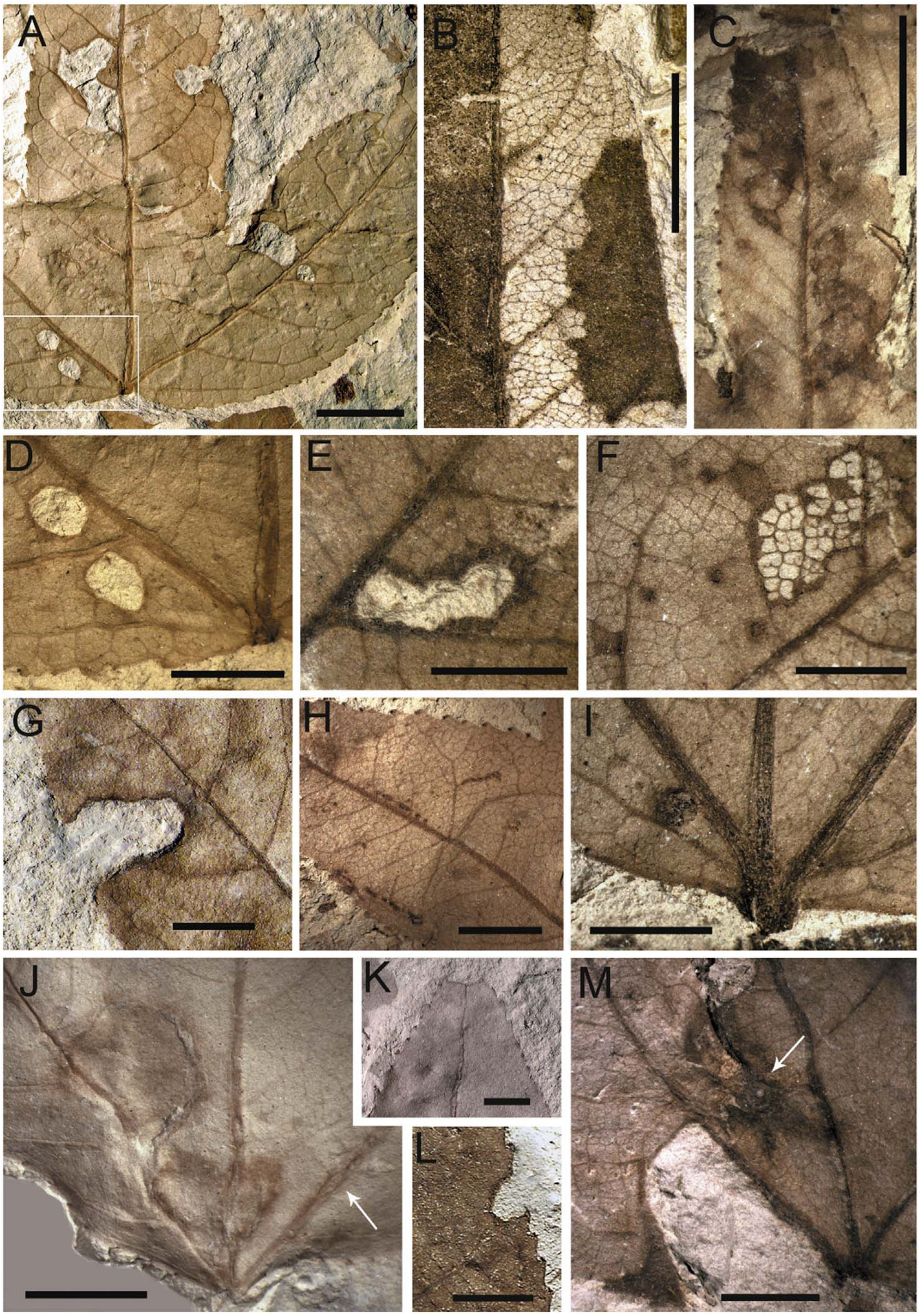

Fig. 2. Damage on the leaves of *Liquidambar maomingensis* N. Maslova, Kodrul, Song et Jin from the upper part of the Huangniuling Formation, Maoming Basin, Eocene, China. A, Circular (DT2) and polylobate (DT3) holes with distinct reaction rim, MMJ3-129a-1. B, Large skeletonized area lacking reaction tissue (DT16), MMJ3-203-1. C, Possible fungal or bacterial infection on the leaf surface, MMJ3-141-1. D, Enlarged view of circular holes from A, MMJ3-129a-1. E, Polylobate hole with well-developed reaction tissue (DT05), MMJ3-326-1. F, Skeletonized area with distinct reaction rim (DT17), MMJ3-788b. G, Margin feeding with an excision that expands toward a primary vein (DT15), MMJ3-022-2. H, Probable surface feeding abrasions, MMJ3-134b-2. I, Circular gall (DT32), MMJ3-788b. J, Probable fungal infection with diffuse reaction front and possible gall similar to DT85 (arrow), MMJ3-062. K, Excision of leaf apex (DT13), MMJ3-772a. L, Margin feeding (DT12) with shallow, semicircular incisions, MMJ3-160-1. M, Marginal feeding (DT13, DT14) and gall with thickened outer rims (DT11), MMJ3-163a-1. Scale bar — 10 mm (A–C) and 5 mm (D–L).

might be assigned to the terrestrial arthropod functional feeding groups (FFG), while three DTs are possibly bacterial or fungal in origin. In total, 18 DTs were found on the leaves, with 79 occurrences for all damage types, 69 of which belong to the external foliage feeding group, four are possible galls and six represent damage traces probably caused by bacteria or fungi (Table 1).

External foliage feeding in *L. maomingensis* includes hole feeding, margin feeding, skeletonization, and surface feeding. Circular perforations and holes (DT01, DT02) range in diameter from 0.6–2.5 mm (Fig. 2A, D). Reaction rims are distinct, and up to 0.5 mm wide (Fig. 2D). Polylobate holes (DT03, DT05) are from 1.5–10.2 mm in length and 0.54–4.1 mm in width (Fig. 2A). Reaction rims are well developed, and up to 0.8 mm wide (Fig. 2E). Margin feeding associations include a semicircular, shallow excision of the leaf margin (DT12) less than 180° of arc (Fig. 2L), measuring 2.5–9 mm wide and 1.5–7 mm deep, a deep excision extending toward the primary veins (DT14; Fig. 2M), an excision of the leaf apex, including the primary vein (DT13; Fig. 2K), and a deeply incised excision of the leaf blade that expands inwardly from the leaf margin (DT15, Fig. 2G). *L. maomingensis* is associated with two skeletonization damage types. The most common of these are large skeletonized areas with a poorly developed reaction rim and with third to fourth order venation intact (DT16; Fig. 2B). The second type of skeletonization is represented by small oval or polylobate areas of leaf lamina with fourth to fifth order venation intact, framed by a distinct reaction rim (DT17; Fig. 2F). Small patches of surface feeding, bound by tertiary and quaternary venation (DT29) or surface abrasion in the form of small scratches (Fig. 2H), are also present.

Three gall damage types caused probably by arthropods are present on *L. maomingensis* leaves. Small darkened circular areas with thickened tissue (DT32) occupy mainly intercostal regions between primary veins. The diameter of these structures ranges between 0.5 and 1.5 mm (Fig. 2F, I). The possibility that this damage type could be caused by fungi cannot be excluded. In general, small structures similar in macromorphology to plant galls may arise as a result of fungal infection, e.g., small button-like structures protruding above the leaf surface of taxodioid conifer, previously considered to be galls (Vasilenko and Karasev, 2006), recently were identified as fruiting body of micromycetes (study in progress).

Other possible circular galls on *L. maomingensis* leaves with a thickened outer rim and a small unhardened central zone are positioned between the midvein and lateral primary veins, or near the leaf margin and surrounded occasionally by a wide polylobate area of darkened leaf tissue (probable DT11; Fig. 2M). The third most likely gall damage type (similar to DT85; Fig. 2J) includes small elliptical to lanceolate structures with a striate surface centered lengthwise on primary veins.

Rounded or ellipsoidal necrotic areas ranging from 1.8 × 4.4 mm to 4.9 × 5.9 mm, surrounded by a broad diffuse reaction front, represent another form of DTs that may have been caused by fungi (Labandeira and Prevec, 2014; Labandeira et al., 2007). These structures are positioned at the leaf base, causing deformation of nearby primary veins (Fig. 2J). One type of damage is represented by irregularly shaped necrotic lesions delimited by distinct reaction rim (Fig. 2C). The cause of these marks is ambiguous, but they may represent fungal or bacterial damage. Small polygonal or oval spots on the leaves of fossil *Liquidambar*, often delimited by higher-order veins, also can be caused by fungi.

3.2. Damage on the leaves of Liquidambar sp.1 (plant fossil locality MMJ2-2, lower part of the Huangniuling Formation)

Of the 41 leaves of *Liquidambar* sp. 1 studied, 20 leaves exhibit at least one type of damage, with a total of 31 occurrences for all damage types (Table 1). In total, 11 DTs are known on these leaves, 10 (28 occurrences) of which could be assigned to the arthropod functional feeding groups. One DT is possibly bacterial or fungal in origin.

The fossil leaves exhibit mostly external foliage feeding, three DTs are probable galls. External foliage feeding on *Liquidambar* sp.1 includes margin feeding, skeletonization, and hole feeding. Margin feeding is characterized by shallow, semicircular excisions of leaf margins, less than 180 degrees of arc (DT12; Fig. 3C, G), measuring 4.5–6 mm wide and 2–2.5 mm deep, with a 0.2–0.6 mm wide reaction rim, a deep excision extending to the primary veins (DT14; Fig. 3C), and an excision of the leaf apex, including the primary vein (DT13; Fig. 3F). Skeletonized areas are exemplified by polygonal patches of completely or partly removed interveinal tissue, with or without reaction rims and third, rarely fourth, order venation preserved (DT16, DT17; Fig. 3C, E, F, I, J).

One specimen was found with several galls and a hole probably remaining following gall loss (Fig. 3A). Dark, circular to ellipsoidal galls, caused possibly by arthropods, are positioned on the primary veins (DT33) and range in diameter from 1.1 to 2.0 mm. Three ellipsoidal galls of another type (DT32) occur on the interveinal regions of the same leaf (Fig. 3A, D). Several elliptical possible galls are centered lengthwise on a midvein of at least one fossil leaf.

One fossil leaf of *Liquidambar* sp.1 exhibits, on both lamina surfaces, small rounded or polygonal marks surrounded by dark thickened tissue (Figs. 3B, H, 4A). The mark diameter varies from 800 μm to 1.5 mm. Other circular thickened rims approximately 200 μm in diameter were revealed within the outer rims by SEM (Fig. 4A). Identifying the cause of this damage is complicated but these traces resemble a consequence of fungal activity.

3.3. Damage on the leaves of Liquidambar sp. 2 (plant fossils from the Changchang Formation)

Of the 56 leaves of *Liquidambar* sp. 2, only 10 exhibited damage traces, most of which have been assigned to the arthropod functional feeding groups (FFG), and two DTs are possibly caused by bacteria or fungi. In total, six DTs were found on the leaves, with 10 occurrences for all damage types, five of which are galls, three belong to the external foliage feeding group, and two represent fungal or bacterial damage (Table 1).

External foliage feeding on *Liquidambar* sp. 2 includes hole feeding and skeletonization. A large-sized, circular perforation was recorded on only one leaf. A lanceolate perforation with a distinct reaction rim on the other leaf also appears to be hole feeding damage (Fig. 5G). One leaf exhibits a small area of skeletonization (DT16; Fig. 5F), two other leaves appear to be infected by fungi or bacteria (Fig. 5C, H, I).

Liquidambar sp. 2 is mostly associated with columnar galls of fusiform shape, adjacent to the primary veins. Earlier, a morphological classification was introduced for three-dimensional fossil gall impressions (Waggoner and Poteet, 1996), which is used here.

4. Systematic paleontology

FAMILY Paleogallidae Vjalov, 1959.

GENUS *Antronoides* Waggoner et Poteet, 1996.

SPECIES *Antronoides changchangensis* sp. nov. N. Maslova et Vasilenko.

Etymology: from the Changchang Basin.

Holotype: CC 1684a-1, CC 1684b, part and counterpart, gall on *Liquidambar* sp. 2 leaf, designated here (Fig. 5A, D).

Repository: Museum of Biology, Sun Yat-Sen University, Guangzhou, China.

Type locality: Changchang Basin, northwest of Jiazi Town, Qiongshan County, northeastern part of Hainan Island, China.

Stratigraphic position and age: Changchang Formation, middle Eocene.

Specific diagnosis: gall columnar, positioned near primary veins, fusiform in shape, protruding above lower leaf surface. Gall attachment area on upper leaf surface circular to ellipsoidal, slightly raised above lamina surface. Circular scars of gall attachment on lower leaf surface marked by finely folded thickened tissue around central core.

4.1. Description

Galls are columnar, protruding significantly above the lower leaf surface, fusiform in shape, tapering in the distal part and at the base. Galls are positioned near primary veins between the secondary veins. 3-D preserved gall on the leaf surface (Figs. 4C, D, 5D) ranges in length from 3 to 7.8 mm and in width from 1.5 to 2.7 mm. Gall attachment areas on the upper leaf surface are circular to ellipsoidal, 2–3 mm in diameter, slightly raised above the lamina surface, with fusainized tissue in a stellate arrangement within the inner area. Circular scars of gall attachment on the lower surface of the leaves are marked by a thickened structure with fine radial folds around a central core (Fig. 5D, E). Gall surface is covered by fusainized tissue (Figs. 4C, D, 5D). Probable early stages of gall development was examined by SEM. Small rounded structures with prominent outer rims, ranging in diameter from 700 to 800 μm, were found on the lower surface of leaves (Fig. 4B).

4.2. Comparison

To date, seven formal fossil species of columnar and horn-shaped galls are known from the Upper Cretaceous to the middle Miocene: two species from the Turonian of Israel (*A. ovatus* (Krassilov) Vasilenko et N. Maslova, 2015, *A. mucronatus* (Krassilov) Vasilenko et N. Maslova,

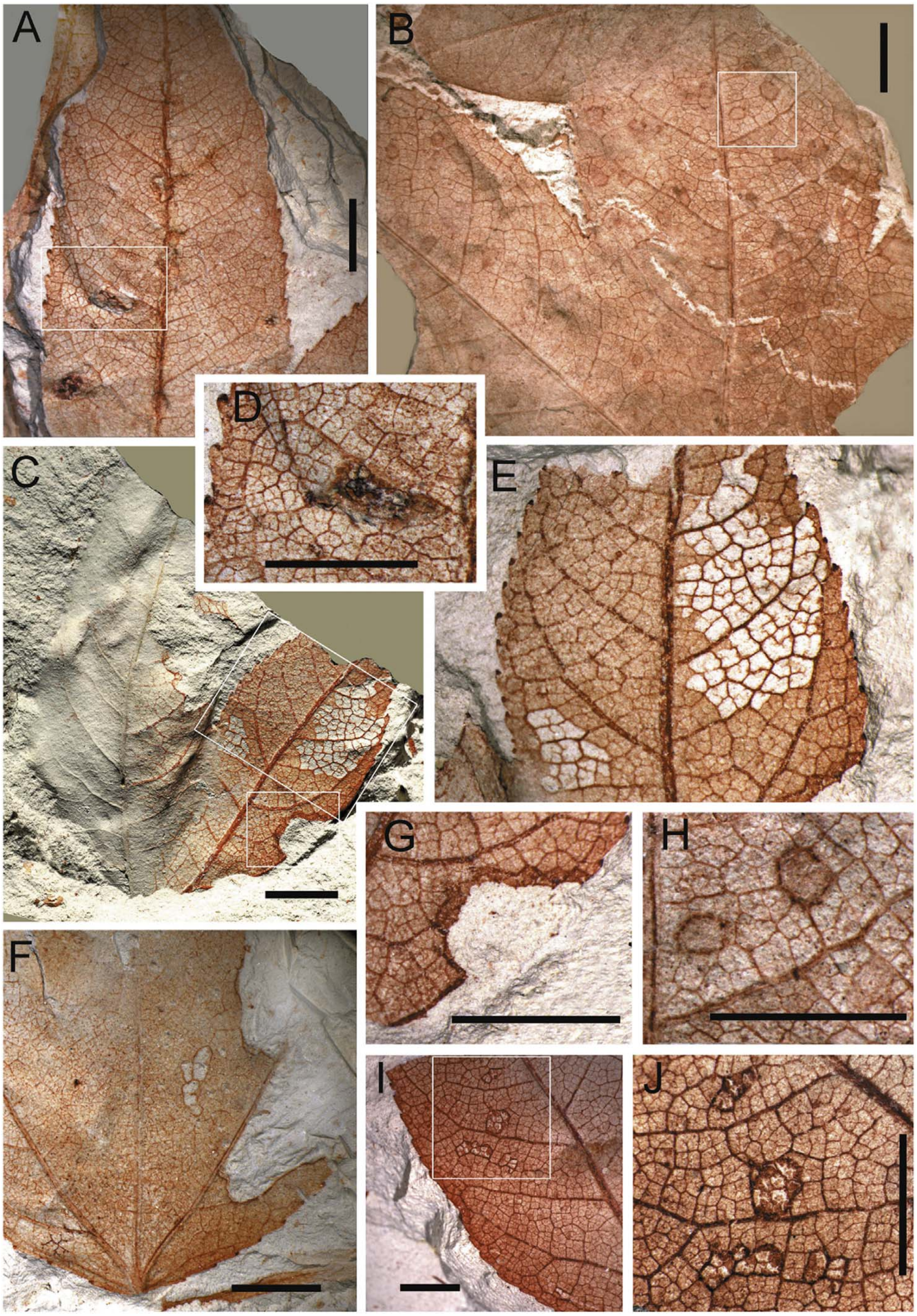

Fig. 3. Damage on the leaves of *Liquidambar* sp. 1 from the lower part of the Huangniuling Formation, Maoming Basin, Eocene, China. A, Circular to ellipsoidal galls positioned on the primary veins (DT33) and three ellipsoidal galls (DT32) occurred on the interveinal regions of the leaf, MMJ2-2-023. B, Probable fungal damage, MMJ2-2-036b. C, Margin feeding (DT12, DT14) and sceletonization (DT16), MMJ2-2-032a-1. D, Enlarged view of gall from box in A. E, Large skeletonized area with poorly developed reaction rim, enlarged view from box in C. F, Margin feeding (DT13) and skeletonization (DT16), MMJ2-2-161b-1. G, Margin feeding (DT12) with relatively shallow, semicircular incisions and distinct reaction tissue, enlarged view from box in C. H, Darkened damage delimited by leaf venation probably caused by fungi, enlarged view from box in B. I, Skeletonization with well-developed reaction rim, MMJ2-2-034b-1. J, Enlarged view from box in I. Scale bar — 5 mm.

2015), one species from the upper Paleocene of Kamchatka (*A. krassilovi* Vasilenko et N. Maslova, 2015), and four species from the Miocene of North America (*A. schorni* Waggoner et Poteet, 1996, *A. oregonensis* Erwin et Schick, 2007, *A. cyanomontanus* Erwin, Schick, 2007 and *A. polygonalis* Waggoner, 1999).

The Turonian *A. mucronatus* and *A. ovatus* are positioned exclusively near the leaf lamina margin. Paleocene galls *A. krassilovi* are scattered over the surfaces of leaves near veins as well as in intercostal areas. In the Miocene species, the galls are typically distributed either more or less evenly over the lamina (*A. cyanomontanus*, *A. polygonalis*, and *A. schorni*) or more densely along the midvein (*A. oregonensis*). *A. cyanomontanus* is the most similar to the new species from the Changchang Basin in the size and shape, a similar attachment scar to the leaf surface with thickened margin and small central pit. The difference is in the localization of *A. cyanomontanus* galls near the secondary veins.

Antronoides changchangensis is similar in gall body shape and attachment type to extant species *Xanthoteras clavuloides* (Kinsey) that develop on the leaves of some species of *Quercus* (Erwin and Schick, 2007; Schick, 2002). *Xanthoteras clavuloides* is distinguished by a lack of drastic deformation of the leaf lamina after gall detachment, only a superficial trace of achlorophyllous tissue remains on the gall attachment scar on the lower surface of the leaf. Galls of this species are induced by representatives of Cynipidae (Hymenoptera). The new species differs from all other species within the genus by the characteristic structure of gall attachment area, which is expressed in both upper and lower surfaces of the leaf. Unlike other species, A. *changchangensis* has a disk of thickened tissue with fine radial folds around a circular core on the lower leaf surface.

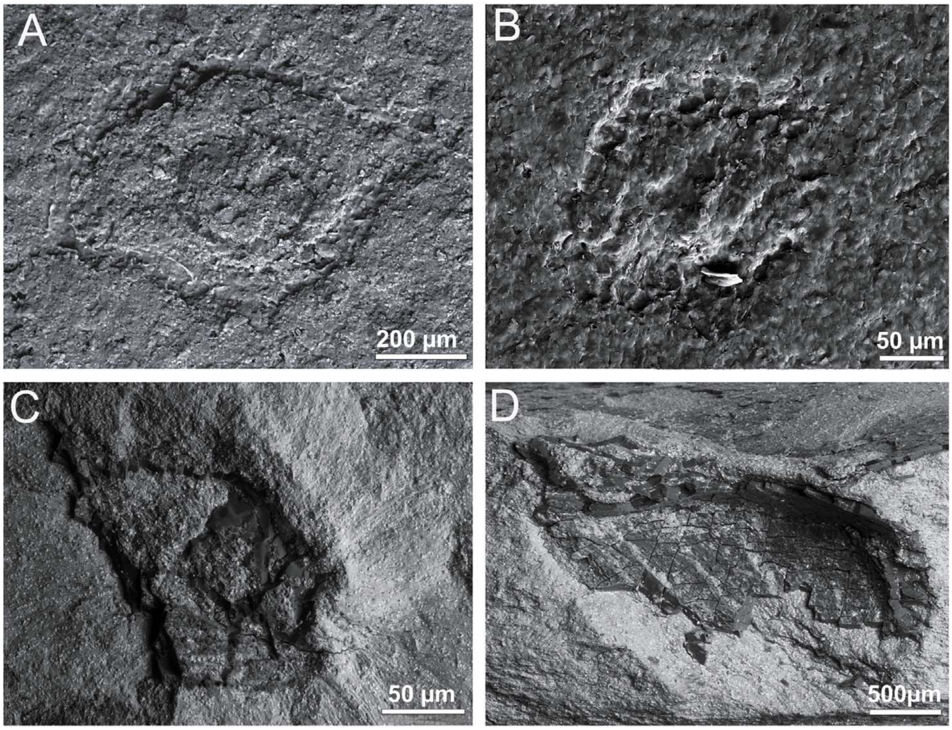

Fig. 4. Damage on the leaves of *Liquidambar* sp. 1 from the lower part of the Huangniuling Formation, Maoming Basin, and *Liquidambar* sp. 2 from the Changchang Formation, Changchang Basin, Eocene, China, SEM. A, *Liquidambar* sp. 1, rounded mark with double rim of thickened tissue, probable fungal damage, MMJ2–2–036b. B–D, Galls *Antronoides changchangensis* sp. nov. on leaves of *Liquidambar* sp. 2. Rounded structure with prominent outer rim on the lower surface of the leaf (B), CC 1684b. The gall attached scar on the lower surface of the leaf with thickened outer rim and fusainized tissue inside (C), CC 1684b. Three-dimensionally preserved gall on the lower leaf surface with fusainized tissue; side view of gall in C (D), CC 1684b.

4.3. Remarks

The genus *Antronoides* was established for Miocene galls with the following diagnosis: “elongated fusiform galls with annulate bases on leaves of *Quercus hannibali*”, an analogue of the modern species *Q. chrysolepis* Liebmann (Waggoner and Poteet, 1996, p. 1081). Subsequently, Waggoner (1999) included in the diagnosis a direct reference to the possibility of using this genus for similar fossil galls. We assign our material to the genus *Antronoides*, which is applicable for columnar and elongate galls in which gall length exceeds the width.

4.4. Material

Three specimens (part and counterpart): CC1684a-1 and CC1684b, holotype; CC1682a-1 and CC1682b-2; CC1683a and CC1683b.

5. Evaluation of results and discussion

Leaves of fossil *Liquidambar* with the studied damage types occur in neighboring sedimentary basins located approximately 250 km from each other and characterized by similar geological settings and age. These fossil leaves have similar morphological features, but can be assigned to different species due to some clear morphological distinctions.

Recently described (Maslova et al., 2015) *L. maomingensis* from the upper part of Huangniuling Formation differs from previously known fossil species of *Liquidambar* in the range of the lamina shape from 3-lobed (occasionally with additional small lobe on one side of the lamina) to unlobed. Similar variability of the lamina shape is observed in extant *Liquidambar* species previously belonging to the genus *Semiliquidambar*. Leaves of the more ancient *Liquidambar* sp. 1 from the lower part of the Huangniuling Formation are exclusively 3-lobed. Along with basal venation that is characteristic of most modern *Liquidambar* species, they possess suprabasal venation characteristic of 3-lobed leaves of the former genus *Semiliquidambar*. Even more ancient *Liquidambar* sp. 2 from the middle Eocene Changchang Formations of Hainan Island is characterized by both 3- and 5-lobed leaves with long narrow lobes. They also include morphotypes with basal and suprabasal venation of the lower pair of lateral primary veins.

Hence, three different taxa of *Liquidambar* occurred in the Eocene of South China. In foliar morphology they were similar to each other but different from the modern species of this genus. They are characterized by a mosaic combination of morphological features inherent to more divergent modern species of the genus previously belonging to different genera (Ickert-Bond and Wen, 2013).

Nevertheless, these three *Liquidambar* taxa possess different associations of leaf damage types. The percentage of each functional feeding group and probable fungal or viral infection in these taxa are shown in Fig. 7. *L. maomingensis* exhibit mostly external foliage feeding (hole feeding, margin feeding, skeletonization, and probably surface feeding), but galling is present only very rarely. Damage types on *Liquidambar* sp. 1 include margin feeding, skeletonization, and hole feeding, while three DTs are probable galls. *Liquidambar* sp. 2 hosts mostly columnar galls. No clearly distinguishable mines have been recorded on the *Liquidambar* leaves from the Maoming Basin. It is possible that this type of arthropod feeding may have been overlooked. Identification of some fossil plant damage types and causative biotic agents can involve certain difficulties (Labandeira and Prevec, 2014; Maslova et al., 2016). Indeed, a variety of holes in the leaves could be result of insect hole feeding, or excision of necrotic leaf tissue of blotch mines, or loss of necrotic tissue surrounding the site of pathogenic (fungal, viral or bacterial) infection.

Overall, most insect DTs on *Liquidambar* leaves from the Maoming Basin belong to the external foliage feeding group. Skeletonization and margin feeding are two predominant types of insect damage for both *L. maomingensis* and *Liquidambar* sp. 1. Both taxa had leaves typically displaying large patches of skeletonized tissue with poorly developed reaction rims. Margin feeding damage of the same types was also present on the leaves of both *Liquidambar* taxa from Huangniuling Formation. Margin excisions differ in morphology and size, and could be caused by different arthropods. The percentage of arthropod endophytic feeding damage types (galls) are higher on *Liquidambar* leaves from the Changchang Basin. Our data indicate a distinct trend toward overall higher damage diversity and frequency on the leaves of *Liquidambar* from the middle Eocene Changchang flora to the upper Eocene Upper Huangniuling flora (Fig. 7). On the other hand, the proportion of endophytic feeding damage (galls) increases significantly

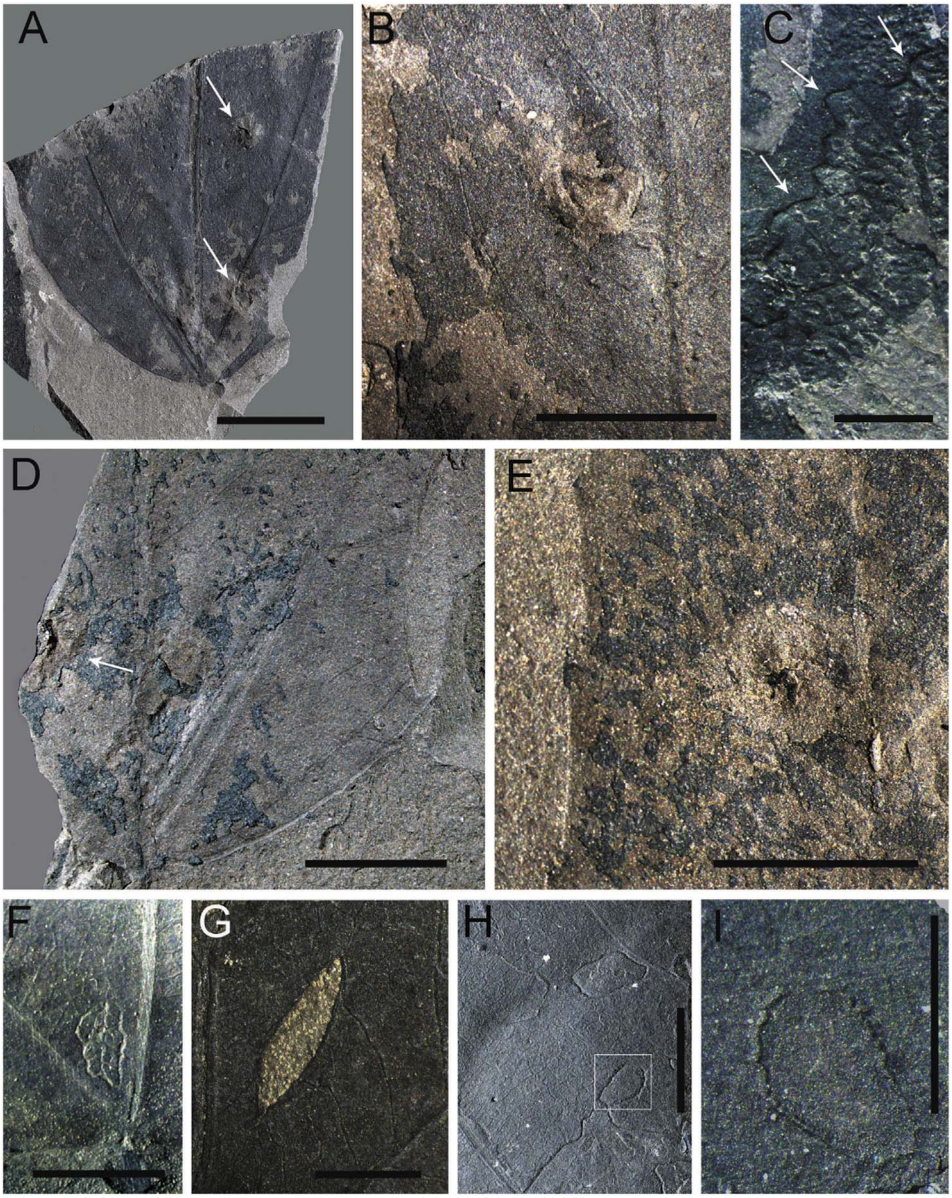

Fig. 5. Damage on the leaves of *Liquidambar* sp. 2 from the Changchang Formation, Changchang Basin, Eocene, China. A, Attachment areas (arrows) of galls *Antronoides changchangensis* sp. nov. on the upper surface of leaf, CC 1684a–1, holotype. B, Attachment area of gall *Antronoides changchangensis* sp. nov. on the upper surface of leaf, CC 1682a–1. C, Probable bacterial or fungal infection, arrows indicate the outer rim of the damaged area, CC 1224. D, Attachment scar (arrow) of gall *Antronoides changchangensis* sp. nov. on the lower surface of leaf, CC 1684b, holotype. E, Attachment scar of gall *Antronoides changchangensis* sp. nov. on the lower surface of leaf, counterpart of leaf shown in B, CC 1682b-2. F, Skeletonized area (DT16), CC 771. G, Hole feeding or possible abiotic tear, CC 880. H, Possible fungal damage, CC 1681b. I, Enlargement of possible fungal damage shown in box in H, counterpart CC 1681a. Scale bar — 10 mm (A), 5 mm (B, D–F, H), and 2.5 mm (C, G, I).

downsection, from *Liquidambar maomingensis* from the Upper Huangniuling flora to *Liquidambar* sp. 2 from the Changchang flora (Fig. 8). A similar, but less pronounced, trend is observed for the percentage of damage probably caused by fungi or bacteria.

An analysis of available data on fossil *Liquidambar* with leaf damage caused by insect or other phytopathogens revealed only evidence of blotch and circular mining on leaves of *Liquidambar europaeum* A. Br. from the lower Miocene of the Most Basin in North Bohemia (Knor et al., 2012).

We compared also the damage types on the leaves of studied fossil *Liquidambar* taxa and similar extant species *L. formosana* Hanse collected from the Zhongshan Arboretum in Guangdong Province. In (sub) tropical climates most temperate broad-leaved species exchange leaves within a few weeks in January/February (Borchert et al., 2005), hence the leaves of *L. formosana* were collected at the end of the growing season (in December). The leaves of extant species exhibit a greater number of damage types and their occurrences. Of the 78 leaves analyzed, 54 leaves were damaged. The most abundant DTs are specialized and caused by miners and gallers. Mine association includes relatively small sized full depth blotch mines with small exit holes (Fig. 6H, I), large mines with serpentine and blotch phases developed often between the leaf margin and primary veins (Fig. 6J), and skeletonized areas damaged by leaf miners (Fig. 6E–G). Galls are represented mainly by very small (less than 1 mm) circular structures occurring on both sides of the leaf, with small openings on the lower leaf surface and thickened small swellings on the upper leaf surface. They are scattered over leaf lamina, and often are locally abundant. Occasionally the gall chambers contain a single white larva. In the dried condition the galls easy fall from the lamina, leaving small rounded holes in the leaf (Fig. 6L, M). In terms of frequency, galling is followed by hole and margin feeding (Fig. 6A–C) and then by fungal damage (Fig. 6K). The remains of possible pests of *Liquidambar* were found on the leaf surface (Fig. 6D, I, M).

The interactions of two dominant groups of terrestrial ecosystems, plants and herbivorous arthropods, are affected by numerous abiotic and biotic factors influenced by environmental variability and evolutionary processes. Among them different rates and compositions of plant pathogen and herbivorous insect traces in fossil and extant *Liquidambar* can be determined in large part by climatic conditions. The quantitative palaeoclimate estimates obtained using CLAMP (Herman et al., 2017; Spicer et al., 2014, 2016) indicate a subtropical to tropical temperature regime for the Changchang, Youganwo and Huangniuling floras. Leaf physiognomic spectra from the Youganwo and

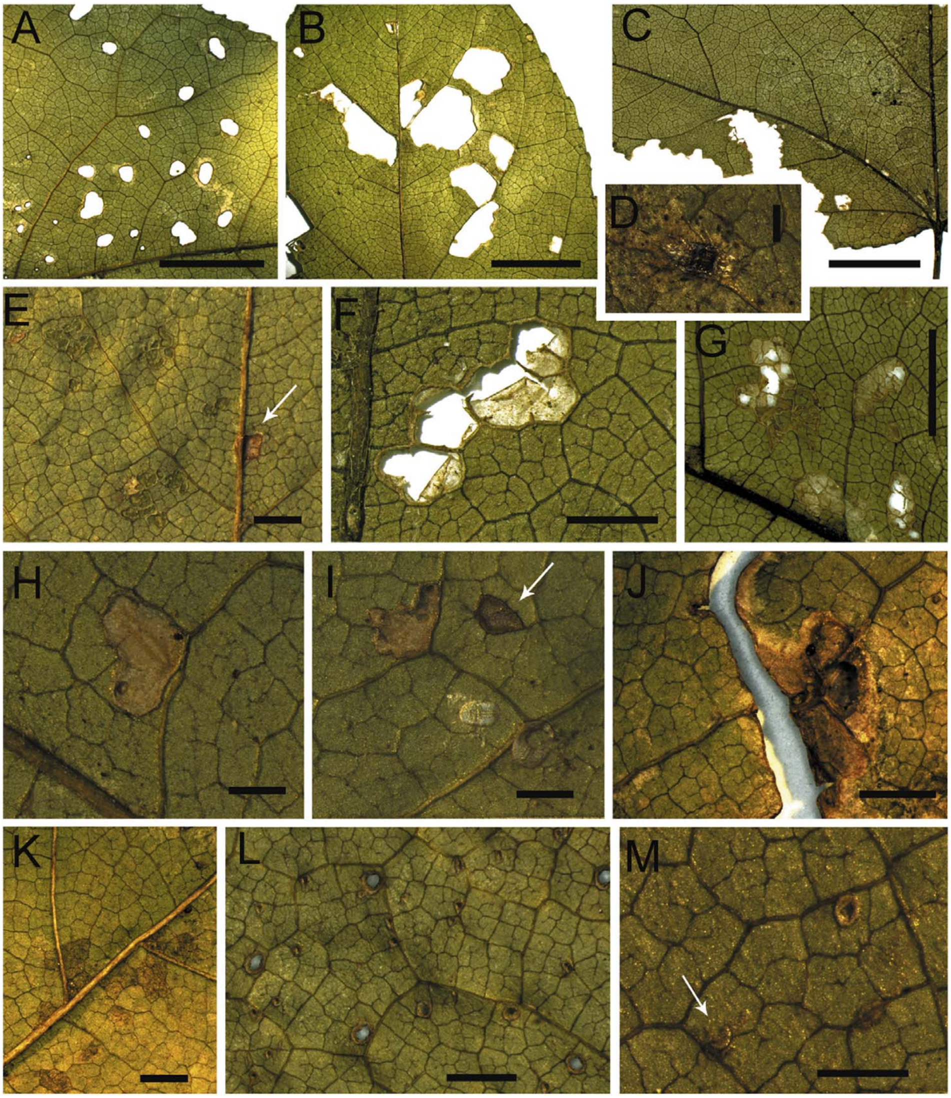

Fig. 6. Damage on the leaves of *Liquidambar formosana* Hanse from the Zhongshan Arboretum of Zhongshan City, southern Guangdong Province, China. A, Small semi-circular feeding holes. B, Large polylobate feeding holes. C, Margin feeding. D, Insect remains on the leaf surface. E–J, Different types of mines caused possibly by Lepidoptera, and probable fungal damage (arrows). Note the insect remains in I. K, Fungal damage. L, M, Small galls, view from lower leaf surface, note the larva inside in M (arrow). Scale bar — 10 mm (A–C), 5 mm (G), 2 mm (E, F, J–L), and 1 mm (D, H, I, M).

Huangniuling formations demonstrate a progressive warming during this time, and a possible increase in the wet/dry season precipitation ratio. Overall the climate was humid, and the length of the plant growing season was close to 12 months. The estimated mean annual temperature (MAT; uncertainty ± 4.7 °C, 2 s.d.) experienced by plants of the Upper Huangniuling flora is 24.0 °C, growing season precipitation (GSP; uncertainty ± 122.0 cm, 2 s.d) is ~2400 mm. The Lower Huangniuling flora experienced a MAT of 20.7 °C and a GSP ~ 2330 mm, and for the Changchang flora the following estimates were obtained: MAT 21.3 °C and GSP ~ 2020 mm (Spicer et al., 2016). Eocene pCO_2 concentration reconstructed based on the regression approach and the stomatal ratio method by using the stomatal density (SD) of *Nageia* fossil leaves from the Youganwo and Huangniuling formations shows a very moderate increase from the middle Eocene to the

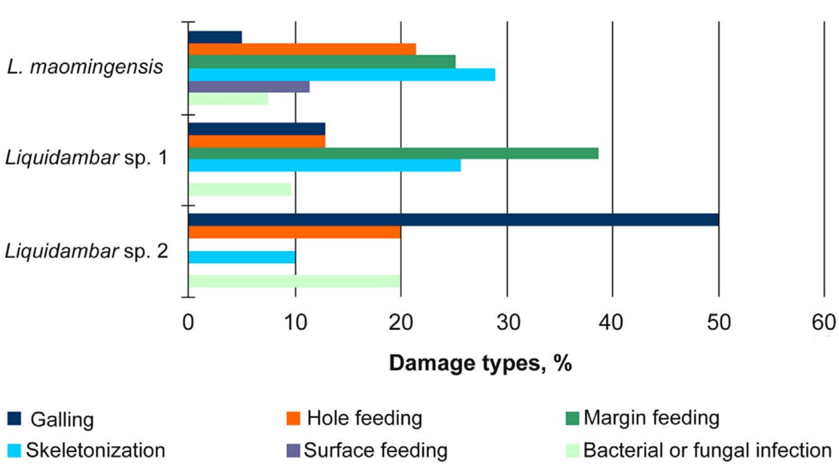

Fig. 7. Percent of occurrences of each damage types (DTs) on the leaves of the Eocene *Liquidambar* from southern China calculated relatively to all damage occurrences on the leaves of each taxon.

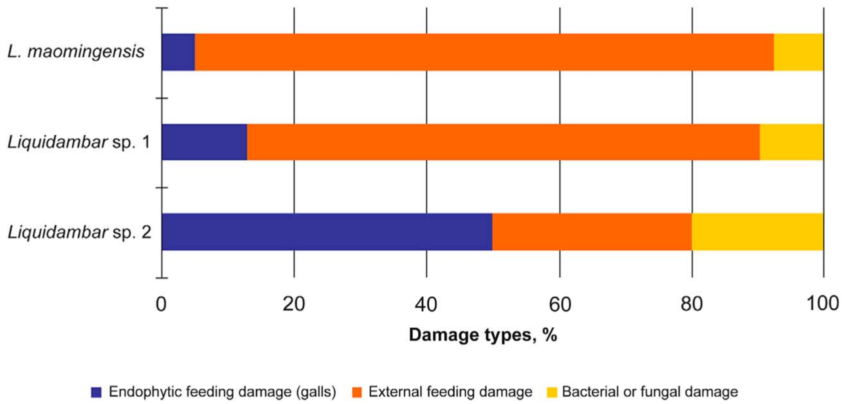

Fig. 8. Relation between percentage of occurrences of arthropod endophytic feeding damage types (galls), external feeding damage types and possible viral or fungal damage on the leaves of the Eocene *Liquidambar* from southern China.

late Eocene (Liu et al., 2016). Although climatic changes in terms of temperature and precipitation variability during the middle–late Eocene was not considerable, rainfall seasonality increased progressively in South China achieving modern monsoon-like wet season/dry season precipitation ratios by the early Oligocene (Spicer et al., 2016). The increase of the climate seasonality from middle to late Eocene in the region may have influenced the abundance and diversity of different insect groups (e.g., Denlinger, 1980; Pinheiro et al., 2002).

At present, a part of southern China, including Guangdong province, experiences a complex climate regime generated by an interaction of two monsoon systems: the South Asia Monsoon and the East Asia Monsoon (Wang and Ho, 2002). On the Updated world map of the Köppen-Geiger climate classification (Peel et al., 2007) the climate of the Guangdong Province is assigned to Cwa (humid subtropical climate with winter dry month precipitation and a hot summer). The observed climatic parameters of Zhongshan city, where modern leaves of *Liquidambar formosana* were collected, indicate a mean annual temperature 22.6 °C and year-round rainfall ~ 1625 mm (Climate-Data.org, n.d., https://en.climate-data.org/location/2735/). December and January are the driest months of the year, with 27–28 mm of rainfall. Most precipitation falls in June and July, with an average of 271 mm. As mentioned above, damage types caused by leaf miners and gallers predominate on the leaves of extant *Liquidambar formosana* from the Zhongshan Arboretum. The relative abundance of galls with some inhabitants inside most probably reflects seasonal reproductive activity of leaf gallers, whose larvae develop and leave the cecidia in the driest months of the year in this region.

According to a range of studies, elevated CO_2 typically increases the concentration of foliar carbohydrates and decreases nitrogen content, resulting in a lowered concentration of leaf protein and an increase in C/N ratio (Bezemer and Jones, 1998; Robinson et al., 2012; Stiling and Cornelissen, 2007). The concentrations of tannins and other phenolics also increase with elevated CO_2, as well as leaf toughness (Stiling and Cornelissen, 2007). Together, these factors contribute to the declining nutritional quality of leaves, causing herbivore compensatory feeding. Experimental field study and meta-analysis conducted by Stiling and Cornelissen (2007) revealed that reductions in insect abundance under elevated CO_2 were much stronger for specialist herbivores than for generalists, and abundance and relative damage were the only effects that significantly differed among herbivore types. Our results for herbivores in the middle–late Eocene of South China are basically in accordance with these data, but a minor difference in estimated atmospheric pCO_2 concentrations (Liu et al., 2016) could not have been a sufficient reason for a simple explanation of significantly different damage level in the fossil *Liquidambar* leaves studied.

Plant physiological responses to elevated CO_2 and the interactions between plants and insects were also studied using free-air CO_2 enrichment (FACE) technology in a closed canopy *Liquidambar styraciflua* plantation in Tennessee (Oak Ridge National Laboratory) and in the Duke forest (North Carolina) dominated by *Pinus taeda*, with *L. styraciflua* and *Liriodendron tulipifera* L. as sub-dominants and forty-eight species of woody plants in the understory (DeLucia and Thomas, 2000; Hamilton et al., 2004; Kim et al., 2015; Knepp et al., 2005). Long-term high CO_2 concentrations stimulated photosynthesis and plant growth, e.g. light-saturated photosynthetic rate for *L. styraciflua* more than doubled at the maximum (DeLucia and Thomas, 2000). Xylem cell sizes and cell wall thickness of *L. styraciflua* wood also were significantly impacted by higher CO_2 concentration (Kim et al., 2015). Leaf chemistry varied distinctly by year and across species but no evidence for statistically significant changes in leaf carbon and nitrogen concentrations, C/N ratio, sugar, starch and total leaf phenolics were found (Hamilton et al., 2004; Knepp et al., 2005). In contrast to predictions that herbivory may increase under elevated CO_2, the FACE experiments revealed a decrease in leaf damage by insect herbivores in these naturally established forest communities (Hamilton et al., 2004; Knepp et al., 2005). *Liquidambar styraciflua* typically experienced low level of insect damage under elevated CO_2 (Knepp et al., 2005). Similar results were obtained from the fossil record of plant–insect associations. Palaeoecological analysis of herbivory in the late Paleocene–early Eocene floras of the Western Interior US demonstrated that temperature and pCO_2 are uncorrelated with total insect consumption at the ecosystem level (Currano et al., 2016).

The widely accepted idea of a latitudinal trend in the intensity of biotic interactions (Coley and Aide, 1991; Coley and Barone, 1996) can scarcely be considered as an explanation for different rate of plant damage in the Eocene floras of South China, particularly since the Youganwo and Changchang floras, which are regarded as contemporaneous, existed almost at the same latitudes (difference is about 2–3°) and experienced equally low level of plant damage. Furthermore, since the broad literature reviews of Coley and Aide (1991) and Coley and Barone (1996), many studies (Adams et al., 2009, 2010; Moles et al., 2011; and references herein) have tested the hypothesis that herbivory and plant defense are more intense at lower latitudes. These recent studies and meta-analyses showed no significant latitudinal trend in herbivory and no significant effect of latitude on plant physical defense, while overall chemical defenses were significantly higher in plants from higher latitudes (Moles et al., 2011).

Taxonomic differences between the Eocene floras of southern China under consideration could be another significant reason for the different overall rates of herbivory in these palaeofloras. The Changchang flora from the Hainan Island is dominated mainly by evergreen taxa of Lauraceae and Fagaceae. Plant species with thick, tough-textured leaves are abundant in this flora. According to a range of studies, leaf mass per unit area (LMA), one of the important morphological leaf functional traits, is generally positively related with leaf thickness and leaf density, but shows negative relationships with foliar nutrient concentration. Leaves with high LMA negatively correlate with herbivory with the leaves tending to have greater toughness, lower nutritional quality and longer life-span (e.g., Coley, 1983; Coley and Barone, 1996; de la Riva et al., 2016; Royer et al., 2007; Wilf, 2008; Wright et al. 2004). Consistent with these data, leaves of *Liquidambar* sp. 2 from the Changchang flora differ from those of the other two Eocene *Liquidambar* taxa by possessing a thicker, presumably coriaceous, leaf texture. However, some previous studies of plant fossils (Currano, 2009; Currano et al., 2008; Wappler et al., 2009) showed no significant correlation between the LMA and insect damage. Because of the preservation condition of plant fossils we cannot estimate LMA for each *Liquidambar* taxa using the Royer et al. (2007) petiole width proxy. Comparative studies of leaf traits in extant species of *Liquidambar* and analysis of associated insect damage, which could help indicate what trends in herbivory we might expect in extinct species, are virtually lacking. Only the bioactivity of chemical constituents from the bark, stems, leaves, and fruits of *Liquidambar* are relatively well studied (Lingbeck et al., 2015). Overall, leaves of the species of *Liquidambar* contain high amounts of tannins. An assessment of leaf toughness, leaf total phenolic and tannin concentrations for 51 tree species from subtropical forests in south-east China revealed the highest tannin concentration in the leaves of *L. formosana*, whereas leaf toughness was one of the lowest (Eichenberg et al., 2015).

Plant leaf traits are one of the main factors that determine palatability of plants for herbivorous insects. Anti-herbivory plant traits comprise a wide range of morphological, chemical, and physiological features. The patterns of plant investment in biotic defense have been emphasized in several fundamental hypotheses for the evolution of plant defense strategies. Among them, the plant apparency hypothesis (Feeny, 1976; Rhoades and Cates, 1976) and the resource availability hypothesis (Coley et al., 1985) are the most known and influential.

According to the apparency theory, the risk of plant discovery by herbivores is responsible for the type and allocation of the plant defense mechanisms. For example, early successional plants (or short-lived and ephemeral plants) with unpredictable distributions in time and space (unapparent plants) can potentially avoid discovery by herbivores and may invest only in less costly allelochemicals in low concentrations (qualitative defenses), which are effective mainly against generalist herbivores. Apparent plants that are distributed predictably should have higher investment in secondary metabolites (e.g., tannins) for effective defense against both generalist and specialist herbivores (quantitative defenses). Based on these statements, several extant species of *Liquidambar* regarded as fast-growing successional pioneer species (Brewer, 2001; Chen et al., 2017) may be considered as typical unapparent plants. One would expect that fossil *Liquidambar* plants from the Maoming Basin, apparently inhabiting an alluvial plain, possessed similar life-history strategies. Despite that, plants of these both *Liquidambar* taxa have been significantly damaged by leaf-chewing insects. In contrast of predictions of the plant apparency theory, high herbivory level on early successional, fast-growing pioneer species was also revealed by meta-analysis and several recent studies (Endara and Coley, 2011; Lemoine et al., 2017).

The resource availability hypothesis (or growth-rate theory) provides an alternative explanation of the observed patterns of herbivory and plant defense. This theory predicts that plant species adapted to resource-rich environments have faster growth rates and shorter leaf lifetimes than species adapted to resource-poor environments, and fast-growing species support higher herbivory rates than slow-growing species because they are less defended (Coley et al., 1985; Endara and Coley, 2011).

Resource availability is often associated with habitat disturbance and successional stage. Consequently, the successional status of plants should be correlated with their defense investment (Coley et al., 1985). These predictions correspond well with the data obtained from our study. The differences in leaf damage types in the Eocene *Liquidambar* taxa might be related to their different successional rank. As noted above, some extant species of *Liquidambar* are generally dominants or companion species during early successional stages, but commonly persist in the later successional stages (An et al., 2001; Brewer, 2001; Chen et al., 2017). Native to East Asia *Liquidambar formosana* and *L. acalycina* Chang occur widely in the late-successional subtropical evergreen broad-leaved forests dominated by species of the families of Fagaceae and Lauraceae (Wang et al., 2007a,b). As already mentioned, apparently, fossil *Liquidambar* taxa from South China could have possessed similar life strategies. Early successional riparian forest habitats on the nutrient-rich alluvial soils were widespread during deposition of the Huangniuling Formation. Well-preserved plant megafossils, including leaves of *L. maomingensis* and *Liquidambar* sp. 1, occur subautochthonously in lenses of siltstones and claystones represented pond deposits in alluvial sandstones. In contrast, *Liquidambar* sp. 2 from the Changchang Basin could have belonged to the late-successional plant communities dominated by evergreen species of the Fagaceae and Lauraceae families. Similar to modern species, fast-growing and long-lived trees of *Liquidambar* sp. 2 could have inhabited bordering the Eocene lake hillside forests as the upper canopy trees and along streamsides.

These assumptions and our data for herbivore damage in fossil *Liquidambar* taxa are in accordance with the results of ecological studies conducted for evaluation of biogeographical, altitudinal, and successional gradients in specialist insect species, particularly in the gall-forming insect species. Several studies have documented a decline of generalist insect species along the successional gradient and a marked increase of specialists in later successional plant communities (Brown, 1985; Fernandes et al., 2010).

A range of studies have focused on a testing of the harsh environment hypothesis predicted that galling species richness should vary in response to environmental variables such as moisture and temperature. Galling species frequency was higher in xeric habitats than in mesic habitats (Fernandes and Price, 1988, 1992; Lara et al., 2002), whereas the richness of free-feeding herbivore species exhibited the opposite pattern (Fernandes and Price, 1988). The lowest richness of plants with gall-forming insects and the smallest number of gallers per individual plant were detected in plants growing on more fertile soil (alluvial). Conversely, the highest number of plants with galls, and the highest gall-forming insect richness per plant, were found at a vegetation site where the poorest soil was recorded (Cuevas-Reyes et al., 2003). A positive relationship between the frequency and diversity of specialist feeders and forest age were demonstrated for two Oligocene tropical floras from Ethiopia (Currano et al., 2011). Overall rate of insect damage diversity was also higher in the later successional forest, which had greater floral richness.

6. Conclusions

Our study presents for the first time previously undocumented information on biotic damage in the Eocene low-latitude floras of southern China. A preliminary comparison of four Eocene floras from the adjacent Changchang and Maoming sedimentary basins confirmed different rates of plant–biotic interactions in these very diverse floras. Our results show significant differences in intensity of arthropod and phytopathogen damage in both bulk floras and in individual taxa. The diversity and frequency of DTs are significantly higher on the leaves of *L. maomingensis* and *Liquidambar* sp. 1 from the Huangniuling Formation of the Maoming Basin than in *Liquidambar* sp. 2 from an older flora of the Changchang Basin. Both *Liquidambar* taxa from the Huangniuling floras exhibited generally external foliage feeding, whereas *Liquidambar* sp. 2 was mainly subjected to endophytic foliage feeding damage like galls.

A combination of multiple biotic and abiotic factors may have affected the intensity and types of plant–arthropod herbivore interactions in these low-latitude floras. A rise in the diversity and frequency of DTs from middle to late Eocene could have been to some extent influenced by a progressive warming and an increase of the climate seasonality in the region. Taxonomic differences of the studied palaeofloras might have been another contributing factor for the different rate of herbivory. The interactions between plants and herbivores are generally highly sensitive to plant leaf traits, the composition of vegetation, and microenvironmental variations in light, temperature, and humidity. More particularly, we hypothesize that the different successional status of the three Eocene *Liquidambar* taxa might be one of the most plausible arguments for the explanation of their different response to the plant pathogens. *L. maomingensis* and *Liquidambar* sp. 1 from the Maoming Basin apparently inhabited the early successional riparian forests on the nutrient-rich alluvial soils, whereas *Liquidambar* sp. 2 from the Changchang Basin, with higher galling frequency, may have been a component of the later successional forests similar to the modern subtropical evergreen broad-leaved forest of China that are dominated by species of the Fagaceae and Lauraceae families.

However, only individual taxa from the Eocene floras of southern China have been investigated for biotic leaf damage at the present time. Further testing of overall plant–biotic interactions on the floras of the Maoming and Changchang basins is needed to explore further the results obtained from this study.

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