

Liquidambar (Altingiaceae) and associated insect herbivory from the Miocene of southeastern China

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ABSTRACT

The infructescences and associated leaves of *Liquidambar* from the middle Miocene Fotan Group, southeastern China, were assigned to a new species, *Liquidambar fujianensis* sp. nov., based on their long persistent styles, fruit morphological and anatomical characters. The comprehensive anatomical information on the infructescences, including the seeds, inner carpel wall cells and outer fruit tissue cells, were discussed and compared in detail. The infructescences and leaves are considered to belong the same plant and have a close relationship with the modern species *Liquidambar formosana*. Insect-mediated damage was investigated on the leaves of *L. fujianensis* sp. nov., and five principal types of damage, hole feeding, margin feeding, surface feeding, skeletonization, and galling, were categorized. The damage richness indicates that our fossils were distributed in a region with a warm and wet climate, and we inferred that the possible phytophagous insect as herbivore culprits against *L. fujianensis* sp. nov. of the middle Miocene Fotan flora belong to the insect orders Coleoptera, Lepidoptera and Hemiptera.

1. Introduction

Based on molecular studies, Altingiaceae Horan. is treated as a separate clade of Saxifragales within a larger rosoid clade (Magallón et al., 1999; Judd et al., 2002; APG, 2003; Takhtajan, 2009). *Liquidambar* L. is a monotypic genus of Altingiaceae, and it consists of 15 species (Ickert-Bond and Wen, 2013) exhibiting an intercontinental disjunction from eastern and western Asia to North and Central America (Ferguson, 1989; Wen, 1999; Ickert-Bond and Wen, 2006). Fossil records of Altingiaceae are abundant in the Cenozoic floras of the Northern Hemisphere, especially the Neogene floras, with numerous occurrences of fossil leaves, infructescences, seeds, pollen, and wood (Tanai, 1976; Ferguson, 1989; Maslova, 1995; Meyer and Manchester, 1997; Maslova et al., 2015). The earliest fossil records confirmed by inflorescences were described from the Late Turonian (Late Cretaceous) Lower Magoghy Formation of New Jersey (Zhou et al., 2001) and the Late Santonian (Late Cretaceous) Allon flora of central Georgia (Herendeen et al., 1999). *Liquidambar* flourished across a wide area during the Miocene, including Japan, China, Korea, Central Asia, Asia Minor, Central Europe and western North America (Hoey and Parks, 1994), and then disappeared in Europe and northwest America during the Pleistocene (Uemura, 1983; Ickert-Bond and Wen, 2006) but still persisted in the lower latitude regions of western and eastern Asia and eastern North America. The spatiotemporal distribution of *Liquidambar*

indicates that the genus apparently arose in the Late Cretaceous of Laurasia, and then it became widespread in North America and Eurasia along the Tethys seaway in the Cenozoic and across the North Atlantic land bridge (Wen, 1999; Pigg et al., 2004).

The complex interactions between plants and insects are hot topics in the paleontological field. Insects are the major group of herbivores in the world based on biodiversity, and almost half of insect species are herbivores in terrestrial ecosystems (Schoonhoven et al., 2005). Insect-mediated damage on leaves can provide direct evidence to verify the evolution of plant-insect interactions (Labandeira, 2006). Insect herbivory data from plant-insect associations can provide valuable information for documenting insect feeding patterns (Iannuzzi and Labandeira, 2008), recognizing insect types (McDonald et al., 2007a,b), and evaluating insect richness (Carvalho et al., 2014). Fossil records of insect damage are numerous, especially in the Cenozoic fossil records, which can provide abundant material to investigate both paleoclimate and paleoentomology. Although there are no insect body fossils preserved with leaves in the Fotan flora, there are abundant and diverse insect-mediated damages on leaves, which allows us to conduct a detailed examination and gain a better understanding of the insect fauna of the middle Miocene in Zhangpu County, Fujian Province.

In this study, we describe comprehensive information on the morphology and micromorphology of both the leaves and infructescences of *Liquidambar* from the middle Miocene Fotan Group of southeastern

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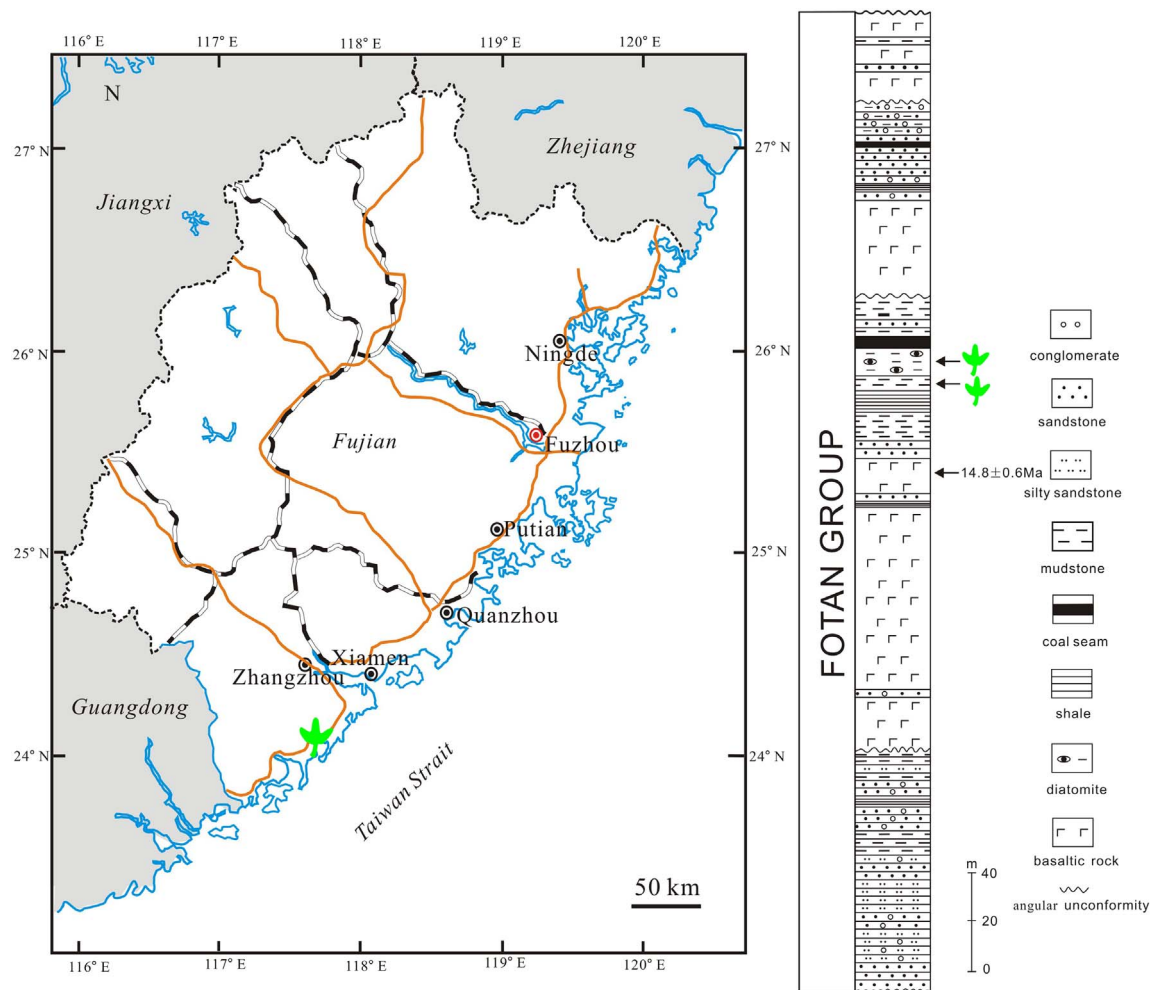


Fig. 1. Map showing the fossil locality and the stratigraphic column of the Fotan Group. Horizons with plant fossils are indicated by the green blade. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

China. A new species, *Liquidambar fujianensis* sp. nov., is established based on infructescences and leaves. These reproductive remains and leaves document the diversity of the floral morphological and anatomical information. Furthermore, we evaluated insect-mediated damage on the leaves of *Liquidambar* and analyzed the diversity and species of the paleoherbivory in the Fotan biota during the Miocene.

2. Materials and methods

2.1. Geologic setting

Fossil specimens were collected from the Fotan Group at Zhangpu County, Fujian Province, southeastern China (Fig. 1). The Fotan Group is dominated by three layers of sedimentary rocks alternating with three layers of intrusive basaltic rocks (Zheng and Wang, 1994). The fossil-bearing layers belong to the secondary unit of sedimentary rocks and are composed of a layer of light brown diatomite and an underlying layer of blue-gray mudstone. Our fossil specimens were found in both the light brown diatomite and blue-gray mudstone. The fossil assemblage represents a tropical rainforest, based on the occurrence of *Dipterocarpaceae* Blume. (Shi and Li, 2010). In addition, the assemblage exhibits a high diversity of angiosperm, including *Fabaceae* Lindley, *Fagaceae* Dumortier, *Lauraceae* Jussieu, and *Euphorbiaceae* Juss. The stratigraphic age of the Fotan Group is considered to be the Langhian Stage of the middle Miocene based on the $^{40}\text{Ar}/^{39}\text{Ar}$ dating (14.8 ± 0.6 Ma) of the basaltic rocks underlying the fossil-bearing layers (Ho et al., 2003) and a palynostratigraphic study (Zheng and

Wang, 1994).

2.2. Materials and terminology

There are 161 leaves and 68 reproductive structures preserved as primary compression fossils with cuticles and partial impression fossils with delicate venation. The fossil specimens were examined and photographed using a digital camera (Sony DSCT70, Japan) and a Leica MZ12.5 stereomicroscope. The extant leaves and infructescences used for the comparisons were collected from the herbarium of the Institute of Paleontology in Lanzhou University, Gansu Province, China, and the campus of Zhejiang Gongshang University, Zhejiang Province, China. The terminology for leaf architecture follows the Manual of Leaf Architecture (Ellis et al., 2009) and Maslova et al. (2015), and the terminology will be used to explain the infructescence architecture following Pigg et al. (2004) and Ickert-Bond et al. (2005).

The experimental treatments, both on fossils and on extant specimens, for identifying anatomical characteristics followed the method explained by Dong et al. (2015). Some cuticles were mounted on slides and observed and photographed with a Leica DM4000B multifunctional biological microscope (LM), and the others were mounted on a stub and examined and photographed with a scanning electron microscope (SEM). All specimens and cuticle slices are stored in the Institute of Paleontology in Lanzhou University, Gansu Province, China.

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