Late Oligocene *Melia* (Meliaceae) from the Nanning Basin of South China and it’s biogeographical implication

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**Abstract**

*Melia* L. is a small genus of only 2–3 species, which is native to Indo-Malesia, India, Pakistan and southern parts of tropical Africa. Fossil records of *Melia* are known from the early Miocene to the Pleistocene. Here we describe some mummified fossil endocarps of *Melia* from the upper part of the Yongning Formation (late Oligocene) in Nanning Basin, South China. These well-preserved stony endocarps are 8–14 mm long and 5–9 mm wide, and have 5 locules with a single spindle seed per locule. We interpret these endocarps as the internal remains of a *Melia* drupe, and assign them as a new species: *M. santangensis* sp. nov. This is the only fossil record of anatomically preserved *Melia* found in China, and also the oldest fossil record of *Melia* so far reported globally. The fossil record confirms the presence of *Melia* in Asia at the late Oligocene, and provides evidence supporting the distribution and dispersal hypothesis of the Meliaceae.

**Keywords:** *Melia*, Endocarp, Mummified fruit, Nanning Basin, Paleogene

**1 Introduction**

The family Meliaceae A. Jussieu, belonging to the order Sapindales Dumortier, is widely distributed throughout the tropics and sub-tropics, and within the family, 49–51 genera, encompassing about 600 species, have been recognized (Pennington and Styles 1975; Mueller et al. 2006; Peng et al. 2008). Meliaceae was traditionally divided into two subfamilies, Melioideae and Swietenioideae, and two monotypic genera *Quivisianthe* Baill. and *Capuronianthus* J.-F. Leroy (Pennington and Styles 1975; Mabberley 2011). However, phylogenetic analysis based on nuclear and plastid DNA sequences tend to place *Quivisianthe* in Melioideae and *Capuronianthus* in Swietenioideae, and two monotypic genera *Quivisianthe* Baill. and *Capuronianthus* J.-F. Leroy (Pennington and Styles 1975; Mabberley 2011). However, phylogenetic analysis based on nuclear and plastid DNA sequences tend to place *Quivisianthe* in Melioideae and *Capuronianthus* in Swietenioideae (Mueller et al. 2003, 2006), which is now renamed as Cedreloideae (Mabberley 2011). Thus, current data suggests Meliaceae can be divided into two subfamilies, Melioideae and Cedreloideae (Mabberley 2011). Generally, species belonging to the subfamily Melioideae have fleshy fruits (drupes) and wingless seeds, while species of Cedreloideae produce capsules and winged seeds, which indicates that the former are typically animal dispersed, while the latter are wind dispersed. For the subfamily Melioideae, 8 tribes with 36 genera are recognized (Mueller et al. 2006; Mabberley 2011), including the Tribe Melieae, which contains only two genera: *Melia* L. and *Azadirachta* A. Jussieu. *Melia* is a small genus containing only 2–3 species and, studies based on molecular clock approaches suggest the divergence of *Melia* occurred in the Eocene (Mueller et al. 2008) or early Oligocene (Mueller et al. 2006). However, the few fossil records of *Melia* so far recovered are all found in strata younger than the Oligocene, e.g. Miocene and Pleistocene (Tsukagoshi et al. 1997; Grote 2007; Pigg et al. 2014).

In the present study, we describe mummified endocarps of *Melia* from the upper Oligocene of Nanning
Basin, South China. This is the oldest Melia record reported so far and provides valuable information for our understanding of the origin, evolution and biogeographic history of Melia and Meliaceae.

2 Material and methods

2.1 Geological setting
The fruits described here were collected from the upper part of the Yongning Formation within the Nanning Basin, from a location in Santang Town, Nanning, Guangxi, South China (22°52′50″N, 108°25′2″E; Fig. 1a). The Yongning Formation is subdivided into three parts based on lithological characteristics. Our fossil fruits were collected from the upper part of the formation, which mainly comprises bluish gray clayey mudstone, interspersed with a few coal seams and thin sandstones (Fig. 1b–d). It is considered to be late Oligocene in age based on the co-occurrence of mammal fossils (Zhao 1983, 1993; Quan et al. 2016).

The fossil fruits reported here are mummified, a form of preservation quite rare in the Paleogene globally (Quan et al. 2016). Because mummified fossils retain many anatomical details, they are preferable for reliable taxonomic determination.

2.2 Specimen preparation
The mummified fruit specimens were washed in water using ultrasonic cleaners (JP-020S, 120 W; Jiemeng, Shenzhen, China) and then air dried. The morphologies were observed, photographed and measured using a stereoscope (Stereo Discovery V20; Zeiss, Jena, Germany). In addition, we used CT-scanning, a non-invasive technology that can observe three-dimensional internal structures of the fruits without damaging the specimens. Specifically, the fruit specimens were scanned using a 450 ICT scanner at the Institute of Vertebrate Paleontology and Paleoanthropology of the Chinese Academy of Sciences (IVPP), Beijing, China. The image data were then imported into VGStudio 2.1 software and reconstructed using Mimics 18.0.

The extant Melia fruits for comparison were collected from Guangzhou, Guangdong Province, China. All specimens are deposited in the Museum of Biology, Sun Yat-sen University (Guangzhou, China). Terminology for describing of the fruits follows that of Grote (2007).

![Fig. 1 Geological setting of the mummified fruit fossil locality. a Fossil location, Nanning Basin. The inset map of China is modified after the Standard Map Service of the National Administration of Surveying, Mapping and Geoinformation of China (http://bzdt.ch.mnr.gov.cn/) (No. GS(2016)1603, and No.GS(2016)2884); b The layer of plant fossils (red arrow); c Overview of the interbedded plants layer; d Lithological column of the outcapped section of the fossil site. c and d modified from Quan et al. (2016) ](image-url)
3 Results

Systematics

Order Sapindales Dumortier, 1892
Family Meliaceae A. Jussieu, 1789
Genus Melia Linnaeus, 1735
Species Melia santangensis Liu, Xu and Jin, sp. nov.
Holotype NNF-352
Paratypes NNF-289, NNF-351, NNF-942, NNF-944, NNF-946, NNF-947
Locality Santang Town, Nanning, Guangxi Zhuang Autonomous Region, South China
Stratigraphic horizon and age Upper part of the Yongning Formation, Nanning Basin, late Oligocene
Repository The Museum of Biology, Sun Yat-sen University, Guangzhou, Guangdong Province, China
Etymology The specific name refers to the collecting locality, Santang Town
Specific diagnosis Fruit stones woody. Endocarp ellipsoidal or oblong, with 5 longitudinally arranged ridges. Endocarp has an inward sunken cavity on both ends, and they are linked by a central tunnel. Axile placenta, locular cavities 5, spindle-like, link with apical cavity. Seed attached subapically with elongated hilar region, spindle-like, slightly pointed at base.
Description Fruit stones woody. Endocarps ellipsoidal or oblong, 8–14 mm long by 5–9 mm wide, covered with fibrous fine stripes (Fig. 2a–h). The fruits have 5 locules, with prominent ridges marking the central rib of the locule, which gives the fruits a five-pointed star shape in cross-section (Figs. 2c, 3d, Supplemental file 1). The width of the ridges is 1–2 mm, with shallow grooves between ridges. The endocarps dehisce longitudinally from the base to the apex along the ridges (Fig. 2k). A conical opening is present, centrally, at the base of the endocarp, and is approximately 3 mm wide at the opening point (Figs. 2c, 3b, c). There is a circular opening at the apex, approximately 3 mm wide, and the opening extends into a cup-like cavity (Figs. 2b, 3b, c). The apex and the base cavities are linked via a central tunnel approximately 0.7 mm wide (Fig. 3c, d). The locular cavities are arranged radially, round in cross-section and spindle-like in longitudinal section, while slightly pointed at the base (Fig. 2i,

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![Fig. 2 Fossil fruits of Melia santangensis sp. nov. (a–k) and extant Melia azedarach Linnaeus (l–o). a–c Endocarp of specimen NNF-352 (holotype) in lateral view (a), apical view (b) and basal view (c); d–h Lateral view of the endocarps of paratypes NNF-946, NNF-947, NNF-944, NNF-942, and NNF-351, respectively; i–j Longitudinal section of paratype NNF-289 showing the locule, central canal, apical and basal cavities, and seeds inside. OP: The openings from the locular cavity extending to the apical cavity; k Apical view of NNF-946, showing loculicidal dehiscence of the endocarp; l–o Endocarp of extant Melia azedarach in lateral view (l, m), apical view (n) and basal view (o). Scale bars = 2 mm](image)
The locular cavities are closed at the base, but each has an apical opening extending to the apical cavity of the endocarp (Figs. 2i, 3b). Each locular cavity is filled by one seed (Figs. 2i, 3a–d). The seeds are subapically attached to the axis of the placenta by an elongate hilar region, spindle-like, approximately 9 mm long and 4 mm wide, broader near the base and slightly pointed at base (Figs. 2i, 3a–d).

4 Discussion

4.1 Comparison with affinities

The mummified fossil endocarps described here are quite distinctive and can be easily assigned to Melia, according to the following characters: 5-locular, loculi 1-seeded, endocarp hard and bony, deeply dimpled at apex and base. They are very similar to those of the extant species Melia azedarach L., which has woody endocarps, 4–5 locules with a prominent ridge along the main axis of each locule, loculicidal dehiscence, and seeds subapically attached by an elongate hilar region (Fig. 2). However, they differ in the shape of locular cavity and seed. The locular cavity of the fossil fruits is spindle-like, with the widest region near the base, and is slightly pointed at base (Fig. 2i, j). By contrast, locular cavity of the extant species is elliptic (Fig. 2i; Table 1).

There are only a few fossil records of the genus Melia. Pigg et al. (2014) had reported fossil fruits of Melia, M. yakimaensis Pigg, from the middle Miocene in Washington State of USA. Their fruits are much smaller than our fruits, being only 2.8–3.7 mm long and 3.2–3.6 mm wide. The shape of their fruits is turbinate to spherical, and have 5–9 locular cavities. By contrast, our fossil fruits are 8–14 mm long and 5–9 mm wide, and have 5 locular cavities, making the two fossil forms easily distinguishable. The fruit fossils of Melia found in the Pleistocene of northeast Thailand area also quite similar to extant M. azedarach L., and have been included in M. azedarach (Grote 2007). These fossils are similar to the Nanning fossils we found, but the locular cavities of Nanning fossils are spindle-like, while those of the Thailand fossils are narrowly elliptic, thus they can be distinguished from each other (Table 1).

Table 1  Comparison of Melia santangensis sp. nov. with other fossil species of Melia and extant species M. azedarach L. --- indicates no description

| Species          | Endocarp Shape | Length (mm) | Width (mm) | Number of locular cavity | Shape of locular cavity | Shape of seed | Length (mm) | Width (mm) | Age | Locality | Reference                |
|------------------|---------------|-------------|------------|--------------------------|-------------------------|---------------|-------------|------------|-----|----------|--------------------------|
| M. santangensis  | Ellipsoidal   | 8–14        | 5–9        | 5                        | Spindle-like             | Spindle-like   | 6.4–9       | 2.4–4      | late Oligocene | Nanning, China          | Present study             |
| M. yakimaensis   | Turbinated    | 2.8–3.7     | 32–3.6     | 5–9                      | Flattened                | Flattened      | 2.4         | 0.6        | middle Miocene | Yakima county, USA      | Pigg et al. 2014          |
| M. azedarach     | Ellipsoidal   | 10.0–11.9   | 8.8        | 5                        | Narrowly elliptic        | ---            | ---         | ---        | middle Pleistocene | Khok, Thailand           | Grote 2007                |
| M. azedarach     | Ellipsoidal   | 12–15       | 8–10       | 4–5                      | Elliptic                 | Elliptic       | 6–9         | 2.1–4      | Extant species   | Guangzhou, China         | Present study             |
4.2 Biogeographic implications

According to molecular clock studies (Muellner et al. 2006), the family Meliaceae is considered to have originated in Africa in the Cretaceous and, seemingly it was also in the Cretaceous that it separated into two subfamilies, namely Cedreloideae and Melioideae (Fig. 4). Fossils of Cedreloideae date back to the Eocene. For example, fossils of *Toona* (Endl.) M. Roem. have been found in the early Eocene London Clay of England (Collinson 1983), and in the middle Eocene of Alaska (Muellner et al. 2006), while fossils of *Cedrela* P. Br. have been found in the early Eocene of California, USA (MacGinitie 1941; Leopold 1984), and in the middle and late Eocene of the USA (MacGinitie 1953, 1974; Manchester 2001; Meyer 2003). Fossils of Melioideae, however, are mostly found in younger sediments. For example, fossils of *Guarea* F. Allam. ex L. have been found in the Oligocene of Puerto Rico (Graham and Jarzen 1969) and in the Miocene of Mexico and Panama (Graham 1991, 1999), but notably a wood fossil showing strong resemblance to the modern genus *Chisocheton* Blume (Melioideae) has been retrieved from the early Eocene of Gujarat, western India (Shukla and Mehrotra 2018).

![Fig. 4](image1.png)

**Fig. 4** Simplified estimated chronogram of Meliaceae based on the molecular clock study of Muellner et al. (2006, 2008). Numbers along the bars indicate million years ago (Ma).

![Fig. 5](image2.png)

**Fig. 5** Distribution of fossil records and extant species of *Melia*. Geographic map is based on Standard Map Service of the National Administration of Surveying, Mapping and Geoinformation of China (http://bzdt.ch.mnr.gov.cn/)
Melia belongs to the Tribe Meliaceae (subfamily Melioidae), which contains only two genera: Melia and Azadirachta. Melia is a small genus of only 2–3 species, including M. azedarach, which is a complex of natural and cultivated forms that have been widely grown, and naturalized, throughout tropical and subtropical areas for over 2500 years (Mabberley 1984). The natural distribution of M. azedarach is uncertain, but is thought to be native to Asia, specifically Indo-Malesia, India and Pakistan (Troup 1921; Mabberley 2011; Liu and Hu 2020). There are one or, possibly, two other species distributed in southern parts of tropical Africa (Mabberley 1984, 2011). Molecular clock studies suggest that Melia might diverge around the early Oligocene (Fig. 4; MueIIner et al. 2006) or middle Eocene (Muellner et al. 2008). However, previous fossil records of Melia are all much later than the early Oligocene, restricted to the early Miocene of Poland (Muellner et al. 2006), the middle Miocene of North America (Pigg et al. 2014), and the Pleistocene of Japan and Thailand (Tsukagoshi et al. 1997; Grote 2007). Pollen grains of Melia (similar to M. azedarach) from the early Miocene have been found in Cameroon (Salard-Cheboldaef 1978).

The fruit fossils reported here represent the earliest fossil record of Melia so far discovered, and demonstrate the presence of Melia in the Paleogene of South China. Based on these fossil records (Fig. 5), we consider that Melia was presented in Asia by at least the late Oligocene, and we speculate that species of this genus diffused westwards to Europe in the early Miocene, and eastwards through the Bering Land Bridge to North America in the middle Miocene. This speculation is in line with the distribution and dispersal hypothesis of the Meliaceae (Muellner et al. 2006).

5 Conclusions

Mummified fossil endocarps from the upper part of the Yongning Formation (late Oligocene) of the Nanning Basin were described. By careful comparison with similar extant and fossil endocarp specimens, these endocarps were recognized as a new species of Melia, namely M. santangensis. The endocarps of the new species are similar to those of the extant species M. azedarach, but the shape of its locular cavity and seed is spindle-like, and so different from the elliptic shape of M. azedarach. This is the oldest fossil occurrence of Melia so far discovered, which narrows the gap between the molecular clock estimates and fossil record, and provides evidence that supports the distribution and dispersal hypothesis of the Meliaceae.

6 Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42501-021-00097-x.
