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Late Oligocene *Melia* (Meliaceae) from the Nanning Basin of South China and its 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 subtropics, and within the family, 49–51 genera, encompassing about 600 species, have been recognized (Pennington and Styles 1975; Muellner 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 (Muellner 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 (Muellner 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 (Muellner et al. 2008) or early Oligocene (Muellner 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

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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).

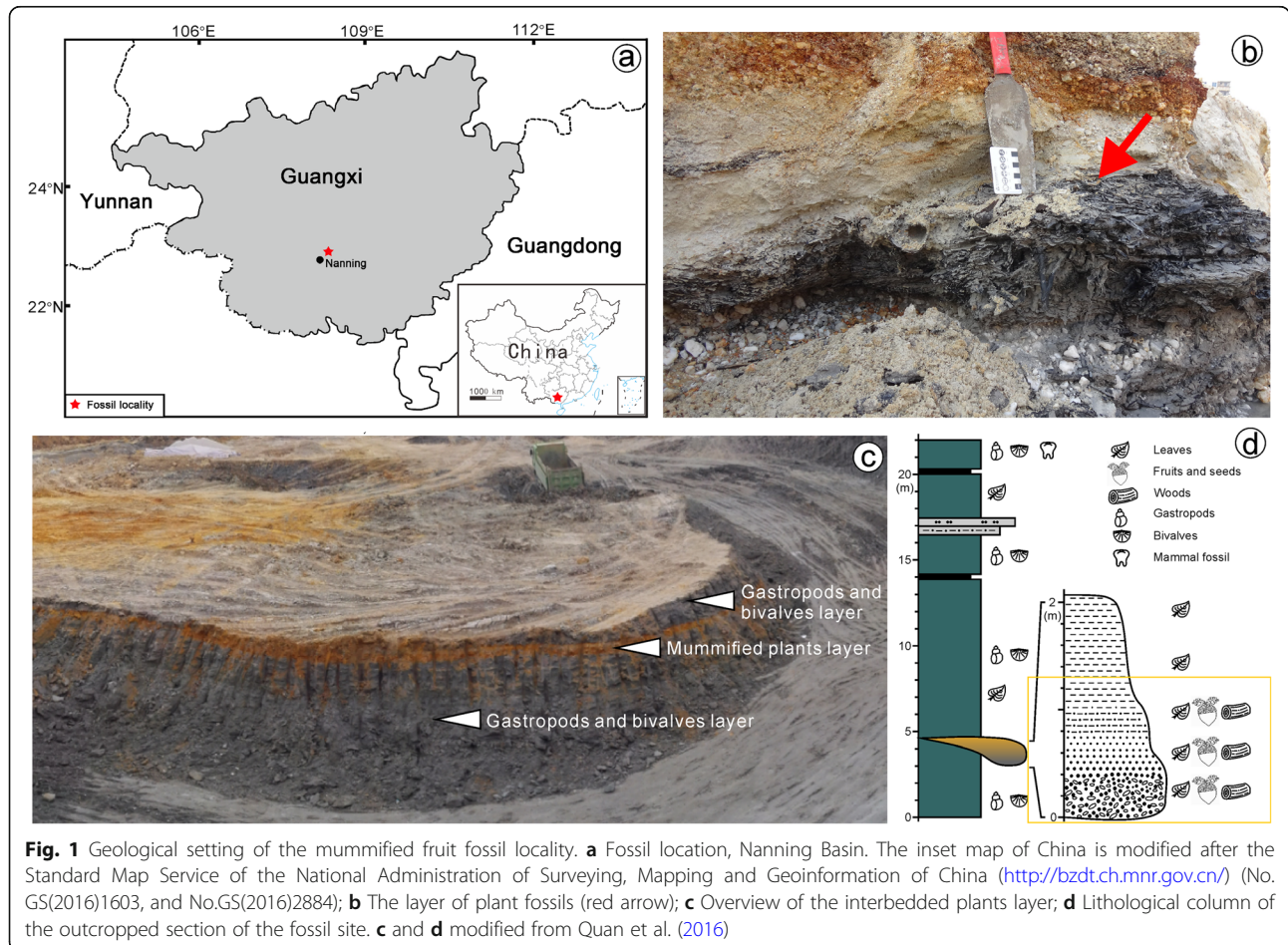
The fossil fruits reported here are mummified, a form of preservation quite rare in the Paleogene globally (Quan et al. 2016). Because mummified fossils retain

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).



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,

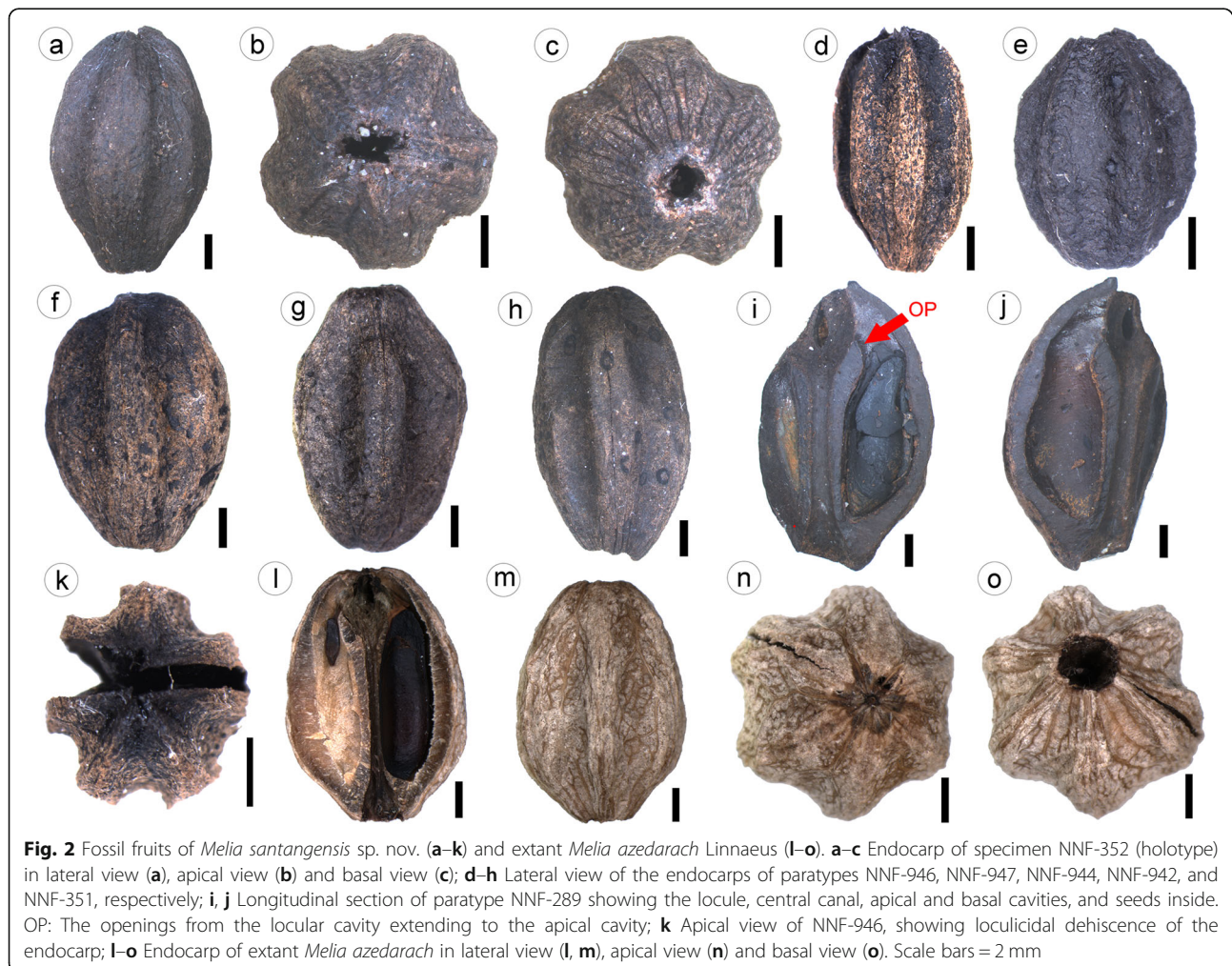
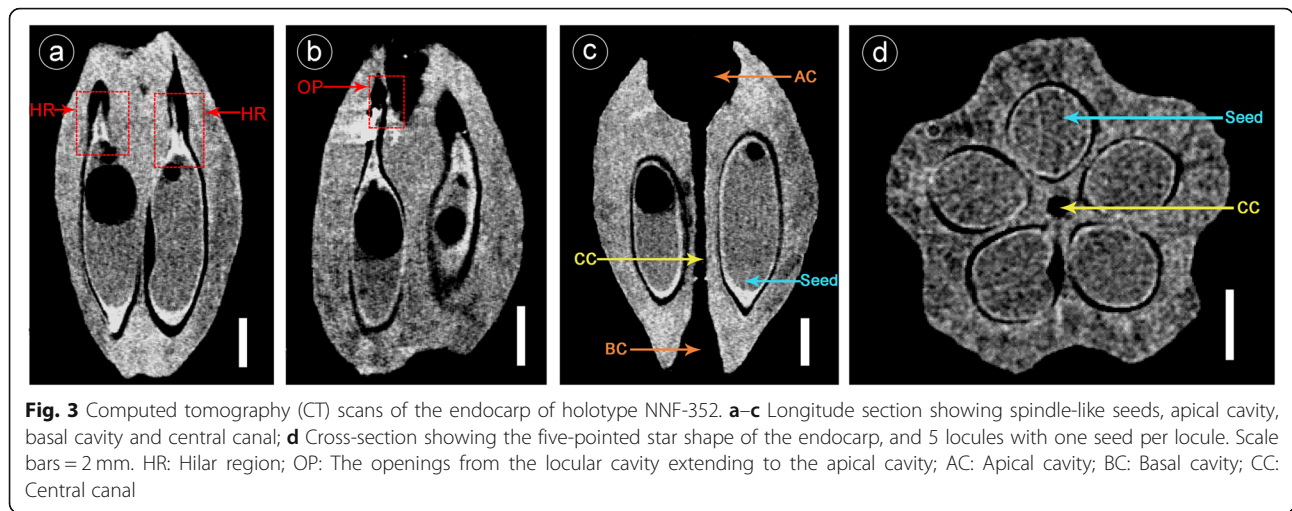


Fig. 2 Fossil fruits of *Melia santangensis* sp. nov. (a–k) and extant *Melia azedarach* Linnaeus (l–o). a–c Endocarp of specimen NNF-352 (holotype) in lateral view (a), apical view (b) and basal view (c); d–h Lateral view of the endocarps of paratypes NNF-946, NNF-947, NNF-944, NNF-942, and NNF-351, 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



j; Supplementary file 2). 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

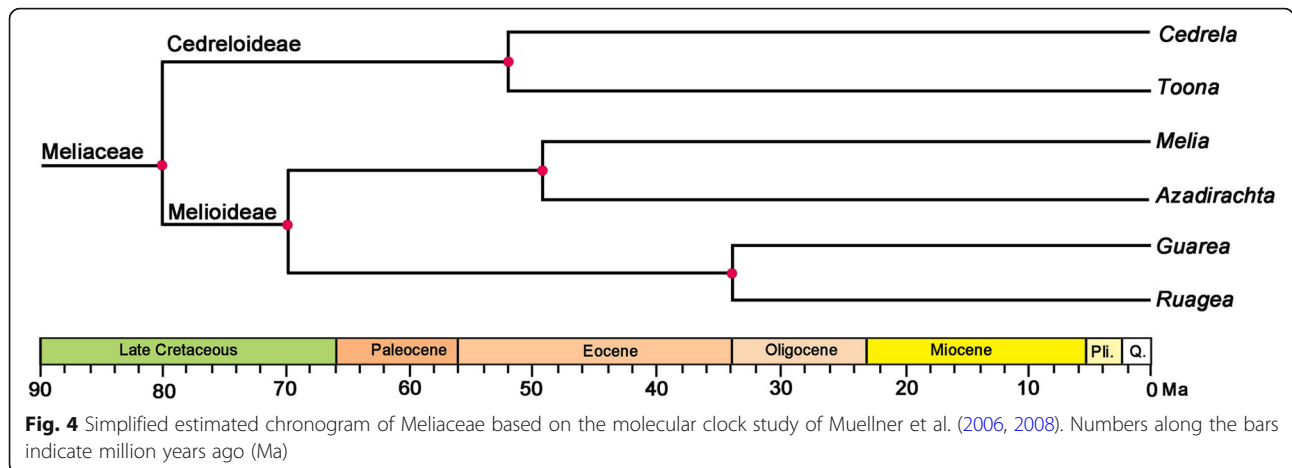
The mummified fossil endocarps described here are quite distinctive and can be easily assigned to *Melia*, according to the following characters: 5-locular, loculi 1-seeded, endocarp hard and bony, deeply dimpled at apex and base. They are very similar to those of the extant species *Melia azedarach* L., which has woody endocarps, 4–5 locules with a prominent ridge along the main rib 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. 2j; 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 turberate 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 are 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

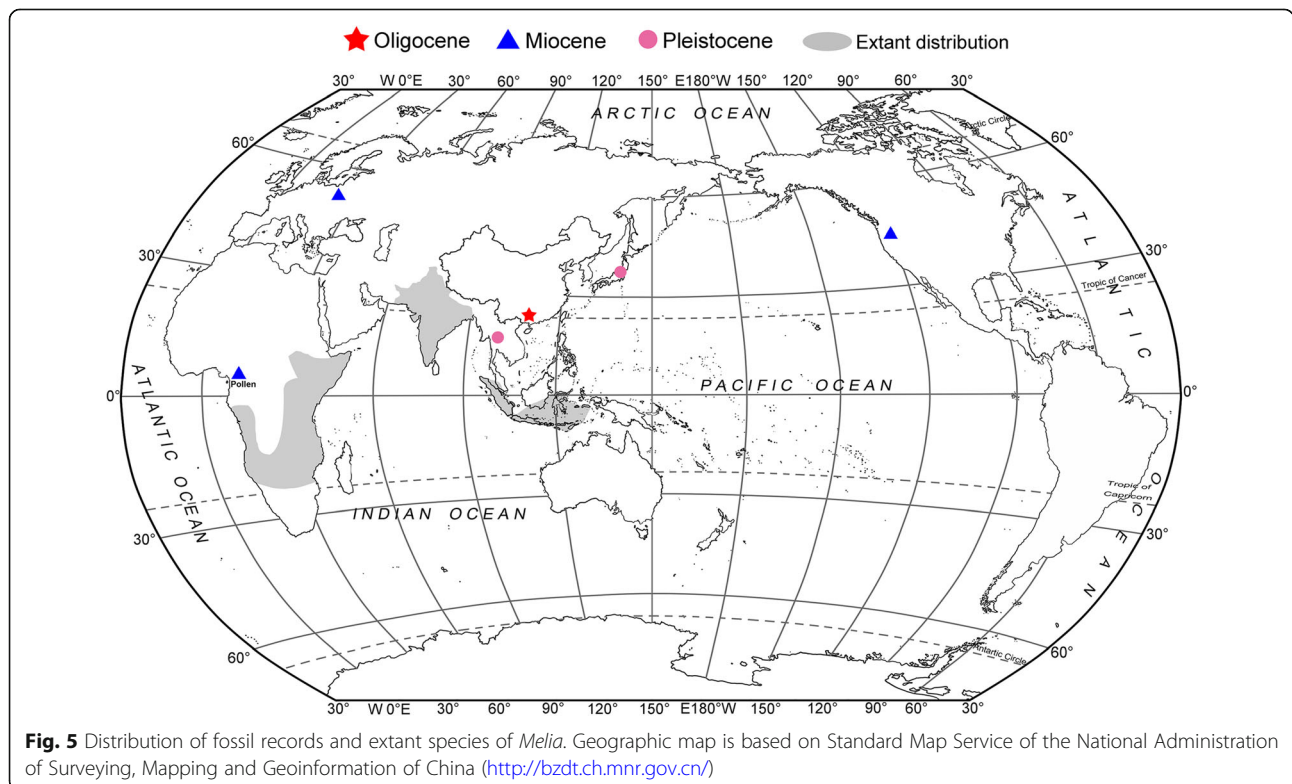
Species	Endocarp					Seed			Age	Locality	Reference
	Shape	Length (mm)	Width (mm)	Number of locular cavity	Shape of locular cavity	Shape	Length (mm)	Width (mm)			
<i>M. santangensis</i>	Ellipsoidal or oblong	8–14	5–9	5	Spindle-like	Spindle-like	6.4–9	2.4–4	late Oligocene	Nanning, China	Present study
<i>M. yakimaensis</i>	Turberate to spherical	2.8–3.7	3.2–3.6	5–9	Flattened	Flattened	2.4	0.6	middle Miocene	Yakima county, USA	Pigg et al. 2014
<i>M. azedarach</i>	Ellipsoidal	10.0–11.9	8.8	5	Narrowly elliptic	---	---	---	middle Pleistocene	Khok, Thailand	Grote 2007
<i>M. azedarach</i>	Ellipsoidal or oblong	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).



Melia belongs to the Tribe Melieae (subfamily Melioideae), 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; Muellner 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-Chebaldieff 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 elliptical 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>.

Additional file 1: Supplementary file 1. Video showing the shape of the endocarp of holotype NNF-352.

Additional file 2: Supplementary file 2. Video showing the internal structure of the endocarp of holotype NNF-352.

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Authors' contributions

WQL and SLX drafted the manuscript. SLX and QYF photographed and CT scanned the fossils. CQ, QYF and JHJ collected the fossils. CQ and JHJ critically revised the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

All fruit fossils are deposited in the Museum of Biology, Sun Yat-sen University, Guangzhou, Guangdong Province, China.

Declarations

Competing interests

The authors declare that they have no competing interests.

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