



# Fossil Leaves of *Meliosma* (Sabiaceae) With Associated Pollen and a Eupodid Mite From the Eocene of Maoming Basin, South China

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## OPEN ACCESS

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### Specialty section:

This article was submitted to  
Paleontology,  
a section of the journal  
Frontiers in Ecology and Evolution

**Received:** 04 September 2021

**Accepted:** 30 November 2021

**Published:** 03 January 2022

### Citation:

Moiseeva MG, Kodrul TM, Tekleva MV, Maslova NP, Wu X and Jin J (2022) Fossil Leaves of *Meliosma* (Sabiaceae) With Associated Pollen and a Eupodid Mite From the Eocene of Maoming Basin, South China.  
*Front. Ecol. Evol.* 9:770687.  
doi: 10.3389/fevo.2021.770687

A first occurrence of the genus *Meliosma* (Sabiaceae) is reported from the upper Eocene of the Maoming Basin of South China. This fossil is one of the oldest reliable records of the genus within its modern center of diversity. Fossil leaves are assigned to a new species, *Meliosma eosinica* sp. nov. based on leaf morphology and epidermal characters. The leaf epidermal anatomy of fossil *Meliosma* is illustrated for the first time. We also provide the first SEM observation of pollen grains associated with *Meliosma*. This study also documents an occurrence of mites within the leaf domatia previously unknown from the fossil record. We presume that the studied mite belongs to the superfamily Eupodoidea (Arthropoda), and probably the family Eupodidae, which comprises very small soft-bodied cosmopolitan mites occupying a wide range of terrestrial habitats. Additionally, we analyze the damage types on the fossil leaves of *Meliosma*. They exhibit exclusively external foliage feeding damage caused by arthropods and traces of probable fungal infection. A review of currently known fossil occurrences of leaves, fruits, and wood of *Meliosma* provides evidence for the geological and geographical distribution of the genus.

**Keywords:** plant fossils, *Meliosma*, mites, Eocene, China

## INTRODUCTION

Sabiaceae are a small family of trees, shrubs, and lianas comprising four genera: *Meliosma* Blume, *Kingsboroughia* Liebm., *Sabia* Colebr., and *Ophiocaryon* Endl. (Yang et al., 2018). The family is distributed in tropical and subtropical regions of eastern and south eastern Asia and Central and South America. The most diverse and widely distributed genus in the family is *Meliosma* (Figure 1). The number of species within *Meliosma* is uncertain and between different publications varies considerably from 25 species (Van Beusekom, 1971) to 80 species (Stevens, 2017) or even 124 species (World Checklist of Selected Plant Families, 2021). In China, 29 species are currently known (Law and Wu, 1982; Guo and Brach, 2007) and over 70 species are estimated for the Neotropical region (Cornejo, 2008, 2009; Ramos and Cornejo, 2012).

The genus *Meliosma*, which in the Paleogene and Neogene was quite widespread in Europe, Asia, and America, now has a disjunct distribution with centers of diversity in southeast Asia (southern China, Myanmar, Thailand, Vietnam, Indonesia), Central America, and in northwest South America (**Figure 1**). Based on phylogenetic and biogeographic studies of Sabiaceae, including the consideration of the fossil record, it is presumed that *Meliosma* originated in Asia, subsequently migrated to Europe and then through the North Atlantic Land Bridge (Raven and Axelrod, 1974; Zúñiga, 2014) or the Bering Land Bridge (Van Beusekom, 1971) moved to America. Molecular dating and ancestral area reconstruction suggest a Eurasian origin of Sabiaceae in the Late Cretaceous followed by a boreotropical range expansion during the Paleogene (Yang et al., 2018).

The family Sabiaceae has an uncertain position in modern plant systematics. Earlier classifications placed it in the Sapindales (Bentham and Hooker, 1862; Takhtajan, 1966, 1987; Dahlgren, 1980), in the Berberidales (Cronquist, 1957), or the Ranunculales, close to Menispermaceae (Cronquist, 1981). Later, Takhtajan (1997) distinguished a separate order, Sabiales. The position of the family relative to orders Proteales and Buxales, or core eudicots has been debated in many publications (Hilu et al., 2003; Soltis et al., 2003; Furness et al., 2007; Wanntorp and Ronse de Craene, 2007; Worberg et al., 2007; Ronse de Craene and Wanntorp, 2008; Zúñiga, 2015; Yang et al., 2018). According to recent phylogenetic studies based on molecular data, the family is placed in Proteales (Angiosperm Phylogeny Group, 2016; Stevens, 2017; Yang et al., 2018). This placement received moderate (74%) bootstrap support, and is corroborated by various alternative hypothesis tests (Yang et al., 2018).

The most comprehensive research on living and fossil representatives of the genus *Meliosma* is the revision of Van Beusekom (1971). He proposed an infrageneric classification of *Meliosma* based primarily on endocarp morphology. The genus was subdivided into subgenera *Kingsboroughia* and *Meliosma*, with the sections *Hendersonia* and *Kingsboroughia*, and *Meliosma* and *Lorenzanea*, respectively. In his monograph, the extant species of *Meliosma* (with the exception of Neotropical sect. *Lorenzanea*) were taxonomically revised and all known fossil species of the genus were evaluated.

The earliest records assigned to the genus *Meliosma* (represented by endocarps) so far reported come from the Maastrichtian of Europe (Knobloch and Mai, 1986). To date, about 15 reliable species of fossil fruits (endocarps) of the genus, as well as 4 species of fossil wood, have been described (see **Supplementary Table 1; Supplementary Figure 1**). Publications with detailed descriptions and illustrations of *Meliosma* fossil leaves are quite rare. To date, more than 18 species of fossil leaves attributed to the genus have been reported from the Paleocene to the Pliocene (e.g., Van Beusekom, 1971; Hickey, 1977; Wolfe, 1977; WGCP (Writing Group of Cenozoic Plants of China), 1978; Manchester, 1981; Peppe and Hickey, 2014). However, the generic assignment of these fossils is often questionable and based on fragmentary material. Van Beusekom (1971, p. 384) remarked that “in *Meliosma* the leaf-types are generally not very characteristic. Especially when they have an entire margin, they may easily be confused with leaves of other taxa.

In fact, it is only the obovate-oblong leaf with dentate margins, such as is found in several subspecies of *Meliosma simplicifolia* (Roxb.) Walp. which, with the help of its rather characteristic nervation pattern, may be referred with reasonable certainty to *Meliosma*. Indeed, it is this type of leaf which predominantly figures in paleobotanical literature under the name of *Meliosma*.”

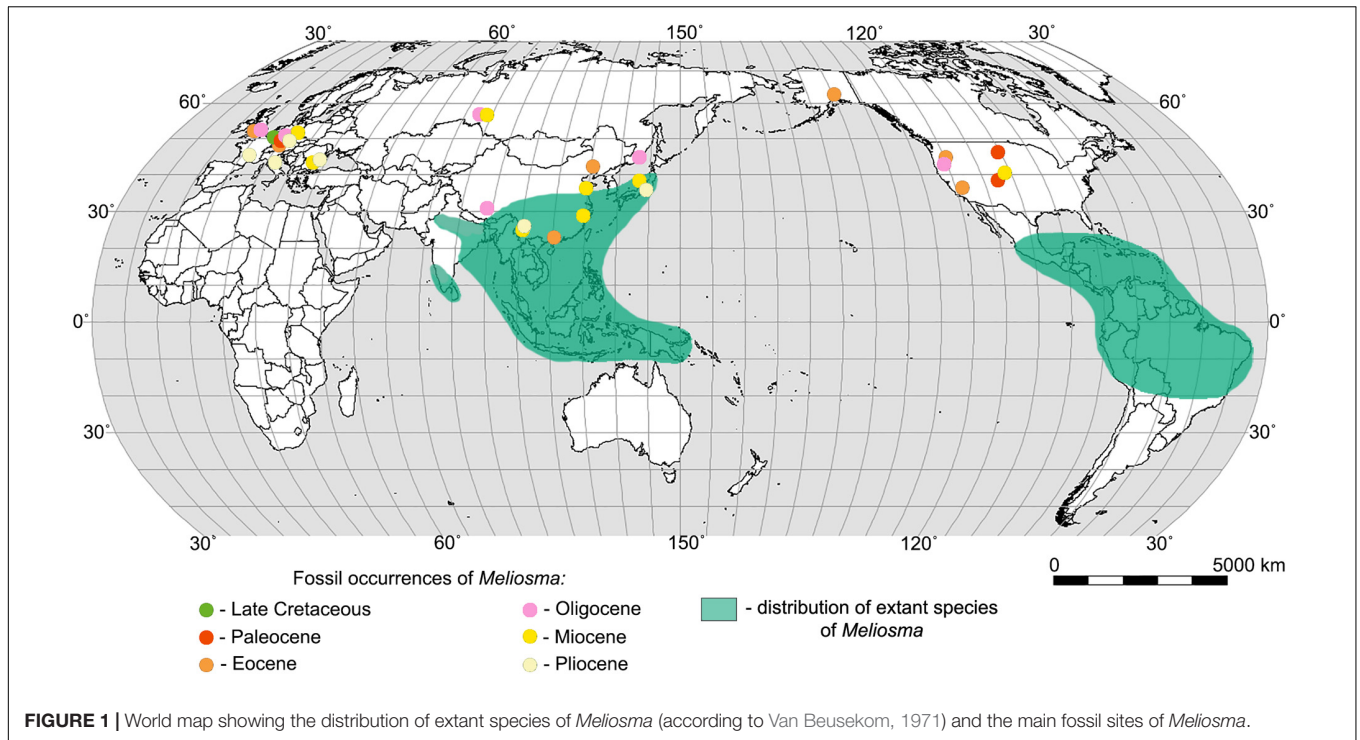
Here, we report well-preserved leaves from the upper Eocene of South China confidently assigned to the genus *Meliosma* based on a detailed comparison of leaf morphology and epidermal characters with those of extant representatives of the genus. Fossil leaves from the Maoming Basin are described as a new species. The leaf epidermal features of fossil *Meliosma* are depicted for the first time. We examine fossil pollen grains found on the leaf of *Meliosma* and compare them with pollen grains of several extant species of this genus using SEM. One of the purposes of this study is to identify the mite found in the fossil leaf domatium and evaluate its possible adaptive relationship. In addition, we document the fossil leaf damage types.

## MATERIALS AND METHODS

Ten specimens studied here were collected by J. Jin (Sun Yat-sen University, Guangzhou, China) and his colleagues and students during the 2010s from the Huangniuling Formation of the Maoming Basin, located in southwest Guangdong Province, South China (**Figure 2**). The leaf fossils preserved as impressions/compressions were recovered from a lens of mudstones in the upper part of the formation together with hundreds of other plant fossils. The Huangniuling flora is highly diverse and has yielded more than 150 species of angiosperms and rare ferns and gymnosperms (e.g., Spicer et al., 2017). The Huangniuling Formation is considered to be late Eocene in age based on paleomagnetic and palynological data (Wang et al., 1994; Aleksandrova et al., 2015). The specimens are housed in the Museum of Biology, Sun Yat-sen University, Guangzhou, China with collection numbers beginning MMJ3.

The morphological study of both fossil and modern leaves was performed using a dissecting microscope (Carl Zeiss Stemi 2000 C) equipped with a Canon G10 Power Shot digital camera. The leaf specimens were photographed under low-angle incident light using a Panasonic GX7 digital camera with Leica DG Macro-Elmarit 1:2.8/45 mm macro lens. Fossil leaf drawings were made by tracing over photographs using a Wacom Intuos3 tablet. For the leaf descriptions, we used a terminology devised by Ellis et al. (2009). The types of insect damage on the fossil leaves were identified following the “Guide to Insect (and Other) damage types on compressed plant fossils” (Labandeira et al., 2007).

The fossil leaves of *Meliosma* studied here almost lack cuticles except for small fragments from the midrib and leaf domatia. These fragments were macerated using Schulze solution (70% HNO<sub>3</sub> and saturated KClO<sub>3</sub> with a volume ratio of 3:1) and ammonium hydroxide and then mounted on glass slides and SEM stubs. We examined the material with a light microscope (LM) Zeiss AxioStar plus at the Geological Institute, Russian Academy of Sciences (GIN RAS), and with an SEM (Tescan Vega)



at the Borissiak Paleontological Institute, Russian Academy of Sciences (PIN RAS).

A cluster of dispersed pollen grains similar in morphology to those of extant species of *Meliosma* was found on the fossil leaf (specimen MMJ3-837-3a). Two mites (one of them was later lost) were obtained from the leaf domatium during maceration.

Pollen grains and fragments of mite cuticle were mounted on an SEM stub, sputtered with gold, and observed with a Tescan, at accelerating voltage 20 kV.

We examined the leaves and pollen of the extant species of *Meliosma* using specimens available in the Herbarium of Sun Yat-sen University (SYS), Guangzhou, China, as well as specimens

collected by S.R. Manchester (Florida Museum of Natural History, Gainesville, United States) in the Xishuangbanna Tropical Botanical Garden (XTBG) and kindly donated to us. The cuticles from small fragments of extant leaves were prepared by immersing them in 70% nitric acid, followed by treatment with ammonium hydroxide for complete removal of the leaf mesophyll. The leaf cuticles and parts of anthers of extant *Meliosma* species were mounted on an SEM stub with nail varnish, sputtered with gold and palladium, and observed using SEM, at accelerating voltage 20 kV, at PIN RAS.

## RESULTS

Order PROTEALES Juss. ex Bercht. et J. Presl, 1820

Family SABIACEAE Blume, 1851

Genus *Meliosma* Blume, 1823

Species *Meliosma eosinica* Moiseeva, Kodrul et Jin (Figures 3A–H, 4A–F, 5A–H, 6A,D,F,H, 7A–E, 8A–C, 9A–E,G,H).

### Holotype

Leaf, specimen no. MMJ3-008-1a (part) and MMJ3-008-1b (counterpart), designated here (Figures 3A,B,D, 4A,B, 5H, 6A,D,F,H).

### Repository

The Museum of Biology of the Sun Yat-sen University, Guangzhou, China.

### Type Locality

Maoming Basin, Guangdong Province, China.

### Stratigraphic Horizon

The Huangniuling Formation, upper Eocene.

### Etymology

From Eocene and Sina (lat.) – China.

### Diagnosis

Leaves are simple, petiolate, laminar size mesophyll, length to width ratio about 3:1. Lamina is obovate, slightly asymmetrical at the base. Laminar apex angle acute with straight or acuminate apex shape, base angle acute with cuneate shape. Primary venation pinnate. The surface of the primary vein is pubescent. Major secondary veins alternate or occasionally opposite, semicraspedodromous or brochidodromous with spacing decreasing proximally. In the axils of primary and secondary veins leaf domatia developed. Leaf margin untoothed undulate or irregularly serrate in the upper half of lamina. Tooth spacing is irregular with one order of teeth. Sinus shape rounded, tooth shapes typically concave/convex or concave/flexuous. Leaves hypostomatic. Abaxial epidermis is composed of polygonal ordinary cells, anomocytic stomata, and trichomes of two types: simple elongate unicellular and glandular with uniseriate 2–3-celled stalk and single-celled head.

Adaxial epidermis is composed of isodiametric ordinary cells with glandular trichomes.

## Description

The leaves are simple, petiolate, with marginal petiole attachment. The incompletely preserved petiole is up to 0.8 cm long and 0.15 cm wide. Laminar size is mesophyll. The biggest specimen is 17.5 cm long and up to 6.1 cm wide, the length-to-width (L/W) ratio is approximately 3:1. The laminar shape is obovate. The leaf apex is acute, straight, or acuminate in shape. The leaf base is slightly asymmetrical, with an acute angle and cuneate shape.

Primary venation is pinnate. The primary vein is straight or slightly curved at the base, thick in the basal half and tapering upward, terminating at the apex. The surface of the primary vein is pubescent. Major secondary veins (14–17 pairs) are alternate or occasionally opposite, mixed semicraspedodromous or brochidodromous (mostly in the lower part of the lamina and near the leaf apex) with spacing that decreases proximally. The secondary vein angle is smoothly increasing proximally (from 45 to 50° in the upper part of the lamina to 70° in the lower part). The leaves possess numerous leaf domatia in the axils between primary and secondary veins (Figures 3H, 4E). Interior secondaries are absent. Minor secondary veins, if present, are semicraspedodromous. Intersecondary veins are occasionally present, usually, their length is less than 50% of the subjacent secondary vein, the intersecondary proximal course is almost perpendicular to midvein, while the intersecondary distal course is perpendicular to subjacent secondary vein. Intercostal tertiary veins are mixed percurrent with an obtuse angle to midvein and consistent vein angle variability. Epimedial tertiary veins are mixed percurrent with proximal course perpendicular to the midvein and distal course parallel to intercostal tertiaries. Exterior tertiaries are looped. Quaternary vein fabric is an alternate percurrent. Quintarnary vein fabric is irregular reticulate. Areolation is well developed. Freely ending veinlets are unbranched. Marginal ultimate venation is looped.

The leaf margin is untoothed undulate or irregularly serrate in the upper half of leaf lamina. Tooth spacing is irregular with one order of teeth and usually less than one tooth per 1 cm. Teeth are small and 1–1.5 mm high. Sinus shape is rounded, tooth shapes are concave/convex or concave/flexuous. The principal vein terminates at the tooth apex.

The leaf epidermal characters were obtained from the cuticle fragmentary preserved on the midvein and near domatia. The cuticle is very thin. Ordinary epidermal cells of a costal area are rectangular in shape, with straight anticlinal walls, 40–70 μm long and 9–15 μm wide, bearing numerous trichome bases (Figures 6A,D,F,H).

The epidermis of the leaf abaxial surface is composed of polygonal ordinary cells, randomly oriented stomata, and trichomes of two types: simple elongate unicellular and glandular (Figures 7A,C, 8A,B). The length of the unicellular non-glandular trichomes is up to 600 μm, their diameter at the base is approximately 20–30 μm (Figures 7D,E, 8A, 9C–E). Glandular trichomes have uniseriate stalks that usually consist of 2–3 cells and a single-celled head, the length of trichomes is 45–60 μm,



**FIGURE 3** | Fossil leaves of *Meliosma eosinica* sp. nov. from the Eocene Huangniuling Formation of the Maoming Basin, South China. **(A,B,D)** Holotype, MMJ3-008-1a. Note insect leaf-feeding damage in **(D)** small circular hole (damage type DT2) and a cluster of three holes located at the divergence point of secondary veins from primary veins (DT57) with a narrow reaction rim. **(C)** Untoothed leaf, MMJ3-2175-1a. Note polylobate insect feeding holes (DT3) with weakly developed reaction tissue. **(E)** Incompletely preserved leaf showing insect marginal feeding (DT15), hole feeding (DT5), and surface feeding (DT31) traces, MMJ3-837-3a. **(F,G)** Enlargement of leaf in **(E)**. **(H)** Enlargement of leaf in **(C)** showing domatia (arrows). Scale bars = 1 cm.

their diameter at the base is about 20  $\mu\text{m}$  (**Figure 8A**). Stomata are anomocytic with four to six subsidiary cells (**Figures 8B, 9B,C,H**), stomatal size ranges between 28 and 33  $\mu\text{m}$  in length and between 25 and 28  $\mu\text{m}$  in width.

The epidermis of the adaxial surface consists of isodiametric cells, usually pentagonal with undulate anticlinal cell walls, 37–60  $\mu\text{m}$  long, 23–36  $\mu\text{m}$  wide (**Figure 8C**). There are only glandular trichomes of the same morphology as on the abaxial surface (**Figures 7B, 9A,G**).

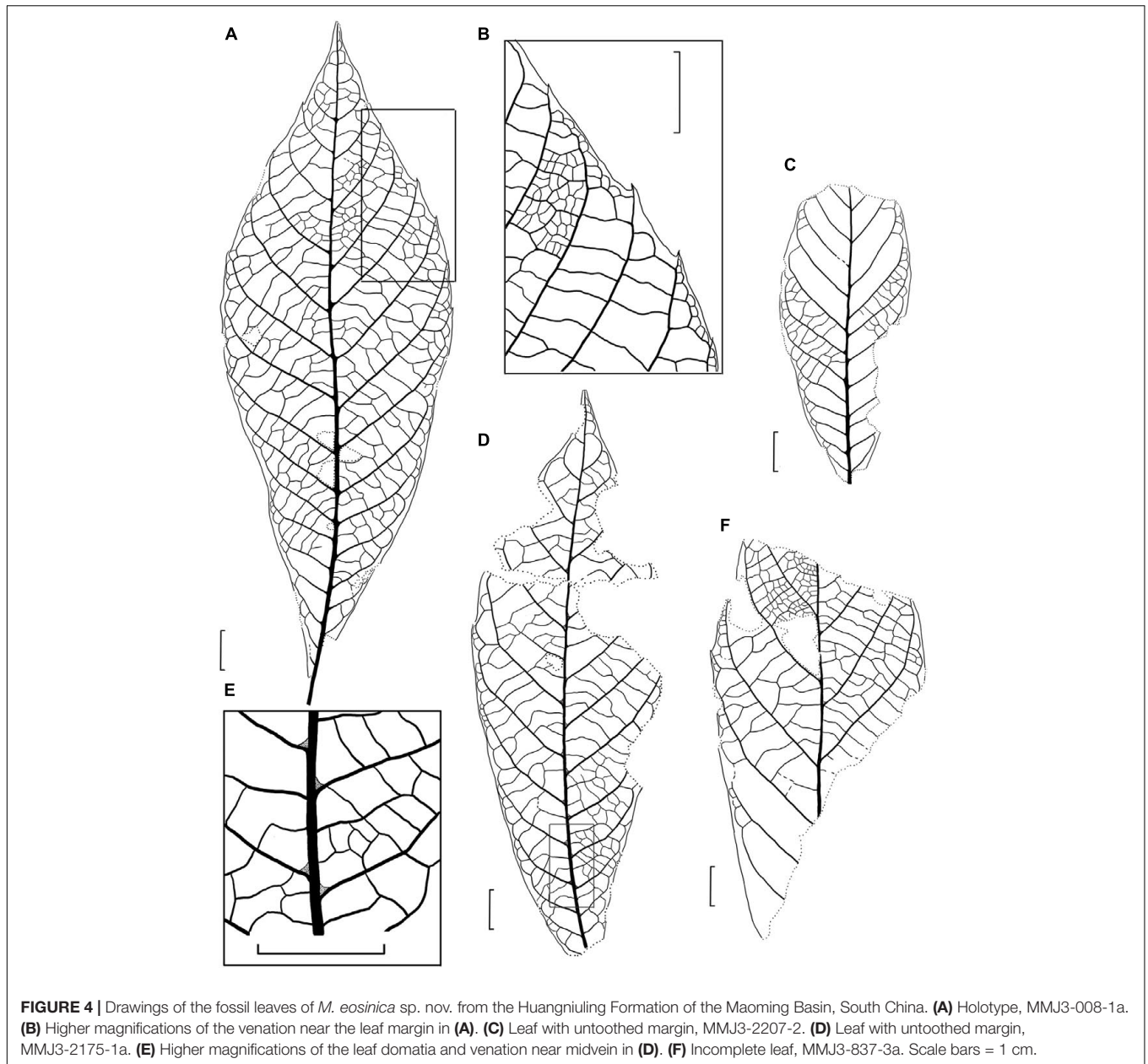
## Material

MMJ3-008-1a, b; MMJ3-321; MMJ3-549-1; MMJ3-837-3a, b; MMJ3-898; MMJ3-2175-1a, b; MMJ3-2205-1; MMJ3-2206-2; MMJ3-2207-1; MMJ3-2207-2.

## DISCUSSION

### Comparison With the Fossil Species of *Meliosma*

Leaves of the new species are most similar to the fossil leaves of *Meliosma* sp. cf. *M. simplicifolia* from the Eocene Clarno Formation of Oregon, United States (Manchester, 1981) in the size and shape of the lamina, the number of secondary veins, as well as the tertiary and higher order venation patterns. *Meliosma eosinica* sp. nov. differs from this species mostly in terms of the leaf margin characters: fossil leaves from the Maoming Basin have irregular small teeth only in the upper half of the lamina or untoothed leaf margin. By contrast, leaves from the Clarno Formation are characterized by more prominent teeth arranged



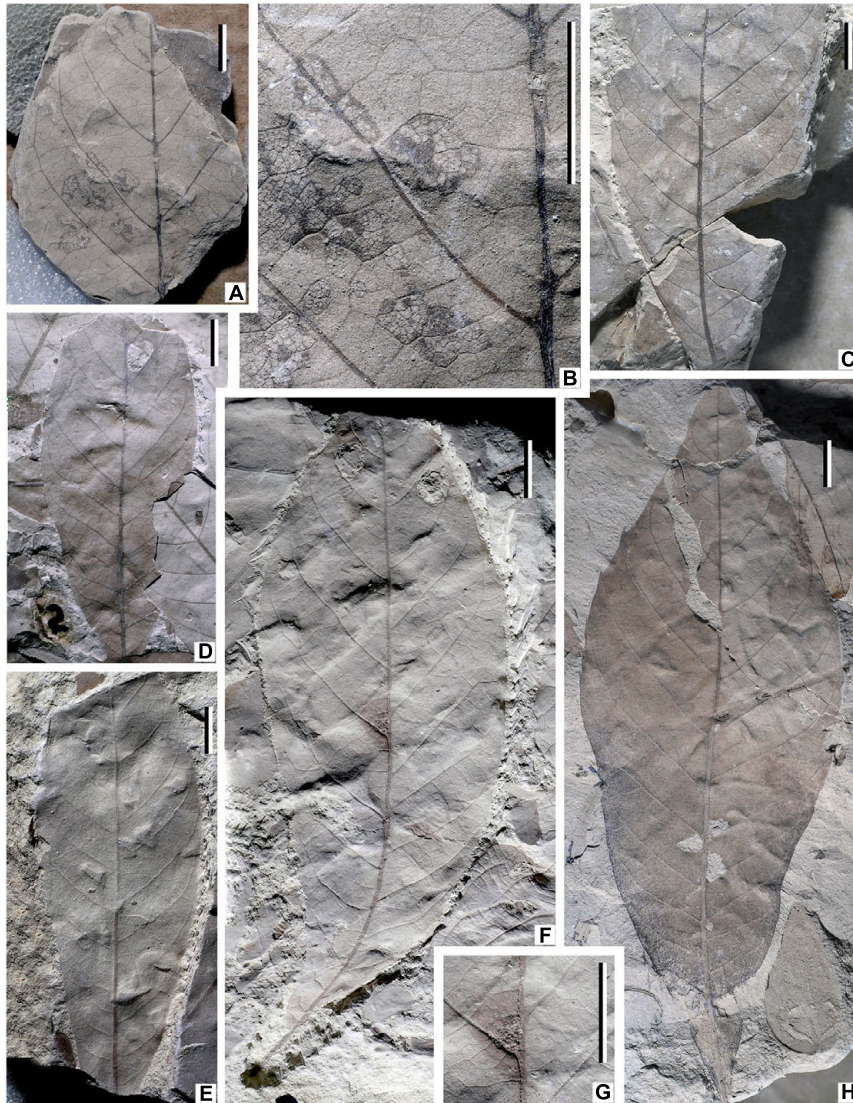
**FIGURE 4** | Drawings of the fossil leaves of *M. eosinica* sp. nov. from the Huangniuling Formation of the Maoming Basin, South China. **(A)** Holotype, MMJ3-008-1a. **(B)** Higher magnifications of the venation near the leaf margin in **(A)**. **(C)** Leaf with untoothed margin, MMJ3-2207-2. **(D)** Leaf with untoothed margin, MMJ3-2175-1a. **(E)** Higher magnifications of the leaf domatia and venation near midvein in **(D)**. **(F)** Incomplete leaf, MMJ3-837-3a. Scale bars = 1 cm.

almost along the whole leaf margin. However, fossil leaves from the Clarno Formation have not been described in detail.

The leaves of *M. eosinica* are also very similar in general morphology to the fossil leaves *M. shanwangensis* Hu et Chaney originally described from the lower-middle Miocene of Shandong, eastern China (Hu and Chaney, 1940). Both species are characterized by an obovate shape of the leaf lamina with an acute or acuminate apex and cuneate base, a similar number of secondary veins (12–16 pairs in *M. shanwangensis* and 14–17 pairs in *M. eosinica*) arising at angles of 50–70° from the midvein and distally curving up to the leaf margin, and a slightly asymmetrical base. Leaves of *M. shanwangensis* differ in having remotely serrate margin and serration starting in some cases from the leaf base.

Leaves of *M. eosinica* resemble leaves of *M. obtusifolia* Tao described also from the lower-middle Miocene of Shandong, eastern China (WGCP (Writing Group of Cenozoic Plants of China), 1978), in respect of their obovate lamina shape and irregularly serrate margin, but differ by having an acute apex. Tao compared these fossil leaves with the leaves of extant *M. parviflora* Lecomte, which also possess an obovate lamina with an obtuse rounded apex. In addition, leaves of *M. eosinica* differ from those of *M. obtusifolia* by their larger lamina size and their greater number of secondary veins (14–17 pairs compared to 10–13 in *Meliosma obtusifolia*).

The leaves of *M. eosinica* are similar to those of *M. longifolia* (Heer) Hickey from the Golden Valley Formation (lower Eocene) of Western Dakota, United States (Hickey, 1977), in the number



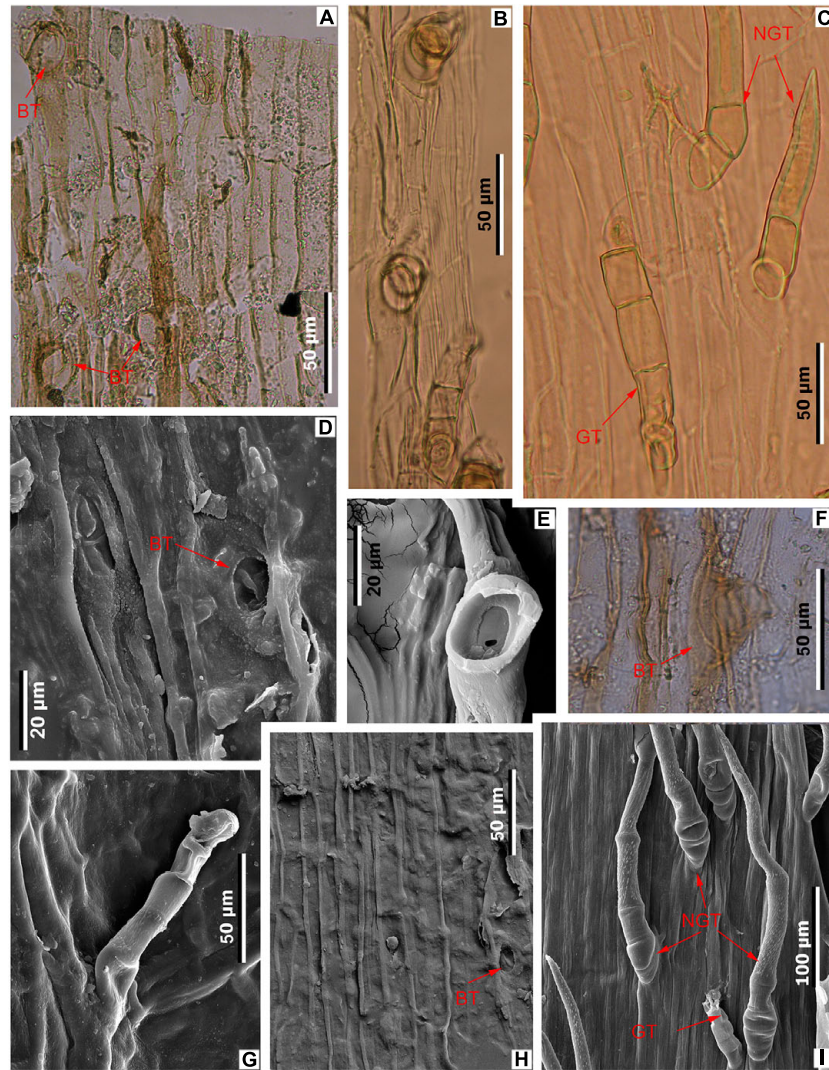
**FIGURE 5** | Fossil leaves of *M. eosinica* sp. nov. from the Eocene Huangniuling Formation of the Maoming Basin, South China. **(A)** Incomplete leaf showing skeletonization insect damage (DT17), MMJ3-321. **(B)** Enlargement of leaf in **(A)**, polygonal skeletonized patches with reaction tissue bounded by tertiary veins. **(C)** Lower part of the leaf, MMJ3-549-1. **(D)** Untoothed leaf with large polylobate perforation (DT5) caused by an insect, MMJ3-2207-2. **(E)** Untoothed leaf, MMJ3-2205-1. **(F)** Leaf with small teeth in the upper third of lamina, MMJ3-2206-2. Note circular holes (DT2, DT4) caused by insects and probable fungal damage in the domatium zone. **(G)** Enlargement of domatium zone in **(F)**. **(H)** Holotype (counterpart), MMJ3-008-1b. Scale bars = 1 cm.

of secondary veins and their angle of divergence. However, *M. eosinica* leaves can be distinguished by their obovate shape and irregularly serrate margin.

Unlike the leaves of two species, *M. duktotensis* Wolfe and *M. kushtakensis* Wolfe, described from the Eocene Kulthieth and Kushtaka formations of the Gulf of Alaska (Wolfe, 1977), *M. eosinica* leaves are characterized by a larger lamina size, a greater number of secondary veins, and an irregularly serrate or undulate leaf margin.

The leaves of *M. eosinica* differ significantly from the leaves of two Paleocene species from North Dakota, United States, *M. thriviensis* Peppe et Hickey from the lower Paleocene Ludlow Member of the Fort Union Formation and *M. vandaelium*

Peppe et Hickey from the middle Paleocene Tongue River Member of the Fort Union Formation (Peppe and Hickey, 2014). Both American species are characterized by a small number of secondary veins, 9–10 pairs in *M. vandaelium* and 8–14 (average 10) in *M. thriviensis*, compared with 14–17 pairs in *M. eosinica*. The secondary vein angle in *M. eosinica* is smoothly increasing proximally (from 45 to 50° in the upper part to 70° in the lower part of the lamina) whereas in *M. vandaelium* the secondary vein angle decreases basally, and in *M. thriviensis* secondary vein spacing and angle are uniform. These species also differ in their leaf margin characteristics. In *M. eosinica*, the teeth are sparse, developed mainly in the upper part of the leaf or the leaf margin is untoothed, while in *M. vandaelium* the margin is



**FIGURE 6** | Midvein epidermal characters in fossil and extant *Meliosma* leaves. *M. eosinica* sp. nov., holotype, MMJ3-008-1a (**A,D,F,H**). (**A**) Trichome bases (BT), light microscopy (LM). (**D**) Trichome base, SEM. (**F**) Glandular(?) trichome base, LM. (**H**) Ordinary cells of the costal area and trichome base, internal view, SEM. *M. rigida* Siebold et Zucc., SYS00085214 (**B,E**). (**B**) Trichomes, LM. (**E**) Base of trichome, external view, SEM. *M. simplicifolia* (Roxb.) Walp., Xishuangbanna Tropical Botanical Garden (XTBG) (**C,G,I**). (**C**) Glandular (GT) and non-glandular (NGT) trichomes, LM. (**G**) Glandular trichome (GT), external view, SEM. (**I**) Glandular (GT) and non-glandular trichomes (NGT), external view, SEM.

serrate to dentate throughout the entire leaf, the teeth are smaller and more frequent (three teeth per 1 cm). In *M. thriviensis* the teeth are uniformly spaced along the entire lamina (one to two teeth per 1 cm).

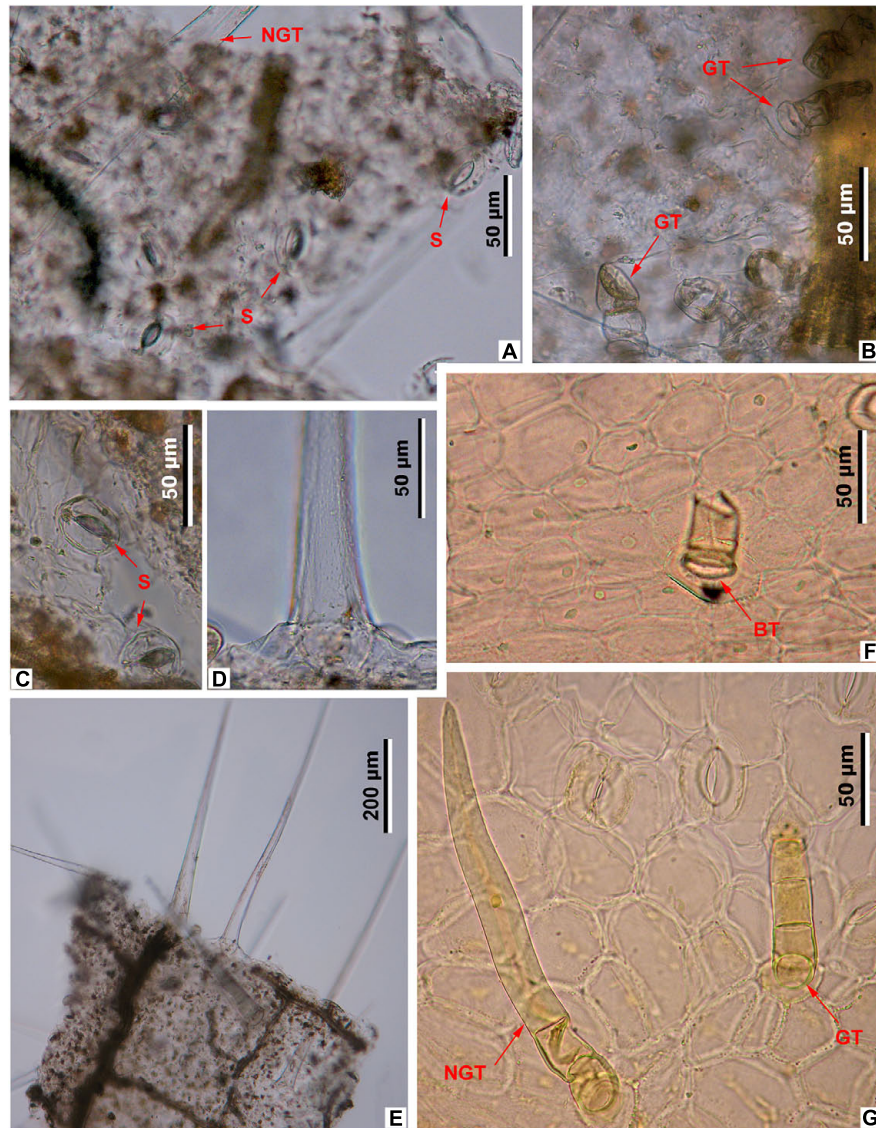
The only fossil leaves of *Meliosma* with studied epidermal characters were reported from the upper Miocene of Tiantai, Zhejiang, China in a conference abstract (Jia and Sun, 2011). Leaves of *M. eosinica* differ from those of *M. cf. flexuosa* Pamp. from Zhejiang in having a larger lamina size (6.2–9.8 cm long and 2.2–4.2 cm wide in *M. cf. flexuosa*), an acute apex (obtuse or narrowly acuminate in *M. cf. flexuosa*), and smaller irregular teeth (compared with sharp coarse marginal teeth in *M. cf. flexuosa*). *Meliosma cf. flexuosa* also differs in having only sparse multicellular hairs composed of 6–7 cells and smaller stomata

(15–20  $\mu\text{m}$  long, 12–15  $\mu\text{m}$  wide). However, these Zhejiang fossils were not subsequently published in full.

### Comparison With Modern *Meliosma* Species

Within living species of *Meliosma*, leaves of *M. rigida* Siebold et Zucc., *M. fordii* Hemsl., and *M. simplicifolia* have the most similar leaf architecture to those of *M. eosinica*. Van Beusekom (1971) treated these species as subspecies of one highly variable species *M. simplicifolia*, but later they were considered as individual species (Guo and Brach, 2007). The leaves of these three extant species are very similar to each other; and like *M. eosinica*, they are obovate or elliptic in shape with an acute or acuminate apex and a cuneate base, pinnate semicraspedodromous or



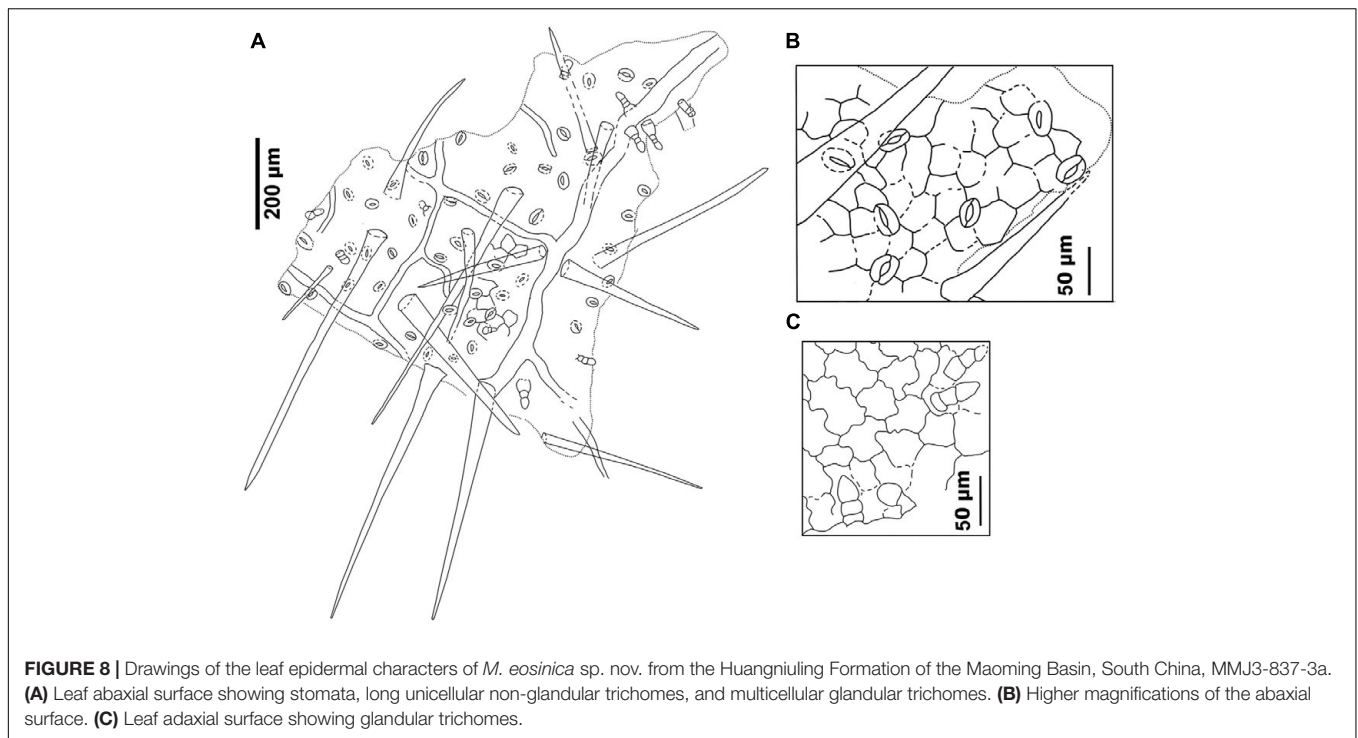


**FIGURE 7** | Leaf epidermal characters of fossil and extant *Meliosma*, LM. *M. eosinica* sp. nov., MMJ3-837-3a (A–E). (A) Abaxial surface with stomata (S) and non-glandular trichomes (NGT). (B) Adaxial surface with glandular trichomes (GT). (C) Abaxial surface with stomata (S). (D) The base of unicellular non-glandular trichome (NGT). (E) Long unicellular trichomes. Extant *M. simplicifolia* (Roxb.) Walp., XTBG (F,G). (F) Adaxial surface with the base of glandular trichome (BT). (G) Abaxial surface with stomata, multicellular glandular (GT), and non-glandular (NGT) trichomes.

brochidodromous venation with distinctly ascending secondary veins, and untoothed or serrate margins usually toothed in the upper half of lamina (Figures 10A–G,I,L). Compared with the new fossil species, *M. simplicifolia* differs in having larger leaves (15–40 × 4–16 cm) and a greater number of secondary veins (15–28 pairs) (Guo and Brach, 2007). The leaves of *M. rigida* and *M. fordii* are usually less than 15 cm long and 5 cm wide, the number of secondary veins is often fewer than 15 pairs. In addition, despite the certain morphological similarity of leaves, extant taxa also differ from each other and fossil species in leaf epidermal features (Figures 6B,C,E,G,I, 11A,D–G, 12).

The epidermal characters of the new fossil species *M. eosinica* are most similar to those of *M. simplicifolia* (Figures 6C,G,I,

7F,G, 9F, 11A,D–G; Supplementary Table 2). The epidermis of the leaf abaxial surface in both extant and fossil species is composed of ordinary cells lacking papillae, with randomly orientated anomocytic stomata and trichomes of two types: non-glandular and glandular, which are especially numerous in the axils between primary and secondary veins forming domatia of hair-tuft type (e.g., O’Dowd and Willson, 1989). On the leaf adaxial surface of both species, mostly glandular trichomes of a similar morphology are presented. The stomata in the modern species are slightly larger, 38–45 μm long and 35–37 μm wide, compared with 28–33 μm long and 25–28 μm wide in *M. eosinica*. *M. eosinica* differs from *M. simplicifolia* in having unicellular non-glandular trichomes.



The non-glandular trichomes of the modern species consist of 2–5 cells (Figures 6C,I), and the length of trichomes varies from 100 to 500  $\mu\text{m}$ . The surface of non-glandular trichomes in the new species is smoother (Figures 9E, 11F). The glandular trichomes of *M. eosinica* are smaller than those of *M. simplicifolia*, in that they consist of 2–3 cells and are up to 60  $\mu\text{m}$  long (compared to 4–5 cells in the trichomes of usually more than 100  $\mu\text{m}$  long in *M. simplicifolia*).

Unlike *M. eosinica*, on the leaf abaxial surface of *M. rigida*, all epidermal cells have papillae, the stomata are smaller (10–14  $\mu\text{m}$  long and 7–9  $\mu\text{m}$  wide compared with 28–33  $\mu\text{m}$  long and 25–28  $\mu\text{m}$  wide in *M. eosinica*), sunken, and surrounded by subsidiary cells with large papillae which partly cover the stomatal pit (Figure 12G; Supplementary Table 2). The epidermal characters similar to those of *M. rigida* are observed also in the leaves of *M. fordii* (Figures 12A–E; Supplementary Table 2): all epidermal cells of the abaxial surface are papillate, the stomata are relatively small (17–23  $\mu\text{m}$  long and 15–18  $\mu\text{m}$  wide), and the ordinary cells of the adaxial surface are non-papillate, polygonal, with straight anticlinal walls, 40–50  $\mu\text{m}$  long, and 26–30  $\mu\text{m}$  wide (Figure 12F). Similar to the fossil leaves of *M. eosinica*, numerous non-glandular and glandular trichomes are present on the leaf abaxial surface of both modern species, particularly on the midvein (Figures 12A,C). As in *M. eosinica*, on the leaves of *M. fordii* and *M. rigida*, simple unicellular non-glandular trichomes are sometimes present (Figure 12C), although more often, they consist of several cells (Figure 12D). Non-glandular trichomes on *M. rigida* leaves are usually elongated with a short basal cell and a cylindrical terminal cell.

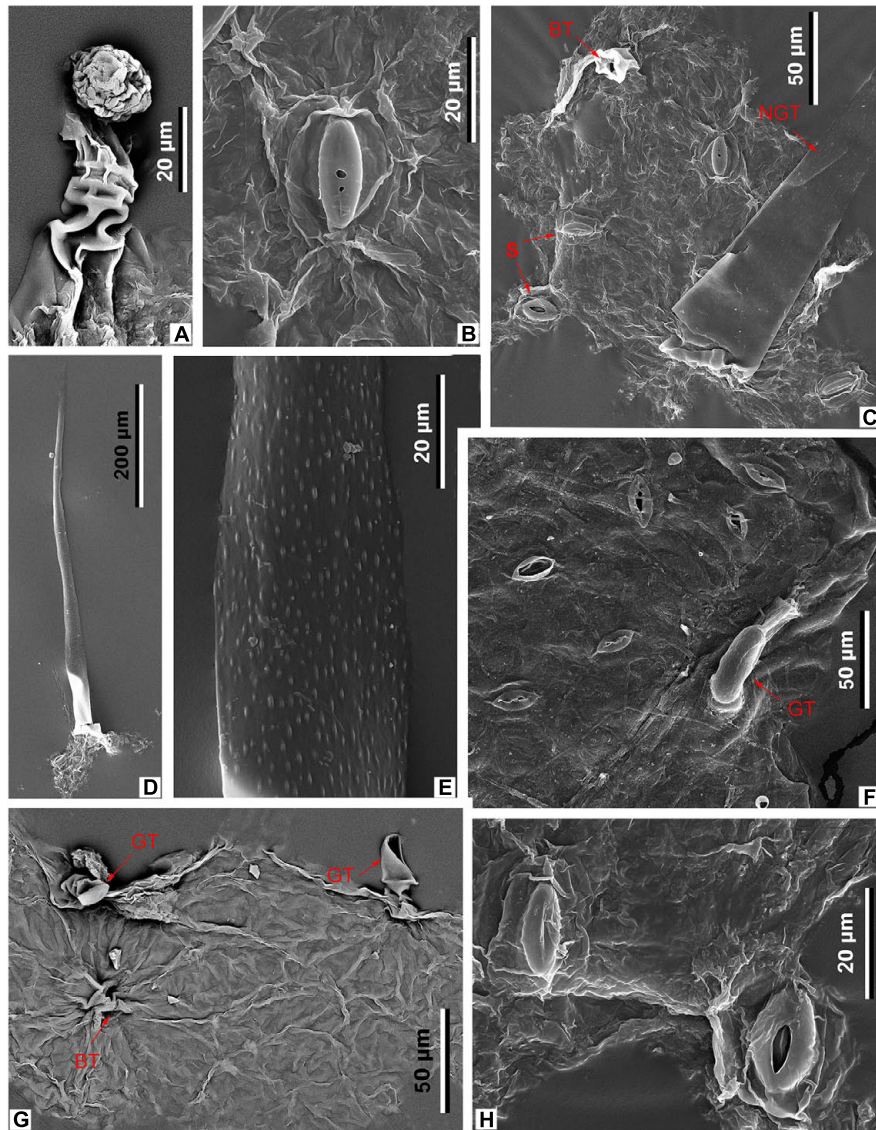
Leaves of the extant Japanese species *M. tenuis* Maxim. differ from those of *M. eosinica* in being of smaller leaf size, having

a mainly elliptic (not obovate) lamina shape, straight secondary veins craspedodromously terminated at the tooth apex and a biserrate leaf margin toothed along the entire length of the lamina (Figures 10H,J,K). The leaf epidermal features of *M. eosinica* are similar to those of *M. tenuis* in stomatal size (26–37  $\mu\text{m}$  long and 15–20  $\mu\text{m}$  wide in *M. tenuis* compared to 28–33  $\mu\text{m}$  long and 25–28  $\mu\text{m}$  wide in *M. eosinica*), with non-papillate ordinary cells on abaxial and adaxial surfaces and numerous trichomes of two types (Figures 11B,C; Supplementary Table 2). However, in contrast to *M. eosinica*, the non-glandular trichomes of *M. tenuis* are much longer (up to 1,000–1,100  $\mu\text{m}$ ) and consist of several cells.

## Pollen Associated With Fossil *Meliosma* Leaves

Pollen grains recovered from the leaf surface of *M. eosinica* are small, prolate to subprolate, tricolpate (probably, tricolpate but this is not detectable on available SEM photos), and perforate (Figure 13). Perforations are distributed more or less regularly, at a distance 3–5 times greater than the perforation diameter. They become smaller on apocolpium regions and toward apertures; there is a narrow smooth margo along the aperture. The aperture membrane is granular. The colpus ends are pointed. The pollen outline is elongated in equatorial view and rounded in polar view (the polar outline is based on one pressed pollen grain and might be incorrect). The polar axis is 16.2–19.2  $\mu\text{m}$ , the equatorial diameter is 10.5–12.5  $\mu\text{m}$ , and the colpus length is 11.2–13.6  $\mu\text{m}$  (based on three pollen grains).

We found no previous data on fossil *Meliosma* pollen. Studies on the pollen grains of extant *Meliosma* species are relatively few with the most detailed study SEM and transmission



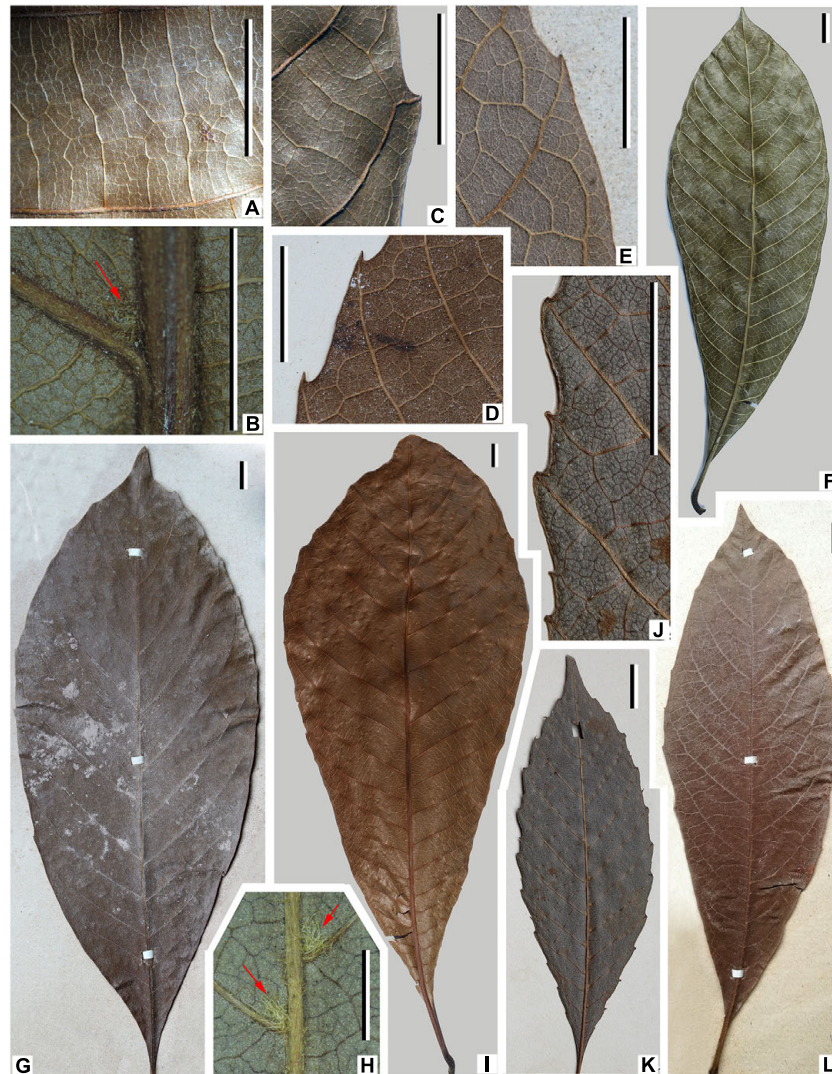
**FIGURE 9** | Leaf epidermal characters of *M. eosinica* sp. nov., MMJ3-837-3a (A–E,G,H), and extant *M. simplicifolia* (Roxb.) Walp., SYS00085373 (F), SEM. (A) Glandular trichome. (B) Stoma. (C) Abaxial surface with stomata (S), unicellular non-glandular trichome (NGT), and base of glandular(?) trichome (BT), external view. (D) Abaxial surface with long unicellular non-glandular trichome. (E) The surface of non-glandular trichome (NGT). (F) Abaxial surface with stomata (S) and glandular trichome (GT), external view. (G) Adaxial surface with glandular trichomes (GT), internal view. (H) Abaxial surface with two stomata, external view.

electron microscopy (TEM) by Furness et al. (2007), and short descriptions of SEM data by Li et al. (2011) and Miyochi et al. (2011). Earlier publications incorporating data from LM (see review in Mondal, 1983) are insufficient for a reliable determination of fossil *Meliosma* pollen. The pollen grains of extant *Meliosma* are small, spheroidal to subprolate, tricolporate, perforate to microreticulate; the exine sculpturing often becomes finer toward the colpi or forms a smooth margo along the colpus. Among the studied species, our fossil pollen grains show the most similarity to *M. pinnata* ssp. *macrophylla* (Merr.) Beusekom (Furness et al., 2007), *M. rhoifolia* Maxim. (Figures 14A,B, this study), and *M. rigida* (Figure 14C, this study). To a lesser extent, due to somewhat larger perforations, the studied fossil pollen

grains also resemble *M. buchananifolia* Merr. (Li et al., 2011) and *M. angustifolia* Merr. (Figure 14D, this study). The pollen grains of *M. fruticosum* Blume (Figure 14E) and *M. simplicifolia* (Figure 14F) show larger perforations (microreticulation) and no smooth margo along the colpi that differentiate the here studied fossils. However, the pollen type and exine sculpturing of the found fossil pollen is rather common for eudicot angiosperms and indistinguishable from several other taxa (e.g., some Menispermaceae taxa, Harley and Ferguson, 1982).

### Leaf Domatia and Associated Mites

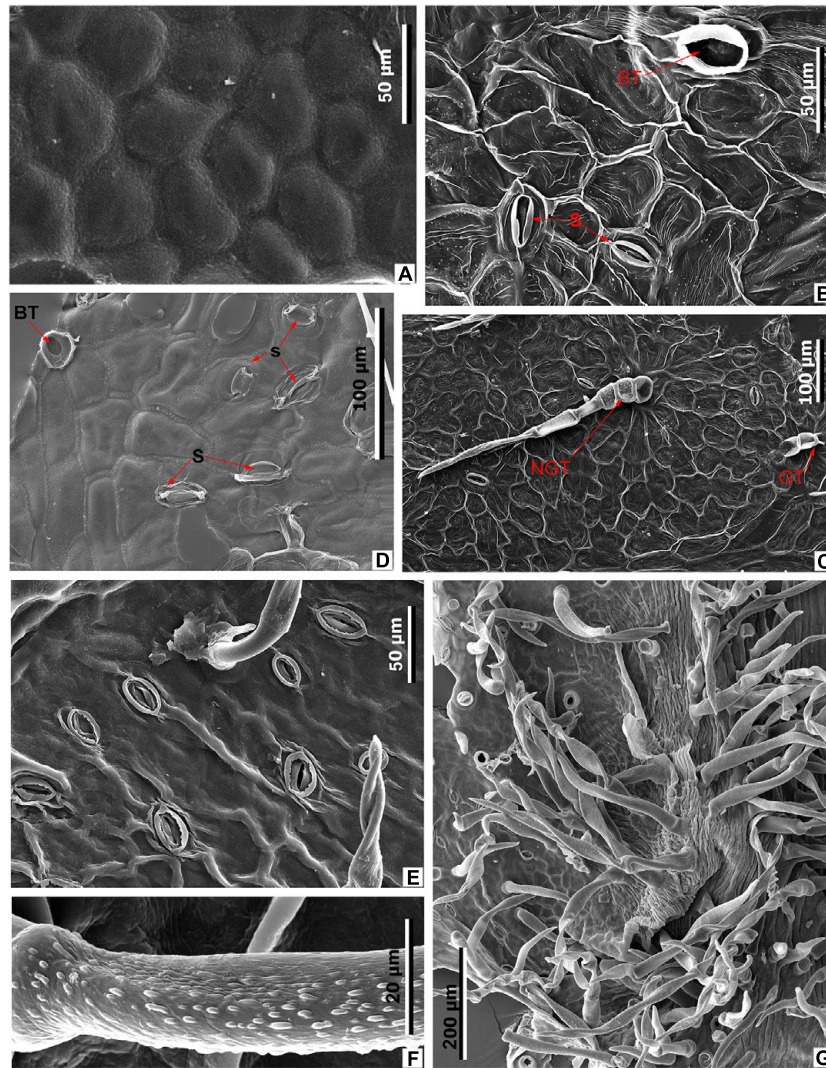
Leaf domatia are tiny structures located on the underside of leaves, usually in the vein axils (Figure 3H). The main types



**FIGURE 10** | Leaf morphology of extant *Meliosma* species. *M. simplicifolia* (Roxb.) Walp., XTBG (**A–C,F,I**). (**A**) Tertiary and higher-order venation. (**B**) Leaf domatium (arrow) in the axil of midvein and secondary vein. (**C**) Marginal tooth. (**F**) Leaf with entire margin. (**I**) Leaf with an irregularly serrate margin. *M. fordii* Hemsl. (**D,L**). (**D**) Marginal tooth, SYS00085158. (**L**) Leaf with irregularly serrate margin, SYS00085144. *M. rigida* Siebold et Zucc., SYS00085219 (**E,G**). (**E**) Marginal tooth. (**G**) Leaf with an irregularly serrate margin. *M. tenuis* Maxim., SYS00085289 (**H,J,K**). (**H**) Tuft of long trichomes (domatia) in axils of midvein and secondary veins. (**J**) Marginal teeth of two orders. (**K**) Leaf with biserrate margin. Scale bars = 1 cm.

of domatia of woody angiosperms are represented by cavities between veins (pockets), partial destruction of the external tissue near the vein bifurcation (pits), and hair tufts covering the area between veins. The combination of hair-tufts with pockets or pits is common for many plants (Nishida et al., 2005; Romero and Benson, 2005). Leaf domatia occur in woody angiosperms of over 80 families, including Sabiaceae, in both temperate and tropical regions but are most abundant in tropical and subtropical zones of Australia, Korea, China, Japan, New Zealand, Africa, and the United States, being limited mainly to humid areas (O'Dowd and Willson, 1989, 1991; Pemberton and Turner, 1989; O'Dowd et al., 1991; Ryu and Ehara, 1991; Willson, 1991; O'Dowd and Pemberton, 1994; Situngu and Barker, 2017). The function of leaf domatia has been debated for a long time (e.g.,

O'Dowd and Willson, 1989, 1991; Pemberton and Turner, 1989; Walter and O'Dowd, 1992a,b; O'Dowd and Pemberton, 1994; Agrawal, 1997; Norton et al., 2000, 2001; Romero and Benson, 2005; Ferreira et al., 2008; Rowles and O'Dowd, 2009; Schmidt, 2014; Situngu and Barker, 2017). Leaf domatia are often called acarodomatia because they are inhabited by mites (e.g., O'Dowd et al., 1991; O'Dowd and Pemberton, 1998; Norton et al., 2000; Romero and Benson, 2004, 2005; Situngu and Barker, 2017; Maccracken et al., 2019). The diversity and reproduction of mites are greater on leaves with domatia (e.g., Walter and O'Dowd, 1992a,b; O'Dowd and Pemberton, 1994; O'Connell et al., 2010). The majority of mites inhabiting leaf domatia are either predators or fungivores (e.g., O'Dowd and Willson, 1989, 1991; Pemberton and Turner, 1989;

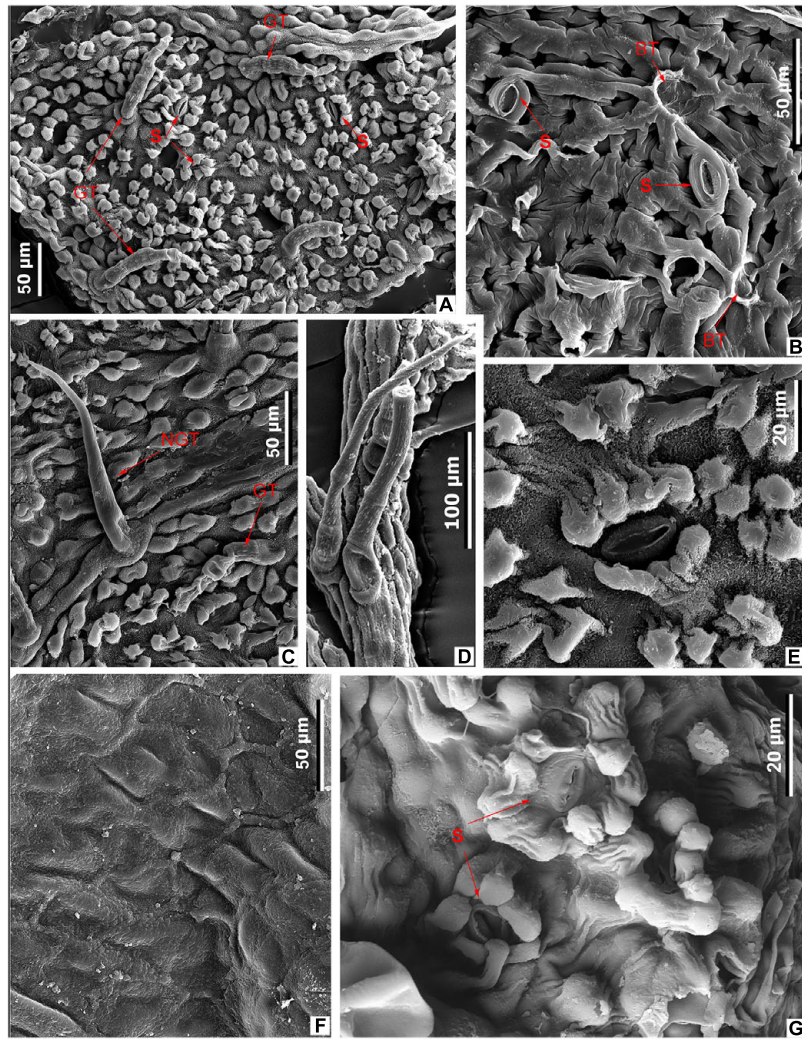


**FIGURE 11** | Leaf epidermal characters of extant *Meliosma*, SEM. *M. simplicifolia* (Roxb.) Walp., XTBG (A,D–G). (A) Ordinary cells on adaxial surface, internal view. (D) Stomata (S) and trichome base (BT) on abaxial surface, internal view. (E) Stomata and trichome base on abaxial surface, external view. (F) Trichome surface. (G) Leaf domatium. *M. tenuis* Maxim. SYS00085289 (B,C). (B) Stomata (S) and trichome base (BT) on abaxial surface, internal view. (C) Abaxial surface with stomata, spinose multicellular non-glandular (NGT) and multicellular glandular (GT) trichomes, external view.

Walter and Denmark, 1991; Willson, 1991; Walter and O’Dowd, 1992a,b; Nishida et al., 2005), but saprophagous mites also utilize domatia (O’Dowd and Willson, 1989). Studies on leaves with several types of domatia revealed that different mite taxa dominate different domatia, even on the same leaf (Nishida et al., 2005). Since numerous tiny mites are characterized by a thin weakly chitinised integument, dry air, and high temperatures are very harmful to them. Domatia help to reduce moisture loss and maintain a relatively constant temperature, thereby preventing the desiccation of mite eggs and mite bodies during molting (Pemberton and Turner, 1989; Willson, 1991; Agrawal, 1997; Norton et al., 2000; Romero and Benson, 2005). Domatia also provide mites with refuges from predatory arthropods (e.g., O’Dowd and Willson, 1989; Agrawal, 1997; Norton et al., 2001; Romero and Benson, 2005; Schmidt, 2014; Situngu and Barker,

2017) and protect young predatory mites from cannibalism (Ferreira et al., 2008). Furthermore, domatia functions as pollen and fungal spore traps, providing some mites (e.g., some Phytoseiidae, Eupodidae) with additional food sources (e.g., Kreiter et al., 2002; Duso et al., 2004; Romero and Benson, 2005; Schmidt, 2014). In return, predaceous and fungivorous mites may protect leaves from epiphyllous pathogenic agents, including herbivorous arthropods and fungi (e.g., Pemberton and Turner, 1989; O’Dowd and Willson, 1991; Agrawal, 1997; Norton et al., 2000; Romero and Benson, 2004; Monks et al., 2007). Thus, leaf domatia facilitate a protective mutualism between mites and plants (Norton et al., 2000; O’Connell et al., 2010; Walter, 2017).

While studies of the modern mite-plant associations are relatively abundant, the fossil record of leaf domatia considered to be inhabited by mites is sporadic. The oldest acrodomatia

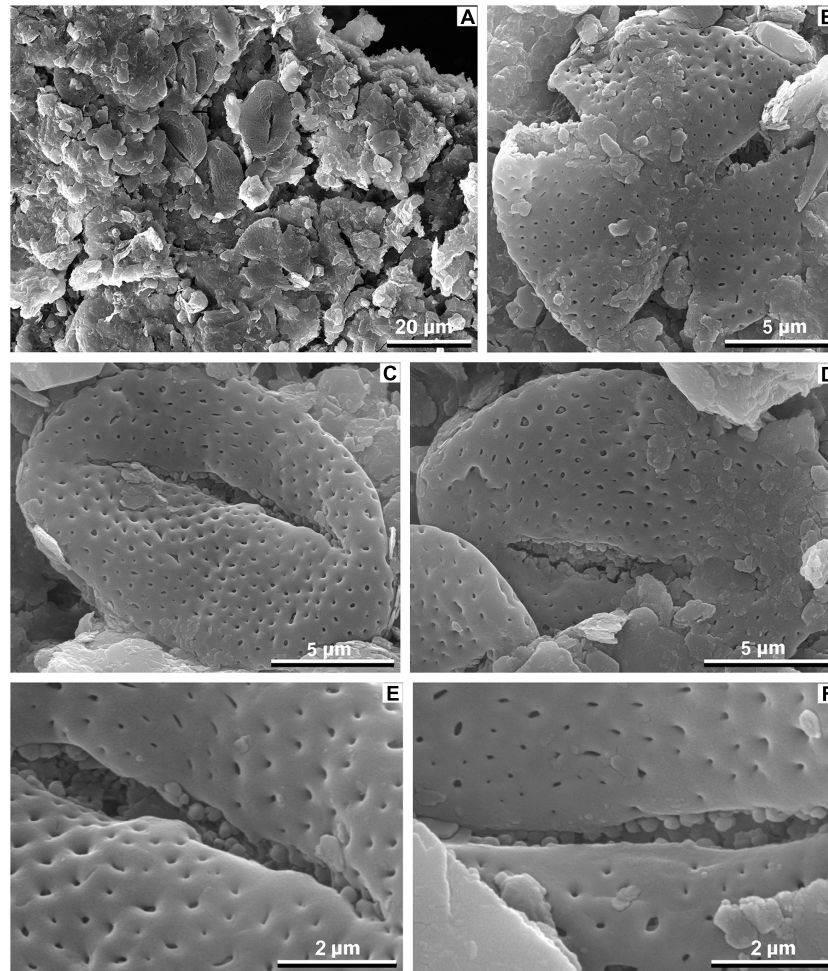


**FIGURE 12** | Leaf epidermal characters of extant *Meliosma*, SEM. *M. fordii* Hemsl., SYS00085139 (A–F). (A) Abaxial surface with papillate cells, stomata (S), and glandular trichomes (GT), external view. (B) Abaxial surface with stomata (S) and trichome base (BT), internal view. (C) Abaxial surface with glandular (GT) and unicellular non-glandular (NGT) trichomes, external view. (D) Multicellular non-glandular trichomes. (E) Stomata surrounded by papillae, external view. (F) Ordinary cells on adaxial surface, internal view. (G) *M. rigida* Siebold et Zucc., SYS00085214, stomata (S) with papillae on abaxial surface, external view.

in the fossil record are known from the Upper Cretaceous of western North America (Maccracken et al., 2019). Fossil acrodomatia have also been described from the middle and upper Eocene of Victoria, Australia (O'Dowd et al., 1991), the middle Eocene of western North America (Liu et al., 2014), and the Miocene of New Zealand (Lee et al., 2010, 2012; Kaulfuss et al., 2015; Conran et al., 2016). However, the interaction between domatia-bearing plants and mites in the fossil record has not been proven by the presence of mites in domatia. In this paper, we report the first occurrence of fossil mites in a leaf domatium of *M. eosinica* (Figure 15). The recovered mite exoskeleton is considerably damaged, the covering was apparently soft, weakly sclerotized, without pronounced shields, and with numerous cuticular papillae and the thinnest of grooves (Figures 15C,D). Several characteristic densely pilose setae are preserved (Figures 15A–D), but a chaetome cannot be

reconstructed due to incomplete preservation of the exoskeleton. Preserved legs are partly deformed, but presumably, they were longer than the body (Figures 15A,B). The gnathostome is not preserved, therefore the type of nutrition is not known with certainty. Based on all visible characters, we interpreted the studied mite as belonging to the superfamily Eupodoidea (Trombidiformes, Arachnida, Arthropoda), and probably the family Eupodidae, which comprises very small (up to 200 μm long) free-living mites with soft and weakly sclerotized bodies. Eupodids can be distinguished from other mites of the superfamily by chaetotaxy, setal and integument ornamentations, and the number of rhagidial solenidia (Strandtmann, 1971; Baker, 1990; Baker and Lindquist, 2002; Krantz and Walter, 2009; Khaustov, 2015a,b).

Eupodoidea has a global distribution, including both polar regions (e.g., Strandtmann, 1971; Olivier and Theron, 2000;



**FIGURE 13** | Fossil pollen associated with *M. eosinica* sp. nov., MMJ3-837-3a, SEM. **(A)** A cluster of pollen grains found on the leaf of *Meliosma*. **(B)** A polar view of the single pollen grain, a smooth margo along the colpus is seen. **(C,D)** Single pollen grain, equatorial view, granular aperture membrane, and probable os in **(C)** are seen. **(E,F)** Close-ups with exine and aperture sculpture.

Baker and Lindquist, 2002; Booth et al., 2009). The most described species of extant mites inhabit temperate to cold regions, whereas mites from tropical areas are much less understood (Baker and Lindquist, 2002; Booth et al., 2009). In China, extant Eupodidae mites were studied from the Shanghai City (Zha et al., 2003), Sichuan (He et al., 2012), Fujian (Zhang and Lin, 2012), and Jiangxi (Ding et al., 2008) provinces.

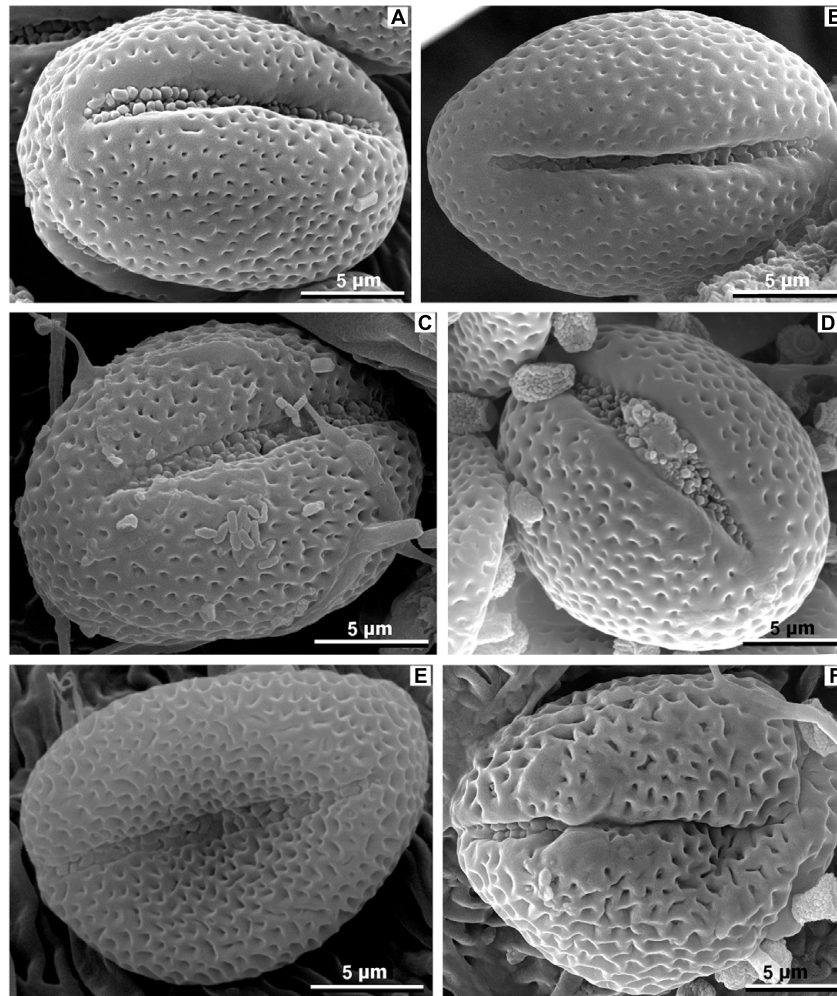
The greatest diversity and frequency of extant Eupodoidea mites are reported from the soil, leaf litter, mosses, lichens, decomposing wood, grasses, and shrubs where they may act as fungivores, predators, bryophytes, or phytophages (e.g., Baker, 1990; Krantz and Walter, 2009; Bizarro et al., 2020). Moreover, abundant Eupodoidea mites inhabit canopies from temperate to tropical forests living on the bark and under the bark of trees, as well as on leaves and stems (e.g., Walter and Behan-Pelletier, 1999; Romero and Benson, 2004; Situngu and Barker, 2017). Mites of the family Eupodidae are often very abundant in soil habitats. They are typically found in moist microhabitats,

many of them are fungivores (Cowles, 2018). Most bark- and leaf-dweller eupodids are algivores, fungivores, and pollen-feeders (Walter and Behan-Pelletier, 1999).

We suppose that the fossil mites studied here lived in the forest canopy occupying the tomentous leaf surface and the domatia of the hair-tuft type.

### Types of Arthropod and Fungal Damage on the Leaves of *Meliosma*

Analysis of plant interactions with arthropods and plant pathogens (especially fungi) in the fossil record provides recent ecological and evolutionary studies with comparative long-term data on the influence of climate change on the ecosystem structure and food-chain relationships (Currano et al., 2008; Wilf, 2008; Wappler, 2010; Wappler et al., 2012; Wappler and Grímsson, 2016), recovery of ecosystems after environmental crises and mass extinctions (Labandeira et al., 2002; Wilf et al., 2006; Wilf, 2008; Donovan et al., 2014, 2016), and their



**FIGURE 14** | Pollen of extant species of *Meliosma*, equatorial view, SEM. **(A,B)** *M. rhoifolia* Maxim., SYS00085206. **(C)** *M. rigida* Siebold et Zucc., SYS00085214. **(D)** *M. angustifolia* Merr., SYS00085105. **(E)** *M. fruticososa* Blume, SYS00085274. **(F)** *M. simplicifolia* (Roxb.) Walp., SYS00085273.

evolutionary implications (Labandeira, 2013, 2021; Labandeira and Currano, 2013).

Damage traces on the leaves of *M. eosinica* are caused mainly by external feeders and, more rarely, by fungi. Insect damage types (DTs) from the external foliage feeding group can be assigned to hole feeding, margin feeding, skeletonization, and surface feeding. The most common DTs are hole feeding types. Medium-sized circular and polylobate holes (DT2, DT3) range in maximum diameter between 2 and 5 mm; with weakly developed reaction tissue present along the edges of polylobate holes (Figures 3C,D, 5F,H). Larger circular holes (DT4) reach 6.5 mm in diameter (Figure 5F). Large-sized polylobate perforations (DT5) showing a narrow reaction rim are confined to the axils between the midvein and secondary veins (Figures 3E, 5D). A cluster of three holes located at the divergence point of secondary veins from primary vein is assigned to DT57 (Figures 3D, 5H). Margin feeding damage (DT15) is present as incisions (up to 7 mm wide and 10 mm deep) extending toward the midvein and showing a distinct reaction rim (Figure 3E).

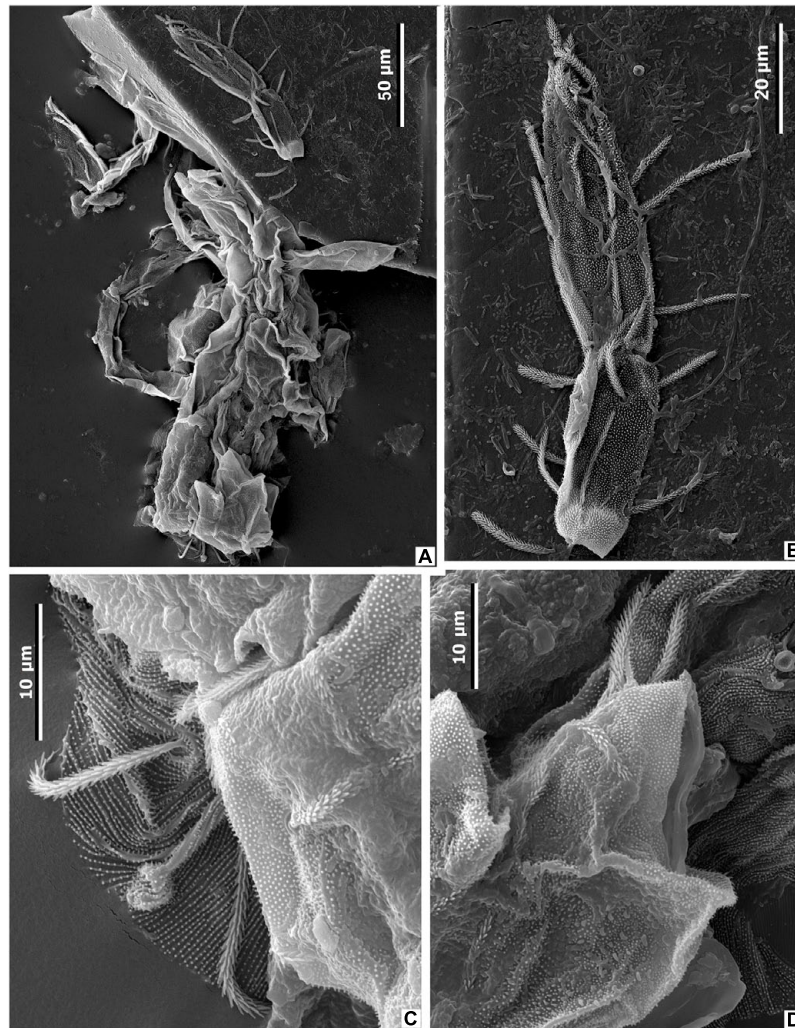
One leaf is skeletonized (Figures 5A,B). Polygonal patches of skeletonized tissue (DT17) are bounded by tertiary veins, with one elongate skeletonized zone adjacent to a secondary vein. Reaction tissue is usually present along the edges of the patches, and high order venation is preserved within skeletonized areas. Surface feeding damage (DT31) recorded on only one leaf is characterized by a circular shape and a distinct reaction rim, and measures 5 mm in diameter (Figure 3E).

A probable fungal infection mark with a wide diffuse reaction front bounded on one side by a tertiary vein is evident in the axillary zone of the primary vein and a secondary vein where domatia are developed (Figures 5E,G).

## Review of the *Meliosma* Fossils (Including Leaves, Fruits, and Wood) and Their Geographical Distribution

*Meliosma* has a rather long and well-documented fossil history and was widespread both in North America and Eurasia





**FIGURE 15** | Mite from the leaf domatia of *M. eosinica* sp. nov., MMJ3-837-3a, SEM. **(A)** Incomplete mite exoskeleton, general view. **(B)** Mite leg. **(C,D)** Details of mite exoskeleton.

during most of the Paleogene and Neogene (**Supplementary Table 1; Supplementary Figure 1**). The earliest records assigned to the genus *Meliosma* have been reported from the Upper Cretaceous (Maastrichtian) of Europe (Knobloch and Mai, 1986). Endocarps of *M. praealba* Knobloch et Mai were described from Walbeck, Germany; this species corresponds to the subgenus *Kingsboroughia* according to the classification of Van Beusekom (1971). In North America, the presence of *Meliosma* is confirmed by endocarps of *M. rostellata* (Lesquereux) Crane, Manchester et Dilcher from the uppermost Cretaceous or lowermost Paleocene Denver Formation near Golden, Colorado, and the Paleocene Sentinel Butte Member of Fort Union Formation near Almont, North Dakota (Crane et al., 1990). Paleocene endocarps are also known in Europe. Mai (1987) described two species, *M. gonnensis* Mai and *M. sheppeyensis* Reid et Chandler, from the lower and upper Paleocene of Gonna near Sangerhausen, Germany. According to Mai (1987), the endocarps of *M. sheppeyensis* are very similar to those from

the Lower Eocene London Clay Formation of southern England (Reid and Chandler, 1933).

The oldest occurrence of fossil leaves assigned to the genus *Meliosma* is from the Paleocene of Williston Basin, North Dakota, United States (**Supplementary Figure 1**). The species *M. thriviensis* was recorded from the lower Paleocene Ludlow Member of the Fort Union Formation, while *M. vandaelium* comes from the middle Paleocene Tongue River Member of the Fort Union Formation (Peppe and Hickey, 2014). Unlike most other *Meliosma* species, these two species are characterized by a relatively small number of secondary veins, 9–10 pairs in *M. vandaelium* and 8–14 in *M. thriviensis*. Peppe and Hickey (2014) compare these species with *M. longifolia* from the lower Eocene Golden Valley Formation of North Dakota, United States, and note a trend toward an increasing number of secondary vein pairs. They suggest that *M. thriviensis*, *M. vandaelium*, and *M. longifolia* might represent a pattern of evolutionary change within the genus. *M. thriviensis* could represent an evolutionary

precursor to *M. vandaelium*, and *M. vandaelium*, in turn, could be a precursor to *M. longifolia* (Peppe and Hickey, 2014).

In the Eocene, the genus *Meliosma* reaches a wide distribution and diversity, confirmed by numerous occurrences of fossil fruits, leaves, and wood, including leaves of the new species *M. eosinica* and associated pollen grains described in this paper. Three species of endocarps, *M. sheppeyensis* Reid et Chandler, *M. cantiensis* Reid et Chandler, and *M. jenkinsii* Reid et Chandler, have been described from the lower Eocene London Clay Formation of southern England (Reid and Chandler, 1933; Chandler, 1961; Collinson, 1983). *M. jenkinsii* also has been reported from the middle Eocene Geiseltal Flora of eastern Germany (Mai, 1976).

The middle Eocene Nut Beds assemblage from the Clarno Formation of Oregon, United States is one of the most interesting fossil floras, which includes five species of *Meliosma* based on endocarps (Manchester, 1994), three species of woods (Wheeler and Manchester, 2002), and leaf species (Manchester, 1981). Manchester (1994) described four species of fossil endocarps, *M. beusekomii* Manchester, *M. bonesii* Manchester, *M. elongicarpa* Manchester, and *M. leptocarpa* Manchester, which correspond to the subgenus *Meliosma*, section *Meliosma*, and one species, *M. cf. jenkinsii* Reid et Chandler, corresponds to the subgenus *Kingsboroughia*. The Clarno Formation fossil wood is the oldest known wood with anatomical characteristics similar to those of extant genus *Meliosma*. There are three types of *Meliosma* wood in the Clarno Formation assemblage, *M. brehmii* Wheeler et Manchester, *M. deweyii* Wheeler et Manchester, and *M. dodsonii* Wheeler et Manchester, distinguished by variation in porosity, ray size, and ray cellular composition. All *Meliosma* woods have characteristics of the subgenus *Meliosma*, section *Meliosma* (Wheeler and Manchester, 2002). Only one well-preserved fossil leaf of *Meliosma* from this locality has been illustrated but so far has not been described (Manchester, 1981). The leaf from the Clarno Formation is most similar in morphology to those of extant *M. simplicifolia*.

Fossil leaves more or less similar in morphology to those of extant *Meliosma* have been described from several Eocene localities in North America and Asia. Two species, *M. duktotensis* and *M. kushtakensis*, were reported from the middle-upper Eocene Kulthieth and Kushtaka formations of the Gulf of Alaska (Wolfe, 1977). *M. longifolia* comes from the lower Eocene Golden Valley Formation of North Dakota, United States (Hickey, 1977). Previously, parts of these same leaves were assigned to *Quercus sullyi* Newberry by Brown (1962). According to Crane et al. (1990) and Manchester (2014), the leaves illustrated by Hickey, and most of those treated as *Q. sullyi* by Brown, appear to represent the extinct genus *Dyrana* Golovneva (Golovneva, 1994; Budantsev and Golovneva, 2009). The glandular (rather than spinose) marginal teeth with rounded sinuses may indicate that these leaves represent Platanaceae, rather than Sabiaceae (Manchester, 2014).

A single leaf from the Chalk Bluffs assemblage, Sierra Nevada, California (United States) assigned to *M. truncata* MacGinitie (1941) is similar in morphology to the leaves of extant *M. parviflora* (Van Beusekom, 1971), but in fact, such an important diagnostic feature as the shape of the leaf apex is unknown, since the apex has not been preserved.

In China, within the distribution area of extant *Meliosma*, occurrences of Eocene *Meliosma*-like leaves have been also repeatedly mentioned (**Supplementary Table 1**), but fragmentary preservation does not afford confidence in determining their taxonomic affinity. Among them, *M. rigidifolia* Guo was described based on one small incomplete leaf from the Guchengzi Formation of Fushun coal mine near Fushun City, Liaoning, northeastern China (WG CPC (Writing Group of Cenozoic Plants of China), 1978). Two poorly preserved incomplete leaves from the Shinao Basin, Panxian County, Guizhou, southwest China (Zhang, 1983) and one fossil leaf from the Nadu Formation, Fengling Town, Nanning City, Guangxi, South China (Feng et al., 1977) were assigned to *Meliosma* sp. *M. augusta* auct. was listed in the assemblage of presumably early Eocene in age from the Yilan coal mine, Heilongjiang, northernmost China, but this plant fossil has not been described and figured (He and Tao, 1997).

Oligocene occurrences of leaf and fruit fossils of *Meliosma* are less common. Three species of fossil leaves morphologically similar to extant *Meliosma* were reported from the Goshen flora (early Oligocene), Lane County, Oregon (United States): *M. rostrata* Chaney et Sanborn (Chaney and Sanborn, 1933, depicted in Van Beusekom, 1971, p. 403, Figures 14-C 1, 2, *M. goshenensis* Chaney et Sanborn (Chaney and Sanborn, 1933, depicted in Van Beusekom, 1971, p. 399, Figure 10-A), and *M. aesculifolia* Chaney et Sanborn (Chaney and Sanborn, 1933, depicted in Van Beusekom, 1971, p. 391, Figure 14-B). *M. goshenensis*, according to Van Beusekom (1971), is very similar in morphology to the extant species *M. rigida* and *M. fordii*. Small lanceolate leaves (or leaflets?) that serrate along the whole lamina margin were described as *M. nevolinae* Pavlyutkin from the lower Oligocene Fatashinskaya Formation of South Primorye, Russia (Pavlyutkin et al., 2014). Furthermore, a single small leaf lacking an apex, probably pubescent, with a serrate margin in the upper part of the lamina, was described as *Meliosma* sp. from the same deposits (Pavlyutkin et al., 2014). A single incomplete leaf of *Meliosma* sp. was described (but not pictured) from the Liuqu Formation of Lazi County, Xizang, southwestern China (Tao, 1988). The age of this formation, according to various reports, has been thought to be Oligocene (Wei et al., 2011), Oligocene–Miocene (Li et al., 2015), or late Paleocene (Ding et al., 2017), this most recent determination being based on radiometric analysis of contained volcanic ashes.

Several *Meliosma* species based on endocarps are known from the Oligocene of Europe. *M. reticulata* (C. et E.M. Reid) Chandler was originally described from Bovey Tracey, Devonshire, England, and subsequently also recovered from the Haselbach member, Saxony, Germany (Chandler, 1957; Mai and Walther, 1978). Endocarps of *M. europaea* C. et E.M. Reid have been reported from several Oligocene and Miocene localities in Western Siberia (Dorofeev, 1963). According to Mai (1964), the older epithet *wetteraviensis* has priority over *europaea*, and, consequently, *M. europaea* was placed by Mai in the synonymy of *M. wetteraviensis* (Ludw.) Mai. This species is also known from the Miocene and numerous Pliocene localities of Europe (**Supplementary Table 1**). Van Beusekom (1971) noted that the similarity of these endocarps (especially from Pliocene) to

modern ones of *M. veitchiorum* Hemsl. is very close; they are probably best attributed to *M. veitchiorum*.

Several species of *Meliosma* endocarps have been also found both in the Miocene and Pliocene of Europe. *M. miessleri* Mai was described from the Miocene of Germany, the Czech Republic, and the Pliocene of Italy (**Supplementary Table 1**; Mai, 1964; Van Beusekom, 1971; Martinetto, 1998; Holý et al., 2012), and *M. pliocaenica* (Szafer) Gregor has been recorded from the upper Miocene Sandanski Formation and upper Miocene–lower Pliocene Noviiskar Formation in Bulgaria (Mai and Palamarev, 1997).

Silicified wood of *Meliosma mio-oldhami* Suzuki et Watari is known from the Lower Miocene Nawamata Formation of central Japan (Watari, 1949; Suzuki and Watari, 1994). This species is similar to the extant species *M. oldhami* Miq. ex Maxim. in wood anatomy.

The only species of *Meliosma* leaves in the upper Miocene of North America, described as *M. predentata* MacGinitie, was reported from the Kilgore flora of Nebraska, United States (Van Beusekom, 1971, p. 402, Figure 10-D).

Fossil leaves of *M. obtusifolia* and *M. shanwangensis* have been described from the lower-middle Miocene Shanwang Formation of Shandong, eastern China (Hu and Chaney, 1940; WGPC (Writing Group of Cenozoic Plants of China), 1978). Species *M. shanwangensis* are also known from the Miocene of Kobe Group, Japan, and South Primorye, Russia (Hori, 1983; Pavlyutkin et al., 2012). Miocene–Pliocene leaves from southwestern China were assigned to *M. lincangensis* Tao et Chen from the Lincang Region, Yunnan (Tao and Chen, 1983; Tao et al., 2000), and extant species *M. buechananifolia* (younger synonym of *M. thorelii* Lecomte) from Tengchong County, Yunnan (Tao and Du, 1982; Tao et al., 2000; Li et al., 2004). *Meliosma* sp. based on a single incomplete leaf was reported from the Tatsumitoge flora (late Miocene), Tottori Prefecture, Southwest Honshu, Japan (Ozaki, 1980).

The only fossil leaves with known epidermal characters assigned to the extant species *M. cf. flexuosa* were reported from the upper Miocene Shengxian Formation of Zhejiang Province, eastern China (Jia and Sun, 2011).

Pliocene endocarps of *M. canavesana* Martinetto, originally described as *Meliosma* aff. *reticulata* (Martinetto, 1998), have been reported from several fossil sites in northwestern and Central Italy (Martinetto, 2001a). Two species of fossil leaves similar to the leaves of modern species *M. myriantha* Siebold et Zucc. and *M. tenuis* were identified from the Kabutoiwa Formation of Central Honshu, Japan (Ozaki, 1991). Fossil endocarps of *Meliosma* cf. *rigida* Siebold et Zucc. were reported from the lower Pliocene of Hatagoya, Central Honshu, Japan (Miki, 1941; Van Beusekom, 1971, p. 402, Figures 13-E 1, 2).

## CONCLUSION

The new species of *M. eosinica* from the Eocene of the Maoming Basin adds to the diversity of the genus in the Paleogene and extends its paleogeographical range to South China. The leaves of the new fossil species are morphologically most similar to

those of the extant Asian species *M. rigida*, *M. fordii*, and *M. simplicifolia*, but extant taxa differ from the fossil species, and each other, in leaf epidermal characters. Pollen grains found on the leaf surface of *M. eosinica* sp. nov. resemble those of the studied extant species *M. pinnata* ssp. *macrophylla* (Furness et al., 2007), *M. rhoifolia*, and *M. rigida*. The first fossil record of a mite associated with leaf domatia increases understanding of co-evolutionary relationships between plants and mites in deep time.

## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

## AUTHOR CONTRIBUTIONS

MM, TK, and JJ conceived the project and designed the research. JJ organized field work and led the data acquisition. MM prepared, imaged fossil and modern specimens, and prepared and studied the cuticles with LM and SEM. MT analyzed and interpreted data on fossil and modern pollen. NM and TK analyzed and interpreted data on fossil mite. MM, TK, MT, NM, XW, and JJ contributed to initial manuscript preparation. All authors contributed to the discussion, final manuscript preparation, and approved submission.

## FUNDING

This study was supported by the National Natural Science Foundation of China (Grant Nos. 41872015, 42111530024 to JJ), State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, CAS) (Grant No. 193118 to JJ), the Fundamental Research Funds for the Central Universities (Grant No. 2021qntd18 to XW), and the Russian Foundation for Basic Research (Grant Nos. 19-04-00046 for NM and 21-54-53001 for MT, NM). The work was carried out within the framework of the State program 0135-2019-0045 GIN RAS.

## ACKNOWLEDGMENTS

We would like to thank Philipp E. Chetverikov (Zoological Institute RAS, Saint Petersburg, Russia) and Alexander A. Khaustov (Tyumen State University, Russia) for their assistance in the identification of the fossil mite. We thank Galina N. Aleksandrova (Geological Institute RAS, Moscow, Russia) for valuable discussions on fossil pollen, Elena I. Kostina (Geological Institute RAS, Moscow, Russia) for her help and advice on macerating fossil and modern leaf cuticles, Robert A. Spicer (School of Environment, Earth and Ecosystem Sciences, The Open University, Milton Keynes, United Kingdom) for valuable advice, and Steven R. Manchester (Florida Museum of Natural History, Gainesville, FL, United States) for helpful comments,

donated leaves of *Meliosma* from his own herbarium, and unpublished photographs of fossils from the Clarno Formation for comparison. We are grateful to Roman A. Rakitov for his help during the SEM examination. We also thank Alexei B. Herman (Geological Institute RAS, Moscow, Russia) for his helpful suggestions on this study. We thank the editor and two reviewers for their constructive comments and useful suggestions.

## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.770687/full#supplementary-material>

**Supplementary Figure 1 |** Plate tectonic maps showing the main fossil occurrences of the *Meliosma* endocarps (blue), leaves (red), and woods (green). Localities: (1). Walbeck (Germany); (2). Almont and Williston Basin, North Dakota

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- Supplementary Table 1 |** Fossil record of *Meliosma*.
- Supplementary Table 2 |** Leaf epidermal characters of *Meliosma eosinica* and similar extant species of *Meliosma*.
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