Fossil evidence for a Cretaceous rise of the mahogany family

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PREMISE: The mahogany family (Meliaceae) is an angiosperm lineage comprising many species that are important elements in tropical ecosystems, and is often used as a study system to understand the evolution of tropical rainforests. While divergence time studies have estimated a Cretaceous origin for the family, no unequivocal fossils of that age have been described. Here, the first Cretaceous evidence for Meliaceae is reported, based on an exceptionally well-preserved fruit from the Upper Cretaceous (79–72 Ma, Campanian) of North America.

METHODS: The fossil fruit was prepared using traditional paleobotanical techniques. Bayesian phylogenetic analyses using morphological and molecular data were conducted to assess the phylogenetic position of the Cretaceous fruit in Meliaceae and to assess the effect of morphology for inferring the overall pattern of phylogeny for the family.

RESULTS: The fruit consists of a fleshy mesocarp and a woody endocarp with a hollow center, nine locules, loculicidal sutures, and one subapically attached seed per locule that has an enlarged sarcotesta near the hilum. The combination of characters in this fruit is strikingly similar to the genus *Melia* L. Phylogenetic analyses recover the Cretaceous fruit as being closely related to *Melia* and highlights the effect of fruit morphological data for inferring the overall pattern of phylogeny in Meliaceae. There are a few structural differences between the fossil fruit of this study and *Melia*; thus, the newly characterized Cretaceous taxon is named *Manchestercarpa vancouverensis* gen. et sp. nov.

DISCUSSION: These results clearly confirm a Cretaceous origin for Meliaceae and that important tropical families were present prior to the development of modern tropical ecosystems in the Cenozoic.

KEY WORDS Cretaceous; fruits; *Melia*; Meliaceae; Sapindales; total-evidence; tropical floras.

The mahogany family, Meliaceae (Sapindales) comprises 702 species within 53 genera of trees and shrubs (Koenen et al., 2015), many of which are highly valuable timbers such as *Swietenia* (mahogany) Jacq. and *Cedrela* P. Browne in the Neotropics, as well as *Khaya* Juss and *Entandrophragma* C. DC. in Africa. In addition, there are many pharmaceutically important members of this family, including *Aglaia* Lour., *Azadirachta* Juss., and *Walsura* Roxb. Moreover, Meliaceae are important components in tropical ecosystems worldwide, especially lowland rainforests (Pennington and Styles, 1975; Mabberley et al., 1995; Koenen et al., 2015). Based on molecular phylogenetic studies, the family is currently circumscribed into two subfamilies (Muellner et al., 2003, 2006): Cedreloideae (81 species) and the much more diverse Melioideae (697 species). Because of the diversity and abundance of Meliaceae in the tropics, it has been used as a study system for elucidating the origin and evolution of

modern tropical biomes (Raven and Axelrod, 1974; Muellner et al., 2006, 2010; Koecke et al., 2013; Koenen et al., 2015; Pennington et al., 2015; Dick and Pennington, 2019).

The estimation of the temporal origin for Meliaceae has been the focus of several studies (Muellner et al., 2006; Koenen et al., 2015; Muellner-Riehl et al., 2016), with the latest divergence time estimates ranging from ca. 90–70 Ma (Muellner-Riehl et al., 2016), suggesting a Cretaceous origin for the family. Unequivocal fossils of that age have yet to be described. Based on fruits, putative Cretaceous Meliaceae have been assigned to extant genera such as *Guarea* F.Allam. ex L. from North America (Graham, 1962) and *Carapa* Aubl. and *Trichilia* P.Browne from western Africa (Monteillet and Lappartient, 1981); because of their preservation, these fossils do not display any apomorphic characters supporting their taxonomic assignments. Hence they are dubious and in need

of critical revaluation (discussed in Pigg et al., 2014). On the other hand, the Cenozoic record of the family is well supported (e.g., Reid and Chandler, 1933; Manchester, 1994; Castaneda-Posadas and Cevallos-Ferriz, 2007; Manchester and McIntosh, 2007; Pigg et al., 2014). Many reported meliaceous fossils are fruits and seeds; for extant taxa, these structures appear to be morphologically diverse and somewhat taxonomically informative (Pennington and Styles, 1975; Cheek, 1989).

Here I provide the first unequivocal evidence for Meliaceae in the Cretaceous, based on an exceptionally preserved fruit from Vancouver Island, British Columbia, Canada. Bayesian phylogenetic analysis of combined morphological and molecular data demonstrates that this fossil is a crown member of tribe Melieae and is closely related to the living genus *Melia*. The newly characterized Cretaceous species provides a minimum clade age for Meliaceae and sheds light on the early evolution of this important tropical family.

MATERIALS AND METHODS

The new species is represented by a single anatomically preserved fruit from Shelter Point on Vancouver Island, British Columbia, Canada. Exposures at Shelter Point are part of the Upper Cretaceous Spray Formation of the Nanaimo Group and include two stratigraphic units that contain fossil plants (Richards, 1975). Exposures of the Spray Formation on Shelter Point are within the *Pachydiscus suciaensis* (Richards, 1975) zone, which is Upper Campanian in age. Furthermore, Ward et al. (2012) places the Shelter Point locality within the *Baculites inornatus* zone, which straddles the magnetochrons C33n and C33r of the global polarity time scale (see Fig. 13 in Ward et al., 2012). Thus, the age range for Shelter Point is here inferred as 79–72 Ma. Although plant fossils at Shelter Point are rare, they are superbly preserved in calcareous concretions and include pinaceous seed cones (Smith and Stockey, 2002), cyatheaceous tree ferns (Stockey and Rothwell, 2004), and angiosperm cornalean fruits (Atkinson et al., 2017).

The fruit described in this study (specimen number SH790 B1 bot-a/side) was sectioned longitudinally (SH790 B1 bot-a) and then in cross section (SH790 B1 side) using the cellulose acetate peel technique (Joy et al., 1956). Microscope slides of the peels were made using Eukitt (O. Kindler GmbH, Freiberg, Germany) xylene soluble mounting medium. Photographs of slides were taken with a Leica DC500 digital camera attached to a Leica MZ16 manual fluorescence stereomicroscope and a Leica DM500B compound microscope (Leica, Wetzlar, Germany). Adobe Photoshop CS 5.0 (Adobe, San Jose, California) was used to process images.

To assess the systematic affinities of the fossil, a combined morphological and molecular Bayesian phylogenetic analysis (hereafter referred to as the total-evidence analysis) was conducted using MrBayes 3.2 (Ronquist and Huelsenbeck, 2003). The analysis used *rbcL*, *matK*, and *trnL-trnF* data from GenBank (Appendix S1). Sequences were aligned in Mafft (Katoh and Standley, 2013), which was spawned through Aliview (Larsson, 2014). A morphological matrix of 49 taxa (46 extant, 2 extinct) and 18 fruit characters was constructed and is available in Appendix S2 and in MorphoBank (O'Leary and Kaufman, 2011; Project 3239). The outgroup consisted of three species of Simaroubaceae: *Quassia amara*, *Simarouba glauca*, and *Ailanthus altissima*. Because of the limited amount of fruit morphological data available for most of

Meliaceae, all taxa were scored according to their generic descriptions (Pennington and Styles, 1975; Cheek, 1989; Mabberley et al., 1995). The relatively small number of characters was sufficient for the goals of this study, but the data set can be easily updated when additional data on characters and taxa are recorded and made available. To assess the effect of fruit morphology on phylogenetic relationships within the family, a morphology-only analysis was performed and the results were compared to those of a molecular-only analysis. Each gene was partitioned and was assigned a GTR + Γ substitution model (see Muellner et al., 2006; Koenen et al., 2015), while the standard model (Mkv) for morphological data (Lewis, 2001) was assigned to fruit characters. The Metropolis-coupled Markov chain Monte Carlo (MCMCMC) had four chains, which ran for 30 million generations, sampled every 1000 generations, and with burn-in set at 25%. The standard deviation of split frequencies was <0.02 at the end of each run. Tracer 1.7 was used to confirm convergence in which all ESS values for each analysis were well over 200. Data statistics (see Appendix S1) were obtained using PAUP* 4.0 (Swofford, 2002). The MrBayes input files from each analysis can be found in the supplements of this paper as Appendices S3, S4, and S5.

RESULTS

Systematics

Order—Sapindales
Family—Meliaceae Juss.
Subfamily—Melioideae Arn.
Genus—*Manchestercarpa* Atkinson gen. nov.
Type— *Manchestercarpa vancouverensis* Atkinson
Generic diagnosis—Fruit drupaceous, containing up to nine locules. Endocarp thick-walled, woody. Center of endocarp hollow. Diameter of central endocarp hollow consistent throughout its entire length. Mesocarp containing radially elongate parenchyma. Endocarp ridges minute. Endocarp ground tissue comprised of interlocking sclereids. Seeds ellipsoidal, one per locule, ellipsoidal, sub-apically attached. Sarcotesta fleshy near hilum.
Etymology—The genus (*Manchester* + *carpa* [fruit]) is named in honor of Dr. Steven R. Manchester for his many contributions to understanding ancient angiosperm diversity while using fossil fruits.
Species—*Manchestercarpa vancouverensis* Atkinson sp. nov.
Specific diagnosis. As for genus.
Etymology. The specific epithet (*M. vancouverensis*) is named for the region, Vancouver Island, where the fossil was recovered.
Holotypus hic designatus: SH790 B1 bot (Figs. 1,2) from beach on Shelter Point, Vancouver, Island, British Columbia, Canada (49°56′39″N, 125°11′10″W), from the Spray Formation, late Campanian (ca, 79–72 Ma).
Repository. Royal British Columbia Museum, Victoria, British Columbia, Canada.

Description

This new taxon is based on a drupaceous fruit with a mesocarp surrounding a thick woody endocarp (Fig. 1A–C). The fruit is 3.5 mm long and 4.0 mm wide. Serial sections reveal nine locules surrounding a hollow central axis (Fig. 1B). Locules are ovate in cross section (Fig. 1D) and each contains a single subapically attached seed

FIGURE 1. *Manchestercarpa vancouverensis* gen. et sp. nov. Holotype SH790. (A) Tangential section of fruit showing fleshy mesocarp, leathery meso-carp (arrow), thick-walled endocarp, and subapically attached seed. B1 bot α #215. Scale = 1.0 cm. (B) Mid-longitudinal section of fruit showing hollow center with a vascular bundle running along ventral (inner) surface of carpel (arrow). B1 bot α #203. Scale bar = 1.0 cm. (C) Tangential section of fruit showing three locules. Note fleshy mesocarp at the apex and leathery mesocarp towards the base. B1 bot α #192. Scale bar = 1.0 cm. (D) Cross section of fruit showing endocarp ridge with loculicidal suture (arrow) opposite of ovate-shaped locule with a single seed. Note leathery mesocarp at bottom right. B1 side #8. Scale bar = 0.5 cm.

(Fig. 1A–C). Opposite of each locule is a small ridge with a loculi-cidal suture (Fig. 1D, arrow).

The mesocarp is preserved with two different textures, one fleshy and one that is interpreted as leathery (Figs. 1A, C, 2A, B). The fleshy mesocarp is preserved at the more apical regions of the fruit (Fig. 1A) and consist of radially elongate parenchyma with amber contents (Fig. 2A). The leathery mesocarp is preserved towards the basal areas of the fruit and is made of shriveled cells (Figs. 1A, C, 2B).

The woody endocarp mostly consists of two types of scler-enchyma: isodiametric sclereids towards the outer periphery (Figs. 1D, 2A, B) and interlocking sclereids (Fig. 2B, C), which com-prise the majority of the ground tissue. There is also a uni- to bise-riate layer of fibers and cuboidal cells that line each locule (Figs. 1D, 2D). Within the hollow center of the fruit, there are some remnant parenchyma cells and robust vascular bundles opposite each locule (Figs. 1B and 2E). These bundles extend from the base to the apex of
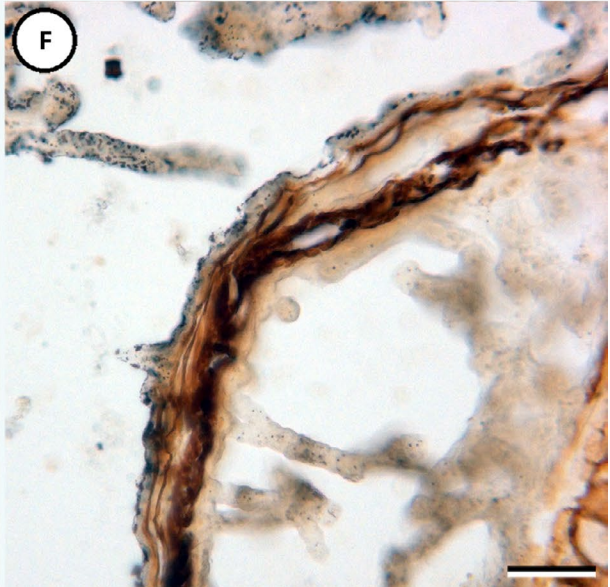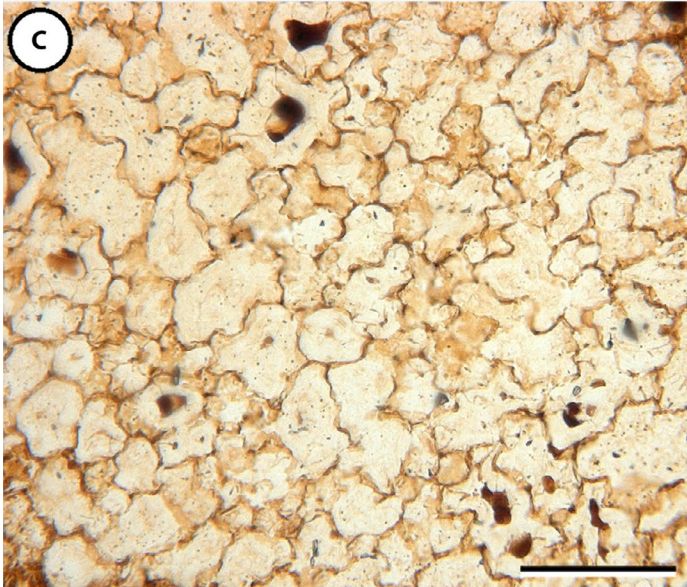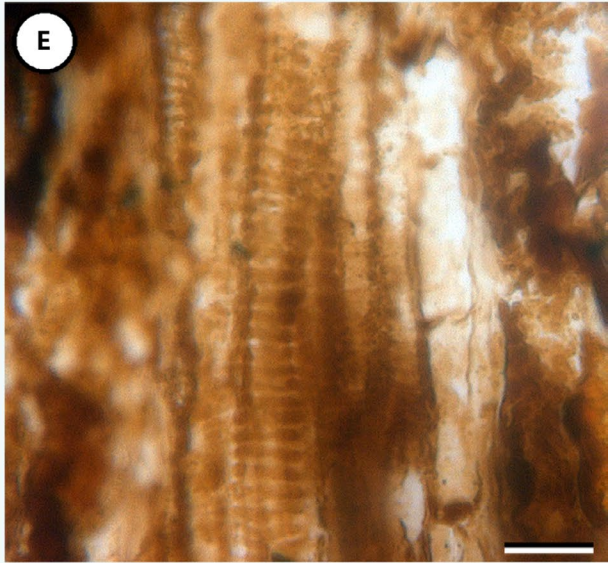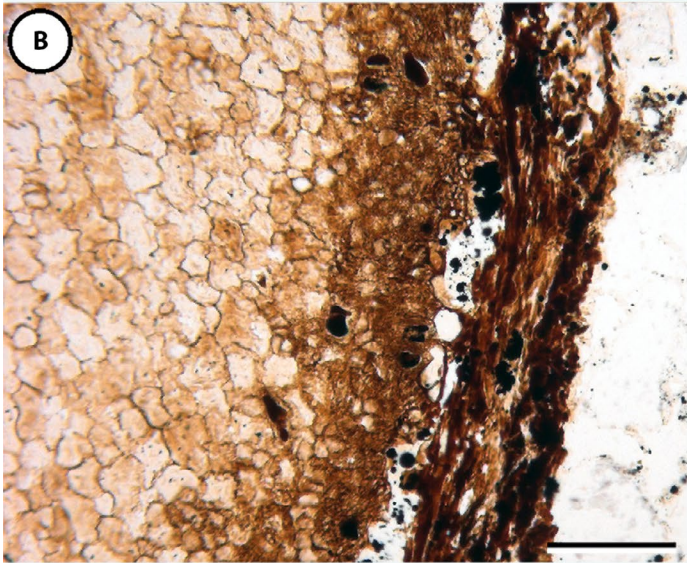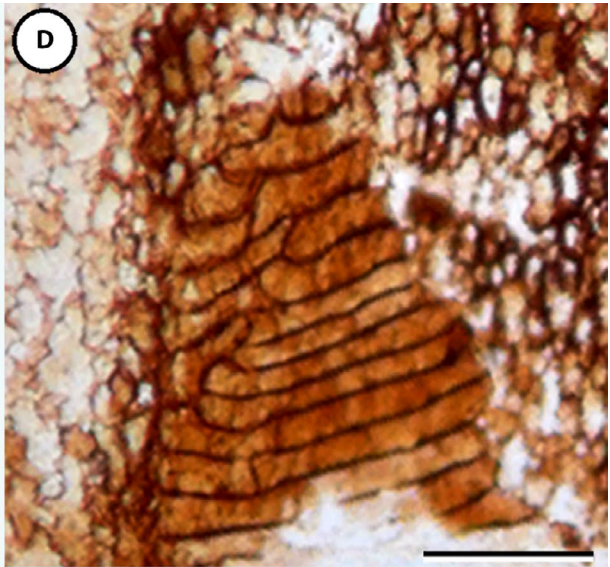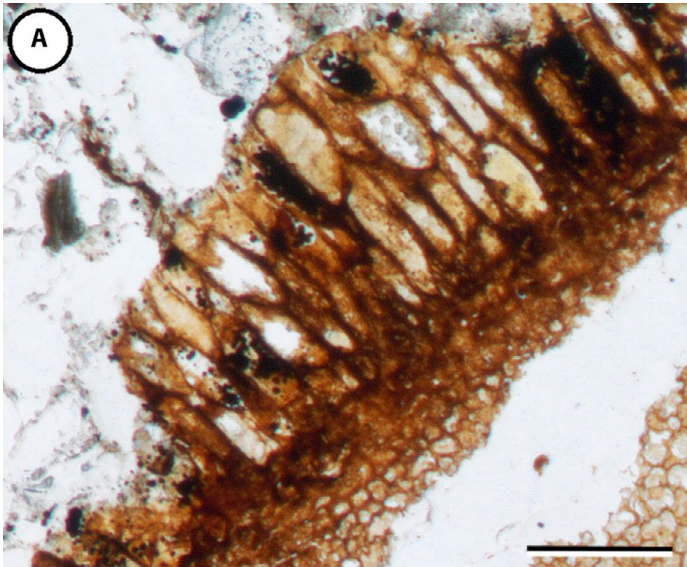
FIGURE 2. *Manchestercarpa vancouverensis* gen. et sp. nov. Holotoype SH790. (A) Longitudinal section of fruit wall showing fleshy mesocarp of radially elongate parenchyma. B1 bot α #215. Scale bar = 0.25 mm. (B) Longitudinal section of fruit wall showing leathery mesocarp and sclerenchymatous endocarp. B1 bot-a #215. Scale bar = 0.25 mm. (C) Histology of endocarp showing interlocking sclereids, some of which contain dark contents. B1 bot α #207. Scale bar = 10 μm. (D) Tangential section of locule showing uni- to biseriate layer of circum-locular fibers. B1 bot α #213. Scale bar = 250 μm. (E) Tangential section of vascular bundle displaying tracheary elements with annular thickenings. B1 bot α #209. Scale bar = 5.0 μm. (F) Cross section of seed coat displaying three to four cell layers including an outer uniseriate zone of thick thick-walled cells. B1 side #8. Scale bar = 20 μm.

the endocarp and branch to supply each seed (Fig. 1A, B). The fruit vascular bundles are made up of tracheary elements with annular thickenings (Fig. 2E).

Each locule has one apically attached seed (Fig. 1A–C). Near the hilum, the seed coat is enlarged and fleshy (Fig. 1A). This fleshy tissue is interpreted as the sarcotesta. The rest of the seed coat is membranous consisting of three to four cell layers (Fig. 2F). The outermost cells are thick walled while the inner cells are thin walled. Because no embryo is preserved, it is difficult to determine whether the membranous seed coat is due to immaturity or if it is characteristic of mature seeds for this species.

Phylogenetic analyses

Bayesian majority rules consensus trees of the total-evidence and molecular analyses revealed a monophyletic Meliaceae with the two major subfamilies, Melioideae and Cedreloideae (Figs. 3,4). Focusing on the Melioideae, two large clades were recovered in the total-evidence analysis and are informally referred to as the Turraeeae-Trichilieae ("TT") clade (posterior probability = 0.84) and the Guareeae-Aglaieae ("GA") clade (posterior probability = 0.62); these two clades form a monophyletic group (posterior probability = 0.99). While the "TT" clade was recovered in the molecular-only analysis (posterior probability: 0.89), the "GA" clade was not. In both analyses, the tribe Melieae is recovered as well (posterior probability in total-evidence tree = 0.98; molecular-only tree = 1). The total-evidence analysis recovered *Manchestercarpa vancouverensis*, *Melia azedarach*, and *Melia yakimahensis* as a trichotomy (posterior probability: 0.97) within the Melieae (Fig. 3). The morphology-only analysis resulted in a majority-rule consensus tree with poor resolution. The *Melia* and *Manchestercarpa* clade were recovered (posterior probability = 0.61), while the "TT" and "GA" clades were not (Fig. S2).

DISCUSSION

The Bayesian phylogenetic analyses of the total-evidence and molecular-only data sets recovered majority-rule consensus trees with consistent higher-level relationships involving two subfamilies: Cedreloideae and Melioideae (see Figs. 3 and 4). These are in agreement with previous analyses (Muellner et al., 2003, 2006, 2008; Koenen et al., 2015). The lower resolution within the "TT" and "GA" clades mirror the phylogenetic relationships that have been difficult to resolve in previous studies (Muellner et al., 2006, 2008; Koenen et al., 2015). In the consensus tree of the total-evidence analysis, *Manchestercarpa vancouverensis* was recovered within the Melioideae and more specifically in a clade (trichotomy) consisting of *Melia azedarach* L. and *Melia yakimaensis* Pigg, DeVore, Benedict & Creekmore with high support. This clade is also supported by having a drupaceous fruit morphology with a thick-walled endocarp, high number of locules, hollow central axis, single

ridge opposite of each locule, loculicidal sutures, one subapically attached seed per locule, and enlarged and fleshy sarcotesta near the hila (Pennington and Styles, 1975; Pigg et al., 2014). The close relationship of *Manchestercarpa* with *Melia azedarach* and *Melia yakimaensis* supports its phylogenetic affinity to Meliaceae and suggests that it is most likely a crown member of the tribe Melieae.

Despite the close relationship between *Manchestercarpa* and *Melia,* there are some differences in fruit structure. *Manchestercarpa* differs from extant *Melia* species by having interlocking sclereids comprising the majority of the endocarp ground tissue rather than interwoven bands of elongate fibers (see Pigg et al., 2014; Appendix S1). The Cretaceous fruit has locules that are ovate in cross section, while those of extant *Melia* species have locules that are laterally compressed (~elliptical) in cross section. In addition, the central hollow within the endocarps of extant *Melia* is constricted in the mid regions as compared to the apical and basal regions of the fruit (Fig. S1B in Appendix S1), while the central hollow of *Manchestercarpa* lacks any such constriction (Fig. 1B). *Manchestercarpa vancouverensis* also differs from the extinct species, *Melia yakimaensis* from the Miocene of western North America (Pigg et al., 2014). In contrast to *Manchestercarpa, Melia yakimaensis* has endocarps with isodiametric and elongate sclereids (potentially fibers) rather than interlocking ones. Because of the morphological differences outlined above, it is most conservative to erect a new genus for this new taxon, *Manchestercarpa* gen. nov.

Assessing the fossil record of tribe Melieae

With the exception of *Manchestercarpa vancouverensis*, the fossil record of the tribe Melieae (*Melia*, *Azadirachta* A. Juss., sensu Muellner et al., 2008) is restricted to *Melia*. There are reports of Paleogene leaves being assignable to *Melia* (e.g., Cockerell, 1908, 1909), but these studies rarely figure the specimens and I find the descriptions too fragmentary to warrant assignment to the genus with confidence. Fruits, however, appear to be the most reliable structures for assessing the fossil record of *Melia*. Pigg et al. (2014) provides a thorough review of fossil *Melia* endocarps. The distribution of this genus appears to have been more extensive in the past than today, with occurrences in the Pleistocene of Japan and Thailand (Tsukagoshi et al., 1997; Grote, 2007), as well as the Miocene of North America and Poland (Pigg et al., 2014 and references therein).

There is a diversity of other fossil fruits that superficially resemble *Melia*, such as *Melicarya* Reid and Chandler from the Eocene London Clay, *Tiffneycarpa* Manchester from the Eocene Clarno nut beds of Oregon (western USA), and *Wetherellia* (Bowerbank) Mazer & Tiffney from the Eocene of eastern North America and the London Clay beds. The fruits of these Eocene taxa are drupaceous with a presumably fleshy mesocarp, a (sub-) woody endocarp that has loculicidal sutures, relatively high number of locules surrounding a hollow axis, and one seed per locule. However, with the exception of Reid and Chandler's (1933) description of *Melicarya*, researchers have been reluctant to formally recognize these taxa
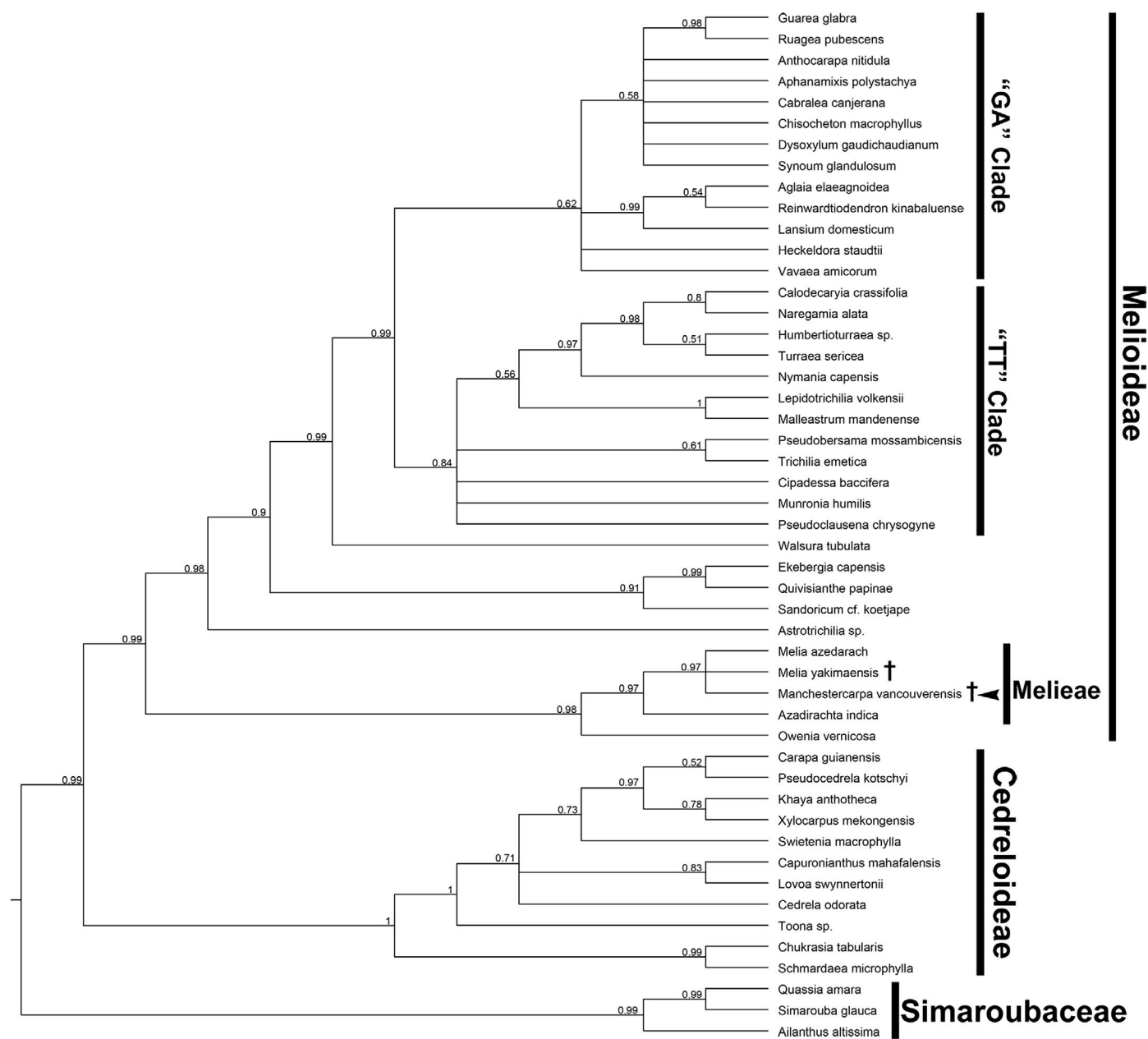
FIGURE 3. Majority-rules consensus tree (branch lengths not shown) from Bayesian total-evidence analysis showing relationships within Meliaceae including selected fossil taxa. Numbers above branches indicate support values (posterior probabilities). Arrowhead marks position of *Manchestercarpa vancouverensis* and † denotes extinct taxa.

as members of Meliaceae based on the fossils' unique combination of characters that do not conform to any genus within the family (Mazer and Tiffney, 1982; Manchester, 1994; Herrera et al., 2012; Pig et al., 2014). This may also reflect our poor understanding of fruit structure across Meliaceae.

Melicarya and *Tiffneycarpa* may be synonyms (Herrera et al., 2012). However, *Melicarya* has endocarps that split into mericarps and ovules with axile placentation (Reid and Chandler, 1933) while *Tiffneycarpa* lacks mericarpy and has ovules with (sub-) apical placentation (Manchester, 1994). The loculicidal sutures of *Tiffneycarpa* extend from the outer periphery of the endocarp to the ventral edge of carpel near the hollow axis (Manchester, 1994), which is not seen in

Melia or any other *Melia*-like taxon. It is unclear whether the seeds of *Melicarya* or *Tiffneycarpa* have an enlarged sarcotesta.

Wetherellia as a whole consists of three species known from drupaceous fruits from the Eocene London Clay Formation and Bracklesham Series of Europe (Reid and Chandler, 1933; Chandler, 1961) as well as the Eocene Nanjemoy Formation of North America (Mazer and Tiffney, 1982). Mazer and Tiffney (1982) provided an extensive review and emendation of the genus. Fruits of *Wetherellia*, specifically *W. variabilis* Bowerbank and *W. marylandica* (Hollick) Mazer & Tiffney, are characterized as syncarpous (up to nine locules) with a thin leathery mesocarp (exocarp in Mazer and Tiffney, 1982), endocarp (mesocarp in Mazer and Tiffney, 1982) of weakly
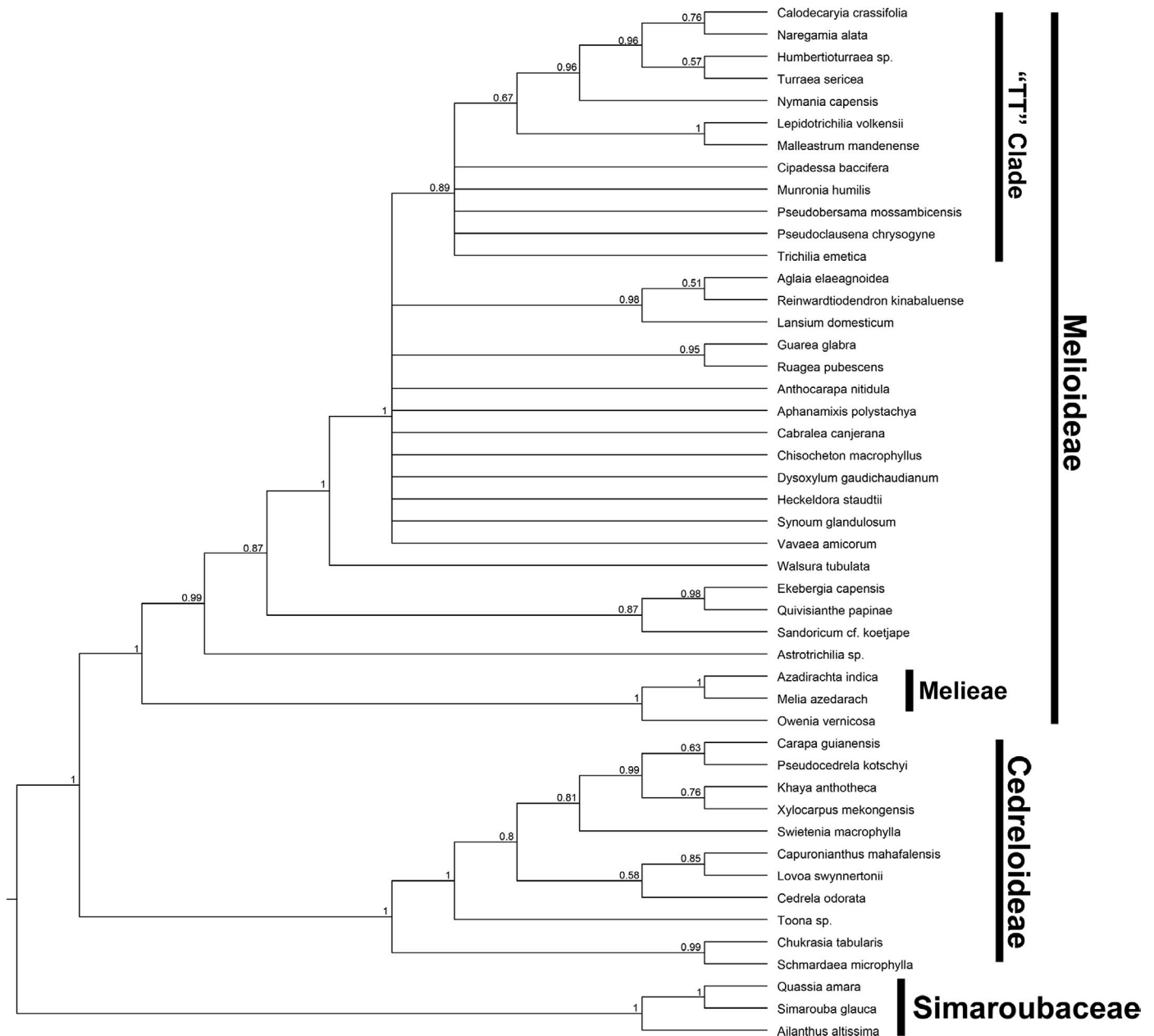
FIGURE 4. Majority-rule consensus tree (branch lengths not shown) from Bayesian molecular-only analysis showing relationships within Meliaceae. Numbers above branches indicate support values (posterior probabilities).

sclerotic cells, endocarp ridges opposite of each locule with lo-culicidal sutures, a hollow central axis, a locule lining of circum-locular fibers (endocarp in Mazer and Tiffney, 1982), laterally compressed locules in cross section, and one (to two) ovules per locule. Furthermore, similar to fruits of *Melia*, those of *Wetherellia* split apart septicidally into mericarps. Tiffney and Mazer cautiously suggested that *Wetherellia* belonged to Meliaceae, but they also noted that the genus was very similar to another fossil taxon, *Palaeowetherellia* (Heer) Chandler, which has been considered to belong to Euphorbiaceae (discussed in Mazer and Tiffney, 1982). However, unlike *W. variabilis, W. marylandica, Palaeowetherellia* fruits have a solid center and the long axis of the seeds are inclined about 60 degrees from the central axis (Mazer and Tiffney, 1982).

Fruits of *Wetherellia* differ from those of *Manchestercarpa* and *Melia* by having endocarps that are less lignified, consisting of relatively thin-walled sclereids and perhaps thick-walled parenchyma (Mazer and Tiffney, 1982). Furthermore, the endocarps of these two Eocene species contain secretory cells, which are lacking in *Manchestercarpa* and *Melia*. *Wetherellia dixonii* Chandler, differs from the other two species in the genus, *Manchestercarpa*, and *Melia* by having a central axis composed of fibers rather than a hollow one.

The unique combination of characters found in *Melicarya*, *Tiffneycarpa*, and *Wetherellia* prevents a confident familial assignment at this time. This issue will be addressed in a forthcoming study. In addition, a thorough survey of Meliaceae fruit anatomy

and morphology is required to more fully assess whether these taxa are assignable to the family.

Inferring phylogenetic relationships of Meliaceae

The results from the total-evidence and molecular-only analyses of this study are in much agreement with those from previous studies (Muellner et al., 2003, 2006, 2008; Koenen et al., 2015; Muellner-Riehl et al., 2016). Muellner et al. (2003, 2008) has thoroughly discussed the effect of different molecular markers for inferring phylogenetic relationships within Meliaceae. An exploration of the morphology and molecular data sets clearly reveals that, when analyzed alone, the combined molecular data provide higher phylogenetic resolution than the morphological data (Figs. 4, S3; also see Table S2), but the "GA" clade was not. However, when fruit morphology is combined with nucleotide sequences in the total-evidence analysis, the "GA" clade is recovered. Thus, I am hopeful that additional fruit characters will help further our understanding of phylogenetic relationships within Meliaceae. As shown in the total-evidence analysis (Fig. 3), morphology plays a crucial role in understanding evolutionary relationships of unequivocal meliaceous fossils and will be critical for reconstructing the overall pattern of phylogeny for the family (including extinct members).

Evolutionary implications

Several studies have attempted to elucidate the timing and evolution of modern tropical forests (those with modern taxonomic compositions and structural diversity) by using molecular divergence time estimates of important eudicot groups such as Meliaceae, Malpighiales, and Menispermaceae (Davis et al., 2005; Muellner et al., 2006; Wang et al., 2012; Koenen et al., 2015; Pennington et al., 2015; Muellner-Riehl et al., 2016). Although many molecular divergence time estimates for these lineages suggest a Cretaceous origin, there has been no fossil evidence to support many of these hypotheses. However, *Manchestercarpa vancouverensis* is the first unequivocal Cretaceous evidence for crown-group Meliaceae and provides a minimal clade age for the family at 72 Ma, which supports the Late Cretaceous age (~80 Ma) estimates for Meliaceae (see Muellner et al., 2006; Muellner-Riehl et al., 2016).

It is worth noting that the presence of important tropical families such as Meliaceae in the Late Cretaceous does not necessarily imply that tropical ecosystems with modern taxonomic compositions and structural characters (e.g., high abundance of entire margined and large leaves and drip tips) were present at that time (Wing and Boucher, 1998; Burnham and Johnson, 2004; Wing et al., 2009). The earliest unequivocal evidence for modern tropical ecosystems are neotropical rainforests from the Paleocene of South America (Wing et al., 2009). The report of *M. vancouverensis* does suggest, however, that important tropical clades, like Meliaceae, were present prior to the Cenozoic development of modern tropical forests (as we know them today), which supports the concept that tropical ecosystems may serve as museums for ancient higher-level taxa.

DATA AVAILIBILITY

The morphological matrix can be found as an online supplement (Appendix S2) and on MorphoBank (Project 3239: Meliaceae fruit matrix): http://morphobank.org/permalink/?P3239.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1. Character descriptions, GenBank accession numbers, phylogenetic statistics, extant *Melia* fruit anatomy, and phylogenetic tree from morphology-only analysis.

APPENDIX S2. Morphological Matrix.

APPENDIX S3. Total-Evidence nexus file with MrBayes block.

APPENDIX S4. Molecular nexus file with MrBayes block.

APPENDIX S5. Morphology nexus file with MrBayes block.

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