ABSTRACT

*Melia yakimaensis* Pigg, DeVore, Benedict & Creekmore (Meliaceae, Melioidae) is described for permineralized endocarps from the Middle Miocene Yakima Canyon flora of central Washington State, U.S.A. Fruits are scleritized endocarps, 2.8–3.7 mm long and 3.2–3.6 mm across, with prominent vertical ridges, a flattened base and a pointed apex. They are 5- to 9-loculate with subapical, axile placentation, and they bear a single, pendulous, mature seed and sometimes several small, presumably abortive seeds per locule. They provide some of the first evidence of Meliaceae subfam. Melioidae in the western North American Neogene and contribute to our understanding of the floristic diversity of the Middle Miocene Yakima Canyon “bog” flora.

Key words: Columbia River Basalt Group, drupe, Melioidae, permineralization, septicidal dehiscence.

The Meliaceae is a family of mostly tropical and subtropical trees and shrubs of Old and New World distribution. Authors have recognized variably two, four, or five subfamilies, with the previous most authoritative treatments recognizing four subfamilies, including Melioidae and Swietenioideae, and the monotypic genera *Quivisianthe* Baill. and *Capuronianthus* J.-F. Leroy (Pennington & Styles, 1975; Mabberley, 2011). Phylogenetic analyses of Meliaceae, based on nuclear and plastid DNA sequences (Muellner et al., 2003, 2006) including representatives of all four subfamilies, supported only Melioidae and Swietenioideae; *Quivisianthe* was placed in Melioidae and *Capuronianthus* in Swietenioideae, which is recognized as Cedreloideae in the most recent taxonomic treatment of the family (Mabberley, 2011). The traditional subfamily Melioidae includes genera with fleshy fruits and seeds lacking wings, such as the chinaberry, *Melia* L., which are typically bird- and fruit bat-dispersed (White, 1986; Voigt et al., 2011). Subfamily Cedreloideae contains taxa with capsules and winged seeds that are wind-dispersed, such as *Swietenia* Jacq. (mahogany) and *Cedrela* P. Browne.

Except for the fossil wood record, particularly of the mahoganies, the fossil record of the family is not extensively distributed; however, it does also
include flowers, fruits, seeds, possible leaves, and pollen. Leaf and fertile remains are from North America and Europe, and wood occurs in Europe, Africa, India, and North America. Of the two currently recognized subfamilies, members of Cedreloideae presumably are more common in the fossil record, although some of these reports are in need of confirmation. Among the megafossil remains attributable to the family, the most commonly recognized forms in the western North American Tertiary are those of the genus Cedrela (Manchester, 2001).

In the current study we describe permineralized endocarps of *Melia* L. from the Middle Miocene Yakima Canyon flora of central Washington State, U.S.A. (Pigg & DeVore, 2005). This material is the oldest known anatomically preserved fruit record of the genus and documents subfamily Melioideae in the Neogene of western North America, where subfamily Cedreloideae is known already from the Paleogene (e.g., *Cedrela*).

**MATERIALS AND METHODS**

Most of the specimens were collected from 1965 to 1990 by T. H. Tuggle and Raymond D. Foisy from the Middle Miocene Yakima Canyon area in Yakima County, central Washington State, between the cities of Yakima and Ellensburg (Burke Museum of Natural History and Culture, University of Washington, Seattle, locality number B4101). Two specimens were found in a collection made in 1993 by the authors. Fossils were recovered from the sites referred to locally as the “County Line Holes,” primarily from the area within the site designated “Hi Hole” by the original collectors (Pigg & DeVore, 2005).

The fossils are found within the Columbia River Basalt Group. Previously we stated that they occur within interbeds of the Sentinel Bluffs Unit of the Grand Ronde Basalt within the Museum Flow Package of N2 Grand Ronde Basalt, which is dated 15.6 million years old by argon-argon (Ar/Ar) dating (Borgardt & Pigg, 1999). Reevaluation of the deposition demonstrates that fossils are found directly within pockets in the basalt flow and not within an interbed (Pigg & DeVore, 2005). Recently obtained dates from the adjacent basalts confirm this previously determined age (Pigg et al., 2007). Specimens that comprise part of the Tuggle/Foisy collection were borrowed from the Burke Museum of Natural History and Culture, University of Washington (UWBM), while other material is housed in the Paleobotanical Collections, School of Life Sciences, Arizona State University (ASU).

Specimens were examined with a Nikon (Melville, New York, U.S.A.) SMZ-10 dissecting microscope and photographed prior to sectioning. Several specimens were sectioned at intervals of 35 μm with a Microslice 2 annular diamond saw (Ultrapract, Santa Ana, California, U.S.A.) with a paper-thin diamond blade, and others were wafered at thicker intervals on a Buehler IsoMet Low Speed Saw. Sections were mounted onto microscope slides with either epoxy or UV-cured adhesive with coverslips mounted in xylene-soluble Permount adhesive (Thermo Fisher Scientific, Inc., Anthem, Arizona, U.S.A.) and studied with reflected and/or transmitted light. Extant endocarps of *Melia azedarach* L. were sectioned freehand or embedded in Ward’s bionplastic and wafered on the Buehler IsoMet Low Speed Saw.

**SYSTEMATICS**

**Family:** Meliaceae Juss.

**Subfamily:** Melioidae Arn.

**Genus:** Melia L.

**Species:** *Melia yakimaensis* Pigg, DeVore, Benedict & Creekmore, sp. nov.

**Holotype:** designated here: Specimen 8, UWBM 56470-50 (Fig. 1H, 2A, E–G).
Paratypes: designated here: Specimen 2, UWBM 56479-7 (Fig. 1E, F); Specimen 5, UWBM 56470-41 (Fig. 1I); Specimen 6, UWBM 56479-15 (Fig. 1A–C); Specimen 9, UWBM 56488 (Fig. 2B); Specimen 12, ASUYC (Arizona State University Yakima Canyon) 59 (Fig. 2C); Specimen 13, ASUYC 60 (Fig. 3A, D). Not figured: Specimen 1, UWBM 56479-14; Specimen 3, UWBM 56470-39; Specimen 4, UWBM 56479-12; Specimen 7, UWBM 56479-6; Specimen 10, UWBM 56478-3; Specimen 11, UWBM 56470.

Type Locality: “Hi Hole” County Line Holes, Yakima Canyon, Washington.

Stratigraphy and age: Columbia River Basalt Group, Middle Miocene.


Etymology: The specific epithet, *yakimaensis*, refers to the collecting locality in Yakima Canyon, Washington State, U.S.A.

Species diagnosis: Endocarps turbinate (top-shaped) to spherical, 2.8–3.7 × 3.2–3.6 mm, 5- to 9-loculate; with prominent vertical ridges marking central rib of locale from base to apex; endocarp tissue highly sclerotic, placenta axial, with seeds attached subapically; seeds flattened, ovate, with elongated hilar region, one mature seed per locale; fruits septicidal, splitting into pyrenes.

Description: This description is based on a total of 13 specimens of fossil endocarps (Figs. 1A–C, E, F, H, I, 2A–C, E–G, 3A, D) that greatly resemble the fruits that we examined of extant *Melia azedarach* (Meliaceae) (Figs. 1D, G, J–L, 2D, H, 3B, C). Of these, 10 specimens were found in the round, weathered out from the matrix (Figs. 1A–C, E, F, H, I, 2A, E–G). These specimens include five complete fruits, four half fruits (the result of weathering and septicidal dehiscence), and one almost complete fruit with a single pyrene removed. Three specimens occur within the chert matrix on weathered surfaces, one oriented in slightly oblique transverse section (Fig. 2B) and the others in oblique longitudinal section (Figs. 2C, 3A, D). Some specimens have a complete fruit axis like those seen in extant endocarps (Figs. 1A–C, 2A, C), while others have a central hollow area corresponding to the central fruit axis (Figs. 1F, I, 2B).

Fruits are 2.8–3.7 × 3.2–3.6 mm, generally turbinate (top-shaped) with the apical half of the fruit extending to a pointed apex (Figs. 1A, E, 3A) and the basal half broader and somewhat flattened at the base (Fig. 1B, H). There is some variation in this general shape, with some endocarps tending toward spherical (Fig. 1E) or vertically flattened (Fig. 1B). Similar variation is seen among extant endocarps, with more tending toward ovate (Fig. 1K). The fruit axis, 0.5 mm in diameter, is seen in some specimens (Figs. 1C, 2A), as in extant forms (Fig. 1L). Prominent vertical ridges that expand in the central part of each locale extend from the fruit apex to the base (Fig. 1A–C, E, H).

Fruits are 5- to 9-loculate endocarps with axile placentation (Fig. 2A–C). The central axis of the endocarps, when preserved, is typically star-shaped, around 500 μm in diameter, and contains a central pith of darker, resinous material (Fig. 2A) that apparently contains bubbles upon fossilization (Fig. 2E). Each locale has a prominent central ridge to the outside and bears a single mature seed that is aligned along the same radius as the central ridge (Figs. 2A–C, 3A). Some specimens have smaller, presumably abortive seeds (Fig. 2C) like those seen in extant fruits (Fig. 2D). Seeds are borne subapically along the central axis and are pendulous within the locale (Fig. 3A, D), as in extant forms (Fig. 3B). The endocarp is composed of highly scleritized, elongate, thick-walled cells with simple pits throughout (macrosclereids) (Fig. 2F). They tend to be aligned somewhat radially, but occur in a swirling pattern around the
FIGURE 2. Fossil and extant *Melia azedarach* L. fruits, transverse sections and anatomical detail. A–C. Fossil *M. yakimaensis*. —A. Transverse section showing pith, radiating lines showing position of septa, and highly scleritized fruit wall; note seed at upper left (holotype, specimen 8, UWBM 56470-50). —B. Fossil fruit in surface of chert matrix showing hollow central axis and seeds aligned along septa (specimen 9, UWBM 56488). —C. Fossil fruit in transverse section, cut at level fairly close to fruit apex, with large (maturing) and small (presumably aborted) seeds near point of attachment (specimen 12, ASUYC 59, #31top). —D. Extant fruit of *M. azedarach*, transverse section cut at level near fruit apex with numerous seeds in attachment, both large (maturing) and small (presumably aborted). Note dark amorphous material in fruit axis. E–G. Fossil fruits, anatomical details of *M. yakimaensis* holotype. —E. Detail of pith in Figure 2A, showing bubblelike structures. —F. Detail of highly sclerified endocarp, showing distribution of sclereids swirling around top edge of seed (appearing as horizontal line). —G. Detail of seed. —H. Extant *M. azedarach* endocarp, detail showing organization of sclereids. Scale bars: A = 2.7 mm; B = 1 mm; C = 1.6 mm; D = 1 cm; E = 2.8 mm; F, G = 2.4 mm.
seeds (Fig. 2A, F), in a manner similar to that in extant *Melia* (Fig. 2H).

Seeds are $2.4 \times 0.6$ mm and flattened, with a straight edge facing the axis and a curved margin to the outside (Figs. 2G, 3A, D) like those of extant *Melia* (Fig. 3C). Like their modern counterparts, they have an elongated hilar region (Fig. 3A, D).

**DISCUSSION**

**ASSIGNMENT TO MELIA**

Fossil endocarps of *Melia yakimaensis* can be assigned easily to *Melia*, a distinctive member of Meliaceae subfam. Melioidae, on the basis of their fruit and seed characters. These include the general fruit organization as small endocarps with prominent vertical ridges; a locule number of five to nine; the subapical attachment of seeds; the highly sclerotic nature of the endocarp; the presence of dark, presumably resinous material in the central axis; and the general shape of the seeds with their distinctive elongate hilar region.

Extant *Melia* fruits are initially drupes, with a fleshy mesocarp and waxy exocarp (Fig. 1D). These outer layers are broken, eaten, and/or mechanically degraded to reveal a highly scleritized, septicidal endocarp (Fig. 1G, J–L). Upon weathering, endocarps eventually split septicidally, usually into either half fruits or, occasionally, with individual locules separating from one another as pyrenes (or mericarps). Our observations of extant *Melia* show that endocarps eventually become free of the fleshy mesocarp after weathering for some months to a year or more. The Yakima Canyon fossils are of fruit endocarps from which the fleshy mesocarp has degraded completely. As in extant *Melia* endocarps, in *M. yakimaensis* the central axis of the fruit may be present (Fig. 1A–C, 2A, E) or sometimes is completely degraded, leaving a hollow center (Fig. 1F, I, 2B, 3A). This hollow central area apparently provides a plane of weakness that contributes to the mechanical splitting of the endocarps upon weathering.

**FIGURE 3.** Fossil and extant *Melia*. —A. Fossil *M. yakimaensis*, oblique longitudinal section through fruit in matrix, showing several seeds in longitudinal view and fruit apex, at top (specimen 13, ASUYC 60). —B. Extant fruit of *M. azedarach* L., longitudinal section near level of apex, showing subapical attachment of several abortive seeds. Note elongate hilar attachment. —C. Extant fruit of *M. azedarach*, longitudinal section through locule, showing elongate hilar attachment of seeds. —D. Fossil *M. yakimaensis*, detail of Figure 3A, showing seeds with elongate hilar attachment. Scale bars: A = 1.7 mm; B = 2 mm; C = 0.8 mm; D = 1.4 mm.
The endocarps of the fossils, like those of the extant forms, are highly scleritized, with five to nine 1-seeded locules (Fig. 2B, D). Fruits also have a centrally placed, radially aligned dehiscence slit along the main rib of each locule, suggesting loculicial dehiscence might also occur on occasion. However, we have seen no evidence of dehisced fruits or isolated seeds. It is more likely that the dehiscence slit is a remnant of a similar feature that is functional in related fruits that are loculically dehiscent capsules.

Fruits of *Melia* are distinctive from the other drupes in Meliaceae, which are known in *Azadirachta* A. Juss. and *Owenia* F. Muell. They differ from these fruits in locule number, endocarp type, and seed coat. In contrast to *Melia* drupes that typically have a highly scleritized endocarp and five to nine 1-seeded locules, *Azadirachta* fruits have 1- or sometimes 2-seeded drupes with a thin, cartilaginous endocarp and seeds with thin, membranous seed coats (Mabberley et al., 1995). *Owenia* fruits are 2- to 3-locular drupes with thin, fleshy, or leathery mesocarps and thick, hard, woody endocarps. In contrast to extant *Melia*, *M. yakimaensis* endocarps are considerably smaller, roughly one half the size of those in living fruits. They also tend to be more turbinate to spherical in shape, while groups of extant endocarps we studied were more often obovate.

*Melia* has been recognized variously as having a single to several species (Mabberley, 2011). Cheek (1989) recognized three species, noting differences in fruit and seed characters in each. In comparison to Cheek's (1989) delimitation, the fruits and seeds of *M. yakimaensis* show a combination of morphological characters found in individual “species.” Endocarps of *M. yakimaensis* are generally most similar in overall isodiametric shape to specimens recognized by Cheek (1989) as *M. azedarach*, in comparison to the elongate fruits he placed in *M. dubia* Cav. and material designated as *M. volkensii* Gürke. *Melia yakimaensis* also has the characteristic star-shaped stele seen in *M. azedarach* sensu Cheek (1989) (Fig. 2L), and in general, seeds appear similar. Several features of *M. dubia* sensu Cheek (1989) are also seen in the fossil *M. yakimaensis*, namely the curved and attenuated region of hilar attachment and a pronounced domelike apical tip of the radicle, as well as a tendency to produce several abortive ovules per fruit (Fig. 2C, D). *Melia volkensii* sensu Cheek (1989) shows both sterile, multiloculate fruits, and those with a single viable seed.

Seed development (Nair, 1959) and anatomy (Netolitsky, 1936; Vaughn, 1970; Corner, 1976; Cheek, 1989) have been described for extant *Melia* with seeds being formed from bitegmic ovules, primarily from the testa (outer integument). In this context, the *M. yakimaensis* seed coat appears more similar to that of *M. azedarach* sensu Cheek (1989), and it lacks the prominent palisade layer of forms that have been designated by Cheek (1989) as *M. dubia*.

**FOSSIL RECORD OF MELIACEAE AND MELIA**

The oldest fossil fruits to be assigned to the Meliaceae are known from the Maastrichtian of Wyoming, Montana, and Saskatchewan, and the Dakota Formation of Kansas (Hollick, 1903). These fossils were described originally as *Ficus* L. (Knowlton, 1911) and later as *Guarea* F. Allam. ex L. (Graham, 1962; Shoemaker, 1977). From our cursory examination of specimens housed in the Museum of Paleontology, University of Michigan, and other specimens given to us by William C. Rember, University of Idaho, we could not conclude with certainty how to interpret them, since they lack the morphological and/or anatomical features needed to be identifiable unequivocally to Meliaceae.

Fruits and seeds described from the Late Cretaceous of Senegal were assigned to Meliaceae and considered to be similar to the genera *Carapa* Aubl. and *Trichilia* P. Browne (Monteillet & Lappartient, 1981). These specimens need to be reevaluated; they cannot be identified on the basis of this report, because there are no photographs.
in the publication to demonstrate the nature of the specimens.

Tertiary fruit and seed occurrences of Meliaceae are found in the Early Eocene London Clay Formation flora, where fruits are attributed to *Toona* (Endl.) M. Roem. (Reid & Chandler, 1933; Collinson, 1983). These fruits clearly belong to the Meliaceae, and presumably to subfamily Cedreloideae, based on their prominent winged seeds; however, their generic assignment is in need of reevaluation (Pigg et al., 2007; Pigg & DeVore, 2010). Pyritized fruits of *Melicarya* Reid & Chandler from the London Clay bear some similarities with Meliaceae; however, they lack the combination of features present in extant genera, and may not belong to the family (Steven R. Manchester, Florida Museum of Natural History, pers. comm., February 2013).

Anatomically preserved fruits compared with *Cedrela* and *Toona* have been recognized recently in the Late Eocene flora of Post, Oregon (Manchester & McIntosh, 2007). The winged seeds of *Cedrela* and related leaves are well-known compression/impression fossils from the Late Eocene Florissant flora of Colorado (MacGinitie, 1953; Manchester, 2001; Meyer, 2003) and the Oligocene of Montana (Becker, 1961, 1962). Leaves from the Florissant flora have been assigned to *Trichilia* by MacGinitie (1953) and are listed without comment in Manchester's (2001) revision of the Florissant megafossil flora. A leaf referred to *Toona* has been reported from the Middle Eocene of Alaska. This report is in need of reevaluation (Wolfe, 1977). Flowers of *Swietenia* have been described in Late Oligocene–Early Miocene amber of Mexico (Castañeda-Posadas & Cevallos-Ferriz, 2007). Fossil endocarps assignable to *Melia* occur in the Miocene of Poland (Czeczott et al., 1959, 1961) and from the Early Pleistocene of Japan (Tsukagoshi et al., 1997) and the Pleistocene of Thailand (Grote, 2007).

Fossil pollen of Meliaceae has been reviewed by Muller (1981), and interested readers should consult this paper for details. He accepts *Guarea* from the Oligocene of Puerto Rico (Graham & Jarzen, 1969); *Psilastephanocolporites grandis* Wingate & Nichols (compared with *Trichilia*) from the Oligocene of Cameroon (see Muller, 1981); and *Meliopollis* Wingate & Nichols from Middle Tertiary sites in western North America (Wingate & Nichols, 2001). He accepted “cf. Melia” cf. azedarach (Salard-Cheboldaef, 1978) as attributable to Meliaceae but not unequivocally to the genus *Melia*. More recent pollen occurrences since Muller (1981) include the Late Oligocene of Ethiopia (Danehy, 2010; Aaron Pan, Southern Methodist University, pers. comm., April 2013).

The fossil wood record for Meliaceae, including the mahoganies, has been compiled in the online compendium InsideWood (2004 onwards). Wood anatomy of Meliaceae has been carefully investigated since the timbers of the family are of considerable economic importance (Kribs, 1930; InsideWood, 2004 onwards; Gregory et al., 2009). Wood in Meliaceae sometimes may be distinctive at infrafamilial levels (Kribs, 1930; InsideWood, 2004 onwards). From a taxonomic standpoint, because of the many genera with overlapping wood anatomical features, using wood anatomical features alone to consistently delimit genera of extant Meliaceae is not possible (Mabberley, 2011). In this context, it is not possible to authoritatively place fossil wood types into modern genera.

**FRUIT AND SEED DISPERSAL IN MELIACEAE**

Within the subfamily Melioidae, fruits in more derived clades are capsules with seeds with fleshy outgrowths originating from localized or generalized meristematic regions of the outer integument (i.e., arils; Corner, 1976; Cheek, 1989). However, the basalmost members have drupes with endocarps that are either hard, or thin and membranous (*Azadirachta*), and that may split septically to produce pyrenes as dispersal units. In contrast, all other members of the Melioidae have seeds that are the principal dispersal units.
Clearly, selection for dispersal has played a major role in the diversification of extant taxa. Furthermore, the role of attraction may not be the sole feature selected for. The Meliaceae contain an impressive array of secondary compounds; fruit evolution may be a balance between attraction of biotic dispersal agents and defense against herbivory (Mulholland et al., 2000).

The much smaller size of the fossil endocarps in comparison to extant *Melia* endocarps (roughly half) is intriguing. Taxa with larger-sized, fleshy fruits have been shown to attract fewer, more specialized species of avian dispersers than do other arboreal plants with smaller, fleshy fruits (McKey, 1975; Howe & Estabrook, 1977; Wheelwright, 1985). Birds with larger beaks, and consequently larger gapes, will eat both small and large fruits, while birds with smaller gapes are capable of dispersing only small fruits. In studies of interactions between bat and bird dispersers of introduced *Melia* in South Africa, Voight and colleagues (2011) documented dispersal of *Melia* fruits by seven species of birds and one species of bats. Of these, the dark-capped bulbul was capable of dispersing propagules into suitable microsites. Clearly, increasing fruit size would decrease the number of bat and bird dispersers of *Melia* propagules. However, field observations (Voight et al., 2011) demonstrate that the genus is capable of linking into local plant dispersal webs where it has been introduced. The potential for documenting a trend for increase of fruit size of *Melia* can only be fully addressed if additional reports of the genus in the fossil record are made in the future.

A second, perhaps stronger, source of evidence for animal-plant relationships of *Melia* can be drawn from the anatomy of the fruits themselves. The Meliaceae have an impressive array of secondary compounds. In *Melia* alone, terpenoids, steroids, alkaloids, flavonoids, anthraquinones, and a variety of other compounds have been isolated. The genus is best known for the production of limonoids, which are tetranolitriterpenoids with a b-substituted furanyl ring at C(17) (Zhao et al., 2010). Antifeeding insect compounds and growth inhibitors are present within *Melia*’s chemical arsenal, as are other compounds with antibacterial, antiviral, and antifungal activities (Zhao et al., 2010). There are reports of poisoning in humans and pigs, but not in birds, sheep, or goats (Mabberley, 2011). Of these studies, some focus on the extracts of the endocarp. In one study (Wand-scheer et al., 2004) a connection was made between the pigmented, dark brown testa and the ability to obtain active compounds from the seeds themselves. Bioassays using only the cotyledons found an active larvicidal compound obtained from the cotyledons. However, the production of the dark material (extant) and resinous material present in the pith of the endocarp’s central axis suggests that this region of the fruit would likely be a source of secondary compounds. Both fossil and extant *Melia* have dark, amorphous, and presumably resinous material in the pith (Fig. 2A, D, E). The anatomy of fossil *Melia* suggests that the endocarp had evolved the ability to produce an array of secondary compounds by the Miocene.

Although the fossil record of fruits and seeds in Meliaceae is scant, we note that the occurrence of capsules with winged seeds in the Early Eocene London Clay (*Toona*) and *Cedrela* in Eocene and Oligocene of western North America is consistent with the basal appearance of subfamily Cedreloideae. The presence of *Melia* in the Miocene of Washington State documents that drupes with endocarps appeared by the Neogene in western North America, and essentially modern *Melia* was present by the Pleistocene in Thailand (Grote, 2007). What the fossil record cannot address is how the complexity of fruit types evolved within Meliaceae and the rates of evolution within the family. As new fossil materials become available for description, and as more paleobotanists recognize that members of the family represented in the Paleogene record may not be identical to their
extant relatives, more information regarding the origin and evolution of this significant tropical family may become clearer.

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