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BEARDIA VANCOUVERENSIS GEN. ET SP. NOV. (JUGLANDACEAE): PERMINERALIZED FRUITS FROM THE EOCENE OF BRITISH COLUMBIA[1]

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Large numbers of permineralized juglandaceous fruits were identified in calcareous nodules from the Eocene Appian Way locality on Vancouver Island, British Columbia, Canada. The fruits, small dorsiventrally flattened nutlets, 4.5–7.0 mm long and 5.5–9.0 × 3–5 mm in diameter, were studied using cellulose acetate peels. They are wingless, ribbed, and have a lobed epicarp that surrounds the nutlet. Cells of the inner epicarp are thin-walled and traversed by a system of branching vascular strands. The stony nutlet wall is composed of fibers, with an outer layer of distinctive idioblasts. The fruits have a symmetry like that in Juglandaceae, subfamily Juglandoideae, tribe Platycaryeae, while the fibrous nut walls are like those of subfamily Engelhardioideae. This unique combination of characters indicates that these fruits represent a new genus and species of Juglandaceae: *Beardia vancouverensis* gen. et sp. nov. The excellent preservation of the Appian Way specimens has allowed a unique view of the internal fruit anatomy and external morphology. As the only wingless, flattened nuts known in the family, they further extend the range of morphological variation in fruits in the family. These fossils further support the hypothesis that North America was an important center of generic diversity for Juglandaceae during the early Tertiary.

Key words: Appian Way; *Beardia*, Engelhardioideae, Eocene, fossil, fruits, Juglandaceae, Platycaryeae.

The walnut family (Juglandaceae) has been extensively studied due to its economic and ecological importance across the northern hemisphere (Manos and Stone, 2001). That it happens to have a very rich fossil record only furthers the status of the family as a model for the integration of extinct and extant taxa in systematic studies (Crane and Manchester, 1982; Manos, 2005). This approach has led to numerous hypotheses on the origin and diversification of Juglandaceae. The addition of newly described fossils of juglandaceous affinity (e.g., Manchester, 1991; Manchester and Dilcher, 1997) continues to reshape these interpretations.

The family, represented by seven to 10 extant genera and 60+ species, is found mainly in the northern hemisphere (Manning, 1978). They are a well-defined group of deciduous or rarely, evergreen trees with pinnately compound leaves, wind borne pollen and unisexual flowers (Manning, 1978). This family has an exceptional fossil record in the Tertiary of the northern hemisphere that includes leaves, wood, inflorescences, fruits, and pollen of both extinct and extant genera (Manchester, 1987). Pollen and fruit records of Juglandaceae indicate that this family radiated in the early Tertiary, especially in the mid-latitudes of North America, ultimately leading to the distribution of genera seen today (Manchester, 1989).

The Juglandaceae are sister to Rhoipteleaceae within the order Fagales, on the basis of morphology, chemistry, and chloroplast, mitochondrial, and nuclear DNA sequence data according to recent phylogenetic analyses (Manos and Steele, 1997; Manos and Stone, 2001; Li et al., 2004). Like other families of Fagales, the Juglandaceae are thought to have had their origins in the *Normapolles* complex of the Late Cretaceous and early Tertiary (Batten and Christopher, 1981; Zaklinskaya, 1981; Friis, 1983). The divergence of juglandaceous taxa from the *Normapolles* complex is thought to be closely associated with adaptive modifications of seed and pollen dispersal systems (Stone, 1973, 1989). Due to adaptive shifts in dispersal, the fruits of Juglandaceae are highly diverse and considered to contain the most important characters for making generic determinations (Manchester, 1987).

Large numbers of fossil juglandaceous fruits have been recovered from the Eocene Appian Way locality in British Columbia. One of the two types identified is described anatomically in this paper and compared to the extensive database of extant and fossil Juglandaceae currently being compiled by Manchester and Manos (S. R. Manchester, Florida Museum of Natural History, personal communication). Unlike most fossil fruits, the Appian Way material is permineralized, providing all of the cellular detail of fruit, seed, and embryo tissues. The relationships of these fossils to other extant and extinct genera of Juglandaceae are considered.

MATERIALS AND METHODS

Specimens used for this study were collected from the Appian Way locality (49°54′42″ N, 125°10′40″ W; UTM 10U CA 5531083N 343646E) on the east coast of Vancouver Island, British Columbia (Fig. 1) on the northern periphery of the Tertiary Georgia Basin (Mustard and Rouse, 1994). Abundant permineralized fossil plant material, gastropods, echinoderms, and bivalves are found in large calcareous nodules embedded in a sandy–siltstone matrix representing a shallow marine environment. Characteristic invertebrates, decapods (Schweitzer et al., 2003), and shark teeth indicate that the calcareous nodules are of Eocene age (Haggart et al., 1997). Based on palynological studies (Sweet, 1997), the site is stratigraphically precarious, with Mesozoic, Paleocene, and Eocene palynomorphs present. The stratigraphy of the area is currently under further investigation (J. W. Haggart, Geological Survey of Canada, personal communication).

Plant material, including abraded wood pieces and fruits representing numerous taxa, is well preserved in the concretions (Little et al., 2001).

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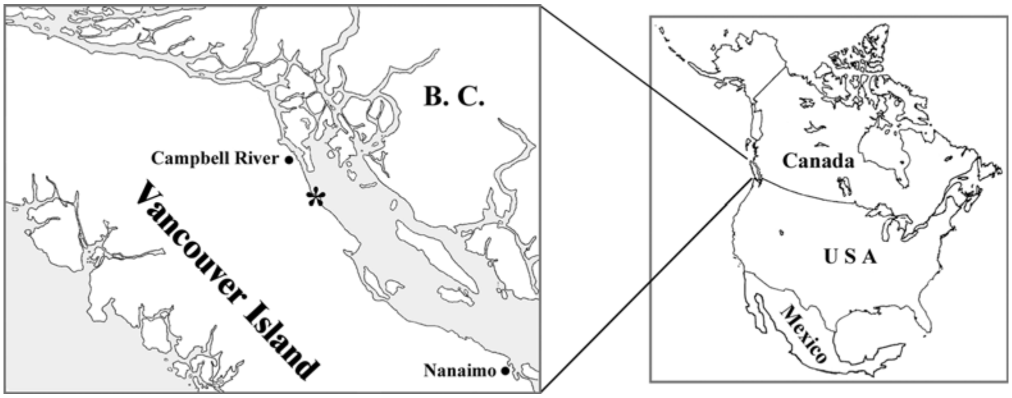


Fig. 1. Map showing location (*) of Appian Way fossil beds, Vancouver Island, British Columbia, Canada.

Taxodiaceous pollen cones (Hernandez-Castillo et al., 2005), gleicheniaceous fern remains (Mindell et al., in press), and shelf fungi (Smith et al., 2004) have been described from the locality.

Nodules were cut into slabs and peeled using the cellulose acetate peel technique (Joy et al., 1956). Of the 292 specimens of juglandaceous fruits that we found within the nodules collected, 290 represent the smaller fruits described in this paper. Microscope slides were made using Eukitt (O. Kindler GmbH, Freiberg, Germany) mounting media.

Images were captured using a PowerPhase digital camera (Phase One, A/S, Frederiksberg, Denmark) and processed using Adobe (San Jose, California, USA) Photoshop 7.0. External morphology of the fruit was reconstructed from serial sections layered, aligned, and connected in three-dimensional space using AMIRA 3.1 visualization software (TGS Software, San Diego, California, USA). All specimens and microscope slides are housed in the University of Alberta Paleobotanical Collections, Edmonton, Alberta, Canada (UAPC-ALTA).

RESULTS

***Systematics*—**
Order: Fagales
Family: Juglandaceae A. Rich. ex Kunth
Genus: *Beardia* Elliott, Stockey et Mindell gen. nov.
Species: *Beardia vancouverensis* Elliott, Stockey et Mindell sp. nov. (Figs. 3–22)

***Generic diagnosis*—**Nutlets flattened in plane of secondary septum, ribbed, wingless, 4.5–7.0 mm long, 5.5–9.0 mm wide, 3–5 mm thick, pedicellate. Nut shape subtriangular in longitudinal view, transversely lenticular. Fruit unilocular, divided by thick primary septum into two main chambers, further partitioned by secondary septum into four chambers at the base. Primary septum one-third to one-half nutshell diameter, secondary septum up to one-third nutshell diameter, lacunae absent. Outer epicarp <1 mm thick, margin undulating. Vascular strands with scalariform tracheary elements extending into the furrows from the inner to outer epicarp. Inner epicarp 1.5–2.0 mm thick, composed of isodiametric parenchyma and vascular bundles. Epicarp thicker at fruit base, measuring up to 6 mm. Nut wall with longitudinal ridges, tapering towards apex, 0.7–2.0 mm thick, composed of fibers with single outer layer of circular idioblasts. Septation formed by wall intrusion into single locule. Placental vascular bundle in center of primary septum. Embryo folded, dicotyledonous.

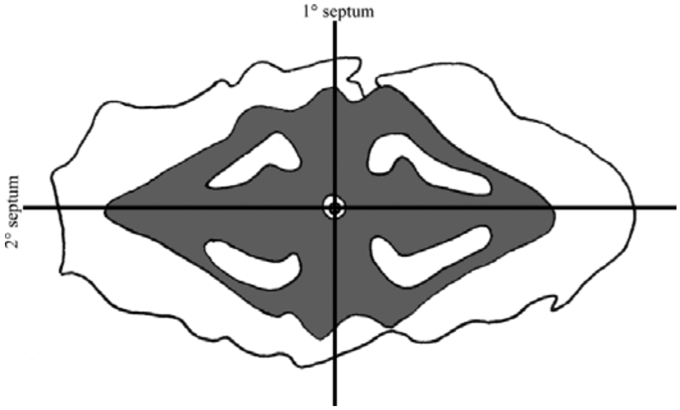


Fig. 2. Diagram of septal orientation for fruits of *Beardia vancouverensis* gen. et sp. nov. Nutlet is flattened in plane of secondary (2°) septum. Primary (1°) septum assumed to be in transverse orientation and secondary septum with median orientation resulting in four-chambered base.

***Specific diagnosis*—**As described in the generic diagnosis.

Holotype—AW 320 Atop (Figs. 3, 4, 13).

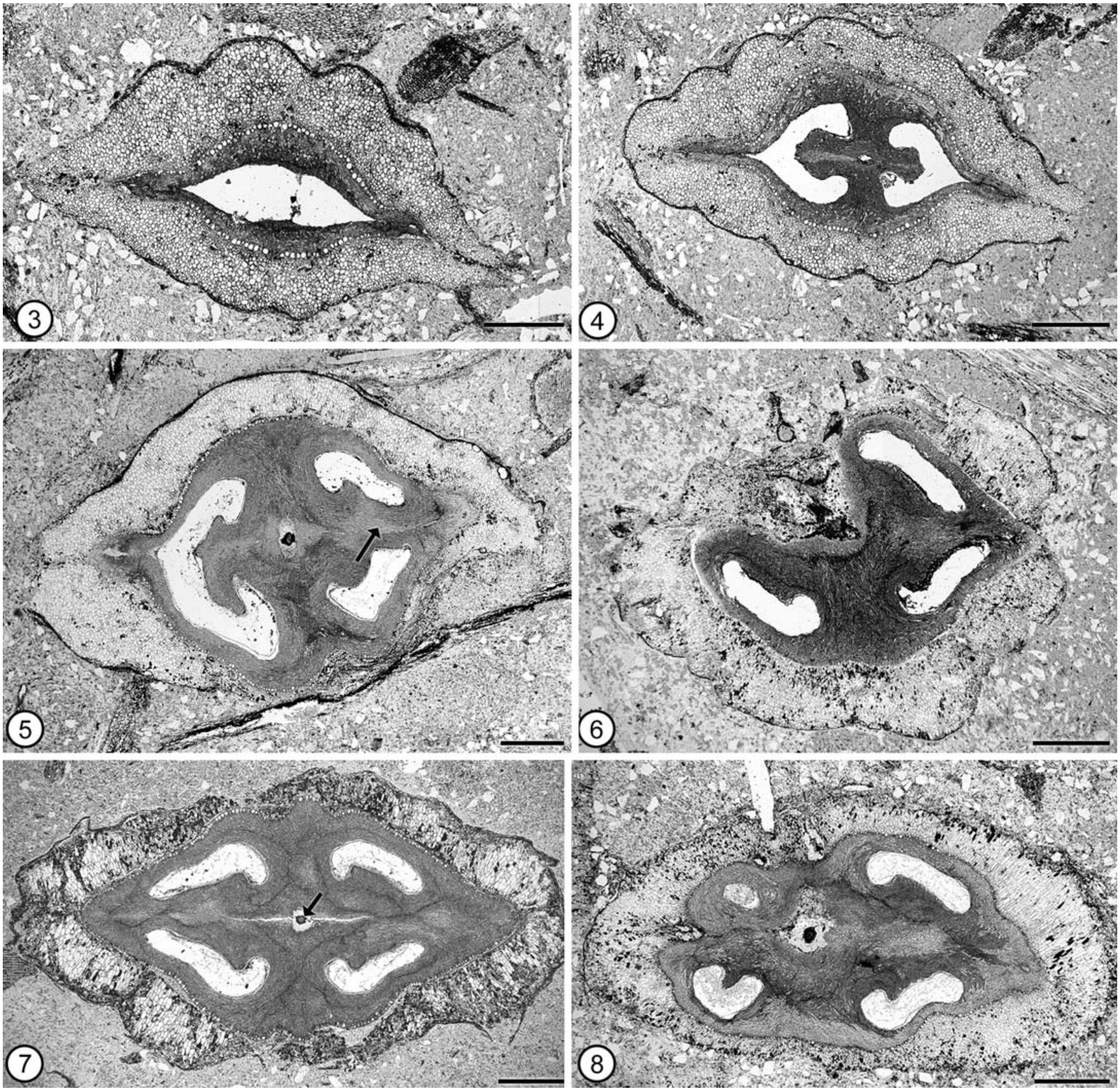
Paratypes—AW 363 F_3bot, AW 253 Gtop, AW 265 Dtop, AW 400 Gbot, AW 378 Jtop, AW 301 Gtop, AW 56 Bbot, AW 3 Bbot, AW 320 Atop, AW 7 Dbot, AW255 Dbot, AW 353 I_2top, AW 292 Ebot (Figs. 5–12, 14–22).

Locality—Appian Way (49°54′42″ N, 125°10′40″ W; UTM 10U CA 5531083N 343646E), Vancouver Island, British Columbia, Canada.

Age—Eocene.

Etymology—The generic name *Beardia* is proposed in recognition of Graham Beard, Qualicum Beach, British Columbia, who has collected and prepared large numbers of fossil plant specimens and generously provided this material for study at the University of Alberta. The specific epithet *vancouverensis* refers to the source of the fossils on Vancouver Island, British Columbia.

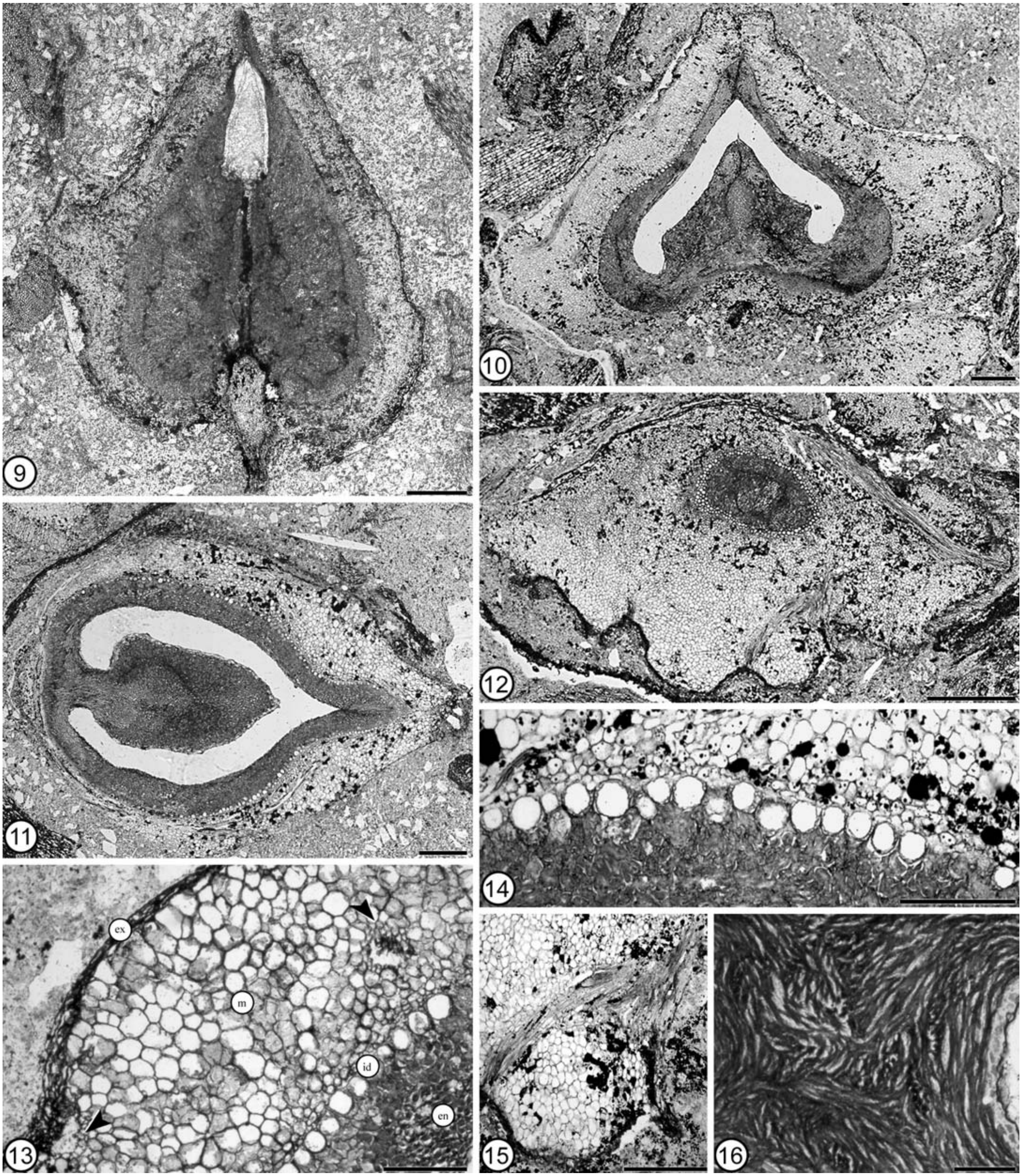
***Description*—**Two hundred and ninety of the 292 identified fruits of Juglandaceae from Appian Way are those of a small, single-loculed fruit of one type (Figs. 3–22). These are dorsiventrally flattened nutlets measuring 5.5—9.0 mm at the widest point in the plane of the secondary septum (Fig. 2). Fruits measure 3.0—5.0 mm in the plane of the primary septum



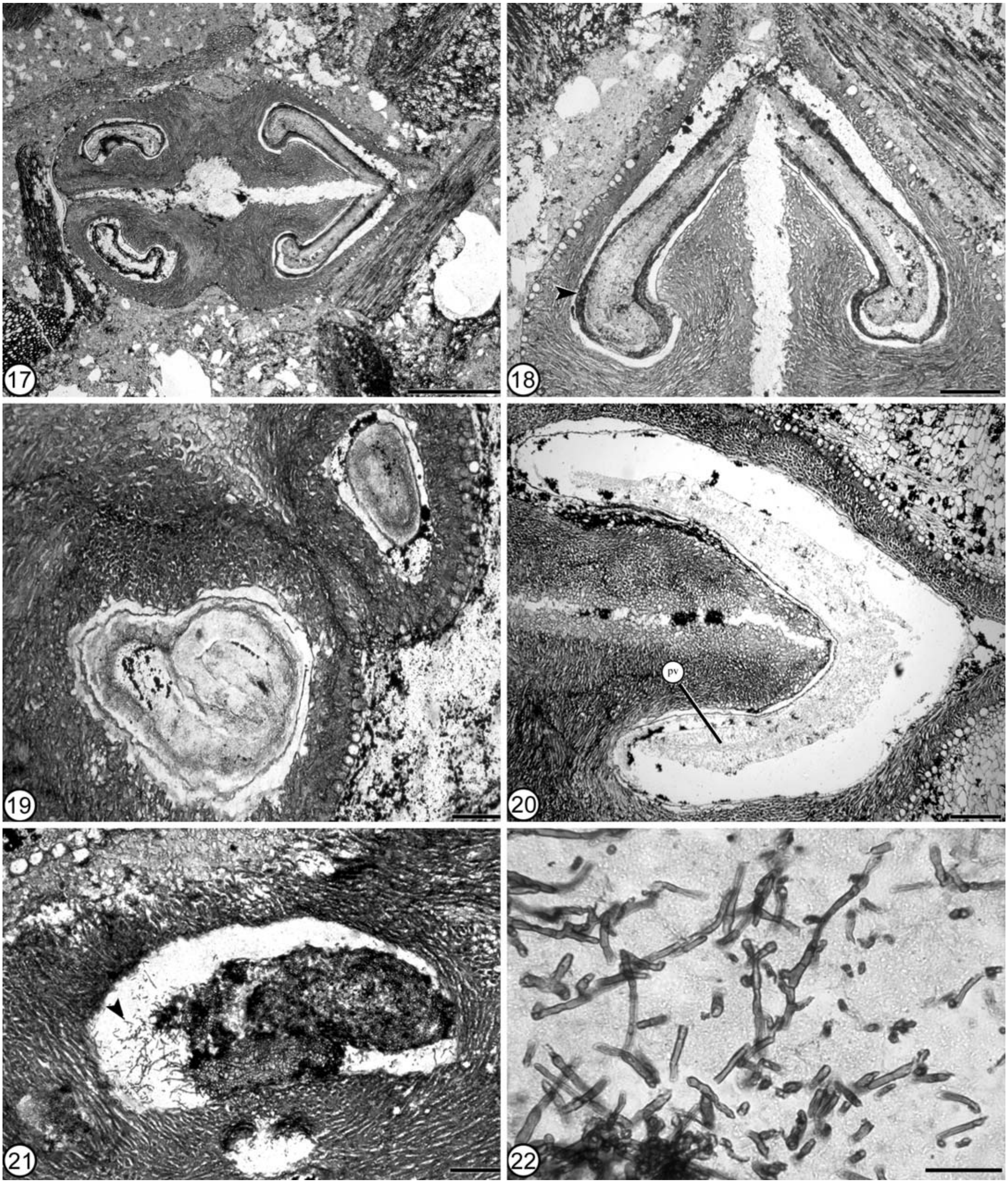
Figs. 3–8. *Beardia vancouverensis* gen. et sp. nov. fruits in transverse section. **3**. Section near apex of flattened fruit showing one chamber and external lobes. Holotype AW 320 Atop #7, ×13.3. Bar = 1 mm. **4**. Section near center of fruit. Primary septum separates chamber into two; secondary septa extend from each side of primary septum. Holotype AW 320 Atop #58, ×12.8. Bar = 1 mm. **5.** Oblique section in middle of fruit near base, showing transition from four chambers to two. Arrow indicates secondary septum. AW 265 Dtop #1, ×10.4. Bar = 1 mm. **6.** Nutlet sectioned transversely near base, at the level of four chambers (one obscured by abrasion). AW 400 Gbot #5, ×12.7. Bar = 1 mm. **7.** Section at base of fruit, showing flattening, nutshell ridges, and four chambers. Arrow indicates vascular bundle. AW 363 F_3bot #9, ×10.9. Bar = 1 mm. **8.** Section near fruit base, four chambers and prominent central vascular bundle. Note lack of lacunae. AW 253 G top #7, ×12.4. Bar = 1 mm.

and 4.5—7.0 mm long in longitudinal section (Figs. 9–11). The primary septum is transverse and incomplete; it only partially extends into the fruit locule. Thus, fruits are one-chambered at the apex and become two-chambered below the apex (Figs. 3, 4). The secondary septum appears near the midpoint of the fruit and separates the two chambers into four (Fig. 5).

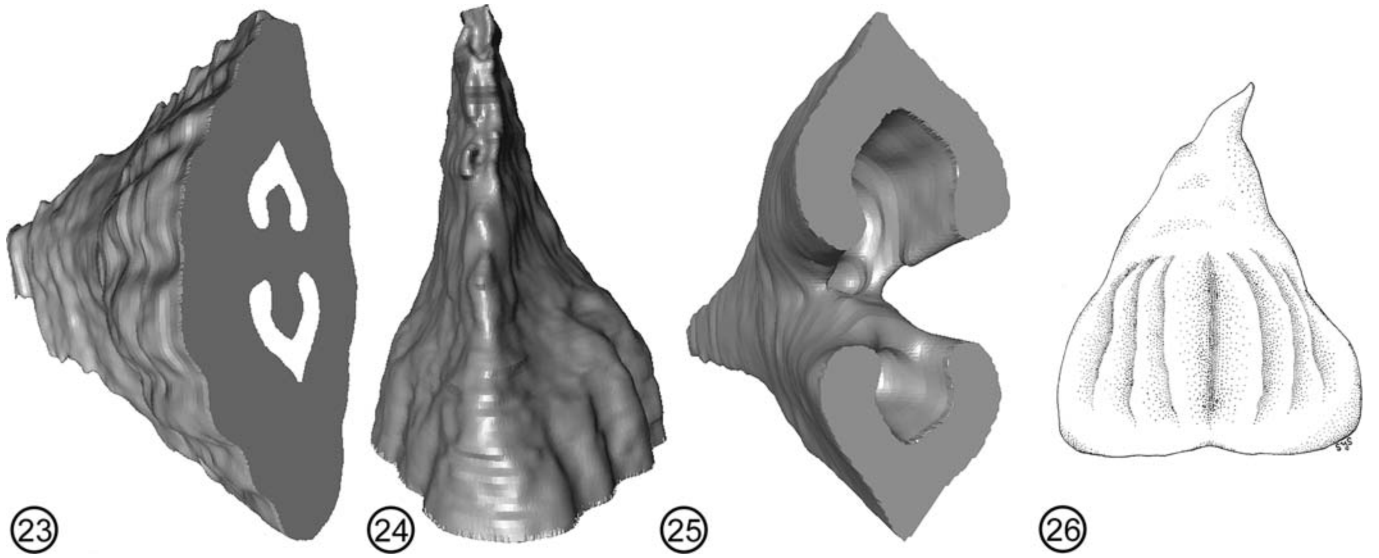
In transverse section, fruits have a lobed epicarp that extends through the peel sections (Figs. 3, 4, 6, 7). In longitudinal section, a column of vascular tissue can be seen between the embryo tissues and the point of fruit attachment, and a pedicel has been found in one specimen (Fig. 9). Fruits are wider at base than at the apex in



Figs. 9–16. Fruits of *Beardia vancouverensis* gen. et sp. nov. **9.** Longitudinal section along primary septum showing apical aperture through which the two main chambers are connected. Note basal attachment and central column of vascular tissue (black). AW 378 Jtop #0, ×11. Bar = 1 mm. **10.** Longitudinal section in plane of secondary septum. AW 301 Gtop #74, ×16. Bar = 0.5 mm. **11.** Section in plane of secondary septum. AW 56 Bbot #18, ×8.7. Bar = 1 mm. **12.** Oblique transverse section of fruit near base, showing vascular traces in lobed epicarp. AW 3 Bbot #24, ×16. Bar = 1 mm. **13.** Transverse section of fruit showing wall layers. *Abbreviations*: N, nut wall; OE, outer epicarp; ID, idioblast; IE, inner epicarp. Holotype AW 320 Atop #7, ×76. Bar = 0.2 mm. **14.** Idioblasts cells indented into outer nut wall. AW 56 Bbot #18, ×84. Bar = 0.25 mm. **15.** Branching vascular trace in epicarp. AW 3 Bbot #24, ×61. Bar = 0.25 mm. **16.** Fibrous nut wall. AW 363 F_3bot #9, ×110. Bar = 0.1 mm.



Figs. 17–22. *Beardia vancouverensis* gen. et sp. nov. fruits. **17.** Oblique section of fruit with embryo. AW 7 Dbot #26, ×17. Bar = 1 mm. **18.** Transverse section of cotyledon; arrow indicates possible fungi. AW 7 Dbot #26, ×54. Bar = 0.2 mm. **19.** Transverse section of fruit showing folded cotyledon. AW 255 Dbot #4, ×89. Bar = 0.1 mm. **20.** Transverse section of cotyledon showing provascular strand (pv). AW 353 I_2top #45, ×46. Bar = 0.2 mm. **21.** Fruit chamber filled with fungal hyphae (arrowhead). AW 292 Ebot #13, ×92. Bar = 0.1 mm. **22.** Septate hyphae in fruit chamber. AW 292 Ebot #3, ×140. Bar = 0.1 mm.



Figs. 23–26. Three-dimensional models of *Beardia vancouverensis* gen. et sp. nov. fruit reconstructed from 255 sections of holotype AW 320 Atop. **23.** External surface of fruit showing dorsiventral shape, external ribbing. Cutaway face shows locule (white) divided into two chambers. ×12. **24.** Longitudinal view of external fruit surface showing external ribbing on both sides of dorsiventrally flattened nut. ×12. **25.** Locule cast showing two chambers and elongate shape. ×24. **26.** Diagrammatic reconstruction of dispersed fruit. ×8.

longitudinal section due to expansion of the mesocarp at the fruit base (Fig. 10).

The outer epicarp is present in some fruits and consists of roughly rectangular cells in a narrow zone 2–3 cells thick that is abraded away in most specimens (Fig. 13). The inner epicarp is lobed, varies from 10 to 46 cells in thickness, and is composed of thin-walled cells (Figs. 12, 13). Vascular bundles with scalariform tracheary elements extend into the epicarp between the lobes (Figs. 12, 13) and appear to dichotomize (Figs. 12, 15).

The nut wall has three ridges on each side of the fruit parallel to the plane of the primary septum (Figs. 2, 7). This layer is 10–22 cells thick outside the chamber and composed of thick-walled fibers (Fig. 16). The shell is thicker in the plane of the secondary septum and extends outward into a prominent ridge (Figs. 3– 5). A distinctive row of round idioblasts, 98–130 μm in diameter, occasionally filled with light-brown contents, forms the outer layer of the nut wall (Figs. 13, 14). These do not have any crystals that can be distinguished from the calcite that fills the lumen under polarized light. although such crystals could have been dissolved during diagenesis. Lacunae are absent in the nut wall.

Embryo tissue is preserved in several of the fruits. The embryo is dicotyledonous (Fig. 17), and the cotyledons appear folded within the chambers (Figs. 18, 19). In one specimen the embryo is surrounded by a dark line of material, which may be the seed integument but most likely represents fungal hyphae (Figs. 17, 18). Fungi with septate hyphae are often found in fruit chambers, usually associated with the embryo tissue (Figs. 21, 22).

The reconstructions of the external fruit surface (Figs. 23, 24) and locule shape (Fig. 25) show the fruit morphology. The wingless, flattened nut is prominently ribbed with eight major lobes towards the base and tapers toward the fruit apex (Figs. 6, 23, 24). The fruit is clearly unilocular and the primary septum divides it into two (Fig. 25) and then four C-shaped chambers at the base (Figs. 7, 8). Evidence from both the reconstruction (Appendix S1, see Supplemental Data with online version of this article) and peels has been used to put together a proposed model for the external fruit shape (Fig. 26).

DISCUSSION

Interpretations of juglandaceous fossil fruits rely heavily on comparisons with extant genera (Manning, 1978; Manchester, 1987). Extant Juglandaceae with unequivocal early Tertiary fruit records include *Juglans* L., *Carya* Nutt., *Cyclocarya* Iljinskaya, *Engelhardia* Lesch. ex Blume, *Oreomunnea* Oerst, *Platycarya* Sieb. & Zucc., and *Pterocarya* Kunth (Manchester, 1987). As yet, no fossil record has been found for *Alfaroa* Standl., but it is believed to be closely related to *Oreomunnea* (Manos and Stone, 2001). Extinct genera of Juglandaceae include *Casholdia* Crane & Manchester, *Paraoreomunnea* Dilcher, Potter & Crepet, *Paleooreomunnea* Dilcher, Potter & Crepet, *Paraengelhardia* Berry, *Juglandicarya* Reid & Chandler, *Hooleya* Reid & Chandler, *Palaeocarya* Saporta, *Paleoplatycarya* Manchester, *Cruciptera* Manchester, *Polyptera* Manchester & Dilcher, and *Sphaerocarya* Dorofeev.

The grouping of genera within Juglandaceae into subfamilies and tribes was originally based on morphological characters (Manning, 1940; Bolick, 1983; Schaarschmidt, 1985). Smith and Doyle (1995) were the first to combine cladistic analyses of chloroplast DNA and morphological data in the recognition of intrafamilial relationships within Juglandaceae, showing the presence of two major clades within the family. Manos and Stone (2001), also using molecular and morphological data, were able to recognize Juglandaceae as having two subfamilies: Engelhardioideae (*Engelhardia*, *Oreomunnea*, *Alfaroa*) and Juglandoideae. According to their data, two tribes exist in the subfamily Juglandoideae: Platycaryeae (*Platycarya)* and Juglandeae (*Juglans*, *Cyclocarya*, *Pterocarya*, *Carya)* (See Fig. 1 in Manos and Stone, 2001).

The morphology, ontogeny, and anatomy of extant juglandaceous fruits have been extensively studied (Holm, 1921; Woodroof and Woodroof, 1927; Shuhart, 1932; Langdon, 1939; Verhoog, 1968), providing a good deal of data with which to compare our fossil fruits (Table 1). Juglandaceous fruits are very diverse in morphology, illustrating the evolution of fruits adapted for wind dispersal, with a large range of wing sizes and shapes, to large, fleshy fruits adapted for animal dispersal (Stone, 1973; Manchester, 1987). Animal-dispersed fruits are thought to have arisen three separate times from winged fruits in the evolution of the modern juglandaceous genera (Stone, 1973). In Juglandaceae, all but *Alfaroa, Carya*, and *Juglans* have wings (Manning, 1978). After examining 290 specimens, some with over 255 consecutive sections, clearly the Appian Way nutlets have a flared and lobed epicarp at the fruit base but lack a distinct wing of any kind. The extent of the epicarp surrounding the fruit and the thickness at the base in these fossil fruits would not have been effective for wind transport. This leaves two possibilities: (1) wings were formed by a subtending bract and/or bracteoles (as in most Engelhardioideae) attached below the fruit, or (2) these fruits were transported by means other than wind. The former seems unlikely because pedicels are present on some fruits and no accessory structures are observed in these specimens. Animals are the common alternative vector for the family, although the fossil nuts are much smaller than those of extant genera.

Fruit shape is highly variable within Juglandaceae, with spherical fruits being the most common (Manning, 1940). Nutlets of subfamily Engelhardioideae are mostly spherical, with the exception of *Engelhardia roxburghiana* Wall. and the extinct genus *Paleooreomunnea*, which has laterally compressed nutlets (Manchester, 1987). Fruits of subfamily Juglandoideae, tribe Juglandeae, have nutlet shapes ranging from spherical (as in *Carya* and *Juglans*), ovate (as in *Pterocarya*) to pyramidal (as in *Cyclocarya*) (Manchester, 1987). The nutlets of the fossil fruits from Appian Way are flattened, although their orientation relative to the bract is unknown. The shape of the Appian Way fruits is similar to the pyramidal nuts of *Cyclocarya*, *Polyptera*, and *Cruciptera*, except that they are flattened and lack a wing. Extant *Carya aquatica* (Michx. f.) Nutt. also has flattened fruits (Fig. 31d, 31e in Manchester, 1987), but accessory tissues do not surround the nut at maturity (Manning, 1978). Only *Playtcarya* have flattened nuts (Manning, 1978) like the Appian Way fossils. In *Platycarya*, the fruits are born in woody, cone-like infructescences (Manning, 1978). No such structures have been recovered as yet from the fossil locality.

Juglandaceous nutlets have one locule with incomplete primary, secondary, and rarely tertiary septa, resulting in two to eight chambers at the base of the fruit (Reid and Chandler, 1933; Manning, 1978). As a result of the fusion of two carpels early in floral development, the single ovule of the Juglandaceae is borne on the apex of the primary septum, and although fruits of all genera have at least two chambers at the base, they are joined apically into a single locule (Manning, 1940). In Juglandaceae, chamber number is a product of the incomplete primary, secondary, and tertiary septation. This septation provides a useful tool in distinguishing genera (Manning, 1978). Little or no secondary septation occurs in fruits of *Platycarya*, *Annamocarya* Dode, and some *Juglans* spp., resulting in a two-chambered base. Tertiary septation occurs in *Alfaroa* and *Oreomunnea*, resulting in eight chambers at the base (Manchester, 1987; Manos and Stone, 2001), although *Alfaroa* has been observed to be four chambered at its base in both mature (Manning, 1949) and immature fruits (Leroy, 1955). Secondary septation in *Carya*, *Cyclocarya*, *Engelhardia*, *Pterocarya*, and certain *Juglans* spp. results in four chambers at the base of the fruit (Manchester, 1987). Four chambered nuts also occur in the extinct genera *Cruciptera* (Manchester, 1991) and *Polyptera* (Manchester and Dilcher, 1997). This seems to be the most common arrangement within the family and is also the type present in the small Appian Way fruits.

The type of nut wall sclerification is an important feature distinguishing the two subfamilies of Juglandaceae (Manchester, 1987; Smith and Doyle, 1995; Manos and Stone, 2001). All fruits of subfamily Juglandoideae have a nut wall consisting of isodiametric sclereids, whereas the walls of fruits within subfamily Engelhardioideae have fibers (Manos and Stone, 2001). Nut wall tissue in the Appian Way fruits is composed of thick-walled fibers, making them more similar to those of subfamily Engelhardioideae in this respect. The presence or absence of lacunae in the nut wall is another important character in Juglandaceae. With the exception of *Platycarya*, all members of subfamily Juglandoideae have lacunae, while this feature is

TABLE 1. Comparison of relevant characters of select extant and fossil Juglandaceae fruits.

Subfamily	Genus	Stratigraphic range	Nutshell sclerenchyma	Nutshell lacunae	Nutshell flattening	Wings	Chambers at base	Secondary septum
Engelhardioideae	*Engelhardia*	Eocene–Recent	Fibers	Absent	Absent	Present	4	Present
	Oreomunnea	Recent	Fibers	Absent	Absent	Present	8	Present
	Alfaroa	Recent	Fibers	Absent	Absent	Absent	8	Present
	*Paleooreomunnea**	Eocene	?	?	Present (?)	Present	4 (8)?	Present (?)
	*Paraoreomunnea**	Eocene	?	Absent (?)	Absent	Present	4–8	Present
	*Pararengelhardia**	Eocene	?	?	Absent	Present	?	?
	*Casholdia**	Paleocene	?	?	Present (?)	Present	2(?)	?
Juglandoideae	*Platycarya*	Eocene–Recent	Sclereids	Absent	In plane perpendicular to primary septum	Present	2	Absent
	Juglans	Eocene–Recent	Sclereids	Present	Absent	Absent	2–4	Present/Absent
	Pterocarya	Eocene-Recent	Sclereids	Present	Absent	Present	4	Present
	Cyclocarya	Paleocene–Recent	Sclereids	Absent	Absent	Present	2	Absent
	Carya	Eocene–Recent	Sclereids	Present, (Occasionally absent)	Absent	Absent	2–4	Present/Absent
	*Cruciptera**	Eocene–Oligocene	?	Present	Absent	Present	4	Present
	*Polyptera**	Paleocene	?	Present	Absent	Present	4	Present
This Paper	*Beardia**	Eocene	Fibers	Present	In plane perpendicular to primary septum	Absent	4	Present

Note: Data from Dilcher et al., 1976; Manning, 1978; Crane and Manchester, 1982; Manchester and Dilcher, 1982; Manchester, 1987, 1991; Manos and Stone, 2001.

* Extinct fossil taxon.

absent in fossil and extant Engelhardioideae (Manning, 1978). The Appian Way fruits likewise lack lacunae.

Carpel orientation and method of fusion are important distinguishing characters of juglandaceous fruits (Manning, 1940, 1978). Carpel fusion can be of two types, median or transverse, with median being the most common type (Manning, 1940; Manchester, 1987; Manos and Stone, 2001). Because the primary septum is formed from the fusion of two carpels, fruits with median carpel fusion are said to have a "median septum" (Manning, 1940). Fruits with median carpel fusion are those from subfamily Engelhardioideae and subtribe Juglandinae (Manning, 1940; Manos and Stone, 2001). The fossil fruits are flattened in the plane of nutshell dehiscence (in the plane of the secondary septum). We assume this flattening is dorsiventral but would need to observe their orientation relative to the bract to confirm a transverse primary septum. Transverse carpel fusion is found in fruits of tribe Platycaryeae and subtribe Caryinae, although only *Platycarya* is known to have flattened fruits (Manning, 1978).

Embryos, rarely seen in fossils, occur in the Appian Way fruits. The cotyledons appear to be folded within the fruit chambers. The folds in juglandaceous cotyledons, as explained by Shuhart (1932), are a consequence of embryo growth and subsequent digestion of endosperm. As the endosperm becomes depleted, the embryo surrounds the endosperm, crushing the endosperm cell walls, resulting in highly folded cotyledons. In addition to folds, provascular elements also develop in mature cotyledons of Juglandaceae (Langdon, 1939). A thin line of material in the embryo tissue of one of our specimens could potentially be provascular in nature (Fig. 20).

The fibrous nutshell without lacunae of the Appian Way fruits is most similar to fruits of subfamily Engelhardioideae. Extant *Engelhardia* typically have globose nuts with large dispersal wings. This genus has a thick primary septum and four chambers at its base (Manning, 1978), but the unflattened shell and winged fruits differ markedly from the condition observed in the Appian Way fruits. *Oreomunnea* fruits are round and winged, and have very thin tertiary septations at their base (Manning, 1978). *Alfaroa* is the only wingless genus in the subfamily Engelhardioideae; the wing is a diminutive remnant at the base of the fruit (Manning, 1978). The fruit is globose and typically has thin, tertiary septa at its base that divides the locule into eight chambers. While the shape is dissimilar to the Appian Way fruits, it should be noted that some fruits in *Alfaroa* have four chambers at their base in both immature (Leroy, 1955) and mature (Manning, 1949) fruits. *Paleooreomunnea, Paraoreomunnea*, *Pararengelhardia*, and *Casholdia* are genera of engelhardioid compression fossils known from the early Tertiary. Of these, *Casholdia* Crane et Manchester, from the Late Paleocene of southern England, is most comparable to the Appian Way fruits. Fruits of *C. microdiptera* Crane et Manchester are dorsiventrally flattened, and Crane and Manchester (1982) speculated that both primary and secondary septa are present, as in the Appian Way fruits. Because *Casholdia* was described from compression specimens, the internal tissues cannot be examined. However, *Casholdia* fruits have a prominent wing with engelhardioid venation (Manchester, 1987) unlike the wingless fruits from Appian Way.

Appian Way fossil fruits are small and flattened in the plane of the secondary septum (assumed to be dorsiventrally flattened) with a transverse carpel fusion like those of *Platycarya* (subfamily Juglandoideae, tribe Platycareae) (Manning, 1978). Both *Platycarya* and the Appian Way fruits lack nutshell lacunae (Manning, 1978) and have prominent ribbing on their external surfaces (Figs. 10D–F in Manchester, 1987). Beyond these similarities, a great number of differences exist between the Appian Way fossils and extant *Platycarya*: (1) the former has a nutshell of fibers, while the nutshell in the latter is made up of sclereids; (2) the Appian Way fruits have no wings; (3) *Platycarya* has only two basal chambers at maturity with a thin primary septum, as opposed to the thick primary and secondary septa of the fossil fruits; (4) the nut wall of the Appian Way specimens is thick, while in extant *Platycarya* it is relatively thin (Manchester, 1987). Additionally, no cone-like infructescences have been recovered from the Appian Way strata, as would be expected if *Platycarya* was present in the area in the Eocene. The numerous species of fossil *Platycarya* fruits from other localities are described based on variations in wing shape and size (Manchester, 1987), a feature not applicable to the Appian Way fruits.

The spherical idioblasts along the outer nutshell of the Appian Way fossils seem to be unique. As yet, no records of these distinctive cells have been published for either extant or extinct genera of Juglandaceae (S. R. Manchester, Florida Museum of Natural History, personal communication). Idioblasts have, however, been noted in the outer endocarp of extinct Betulaceae (e.g., *Palaeocarpinus*, Fig. 3E in Manchester et al., 2004); Betulaceae, like Juglandaceae, are placed in the Fagales clade (Manos and Steele, 1997; Li et al., 2004). This could be a useful taxonomic character and could be surveyed in extant and fossil fagalean fruits.

While no pollen grains were found in connection with the fossil fruits from Appian Way, two types of pollen often associated with Juglandaceae were previously identified there: *Momipites* Wodehouse and *Caryapollenites* Raatz (Sweet, 1997). *Momipites*-type grains are typically associated with Engelhardioideae fossils from the Middle Eocene (Manchester, 1987). Because at least two types of juglandaceous fruits and two types of pollen are known at the Appian Way locality, it is impossible at present to make a correlation. The absence of *Platycarya*-type pollen from Appian Way should be noted, because it is otherwise common at many Eocene localities in northwestern North America (Newman, 1981). Style orientation relative to the primary septum is another useful taxonomic character (Manos and Stone, 2001), but in *Beardia* the styles are not preserved, because they were likely abraded away during transport and deposition.

Thus, the small Appian Way fruits appear to represent a new genus and species of Juglandaceae, *Beardia vancouverensis* Elliott, Stockey et Mindell gen. et sp. nov., with characters spanning the two recognized subfamilies, Engelhardioideae and Juglandoideae (tribe Platycaryeae). While these fruits are small and flattened, like those of wind-dispersed types, they did not have distinct wings and the nutlet wall is thick and fibrous, similar to *Alfaroa*, an animal dispersed taxon. *Beardia* fruits, however, are smaller than most extant, animal-dispersed fruits and may show a transitional stage from wind to animal dispersal. While *Beardia* fruits have structural similarities to those of *Platycarya*, the single partition and isodiametric sclereids in the nutlet wall of this taxon differ from the thick zone of fibers in *Beardia*. We are, therefore, unable to place these fruits in any extant subfamily. This is of particular interest because it is another corroborating line of evidence for the explosive radiation of the family in the Eocene of North America (Manchester, 1987).

The excellent preservation of all tissues makes *Beardia vancouverensis* the best-preserved fossil juglandaceous fruit known. Further work on the Appian Way site will hopefully result in the reconstruction of whole plants, because various angiosperm leaves, twigs, wood, pollen, and reproductive structures are present in the nodules. *Beardia vancouverensis* from Appian Way has added to our knowledge of diversity of Juglandaceae in North America and is among the oldest known remains in the family. Wingless and flattened, it provides still another example of fruit morphology that would be otherwise anomalous in the framework of extant Juglandaceae systematics. *Beardia* fruits, with a unique combination of characters, reinforce the hypothesis (Manchester, 1987) that North America may be the earliest center of generic diversity for the family.

LITERATURE CITED

Batten, D. J., and R. A. Christopher. 1981. Key to the recognition of *Normapolles* and some morphologically similar pollen genera. *Review of Palaeobotany and Palynology* 35: 359–383.

Bolick, M. R. 1983. A cladistic and biogeographic analysis of the Juglandaceae. *American Journal of Botany* 70 (Supplement): 106.

Crane, P. R., and S. R. Manchester. 1982. *Casholdia*, an extinct juglandaceous fruit from the Upper Paleocene of southern England. *Botanical Journal of the Linnaean Society* 85: 89–101.

Dilcher, D. L., F. W. Potter, and W. L. Crepet. 1976. Investigations of angiosperms from the Eocene of North America: juglandaceous winged fruits. *American Journal of Botany* 63: 532–544.

Friis, E. M. 1983. Upper Cretaceous (Senonian) floral structures of juglandalean affinity containing Normapolles pollen. *Review of Palaeobotany and Palynology* 39: 161–188.

Haggart, J. W., W. A. Hessin, A. McGugan, D. R. Bowen, G. Beard, R. Ludvigsen, and T. Obear. 1997. Paleoenvironment and age of newly-recognized Tertiary marine strata, east coast Vancouver Island, British Columbia. Proceedings of the Second British Columbia Paleontological Symposium, Vancouver, British Columbia, Canada, 25 (Abstract).

Hernandez-Castillo, G. R., R. A. Stockey, and G. Beard. 2005. Taxodiaceous pollen cones from the early Tertiary of British Columbia, Canada. *International Journal of Plant Sciences* 166: 339–346.

Holm, T. 1921. Morphological study of *Carya alba* and *Juglans nigra*. *Botanical Gazette* 72: 375–389.

Joy, K. W., A. J. Willis, and W. S. Lacey. 1956. A rapid cellulose peel technique in paleobotany. *Annals of Botany,* new series 20: 635–637.

Langdon, L. M. 1939. Ontogenic and anatomical studies of the flowers and fruits of Fagaceae and Juglandaceae. *Botanical Gazette* 101: 301–327.

Leroy, J. F. 1955. Étude sur les Juglandaceae. *Mémoires Musée Paris II, Botany* 6: 1–246.

Li, R., Z. Chen, A. Lu, D. E. Soltis, P. S. Soltis, and P. S. Manos. 2004. Phylogenetic relationships of Fagales based on DNA sequences from three genomes. *International Journal of Plant Sciences* 165: 311–324.

Little, S. A., R. A. Stockey, and G. Beard. 2001. Angiosperm fruits and seeds from the Eocene of Vancouver Island. Botany 2001: Annual Meeting of The Botanical Society of America, Albuquerque, New Mexico, USA (Abstract, online http://www.botany2001.org/botany2001a.pdf: 66).

Manchester, S. R. 1987. The fossil history of Juglandaceae. *Monographs in Systematic Botany Missouri Botanical Garden* 21: 1–137.

Manchester, S. R. 1989. Early history of the Juglandaceae. *Plant Systematics and Evolution* 162: 231–250.

Manchester, S. R. 1991. *Cruciptera*, a new juglandaceous winged fruit from the Eocene and Oligocene of western North America. *Systematic Botany* 16: 715–725.

Manchester, S. R., and D. L. Dilcher. 1982. Pterocaryoid fruits (Juglandaceae) in the Paleogene of North America and their evolutionary and biogeographic significance. *American Journal of Botany* 69: 275–286.

Manchester, S. R., and D. L. Dilcher. 1997. Reproductive and vegetative morphology of *Polyptera* (Juglandaceae) from the Paleocene of Wyoming and Montana. *American Journal of Botany* 84: 649–663.

Manchester, S. R., K. B. Pigg, and P. R. Crane. 2004. *Palaeocarpinus dakotensis* sp. nov. (Betulaceae: Coryloideae) and associated staminate catkins, pollen, and leaves from the Paleocene of North Dakota. *International Journal of Plant Sciences* 165: 1135–1148.

Manning, W. E. 1940. The morphology of the flowers of Juglandaceae. II. The pistillate flowers. *American Journal of Botany* 27: 839–852.

Manning, W. E. 1949. The genus *Alfaroa*. *Bulletin of the Torrey Botanical Club* 76: 196–209.

Manning, W. E. 1978. The classification within the Juglandaceae. *Annals of the Missouri Botanical Garden* 65: 1058–1087.

Manos, P. S. 2005. A comprehensive systematic appraisal of the Fagales with particular attention to the Juglandaceae. XVII International Botanical Congress, Vienna, Austria, 135 (Abstract).

Manos, P. S., and K. P. Steele. 1997. Phylogenetic analyses of 'higher' Hamamelidae based on plasmid sequence data. *American Journal of Botany* 84: 1407–1419.

Manos, P. S., and D. E. Stone. 2001. Evolution, phylogeny and systematics of the Juglandaceae. *Annals of the Missouri Botanical Garden* 88: 231–269.

Mindell, R. M., R. A. Stockey, G. W. Rothwell, and G. Beard. In press. *Gleichenia appianense* sp. nov. (Gleicheniaceae), a permineralized rhizome and associated vegetative remains from the Eocene of Vancouver Island, British Columbia. *International Journal of Plant Sciences.*

Mustard, P. S., and G. E. Rouse. 1994. Stratigraphy and evolution of the Tertiary Georgia Basin and subjacent Late Cretaceous strata of the Greater Vancouver area, British Columbia. *In* J. W. H. Monger [ed.], Geology and geological hazards of the Vancouver region, southwestern British Columbia. *Geological Survey of Canada Bulletin* 481: 97–161.

Newman, K. R. 1981. Palynological biostratigraphy of some early Tertiary nonmarine formations in central and western Washington. *In* J. M. Armentrout [ed.], Pacific Northwest Cenozoic biostratigraphy. *Geological Society of America Special Paper* 84: 49–65.

Reid, E. M., and M. E. J. Chandler. 1933. London Clay flora. British Museum (Natural History), London, UK.

Schaarschmidt, H. 1985. The relationship between *Carya* and *Platycarya* (Juglandaceae) and the natural classification of the family. *Feddes Repertorium* 96: 345–361.

Schweitzer, C. E., R. M. Feldmann, J. Fam, W. A. Hessin, S. W. Hetrick, T. G. Nyborg, and R. L. M. Ross. 2003. Cretaceous and Eocene decapod crustaceans from southern Vancouver Island, British Columbia, Canada. National Research Council Press, Ottawa, Canada.

Shuhart, D. V. 1932. Morphology and anatomy of the fruit *Hicoria pecan*. *Botanical Gazette* 93: 1–20.

Smith, J. F., and J. J. Doyle. 1995. A cladistic analysis of chloroplast DNA restriction site variation and morphology for the genera of Juglandaceae. *American Journal of Botany* 82: 1163–1172.

Smith, S. Y., R. S. Currah, and R. A. Stockey. 2004. Cretaceous and Eocene poroid hymenophores from Vancouver Island, British Columbia. *Mycologia* 96: 180–186.

Stone, D. E. 1973. Patterns in the evolution of amentiferous fruits. *Brittonia* 25: 371–384.

Stone, D. E. 1989. Biology and evolution of temperate and tropical Juglandaceae. *In* P. R. Crane and S. Blackmore [eds.], Evolution, systematics and fossil history of the Hamamelidae, vol. 2, 'Higher' Hamamelidae. Systematics Association Special Volume 40B, 117–145. Clarendon Press, Oxford, UK.

Sweet, A. R. 1997. Applied research report on 2 samples from Vancouver Island, southwestern British Columbia as requested by J. Haggart. Geological Survey of Canada Paleontological Report ARS-1997-06. Geological Survey of Canada, Calgary, Alberta, Canada.

Verhoog, H. 1968. A contribution towards the developmental gynoecium morphology of *Engelhardia spicata* Lechen. ex Blume (Juglandaceae). *Acta Botanica Neerlandica* 17: 137–150.

Woodroof, J. G., and N. C. Woodroof. 1927. The development of the pecan nut (*Hicoria pecan*) from flower to maturity. *Journal of Agricultural Research* 34: 1049–1063.

Zaklinskaya, E. D. 1981. Phylogeny and classification of the Normapolles. *Review of Palaeobotany and Palynology* 35: 139–148.