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CASCADIACARPA SPINOSA GEN. ET SP. NOV. (FAGACEAE): CASTANEOID FRUITS FROM THE EOCENE OF VANCOUVER ISLAND, CANADA[1]

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Documenting the paleodiversity of well-studied angiosperm families serves to broaden their circumscription while also providing a time-specific reference point to mark the first occurrence of characters and appearance of lineages. More than 80 anatomically preserved specimens of spiny, cupulate fruits in various developmental stages have been studied from the Eocene Appian Way locality of Vancouver Island, British Columbia, Canada. Details of internal anatomy and external morphology are known for the cupules, fruits, and pedicels. Cupule spines branch and are often borne in clusters. Cupules lack clear sutures and are adnate to a single nut that is enclosed entirely with the exception of the apical stylar protrusion of the pistil. A central hollow cylinder of vascular tissue can be seen extending up the peduncle to the base of the fruit and along the inner wall of the cupule. The fruit has a sclerotic outer pericarp that grades into a parenchymatous mesocarp and a sclerotic endocarp lining the locules. Early in development, the two locules are divided by a thin septum to which the ovules are attached. Only one seed develops to maturity as evidenced by an embryo occupying the locule alongside an abortive apical ovule. Three-dimensional reconstructions of these fruits have allowed for comparisons to both extinct and extant fagaceous taxa. The Appian Way fruits are most similar to extant *Castanopsis* species (Fagaceae) but differ in having only two locules. *Cascadiacarpa spinosa* gen. et sp. nov. Mindell, Stockey et Beard is the first occurence of a bipartite gynoecium and earliest known occurrence of hypogeous fruits in Fagaceae. The appearance of *Casacadiacarpa* in the Eocene of British Columbia supports a Paleogene radiation of the family. The numerous derived characters of these fruits show that evalvate, spiny, single-fruited cupules of Fagaceae were present in the Paleogene of North America.

Key words: Appian Way; Castaneoideae; *Castanopsis*; Eocene; Fagaceae; Fagales.

The beech family (Fagaceae) is an integral component of the canopy in the deciduous forests of the northern hemisphere (Manos and Stanford, 2001). Given the economically important hardwoods and edible nuts harvested from trees of this family, it has been the subject of many systematic, morphological, anatomical, and ecological studies (Manos et al., 2001). Given the diverse fossil record of Fagaceae (Crepet, 1989) and the abundance of data on extant taxa, it serves as a model family for the integration of paleobotanical and neobotanical knowledge (Manos, 2005).

The family is divided into eight genera that are defined predominantly by characters of the flowers and cupulate fruits. Highest generic and specific diversity is found in the tropics of Southeast Asia, where the endemic genus *Castanopsis* Spach. occurs, as does *Quercus* L., *Lithocarpus* Blume, *Castanea* Mill., and *Fagus* L. (Soepadmo, 1972). The three anomalous and monotypic trigonobalanoid genera have small ranges, with *Trigonobalanus* Forman restricted to Malaysia, *Formanodendron* Nixon & Crepet found in Thailand and China, and *Columbobalanus* Nixon & Crepet known only from the cloud forests of Columbia (Nixon and Crepet, 1989). There are more than 300 species of *Quercus* found throughout North and Central America (Nixon, 1997). *Fagus* is found across the northern hemisphere, though the majority of species are endemic to Europe. *Chrysolepis* Hjelmqvist is represented by two species from western North America, though both have frequently been placed in other genera (Nixon, 1997).

Systematically, Fagaceae were traditionally placed in the Hammamelidae (Cronquist, 1981) for their reduced, mostly wind-pollinated flowers. Like many families in that artificial construct, it has since been placed among the "core" eudicots within the Fagales as sister to Nothofagaceae in a clade with Juglandaceae, Betulaceae, Casuarinaceae, Ticodendraceae, Myricaceae, and Rhoipteleaceae (Manos and Steele, 1997; Li et. al., 2004).

The family was traditionally divided into three subfamilies, but recent phylogenetic studies nest *Quercus* within subfamily Castaneoideae alongside *Castanea*, *Castanopsis*, *Lithocarpus*, and *Chrysolepis* (Manos and Steele, 1997; Manos et al., 2001; Li et al., 2004). *Quercus* was traditionally placed in subfamily Quercoideae (Forman, 1964), alongside *Trigonobalanus*, which has since been segregated into three genera (Nixon and Crepet, 1989), and placed with *Fagus* in subfamily Fagoideae (Manos et al., 2001). Fruits in all genera of Fagaceae are readily recognizable from the cupules that subtend or enclose them. The subfamilies and genera of Fagaceae are divided on the basis of diagnostic flower and cupule characters, including number of flowers per cupule, cupule valve number, and carpel number (Forman, 1966b).

The fossil record for the family is extensive, going back to the late Cretaceous, where the family is represented by flowers with in situ Normapolles-type triaperturate pollen (Herendeen et al., 1995). During the Paleogene, fossil fruits and flowers appear that can be easily accommodated in the diagnoses of

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extant genera. These include *Quercus* from Europe (Kvaček and Walther, 1989; Palamarev and Mai, 1998) and North America (Daghlian and Crepet, 1983; Manchester, 1994); *Trigonobalanus* from Europe (Kvaček and Walther, 1989); *Castanea* from Tennessee, USA (Crepet and Daghlian, 1980); and *Fagus* (Manchester and Dilhoff, 2004), *Lithocarpus*, and *Castanopsis* (Manchester, 1994) from North America. The rich fossil record for these genera have made Fagaceae a model family for the integration of paleobotanical and neobotanical data in phylogenetic (Manos et al., 2001; Manos, 2005) and biogeographic (Manos and Stanford, 2001) studies.

This paper furthers this goal, describing a new genus of fagaceous fruits from the Eocene of Vancouver Island. These fossils represent the first of three types of anatomically preserved fagaceous fruits (Stockey et al., 2005) to be formally described from the Appian Way locality and contributes to the known paleodiversity of Fagaceae.

MATERIALS AND METHODS

The 85 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 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 silty mudstone matrix representing a shallow marine environment. Characteristic molluscs, decapods (Schweitzer et al., 2003), and shark teeth indicate that the calcareous nodules are of Eocene age (Haggart et al., 1997). Sweet (2005) has studied the pollen from the site and has found it to be stratigraphically precarious, with both late Paleocene and early Eocene signatures present. The stratigraphy of the area is currently being examined (J. W. Haggart, Geological Survey of Canada, personal communication).

Plant material, including abraded wood and fruits representing numerous taxa, is well preserved in the concretions (Little et al., 2001). Juglandaceae fruits (Elliott et al., 2006), Platanaceae inflorescences (Mindell et al., 2006a), taxodiaceous pollen cones (Hernandez-Castillo et al., 2005), schizaeaceous (Trivett et al., 2006) and gleicheniaceous (Mindell et al., 2006b) fern remains, and shelf fungi (Smith et al., 2004) have been described from the locality.

Nodules were cut transversely and peeled using the cellulose acetate peel technique (Joy et al., 1956). Microscope slides were made using Eukitt (O. Kindler GmbH, Freiberg, Germany) mounting medium. Images were captured using a PowerPhase digital camera (Phase One, A/S, Frederiksberg, Denmark) and processed using Photoshop 7.0 (Adobe, San Jose, California, USA). External morphology of the fruit was reconstructed from serial sections layered, aligned, and correlated in three-dimensional space using AMIRA 3.1.1 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: Fagaceae
Genus: *Cascadiacarpa* Mindell, Stockey et Beard gen. nov.

Generic diagnosis—Fruit cupulate. Cupule spiny, indehiscent, enclosing, and adnate to single nut; pedicellate. Nut ovoid to spherical, with apical protrusion. Fruit with two carpels separated by thin septum. Trichomes absent from locule. Ovules apical. Single seed at maturity; embryo large, straight, dicotyledonous.

Species—*Cascadiacarpa spinosa* Mindell, Stockey et Beard sp. nov. (Figs. 1–21).

Specific diagnosis—Pedicel spiny. Cupule spines scattered on surface, branching one to several times, circular in transverse section, vascularized, central vascular bundle ensheathed by sclerenchyma. Nut 5–8 mm long, 4–8 mm in diameter, circular in transverse section, ovoid to circular in longitudinal section. Exocarp present, underlain by sclerotic layer 2–7 cells wide, grading to parenchymatous zone up to 30 cells thick. Locule lining sclerenchymatous. Septum absent at maturity, single seed filling cavity.

Holotype—P 13105 Dtop.

Paratypes—AW 357 A, AW 507 Hbot, AW 532 L_2bot, AW 646 Bbot, AW 647 Btop, AW 669 Gtop, AW 699 B Surface.

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

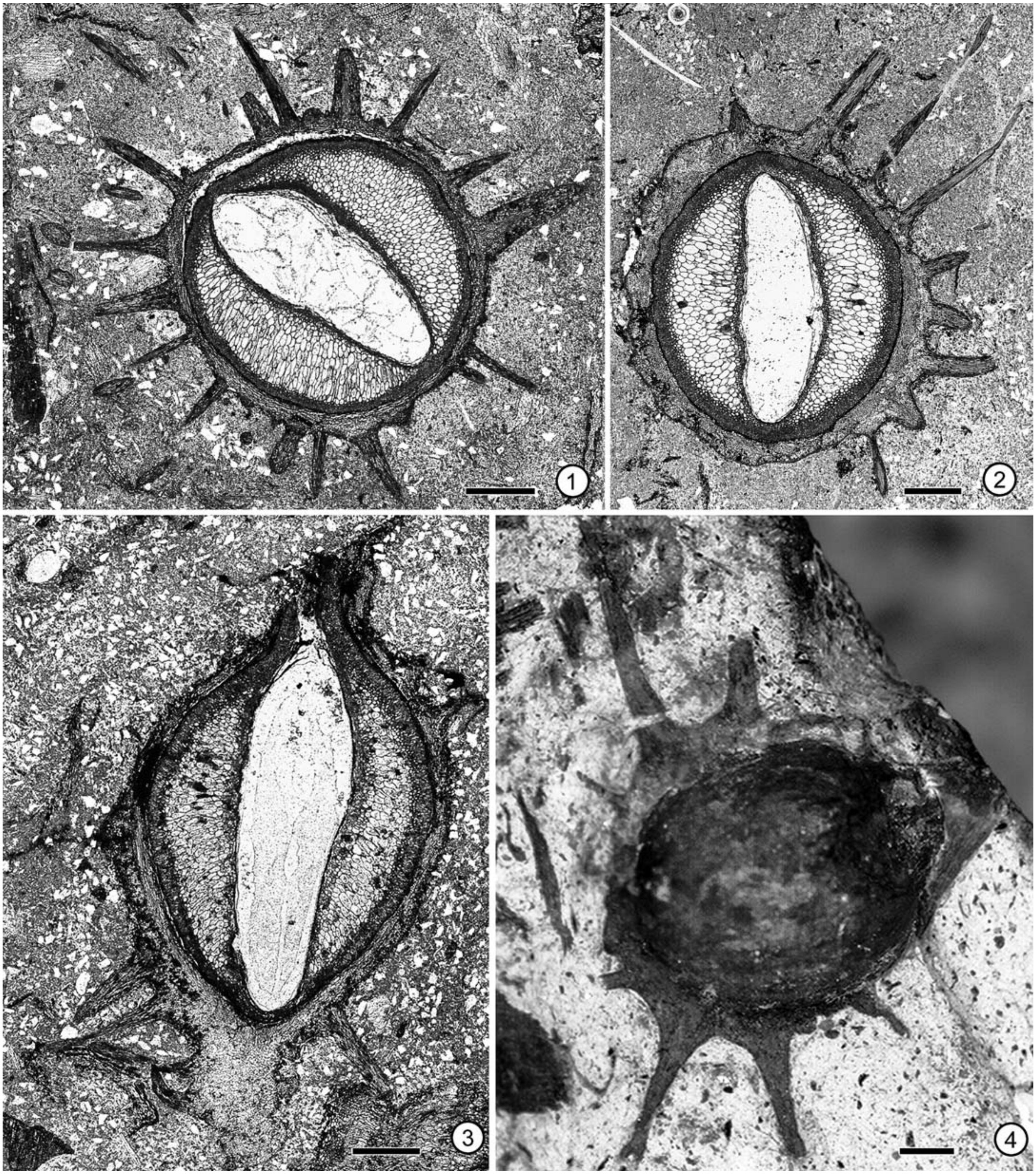
Age—Eocene.

Etymology—The generic name refers to the natural geographic province of Cascadia, where the fossils were found. The specific epithet refers to the spiny nature of this cupulate fruit.

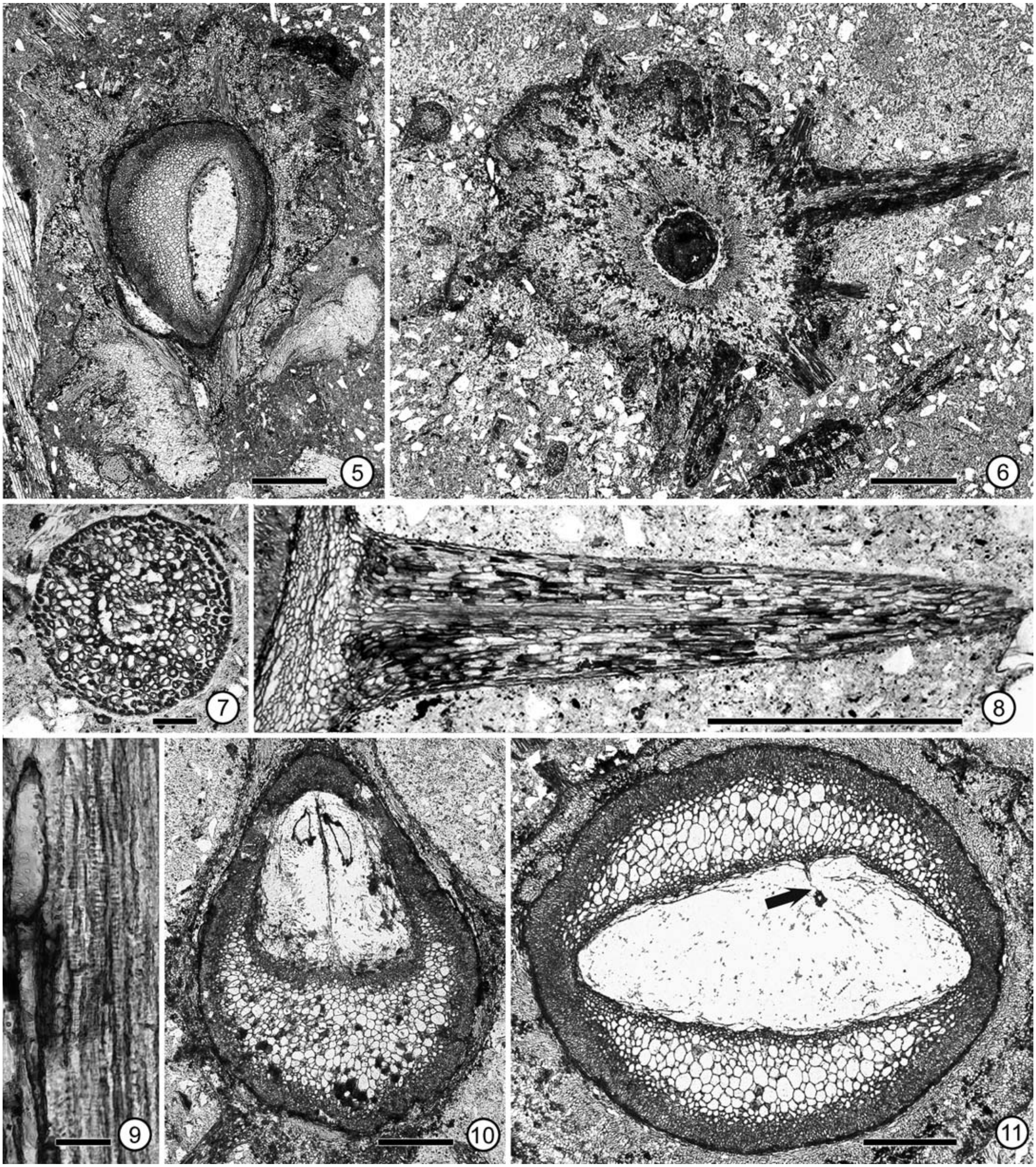
Description—The 85 specimens are known as both cupulate fruits and isolated nuts. The globose shape and spiny cupules distinguish these fruits from others present in the concretions. They are known from both internal anatomy (Figs. 1–3, 5–17) and fractured surfaces (Fig. 4). Fruits are preserved in different developmental stages and were subjected to varying degrees of abrasion prior to final deposition. Bacterial degradation is evidenced by the abundant pyrite crystals found throughout the tissues.

Cupule—The sclerenchymatous cupule is adnate to the nut wall and entirely encloses the fruit (Figs. 1–5). There are no tissue zones in the cupule that would indicate a suture (Figs. 1, 2), and the surface reconstruction shows no signs of dehiscence (Figs. 18–20). Cupules are circular to ovoid in transverse section (Figs. 1, 2) and ovoid in longitudinal section (Figs. 3, 5). The cupule wall is up to 1.5 mm thick, thinning from base to tip (Fig. 3). A spiny pedicel is evident at the base of the cupule in which a continuous ring of vascular tissue is present (Fig. 6). At the base of the cupule numerous lobed spine bases are evident, while distally spine bases are narrower. Spines along the pedicel are continuous with those on the surface of the cupule. They are numerous, frequently branched, elongate, conical, up to 5 mm long, 1 mm wide at the base, and randomly distributed across the entire cupule surface. Spines can be simple or branched up to five times (Figs. 4, 6, 20). In transverse section, spines are circular (Figs. 6, 7) with a central vascular strand surrounded by sclerenchyma fibers (Figs. 7, 8). Secondary wall thickenings of the tracheary elements in these spines are scalariform (Fig. 9).

Nut—Nuts are globose, circular in transverse section, up to 8 mm in diameter, and ovoid in longitudinal section, up to 8 mm long. One specimen found on a fractured rock surface (Fig.



Figs. 1–4. *Cascadiacarpa spinosa* gen. et sp. nov. fruits. Scale bar = 1 mm in all figures. **1.** Transverse section of cupule and nut. Holotype P 13105 Dtop #29. **2.** Transverse section of cupule and nut showing large cupule spines. AW 357 A #2. **3.** Longitudinal section of cupule enclosing nut. Note apical protrusion of nut and pedicel. AW 654 A #1. **4.** Surface view showing external morphology. Note smooth nut wall and distally branching cupule spines at bottom left. AW 699 B Surface.



Figs. 5–11. *Cascadiacarpa spinosa* gen. et sp. nov. fruits. **5.** Longitudinal section showing lobed spine bases and vascular tissues of pedicel and cupule. AW 507 Hbot #3. Scale bar = 1 mm. **6.** Transverse section through basal portion of cupule. Note sclerotic nut wall at center, ring of vascular tissue (arrow) along inner wall of cupule, and spines. AW 532 L$_2$bot #13. Scale bar = 1 mm. **7.** Transverse section of cupule spine showing sclerotic ground tissue enclosing vascular bundle. Holotype P 13105 Dtop #153. Scale bar = 100 μm. **8.** Longitudinal section of simple cupule spine. Note thin strand of vascular tissue. Holotype P 13105 Dtop #40. Scale bar = 1 mm. **9.** Longitudinal view of vascular tissue in cupule spine. Holotype P 13105 Dtop #40. Scale bar = 20 μm. **10.** Oblique transverse section near fruit apex showing ovules attached to thin septum. AW 103 Etop #1. Scale bar = 1 mm. **11.** Transverse section of nut showing septal remnant (arrow) at later stage of fruit development. AW 357A #38. Scale bar = 1 mm.

4) shows the three-dimensional shape of the nut and its smooth external wall. Nuts are always found in attachment to cupular tissues, though these are often abraded (Fig. 14); thus, they are adnate to the cupule. The exocarp is represented by small-diameter parenchymatous cells underlain by a layer composed of small-diameter sclerenchyma cells up to seven cells thick (Figs. 11, 13). The middle layer of the fruit wall is parenchymatous up to 30 cells thick (Figs. 11, 13). The innermost layer of the nut wall is made up of small-diameter sclerenchymatous cells (Figs. 11, 13). In transverse section, two sutures are observed traversing the nut wall (Figs. 14, 16). Numerous specimens have been peeled through entirely and have no evidence of an enclosing "fruit receptacle" as observed in some species of *Lithocarpus* and *Castanopsis* (Cannon and Manos, 2000).

The fruit is bilocular, the locules divided by a thin septum present early in development (Fig. 10). In mature fruits with seed and embryo tissues, this septum is present as a broken remnant (Fig. 11). Placentation is axile with at least one ovule per locule attached near the apex of the fruit (Figs. 10, 15). In one specimen, an abortive apical ovule can be observed alongside remnants of a mature seed (Fig. 15). Remnants of the seed commonly fill the area of both locules in mature fruits (Figs. 12, 13, 15). The integuments are one to several cells thick, mostly represented by cuticle and commonly invaded by fungi. Embryos are present in several specimens (Figs. 3, 12, 15). In most specimens, cellular detail is obscured by fungi, but it can be seen in one specimen (Fig. 12). The embryo is straight and large, filling the entire seed cavity (Fig. 12), with two elongate cotyledons, a dome-shaped shoot apex, and a short hypocotyl (Figs. 3, 15). Endosperm is apparently absent.

An apical protrusion of the nut and cupule is seen in numerous specimens (Figs. 3, 15). In transverse section, possible perianth and stylar remnants are present (Fig. 17). At the apex of the fruit, the cupule is absent, and the fruit wall becomes lobed. Vascular tissue in this region suggests that up to 12 perianth parts or floral organs were attached (Fig. 17).

Three-dimensional reconstruction reveals a profusely spiny cupule surface, with spines extending down the pedicel (Figs. 18–21; Appendix S1, see Supplemental Data with online version of this article). Spines lack a clear arrangement, and the cupule surface is devoid of sutures (Figs. 18–21). The morphology of spines is readily seen from this model, with enlarged bases branching up to five times (Fig. 20).

DISCUSSION

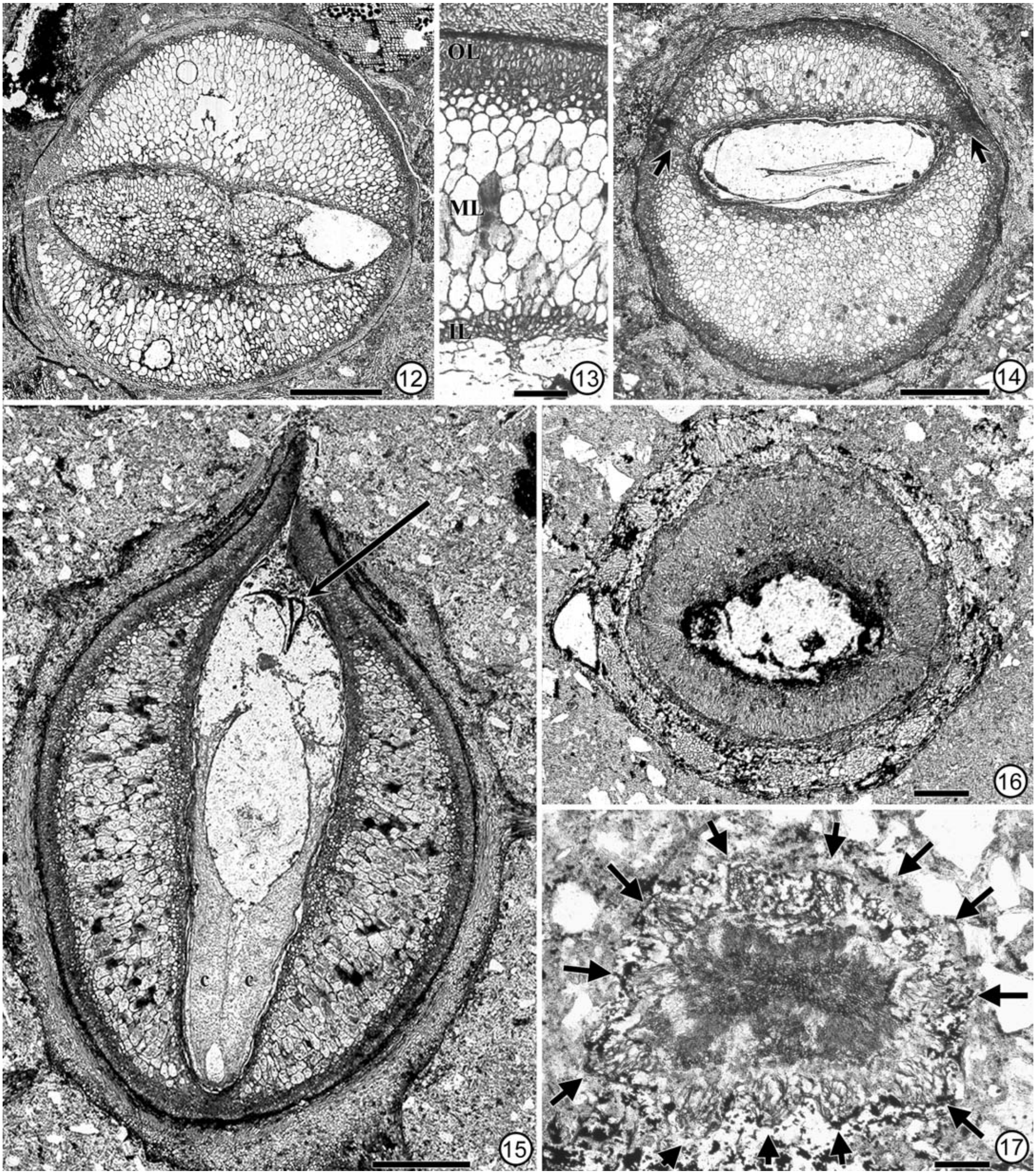
The fruits described in this paper have a suite of characters consistent with Fagaceae: cupules, nuts, abortive apical ovules, large, straight embryos, and a lack of endosperm (Cronquist, 1981; Kubitzki, 1993). Furthermore, at the apex of the nut in the Appian Way fossil fruits is a protrusion with thin, vascularized lobes surrounding a sclerotic central mass to which styles and tepals were likely attached. The 12 vascularized lobes most likely represent perianth parts, while the sclerotic central tissue may have terminated in two styles. In extant Fagaceae, perianth members are highly reduced, scale-like appendages (Abbe, 1974; Kubitzki, 1993), and this seems a likely case for the fossil. Only the very apex of the fruit is not enclosed by the cupule at maturity, and two styles probably protruded earlier in development. The large, non-endospermic seed, with an embryo filling both locules at maturity with two fleshy cotyledons is consistent with many taxa of extant Fagaceae with hypogeal germination (Forman, 1964; Corner, 1976). This type of embryo observed in the indehiscent cupulate fruits suggests that the seeds and fruits were dispersed in the cupule, as in many extant Fagaceae, subfamily Castaneoideae (Manos et al., 2001). The fruit is interpreted as being bilocular because of the numerous specimens that occur with a thin septum dividing the two locules. This septum can be distinguished from the woody partitions that occur in some species of Fagaceae in having ovules attached. Furthermore, the locule space is always lenticular in transverse section, having no evidence of a third chamber as would by expected in a tripartite gyneocium.

Within Fagaceae, genera are distinguished primarily by cupule, fruit, and inflorescence characters (Forman, 1966a, b). Cupule shape, attachment, valve number, presence of internal valves, spines, trichomes, fruit shape, number of nuts per cupule, presence of wings, germination type, number of nuts per cupule, and number of carpels per nut are all relevant characters that can be used to key out living genera (Table 1; Brett, 1964; Forman, 1966a; Soepadmo, 1972; Nixon, 1997; Soepadmo et al., 2000).

Through time, taxonomy within the family has been unstable due to varying interpretations of the homology of cupule structure (Brett, 1964; Forman, 1964b; Fey and Endress, 1983; Nixon, 1989; Corner, 1990). Presently, nine genera are recognized: *Fagus*, *Trigonobalanus*, *Colombobalanus*, *Formanodendron*, *Quercus*, *Lithocarpus*, *Chrysolepis*, *Castanea*, and *Castanopsis* (Nixon, 1989; Manos et al., 2001). The southern hemisphere genus *Nothofagus*, once placed in the family based on its cupulate trigonal fruits has since been placed in its own family, Nothofagaceae (Nixon, 1989; Hill and Jordan, 1993; Manos and Steele, 1997; Li et al., 2004). The remaining genera have, through time, been placed in various subfamilies. Using morphology, Nixon (1989) placed *Fagus*, *Quercus*, *Trigonobalanus*, *Colombobalanus*, and *Formanodendron* in the subfamily Fagoideae and distinguished the subfamily by morphological features conducive to anemophily (e.g., unisexual inflorescences and broad stigmatic surfaces). The remaining genera have long been placed in subfamily Castaneoideae (Forman, 1966b). Molecular phylogenetic analyses (Manos and Steele, 1997; Manos et al., 2001; Li et al., 2004) have since supported the placement of *Quercus* in the subfamily Castaneoideae, subsequently interpreting an independent derivation of wind pollination in the genus and suggesting hypogeous fruits as a synapomorphy for the subfamily.

The four remaining genera of Fagoideae have trigonal, epigeous fruits enclosed or partially enclosed in scaly cupules (Table 1). In the common beech (*Fagus*), fruits are always two per cupule, the cupule having four valves (Langdon, 1939). In *Trigonobalanus*, *Colombobalanus*, and *Formanodendron*, the number of fruits per cupule varies substantially along the inflorescence axis (Forman, 1964; Nixon and Crepet, 1989). As in *Fagus*, the cupules are split between the valves at maturity, releasing the nuts. The fossils described in this paper can be easily distinguished from these genera in having globose, likely hypogeous fruits, which occur singly in each cupule. Furthermore, the cupules in the Appian Way fossils have no obvious valves, and at maturity, the fruit is still enclosed.

The fossil fruits can be readily distinguished from those of some genera within the subfamily Castaneoideae (Table 1). This group is united by hypogeous fruits (Manos et al., 2001), a condition strongly suggested by the presence of large



Figs. 12–17. *Cascadiacarpa spinosa* gen. et sp. nov. fruits. **12.** Transverse section of isolated nut showing embryo tissue filling both locules. P 13105 Dtop #92b. Scale bar = 1 mm. **13.** Detail of pericarp showing sclerenchyma of outer layer (OL), parenchyma of middle layer ML, and sclerenchyma of inner layer (IL). AW 357 A#2. Scale bar = 0.25 mm. **14.** Transverse section near apex of nut showing seed coat remnants and lateral nut sutures (arrows). AW 532 L$_2$bot #1. Scale bar = 1 mm. **15.** Longitudinal section of cupulate nut showing apical protrusion of nut, embryo with cotyledons (c), and abortive apical ovule (arrow). AW 669 Gtop #1. Scale bar = 1 mm. **16.** Transverse section through apex of cupulate fruit showing ensheathing cupule and lateral sutures of fruit wall (arrows). AW 646 Bbot #53. Scale bar = 0.25 mm. **17.** Transverse section through most distal portion of fruit showing vascularized lobes at arrowheads. AW 646 Bbot #67. Scale bar = 100 μm.

TABLE 1. Cupulate fruit characters of extant and relevant fossil genera of Fagaceae.

Genus	Stratigraphic range	Cupule shape	Attachment of cupule	Valves	Internal valves	Cupule Spines	Nuts enclosed by cupule	Nuts per cupule	Fruit shape in cross section	Fruit winged	Number of carpels	Germination
Chrysolepis	Recent	Subglobose	Sessile	2–many	Present	Present	Yes	(1–)3–many	Circular to Trigonous	No	3	Hypogeal
Castanea	Recent	Subglobose	Solitary on rachis	2–4	Absent	Present	Yes	1–3	Plano-convex to circular	No	6(–9)	Hypogeal
Castanopsis	Eocene to Recent	Subglobose	Solitary on rachis	0–many	Absent	Present	Yes	1–3(–7)	Circular to sub-triangular	No	3	Hypogeal
Lithocarpus	Eocene to Recent	Cup-shaped	Sessile	0	Absent	Present/ Absent	Yes/No	1	Circular	No	3	Hypogeal
Quercus	Paleocene to Recent	Cup-saucer-goblet-shaped	Sessile	0	Absent	Absent	Rarely	1	Circular	No	3–6	Hypogeal
Trigonobalanus	Eocene to Recent	Irregular	Sessile	(2–)4–(many)	Absent	Absent	Yes	(1–)3–7(–15+)	Trigonous	No	3	Epigeal
Formanodendron	Recent	Irregular	Sessile	(2–)4–(many)	Absent	Absent	No	(1–)3–7(–15+)	Trigonous	Yes or No	3	Epigeal
Colombobalanus	Recent	Irregular	Sessile	(2–)4–(many)	Absent	Absent	Yes	(1–)3–7(–15+)	Trigonous	Yes	3	Epigeal
Fagus	Eocene to Recent	Pyramidal	Solitary on rachis	4	Absent	Present	Yes	2	Trigonous	Yes or No	3	Epigeal
Fagopsis	Oligocene	Triangular	Sessile in conical inflorescence	?	Absent	Absent	Yes	3	Round (?)	Yes	3?	?
Cascadiacarpa	Eocene	Subglobose	Solitary on rachis	0	Absent	Present	Yes	1	Circular	No	2	Hypogeal

Note: Data from Berridge, 1914; Langdon, 1939; Forman, 1966a; Soepadmo, 1972; Manchester et al., 1983; Nixon and Crepet, 1989; Nixon, 1997; Palamarev and Mai, 1998; Cannon and Manos, 2000.

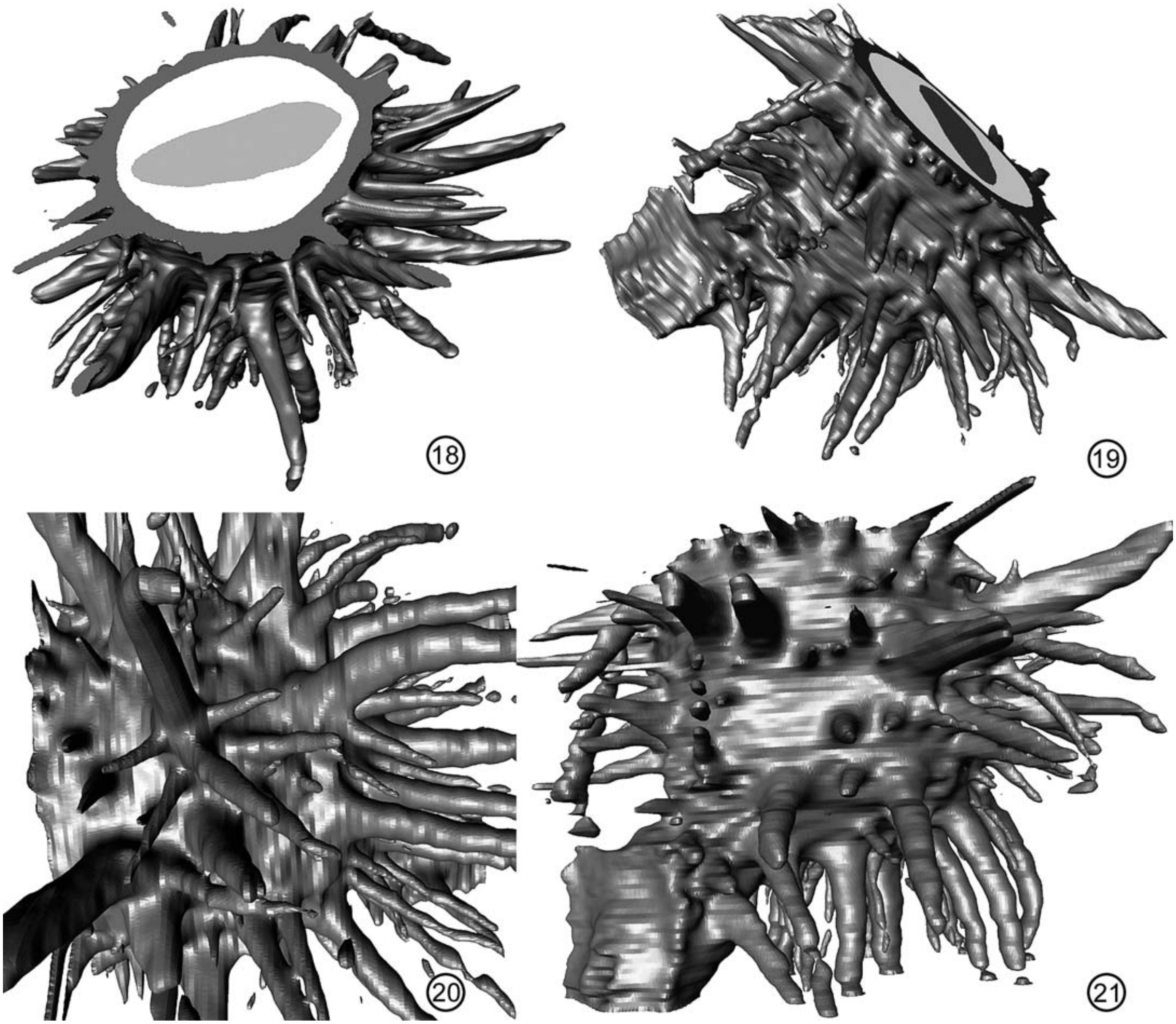
cotyledons and a stony nut wall in the Appian Way fruits. *Quercus*, like the Appian Way fruits, can have globose nuts, but these solitary fruits are typically subtended by a scaly cupule and the ovary is trilocular (Kubitzki, 1993; Nixon, 1997), whereas in the fossil fruits the enclosing cupule is spiny and the ovary is bilocular.

Lithocarpus, a speciose (~300 sp.) East Asian genus (with the exception of *L. densiflorus* (Hooker & Arnott) Rehder of western North America) also has globose, trilocular solitary nuts borne typically on scaly, indehiscent cupules (Forman, 1966b; Soepadmo, 1972; Kaul, 1987, 1989; Soepadmo et al., 2000). While most members in this genus lack totally enclosing cupules, some species of *Lithocarpus* have a cupule that almost entirely encloses the nut (Cannon, 2001) as in the Appian Way fruits. Spines are present in a few species of *Lithocarpus*; however, they are unbranched (Soepadmo, 1970; Cannon and Manos, 2000). Many species of *Lithocarpus* (e.g., those in section *Synaedrys*) have a differentiated mass of tissue at the base of the nut, which encloses the seeds and is referred to as the "fruit receptacle" (Cannon and Manos, 2000). While the Appian fruits are entirely enclosed in a cupule as in some *Lithocarpus,* no fruit receptacle occurs in the fossils, and cupule spines are branched.

The North American genus *Chrysolepis* has formerly been placed within *Castanopsis* (see Berridge, 1914; Hjelmqvist, 1948; Brett, 1964; Forman, 1966b). While molecular phylogenies have grouped *Chrysolepis* with the anomalous *L. densiflorus* (Manos et al., 2001), *Chrysolepis* has morphologically distinct fruiting structures useful for comparison to the Appian Way fruits. As in the fossils, it has a spiny cupule wall, and the nut is occasionally globose, but unlike the fossils, the cupules have numerous valves, external and internal, that typically enclose many trilocular fruits (Berridge, 1914; Hjelmqvist, 1948; Brett, 1964; Forman, 1966b; Nixon, 1997). In the Appian Way fossils, there is only one bilocular fruit per cupule, and no obvious valves can be observed.

Fruits of *Castanea* superficially resemble the fossils in having an enclosing cupule with branched spines (Prantl, 1889; Langdon, 1939; Fey and Endress, 1983). Furthermore, species in this genus can have cupules enclosing only one globose nut. However, the Appian Way fruits are significantly different in having a bilocular ovary, as opposed to the 6–9 locular condition known in *Castanea* (Table 1). The spine bases, while branched in *Castanea*, form a distinctive banded pattern on the cupule wall (Brett, 1964; Forman, 1966b), while in the fossils their distribution is apparently random. Lastly, the cupule of *Castanea* is divided into valves. Such valves are clearly lacking in the Appian Way fruits.

The genus of Fagaceae most comparable to the fruits described in this paper is *Castanopsis*. Compression leaves attributed to the genus are known from the Upper Eocene of Europe (Kvaček and Walther, 1989; Palamarev and Mai, 1998), and isolated fruits are known from the Eocene of Europe (Kvaček and Walther, 1989; Palamarev and Mai, 1998) and North America (Manchester, 1994). Extant species in the genus are endemic to East Asia (Camus, 1929; Soepadmo, 1968a, 1972) and have great variability in fruit and cupule morphology (Langdon, 1966a; Soepadmo, 1972; Kaul, 1988; Soepadmo et al., 2000). Spiny, indehiscent cupules enclosing solitary nuts like those described in this paper are known in *Castanopsis* (Forman, 1966b; Soepadmo, 1972; Kaul, 1988; Soepadmo et al., 2000). As in the Appian Way fruits, the spines branch, and the nuts are typically ovoid to globose. The fossils



Figs. 18–21. Three-dimensional reconstructions of *Cascadiacarpa spinosa* gen. et sp. nov. fruits from Holotype P 13105 Dtop. **18.** Cutaway view of cupulate fruit. Cupule is dark grey, nut is white, and locule is light grey. **19.** View of cupule wall and spiny pedicel. **20.** Detail of spines showing enlarged spine base and five branches. **21.** Lateral view of pedicel and cupule wall. Note lack of sutures and valves.

described in this paper are morphologically identical externally to some extant species of *Castanopsis* (e.g., *C. hypophoenicea* (Von Seeman) Soepadmo and *C. malacennsis* Gamble (Soepadmo, 1972)). Soepadmo (1968b) described fruit wall anatomy in *C. javanica* as being composed of at least five different layers of cells, including a palisade layer, several layers of parenchyma, and scattered, very distinct sclerenchyma bundles. In the fossil fruits, the wall is differentiated into three layers, lacks a palisade, and has only one parenchymatous zone. Soepadmo (1968b) described only one of more than a hundred species in *Castanopsis*, and a more extensive survey of fruit anatomy needs to be undertaken. However, the bilocular and thus bicarpellate ovary in the *Cascadiacarpa* differs from the trilocular condition in *Castanopsis*.

The fossil record for the family has been greatly extended by the discovery of three kinds of charcoalified Upper Cretaceous (Santonian) cupulate nuts from Georgia, USA (Herendeen et al., 1995). By the Paleocene/Eocene boundary, well-studied flowers and fruits of both Castaneoideae and Fagoideae are present (Crepet and Nixon, 1989). By the Middle Eocene, modern genera are easily recognized from fruits and leaves (Kvaček and Walther, 1989; Manchester, 1994). Around the Eocene-Oligocene boundary, fruits occur that do not fit existing generic concepts (Manchester and Crane, 1983; Crepet, 1989).

Protofagacea allonensis Herendeen, Crane and Drinnan (1995) is the earliest known macrofossil of Fagaceae s.l. Herendeen et al. (1995) described fossil staminate flowers along with associated fruits and cupules from Santonian (Late Cretaceous) age sediments in eastern North America. Cupules associated with *Protofagacea* have three fruit scars, and the associated fruits are typically trigonous. These remains bear little resemblance to the single-fruited cupule of the Appian Way fossils, but are relevant because of the occurrence of lenticular fruits with only two styles (Herendeen et al., 1995). Either these fruits were formed from a bipartite ovary, as in the fruits described in this paper, or the third style did not develop, as is occasionally observed in lenticular fruits of extant *Nothofagus*.

Antiquacupula sulcata Sims, Herendeen and Crane (1998) is represented by fossil flowers, both staminate and bisexual, along with fruits and cupules, from the Santonian (Late Cretaceous) of Georgia. The fruits of *Antiquacupula* are sharply trigonal, tricarpellate, and occur in clusters of at least six per cupule (Sims et al., 1998), like the condition observed in some trigonobalanoids (Nixon and Crepet, 1989). The locules of *Antiquacupula*, like those of the Appian fruits, are not lined with trichomes, but otherwise, the two fossils share little similarity.

After the Paleocene–Eocene boundary, trigonal fruits with affinities to subfamily Fagoideae become common (Crepet, 1989; Crepet and Nixon 1989a, b; Kvaček and Walther, 1989; Denk and Meller, 2001; Manchester and Dilhoff, 2004). The anomalous genus *Fagopsis* Manchester and Crane (1983) was described from fruits, flowers, inflorescences, and leaves from the Oligocene of Colorado (Table 1). With a globose inflorescence and minute, wedge-shaped, three-fruited cupules, they have no clear subfamilial affinities and differ from the large, globose, single-fruited, spiny cupules of the Appian Way fruits. Furthermore, fruits of *Fagopsis* are observed to have three styles and, by inference, develop from the fusion of three carpels (Manchester and Crane, 1983), while the fossils described in this paper clearly develop from the fusion of two carpels.

The oldest castaneoid fruits are known from compressions from the Paleocene–Eocene boundary of Tennessee (Crepet and Nixon, 1989a). *Castanopsoidea columbiana* Crepet & Nixon has scaly cupules enclosing three fruits, each with three styles (Crepet and Nixon, 1989a). Thus, it can be inferred that this castaneoid fruit formed from a trilocular ovary. This is in considerable contrast to the bilocular Appian Way fruits, which occur singly in spiny cupules.

Crepet and Daghlian (1980) describe staminate castaneoid flowers of *Castaneoidea puryearensis* Crepet & Daghlian associated with fruits from the Middle Eocene of Tennessee. These authors suggest that an unnamed spiny cupulate fruit compression (Fig. 37 in Crepet and Daghlian, 1980) from this locality could represent the first occurrence of extant *Castanea*. The Eocene also marks the first appearance of *Fagus* (Manchester and Dilhoff, 2004), *Quercus* (Manchester, 1994), and *Castanopsis* (Kvaček and Walther, 1989; Manchester, 1994).

The unique bilocular condition of the Appian Way fruits distinguishes them from all extant and fossil genera of Fagaceae. In every other respect, the fossils share the characters of the family (Table 1). Ovaries in Fagaceae are three-parted, with the exception of *Castanea*, where the ovary can be 6–9 loculed. The construction of the fruit in the Appian Way fossil is identical in almost all other respects to that found in extant Fagaceae. This includes the sclerotic outer wall of the nut, axile placentation, and abortive apical ovules alongside one mature seed. No generic diagnosis within Fagaceae, extinct or extant, however, can accomodate the bilocular form present in the Appian Way fossil. Thus, we place it in *Cascadiacarpa spinosa* gen. et sp. nov. These fruits clearly fall within the boundaries of subfamily Castaneoideae and are most similar to extant *Castanopsis*.

While the bilocular ovaries of *Cascadiacarpa spinosa* are unique for the family, they are present in other taxa of the order (Stone, 1973; Abbe, 1974; Endress, 1977). Nothofagaceae, now considered sister to all other Fagales (Manos and Steele, 1997; Li et al., 2004) typically has three fruits per cupule. The central fruit in these cupules, lenticular and compressed between two trigonous lateral fruits, has been observed to be bilocular (Langdon, 1947). The gynoecia in Betulaceae, Rhoipteleaceae, Myricaceae, Casuarinaceae, and Juglandaceae are also fundamentally two-parted (Stone, 1973). Thus, the bipartite ovary of *Cascadiacarpa* could represent a holdover of an ancestral condition within the order or an autapomorphic state within the family. The former scenario if correct calls to question the long-held and well-supported hypotheses that indehiscent, evalvate, single-fruited cupules are the result of fusion and reduction from a multifruited, valvate ancestor (Forman, 1966b; Manos et al., 2001).

Attachment of the isolated, cupulate fruits of *C. spinosa* with other organs of the plants that bore them could provide very useful information in light of the extensive record of fagaceous leaves from the Tertiary of western North America (MacGinitie, 1941; Axelrod, 1983). Fruits that do not fit within extant genera have been described from other localities attached to leaves that in isolation could be placed in extant genera (Smiley and Huggins, 1981; Manchester and Crane, 1983). The existence of another distinct fruit serves as a reminder that we should cautiously approach the assignment of generic affinities to isolated leaves of Fagaceae. At present, no leaves, staminate flowers, or whole inflorescences are known from the Appian Way locality. Characters of pollen are another useful tool in distinguishing generic affinities of fossil Fagaceae (Crepet and Daghlian, 1980). No pollen grains are found in proximity to any of the specimens described in this paper. It is curious that pollen reports from the locality (Sweet, 2005) are devoid of any definitively fagaceous pollen. Castaneoid pollen forms a significant palynological component of many Tertiary localities in northwestern North America (e.g., Mustard and Rouse, 1994; Moss et al., 2005). Given the predominance of Fagaceae fruits in the concretions (Stockey et al., 2005), pollen would be expected. However, these fossils were deposited in a shallow marine environment, likely transported some distance from their source area. The absence of pollen suggests that the source area for the macrofossils may not be the same as the source area of the microfossils.

Radiation of Fagaceae in the Paleogene is not limited to extant genera. Some forms that appeared during this time are entirely novel. The bizarre inflorescences of *Fagopsis* (Manchester and Crane, 1983) have cupules and fruits that were seemingly wind-dispersed. Almost all other fruits in the family are large and almost exclusively animal-dispersed (Tiffney, 1986). Members of Fagaceae, subfamily Fagoideae have varying degrees of wing development, suggesting past wind dispersal (Tiffney, 1986; Manchester and Dilhoff, 2004). *Cascadiacarpa spinosa* is small, but its spiny, indehiscent cupule was certainly not conducive to wind dispersal. If living spiny cupules of Fagaceae are any indication, the large spines could be interpreted as a defense mechanism against fructivory (Vander Wall, 2001). The first clear association of Fagaceae fruits with rodents occurs in the Miocene of Germany, where *Castanopsis* nuts occur in burrows (Gee et al., 2003).

Borghardt and Pigg (1999) speculated that abrasion marks on the surface of Miocene *Quercus* from Washington State might have been caused by rodents. Fruits of *Cascadiacarpa spinosa* are adnate to the spiny cupule wall and were likely dispersed by rodents, as is observed in extant Fagaceae with this type of morphology (Vander Wall, 2001).

Historical biogeography of Fagaceae has been summarized by Manos and Stanford (2001). Among living castaneoids, *Castanopsis* is endemic to Southeast Asia. The roughly 150 species of *Lithocarpus* are concentrated in Southeast Asia, with the exception of two species in western North America, where they overlap with the monotypic genus *Chrysolepis* (Soepadmo, 1972; Kubitzki, 1993; Manos and Stanford, 2001). *Quercus* is found across the northern hemisphere, but is most diverse in North and Central America (Nixon, 1997). *Castanea*, the true chestnuts, are known across the northern hemisphere (Manos and Stanford, 2001). By the Eocene–Oligocene boundary, all castaneoid genera are known from North America with the exception of *Chrysolepis* (Crepet, 1989; Manchester, 1994; Manos and Stanford, 2001). The occurrence of a new genus within Castaneoideae during the Eocene of North America lends more support to the continent being a center of generic diversification in the Eocene (Crepet, 1989). Furthermore, it adds another dimension to the predominance of Fagaceae in the Eocene of Cascadia.

The abundance of data—fossil and living, morphological and molecular—accumulating for Fagaceae makes it a model family for the integration of neobotanical and paleobotanical information (Manos, 2005). The diagnostic cupules are an ideal focus for testing hypotheses on reproductive trait evolution. *Cascadiacarpa spinosa* contributes to this framework as the earliest fossil castaneoid fruit known both anatomically and developmentally. Brett (1964) and Forman (1966b) postulated that indehiscent, single-fruited cupules were a highly evolved character in Fagaceae resulting from the reduction in flower number and fusion of cupule valves. This hypothesis was later supported by phylogenetic work (Manos and Steele, 1997; Manos et al., 2001; Li et al., 2004). The Appian Way fossil fruits suggest that this type of fruit and cupule configuration was present by the Middle Eocene. *Cascadiacarpa spinosa* also provides the earliest evidence in the family for hypogeous fruits. The bicarpellate gynoecium of this new taxon represents a novel configuration for the family. *Cascadiacarpa spinosa* has a unique combination of characters, where highly derived features, such as spiny, indehiscent cupules bearing a single nut, co-occur with an anomalous two-parted gynoecium.

LITERATURE CITED

Abbe, E. C. 1974. Flowers and inflorescences of the "Amentiferae." *Botanical Review* 40: 159–261.

Axelrod, D. I. 1983. Biogeography of oaks in the Arcto-Tertiary Province. *Annals of the Missouri Botanical Garden* 70: 629–657.

Berridge, E. M. 1914. The structure of the flower of Fagaceae, and its bearing on the affinities of the group. *Annals of Botany* 28: 509–526.

Borgardt, S. J., and K. B. Pigg. 1999. Anatomical and developmental study of petrified *Quercus* (Fagaceae) fruits from the Middle Miocene, Yakima Canyon, Washington, USA. *American Journal of Botany* 86: 307–325.

Brett, D. W. 1964. The inflorescence of *Fagus* and *Castanea*, and the evolution of the cupules of the Fagaceae. *New Phytologist* 63: 96–118.

Camus, A. 1929. Les chataigniers: monographie des *Castanea* et *Castanopsis*. Encyclopédie Économique de Sylviculture, vol. 3. Académie des Sciences, Paris, France.

Cannon, C. H. 2001. Morphological and molecular diversity in *Lithocarpus* (Fagaceae) on Mount Kinabalu. *Sabah Parks Nature Journal* 4: 45–69.

Cannon, C. H., and P. S. Manos. 2000. The Bornean *Lithocarpus* Bl. section *Synaedrys* (Lindl.) Barnett (Fagaceae): its circumscription and description of a new species. *Botanical Journal of the Linnean Society* 133: 345–357.

Corner, E. J. H. 1976. Seeds of dicotyledons, vol. I. Cambridge University Press, Cambridge, UK.

Corner, E. J. H. 1990. On *Trigonobalanus* (Fagaceae). *Botanical Journal of the Linnean Society* 102: 219–223.

Crepet, W. L. 1989. History and implications of the early North American fossil record of Fagaceae. *In* P. R. Crane and S. R. Blackmore [eds.], Evolution, systematics, and fossil history of the Hamamelidae, vol. 2, 'Higher' Hamamelidae. Systematic Association Special Volume 40B, 45–66. Clarendon, Oxford, UK.

Crepet, W. L., and C. P. Daghlian. 1980. Castaneoid inflorescences from the middle Eocene of Tennessee and the diagnostic value of pollen (at the subfamily level) in the Fagaceae. *American Journal of Botany* 67: 739–757.

Crepet, W. L., and K. C. Nixon. 1989a. Earliest megafossil evidence of Fagaceae: phylogenetic and biogeographic implications. *American Journal of Botany* 76: 842–855.

Crepet, W. L., and K. C. Nixon. 1989b. Extinct transitional Fagaceae from the Oligocene and their phylogenetic implication. *American Journal of Botany* 76: 1493–1505.

Cronquist, A. 1981. An integrated system of classification of flowering plants. Houghton Mifflin, Boston, Massachusetts, USA.

Daghlian, C. P., and W. L. Crepet. 1983. Oak catkins, leaves and fruits from the Oligocene Catahoula Formation and their evolutionary significance. *American Journal of Botany* 70: 639–649.

Elliott, L. E., R. A. Mindell, and R. A. Stockey. 2006. *Beardia vancouverensis* gen. et sp. nov. (Juglandaceae): permineralized fruits from the Eocene of British Columbia. *American Journal of Botany* 93: 557–565.

Endress, P. K. 1977. Evolutionary trends in the Hamamelidales-Fagales Group. *Plant Systematics and Evolution* 1 (Supplement): 321–347.

Fey, B. S., and P. K. Endress. 1983. Development and morphological interpretation of the cupule in Fagaceae. *Flora* 173: 451–468.

Forman, L. L. 1964. *Trigonobalanus*, a new genus of Fagaceae, with notes on the classification of the family. *Kew Bulletin* 17: 381–396.

Forman, L. L. 1966a. Generic delimitation in the Castaneoideae (Fagaceae). *Kew Bulletin* 18: 421–426.

Forman, L. L. 1966b. On the evolution of cupules in the Fagaceae. *Kew Bulletin* 18: 385–419.

Gee, C. T., P. M. Sander, and B. E. M. Petzelberger. 2003. A Miocene rodent nut cache in coastal dunes of the Lower Rhine Embayment, Germany. *Palaeontology* 46: 1133–1149.

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. *In* Program and abstracts of the Second British Columbia Paleontological Symposium, 25, Vancouver, British Columbia, Canada.

Herendeen, P. S., P. R. Crane, and A. N. Drinnan. 1995. Fagaceous flowers, fruits and cupules from the Campanian (Late Cretaceous) of central Georgia, USA. *International Journal of Plant Sciences* 156: 93–116.

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.

Hill, R. S., and G. J. Jordan. 1993. The evolutionary history of *Nothofagus* (Nothofagaceae). *Australian Systematic Botany* 6: 111–126.

Hjelmqvist, H. 1948. Studies in the floral morphology and phylogeny of the Amentiferae. *Botaniska Notiser* (Supplement 2): 1–171.

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

Kaul, R. B. 1987. Reproductive structure of *Lithocarpus* sensu lato (Fagaceae): cymules and fruits. *Journal of the Arnold Arboretum* 68: 73–104.

Kaul, R. B. 1988. Cupular structure in paleotropical *Castanopsis* (Fagaceae). *Annals of the Missouri Botanical Garden* 75: 1480–1498.

Kaul, R. B. 1989. Fruit structure and ecology in paleotropical *Lithocarpus* (Fagaceae). *In* P. R. Crane and S. R. Blackmore [eds.], Evolution, systematics, and fossil history of the Hamamelidae, vol. 2, 'Higher' Hamamelidae. Systematic Association Special Volume 40B, 67–86. Clarendon, Oxford, UK.

Kubitzki, K. 1993. Fagaceae. *In* K. Kubitzki, J. G. Rohwer, and V. Bittrich [eds.], The families and genera of vascular plants, vol. 2, 301–309. Springer-Verlag, Berlin, Germany.

Kvaček, Z., and H. Walther. 1989. Paleobotanical studies in Fagaceae of the European Tertiary. *Plant Systematics and Evolution* 162: 213–229.

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

Langdon, L. M. 1947. The comparative morphology of the Fagaceae. I. The genus *Nothofagus*. *Botanical Gazette* 108: 350–371.

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. *In* Proceedings of Botany 2001, annual meeting of the Botanical Society of America, Albuquerque, New Mexico, USA, p. 66 (abstract). Website http://www.botany2001.org/section7/abstracts/48.shtml.

MacGinitie, H. D. 1941. A Middle Eocene flora from the central Sierra Nevada. *Carnegie Institution of Washington Publication* 534: 1–178.

Manchester, S. R. 1994. Fruits and seeds of the Middle Eocene Nut Beds Flora, Clarno Formation, Oregon. *Palaeontographica Americana* 58: 1–205.

Manchester, S. R., and P. R. Crane. 1983. Attached leaves, inflorescences, and fruits of *Fagopsis*, an extinct genus of fagaceous affinity from the Oligocene Florissant flora of Colorado, USA. *American Journal of Botany* 70: 1147–1164.

Manchester, S. R., and R. M. Dillhoff. 2004. *Fagus* (Fagaceae) fruits, foliage, and pollen from the middle Eocene of Pacific northwestern North America. *Canadian Journal of Botany* 82: 1509–1517.

Manos, P. S. 2005. A comprehensive systematic appraisal of the Fagales with particular attention to the Juglandaceae. Abstract 8.10.1. Seventeenth International Botanical Congress, Vienna, Austria.

Manos, P. S., and A. M. Stanford. 2001. The historical biogeography of Fagaceae: tracking the Tertiary history of temperate and subtropical forests of the northern hemisphere. *International Journal of Plant Sciences* 162: S77–S93.

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

Manos, P. S., Z. Zhou, and C. H. Cannon. 2001. Systematics of Fagaceae: phylogenetic tests of reproductive trait evolution. *International Journal of Plant Sciences* 162: 1361–1379.

Mindell, R. A., R. A Stockey, and G. Beard. 2006a. Anatomically preserved staminate inflorescences of *Gynoplatananthus oysterbayensis* gen. et sp. nov. (Platanaceae), and associated pistillate fructifications from the Eocene of Vancouver Island, British Columbia. *International Journal of Plant Sciences* 167: 591–600.

Mindell, R. M., R. A. Stockey, G. W. Rothwell, and G. Beard. 2006b. *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* 167: 649–647.

Moss, P. T., D. R. Greenwood, and S. B. Archibald. 2005. Regional and local vegetation community dynamics of the Eocene Okanagan Highlands (British Columbia–Washington State) from palynology. *Canadian Journal of Earth Science* 42: 187–204.

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.

Nixon, K. C. 1989. Origins of Fagaceae. *In* P. R. Crane and S. R. Blackmore [eds.], Evolution, systematics, and fossil history of the Hamamelidae, vol. 2, 'Higher' Hamamelidae. Systematic Association Special Volume 40B, 23–43. Clarendon, Oxford, UK.

Nixon, K. C. 1997. Fagaceae. *In* Flora of North America Editorial Committee [ed.], Flora of North America north of Mexico, vol. 3, 436–506. Oxford University Press, New York, New York, USA.

Nixon, K. C., and W. L. Crepet. 1989. *Trigonobalanus* (Fagaceae): taxonomic status and phylogenetic relationships. *American Journal of Botany* 76: 828–841.

Palamarev, E., and D. H. Mai. 1998. Die palaogenen Fagaceae in Europa: Artenvielfalt und Leitlinien ihrer Entwicklungsgeschichte. *Acta Palaeobotanica* 38: 227–299.

Prantl, K. 1889. Fagaceae. *In* A. Engler and K. Prantl [eds.], Die Natürlichen Pflanzenfamilien, Band III, Tl. 1, 47–58. Wilhelm Engelmann, Leipzig, Germany.

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

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. NRC Press, Ottawa, Canada.

Sims, H. J., P. S. Herendeen, and P. R. Crane. 1998. New genus of fossil Fagaceae from the Santonian (Late Cretaceous) of central Georgia, USA. *International Journal of Plant Sciences* 159: 391–404.

Smiley, C. J., and L. M. Huggins. 1981. *Pseudofagus idahoensis*, n. gen. et sp. (Fagaceae) from the Miocene Clarkia Flora of Idaho. *American Journal of Botany* 68: 741–761.

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.

Soepadmo, E. 1968a. Flora Malesiana precursors XLVII: census of Malesian *Castanopsis*. *Reinwardtia* 7: 383–410.

Soepadmo, E. 1968b. A revision of the genus *Quercus*. *Gardens' Bulletin, Singapore* 22: 355–428.

Soepadmo, E. 1972. Fagaceae. *In* C. G. G. J. Van Steenis [ed.], Flora Malesiana, series I, 7, 265–403. P. Noordhoff, Leyden, Netherlands.

Soepadmo, E., S. Julia, and R. Go. 2000. Fagaceae. *In* E. Soepadmo and L. G. Shaw [eds.], Tree flora of Sabah and Sarawak, vol. 3, 1–118. Forest Research Institute Malaysia, Kepong, Malaysia.

Stockey, R. A., R. A. Mindell, and L. E. Elliott. 2005. Anatomically preserved Fagalean fruits from the Eocene of western North America and their systematic implications. *In* Proceedings of the Seventeenth International Botanical Congress, Vienna, Austria, Abstract 8.10.5. Website http://www.ibc2005.ac.at.

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

Sweet, A. R. 2005. Applied research report on four Tertiary samples from Appian Way plant locality, East Coast of Vancouver Island near Campbell River. Geological Survey of Canada Paleontological Report 02-ARS-2005. Geological Survey of Canada, Calgary, Canada.

Tanai, T. 1974. Evolutionary trend of the genus *Fagus* in the northern Pacific Basin. *Birbal Sahni Institute of Palaeobotany, Special Publication* 1: 62–83.

Tiffney, B. H. 1986. Fruit and seed dispersal and the evolution of the Hamamelidae. *Annals of the Missouri Botanical Garden* 73: 394–416.

Trivett, M. L., R. A. Stockey, G. W. Rothwell, and G. Beard. 2006. *Paralygodium vancouverensis* sp. nov. (Schizaeaceae): additional evidence for filicalean diversity in the Paleogene of North America. *International Journal of Plant Sciences* 167: 675–681.

Vander Wall, S. B. 2001. The evolutionary ecology of nut dispersal. *Botanical Review* 67: 74–117.