University of Alberta

Paleobotanical Studies of the Appian Way Fossil Locality

by

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ABSTRACT

The Eocene Appian Way locality of Vancouver Island, British Columbia, Canada, has been surveyed for plant fossils. More than sixty taxa of mosses, ferns, conifers and flowering plants have been identified. This dissertation presents data on five new fossil taxa in three vascular plant families (Gleicheniaceae, Platanaceae and Fagaceae). The plants are anatomically preserved in calcium carbonate concretions, often at different developmental stages. This three-dimensional preservation allows for correlation of internal anatomy to external morphology. A branching fern rhizome and associated stipes are described and placed in the family Gleicheniaceae based on stelar anatomy and leaf trace divergence. The protostelic rhizome is designated as a new species of the extant genus *Gleichenia* and is the only Cenozoic fossil record of the family in North America. Globose, staminate inflorescences of Platanaceae (sycamores) from the locality have five-parted flowers with in situ pollen and rudimentary carpels. This is the first occurrence of rudimentary bisexuality in the fossil record of the family and the inflorescences are described as a new genus, *Gynoplatananthus*. Cupules and nuts of the beech family (Fagaceae) are the most common angiosperm fruiting structures in the concretions. The three species described in this thesis represent both Castaneoideae and Fagoideae, the two major subfamilies of Fagaceae. Trigonal, wingless, single-seeded, tricarpellate nuts are placed as a fossil species of the genus *Fagus* and represent the earliest wingless fruits of subfamily Fagoideae. Two species of spiny, cupulate, ovoid to globose fruits are described and placed in a new genus, *Cascadiacarpa*. They differ from all extant and fossil species of Fagaceae in being strictly bicarpellate. Their placement in subfamily Castaneoideae is supported by a phylogenetic analysis of morphological characters. The diversity and abundance of Fagaceae at the locality supports a Paleogene radiation of the family. A framework for studying fossil plants from the Appian Way locality has been established and taxa described, thus far, suggest a unique and diverse assemblage that will broaden our understanding of Eocene vegetation.

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The paleo people of Vancouver Island are perhaps a 21st Century equivalent to a legendary Norse—make that Welsh—tribe, only armed with rock hammers in place of swords and fighting with bedrock in place of other humans. In my experience, I came to see Graham and Tina Beard of Qualicum Beach, British Columbia as the leaders of this noble enterprise. Their pure passion for fossils was matched only by their hospitality and graciousness. Were it not for the efforts of the Beards and their people, none of these fossils would ever have been known to exist, let alone available for study.

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CHAPTER 1: INTRODUCTION

Fossil evidence of Eocene plant life is abundant. However, most macrofossil localities from this period preserve compression/impression fossils (Lesquereux 1892, Penhallow 1908, Berry 1916, MacGinitie 1941, 1969, Wolfe 1977, McIver and Basinger 1999, Manchester 1999, Pigg and Wehr 2002). Such fossils have contributed extensively to our understanding of Eocene climate, paleoecology and floristics (e.g., Wolfe 1977, Wing and Greenwood 1993, Wolfe 1994, Wing et al. 2005). Compression localities have contributed large amounts of data, predominantly on fossil leaves. Higher resolution systematic studies of plant macrofossils are often reliant on fine scale preservation of reproductive structures. This can be found in fine-grained compressions (e.g., Manchester 1991, Boucher et al. 2003), charcoalifications (e.g., Magallon-Puebla et al. 1997) and permineralizations (e.g., Reid and Chandler 1933, Manchester 1994). These latter two types of fossils provide both anatomical and morphological lines of data, however, charcoalified macrofossils are uncommon in the Eocene.

Permineralizations provide an optimal medium for systematic and taxonomic studies of fossil plants in the Eocene. Fossil localities with cellular preservation via precipitated pyrite, siderite, calcite or silica are rare. The Eocene Appian Way fossil locality on the east coast of Vancouver Island, British Columbia (Fig. 1.1) provides a new perspective on Paleogene plants. With anatomical preservation of fungi, mosses, ferns, conifers, angiosperm leaves, flowers, fruits and seeds (Little et al. 2001, Mindell et al. 2007a), the locality represents a diverse, permineralized assemblage.

Localities of a similar age from around the world have provided a wealth of data. The Lower Eocene London Clay Flora (Reid and Chandler 1933) is thought to represent a shallow marine deposit. The beds are extensive and varied, with plant macrofossils showing an array of preservation, including pyritization, molds, casts and three-dimensional calcium carbonate permineralization. The flora has been under study since the pioneering work of Reid and Chandler (1933) and work to date has yielded more than 300 fossil plant species (Collinson 1983).

Likewise, the Middle Eocene fruit and seed beds of Messel, Germany have been extensively studied due to exquisite preservation (Collinson 1988). The isolated fruits, flowers and seeds occur in oil shales and the three-dimensionally preserved fossils are made up of original, if degraded, organic tissues. Species described from Messel, as in other Eocene localities with fine scale preservation, allow for exhaustive comparisons to extant and extinct species (Collinson 1988).

Regionally, only the Princeton Chert and Clarno Nut Beds localities in the Pacific northwestern quarter of North America offer comparable preservation. The Lower Eocene Princeton Chert locality of south central British Columbia is thought to represent a freshwater environment. Exceptional preservation of vegetative and reproductive organs, often in attachment or association conducive to whole plant reconstructions, has allowed detailed study of diversity, development, reproduction and ecology in an Eocene freshwater environment (Pigg and Stockey 1996).

The Middle Eocene Clarno Nut Beds locality of central Oregon, U.S.A. have been monographed by Manchester (1994). Macrofossils are preserved as molds and casts, with occasional permineralization and preservation of cellular detail. Like Princeton, Clarno is thought to represent a terrestrial, inland deposit. As in the Appian Way locality, reproductive and vegetative organs are typically found in isolation, thus the plants preserved represent an assemblage as opposed to a community. One-hundred and forty-five genera and 170 species are recognized here. Manchester (1994) places 102 of these species in 35 extant families. Clarno, like Messel, Princeton and the London Clay, has had a strong impact on interpretations of the antiquity and paleodiversity of different plant groups. The morphological, anatomical and age data coming out of these kinds of localities is particularly useful to calibrate, test and generate phylogenetic and phytogeographic hypotheses, which typically sample only extant plants.

THE APPIAN WAY LOCALITY

Plant fossils of Vancouver Island have been well known since the end of the 19th century, when there was active coal mining in the area (Bell 1957, Gardner 1999). The earliest paleobotanical studies come from the Upper Cretaceous Nanaimo Group, which was monographed by Bell (1957). While plant fossils have been described from numerous Cretaceous localities on the Island (McIver 1994, Mickle and Delvoryas 1995, Stockey and Rothwell 2003, Smith et al. 2003, Stockey and Rothwell 2004), formal scientific work on the Eocene Appian Way locality did not commence until 1997 (Haggart et al. 1997). A number of gastropods and bivalves have been identified from the locality (Cockburn and Haggart 2007), but the only invertebrate paper published thus far describes a single decapod (Schweitzer et al. 2003).

Paleobotanical studies of the locality were initially undertaken by Graham Beard, a retired high school science teacher working out of Qualicum Beach. He began collecting at the locality in the late 1980's. At present, 11 fossil species have been described (Table 1.1). An initial systematic survey of plant fossils was presented by Little et al. (2001) and included flowers, fruits and seeds of Lauraceae and seeds of

Annonaceae. The first paper published on anatomically preserved material from the concretions was a poroid hymenophore (fungus) described by Smith et al. (2004). Hernandez-Castillo et al. (2005) described *Homalcoia,* a new genus of taxodiaceous/cupressaceous pollen cones. Elliott et al. (2006) described *Beardia vancouverensis*, a new genus and species of walnut family fruits (Juglandaceae). Trivett et al. (2006) described *Paralygodium vancouverensis*, a new species of an extinct schizaeaceous fern genus based on fertile pinnules. Rankin et al. (2008) described three different species of *Palaeophytocrene* (Icacinaceae) fruits. Numerous other families are known from the locality (see table 7.1) and await formal study (Little et al. 2001, Mindell et al. 2007a).

GEOLOGICAL SETTING

Regional geology is complex since Vancouver Island has been subject to intense deformation as a consequence of its long time proximity to the subduction zone between the North American Plate and the Kula and Farrallon oceanic plates (Mustard 1994). This is further complicated by extensive strike-slip faulting throughout the Tertiary (Mustard 1994, Mustard and Rouse 1994). The Tertiary rocks of Appian Way outcrop as an anomaly among those of the Upper Cretaceous Nanaimo Group that occur over much of Vancouver Island's east coast (Mustard 1994). The nearest Paleogene sedimentary units (Chuckanut Formation) occur in the southern Gulf Islands of Canada, the northern San Juan Islands of Washington State between Vancouver and Bellingham (Mustard and Rouse 1994). All of these nearby outcrops are considered to be exposures of the Chuckanut/Huntingdon Formation of northwest Washington and southwest British

Columbia (Johnson 1984, 1985, 1991, Mustard and Rouse 1994; Evans and Ristow 1994; Gilley 2004).

Major regional tectonic events in the Paleogene are thought to have led to significant depositional basin formation in the area (Johnson 1984, 1985, Evans and Ristow 1994, Mustard and Rouse 1994). Dextral strike-slip faulting as a consequence of early Paleogene oblique northward subduction of the Kula Plate beneath North America is thought to have led to a system of basins all along the Pacific margin of the continent (Johnson 1985, Mustard and Rouse 1994). This system of basins, called the Tertiary Georgia Basin by Mustard and Rouse (1994) finished filling at the end of the Eocene and has since been faulted and folded, along with underlying Nanaimo Group rocks, by deformational events associated with the accretion of the Pacific Rim and Crescent terranes onto southern Vancouver Island during the Late Eocene (Mustard and Rouse 1994).

This model of faulting and basin formation has been developed to explain neighboring Paleogene sedimentary rocks. It should be noted, however, that all of these Chuckanut/Huntingdon Formation rocks represent terrestrial environments (Mustard and Rouse, 1994). Johnson (1984) noted that despite the grading of extensive fluvial deposits, no marine correlative has ever been found for these rocks. He suggests that the marine end of the basin has been displaced by subsequent northwest faulting. Interestingly, the Appian Way fossil locality represents a shallow marine environment (Haggart et al. 1997) as evidenced by the rich invertebrate fauna. Its geographical proximity northwest of Chuckanut/Huntingdon outcrops makes Appian Way a possible candidate for the marine side of the basin system proposed by other workers (Johnson 1984, Mustard and Rouse 1994).

Local Geology

The Appian Way beds are exposed in two areas. A massive outcrop occurs in the intertidal area on the northern side of the mouth of the Oyster River. The Lorna Lane exposure (Jim Haggart, Geological Survey of Canada, pers. comm. 2007) is a much smaller outcrop along the river bank roughly 1.0 km west of the mouth. It is overlain by Quaternary glacial and marine sediments. While no underlying contact is exposed, proximity to exposed Upper Cretaceous Nanaimo Group rocks suggests an unconformity (Haggart et al. 1997). The section itself is divided into three units. The lowermost unit is a coarse grained sandstone that is moderately fossiliferous, bearing invertebrates and shark teeth (Haggart et al. 1997). The middle unit grades from a sandy siltstone to silty mudstone (Haggart et al. 1997). This middle unit is very fossiliferous and contains the plant bearing calcium carbonate concretions (Fig. 1.2). The upper unit is a cross-stratified sandstone relatively depauperate in fossil material, though some wood is evident. Concretions in the upper unit typically only preserve wood, while those in the middle (Fig. 1.3) unit preserve leaves, twigs, wood, flowers, fruits, ferns, cones, mosses and a host of invertebrate shells (Fig. 1.4).

Age

Two conflicting lines of evidence have been provided for the age of the locality (Fig. 1.5). Bivalve and gastropod fossils were studied by Cockburn and Haggart (2007) and show both Late Paleocene and Middle Eocene affinities. Sweet (Thesis appendix 1, 1997, 2005) has looked at the palynomorphs from the site and found significant reworking of Cretaceous and early Paleocene pollen. Of the pollen that was not reworked, types correlating to late Paleocene and early Eocene were found. Plant macrofossil correlations are few, though *Palaeophytocrene pseudopersica* Scott emend. Manchester (Rankin et al. 2008) and *Tiffneycarpa scleroidea* Manchester (Mindell et al., 2007a), present at Appian Way, both occur in the Clarno Nut Beds, which are dated radiometrically at 44 million years old (Manchester 1994). The only overlap between these age estimates is Upper to Middle Eocene, but further biostratigraphic work at the locality needs to be undertaken to refine this broad range.

Preservation of fossils

The anatomically preserved fossils that form the basis of this dissertation occur in calcium carbonate concretions (Figs. 1.3, 1.4). Concretions are mineralogically identical to surrounding bedrock but are cemented by a fine, microcrystalline calcite (Fig. 4). Fine details of preservation of delicate tissues such as embryos of Juglandaceae (Elliott et al. 2006) and *in situ* ascospores (Mindell et al. 2007c) suggest rapid preservation (Canfield and Raiswell 1991, Raiswell and Fisher 2000, Seilacher 2001). Organic material is present outside the concretions as a coarse black carbon film, suggesting that the early cementation of the material inside the concretions led to differential preservation of organic material, leaving concretion material mechanically unaltered while the host rock was compressed (Seilacher 2001). The presence of abundant pyrite within fossil tissues (Figs. 1.6, 1.7) suggests that local microenvironments with water chemistry hospitable to calcite and pyrite deposition were formed by microbial degradation of organic matter in the concretions (Canfield and Raiswell 1991, Raiswell and Fisher 2000). This process would involve the formation of carbonate supersaturated waters via oxic respiration, denitrification, sulfate reduction and methane production by bacteria (Canfield and Raiswell 1991). The high concentration of carbonate ions (CO_3^{2-}) leads to the spontaneous precipitation of calcite ($CaCO_3$) in the presence of calcium ions, which are abundant in seawater (Canfield and Raiswell, 1991). The pyrite is an indicator of sulphur reducing bacteria, which produce hydrogen sulphide (H_2S) which readily reacts with iron in seawater to form pyrite. The presence of pyrite framboids (Fig. 1.7) is thought to be indicative of sulfur-reducing bacteria in seawater (Popa et al. 2004).

THE PRESENT WORK

The foundation of this thesis involved a broad survey of plant fossils present at the Appian Way locality. The dissertation aims to utilize the preservation of plant macrofossils at the Appian Way fossil locality to extract useful data on both the external morphology and anatomy of select ferns, flowers, fruits and seeds recovered from the concretions.

The second chapter describes and identifies a fern based on rhizome anatomy and histology of the departing leaf trace. Results of this investigation support the utility of anatomical preservation and characters in the relatively scant (see: Collinson 2001) record of Eocene ferns.

Chapter Three deals with novel inflorescences from the sycamore family, Platanaceae. Among angiosperms, this family has one of the richest and deepest fossil records (Manchester 1986; Crane 1989). The majority of these records are leaf compression/impressions, although most systematically significant data has been derived from rare inflorescences (Manchester 1986; Crane 1989; Magallon-Puebla et al. 1997). Most of these fossils are known strictly from external morphology. The family has been at the confluence of two conflicting streams of data in the longstanding debate on the utility of molecular and morphological data in phylogenetic studies, owing to recent molecular phylogenetic hypotheses (Hoot et al. 1999, Hilu et al. 2003) that group Platanaceae with flowering plant families (Proteaceae, Nelumbonaceae) that show no obvious morphological similarity. Fossils provide "real", time-anchored data sources that contribute to the resolution of these sorts of conflicts. The third chapter demonstrates this by revealing an important but hidden character previously unconfirmed to be present in the fossil record of the family.

Chapters Four through six deal with the beech family, Fagaceae. Like Platanaceae, this family has a rich fossil record, predominantly of compression leaf material (Crepet 1989). Inflorescences are known from the Paleocene and Eocene and compression fruits thought to represent modern genera emerge around the boundary between these two epochs (Crepet 1989). These chapters describe some of the earliest and only anatomically preserved fruits of Fagaceae.

Chapter Four describes fruits of the genus *Fagus* L. (Beech). Species of *Fagus* grow across much of the Northern Hemisphere and are an important source of lumber and habitat for wildlife (Manos and Stanford 2001). The genus has been well studied because of its economic and ecological importance. The specimens examined in this chapter provide useful anatomical, temporal and paleophytogeographical data to test, support and contradict current hypotheses on the origin of the genus. My study also provides a framework for interpreting fossilized trigonous fruits of Fagaceae.

One of the distinguishing characters of Fagaceae is the cupule, a structure that surrounds or encloses the fruit at maturity (Forman 1966). Chapter Five describes a new genus and species of Fagaceae based on cupulate fruits. I employed three-dimensional reconstruction techniques to generate the external morphology of the cupulate fruit. This information, when combined with anatomical data makes *Cascadiacarpa* gen. nov. the only fossil genus of Fagaceae where cupule, nut and anatomical characters are all known. This chapter also presents an updated morphological character matrix for the genera of Fagaceae, the first since Nixon (1984), and attempts to put the fossil genus in a phylogenetic context via cladistic analysis. Thus this chapter employs all the tools available for detailed systematic study due to the preservation at the Appian Way fossil locality.

The sixth chapter of this dissertation builds on the fifth, describing another species of the extinct genus *Cascadiacarpa*. The specimens described in this last study are the most common fruit type at the Appian Way locality. I use the data derived from these fossils to address the potential for misidentification of compression fossils of similar morphology.

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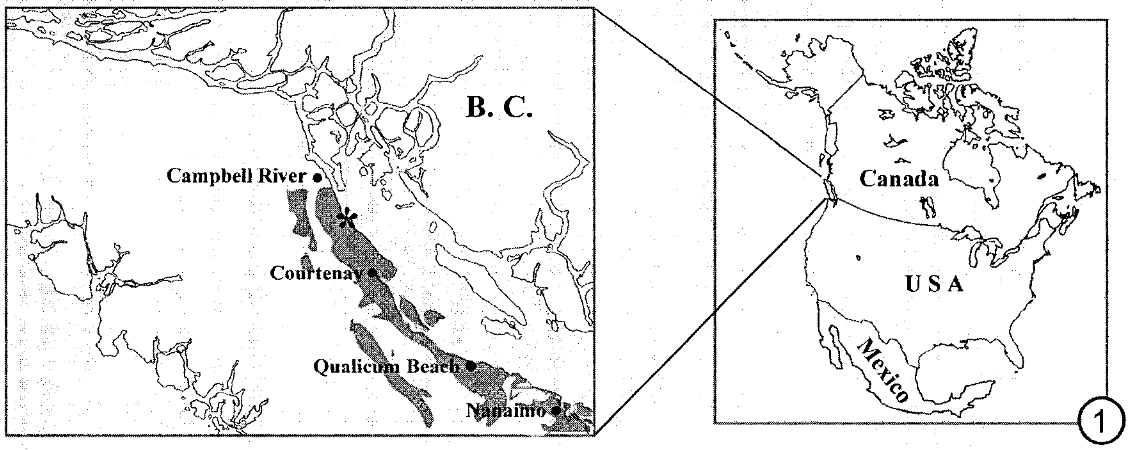
TABLE 1.1 Plants and fungi described from the Appian Way fossil locality.

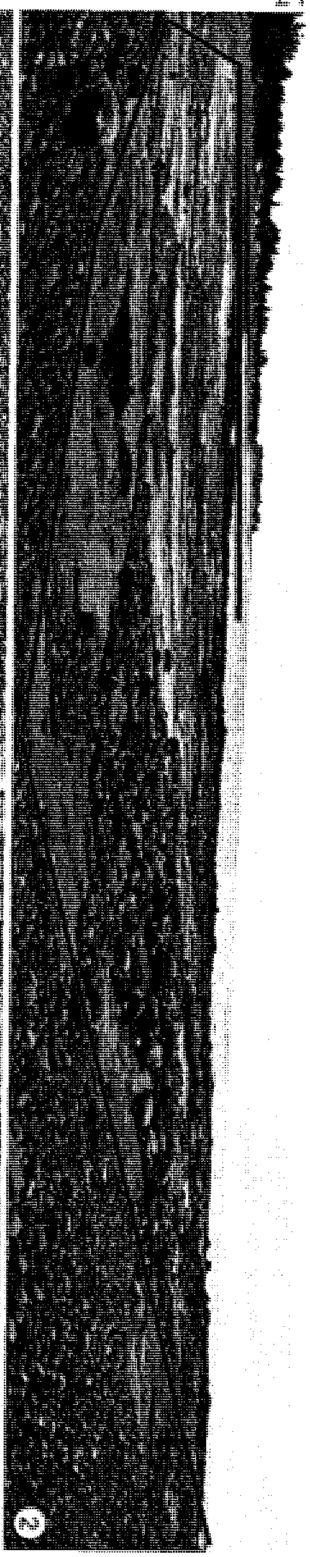
Taxon	References	Affinities	Organs / Structures
Basidiomycota			
Appianoporites vancouverensis	Smith et al. 2004	Hymenochaetales	Hymenophore
Ascomycota			
Margaretbarromyces dictyosporus	Mindell et al. 2007c	Pleosporales	Ascocarp, Asci, Ascospores
Pteridopsida			
Filicales			
Gleichenia appianensis	Mindell et al. 2006b	Gleicheniaceae	Rhizome and associated stipes
Paralygodium vancouverensis	Trivett et al. 2006	Schizeaeceae	Fertile pinnules, sporangia, spores
Coniferopsida			
Coniferales			
Homalcoia littoralis	Hernandez-Castillo et al. 2005	Cupressaceae	Leaves, pollen cones, pollen
Angiosperms			
Laurales	Little et al. 2001	Lauraceae	Flowers, fruits, seeds
Magnoliales	Little et al. 2001	Annonaceae	Seeds
Proteales			
Gynoplatananthus oysterbayensis	Mindell et al. 2006a	Platanaceae	Inflorescences, flowers, pollen
Fagales			
Cascadiacarpa spinosa	Mindell et al 2007b	Fagaceae	Cupulate fruits
Beardia vancouverensis	Elliott et al. 2006	Juglandaceae	Fruits
Celastrales			
Palaeophytocrene pseudopersica	Rankin et al. 2008	Icacinaceae	Fruits
Palaeophytocrene vancouverensis	Rankin et al. 2008	Icacinaceae	Fruits
Palaeophytocrene manchesterii	Rankin et al. 2008	Icacinaceae	Fruits

FIGURE 1.1 Map showing the location of Paleogene Appian Way fossil locality (*) on Vancouver Island and surrounding Upper Cretaceous Nanaimo Group rocks (shaded). Modified from Mustard (1994) and Elliott et al. (2006).


B. C.
Campbell River
Courtenay
Qualicum Beach
Nanaimo
Canada
U S A
Mexico

①

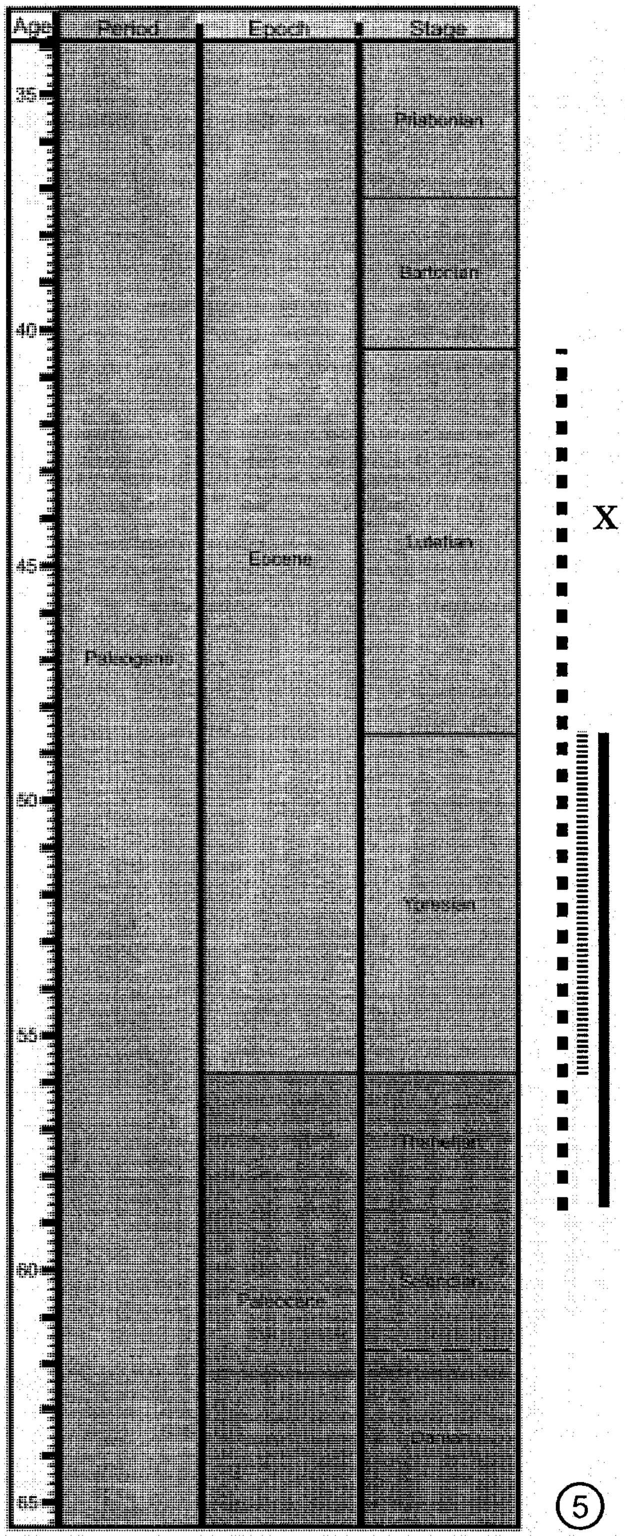
FIGURES 1.2-1.4 Geology of Appian Way. **1.2** Panorama of outcrop. Fossiliferous concretion horizon within lines. **1.3** Portion of concretionary horizon showing extracted concretion surrounded by cavities from previously extracted concretions. Hammer for scale. **1.4** Detail of broken concretion showing dark plant material and white shell fossils. Scale bar = 1 cm.


2

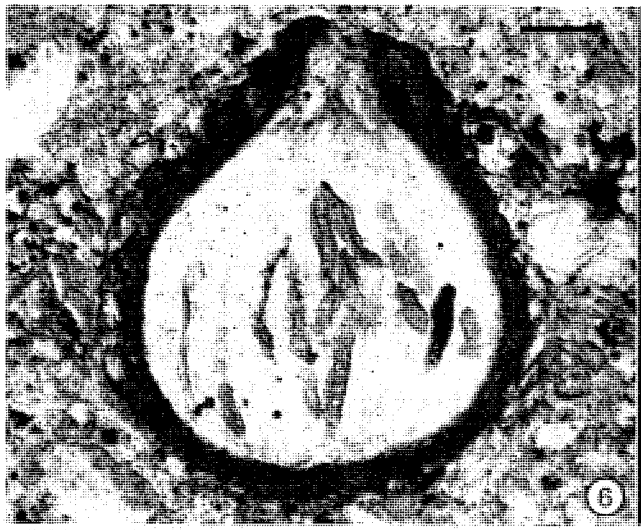

3

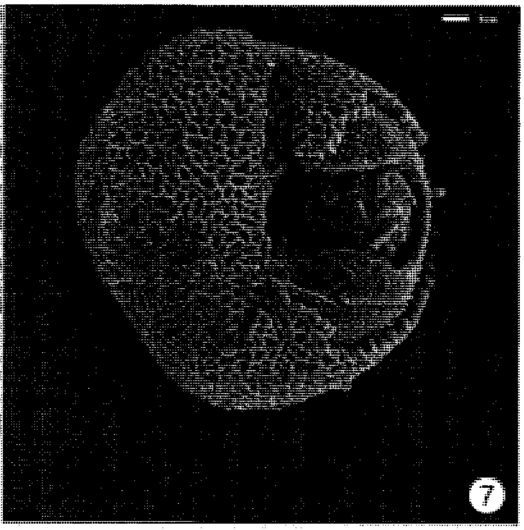

4

FIGURE 1.5 Stratigraphic column showing age estimates for Appian Way fossil locality. Thickly dashed line represents estimate based on invertebrate fauna (Cockburn and Haggart 2007), black line represents range of palynomorphs (Sweet 2005), "X" represents correlation to Clarno Nut Beds based based on plant macrofossils (Mindell et al. 2007a, Rankin et al. 2008). Finely dashed line represents stratigraphic range of London Clay beds.


Age
Period
Epoch
Stage
35
40
45
50
55
60
65
Paleogene
Eocene
Paleocene
Priabonian
Bartonian
Lutetian
Ypresian
Thanetian
Selandian
Danian
X
⑤

FIGURES 1.6-1.7 Preservation in concretions. **1.6** Fungal ascocarp with *in situ* ascospores embedded in peridium of unknown vascular plant. Note abundant pyrite, represented by black spots throughout fungal and plant tissues (Mindell et al. 2007c). Scale bar= 100 µm **1.7** Framboidal pyrite within pollen grain of *Gynoplatananthus oysterbayensis*.


⑥


⑦

CHAPTER 2

Gleichenia appianense sp. nov. (Gleicheniaceae), a permineralized rhizome and associated vegetative remains from the Eocene of Vancouver Island, British Columbia.[A1]

INTRODUCTION

Gleicheniaceae is a tropical to subtropical family of three to five living genera (Tryon and Tryon 1982; Kramer 1990) that have long been considered to be basal leptosporangiate ferns based on morphological and anatomical characters (Bower 1926; Copeland 1947). Most notable of these characters are the protostelic rhizomes, exindusiate sori with simultaneous maturation, and large sporangia (Bower 1926). Phylogenetic relationships of the Gleicheniaceae have been clarified by recent cladistic analyses using morphological and molecular characters (Hasebe et al. 1995; Pryer et al. 1995; Stevenson and Loconte 1996; Rothwell 1999).

Probable gleicheniaceous fossil remains are known as early as the Permian (Yao and Taylor 1988). Mesozoic records of the family are more common, including fronds, rhizomes with attached stipes, and isolated fertile material (Tidwell and Ash 1994; Collinson 1996; Skog 2001). By the mid-Cretaceous gleicheniaceous fossils are abundant, with a large number of specimens being assigned to *Gleichenia* (Berry 1922; Andrews and Pearsall 1941). Despite this relatively rich Mesozoic history, there are no Tertiary records of the family in the New World (Tidwell and Ash 1994; Collinson

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[1] A version of this chapter has been published. Mindell, Stockey, Rothwell and Beard 2006. International Journal of Plant Sciences. 167: 639-647.

2001). The Eocene Appian Way flora of Vancouver Island is dominated by angiosperm fruits and seeds (Little et al. 2001), but several kinds of taxodiaceous conifers are present (Hernandez-Castillo et al. 2005), as well as a polypore fungus (Smith et al. 2004) and many types of filicalean ferns. The ferns of Appian Way have only recently begun to be investigated in detail. Sori of a schizaeaceous fern have been described (Trivett et al. 2002), and a general description of fern diversity is underway. In this paper I describe *Gleichenia appianense* sp. nov., a new species of gleicheniaceous ferns based on a permineralized rhizome with an attached stipe. This rhizome and several associated stipes represent the first record of Gleicheniaceae in the Tertiary of North America.

MATERIAL AND METHODS

Specimens were collected from the Appian Way fossil locality south of Campbell River on the east coast of Vancouver Island, British Columbia Canada (49° 56' 00" N 125° 11' 15" W; UTM 10U CA 433331). Plant remains occur in marine calcareous concretions in a sandy-siltstone matrix. These shallow marine sediments have been dated as Eocene based on fossil molluscs, decapods and shark teeth (Haggart et al. 1997) and stratigraphic studies are currently being conducted at the site (J. W. Haggart pers commun. 2004).

The fossiliferous concretions were cut into slabs and peels were made using the cellulose acetate peel technique (Joy et al. 1956). Slides were mounted using xylene-soluble Eukitt (O. Kindler GmbH, Freiberg, Germany) mounting medium. Images were captured using a PowerPhase digital scanning camera (Phase One, Copenhagen, Denmark) and processed using Adobe Photoshop 7.0.

SYSTEMATICS

Order: Filicales

Family: Gleicheniaceae

Genus: *Gleichenia*

Species: *G. appianense* Mindell, Stockey, Rothwell, et Beard sp. nov. (Figs. 2.1a-g, 2.2a-f)

Specific Diagnosis. Rhizome small, at least 3.4 mm in diameter. Protostele mixed, ca. 1.4 mm in diameter; tracheids in chains or groups. Parenchyma cells between tracheids, thin-walled, 10-20 µm in diameter. Protoxylem strands 5-6; stele marginally-mesarch; protoxylem tracheids ca. 10 µm in diameter, thickenings helical. Metaxylem tracheids scalariform, 25-63 µm in diameter. Cortex two-zoned, at least 1 mm thick; outer parenchymatous, up to 950 µm thick, cells 25-63 µm in diameter; inner sclerenchymatous, 125-188 µm wide, fibers 13-38 µm in diameter. Roots diarch, numerous, arising on all sides of rhizome. Frond trace C-shaped, originating as an arc, forming nodal island of sclerenchyma fibers on divergence; metaxylem tracheids scalariform, up to 200 µm in diameter, some with numerous regularly-spaced, horizontal to slightly oblique septations.

Holotype. Rhizome with diverging stipe; specimen AW 258 C_2 bot and D_2 top, University of Alberta Paleobotanical Collections (UAPC-ALTA)

Stratigraphic position and age. Oyster Bay Formation, Middle Eocene.

Description. The rhizome of *Gleichenia appianense* is 7.5 mm long and 3.0 mm in diameter (figs. 2.1a, 2.1b), but the specimen has been abraded, and was probably at least 3.4 mm in diameter in life. No epidermis is preserved on the specimen. Therefore, the presence of possible scales or trichomes cannot be determined. The cortex is at least 1.1 mm thick and shows two distinct zones (fig. 2.1a). The outer cortex is up to 950 μm in thickness and up to 25 cells wide in the most completely preserved area. Cells in this zone are thick-walled parenchyma, 25-63 μm in diameter. The inner cortex, measures 125-188 μm in thickness, and is composed of thick-walled, sclerenchyma fibers, 13-38 μm in diameter.

The rhizome has a mixed protostele up to 1.4 mm in diameter (figs. 2.1a-c, 2.1g). In cross sections metaxylem tracheids, 25-63 μm wide, appear to be arranged in chains up to five cells long (figs. 2.1a-d). Thin-walled parenchyma cells 10-20 μm in diameter occur between groups of metaxylem tracheids (fig. 2.1d). Five to six marginally mesarch protoxylem strands correspond to subtle lobes of the stele (figs. 2.1a, 2.1b, 2.1f). Helically-thickened protoxylem elements 10 μm in diameter (fig. 2.1e, at right) occur in clusters among scalariform metaxylem tracheids near the periphery of the xylem (fig. 2.1e, 2.1f). Encircling the xylem is a poorly preserved layer of putative phloem and pericycle up to five cells wide and 60 μm across (fig. 2.2f, at arrow).

Diarch root traces occur on all sides of the rhizome (figs. 2.1a, 2.1b; at arrows) except in the area of leaf trace divergence (fig. 2.1g). Root traces are surrounded by thick-walled parenchyma, and their course of growth through the cortex is oblique. No isolated roots have been identified in the matrix.

Leaf trace divergence is initiated by the formation of an arc of xylem at the periphery of the stele (fig. 2.2a, at top). In slightly more distal transverse sections, a sub-circular nodal island of sclerenchyma forms in the space between the xylem of the leaf trace and that of the stele (fig. 2.2b). Continuing distally, the leaf trace and sclerotic bundle grow larger, as does the cortex surrounding them (figs. 2.2c, d). The trace itself has endarch xylem maturation with metaxylem tracheids that measure up to 200 μm wide; these tracheids having scalariform secondary wall thickenings and regular septa (figs. 2.1g, 2.2e, f). Spacing between these planar septa increases with tracheid width.

Associated Foliage

Two branching specimens and at least 15 isolated frond segments with gleicheniaceous characters have been found associated with the rhizome (figs. 2.2g, 2.2h, 2.3a-e). Frond segments show significant variation in size, ranging from 2.5 mm-8.0 mm in width. All have C-shaped traces with well-developed, infolded adaxial hooks (fig. 2.2g). Protoxylem strands vary (5 or more) and show endarch maturation (fig. 2.2h). Xylem at the lateral edges of the trace is constricted, giving the trace an angular shape (fig. 2.2g, at arrows). The vascular tissue is surrounded by a narrow sheath of sclerenchymatous tissue (fig. 2.2g). To the outside of this sheath the remaining extraxylary ground tissues are usually thick walled towards the periphery and relatively thin walled near the vascular trace (fig. 2.2g).

At levels of frond branching, the stipe and abaxial arc both widen and the vascular trace divides to form three separate traces before the frond divides. The changes in xylem configuration that lead to formation of the three traces are similar in each specimen. Proceeding distally through a series of transverse sections in the branching region, both adaxial hooks close to form rings that each enclose ground tissue (fig. 2.3a) and then separate abaxially to form two rings of vascular tissue (fig. 2.3b). Distally, the rings begin to open up on their abaxial side, coincident with the development of two constrictions on the abaxial arc (fig. 2.3c). At the level of constriction, the xylem of the abaxial arc unites with to the abaxial side of the xylem of the remnant rings (fig. 2.3d). Distal to this level the trace divides to produce three separate bundles (fig 2.3d). In both branching specimens, only two of the resulting pinnae persist (fig. 2.3e). In each specimen, the central segment truncates and terminates as incompletely preserved tissue.

DISCUSSION

Rhizomes with vitalized protosteles occur in several fern families, most notably in the basal leptosporangiate ferns (Bower 1926; Ogura 1972). Anatomical studies of Gleicheniaceae (Boodle 1901b), Schizaeaceae (Boodle 1901a), Hymenophyllaceae (Boodle 1900) and Cheiropleuriaceae (Bower 1915) have revealed protosteles that differ from family to family. *Lygodium* Sw., the only protostelic genus in Schizaeaceae, shows a round cylinder of xylem with exarch maturation and indistinct protoxylem strands (table 1). By contrast, the Appian Way rhizome shows distinct marginally mesarch protoxylem strands. The leaf trace in *Lygodium* diverges as a solid cylinder (Boodle 1901a), as opposed to the arc of xylem enclosing sclerenchyma that characterizes the frond trace in the Appian Way rhizome.

The Hymenophyllaceae has several protostelic genera that were formerly grouped in the genus *Trichomanes* L. (Ogura 1972, Dubuisson 1997). Like those of *Lygodium*, the rhizomes of these taxa are characterized by exarch primary xylem maturation, but the leaf trace diverges as a hollow cylinder of xylem that encloses sclerenchyma (table 1; Boodle 1900). In the Appian Way fern, the leaf trace appears as an arc of xylem with a nodal island, that opens up into the characteristic C-shaped trace as it diverges from the stele (table 1). Like the Appian Way rhizome, *Cheiropleuria* Nakai has mesarch primary xylem maturation, but the protoxylem strands are indistinct and the leaf trace diverges as a solid cylinder that rapidly dichotomizes as it leaves the stele (Bower 1915).

The Appian Way rhizome is most similar to species of Gleicheniaceae. This family is composed exclusively of protostelic forms except for one solenostelic species, *Dicranopteris pectinata* (Willd.) Underw. (Ogura 1972; Boodle and Hiley 1909). All other described gleicheniaceous species also have characters in common with the Appian fern. In the subfamily Stromatopteroideae, *Stromatopteris monofilaformis* Mett. (the sole representative of the genus) is similar in stelar construction to the Appian Way fern, except that tracheid chains are significantly longer (5+) and in this species there are no obvious protoxylem strands (table 1; Bierhorst 1969, 1971).

The remaining four gleicheniaceous genera, *Diplopterygium* Nakai, *Sticherus* C. Presl, *Gleichenia* J.E. Smith and *Dicranopteris* Bernhardi (subfamily Gleichenioideae), have been subject to substantial taxonomic revision (Holttum 1957, Tryon and Tryon 1982, Kramer 1990) with most authors recognizing *Diplopterygium* and *Sticherus* as subgenera within *Gleichenia*. Rhizomes of these protostelic taxa have an inner cortex of thick-walled cells and relatively thin-walled cells in the outer cortex. Like those of *G. appianense*, steles of these species are small with obvious protoxylem strands, marginally mesarch xylem maturation, and protoxylem strands varying in number from 5 to15 (table 1; Ogura 1972).

Dicranopteris has similar stelar construction to *G. appianense*, but the frond trace diverges as a hollow cylinder rather than an arc (table 1; Boodle 1901b; Ogura 1972). There has been some confusion about this because *Dicranopteris dichotoma* (Thunb. ex Murray) Willd. is a synonym of *D. pedata* (Houtt.) Nakaike, that Boodle originally figured as *Gleichenia dichotoma* Willd. and Ogura figured as *D. dichotoma*. In *Diplopterygium* the stele is unlobed and Ogura (1972) shows 11 protoxylem strands, a number far greater than the five to six observed in *G. appianense* (table 1). In *Sticherus flabellatus* (R. Br.) H. St. John. (figured by Boodle as *Gleichenia flabellata* Br.; table 1), the frond trace diverges as an arc of xylem enclosing a nodal island, as in *G. appianense* (Boodle 1901b; Bierhorst 1971). However, the stele is unlobed, and Boodle (1901b) shows 14 protoxylem strands.

As in *G. appianense*, living species of *Gleichenia* s.s. have a lobed stele with 5-15 protoxylem strands and a frond trace that diverges as an arc of xylem enclosing a nodal island (table 1; Boodle 1901b; Ogura 1972). Our specimen is most similar to *Gleichenia dicarpa* R. Br. (= *Gleichenia circinnata* Sw.) as illustrated by Boodle (1901b) and Ogura (1972). This species has five protoxylem strands, a lobed stele, and a similar mode of leaf trace divergence (Ogura 1972). The nodal island formed in *G. dicarpa* is parenchymatous (Ogura 1972), while that of the Appian Way rhizome is sclerenchymatous.

The presence of planar septa in the long metaxylem tracheids of the frond trace of *G. appianense* is a feature unknown in extant *Gleichenia*. However, such septa likely represent tyloses, which have been observed in the stipes of numerous fern families (Ogura 1972), and specifically in the protoxylem of *Gleichenia* (Chrysler 1943).

The fossil record of Gleicheniaceae has been reviewed by several authors (Tidwell and Ash 1994; Collinson 1996, 2001, 2002; Skog 2001). Remains are predominantly compression/impressions, and are described from as far back as the Permian (Yao and Taylor 1988). The fossil record of North American Gleicheniaceae begins in the Triassic, with spores from eastern North America (Cornet and Traverse 1975), fertile frond compressions and spores from New Mexico (Ash 1969), and fronds from Virginia (Cornet and Olsen 1990). While Cretaceous compression records are abundant (Andrews and Pearsall 1941; Rushforth 1971; Crabtree 1988; Wing et al. 1993; Skog and Dilcher 1994) Tertiary remains of any sort are scarce worldwide (Tidwell and Ash 1994; Collinson 2001).

Anatomically preserved rhizomes of Gleicheniaceae are rare in the fossil record. *Antarctipteris sclericaulis* Millay and Taylor (1990), a rhizome from the Triassic of Antarctica, was suggested to have gleicheniaceous affinities based on its mixed protostele, simple frond trace and scalariform tracheids. Unlike *G. appianense*, the Antarctic specimens lack any clear protoxylem strands in the stele (Millay and Taylor 1990). *Antarctipteris sclericaulis* also has axially elongate sclerenchyma strands surrounding the stele and bar-shaped leaf traces (Millay and Taylor 1990) that do not occur in *G. appianense*.

Gandolfo et al. (1997) described the charcoalified remains assignable to Gleicheniaceae from the Turonian (Late Cretaceous) of New Jersey. Rhizomes with attached frond bases of *Boodlepteris turoniana* Gandolfo have a dorsiventral protostele without distinguishable protoxylem strands (Gandolfo et al. 1997), while the protoxylem strands in *G. appianense* are distinct and there is no evidence of dorsiventrality.

Thus, we have placed the Appian rhizome in a new species, *Gleichenia appianense* Mindell, Stockey, Rothwell et Beard sp. nov. Of those extant species of *Gleichenia* studied anatomically, *G. appianense* is most similar to *G. dicarpa*. It should be noted that while a few species of all gleicheniaceous genera have been studied in anatomical detail, there are a large number of species that have not been sectioned. Nevertheless, with the current body of literature, the anatomical distinctions among the gleicheniaceous genera seem to be clear (table 1).

The numerous associated frond segments known from Appian Way could be those of *G. appianense*, however, they have not been found in attachment. The infolded, angular C-shaped traces with characteristic constrictions are indicative of the Gleicheniaceae, as is the pseudodichotomous branching (Chrysler 1943, 1944; Ogura 1972). The latter clearly represent fronds that follow the same branching sequence as that described for *Sticherus intermedius* (Bak.) Chrysler (Chrysler 1943, 1944). While the bifurcating frond in Gleicheniaceae appears superficially to be an even dichtomomy, a central terminal or dormant bud occurs between the lateral axes. Histological studies through this region show that the lateral traces diverge from the margins of the central trace, the latter persisting in the form of a bud, thus, the pseudodichotomy (Chrysler 1943).

Permineralized frond segments are known from the Mesozoic. These are all placed in Gleicheniaceae based on the characteristic C-shaped trace and, sometimes, the fertile structures that are present. Phipps et al. (2000) assign *Gleichenipteris antarcticus* to the family based on sporangial shape and arrangement, and point to a close association with rachides of *Antarctipteris sclericaulis* (Millay and Taylor 1990). It should be noted, however, that *A. sclericaulis* lacks the characteristic C-shaped trace near the level of stipe divergence from the rhizome.

Sharma and Bohra (1977) describe gleicheniaceous stipes from the Jurassic Rajmahal Hills of India. These show the constricted, infolded, C-shaped trace observed in many extant species of *Gleichenia* (Chrysler 1944). Gandolfo et al. (1997) described charcoalified fertile frond remains that gave enough characters to place *Boodlepteris turoniana* within the Gleicheniaceae as a sister group to *Stromatopteris* in a cladistic analysis based on morphological and anatomical characters. The trace in these fossil fronds is C-shaped with two visible endarch protoxylem strands and is surrounded by a cortex of thick-walled sclerenchyma. The stipe traces associated with *G. appianense* are superficially similar to those of *Boodlepteris* in that they have endarch xylem maturation and scalariform metaxylem tracheids, but they differ from the Appian Way stipes in having numerous protoxylem strands and a cortex that is typically parenchymatous towards the trace and sclerenchymatous towards the periphery of the stipe. Branching of the fronds in *Boodlepteris turoniana* was observed only externally and suggests that branching was either dichotomous or pseudodichotomous (Gandolfo et al. 1997). Branching in *G. appianense* fronds is preserved anatomically, and clearly shows a pseudodichotomous pattern as illustrated by Chrysler (1943) for a living gleicheniaceous species.

Gleichenia chaloneri Herendeen et Skog (1998) has been described from fusainized frond segments from the early Cretaceous (Albian) of Bedfordshire, England. These frond fragments have a C-shaped trace with incurved arms and 7-8 protoxylem strands. Like the Appian Way frond remains, sclerenchyma immediately surrounds the vascular tissue. Histology of the branching regions is not known in the branching specimens described by Herendeen and Skog (1998), but they are similar in most respects to our isolated stipes and rachides.

The specimens described in this paper are the only Tertiary macrofossils of the Gleicheniaceae thus far described from the New World, and they provide direct evidence for Gleicheniaceae in the Eocene of North America. In addition to the vegetative remains described in this paper, spores of *Gleicheniidites* Ross have also been identified from the Appian Way locality by Sweet (1997). Biogeographic reviews of the ferns (Tidwell and Ash 1994; Skog 2001; Collinson 2001, 2002) all suggest a poor worldwide record of Gleicheniaceae in the Paleogene. The family is well represented in North America in the Triassic (Tidwell and Ash 1994) and Cretaceous (Berry 1922; Andrews and Pearsall 1941; Rushforth 1971; Crabtree 1988; Skog and Dilcher 1994; Gandolfo et al. 1997). However, in addition to some spore records and ambiguous compressions known from Europe and South America (Collinson 2001), clear Tertiary records are known only from the Eocene of southeast England (Holttum 1957) and the Oligocene of Australia (Blackburn and Sluiter 1994). Today, the family's Northern Hemisphere distribution is restricted to tropical and subtropical latitudes (Tryon and Tryon 1982).

The branching frond segments described here from Appian Way represent the first anatomically preserved bifurcating leaves of Gleicheniaceae in the fossil record, and they demonstrate that the pseudodichotomous branching pattern of Gleicheniaceae was established by at least the early Tertiary. The presence of anatomically preserved rhizomes, fronds and spores confirms that this long-lived family persisted at the northwestern margin of the North American continent at least until the Eocene.

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TABLE 2.1 Comparison of Appian rhizome stelar anatomy and leaf trace divergence to extant fern genera with ectophloic, protostelic rhizomes.

Table 2.1

Family	Genus	Primary Xylem Maturation	Protoxylem Groups	Stele Lobed	Leaf Trace Divergence
Schizaeaceae	*Lygodium*	Exarch	Indistinct	No	Solid cylinder of xylem
Hymenophyllaceae	*Trichomanes* s.l.	Exarch	Indistinct	No	Hollow cylinder of xylem
Dipteridaceae	*Cheiropleuria*	Mesarch	Indistinct	No	Dichotomizing solid cylinder of xylem
Gleicheniaceae	*Stromatopteris*	Marginally mesarch	Indistinct	Yes	Solid cylinder of xylem
	Dicranopteris	Marginally mesarch	Distinct (5-15)	Yes	Hollow cylinder of xylem
	Diplopterygium	Marginally mesarch	Distinct (11)	No	Arc of xylem enclosing sclerenchyma
	Sticherus	Marginally mesarch	Distinct (14)	No	Arc of xylem enclosing sclerenchyma
	Gleichenia	Marginally mesarch	Distinct (5-15)	Yes	Arc of xylem enclosing parenchyma
	Appian Rhizome	Marginally mesarch	Distinct (5-6)	Yes	Arc of xylem enclosing sclerenchyma

Data from Boodle 1900a, 1900b, 1901; Bower 1915; Chrysler 1943; Bierhorst 1969, 1972; Ogura 1972.

FIGURE 2.1

Gleichenia appianense Mindell, Stockey, Rothwell et Beard sp. nov. Holotype. *a*, Transverse section of rhizome showing lobed stele, root traces (arrows) and thick, two-zoned cortex. Note that position of protoxylem strands correlate with subtle lobes of stele (numbered 1-5). AW258 C bot 16. Scale bar = 500 µm. *b*, Transverse section of rhizome showing root traces (arrows) and two-zoned cortex. AW 258 C_3 side 5. Scale bar = 500 µm. *c*, Transverse section of stele showing tracheary elements in chains surrounded by parenchyma cells. AW 258 C_3 side 5. Scale bar = 100 µm. *d*, Detail of mixed protostele showing parenchyma between large metaxylem tracheids. AW 258 C_3 side 5. Scale bar = 50 µm. *e*, Longitudinal section near stele margin showing spirally thickenened protoxylem (px) and scalariform metaxylem tracheids (mx). AW 258 C_3 side 9. Scale bar = 10 µm. *f*, Transverse section showing stele periphery with marginally mesarch protoxylem strand (px) and zone of putative phloem and pericyle (arrow). AW 258 C_3 side 5. Scale bar = 50 µm. *g*, Oblique transverse section though rhizome showing diverging leaf trace and internodal island of sclerenchyma. AW 258 D_2 top 2. Scale bar = 1 mm.

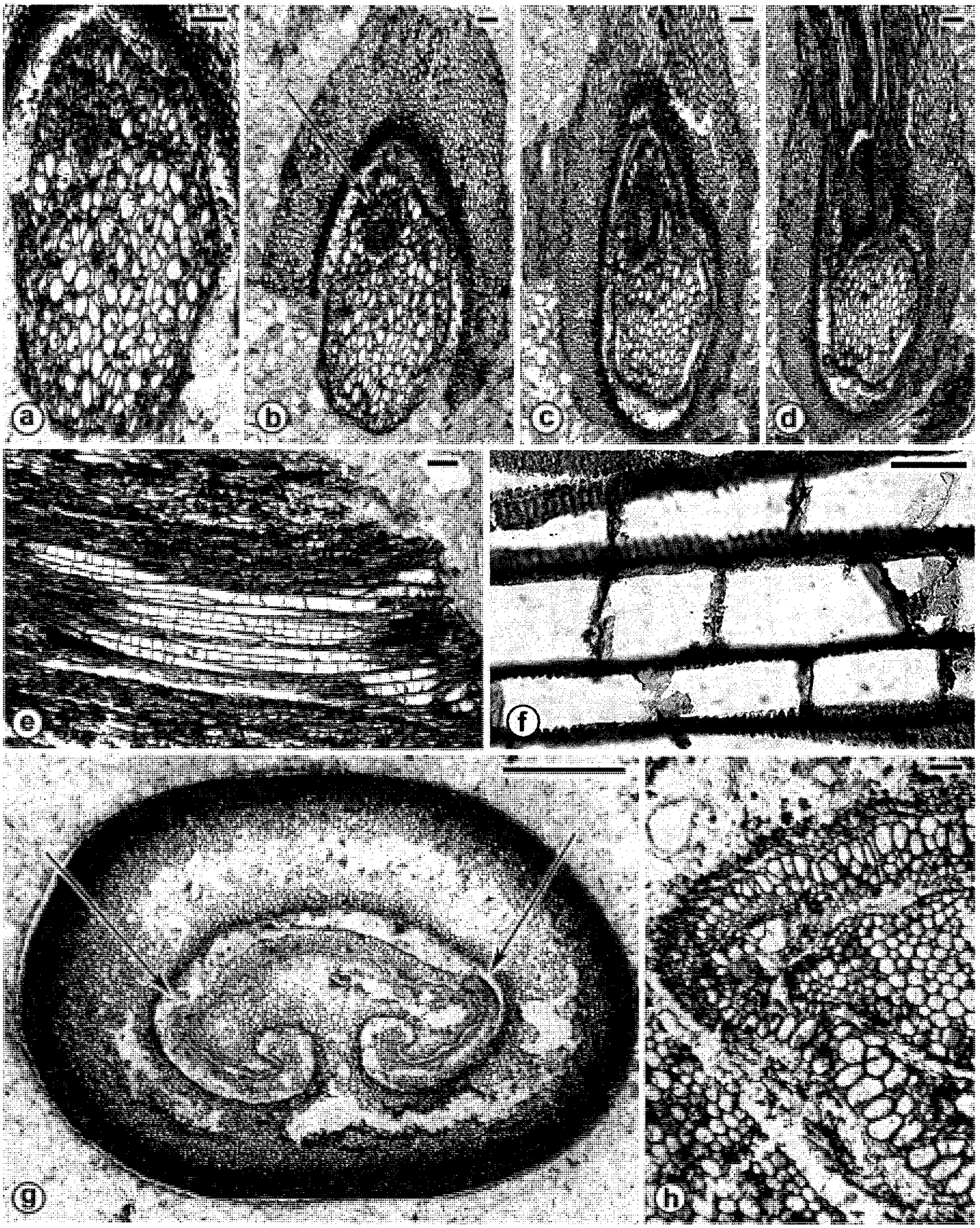
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FIGURE 2.2

a-f *Gleichenia appianense* Mindell, Stockey, Rothwell, Beard sp. nov. Holotype. g-h Associated frond segments. *a*, Oblique transverse section of stele at base of stipe divergence. AW 258 D_2 top 50. Scale bar = 100 µm. *b*, Oblique transverse section of rhizome distal to that in 2a showing sclerenchymatous internodal island (arrow) developing between arc of xylem and stele. AW 258 D_2 top 39. Scale bar = 100 µm. *c*, Section distal to 2b showing well developed arc of xylem, cortical expansion and larger internodal island. AW 258 D_2 top 12. Scale bar = 100 µm. *d*, Transverse section through rhizome at level of leaf trace departure. AW 258 D_2 top 2. Scale bar = 100 µm. *e*, Longitudinal section through departing leaf trace showing elongate metaxylem tracheids with regular septa. AW 258 D_2 top 4. Scale bar = 100 µm. *f*, Longitudinal section of metaxylem tracheids in stipe base showing planar septa and scalariform secondary wall thickenings. AW 258 D_2 top 4. Scale bar = 50 µm. *g*, Isolated frond segment in transverse section showing angular, C-shaped trace with lateral constrictions (arrows) and adaxial hooks. AW 103 D bot 0. Scale bar = 1 Mm. *h*, Transverse section through isolated frond segment showing lateral constriction and endarch primary xylem maturation. AW 4 C top 4. Scale bar = 100 µm.

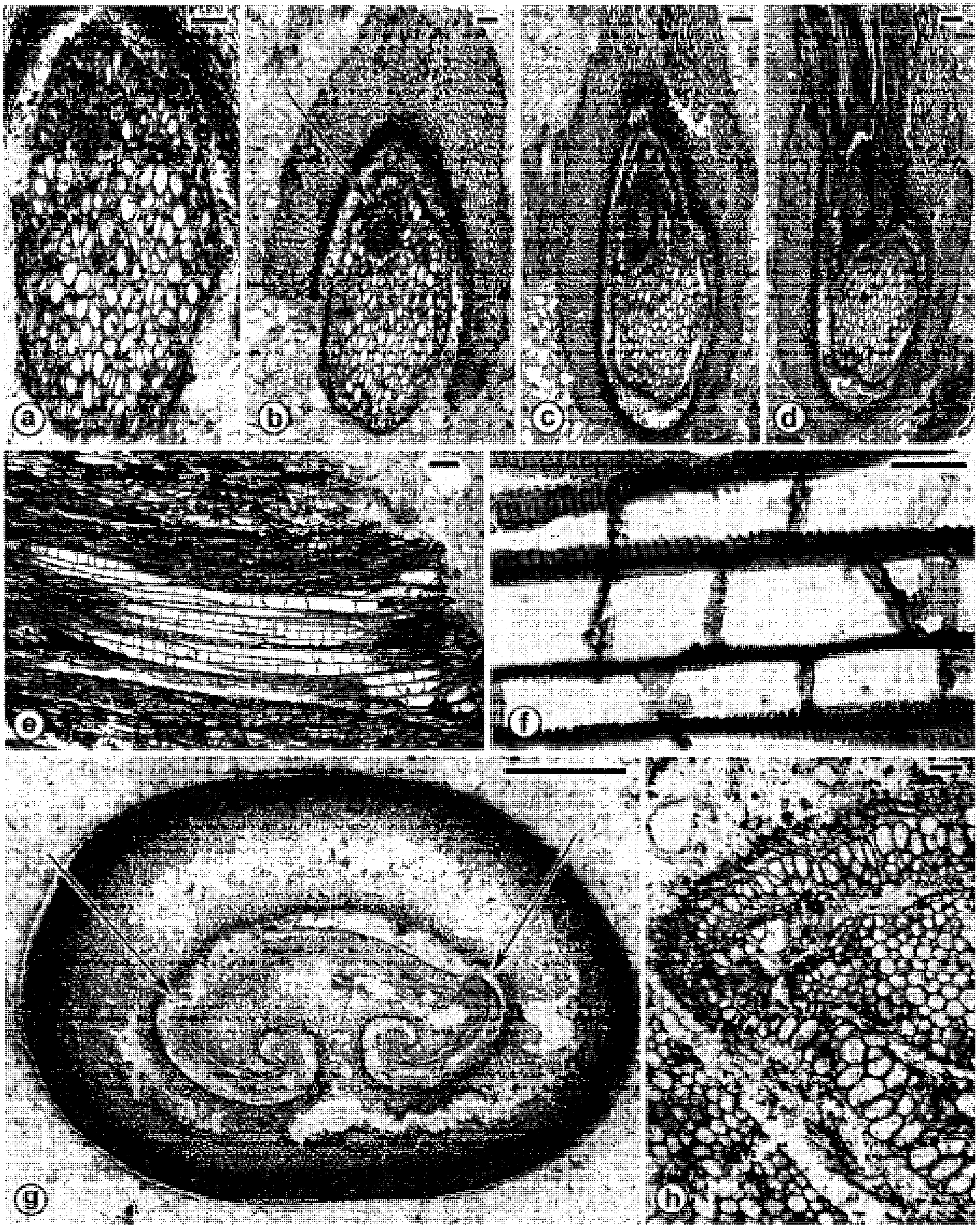
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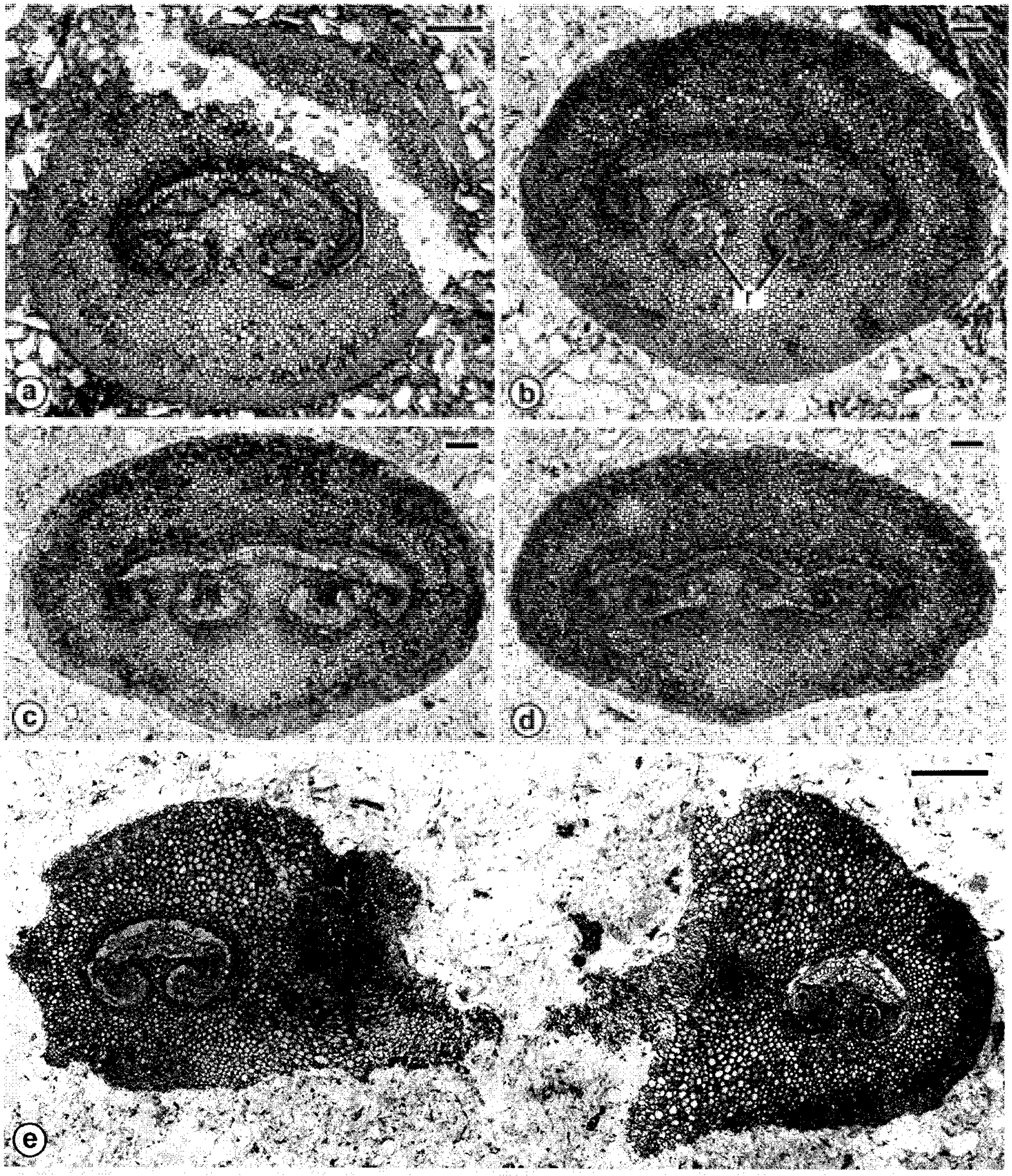
FIGURE 2.3

Transverse sections showing branching of gleicheniaceous fronds. *a*, Base of frond segment showing single trace with adaxial rings of vascular tissue forming at hooks of C-shaped trace. AW 503 C2 top 7. Scale bar = 100 µm. *b*, Frond segment distal to 3a with two free adaxial rings (R) and abaxial arc with adaxial hooks. AW 503 C top 171. Scale bar = 100 µm. *c*, Adaxial rings of vascular tissue open on abaxial side, coincident with indentations of abaxial arc. AW 503 C top 42. Scale bar = 100 µm. *d*, Section distal to 3c showing fusion of three-lobed abaxial arc with tissue of flattened remnants of adaxial rings, and proximal to the level shown in fig. 2h. AW 503 C top 2. Scale bar = 100 µm. *e,* Transverse section through frond at point above bifurcation showing two separate axes both with angular C-shaped trace. AW 503 Bbot 0. Scale bar = 100 µm.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CHAPTER 3

Anatomically preserved staminate inflorescences of *Gynoplatananthus oysterbayensis* gen. et sp. nov. (Platanaceae), and associated pistillate fructifications from the Eocene of Vancouver Island, British Columbia.[1]

INTRODUCTION

Known from Early Cretaceous sediments and abundant in the Tertiary, fossils of platanaceous affinity attest to a past diversity that outstrips that known in extant species (Crane 1989, Pigg and Stockey 1991, Kvaček and Manchester 2004). Modern *Platanus* L. species are distinguished by their pedunculate, globose unisexual inflorescences and alternating, palmately-lobed leaves (Kubitzki 1993). The one exceptional species, *P. kerrii* Gagnepain from Vietnam, has a sessile inflorescence and entire elliptical leaves. One species, *P. orientalis* L., is endemic to Mediterranean Europe, while the remaining eight taxa are found in North and Central America, with the highest diversity found in Mexico (Nixon and Poole 2003). Interspecific hybridization is common, and the common London Plane Tree, *Platanus* x *acerfolia* (Aiton) Willdenow is grown as an ornamental throughout much of the Northern Hemisphere (Kaul 1997).

Traditionally, the family Platanaceae was placed in the polyphyletic "Amentiferae" (Thorne 1973) and until recently was grouped within the Hamamelidales (Cronquist 1981; Schwarzwalder and Dilcher 1991; Tahktajan 1997), based mainly on gross morphological similarities in leaf and inflorescence structure to extant species within the group, specifically those now placed within the family Altingiaceae (Nixon

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[1] A version of this chapter has been published. Mindell, Stockey and Beard 2006. International Journal of Plant Sciences. 167: 591-600.

and Poole 2003). However, recent molecular phylogenetic analyses (Chase et al. 1993, Hoot et al. 1999, Soltis et al. 2003) have placed Platanaceae in the Proteales as sister group to either Proteaceae or Nelumbonaceae. So far, this unexpected and counterintuitive relationship has been supported by embryological studies (Floyd et al. 1999) and leaf cuticular morphology (Carpenter et al. 2005); and both Hoot et al. (1999) and Soltis et al. (2003) have used the fossil record of Platanaceae as evidence for a relationship with Proteaceae.

Crane (1989) and Crabtree (1987) have reviewed the diversity of Cretaceous platanoid leaves, which are a common component of North American floras from that period. The fossil record for the family extends into the Early Cretaceous. Leaf compressions (Hickey and Doyle 1977) and inflorescences (Friis et al. 1988; Crane et al. 1993; Pedersen et al. 1994) of platanaceous affinity are known from the Albian of Eastern North America. Three-dimensionally preserved inflorescences from the Late Cretaceous of Sweden (Friis et al. 1988) and North America (Friis et al. 1988; Magallon-Puebla et al. 1997) have shown characters unknown in extant Platanaceae, specifically, elongate tepals and a regular, invariable arrangement of floral parts. These characters are also known in the Cretaceous to Tertiary genera *Platananthus* Manchester, and *Macginicarpa* Manchester, the Paleogene genus of pistillate fructifications (Manchester 1986); whereas extant *Platanus* have a highly variable merosity and diminutive "petals" (Boothroyd 1930).

The current paper describes permineralized staminate inflorescences and pistillate fructifications from the Eocene Appian Way locality of Vancouver Island, British

Columbia. The platanaceous specimens show floral anatomy and, thus, can be useful in the interpretation of floral evolution within the family. These are the first of many angiosperm fossils that will be described from the locality.

MATERIAL AND METHODS

Three pistillate fructifications and four staminate inflorescences were found in rocks collected from the Appian Way fossil locality south of Campbell River on the east coast of Vancouver Island, British Columbia Canada (49°54' 42" N 125°10'40" W; UTM 10U CA 5531083N 343646E). So far this locality has yielded decapod crustaceans (Schweitzer et al. 2003), polypore fungi (Smith et al. 2004), gleicheniaceous (Mindell et al. 2005) and schizaeaceous (Trivett et al. 2002, 2006) fern remains, taxodiaceous pollen cones (Hernandez-Castillo et al. 2005) and more than forty taxa of dispersed angiosperm fruits and seeds (Little et al. 2001). Plant remains occur in marine calcareous concretions in a sandy-siltstone matrix. Palynological investigations of the locality have dated these shallow marine sediments as late Paleocene to early Eocene (Sweet 1997). Using an assortment of fossil decapods (Schweitzer et al. 2003), molluscs and shark teeth, Haggart et al. (1997) gave these rocks a middle to late Eocene age. Stratigraphic studies are currently being conducted at the site (J. W. Haggart pers. commun. 2004).

The fossiliferous concretions were cut into slabs and peels were made using the cellulose acetate peel technique (Joy et al. 1956). Slides were mounted using xylene-soluble Eukitt (O. Kindler GmbH, Freiberg, Germany) mounting medium. Images were captured using a PowerPhase digital scanning camera (Phase One, A/S, Copenhagen, Denmark) and whole specimens in rock with a Microlumina digital scanning camera

(Leaf Systems, Bedford, Mass.). Images were processed using Adobe Photoshop 7.0. Pollen was coated with 15 nm of gold using a Nanotek sputter coater and examined with a Japan Electronics Optics (JEOL 6301F) scanning electron microscope (SEM) at 5 kV. All specimens are housed in the University of Alberta Palaeobotanical Collections, Edmonton, Alberta (UAPC-ALTA).

SYSTEMATICS

Family: Platanaceae T. Lestib.

Genus: *Gynoplatananthus* gen. nov. Mindell, Stockey et Beard

Generic diagnosis: Inflorescences staminate with rudimentary carpels, globose. Flowers numerous, borne on sclerotic, spheroidal receptacular core; floral vascular trace pentagonal; tepal whorls at least 2. Stamens five, elongate, spatulate; anthers elongate, connective enlarged apically. Gynoecium nonfunctional, rudimentary carpels five, strongly developed. Pollen tricolpate, semitectate columellate.

Type Species: *G. oysterbayensis* Mindell, Stockey et Beard sp. nov. (figs.3.1, 3.2)

Specific diagnosis. Inflorescence staminate, diameter 8-9.5 mm with more than 40 flowers, tightly packed. Flowers up to 4.0 mm long, 1.1 mm wide. Tepals spatulate, innermost whorl fused at base. Stamens in single whorl. Rudimentary carpels ovoid to subtriangular, styles lacking. Pollen (14-)16(-18) μm polar diameter, (12)-13-(14) μm equatorial diameter.

Holotype. AW 263 Fbot, Gtop (UAPC-ALTA)

Paratypes. AW 120 A, Btop, AW 103 Gbot, Htop, AW 289 Etop

Stratigraphic position and age. Oyster Bay Formation, Middle Eocene.

Locality. Appian Way locality, south of Campbell River, British Columbia,
Canada (49E 56' 00" N 125E 11' 15" W; UTM 10U CA 433331)

Etymology. Generic name derived from the Latin *gyno*, refers to the gynoecium present in functionally staminate flowers and *Platananthus*, a fossil genus encompassing five-parted staminate inflorescences with elongate tepals. The specific epithet *oysterbayensis* refers to Oyster Bay, Vancouver Island, the locality from which the specimens were collected.

Description. The four isolated staminate inflorescences occur within the concretions. Inflorescences are commonly abraded with deposits of pyrite found within pollen grains and in between floral organs. No peduncles have been observed, so the type of inflorescence attachment (sessile or pedunculate) is unknown. The compound globose inflorescences measure 9.0-9.5 mm in maximum diameter and have numerous (at least 40) flowers centrally attached to a sclerotic receptacular core up to 3 mm in diameter (figs. 3.1a, b). Vascular tissue diverges as a circular to pentagonal bundle that supplies the base of each flower (figs. 3.1a, c). In transverse section, at the base of every flower, a perianth of at least two whorls of tepals can be seen (figs. 3.1b-e). In longitudinal section, at least one whorl of these tepals is elongate and strap shaped up to 4 mm long, extending above the level of the stamens (figs. 3.1b, g). Stamens occur in a single whorl of five, and most anthers have dehisced. Anthers are elongate and have a very thick connective (fig. 3.2a) that has an apical extension. Pollen both in the anthers and between flowers occurs in large clumps (figs. 3.2a-c). Pollen grains are tricolpate, wider in polar diameter (14-)16(-18) μm than in equatorial diameter (12-)13(-14) μm. Pollen is semitectate, columellate, with a dense reticulate ornamentation and the exine is 1 μm thick (figs. 3.2d-g). There are five ovoid to sub-triangular rudimentary carpels (rarely four) in each flower. These carpels have been followed through completely and lack developed styles, obvious trichomes and ovules and thus are interpreted as rudimentary (figs. 3.1b-e, g).

Associated infructescences

Three platanaceous infructescences derived from pistillate flowers have also been found in Appian Way concretions (figs. 3.3a-g). These infructescences are larger than the staminate heads, measuring up to 20 mm in diameter. Two of these are mature fruiting specimens and the third has flowers and fruits. Flowers and fruits are clustered around a spheroidal, parenchymatous receptacular core 5-6 mm wide (figs. 3.3a, b). Vascular traces to the flower originate as a hollow cylinder that changes distally with proximity to the flower, first to a pentagonal trace and then to five individual ovoid strands (figs. 3.3b, c). Flowers have at least two whorls of tepals (figs. 3.3d, e). Outside these tepals are numerous thin, filiform appendages that can be seen in both transverse (figs. 3.3c, d) and longitudinal section (fig. 3.3e). Tepals are elongate and strap shaped (fig. 3.3b).

In all three specimens there are five carpels per flower. Carpels are ovoid to subtriangular in shape in transverse section (figs. 3.3b, d). Styles are elongate (up to 4 mm) and persistent with no obvious trichomes (figs. 3.3a, f). Fruits are achenes measuring up to 8 mm long from base to tip of the persistent style, and lack dispersal hairs (figs. 3.3a, f, g). Fruits have an exocarp one cell thick and a parenchymatous mesocarp, 4-5 cells thick (fig. 3.3g). The endocarp is represented by a single palisade layer of sclerenchyma (fig. 3.3g).

Large amounts of pollen of the same type and dimensions as that found in the anthers of *G. oysterbaysensis* are found among the styles of the fructifications along with septate fungal hyphae (fig. 3.3h). Given that this pollen is not observed in association with other fossils in the concretion, nor scattered in the surrounding sediment, it is assumed to have landed in the inflorescences prior to burial.

DISCUSSION

Globose flowering heads, free carpels, elongate anthers, apical connective extensions, and tricolpate, semitectate, columellate pollen place these fossils within Platanaceae (Kubitzki 1993, Nixon and Poole 2003). The staminate inflorescences from Appian Way are unlike any extant Platanaceae in their possession of elongate tepals and a consistent arrangement of parts in fives. Extant species typically have a highly reduced perianth and a variable number of stamens (Nixon and Poole 2003; Boothroyd 1930). The small parts in the highly reduced perianth of Platanaceae have over time been interpreted as staminodes (Niedenzu 1910) pistils (Griggs 1909) and bracts (Brouwer 1924). However, work by Boothroyd (1930) showed that these structures are true petals and sepals. The presence of rudimentary carpels has been reported sporadically in some staminate flowers in the inflorescence of *P. occidentalis* L., *P. acerifolia* (Aiton) Willdenow, *P. racemosa* Nutt. and *P. orientalis* L.; however, the consistent appearance of rudimentary carpels in a regular arrangement of five is a feature unknown in extant

Platanus (Boothroyd 1930; Schwarzwalder and Dilcher 1981).

The Appian Way staminate inflorescences show no evidence of peduncle attachment as they are found isolated in the concretions, and serial sectioning reveals no obvious point of entry for vascular tissues. Since we completely peeled through three specimens, it is unlikely that this part was missing in the saw cut. This leaves two possibilities: 1) attachment was eroded off before or during deposition, 2) the inflorescences were sessile. The number and arrangement of flowering heads along the peduncle is an important character (Kvaček et al. 2001) in Platanaceae, though both the stalked and sessile conditions are known within and between species of the subgenus *Platanus*, while in subgenus *Castaneophyllum* globose heads are sessile (Nixon and Poole, 2003).

Diversity of Platanaceae is best understood in the fossil record, where most species occur (Crane 1989; Kvaček et al. 2001; Maslova 2003; Kvaček and Manchester 2004). Leaf compression/impressions are common throughout the Cretaceous and Tertiary and have been assigned numerous generic names (Crane 1989; Crabtree 1987; Manchester et al. 1997; Manchester 1999; Kvaček and Manchester 2004). Inflorescences are usually assigned to morphotaxa (Friis et al. 1988; Pedersen et al. 1994; Magallon-Puebla et al. 1997; Maslova and Krassilov 2002; Maslova 2002), but in exceptional cases, these parts have been hypothesized to represent whole plants (Manchester 1986, Pigg and Stockey 1991).

Inflorescences of Platanaceae are common in the fossil record, but few are preserved well enough to deduce floral structure and anatomical details. Staminate inflorescences assigned to the genus *Platananthus* Manchester are characterizd by an arrangement of parts in fives, well developed tepals and an apically extended connective that unites the stamens into groups (Manchester 1986). The earliest *Platananthus* comes from the Early Cretaceous of North America. Friis et al. (1988) describe *Platananthus potomacensis* Friis, Crane et Pedersen from the Late Albian of Maryland, USA, as having a five-parted androecium and elongate tepals, but unlike the platanoids described in this paper, these specimens lack rudimentary carpels and possess smaller pollen (8.5-12 µm polar diameter). The inflorescence of *Platananthus hueberi* Friis, Crane & Pedersen (1988) from the Late Cretaceous of North Carolina, USA, is much smaller in diameter (1.9-3.6 mm) than those from Appian Way.

Hamatia elkneckensis Pedersen, Friis and Crane (1994) is an anomalous lignitic compression from the latest Albian of Maryland. While the flowers this species are seemingly five parted and have a well developed perianth, the inflorescence is significantly smaller (3-4 mm) than those described from Appian Way. Pollen from *Hamatia* is distinguished from that of all other extant and fossil species, including pollen described here, in being tricolporate, as opposed to the typical tricolpate condition (Pedersen et al. 1994).

Quadriplatanus georgianus Magallon-Puebla, Herendeen & Crane (1997) is represented by both staminate and pistillate inflorescences linked by similarity in structure. Stamens are in groups of four surrounded by two whorls of perianth of elongate tepals (Magallon-Puebla et al.1997). At the center of the staminate flowers, between the stamens, is a central, undifferentiated mass that is interpreted as similar to carpel bases in the pistillate flowers (Magallon-Puebla et al. 1997). This structure seems similar to the Appian Way inflorescences, but our flowers have parts arranged in fives, not fours. This arrangement of four stamens is also known in another late Cretaceous species, *Sarbaya radiata* Krassilov et Shilin (1995). These staminate inflorescences from Kazakhstan lack a well-developed perianth and are estimated to have only 24 flowers per head. A tetramerous arrangement has also been observed in *Archaranthus krassilovii* Maslova et Kodrul (2003), a fossil from the Cretaceous-Paleocene boundary of the Amur region in eastern Russia. While the perianth in this species is more developed than in *Sarbaya*, only 15 flowers are estimated per head. The Appian Way staminate inflorescences have at least 40.

Staminate inflorescences of *Platanus neptuni* (Ettingshausen) Bůžek, Holý & Kvaček, a widespread taxon from the Neogene of Europe (Kvaček and Manchester 2004), have been reported with what have been described as 5-8 short, central protrusions of tissue within a whorl of 6-7 stamens (Friis 1985). Specimens from the Miocene of Denmark (Friis 1985), show that the central protrusions are "probable reduced carpels", a conclusion with which we are inclined to agree. Staminate inflorescences of *Platanus neptuni* unlike those at Appian have a small ellipsoidal receptacular stalk, variable arrangement of parts, and larger pollen (20 µm polar diameter).

Stamens in *Platananthus synandrus* Manchester, a species known from the Eocene Clarno Nut Beds of Oregon, probably dispersed their stamens in groups held together by intertwining trichomes of the connective extension (Manchester 1986). The fossils from Appian Way show no evidence of this type of dispersal, and instead suggest that the anthers dehisced singly within the flower, as evidenced by the presence of withered pollen sacs within the perianth. All species of *Platananthus* have been described as having a well-developed perianth and smaller pollen than *Gynoplatananthus*, but stamens are often found in dispersed groups held together by the intertwining of the apical connective extension (see tables in Manchester 1986; Pigg and Stockey 1991). The Appian Way staminate inflorescences show evidence of dehisced stamens and suggest that pollen dispersed directly from the head. In combination with its prominent tepals, this could be evidence of insect pollination within the family in the Eocene, a condition that has been hypothesized as being present in Cretaceous species (Friis et al. 1988; Crane 1989).

Given these above differences, we have placed the Appian Way staminate platanoids into a new genus and species, *Gynoplatananthus oysterbayensis*, which is similar in most respects to species of *Platananthus* but differs in the presence of rudimentary carpels in every flower. This feature has not been reported in any genus of fossil or extant Platanaceae and cannot be accommodated by any existing diagnoses.

Infructescences

Morphologically, the infructescences from Appian Way are also unlike any extant Platanaceae. While there are similarities in size and fruit structure, no living species has either elongate tepals or a consistent arrangement of parts in fives. As is the case for staminate inflorescences, these features are more common in the fossil record (Manchester 1986; Friis et al. 1988; Pigg and Stockey 1991; Pedersen et al. 1994).

The infructescences from Appian Way contain flowers at different stages of development, so it is possible to deduce floral morphology, fruiting features and anatomy from the some infructescences. Size differences between Appian Way infructescences and other fossil pistillate inflorescences may in some part be due to completeness of preservation or development, as a fruiting specimen is going to be larger than fossils of the flowering stage, but they are otherwise ideal for comparison to both fruiting and flowering pistillate inflorescences.

Platanocarpus Friis, Crane & Pedersen (1988), a Cretaceous genus known from both Europe and North America has pistillate inflorescences that are similar to those of Appian Way, having a pentamerous construction and hairless achenes. *Platanocarpus* is much smaller in size (3-4 mm in diameter) and has a poorly developed style (Friis et al. 1988) compared to the elongate and persistent styles known from the flowers and fruits at Appian Way.

The exceptionally preserved, fusainized pistillate inflorescences of *Quadriplatanus georgianus* from the Late Cretaceous of Georgia, USA, have elongate tepals in numerous whorls (Magallon-Puebla et al. 1997). The inflorescences are significantly smaller (1.1-2.4 mm) than those known from Appian Way. Furthermore, individual flowers of *Q. georgianus* have a tetramerous arrangement of basally-connate parts, as opposed to the pentamerous arrangement in the Appian Way infructescences.

The Paleogene fossils assigned to the genus *Macginicarpa* Manchester (1986) compare most strikingly to the pistillate fructifications from Appian Way. The five-parted arrangement, numerous elongate tepals, mixed fruit maturation, hairless achenes, elongate persistent styles and fruit anatomy of permineralized *Macginicarpa glabra*

Manchester (1986, 1994) from the Middle Eocene Clarno Nut Beds of Oregon, are very similar to the pistillate remains described in this paper. While the two differ nominally in size, the only significant difference is the presence of thin, elongate and planated appendages present at the base of each flower in the Appian Way fossils.

The hairless achenes of the infructescences from Appian Way are noteworthy. The absence of hairs is not due to preservation, as many other fine structures, such as fungal hyphae have been observed. Hairless achenes are present in numerous fossil species of Platanaceae (Lesquereux 1892; Manchester 1986, 1994; Friis et al. 1988). This character merits further consideration, given that modern members of the family have wind-dispersed achenes with a dense basal tuft of trichomes to aid in dispersal (Tiffney 1986). The Appian Way locality has been interpreted as a shallow marine environment based on the presence of decapods (Schweitzer et al. 2003). The presence of entire infructescences suggests the plants were growing in a riparian environment, like most extant members of the family (Nixon and Poole 2003), and that the infructescenses floated downstream to the shallow marine environment into which they were finally deposited. Given the lack of disperal hairs, it is plausible that the fruits of this species, like those of *Macginicarpa* were dispersed by water (Manchester 1986).

Relationship between staminate and pistillate flowers

A relationship between the staminate and pistillate platanoids at Appian Way is supported by similarities in vascular and floral structure and the presence of the same pollen type in both flowers. Both pistillate and staminate flowers are supplied by pentagonal vascular traces which subsequently divide into five major ellipsoidal traces.

Both types of flowers have their parts in fives and elongate, strap-shaped tepals. The carpels when immature in the pistillate flowers are the same shape as the rudimentary carpels in the staminate flowers. The only difference between the two types of flowers is that the pistillate flowers lack stamens, while their gynoecium is fully developed with an elongate style and ovules. The presence of pollen of the same dimensions and shape as that found in the anthers of *Gynoplatananthus oysterbayensis*, proximal to the styles in the pistillate flowers, supports the idea that these two inflorescence types are likely of the same species, though further evidence in the form of attached vegetative parts linking the two is needed to confirm this relationship.

In the fossil record of Platanaceae *Gynoplatananthus oysterbayensis* has the clearest record of rudimentary carpels, as evidenced by the absence of a style or stigmatic surface. While some Cretaceous species are known to have short styles (Friis et al. 1988) or even lack styles (Magallon-Puebla et al. 1997), these species have elongate carpels and specialized apical platforms. They are clearly functional, as evidenced by the presence of ovules and seeds. The rudimentary carpels of *G. oysterbayensis* have been followed through successive peels and lack any evidence of styles, stigmatic surfaces, apical platforms, trichomes or any other structure conducive to pollen trapping.

These rudimentary carpels occur in fives in the center of every staminate flower. An arrangement of five carpels is common in pistillate flowers of extant *Platanus* species (Cronquist 1981), but has been reported only sporadically in staminate inflorescences (Boothroyd 1930, Schwarzwalder and Dilcher 1981). Pistillate flowers of *P. racemosa* have staminodia (Boothroyd 1930, Floyd et al. 1999), while stamens in some pistillate flowers of *P. occidentalis* have been shown to intergrade between between a rudimentary condition to fully functional, the latter being part of truly perfect flowers (Schwarzwalder and Dilcher 1981). While inflorescences of *Platanus* are generally unisexual, the co-occurrence of separate male and female flowers on the same globose head is known to occur in *P. racemosa* (Floyd et al. 1999). This same type of arrangement has been observed in both Eocene and Oligocene fossils (S.R. Manchester pers. comm. 2005).

While the idea of an ancestral bisexual condition in Platanaceae has been put forth (Schwarzwalder and Dilcher 1981), fossil species do not provide clear evidence for this. As discussed above, some fossil staminate inflorescences have flowers with central protrusions of tissue between the stamens. Due to their exceptional preservation, Late Cretaceous *Quadriplatanus georgianus* (Magallon-Puebla et al. 1997) and Miocene *Platanus neptuni* (Friis 1985) show these protrusions, and in both cases these are interpreted as rudimentary carpels. The presence of rudimentary carpels in *Gynoplatananthus oysterbayensis* confirms that this feature is long-lived within the family, arising possibly in the Late Cretaceous (Magallon-Puebla et al. 1997), certainly by the Eocene, and persisting through to the present. The occurrence of these features in fusainized and permineralized material suggests the possibility of a preservation bias, as such cryptic characters would be difficult to deduce from compression/impression fossils. The presence of rudimentary carpels in fossil Platanaceae could be far more prevalent than current estimates. If these rudimentary carpels are the result of a reduction from earlier bisexual flowers, we would expect to see evidence of this in the early fossil record for the family.

The fossil inflorescences and infructescences from Appian Way are of interest in debating the validity of hypothesized relationships between Platanaceae, Nelumbonaceae and Proteaceae within the Proteales as put forth by recent molecular phylogentic studies (Chase et al. 1993, Hoot et al. 1999, Hilu et al. 2003). The initial grouping of Platanaceae with Nelumbonaceae and Proteaceae in what is presently known as the "Proteales clade" was thought to be a product of the small number of species sampled (Chase et al. 1993). The group has very little morphological or anatomical continuity, but molecular phylogenies have consistently grouped these families together (Hoot et al. 1999, Soltis et al. 2003). As a consequence, there has been an effort to find features in common. Hoot et al. (1999) point to the fossil record to show a relationship between Platanaceae and Proteaceae, suggesting that the Cretaceous *Quadraplatanus georgianus* points to an ancestral tetramerous arrangement. Using extant taxa in a combined analysis (morphology, rbcL, 18S and *atp*B sequences), Doyle and Endress (2000), generated the same grouping of families (though morphology alone could not resolve the same grouping) and pointed to orthotropous ovules, nuclear endosperm and large embryos as features uniting Platanaceae and Proteaceae as sister taxa.

Gynoplatananthus oysterbayensis, much like living Platanaceae, has characters that could be employed to both support and refute the Proteales grouping. Hoot et al. (1999) state that the regular merosity of fossil Platanaceae suggests derivation from a four-parted ancestral condition, as is the case with the perianth and androecium of Proteaceae. Regularly (Magallon-Puebla et al. 1997) and irregularly tetramerous

(Manchester 1994) Platanaceae flowers are known from the fossil record. *Gynoplatananthus* falls among the Tertiary constituents of a long line of pentamerous flowers with a deeper stratigraphic range, stretching from the Lower Cretaceous (Friis et al. 1988; Pedersen et al. 1994), through the Paleocene (Pigg and Stockey 1991) to the Eocene (Manchester 1986; Maslova 2003). Extant Proteaceae and Nelumbonaceae both have perfect flowers, while Platanaceae is strictly unisexual. While functionally bisexual flowers have been observed (Schwarzwalder and Dilcher 1981) in extant *Platanus* and *Gynoplatananthus* does have rudimentary carpels, caution should be taken to avoid extrapolating bisexual ancestors in the absence of a clear Cretaceous fossil example.

In conclusion, staminate and pistillate platanaceous inflorescences from Appian Way, linked by similarities in structure and pollen, are among the best preserved fossils of Platanaceae. Three dimensional permineralization has revealed details of anatomy and presence of structures that would not be observable in compressions. The occurrence of rudimentary carpels in staminate flowers of *G. oysterbayensis* suggests this condition, occasionally reported in extant *Platanus*, has long been held within the family and could represent an intermediate step from an ancestral perfect flower to the present unisexual condition. The recovery and recognition of fossil platanoid flowers containing fully developed stamens and carpels would clarify the validity of this proposed transition. A well-developed perianth and anthers dehiscing within the flower suggest possible insect pollination (Crane 1989), and the hairless achenes of the infructescences suggest water dispersal of fruits, as is observed in both living (Tiffney 1986) and fossil (Manchester 1986) fruits of Platanaceae.

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FIGURE 3.1

Gynoplatananthus oysterbayensis Mindell, Stockey et Beard gen. et sp. nov. Holotype. *a*, Transverse section of staminate inflorescence; sclerotic receptacular core with pentagonal floral traces. AW 263 Fbot 50. Scale bar = 1 mm. *b*, Tangential section through inflorescence showing individual flowers. AW 263 Fbot 6. Scale bar = 1 mm. *c*, Transverse section of inflorescence showing pentagonal floral vascular traces. Note carpels in longitudinal section lacking styles. AW 263 Fbot 60. Scale bar = 1 mm. *d*, Oblique section through cluster of flowers showing regular arrangement of five subtriangular carpels and two-whorled perianth. AW 120 Btop 44. Scale bar = 1 mm. *e*, Transverse section through base of flower showing five carpels, inner fused whorl of tepals and outer free whorl of tepals (arrows). AW 120 Btop 42. Scale bar = 100 μm. *f*, Transverse section through distal region of flower showing five dehisced stamens and five prominent thick tepals (1-5). AW 120 Btop 147. Scale bar = 100 μm. *g*, Longitudinal section through single flower showing carpels (c) at base and tepals (t) surrounding anthers. AW 120 Btop 1. Scale bar = 100 μm.

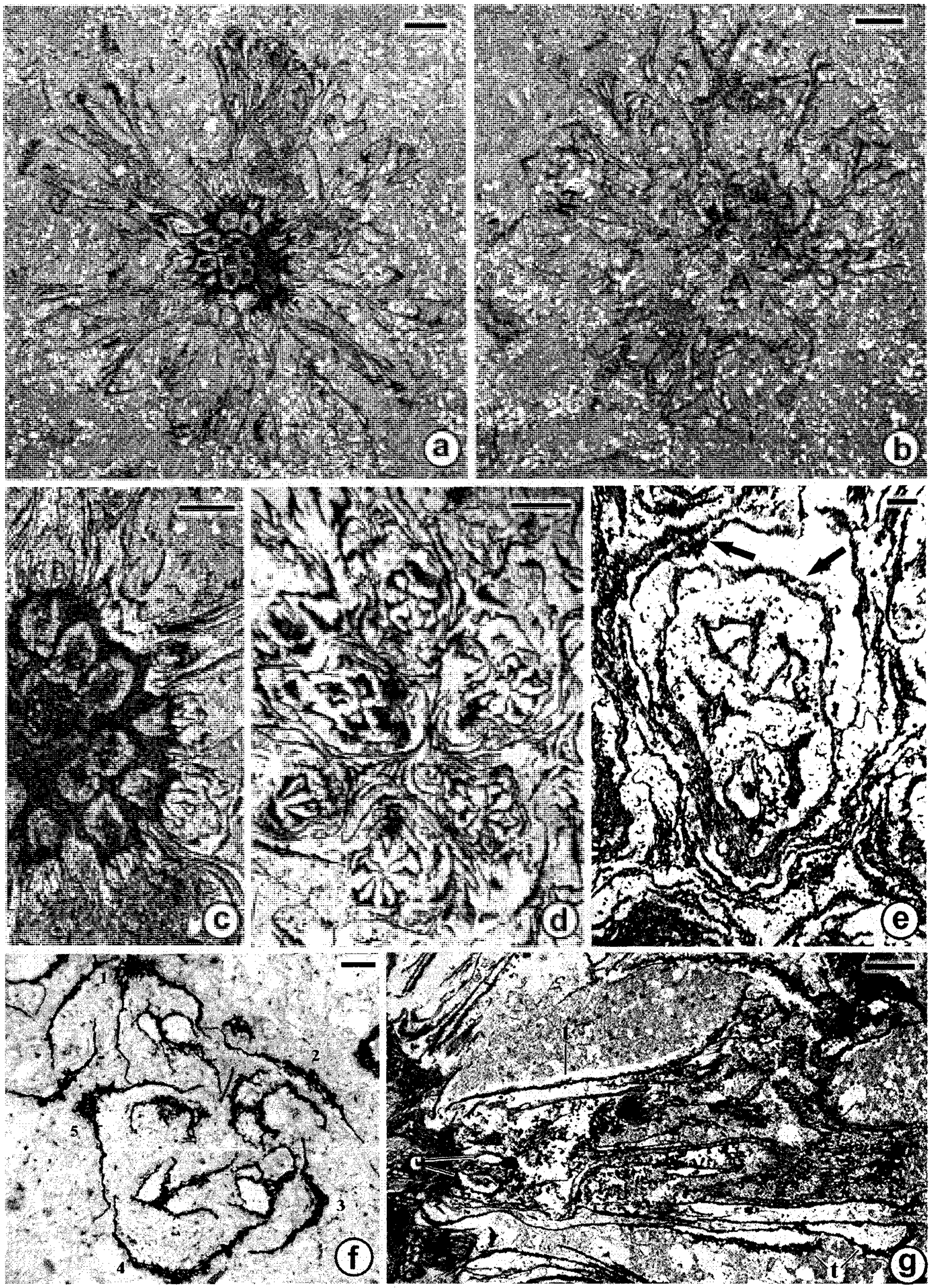
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FIGURE 3.2

Gynoplatananthus oysterbayensis Mindell, Stockey et Beard gen. et sp. nov. *a*, Transverse section through apical portion of stamen, showing thick connective, anthers and in situ pollen. AW 120 Btop 59. Scale bar = 100 µm. *b*, Single pollen sac with in situ pollen. AW 120 Btop 59. Scale bar = 100 µm. *c,* In situ tricolpate pollen grains. AW 120 Btop 1. Scale bar = 10 µm. *d*, SEM showing polar view of reticulate, tricolpate pollen. AW 120 Btop 4. Scale bar = 1 µm. *e*, SEM showing near equatorial view of reticulate, tricolpate pollen. AW 120 Btop 4. Scale bar = 1 µm. *f*, SEM showing near polar view of pollen. AW 120 Btop 4. Scale bar = 1 µm. *g*, SEM micrograph of tectate-columellate pollen wall. AW 120 Btop 4. Scale bar = 1 µm.

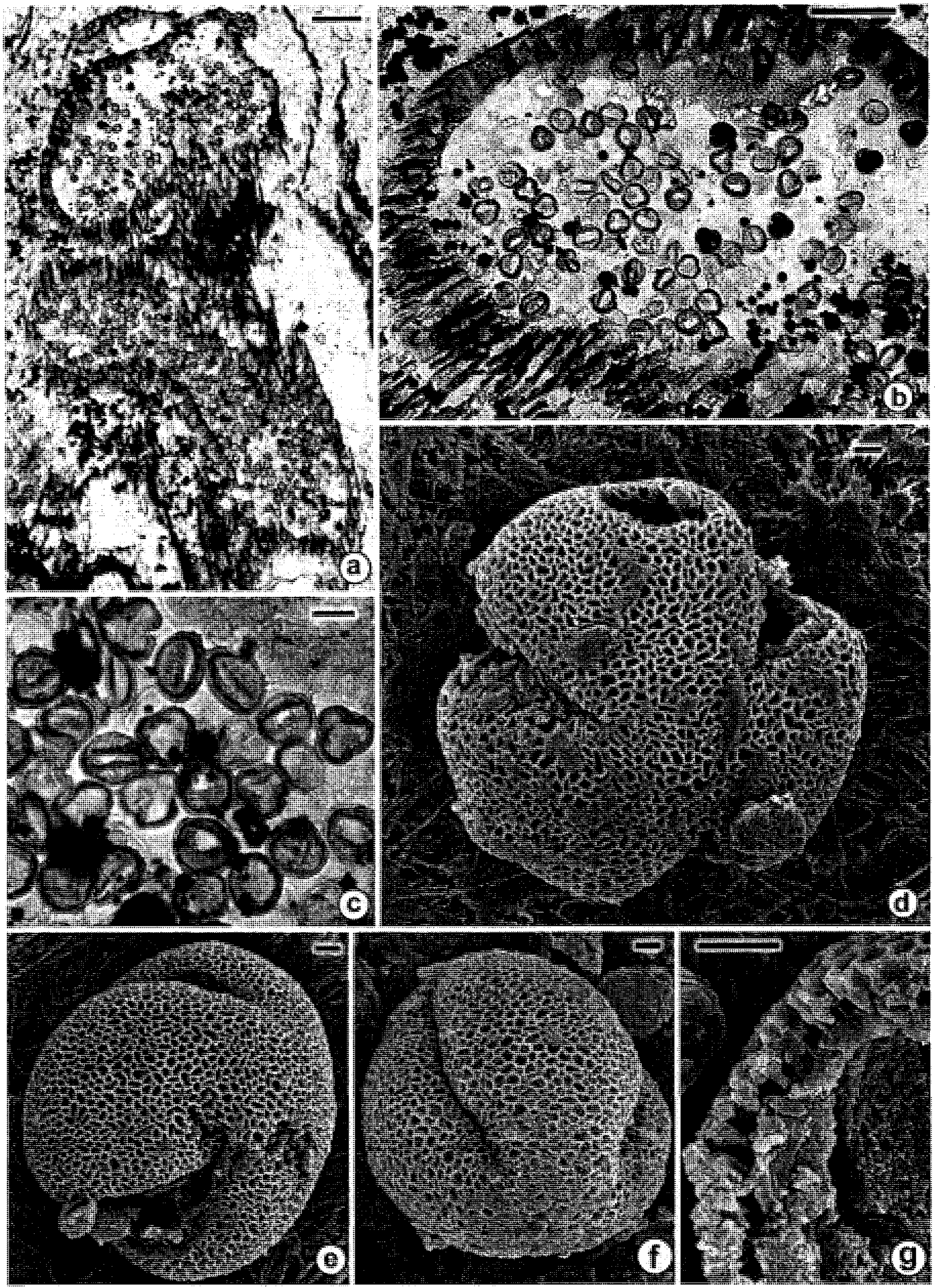
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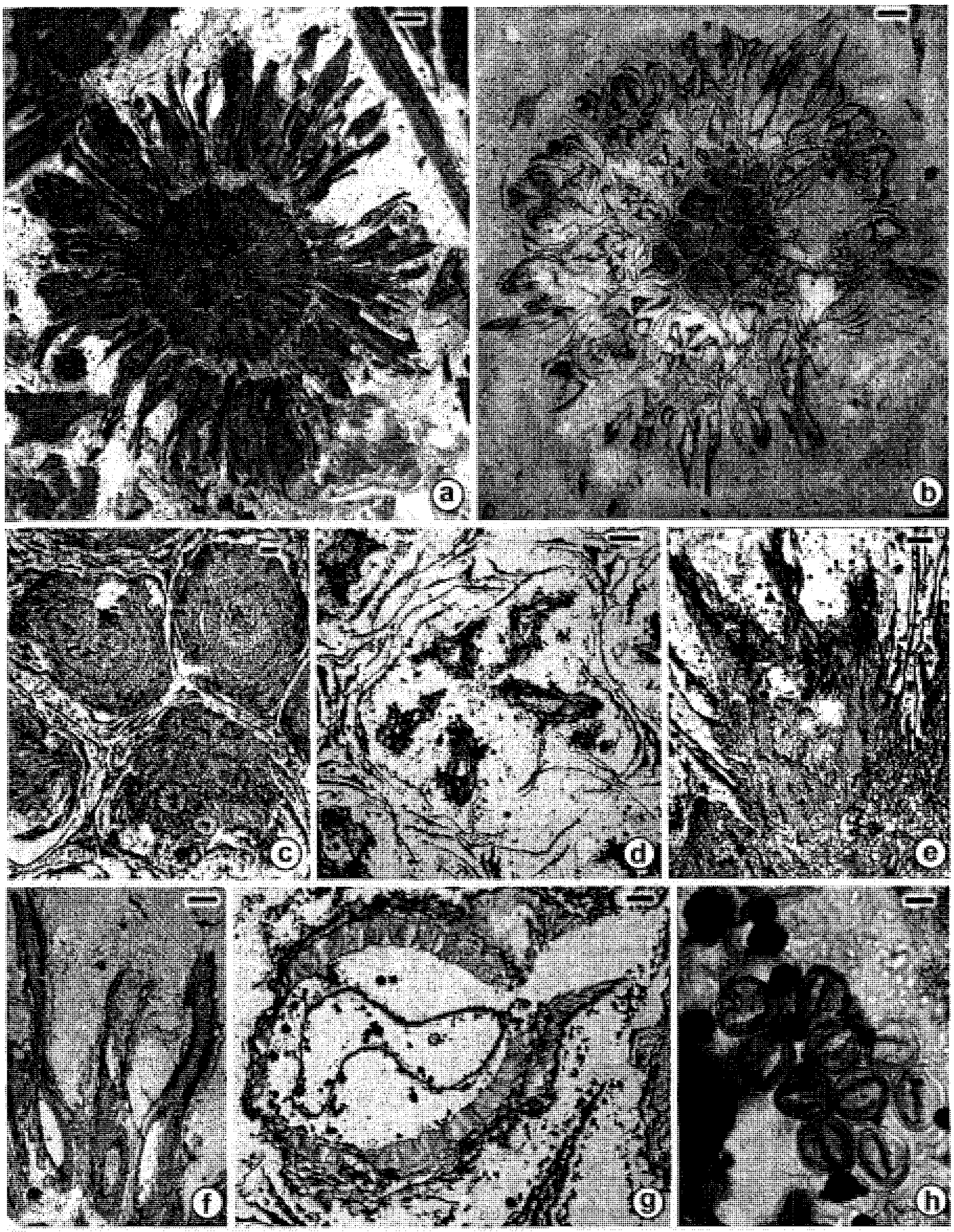
FIGURE 3.3

Associated pistillate infructescences. *a*, Permineralized fructification exposed on surface of rock. AW 699 B. Scale bar = 1 mm. *b*, Transverse section through pistillate fructification showing five-carpelled flowers. AW 142 Ltop 76. Scale bar = 1 mm. *c*, Transverse section through base of flowers showing parenchymatous receptacle, pentagonal floral trace (top) and circular carpel traces (bottom right). AW 142 Ltop 76. Scale bar = 100 µm. *d*, Transverse section through flower showing five carpels and two whorls of thin tepals. AW 142 Ltop 83. Scale bar = 100 µm. *e*, Longitudinal section through base of flower showing numerous whorls of basal appendages. AW 142 Ltop 18. Scale bar = 100 µm. *f*, Longitudinal section of mature achenes showing persistent styles (s). AW 699 B 2. Scale bar = 1 mm. *g*, Transverse section through base of mature fruit with palisade-like endocarp surrounded by remnant mesocarp. Note seed remnant inside. AW 142 Ltop 8. Scale bar = 1 mm. *h*, Tricolpate pollen found between styles of pistillate flowers. AW 142 Ltop 5. Scale bar = 10 µm.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CHAPTER 4

Permineralized *Fagus* nuts from the Eocene of Vancouver Island, Canada.

INTRODUCTION

Nuts of the beech family, Fagaceae, are among the most widespread fruits in both modern and historical landscapes (Crepet 1989; Manos and Stanford 2001). The dispersal of these nuts is typically aided by rodents and birds (Vander Wall 2001), and vast tracts of modern forests are dominated by oaks (*Quercus* L.) and beeches (*Fagus* L.) (Peters 1997; Manos and Stanford 2001).

The family is presently segregated into two subfamilies that are distinguished by the presence (Castaneoideae) and absence (Fagoideae) of hypogeous fruits (Manos et al. 2001). While both subfamilies have considerable variation in cupule morphology and nut arrangement (Forman 1966; Nixon and Crepet 1989), fruits in subfamily Fagoideae are always sharply triangular in transverse section, while those in subfamily Castaneoideae are circular to sub-triangular (Kubitzki 1993). While subfamily Castaneoideae was initially thought to contain the basal genera within the family (Nixon 1984; 1989; Crepet and Nixon 1989), molecular data suggests that the genera of Fagoideae are a paraphyletic grade basal to all other Fagaceae (Manos et al. 2001; Li et al. 2004).

Generic delimitation within subfamily Fagoideae is unsettled (See Nixon and Crepet 1989; Manos et al. 2001). The genus *Fagus* stands alone in having two fruits enclosed in a four-valved cupule, while the remaining taxa have been treated as a single genus, *Trigonobalanus* Forman (Forman 1964; Lozano et al. 1979; Kubitzki 1993) and alternately as three monotypic genera: *Trigonobalanus, Formanodendron* Nixon & Crepet (1989) and *Colombobalanus* Nixon & Crepet (1989) (Li et al. 2004). Given the small number of species within subfamily Fagoideae, fossils, specifically those which provide data on reproductive characters, serve to extend the known morphological diversity within the group and provide valuable data for testing hypotheses about the temporal, geographic and evolutionary origins of these genera (Manos and Stanford 2001; Denk and Meller 2001; Denk at al. 2002; Denk 2003).

The Appian Way locality on Vancouver Island, British Columbia provides a great window for assessing diversity within Fagaceae during the Eocene due to the quality of preservation. The family is represented by three permineralized fruit types ideal for studying in three dimensions (Mindell et al. 2005; Mindell et al. 2007a). This chapter describes a new species of anatomically-preserved trigonous nuts from the locality.

MATERIAL AND METHODS

The 60 specimens in this study were collected from the Appian Way locality (49°54′42″ N, 125°10′40″ W; UTM 10U CA 5531083N, 343646E) on the eastern shore of Vancouver Island, British Columbia, at the northern margin of the Tertiary Georgia Basin (Mustard and Rouse 1994). Fossil plant material is permineralized and occurs with echinoderms, gastropods, bivalves, fish bones and shark teeth in large calcareous nodules. The nodules are embedded in a silty sandstone matrix that, on the basis of the faunal assemblage and lithology, is interpreted to represent a shallow marine environment (Haggart et al. 1997). Characteristic molluscs, decapods (Schweitzer et al. 2003), and gastropods indicate a Early-to-Middle Eocene age (Haggart et al. 1997, Cockburn and Haggart 2007). Pollen from the site has yielded a less certain age for the locality, with both late Paleocene and early Eocene signatures present (Sweet 2005). The formal stratigraphy of the Appian Way fossil beds is presently under investigation (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). Fruits of Juglandaceae (Elliott et al. 2006) and Fagaceae (Mindell et al. 2007a), inflorescences of Platanaceae (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, poroid hymenophores (Smith et al. 2004) and a pleosporalean ascoma (Mindell et al. 2007b) have been described from the locality.

Nodules were cut into serial slabs and peeled using the cellulose acetate peel technique (Joy et al. 1956). Microscope slides were prepared using Eukitt (O. Kindler GmbH, Freiberg, Germany) mounting medium. Images were captured on a PowerPhase digital scanning camera (Phase One, A/S, Frederiksberg, Denmark) and processed with Photoshop 9.0 (Adobe, San Jose, California, USA). All specimens and microscope slides are housed in the University of Alberta Paleobotanical Collections, Edmonton, Alberta, Canada (UAPC-ALTA).

SYSTEMATICS

Family: Fagaceae Dumortier

Genus: Fagus L.

Species: *Fagus schofieldii* Mindell, Stockey et Beard. (Figs 4.1-4.3)

Specific diagnosis: Nut trigonous; lacking wings. Fruit surface glabrous, tomentose near apex. Outer nut wall sclerenchymatous, up to 15 cells thick; inner wall parenchymatous. Mesocarp vascular bundles three, median between corners. Endocarp tomentose. Styles three, ovary tricarpellate, locules divided by thin septum. Placentation axile, ovules 2 per locule, apical. Seed single, filling ovarian cavity at maturity, three lobed.

Holotype. P13417 Bbot, Ctop (UAPC-ALTA).

Paratypes. AW 104 Cbot, Dtop, AW 116 Ibot, AW 116 D2top, AW 601 A, AW 650 Btop.

Stratigraphic position and age. Oyster Bay Formation, Middle Eocene.

Locality. Appian Way locality, south of Campbell River, British Columbia, Canada (49^0 54' 42"N $125^0$10' 40"W; UTM 10U CA 5531083N, 343646E)

Etymology. The specific epithet is in recognition of Dr. Wilf Schofield, Professor Emeritus in the Department of Botany, University of British Columbia, for his contributions to botany in British Columbia.

Description. Of the 60 specimens, two are known from surface features, while the remaining specimens were studied anatomically. Corresponding cupules are absent, but it is assumed that nuts were deposited in their dispersed state. Nuts are sharply three-angled (Figs. 4.1a-d), up to 11 mm in diameter, tapering from base to tip, with typically planar (Figs. 4.1a, d) but occasionally convex walls (Figs. 4.1b, c) between the angles. In longitudinal view, fruits are obtriangular (Figs. 4.2a-c), up to 12 mm long, giving a slightly elongate tetrahedral shape to the nut. The surface of the nut is glabrous (Figs. 4.1a-d, 4.2a-f), with the exception of the tomentose apex (Fig. 4.3d). Except at the corners, ridges and furrows are absent along the nut surface (Figs. 4.1a-d, 4.2f). Fruit wall is differentiated into three distinct zones (Fig. 4.2f). The epidermis of the nut has numerous small idioblasts scattered among sclereids (Figs. 4.2e, f). Many specimens show an intact, unabraded epidermis with neither trichomes nor remnants of them (Fig. 4.2f). The outer sclerenchymatous layer is continuous around the margin of the nut and measures 5-8 cells in thickness (Figs. 4.2d-f). Immediately inside this layer is a relatively thick band of parenchymatous tissue up to 32 cells thick (Figs. 4.1a, 4.2f). It is continuous around the nut except in the area of the angles, where it grades into sclerenchyma (Fig. 4.2d). The endocarp layer of the nut wall is thin and appears as a dark band, 2-4 cells thick and made up of crushed, thin-walled parenchyma (Figs. 4.1a-d, 4.2f). Multicellular, uniseriate trichomes are borne on the inner surface of the endocarp and line the locule (Figs. 4.1b-d, 4.2a, 4.3a-c). Major vascular tissues are present in a regular arrangement of discreet bundles median between the angles (Figs. 4.1a, 4.2f). Amorphous dark bands and areas of decay are common in the nuts and tend to be concentrated in the middle tissue zone (Figs. 4.1a-d, 4.2f). The corners of the nut have a distinct, sclerified zone that shows a radial fracture (Figs. 4.1a, 4.2d), that may represent a dehiscence line because it is present only at the corners and extends from the locule through all tissue layers.

Fruits have three locules divided by thin septa radiating from a vascularized placental column at the apex of the locules (Figs. 4.1b, 4.1d, 4.3b) that is absent in the lower two-thirds of the nut (Fig. 4.1a). Trichomes from the inner endocarp extend throughout the locules in all specimens (Figs. 4.3a, b) but are confined to a narrow, marginal band in mature nuts (Figs. 4.1a, 4.2f). Six ovules are present, two per locule, with axile placentation near the apex of the fruit (Figs. 4.3a, b). Three styles have been observed in transverse section at the very apex of the nut in one specimen (Fig. 4.3d). No staminodia or pollen are observed in this area, but thin, membraneous structures present near the fruit apex could represent the remains of tepals (Fig. 4.3d). Cuticular seed coat remnants fill the common area of all three locules at maturity (Figs. 4.1a, 4.2f). In specimens with preserved seed coat, the seed occupies the entire cavity.

DISCUSSION

Nuts formed from a tricarpellate ovary with axile placentation, six apical ovules, two in each locule, only one of which matures into a seed, are diagnostic characters for the family Fagaceae (Kubitzki 1993). Traditionally, this family has included the genus *Nothofagus* Blume, however, multiple lines of evidence have supported placement of this genus in its own family, Nothofagaceae (Nixon 1989; Manos and Steele 1997). Nuts of *Nothofagus* share all these fagaceous characters (Table 4.1) but also tend to show variation in shape and locule number due to the arrangement of fruits in the cupule (Langdon 1947). Typically, each cupule contains three nuts in a row. Lateral nuts are trigonal and trilocular, while the central nut is lenticular and bilocular (Langdon 1947). Fruits of *Nothofagus*, regardless of their shape, lack trichomes lining the locules (Soepadmo 1968; Nixon and Crepet 1989). Furthermore, in the few species studied anatomically, sclerenchyma is concentrated in a band that runs through the middle of the fruit wall (Soepadmo 1968). Thus, the genus can be distinguished from the Appian Way fossils, which are strictly trigonal, have a tomentose endocarp and a fruit wall hardened by an outer band of sclerenchyma.

Comparison to Extant Fagaceae

Extant genera in Fagaceae *sensu stricto* are divided into two to three subfamilies based on cupule, nut and inflorescence characters (Nixon and Crepet 1989; Kubitzki 1993; Manos et al. 2001; Oh and Manos 2008). Genera of subfamily Castaneoideae

(*Castanea* Mill., *Lithocarpus* Blume, *Chrysolepis* Hjelmqvist, *Castanopsis* Spach.) are united by hypogeous fruits but otherwise show great diversity in cupule and nut morphology and anatomy (Manos et al. 2001). These genera have more complex fruit wall anatomy (Soepadmo 1968; Borghardt and Pigg 1999) than that observed in the Appian Way fossil. Typically, the wall in castaneoid fruits is differentiated into 5 distinct layers and vascular bundles are numerous and regular throughout the mesocarp (Soepadmo 1968). In the Appian Way nut, the wall is differentiated into only three layers at maturity and bundles are few, occurring only at midway points on the lateral walls. Furthermore, these genera typically have globose nuts, with the exception of subtriangular fruits known in some species of *Castanea* and *Chrysolepis* (Table 4.1; Hjelmqvist 1948; Kubitzki 1993). In *Castanea*, fruits are typically 6-9 loculed (Nixon 1997), while in the fossils from Appian Way there are clearly only three locules. *Chrysolepis* can be round to triangular in cross section (Hjelmqvist 1948), but can be easily distinguished from the fossil fruits in having six differentiated layers in the fruit wall (Soepadmo 1968), as opposed to three in the fossils (Table 1). It should also be noted that the Appian Way fruits are strictly trigonal, showing none of the variation that is observed in *Chrysolepis* species.

The genus *Quercus* has been placed in subfamily Quercoideae (Forman 1964, 1966) or subfamily Fagoideae (Nixon and Crepet 1989). Oh and Manos (2008) have shown that the genus is nested within a clade containing all the genera of subfamily Castaneoideae. Regardless of their placement, they can be distinguished from the trigonal Appian Way nuts in having globose, acorn-type fruits and a more complex nut wall anatomy (Soepadmo 1968).

The genera of subfamily Fagoideae are most similar to the Appian Way specimens. The group is presently interpreted as a paraphyletic grade that encompasses a suite of ancestral characters (Nixon and Crepet 1989; Manos et al. 2001). The taxonomic affinities and delimitation of the genus *Trigonobalanus* has been the cause of much debate since its initial description (Forman 1964, 1966; Lozano et al. 1979; Nixon and Crepet 1989; Corner 1990; Li et al. 2004). Frequently treated as three disjunct species of the same genus (Kubitzki 1993; Soepadmo 1972; Soepadmo et al. 2000), the group was formally divided into three monotypic genera by Nixon and Crepet (1989).

Trigonobalanus verticillata Forman was described from trees growing in Southeast Asia that were originally placed in the genus *Quercus* (Forman 1964). Like the fossil fruits, the nuts of this species are trigonal in cross section, have three styles and a tomentose locule lining (Table 1) (Forman 1964). However, they differ in having abundant trichomes on the outer surface, possessing staminodia, frequently bearing wings, and having a fruit wall differentiated into two layers (Forman 1964; Soepadmo 1968). In the fossil nuts, staminodia are absent. This could be attributed to abrasion, however delicate styles, trichomes and probable perianth parts are preserved in the area where staminodia would be present. Also, wings are absent, and the fruit wall is differentiated into three layers in the Appian Way fruits. Furthermore, the external surface of the fossil nuts lack surface trichomes on all portions with the exception of the very apex.

Formanodendron doichangensis (Forman) Nixon and Crepet was initially treated as a species of *Trigonobalanus* that Nixon and Crepet (1989) placed in its own genus based on leaf arrangement and pollen morphology. Like *T. verticillata*, the fruits in this species are trigonous nuts with persistent staminodia (Forman 1964). They occur in a cupule that holds between 1 and 15 small (< 5 mm long) nuts of varying shape depending on arrangement in the cupule (Forman 1964; Table 1). Persistent staminodia occur at the apices of the nuts of *Formanodendron* (Nixon and Crepet 1989). The Appian Way nuts are substantially larger than those of *Formanodendron*, but more importantly, they show little variation in shape in both the longitudinal and transverse planes and lack staminodia. Furthermore, nut walls in *Formanodendron* are differentiated into two layers: an outer stony layer and inner parenchymatous layer (Min Deng, Kunming Institute of Botany, pers. comm. 2006). In the fossil fruits there are three layers with a thick inner endocarp layer in addition to those observed in *Formanodendron*.

Colombobalanus excelsa (Lozano, Hdz-C & Henao) Nixon & Crepet was initially described from three populations in the cloud forests of Colombia (Lozano et al. 1979). Like the other two trigonobalanoid species, *C. excelsa* shows great variability in fruit and cupule morphology. This species was placed in its own genus by Nixon and Crepet (1989) based on pollen shape and bud morphology. While the anatomy of these fruits has not been studied, they can still be distinguished from the Appian Way fossils in having mature nuts with persistent staminodia (Lozano et al. 1979; Table 1). As in *Formanodendron* and *Trigonobalanus*, nuts are frequently winged and have a tomentose surface (Lozano et al. 1979), as opposed to the glabrous and clearly wingless fruits from Appian Way.

The genus *Fagus* L. is distinguished from other genera in subfamily Fagoideae in having four-valved, two-fruited cupules (Table 1). The 8-10 species within the genus are predominantly east Asian (Liao 1971; Chengjiu et al. 2001), with the exception of *Fagus* *sylvatica* L., endemic to western Eurasia and *Fagus grandifolia* Ehrh., a dominant component of the deciduous forests of eastern North America (Peters 1997). The genus possesses a suite of characters identical to those found in the fossil fruits: three layered fruit wall, three styles, membranous perianth, wingless trigonal nuts, tomentose locule lining, six ovules, axile placentation and sclerified dehiscence zones at the angles (Langdon 1939; Nixon 1997; Chengjui et al. 2001). Some species (e.g., *Fagus lucida* Okamoto) lack wings, while the extent and density of trichomes on the nut surface varies from species to species (Chengjui et al. 2001, Denk and Meller 2001). Unlike trigonobalanoid genera, staminodia are absent in mature nuts of *Fagus*, as in the Appian Way fossils.

Comparison to fossil Fagaceae

Fagaceous fossils appear first in the Late Cretaceous of Japan and North America (Herendeen et al. 1995; Sims et al. 1998; Takahashi et al. 1999). These earliest fossils are trigonous and cupulate. An unnamed fossil fruit common in the Coniacian (Upper Cretaceous) of Japan is triangular in transverse section and, like the Appian Way fossils, is trilocular, with possibly six ovules found near the apex of the ovary in axile placentation (Takahashi et al. 1999). The major vascular bundles in the Japanese fossils are found along the ridges (Takahashi et al. 1999), whereas in the Appian fruits, they are found midway between the ridges on the lateral walls. The absence of further anatomical data for the Japanese fossils makes further comparisons difficult.

Two fagaceous fruits from the Santonian (Late Cretaceous) of Georgia, U.S.A. also have some general similarities to the Appian Way nuts. *Antiquacupula* Sims, Herendeen & Crane (1998) has three styles, three locules and six ovules in the same arrangement as in the Appian Way specimens. The fruit wall in *Antiquacupula*, however, is prominently ribbed and covered in trichomes (Sims et al. 1998), while the Appian Way fruits have, glabrous walls. Furthermore, the perianth in *Antiquacupula* is composed of very prominent tepals (Sims et al. 1998), while the Eocene nuts described in this paper suggest a very diminutive perianth in close proximity to the styles.

Protofagacea Herendeen, Crane & Drinnan (1995) comes from the same Santonian locality as *Antiquacupula* and is used to describe staminate flowers. Cupules and fruits associated with *Protofagacea* flowers are linked by the presence of pollen identical to that found in the staminate flowers (Herendeen et al. 1995). These fruits vary in shape from triangular (three styles) to lenticular (two styles) and the associated cupules suggest that this variation is a result of their arrangement in the cupule, much like living *Nothofagus* (Langdon 1947; Herendeen et al. 1995). In the Appian Way fruits, there is little variation in fruit shape among the 60 specimens studied.

Trigonal fossil fruits of Fagaceae *sensu stricto* emerge in the Paleogene (Crepet 1989). The Paleocene/Eocene boundary of southeastern North America has yielded numerous informative fossil genera of Fagaceae (Crepet 1989). These compression fossils from Tennessee document the first megafossil evidence for subfamilies Fagoideae and Castaneoideae (Crepet and Nixon 1989b). Trigonal nuts are known from the Tennessee locality and are assigned to the genus *Trigonobalanoidea* Crepet & Nixon (1989a). These fruits, like the Appian Way specimens, have three styles and a diminutive perianth, however they differ by having very prominent, membraneous wings (Crepet and Nixon 1989a).

Crepet and Nixon (1989b) describe compression/impressions of dispersed, winged fruits of *Parvobalanus* Crepet & Nixon and *Amplobalanus* Crepet & Nixon from the Oligocene of Texas. While both are trigonal and have three styles, as in the unwinged Appian Way fruits, lack of anatomical detail prevents further comparison.

Fruits of *Fagopsis* Manchester & Crane are known from the Oligocene of Colorado. These specimens, if truly fagaceous, represent an extreme variation in morphology, as they are enclosed in a globose arrangement of laminar cupules or "fruit wedges". Each cupule bears three microscopic fruits (Manchester and Crane 1983). While nothing is known about the anatomy of these fruits, they can be easily distinguished from the trigonous Appian fruits by their ovoid shape. Interestingly, leaves attached to the infructescence were previously interpreted as belonging to *Fagus*, thus providing a caution to the assignment of fossil leaves to living genera in extant Fagaceae (Manchester and Crane 1983).

Fruits of *Pseudofagus* Smiley & Huggins (1981) are found in the Miocene of Idaho. These fruits, attached to cupules, in turn attached to leafy shoots, are unique among Fagaceae in having only solitary trigonous fruits in each cupule (Smiley and Huggins 1981). They are trigonal in transverse section and have prominent "keels" at the angles. They differ from the fossil fruits from Appian Way in having a tomentose fruit wall and a complex, "star-shaped" pattern to the epidermis (Smiley and Huggins 1981). Like fruits of *Fagopsis*, these anomalous nuts are found in attachment to leaves that would otherwise be classified as *Fagus.*

In the Miocene of Europe, trigonal fruits of *Trigonobalanopsis exacantha* Kvaček & Walther (1989) occur solitarily or in pairs in 3-4 valved cupules. The nuts themselves differ from the Appian Way fossils in having radially elongate sclereids in the pericarp and a densely tomentose surface. Both of these characters are absent in the Appian Way fruits.

The genus *Fagus* has an extensive fossil record based primarily on leaves and cupulate nuts (Tanai 1974; Kvaček and Walther 1989; Denk and Meller 2001; Denk et al. 2002; Denk 2004; Manchester and Dilhoff 2004). The earliest fruits of the genus were recently described from the Middle Eocene of British Columbia, Canada and Washington State, U.S.A. *Fagus langevinii* Manchester & Dilhoff has foliage with attached fruits, cupules, and in situ pollen preserved in compressions/impressions (Manchester and Dillhoff 2004). The nuts of this species are winged, but are otherwise similar in construction to the relatively contemporaneous nuts from Appian Way. *Fagus pacifica* Chaney (1927) from the Oligocene of Oregon also has distinct wings along its lateral edges and likewise can be distinguished from the wingless trigonal fruits described in this paper.

The Appian Way fossil fruits have a suite of characters that can only be accommodated by one genus of Fagaceae. The absence of wings, fruit wall anatomy, glabrous surface, probable membraneous perianth, three styles and consistent shape are all traits that are encompassed by the genus *Fagus* (Langdon 1939; Shen 1992; Kubitzki 1993; Denk and Meller 2001; Denk 2003). However, in the absence of attached or associated staminate flowers and vegetative organs, placement of this fossil in any extant species is impossible. The fossil record for the genus is predominantly based on compression/impression and mold/cast material that offers little in the way of internal anatomy for comparison. Thus, I have designated it as a new species of isolated nuts, *Fagus schofieldii* Mindell, Stockey & Beard sp. nov. As the study of the Appian Way fossil locality progresses, attached and associated cupules and staminate flowers could further our knowledge of the affinities of these specimens.

Fagus pollen is common in the Eocene sediments of British Columbia (Manchester and Dilhoff 2004; Moss et al. 2005). Not only is it absent from the apices of *Fagus schofieldii* nuts, but it is absent entirely from the Appian Way fossil locality (Sweet 2005). Given the prevalence of these nuts in the concretions, it is assumed that the plants that bore them made up a significant component of the vegetation in the depositional system from which they are derived. The absence of *Fagus* pollen suggests that the nuts may have traveled a long distance between where they fell to the ground and where they finally came to rest in a shallow marine environment. In situ pollen (Mindell et al. 2006a) and spores (Trivett et al. 2006) have been reported from the concretions, so a preservational bias seems unlikely.

Of the 11 extant species of *Fagus,* seven are winged while the remaining four are wingless, though the distribution of this character shows little phylogenetic pattern (Denk and Meller 2001; Denk 2003). Thus, the fossil record provides a neccessary line of evidence for interpreting the morphology of ancestral *Fagus*. Manchester and Dillhoff (2004) suggested the winged nuts of *F. langevinii* from the Eocene provide strong support for the hypothesis of ancestral wind dispersal of the fruits in the genus. However, wingless *Fagus schofieldii* nuts are contemporaneous with this earliest fossil occurrence and provide evidence of an equally probable ancestral state. At the least, they suggest that, as in extant *Fagus*, both animal and wind vectors may have been responsible for dispersal of the genus by the Middle Eocene.

Manos and Stanford (2001) undertook an extensive phylogeographic study of living *Fagus* using molecular techniques. Their research suggested an Asian origin for the genus, in keeping with its' present center of diversity. Nevertheless, the earliest fossils clearly assignable to *Fagus* both occur in British Columbia (this paper; Manchester and Dillhoff 2004). These findings support the hypothesis of Denk et al. (2005), who suggest an Eocene, North Pacific origin of the genus and subsequent dispersal to Asia. If the genus did have its origins in Asia, this means that dispersal to North America occurred by the Middle Eocene. Alternately, the fossil data could support a North American origin for *Fagus*, as previously suggested by Manchester and Dillhoff (2004).

The presence of extant *Fagus* had long been suspected in the Eocene of North America. However, *Fagus*-type leaves have been found in attachment on two occasions to fruits of other fossil genera (Manchester and Crane 1981; Smiley and Huggins 1983). Prior to the reports of Manchester and Dilhoff (2004), the earliest known certain occurrence of *Fagus* was from the Oligocene of Oregon (Meyer and Manchester, 1997). Two-fruited cupules found in attachment to leaves provide strong evidence for a Middle Eocene earliest occurrence of the genus (Manchester and Dilhoff 2004). *Fagus* from Appian Way suggests that the genus was a common component at least in two distinct Eocene environments. The specimens from the MacAbee locality in south central British Columbia were deposited in an inland low energy fluvial environment, while, the Appian Way nuts were deposited in a shallow marine environment, suggesting a proximally coastal source.

The exact age of the Appian Way locality is unknown. While the only formal description (Haggart et al. 1997) describes it as Middle Eocene, Late Paleocene and Early Eocene ages have been suggested by the palynological assemblage (Sweet 2005) and the gastropods (Schweitzer et al. 2003) from the locality. As formal stratigraphy of the area is worked out, *F. schofieldii* could turn out to be an Early Eocene and *ergo* first occurrence of the genus *Fagus.*

Fagus schofieldii shows that wingless nuts, likely dispersed by animals, were present in the Eocene. It also contributes to a growing picture of the vegetation that populated the depositional system responsible for the fossils at the Appian Way locality. Along with *Cascadiacarpa* (Mindell et al. 2007a), the fossil *Fagus* nuts are further evidence of the predominance of Fagaceae at the locality and in the Eocene of North America. The presence of *Quercus* and purported *Castanopsis* at the Eocene Clarno Nut Beds of Oregon (Manchester 1994) and *Fagus* from the Okanagan Highlands region of Washington and British Columbia (Manchester and Dilhoff 2004) suggests that the Pacific Northwest, like the southeastern United States (Crepet 1989), was particularly diverse with respect to Fagaceae in the Paleogene.

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TABLE 4.1 Fruit characters in trigonal genera of Fagaceae *sensu lato*.

Table 1. Fruit characters in trigonal genera of Fagaceae *sensu lato*.

Taxon	Carpels	Fruits/Cupule	Endocarp	Staminodia	Stigma	Persistent perianth	Shape in Transverse Section	Wings	Pericarp Layers
Trigonobalanus	3	1-15	Tomentose	Present	Capitate	Present	Trigonal, frequently compressed	Present/Absent	2
Colombobalanus	2-3	1-15	Tomentose	Present	Capitate	Present	Trigonal, frequently compressed	Present/Absent	?
Formanodendron	3	1-15	Tomentose	Present	Capitate	Present	Trigonal, frequently compressed	Present/Absent	2
Chrysolepis	3	1, 3, 5, 7(+)	Tomentose	Present	Punctate	Present	Subtriangular	Absent	6
Fagus	3	2	Tomentose	Absent	Decurrent	Present	Triangular	Present/Absent	3
Nothofagus	3	2-3(+)	Glabrous	Absent	Capitate	Present	Triangular-Lenticular	Present/Absent	4
Appian Fruits	2-3	?	Tomentose	Absent	?	Present	Triangular	Absent	3

With data from Langdon 1939, 1947; Hjelmqvist 1948; Forman 1964; Loranz et al 1979; Soepadmo 1968; Nixon and Crepet 1989; Denk and Meller 2002

FIGURE 4.1

Transverse sections of *Fagus schofieldii* Mindell, Stockey & Beard sp. nov. A, Nut showing trigonal shape, tissue zonation, dehiscence lines (through sclerified angles) and major vascular bundles (numbered 1, 2, 3). Note smooth external surface and thin seed coat remnant. Holotype P13417 Ctop #4. B, Nut with convex edges, thick mesocarp and three locules. AW 116 Ibot #17. C, Nut with convex edges showing dark endocarp lining and trilocular ovarian cavity. AW 650 Btop #1. D, Largest specimen showing triangular shape, dehiscence lines and degenerating central partition. AW 601 A #1. All scale bars = 1.0 mm.

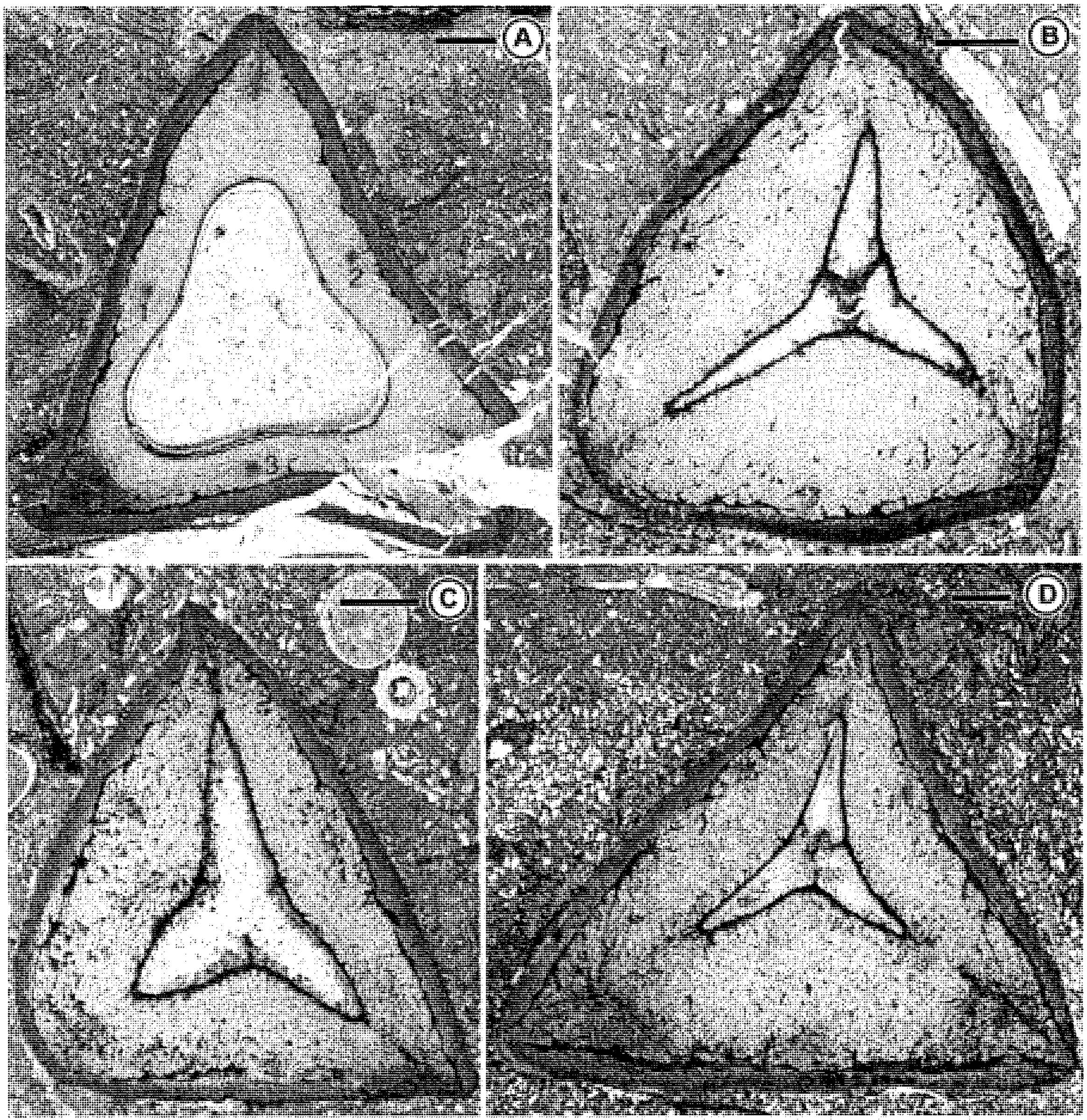

A
B
C
D

FIGURE 4.2

Nut characters of *Fagus schofieldii* Mindell, Stockey & Beard sp. nov. A, Longitudinal section of nut showing obtriangular shape and elongate locules. Note central column of vascular tissue at arrow. AW 104 Dtop #1a. Scale bar = 1.0 mm. B, Oblique longitudinal section of nut showing obtriangular shape and flattened base. AW 116 D_2top #11a. Scale bar = 1.0 mm. C, Longitudinal section near angular margin of nut. AW 104 Cbot #2. Scale bar = 1.0 mm. D, Transverse section through angled area of nut showing mesocarp sclerification. Holotype P13417 Ctop #4. Scale bar= 100 µm. E, Paradermal section through nut showing large idioblasts of epidermis. AW104 Dtop #100b Scale bar= 100 µm. F, Detail of nut wall showing sclerified outer layer (OL), parenchymatous mesocarp (ML) crushed endocarp (EC) and oscillating black band of decaying tissues. (Arrow indicates seed coat remnant). Holotype P13417 Ctop #4. Scale bar= 500 µm.

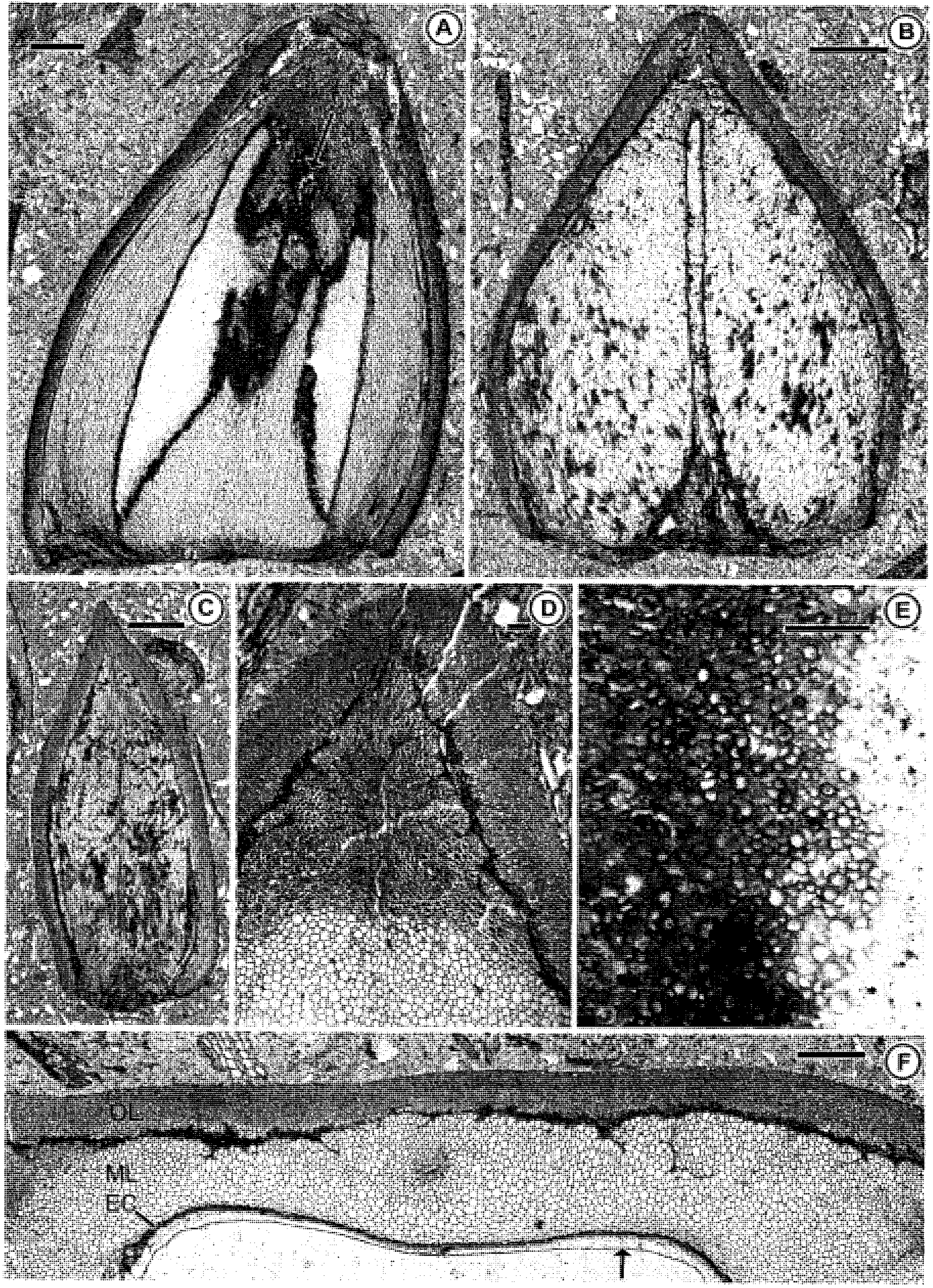
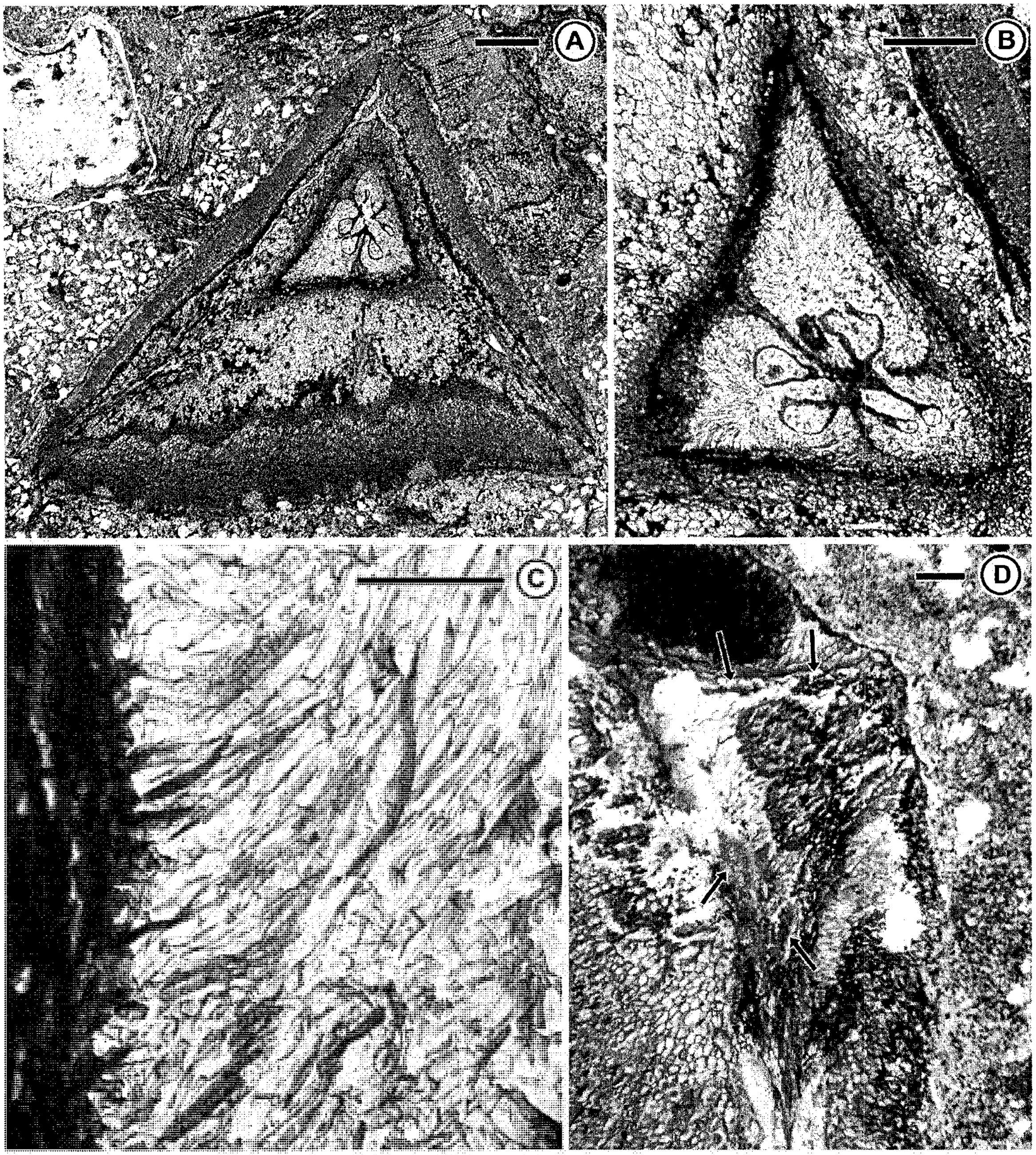

A
B
C
D
E
F
OL
ML
EC

FIGURE 4.3

Nuts of *Fagus schofieldii* Mindell, Stockey & Beard sp. nov. A, Transverse section showing axile placentation of six ovules (two per locule) near apex of nut. AW 601 A #9. Scale bar = 1.0 mm. B, Detail of orthotropous ovules in three locules and three armed septum. Note tomentose locule lining. AW 601 A #11. Scale bar = 500 µm. C, Detail of uniseriate, multicellular trichomes lining endocarp wall. AW 601 A #9. Scale bar = 100 µm. D, Oblique transverse section through apex of nut showing three central styles, possible membraneous perianth remnants (at arrows) and trichomes. Holotype P13417 B2bot #53. Scale bar = 100 µm.


A
B
C
D

CHAPTER 5

Cascadiacarpa spinosa gen. et sp. nov. (Fagaceae): castaneoid fruits from the Eocene of Vancouver Island, Canada.[1]

INTRODUCTION

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 *Colombobalanus* Nixon & Crepet known only from the cloud forests of Colombia (Nixon and Crepet, 1989). There are more than 300 species of *Quercus* found throughout North and Central America (Nixon,

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[1] A version of this chapter has been published: Mindell, Stockey and Beard 2007. American Journal of Botany. 94: 351-361.

1997). *Fagus* is found across the Northern Hemisphere, though the majority of species are endemic to Asia. *Chrysolepis* Hjelmqvist is represented by two species from western North America (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 surround 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 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 Middle 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 (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 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).

Phylogenetic analyses: The data matrices of Nixon (1984) and Denk (2003) were modified with new characters and fossil data were added to form a new morphological data set of 9 taxa, 22 characters (Table 5.2, Appendix 5.1). Phylogenetic analyses based on molecular data have recognized Nothofagaceae as sister to all other families of Fagales (Manos and Steele, 1997; Li et al., 2004). Analysis of the relationships of the fossil taxon and extant genera used *Nothofagus* Blume (Nothofagaceae) as an outgroup. The ingroup consisted of *Fagus* L., *Trigonobalanus* Forman, *Castanea* Mill., *Castanopsis* Spach., *Lithocarpus* Blume, *Chrysolepis* Hjelmquist and *Quercus* L. The use of genera in the analysis necessitated the coding of multistate characters as polymorphic.

Phylogenetic analyses were executed with PAUP* version 4.0b10 (Swofford, 2002). The basic parsimony model was used. Trees are a product of heuristic searches using 10000 random addition replicates with tree bisection-reconnection (TBR) branch swapping and MULTREES on. Bootstrap analyses (Felsenstein, 1985) using the same criteria as heuristic searches with 1000 bootstrap replicates were used to assess branch support. Characters were unordered and equally weighted, with multistate characters treated as polymorphisms at the generic level. Analyses with and without the fossil taxon were run, as were analyses with and without a backbone constraint to keep subfamily Castaneoideae monophyletic.

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. 5.3–5.22).

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: Middle 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. 5.1–5.3, 5.5–5.17) and fractured surfaces (Fig. 5.4). 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. 5.1–5.5). 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. 5.18–5.20). Cupules are circular to ovoid in transverse section (Figs. 5.1, 5.2) and ovoid in longitudinal section (Figs. 5.3, 5.5). The cupule wall is up to 1.5 mm thick, thinning from base to tip (Fig. 5.3). A spiny pedicel is evident at the base of the cupule in which a continuous ring of vascular tissue is present (Fig. 5.6). 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. 5.4, 5.6, 5.20). In transverse section, spines are circular (Figs. 6, 7) with a central vascular strand surrounded by sclerenchyma fibers (Figs. 5.7, 5.8). Secondary wall thickenings of the tracheary elements in these spines are scalariform (Fig. 5.9).

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. 5.4) 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. 5.14); 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. 5.11, 5.13). The middle layer of the fruit wall is parenchymatous up to 30 cells thick (Figs. 5.11, 5.13). The innermost layer of the nut wall is made up of small-diameter sclerenchymatous cells (Figs. 5.11, 5.13). In transverse section, two sutures are observed traversing the nut wall (Figs. 5.14, 5.16). 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. 5.10). In mature fruits with seed and embryo tissues, this septum is present as a broken remnant (Fig. 5.11). Placentation is axile with at least one ovule per locule attached near the apex of the fruit (Figs. 5.10, 5.15). In one specimen, an abortive apical ovule can be observed alongside remnants of a mature seed (Fig. 5.15). Remnants of the seed commonly fill the area of both locules in mature fruits (Figs. 5.12, 5.13, 5.15). The integuments are one to several cells thick, mostly represented by cuticle and commonly invaded by fungi. Embryos are present in several specimens (Figs. 5.3, 5.12, 5.15). In most specimens, cellular detail is obscured by fungi, but it can be seen in one specimen (Fig. 5.12). The embryo is straight and large, filling the entire seed cavity (Fig. 5.12), with two elongate cotyledons, a dome-shaped shoot apex, and a short hypocotyl (Figs. 5.3, 5.15). Endosperm is apparently absent.

An apical protrusion of the nut and cupule is seen in numerous specimens (Figs. 5.3, 5.15). In transverse section, possible perianth and stylar remnants are present (Fig. 5.17). 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. 5.17).

Three-dimensional reconstruction reveals a profusely spiny cupule surface, with spines extending down the pedicel (Figs. 5.18–5.21). Spines lack a clear arrangement, and the cupule surface is devoid of sutures (Figs. 5.18–5.21). The morphology of spines is readily seen from this model, with enlarged bases branching up to five times (Fig. 5.20).

Phylogenetic analyses—Analyses with the fossil taxon, with or without the backbone constraint to keep subfamily Castaneoideae monophyletic, result in 10 most parsimonious trees of 33 steps (CI=.788, RI=.774). A strict consensus of these 10 trees (Fig. 5.22) places *Cascadiacarpa* within the monophyletic subfamily Castaneoideae, with subfamily Fagoideae (*Trigonobalanus* and *Fagus*) forming a basal grade. Within subfamily Castaneoideae, (*Quercus* + *Lithocarpus*) form a polytomy with *Cascadiacarpa*, *Castanopsis*, *Castanea* and *Chrysolepis*. When the fossil is excluded without a constraint, three most parsimonious trees are produced with 31 steps (CI=.875, RI=.840). A strict consensus produces a polytomy of *Fagus* + *Trigonobalanus* + Castaneoideae. Subfamily

Castaneoideae is resolved with (*Lithocarpus* + *Quercus*) sister to a clade of (*Chrysolepis* + (*Castanea* + *Castanopsis*)). Results from the extant-only analysis are congruent with the strict consensus of the extant+fossil analysis.

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, nonendospermic 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 be 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 5.2; 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; however, the number of fruits per cupule is typically equal to the number of cupule valves less one (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 Castanoideae (Table 5.2). This group is united by hypogeous fruits (Manos et al., 2001), a condition strongly suggested by the presence of large 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 Way 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; Hjelmquist, 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; Hjelmquist, 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 distinct lamellae 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 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 et 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 5.2). 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 bilolular 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*.

Phylogenetic analysis of extant genera of Fagaceae with the fossil produces little resolution save for resolving subfamily Castaneoideae and placing *Cascadiacarpa* within it. This analysis emphasizes fruit and cupule characters, as opposed to the vegetative and floral characters emphasized by Nixon (1984). This analysis supports the placement of *Quercus* within subfamily Castaneoideae, whereas Nixon's (1984) analysis nested *Quercus* within a monophyletic *Fagoideae*. The nesting of *Quercus* with genera traditionally placed in subfamily Castaneoideae has been shown in all recent molecular phylogenetic analyses (Manos and Steele, 1997; Manos et al., 2001; Li et al., 2004; Oh and Manos, 2008). Mine is the first analysis based on morphological data to support this grouping. The clade is supported morphologically by straight cotyledons, hypogeous fruits and subtriangular-globose nuts. *Cascadiacarpa* fruits posess two autapomorphies: bilocular fruits and a tomentose endocarp. The resolution of intergeneric relationships is hampered by morphological diversity within genera. The integration of fossil and extant morphological data in Fagaceae is limited by the incomplete sampling of taxa. Given the amount of sequence data available and the richness of the fossil record, a total evidence approach (Gautier et al. 1988), as has been successful in another fossil-rich family of Fagales (Juglandaceae, see Manos et al., 2007), could produce more robust results once intrageneric characters are more completely understood.

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 from 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 diagnostic cupules of Fagaceae 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.

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TABLE 5.1. Morphological data matrix used for phylogenetic analysis.

Character	1	10	20
Taxon			
Nothofagus	010001010	2101(01)01100	000
Fagus	110001010	1111110100	111
Trigonobalanus	010001010	2111110100	111
Castanea	110000100	2110210011	211
Castanopsis	11(01)(01)00100	(02)010110011	211
Lithocarpus	001000010	0010110011	211
Quercus	001000010	0010110010	111
Chrysolepis	110012101	2110110011	211
Cascadiacarpa	111102100	001000001?	???

Sources: Berridge, 1914; Langdon, 1939; Langdon, 1947; Hjelmquist, 1948; Brett, 1964; Forman, 1964; Forman 1966a; Soepadmo 1968b, Soepadmo, 1972; Corner, 1976; Crepet and Daghlian, 1980; Nixon, 1984; Nixon and Crepet, 1989; Kubitzki, 1993; Nixon 1997; Canon and Manos, 2000; Soepadmo et al., 2000.

TABLE 5.2 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.

APPENDIX 5.1. Characters used in morphological analysis. * denotes characters and scoring from Nixon (1984), # from Denk (2003).

1. Cupule attachment
    - 0: sessile
    - 1: stalked
2. Cupule enclosure
    - 0: basal
    - 1: complete
3. Cupule type *
    - 0: valvate
    - 1: evalvate
4. Dehiscent cupule #
    - 0: present
    - 1: absent
5. Internal valves
    - 0: absent
    - 1: present

Internal valves present between fruits, in addition to cupule vales surrounding fruits are present in *Chrysolepis* and absent in *Nothofagus* and remaining genera of Fagaceae (Hjelmquist, 1948; Nixon, 1997).

6. Cupule appendage arrangement
    - 0: concentric
    - 1: absent

Lithocarpus, Castanea and *Castanopsis* typically have cupule appendages (spines/scales) arranged concentrically.

7. Cupule scales
    - 0: present
    - 1: absent
8. Cupule spines
    - 0: present

1: absent

9. Multicellular glands on cupule

0: absent

1: present

10. Nuts per cupule #

0: one

1: two

2: three or more

11. Nut-cupule adnation

0: present

1: absent

In *Castanopsis, Lithocarpus* and *Quercus*, the nut is fused to the cupule wall (Soepadmo, 1972), while in all other genera, nuts are basally attached but otherwise free.

12. Dimorphic fruits in same cupule

0: present

1: absent

Nothofagus cupules contain fruits formed from tricarpellate and bicarpellate flowers (Langdon, 1947). Genera of Fagaceae have cupules that enclose one type of fruit (Kubitzki, 1993).

13. Nuts winged #

0: absent

1: present

Nixon and Crepet (1989) note wings on *Fagus* and *Trigonobalanus* s.l.. All other genera of Fagaceae are wingless and grade from rounded and pyramidal to ovoid or globose.

14. Number of locules *

0: two

1: three

2: six

15. Endocarp ornamentation *

0: glabrous

1: tomentose

16. Stony layer in nut

    0: outer

    1: middle

Soepadmo (1968b) notes that the sclerotic layer in *Nothofagus* is in the middle of the fruit wall, while in Fagaceae *sensu stricto* it is the outer layer.

17. Cotyledons

    0: straight

    1: folded

18. Germination *

    0: epigeal

    1: hypogeal

19. Inflorescences

    0: unisexual

    1: bisexual

20. Pollen shape #

    0: oblate

    1: spheroidal

    2: prolate

21. Aperture number #

    0: 4+

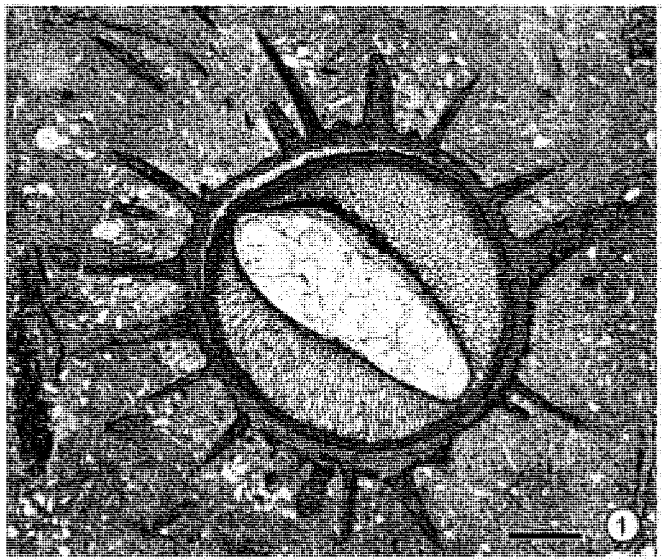
    1: 3

22. Colpi #

    0: poorly developed

    1: well developed

FIGS. 5.1–5.4. Light micrographs of *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, pedicel, embryo remnants in seed cavity, and cotyledons. 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.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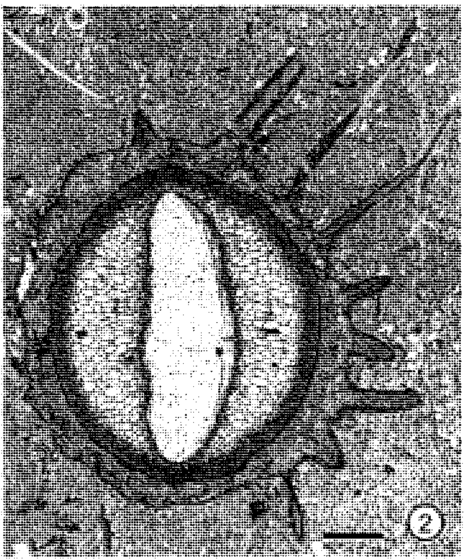
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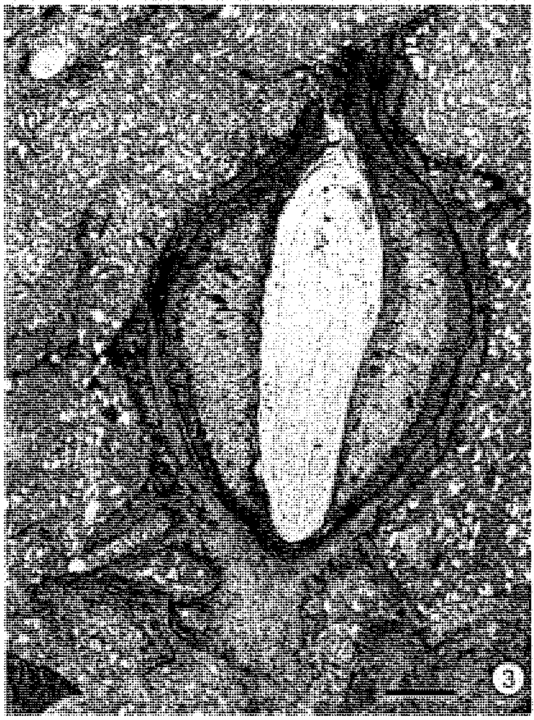
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FIGS. 5.5–5.11. Light micrographs of *Cascadiacarpa spinosa* gen. et sp. nov. fruits. **5.** Longitudinal section showing lobed spine bases and vascular tissues (VT) of pedicel and cupule. AW 507 Hbot #3. Scale bar = 1 mm. **6.** Transverse section through basal portion of the cupule. Note sclerotic nut wall at center, ring of vascular tissue along inner wall of cupule, and spines. AW 532 L_2bot #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.


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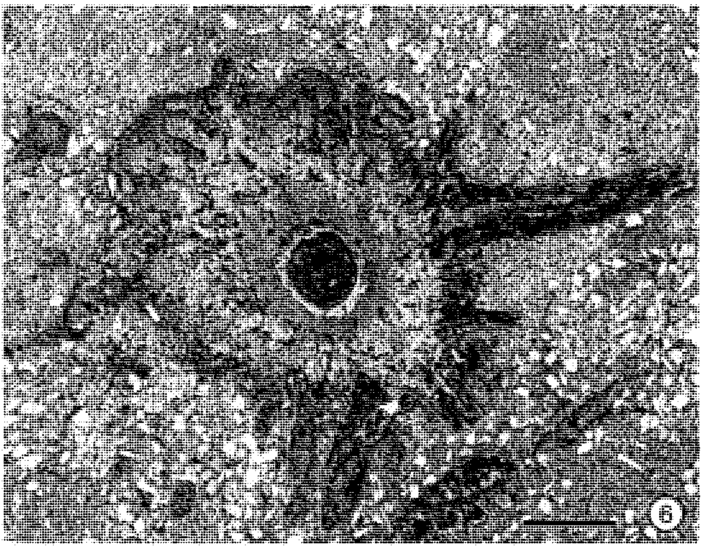
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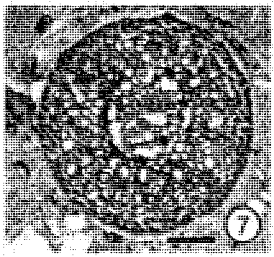
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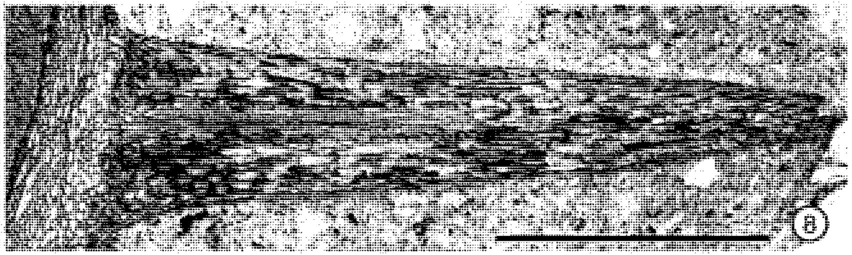
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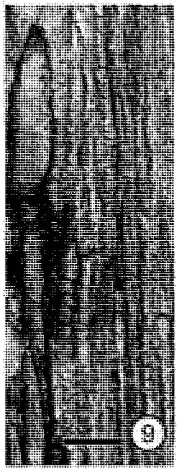
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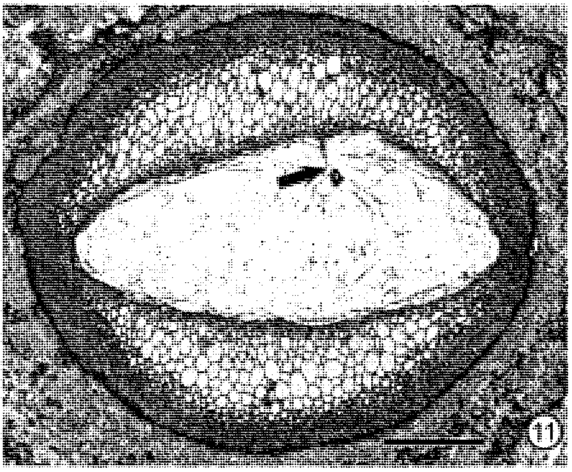
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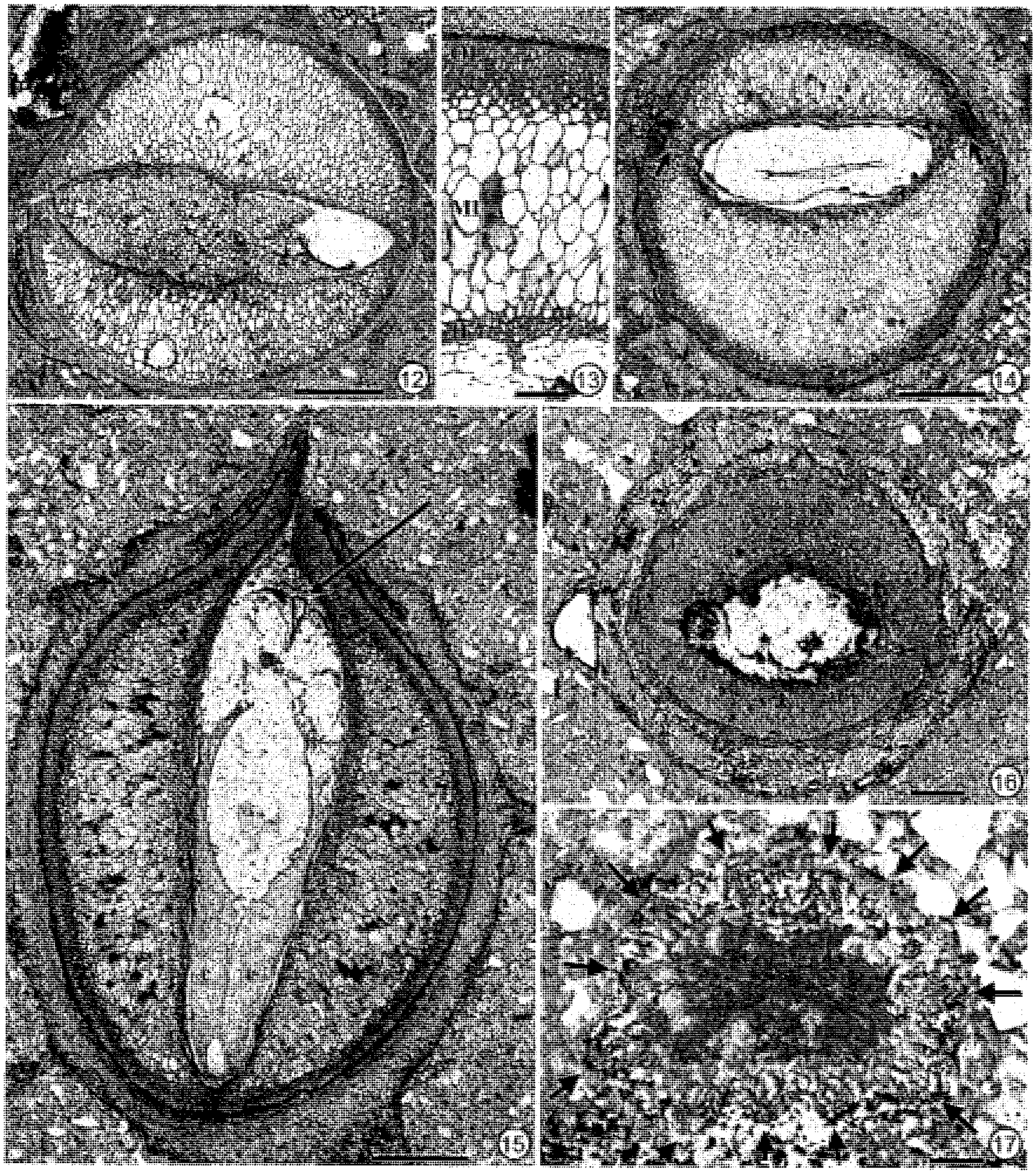
FIGS. 5.12–5.17. Light micrographs of *Cascadiacarpa spinosa* gen. et sp. nov. fruits. **12.** Transverse section of isolated nut showing embryo tissue filling both locules. P 13105 Dtop #92b. Scale bar = 1 mm. **13.** Detail of pericarp showing sclerenchyma of outer layer (OL), parenchyma of middle 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_2bot #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. 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.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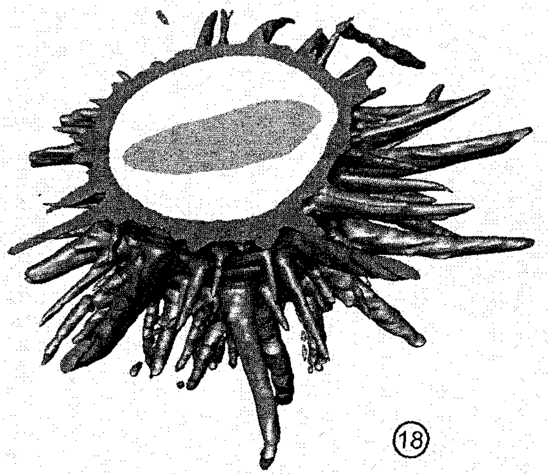
FIGS. 5.18–5.21. Three dimensional reconstructions of *Cascadiacarpa spinosa* gen. et sp. nov. fruits from Holotype P 13105 Dtop . **18.** Cutaway view of cupulate fruit. Cupule is dark grey, nut is white, and locule is light grey. **19.** View of cupule wall and spiny pedicel. **20.** Detail of spines showing enlarged spine base and five branches. **21.** Lateral view of pedicel and cupule wall. Note lack of sutures and valves.



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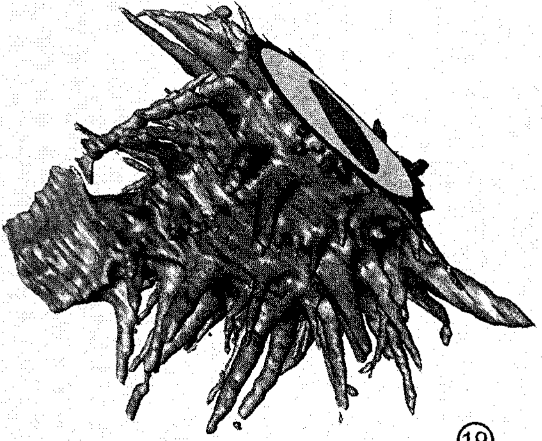

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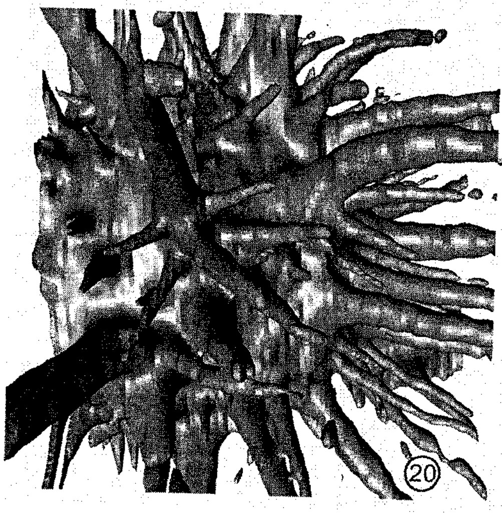

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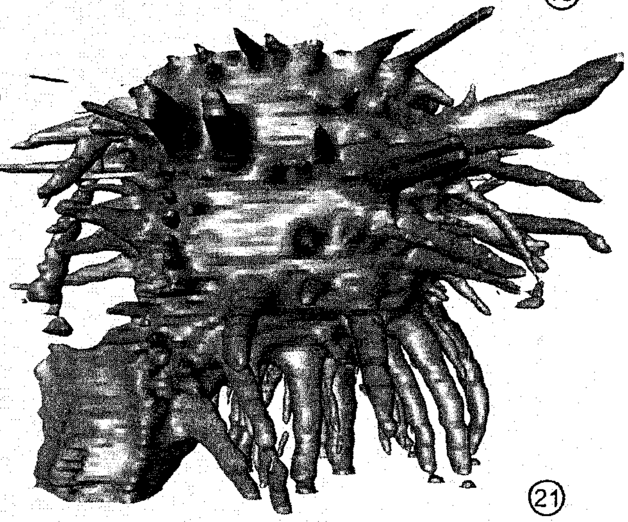

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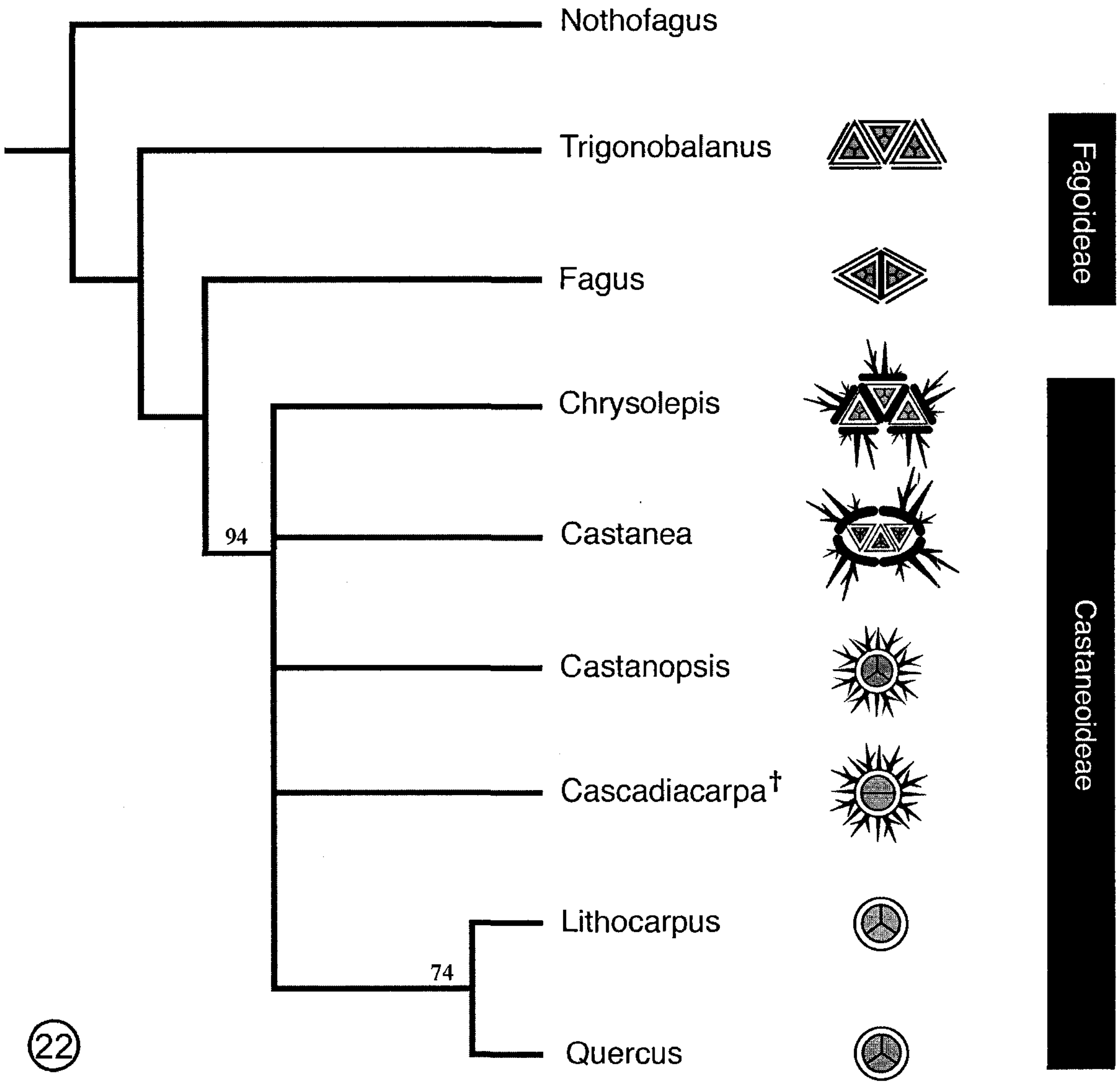
FIG. 5.22. Strict consensus tree from phylogenetic analysis with fossil taxon included, resulting from heuristic search including 8 extant genera and fossil genus *Cascadiacarpa* (Length=33, CI=.788, RI=.774). Bootstrap values above branches with greater than 50% support. Fossil species is denoted by †. Carpel number, nut shape, valve arrangement and cupule ornamentation for genera of Fagaceae are shown at right.


Nothofagus
Trigonobalanus
Fagus
Chrysolepis
Castanea
Castanopsis
Cascadiacarpa†
Lithocarpus
Quercus
94
74
Fagoideae
Castaneoideae

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Chapter 6

Cascadiacarpa exilis sp. nov (Fagaceae) from the Eocene of British Columbia.

INTRODUCTION

The fossil record of Fagaceae is one of the most extensive and diverse among angiosperm families (Kvaček and Walther, 1989; Crepet, 1989; Sims et al., 1998). While most extant genera are represented in the fossil record (Crepet, 1989; Manchester, 1994; Palamarev and Mai, 1998; Pigg and Wehr, 2002; Manchester and Dilhoff, 2004), extinct genera placed in the family vastly expand the diversity of Fagaceae (Crepet and Daghlian, 1980; Smiley and Huggins, 1981; Manchester and Crane, 1983; Crepet and Nixon, 1989a, b; Crepet, 1989; Mindell et al., 2007a).

Extant Fagaceae are most diverse in tropical and subtropical southeast Asia (Soepadmo 1972; Soepadmo et al., 2000; Manos et al., 2001). Because the family is of such economic and ecological importance, it has been the subject of extensive taxonomic and phylogenetic scrutiny (Prantl, 1889; Camus, 1929; Hjelmquist, 1948; Brett, 1964; Forman 1966a,b; Soepadmo 1968a, b, 1972; Abbe, 1974; Nixon, 1984, 1989; Manos and Steele, 1997; Manos et al., 2001; Li et al. 2004; Oh and Manos, 2008). The large number of morphological, anatomical and reproductive studies has made it ideal for studies of character evolution (Brett, 1964; Forman, 1966b; Fey and Endress, 1983; Nixon and Crepet, 1989; Manos et al., 2001; Oh and Manos, 2008). As such, contributions from the fossil record can serve to support, falsify or modify hypotheses on the evolution of flowers, fruits, cupules and inflorescences in the family.

Permineralized fossils provide gross morphological and anatomical data that is not readily available from most compression fossils. In angiosperm paleobotany, perhaps due to rules of botanical nomenclature, there has been very little correlation between anatomically preserved specimens and compression material. Correlation between preservation types allows for new data to call in to question, if not falsify, previous interpretations of compression fossils. Due to the isolated nature of most plant macrofossils and the convergent nature of angiosperm reproductive structures, potential for misidentification of fossil fruits is only exacerbated by the limited data available from some compression material.

This paper proposes a second species of the recently erected genus *Cascadiacarpa* Mindell, Stockey et Beard. Like the type species, these specimens come from the Eocene Appian Way locality of southwestern British Columbia, Canada. They represent a third fagaceous fruit type from the locality (Mindell et al. 2007a, Chapter 4 of this thesis). Results are used to compare the genus to compression fossils from other Pacific Northwest localities.

MATERIALS AND METHODS

The 800 permineralized 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 concretions are of Eocene age (Haggart et al., 1997; Cockburn and Haggart 2007). Sweet (2005) has studied the pollen from the site and has found 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), cupules of Fagaceae (Mindell et al. 2007a), endocarps of Icacinaceae (Rankin et al., 2008), 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, shelf and cup fungi (Smith et al., 2004; Mindell et al. 2007b) have been described from the locality.

Concretions 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) Specimens and microscope slides are housed in the University of Alberta Paleobotanical Collections, Edmonton, Alberta, Canada (UAPC-ALTA).

Compression specimens used in this study come from the Lower Eocene Renton Formation near Issaquah, Washington and the Taneum Creek, Kittitas County (Eocene Naches Formation). All compression specimens studied and figured in this paper are housed in the University of Washington Thomas Burke Memorial Museum of Natural History (UWBM). Compression specimens were captured using a Microlumina scanning camera (Leaf Systems, Inc., Bedford, Massachusetts, USA) and processed using Adobe Photoshop 7.0, San Jose, California, USA).

RESULTS

Systematics

Order: Fagales

Family: Fagaceae

Genus: *Cascadiacarpa* Mindell, Stockey et Beard

Species: *Cascadiacarpa exilis* sp. nov. Mindell, Stockey et Beard. (Figs. 6.1-6.27)

Specific diagnosis—Pedicel spiny, elongate. Cupule spines branching one to several times, circular in transverse section, vascularized, central vascular bundle ensheathed by sclerenchyma. Large cupule lobes present at base of fruit. Nut 3–6 mm long, 2–4 mm in diameter, ovoid in transverse section, ovoid in longitudinal section. Nut wall sclerotic with exocarp idioblasts. Septum absent at maturity, single seed filling cavity.

Holotype: AW 116 D_2top (UAPC-ALTA)

Paratypes: AW 51 Bbot, AW 257 Etop, AW 259 Dtop, AW 263 Fbot, AW 301 Bbot, AW 301Etop, AW 355 G_2bot, AW 505 Htop, AW 509 Ctop, AW 541Btop, AW 641 Gbot, P14349 Kbot.

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 specific epithet *exilis* refers to the small, diminutive form of the fossil fruits relative to those of the type species of the genus.

Description—More than 800 specimens are known as both cupulate fruits and isolated nuts. The small, ovate, elongate nut and its sclerotic wall distinguishes this fruit from all others present at the locality. All fruits are anatomically preserved and were studied in a multitude of planes and developmental stages. Cupules are often abraded such that spines are not apparent, and often nuts are often found in isolation. Fungi are common throughout the cupules. Abundant pyrite found throughout specimens provides evidence of organic tissue degradation and breakdown via microbial sulphate reduction.

Cupule- Cupules completely enclose nuts (Figs. 6.1-6.11). No evidence of sutures or valves is present in any section of the cupules ((Figs 6.1, 6.2, 6.6-6.11). Cupules roughly mimic nut shape and are up to 9 mm long and 6 mm wide. Cupule tissues are continuous with pedicel (Figs 6.3, 6.5). Cupules are circular and thick walled in basal section (Figs. 6.6, 6.7). A cylinder of vascular tissue is continuous from the pedicel to the base of the nut (Figs. 6.3, 6.5, 6.6, 6.16). Distally, this vascular tissue is present around the inner wall of the cupule, surrounding the nut (Figs. 6.7, 6.8, 6.17). Cupule ornamentation varies between pedicel and apex. Spines are present along the pedicel (Figs. 6.5, 6.16) and across the entire surface of the nut (Figs. 6.1-6.13, 6.16, 6.23). These spines are often born on large, bulbous spine bases (Figs 6.1, 6.2, 6.6-6.8, 6.13), which are in highest concentration at the base of the cupule (Figs. 6.6-6.8). Spines can be simple (Figs 6.1, 6.4, 6.9, 6.10, 6.12) or branching (Figs. 6.2, 6.7, 6.13), reaching a maximum length of 3.5 mm. In longitudinal section (Fig. 6.12), the spines taper from the base, where they reach a maximum diameter of 1 mm, to a fine point at the tip. The spines are vascularized (Fig. 6.15), with a central cylinder of vascular tissues (Fig. 6.14) observable in transverse section. The cupule wall thins distally (Figs. 6.6-6.11, 6.23, 6.24) and is free from the fruit only in the area of the stylar protrusion (Figs. 6.23, 6.24). At the apex of the fruit (Figs. 6.5, 6.20-6.22), cupule tissues encircle the stylar protrusion. This is the only place where trichomes are observed on the cupule (Figs. 6.21, 6.22).

Nut— Nuts are ovoid in both transverse (Figs. 6.1, 6.2, 6.9, 6.10, 6.19, 6.26) and longitudinal (Figs. 6.3-6.5, 6.27) section. Nuts are up to 6 mm long and 4 mm wide and are flattened perpedicular to the septum (Figs. 6.2, 6.9-6.11, 6.18, 6.19). The base of the nut is rounded (Fig. 6.7) and is attached immediately above vascularized cupule tissue. Nut wall is uniformly sclerotic and 6-to-10 cells wide with an epidermis containing numerous idioblasts (Fig. 6.17). The inner nut wall is glabrous (Fig. 6.17). The nut is completely adnate to the cupule wall and a layer of dark, compressed cells of the cupule is present immediately outside the epidermis (Fig. 6.17). Sutures are present distally along the plane of flattening (Figs. 6.2, 6.11, 6.23). None of the specimens has shown any evidence of an enclosing “fruit receptacle” (Cannon and Manos, 2000).

The central cavity appears hollow in some specimens (Figs. 6.1, 6.3-6.5), however, many specimens show it to be bilocular (Figs. 6.2, 6.8, 6.18, 6.19). This is evident either from the lobing of the locules (Fig. 6.8) or the thin septum that divides the two locules (Figs. 6.2, 6.18, 6.19). Ovules are attached to the septum. Ovules are apical and number at least one per locule (Figs. 6.2, 6.21). A single seed occupies the locules at maturity (Figs. 6.25-6.27). Seed coat remnants, in the form of a thick cuticle, have been observed filling the area of both locules in mature specimens (Fig. 6.25). Straight, dicotyledonous embryos are present in some specimens (Figs. 6.10, 6.26, 6.27). Endosperm is absent in the preserved fossil seeds.

A prominent apical protrusion of the nut is present in several specimens (Figs. 6.5, 6.20-6.24). In longitudinal section, it extends through an opening at the top of the cupule (Figs. 6.5, 6.20, 6.21). The surface of this protrusion (Fig. 6.22) is covered in minute trichomes and as such it could represent a stigmatic surface. In transverse sections (Figs. 6.23, 6.24), this protrusion is surrounded by, but free from, cupular tissues. In the most distal section, the central protrusion has outer lobes which could represent perianth parts or other remnant floral organs (Fig. 6.24).

Pollen has not been observed in association with the fruits. Staminodes are absent. Fungal hyphae have been observed in the nut (Figs. 6.1, 6.4) and cupule (Fig. 6.25).

Compression Material.

Taneum Creek Locality (UWBM Locality 6202): UWBM 93591a, 93591b (counterpart)

Issaquah Locality (Renton Fm, UWBM Locality B5506): UWBM 57425, 57426, 57427, 57431, 57433, 57434, 57435.

Burke Museum specimens come from the Eocene of Washington State. The single specimen from the Taneum Creek Locality, near Ellensburg, WA (47°06.195'N, 120°58.715'W) comes from the Manastash Formation and was collected by Don Hopkins. It was identified in the collections as *Ceratophyllum*. The compression is spiny, pedicillate and ovate (Fig. 6.28). It measures 9 mm from pedicel base to fruit tip and spines are present along the pedicel and more densely along the perimeter of the fruit.

Their appears to be an apical opening represented by three spine-like protrusions. Spines are simple.

The majority of specimens identified as *Ceratophyllum* come from the Renton Formation near Issaquah and were also collected by Don Hopkins. These specimens display finer preservation than the Taneum Creek specimen. A dark ovoid central mass is encircled by a surrounding layer of spiny, vascularized tissue (Figs. 6.29-6.31). Spines are predominantly simple, though could be interpreted as branching near their base (Fig. 6.29). The body of the fruit is up to 3 mm wide and 5 mm long. In some specimens, a large apical protrusion can be seen emergent from the dark, central fruit tissue (Figs. 6.29, 6.31). In one specimen, this protrusion is bifurcated at its tip (Fig. 6.32).

DISCUSSION

Placement of the fossil fruits from Appian Way hinges on the interpretation of its outermost layer as a spiny cupule as opposed to a drastically differentiated fruit wall. The specimens clearly make the case for the former, as the outer tissues are continuous with those of the pedicel, have separate vasculature and are free from the rest of the fruit in the apical regions. Thus the fruits are interpreted as cupulate nuts, the fruit wall adnate to the cupule wall except in the area of the apical protrusion, which is likely a remnant of the style.

The combination of spiny cupules, stony nuts, straight embryos with large cotyledons, and an absence of endosperm, places these fossil fruits within Fagaceae (Cronquist 1981; Kubitzki 1993). The opening of the cupule at the apex of the fruit allowed for the styles to protrude . The absence of any sutures along the cupule wall suggests these fruits were valveless and indehiscent, as observed in many species of extant Fagaceae (Soepadmo, 1972). Non-endospermic seeds with large cotyledons in extant representatives of the family are synonymous with hypogeal germination (Corner, 1976; Manos et al., 2001). Non-endospermic seeds with large, straight cotyledons are present in the fossil cupulate fruits from Appian Way, suggesting that the seed was dispersed and possibly germinated while still in the fruit. Fruits are clearly bilocular as evidenced by the lobing of the ovarian cavity and the ovule-bearing septum that divides the chamber. The locule space is always lenticular in transverse section and shows no evidence of the trigonal symmetry present in tripartite gynoecia. Thus, it is assumed that these fruits are products of bicarpellate flowers.

Fagaceae as a family has been the subject of numerous systematic studies and subsequent taxonomic revisions (Prantl, 1889; Berridge, 1914; Camus, 1929; Hjelmquist, 1948; Brett, 1964; Forman, 1964, 1966a; Soepadmo, 1968b, 1972; Cronquist, 1981; Nixon, 1984, 1989; Nixon and Crepet, 1989; Hill and Jordan, 1993; Kubitzki, 1993; Manos and Steele, 1997; Manos and Stanford, 2001; Manos et al., 2001; Li et al. 2004; Oh and Manos, 2008). Generic delimitation is based typically on cupule, fruit and inflorescence characters (Forman, 1966a, b; Kubitzki, 1993; Nixon, 1997). Current interpretations (Manos et al., 2001; Li et al., 2004; Oh and Manos, 2008) place the once included genus *Nothofagus* Blume in its own family, Nothofagaceae, considered sister to all other familes of Fagales (Fagaceae, Casuarinaceae, Ticodendraceae, Betulaceae, Myricaceae, Rhoipteleaceae and Juglandaceae). Fagaceae *sensu stricto* presently consists of nine genera. *Fagus* L., *Trigonobalanus* Forman, *Colombobalanus* (Lozano, Hern. Cam. & Henao) Nixon & Crepet and *Formanodendron* (A. Camus) Nixon & Crepet, placed by Nixon (1989) in subfamily Fagoideae together form a basal paraphyletic grade of Fagaceae (Manos et al. 2001). Subfamily Castaneoideae, traditionally encompassing *Castanea* Mill., *Castanopsis* Spach., *Lithocarpus* Blume and *Chrysolepis* Hjelmquist (Forman, 1966a, b; Kubitzki, 1993) forms a monophyletic clade with *Quercus* L., all sharing hypogeous fruits (Manos et al. 2001; Oh and Manos, 2008).

Fruits of *Nothofagus* are readily distinguishable from the evalvate, single-fruited Appian Way fossils in having open, valvate cupules with (typically) more than one fruit per cupule (Langdon, 1947; Kubitzki, 1993; Hill and Jordan, 1993). Furthermore, appendages on *Nothofagus* cupules are scales, whereas cupules of the Appian Way fruits have numerous simple and branching spines. Species of extant *Nothofagus* have fruits with a glabrous endocarp and, while pistillate flowers are predominantly trimerous, many three-flowered cupules have bicarpellate, lenticular central flowers (Langdon, 1947). The Appian Way fossil fruits are bicarpellate and have a glabrous endocarp as well. Neither of these features is present in the fruits of extant Fagaceae *sensu stricto*.

Genera of subfamily Fagoideae have trigonal fruits and seeds with folded cotyledons (Nixon and Crepet, 1989; Kubitzki, 1993). These are distinct from permineralized nuts from Appian Way, which are ovoid and contain seeds with straight cotyledons. The cupules in species of Fagoideae are valvate and scaly, whereas the fruits from Appian Way have spiny and indehiscent cupules. Furthermore, the fossil cupules from Appian Way bear only one fruit, while cupules of *Fagus* bear two (Langdon, 1939; Denk and Meller, 2001) and *Trigonobalanus*, *Colombobalanus* and *Formanodendron* cupules typically have between three and seven nuts per cupule depending on their position along the inflorescence (Forman, 1964; Nixon and Crepet, 1989).

Quercus has been placed in several groupings through time. Traditionally, it was placed in subfamily Quercoideae (Forman, 1964, 1966a; Abbe, 1974). Nixon (1989) placed the genus within subfamily Fagoideae along with the other wind-pollinated genera of Fagaceae. Recent molecular phylogenetic hypotheses (Manos and Steele, 1997; Manos et al., 2001; Li et al., 2004; Oh and Manos, 2008) have suggested the genus is more closely related to the hypogeous fruit-bearing genera of subfamily Castaneoideae. The cupulate nuts of *Quercus* are tricarpellate with a tomentose endocarp lining and have a subtending, scaly cupule (Nixon, 1997; Kubitzki, 1993). This differs from the Appian Way fossil fruits, which have bicarpellate nuts with a glabrous endocarp wall totally enclosed in a spiny cupule.

Like *Quercus,* the genera of subfamily Castaneoideae all have hypogeous fruits (Manos et al., 2001). This condition involves large (filling the seed), straight cotyledons remaining in the non-endospermic seed, which remains in the fruit, during germination. The Appian Way fossil nuts seem to share this syndrome as evidenced by the lack of endosperm and large, straight cotyledons.

Lithocarpus comprises more than 300 species in East Asia (Soepadmo, 1972; Kaul, 1987, 1989; Cannon and Manos, 2000; Cannon, 2001). A single North American species, *L. densiflorus* (Hooker & Arnott) Rehder has been shown based on molecular data to be misplaced (Oh and Manos, 2008). Regardless of generic delimitation, species of *Lithocarpus sensu lato* are similar to the Appian Way specimens in having evalvate cupules and sub-globose nuts. Cupules in some species can almost enclose the nut (Soepadmo, 1972; Cannon, 2001), as in the fossil fruits, but the cupule appendages are scales, often following concentric rings along the outer wall of the cupule. The Appian

Way fruits have spiny cupules that follow no discernable pattern. Furthermore, the pedicillate fossil fruits are bicarpellate and have a glabrous endocarp wall, while *Lithocarpus* fruits are sessile, tricarpellate and have a tomentose endocarp wall (Soepadmo, 1968, 1972; Abbe, 1974; Kaul, 1989).

The genus *Chrysolepis* also has spiny cupules with branched spines, as in the Appian Way fossil fruits, but clear cupule valves are present, both outside (external valve) and between (internal valves) the tricarpellate fruits (Berridge, 1914; Hjelmquist, 1948; Nixon, 1997). The Appian Way fruits lack valves altogether and are bicarpellate.

Fruits of the true chestnut genus, *Castanea*, are similar to the Appian Way fossil fruits in having pedicellate, spiny cupules that can entirely enclose a solitary nut in some species (Prantl, 1889; Langdon, 1939; Fey and Endress, 1983; Nixon 1997). *Castanea*, like the Appian Way specimens, differs from all other Fagaceae in carpel number. While all other genera of extant Fagaceae are tricarpellate, flowers of *Castanea* have either six or nine carpels (Kubitzki, 1993). The Appian Way fruits differ from other species, *Castanea* included, in being the product of a bicarpellate gynoecium. Spines on the cupule of *Castanea* fruits are also branched or simple and can have enlarged bases, as in the permineralized fossils, but they are arranged in a concentric pattern (Prantl, 1889; Brett, 1964). No such pattern exists in the fossil cupules.

The permineralized nuts described in this chapter are most similar to those of *Castanopsis*. *Castanopsis* represents another genus of Fagaceae endemic to Asia (Camus, 1929; Soepadmo, 1968a, 1972; Soepadmo et al., 2000). The genus has a fossil record dating back to the Eocene of western North America (Manchester, 1994) and is also common in the Paleogene of Europe (Kvaček and Walther, 1989; Gee et al. 2003). Fruits of *Castanopsis* are most similar to the Appian Way fossil fruits, sharing spiny, pedicellate, evalvate, indehiscent cupules that can enclose a single nut (Forman, 1966b; Soepadmo, 1972). Cupule spines in *Castanopsis* are also branched and can emerge from enlarged bases, as in the fossil fruits. While extant *Castanopsis* fruits vary considerably in shape, they too can be ovoid (Soepadmo, 1972), however, they are trilocular and have a tomentose endocarp lining (Soepadmo, 1968b, 1972), whereas the Appian Way cupulate nuts are bilocular and have a glabrous endocarp lining. These two characters differentiate the permineralized fruits from those found in *Castanopsis* and all extant Fagaceae.

Fossil fruits and flowers of fagaceous affinity to which the Appian Way fossils can be compared first appear in the Late Cretaceous (Herendeen et al. 1995). Cupules associated with *Protofagacea allonensis* Herendeen, Crane and Drinnan (1995) from the Santonian of eastern North America have three fruit scars and the associated fruits are typically trigonal. These fossils are unlike the Appian Way specimens, which have only one ovoid fruit per cupule. However, much like extant *Nothofagus*, some fruits associated with *Protofagacea* are lenticular and have two styles (Herendeen et al. 1995). This is one of only two other instances of bicarpellate fagaceous fruits in the fossil record, in addition to the specimens described in this paper.

One anomalous character of the Appian Way fossil fruits is the lack of trichomes on the inner wall of the endocarp, which is typically tomentose in extant Fagaceae (Soepadmo, 1968b; Nixon and Crepet, 1989). This absence is also noted in the fruits of *Antiquacupula sulcata* Sims, Herendeen and Crane (1998). These charcoalified fagaceous specimens from the Santonian (Late Cretaceous) of Georgia have cupules with at least six trigonal and tricarpellate flowers (Sims et al. 1998). In contrast, the Appian Way cupules hold only one ovoid, bicarpellate nut. Both fossils, however, call to question whether or not tomentose endocarp walls are ancestral in Fagaceae.

By the Paleogene we see the emergence of modern subfamilies and genera of Fagaceae (Crepet and Daghlian, 1980; Daghlian and Crepet, 1983; Crepet, 1989; Crepet and Nixon 1989a, b; Kvaček and Walther, 1989; Manchester, 1994; Manchester and Dilhoff, 2004). While most of these fossil genera fit well within the framework of extant Fagaceae (eg. *Contricuparius* Crepet & Nixon, *Trigonobalanoidea* Crepet & Nixon), the Oligocene genus *Fagopsis* Manchester and Crane (1983) is anomalous in its dense, globose aggregation of minute, three-fruited cupules. The three styles of the fruits suggest that they conform to the tricarpellate body plan of the family from which the bilocular, single fruited, solitary cupules from Appian Way may have diverged.

The emergence of subfamily Castaneoideae is first marked in the fossil record by cupulate fruits and flowers from the Paleocene/Eocene boundary of Tennessee. Cupules of *Castanopsoidea columbiana* Crepet & Nixon (1989a) enclose three tricarpellate fruits as in some species of extant *Castanopsis*. The cupules of *Castanopsoidea* are scaly, as in extant *Quercus* and *Lithocarpus* (Nixon and Crepet, 1989a). The Appian Way fossil fruits show little affinity with these genera, as they are bicarpellate and occur solitarily in spiny cupules.

The genus *Cascadiacarpa* Mindell, Stockey et Beard was described from fruits from the Appian Way locality (Mindell et al., 2007a). Like the fossils described in this paper, these fruits have spiny, evalvate cupules adnate to and entirely enclosing a single nut. Like the nuts described in this paper, fruits of *Cascadiacarpa* are bilocular, have a glabrous endocarp wall, and bear a single non-endospermic seed with a straight embryo and large cotyledons (Mindell et al., 2007a). The type species, *C. spinosa* shares nearly identical spine morphology (see Figs. 7, 8, 20 of Mindell et al., 2007a) with the fossils described in this paper. These specimens fit the generic diagnosis of *Cascadiacarpa* but differ from the type species in having an ovoid-lenticular shape in transverse section and a sclerotic nut wall, whereas the type species is circular and has a nut wall differentiated into three distinct zones (Mindell et al., 2007a). The cupules of *C. spinosa* also lack the enlarged spine bases of the specimens described in this paper.

From comparisons of the Appian Way permineralized fruits to extant and fossil fagaceous taxa, it is clear that they belong in the genus *Cascadiacarpa.* They differ from *C. spinosa* in nut shape and anatomy and by their possession of enlarged spine bases on their cupules. Since they are morphologically distinct from the type species, they are designated as a second species of *Cascadiacarpa. Cascadiacarpa exilis* Mindell, Stockey and Beard fruits are the most common in the concretions at the locality, known from more than 800 specimens, while *C. spinosa* is known from less than 100 specimens. The predominance of *Cascadiacarpa* fruits in the concretions at Appian Way suggests that the plant to which these fruits belong was a significant component in the regional vegetation at the time of deposition.

Phylogenetic analyses based on ribosomal DNA sequences (Manos et al. 2001) have found support for a *Quercus*, *Lithocarpus* (North American and Asian) and *Chrysolepis* clade and suggested a single origin within this group of “flower cupules”, a condition wherein individual pistillate flowers are each surrounded by their own cupule. More recent analyses (Oh and Manos, 2008) have used sequence data from the CRAB CLAW (CRC) nuclear gene, which is thought to regulate carpel development in angiosperms. Results of this work suggest a relationship of *Quercus* + North American *Lithocarpus* sister to *Castanea* + *Castanopsis*. This would suggest numerous independent derivations of the pistillate flower cupules. Species of *Cascadiacarpa* contribute to this conflict in presenting the earliest occurrence of single-fruited, spiny cupules. The vasculature of the pedicel in *C. exilis* shows no evidence of any other floral traces, the adnate cupules hold only one fruit and show no trace of suppressed lateral flowers. As such, *Cascadiacarpa* supports an early derivation of this condition. This is also supported by the arrangement of fruits in the earliest fossil castaneoid cupules, which, excepting *Castanopsoidea* (Crepet and Nixon 1989a), are all have single-flowered/fruited cupules (see: Manchester 1994, Mindell et al. 2007a).

Significance with regard to compression fossils

Superficially, both the Appian Way fruits and the compression fossils have strong similarities to those of extant *Ceratophyllum* L.. *Ceratophyllum* fruits are small, stalked, spiny and have an elongate apical style (Les 1988). The Appian Way fossils can easily be distinguished from extant Ceratophyllaceae on the basis of spine morphology and distribution, fruit wall anatomy and gynoecium structure. Fruits of Ceratophyllaceae have simple spines in planes (Les 1988), whereas the Appian specimens have simple and branching spines distributed all along the cupule wall. Furthermore, extant *Ceratophyllum* fruits have a papillate or punctate surface due to the presence of sclerotic nests underneath a transparent sheath (Les 1988). No such surface ornamentation exists on the fossil fruits from Appian Way. While *Cascadiacarpa* fruits could be interpreted as having apical placentation, the ovules are borne in a bilocular ovary, unlike *Ceratophyllum* which is unilocular.

The Eocene compression fossils from Washington State studied here were informally identified as *Ceratophyllum* in the Burke Museum collections, probably because of their size and spines. None of the specimens, however, displays the sclerotic, papillate ornamentation on the surface of the fruit wall present in extant *Ceratophyllum* (Les 1988). Likewise, when stalks are preserved, spines are evident along their length, a character absent in *Ceratophyllum* fruits, which are delimited from the stalk by a subtending whorl of connate bracts (Les 1997), also absent in the Burke Museum specimens.

These "*Ceratophyllum*" fruits from the Eocene of Washington State could alternately be interpreted as spiny, cupulate fruits of Fagaceae, with the central dark body being the fruit (i.e. nut) proper and the surrounding spiny tissue representing the cupule. Based on size, shape and spine arrangement, any of these specimens could be interpreted as compressed equivalents of *Cascadiacarpa*. The Taneum Creek specimen is larger and more globose than the Issaquah specimens. In size and shape, it bears a striking resemblance to *Cascadiacarpa spinosa* (see Figs. 3, 4, 21 of Mindell et al., 2007a). The smaller, more elongate specimens are more similar to *C. exilis* cupulate fruits, which bear an elongate apical protrusion. One specimen shows this protrusion bifurcated at the tip. Since this protrusion is continuous with the central dark body of the fruit, I interpret it as two remnant styles at the top of the fruit. This supports an affinity with the bicarpellate nuts of *Cascadiacarpa*.

The identification of the compression fossils as probable *Cascadiacarpa* is of consequence when considering the sparse fossil record of *Ceratophyllum*. While definitive vegetative material occurs in the Cenozoic fossil record (Herendeen et al., 1990; Wang et al., 2005), the occurrence of small, spiny fruits lacking any association with vegetative material might be mistaken for the presence of *Ceratophyllum*. Work by Herendeen et al. (1990) summarizes more than 35 specimens from the Tertiary of North America. Of these specimens, 33 represent isolated fruits from four separate localities. The last specimen is a vegetative axis found at another locality. These are placed by Herendeen et al. (1990) in two extant and one fossil species of *Ceratophyllum* based on fruit shape and spine arrangement. While two of these placements are well supported, the characters used to diagnose the fossil species, *Ceratophyllum furcatispinum* Herendeen, Les and Dilcher are not unique to those specimens in light of the description of *Cascadiacarpa exilis*. In fruit length, fruit width, spine length, spine baranching and seed morphology, they fit the description of *Cascadiacarpa exilis*. The fruits of *Ceratophyllum furcatispinum*, which come from the Paleocene of Montana are also noted as having spines that protrude from a thin webbing, which could very well be cupule material as opposed to fruit wall. The lack of a basal involucre and papillate surface sculpture (Herendeen et al. 1990) also casts doubt on the affinities of these specimens. In the absence of supporting vegetative material, we suggest a cautious approach to the description of ceratophyllaceous fruits in the fossil record.

Conclusions

Cupulate nuts of *C. exilis* are the most common fruit in the Appian Way concretions. They represent a second form of *Cascadiacarpa* that differs from the type species, *C. spinosa*, in shape, size, wall anatomy and spine arrangement. The spiny cupule encloses a single ovoid nut, a condition found in extant castaneoid genera. The presence of this arrangement in the Paleogene is interesting in light of the hypothesis of Oh and Manos (2008) for multiple origins of the flower cupule. These fruits would represent another variation of the "acorn"-type cupule, which they propose to have multiple origins. *Cascadiacarpa exilis* is the third species of Fagaceae described at the Appian Way locality (Mindell et al. 2007a, this thesis) and, together with those species previously reported from the Clarno Nut Beds of Oregon (Manchester, 1994) and the Okanagan Highlands of British Columbia and Washington (Pigg and Wehr, 2002; Manchester and Dilhoff, 2004; Moss et al. 2005), suggests the family was very prominent at the continental margin in the Eocene of western North America. The slender cupules and fruits of *C. exilis* correspond to compressed fossil fruits identified as *Ceratophyllum* from other Eocene localities of western North America. These fruits show large overlap with the diagnosis of *C. exilis* and *C. spinosa* and draw attention to the need for more cautionary evaluations of isolated *Ceratophyllum*-like fruits in the fossil record.

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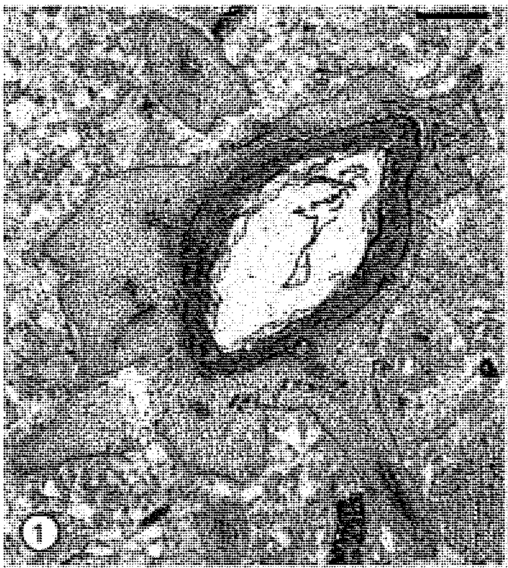
Figs. 6.1–6.5. *Cascadiacarpa exilis* sp. nov. fruits. **1.** Transverse section of cupulate nut. AW 387 D_2bot #7. Scale Bar= 1 mm **2.** Transverse section of cupule and nut showing two locules divided by thin septum. Note two ovules at center and large spine base. AW 51 Bbot #54. Scale Bar= 500 um **3.** Oblique longitudinal section of cupule enclosing nut. Note vascular tissue in cyclinder near base AW 301 Bbot #1b. Scale bar=1 mm. **4.** Oblique section through cupulate flattened nut showing variation in spine morphology. AW 301 B_5bot #37a. Scale bar= 1 mm. **5.** Longitudinal section through cupulate nut showing long pedicel and cupule lobes surrounding apex of nut. AW 355 G_2Bot #17a. Scale bar= 1 mm.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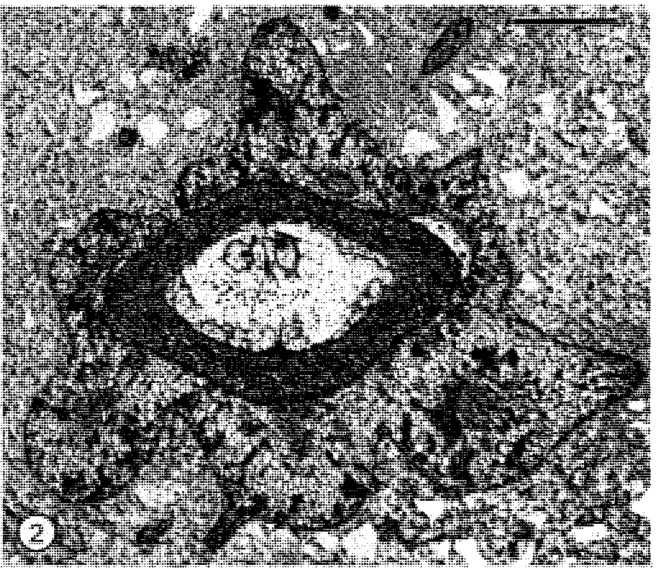
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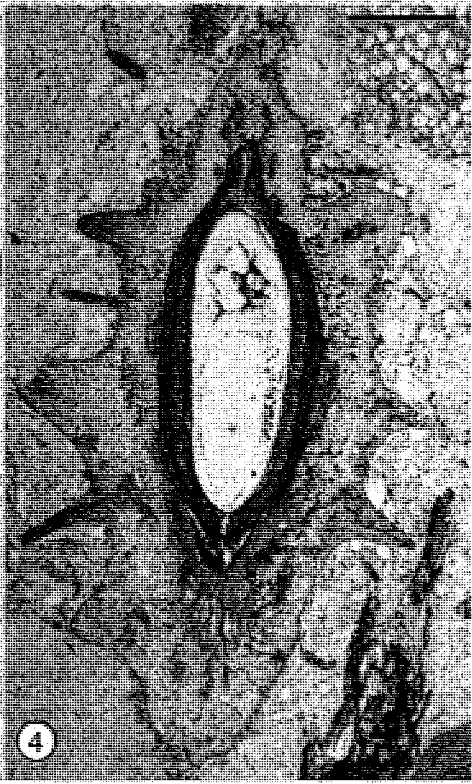
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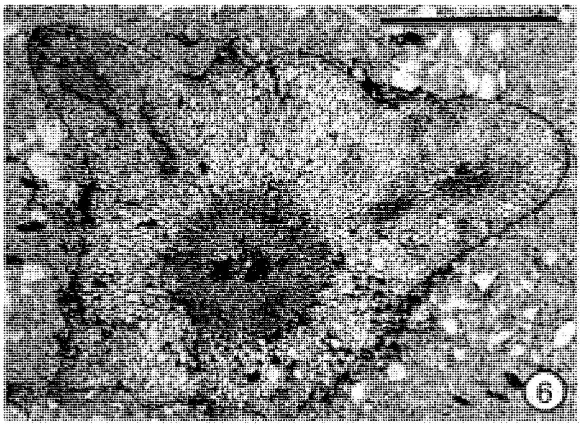
Figs. 6.6–6.11. Successive transverse sections of *Cascadiacarpa exilis* sp. nov. fruits. Holotype. AW 116 D_2bot. All scale bars=1mm. **6.** Section below fruit base showing large lobes of cupule and central cylinder of vascular tissue. AW 116 D_2top #44b. **7.** Section showing rounded base of nut (center) surrounded by ring of vascular tissue on inner wall of cupule. AW 116 D_2top #45b. **8.** Section above base of nut showing two locule lobes. Cupule wall thick and large lobes still present. AW 116 D_2top #46b. **9.** Section showing ovoid nut and numerous spines on cupule. Section AW 116 D_2top #47b. **10.** Section showing embryo in nut and variation in spine morphology. AW 116 D_2top #51b **11.** Section near apex of nut showing increasingly flattened fruit with septa (arrows). Note cupule free from nut in some places. AW 116 D_2top #58b.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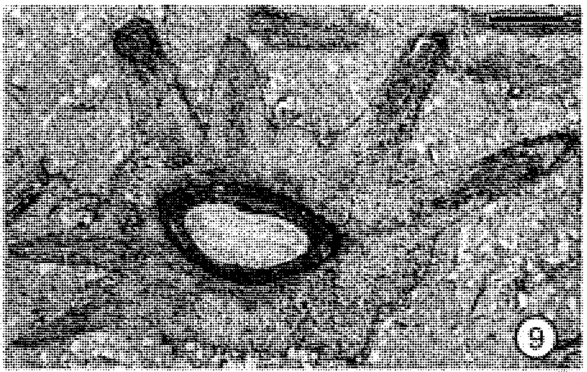
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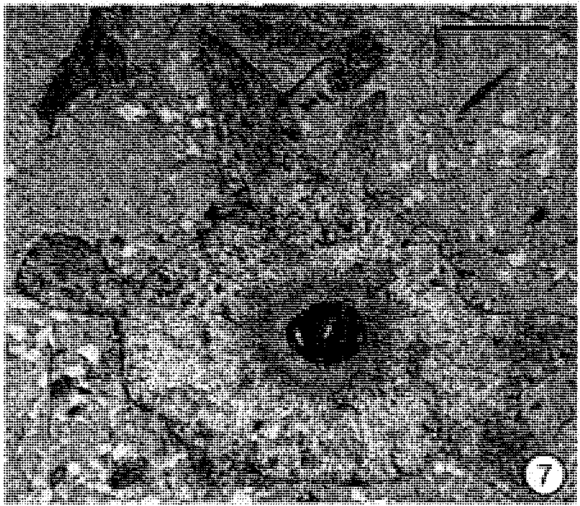
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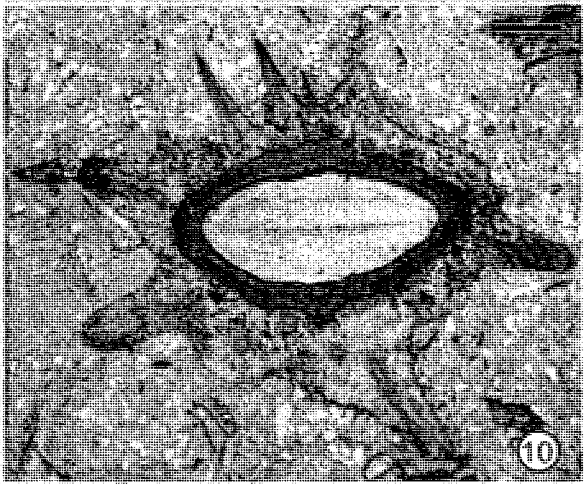
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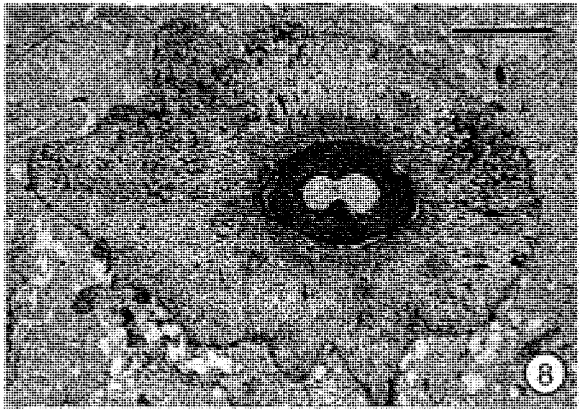
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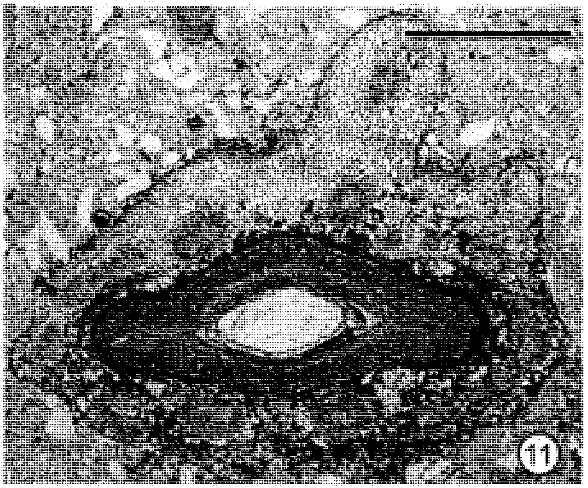
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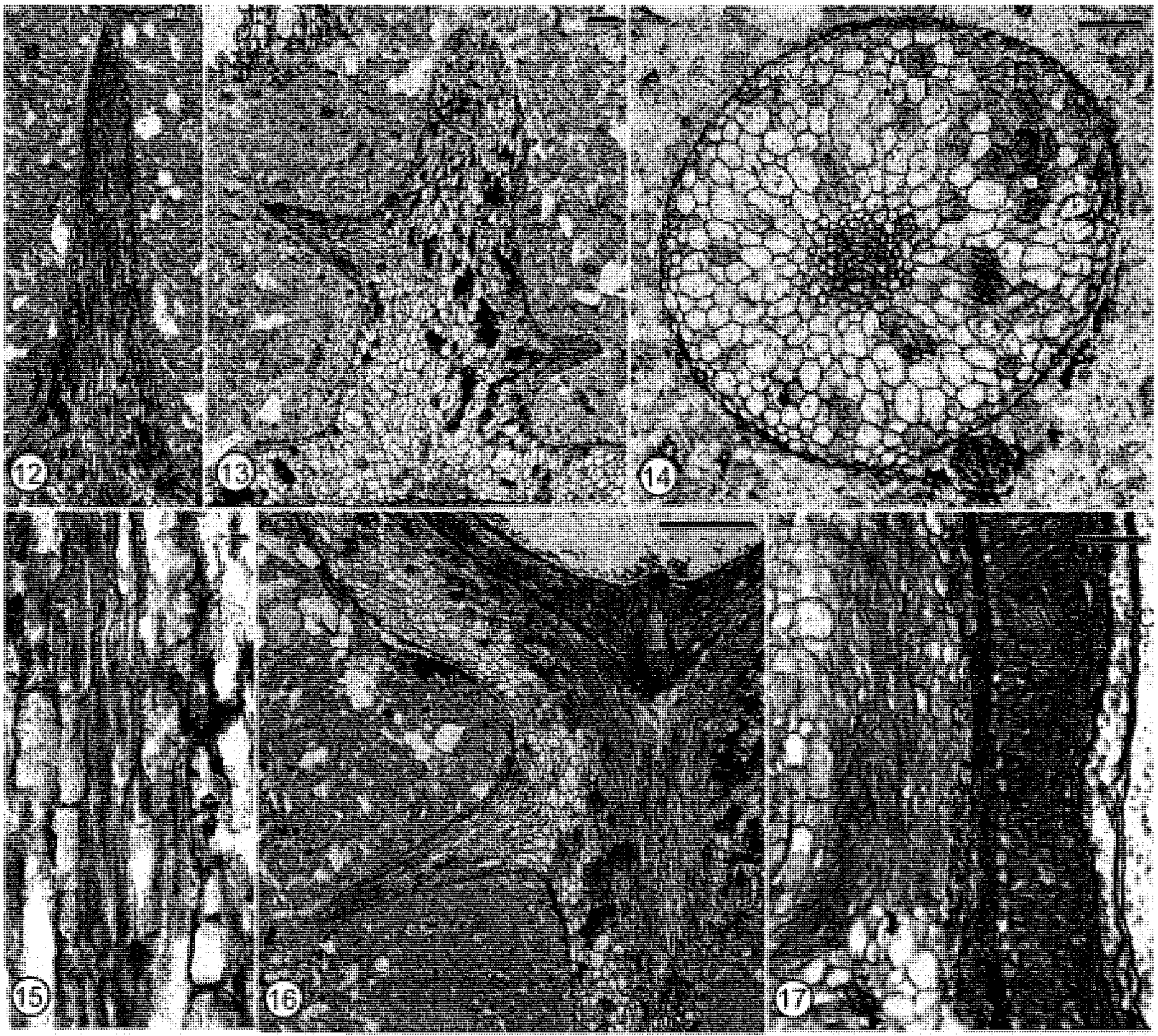
Figs. 6.12–6.17. Cupule wall and spine anatomy of *Cascadiacarpa exilis* sp. nov. fruits. **12.** Longitudinal section of simple tapering spine. AW 257 Etop #20. Scale bar= 100 µm. **13.** Longitudinal section through branching spine. AW 51 Bbot #4. Scale bar= 100 µm. **14.** Transverse section through spine showing circular shape and central strand of vascular tissue. Note minor spine at bottom right. AW 310 B5bot #86b. Scale bar= 100 µm. **15.** Longitudinal section through vascular tissue of spine. AW 257 Etop #20. Scale bar = 10 µm. **16.** Longitudinal section through base of of cupule showing spine on pedicel, adnation of fruit to cupule and elongate vascular tissue on inner wall of cupule. AW 263 Fbot #71b. Scale bar=500 µm. **17.** Section through cupule (CW) and nut wall (NW) showing seed coat (SC) and idioblast layer (IL). Note vascular tissue along inner wall of cupule. AW 641 Gbot #1a.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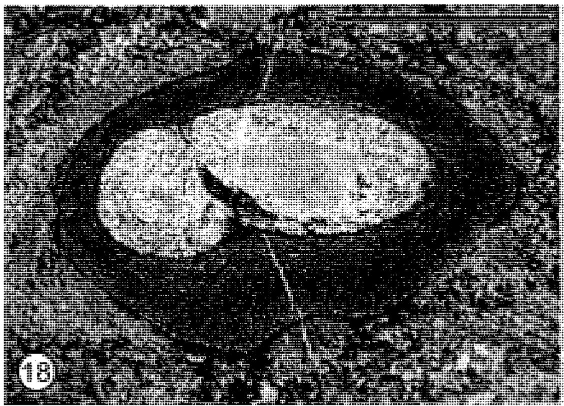
Figs. 6.18–6.24. Fruit characters of *Cascadiacarpa exilis* sp. nov . **18.** Transverse section of bilocular fruit with abraded cupule. Note remnants of septum, at center. AW 301 Etop #18. Scale bar=1 mm. **19.** Transverse section of bilocular fruit with abraded cupule. Note thin septum. AW 505 Htop #1b. Scale bar=1 mm. **20.** Narrow apical extension of fruit tissue, possibly style, in longitudinal section. AW 541 Btop #0. Scale bar = 100 um. **21.** Apex of nut in longitudinal section showing undeveloped apical ovule and tapering extension of nut wall surrounded by cupule tissue. AW 509 Ctop #3. Scale bar=100 um. **22.** Detail of previous figure, showing trichomes lining apical extension of nut and surrounding cupule. Note cupule free from nut at apex. AW 509 Ctop # 3. Scale bar=100 um. **23.** Transverse section through apical region of cupulate nut, showing nut free from cupule. AW 51 Bbot #115. Scale bar=100 um. **24.** Transverse section through distal portion of cupulate nut showing cupule tissue enclosing narrow protrusion of nut. Note possible perianth tissue (arrow). AW 259 Dtop #4. Scale bar=100 um.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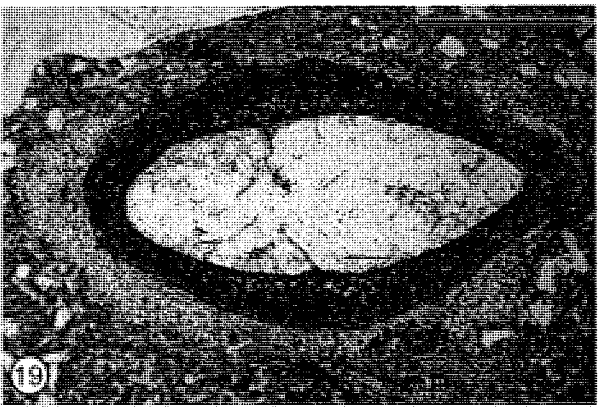
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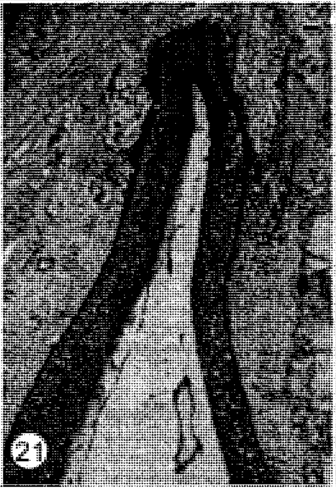
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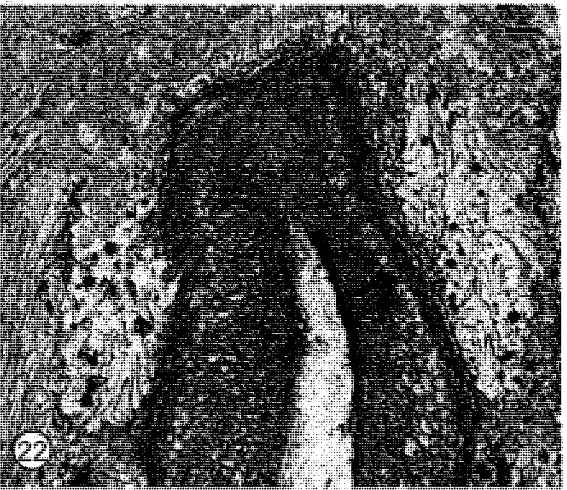
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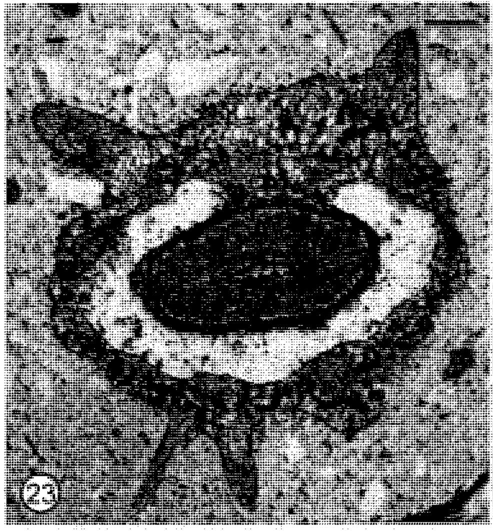
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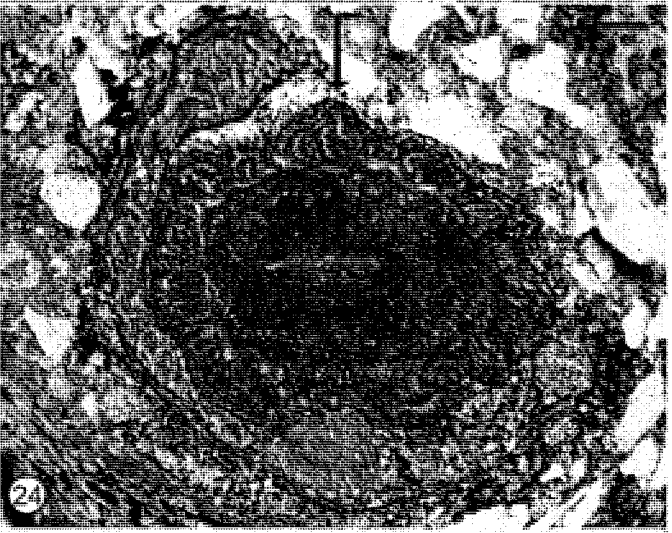
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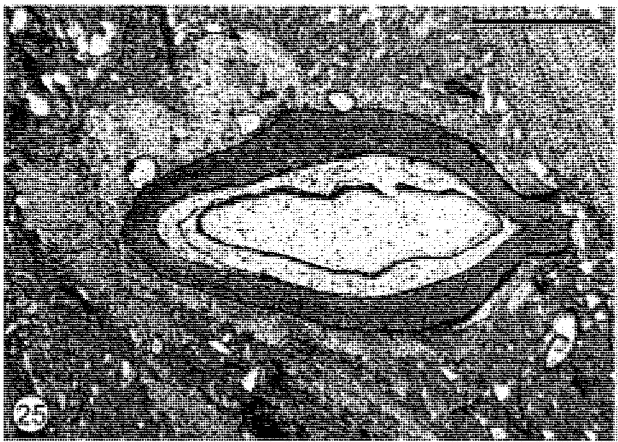
Figs. 6.25-6.27. Seeds of *Cascadiacarpa exilis* sp. nov. **25.** Seed coat (at arrow) in ovarian cavity of cupulate nut. AW 641 Gtop 16b. Scale bar= 1 mm. **26.** Transverse section through mature fruit showing two cotyledons, at center. Holotype AW 116 D_2top #51b. **27.** Oblique longitudinal section through embryo. P14349 Kbot #1b. Scale bar= 100 um.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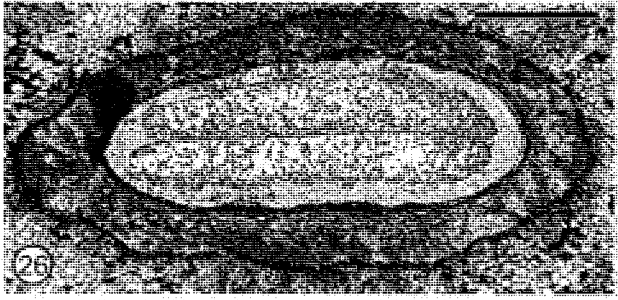
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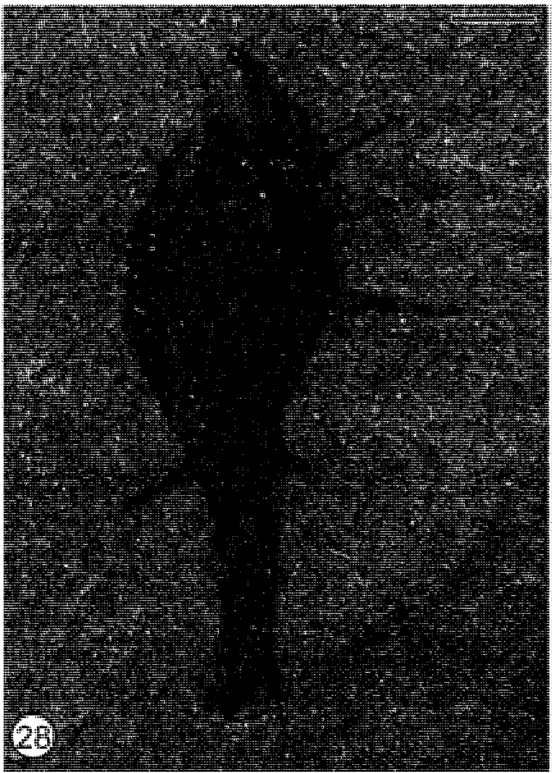
Figs. 6.28-6.32. Eocene compression fossils from Washington State. **28.** Pedicellate fruit showing spines and apical lobes. Taneum Locality, UWBM 93591. **29.** Spiny margined fruit with apical continuation of central tissues. Issaquah Locality, UWBM 77802. **30.** Spiny margined fruit. Issaquah locality, UWBM 5149. **31.** Spiny margined fruit with birfucating apical protrusion. Issaquah locality, UWBM 98263. **32.** Detail of apex of UWBM 98263 showing branched apical protrusion. All scale bars = 1 mm.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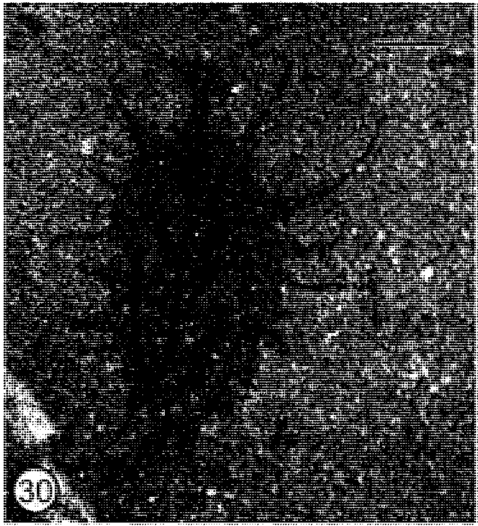
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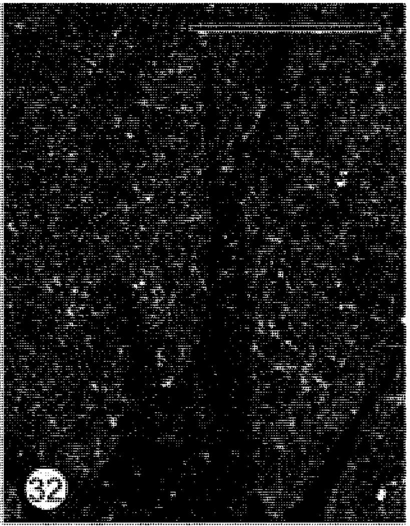
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Chapter 7: Conclusions

The cellular preservation of specimens at the Eocene Appian Way locality affords high resolution fossil plant taxonomy. The taxa described in this thesis and in papers published to date represent isolated organs of plants that likely grew far from their place of deposition.

This thesis, in combination with other papers published on plant fossils from the locality (Hernandez-Castillo et al. 2005, Elliott et al. 2006, Trivett et al. 2006, Rankin et al. 2008), represents the initial study of a vast assemblage of Eocene plants at Appian Way. In the broad survey on which this work is based, more than 60 morphotaxa of mosses, ferns, conifers and angiosperms have been identified (Table 7.1). With the species described in this thesis, seven plant families have now been formally recognized from the locality: Schizaeaceae (Trivett et al. 2006), Gleicheniaceae (Mindell et al. 2006b, this thesis), Cupressaceae (Hernandez-Castillo et al. 2005), Platanaceae (Mindell et al. 2006a, this thesis), Juglandaceae (Elliott et al. 2006), Fagaceae (Mindell et al. 2007a, this thesis) and Icacinaceae (Rankin et al. 2008). However, many other families and genera remain to be described. These include Osmundaceae, Dennstaedtiaceae, Cyatheaceae, Lauraceae, Annonaceae, Magnoliaceae, Menispermaceae, Meliaceae and Cornaceae, in addition to the many others that are as yet unknown (Table 7.1, Little et al. 2001, Mindell et al. 2007b).

GLEICHENIACEAE

Chapter 2 describes a permineralized gleicheniaceous rhizome with an attached stipe base. Gleicheniaceae is one of the earliest diverging groups of extant Filicales (Stevenson and Loconte 1996; Rothwell 1999) and one the oldest living families of ferns, with a fossil record stretching into the Paleozoic (Yao and Taylor 1988). The marginally mesarch rhizome has a vitalized protostele, protoxylem elements with helical wall thickenings, and scalariform metaxylem tracheids that occur in clusters. A continuous band of phloem and pericycle surrounds the xylem. The inner cortex consists of a layer of small diameter sclerenchyma fibers, while the outer cortex is composed of larger parenchyma cells. A nodal island of sclerenchyma is present between the leaf trace and protostele at the level of frond trace divergence. Long metaxylem tracheids in the frond trace show septa in longitudinal section that likely represent tyloses, as have been observed in extant Gleicheniaceae (Ogura 1972). Roots diverge from all sides of the rhizome, with traces that run obliquely through the cortex. Numerous associated but isolated frond segments are found in the Appian Way nodules that show a pinched and inrolled C-shaped vascular trace and pseudodichotomous branching, a diagnostic feature of Gleicheniaceae (Holttum 1957) . The frond traces have numerous protoxylem strands, and the general anatomy is comparable to that of gleicheniaceous stipes (Chrysler 1943, 1944).

Rhizome anatomy, while broadly similar to other families of basal Filicales (Boodle 1900, 1901a, 1901b) places the fossil stem within Gleicheniaceae. The number of protoxylem poles and the divergence of the stipe from the rhizome is identical to that described in extant *Gleichenia*. Thus, the rhizome is described as a new species of *Gleichenia*, *G. appianense*. The family, while common throughout the Mesozoic (Tidwell and Ash 1994), especially in the Cretaceous of North America, is noticeably rare in the Cenozoic (Collinson 1996, 2001, 2002). *Gleichenia appianense* represents the first record of Gleicheniaceae in the Tertiary of North America.

PLATANACEAE

Chapter 3 describes specimens of globose staminate and pistillate inflorescences belonging to Platanaceae. Among extant angiosperm families, the sycamores have one of the deepest (Hickey and Doyle 1977) and most diverse (Manchester 1986, Crane 1989, Magallon-Puebla et al. 1997) fossil records. The extant family is represented by only a handful of species in one genus, *Platanus*, that shows little gross morphological or floral diversity (Crane 1989, Nixon and Poole 2003), so the family serves as an example for how the fossil record can expand familial concepts.

Flowers occur on globose unisexual heads and are supplied at their bases by branching pentagonal vascular traces. Flowers of staminate inflorescences have a well-developed perianth with at least two whorls of tepals. Five stamens with elongate anthers surround a single whorl of five (rarely four) free, nonfunctional carpels that are ovate in longitudinal section and roughly triangular in transverse section. *In situ* tricolpate pollen 16 µm in polar diameter is found in the anthers. This same pollen is found among the persistent styles of larger pistillate fructifications. The pistillate flowers are identical in structure to staminate flowers but have five fully-developed carpels, and they lack stamens. Fruits are glabrous achenes up to 8 mm long.

Staminate inflorescences compare most closely to those of *Platananthus* sp. (Manchester 1986), but the regular co-occurrence of both stamens and rudimentary carpels in the same flower has not previously been reported in the fossil record and, thus, these specimens have been placed in a new genus and species, *Gynoplatananthus oysterbayensis*. These platanaceous inflorescences provide evidence that rudimentary carpels are an ancient feature within staminate flowers of Platanaceae. This is important in light of recent molecular phylogenetic hypotheses which have posited a relationship between Platanaceae, a family exclusive to the Northern Hemisphere, and Proteaceae, a Southern Hemisphere family (Chase et al. 1993, Hoot et al. 1999, Hilu et al. 2003, Doyle and Endress 2000). This relationship is weakly supported by morphological characters of extant representatives of the two families (see Doyle and Endress 2000, Carpenter et al. 2005), however, the fossil record now provides a few more lines of evidence linking the two families, with documentation of rudimentary bisexual flowers in *G. oysterbayensis* and the presence of tetramerous flowers in *Quadriplatanus* (Magallon-Puebla et al. 1997).

FAGACEAE

The last three data chapters of this thesis describe fruits of Fagaceae. Like Platanaceae, the family has a rich fossil record (Crepet 1989, Manchester 1994, Kvaček and Walther 1989). Unlike Platanaceae, the family is represented by a diverse assemblage of living genera of great economic and ecological importance (Kubitzki 1993). Consequently, a wide body of genetic, anatomical and morphological data has been produced, making the family ideal for systematic and phytogeographic studies (Manos et al. 2001, Manos and Stanford 2001). While evidence of the family first appears in the Late Cretaceous (Herendeen et al. 1995, Sims et al. 1999), greatest diversification of genera occurs in the Paleogene (Crepet 1989, Manchester 1994, Manchester and Dilhoff 2004). In light of this, the abundance of the family at the Eocene Appian Way locality is not surprising.

FAGUS

Chapter 4 describes 60 trigonal fagaceous fruits known at various developmental stages. In transverse section, fruits are triangular with lateral ridges that vary in shape from rounded to sharply angled. In longitudinal section, the nuts show a broad base and a tapered distal tip. The ovary is partitioned into three locules at the apex, and placentation is axile with two ovules per locule. Locules merge near the base, giving the appearance of a three-lobed ovarian cavity. This area is occupied by a single seed at maturity. The inner wall of the endocarp is tomentose. Major vascular bundles in the mesocarp occur midway between and at the lateral ridges of the nut. The nut is wingless and has an exocarp of dense sclerenchyma interrupted at the ridges by dehiscence lines that traverse the entire fruit wall. The nut surface is glabrous, except near the distal end, where trichomes emerge in proximity to three styles and surrounding perianth remnants.

These nuts are placed in the genus *Fagus* and are roughly contemporaneous with the earliest fossils of the genus (Manchester and Dilhoff 2004). While subfamily Fagoideae is well represented in the Paleogene fossil record (Crepet 1989, Crepet and Nixon 1989; Kvaček and Walther 1989), all occur as compression fossils. The Appian Way specimens represent the first permineralized Fagaceae subfamily Fagoideae in the fossil record. *Fagus schofieldii* sp. nov. provides the earliest evidence of winglessness in Fagoideae and lends support for a North American origin for the genus.

CASCADIACARPA SPINOSA

Chapter 5 of this thesis erects a new genus of Fagaceae, employing a three-dimensional reconstruction to correlate internal anatomy to external morphology. More than 80 anatomically preserved specimens of spiny, cupulate fruits in various developmental stages were studied. 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 three-dimensional reconstruction of the cupulate nut allowed for correlation of internal anatomy to external morphology. Based on this complete set of fruit and cupule characters, the Appian Way fruits are placed in Fagaceae subfamily Castaneoideae. They are most similar to extant *Castanopsis* species but differ in having only two locules and a glabrous endocarp lining. A cladistic analysis supports the placement of the fossil within subfamily Castaneoideae along with *Quercus*, *Lithocarpus*, *Castanea*, *Castanopsis* and *Chrysolepis*. *Cascadiacarpa spinosa* gen. et sp. nov. is the first occurence of a bipartite gynoecium and earliest known occurrence of hypogeous fruits in Fagaceae. The appearance of *Cascadiacarpa* in the Eocene of British Columbia supports a Paleogene radiation of the family (Crepet 1989). The numerous derived characters of these fruits show that evalvate, spiny, single-fruited cupules of Fagaceae were present in the Paleogene of North America and as such these characters arose early within subfamily Castaneoideae. This is corroborated by the Eocene occurrences of single fruited cupules of *Quercus* and *Castanopsis* (Manchester 1994).

CASCADIACARPA EXILIS

Chapter 6 describes the most common fruit from the Appian Way locality. These small, narrow, spiny-margined fruits are represented by more than 800 specimens. Because of the exceptional preservation, the spiny outer tissues can be interpreted as cupule wall, as opposed to fruit wall. The cupule is borne on a spiny pedicel and has both simple and branched spines. The cupule is adnate to and almost entirely encloses a single nut, except at the apex. Nuts are small (less than 5 mm long) and ovoid. The nut wall is entirely sclerotic, though idioblast-like cells line the epidermis, while the locule lining is tomentose. The nuts are bilocular and early in development show a thin partition dividing these locules. Ovules are apical and attached to this septum. The apex of the nut protrudes through the cupule, likely representing the place of style attachment.

These fruits are placed in the family Fagaceae based on the presence of a spiny cupule enclosing a single nut, a feature diagnostic for the family (Kubitzki 1993). They are described as a second species of *Cascadiacarpa*. *Cascadiacarpa exilis* sp. nov. differs from the type species in nut shape, nut wall anatomy and the presence of basal lobes on the cupule. Both species of *Cascadiacarpa* share a suite of characters (spines, single-fruited cupules, ovoid-globose nuts) that place them firmly in subfamily Castaneoideae (Kubitzki 1993). The sheer number of single fruited specimens and the three-dimensional reconstruction corroborate the observation that *Cascadiacarpa* fruits possess cupules that surround a single flower, suggesting an early derivation of this condition among spiny-cupuled members (*Chrysolepis*, *Castanea*, *Castanopsis*) of subfamily Castaneoideae.

Cascadiacarpa exilis fruits also demonstrate the utility of permineralized fruits from Appian Way for broad comparisons to both living and fossil taxa. Eocene compressions from Washington State are identified in museum collections as *Ceratophyllum,* the only extant genus of Ceratophyllaceae, a family of weedy, aquatic plants (Les 1988) with a patchy Cenozoic fossil record (Herendeen et al. 1990). The compression fossils overlap with *C. exilis* in shape, size and spine morphology. As they are compressions, there is no way of knowing their internal anatomy. However, the results of this study suggest a more cautious approach to interpreting isolated ceratophyllaceous fruits in the fossil record, as they may be confused with the small fruits of *C. exilis*.

COMPARISON TO OTHER EOCENE FOSSIL LOCALITIES

Work done so far with the fossils from the Appian Way locality has shown broad affinities at the familial level with other Eocene localities. Angiosperm families identified from the locality (Platanaceae, Icacinaceae, Cornaceae, Juglandaceae, Fagaceae, Annonaceae, Menispermaceae, Meliaceae and Lauraceae) are common components of Eocene plant assemblages (Manchester 1999). All of these families are present in the Clarno Nut Beds of Oregon (Manchester 1994) and likewise all except for Fagaceae are present in the London Clay beds (Reid and Chandler 1933). However, at higher levels of taxonomic resolution there is little overlap between the fossils described from Appian Way thus far and those from other localities.

Regionally, Fagaceae is represented at Clarno by cupulate fruits of *Castanopsis* and *Quercus* (Manchester 1994). Pollen from the family is present in the Chuckanut/Huntingdon Formation around Vancouver (Mustard and Rouse 1994) and at many of the Okanagan Highlands localities of south-central British Columbia and north-central Washington State (Moss et al. 2005), however correlative macrofossils are scarce.

Fruits and vegetative material of *Fagopsis* and *Fagus* are known from the Okanagan Highlands (Pigg and Wehr 2002, Manchester and Dilhoff 2004), but otherwise fossil and extant genera of Fagaceae are disproportionately represented by pollen records along the Pacific margin of the North American continent. This disparity is also manifest at Messel, Germany, where the Eocene beds are laden with Fagaceae pollen type, but macrofossils from the family are entirely absent (Collinson 1988). At Appian Way, the opposite is true, where Fagaceae fruits are the most abundant angiosperm fossils but a survey of pollen (Sweet 2005) lacks any fagaceous signature. This discrepancy could be the result of a depositional bias between low energy freshwater environments (Messel) and higher energy, disturbed marine environments (Appian Way).

The Princeton Chert of southern British Columbia is geographically proximal in present day terms but because of the complex tectonic history of the area, no certain statements can be made about its proximity to the Appian Way locality in the Eocene. The Princeton Chert has been radiometrically dated as approximately 49 million years old. Like Appian Way, Princeton plant fossils are permineralized, though the latter locality is thought to represent a low energy freshwater environment, and many of the plants are interpreted being preserved *in situ* (Pigg and Stockey 1996, Stockey 2001). The two localities both preserve leafy shoots of Cupressaceae, flowers of Lauraceae flowers and possible cornalean fruits (Pigg and Stockey 1996); however, the wealth of aquatic plants preserved at Princeton are absent from Appian Way. Fagaceae fruits, so prominent at Appian Way and present at various Eocene localities (Pigg and Wehr 2002, Manchester and Dilhoff 2004), are absent from Princeton, as are inflorescences of Platanaceae. The Princeton Chert has a relatively diverse assemblage of ferns (see Smith et al. 2006 for a review), and while Osmundaceae and Dennstaedtiaceae are present at the two localities, Gleicheniaceae is present only at Appian Way. These major differences between the localities could be due to a disparity in age, geography or depositional environment.

The lack of Fagaceae fruits in the London Clay, by far the most extensive fruit and seed assemblage of the Eocene (Reid and Chandler 1933, Collinson 1983) seems to represent a real geographical disparity, as it, like Appian Way, represents a marine depositional environment (Reid and Chandler 1933). Given the concentration of Fagaceae fossils in the Paleogene of North America (Crepet 1989, Manchester 1994) and continental Europe (Kvaček and Walther 1989) it seems the family was not present in the terrestrial environment from which London Clay fossils originated. Interestingly, the only other North Hemisphere occurrence of the family Gleicheniaceae in the Paleogene outside of Vancouver Island is *Gleichenia hantonensis* from the Middle Eocene of southern England (Gardner and Ettinghausen 1882, Holtumm 1957).

The presence of *Palaeophytocrene pseudopersica* (Rankin et al. 2008), *Tiffneycarpa scleroidea* (Mindell et al. 2007b) and pistillate inflorescences of Platanaceae almost indistinguishable from *Macginicarpa glabra* (Mindell et al. 2006a) at Appian Way provides a macrofloral link to the Clarno Nut Beds of central Oregon (Manchester 1994). This serves as another line of evidence for an Eocene age for the Appian Way locality. The Clarno Nut beds have been given an absolute age of roughly 44 million years (Manchester 1994). This is congruent with the Late Paleocene-Middle Eocene range suggested by invertebrate fossils (Cockburn and Haggart 2007), but does not fit within the age range suggested by the palynological assessment of the locality (Sweet

2005). The incongruence of the macrofossils at Appian Way with the pollen assemblage suggests that palynology does not accurately reflect the age of the locality. However, the Eocene is a long epoch, and more exhaustive biostratigraphic lines of evidence will be needed to clarify the age of the locality. Exhaustive surveys of microfauna (dinoflagellates, foraminifera) might help refine age estimates.

CONCLUDING REMARKS

Fossils from the Appian Way locality described in this thesis as well as those already published in the literature have all contributed significant information on the age, origin, evolution and paleobiogeography of the groups to which they belong. They represent only a small fraction of the diversity of fossils from the concretions. Fossil fungi, exceedingly rare throughout the geological record (Tiffney and Barghoorn 1974, Taylor 1994), are present in abundance throughout the concretions. Two species have been described thus far (Smith et al. 2004, Mindell et al. 2007c), but many more occur within and on the surface of the permineralized plant material (See Elliott et al. 2006, Mindell et al. 2006a, Mindell et al. 2007a). The potential systematic utility of fossil ferns at Appian Way is best considered in light of the scant Cenozoic record of ferns (Collinson 2001). The Princeton Chert has demonstrated that Eocene fern diversity can be documented through anatomically preserved vegetative material (Smith et al. 2006). *Gleichenia* described from Appian Way represents an early entry in what could be one of the more diverse fern assemblages of the Paleogene. Only one conifer has been described thus far (Hernandez-Castillo et al. 2005), but an abundance of wood, shoots, leaves and cone material remains to be described.

Angiosperm families present at the locality have thus far provided characters rarely preserved in the fossil record (e.g., embryos, *in situ* pollen, trichomes). Thousands of specimens representing many morphotaxa are as yet undescribed from Appian Way, and this thesis and the work that preceded it exemplifies the utility and application of these fossils in angiosperm systematics. With the inventory of fossils and framework for studying them having been established with this thesis, future studies can continue to document diversity at the locality. As taxonomic resolution of the assemblage is refined, more exacting and exhaustive comparisons can be made to other Paleogene localities.

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Table 7.1. Preliminary list of plants and fungi preserved at the Appian Way locality.

TAXON	REFERENCES	ORGANS / STRUCTURES
Basidiomycota		
Hymenochaetales		
Appianoporites vancouverensis	Smith et al. 2004	Hymenophore
Ascomycota		
Pleosporales		
Margaretbarromyces dictyosporus	Mindell et al. 2007c	Ascocarp, asci, ascospores
Bryopsida		Gametophytes
Pteridopsida		
Filicales		
Osmundaceae		Stipes
Gleicheniaceae		
Gleichenia appianensis	Mindell et al. 2006b	Rhizome and associated stipes
Schizaeaceae		
Paralygodium vancouverensis	Trivett et al. 2006	Fertile pinnules, sporangia, spores
Blechnaceae		Stipes
Dennstaedtiaceae		Stipes
Cyatheaceae		Stipes
Coniferopsida		
Coniferales		
Cupressaceae		
Homalcoia littoralis	Hernandez-Castillo et al. 2005	Leaves, pollen cones, pollen
Cupressaceae		Wood, leaves, ovulate cones
Pinaceae		Ovulate cones, leaves
Angiosperms		
Magnoliales		
Annonaceae	Little et al. 2001	Seeds
Laurales		
Lauraceae	Little et al. 2001	Flowers, fruits, seeds
MONOCOTS		Roots, Stems
Zingiberales		Seeds

Table 7.1 continued.

TAXON			REFERENCES	ORGANS / STRUCTURES
EUDICOTS				
Ranunculales				
	Menispermaceae			Fruits
Proteales				
	Platanaceae			
		Gynoplatananthus oysterbayensis	Mindell et al. 2006a	Inflorescences, flowers, pollen
		Macginicarpa glabra	Mindell et al. 2006a	Inflorescences, flowers, pollen
Celastrales				
	Icacinaceae			
		Palaeophytocrene pseudopersica	Rankin et al. 2008	Fruits
		Palaeophytocrene vancouverensis	Rankin et al. 2008	Fruits
		Palaeophytocrene manchesterii	Rankin et al. 2008	Fruits
Fagales				
	Fagaceae			
		Cascadiacarpa spinosa	Mindell et al 2007b	Cupulate fruits
		Cascadiacarpa exilis	This thesis	Cupulate fruits
		Fagus schofieldii	This thesis	Fruits
	Juglandaceae			
		Beardia vancouverensis	Elliott et al. 2006	Fruits
		Unknown	Elliott et al. 2006	Fruits
	Betulaceae			Fruits
Sapindales				
	Meliaceae			
		Tiffneycarpa scleroidea		Fruits
Cornales				
	Mastixiaceae			Fruits (two kinds)
	Cornaceae			Fruits (two kinds)
INCERTAE SEDIS				
	Ferns			
		Siphonostelic fern rhizome		
		Matoniaceous fern rhizome		
		Onocleoid fern stipe		
	Gymnosperms			
		Ginkgo-like seed		
		Conifer leaves (four types)		
		Large conifer seed		

Table 7.1 continued.

TAXON

- *INCERTAE SEDIS*
  - Flowers
    - Apocarpous flower
  - Fruits
    - Apocarpous fruit with two locules, two seeds per locule
    - Three-loculed fruit
    - Trilocular fusiform fruit
    - Two-loculed fruit (two types)
    - Fleshy winged fruit
    - Fig-like fruit
    - Star-shaped fruit
    - Five-seeded fruit
    - Flask-shaped fruit
    - Large ovoid four-layered fruit
    - Conical infructescence
    - Large apocarpous fruit with four carpels
    - Five-locular fruit
    - Bubbly fruit
  - Seeds
    - Two-winged seed
    - Triangular seed
    - Small fusiform seeds
    - Ridged seed (three types)
    - Hairpin seed
    - *Allenbya*-like seed

Appendix 1. Palynomorphs from the Eocene Appian Way locality recorded by Sweet (2005). # denotes reworked Cretaceous palynomorphs, * represents palynomorphs diagnostic for the Eocene.

Spores
Biretisporites sp.
Cicatricosisporites sp.
Cranwellia sp. #
Cyathidites sp.
Distaltriangulisporites sp.
Echinatisporis sp.
Gleicheniidttes sp. #
Hazaria sp.
Laevigatosporites sp.
Lycopodiumsporites sp.
Osmundacidites sp.
Schizaea sp.
Selaginella sp.
Sphagnum sp.
Umbosporites sp. #
Zilvisporis sp.
Gymnosperm Pollen
Cupressaceae pollen
Tsuga sp. *
Ephedripites sp.#
Angiosperm Pollen
Alnus sp. *
Aquilapollenites reductus #
Betulaceae pollen
Caryapollenites sp. *
Cupanieidites sp.
Erdtmanipollis sp.
Liliacidites sp.
Momipites coryloides Wodehouse *
Normapolles pollen
Nyssapollenites sp.
Paraalnipollenites sp.
Pulcheripollenites sp. #
Platanoid pollen
Plicatopollis sp.
Proteacidites sp.
Retimonocolpites sp.
Retitricolpites sp. cf. *R. crassus* Samoilovich
Tiliapollenites sp. *