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Angiosperm wood from the Upper Cretaceous (Coniacian) of British Columbia, Canada

Nathan A. Jud[1], **Elisabeth A. Wheeler**[2], **Gar W. Rothwell**[3], and **Ruth A. Stockey**[3]

[1]L.H. Bailey Hortorium, Plant Biology section, School of Integrative Plant Science, Cornell University, Ithaca, NY 14853, U.S.A.
[2]Department of Forest Biomaterials, N.C. State University, Raleigh, NC 27695-8005, U.S.A.
[3]Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331, U.S.A.
Corresponding author; e-mail: nathan.jud@cornell.edu

ABSTRACT

Fossil angiosperm wood was collected from shallow marine deposits in the Upper Cretaceous (Coniacian) Comox Formation on Vancouver Island, British Columbia, Canada. The largest specimen is a log at least 2 m long and 38 cm in diameter. Thin sections from a sample of this log reveal diffuse-porous wood with indistinct growth rings and anatomy similar to *Paraphyllanthoxylon*. Occasional idioblasts with dark contents in the rays distinguish this wood from previously known *Paraphyllanthoxylon* species and suggest affinity with Lauraceae. The log also includes galleries filled with dry-wood termite coprolites. This trunk reveals the presence of tree-sized angiosperms in what is now British Columbia, and the association of dry-wood termites with angiosperm woods by the Coniacian (89 Ma). To understand the significance of this discovery, we reviewed the record of Cretaceous woods from North America. Our analysis of the distribution of fossil wood occurrences from Cretaceous deposits supports the conclusion that there was a strong latitudinal gradient in both the size and distribution of angiosperm trees during the Late Cretaceous, with no reports of Cretaceous angiosperm trees north of 50 °N paleo-latitude in North America. The rarity of angiosperm wood in the Cretaceous has long been used to support the idea that flowering plants were generally of low-stature for much of the Cretaceous; however, large-stature trees with *Paraphyllanthoxylon*-like wood anatomy were widespread at lower–middle paleo-latitudes at least in North America during the Late Cretaceous. Thus, the presence of a large *Paraphyllanthoxylon* log in the Comox Formation suggests that Vancouver Island has moved significantly northward since the Coniacian as indicated by other geological and paleo-botanical studies.

Keywords: Lauraceae, Coniacian, fossil, biogeography, latitudinal gradient, termites.

[In the online version of this paper Figure 1–4 are reproduced in colour.]

INTRODUCTION

Flowering plants dominate the tropical and temperate forests of the world both in terms of species richness and percent cover; however, despite considerable diversity known from fossilized pollen, leaves, flowers and fruits, the fossil record of angiosperm wood is surprisingly sparse until the Cenozoic. Gymnosperm wood is common in Cretaceous deposits, but there are fewer than 300 Cretaceous angiosperm wood types known that have reasonably detailed anatomical descriptions and good age and stratigraphic control (Wheeler & Baas 1991; InsideWood 2004-onwards; Wheeler & Lehman 2009; Peralta-Medina & Falcon-Lang 2012). More than two-thirds of those occurrences are from the uppermost Cretaceous (Campanian-Maastrichtian) (InsideWood 2004-onwards; Wheeler & Lehman 2009). Thus, any wood from an earlier stage of the Cretaceous has significance for broadening our knowledge of ancient angiosperm diversity and the rise of angiosperm-dominated communities.

Many fossil angiosperm woods from the Cretaceous fall into one of two broad categories: first, the icacinoid/platanoid xylotype represented by *Icacinoxylon* Shilkina and *Plataninium* Unger emend. Vater, and second, the phyllanthoid xylotype represented by *Paraphyllanthoxylon* Bailey and the very similar taxa, *Bridelioxylon* Ramanujam, *Glochidioxylon* Ramanujam, and *Carlquistoxylon* Wheeler, McClammer & Lapasha (*e.g.*, Thayn & Tidwell 1984; Wheeler *et al*. 1995; Oakley *et al*. 2009). Fossils assigned to the genus *Paraphyllanthoxylon* are among the oldest and largest angiosperm woods in Cretaceous assemblages. They have been found in Albian and younger deposits in North America, Europe, and Asia (*e.g.*, Bailey 1924; Herendeen 1999; Takahashi & Suzuki 2003; Gryc *et al*. 2009), and some specimens are nearly a meter or more in diameter (Cahoon 1972; Wheeler & Lehman 2009; Parrott *et al*. 2013). The characteristics of these early angiosperm trees have been reviewed multiple times (*e.g.*, Mädel 1962; Thayn & Tidwell 1984; Herendeen 1991; Takahashi & Suzuki 2003; Gryc *et al*. 2009; Méndez-Cárdenas & Cevallos-Ferriz 2013) and it is likely that they represent more than one natural group. At least some specimens likely belong to the Laurales because a char-coalified twig with wood anatomy similar to the juvenile wood of *Paraphyllanthoxylon marylandense* Herendeen was found attached to a lauraceous reproductive structure (Herendeen 1991). Others may be more closely related to Malpighiales or Sapindales (Wheeler & Lehman 2009). Affinities with Verbenaceae, Apocynaceae, Hamamelidaceae, and Samydaceae have also been suggested (Mädel 1962; Thayn & Tidwell 1984).

We describe a large permineralized log from the Coniacian of Vancouver Island, British Columbia, Canada, with phyllanthoid-type anatomy, but with unusually tall cells in the rays. Next, we compare the anatomy of this wood with other selected fossil woods attributed to *Paraphyllanthoxylon* and Lauraceae and show that this one is distinct. The log includes galleries with coprolites similar to those produced by kalotermitid (dry-wood) termites and provides the earliest evidence for an association between dry-wood termites and angiosperm wood. Finally, we examine the size and distribution of Cretaceous angiosperm woods from North America and discuss the implications of this new occurrence for understanding the ecology of Cretaceous angiosperms and the paleogeographic history and paleoclimate of Vancouver Island.

MATERIALS AND METHODS

Fossil angiosperm woods were collected from several sites on Vancouver Island, British Columbia, Canada, in the Upper Cretaceous Dunsmuir Member of the Comox Formation (Nanaimo Group) (Karafit *et al*. 2006; Karafit 2008; Mindell *et al*. 2014). The largest fossil specimen is a log found in the Eden Main Quarry (N 49° 49' 52.04", W 125° 25' 10.41"), 35 km northwest of Courtenay, where ~10 m of muddy to silty conglomeratic sandstone and greywacke breccia were exposed to make gravel (Schweitzer *et al*. 2003; Karafit & Stockey 2008; Klymiuk *et al*. 2015). The Comox Formation is diachronous and spans the Turonian to early Campanian (Haggart *et al*. 2003; Johnstone *et al*. 2006), but the presence of the collignonceratid ammonite *Prionocycloceras* at the Eden Main quarry constrains the age of that site to Coniacian (Klymiuk *et al*. 2015). Fossil decapods that co-occur with the plants support the interpretation of the Eden Main quarry site as a shallow-marine depositional setting with significant alluvial contribution (Mustard 1994; Schweitzer *et al*. 2003).

Plant fossils from the Comox Formation identified by Karafit (2008) include calcareous permineralizations of mosses, lycophytes, ferns, cycadeoids, conifers (Pinaceae, Cupressaceae), and angiosperm flowers, fruits, and wood; but only four taxa have been described in detail. Karafit and Stockey (2008) described a schizaeaceous fern from the Eden Main locality based on fertile fern pinnae. Two gymnosperms have been described: an unusual bennettitalean plant based on a single fossil stem (Jud *et al*. 2010), and a cupressaceous conifer based on a leafy branch with an attached seed cone (Klymiuk *et al*. 2015). Finally, Mindell *et al*. (2014) described inflorescences with bisexual flowers produced by an extinct member of the Platanaceae.

Figure 1. *Paraphyllanthoxylon vancouverense* sp. nov. Holotype; Condon Collections specimen number F-55441. Large log in Eden Main Quarry, 38 cm in diameter, extending at least 2 m into quarry wall. – N. A. Jud for scale.
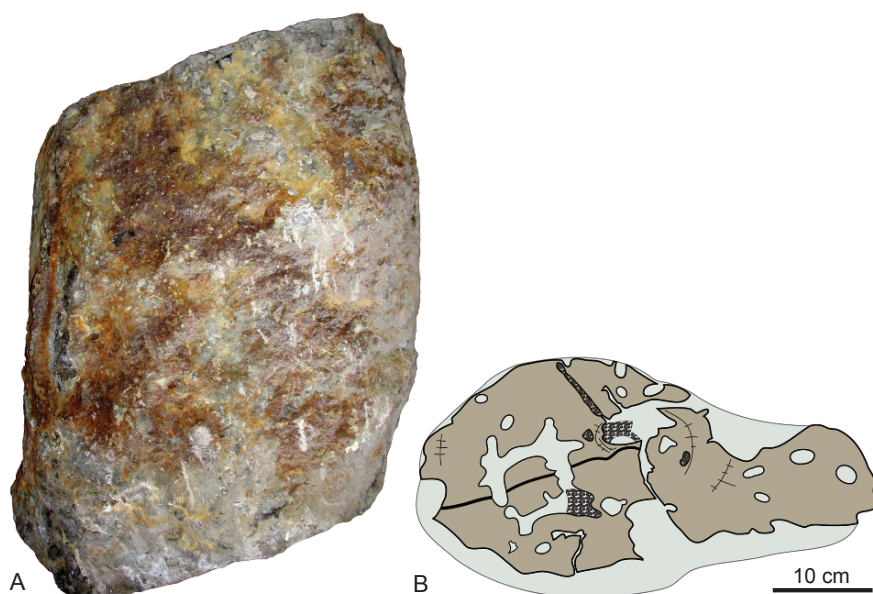
Figure 2. *Paraphyllanthoxylon vancouverense* sp. nov., holotype.
Condon Collections specimen number F-55441. – A: Segment of the fossil log, 56 cm long, 38 cm in diameter. – B: diagram of transverse section showing features of the fossil including wood with indistinct growth rings (dark gray), sediment filled galleries (gray), and coprolite-filled galleries (stippled).

Small fragments of fossil angiosperm wood are common at the Eden Main site, but the focus of this study is a permineralized, decorticated log, with one end originally exposed at the rock face extending at least 2 m before disappearing into the matrix (Fig. 1). Two segments of the log have been collected at different times. The first is c. 30 cm long and is deposited in the Paleobotanical Collections, University of Alberta (UAPC-ALTA). The second segment (Fig. 2) is 56 cm long and 38 cm in maximum diameter and housed in the Condon Museum collections at the University of Oregon Museum of Natural and Cultural History in Eugene, OR under specimen number F-55441. A sample of segment one was cut and prepared for thin sections in transverse section (XS), tangential longitudinal section (TLS), and radial longitudinal section (RLS) using the cellulose acetate peel technique (Joy *et al*. 1956). Peels were mounted on 25 × 75 mm slides for light microscopy using the xylene-soluble mounting medium Eukitt (O. Kindler GmbH, Freiburg, Germany). Segment two was cut, thin sectioned transversely, and slides made of the coprolite-filled galleries on 50 × 75 mm slides as above. Small fragments of wood with anatomy similar to the log were collected from the same quarry and four other nearby sites with similar lithology were described by Karafit (2008) before the discovery of our log (UAPC-ALTA P14457, P15041).

Images were captured using an Olympus DP70 digital camera and processed using Adobe Photoshop (San Jose, California, USA). Description of wood anatomy is based on the IAWA Hardwood List features (IAWA Committee 1989), with vessel diameter

and ray height averages based on 25 measurements, and total vessels (not vessel groupings) per square millimeter and rays per mm based on 10 counts. Finally, the fossil wood was compared with descriptions and images available on the InsideWood database (InsideWood 2004-onwards; Wheeler 2011) and in the literature.

A spreadsheet of Cretaceous fossil wood occurrences in North America was compiled using the InsideWood database (2004-onwards) and the dataset of Peralta-Medina & Falcon-Lang (2012). Then occurrences were cross-checked with the primary literature. We also included the largest minimum stem diameter estimate for each angiosperm wood type at each locality. These measurements were compiled either from original sources, by direct measurements of the fossils, or by calculating minimum diameter from the radius, by projecting the course of the rays inward to find the center and estimate the radius. Very small fragments were assigned minimum diameters of 1 cm or 10 cm.

SYSTEMATICS

Genus *Paraphyllanthoxylon* Bailey

Species *Paraphyllanthoxylon vancouverense* Jud, Wheeler, Rothwell et Stockey sp. nov. (Fig. 1–4).

Specific diagnosis: Tree-sized plant producing diffuse-porous wood with indistinct growth rings; vessels solitary and in short radial multiples; perforation plates simple; tyloses common; intervessel pits polygonal, alternate, crowded; vessel-ray pits with reduced borders wider than tall, irregularly distributed within ray cells, and throughout body of ray; fibers septate and nonseptate; scanty paratracheal axial parenchyma rare; uniseriate and multiseriate (1–4 cells), heterocellular rays with procumbent and upright cells mixed throughout rays; occasional taller cells with dark contents present in ray body. Storied structure, canals, and cambial variants absent; crystals not observed.

Etymology: The specific epithet *vancouverense* refers to Vancouver Island, where the fossil was collected.

Holotype: Large log, at least 2 m long, collected in two segments. One segment, including all figured parts, deposited as specimen number F-55441 in the Condon Collections, University of Oregon Museum of Natural and Cultural History, Eugene, OR, USA. The other segment of the holotype log has been deposited at the University of Alberta Paleobotanical Collections (UAPC-ALTA), Edmonton, AB, Canada.

Other specimens: UAPC-ALTA P15041; P14457.

Type locality: Eden Main Quarry (N 4° 49′52.04″, W 125° 25′10.41″).

Stratigraphic position and Age: Dunsmuir Member, Comox Formation, Nanaimo Group; Coniacian, Late Cretaceous, c. 89 Ma.

Description: The large, slightly compressed log is at least 38 cm diameter and over 2 m long (Fig. 1 & 2). Growth rings are indistinct, with a few rows of radially flattened fibers, and wood is diffuse porous (Fig. 3A). Vessels are evenly dispersed; solitary (37%) and in radial multiples of 2–4, with an average tangential diameter of 118 μm (sd = 17, range 82–167 μm) and a frequency of 7 (6–10) per mm^2 (Fig. 3A, B). Perforation plates are simple (Fig. 3C) and intervessel pitting is crowded alternate. Intervessel pits are 7–10 μm across, hexagonal in outline, and with narrow oval apertures
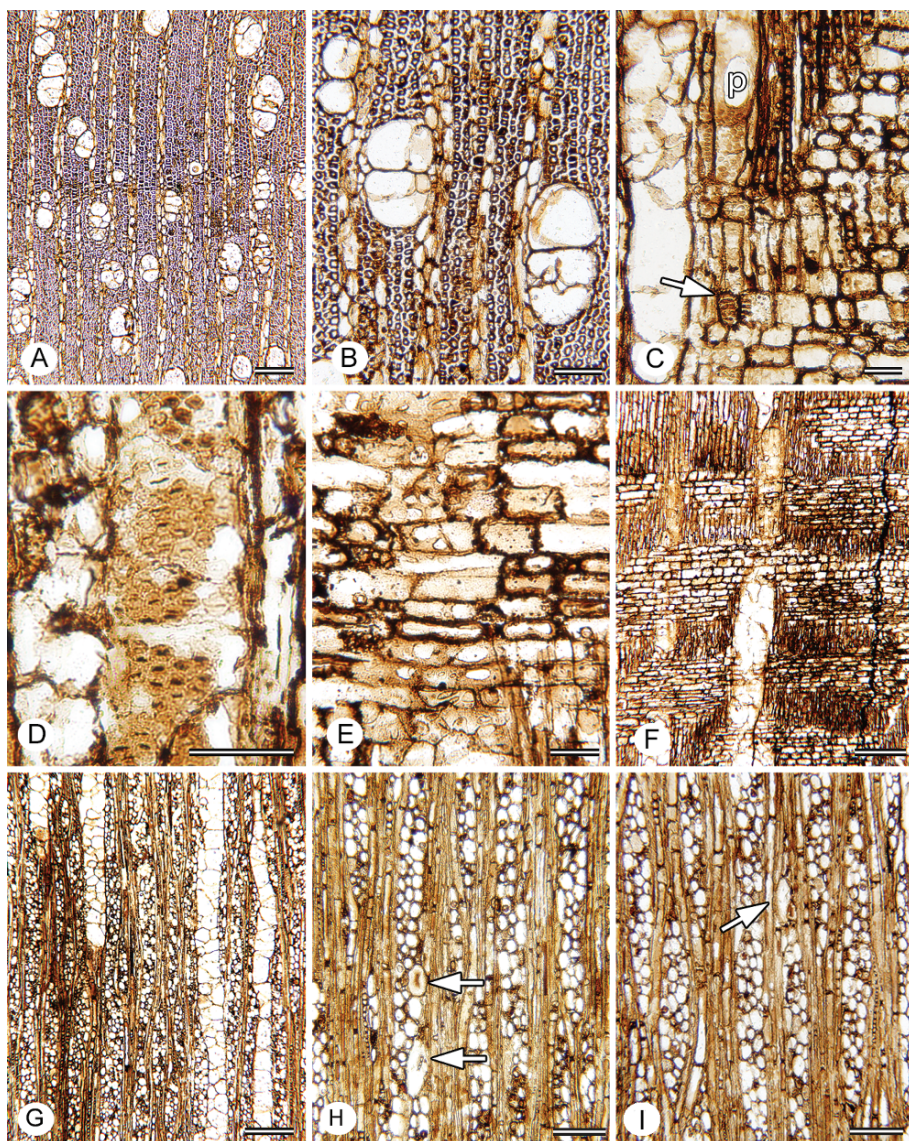
Figure 3. Wood anatomy of *Paraphyllanthoxylon vancouverense* sp. nov. Holotype; Condon Collections specimen number F-55441. – A: Diffuse porous wood with vessels solitary and in radial multiples of 2–3, growth rings indistinct, axial parenchyma rare (TS). – B: Radial multiples of 2, axial parenchyma rare (TS). – C: Simple perforation plate indicated by the letter "p", tyloses, horizontally elongate vessel-ray parenchyma pits (arrow) (RLS). – D: Alternate intervessel pitting (TLS). – E: Vessel-ray parenchyma with much reduced borders, oval to horizontally elongate (RLS). – F: Body of ray composed mostly of procumbent cells, with intermixed square and upright cells (RLS). – G: Vessels filled with bubble-like tyloses (TLS). – H & I: Rays predominantly 3–4-seriate, cells variable in size, arrows point to enlarged ray cells, resembling oil cells (TLS). — Scale bars: 200 μm in A, F, G; 100 μm in B, H, I; 50 μm in C, D, E.

extending almost to the edge of the border (Fig. 3D). The vessel-ray parenchyma pits have reduced borders and are oval to horizontally elongate, irregularly distributed within the ray cells and, throughout the body of the ray, similar to Richter's class b vessel-ray pits for Lauraceae (Richter 1987) (Fig. 3F). Tyloses are abundant and bubble-like (Fig. 3C, F, G). Axial parenchyma is rare, with some scanty paratracheal parenchyma. Fibers are thin- to medium-thick-walled, and some are septate, but others are non-septate. Fiber pits were not observed. Rays are mostly 2–4-seriate, uniseriate rays are rare (Fig. 3G). Ray cell size is variable, and cells have thin, smooth walls (Fig. 3G, H, I). Uniseriate margins of multiseriate rays are 1–2 cells high as viewed in tangential section. The ray body consists mostly of procumbent cells, with some intermixed square, and upright cells, but the upright cells are not in long horizontal series like tile cells (Fig. 3C, E, F). In tangential and transverse sections, some enlarged ray cells have dark contents, but we did not observe the characteristic swollen-look in radial section that is typical of enlarged oil cells in many, but not all, Lauraceae (Fig. 3H, I). Mean ray height 23 cells (sd = 8.5; n = 25), range 10–36 cells, or 658 (sd = 278; n = 25) μm, range 228–1188 μm. Ray frequency ranges from 6–10 rays per tangential mm. Crystals, storied structure, canals, cambial variant structure have not been observed.

Comments: If the 0.38 m segment of trunk that represents *P. vancouverense* was located at breast height on the stem, then the tree is predicted to be at least 23.5 (16.3–34.1) m tall using the allometric scaling equations of Rich *et al*. (1986) and Feldpausch *et al*. (2011) for tropical angiosperm trees. It was not possible to reliably measure vessel element lengths because of abundant tyloses obscuring the vessel element end walls.

Galleries

The log has internal cracks and irregular galleries that are visible in transverse section (Fig. 2). One of these galleries obscures the pith. Some of these galleries are filled with sediment, but others are filled with dark brown, homogeneous/amorphous bodies in a light-brown, homogeneous matrix. These bodies are 0.73–1.13 mm in diameter, ~1130 μm by 730 μm (n = 17), oblong in longitudinal section, and hexagonal with convex to straight, (rarely concave) sides in transverse section (Fig. 4).

Figure 4. *Paraphyllanthoxylon vancouverense* sp. nov. Holotype; Condon Collections specimen num–ber F–55441. Transverse section of wood showing gallery filled with light brown frass and dark brown, oblong, hexagonal coprolites. – Scale bar: 1 mm.

Table 1. Comparison of the Cretaceous *Paraphyllanthoxylon* species and *Aplectotremas*.

Taxon	Specimens	Origin	Age	GR	PP	%S	MVG
A. halistichum	UPTN 259A	TX, USA	Al	–	–	~20	3
P. utahense	BYU 2190	UT, USA	Al	–	–	?	5
P. arizonense	USNM 4263; YPM 30151, 30155, 30156	AZ & NM, USA	Ce-Ma	–	–	?	4
P. idahoense	Henry Shaw School of Botany Coll. slides 1482–1484	ID, USA	Ce	–	–	?	4
P. aff. *utahense*	102/04	Czech Rep.	Ce	–	–	29	5
P. alabamense	W5, W11, W18, W19, W21, W24, W27, W28, W34	AL, USA	Tu	+/-	–	30–70	7
P. vancouverense	**Codon Coll. F-55441**	**BC, Canada**	**Co**	**–**	**–**	**37**	**4**
P. cf. *marylandense*	LPPU 1747	Belgium	Sa	–	–	?	6
P. obirense	TK 98141	Hokkaido, Japan	Sa	–	–	52	5
P. anasazii*	USNM 507032; TXSTATE 1205; YPM 30147, 30159	TX & NM, USA	Ca-Ma	–	–	33–64	4
P. capense	SMB 9084/2	South Africa	Ca-Ma	–	–	?	6
P. illinoisense*	SIPC 607.9 (and 9 others)	IL, USA	Ma	–	–	low	8
P. romanicum	University of Cluj-Napoca Paleobot. Coll. No. 439	Romania	Ca-Ma	–	–	12	9
P. bacense*	G.I.R. 26357, 26358	Romania	Ma-Da	–	-/+	?	3
P. sp.*	UNAM LPb No. 50	Mexico	Ma	–	–	54	4

<div align="right">⟶</div>

Legend: The subject of this study is in bold. Data were obtained from new measurements and from the literature (Bailey 1924; Spackman 1942; Mädel 1962; Cahoon 1972; Petrescu *et al*. 1978; Serlin 1982; Thayn 1983; Wheeler *et al*. 1987; Wheeler 1991; Cevallos-Ferriz & Weber 1993; Wheeler *et al*. 1995; Iamandei & Iamandei 2000; Meijer 2000; Wheeler & Lehman 2000; Takahashi & Suzuki 2003; Gryc *et al*. 2009; Estrada-Ruiz *et al*. 2012).

Age: Al = Albian, Ce = Cenomanian, Tu = Turonian, Co = Coniacian, Sa = Santonian, Ca = Campanian, Ma = Maastrichtian, Da = Danian (Paleocene); GR = growth rings, (–) indistinct (+) distinct; PP = perforation plates, (–) simple, (+) scalariform; %S = percent solitary vessels; MVG = maximum number of vessels in radial multiples.

(Legend continued on the next page)

(Table 1 continued)

Taxon	MTD	VF	Ty	AP	l-r	MR	RCC	MUs	RF	Id	Crys
A. halistichum	193	?	?	1	?	4	1	?	?	–	–
P. utahense	93	12	2	1	–	5	1	2	9.5	–	–
P. arizonense	143–184	6	1	1	+	7	1	1/2	4	–	–
P. idahoense	100	?	1	1	–	4	1	2	?	–	–
P. aff. *utahense*	84–95	20	1	1	–	7	1	2	?	–	–
P. alabamense	83–136	5–14	1/3	1	'-/+	4	1	1	4.3–5.5	–	–
P. vancouverense	**118**	**7**	**1**	**1**	**–**	**4**	**1**	**1**	**8**	**+**	**–**
P. cf. *marylandense*	60–200	29–47	?	1	–	4	1	2	11	–	–
P. obirense	96	27	2	1	–	3	1	?	?	–	–
*P. anasazii**	74–120	5–24	2	1	'-/+	3	2	1	8.5	–	–
P. capense	74	39	1	1	–	?	?	2	7.5	–	–
*P. illinoisense**	118	22	2	1	+	6	2	2	?	–	+
P. romanicum	86	?	1	1	–	7	1	1/2	?	–	–
*P. bacense**	~105	~25	3	2	+	3	1	2	15	–	+
P. sp.*	68	10	?	1	–	5	2	1	11	–	–

←

(Legend continued) MTD = mean tangential vessel diameter (ranges were obtained from multiple specimens in μm); VF = vessels per square millimeter (ranges were obtained from multiple specimens); Ty = Tyloses: 1 = bubble-like, 2 = segmenting vessel, 3 = sclerotic; AP = axial parenchyma, 1 = rare to scanty paratracheal, 2 = diffuse or diffuse-in-aggregates; 1-r = uniserate rays, (–) rare, (+) common; MR = maximum multiseriate ray width; RCC = ray cellular composition, 1 = mixed upright & procumbent, 2 = homocellular, procumbent; MUs = rows of marginal upright cells associated with rays; 1 = one or rarely two rows of marginal uprights, 2 = commonly two or more rows of marginal upright cells; RF = ray frequency per linear millimeter; Id = Idioblasts: (–) not observed, (+) present, tall cells in rays with dark contents; Crys = Crystals: (–) not observed, (+) present in ray cells. Species marked with an asterisk are in need of revision and may not fit the diagnosis of *Paraphyllanthoxylon*.

DISCUSSION

Comparison with extant and fossil plants

The fossil wood from Eden Main described here has vessels that are solitary and in short radial multiples, simple perforation plates, medium-large and alternate intervessel pits, simple and rounded vessel-ray pits with reduced borders, rare-scanty paratracheal parenchyma, multiseriate heterocellular rays, and septate fibers without distinctly bordered pits. It thus conforms to the genus *Paraphyllanthoxylon*; however, it is unusual for the genus in having enlarged ray cells with dark contents which may have been oil or mucilage cells. No such cells occur in sections of the type (*P. arizonense* Bailey) or in more recent collections from the type locality, nor in other species of Cretaceous *Paraphyllanthoxylon* (Table 1). When oil cells are present in the rays of wood with otherwise *Paraphyllanthoxylon*-like anatomy, the combination of characters indicates affinity with Lauraceae (Metcalfe & Chalk 1950; Stern 1954; Richter in Metcalfe 1987; Dupéron-Laudoueneix & Dupéron 2005). We searched for the distinctive enlarged or swollen shape of lauraceous oil cells in radial section, but we did not find them. Although we think this wood is most probably Lauraceae, it should not be assigned to *Laurinoxylon* Felix emend. Dupéron, Dupéron-Laudoueneix, Sakala & De Franceschi because typical oil cells are not present (Mantzouka *et al*. 2016). Therefore, in order to avoid the multiplication of fossil genera based on a few characters of equivocal systematic importance, we assign this wood to the genus *Paraphyllanthoxylon*.

The diversity of *Paraphyllanthoxylon* woods has been reviewed several times (*e.g*., Mädel 1962; Thayn & Tidwell 1984; Herendeen 1991; Takahashi & Suzuki 2003; Gryc *et al*. 2009) and there are now at least 10 species assigned to the genus from Cretaceous deposits (Table 1). The relationships among these species are uncertain and the genus is likely polyphyletic (Herendeen 1991; Oakley *et al*. 2009; Méndez-Cárdenas *et al*. 2013). We compiled data from the literature to compare *P. vancouverense* with previously described species (Table 1). In the process, we noticed that Cahoon (1972) reported radial vessel diameters rather than tangential vessel diameters, so we made new observations and measurements from slides of nine of the eleven original specimens following the same methods used to describe *P. vancouverense*. We did not find, as reported previously, that *Paraphyllanthoxylon* species are readily grouped into those with rare uniseriate rays and only a few rows of marginal upright cells in the multiseriate rays versus those with common uniserate rays and many rows of upright marginal cells in the multiseriate rays (Wheeler *et al*. 1987; Herendeen *et al*. 1991). The most obvious difference between *P. vancouverense* and the other species is the presence of tall ray cells with dark contents visible in tangential section, but the combination of short radial vessel multiples (up to 4), low vessel frequency, rare uniseriate rays, and rays typically with one row of upright marginal cells also served to distinguish *P. vancouverense* from other species in the genus (Table 1).

Woods assigned to the Lauraceae (Table 2) are relatively common in the fossil record, occurring on all continents, including Antarctica (Gregory *et al*. 2009). No doubt this reflects, in part, the past abundance and diversity of Lauraceae. However, the heartwood of many Lauraceae species is resistant to decay, potentially leading to better

representation in the fossil record compared to most other families. Süss and Mädel (1958), and later Dupéron-Laudoueneix and Dupéron (2005), reviewed fossil woods assigned to Lauraceae and commented on the reliability of the assignments. The latter authors accepted seven fossil wood genera as properly used for Lauraceae: *Caryodaphnopsoxylon* Gottwald (1992), *Cinnamonoxylon* Gottwald (1997), *Cryptocaryoxylon* Leisman (1986), *Laurinoxylon* Felix emend. Dupéron, Dupéron-Laudoueneix, Sakala & De Franceschi (2008) (essentially a synonym of *Ulminium* Unger, see Page 1967; Dupéron *et al.* 2008 for discussions of which name has priority), *Mezilaurinoxylon* Wheeler & Manchester (2002), *Paraperseoxylon* Wheeler & Manchester (2002), and *Sassafrasoxylon* Březinová & Süss (1988). They also recognized *Paraphyllanthoxylon marylandense* as Lauraceae, which lacks oil cells in the rays like other *Paraphyllanthoxylons*, but was associated with a lauraceous inflorescence (Herendeen 1991). An eighth genus, *Sabulia* Stopes, was also assigned to the Lauraceae by Crawley (2001) because he observed "possible oil cells at ray margins", which were only figured in tangential section (Crawley 2001: p. 65).

Since the work of Dupéron-Laudoueneix and Dupéron (2005), three other genera have been proposed for fossil Lauraceae woods: *Richteroxylon* Wheeler & Dillhoff (2009) from the middle Miocene of Vantage, Washington, USA, *Olmosoxylon* Estrada-Ruiz *et al.* (2010) from the late Campanian-early Maastrichtian of northern Mexico, and *Argapaloxylon* Castañeda-Posadas, Calvillo-Canadell & Cevallos-Ferriz (2009) from the Miocene of Mexico. The assignment of *Argapaloxylon* to Lauraceae is suspect because the generic diagnosis mentions presence of vasicentric tracheids, a cell type that does not occur in extant Lauraceae (Metcalfe & Chalk 1950; Stern 1954; Richter in Metcalfe 1987), and homocellular rays. All species of Lauraceae have heterocellular rays with one or more marginal rows of square and upright cells, although in some species some homocellular rays co-occur (Metcalfe & Chalk 1950). The generic diagnosis does not mention oil cells, but the specific diagnosis of *A. richterii* does. Unfortunately, the figures do not clearly show oil cells. We accept *Olmosoxylon* and *Richteroxylon* as additional genera for lauraceous woods (Table 2).

Most, but not all, Lauraceae have oil cells in the wood; but when they are present they are not necessarily distributed throughout stems and roots (Page 1967). Oil cells vary in their distinctiveness, size, and location (ray parenchyma, axial parenchyma, amongst fibers, or a combination of these; Richter 1987; Mantzouka *et al.* 2016). They can also be rare or variable in occurrence within a species, so that a section of a particular sample may not show oil cells. Oil cells associated with rays are typically at the ray margins, but a few species have them in the body of the rays, *e.g.*, *Cinnamomum parthenoxylon* (Jack) Meisn. (Ilic 1991, p. 240) and the Cretaceous *Olmosoxylon*. An assemblage of late Campanian woods from New Mexico includes a group of woods with a continuum of oil cell development – some samples have obvious oil cells in the body of the ray, whereas others have somewhat enlarged cells with dark contents (J. Parrott, pers. comm.; Parrott *et al.* 2013). The variability of ray cell sizes and shapes in *Paraphyllanthoxylon vancouverense* is similar to that seen in tangential sections of the Cretaceous *Olmosoxylon* (Estrada-Ruiz *et al.* 2010: fig. 6H) and (although not as pronounced) in some rays of some present-day Lauraceae species (*e.g.*, *Cinnamomum*

Table 2. Comparison of the anatomical features of lauraceous fossil woods.   →

Taxon	NS	GR	VG	%S	PP	IVP	MTD	VF	VEL
***Paraphyllanthoxylon vancouverense* n.sp.**	**1**	**–**	**1–4**	**37**	**–**	**7–10**	**118**	**7 (6–10)**	**?**
Laurinoxylon	4	srp	1–4	?	-/+	7–10	100–154	9–16	300–550
Olmosoxylon	1	–	1–4	77	–	5–11	109	9 (4–14)	449
Beilschmiedioxylon	1	mp	1–3	57	–	10–12	185	3–9	~500
Caryodaphnopsoxylon	1	+	1–4	?	–	8–13	~160	?	?
Cinnamomoxylon	1	+/-	1–4	?	-/+	7–12	~100	~16–34	?
Cryptocaryoxylon	1	+/-	1–4	?	–	10–13	~150	?	80–550
Mezilaurinoxylon	5	–	1–4	?	–	>10	84–125	16–38	500
Paraperseoxylon	2	–	1–3	?	-/+	5	<100	14 (7–28)	280
Richteroxylon	1	+	1–3	54	–	6–8	90	50–65	~350
Sabulia	3	+	1–3	~60	–	6–10	59–134	11–29	132–330

                                                                              →

Legend: The subject of this study is in bold. Data for extinct lauraceous genera known from fossil woods were obtained from the literature (Felix 1883; Stopes 1913; Leisman 1986; Gottwald 1992, 1997; Wheeler & Manchester 2002; Dupéron-Laudoueneix & Dupéron 2005; Estrada-Ruiz *et al*. 2010). NS = number of specimens on which the generic diagnosis and description of the type species are based; GR = growth rings, (–) indistinct (+) distinct, srp = semi-ring porous, mp = marginal parenchyma; VG = vessels per radial grouping; %S = percent solitary vessels in transverse section; PP = perforation plates, (–) = simple, (+) = scalariform; IVP = alternate intervessel pit size (ranges measured in μm); MTD = mean tangential vessel diameter (ranges in μm were obtained from multiple specimens or multiple fields of view); VF = vessels per square millimeter; VEL = vessel element length, lengths reported in μm.

daphnoides Sieb. & Zucc., *Cryptocarya aschersoniana* Mez, *C. barbellata* A.C.Sm., *C. glaucescens* R.Br., *Lindera umbellata* Thunb.; InsideWood 2004-onwards). So whereas the Eden Main wood cannot be confidently assigned to *Laurinoxylon* because oil cells were not seen in radial section, the variability and continuum in oil cell distinctiveness in the Lauraceae supports considering the Eden Main wood Lauraceae. Lauraceous foliage was common throughout the Cretaceous of North America, albeit not in the northern Rocky Mountains (*e.g.*, Crabtree 1987; Kvaček 1992; Wing & Boucher 1998; Doyle & Upchurch 2014), so wood of this arborescent family should also be present. In the future, investigating whether there are repeated co-occurrences of lauraceous leaves and *Paraphyllanthoxylon* wood could help to establish which phyllanthoid woods are Lauraceae.

Plant-arthropod interactions

We interpret the contents of the galleries (Fig. 4) as coprolites that are rather tightly packed in a frass-supported matrix. Based on the size, shape, arrangement, and texture they are assignable to the *Microcarpolithes hexagonalis* Vangerow, an ichnotaxon used

(Table 2 continued)

Taxon	VRP	RW	RH	RF	RCC	MU	Fibers	AP	Id
Paraphyllanthoxylon vancouverense n. sp.	**r**	**(1–)2–3**	**658**	**6–10**	**he**	**1**	**s/n**	**s**	**rm/rb**
Laurinoxylon	r	1–5	< 1 mm	6–7	he	1–3	?	s-v	rm
Olmosoxylon	r	3–7	400–1430	?	he/ho	1	s/n	s	rb
Beilschmiedioxylon	r	1–6	100–850	4–8	he	1–4	n	v/b	f
Caryodaphnopsoxylon	r	1–8 (–12)	>1 mm	?	he	1–2	s	v	rb/ap
Cinnamomoxylon	r	1–3	300–590	12–14	he	1	s/n	v/a-c	rm/ap
Cryptocaryoxylon	r	1–5	< 1 mm	?	ho	0	n	s/b-c	f
Mezilaurinoxylon	w	1–4 (–5)	437–1423	6–7	he	1	s	s	rb
Paraperseoxylon	c	1–2 (–3)	340–370	6–7	he	1	n	v-c	rm/f
Richteroxylon	s	1–2	168–552	5–8	he	1	n	s-v	rm/rb
Sabulia	r	1–4	208–550	?	he	1	s/n	s-v/a/b	rm

←

(Legend continued) VRP = vessel-ray parenchyma pits, r = with reduced borders and oval to horizontally elongate, c = with reduced borders; horizontally elongate, curved, and small rounded, w = with reduced borders and window-like, s = similar to intervessel pits; RW = maximum multiseriate ray width; RH = ray height in μm; RF = ray frequency per linear mm; RCC = ray cellular composition, he = heterocellular, ho = homocellular; MU = number of rows of marginal upright cells associated with rays; Fibers: s = septate, n = non-septate; AP = axial parenchyma, s = scanty paratracheal, v = vasicentric, a = aliform, c = confluent, b = banded; Id = idioblasts, rm = at ray margins, rb = in ray bodies, f = amongst fibers, ap = among axial parenchyma.

for kalotermitid (dry-wood) termites and mastotermitid (giant northern) termite coprolites (Rohr *et al*. 1986; Labandeira *et al*. 1997; Hasiotis 2003; Grimaldi & Engel 2005; Massini & Pujana 2013). The shape of the galleries, their presence in angiosperm wood, and the rarity of fungal hyphae in the wood specimen suggests the termite coprolites were most likely produced by kalotermatid termites (Rohr *et al*. 1986; Wheeler *et al*. 1994; Boucot 2013).

Recent phylogenetic work suggests that kalotermitid termites are not primitive, but rather are deeply nested within Euisoptera, and that their appearance and diversification may be correlated with the diversification of woody flowering plants in the later part of the Early Cretaceous and the Late Cretaceous (Engel *et al*. 2009). The termite fossil record consists of both body fossils (often in amber), wings, and the distinctive hexagonal coprolites with worldwide distribution by the end of the Late Cretaceous (Thorne *et al*. 2000; Engel *et al*. 2009, 2011; Colin *et al*. 2011). Although termite fossils are known from Lower Cretaceous deposits (Thorne *et al*. 2000; Engel *et al*. 2008, 2011), the presence of Coniacian *Microcarpolithes hexagonalis* in this log is early evidence of termite activity on angiosperm trees. Similar coprolites have been

found dispersed in mid-Cretaceous deposits of Iowa (Hall 1963), Kansas (Kovach & Dilcher 1988), Alberta (McLean & Wall 1981), and Nova Scotia (Calder *et al*. 1998; Scott & Stea 2002); in permineralized *Cycadeoidea* trunks from the Aptian-Albian of Utah (Dayvault & Hatch 2005), in true cycads from the Cretaceous of Argentina (Genise 1995); in conifer wood from the Barremian of the Isle of Wight (UK) (Francis & Harland 2006) and the Maastrichtian of Texas (Rohr *et al*. 1986). Termite fossils have been collected from the Cenomanian of Labrador (Emerson 1967) and the Turonian of New Jersey (Krishna & Grimaldi 2000), but neither of these are kalotermitids. Until now, the earliest published evidence for termite activity in angiosperm wood came from the Maastrichtian of Texas (Wheeler *et al*. 1994; Boucot 2013).

Paleogeography

There was a strong latitudinal gradient in the distribution and size of angiosperm trees during the Late Cretaceous in North America (Fig. 5). By the start of the Late
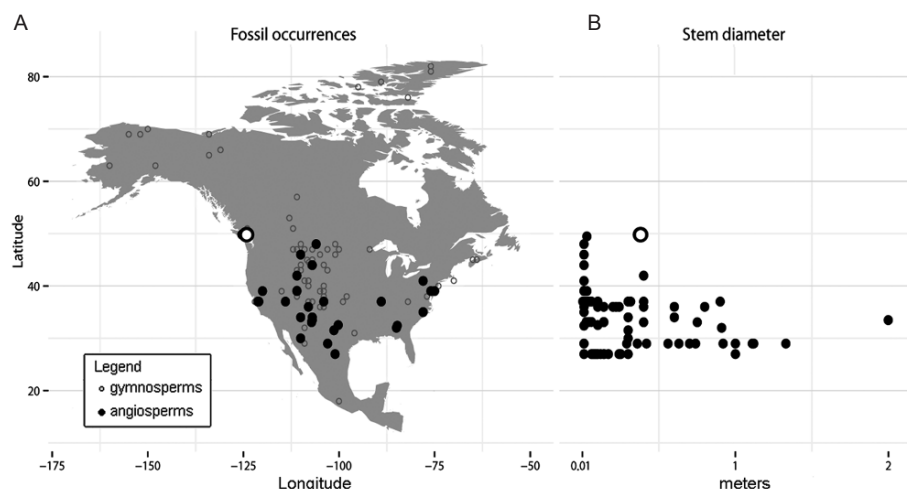
Figure 5. Fossil record of Cretaceous angiosperm woods from North America. Black dots represent occurrences of angiosperm woods, small open circles represent gymnosperm wood occurrences, and the bold open circle represents location and diameter of the *Paraphyllanthoxylon vancouverense* log. – A: Fossil wood occurrences from Albian–Maastrichtian (Cretaceous) deposits in North America (left). Note widespread distribution of gymnosperm woods from the Cretaceous of Canada and Alaska, but paucity of Cretaceous fossil woods from Mexico and Central America. Gymnosperm fossil wood location data from Peralta–Medina & Falcon-Lang (2012). – B: Scatterplot of latitude of angiosperm wood occurrences against minimum diameter estimates. Each point represents the largest minimum diameter estimate for each angiosperm wood type at each site. Note strong latitudinal gradient in size and frequency of occurrences. (Bailey 1924; Spackman 1948; Page 1967, 1968, 1970, 1979, 1980; Cahoon 1972; Serlin 1982; Cevallos-Ferriz 1983, 1992; Thayn *et al*. 1983; Tidwell & Thayn 1985; Wheeler *et al*. 1987, 1994, 1995; Wolfe & Upchurch 1987; Herendeen 1991; Wheeler & Lehman 2000, 2009; Lehman & Wheeler 2001; Hudson 2006; Estrada-Ruiz *et al*. 2007, 2010, 2012; Sweeney *et al*. 2009; Davies-Vollum *et al*. 2011; Falcon-Lang *et al*. 2012; Peralta-Medina & Falcon-Lang 2012; Parrott *et al*. 2013; Smith *et al*. 2013).

Cretaceous, angiosperm pollen and leaves were globally distributed (Hickey & Doyle 1977), but as far as we know, fossilized angiosperm wood has not been found in Cretaceous deposits north of ~50 °N (InsideWood 2004-onwards) despite the abundance of gymnosperm wood (Peralta-Medina & Falcon-Lang 2012). This northern limit of ~50 °N matches the range of megathermal climates inferred based on leaf physiognomy and the distribution of crocodilians during the Late Cretaceous (Wolfe & Upchurch 1987; Markwick 1998), but contrasts with the emerging pattern from South America and Antarctica, which indicates that angiosperm trees were present on Antarctica at southern high latitudes by the Coniacian-Santonian (Francis 1986; Rees & Smellie 1989; Francis & Poole 2002; Cantrill & Poole 2005).

The distribution of Cretaceous angiosperm and gymnosperm woods in North America is consistent with the hypothesis that, although angiospermous herbs and shrubs were globally distributed by the mid-Cretaceous (Spicer & Parrish 1986; Wing *et al.* 1993, 2011; Cantrill & Nichols 1996; Wing & Boucher 1998), in North America large angiosperm trees were restricted to middle latitudes probably because of the distribution of subtropical/warm temperate conditions (*e.g.*, Bailey 1924; Cahoon 1972; Wheeler *et al.* 1987, 1995; Wolfe & Upchurch 1987; Wheeler & Lehman 2000, 2009; Lehman & Wheeler 2001; Estrada-Ruiz *et al.* 2010, 2012; Parrott *et al.* 2013). Additional field work is necessary to determine whether the pattern of increasing abundance and size of angiosperm trees with decreasing latitude extended to low latitudes, south of ~25 °N during the Late Cretaceous, because reports of fossil woods of any kind from the Cretaceous of Southern Mexico and Central America are rare (Fig. 5). A single occurrence reported from the Cretaceous of Oaxaca (Müller-Stoll & Mädel 1967) may in fact be Cenozoic (Calvillo-Canadell & Cevallos-Ferriz 2002).

At N 49° 49'52.04" *Paraphyllanthoxylon vancouverense* is the northernmost occurrence of a Cretaceous angiosperm tree to date from North America. However, the Eden Main site occurs on a portion of the allochthonous Wrangellia Terrane that has migrated northward along the western margin of North America since the Early Cretaceous as the North American plate has rotated counter-clockwise. During the Coniacian, alternative models suggest that the Eden Main site may have been located as far north as ~51 °N and thus has roughly maintained its position as North America rotated, or as far south as 29.0 °N (Krijgsman & Tauxe 2006; Miller *et al.* 2006). The presence of lauraceous trees at least 23 meters tall and with indistinct growth rings in the Eden Main assemblage suggests that the Coniacian flora of Vancouver Island grew under warm conditions to the south and supports the hypothesis that Wrangellia has migrated north since the Late Cretaceous.

CONCLUSIONS

Plant fossils from the Eden Main locality on Vancouver Island provide evidence that large lauraceous trees co-occurred with platanoids and conifers during the Coniacian on the allochthonous terrane Wrangellia in western North America. The Eden Main fossils also indicate that drywood termites began exploiting the wood of angiosperms relatively early in angiosperm evolution. A review of the literature suggests that warm,

equable climates were important for the development of large angiosperm trees during the Late Cretaceous. Tectonic evidence, the absence of growth rings in *Paraphyllanthoxylon vancouverense*, and co-occurring fossils, all indicate that the Eden Main flora grew under mesic conditions south of ~50 °N.

ACKNOWLEDGEMENTS

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APPENDIX

Supplement 1. Age and distribution of occurrences of Cretaceous angiosperm wood fossils from North America, including minimum diameter estimates. The dataset is available in *.csv format at https://figshare.com/s/e2b83e2964c8e929ffaf