The Middle Miocene Wood Flora of Vantage, Washington, USA

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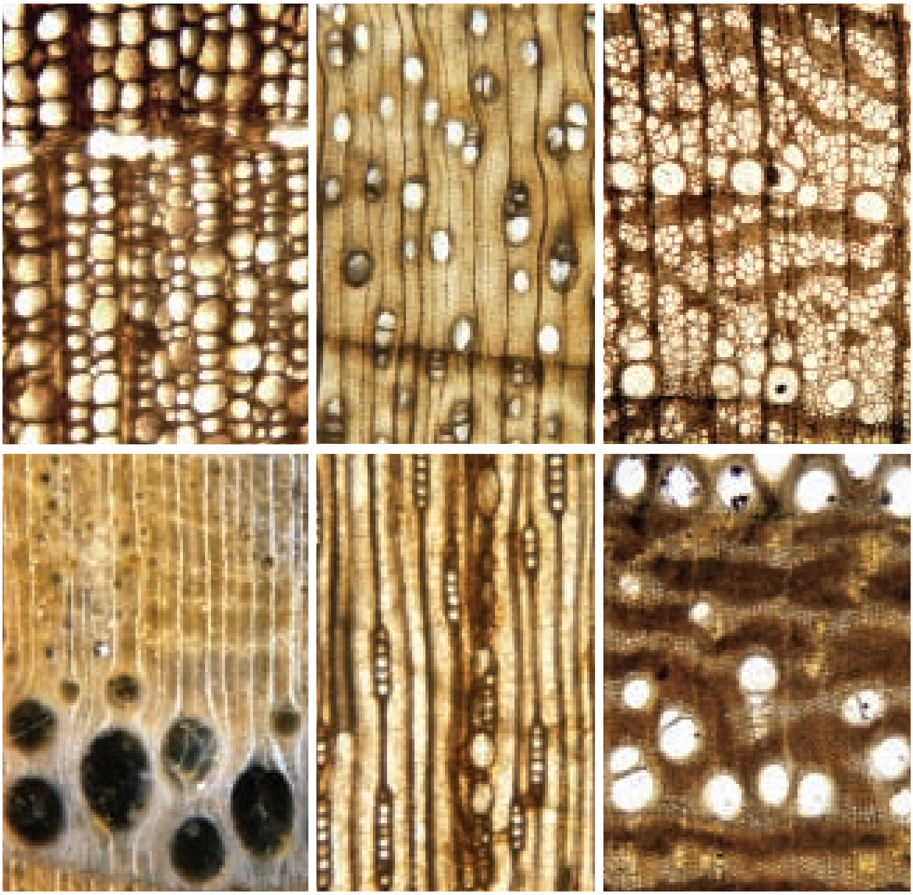

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The Middle Miocene Wood Flora of Vantage, Washington, USA

by

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Cover. Top row (from l to r): *Ginkgo beckii* (Ginkgoaceae), *Acer berkhoffii* (Sapindaceae), *Ulmus miocenica* (Ulmaceae). Bottom row (from l to r): *Quercus leuca* (Fagaceae), *Ginkgo beckii* (Ginkgoaceae), cf. *Sapindus* sp. (Sapindaceae)

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Contents

SUMMARY

The mid-Miocene Vantage Forest, conserved in the Ginkgo Petrified Forest State Park, Washington, U.S.A., is the single most diverse locality of Miocene woods in North America, with 34 angiosperm and 6 gymnosperm species. The composition of the Vantage forest is a mixture of plants now restricted to the eastern U.S. (*e.g.*, hard elm group of *Ulmus*) and to Asia (*Ginkgo*), classic examples of disjunct genera (*e.g.*, *Liquidambar*), and genera now widespread in the Northern Hemisphere (*e.g.*, *Quercus, Acer, Prunus*). For many Vantage woods their relationships to extant taxa were evaluated in the context of recent phylogenetic work to see if there were wood anatomical features consistent with the groupings recovered in those studies and useful for determining which continent the closest living relatives inhabit. For *Gleditsia* such features were found. Ring porous and semi-ring porous woods are common in the Vantage assemblage, but there also are diffuse porous woods with relatively few wide vessels, a combination of features that today does not occur in temperate North America, Europe, or Asia, but does occur in the subtropics. The 15.5 Ma Vantage woods grew during one of the warmer intervals of the Miocene and this mixture of wood types indicates that while there was a seasonal climate, it was less pronounced than in the Late Miocene-Pliocene when many Asian elements disappeared from North America as the climate cooled. MAT estimates for Vantage based on the assemblage's wood anatomical features are 12.1 and 12.8 °C, values within the range of the present-day Mixed Mesophytic forest type of eastern Asia. The Vantage assemblage shares genera with compression/impression and pollen floras of the Columbia Plateau, providing opportunities to eventually do whole plant reconstructions.

Key words: fossil wood, Miocene, Vantage, *Acer*, *Gleditsia*, *Quercus*, Juglandaceae, *Ulmus*, Fabaceae, *Pseudotsuga*, *Picea*, *Liquidambar*, Columbia River Basalts.

INTRODUCTION

The Tertiary floras of the Columbia Plateau, western U.S., are described as "among the richest in the world" (Graham 1999). In addition to compression floras and pollen-rich sediments, there are thousands of petrified logs of Miocene age entombed in the Columbia River Basalts of Central Washington, U.S.A. These Miocene woods are prized by amateur collectors because of their attractive coloration coupled with their superficial resemblance to common commercial woods of the Northern Hemisphere. Most collections of petrified wood include sections from at least one of the Vantage logs, and books documenting the beauty of polished petrified wood sections invariably feature macroscopic views of Vantage woods (*e.g*., Daniels & Dayvault 2006). The first question asked about petrified woods usually is "What kind of wood is it?"

In the 1930's, Professor George Beck of the Washington State Normal School (now Central Washington University) began work to answer this question for fossil woods of the Pacific Northwest, particularly woods of the Columbia River Basalts. Beck published a series of informal papers highlighting diagnostic features of the different wood types. Many of these papers discussed categories of woods, *e.g*. maple woods (Beck 1944). These papers were not accompanied by formal species diagnoses or photographs, but by general descriptions and line drawings of light microscope observations of a wood type. A 1945 paper in the Journal of Forestry listed the wood types Beck recognized at 12 localities in the Columbia River Basalts. The amount of work represented by this 5-page paper is remarkable as it resulted from the examination of thousands of thin sections made over more than two decades. Of the 12 localities mentioned in the 1945 paper, the Vantage assemblage was the most diverse, and, to our knowledge, is the single most diverse Miocene wood locality in North America.

Beck was an astute observer, and cautious with his comparative work and assigning names. His identifications of woods, done to genus or species group, were done before the publication of the standard reference "Anatomy of the Dicotyledons" (Metcalfe & Chalk 1950), and many decades before the availability of computerized multiple entry keys. If Beck was unsure of a wood's affinity, he refrained from assigning it a name. Among the woods he noted as being common at Vantage are Wood Type A, Wood Type B, and Wood Type C, which had distinctive anatomy, but were ones that he was unable to assign to family or genus. Beck did not define the criteria for abundant or common, but noted that *Pseudotsuga* and *Ulmus* were abundant and that *Abies, Picea, Acer, Carya, Fraxinus, Gleditsia, Gordonia, Juglans, Liquidambar, Quercus* were common at Vantage.

In the 1960's Prakash and Barghoorn (Prakash & Barghoorn 1961a, 1961b; Prakash 1968) published a series of papers describing 23 species of Vantage woods (2 conifers and 21 angiosperms). Their studies were dedicated to Beck and meant to formalize his work. Except for *Juglans fryxellii* ("few, small samples") and "*Albizzia vantagiensis"* (two samples), diagnoses and descriptions of each species were based on a single sample, provided by a Harvard undergraduate, Jay O'Leary. It is not known whether O'Leary collected this material himself or acquired it from Beck. Prakash and Barghoorn did not describe some of the woods that Beck (1945a) said occurred at Vantage, including some that Beck said were abundant (*Pseudotsuga*) or common (*Gordonia*, Hardwoods A, B, and C).

Among the objectives of our study are 1) to describe and illustrate wood types that Prakash and Barghoorn did not, and 2) using wood anatomical information that has become available in the decades since their work to investigate whether it is possible to provide more detail about the affinities of the Vantage woods. We are especially interested in determining whether it is possible to recognize subgeneric relationships. This information has value for those studying the biogeography and phylogeny of Northern Hemisphere plants.

The Vantage forests grew during the Mid-Miocene Climatic Optimum that lasted from 17 to 15 million years ago (Zachos *et al*. 2001). During the Miocene, global temperatures warmed from the cooler temperatures of the Oligocene to a peak in the mid Miocene, and then began a long cooling trend into the following Pliocene and the ice ages of the Pleistocene (Graham 1999). Global cooling plus altered rainfall patterns

Formation	**Member**	**Approximate Isotopic Age**
Saddle Mountains Basalt	Elephant Mountain Member	10.5 Ma
	— *EROSIONAL UNCONFORMITY* —	
	Pomona Member	12 Ma
	— *EROSIONAL UNCONFORMITY* —	
Wanapum Basalt	Priest Rapids Member	14.5 Ma
	Roza Member	
	Frenchman Springs Member	
	– Basalt of Sentinel Gap	
	– Basalt of Sand Hollow	15.3 Ma
	– Basalt of Ginkgo	15.5 Ma
	VANTAGE HORIZON	
Grande Ronde Basalt	– Magnetostratigraphic Unit N_2	
	– Member of Sentinel Bluffs	15.6 Ma
	– Member of Slack Canyon	
	– Member of Umtanum	
	– Member of Ortley	
	Magnetostratigraphic Unit R_2	
	– Member of Grouse Creek	
	– Member of Wapshilla Ridge	
	– Member of Mt. Horrible	
	Magnetostratigraphic Unit N_1	
	– Member of China Creek	
	Magnetostratigraphic Unit R_1	
	– Member of Center Creek	
	– Member of Teepee Butte	
		16.5 Ma

Figure 1. Stratigraphy of the Columbia River Basalts in the Vantage area (based on stratigraphic tables and basalt flow maps from Tolan *et al*. (1989) and Reidel *et al*. (1989). The Vantage wood assemblage is preserved within the Ginkgo Flow (highlighted).

due to increasing tectonic activity in both Asia and North America, resulted in dramatic changes in the vegetation of western North America. Vantage helps broaden our understanding of the woody vegetation that inhabited the Northern Hemisphere prior to the cooling and increasing seasonality of the latest Tertiary. The Vantage woods can also serve as a reference point for future studies of Miocene woods of North America and Asia. We present in alphabetical order by family and genus information on the woods that occur at Vantage.

GEOGRAPHIC SETTING AND GEOLOGY

The Vantage site is located in central Washington state, U.S., surrounding the town of Vantage in eastern Kittitas County. Fossilized wood is found in a series of discontinuous exposures that occur over an area of approximately 3000 hectares. The occurrence was discovered in the early part of the 20th century and, ultimately, thousands of fossilized logs and wood fragments were discovered in the area. When Professor Beck started working in the area in the early 1930s, he immediately recognized the scientific importance of the deposit and spearheaded an effort to preserve the locality. The area was designated as the Ginkgo Petrified Forest State Park and opened to the public in 1938.

The main wood horizon at Vantage is preserved in the Ginkgo flow, Frenchman Springs Member of the Wanapum Formation within the Columbia River Basalt Group (Fig. 1). This flow has been radiometrically dated at approximately 15.5 Ma (Reidel & Fecht 1987).

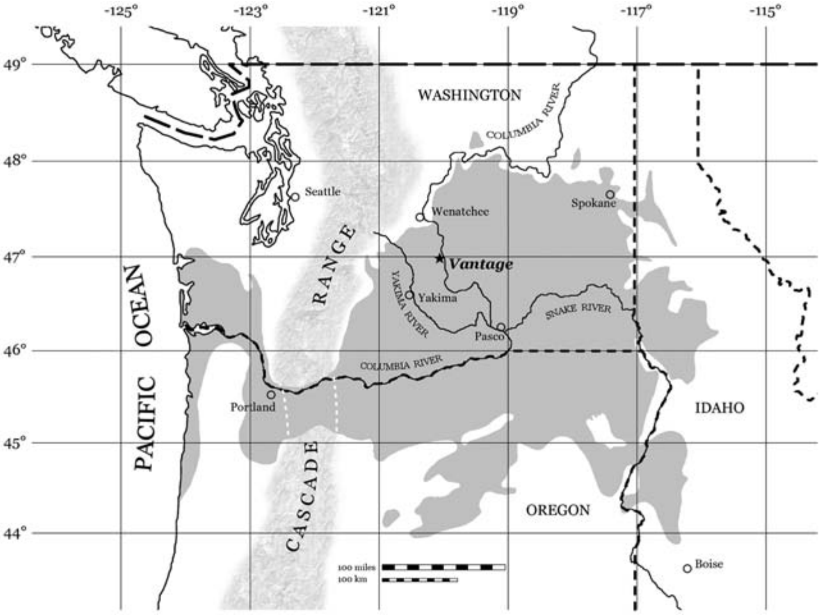


Figure 2. Map of study area. Shaded region shows the approximate overall extent of the Columbia River Basalt flows. Modified from Wells *et al.* (1989).

The Columbia River Basalts are a series of very fluid flood basalts that erupted from volcanic vents in the area of southeastern Washington, northeastern Oregon, and southwestern Idaho. These eruptions occurred between 17.5 and 6 million years ago, with over 80 % of the lava erupting during the first two million years of the cycle that made up the Grand Ronde Basalt Formation, extending from 16.5 to 15.6 million years ago (Reidel *et al*. 1989). The extent of these eruptions was enormous (Fig. 2) – the lavas covered an area of approximately 164,000 km^2 (an area 4× the size of the Netherlands), with a total volume of approximately 174,000 km^3 (Tolan *et al*. 1989). This volume would be sufficient to cover all of Germany to a depth of nearly 500 meters. Recent work has attributed the source of the lavas to a mantle plume associated with a volcanic hotspot that is the source of current volcanic activity at Yellowstone National Park (Camp 1995; Camp & Ross 2004). These authors theorize that the hotspot manifested itself in a series of flood basalt eruptions that began in northern Nevada and southeastern Oregon in the Middle Miocene, and migrated northwards into southeastern Washington and western Idaho.

Hiatuses between many of the eruptive cycles allowed the establishment of forest and swamp ecosystems. Subsequent eruptions buried remains of these forests and the wood was sometimes preserved by silica dissolved from volcanic ash and the basalts. This happened several times during the ten million years of volcanic eruptions, resulting in numerous deposits of fossilized wood across the Columbia Plateau. It is currently thought that there was a pause of approximately 100,000 to 200,000 years between the end of eruptions of the Grand Ronde Basalt Formation and the beginning of the

Figure 3. Section of fossilized log on display at the Ginkgo Petrified Forest State Park in Vantage, WA.

Wanapum Basalt Formation eruptions (Tolan, personal communication). This hiatus is marked by the Vantage Horizon: a sedimentary interbed that outcrops extensively across the Columbia Plateau and directly underlies the fossil wood-bearing Ginkgo basalt flow in the Vantage area.

The deposit at Vantage is the most diverse and well collected of the Columbia River Basalt fossil wood localities. The wood is preserved in prostrate log rafts, with thousands of logs representing trees from a variety of habitats. Bark, limbs and roots are typically absent, and the external surfaces of the wood show signs of abrasion, indicating transport of the logs prior to burial (Fryxell 1963). Beck (1935) presented several lines of evidence for the logs being afloat in a lake at the time of burial, including the fact that the logs are preserved directly in the basalt flow rather than in the underlying sediments; the basalt is a pillow-palagonite type indicating that the lava flow entered a water environment, and the logs show a consistent dip and direction as if they were afloat in a log raft that was buried by the encroaching lava flow. Figure 3 shows a section of a Vantage log on display at the Ginkgo Petrified Forest State Park, Vantage, Washington.

In his field notes Beck hypothesized that the deposit represented a watershed drainage where trees fell into rivers and were washed into a large lake at Vantage. Once there, the tree trunks would have drifted in the lake and became waterlogged, and were preserved when the lava flow swept through the region and buried the logs (Beck 1935). More recently, workers have postulated that the logs were transported into the Vantage area by a lahar from a regional volcano. They theorize that the lahar carried logs into a lake formed when a lava dam blocked the ancestral Columbia River. Once the flows entered the lake, the logs were floated up out of the sediment carried by the lahar and then entombed by the encroaching Ginkgo Flow (Tolan *et al.* 1991). This theory is based on several lines of evidence. The wood is entombed directly within the basalt flow and only rarely found in the underlying sediments of the Vantage Horizon. In a slow buildup of a lake, one would expect some of the wood to become waterlogged and sink to the bottom, where it would be buried in sediments and later preserved. Additionally, the composition of the sediments is rhyolitic, which is consistent with Cascade Mountain volcanism rather than the mafic Columbia River Basalts. There is also abundant pumice present in the upper sediments of the Vantage Horizon, including a report of one fossilized log that had pieces of pumice imbedded in the wood (Tolan, personal communication).

Professor Beck generally did not keep detailed notes about the diameter of woods that he found in the field, thus it is not feasible to directly correlate samples examined in this study with the size of the log that they came from. Additionally, some of the specimens are known to be from fragments found loose on the ground rather than from an exposed log. Vantage wood specimens seen in private and public collections can range from a few centimeters to over a meter in diameter.

The one case where there are good records of log size is from Beck's main collecting locality (Beck site 11). In his unpublished field notes, Professor Beck provided estimates of log diameter for over 100 specimens from this locality. These data were obtained during surveys for construction of walking trails in the state park. Table 1 lists the log type and size estimates that Beck recorded. Note that identifications were done in the field and were tentative; in his field notes, Professor Beck put question marks next to several of the identifications.

As can be seen from Table 1, the majority of the logs apparently represent boles from mature trees. Smaller limbs and roots are rare, possibly due to their being stripped from the tree during transport. Another possibility is that the smaller pieces were more portable and had been gathered by local collectors prior to establishment of the state park. In either case, the size estimates for the larger logs are consistent with the few

Table 1. Sizes of Vantage logs. Information compiled from Beck's field notes.

Wood type (based on initial ID in field notes)	**Range in diameter (cm)**	**Average diameter (cm)**	**Number of logs**	**Comments**
Piceoxylon	25–120	75	45	Plus one small diameter section not counted as a log (it likely represents a root or limb). Includes specimens field identified as *Picea, Pseudotsuga*, or *Piceoxylon*, since these cannot be reliably separated without thin sections
Ulmus	30–90	45	18	Plus four small diameter sections not counted as logs
Acer	15–90	38	15	Plus one small diameter section not counted as a log
Liquidambar	20–90	45	7	
Gordonia	15–25	20	7	= *Hamamelis*
Juglans	30–137	68	6	Plus two small diameter sections not counted as logs
"Locust"	30–60	45	3	Assumed to include both *Gleditsioxylon* and *Robinia* types
Quercus	45–120	84	2	
Ginkgo	90	N/A	1	
Cupressus	45	N/A	1	Field identified as *Cupressus* – this log is the source of the type specimen for *Taxus*
Sophora	40	N/A	1	= *Ulmus*
"Yellow wood"	20	N/A	1	Unclear which taxon this is supposed to represent
Total			107	

reports from other Vantage localities; and therefore appear representative of the Vantage assemblage as a whole. The largest recorded log from the Vantage localities is a hollow section of *Dichrostachyoxylon occidentale* that was reported to be nearly 2.75 meters in diameter with intact bark (Beck 1956).

MATERIALS AND METHODS

We examined slides on loan from the Harvard Paleobotanical Collections (HU) and Burke Museum, University of Washington (UWBM). Samples examined by Prakash and Barghoorn and presumably provided by Jay O'Leary only have HU numbers. Sections prepared by Beck, but not examined by Prakash and Barghoorn, are referred to by both their HU number and Beck collection number. Samples from the Burke Museum are referred to by their UWBM number and Beck collection number.

The terminology generally follows the IAWA Hardwood Feature List (IAWA Committee 1989) and IAWA Softwood Feature List (IAWA Committee 2004). When preservation permitted and digital images had good detail, vessel diameter and ray height were measured using ImageJ software, otherwise measurements were made by using an ocular micrometer.

Information from the InsideWood web site, the FFPRI Database of Japanese Woods [http://f030091.ffpri.affrc.go.jp/index-E1.html], Wood Anatomy of Central European Species [Schoch *et al*. 2004], literature referenced by Gregory (1994) and on the Kew Micromorphology Website were used to evaluate the relationships of the Vantage woods to extant woods. Slides of extant woods are referenced by their wood collection numbers (Stern 1988), *e.g*., BWCw 8148. Additional images of the woods described in this paper are available on the InsideWood website [http://insidewood.lib.ncsu.edu/search].

Some of the macroscopic images of transverse sections were prepared by placing the thin section directly on a flat bed scanner and scanning it as a transparency at 2400 dpi. Higher magnification digital images were taken with an Olympus DP70 camera and Olympus compound microscope.

DISCUSSION

Table 2 lists the wood types we recognize at Vantage. There are 34 dicots and at least 6 gymnosperms. Five of the dicots cannot be assigned with confidence even to the family level. As with any study of a fossil assemblage, we questioned how much comparative work per sample should be done, how many new sections of extant plants should be prepared, and how could it be established that the fossil wood has characteristics unique to a single extant taxon. It is frustrating that these five wood types eluded identification to family because they are distinctive. The mid-Miocene is a time when many plants have characteristics of extant genera. Our inability to identify these woods in part reflects the reality that there is still much work to be done on extant wood anatomy, and that different genera and different families can share similar anatomy, as well as our reaching a point of needing to bring the study of this assemblage to a close. It is possible that

Table 2. List of Vantage Woods.

Altingiaceae	cf. *Liquidambar hisauchii* Suzuki & Watari (1994)
Araliaceae	*Araliaceoxylon miocenica* gen. et sp. nov.
Betulaceae	*Betula scammonii* (Prakash) comb. nov.
Fabaceae	*Dichrostachyoxylon occidentale* (Prakash & Barghoorn) Müller-Stoll & Mädel 1967
	"Albizzia vantagiensis" Prakash & Barghoorn 1961a
	Gleditsioxylon columbianum (Prakash & Barghoorn) Müller-Stoll & Mädel 1967
	Robinia zirkelii (Platen) Matten, Gastaldo, Lee 1977
Fagaceae	*Fagus manosii* sp. nov.
	Quercus leuca Prakash & Barghoorn 1961a
Hamamelidaceae	*Hamamelidoxylon beckii* sp. nov.
	Hamamelidoxylon suzukii sp. nov.
Juglandaceae	*Rhysocaryoxylon tertiarum* (Prakash & Barghoorn) Dupéron 1988
	Rhysocaryoxylon fryxellii (Prakash & Barghoorn) Dupéron 1988
Lauraceae	*Richteroxylon micropunctatum* gen. et sp. nov
Nyssaceae	*Nyssa eydei* Prakash & Barghoorn 1961b
Oleaceae	*Fraxinus washingtoniana* (Prakash & Barghoorn) comb. nov.
	Fraxinus macropunctatum sp. nov.
Platanaceae	*Platanus americana* Prakash & Barghoorn 1961a
Rosaceae	*Prunus rodgersae* sp. nov
	Prunus barnetti sp. nov.
Sapindaceae	*Acer beckianum* Prakash & Barghoorn 1961a
	Acer puratanum Prakash & Barghoorn 1961a
	Acer olearyi Prakash & Barghoorn 1961a
	Acer berkhoffii sp. nov.
	Aesculus hankinsii Prakash & Barghoorn 1961b
	cf. *Sapindus* sp.
Ulmaceae	*Ulmus baileyana* Prakash & Barghoorn 1961b
	Ulmus miocenica Prakash & Barghoorn 1961a
	Ulmus pacifica Prakash & Barghoorn 1961a
Incertae Sedis	Beck's Hardwood C
	Vantage Unknown Dicot 1
	Vantage Unknown Dicot 2
	Vantage Unknown Dicot 3
	Vantage Unknown Dicot 4
CONIFERAE	
Cupressaceae	*Cupressinoxylon* spp.
	Taxodioxylon antiquum Prakash 1968
Pinaceae	*Picea tertiarum* (Prakash) comb. nov.
	Pseudotsuga pseudotsugae (Gothan) Beck 1945b
Taxaceae	*Taxus* sp.
GINKGOALES	
Ginkgoaceae	*Ginkgo beckii* Scott, Barghoorn & Prakash 1962

the affinities of these woods might be determined later when more systematic wood anatomical work has been done and more information on Asian woods is available.

Many of the genera present at Vantage contain modern species that inhabit a variety of habitats, from riparian/floodplain to uplands. Since the fossil trees are preserved as transported log rafts rather than being preserved *in situ*, it is difficult to reconstruct the forest environment around the lake. It is believed that the topography at the time was of low relief, primarily due to leveling of the area by the high volume lava flows of the Grande Ronde Basalt (Tolan, personal communication). Upland/drier habitat species are represented by *Ginkgo beckii*, *Pseudotsuga pseudotsugae*, and *Picea tertiarum*. Presumed swamp/lowland tree types, such as *Nyssa eydei* and *Taxodioxylon antiquum,* are present at Vantage, but are rare. These species are common at other wood localities in the Columbia River Basalts and their rarity at Vantage would indicate that there was not a well-developed swamp habitat nearby. This is consistent with the theory that the lake was formed by blockage of the ancestral Columbia River shortly before deposition of the woods.

Climatic inferences

The modern climate at Vantage is characterized by cold winters, dry, hot summers, and less than 20 cm of annual precipitation. The low amount of precipitation is due to the rain shadow created by the north-south trending Cascade mountain range that intercepts much of the moisture coming in from the Pacific Ocean. The modern flora is a shrub-steppe habitat, dominated by sagebrush (*Artemisia tridentata*), rabbit brush (*Chrysothamnus* spp.), and native bunchgrasses (Fig. 4).

Figure 4. Looking east from the main wood locality at Vantage towards the Columbia River.

In the Middle Miocene, however, the climate was very different. The Vantage forests were established during the Middle Miocene climactic optimum, which occurred between 17 and 15 Ma (Zachos *et al*. 2001). During this period, global temperatures were higher overall and there was less of a latitudinal temperature gradient than in modern times (Wolfe 1978). Fossil floras from western North America bear this out. At high latitudes in Alaska (Wolfe 1980; White & Ager 1994; Leopold & Liu 1994), Miocene leaf and pollen floras shared many taxa with the Vantage woods. The closest modern analog to the Middle Miocene forests of northwestern North America in terms of climatic preferences, diversity, and floristic composition is the Mixed Mesophytic Forest type of eastern Asia and eastern North America as defined by Wang (1961) and Braun (1950).

The modern Mixed Mesophytic Forest type lives in a temperate climate with a long growing season and 1000 to 1500 cm of precipitation spread throughout the year (Wang 1961). These forests are characterized by high diversity, a high proportion of deciduous broad-leaved angiosperms, and lack of dominance by any single species. The Vantage assemblage generally fits this model, with one major exception (*Piceoxylon*) as discussed later in this paper.

In the Middle Miocene, the Cascade Mountain range had not achieved sufficient altitude to cast a rain shadow (Reiners *et al*. 2002), and there was abundant rainfall during the growing season as evidenced by the affinity of the Vantage assemblage with the modern forests of eastern Asia and eastern North America. The combination of warmer regional temperatures and adequate summer rainfall allowed the establishment of forests in the Miocene that were quite distinct from the modern dry summer climate forests of the Pacific Northwest region.

Wood anatomical characteristics of the Vantage dicot woods — Various wood anatomical features have featured prominently in discussions of ecological wood anatomy, particularly porosity (ring vs. diffuse), vessel diameter and density (narrow and many vs. wide and few), helical thickenings in vessel elements, vessel groupings and arrangement (*e.g*., Baas 1986; Carlquist 1988, 2001).

None of the Vantage woods have the syndrome of few (<10 vessels per sq.mm) and wide vessels (>200 µm) that occurs in modern lowland tropical rainforest trees. At Vantage there is a curious mixture of a relatively high proportion of ring porous (20 %) and semi-ring porous (20 %) woods co-occurring with diffuse porous woods with relatively few (<20/mm^2) and medium-wide vessels (mean tangential diameter >150 µm). Ring porous and semi-porous woods are produced by deciduous trees and correlated with seasonal climates. Helical thickenings are common in modern woods of the temperate zone (c. 45 %) and rare in the tropics (4 %); the 47 % incidence of helical thickenings at Vantage is close to that of present-day temperate regions. However, diffuse porous woods with relatively few, medium-wide vessels are not suggestive of temperate climates, but of less seasonal climates.

MAT Inferences — Wiemann *et al*. (1998, 1999) developed regression equations for estimating Mean Annual Temperature (MAT) from wood anatomical characteristics.

Two of the many regression equations (Eq. 12, 15, given below) tested were considered best for estimating MAT because of how well they worked as MAT predictors at a range of present-day sites (Wiemann *et al.* 1999). Both equations are based on arcsine transformations of the relative proportions of species having the anatomical features: storied rays (stor), marginal parenchyma (marg), axial parenchyma rare to absent (abs), and septate fibers (sept). On an individual basis, these particular features are not those that correlate best with MAT. As classic studies predict (*e.g.* Carlquist 1975; Baas 1986), vessel diameter and incidence of spiral thickenings are more highly correlated with MAT (Wiemann *et al.* 1999).

Eq. 12) $\text{MAT } ^\circ\text{C} = 24.78 + 36.57 \text{ (stor)} - 15.61 \text{ (marg)} - 16.41 \text{ (abs)}$
Eq. 15) $\text{MAT } ^\circ\text{C} = 17.07 + 25.23 \text{ (stor)} - 23.17 \text{ (abs)} + 13.79 \text{ (sept)}$

When Wiemann *et al.* (1998, 1999) applied these equations to Vantage, they based their estimates on 19 wood types and got MAT estimates of 16.2 °C and 15.8 °C from Equations 12 and 15, respectively. We now recognize 34 angiosperm wood types at Vantage. We do not feel confident about using Equation 15, as the preservation of many of the Vantage woods is not good enough to determine confidently whether septate fibers are present or absent.

If the Vantage *Fraxinus washingtoniana* is considered to have a tendency to storied rays, Equation 12 yields a MAT estimate of 12.8 °C, if storied rays are considered absent, *i.e.* there is a frequency of 0 for storied rays at Vantage, the MAT estimate is 12.1 °C.

While using wood anatomical features may not prove the best method for estimating MAT, wood can help reveal how variable the climate was during the lifetime of a tree, and should prove useful for inferring degree of seasonality and length of growing season. Also, if woods were collected from a series of localities in a restricted geographic locality, they would be useful for evaluating general climatic trends through time, by using incidence of such features as distinct growth rings, vessel diameter and density, and ring porosity. There is opportunity for such studies in the Pacific Northwest of the U.S., and the Vantage woods can be a reference point for these studies.

MAT estimates for other Miocene floras of the Pacific Northwest

Several studies have looked at the Miocene leaf floras of the Pacific Northwest and discussed their paleoclimates (Chaney & Axelrod 1959; Smiley & Rember 1985; Fields 1996; Wiemann *et al.* 1999). These studies found forest assemblages generally similar to the one found in the Vantage deposit. In some instances, climate proxies were used to estimate paleotemperatures of the deposits. Takeuchi *et al.* (2007) used paleosols as a climate proxy to estimate MAT for several middle Miocene sites in the region and calculated paleotemperatures which ranged from 15.7 to 20.9 °C. Their paleosol sample site closest in age and proximity to Vantage returned a MAT estimate of 16.1 °C. Wiemann *et al.* (1999) calculated MAT estimates for the Succor Creek assemblage and for the Latah assemblages by using percentage of entire margined leaves and the relationships between MAT and percentage of leaf margin type found by Wolfe (1979), Greenwood (1992), and Wilf (1997). The Succor Creek flora of Idaho and Oregon with

Table 3. MAT estimates for Middle Miocene Pacific Northwest floras.

Locality	**MAT estimate**	**Stated error**	**Method used**	**Reference**
Vantage	12.1–12.8 °C	+/– 3 °C	Wood anatomy (per Wiemann *et al*. 1998; Wiemann *et al*. 1999)	This study
Clarkia, Idaho Site P-33	10.1 °C	+/– 1.7 °C	CLAMP (per Wolfe 1993)	Unpublished data
Latah (Washington & Idaho)	6.6–8.4 °C	Not given	Leaf margin analysis (per Wolfe 1979; Wilf 1997; Greenwood 1992)	Wiemann *et al*. 1999
Succor Creek	7.3–8.8 °C	Not given	Leaf margin analysis (per Wolfe 1979; Wilf 1997; Greenwood 1992	Wiemann *et al*. 1999
46° 37.93' N 118° 38.32' W (~100 km ESE of Vantage)	16.1 °C	+/–0.6 °C	Paleosol analysis (per Sheldon 2006)	Takeuchi *et al*. 2007

98 species and 20 % entire-margined leaves had MAT estimates of 7.3, 8.0, and 8.8 °C. The MAT estimates for the Latah flora from Idaho and Washington with 66 species and 18 % entire-margined leaves were 6.6, 7.4, and 8.4 °C.

Table 3 shows estimates of MAT for Middle Miocene floras of the Pacific Northwest and the methods used for each. It is interesting to note the disparity in temperature estimates between the various methods and localities. The data in the table are provided for reference; we caution against drawing any firm conclusions based on these values. Each method has its own biases and errors, plus each site has its own taphonomic and collecting biases that may affect the temperature estimates, thus making it difficult to directly compare the results.

The regional paleosol temperature estimates seem unreasonably high considering the composition of coeval wood, leaf and pollen floras. If the paleosol estimates were correct, one would expect to see assemblages with a more subtropical aspect rather than the temperate forests present in the fossil record. Given the composition of the wood assemblage at Vantage and the climate preferences of the modern analogs of this assemblage, the MAT estimate of 12.1–12.8 °C based on wood anatomy appears reasonable.

To put the regional temperature estimates in perspective, Wolfe (1979) gave a MAT range of 10–13 °C for the Mixed Mesophytic and 9–13 °C for the Mixed Broad-leaved Deciduous forest types of eastern Asia, values similar to those given by Wang (1961). Although the temperature ranges of these two forest types overlap, one of the characteristics of the Mixed Broad-leaved Forest noted by Wolfe is the dominance of deciduous oaks. Oaks are common in the Vantage assemblage, but are by no means dominant. Therefore we feel that Vantage is more closely aligned with the Mixed Mesophytic Forest type.

Many of the taxa found at Vantage are related to components of the modern Mixed Mesophytic Forest (*sensu* Wang 1961; Braun 1950), including *Acer, Aesculus, "Albizzia", Betula, Carya, Fagus, Fraxinus, Gleditsia, Hamamelis, Juglans, Liquidambar, Nyssa, Platanus, Quercus,* and *Ulmus*. Additionally, gymnosperms such as *Ginkgo, Taxus,* and *Pseudotsuga* are associated with the east Asian Mixed Mesophytic Forest, and *Picea* is considered a montane element (Wang 1961).

Vantage is not a perfect match for the Mixed Mesophytic Forest, however. Two of the main characteristics of the Mixed Mesophytic Forests are high species diversity and lack of dominance of the forest canopy by any single tree type. In Beck's unpublished field notes, he gives the following relative abundances for the Vantage woods:

50 % *Piceoxylon* types (includes *Picea* and *Pseudotsuga*), as they cannot be reliably separated without examination of well preserved thin sections)
20 % *Ulmus*
5 % Juglandaceous types
5 % *Liquidambar* types
5 % *Acer* types
5 % *Quercus* types
3 % Locust types (includes *Gleditsioxylon* & *Robinia*)
2 % *Gordonia* types (= *Hamamelis*).

The rest of the Vantage taxa each comprise 1% or less of the total. It is not feasible to go back and verify Professor Beck's numbers due to the heavy collecting that took place during and after his field work, but we accept his conclusions based on his careful studies, large collections, and detailed note keeping.

While the Vantage assemblage does show the high diversity characteristic of Mixed Mesophytic Forests, the dominance of *Piceoxylon* types does not fit Wang's model. This dominance is unique to Vantage among the wood floras found in the Columbia River Basalts and is not characteristic of the regional megafossil floras. *Piceoxylon* is common at some of the other wood sites, but nowhere is it nearly as dominant as it is in the Vantage site. The nearest in abundance is Beck's Squaw Creek forest in the Columbia River Basalts, where Beck (1943) estimates that *Piceoxylon* types comprise approximately 15 % of the flora.

Beck (1936) postulated that *Picea* in the Miocene was adapted to swamps, thus explaining its relative abundance in the Vantage assemblage. A possible modern analog would be *Picea sitchensis,* which grows from sea level to 900 meters along coastal areas of northwestern North America (Farjon 1990). Although it is not a swamp species, it is often found in river valleys. Other studies of regional megafossil and microfossil deposits do not support Beck's suggestion, however. Research by Chaney and Axelrod (1959), Graham (1963), Smiley and Rember (1985), and Fields (1996) unanimously interpret *Picea* as an upland / montane element in the Miocene floras of the northwest. *Picea* is generally rare in these deposits and is represented mainly by winged seeds, pollen, and occasional cone scales. It is unlikely that Vantage was at a significantly higher elevation than the other deposits because of the leveling effects of the vast Grande Ronde basalt flows that immediately preceded the establishment of the Vantage forest. If the Vantage site had been a high montane region at the time, it likely would not have been inundated by the Grande Ronde and subsequent Ginkgo basalt flows.

A possible explanation for the high proportion of upland conifers in the Vantage assemblage is the lahar theory proposed by Tolan *et al.* (1991) for deposition of the wood. The eruption of Mount St. Helens in 1980 demonstrated the ability for mudflows derived from a volcanic eruption to transport large numbers of logs over 100 km away from the source. Eyewitness accounts of this event reported mudflows full of logs moving downriver, snapping off additional trees as they went. At one site 50 km from the mountain, an observer stated that while it flowed by the surface of the Toutle River was covered with logs for approximately 25 minutes (Cummans 1981). It is possible that the high proportion of *Piceoxylon* wood in the Vantage deposit is the result of logs being transported into the lake by a lahar flow from a relatively distant montane source.

Comparison of the composition of Vantage with other Pacific Northwest Miocene floras

Northwest U.S. Miocene floras have been the subjects of several previous studies. Many of these floras are considered close in age to the Vantage woods. The best known include the lacustrine pollen and megafossil flora at Clarkia, Idaho (Smiley & Rember 1985; Gray 1985; White *et al.* 2002), the Spokane flora of northeastern Washington (Knowlton 1926; Berry 1929; Brown 1937a, 1937b; Chaney & Axelrod 1959), the Mascall flora of northeastern Oregon (Chaney & Axelrod 1959), and the Succor Creek flora of southeastern Oregon and southwestern Idaho (Chaney & Axelrod 1959; Graham 1963; Taggart 1973, Fields 1996). Two less well known floras that are close in age and geographical proximity to the Vantage wood deposit include the leaf flora at Grand Coulee, Washington (Berry 1931, 1938; Chaney & Axelrod 1959) and the pollen flora of the Palouse Falls interbed in southeastern Washington (Barnett & Fisk 1980). Figure 5 shows the relative locations of the sites, and approximate ages for each of these floras are given below:

Vantage: 15.5 Ma (Reidel & Fecht 1987)
Clarkia: 14.5–15 Ma (William C. Rember, personal communication)
Spokane: 12.4–14.9* Ma (Evernden & James 1964; Gray & Kittleman 1967)
Grand Coulee: 16* Ma (Gray & Kittleman 1967)
Palouse Falls: 15.5 Ma (Barnett & Fisk 1980)
Mascall: 16 Ma (Bestland *et al.* 2008)
Succor Creek: 15 Ma (Fields 1996)
*) published K-Ar dates modified by revised decay constants per Dalrymple (1979)

Table 4 compares the composition of Vantage wood flora to these other regional Miocene floras. The table is intended as a coarse comparison of the woody plants in the floras. Caution should be used when interpreting the data, since some of the localities have been studied more recently and/or thoroughly than others, and some identifications may need revision, particularly those made in the early publications. There are also

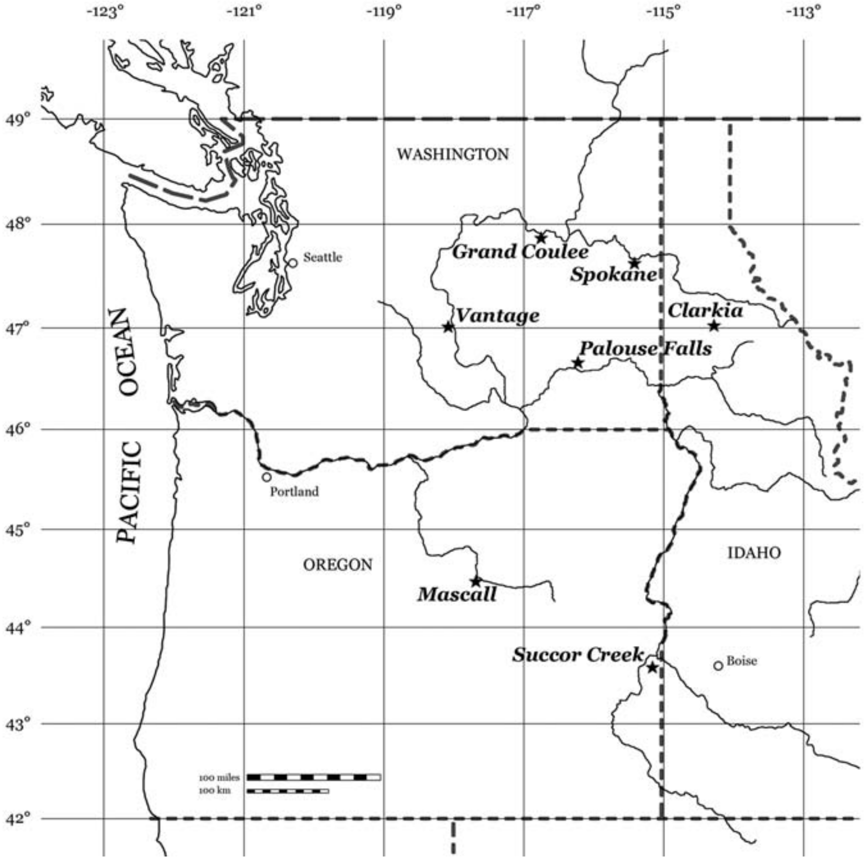


Figure 5. Map showing location of the fossil sites used in the comparison table (Table 4).

taphonomic biases associated with each deposit as well as variation in preservation of different plant organs. It should be noted that since the focus of this paper is on fossil wood, only taxa that form trees or large shrubs are included in the table.

The genera present in the Vantage flora correlate well with other regional floras from the Miocene. The woods at Vantage include a mixture of temperate conifers and deciduous warm temperate angiosperm genera with affinities to modern equivalents that inhabit a variety of microclimates in eastern Asia, western North America, and eastern North America. Gymnosperms are well represented in all of the floras. *Ginkgo* is present in five of the seven listed floras. It had become rare in North America by middle Miocene, and these deposits represent some of the last occurrences of *Ginkgo* on the continent. According to Tralau (1967), *Ginkgo* fossils are not found in North America after the Miocene. *Ginkgo* type pollen was recently reported from the Pliocene of Florida (Hansen *et al*. 2001), but *Ginkgo* pollen is difficult to separate from that of some cycads (Uemura 1997) and the lack of supporting macrofossil evidence in the Tertiary of eastern North America causes us to question this occurrence.

Table 4. Comparison of Vantage with other regional floras.

W = wood, M = macrofossil other than wood, P = pollen (pollen occurrences with question marks are as reported by the original authors).

	Vantage[1]	Clarkia[2,3,9,10]	Spokane[4,9,11]	Grand Coulee[4,9,11]	Palouse Falls Interbed[5]	Mascall[4]	Succor Creek[4,6,7,8]
Gymnosperms							
Cephalotaxaceae							
Cephalotaxus						M	M, P?
Cupressaceae							
Calocedrus		M				M	M
Chamaecyparis		M					
Cunninghamia		M					
Cupressinoxylon[e]	W						
Fokienia			M	M			
Glyptostrobus		M					M
Metasequoia		M				M	M
Sequoia		M					M
Taxodium		M	M	M	P	M	M
Taxodioxylon[f]	W						
Tetraclinus		M	M	M			
Thuja		M	M		P[b]	M	M
Ginkgoaceae							
Ginkgo	W		M	M		M	M
Pinaceae							
Abies		M, P			P	M, P	M, P
Cedrus		P			P?		P
Keteleeria		M	M			M, P	M, P
Picea	W	P			P	M, P	M, P
Pinus		M, P	M		P	M, P	M, P
Pseudotsuga	W	P?					P?
Tsuga		P			P	P	M, P
Podocarpaceae							
Podocarpus		P			P		P
Taxaceae							
Amentotaxus		M					
Taxus	W	M, P					
Undifferentiated T-C-T		P			P	P	P
Angiosperms							
Altingiaceae							
Liquidambar	W	M, P	M	M	P	M, P	M, P
Anacardiaceae							
Rhus		M, P					M
Aquifoliaceae							
Ilex		M, P	M		P	P	M, P
Araliaceae	W						
Oreopanax							M

Table 4 continued	Vantage[1]	Clarkia[2,3,9,10]	Spokane[4,9,11]	Grand Coulee[4,9,11]	Palouse Falls Interbed[5]	Mascall[4]	Succor Creek[4,6,7,8]
Betulaceae							
Alnus		M, P	M	M	P	M, P	M, P
Betula	W	M, P	M	M	P	M, P	M, P
Carpinus					P		M, P
Corylus		M, P			P		P
Ostrya		M, P	M		P	M, P	M, P
Buxaceae							
Pachysandra						P	P
Celastraceae							
Euonymus			M				
Cercidiphyllaceae							
Cercidiphyllum		M				M	M
Cornaceae							
Cornus		M, P	M	M			P
Ebenaceae							
Diospyros		M	M	M		M	M
Ericaceae							P
Arbutus							M, W
Gaultheria			M				
Kalmia							M
Rhododendron							M
Vaccinium		M?	M		P	P?	M
Fabaceae							M, P
"*Albizzia*"	W[a]					M	
Cercis		M					M
Cladrastis							M
Dichrostachyoxylon	W						
Gleditsia	W[a]	M					
Gymnocladus		M				M	M
Robinia	W[a]	M					
Sophora			M	M			M
Fagaceae							
Castanea		M, P?[c]	M	M		M	M, P
Castanopsis		M	M				M?
Chrysolepis							M
Fagus	W	M, P	M	M	P	P	M, P
Lithocarpus		?M, P[c]					M, P
Pseudofagus		M					
Quercus	W	M, P	M	M	P	M, P	M, P
Hamamelidaceae							
Exbucklandia		M	M	M			
Hamamelis	W	M				M	
Juglandaceae							
Carya	W[a]	M, P		M	P	M, P	M, P
Engelhardtia		M, P?					

Table 4 continued	Vantage[1]	Clarkia[2,3,9,10]	Spokane[4,9,11]	Grand Coulee[4,9,11]	Palouse Falls Interbed[5]	Mascall[4]	Succor Creek[4,6,7,8]
(Juglandaceae contd*)*							
Juglans	W[a]	M, P			P	M, P	M, P
Pterocarya		M, P	M		P	P	M, P
Lauraceae	W						
Laurophyllum						M	
Lindera		M				M	
Machilus			M				
Persea		M	M	M		M	M
Sassafras		M				M	M
Magnoliaceae							
Magnolia		M, P	M				M
Liriodendron		M, P	M	M			
Malvaceae							P
Anoda							M
Malvacipollis					P		
Malvacearumpollis					P		
Sphaeralcea							P
Tilia		M, P	M		P	P	M, P
Meliaceae							
Cedrela		M	M	M		M	M
Moraceae							
Morus					P		
Nyssaceae							
Nyssa	W	M, P	M	M	P	M, P	M, P
Oleaceae							
Fraxinus	W	M, P			P	M, P	M, P
Platanaceae							
Platanus	W	M, P	M	M	P	M, P	M, P
Rhamnaceae	W[a]						
Berchemia		M					
Paliurus		M	M	M			M
Rosaceae		P					
Amelanchier		M	M	M		M	M
Crataegus		M				M	M
Heteromeles							M
Malus							M
Prunus	W	M					M
Rutaceae							
Ptelea			M	M		M	M
Salicaceae							
Populus		M	M		P	M, P	M, P
Salix		M, P	M	M	P	M, P	M, P
Sapindaceae							
Acer	W	M, P	M	M	P	M, P	M, P
Aesculus	W	P					

Table 4 continued	Vantage[1]	Clarkia[2,3,9,10]	Spokane[4,9,11]	Grand Coulee[4,9,11]	Palouse Falls Interbed[5]	Mascall[4]	Succor Creek[4,6,7,8]
(Sapindaceae contd)							
Dilodendron			M				
cf. *Sapindus*	W						
Simaroubaceae							
Ailanthus							M
Leitneria						M	
Styracaceae							
Halesia		M					
Theaceae							
Gordonia		M?	M	M	P		M
Trochodendraceae							
Nordenskioldia		M	M	M			
Trochodendron							M
Zizyphoides		M	M				
Ulmaceae							
Celtis		M, P			P	M, P	M, P
Ulmus	W	M, P	M	M	P[d]	M, P	M, P
Zelkova		M, P?	M			M, P	M, P

1 This study
2 Smiley & Rember (1985)
3 White *et al*. (2002)
4 Chaney & Axelrod (1959)
5 Barnett & Fisk (1980)
6 Graham (1963)
7 Taggart (1973)
8 Fields (1996)
9 Manchester *et al*. (1991)
10 Kvaček & Rember (2000)
11 Kvaček *et al*. (2000)

[a] Wood does not match the characteristics of a modern genus well enough to be included in that genus, but has some similarity to it. The fossil wood is listed with the modern genus or a family on the table to facilitate comparison among the floras.

[b] Author lists pollen type as *Thuja* or *Juniperus*.

[c] *Castanea*/*Lithocarpus* type.

[d] Reported as *Ulmus* and/or *Zelkova*.

[e] *Cupressinoxylon* wood could represent any one or more of the genera *Calocedrus, Chamaecyparis, Tetraclinis*, and *Thuja*.

[f] *Taxodioxylon* wood could represent any one or more of the genera *Taxodium, Sequoia, Metasequoia*, and *Glypostrobus*.

Cupressinoxylon wood may represent one or more cupressaceous genera, and thus is difficult to correlate with particular cupressaceous foliage or reproductive structures from other Miocene deposits. Similarly, the wood of *Taxodioxylon antiquum* could represent *Taxodium*, *Glyptostrobus, Sequoia*, or *Metasequoia*, all of which are reported from the lacustrine floras. Beck reported both *Taxodium* and *Sequoia* wood from various localities in the Columbia River Basalt (Beck 1945a). He based the presence of *Sequoia* on specimens at his Squaw Creek and Roosevelt Grade localities that clearly showed traumatic resin canals. According to Beck (1941), *Sequoia* is the only wood of his *Cupressinoxylon* type to exhibit this feature. Later work has shown that traumatic resin canals also occur in *Glyptostrobus* and *Metasequoia* (Visscher & Jagels 2003) and therefore this feature is not useful for separating these genera. *Taxodium* fossils are reported from all of the localities with the exception of Succor Creek (Table 4), and *Taxodium* is reported as the dominant taxon in the Mascall flora (Chaney & Axelrod 1959).

Pinaceous fossils are well represented in the Miocene compression and pollen floras of the Pacific Northwest. However, *Pinus* does not occur at Vantage and is only rarely reported from other wood localities in the Columbia River Basalts. Given that *Pinus* wood is easy to recognize, its absence from wood floras seems real and may reflect some taphonomic bias we do not understand.

Acer, *Betula*, *Fagus*, *Liquidambar*, *Nyssa*, *Platanus*, *Quercus*, and *Ulmus* are reported from all seven deposits. *Alnus* is present in all of the floras except Vantage, although *Alnus* wood has been found in at least two other wood localities in the Columbia River Basalts (Beck 1945a). *Ilex* is reported from five of the floras, as are *Ostrya*, *Cedrela*, *Diospyros*, *Fraxinus*, *Castanea*, *Carya*, *Pterocarya, Persea*, *Tilia*, *Amelanchier*, *Gordonia* and *Populus*.

At the family level, the Betulaceae, Fagaceae, Juglandaceae, Lauraceae, Salicaceae, Sapindaceae, and Ulmaceae show a high diversity among the various floras. It is somewhat surprising that *Populus* and *Salix* are absent from the wood flora, given that they are reported from almost all of the leaf floras. However, woods of *Populus* and *Salix* are not resistant to fungi and consequently might be less likely to enter the fossil record and many of the "*Populus*" leaves from Latah and Clarkia are not *Populus* (Manchester *et al*. 1991). There have been several reports of salicaceous woods from the Columbia River Basalts, but these reports have not yet been confirmed by microscopic anatomy. The Fabaceae appear to be reasonably diverse at Vantage and Clarkia; however, they are relatively uncommon at the other sites. Likewise, the Rosaceae are represented by at least three genera at Clarkia and Succor Creek, but not common elsewhere and absent from the Palouse Falls pollen flora. *Prunus* is present but rare at Vantage.

DESCRIPTIONS AND COMMENTS

The descriptions in the 1961 Prakash and Barghoorn papers (1961a, 1961b) and the Prakash 1968 paper provided information on most, but not all, features of the IAWA Hardwood List (IAWA Committee 1989). For example, sometimes ranges of tangential diameter of vessels were reported, but not the mean. The descriptions below combine data from those papers with our observations. The number in parentheses given after an average is the standard deviation.

ALTINGIACEAE

LIQUIDAMBAR L.

cf. *Liquidambar hisauchii* Suzuki & Watari (1994) (Fig. 6)

[*Liquidamba*r cf. *styraciflua* Prakash & Barghoorn 1961a]

Growth rings distinct, marked by 1–2 rows of radially narrow fibers.

Diffuse porous. Vessels predominantly solitary, with short multiples; oval to somewhat square in outline; average tangential diameters 51(10)–55(7) µm, range 23–76 µm; >100 per sq. mm; perforation plates exclusively scalariform with 15–30 bars; intervessel pits scalariform-transitional; vessel–ray parenchyma pits with slightly reduced borders and usually horizontally elongate; Prakash and Barghoorn reported spiral thickenings at the end of the vessel elements; vessel element lengths up to 1070 µm long; widely spaced tyloses present.

Fibers non-septate, with distinctly bordered pits, on radial and tangential walls; walls thick.

Axial parenchyma rare, isolated diffuse or occasional cells touching the vessels.

Rays 1–3 (4)-seriate; uniseriate rays common. Multiseriate rays heterocellular, body ray cells procumbent, often asymmetric, with one margin with 1–2 cells and other margin with up to 8 cells, total multiseriate height averages 362 (92) µm, range 236–595 in HU 55240; 9–12 rays per mm.

Traumatic axial canals in tangential bands at the beginning of the growth ring in sample HU 56643.

Storied structure absent, crystals not observed.

Material: HU 55240, HU 56642 (Beck 463), HU 56643 (Beck 889), HU 65004 (Beck 466).

Comments: *Liquidambar* has long been used as an example of a North Temperate disjunct, with two species in eastern Asia (*L. formosana, L. acalycina*), one species in western Asia (*L. orientalis*), and one (*L. styraciflua*) occurring in eastern North America, and from central Mexico to Belize (Wen 1999). Consequently, it is of interest to determine the relationships of fossil *Liquidambar* to extant species to better understand the timing of the differentiation of the species. Suzuki and Watari (1994) suggested that relative percentages of 1-, 2-, 3-seriate rays could be used to distinguish woods of *Liquidambar styraciflua* (35, 61, 4 %) from *L. formosana* (18, 61, 22 %). Lee and Baas (1998, unpub. data) noted that ray width in *L. styraciflua* was 1–2 (3)-seriate, in *L. formosana* 1–3, in *L. orientalis* 1–3 (5). Unfortunately, while three of the *L. styraciflua* samples (Uw 6759, CSIRO FPAw u.45, BWCw 8148) we examined rarely had 3-seriate rays, one (Hw 17232) commonly had 3-seriate rays and 4-seriate rays were present; and one sample of *L. formosana* (CAFw 18047) rarely had 3-seriate rays (<5 %). Consequently, ray width does not seem a reliable way to distinguish between these two species. The sample of *L. orientalis* (MADw 14115) we examined had wider rays, to 4 (5)-seriate, than the other species, but more samples should be examined to see if this is a consistent characteristic.

So, although this Vantage wood originally was considered comparable to only the North American species *Liquidambar styraciflua*, it is also similar to the Asian *L. formosana* and *L. orientalis*. Therefore, it does not seem appropriate to refer to this

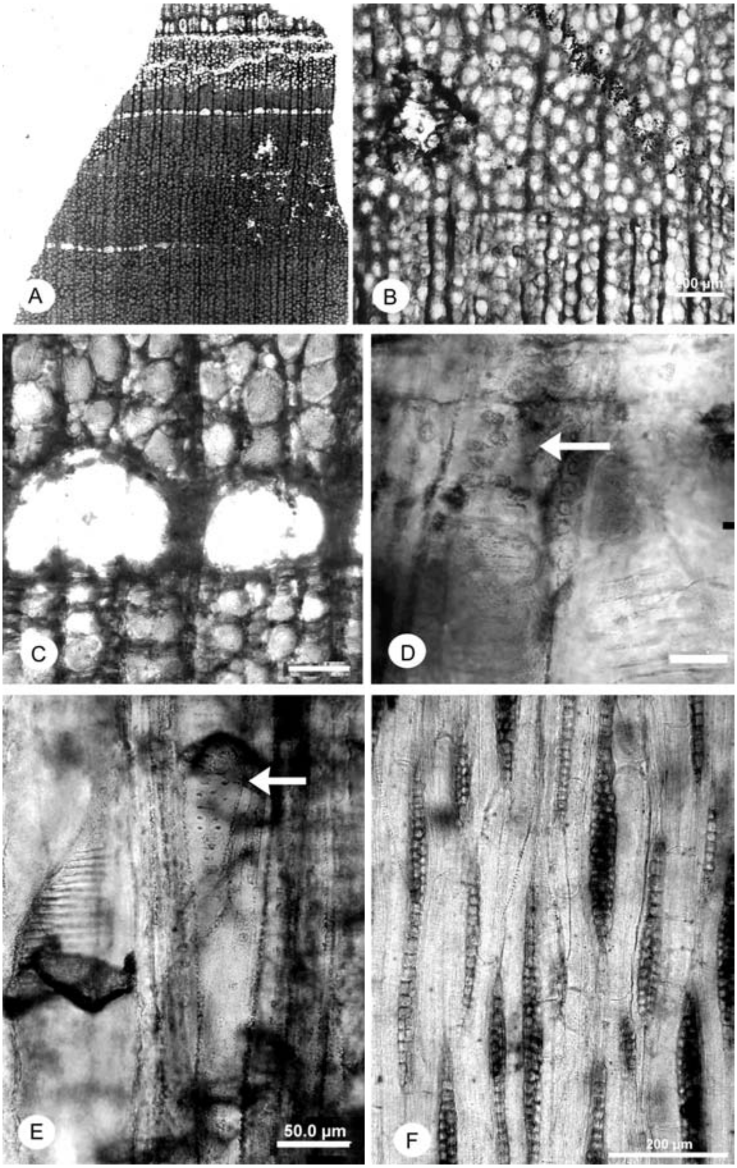


Figure 6. Altingiaceae. cf. *Liquidambar hisauchii*. – A: Diffuse porous wood with crowded narrow vessels, traumatic canals present at beginning of some growth rings, HU 56643. Width of sample at point of longest line of traumatic canals = 7.1 mm. XS. – B: Diffuse porous wood, growth ring marked by a few radially narrower fibers, axial parenchyma not obvious, HU 55240. XS. – C: Detail of growth ring boundary with traumatic canals, HU 56643. XS. – D: Vessel–ray parenchyma pits horizontally elongate (arrow), HU 55240. RLS. – E: Scalariform perforation plate, fibers with distinctly bordered pits, opposite intervessel pits (arrow), HU 55240. RLS. – F: Rays 1–3- (4-)seriate, heterocellular, widely spaced tyloses, HU 55240. TLS. — Scale bar = 200 µm in B, F; 100 µm in C; 50 µm in E; 20 µm in D.

Vantage wood as *Liquidambar* cf. *styraciflua*, as this suggests a relationship only to that present-day species.

Fossil woods similar to *Liquidambar* also are known from the Eocene, Oligocene, and Miocene of Europe (Gottwald 1992; Sakala & Privé-Gill 2004; Van der Burgh 1973), Miocene of Japan (Suzuki & Watari 1994), and Oligocene of Canada (Roy & Stewart 1971). Suzuki and Watari (1994) distinguished the Miocene Japanese *Liquidambar hisauchii* (16% uniseriate, 11% biseriate, 51% 3-seriate, and 22% 4-seriate rays) from most European *Liquidambaroxylon* because the European species have predominantly 1–2-seriate rays. *Liquidambar speciosum* Roy & Stewart (1971) from the Oligocene of Canada also has predominantly 1–2-seriate rays like the European samples assigned to that species. The Vantage *Liquidambar* has 15% uniseriate rays, 38% biseriate rays, 28% 3-seriate rays, and 18% 4-seriate rays. Because over 40% of the Vantage *Liquidambar* wood's rays are 3–4-seriate, it is structurally closer to the Japanese *L. hisauchii* than to the *Liquidambar*-type Canadian and European fossil woods, and we are referring to it as cf. *Liquidambar hisauchii*. The phylogenetic analyses of Ickert-Bond *et al*. (2005) found that the Middle Miocene *Liquidambar* infructescence from Yakima Canyon, Washington, was somewhat closer to the extant Asian species than to extant *Liquidambar styraciflua*.

ARALIACEAE

ARALIACEOXYLON gen. nov.

Wood semi-ring porous. Growth rings distinct. Vessels predominantly in multiples, tendency to diagonal arrangement. Perforation plates scalariform, less than 25 bars. Intervessel pits crowded alternate, medium-sized; vessel-ray parenchyma pits oval to horizontally elongate. Fiber pits not distinctly bordered. Axial parenchyma scanty paratracheal. Rays 1–6-seriate; heterocellular, to more than 1 mm high.

Araliaceoxylon miocenica sp. nov. (Fig. 7)

Growth rings present.

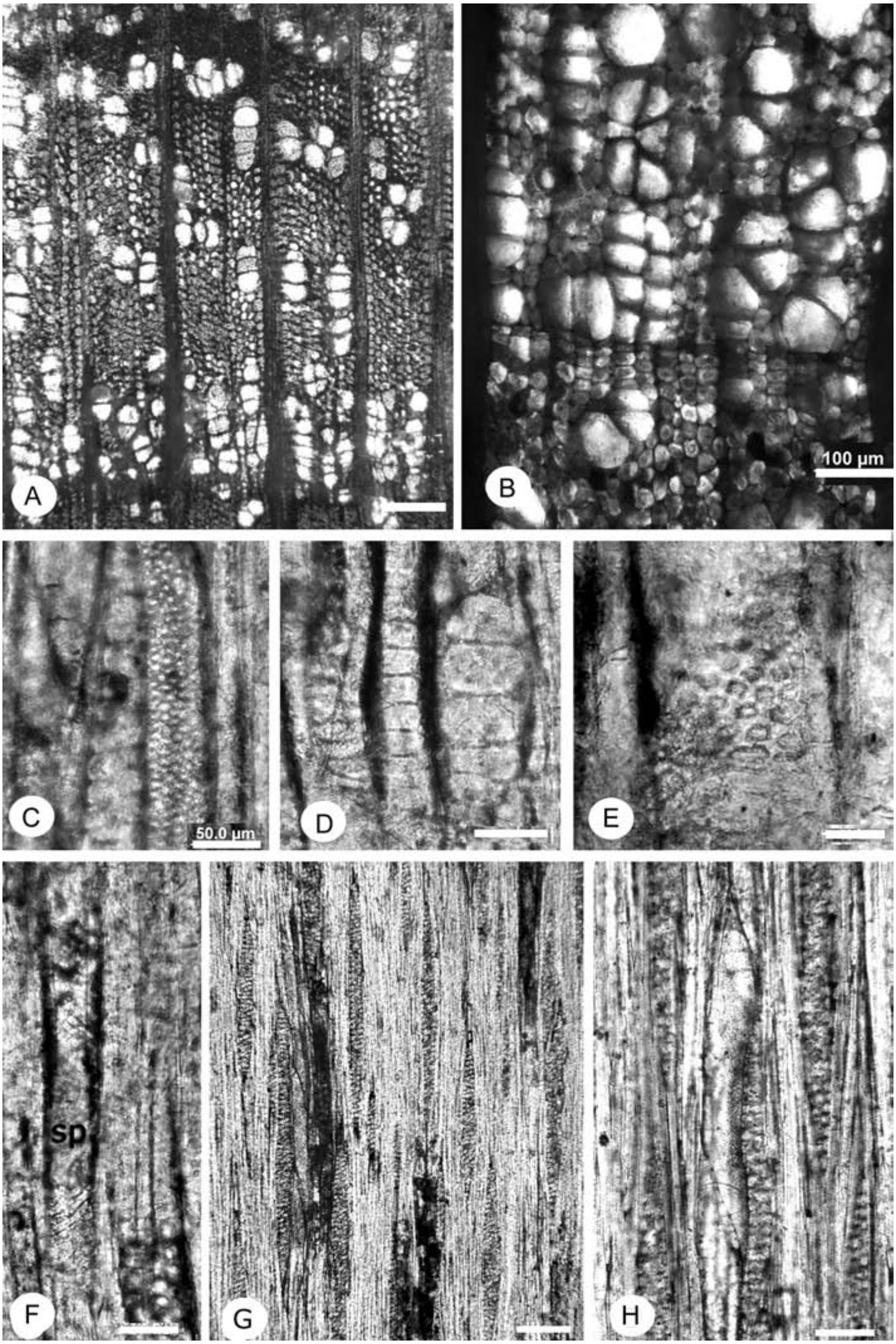
Wood semi-ring porous, with a higher vessel density in the earlywood, and with tendency to a diagonal vessel arrangement in the latewood. Vessels predominantly in multiples, some clusters in earlywood, average tangential diameter in earlywood 62 (12) µm, in latewood 52 (6) µm. Perforation plates scalariform, with 4–20 bars, usually fewer than 5 bars, with the narrower vessels elements having the most bars. Intervessel pits crowded alternate, somewhat angular in outline, 6 to 8 µm across, apertures included. Vessel–ray parenchyma pits oval to slightly horizontally elongated, borders somewhat reduced. Vessel elements 602–749 µm long. Helical thickenings in some narrower vessel elements.

Fibers thick-walled. No pits observed.

Axial parenchyma rare, scanty paratracheal, > 4 cells per strand.

Rays mostly 4-seriate. Multiseriate ray height 380–1314 µm, mean 746 (286) µm. Heterocellular with procumbent body cells and with 1(–3) marginal rows of square to slightly upright cells; body ray cells isodiametric as viewed in tangential section, 3–5 per mm.

Storied structure absent, crystals not observed.


A
B
100 µm
C
50.0 µm
D
E
F
sp
G
H

Holotype: HU 65005 (Beck 467).

Etymology: The generic name indicates the wood has characteristics seen in the Araliaceae; the specific epithet indicates the age of the wood.

Comments: The preservation of this sample was not good enough to determine whether septate fibers were present. Helical thickenings were observed in a few narrow tracheary elements in both tangential and radial sections.

The combination of semi-ring porous wood, with vessels commonly in groups, exclusively scalariform perforation plates with few widely spaced bars, alternate intervessel pitting, vessel–ray parenchyma pits slightly horizontally elongated and rare axial parenchyma is not common in the extant flora. Woods with these features occur in the Araliaceae (*e.g.*, *Fatsia* and *Schefflera*) and Sabiaceae (*Meliosma*). The tendency to a diagonal vessel arrangement, occurrence of helical thickenings in narrow vessel elements, and rays predominantly multiseriate is consistent with the Araliaceae, not Sabiaceae. One of the groups recovered by recent phylogenetic analyses of Araliaceae is the Asian Palmate Group, which includes *Fatsia* and Asian species of *Schefflera* (Plunkett *et al.* 2004), and this wood has characteristics of that group.

Fossil wood believed to represent Araliaceae has been reported from western North America. Platen (1908) described 4 species of *Aralinium* from the Eocene "auriferous gravels" of California. Wheeler and Manchester (2002) described two species of *Plerandreoxylon* from the middle Eocene Nut Beds of Oregon. Both *Aralinium* and *Plerandreoxylon* have predominantly simple perforation plates, while this Vantage wood has exclusively scalariform perforation plates.

Consequently, we are establishing a new genus *Araliaceoxylon*. This wood's characteristics are those of the Araliaceae, but we are unable to determine with certainty which genus/genera it might represent. General knowledge of Miocene floras indicates that they are composed of plants with affinities to extant genera (Graham 1999). Although the wood anatomy of Araliaceae has been studied extensively by Oskolski (1995, 1996, 2001), the wood of many East Asian species of Araliaceae have not been described or illustrated. Megafossils (other than wood) of Araliaceae have been reported from the Tertiary of the North America, mostly leaves assigned to *Aralia*, although *Oreopanax* is reported from Succor Creek (Graham 1963). Dilcher and Dolph (1970) determined that fossil leaves from the Eocene of the southeastern U.S. assigned to *Aralia* are *Dendropanax*. They noted that *Aralia* had been used as a catchall category for a variety of Tertiary leaves, and that the affinities of these needed reassessing. Manchester (1994) described araliaceous fruits from the Middle Eocene Clarno Nut Beds flora that he as-

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←

Figure 7. Araliaceae. *Araliaceoxylon miocenica* gen. et sp. nov. HU 65005 (Beck 467). – A: Vessels solitary, in radial multiples, and irregular groups. XS. – B: Growth ring boundary, earlywood zone characterized by radial multiples and vessel groups being common. XS. – C: Crowded alternate intervessel pits. RLS. – D: Scalariform perforation plates, with widely spaced bars. RLS. – E: Vesselray parenchyma pits oval to horizontally elongate. RLS. – F: Vessel element with helical thickenings (HT). RLS. – G: Tall multiseriate rays, with relatively wide spacing. TLS. – H: Vessel element with scalariform perforation plates, heterocellular multiseriate rays. TLS. — Scale bar = 200 µm in A, G; 100 µm in B, H; 50 µm in C, D; 20 µm in E, F.

signed to the fossil genus *Paleopanax*. Similar fruits occur in the Early Eocene McAbee flora in central British Columbia (Dillhoff *et al*. 2005). Mathias (1965) summarized the putative occurrences of Araliaceae in the Cenozoic of North America; most reports were for the Paleocene and Eocene and are from older literature. These records need re-evaluation.

BETULACEAE

BETULA L.

Betula scammonii (Prakash) comb. nov. (Fig. 8)

[*Betuloxylon scammonii* Prakash 1968]

Growth rings distinct, marked by radially narrower fibers.

Diffuse porous. Vessels solitary (41%) and in radial multiples of 2–4; solitary vessels oval in outline; average tangential diameter 120 µm (range 60–180 µm), 111 (16) µm in HU 56614; 10–23 per sq.mm; perforation plates exclusively scalariform, 8 to 25 bars, average 13 bars; intervessel pitting crowded alternate, minute, c. 4 µm across, frequently coalescent; vessel–ray parenchyma pits similar to intervessel pits; average vessel element length 1070 (132) µm, range 870–1300 µm.

Fibers non-septate, walls thin, pitting not observed.

Axial parenchyma diffuse to diffuse-in-aggregates; 6–8 cells per strand.

Rays 1–4 (5-)seriate. Homocellular, composed of procumbent cells. Individual ray cells isodiametric (rounded to slightly polygonal in outline) in tangential section. Multiseriate ray height averages 325 (120), 148–649 µm; 4–6 per mm.

Storied structure absent, crystals not observed.

Material: HU 56286 (holotype), HU 56614 (Beck 1536).

Comments: *Betula* wood is distinctive, with its combination of minute alternate intervessel pits (Fig. 8F), scalariform perforation plates, vessel–ray parenchyma pits similar to intervessel pits (Fig. 8E), apotracheal parenchyma, and homocellular rays. Although Prakash (1968) wrote that the Vantage birch differed from *B. lenta* in "only minor details", he followed the tradition of many Indian and European workers in assigning fossil woods to an organ genus using the -oxylon ending. This Vantage wood has features seen only in *Betula*, so to indicate that it has an anatomy equivalent to a single modern genus we propose the new combination *Betula scammonii* (Prakash) comb. nov.

Although it is relatively easy to assign isolated pieces of wood to the genus *Betula*, distinguishing individual species is not so easy. Miller and Cahow (1989) in their study of six North American birch woods (*B. alleghaniensis, B. lenta, B. nigra, B. occidentalis, B. papyrifera*, *B. populifolia*) and two European species (*B. pendula, B. pubescens*) found that ray width, ray shape, and ray cell shape as viewed in tangential section, and average number of bars per perforation plate were useful diagnostic features. Another feature they found useful, which normally would be of limited value for fossil wood identification, was whether ray parenchyma cells had russet colored contents. They did not examine any Asian species, but their work allows us to determine that the Vantage wood does not have characteristics of *B. papyrifera* or *B. occidentalis,* both of which have 2–3-seriate rays with individual ray cells laterally flattened, or of *B. nigra* with

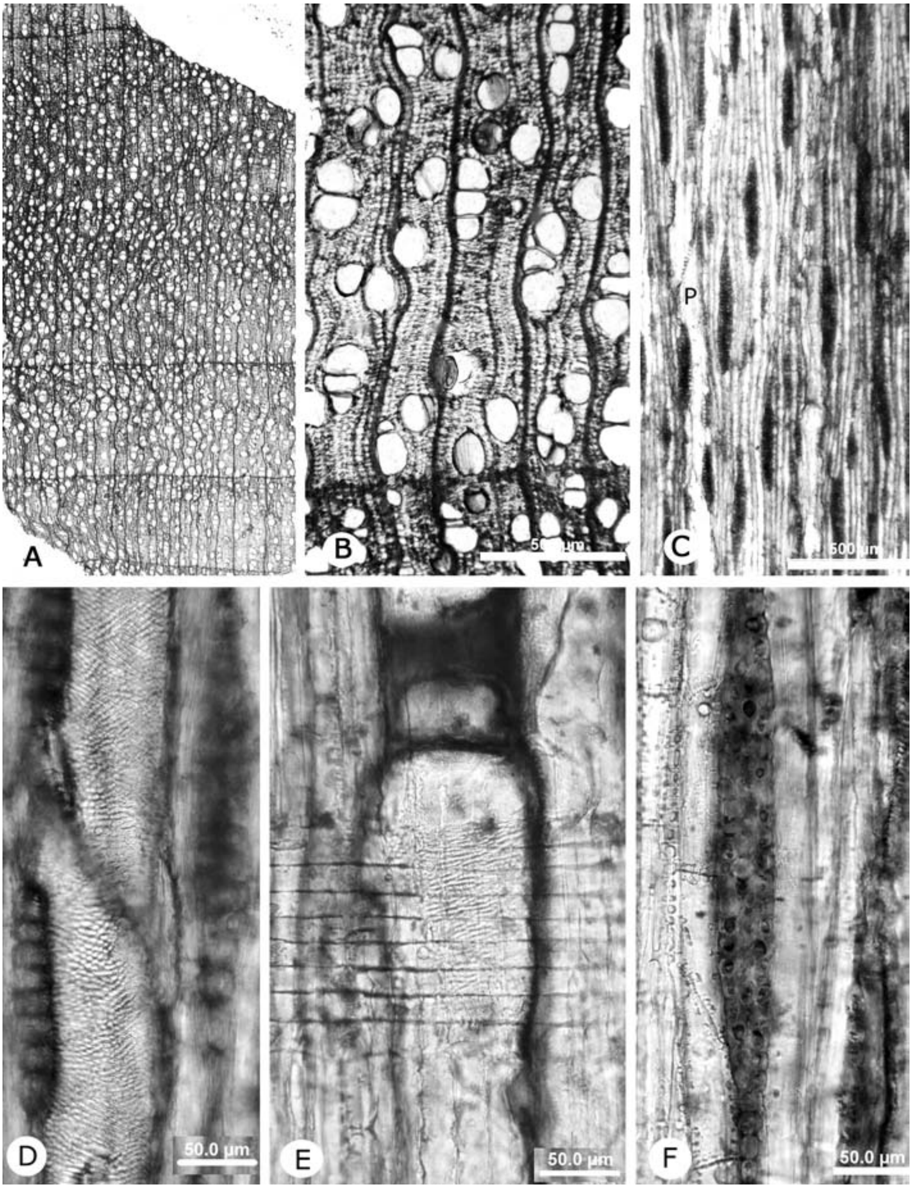


Figure 8. Betulaceae. *Betula scammonii* (Prakash) comb. nov. HU 56614. – A, B: Diffuse porous wood with vessels solitary and in short radial multiples (2–3 vessels), solitary vessels oval in outline. Width of bottom growth ring in A = 2 mm. XS. – C: Rays fusiform to elongate in shape, vessel element with scalariform perforation plate (P). TLS. – D: Minute crowded alternate intervessel pitting, apertures often coalescent. TLS. – E: Vessel–ray parenchyma pitting similar to intervessel pitting. RLS. – F: Individual ray cells circular to polygonal, axial parenchyma strand with end walls slightly nodular. TLS. — Scale bar = 500 µm in B, C; 50 µm in D, E, F.

an average number of bars per perforation plate of 6 to 10. The Vantage birch wood has a ray width (3–4), ray shape (near fusiform, Fig. 8C), ray cell shape (circular in tangential view, Fig. 8F), and an average number of bars (13) per perforation plate similar to that found in extant *B. alleghaniensis, B. lenta, B. pendula, B. pubescens,* and *B. populifolia*. There are colored contents in the Vantage wood's ray cells and this is a feature of the American species, not the European species.

Information on nine Japanese *Betula* species is available on the FFPRI Database of Japanese Woods web site. Of those nine, *Betula ermanii* and *B. grossa* have an average number of bars between 10–20, and rays that are 4-seriate or more and so also resemble the Vantage *Betula*.

Helleberg and Carcaillet (2003) investigated whether woods of the western European *Betula pendula, B. pubescens, B. tortuosa,* and *B. nana* could be distinguished. They examined multiple samples of stem and branch wood, which they charcoalified as they were concerned with the identification of archaeological charcoals. Their principal component analysis of quantitative vessel and ray features indicated that it was not possible to reliably distinguish *Betula pendula* and *B. pubescens*. The shrubby *B. nana* had narrower vessels and more vessels per group than the tree species. They suggested that *B. tortuosa* could be distinguished from the other two tree species because it had more vessels per group.

The aforementioned wood anatomical studies cover 17 *Betula* species. Taxonomy and phylogeny of *Betula* has been termed problematic, with estimates of species numbers ranging from 30 to more than 60 (Järvinen *et al.* 2004). For an investigation of the phylogenetic relationships within the genus (nuclear ADH gene and MATk chloroplast gene used), Järvinen *et al.* (2004) chose 14 species (6 of which were also included in the wood anatomical studies reviewed above) representing the 5 subgenera that De Jong (1993) recognized. Different hypotheses of phylogenetic relationships resulted. The MATk analysis produced two groups – one comprised of three American species, *B. lenta, B. alleghaniensis*, and *B. papyrifera*, the other comprised of the other 11 species they examined. The ADH analysis produced three groups at variance with the MATk results, with *B. lenta* and *B alleghaniensis* in Group II and *B. papyrifera* in Group III. A more recent phylogenetic analysis of 11 species (6 of which had been included in the Järvinen analysis) used the Nia gene and resulted in yet another set of hypotheses for phylogenetic relationships within the genus (Li *et al.* 2007). This study did not include the North American *B. alleghaniensis* or European *B. pendula* species with anatomy similar to *B. lenta* and *B. pubescens,* respectively, so that it cannot be determined whether this similarity in wood anatomy reflects the proposed phylogeny. It is unfortunate that different phylogenetic analyses of a genus do not sample the same species so that their hypotheses can be better compared and morphological and anatomical data can more effectively be used to complement the molecular analyses.

A comprehensive analysis and comparison of Asian, North American, and European *Betula* woods is needed to see whether there are any differences that enable distinguishing woods from these three regions, and how wood anatomical groupings compare to the De Jong subgeneric delimitations, and to the groupings hypothesized on the basis of the ADH data for 14 species, and to the Nia data for 11 species.

FABACEAE

DICHROSTACHYOXYLON Müller-Stoll & Mädel

Dichrostachyoxylon occidentale (Prakash & Barghoorn) Müller-Stoll & Mädel 1967 (Fig. 9 A–D)

[*Leguminoxylon occidentale* Prakash & Barghoorn 1961b]

Growth rings distinct, marked by marginal parenchyma.

Diffuse porous. Vessels solitary (39%) and in radial multiples of 2–3; average tangential diameter 167 (48), range 111–232 µm; 5–7 per sq. mm; perforations exclusively simple; intervessel pits crowded alternate, 6–8 µm; apertures often coalescent; vessel–ray parenchyma pits similar to intervessel pits; vessel element lengths 200–450 µm.

Fibers non-septate according to Prakash and Barghoorn, some possibly septate, walls thick, pitting not observed.

Axial parenchyma vasicentric, aliform (lozenge), and distinct marginal bands mostly 3–5 cells wide; 4–7 cells per strand.

Rays 1–5-seriate, 1–2-seriate rays rare. Multiseriate rays homocellular, composed of procumbent cells, multiseriate ray height averages 358 (120) µm, range 139–698 µm (HU 55076), 6–10 per mm.

Crystals and storied structure not observed.

Material: HU 55076 (holotype), HU 56702 (Beck 622).

Comments: Prakash and Barghoorn thought this wood most similar to species of *Acacia* (Mimosoideae/Fabaceae). The wood that Beck called Hardwood A (Beck 622/HU 56702) appears to be another sample of this legume wood type. The marginal/zonate parenchyma bands are more closely spaced in HU 56702, but otherwise its characteristics are similar to HU 55076.

It often is not possible to distinguish groups of extant legume genera from one another on the basis of wood anatomy, but there are syndromes of wood anatomical characters shared among particular suites of genera. Consequently, Müller-Stoll and Mädel (1967) erected a number of form genera with characteristics of these groups of legume genera. *Dichrostachyoxylon* was one such genus, based on the Mimosoideae genus *Dichrostachys,* but it also accommodates woods with characteristics seen in *Acacia*. Characteristics mentioned in the diagnosis of *Dichrostachyoxylon* include: wood diffuse porous, vessels solitary and in short radial multiples, simple perforations, medium-sized alternate pitting, vessel–ray parenchyma and vessel–axial parenchyma pitting similar to intervessel pitting; non-septate libriform fibers; axial parenchyma vasicentric, aliform, and occasionally confluent, marginal parenchyma often present; rays 1–10-seriate, usually more than 3-seriate, homogeneous to weakly heterogeneous [translated from the German]. Müller-Stoll and Mädel transferred *Leguminoxylon occidentale* Prakash & Barghoorn to this genus.

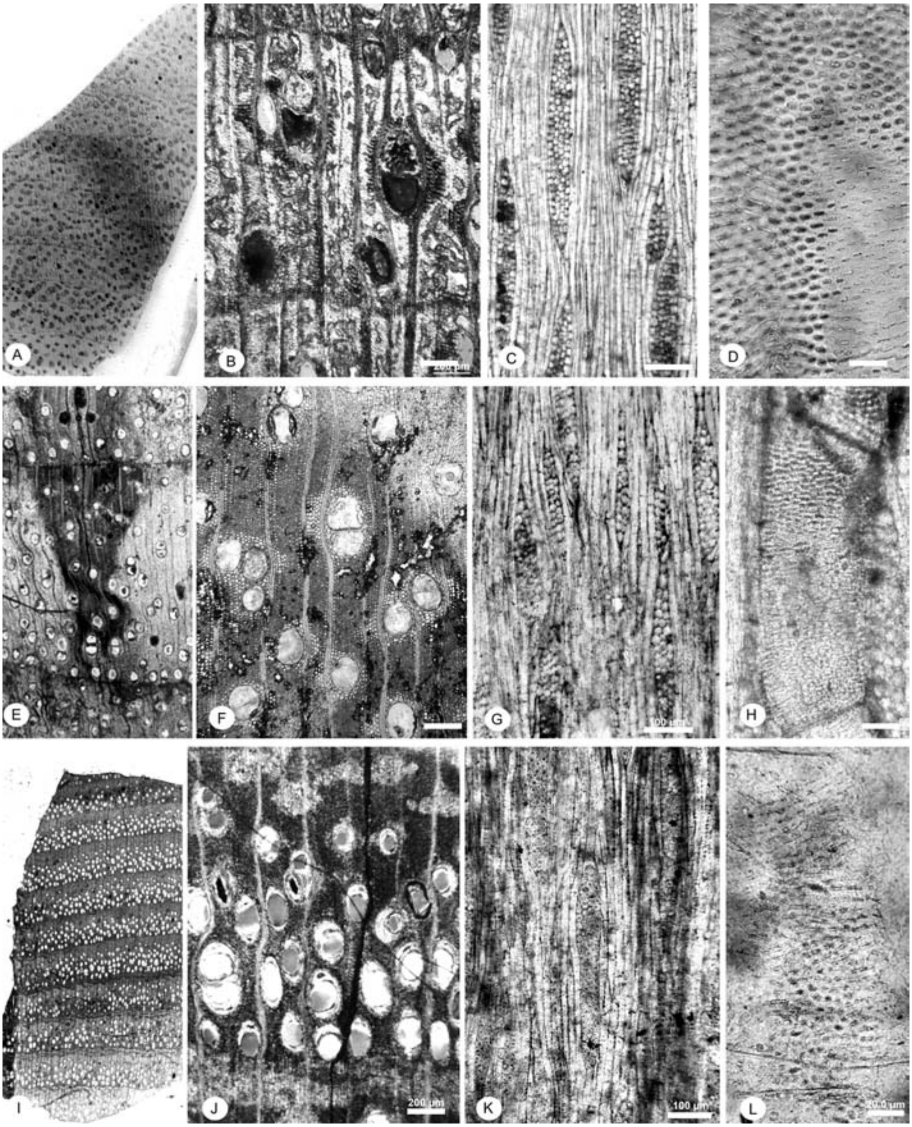
Recent work on extant legume woods, including mimosoid woods, still indicates that often it is not possible to distinguish genera (Evans *et al*. 2006) and so it seems appropriate to continue to use Müller-Stoll and Mädel's (1967) name.

“***Albizzia vantagiensis***” Prakash & Barghoorn 1961a (Fig. 9E–H)

[*Tetrapleuroxylon vantagiense* (Prakash & Barghoorn) Müller-Stoll & Mädel 1967]

Growth rings distinct, marked by radially narrower fibers.

Diffuse porous. Vessels solitary (72%) and in radial multiples of 2–3 (mostly 2); average tangential diameter 168 (35) μm, range 96–229 μm; vessel frequency of 3–5 per sq. mm; perforations simple, intervessel pits crowded alternate, polygonal in outline, 5–8 μm across; vessel–parenchyma pits similar in size and shape to intervessel pits; vessel element lengths 180–484 μm; tyloses not observed.



Fibers mostly non-septate, possibly a few septate fibers, walls thick, pitting not observed.

Axial parenchyma mostly vasicentric, with some tendency to aliform-lozenge; narrow lines of marginal parenchyma, usually 4 cells per strand.

Rays 1–4-seriate. Multiseriate rays homocellular, composed of procumbent cells, average multiseriate ray height 492 (202) µm, range 179–1182 µm, 1–2-seriate rays rare, rays 6–10 per mm.

Storied structure absent, crystals not observed.

Material: HU 55237 (holotype).

Comments: Müller-Stoll and Mädel (1967) believed that this wood could not be assigned to *Albizia* as *Albizia* has septate fibers, and this Vantage fossil was described as having non-septate fibers. However, five of the 25 *Albizia* species that Evans *et al.* (2006) examined are listed as lacking septate fibers. Also, we observed some places in the Vantage wood that looked as if some fibers might be septate. The diagnosis of *Tetrapleuroxylon*, the genus this Vantage wood was transferred to, states that diffuse axial parenchyma is common, but according to Prakash and Barghoorn's description of this sample it is scanty. We could not confirm the presence of diffuse axial parenchyma. Thus, what to call this wood is problematic. It does not fit the diagnosis of *Tetrapleuroxylon*. The presence or absence of septate fibers is an important diagnostic feature for legume wood, it seems that the bulk of this wood's fibers are non-septate, but it appears that there are some septate fibers. This wood has characteristics observed in *Albizia*, but these characteristics occur in other extant mimosoid woods (Evans *et al.* 2006). Our main objective is to document the wood types at Vantage. Until a better preserved example of this wood type is found so that presence and abundance of diffuse parenchyma and septate fiber presence can be determined, we are going to refer to this sample as *"Albizzia vantagiensis"* with the Prakash and Barghoorn name in quotes to indicate that while this mimosoid wood has characteristics reminiscent of *Albizia* it should ***not*** be considered equivalent to only that genus.

GLEDITSIOXYLON Müller-Stoll & Mädel

Gleditsioxylon columbianum (Prakash & Barghoorn) Müller-Stoll & Mädel 1967 (Fig. 9 I–L)

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Figure 9. Fabaceae. – A–D: *Dichrostachyoxylon occidentale* (*Leguminoxylon occidentale*). HU 55076. – A, B: Diffuse porous wood, vessels solitary and in short radial multiples, vasicentric and lozenge-aliform parenchyma, distinct marginal parenchyma bands. Vertical dimension of image = 27.0 mm. XS. – C: Multiseriate rays to 4–5-seriate, uniseriate rays rare. TLS. – D: Crowded alternate intervessel pits. TLS. – E–H: "*Albizzia vantagiensis*". HU 55237. – E, F: Diffuse porous wood, vessels solitary and in radial multiples of 2–3, vasicentric and lozenge-aliform axial parenchyma. Width of growth ring in E = 4.4 mm. XS. – G: Rays 2–4-seriate. TLS. – H: Crowded alternate intervessel pits, with some coalescent apertures. TLS. – I–L: *Gleditsioxylon columbiana*. HU 55204. – I: Ring porous wood, broad earlywood zone. Vertical dimension of sample = 19.3 mm. XS. – J: Growth ring boundary, earlywood with vessels solitary and in radial multiples, latewood with vessels in clusters, paratracheal parenchyma. XS. – K: Rays mostly 4–6 cells wide. TLS. – L: Crowded alternate intervessel pits, some coalescent apertures. TLS. — Scale bar = 200 µm in B, F, J; 100 µm in C, G, K; 50 µm in H; 20 µm in D, L.

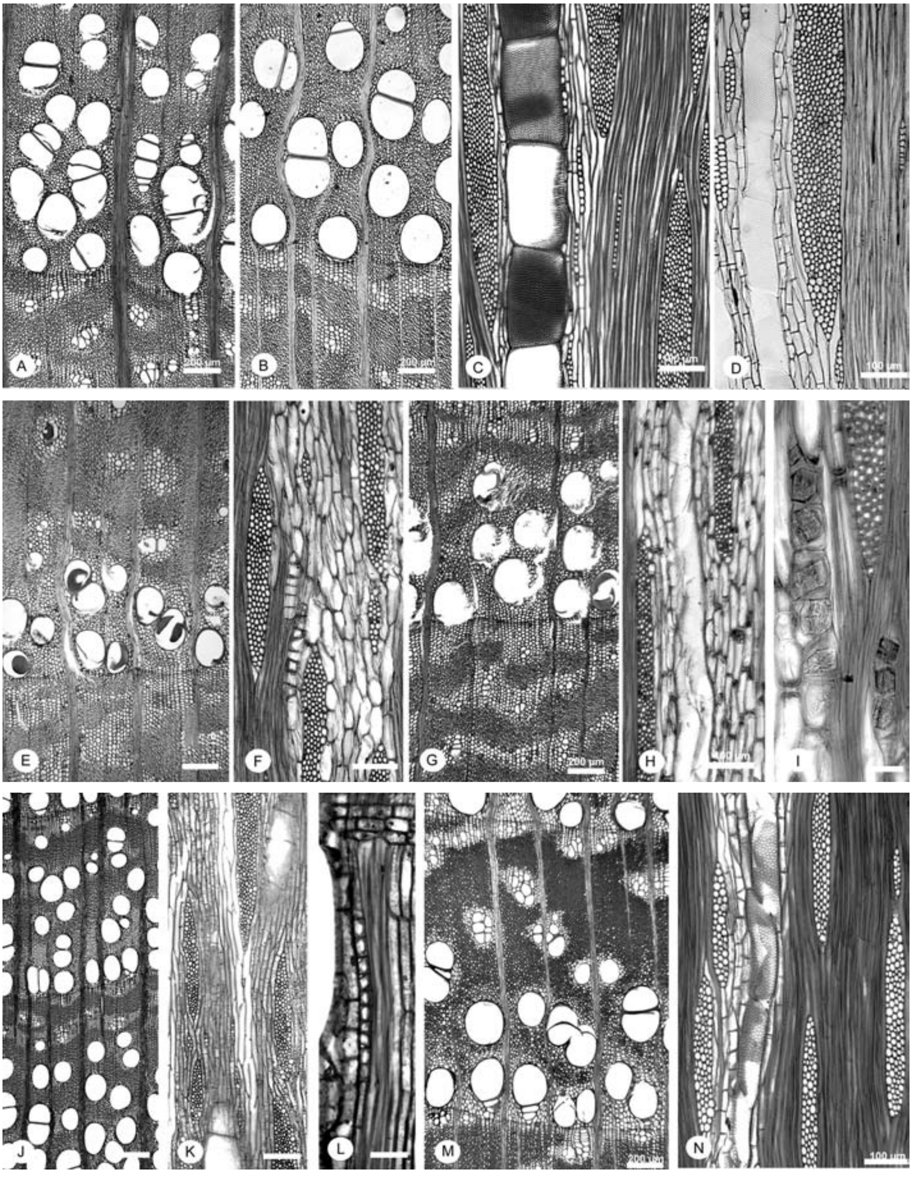

Figure 10. Fabaceae. – A–L: Extant *Gleditsia*. M–N: Extant *Gymnocladus*. – A: *Gleditsia aquatica*. BWCw 8525. Broad earlywood zone, latewood with clusters. XS. – B: *Gleditsia triacanthos*. BWCw 8716. Broad earlywood zone, latewood with clusters. XS. – C: *Gleditsia aquatica*. BWCw 8525. Rays more than 10 cells wide. TLS. – D: *Gleditsia triacanthos*. BWCw 8716. Rays more than 10 cells wide. – E, F: *Gleditsia sinensis* China A140. – E: Ring porous wood, earlywood zone with solitary vessels and short radial multiples, latewood vessels in clusters intermixed with axial parenchyma and narrow vessel elements. XS. – F: Rays less than 10 cells wide. Crystals in chambered axial parenchyma. TLS. – G–I: *Gleditsia macrantha* China A139. – G: Ring porous wood, earlywood zone with solitary vessels and short radial multiples, latewood

[*Gleditsia columbiana* Prakash & Barghoorn 1961a]

Growth ring boundaries distinct.

Ring porous. Earlywood broad, with most earlywood vessels solitary and a few short radial multiples. Mean diameter of earlywood vessels 148 (26) µm, range 102–200 µm (HU 55204); 173 (27) µm, 131–244 µm (HU 56712). Latewood with vessels mostly in clusters, in the latest latewood vessels very narrow. Perforation plates exclusively simple. Intervessel pits crowded alternate, 7–10 µm. Vessel–ray pits with distinct borders; similar to intervessel pits in size and shape throughout the ray. Helical thickenings in the narrowest vessel elements (observed by Prakash & Barghoorn). Vessel element length averages 252 (32) µm, range 200–311 µm in HU 56712. Tyloses not observed, but vessels appear to have gum deposits.

Fibers with simple pits. Non-septate fibres. Fibers medium-thick to thick-walled.

Axial parenchyma vasicentric, aliform-lozenge, to confluent. In latter part of growth ring confluent parenchyma more common, 2–4 cells per strand.

Multiseriate rays commonly 3–5-seriate; 1–2-seriate rays rare; homocellular, composed of procumbent cells, average multiseriate ray height 453 (141), range 190–806 µm in HU 55204 and 433 (219), 207–1177 µm in HU 56712; 6–8 per mm.

Storied structure absent, crystals not observed.

Material: HU 55204 (holotype), HU 56712 (Beck 169, Loc. 11, "12" log).

Comments: When Prakash and Barghoorn (1961a) described this wood they noted that its rays were narrower (mostly 3–4-seriate, Fig. 9 K) and shorter than rays of extant *Gleditsia triacanthos* whose rays typically are 10-seriate or more. Such wide rays also characterize the eastern U.S. *Gleditsia aquatica*. Although it was assigned to *Gleditsia*, Prakash and Barghoorn left open the possibility that this Vantage wood "may be the wood of a *Gymnocladus"*, which has rays 1–5-seriate. *Gleditsia* (Fig. 10 A–L) and *Gymnocladus* (Fig. 10 M, N) are closely related (Lewis *et al*. 2005) and share many wood anatomical features. Gasson *et al*. (2003) noted that *Gleditsia* had larger rays and occasionally had druses. An additional feature that Panshin and De Zeeuw (1980) suggested that distinguished the eastern U.S. *Gleditsia triacanthos* from the eastern U.S. *Gymnocladus dioica* was that individual vessels in latewood clusters of *Gleditsia* are very narrow and it is difficult to distinguish individual vessel outlines, while in *Gymnocladus* it is easier to distinguish individual vessels in the latewood clusters. The size and distinctiveness of the latewood vessels of this Vantage wood resemble those of *Gleditsia* more than those of *Gymnocladus dioica*, but we were not able to examine woods of all species of *Gymnocladus*. Schnabel, McDonel, and Wendel (2003) used ITS and cpDNA to investigate the relationships of *Gleditsia* species. They were unable

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vessels in clusters intermixed with axial parenchyma and narrow vessel elements. XS. – H: Rays less than 10 cells wide. TLS. – I: Prismatic crystals in chambered axial parenchyma. TLS. – J–L: *Gleditsia japonica*. – J: Ring porous wood, with broad earlywood zone. TWTw 13677. XS. – K: Multiseriate rays. TWTw 16316. TLS. – L: Crystals in chambered axial parenchyma. TWTw 13677. RLS. – M, N: *Gymnocladus dioica*. BWCw 8009. – M: Broad earlywood zone, latewood vessels in clusters. XS. – N: Rays mostly 4–5-seriate. TLS. — Scale bar = 200 µm in A, B, E, G, J, M; 100 µm in C, D, F, H, K, N; 50 µm in L; 20 µm in I.

to obtain material of *Gleditsia assamica* (northeastern India) or *G. macrantha* (south coast of Caspian Sea). In all of their analyses of the 11 species available, they recovered four *Gleditsia* clades: the *G. japonica* clade, the *G. triacanthos* clade (including *G. aquatica*), the *G. australis* clade (including *G. ferox*), and the *G. sinensis* clade, with the South American *G. amorphoides* sister to the rest of the genus.

The *Gleditsia* wood samples available to us suggest that it may be possible to distinguish wood anatomically between some of the clades. In *Gleditsia japonica* (Fig. 10 J–L) rays usually do not exceed 8-seriate and prismatic crystals are in chambered axial parenchyma cells (8 or more chambers); in the eastern U.S. clade of *G. triacanthos* and *G. aquatica* (Fig. 10 A–D) rays are typically 10-seriate or more and have druses in ray parenchyma cells. *Gleditsia sinensis* (Fig. 10 E, F) and *G. macrantha* (Fig. 10 G, H) have large crystals in short strands of chambered axial parenchyma, usually 4 crystalliferous cells in a strand, which suggests that *G. macrantha* may belong to the *Gleditsia sinensis* clade. We did not observe crystals of any type or chambered axial parenchyma cells in the Vantage *Gleditsia*.

Müller-Stoll and Mädel (1967) reviewed fossil legume woods and they considered the Vantage wood to resemble *Gymnocladus* wood as much as *Gleditsia* wood. We agree with this evaluation. They proposed the form genus *Gleditsioxylon* and transferred *Gleditsia columbiana* to it. If this wood is *Gleditsia*, its features are not consistent with a relationship to the eastern U.S. *G. triacanthos* clade.

Both the Miocene *Gleditsia paleojaponica* Suzuki & Watari (1994) from Honshu, Japan, and *Gleditsia montanense* Prakash, Barghoorn & Scott (1962) from Montana, USA, have crystal distribution and ray sizes consistent with the extant *Gleditsia japonica* clade.

ROBINIA L.

Robinia zirkelii (Platen) Matten, Gastaldo, Lee 1977 (Fig. 11)
[*Cercidioxylon zirkelii* Platen 1908]
[*Robinia alexanderii* Webber 1933]
[*Robinia breweri* Prakash, Barghoorn & Scott 1962]
[*Robinioxylon zirkelii* (Platen) Müller-Stoll & Mädel 1967]
[*Robinioxylon alexanderi* (Webber) Müller-Stoll & Mädel 1967]
[*Robinioxylon breweri* (Prakash, Barghoorn & Scott) Müller-Stoll & Mädel 1967]

Growth rings present, distinct.

Ring porous. Earlywood vessels circular in outline, earlywood zone usually 3–4 vessels wide. Mean tangential diameter of earlywood vessels 200 μm, range 130–270 μm. Latewood vessels mostly in clusters and intermixed with axial parenchyma. Perforation plates exclusively simple. Intervessel pits crowded alternate, 5–7 μm. Vessel–ray pits with distinct borders; similar to intervessel pits in size and shape throughout the ray. Vessel element lengths 150–350 μm. Helical thickenings in the narrowest vessel elements. Earlywood vessels with abundant thin-walled tyloses.

Thick-walled fibers, fiber pits not observed, fibers non-septate.

Axial parenchyma paratracheal, intermixed with the latewood vessel clusters. Fusiform cells and strands of 2–4 cells, storied.

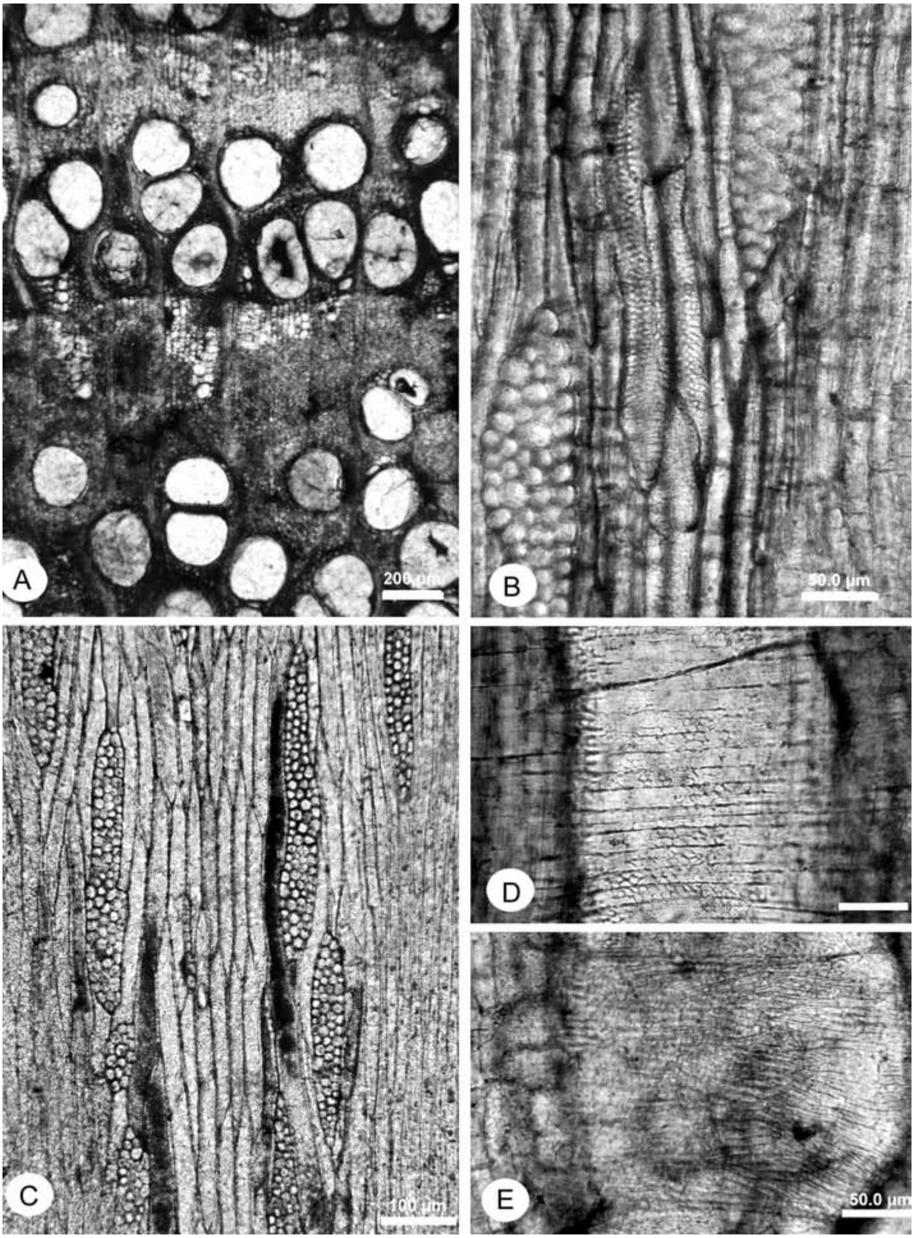

Figure 11. Fabaceae. – A–E: *Robinia zirkelii*. – A: Ring porous wood, latewood vessels in clusters, tyloses visible in some wide earlywood vessels. UWBM 98702 (Beck 290). XS. – B: Latewood vessels with helical thickenings, simple perforation plates, and crowded alternate pitting. UWBM 98702 (Beck 290). TLS. – C: Rays mostly 3–4-seriate, homocellular, storied axial elements. UWBM 98702 (Beck 290). TLS. – D: Vessel–ray parenchyma pits. RLS. – E: Crowded alternate intervessel pits, angular in outline. UWBM 98701 (Beck 228). RLS. — Scale bar = 200 µm in A; 100 µm in C, 50 µm in B, D, E.

Rays 1–5-seriate, mostly 3–4-seriate. Homocellular composed of all procumbent cells. Multiseriate ray height averages 417 (246) µm, range 93–1017 µm; 1-seriate rays usually less than 10 cells high. Rays 4–6 per mm. Non-storied.

Material: HU 56285, UWBM 98700 (Beck 220), UWBM 98701 (Beck 228), UWBM 98702 (Beck 290), UWBM 98703 (Beck 353), UWBM 98705 (Beck 637).

Comments: Matten *et al*. (1977) reviewed characteristics of fossil woods assigned to *Robinia* and found overlap in the quantitative features of the three species from North America. Differences between the fossil species were comparable to differences they found between samples of the extant *Robinia pseudoacacia*. Consequently, they proposed that North American fossil *Robinia* woods be consolidated into a single species, *Robinia zirkelii* (Platen) Matten, Gastaldo, Lee (1977). Page's (1993) study of fossil *Robinia* woods from two different Miocene localities and wood from different parts of a single extant *R. pseudoacacia* tree supported Matten *et al*.'s proposal.

Fossil woods of *Robinia* have been reported from the late Eocene of Nebraska and Colorado (Wheeler 2001; Wheeler & Landon 1992), Miocene of California and Nevada (Webber 1933; Page 1993) and Montana (Prakash *et al*. 1962), and the Pliocene of Oklahoma (Matten *et al*. 1977).

The Vantage sample (HU 56285) that Prakash (1968) assigned to *Robinioxylon breweri* was not located. Among Beck's collection there were other samples Beck had referred to *Robinia*. These samples had characteristics consistent with assignment to *Robinia zirkelii*, although abundant tyloses were not obvious in all samples as would be characteristic of *Robinia*. In these samples the infilling of the vessels and subsequent crystallization created patterns that made it difficult to distinguish tyloses. The *Robinia* woods that Beck collected had quantitative features similar to those reported by Prakash and given above. For example, the tangential diameters of earlywood vessels in Beck 290 averaged 195 (20) µm, with a range of 156–225 µm.

FAGACEAE

FAGUS L.

Fagus manosii sp. nov. (Fig. 12)

Growth ring boundaries distinct and noded. Wood diffuse porous, tending to semi-ring porous; with the latewood with narrower vessels. Vessels solitary and in small multiples, tending to be angular in outline; average earlywood tangential diameter 52 (11) µm; vessel frequency in earlywood 110–130 per sq.mm. Perforation plates mostly simple and occasionally scalariform, with fewer than 10 bars, scalariform perforations in narrow vessel elements at the end of the growth ring. Intervessel pits scalariform to opposite, opposite intervessel pits more than 10 µm in the horizontal dimension. Vessel–ray parenchyma pits with reduced borders and horizontally elongate (scalariform).

Fibers non-septate, some imperforate elements at the end of the growth ring with distinctly bordered pits on the radial walls, walls medium thick.

Axial parenchyma diffuse, not common, strands of 5–8 cells.

Rays uniseriate and multiseriate, with multiseriate rays to 16 cells (150 µm) wide; rays 3–6-seriate common, wide rays irregularly spaced, ray height to 1.7 mm.

Homocellular to heterocellular with 1–3 marginal rows of square to upright cells; 5–7 per mm.

Storied structure absent, crystals not observed.

Holotype: HU 56631 (Beck 1823).

Etymology: Specific epithet recognizes Paul Manos, who has extensively studied the Fagaceae.

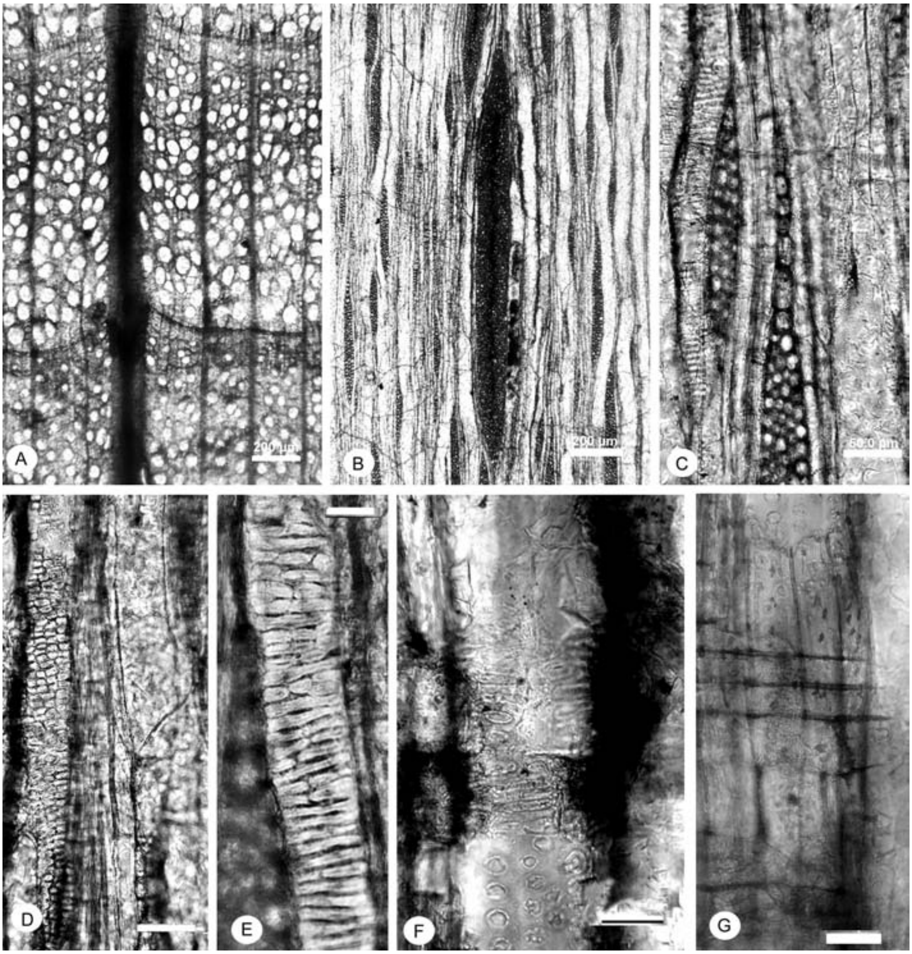

Figure 12. Fagaceae. *Fagus manosii* sp. nov. HU 56631. – A: Diffuse porous wood, with distinct latewood zone with narrower vessels, tendency for vessels to be tangentially arranged. XS. – B: Rays of two distinct sizes, wide ray more than 10 cells wide. TLS. – C: Multiseriate rays with uniseriate margins of upright cells, TLS. – D: Crowded opposite intervessel pits, vessel element end wall with simple perforation viewed from the side. TLS. – E: Scalariform intervessel pits. TLS. – F: Vessel–ray parenchyma pits with reduced borders and horizontally elongated. RLS. – G: Fibers with distinctly bordered pits. RLS. — Scale bar = 200 µm in A, B; 50 µm in C, D; 20 µm in E, F, G.

Comments: Beck labeled his sample 1823 *Fagus*. The combination of characters: diffuse porous (Fig. 12 A), simple and scalariform perforations (Fig. 12 C, D), opposite to scalariform intervessel pits (sometimes alternate) (Fig. 12 C–E), and vessel–ray parenchyma pits with reduced borders (Fig. 12 F), diffuse and diffuse-in-aggregates parenchyma (Fig. 12 A) and large, heterocellular rays (Fig. 12 B) is diagnostic of the genus *Fagus* and confirms Beck's identification. Cupules, leaves and pollen of *Fagus* have been reported from other Pacific Northwest Miocene floras (Table 4).

To our knowledge, there is no reliable way of distinguishing the wood of extant *Fagus* species from different geographic regions. This is unfortunate as it would be useful for biogeographic and phylogenetic studies to know whether a fossil *Fagus* wood resembled a European, Asian, or American species. It may be possible, with examination of multiple specimens of the various *Fagus* species, to find a way to statistically differentiate between the species based on maximum ray width or relative frequency of simple vs. scalariform perforations or opposite vs. alternate vs. scalariform intervessel pitting. Whether this would help with assigning isolated samples of fossil wood to species or species group is debatable. Shimaji (1952) and Brazier and Franklin (1961) noted that *Fagus crenata* and *F. grandifolia* wood had crystals, while *F. japonica* and *F. sylvatica* did not. However, crystal occurrence is variable within a species. Some specimens of *F. grandifolia* had crystals; others did not (Brazier & Franklin 1961). We did not observe crystals in the Vantage *Fagus* wood.

Süss (1986) reviewed the fossil record of *Fagus*-like woods, which have been described under the generic names of *Fagus, Fagoxylon,* and *Fegonium*. There are Paleogene fossil woods described as having wood structure comparable to extant *Fagus*: *F. grandiporosum* Beyer (1954) from the Eocene of Yellowstone National Park, Wyoming, and *F. kraeuselii* Hofmann (1952) from the Oligocene of Austria. Unfortunately, the description of the Austrian wood is not detailed, so it is not possible to re-evaluate the affinities of this wood and to compare it to the Vantage *Fagus*. The Yellowstone *Fagus* has fewer, wider vessels, vessel–ray parenchyma pits were not described or illustrated, and only widely spaced alternate intervessel pits were figured. At least ten *Fagus*-like woods are known from the Mio-Pliocene of Europe, with the descriptions of many lacking some information that would allow comparison of the Vantage wood to them. To our knowledge this is the first description of a *Fagus* wood from the Neogene of North America.

QUERCUS L.

Quercus leuca Prakash & Barghoorn 1961a (HU 54916) (Fig. 13 A)

[*Quercus sahnii* Prakash & Barghoorn 1961b (HU 54968) (Fig. 13 B)]

[*Quercoxylon compactum* Prakash 1968 (HU 55015) (Fig. 13 C)]

Growth rings distinct.

Ring porous. Vessels exclusively solitary, earlywood vessels round in outline, earlywood zone usually two vessels deep, earlywood vessels with mean tangential diameters of 233–269 µm; latewood vessels angular in outline; perforations simple. Vessel–vasicentric tracheid pitting alternate, vessel–ray parenchyma pits irregularly shaped. Vessel element lengths 240–540 µm.

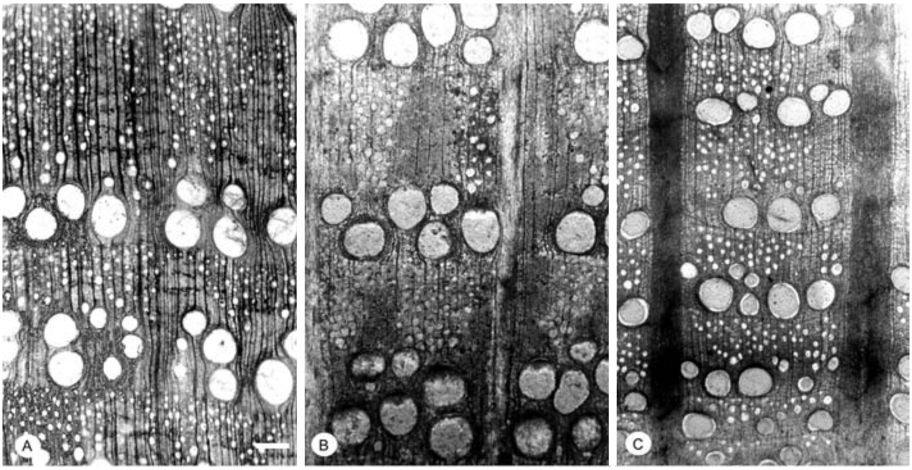

Figure 13. Fagaceae. *Quercus leuca*. – A–C: Ring porous wood with exclusively solitary vessels, two distinct width classes of rays, apotracheal banded parenchyma, abrupt transition to a latewood zone with narrow thin-walled vessels tending to be angular in outline, all are XS. – A: HU 54916. – B: HU 54968. Sample called *Quercus sahnii*. – C: HU 55015. Sample called *Quercoxylon compactum*. — Scale bar in A applies to B and C = ~200 µm.

Vasicentric tracheids present, some fibers with simple pits, some with bordered pits usually restricted to radial walls. Medium-thick to thick-walled.

Axial parenchyma diffuse in aggregates to banded.

Rays of two distinct sizes, uniseriate and broad rays over 10 cells wide, often to more than 20 cells wide. Homocellular, composed of procumbent cells.

Crystalliferous axial parenchyma strands.

Storied structure absent.

Additional material: HU 56676 (Beck 601) from Beck's Vantage locality 35.

Comments: It is frequently noted that while it is relatively easy to recognize an isolated wood sample as an oak (two size classes of rays, solitary medium-wide vessels, enlarged vessel–ray parenchyma pits, vasicentric tracheids, apotracheal axial parenchyma, homocellular rays), it is usually only possible to identify it to group: white oaks (ring porous, latewood vessels thin-walled, narrow and angular in outline), red oaks (ring porous, latewood vessels thick-walled, round to oval in outline), or live oaks (wood diffuse to semi-ring porous) (*e.g.*, Brazier & Franklin 1961; Panshin & DeZeeuw 1980).

Prakash and Barghoorn (1961a, 1961b) and Prakash (1968) described three species of oak from Vantage: (*Quercus leuca, Q. sahnii*, and *Quercoxylon compactum*). While it is possible that there were three distinct species of oak at Vantage, it is equally possible that the three Vantage oak samples described by Prakash and Barghoorn represent different trees of the same species. *Quercoxylon compactum* has narrower growth rings than the other samples. Ring width varies from tree to tree as well as with position in a single tree and affects the general appearance of a ring-porous wood. Figures 13A, B & C show transverse sections taken at the same magnification. Although Prakash compared *Quercus sahnii* to the red oak group, its latewood pores are thin-walled and angular in outline, characteristics of the white oak group. Tyloses are not obvious in the sample called *Quercus sahnii*, so this may be why it was called a red oak; white oaks usually have abundant tyloses, red oaks have tyloses, but they are not abundant. It is our opinion that the differences between these three samples are minor and not sufficient to recognize them as separate species. *Quercus leuca* was the first name applied to the Vantage oaks, and so has precedence and is applied to the samples called *Quercus sahnii* and *Quercoxylon compactum,* with these two names being superfluous.

Borgardt and Pigg (1999) studied silicified acorns from Yakima Canyon in the Columbia River Basalts. They described the species *Quercus hiholensis* based on these fruits, which they assigned to the white oaks. Fossilized *Quercus* woods are common in a number of deposits of the Columbia River Basalts, some of which have been informally described as red oaks. Further study is needed to determine if both red oaks and white oaks were present in the overall wood flora of the region.

HAMAMELIDACEAE

Hamamelidoxylon Lignier 1907

Hamamelidoxylon beckii sp. nov. (Fig. 14)

Growth rings visible microscopically, marked by 1–2 rows of radially narrower fibers.

Wood diffuse porous. Vessels solitary, slightly angular in outline. Mean tangential diameter 54 (6.7) µm, range 40–67 µm; 77–94 per sq.mm; perforation plates exclusively scalariform, 14–24 bars, usually 19 to 22, intervessel pits scalariform. Vessel–ray parenchyma pits horizontally elongate. Vessel element lengths 508–680 µm.

Fibers with distinctly bordered pits, on both radial and tangential walls, non-septate, thick-walled.

Axial parenchyma rare.

Rays predominantly uniseriate, average ray height 20 (7) cells, 369 (172) µm, range 174–858 µm. Heterocellular, body cells procumbent, usually with 1–2 rows of square/upright cells with nodular walls; 10–16 per mm.

Crystals in chambered ray cells that are somewhat enlarged.

Holotype: HU 56634 (Beck 144).

Etymology: Specific epithet is in honor of George Beck, in recognition of his contributions to paleobotany of the Pacific Northwest, and his extensive studies of fossil woods of the Columbia River Basalts.

Comments: Beck labeled this specimen *Gordonia* (Theaceae). Woods of *Gordonia lasianthus* are diffuse porous, have predominantly solitary vessels that are narrow and numerous, scalariform perforation plates, scalariform pitting, rare axial parenchyma, and exclusively uniseriate rays. These features are also found in woods of the Hamamelidaceae, particularly *Chunia, Exbucklandia, Fothergilla,* and *Hamamelis*. This Vantage wood has crystals in chambered ray parenchyma (Fig. 14 E), a feature that occurs in Hamamelidaceae, but not in *Gordonia*. Moreover the vessel–ray parenchyma pits of

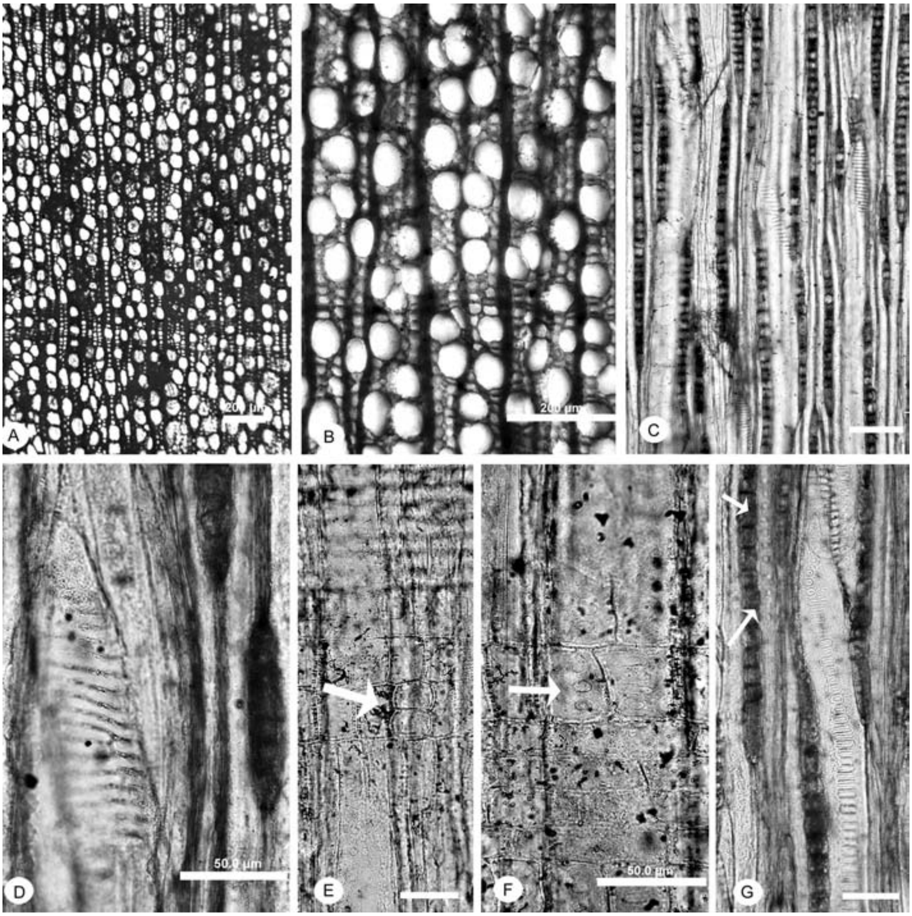

Figure 14. Hamamelidaceae. *Hamamelidoxylon beckii* sp. nov. HU 56634. – A: Diffuse porous wood, vessels predominantly solitary. XS. – B: Growth ring boundary of a few rows of radially narrower fibers, vessels tending to be angular in outline. XS. – C: Rays uniseriate. TLS. – D: Scalariform perforation plate. TLS. – E: Body ray cells procumbent with square/upright marginal cells. Crystals in chambered ray cell (arrow). RLS. – F: Vessel–ray parenchyma pits with reduced borders and horizontally elongated (arrow). RLS. – G: Scalariform pits on vessel wall. Fiber pits distinctly bordered (arrows). TLS. — Scale bar = 200 µm in A, B; 100 µm in C; 50 µm in D, E, F, G.

this Vantage wood (Fig. 14 F) resemble Hamamelidaceae rather than *Gordonia,* which has vessel–ray parenchyma pits that are usually slender and much elongated horizontally. Horizontally elongated vessel–ray parenchyma pits occur in *Hamamelis*, but they are commonly accompanied by oval vessel–ray parenchyma pits and the horizontally elongated vessel–ray parenchyma pits are not as slender as those in *Gordonia*. The vessel–ray parenchyma pits of this fossil resemble those of the Hamamelidaceae, rather than *Gordonia*.

Lee and Baas (1998) surveyed the wood anatomy of Hamamelidaceae and noted that, although there is limited wood anatomical diversity in the family, it is possible to key out most genera using a combination of qualitative and quantitative characters. In the Hamamelidaceae, the occurrence of crystals in ray and axial parenchyma is only reported for *Hamamelis*.

This wood conforms to the diagnosis of *Hamamelidoxylon* Lignier: solitary vessels, scalariform perforation plates, apotracheal diffuse parenchyma, scalariform vessel–ray parenchyma pits, and exclusively uniseriate (very rarely biseriate) rays. *Hamamelidoxylon uniseriatum* from the middle Eocene Clarno Formation differs as it lacks crystals and has more bars per perforation plate (mostly 24, up to 30–40 bars). The Cretaceous *H. obiraense* (Japan, Takahashi & Suzuki 2003), Eocene *H. dapniphylloides* (Europe, Gottwald 1992), and Miocene *H. maegdefrauii* (Europe, Van der Burgh 1973) also have more numerous bars, 40 bars per perforation plate. Other European *Hamamelidoxylon,* the Miocene *H. castellanense* Grambast-Fessard (1969) and *H. rhenanum* Van der Burgh (1973), and the Eocene *H. daphniphylloides* (Gottwald 1992) all have multiseriate rays. It may be that the *Hamamelidoxylon* of Europe with multiseriate rays are more closely related to the Asian *Hamamelis*, *e.g.*, *H. japonica* commonly has biseriate rays, while *Hamamelidoxylon beckii* is related to the eastern U.S. *Hamamelis virginiana,* which has predominantly uniseriate rays and crystals in both ray and axial parenchyma. More samples of the different extant species need to be examined to confirm this is a consistent difference.

Hamamelidoxylon suzukii sp. nov. (Fig. 15)

Growth rings distinct, marked by radially narrower latewood fibers.

Diffuse porous. Vessels predominantly solitary, occasional radial pairs; solitary vessels tending to be square-rectangular, somewhat angular, in outline; mean tangential diameter 53 (7) µm; range 34–66 µm; 60–86 per sq.mm. Exclusively scalariform perforation plates with 16–27 bars, most plates with some forked bars. Intervessel pits scalariform. Vessel–ray parenchyma pits horizontally elongate, borders reduced; vessel elements 550–990 µm long.

Fibers non-septate, walls thick.

Axial parenchyma rare.

Rays 1–2-seriate, predominantly uniseriate. Heterocellular with procumbent body cells and square to upright marginal ray cells, marginal ray cells with nodular end walls. Mean ray height 426 (157), range 185–942 µm; 9–14 per mm.

Crystals in chambered ray parenchyma cells.

Material: HU 56635 (Beck 153).

Etymology: Named for Mitsuo Suzuki in recognition of his contributions to our knowledge of Asian woods, fossil and modern.

Comments: Beck named his sample 153 *Hamamelis*. This sample is similar to *Hamamelis beckii* in vessel element diameter, frequency, and length, number of bars per perforation plate, and presence of prismatic crystals in chambered ray cells. However, this sample differs as it has predominantly biseriate rays. As mentioned above, some European *Hamamelidoxylon* species have multiseriate rays. This Vantage wood shares

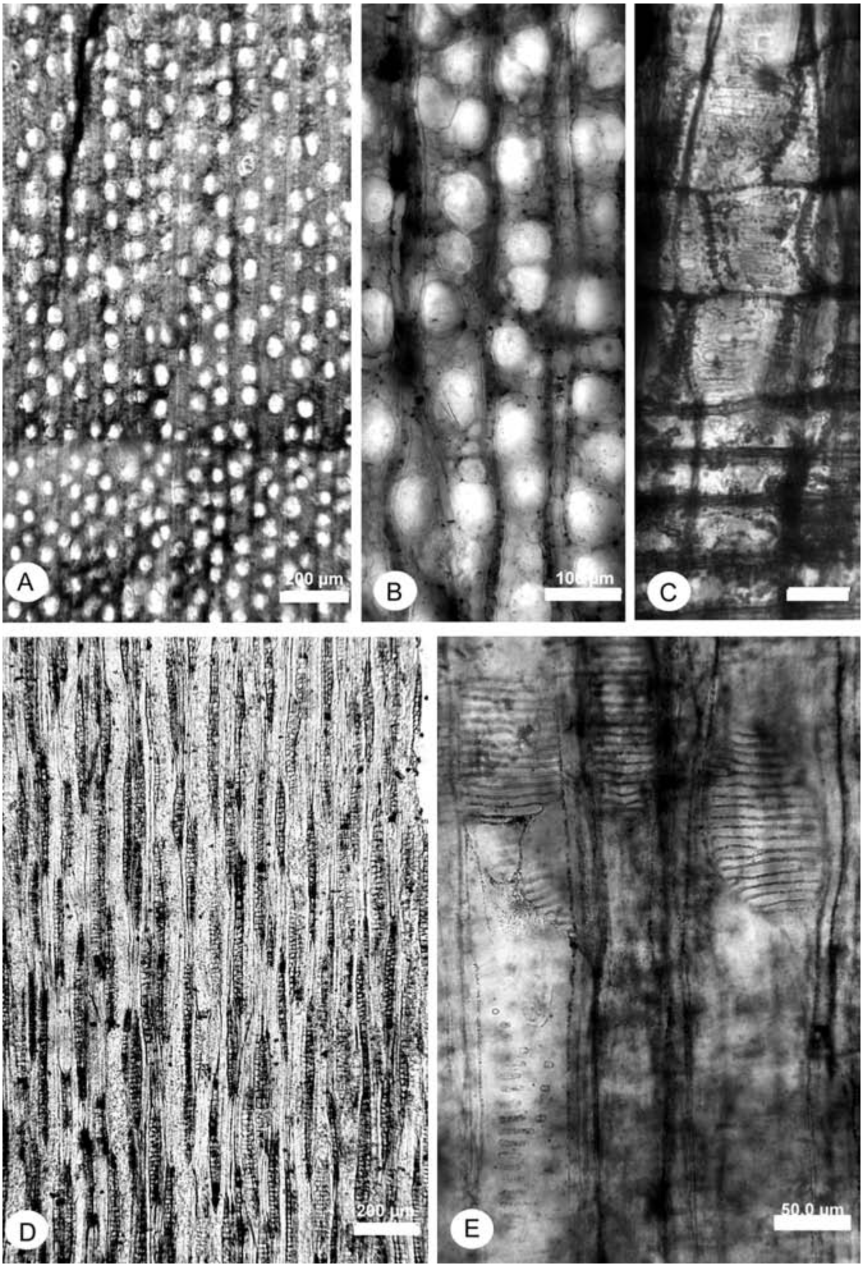

Figure 15. Hamamelidaceae. *Hamamelidoxylon suzukii* sp. nov. HU 56635. – A: Diffuse porous wood, growth rings present but not distinct. XS. – B: Vessels predominantly solitary and mostly circular in outline, axial parenchyma rare. XS. – C: Vessel–ray parenchyma pits with reduced borders and horizontally elongated. RLS. – D: Rays mostly biseriate. TLS. – E: Scalariform perforation plates, scalariform intervessel pits. RLS. — Scale bar = 200 µm in A, D; 100 µm in B; 50 µm in E; 20 µm in C.

some features with both the Miocene *H. rhenanum* and *H. castellanense*. *Hamamelidoxylon rhenanum* has a similar number of bars per perforation plate and rays appear similar to this Vantage wood. However, crystals were not reported for *H. rhenanum,* axial parenchyma is more common, and information on vessels per sq. mm, vessel element lengths, and ray height was not given. *Hamamelidoxylon castellanense* has few uniseriate rays and rays are markedly heterocellular; it was difficult to count the number of bars per perforation plate in this species, but it was estimated there were few bars (~10). However, *H. castellanense* has crystals in ray parenchyma. Consequently, this Vantage wood is not fully congruent with any other *Hamamelidoxylon* species, and has differences of a type used in the past to establish new species of the *Hamamelidoxylon*.

JUGLANDACEAE

RHYSOCARYOXYLON Dupéron

Rhysocaryoxylon tertiarum (Prakash & Barghoorn) Dupéron 1988 (Fig. 16 A–C)

[*Carya tertiara* Prakash & Barghoorn 1961a]

[*Caryojuglandoxylon tertiarum* (Prakash & Barghoorn) Müller-Stoll & Mädel-Angeliewa 1983]

Growth rings distinct.

Semi-ring porous. Vessels solitary and in short radial multiples, solitary vessels oval in outline; earlywood mean tangential diameter 224 (37), 165–320 µm; perforation plates simple; intervessel pits crowded alternate, angular in outline, 7–12 µm; vessel element lengths 255–485 µm.

Fibers non-septate, thick-walled, pitting not observed.

Axial parenchyma scanty paratracheal to vasicentric, in narrow, straight bands (1–2 cells deep), 5–8 cells per strand.

Rays 1–4-seriate, homocellular, composed of procumbent cells, shape of body cells in tangential section circular, total multiseriate ray height averages 477 (93) µm, range 333–777 µm, 9–12 per mm.

Crystals in chambered axial parenchyma cells, crystalliferous cells enlarged, number of chambers variable, 2 to >8, usually 3–4 enlarged crystalliferous cells in a parenchyma strand.

Material: HU 55210 (holotype), HU 65002 (Beck 452).

Rhysocaryoxylon fryxellii (Prakash & Barghoorn) Dupéron 1988 (Fig. 16 D–F)

[*Juglans fryxellii* Prakash & Barghoorn 1961b]

[*Caryojuglandoxylon fryxellii* (Prakash & Barghoorn) Müller-Stoll & Mädel-Angeliewa 1983]

Growth rings distinct.

Semi-ring porous. Vessels solitary and in short radial multiples, diagonally arranged, solitary vessels oval in outline; earlywood mean tangential diameter 214, 150–320 µm; perforation plates simple; intervessel pits crowded alternate, angular in outline, 7–12 µm; vessel element lengths 255–485 µm.

Fibers non-septate, thick-walled, pitting not observed.

Axial parenchyma scanty paratracheal to vasicentric, in narrow bands (1–2 cells deep), 5–8 cells per strand.

Rays 1–3- (4-)seriate, homocellular, composed of procumbent cells, although rays often have uniseriate tails these are composed of procumbent cells, shape of body cells in tangential section mostly circular to slightly oval, total multiseriate ray height averages 317 (66), range 227–551 µm, 9–12 per mm.

Crystals in chambered axial parenchyma cells, crystalliferous cells slightly enlarged.

Material: HU 55045 (holotype).

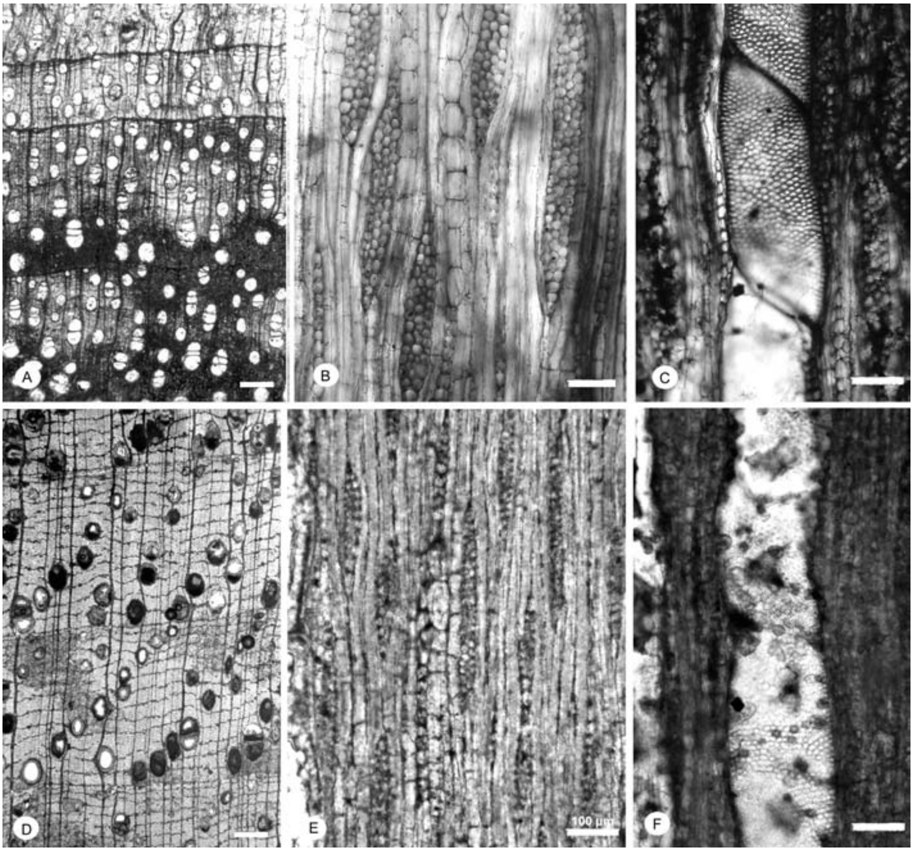

Figure 16. Juglandaceae. – A–C: *Rhysocaryoxylon tertiarum*. HU 55210. – A: Semi-ring porous wood, vessels solitary and in short radial multiples, narrow lines of axial parenchyma. XS. – B: Rays 1–3 (4) cells wide, chambered axial parenchyma with prismatic crystals, somewhat inflated. TLS. – C: Crowded alternate intervessel pits. TLS. – D–F: *Rhysocaryoxylon fryxellii*. HU 55045. – D: Semi-ring porous wood, vessels solitary and in short radial multiples, vessels in diagonal arrangement, regularly spaced lines of axial parenchyma. XS. – E: Rays 1–3-seriate, short chains of crystalliferous axial parenchyma. TLS. – F: Crowded alternate intervessel pits. TLS. — Scale bar = ~250 µm in A, D; 100 µm in B, C, E, F.

Comments: Prakash and Barghoorn considered sample HU 55210 similar to the present-day True Hickory *Carya leiodermis*, and sample HU 55045 similar to the present-day Black Walnut *Juglans nigra*. However, HU 55210 is semi-ring porous and has parenchyma bands in the earlywood. These are not characteristics of *C. leiodermis* or any other True Hickory (Stark 1953; Brazier & Franklin 1961; Panshin & De Zeeuw 1980). Stark noted that it was difficult to distinguish semi-ring porous species of *Carya* from *Juglans*. Dupéron (1988) created the genus *Rhysocaryoxylon* for such woods. Characteristics of this genus and seen in both HU 55210 and HU 55045 are: wood semi-ring porous, vessels solitary and in radial multiples of 2–4, simple perforations, alternate intervessel pits that are polygonal in outline, scanty paratracheal parenchyma, apotracheal parenchyma in narrow bands present throughout the growth ring, crystals in enlarged axial parenchyma cells, rays 1–3(–5)-seriate, homocellular or slightly heterocellular. Consequently, in his revision of Juglandaceous fossil woods Dupéron assigned the two Vantage Juglandaceae woods to *Rhysocaryoxylon*. Dupéron did not comment on the differences between these two species. Vessels in *Rhysocaryoxylon fryxellii* have an obvious diagonal arrangement (Fig. 16D), while vessels in *R. tertiarum* are randomly arranged (Fig. 16A); *R. fryxellii* (Fig. 16E) has shorter crystalliferous chains (rarely more than 4) and narrower rays (mostly 3-seriate) than *R. tertiarum* (Fig. 16B, crystalliferous chains up to 10, rays often 4-seriate).

Miller (1976) divided the walnuts into four wood anatomical groups: North Temperate Black Walnuts, Tropical Black Walnuts, English Walnut, and Butternuts and outlined features to distinguish them (Table 5).

Table 5. Characteristics of *Juglans* species groups. Based on Miller (1976).

	Porosity	Reticulate thickening	Crystals	Ray cellular composition	Ray cell shape
N. Temperate Black Walnuts	Semi-ring porous	Present	Short chains, <10	Homocellular & Heterocellular	Mostly circular
Tropical Black Walnuts	Diffuse porous	Absent	Long chains, often >10	Heterocellular	Mostly circular
English Walnut	Semi-ring porous	Absent	Absent	Homocellular	Mostly circular
Butternuts	Semi-ring porous	Absent	Absent	Homocellular	Oval

Both *Rhysocaryoxylon tertiara* and *R. fryxellii* resemble North Temperate Black Walnuts in porosity, crystal occurrence, ray composition, and ray cell shape, but we did not observe reticulate thickenings in the vessel elements – a distinctive feature of North Temperate Black Walnuts (Brazier & Franklin 1961; Miller 1976; see images of BWCw 8274 - *Juglans nigra* on InsideWood). However, Miller found that reticulate thickenings were less common in *J. major* and *J. microcarpa* than in *J. nigra* and concluded “reticulate thickenings become more sparse and eventually do not occur in species and specimens of the lower latitudes or more tropical regions.” The absence of reticulate thickenings in the Vantage Juglandaceae may be correlated with the Vantage forest growing during the mid-Miocene warm interval and growing in a climate consistent with present-day species growing at lower latitudes.

Pollen assigned to *Pterocarya, Juglans* and *Carya* is present in regional Miocene floras (Table 4), plus fossilized *Carya washingtonensis* fruits were described from a possible rodent cache found inside a hollow petrified log at one of the other Columbia River Basalt wood deposits (Manchester 1987). Further investigation of fossil woods from other regional localities may help to clarify which juglandaceous wood genera were present at the time.

LAURACEAE

RICHTEROXYLON gen. nov.

Wood diffuse porous. Growth rings distinct to indistinct. Vessels solitary and in short radial multiples. Perforation plates predominantly simple. Intervessel pits crowded alternate, small to medium; vessel–ray parenchyma pits similar to intervessel pits in size and shape. Fibers predominantly non-septate. Scanty paratracheal to vasicentric axial parenchyma. Rays 1–3-seriate. Oil cells present, predominantly associated with rays. Storied structure absent.

Richteroxylon micropunctatum sp. nov. (Fig. 17)

Growth rings distinct, marked by radially narrow fibers.

Diffuse porous. Vessels solitary (54%) and in radial multiples of 2(–3). Solitary vessels rounded in outline. Average tangential diameter 90 (14) μm, range 66–122 μm; 50–65 per sq.mm. Perforation plates simple, intervessel pits crowded alternate, polygonal in outline, usually 6–8 μm across. Vessel–ray parenchyma pits of similar size to intervessel pits. Vessel element lengths 238–462 μm.

Fibers non-septate, pits not observed.

Axial parenchyma scanty paratracheal, 2–4 cells per strand.

Rays mostly 2-seriate. Heterocellular, body ray cells procumbent, with 1 row of square to upright cells. Average ray height 286 (94) μm, range 168–552 μm, occasionally with oil cells; 5–8 per mm.

Storied structure absent, crystals not observed.

Holotype: HU 56645 (Beck 849).

Etymology: The genus name is in honor of H.G. Richter in recognition of his work on the Lauraceae. The species name is for the vessel–ray pits of the species, pits that are small for the Lauraceae.

Comments: Beck thought that this sample might be *Malus* in the Rosaceae. There is some resemblance to *Malus* in vessel distribution. However, the occurrence of oil cells in the rays (Fig. 17E, F), scanty paratracheal parenchyma (Fig. 17B), narrow heterocellular rays (Fig. 17C), and fibers with simple pits indicates that it is Lauraceae. Of the 31 genera of Lauraceae in the InsideWood database, those with some species that have non-septate fibers, only scanty paratracheal to narrow vasicentric parenchyma, idioblasts in rays, intervessel pits neither minute nor large, and narrow rays include: *Beilschmiedia, Cinnamomum, Endlicheria, Laurus, Lindera, Litsea, Nectandra,*

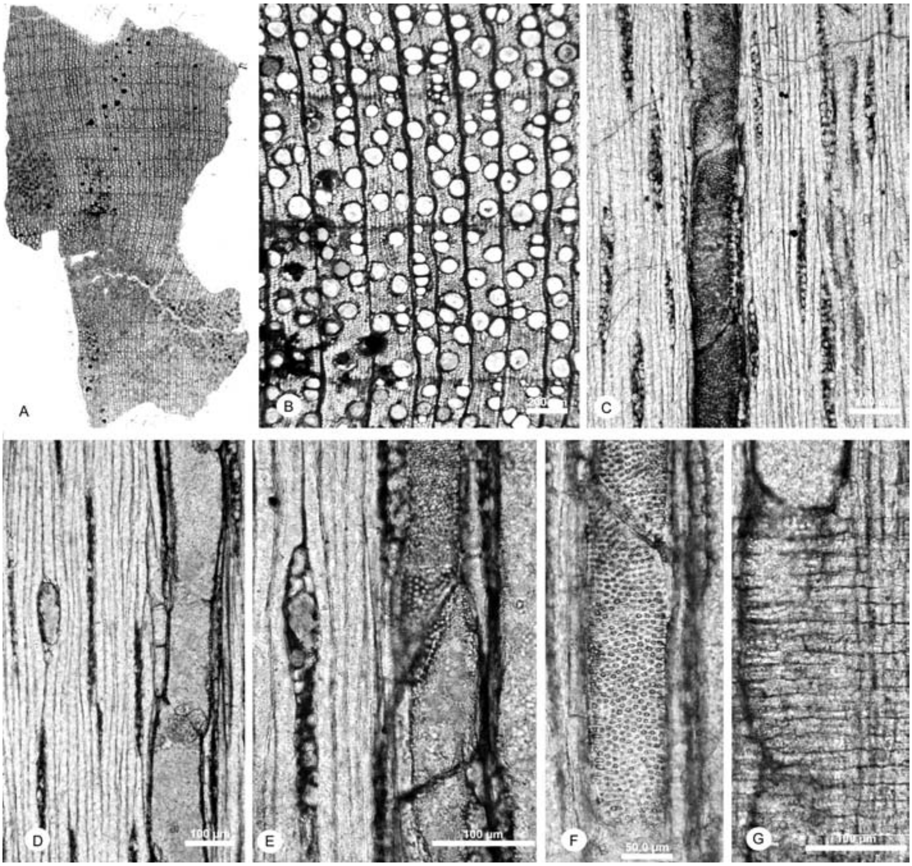

Figure 17. Lauraceae. *Richteroxylon micropunctatum*. HU 56645. – A: Diffuse porous wood with distinct growth rings. Sample width at widest point = 9 mm. XS. – B: Vessels solitary and in short radial multiples. Vessels rounded in outline. XS. – C: Rays predominantly biseriate. TLS. – D: Idioblast in ray, axial parenchyma strand adjacent to vessel element. TLS. – E: Ray with idioblast. TLS. – F: Crowded alternate intervessel pitting. TLS. – G: Vessel–ray parenchyma pits of similar size and shape as intervessel pits. RLS. — Scale bar = 200 µm in B; 100 µm in C, D, E, G; 50 µm in F.

Neolitsea, Ocotea (many *Ocotea* species have septate fibers though), and *Persea*. Richter (1981, 1987) reviewed the wood anatomy of extant Lauraceae. One of the features that Richter considered useful in distinguishing groups of genera was vessel–ray parenchyma pit class, which correlated with intervessel pit size. These classes are Class a: intervessel pits from 3–7 (8) µm and vessel–ray parenchyma pits of similar size and shape as intervessel pits, sometimes opening into compound pits that are horizontally or vertically enlarged, or are curved, Class b: intervessel pits 8–12 µm with vessel–ray pits variable in shape, round to oval, to elongated horizontally, vertically or diagonally, and Class c: intervessel pits 10–15 µm diameter, vessel–ray pits very large and window-like. The Vantage wood fits Class a. The genera that Richter (1987) lists as belonging to Class a are *Actinodaphne p.p., Laurus, Lindera p.p., Litsea chinensis, Neolitsea, Persea p.p.* (North American species), *Sassafras,* and *Umbellularia.*

Dupéron-Laudoueneix and Dupéron (2005), Gottwald (1992, 1997), and Süss (1958) reviewed fossil woods assigned to Lauraceae. Most fossil woods of Lauraceae have been assigned to the genus *Laurinoxylon,* which contains a variety of wood types that differ in features that Richter (1981, 1987) used to distinguish groups of extant genera. *Paraperseoxylon scalariforme* from the middle Eocene Clarno Nut Beds (Wheeler & Manchester 2002) is the only other lauraceous fossil wood known to have Class a vessel-ray parenchyma pits. However, the genus was erected to accommodate woods with both simple and scalariform perforation plates and idioblasts scattered among the fibers in addition to occurring in rays. Consequently, as this wood represents a distinctive type of lauraceous wood with features that have been demonstrated to be useful in separating groups of extant lauraceous genera we propose the genus *Richteroxylon.*

NYSSACEAE

NYSSA L.

Nyssa eydei Prakash & Barghoorn 1961b (Fig. 18)

Growth rings present, but not obvious, marked by only a band of 1–2 rows of radially narrower fibers.

Diffuse porous. Vessels solitary and in radial multiples, solitary vessels squarish to somewhat polygonal in outline; average tangential diameter 62 µm (range 45–90 µm); perforation plates exclusively scalariform with more than 20 bars, intervessel pits opposite, c. 5 µm across; vessel–ray parenchyma pits not observed; vessel element lengths average 1251 (127) µm.

Fibers non-septate, walls thin, pits not observed.

Axial parenchyma diffuse to diffuse-in-aggregates, fairly abundant; 10–12 cells per strand.

Rays 1–3- (4-)seriate. Multiseriate rays heterocellular, with 2 to more than 10 rows of upright marginal cells, rays usually asymmetric with different numbers of marginal rows on different ends of the rays; average total multiseriate ray height 517 (164) µm, range 279–896 µm (Prakash and Barghoorn report to >1 mm high in HU 54972); 7–13 per mm.

Chambered crystalliferous strands of axial parenchyma occasional, with more than 12 chambers.

Material: HU 54972 (holotype), HU 56648 (Beck 515).

Comments: The combination of characters diffuse porous wood with narrow vessels that are solitary and in radial multiples and randomly arranged, exclusively scalariform perforation plates with more than 20 bars, small opposite intervessel pits, fibers with thin walls, diffuse-in-aggregates axial parenchyma, and markedly heterocellular 1–3-seriate rays occurs in *Nyssa*. Noshiro and Baas (1998) reviewed the systematic wood anatomy of the Cornaceae *s.l.*, including *Nyssa*. The distinct growth rings of the Vantage wood indicate that it belongs to the temperate to subtropical species group of the genus. Prakash and Barghoorn (1961b) equated *Nyssa eydei* with *Nyssa ogeche* of

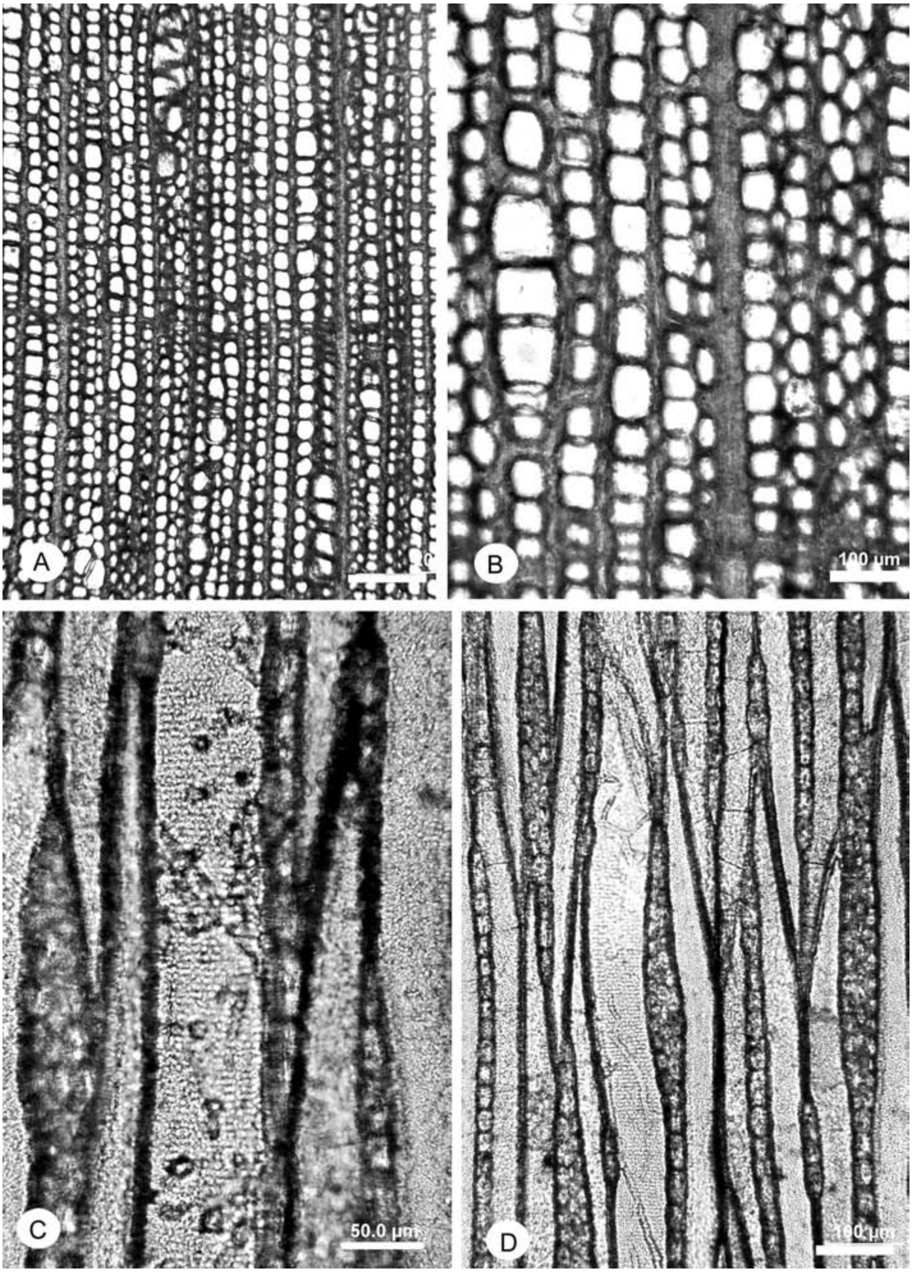

Figure 18. Nyssaceae. *Nyssa eydei*. HU 56642. – A: Growth ring boundary only a few radially narrow fibers, diffuse porous, vessels solitary and in radial multiples. XS. – B: Narrow vessels in radial multiples, not much wider than thin-walled fibers. XS. – C: Opposite intervessel pits. TLS. – D: Heterocellular rays, multiseriate rays with long uniseriate margins, uniseriate rays composed of upright cells, vessel elements with steeply inclined end walls and scalariform perforation plates. TLS. — Scale bar = 200 µm in A; 100 µm in B, D; 50 µm in C.

the southeastern U.S. because both have very thin-walled fibers, and narrow, angular vessel elements. However, these characteristics also can be seen in some samples of *N. biflora* and *N. aquatica*. All three of these southeastern U.S. species grow in moist sites, usually along the borders of rivers, swamps, and ponds.

Fossil woods assigned to *Nyssoxylon* or *Nyssa* are reported from the Cretaceous of Europe (Gottwald 2000; Meijer 2000), Paleocene of the southeastern U.S. (Melchior 1998), Eocene of Europe (Gottwald 1992), Japan (Suzuki 1975), and Yellowstone National Park, U.S. (Wheeler *et al*. 1978). These older woods resemble tropical to subtropical species, such as *Nyssa javanica*, rather than the species now growing in the southeastern U.S.

OLEACEAE

FRAXINUS L.

Fraxinus washingtoniana (Prakash & Barghoorn) comb. nov. (Fig. 19)

[*Diospyros washingtoniana* Prakash & Barghoorn 1961a]

Growth rings distinct.

Semi-ring porous. Vessels solitary and in short radial multiples, solitary vessels oval in outline; earlywood mean tangential diameter 212 (41); perforation plates simple; intervessel pits crowded alternate, minute-small; vessel element lengths 190–310 µm.

Fibers non-septate, thick-walled, pitting not observed.

Axial parenchyma paratracheal, vasicentric, aliform to confluent.

Rays 1–2-seriate, homocellular, composed of procumbent cells, 2–8 cells high, mean biseriate ray height 221 (34) µm, range 146–289 µm; 7–10 per mm.

Crystals not observed, areas with rays in echelon (tending to irregular storying).

Material: HU 55305 (holotype), UWBM 98706 (Beck 1311).

Comments: Given that sample HU 55305 is semi-ring porous (Fig. 19A), has minute-small intervessel pits, and rays that are locally irregularly storied (Fig. 19C), it is understandable that it was assigned to *Diospyro*s. However, *Diospyros* has abundant apotracheal axial parenchyma, either in regular narrow tangential bands or diffuse-in-aggregates; this sample does not appear to have this type of axial parenchyma (Fig. 19A). There are regions in cross section that Prakash and Barghoorn evidently interpreted as "metatracheal" parenchyma, *i.e.* narrow bands. However, these regions seem to reflect differential preservation. In radial section, parenchyma strands are only visible near the vessels – not in the midst of fibers as would occur in woods with apotracheal parenchyma bands. Also, in one area of the sample, vasicentric, aliform to confluent parenchyma is visible. Aside from the axial parenchyma distribution, the original description of Prakash and Barghoorn is consistent with our observations. These features in combination with paratracheal parenchyma, rather than apotracheal parenchyma, indicate that this wood is *Fraxinus*. The mean tangential diameter of the earlywood vessels is more consistent with characteristics of *Fraxinus* (often earlywood >200 µm) than with *Diospyros* (usually medium diameter 100–200 µm). Süss (1987) did not think that this Vantage wood was correctly assigned to the Ebenaceae because its original description mentioned the presence of tyloses; tyloses do not occur in *Diospyros*, but do occur in *Fraxinus*.

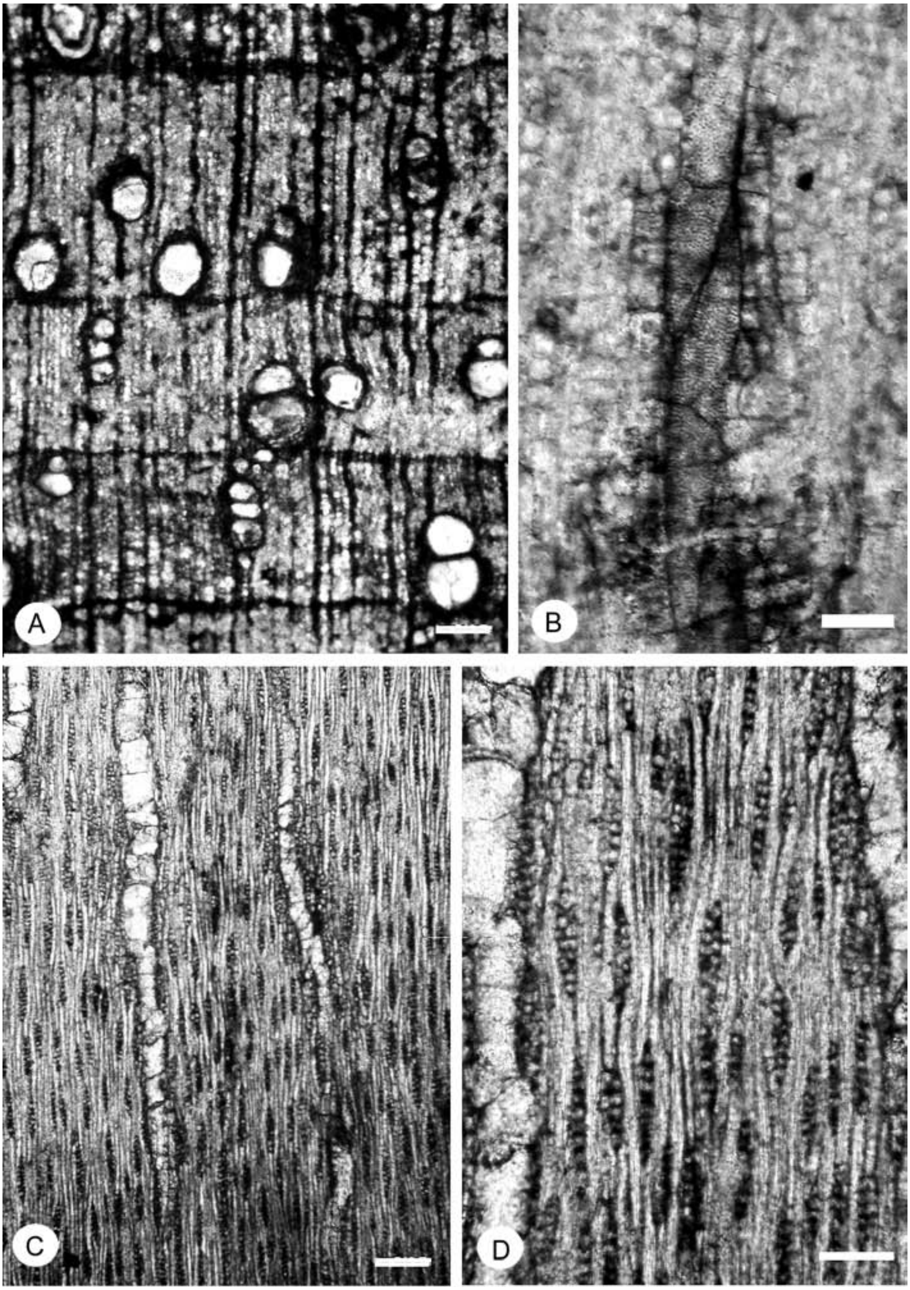

Figure 19. Oleaceae. *Fraxinus washingtoniana*. HU 55305. – A: Semi-ring porous wood. Vessels solitary and in radial multiples, paratracheal axial parenchyma. XS. – B: Vessel–ray parenchyma pits minute to small with distinct borders. XS. – C: Narrow rays, some areas irregularly storied, vessels with thin-walled tyloses. TLS. – E: Rays predominantly 2-seriate. TLS. — Scale bar = 200 μm in A, C; 100 μm in D; 50 μm in D.

Although the extant *Fraxinus* species of North America are ring porous, there are Asian species of *Fraxinus* that are diffuse to semi-ring porous (Baas *et al*. 1988). Beck (1945a) reported both *Diospyros* and *Fraxinus* as occurring at Vantage. This sample is an example of *Fraxinus* rather than *Diospyros*. Therefore, we propose the new combination: *Fraxinus washingtoniana* (Prakash & Barghoorn) Wheeler and Dillhoff.

HU 56632 (Beck 401) from the Miocene Yakima Canyon was labeled *Fraxinus*. This sample with irregularly storied rays more clearly shows aliform-confluent parenchyma than the Vantage sample. We consider it another example of *Fraxinus washingtoniana*.

Süss (2005) reviewed the fossil woods with characteristics of *Fraxinus*, including those assigned to the morphogenus *Ornoxylon*. This Vantage wood differs from all other fossil *Fraxinus* and *Ornoxylon* species in being semi-ring porous, rather than distinctly ring porous with a well-defined earlywood pore zone.

Fraxinus macropunctatum sp. nov. (Fig. 20)

Growth rings present, boundaries marked by radially narrower fibers, and changes in vessel diameter.

Ring porous. Earlywood zone usually 2–3 pores deep. Vessels mostly solitary and with a few radial multiples of 2 (3). Mean tangential diameter of earlywood vessels 222 (32) µm, range 174–289. Simple perforation plates. Crowded alternate pits, often with coalescent apertures, 6–10 µm. Vessel–ray parenchyma pits similar in size to intervessel pits, but with somewhat reduced borders. Vessel element lengths 179–392 µm. Tyloses abundant in the earlywood vessels.

Fibers with thin to medium-thick walls. Pits not observed.

Axial parenchyma scanty paratracheal to vasicentric.

Rays predominantly uniseriate, biseriate rays found occasionally, body ray cells procumbent, in radial section marginal cells shorter than body cells and tending to be square. Around 4 rays per mm.

Storied structure and crystals not observed.

Material: Holotype HU 65006 (Beck 487).

Etymology: Specific epithet refers to the relatively large intervessel pit size which characterizes species of section *Fraxinus*.

Comments: Beck had assigned this wood to *Fraxinus*, and the combination of ring porosity, randomly arranged latewood vessels not in clusters or long radial multiples, vessel–ray parenchyma pits similar to intervessel pits, absence of diffuse-in-aggregates and banded parenchyma, narrow rays that are not markedly heterocellular occurs in *Fraxinus*. The cross-sectional appearance of this Vantage wood resembles samples of extant *Fraxinus nigra* (native to North America, USGSw 786), *F. excelsior* (native to Europe, Kw *s.n.*) and *F. mandshurica* (native to temperate Asia, TWTw 18046) (see InsideWood for images) that have narrow growth rings. These three species belong to section *Fraxinus*; section *Fraxinus* is comprised of five species, with *F. nigra* the only American species in this otherwise Eurasian group (Wallander 2008). The intervessel pits of this sample are larger (> 5 µm) and the incidence of uniseriate rays is higher than is typical of most extant *Fraxinus*, the Vantage *Fraxinus washingtoniana* and

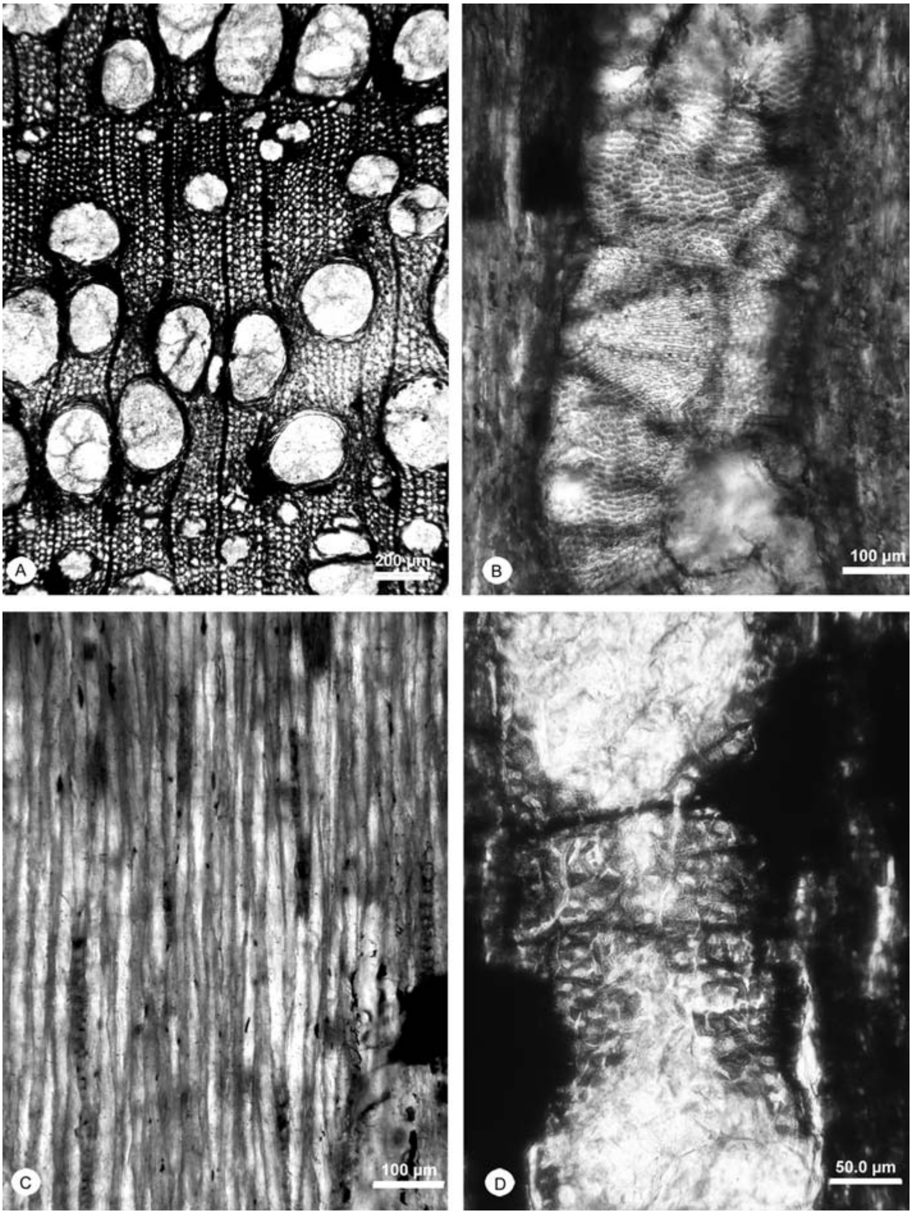

Figure 20. Oleaceae. *Fraxinus macropunctatum*. HU 65006 (Beck 487). – A: Ring porous wood, vessels mostly solitary, radial multiples rare. XS. – B: Thin-walled tyloses filling vessels, crowded alternate intervessel pits. TLS. – C: Narrow rays, widely spaced. TLS. – D: Vessel–ray parenchyma pits similar in size to intervessel pits. RLS. — Scale bar = 200 µm in A; 100 µm in B, C; 50 µm in D.

all other fossil *Fraxinus* woods. However, *Fraxinus nigra* and *F. mandshurica* have similar sized intervessel pits (Baas & Zhang Xinying 1986; Baas *et al*. 1988), and so this Vantage wood can be considered to provide evidence of the presence of wood of section *Fraxinus* in western North America

The presence of *Fraxinus* in the middle Miocene of the Pacific Northwest is also confirmed by the presence of fruits from the Mascall Formation of northeastern Oregon (Chaney & Axelrod 1959).

PLATANACEAE

PLATANUS L.

Platanus americana Prakash & Barghoorn 1961a (Fig. 21)

Growth rings distinct, marked by radially narrower fibers, noded rays.

Diffuse porous, but with a latewood zone of narrower vessels. Vessels solitary and in small groups, with a tendency to a tangential arrangement; in earlywood average tangential diameter 55 (7) µm (range of 30–77 µm); c. 120–140 vessels per sq.mm in earlywood regions between the large rays; perforations mostly simple, some latewood vessels with scalariform perforations with 2–11 widely spaced bars; intervessel pitting crowded opposite, 9–15 µm wide; vessel element lengths 305–765 µm.

Fibers non-septate, pits not observed, thick-walled.

Axial parenchyma diffuse, occasional cells touching vessels.

Rays to more than 15 cells wide, but less than 20, broad rays evenly spaced and to more than 3.5 mm tall. Rays homocellular, composed of procumbent cells; 3–4 rays per mm.

Storied structure absent, crystals not observed.

Material: Holotype HU 55218.

Comments: The combination of characters of diffuse porous, numerous narrow vessels with a tendency to a tangential grouping, opposite intervessel pits, scalariform and simple perforations, diffuse axial parenchyma, rays more than 10-seriate and 1 mm high that are composed of procumbent cells and uniformly spaced is unique to *Platanus*. The modern *Platanus kerrii* of southeast Asia has markedly wider rays (more than 20-seriate) than all other modern *Platanus* species (Wheeler 1995). The other modern *Platanus* species are similar to one another. Prakash and Barghoorn (1961a) suggested "the nearest affinity of the fossil within this genus [*Platanus*] is with *P. wrightii* Wats." This suggestion was based on their observation that *Platanus wrightii* has irregular groups of vessels and a conspicuous difference in diameter between the latewood vessels and earlywood vessels as seen in the Vantage *Platanus*. However, these features also occur in some samples of *P. occidentalis* (FHOw 137, FPAw 9578) and *P. racemosa* (SJRw 11756) (images on InsideWood). They noted differences between *Platanus wrightii* and the fossil: in *P. wrightii* scalariform perforation plates are more common than simple perforation plates and axial parenchyma is more abundant, with diffuse and diffuse-in-aggregates rather than just diffuse. More information on the wood anatomical variation of *Platanus* is needed to determine if the differences Prakash and Barghoorn noted are reliable, and if *P. occidentalis, P. orientalis,* and *P. racemosa* can be distinguished from one another.

Platanus type woods are common as fossils. Cretaceous and early Tertiary *Platanus* woods typically have exclusively scalariform perforations in contrast to the Late Tertiary and Recent species, which have both simple and scalariform perforation plates (Wheeler & Manchester 2002). Ray widths of most of the Cretaceous and Early Tertiary platanoids are comparable to *P. kerrii*. *Platanus americana* and other Miocene platanoids have a mixture of simple and scalariform perforation plates.

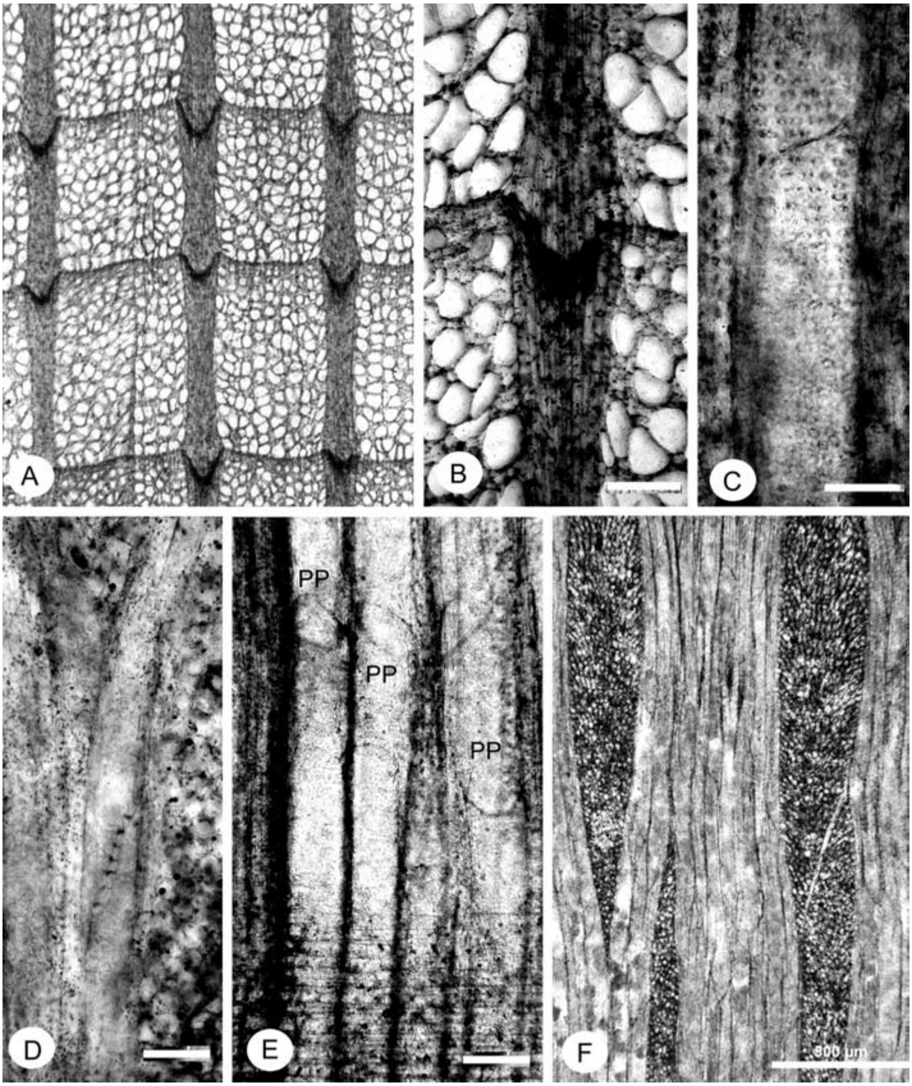

Figure 21. Platanaceae. *Platanus americana*. HU 55218. – A: Diffuse porous wood, numerous narrow vessels, wide rays evenly spaced, average growth ring width 1.27 mm. XS. – B: Detail of growth ring boundary. Wide ray indented. XS. – C: Opposite intervessel pitting. TLS. – D: Scalariform perforation plate in side view. TLS. – E: Simple perforations (PP). RLS. – F: Wide rays. TLS. — Scale bar = 500 µm in F; 100 µm in B; 50 µm in D, E; 20 µm in C.

ROSACEAE

PRUNUS L.

Prunus rodgersae sp. nov (Fig. 22)

Growth rings present, distinct, marked by radially narrower fibers.

Diffuse porous. Vessels mostly in groups, solitary vessels occasional and oval in outline; average tangential diameter 52 (9.5) µm, range 35–70 µm, vessel frequency 100–130 per sq. mm; perforations simple; intervessel pits alternate, round to oval and polygonal in outline, 6.5–8 µm across; vessel–ray parenchyma smaller than intervessel pits; helical thickenings throughout length of narrower vessel elements; average vessel element length 416 (60) µm, range 289–588 µm.

Fibers non-septate, thick-walled, fiber pits not obvious.

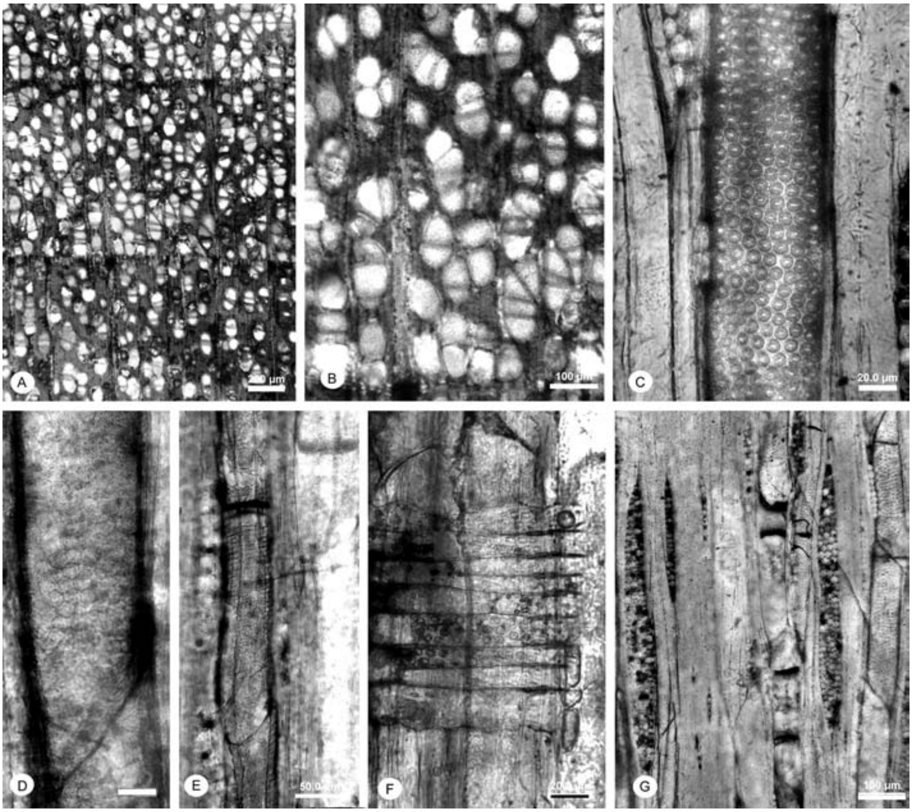

Figure 22. Rosaceae. *Prunus rodgersae*. UWBM 98704 (Beck 612). – A, B: Diffuse porous wood. Vessels solitary and in groups, thick fiber walls, growth ring boundaries marked by radially narrower fibers. XS. – C: Alternate intervessel pits, circular in outline. TLS. – D: Alternate intervessel pits, polygonal in outline. TLS. – E: Vessel element with helical thickenings along entire length, simple perforation plate. TLS. – F: Vessel–ray parenchyma pits similar in size to intervessel pits, body ray cells procumbent. RLS. – G: Rays tending to two sizes. — Scale bar = 200 µm in A; 100 µm in B, G; 50 µm in E; 20 µm in C, D, F.

Axial parenchyma scanty paratracheal and marginal. Enlarged chambered crystal-bearing axial parenchyma not observed.

Rays 1–6-seriate, tending to two sizes, homocellular, composed of procumbent cells, to heterocellular. Uniseriate rays usually less than 10 cells high, multiseriate ray heights average 528 (196) µm, range 244–910 µm.

Crystals not observed.

Material: Holotype UWBM 98704 (Beck 612).

Etymology: Named for Shirley Rodgers, NC State Library Systems Department, with thanks for her work on developing the InsideWood web site.

Comments: The combination of diffuse porosity, narrow vessels that are not exclusively solitary, simple perforation plates, alternate intervessel pits, helical thickenings throughout the vessel element, and rays that are more than 4-seriate occurs in *Prunus s.l.* (Rosaceae) and *Acer* (Sapindaceae). The high proportion of vessel multiples, the tendency to radial/diagonal vessel arrangement, the relatively widely spaced helical thickenings indicate this wood has affinities with *Prunus*. *Prunus s.l.* includes *Amygdalus, Armeniaca, Cerasus, Laurocerasus*, *Padus, Prunus s.str.,* and *Pygeum*.

Zhang reviewed the systematic anatomy of the Rosaceae (1992) and recognized 12 wood anatomical groups in the family. His Groups XI and XII include *Prunus s.l.* Group XI woods have vessel–ray parenchyma pits similar in size to intervessel pits and marginal parenchyma; Group XII woods have vessel–ray parenchyma pits clearly smaller than the intervessel pits and lack marginal parenchyma. Thus, this wood is intermediate between Zhang's two groups. We did not see any distinctly bordered fiber pits in this Vantage wood, although that could be because the preservation was not good enough to allow seeing that feature. On the basis of Zhang's Table 2, if the ground tissue is composed of libriform fibers this suggests relationships to *Laurocerasus* B of Zhang's phenetic group XI or to *Amygdalus* and *Cerasus* of his group XII. In *Laurocerasus* B intervessel pits are smaller (2–4 µm in diameter) than in this Vantage wood and intervessel pits are mainly polygonal in outline. *Amygdalus* woods are ring porous unlike this Vantage wood. In *Cerasus*, intervessel pit size is similar to that of this Vantage wood, but in *Cerasus* intervessel pits also are mainly polygonal in outline. On the basis of both intervessel pit size and pit outline being both polygonal and round to oval this Vantage wood is similar to species of *Padus* and *Prunus s.str*.

Recent molecular and morphological phylogenetic analyses of the genus differ in details, particularly for placement of species and sections of subgenus *Cerasus*. However, these studies usually recover two groups: one that always contains subgenera *Padus* and *Laurocerasus*; another group that always contains subgenera *Prunus, Amygdalus,* and *Emplectocladus* (Bortiri *et al*. 2006). Although wood anatomical features have not figured in any of the recent phylogenetic analyses of *Prunus*, crystal type and location, vessel–ray parenchyma pit size, and axial parenchyma type and abundance have potential for helping to resolve relationships between the sections and species within subgenera.

Fossil woods of the Prunoideae have been reported from the early, middle, and late Eocene of North America (Wheeler *et al*. 1978; Süss & Müller-Stoll 1980; Cevallos-Ferriz & Stockey 1990; Wheeler & Landon 1992; Wheeler & Manchester 2002), Oligocene of Europe (Dupéron 1976), and Oligocene and Miocene of Asia (Suzuki 1984; Suzuki & Watari 1994; Suzuki & Terada 1996). This Vantage wood differs from all other North American fossil Prunoideae woods as it has a higher proportion of vessel multiples, fibers without distinctly bordered pits, and does not have crystals. Devore and Pigg (2007) have recently reviewed the fossil record of Rosaceae, especially of *Prunus,* whose fossil record extends back to the Eocene of North America.

Prunus barnetti sp. nov. (Fig. 23)

Growth rings present, marked by 1–2 rows of radially narrower fibers.

Diffuse porous. Vessels solitary, in radial multiples and irregular groups, solitary vessels somewhat rectangular-square in outline, average tangential diameter 41 (10) µm, range 29–59 µm; vessel frequency 62–94 per sq. mm, perforations simple, intervessel

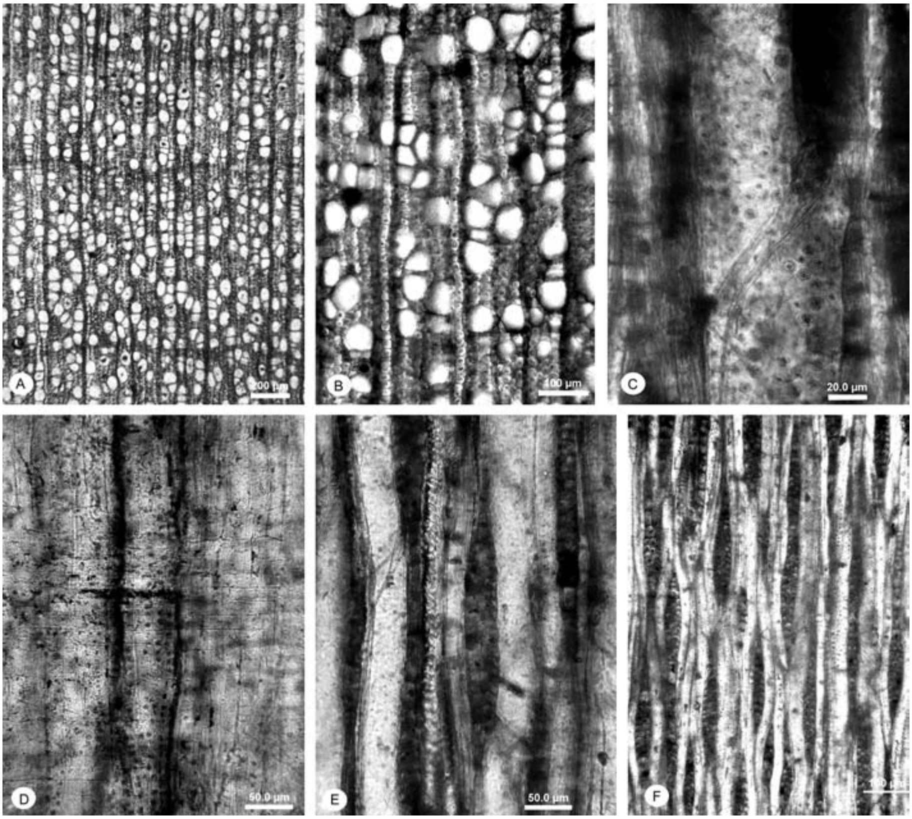

Figure 23. Rosaceae. *Prunus barnetti* sp. nov. HU 55201. – A, B: Diffuse porous wood. Vessels solitary and in groups. Fiber walls medium-thick to thick, growth ring boundaries marked by radially narrower fibers. XS. – C: Alternate intervessel pits, simple perforation plate. TLS. – D: Vessel ray parenchyma pits small, borders not reduced. Body of ray composed of procumbent cells. RLS. – E: Narrow vessel with coarse helical thickenings along entire length of vessel element. TLS. – F: Rays 1–5-seriate. — Scale bar = 200 µm in A; 100 µm in B, F; 50 µm in D, E; 20 µm in C.

pits alternate, 6–8.5 µm across; vessel–ray parenchyma pits similar to intervessel pits; helical thickenings throughout length of the narrower vessel elements, vessel element lengths 376–482 µm.

Fibers non-septate medium-thick to thick-walled, some distinctly bordered fiber pits visible in both radial and tangential sections.

Axial parenchyma rare, scanty paratracheal.

Rays 1–4- (5-)seriate, body of ray procumbent cells, usually with 1 marginal row of square cells. Multiseriate ray heights average 320 (102) µm, range 132–518 µm; 7–10 per mm.

Crystals not observed.

Material: Holotype HU 55201.

Etymology: Named for John Barnett on the occasion of his retirement from Reading University and in recognition of his many contributions to our understanding of cambial activity and wood formation.

Comments: The combination of diffuse porosity, narrow vessels that are not exclusively solitary, simple perforation plates, alternate intervessel pits, helical thickenings throughout the vessel elements, some fibers with distinctly bordered pits, and rays that are 4- or more-seriate occurs in *Prunus s.l.* (Rosaceae). This *Prunus* wood differs from *Prunus rodgersae* because the intervessel and vessel–ray parenchyma pits are the same size, distinctly bordered pits are visible in some fibers, ray heights are rarely > 500 µm, and rays do not tend to be of two distinct sizes. Vessels are somewhat narrower as well. This species also is intermediate between Zhang's phenetic groups XI and XII as defined in his Table 2 (Zhang 1992, ch. 3), as it has vessel–ray parenchyma similar in size to intervessel pits as in Group XI and scanty axial parenchyma as in Group XII. *Laurocerasus* has species in both Zhang's Group XI and XII; Zhang pointed out that few species and few samples of *Laurocerasus* were examined and that further study of vouchered samples of more species is needed. Additional study might reveal that some *Laurocerasus* species have woods that are intermediate between Zhang's two distinct groups of *Laurocerasus*, and share characteristics with these two Vantage *Prunus* woods.

SAPINDACEAE

ACER L.

Acer beckianum Prakash & Barghoorn 1961a (HU 55226) (Fig. 24A, B)
Acer puratanum Prakash & Barghoorn 1961a (HU 55200) (Fig. 24C, D)
Acer olearyi Prakash & Barghoorn 1961a (HU 55311) (Fig. 24G, H)
Acer berkhoffii sp. nov. (HU 56284) (Fig. 24E, F)
[*Aceroxylon pennsylvanicum* Prakash 1968]

The description below applies to the genus *Acer*, with Table 6 detailing differences between the Vantage *Acer* wood types.

Growth rings distinct, marked by radially narrower fibers.

Diffuse porous. Vessels solitary and in radial multiples, average tangential diameter less than 100 µm; perforations exclusively simple, intervessel pits crowded alternate, generally polygonal in outline with included apertures; vessel–ray parenchyma pits

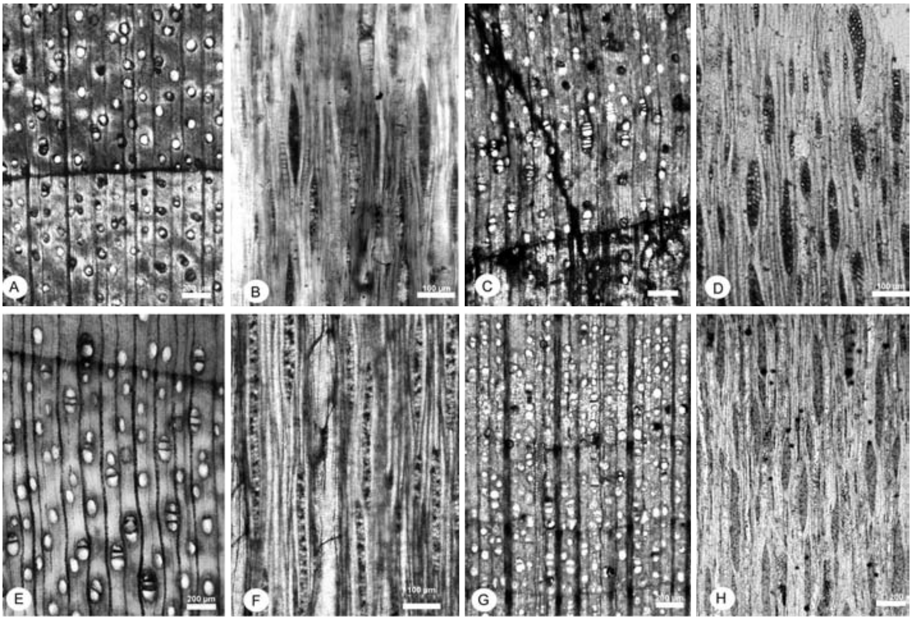

Figure 24. Sapindaceae. – A–H: *Acer.* – A, B: *Acer beckianum*. HU 55226. – A: High proportion of solitary vessels that are rounded in outline. Fibers surrounding vessels probably reflecting different wall structure than ground tissue fibers. XS. – B: Rays predominantly 3-seriate, tending to fusiform shape. Strands of crystalliferous axial parenchyma. TLS. – C, D: *Acer puratanum*. HU 55200. – C: Vessel multiples of up to 4 or more. XS. – D: Rays predominantly 3–4-seriate, ray cells rounded in outline, ray shape tending to fusiform. TLS. – E, F: *Acer berkhoffii*. HU 56284. – E: Vessels solitary and in radial multiples of 2–3. Evidence of two types of fibers with fibers surrounding vessels likely with different wall structure than ground tissue fibers. XS. – F: Narrow, mostly 2–3-seriate rays that are uniformly narrow and not fusiform in shape. TLS. – G, H: *Acer olearyi*. HU 55311. – G: Vessels solitary and in radial multiples, wide rays as wide or wider than vessels. XS. – H: Rays tending to two width classes, wider rays commonly more than 8-seriate. TLS. — Scale bar = 200 µm in A, C, E, G, H; 100 µm in B, D, F.

Table 6. Comparison of Vantage *Acer* woods.

MTD = mean tangential diameter of vessels; % Sol. = percentage of solitary vessels counting all pores as 1; V/MM^2 = vessels per square mm; RW = ray width in cell number; MRH = multiseriate ray height (µm).

Species	MTD	% Sol.	V/MM^2	RW	MRH	Crystals
A. beckianum	60 (31–82)	61	23–35	1–3	237 (65) 141–355	Yes
A. puratanum	53 (30–72)	41	18–26	1–4 (5)	230 (60) 119–326	Yes
A. olearyi	59 (30–80)	26	53–71	1–7, mostly 5–6	437 (239) 139–1157	No
A. berkhoffii	65 (35–90)	49	17–24	1–3	365 (135) 162–627	No

similar in size and shape to intervessel pits; helical thickenings along the whole length of the vessel element.

Fibers non-septate, walls thin to thick, pits indistinct.

Axial parenchyma rare.

Multiseriate rays homocellular, composed of procumbent cells.

Storied structure absent.

Comments: Commercially important maple woods usually are divided into two groups on the basis of ray width: the 'hard maple' group in which rays are commonly 5- to 7-seriate, and up to 10-seriate, and the 'soft maple' group in which rays are commonly 3- to 5-seriate (*e.g.*, Brazier & Franklin 1961; Panshin & DeZeeuw 1980). *Acer beckianum* (Fig. 24A, B)*, A. puratanum* (Fig. 24C, D) and *A. berkhoffii* (Fig. 24E, F) have characteristics of the soft maple group; *Acer olearyi* (Fig. 24G, H) has characteristics of the hard maple group. Ogata (1967), in his study of woods from 22 sections of *Acer*, found that ray shape, whether fusiform or more elongate, and occurrence of crystalliferous axial parenchyma were also useful features. Figure 24 shows cross and tangential sections of the Vantage *Acer* species of Prakash and Barghoorn. As shown by these photographs and Table 6, the Vantage maples can be distinguished from one another by ray width, percentage of solitary vessels, vessels per sq. mm., and crystal occurrence.

Prakash and Barghoorn only cite one sample per Vantage *Acer* species; however, Beck (1944) found that maple-like wood was common in the main Vantage forest. HU 65003 (Beck 465) resembles *Acer berkhoffii*. Beck plotted ray width and height of selected modern woods and samples of Vantage and Yakima Canyon maple-like woods. Beck was circumspect about how many fossil *Acer* species were present, as there was overlap between the ray characteristics of many of the samples; his text implies that he thought there are at least four types. This would be consistent with the results of Prakash and Barghoorn.

Acer was reviewed by De Jong (1994), incorporating all known extant species. His study included many Asian species that were not available to Ogata for his wood anatomical study, as well as biochemical data that was published after Ogata's 1967 monograph. Several molecular phylogenies have since been published for the genus (Hasebe *et al*. 1998; Suh *et al*. 2000; Tian *et al*. 2002), but each of these studies looked at incomplete species subsets, different DNA markers, and resulted in a variety of possible phylogenies; therefore we chose to use De Jong's treatment for our analysis of the relationships between the fossil species and the modern genus.

Fossil leaves and seeds of *Acer* are well represented in Cenozoic floras of the Northern Hemisphere. The oldest known wood with characteristics of *Acer* is from the middle Eocene Clarno Nut Beds, Oregon, USA (Wheeler & Manchester 2002). Wolfe and Tanai (1987) published an extensive monograph on the fossil history of the genus in western North America. Their work places the earliest known fossil attributable to *Acer* in the late Paleocene of south central Alaska.

In their first Vantage paper, Prakash and Barghoorn (1961a) state that the nearest living relative to *Acer beckianum* is *A. negundo*, which has a wide distribution in the central and eastern United States, as well as southern Canada and parts of Mexico. They do note some differences between the fossil and modern species, however, including the shape of the vessels and the lower and slightly wider rays in *Acer negundo*. We also noted that the rays are more irregularly shaped in *A. negundo* than in the fossil species. Our survey found that some species of *Acer* in Section *Platanoidea* are also similar in wood anatomy to the fossil species, especially *Acer campestre*. The ray width and shape in *A. campestre* is similar to *A. beckianum*, as well as the high percentage of solitary vessels and their often-rounded shape. The apparent fiber dimorphism of *Acer beckianum* (Fig. 24 A) is also similar to *Acer campestre* (FPAw 3638 on InsideWood). Many species of *Acer* have two fiber types with different microfibil angles, chemistry, and pit distribution that cause them to appear different in cross section (Vasquez-Cooz & Meyer 2006, 2008). The abundance and distribution patterns of the two fiber types differed in the 15 species that Vasques-Cooz and Meyer examined; a more comprehensive survey of *Acer* species for abundance and distribution patterns of libriform fibers would be of value for determining whether such variation has systematic value. *Acer beckianum* indicates that fiber dimorphism was present in *Acer* by the mid-Miocene.

According to Wolfe and Tanai (1987), fossils of both Section *Negundo* and Section *Platanoidea* are present in western North America during the Middle Miocene. They propose that Section *Negundo* first appeared in North America in the late Eocene. The section became disjunct sometime during the Miocene, with the modern section divided into Series *Cissifolia* in eastern Asia and Series *Negundo* in North America (*sensu* De Jong 1994). Modern species of Section *Platanoidea* are restricted to eastern Asia. Wolfe and Tanai postulate that species of *Platanoidea* were present in western North America in the Eocene and then again from the early Miocene until the early late Miocene.

Acer puratanum shows anatomical similarity to species in Section *Palmata*, although many species of *Palmata* have rays that are slightly higher and wider than *A. puratanum*. Prakash and Barghoorn (1961a) compared *Acer puratanum* to the modern species *A. circinatum* (Section *Palmata*) and *A. mandshuricum* (Section *Trifoliata*). We did not have wood samples of *Acer mandshuricum* or other species of Section *Trifoliata* available for comparison. Modern species of *Trifoliata* are exclusively Asian and *Palmata* is Asian with the single exception of *Acer circinatum*, which is native to the coastal and Cascade mountain region from southern British Columbia to northern California. Wolfe and Tanai (1987) do not report any fossils of either *Palmata* or *Trifoliata* in the Tertiary compression floras of North America.

The wood of *Acer olearyi* matches characteristics of modern woods in Section *Acer* with relatively wide, smooth rays, narrow vessels that commonly occur in radial multiples, and the absence of crystals in parenchyma cells. Prakash and Barghoorn (1961a) noted the similarity of *A. olearyi* with *A. grandidentatum* in Section *Acer*, although we prefer to align the wood with the section rather than with a particular modern species. This section is represented in modern floras by species in Europe, Asia, and eastern North America, with the greatest diversity in Europe and western Asia. Wolfe and Tanai (1987) attribute several fossil species of the Miocene of western North America to Section *Acer*. Of these, leaves and fruits of *Acer tyrellense* are found in floras of the Columbia Plateau close in age to the Vantage woods.

As its name implies Prakash (1968) concluded that the nearest modern relatives of the sample he called *Aceroxylon pennsylvanicum* was with *Acer pennsylvanicum*, which is in Section *Macrantha* and native to eastern North America. Prakash (1968) followed the tradition of assigning any isolated piece of fossil wood to a genus ending in -oxylon. *Aceroxylon pennsylvanicum* has a combination of characteristics unique to extant *Acer* wood. Therefore, assigning it to *Aceroxylon* was unfortunate as this implies that this wood's relationship to extant *Acer* woods is more tenuous than the other Vantage *Acer* woods, and this is not the case. We believe it should be transferred to *Acer*. However, it cannot be renamed *Acer pennsylvanicum* because this is the name of the extant species, and the structure of this Vantage wood is not unique to that species. Consequently, we assign it to a new fossil species, *Acer berkhoffii*. Based on the criteria established by Ogata (1967) and our own examination of modern wood thin section images, we concur that the wood is likely associated with Section *Macrantha*. This section contains modern species native to both eastern North America and eastern Asia. *Acer berkhoffii* (Fig. 24E) also shows fiber dimorphism, with a distribution and abundance comparable to that seen in *Acer pennsylvanicum* (BWCw 8143), but not to *A. capillipes* (TWTw 17534) or *A. rufinerve* (TWTw 14817), which are Asian species of Section *Macrantha*. Wolfe and Tanai (1987) indicate that fossil species of *Acer* attributable to *Macrantha* were present in western North America by the late Middle Eocene, and that disjunct populations formed in Asia and North America due to climate deterioration in the late Middle Miocene. Based on their examination of Cenozoic fossil leaves and fruits of *Acer*, they assigned several species from western North America to Section *Macrantha*. Notably, they conclude that *Acer latahense* from the Middle Miocene of northeastern Washington State is also related to extant *Acer pennsylvanicum* and similar Asian species. The Latah flora is close in age and geographical location to the Vantage wood flora.

AESCULUS L.

Aesculus hankinsii Prakash & Barghoorn 1961b (Fig. 25)

Growth rings present, marked by radially narrower fibers.

Diffuse porous. Vessels solitary and in radial multiples of 2–5 (mostly 2–3), solitary vessels mostly oval in outline, with a slight tendency to angularity; in HU 56640 average tangential diameter 52 (9) µm, range 35–80 µm; in HU 56111 average tangential diameter 53 (9) µm, range 39–77 µm; 95–170 per sq.mm; perforations exclusively simple; intervessel pits crowded alternate, polygonal in outline, 5–7 µm across; vessel–ray parenchyma pits similar in size and shape to intervessel pits; vessel element lengths to 500 µm. Helical thickenings present throughout body of vessel elements.

Fibers non-septate, thin-walled, pitting not observed.

Axial parenchyma rare.

Rays exclusively uniseriate, homocellular, composed exclusively of procumbent cells, 2–32 cells high (mostly 8–15 cells), 322 (73) µm, 202–454 µm; 8–12/mm.

Rays and fibers with a tendency to storied structure.

Crystals not observed.

Material: HU 56640 (holotype) and HU 56611 (Beck 1828).

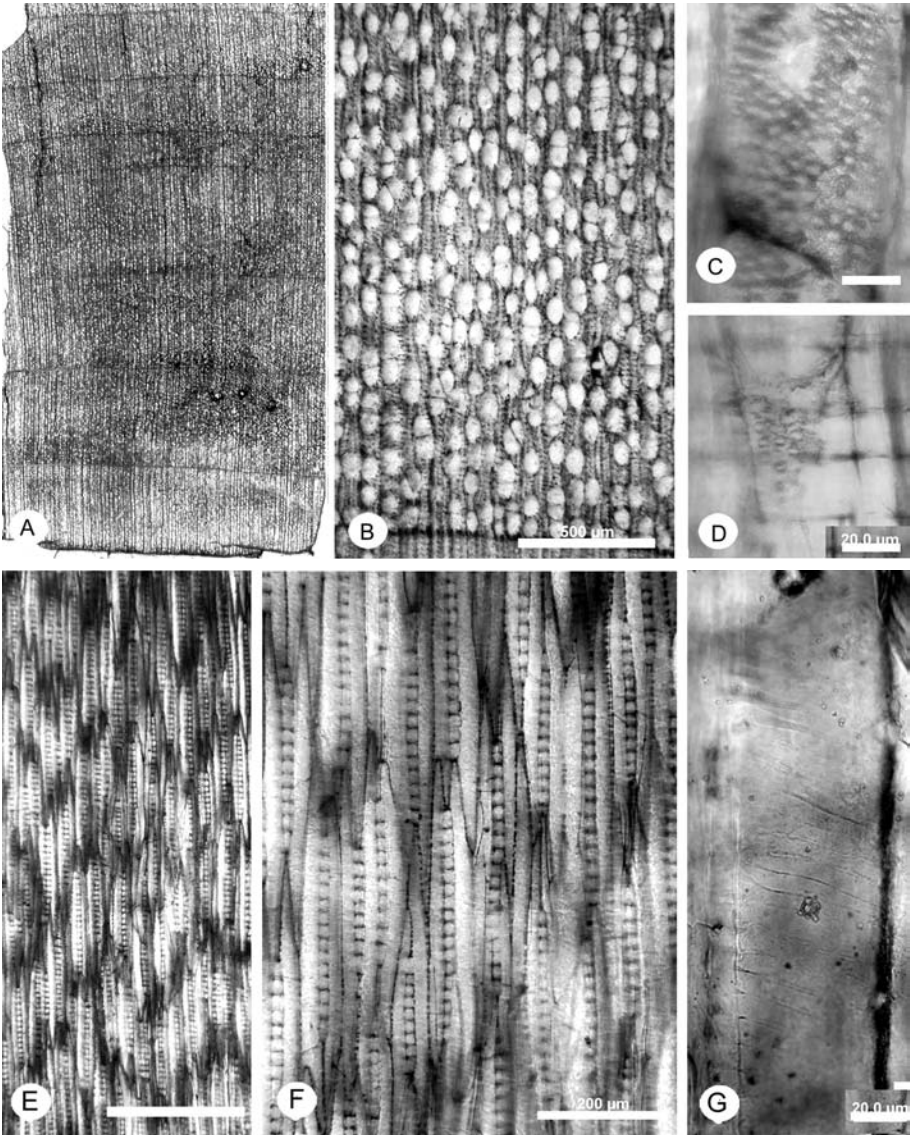

Figure 25. Sapindaceae. *Aesculus hankinsii*. – A–F: HU 56240. – A: Diffuse porous wood. Growth rings present. Width of sample at bottom of photo = 8.3 mm. XS. – B: Vessels solitary and in radial multiples. XS. – C: Crowded alternate intervessel pitting, angular in outline. RLS. – D: Vessel–ray parenchyma pits similar in size and shape to intervessel pits. RLS. – E: Rays exclusively uniseriate, some regions irregularly storied. TLS. – F: Irregularly storied homocellular uniseriate rays, fibers also tending to storied structure. TLS. – G: Vessel element with helical thickenings. HU 56611. TLS. — Scale bar = 500 µm in B, E; 200 µm in F; 20 µm in C, D, G.

Comments: The original description of *Aesculus hankinsii* mentioned helical thickenings in the vessels; we did not observe this feature in the type but did in HU 56611, a Beck sample not cited and apparently not examined by Prakash and Barghoorn. As noted by Panshin and De Zeeuw (1980) the wood of *Aesculus* is often confused with that of *Populus*. Both genera have narrow, numerous vessels that are solitary and in radial multiples, crowded alternate pitting, rare axial parenchyma, and homocellular uniseriate rays. *Populus* never has helical thickenings or storied rays, but some *Aesculus* species do. Vessel–ray parenchyma pitting was not mentioned in the original diagnosis of *A. hankinsii*, but we found that it was similar to the intervessel pitting (Fig. 25F), unlike *Populus*, which has vessel–ray parenchyma pits with reduced borders. The irregularly storied rays (Fig. 25C, D) also are characteristics of *Aesculu*s, rather than *Populus*.

Hardin (1957, 1960) proposed groups of *Aesculus* species based on morphological characters and proposed scenarios for the origin and diversification of the genus. More recently Xiang *et al*. (1998) did a molecular phylogenetic analysis of *Aesculus*, and Forrest *et al*. (2001) did a morphological phylogenetic analysis of *Aesculus* and the closely related *Billia*. Although there are some differences between the two studies, both phylogenetic studies yielded general support for Hardin's groupings, with the groupings in part corresponding to the present-day distribution of species.

Within *Aesculus*, there is variation in the presence and distinctiveness of storied rays. According to Panshin and De Zeeuw (1980), of the common North American species, *Aesculus octandra* has storied rays and *A. glabra* does not. We did not observe storied rays in *A. neglecta* from the southeastern U.S. Irregularly storied rays are reported for the Asian species *A. indica* and *A. turbinata*; *A. indica* is distinct as it has a radial/diagonal arrangement of vessels (Suzuki *et al*. 1991), and so differs from the Vantage *Aesculus*. Irregularly storied rays are of variable occurrence in the European *A. hippocastanum*. A comprehensive wood anatomical study of the genus is needed. In particular, such a study would be useful for determining 1) whether fossil *Aesculus* woods have characteristics of a particular section and that has potential for help with timing divergences of the sections, 2) whether there are wood anatomical characteristics of *A. indica* that help resolve its placement, traditionally in Section *Calothrysus*, but some analyses show it as part of Section *Aesculus* which includes the European *A. hippocastanum* and Asian *A. turbinata*, and 3) whether there are any wood anatomical characteristics distinctive to the western U.S. species *A. parryi* (Section *Parryanae*) which was recovered as sister to all other *Aesculus* in the study by Forrest *et al*. (2001).

To our knowledge, this is the only fossil wood of *Aesculus* described from North America. However, Beck indicated woods of the genus occur at other Tertiary localities in the western U.S. (Beck 1945a). Distinctive palmately compound leaves and fruit remains indicate the genus has been present in North America since the Paleocene (Manchester 2001). Fossil wood resembling *Aesculus* has been reported from the Miocene of Japan (Suzuki & Terada 1996) and the Deccan Intertrappean Beds of India (Trivedi & Srivastava 1982).

cf. ***Sapindus*** sp. (Fig. 26)

Growth rings distinct, marked by latewood with thick-walled fibers, and narrow vessels.

Ring porous, earlywood vessels mostly solitary, widely spaced, earlywood zone more than 2 rows of vessels deep. Sometimes a radial multiple with one wide vessel and more than 4 narrow vessels. Latewood with vessels in clusters. Mean tangential diameter of earlywood vessels 144 (21), range 95–191 µm. Perforation plates exclusively simple. Intervessel pits crowded alternate, polygonal in outline, with apertures extending to the borders; 5–7 µm wide; vessel–ray parenchyma pits similar in size and shape to intervessel pits; helical thickenings along whole length of narrowest vessel elements.

Fibers septate, thick-walled, pits not visible.

Axial parenchyma aliform (mostly winged) to confluent-banded. Latewood with broad bands of parenchyma intermixed with narrow vessels, mostly 4 cells per strand.

Rays 1–3 (–4)-seriate. Homocellular, composed of procumbent cells, isodiametric in tangential view. Multiseriate ray height 109–394 µm (average 230 µm, n = 18); c. 4–6 rays per mm.

Crystals in long strands of chambered cells, ~20 chambers per strand.

Storied structure not observed.

Material: HU 56680 (Beck 350).

Comments: In both the InsideWood and FFPRI Microscopic Identification of Japanese Woods databases, only *Sapindus saponaria* L. (syn. *S. mukorossi* Gaertn.) has the combination of characters: ring porous (Fig. 26A), latewood vessels in clusters (Fig. 26B), intervessel pits that are not large, vessel–ray parenchyma pits similar to intervessel pits (Fig. 26D), septate fibers, vasicentric, confluent and marginal parenchyma, rays 1–3-seriate (Fig. 26C) and prismatic crystals in chambered cells. We examined three samples of *S. saponaria;* FPAw 1732 and TWTw 18520 often have rays that are wider than the Vantage wood, Uw 33589 has rays that are commonly 2-seriate.

Most fossil woods of Sapindaceae (aside from *Acer*, now included in the Sapindaceae) have been assigned to *Sapindoxylon* and have characteristics of extant evergreen species in the family, that is, they are diffuse porous and without obvious helical thickenings in the vessel elements (Klaassen 1999). To the best of our knowledge, there have been no earlier descriptions of ring porous fossil *Sapindus* wood. This wood is problematic in that there are no reliable reports of *Sapindus* fruits in the Tertiary of North America. Leaves previously assigned to *Sapindus* have not stood up to close scrutiny. Hickey (1977) transferred *Sapindus affinis* to an extinct genus, *Averrhoites*, and Dilcher's unpublished analyses of cuticles from leaflets assigned to *Sapindus* by Berry from the Eocene Claiborne Formation indicated that the leaflets were incorrectly identified (Manchester, pers. comm.), Thus in spite of this wood having characteristics indicating affinities with *Sapindus*, we are concerned about assigning it to *Sapindus* outright.

Septate fibers appear to be present in this wood, but it is possible that we are incorrect and what appear to be septae are numerous fine fungal hyphae and the fibers are non-septate.

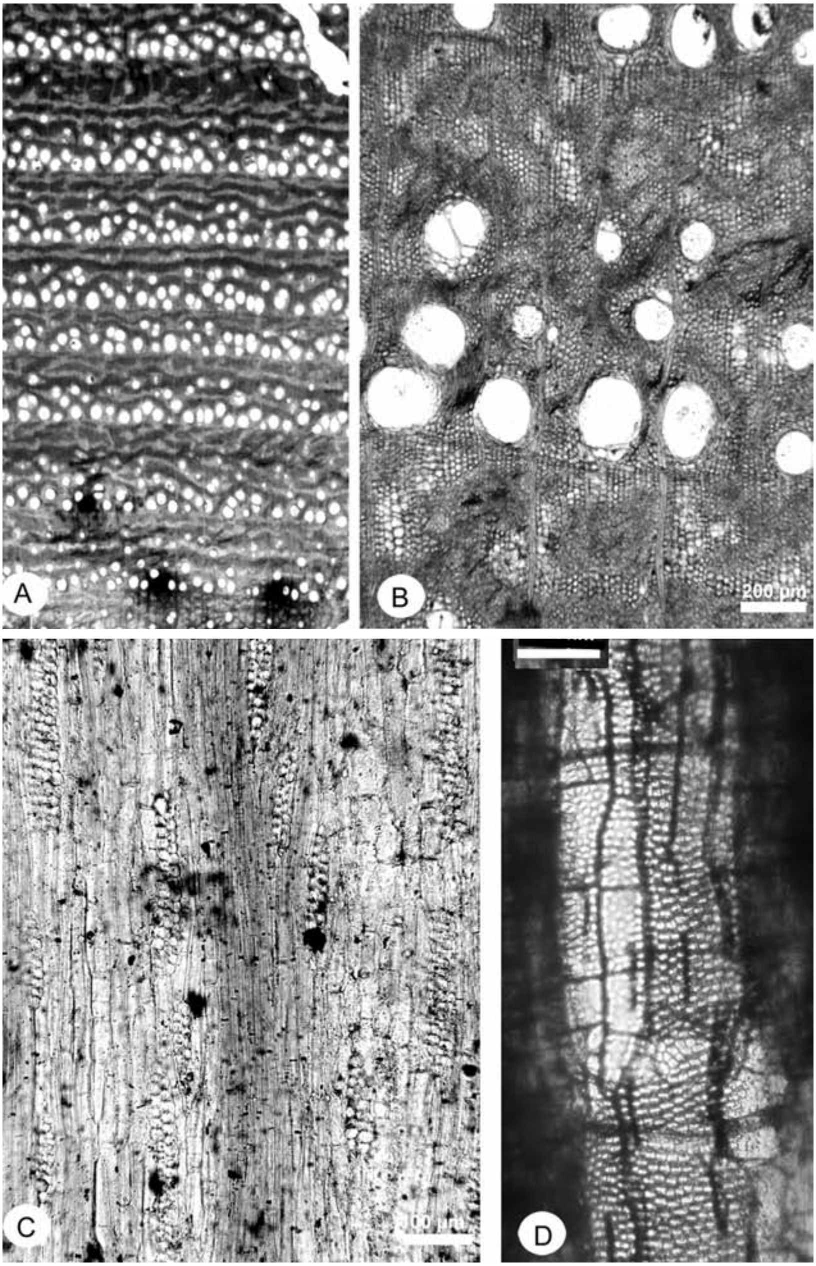

Figure 26. Sapindaceae. cf. *Sapindus* sp. HU 56680. – A, B: Ring porous wood, earlywood vessels mostly solitary, latewood vessels in clusters, axial parenchyma confluent. Width of the complete growth ring at top of A = 2.1 mm. XS. – C: Predominantly 2-seriate homocellular rays. TLS. – D: Crowded alternate intervessel pits, vessel–axial parenchyma pits similar to intervessel pits, axial parenchyma strands of 4 cells. RLS. — Scale bar = 200 µm in B; 100 µm in C, 50 µm in D.

ULMACEAE

ULMUS L.

Ulmus baileyana Prakash & Barghoorn 1961b (HU 54918, Fig. 27A, D, G)

Ulmus miocenica Prakash & Barghoorn 1961a (HU 55213, holotype, Fig. 27B, E, H; HU 55215, HU 56695 (Beck 200), HU 56696 (Beck 638)

Ulmus pacifica Prakash & Barghoorn 1961a (HU 55229, Fig. 27C, F, I; HU 55327)

The description below gives the features common to all Vantage *Ulmus*; Table 7 presents information on selected features that enable distinguishing the *Ulmus* species at Vantage.

Table 7. Comparison of Vantage *Ulmus* woods.

MTD = mean tangential diameter of earlywood vessels (μm); EW = number of rows in earlywood pore zone; d = discontinuous; c = continuous; FW = fiber wall thickness; RW = ray width in cell number; MRH = multiseriate ray height (μm). – * HU 56696.

Species	MTD	EW	FW	RW	MRH	Crystals
U. baileyana	190 (160–265)	Multiple rows, c	Thick to very thick	1–5	507 (248) 141–355	Present
U. miocenica	118 (81–179)	1 row, d	Thick to very thick	1–4	364 (121)* 189–616	Present
U. pacifica	114 (70–160)	1 row, d, widely spaced	Thick	1–7 187–991	421 (175)	Absent

Growth rings distinct, marked by latewood with thick-walled fibers, narrow vessels, marginal parenchyma.

Ring porous. Latewood with vessels in clusters, arranged in wavy tangential bands. Perforation plates exclusively simple. Intervessel pits crowded alternate, polygonal in outline, with included apertures; medium to large, 6–11 μm; vessel–ray parenchyma pits similar in size and shape to intervessel pits but with reduced borders; helical thickenings along whole length of narrow vessel elements. Vessel elements short, average length < 350 μm. Thin-walled tyloses present.

Fibers non-septate without obvious pits; vascular tracheids likely, intermixed with narrow latewood vessel elements.

Axial parenchyma paratracheal, mostly 4 cells per strand.

Rays homocellular, uniseriate and multiseriate rays, uniseriate rays not common, short (less than 10 cells high); multiseriate ray height averages less than 500 μm.

Crystals, if present, in chambered axial parenchyma.

Comments: There is more information on the wood anatomy of *Ulmus* available now than there was in 1961 when Prakash and Barghoorn published on the Vantage woods. This additional information indicates that the relationships of the Vantage *Ulmus* species with extant *Ulmus* species suggested in 1961 need modification.

Ulmus baileyana (Fig. 27A, D, G) has multiple rows of wide earlywood vessels and Prakash and Barghoorn commented that this species closely resembles the extant *U. rubra*, subgenus *Ulmus*, section *Ulmus*. However, elm species with multiple rows

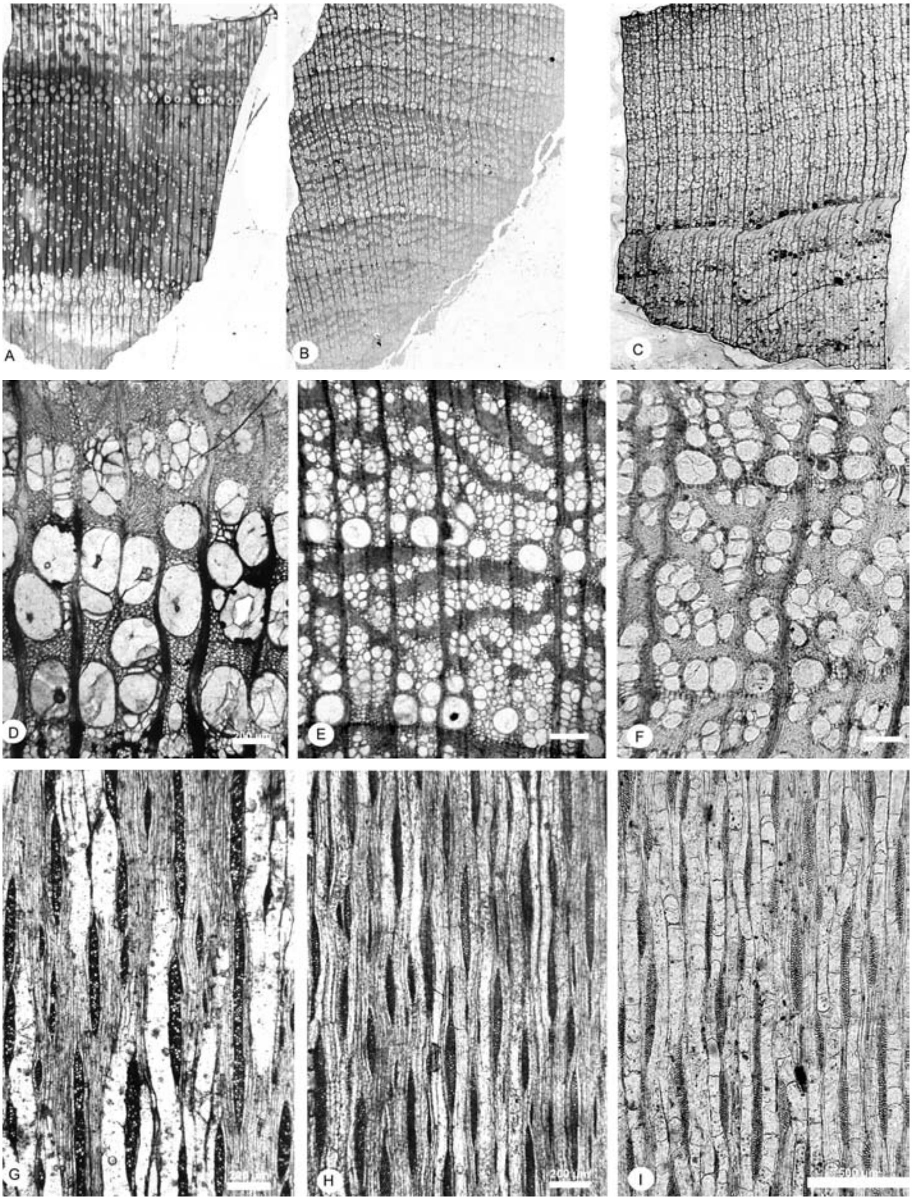

Figure 27. Ulmaceae. *Ulmus*. – A, D, G: *Ulmus baileyana*. HU 54918. – B, E: H: *Ulmus miocenica*. HU 55213. – C, F, I: *Ulmus pacifica*. HU 55229. – A: *U. baileyana*, ring porous wood, earlywood with multiple rows of wide pores that are solitary and in radial multiples. Width of complete growth ring = 7.3 mm. XS. – B: *U. miocenica,* ring porous wood, earlywood with widely spaced solitary earlywood pores. Sample at widest point = 6.8 mm. XS. – C: *U. pacifica,* solitary pores at beginning of growth ring, without a marked difference in width of solitary earlywood pores and latewood pores in clusters. Sample at widest point = 8.0 mm. XS. – G, H, I: Tangential sections showing multiseriate homocellular rays. — Scale bar = 500 µm in I; 200 µm in D–H.

of wide vessels also occur in Asia, and *Ulmus baileyana* also resembles *U. parvifolia* Jacq., which according to Wiegrefe *et al*. (1994) belongs to subgenus *Ulmus*, section *Microptelea*. Given that there can be variation within *Ulmus* species (Wheeler *et al*.1989; Wheeler & Manchester 2007), more samples of the Asian, American, and European species of *Ulmus* need to be studied to see if *Ulmus* species of different geographic regions can be reliably distinguished on wood anatomy alone.

According to Prakash and Barghoorn (1961a) *Ulmus miocenica* (Fig. 27B, E, H) has "nearest affinity … with *U. americana* L." However, *U. miocenica* has a solitary row of earlywood vessels with a mean diameter of 118 µm, the row of earlywood vessels is discontinuous, rather than continuous, and fibers are thick to very thick-walled. *Ulmus americana* has a solitary row of earlywood vessels with mean tangential diameters near or more than 200 µm, earlywood vessels are in a continuous or near-continuous row, and fiber walls are medium thick-walled. The characteristics of *U. miocenica* occur in the Hard Elm species (*U. alata, U. crassifolia, U. serotina, U. thomasii*). According to Wiegrefe, Sytsma, and Guries (1994), who did a phylogenetic analysis of 14 *Ulmus* species, these species belong to the subgenus *Oreoptelea*, with *U. thomasii*, *U. serotina*, and *U. crassifolia* in section *Trichoptelea*, and *U. alata* and *U. mexicana* in section *Chaetoptelea*. The anatomy of *U. thomasii, U. serotina,* and *U. crassifolia* is similar, and distinguishing between the species based on wood anatomy is not always possible (Wheeler *et al*. 1989). We suggest that *U. miocenica* belongs to subgenus *Oreoptelea*. *Ulmus miocenica* also occurs at Squaw Creek, another Miocene Columbia River Basalts wood assemblage (HU 56697, Beck 1673). Between the samples there is some variation in spacing of the earlywood vessels and in the differences between earlywood and latewood pore diameters. However, these differences are less than seen within wood of a single extant *Ulmus* species (Wheeler *et al*. 1989; Wheeler & Manchester 2007).

Prakash and Barghoorn noted that *Ulmus pacifica* (Fig. 27C, F, I) "does not compare in all details with any extant species of *Ulmus,* but it shows some structural resemblance with *Ulmus mexicana* (Liebm.) Planch. … both [are] semi-ring porous." However, *Ulmus mexicana* differs from all other elm species as it lacks vessel clusters and tangentially arranged vessels and has banded axial parenchyma (PACw 8180). *Ulmus pacifica* has tangentially arranged latewood vessels and the vessels often are in clusters. The earlywood vessels of *Ulmus pacifica* are not much wider than the latewood vessels; this characteristic is seen in some samples of *U. crassifolia* and *U. thomasii*. Consequently, we suggest that *U. pacifica* belongs to subgenus *Oreoptelea*, section *Trichoptelea*, and is not comparable to *Ulmus mexicana*.

INCERTAE SEDIS

The woods described and discussed below have distinctive anatomy, but we were unable to determine with certainty their relationships to extant taxa. In some cases this is because the preservation of the sample did not allow determining critical diagnostic features; in others preservation was good, but we were not able to establish that the wood had characteristics unique to a single family or genus using currently available information. These woods' features were also used in estimating the MAT (mean annual temperature) of the Vantage assemblage, so we are documenting their characteristics in the descriptions below. We think that if these Vantage woods belong to genera now occurring in the USA we likely would have been able to determine their relationships. They probably are either extinct or extirpated and now exotic to temperate North America. In the future, as more information on woods of temperate and subtropical Asia becomes available and comprehensive wood anatomical studies of some families and genera are done, it may be possible to establish the relationships of these woods to extant plants.

URTICALES ?

Beck's "Hardwood C" (Fig. 28)

Growth rings present, marked by marginal parenchyma.

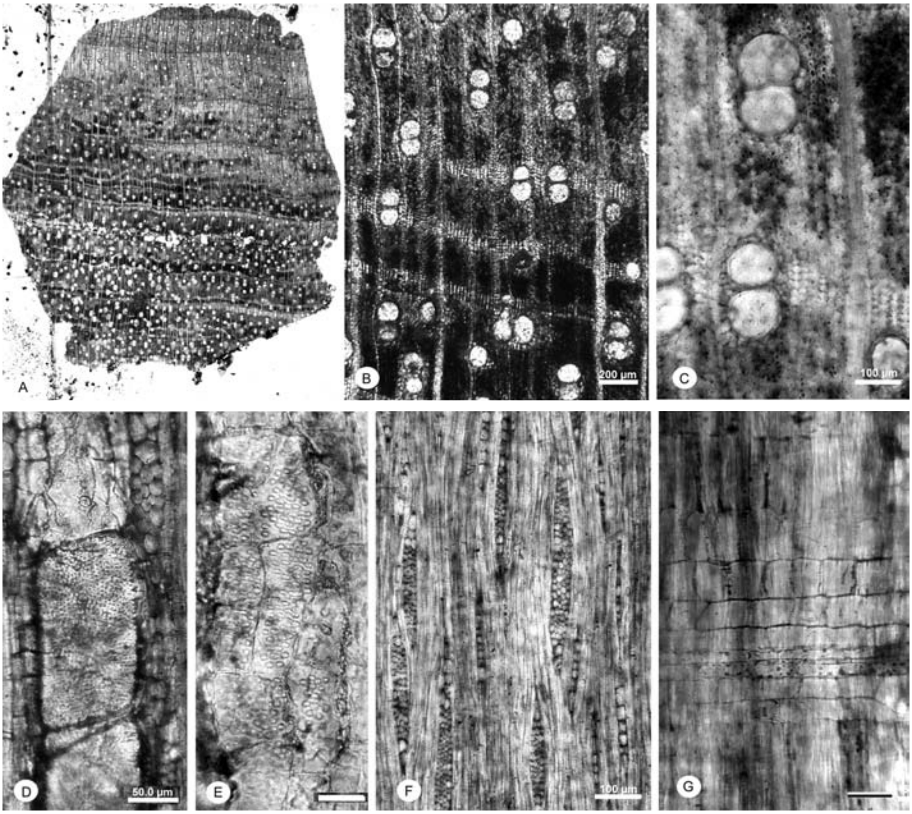

Figure 28. Beck's Hardwood C. HU 56719 (Beck 1539). – A–C: Diffuse porous wood, with vessels solitary and in short radial multiples, solitary vessels rounded in outline, axial parenchyma banded. In A total sample width at widest point = 13 mm. XS. – D: Crowded alternate intervessel pits, vessel elements with simple perforation plates. TLS. – E: Vessel–ray parenchyma pits. RLS. – F: Heterocellular multiseriate rays, TLS. – G: Body ray cells procumbent, square and upright marginal cells. RLS. — Scale bar = 200 µm in B; 100 µm in C, F; 50 µm in D, E; 20 µm in G.

Wood diffuse porous. Vessels solitary (43 %) and in radial multiples of 2–3, solitary vessels round to slightly oval in outline, radial multiples figure 8-shaped; average tangential diameter 110 (19) µm, range 83–158 µm; c. 10–15 per sq.mm. Perforation plates exclusively simple; intervessel pitting crowded alternate, apertures narrow, sometimes pit apertures coalescent, 4–6 µm; vessel–ray parenchyma pits similar in size to intervessel pits but with borders reduced. Vessel elements 295–330 µm long.

Fibers thick-walled, mostly non-septate, pits not observed.

Axial parenchyma scanty paratracheal to vasicentric and banded, with bands generally 4 to 6 cells wide. Marginal parenchyma. Strands usually of 4 cells.

Rays tending to two sizes. Multiseriate rays usually 4–6 (–7)-seriate, uniseriate rays rare and high. Heterocellular, with procumbent body cells and 1–2 marginal rows of square to upright cells, some rays with uniseriate rays of 8 or marginal rows, but based on appearance in radial section not all cells in these longer marginal rows are upright. Total height of multiseriate rays 255–440 µm; 5–8 per mm.

Storied structure absent, crystals not observed.

Material: HU 56719 (Beck 1539).

Comments: Diffuse porous woods with vessels solitary and in radial multiples, exclusively simple perforation plates, crowded alternate pits, vessel–ray parenchyma pits similar in size to intervessel pits, banded and marginal parenchyma occur in some species of Boraginaceae, Cannabaceae, Meliaceae, Moraceae, Rhamnaceae, and Rutaceae. The reduced borders of many of the vessel–ray pits as seen in this Vantage wood are found in the Cannabaceae and Moraceae, as are species with rays tending to be of two sizes. Consequently, we suggest that this wood represents a member of the order Urticales. The cross-sectional appearance of this Vantage wood bears similarity to some diffuse porous *Celtis* species and to *Pteroceltis* (SJRw 32043) of the Cannabaceae. However, crystals are a regular feature of *Celtis* and *Pteroceltis* wood.

Vantage Unknown Dicot I (Fig. 29)

Growth rings distinct. Wood semi-ring porous, earlywood zone with vessels closely spaced, latewood zone with vessels widely spaced. Earlywood and latewood vessels similar in diameter, mean tangential diameter 64 (10) µm. Solitary vessels rare, most vessels in groups, radial multiples more than 4 and clusters present. Scalariform perforation plates, c. 15 bars. Intervessel pits crowded alternate with included circular-oval apertures, 6–9 µm in horizontal direction. Vessel element lengths more than 750 µm.

Fibers medium thick-walled.

Axial parenchyma rare.

Rays to 6-seriate, tending to two size classes, multiseriate rays commonly 0.85 to 1.18 mm high, about 8 rays per mm.

Material: HU 56705 (Beck 628).

Comments: This wood is clearly distinct from other Vantage woods because of the broad earlywood zone that is composed of virtually all vessels in groups. Unfortunately its preservation is not good and we could not determine vessel–ray parenchyma pit type or fiber type or ray cellular composition. It was difficult to distinguish individual ray cells, but it was possible to see that rays were at least 6-seriate. In cross section, bars of

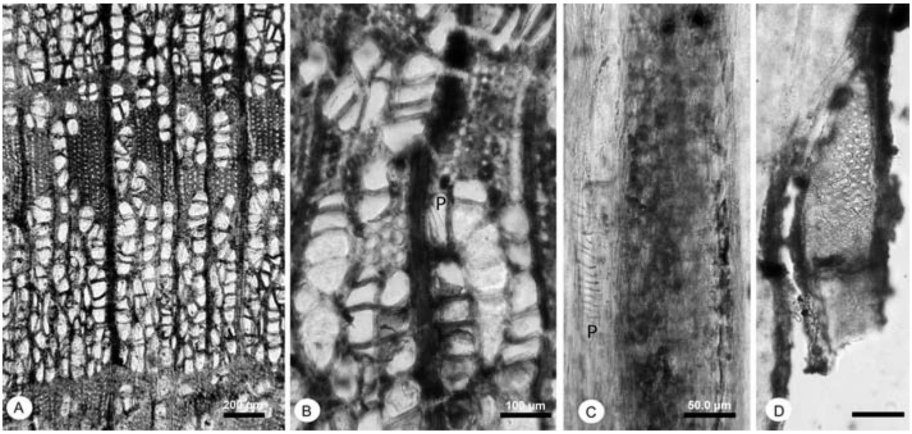

Figure 29. Vantage Unknown Dicot 1. HU 56704 (Beck 628). – A: Semi-ring porous wood, with earlywood zone with crowded vessels in radial multiples, latewood with vessels more widely spaced, but of similar width as the earlywood vessels. XS. – B: Detail of earlywood zone, portion of scalariform perforation plate (P) visible in one vessel element. XS. – C: Multiseriate ray with individual cells indistinct, but seemingly more than 4 cells wide, portion of a scalariform perforation plate (P). TLS. – D: Crowded alternate intervessel pitting. TLS. — Scale bar = 200 µm in A; 100 µm in B; 50 µm in C, D.

scalariform perforation plates were visible in vessel lumens, and in longitudinal sections a few scalariform perforation plates were seen. We did not observe simple perforation plates, but cannot with certainty say they are entirely absent from this wood. Only a few regions with intervessel pitting were found, and these had alternate intervessel pits, it is possible that opposite intervessel pits also could be present.

Woods with the combination of semi-ring porosity, vessels commonly in radial multiples of 4 or more, scalariform perforation plates, alternate intervessel pits, rare axial parenchyma, and rays that are not exclusively uniseriate or commonly more than 10-seriate occur in the Araliaceae, Ericaceae, and Nothofagaceae (InsideWood accessed 18 October 2008), the last being a Southern Hemisphere family without a fossil record in the Neogene of North America. If one allows for mismatches, i.e. searches for woods that have any 5 of the 6 features listed above the possibilities are expanded to include the Aquifoliaceae, Atherospermataceae, Corylaceae, Elaeocarpaceae, Rhamnaceae, Rutaceae, Salicaceae (*Scolopia*), Styracaceae, and Tapisciaceae. The broad earlywood zone with crowded grouped vessels is the most distinctive feature of this wood. Examination of samples or available images of these families did not reveal a good match for this wood, although some *Styrax* species tended to have an earlywood zone with crowded vessels, *e.g.*, some samples of *S. japonica* (UN 412).

There is only one wood sample of this type known at present. Given that there are many fossil wood localities in the Pacific Northwest, it is possible that another, hopefully better preserved, sample will be recovered, so that the affinities of this wood might be resolved. We also think that sectioning additional samples of *Styrax* would be worthwhile as well.

RHAMNACEAE ?

Vantage Unknown Dicot 2 (Fig. 30)

Growth rings distinct. Diffuse to semi-ring porous. Vessels solitary (54 %) and in radial multiples of 2 (3). Mean tangential diameter of vessels in the first half of the growth ring 170 (26) µm, range 127–220 µm. Simple perforation plates, alternate intervessel pits, oval in outline with narrow slit-like apertures extending to the end of the border, horizontal diameter 6–7 µm, vessel–ray parenchyma pits similar to intervessel pits. Mean vessel element length 344 (88) µm. Helical thickenings probable, but difficult to distinguish from coalescent pit apertures.

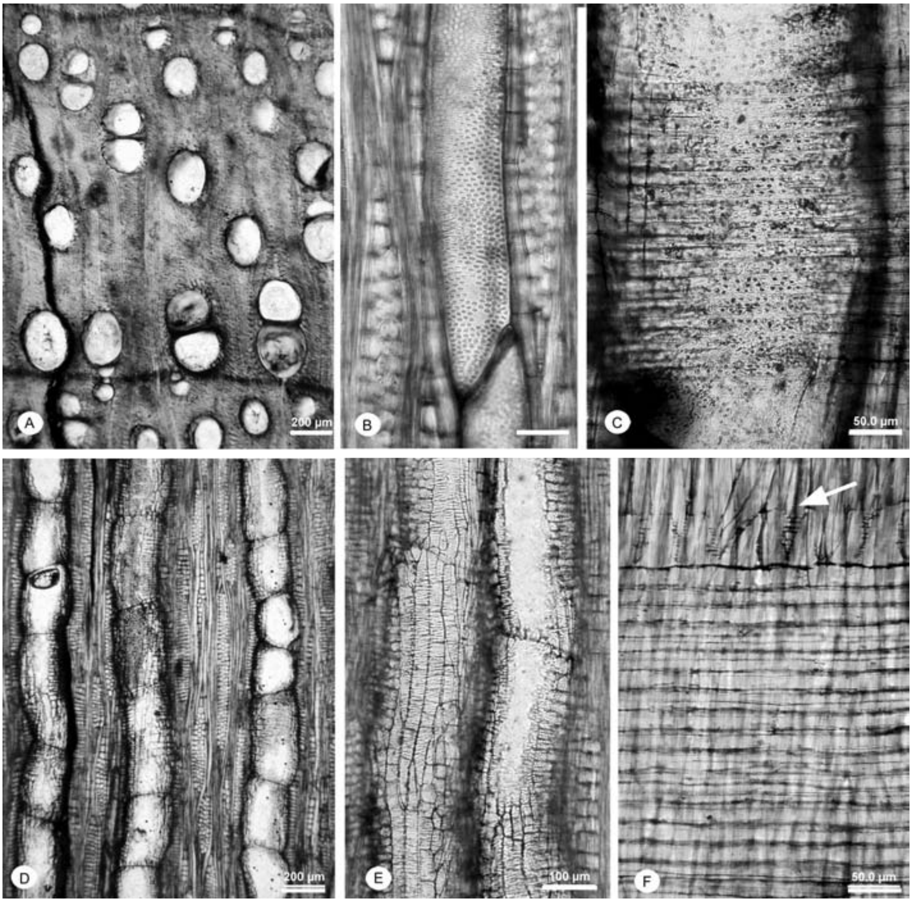

Figure 30. Vantage Unknown Dicot 2. UWBM 98699 (Beck 185). – A: Wood semi-ring porous to diffuse porous. Vessels solitary and in short radial multiples. XS. – B: Crowded alternate intervessel pits. TLS. – C: Vessel–ray parenchyma pits similar to intervessel pits. RLS. – D: Narrow rays, series of vessel element with simple perforation plates. TLS. – E: Storied axial parenchyma strands. TLS. – F: Ray body cells procumbent, marginal row of upright cells, arrow points to disjunct end walls. RLS. — Scale bar = 200 µm in A, D; 100 µm in E; 50 µm in B, C, F.

Fiber walls of medium thickness. Fiber pits not observed.

Axial parenchyma paratracheal, usually 4–8 cells per strand, locally storied.

Rays 1–4-seriate, heterocellular, with 1–3 marginal rows of upright cells, marginal cells twice the height of the procumbent cells, disjunctive ray parenchyma cells; mean multiseriate ray height 489 (168) µm, range 257–833 µm.

Crystals not observed.

Material: UWBM 98699 (Beck 185).

Comments: Species with the combination of semi-ring porous wood, randomly arranged vessels in short multiples having a mean tangential diameter between 100–200 µm, simple perforation plates, minute–small alternate intervessel pits, vessel–ray parenchyma pits similar to intervessel pits, predominantly paratracheal parenchyma, and heterocellular rays that are not exclusively uniseriate or more than 10-seriate occur in the families Bignoniaceae, Malvaceae, Meliaceae, and Rhamnaceae. Disjunctive ray parenchyma cells (Fig. 30 F) occur in this Vantage wood. The distribution of this feature is not well documented in the literature. We examined samples of the aforementioned families and found disjunctive ray cells only in the Rhamnaceae (*Hovenia*), which suggests that its affinities are likely to be with this family.

Recent work has established the occurrence of the Rhamnaceae in the Upper Cretaceous of North America (leaves - Fox Hills Formation, North Dakota, Peppe *et al.* 2007; flowers - Cerro del Pueblo Formation, Cohuila, Mexico, Calvillo Canadell & Cevallos-Ferriz 2007). Calvillo Canadell and Cevallos-Ferriz (2007) listed other occurrences of fossil Rhamnaceae in the Northern Hemisphere, most being fruits of *Paliurus*. *Paliurus* has exclusively uniseriate rays, so this wood cannot be assigned to *Paliurus*.

Vantage Unknown Dicot 3 (Fig. 31)

Growth rings present, marked by marginal parenchyma.

Diffuse porous. Vessels solitary (23 %) and in radial multiples of 2 (3). Mean tangential diameter 140 (28) µm, 76–197 µm. Vessel density < 5 per sq. mm. Simple perforation plates. Crowded alternate intervessel pits, 4–6 µm across. Vessel–ray parenchyma pits crowded and similar to intervessel pits. Vessel element lengths between 500–600 µm.

Fibers thin-walled, non-septate, without obvious pits, short, less than 900 µm long, with a tendency to storied structure.

Axial parenchyma marginal, and scanty paratracheal to vasicentric. Strands usually of 4 cells.

Rays 1–2-seriate (mostly 1-seriate). Homocellular, composed of procumbent cells. Irregularly storied (en echelon). Average ray height 248 (40), 183–329 µm; 7–11 per mm.

Crystals not observed.

Material: UWBM PB1 (Beck 222).

Comments: Species with short (<900 µm), thin-walled fibers that are storied in combination with marginal parenchyma occur in the Malvaceae *s.l.* (Malvaceae, Sterculiaceae, and Tiliaceae) and Simaroubaceae. Species with the combination of thin-walled fibers and irregularly storied narrow rays occur in the Sapindaceae and Simaroubaceae. It seems unlikely this wood has affinities with the Simaroubaceae as species

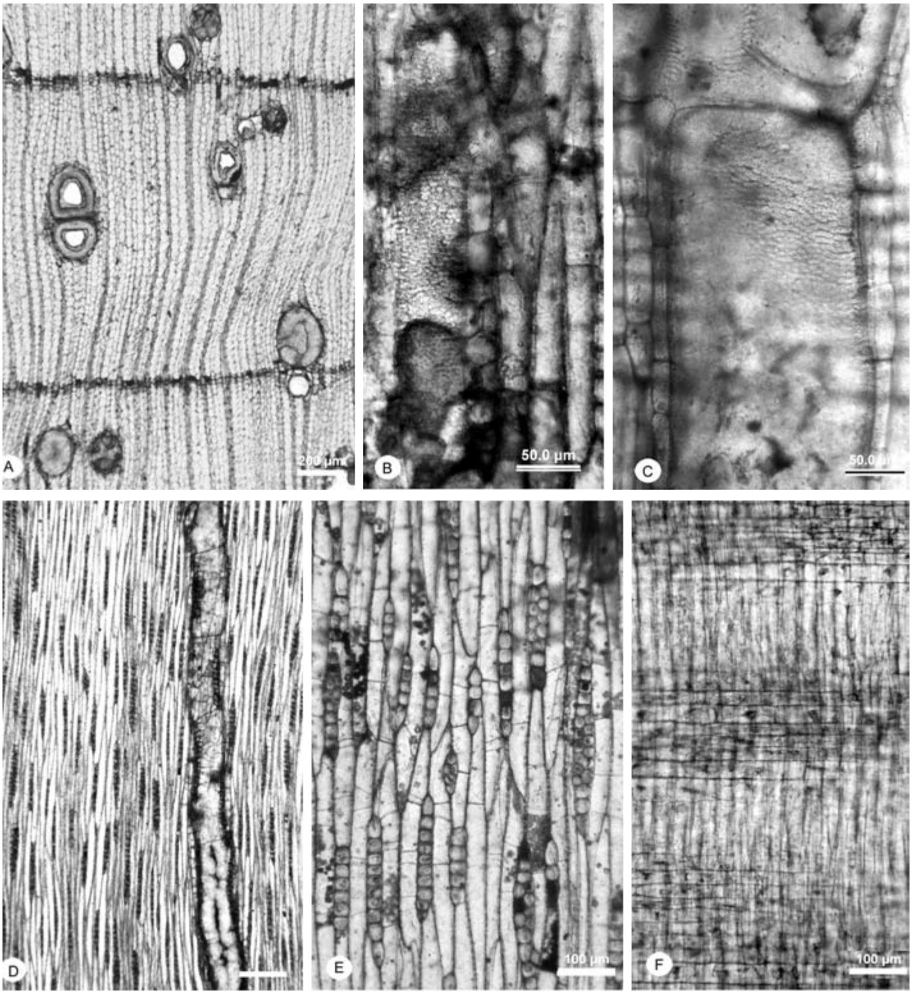

Figure 31. Vantage Unknown Dicot 3. UWBM PB1 (Beck 222). – A: Diffuse porous wood, low vessel density, vessels solitary and in radial multiples of 2. XS. – B: Crowded alternate intervessel pitting. TLS. – C: Vessel–ray parenchyma pits, axial parenchyma strands next to vessels. RLS. – D: Narrow rays and fibers irregularly storied ('en echelon'). TLS. – E: Rays 1–2-seriate. TLS. – F: Rays composed of procumbent cells. RLS. — Scale bar = 200 µm in A, D; 100 µm in E, F; 50 µm in B, C.

in this family usually have aliform-confluent parenchyma, a feature not present in this Vantage wood. The ray structure of this wood (narrow and homocellular) does not occur in the Malvaceae. Narrow homocellular rays, storied structure, marginal parenchyma, small alternate intervessel pits, vessel–ray parenchyma pits similar to intervessel pits occur in the Sapindaceae, with *Aesculus* being the only genus with storied structure. A review of the literature and our own observations did not find any *Aesculus* species with a low vessel density and relatively wide vessels.

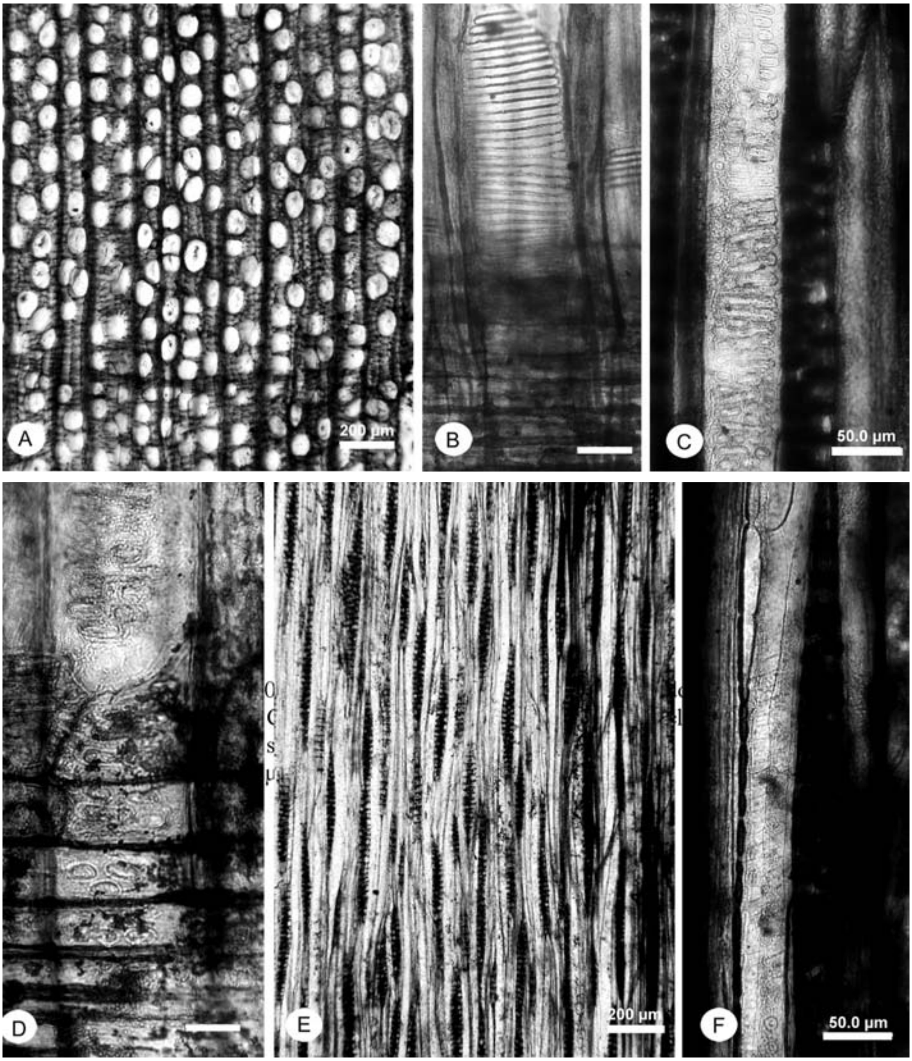

Figure 32. Vantage Unknown Dicot 4. HU 65000 (Beck 305). – A: Diffuse porous wood, vessels predominantly solitary, axial parenchyma rare. XS. – B: Scalariform perforation plate. RLS. – C: Crowded opposite-scalariform intervessel pits. TLS. – D: Vessel–ray parenchyma and intervessel pits. RLS. – E: Heterocellular rays 1–3-seriate. TLS. – F: Vessel element with fine spiral thickenings along the length of the cell. RLS. — Scale bar = 200 µm in A, E; 50 µm in C, F; 20 µm in B, D.

Vantage Unknown Dicot 4 (Fig. 32)

Growth rings present, marked by 2–3 rows of radially narrower fibers.

Diffuse porous. Vessels mostly solitary, but with some short multiples. Average tangential diameter 59 (9) µm, range 43–80 µm. Vessel density 65–104 per sq.mm. Exclusively scalariform perforation plates, with 21–28 bars. Scalariform and opposite intervessel pits. Vessel–ray parenchyma pits horizontally elongated with somewhat reduced borders. Vessel element lengths average 953 (192) µm, 577–1197 µm. Helical thickenings along entire length of some narrower vessel elements and at the tips of others.

Fibers medium-thick-walled, non-septate, with distinctly bordered pits on both radial and tangential walls.

Axial parenchyma rare.

Rays 1–3-seriate. Heterocellular, usually with 1 marginal row of upright to square cells. Average ray height 504 (163) µm, 280–980 µm; 6–10 per mm.

Crystals not observed.

Material: HU 65000 (Beck 305).

Comments: In Beck's collections, this wood had been labeled *Liquidambar* and it is similar to that genus in general appearance. However, this wood has some vessel elements with helical thickenings along their entire length; *Liquidambar* has helical thickenings only at the tips of vessel elements. The combination of narrow (< 100 µm average tangential diameter), randomly arranged vessels with scalariform and opposite intervessel pits, exclusively scalariform perforation plates, helical thickenings along the entire length of the vessel elements, non-septate fibers with distinctly bordered pits, narrow (1–3-seriate) heterocellular rays that have 1–3 marginal rows of square to upright cells, and rare axial parenchyma occurs in species of the families Adoxaceae, Ericaceae, Eucryphiaceae (a Southern Hemisphere family), Hamamelidaceae, Illiciaceae, Pentaphylacaceae, Symplocaceae, and Theaceae. Distinguishing woods of many members of the aforementioned families has long been recognized as problematic (*e.g*., Brazier & Franklin 1961). We think that some of the aforementioned families can be eliminated as candidates for relationships to this Vantage wood: 1) Eucryphiaceae, because it does not occur in the Northern Hemisphere, 2) Illiciaceae usually have more bars per perforation plate and rays with more than 4 marginal rows are relatively common, 3) Theaceae have vessel–ray pits that are more horizontally elongated and have much reduced borders compared to this Vantage wood. At this time, our examination of reference material (slides, literature, and information on InsideWood) did not reveal a way to determine whether this wood has features unique to the Adoxaceae, Ericaceae, Hamamelidaceae, Pentaphylacaceae, or Symplocaceae.

CONIFERAE

Many species of fossil conifer woods reflect differences in geography and age and author rather than significant differences in anatomy. Fossil woods of conifers have always been problematic. Cross-field pit type is a critical diagnostic feature in conifers and can be difficult to determine in many fossil woods. In woods with distinct growth rings, cross-field pit type should be determined from the earliest earlywood and at times that area is not well-preserved. Woods with taxodioid cross-field pits in their earlywood may have cupressoid cross-field pits in their latewood. Preservation of fossil woods may be such that cross-field pits are not visible in the earlywood, only in narrower latewood tracheids, if visible at all. Also, fungal and bacterial attack on the cell wall can alter the appearance of cross-field pits.

Compression wood occurs in fossil woods and the helical cavities in compression wood tracheid cell walls have been confused with helical thickenings. True helical thickenings usually are at near right angles to the longitudinal cell wall, the inclination of the helical cavities in compression wood tracheids varies, but they often are inclined c. 45° from the longitudinal cell wall. Woods of the cupressoid group are especially difficult to distinguish from one another on the basis of wood anatomy alone (Phillips 1948).

CUPRESSACEAE

Cupressinoxylon spp.

Lack of resin canals, combined with absence of helical thickenings in the longitudinal tracheids, presence of cupressoid cross-field pits, and relatively short uniseriate rays indicate affinities with Cupressaceae, cupressoid group. *Cupressinoxylon* is the name applied to such woods. Two of the Vantage woods that have characteristics of *Cupressinoxylon* had been labeled as other genera, one as *Torreya,* one as *Callitris* (see below). We could not find wood of *Torreya* or *Callitris* in the samples we examined. The anatomy of extant Cupressaceae woods is quite homogeneous, with genera and species often distinguished solely on the basis of heartwood color and odor. There are more species of *Cupressinoxylon* than there are distinctive wood anatomical types within extant Cupressaceae, and differences between the fossil species usually are slight. Because of the relatively poor preservation and presence of compression wood in the Vantage cupressoid woods it is difficult to determine how many distinctive wood types there are. We are choosing not to assign the Vantage *Cupressinoxylon* woods to species.

Beck sample 625 (HU 56693, Fig. 33) was labeled *Torreya*. The defining characteristics of *Torreya* are lack of resin canals, and helical thickenings in the longitudinal tracheids. However, the presence of helical thickenings in this sample cannot be confirmed and it seems better to refer it to *Cupressinoxylon*. The regions that at low magnification (10× objective lens) look to have helical thickenings, at higher magnifications (40× objective lens) look to be regions with fine fungal hyphae whose path through the cell wall went around the pits. In places these fine lines ("hyphae") appear to go from tracheid to tracheid, which would be consistent with them being hyphae rather than helical thickenings (Fig. 33 G, H). Also there were regions with 'checks' in the cell wall that appear to follow the microfibril angle of the S_2 layer, and likely result from bacterial or fungal degradation of the wall (Fig. 33F). The inclination of these 'checks' is not near horizontal as is typical for true helical thickenings.

Areas with preservation good enough to clearly see cross-field pits were rare in sample HU 56693, and were especially difficult to see in the earliest earlywood, the region that should be used to view cross-field pits for identification purposes. There appeared to be small cupressoid pits, generally 2 per cross field, so that this sample can be considered a type of *Cupressinoxylon*.

Beck sample 1618 (Fig. 34 A–C) had been labeled *Callitris*. However, this sample appears to be compression wood of Cupressaceae. The longitudinal tracheids are rounded in outline (Fig. 34 A) and the S_2 wall layer appears inclined from the longitu-

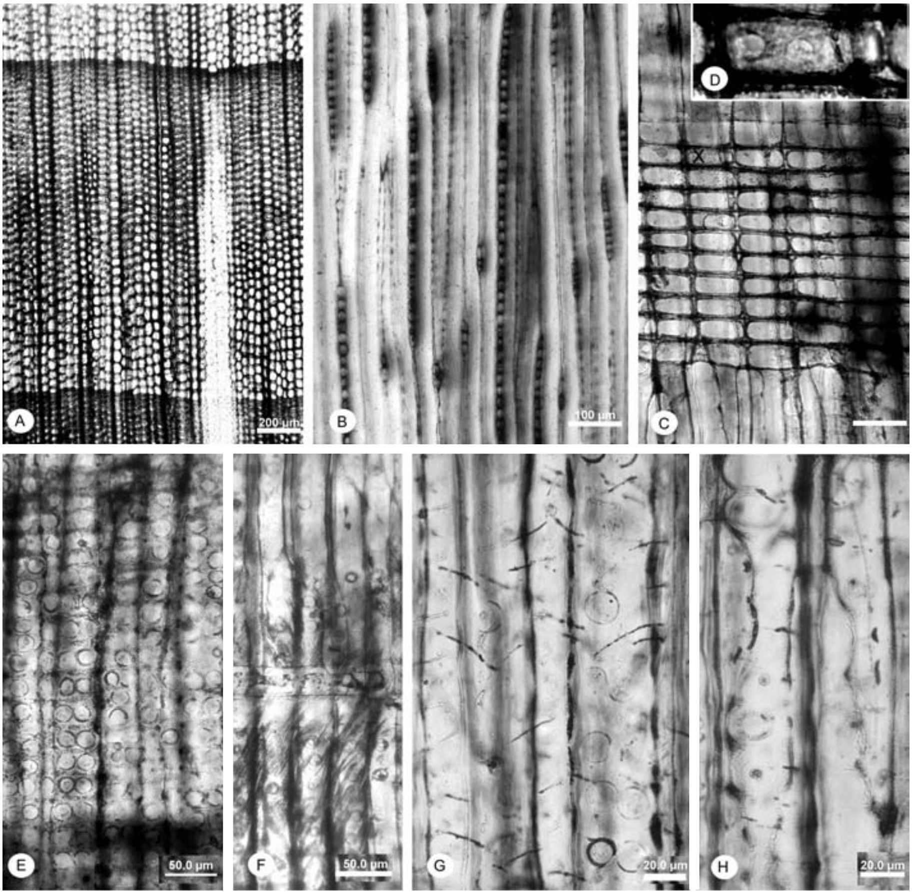

Figure 33. Cupressaceae. *Cupressinoxylon* sp. 1. HU 56693. – A: Growth rings present, gradual earlywood to latewood transition. XS. – B: Uniseriate rays of variable height. TLS. – C: Rays composed of ray parenchyma cells, ray tracheids absent. X in the cross-field shown in D. RLS. – D: Cupressoid cross-field pit. RLS. – E: Intertracheary pits opposite. RLS. – F: Tracheid walls with checks. RLS. – G, H: Tracheids with fine fungal hyphae. RLS. — Scale bar = 200 µm in A; 100 µm in B; 50 µm in C, E, F; 20 µm in G, H.

dinal cell wall to a degree (near 45°) that is usual for compression wood. The helical cavities in compression wood tracheid walls are often especially well developed near pits and these splits may have been interpreted as callitroid thickenings. However, true callitroid thickenings have a horizontal orientation. The preservation of this sample was not good, and it was not possible to find many cross fields in which to count the num-ber of pits per cross field, a feature often used in characterizing species of fossil wood.

Macrofossils of the Cupressaceae (*sensu stricto*) are common in the Cenozoic of the Pacific Northwest. *Calocedrus*, *Chamaecyparis* and *Thuja* are represented by foliage

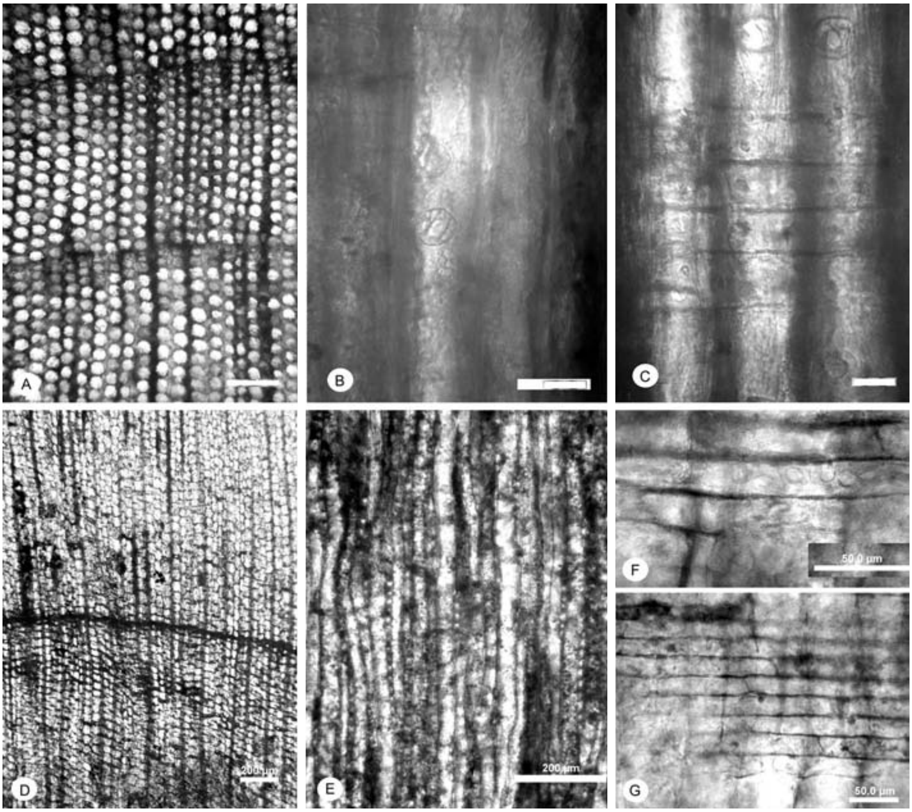

Figure 34. Cupressaceae. – A–C: *Cupressinoxylon* sp. 2. Beck 1618. – A: Growth rings present, longitudinal tracheids rounded in outline, narrow latewood. XS. – B: Intertracheary bordered pits. RLS. – C: Cupressoid cross-field pits, rays with smooth walls. RLS. – D–G: *Taxodioxylon antiquum*. HU 56247. – D: Distinct growth rings, narrow latewood. XS. – E: Uniseriate rays. TLS. – F: Taxodioid cross-field pits. RLS. – G: Rays with smooth end walls. RLS. — Scale bar = 200 µm in D, E; 100 µm in A; 50 µm in F, G; 20 µm in B, C.

and preserved cones in a number of localities, from the Early/Middle Eocene sites of the Okanagan Highlands (Dillhoff *et al*. 2005) through modern times. All three of these taxa are found in Middle Miocene lacustrine deposits around the margins of the Columbia River basalts (Chaney & Axelrod 1959; Smiley & Rember 1985), therefore the cupressaceous woods found at Vantage may represent one or all of these genera. Cuticular foliage and seeds of *Tetraclinus* (today native to warm, summer-dry climates of northern Africa, Malta, and southern Spain) are reported from the Miocene Latah Formation of Oregon and Washington (Kvacek *et al*. 2000; Kvacek & Rember, 2000).

Taxodioxylon antiquum Prakash 1968 (Fig. 34)

Growth rings present, marked by a few rows of radially narrower tracheids. Mean tangential diameter 38 (6) µm, range 25–52 µm. Longitudinal and radial resin canals absent. Helical thickenings absent. Intertracheary pitting opposite. Rays 2–24 cells high, smooth-walled ray parenchyma. Cross-field pits taxodioid.

Material: HU 56247 (holotype), HU 56608.

Comments: This wood has characteristics of the genus *Taxodioxylon* as it lacks resin canals, has relatively large taxodioid cross-field pits and smooth-walled ray parenchyma. The preservation of both specimens is poor and intertracheary pits are difficult to see. There appears to be some scattered axial parenchyma, but that is not definite. This wood could be related to *Taxodium, Glyptostrobus, Sequoia, Metasequoia,* or *Sequoiadendron*. HU 56608 (Beck 1114, Loc. 89) was labeled as *Abies*, but it lacks nodular end walls in the ray parenchyma, and the size of the cross-field pits is consistent with this wood being *Taxodioxylon*.

Taxodioid fossils are common throughout the Cenozoic of the Pacific Northwest. Macrofossils of *Cunninghamia*, *Sequoia*, *Metasequoia*, *Taxodium*, and *Glyptostrobus* are reported from the Early / Middle Eocene Okanagan Highlands (Dillhoff *et al*. 2005) through the Miocene. Today *Sequoia* is restricted to southern Oregon and northern California, while the other taxa are extinct in northwestern North America. *Cunninghamia*, *Glyptostrobus*, and *Metasequoia* are restricted to eastern Asia and *Taxodium* occurs in the southeastern United States, Mexico, and Guatemala (Farjon 2005). Many of the Middle Miocene lacustrine floras around the margins of the Columbia River basalts report one or more of these taxa and therefore it is unclear which genera are represented in the wood assemblage at Vantage.

PINACEAE

We examined sections of five of the woods in Beck's collections that had been labeled *Abies*. In only one of the samples could we see what might be nodular ray parenchyma end walls as well as what might be taxodioid cross-field pits, a combination of features that is necessary to be able to identify a wood as *Abies*. We cannot with certainty assign any of the samples to *Abies*, and the poor preservation of these samples made it difficult to decide whether they were Cupressaceae or Pinaceae.

PICEA A. Dietr.

Picea tertiarum (Prakash), comb. nov. (Fig. 35 A–D)

[*Piceoxylon tertiarum* Prakash 1968]

Growth rings distinct. Gradual transition from earlywood to latewood. Longitudinal and radial resin canals present, with thick-walled epithelial cells, longitudinal canals often at beginning of transition to latewood. Helical thickenings not observed. Intertracheary pitting opposite, pit membranes appear to have distinct tori. Rays with ray parenchyma and ray tracheids. Ray tracheid pits with small teeth. Cross-field pitting small, likely piceoid.

Material: Holotype HU 55306.

Comments: The combination of longitudinal (Fig. 35 A) and radial resin canals with thick-walled epithelial cells (Fig. 35 B, C), a gradual transition from earlywood to latewood (Fig. 35 A), and ray tracheids with small teeth (Fig. 35 D) are characteristics

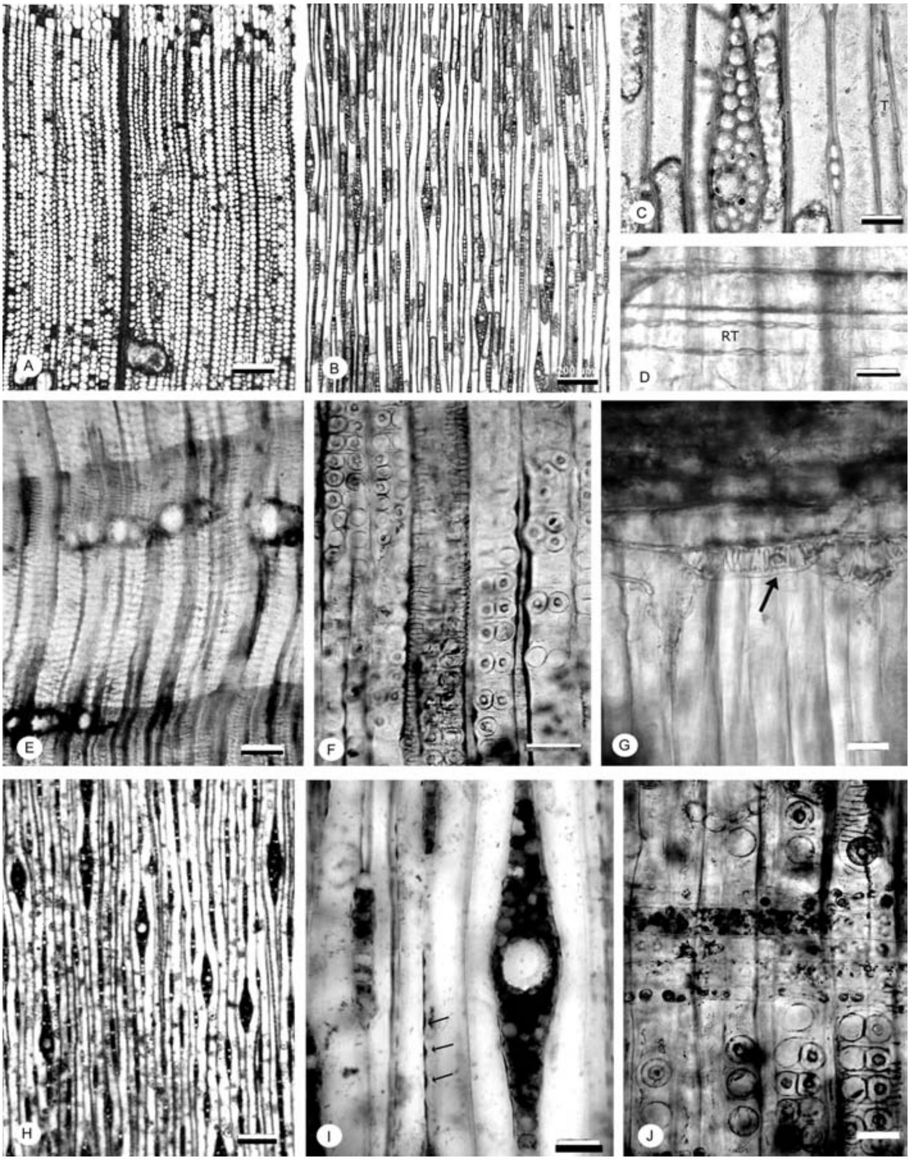

Figure 35. Pinaceae. – A–D: *Picea tertiarum*. HU 55306. – A: Distinct growth rings with broad zone of tracheids gradually becoming radially narrower. Axial resin canals. XS. – B: Fusiform rays and uniseriate rays. TLS. – C: Fusiform ray with thick-walled epithelial cells. Intertracheary pits with tori, at right. TLS. – D: Ray tracheids (RT) minutely dentate. RLS. – E–J: *Pseudotsuga pseudotsugae*. HU 65007 (Beck 1726). – E: Distinct growth rings with distinct latewood band. Axial resin canals in tangential lines. XS. – F: Opposite biseriate intertracheary pitting, helical thickenings in longitudinal tracheids. RLS. – G: Ray tracheid with helical thickening (arrow). RLS. – H: Fusiform rays and uniseriate rays. TLS. – I: Fusiform ray with thick-walled epithelial cells. Intertracheary pits with tori (arrows). TLS. – J: Cross-field pits small, opposite intertracheary pitting. RLS. — Scale bar = 200 µm in A, B, E, H; 50 µm in F; 20 µm in C, D, G, I, J.

of *Picea*. Prakash (1968) thought this wood "may belong to either *Pseudotsuga* or *Picea*", but we did not observe spiral thickenings as he reported, and ray tracheids with small teeth are characteristics of *Picea* rather than *Pseudotsuga*. Given that this wood's characteristics are only seen in *Picea*, we transfer it from *Piceoxylon* to *Picea*.

Fossil woods assigned to *Piceoxylon* have been reported from the Cretaceous of Asia (Nishida & Nishida 1995), Europe (Philippe *et al*. 2006), and North America (Tidwell & Thayn 1985), as well as in a number of younger deposits (Dijkstra & van Amerom 2000). In western North America, remains of *Picea* are common in many compression floras throughout the Cenozoic (Axelrod 1976), including seeds, foliage, cones and pollen.

PSEUDOTSUGA Carrière

Pseudotsuga pseudotsugae (Gothan) Beck 1945b (Fig. 35E–J)

[*Piceoxylon pseudotsuga* Gothan]

Growth rings distinct. Clearly defined band of latewood. Longitudinal and radial resin canals present, longitudinal canals often in tangential groups. Epithelial cells thick-walled. Longitudinal and ray tracheids with helical thickenings. Intertracheary pitting opposite, pit membranes appear to have distinct tori. Rays with ray parenchyma and ray tracheids. Cross-field pitting small, likely piceoid.

Material: HU 65007 (Beck 1726).

Comments: The combination of longitudinal (Fig. 35E) and radial resin canals (Fig. 35H, I) and helical thickenings in both longitudinal (Fig. 35F) and ray tracheids (Fig. 35G) only occurs in *Pseudotsug*a. It has been noted that helical thickenings in ray tracheids of mature wood are of more common occurrence in *Pseudotsuga japonica* than they are in *P. menziesii* (IAWA Committee 2004) suggesting that the Vantage species is related to the present-day Asian species rather than western North American *Pseudotsuga menziesii*. Axelrod (1964) described *Pseudotsuga longifolia* from the Middle Miocene Trapper Creek flora of southern Idaho, based on foliage and winged seeds. In his description, he noted that the features of this taxon were most similar to *P. forrestii* from southern China.

Today *Pseudotsuga* has a disjunct distribution with species in eastern Asia and western North America. Its fossil history is somewhat spotty, in part because of the difficulty in distinguishing its seeds and foliage from other Pinaceae. *Pseudotsuga* seeds, cones, and foliage were reported from the Eocene Thunder Mountain flora of Idaho (Axelrod 1998) and the Eocene Copper Basin flora of Nevada (Axelrod 1966).

Beck (1945b, 1948) referred to "countless logs and specimens of Douglas Fir from Vantage." He considered all structurally similar to one another and not different in any significant features from extant *Pseudotsuga* and the wood Gothan described as *Piceoxylon pseudotsuga*. Beck (1945b) proposed the combination *Pseudotsuga pseudotsugae* (Gothan) Beck.

Wood with characteristics of *Pseudotsuga* was recovered from the high-latitude Eocene fossil forests of the Geodetic Hills, Axel Heiberg Island (Obst *et al*. 1991). Torrey (1923) described *Pseudotsuga annulata* from the Middle Miocene Cape Blanco locality in western Oregon. He considered the Oregon wood to be identical to *Pityoxylon*

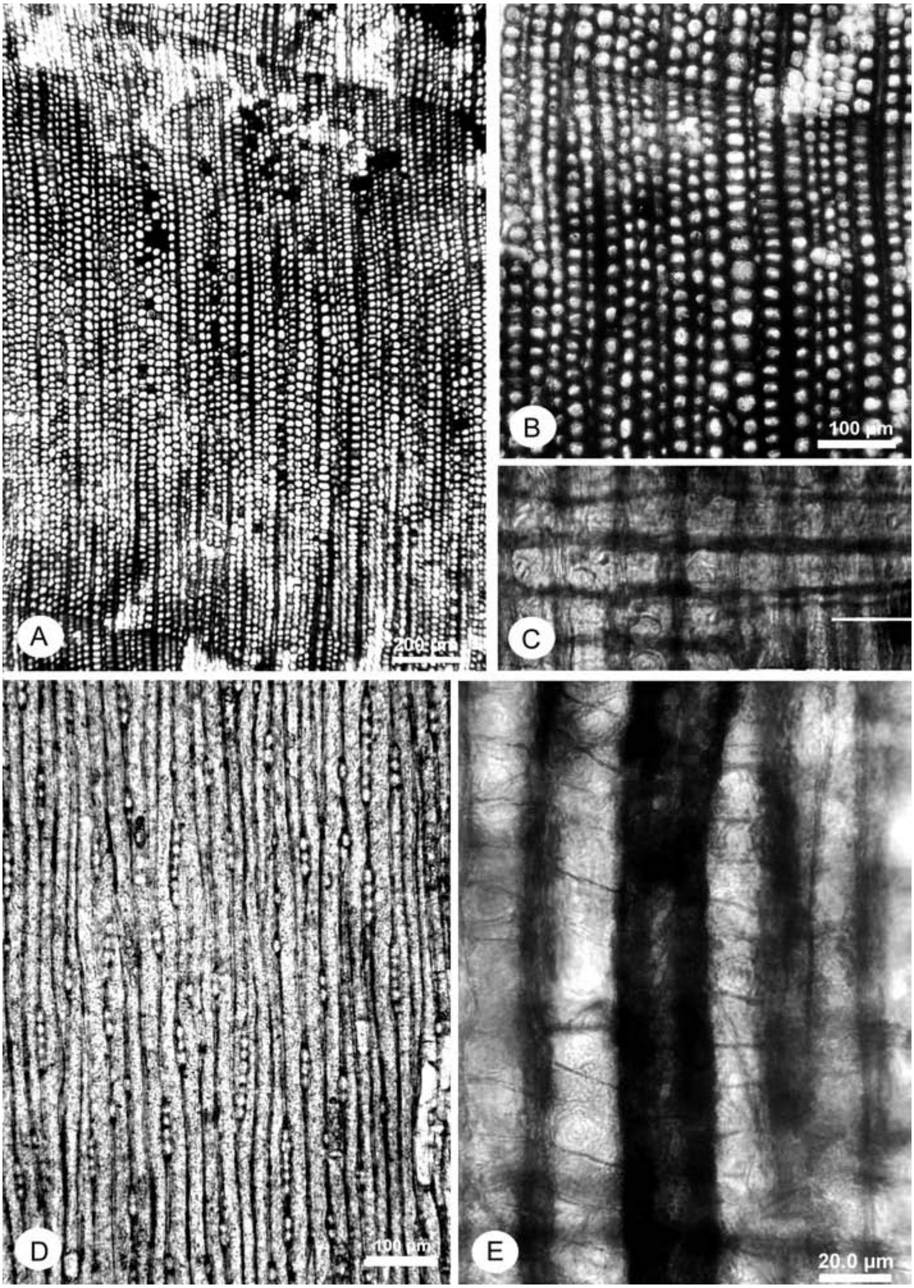

Figure 36. Taxaceae. *Taxus* sp. HU 56687. – A: Latewood not distinct, end of growth ring marked by a few rows of radially narrower tracheids. XS. – B: Growth ring boundary. XS. – C: Cupressoid cross-field pits. – D: Uniseriate rays, typically less than 10 cells high. TLS. – E: Widely spaced helical thickenings in longitudinal tracheids, solitary row of intertracheary pits. RLS. — Scale bar = 200 µm in A; 100 µm in B, D; 50 µm in C; 20 µm in E.

annulatum Platen from the Pliocene of California, and assigned it to the modern genus. *Pseudotsugoxylon pavlovskiense,* said to be closely similar to *Pseudotsuga menziesii* and *P. macrocarpa, is* reported from the Pliocene of the Russian Far East (Blokhina & Bondarenko 2004).

TAXACEAE

Taxus L.

Taxus sp. (Fig. 36)

Growth rings present, marked by only a few rows of radially narrower tracheids; mean tangential diameter 21 (4.3) µm. Longitudinal and radial resin canals absent. Widely spaced helical thickenings present, orientation near right angle to the long axis of the longitudinal tracheids. Intertracheary pitting opposite; average ray height 4 cells (1–12 cells high), smooth-walled ray parenchyma, end walls apparently lacking pitting. Cross-field pitting not observed with certainty, likely cupressoid. Axial parenchyma not observed.

Material: HU 56687 (Beck 853).

Comments: Woods of the Taxaceae have the combination of helical thickenings in longitudinal tracheids and absence of resin canals. The spirals do not look to be in pairs so according to Phillips (1948) and Nishida (1973) this wood resembles *Taxus,* not *Torreya* which has frequent pairing of the helical thickenings. Phillips noted that *Torreya* typically has smaller cross field pits than *Taxus*, but we were not able to measure cross-field pit size reliably. Separation of different species of *Taxus* by wood anatomy alone is not practical (Phillips 1948), and therefore we have elected to not assign a species name to this fossil wood.

Wheeler and Manchester (2002) described a possible taxaceous wood from the Middle Eocene Clarno Formation of central Oregon, but were unable to observe the features necessary to positively identify it. Manchester (1994) identified seeds of *Taxus* from the same formation. Recently, Kvacek and Rember (2007) described foliar remains of *Taxus schornii* based on preserved needles with cuticle from the Middle Miocene Clarkia deposit in Idaho.

GINKGOALES — GINKGOACEAE

Ginkgo L.

Ginkgo beckii Scott, Barghoorn & Prakash 1962 (Fig. 37)

Growth rings distinct. Longitudinal tracheids of two sizes, wider tracheids 40–70 µm, narrower tracheids 20–40 µm in tangential diameter, tending to be rounded to elliptical in outline and with intercellular spaces, intertracheary bordered pits on radial walls opposite, usually 2 rows. In longitudinal sections chains of enlarged axial parenchyma. Rays uniseriate, height 2–15 cells, average 6 cells, composed exclusively of ray parenchyma, end walls smooth.

Material: HU 56262 (holotype).

Comments: In their discussions of the affinities of this sample, Scott *et al*. (1962) noted that “In contrast to the regular, radial arrangement and predominantly equal

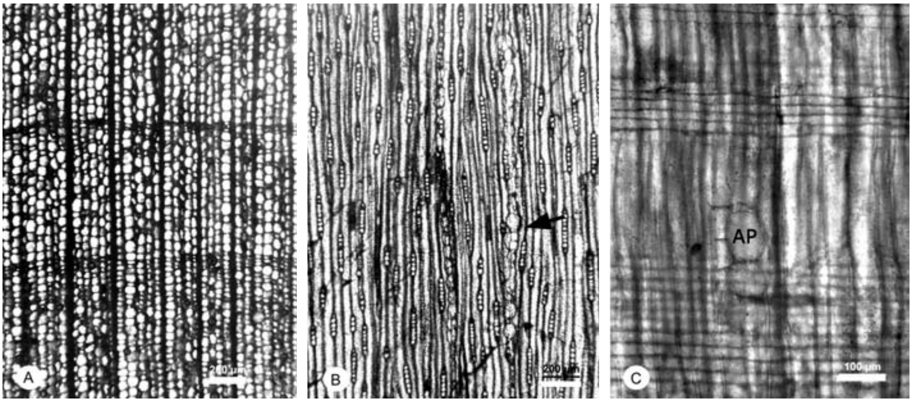

Figure 37. Ginkgoaceae. *Ginkgo beckii*. HU 56262. – A: Growth rings present, marked by a few rows of radially narrower tracheids. Variation in widths of longitudinal tracheids. XS. – B: Uniseriate rays, strands of inflated axial parenchyma (arrow, right of center of photo), TLS. – C: Rays composed of ray parenchyma. Inflated axial parenchyma (AP). RLS. — Scale bar = 200 µm in A, B; 100 µm in C.

size, except at growth ring transitions, of most coniferous tracheids, those of *Ginkgo* are highly variable in both size and linear arrangement. Tracheids of *Ginkgo* present a 'disordered' appearance." The inflated axial parenchyma strands are equivalent to the crystal (druse) containing cells of present-day *Ginkgo*. Apparently the calcium oxalate crystals did not preserve, but the inflated cells are left. Such cells do ***not*** occur in any conifer and among gymnosperms are unique to *Ginkgo*.

Leaf fossils assigned to *Ginkgo* are known in North America from the Middle Jurassic through the Miocene (Tralau 1967). Foliar remains are common in the Eocene Okanagan Highlands floras of northwestern North America (Dillhoff *et al*. 2005), and *Ginkgo bonesii* wood was described from the Middle Eocene Clarno Formation (Scott *et al*. 1962). While it has not yet been established exactly when *Ginkgo* went extinct in North America, there are no known occurrences of *Ginkgo* fossils in western North America after the Miocene (Tralau 1967). The *Ginkgo* woods in the Columbia River basalts and leaves in Middle Miocene compression floras of northwestern North America represent some of the last occurrences of the genus in the region.

ACKNOWLEDGMENTS

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