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Middle Eocene trees of the Clarno Petrified Forest, John Day Fossil Beds National Monument, Oregon

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One of the iconic fossils of the John Day Fossil Beds National Monument, Oregon, USA, is the Hancock Tree—a permineralized standing tree stump about 0.5 m in diameter and 2.5 m in height, embedded in a lahar of the Clarno Formation of middle Eocene age. We examined the wood anatomy of this stump, together with other permineralized woods and leaf impressions from the same stratigraphic level, to gain an understanding of the vegetation intercepted by the lahar. Wood of the Hancock Tree is characterized by narrow and numerous vessels, exclusively scalariform perforation plates, exclusively uniseriate rays, and diffuse axial parenchyma. These features and the type of vessel-ray parenchyma indicate affinities with the Hamamelidaceae, with closest similarity to the Exbucklandoideae, which is today native to Southeast and East Asia. The Hancock Tree is but one of at least 48 trees entombed in the same mudflow; 14 others have anatomy similar to the Hancock Tree; 20 have anatomy similar to *Platanoxylon haydenii* (Platanaceae), two resemble *Scottoxylon eocenicum* (probably in order Urticales). The latter two wood types occur in the nearby Clarno Nut Beds. Two others are distinct types of dicots, one with features seen in the Juglandaceae, the other of unknown affinities, and the rest are very poorly preserved and of unknown affinity. Leaf impressions in and immediately below the layer containing the trees include the extinct genera *Macginitiea* and *Platimeliphyllum* (Platanaceae), and *Trochodendroides* (Saxifragales).

Keywords: Eocene, Clarno Formation, paleobotany, fossil wood, Hamamelidaceae, Platanaceae, wood anatomy

INTRODUCTION

The Nut Beds locality in the Clarno Formation of north-central Oregon contains one of North America's most diverse and well-documented assemblages of middle Eocene plants, with fruits, seeds, leaves, and woods (Scott 1954, Manchester 1981, Manchester 1994, Wheeler and Manchester 2002). About two km east of the Nut Beds in Hancock Canyon, Wheeler County, and in what is today the John Day Fossil Beds National Monument, there is a petrified forest preserved in a volcanic lahar. Compared to the Nut Beds the quantity and diversity of the Hancock Canyon woods is low, but there are logs and standing trunks up to 60 cm diameter contrasting with the fragmentary eroded woods of the Nut Beds. One of the large standing trunks, visible along the US Park Service's Hancock Canyon trail, is named the Hancock Tree. This canyon, the tree, and the nearby field station operated by the Oregon Museum of Science and Industry (OMSI), are named for Alonzo W. "Lon" Hancock, a devoted amateur paleontologist who collected extensively in John Day Basin in the 1950s and 60s, especially in the Clarno Formation (Ashwill 1987).

Bestland et al. (1999) place the Hancock Canyon floras in the same subhorizon of the Clarno Formation as the Nut Beds and consider the two floras to be essentially coeval, although the beds cannot be physically traced from one to the other due to an intervening dacite dome. On the other hand, Hanson (1996, and pers. comm. 2014) maps the Hancock Canyon flora in a higher stratigraphic level (his unit C), considered to have been deposited subsequent to the folding, faulting, intrusion and erosion of the strata that include the Nut Beds (his unit B). Whereas the Hancock Canyon lahar contains large tuffaceous clasts up to 30 cm in diameter, clasts in the Nut Beds deposits generally do not exceed five cm. Although woods of the Nut Beds are highly abraded and evidently allochthonous (i.e., transported), those of Hancock Canyon are logs and stumps with minimal abrasion and may represent more or less *in situ* forest intercepted by a lahar.

The botanical affinities of the Hancock Canyon trees have not been examined in detail. Here we provide an overview of the wood anatomical types occurring in the Hancock Canyon area, and document associated leaf impressions. This information will further our understanding of the diversity of woody plants in the Eocene of northwestern North America, as well as aid Monument personnel in reconstructing the paleoenvironment of the John Day basin for their public exhibits.

MATERIALS AND METHODS

Collections

Samples were obtained during the summers of 1970 and 1971, prior to the collecting restrictions imposed when this area became part of the John Day Fossil Beds National Monument. Specimens, slides, and detailed locality information are archived at the Florida Museum of Natural History. Although the woods occur in a single horizon, they are exposed in different outcrops within a 0.2 km radius of the Hancock Tree (N44.92884°, W120.415686°), with the following locality numbers: UF48 (outcrop B); UF49 (outcrop C); UF68 (outcrop D), UF69 (outcrop E). Samples are cataloged with the 5-digit specimen number of the Florida Museum of Natural History at University of Florida (UF) preceded by the UF locality number. Original field numbers (e.g., C1, indicating first sample collected from outcrop C) are also indicated. Samples for thin sections were not taken from all of the Hancock Canyon logs, and these logs are referred to by their field number only.

Sample preparation

A diamond lapidary saw was used to cut thick sections (wafers) of transverse, tangential, and radial surfaces. One side of the wafer was smoothed to remove saw marks, and then affixed to a glass side using 24-hour transparent epoxy. The sections were then ground to an initial thickness of about 50 µm, either by hand on a lapidary grinding wheel, or with the aid of a Buehler petrographic thin section grinding machine. Further fine grinding was done by hand, using a glass plate and a slurry of 400 grade silicon carbide grit, until they were thin enough (ca 30 µm) to allow seeing anatomical details with transmitted light microscopy. Cover slips were mounted using Canada Balsam to improve clarity for light microscopy.

Descriptions

Our descriptions of the woods generally conform to the IAWA Hardwood List (IAWA Committee 1989), with vessel diameter and ray height averages based on 25 measurements; rays per mm based on 10 counts; vessels per mm^2 from counts of vessels in 10 fields of view. Relationships to extant groups were investigated using the InsideWood web site (InsideWood 2004-onwards; Wheeler 2011) and references found on the Kew Micromorphology Bibliography web site. Diameters (diam) of the logs are presented based on measurements in the field.

Determining affinities

The identification procedure was begun with searches of the InsideWood web site (Wheeler 2011; InsideWood 2004-onwards) and included consultation of descriptions in “Anatomy of the Dicotyledons” (Metcalfe and Chalk 1950, Metcalfe 1987, Cutler and Gregory 1998). Subsequently, comparisons were made to extant wood samples in the Bailey-Wetmore Laboratory of Plant Anatomy and Morphology of Harvard University, Universiteit Leiden Branch of the Nationaal Herbarium Nederlands, University of Utrecht, Jodrell Laboratory of the Royal Botanic Gardens, and the David A. Kribs (NC State University) wood collections and illustrations and descriptions in standard references (Ilic 1991; and as listed in Gregory 1980, 1994) and the on-line Kew Micromorphology Database.

SYSTEMATIC PALEONTOLOGY

The Hancock Tree

FAMILY: HAMAMELIDACEAE R. Br. 1818

SUBFAMILY: EXBUCKLANDIOIDEAE Harms 1930

cf. *Hamamelidoxylon uniseriatum* Wheeler and Manchester 2002

(Figs. 1–6)

Description—The growth rings are distinct and marked by radially flattened fibers, with vessels at the end of a growth ring being narrower than those in the earlywood of the succeeding growth ring (Figs. 1, 2). Vessels are predominantly solitary, vessel outline is oval to angular (Figs. 1, 2), with a mean tangential diameter of 55 µm (sd=-11; the range is 31–80 µm), there are 50–82 vessels per mm^2; the vessel elements are 874–1273 µm long (average 1062, n=12). Perforation plates are exclusively scalariform, with 20–36 bars per perforation plate (Fig. 3), the intervessel pits are rare because the vessels are predominantly solitary, but some scalariform pits have been observed. Vessel-ray parenchyma pits are elongate (scalariform) and apparently with reduced borders (Fig. 5). Fibers are non-septate, with walls medium-thick to thick. Axial parenchyma is diffuse, with strands of 5–8 cells, mostly 8 cells per strand. Rays are exclusively uniseriate (Fig. 4) and consist predominantly of procumbent cells 24–45 cells high (Fig. 6), with an average of 22 cells (sd=11). There are 12–17 rays per mm. Crystals were not observed. Storied structure is absent.

Specimen number: UF69-47252/E13, upright stump approximately 50 cm diameter at base.

Comments—Five of the sectioned Hancock Canyon woods have anatomy similar to the Hancock Tree. They have similar qualitative features and overlap in quantitative vessel features (Table 1). Eight other logs were not sectioned, but appeared similar macroscopically, having many narrow vessels and narrow rays; these are UF49-47372/C2 (diam=34 cm), UF49-47374/C4 (diam=18 cm), UF49-47376/C6 (diam=13 cm), UF49-47379/C9 (diam=46 cm), UF49-473781/C11 (diam=7 cm), UF49-045385/C15 (diam=12 cm), UF48-47351/B1 (diam=11 cm), UF69-47253/E14 (diam=35 cm). Stem diameters for this wood type range from 7 to 50 cm.

Affinities—Members of the Hamamelidaceae (*Chunia* H.T. Chang and *Exbucklandia* R.W. Br., subfamily Exbucklandoideae*; Fothergilla* L. and *Hamamelis* L., subfamily Hamamelidoideae Reinsch; Pentaphylacaceae Engler (*Cleyera*

► **Figures 1–6**. The Hancock Tree. UF69-47252. **1.** Distinct growth rings, vessels mostly solitary, XS, scale bar = 200 µm. **2.** Growth ring boundary, fiber walls of medium thickness, diffuse axial parenchyma, XS, scale bar = 100 µm. **3.** Scalariform perforation with many bars, viewed from the side, TLS, scale bar = 20 µm. **4.** Exclusively uniseriate rays, vessel elements with scalariform perforation plates (PP), TLS, scale bar = 100 µm. **5.** Vessel-ray parenchyma pits horizontally elongated (arrows), RLS, scale bar = 20 µm. **6.** Ray composed mostly of procumbent cells, RLS, scale bar = 50 µm. **XS**=cross section; **RLS**=radial longitudinal section; **TLS**=tangential longitudinal section.

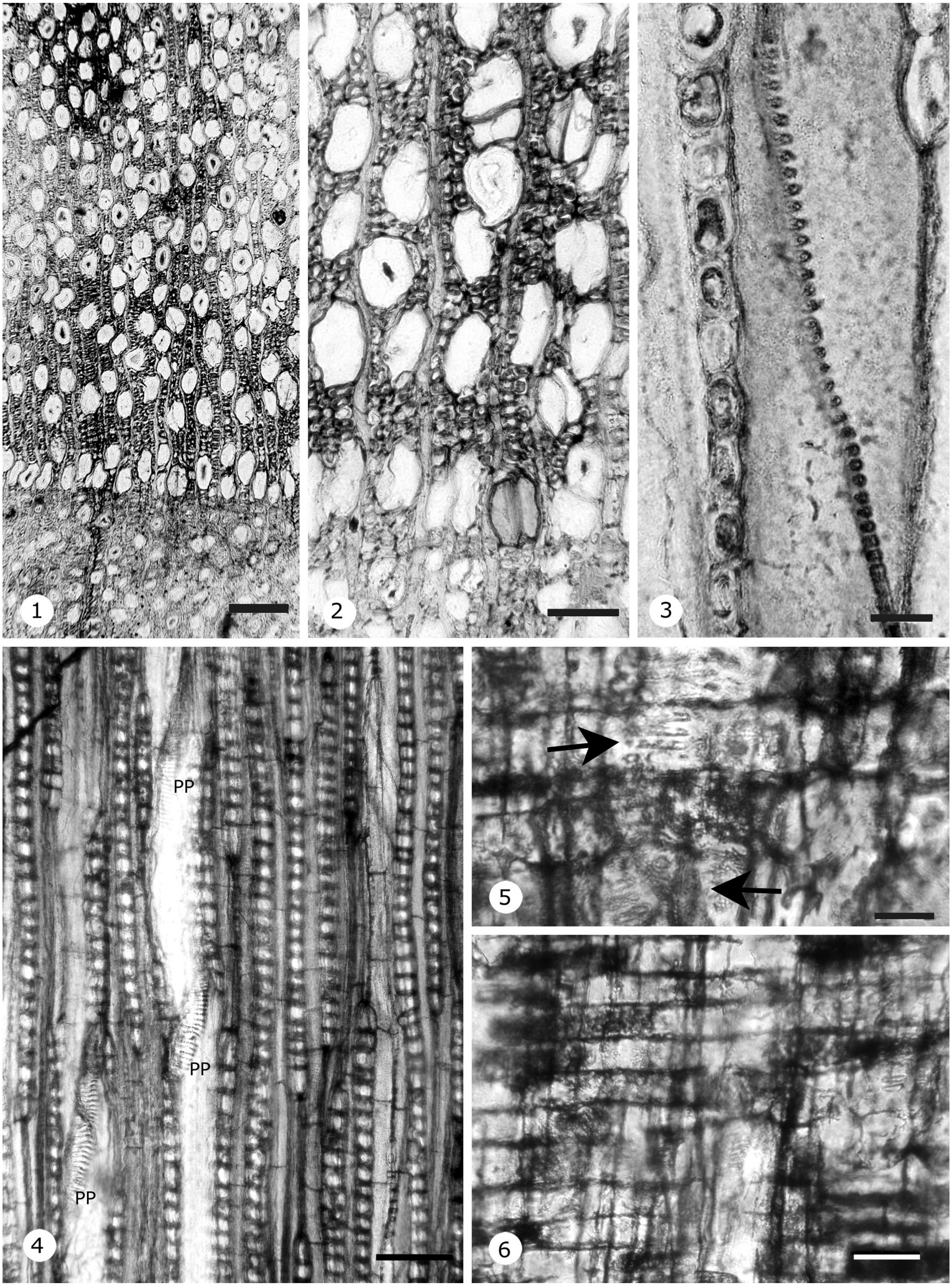
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Table 1. Characteristics of the Hancock Canyon Hamamelidaceae woods. MTD=mean tangential diameter of the vessels, standard deviation in parenthesis. V/MM2=mean number of vessels per square mm.

Specimen No.	Field No.	Log Diam	MTD µm	V/MM2
UF49-47371	C1	31 cm	55 (9) µm	67
UF49-47389	C19	> 20 cm	51 (9) µµ	85
UF68-47260	D6	40 cm	51 (8) µm	71
UF68-47261	D7	45 cm	57 (10) µm	91
UF69-47246	E1	45 cm	40 (7) µm	107

Thunb.), and Theaceae D. Don. (*Gordonia* Ellis.) are the only extant plants with the combination of predominantly solitary vessels that are narrow and very numerous, exclusively scalariform perforation plates, scalariform intervessel pitting, diffuse axial parenchyma, and exclusively uniseriate rays. The type of vessel-ray parenchyma pitting is a useful feature for distinguishing between these woods. *Cleyera* differs from the Hancock tree because its vessel-ray parenchyma pits are small and not elongated, while *Gordonia* differs as the vessel-ray parenchyma pits are consistently narrow and quite elongated. Thus, this wood is assigned to the Hamamelidaceae. The number of bars per perforation plate of this fossil (20–36) is consistent with extant Exbucklandoideae (Wheeler et al. 2010), a subfamily of large trees, whereas the other subfamilies of Hamamelidaceae are mostly shrubs to small trees. Although no leaves or fruits of *Exbucklandia* have been found in the Clarno Formation, infructescences of this distinctive genus, now endemic to southeast Asia, have been recognized previously from the Oligocene and Miocene of the Pacific Northwest (Manchester 1999) and fruits and seeds and inflorescences of the Hamamelidoideae are known from the Nut Beds (Manchester 1994). The Hancock Tree is similar to *Hamamelidoxylon uniseriatum* from the nearby Clarno Nut Beds (Wheeler and Manchester 2002). There are some differences in quantitative features; vessel frequency is somewhat higher in the Nut Beds wood (72–133 per mm^2) than in the Hancock Tree. Axial parenchyma is more abundant in the Hancock Tree. These differences likely are related to the larger diameter of the Hancock Tree.

Additional wood types

Some of Hancock Canyon trees are similar to two other species that occur in the Clarno Nut Beds: *Platanoxylon haydenii* (Felix) Süss & Müller-Stoll (Platanaceae T. Lestibudois) and *Scottoxylon eocenicum* Wheeler & Manchester (probably order Urticales Juss.). Unfortunately, preservation of the Hancock Canyon woods is not as good as the Nut Beds woods. The combination of features that indicates these woods are similar to *Platanoxylon haydenii* and *Scottoxylon eocenicum* are given in the descriptions below. Two additional wood types, each represented by a single sample, can be distinguished but their affinities cannot be determined because some of the necessary diagnostic features cannot be clearly seen due to poor preservation.

FAMILY: PLATANACEAE T. Lestibudois 1826

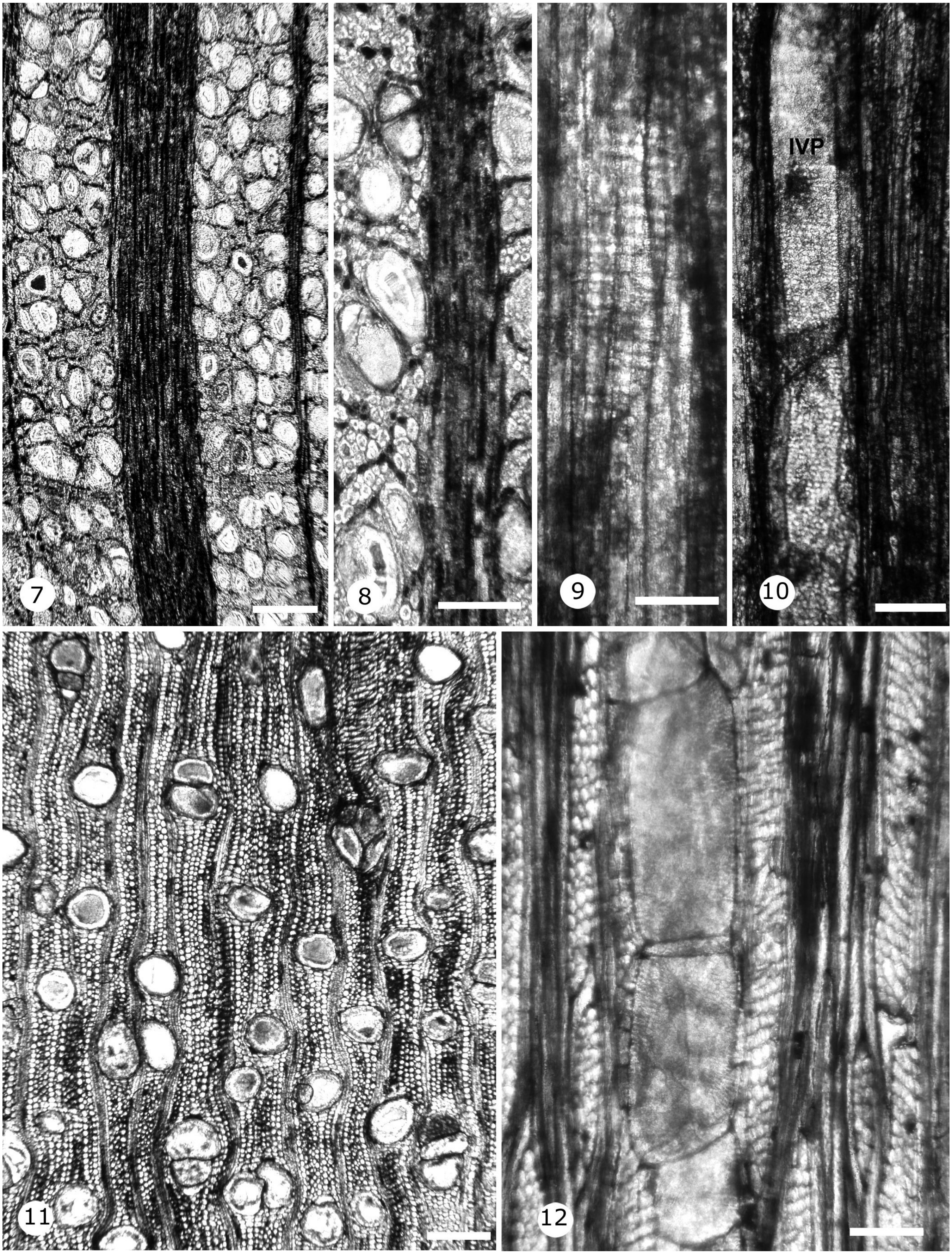
GENUS: *PLATANOXYLON* Andreansky Emend Süss & Müller-Stoll 1977

Platanoxylon haydenii (Felix) Süss & Müller-Stoll 1977
(Figs. 7–10)

Description—Growth rings are distinct, marked by radially narrow fibers, with differences in vessel diameter between the last-formed latewood and subsequent earlywood, and slightly noded rays (Fig. 7). Diffuse porous wood with vessels solitary and in small multiples (mostly tangential or oblique) (Fig. 7), the mean tangential diameter is 69 µm (sd=12) and there are 35 vessels per mm^2. Although the vessels are crowded, when counted using low magnification in an area that includes the wide rays, the values for vessels per mm^2 are not high. Vessels with scalariform perforation plates (Fig. 9), but poor preservation of the samples allowed counting bars in only a few perforation plates, 12–23 bars. Intervessel pits opposite (Fig. 10), pits to parenchyma not observed, and the only vessel element length obtained measured 550 µm. Fibers are non-septate, thick walled, and pits were not observed. Axial parenchyma is diffuse-in-aggregate occurring as short interrupted uniseriate lines (Fig. 8). Rays are predominantly multiseriate, up to 22 cells wide, up to more than 4.8 mm high (avg. 2.7 mm high) and composed predominantly of procumbent cells. Fewer than 4 rays per mm. Storied structure is absent and crystals were not observed.

Comments—UF49-47388 [C18] was the best preserved of the *Platanoxylon haydenii* samples and the quantitative features in the description above are based on it. There are 15 other Hancock Canyon trees with the wide rays, diffuse-in-aggregates axial parenchyma and crowded vessels with a tendency to tangential grouping typical of *Platanoxylon*: UF49-47375/C5 (diam=10 cm); UF49-47384/C14 (diam=18 cm); UF49-47387/C17 (diam=12 cm); UF48-47352/B2 (diam=35 cm); UF48-47354/B4 (diam=32 cm); UF68-47256/D1 (diam=40 cm); UF68-

► **Figures 7–12.** Additional Hancock Canyon woods. **Figs. 7–10.** *Platanoxylon haydenii,* UF69-47388. **7.** Diffuse porous with distinct growth ring boundaries, marked by radially narrow fibers, vessels solitary and in small groups, XS, scale bar = 200 µm. **8**. Diffuse-in-aggregates parenchyma, thick-walled fibers, XS, scale bar = 100 µm. **9**. Scalariform perforation plate, RLS, scale bar = 50 µm. **10**. Opposite intervessel pits (IVP). **11, 12.** *Scottoxylon eocenicum.* UF69-47380. **11**. Diffuse porous wood, vessels solitary and occasionally in radial multiples of two, solitary vessels rounded in outline, XS, scale bar = 200 µm. **12**. Multiseriate rays to 5-seriate, simple perforation plates, and crowded alternate intervessel pits, TLS, scale bar = 100 µm.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47262/D8 (diam=12 cm); D9 (diam=9 cm); UF68-47264/D11 (diam=12 cm;) UF69-47247/E2 (diam=15 cm); E7 (diam=10 cm); E8 (diam=34 cm); E9 (diam=13 cm); UF69-47249 E10 (diam=15 cm); UF69-47250/E11 (diam=30 cm). Diameters of the Hancock Canyon *Platanoxylon* range from 9 to 40 cm. These apparently are additional occurrences of wood of the Clarno Plane Tree (Manchester 1986), one of the few whole plants known from the Eocene.

ORDER: URTICALES Juss. 1820

GENUS: SCOTTOXYLON Wheeler and Manchester 2002

Scottoxylon eocenicum Wheeler and Manchester 2002

(Figs. 11, 12)

Description—Diffuse porous wood with vessels solitary and in short radial multiples, vessels rounded to oval in outline (Fig. 11), with mean tangential diameters equal to140 µm (sd=22) in UF49-47380 [C10] and 136 µm (sd=22) in UF49-47386 [C16]. There are 9 vessels per mm² in both samples. Perforation plates are simple, the intervessel pits are crowded alternate, angular in outline with circular to slightly oval apertures (Fig. 12), and measure 8–11 µm across. Vessel-ray parenchyma pits were not observed, but vessel-axial parenchyma pits have reduced borders and are horizontally elongate, and so vessel-ray parenchyma pits should be similar. Helical thickenings on vessel walls were not observed. The mean vessel element length is 305 µm (sd=51) in UF-49-47380 [C10] and 402 (sd=97) in UF49-47386 [C16]. Fibers are thin-medium thick walled, pits and septae were not observed. Axial parenchyma is scanty paratracheal to vasicentric. Rays are mostly 3-5 seriate with uniseriate rays rare (Fig. 12). The mean total height of multiseriate rays is 482 µm (sd =155) in UF49-47380 [C10] and 758 µm (sd=259) in UF49-47386 [C16]. The rays are heterocellular with procumbent body cells and 1 (-2) marginal rows of square to upright cells. Storied structure is absent and crystals were not observed.

Specimen numbers: UF49-47380 [C10], UF49-47386 [C16].

Comments—The rays of UF49-47380 [C10] are shorter than rays of UF49-47386 [C16], but otherwise the samples are similar and we consider them to belong to the same taxon. This difference in ray size likely is related to the differences in sizes of the source plant, UF49-47380 [C10] having a diameter of 15 cm and UF49-47386 [C16] having a diameter of 25 cm. *Scottoxylon eocenicum* was one of the most common woods in the Nut Beds assemblage. Its general features coincide with those of the Moraceae and Cannabaceae, both families in the Urticales.

FAMILY JUGLANDACEAE Perleb 1818

(Figs. 13–15)

Description—Growth rings are distinct and marked by radially flattened cells at the growth ring boundary. Wood is semi-ring porous with vessels solitary and in radial multiples of 2–3, with a tendency toward a diagonal arrangement of the vessels (Fig. 13). Mean tangential diameter of the earlywood vessels is 121 µm (sd = 15). Vessel elements have simple perforation plates, crowded alternate intervessel pits, pits are angular in outline (Fig. 14), and measure approximately 7.5–10 µm across. Vessel-ray parenchyma pits were not observed due to poor preservation. The only vessel element length measured was 420 µm. Vessel elements with thin-walled, widely spaced tyloses. Fibers medium-thick walled, neither pits nor septae observed, but preservation is poor. Possible axial parenchyma occurs in narrow apotracheal bands. In radial section strands of cells with colored contents are observed and interpreted as apotracheal axial parenchyma. Rays are 1–4 seriate, mostly 2–3 seriate (Fig. 15), multiseriate ray height averages 371 µm (sd = 81), with body of the ray composed of procumbent cells, there appears to be one row of square to upright marginal cells. There are 5-8 rays per mm. In a few rays some slightly enlarged cells occur, possibly crystalliferous.

Specimen number: UF69-47248 [E6].

Affinities—The combination of semi-ring porosity, vessels solitary and in radial multiples with a tendency to a diagonal arrangement, simple perforation plates, crowded medium-large alternate intervessel pits, thin-walled tyloses, narrow rays, and narrow apotracheal bands occurs in the Juglandaceae. Two types of Juglandaceae wood, *Clarnoxylon blanchardii* Manchester & Wheeler and *Engelhardioxylon nutbedensis* Manchester (1983) occur in the Nut Beds. Idioblasts were not observed in this Hancock Canyon wood so it differs from *Clarnoxylon* Manchester & Wheeler, which has commonly occurring idioblasts. The preservation of this wood is poor so it cannot be determined if occasional scalariform perforation plates are present, which is a characteristic of *Engelhardioxylon* Manchester. Five types of juglandaceous fruits occur in the Clarno Formation (Manchester 1994).

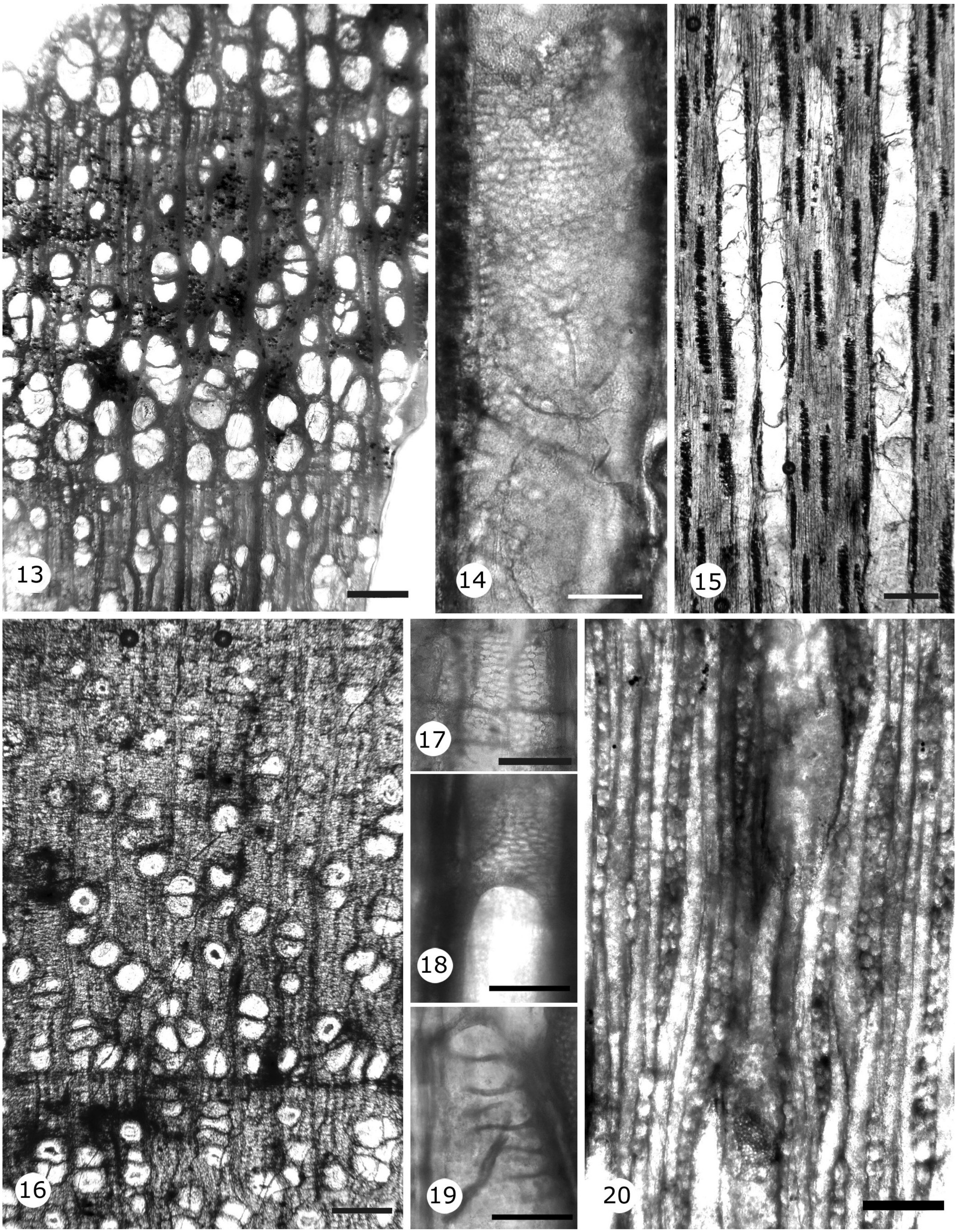
Incertae Sedis

?ARALIACEAE Juss. 1789

(Figs. 16–20)

Description—Growth rings are distinct, marked by radially flattened cells at the growth ring boundary and show slight differences in vessel diameters in the last-formed latewood and

► **Figures 13–20. 13–15.** Hancock Canyon Woods. **13, 14.** Probable Juglandaceae, UF69-47248. **13**. Semi-ring porous wood with vessels solitary and in radial multiples, vessels tending to a diagonal arrangement, XS, scale bar = 200 µm. **14**. Crowded alternate intervessel pits, TLS, scale bar = 50 µm. **15.** Vessels with thin-walled tyloses, rays mostly 3-seriate, TLS, scale bar = 200 µm. **16–20.** *Incertae Sedis.* Araliaceae? UF49-47378. **16.** Distinct growth ring boundary, vessels solitary and in radial multiples of 2-4, solitary vessels rounded in outline, XS, scale bar = 200 µm. **17**. Vessel-ray parenchyma pits, RLS, scale bar = 50 µm. **18**. Simple perforation plates and crowded alternate intervessel pits, RLS, scale bar = 50 µm. **19**. Scalariform perforation plate, RLS, scale bar=50 µm. **20.** Rays 1-2 seriate, TLS, scale bar = 100 µm.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earlywood of the next growth ring. Wood is diffuse porous to slightly semi-ring porous with vessels solitary and in radial multiples of 2 to 4, mostly 2, with a tendency to a diagonal vessel arrangement. The solitary vessels are rounded in outline (Fig. 16). The mean tangential diameter of earlywood vessels is 125 µm (sd=22) and there are 19–30 vessels per mm^2 in the latewood. Perforation plates are simple (Fig. 18) and scalariform with fewer than 10 bars or irregular with branching (Fig. 19). Crowded alternate intervessel pits, angular in outline, and approximately 5 µm across (Fig. 18). Vessel-ray parenchyma pits are similar in size to the intervessel pits, and apparently have reduced borders (Fig. 17). Vessel element lengths range from 620–920 µm (only 4 measured). Fibers are medium thick-walled and neither pits nor septae were observed, but preservation is poor. The presence and distribution of axial parenchyma is not obvious, but appears to be rare. Rays 1-2 seriate, heights of 2-seriate rays variable (Fig. 20), averaging 725 µm (sd=340), with a range of 316–1639 µm, likely intermixed procumbent and square cells, but difficult to determine because of poor preservation. There are 6–10 rays per mm.

Specimen number: UF49-47378 [C8] (diam = 32 cm).

Comments—The combination of distinct growth rings, vessels not exclusively solitary or tangentially arranged, presence of both simple and scalariform perforation plates, alternate intervessel pits that are < 10 µm across, absence of confluent and wide bands of axial parenchyma, and presence of 1–3 seriate rays occurs in species of Araliaceae, Cunoniaceae R. Br., Juglandaceae, Lauraceae Juss., Myristicaceae R. Br., and Salicaceae Mirbel. (*sensu* APG III 2009). The occurrence of rays more than one mm high argues against affinities with the Juglandaceae and Lauraceae. The combination of a tendency to diagonal vessel arrangement, semi-ring porosity and the presence of some irregular perforation plates is more consistent with Araliaceae than with Cunoniaceae and Myristicaceae (Metcalfe and Chalk 1950; InsideWood 2004-onwards).

Associated leaf and fruit impressions

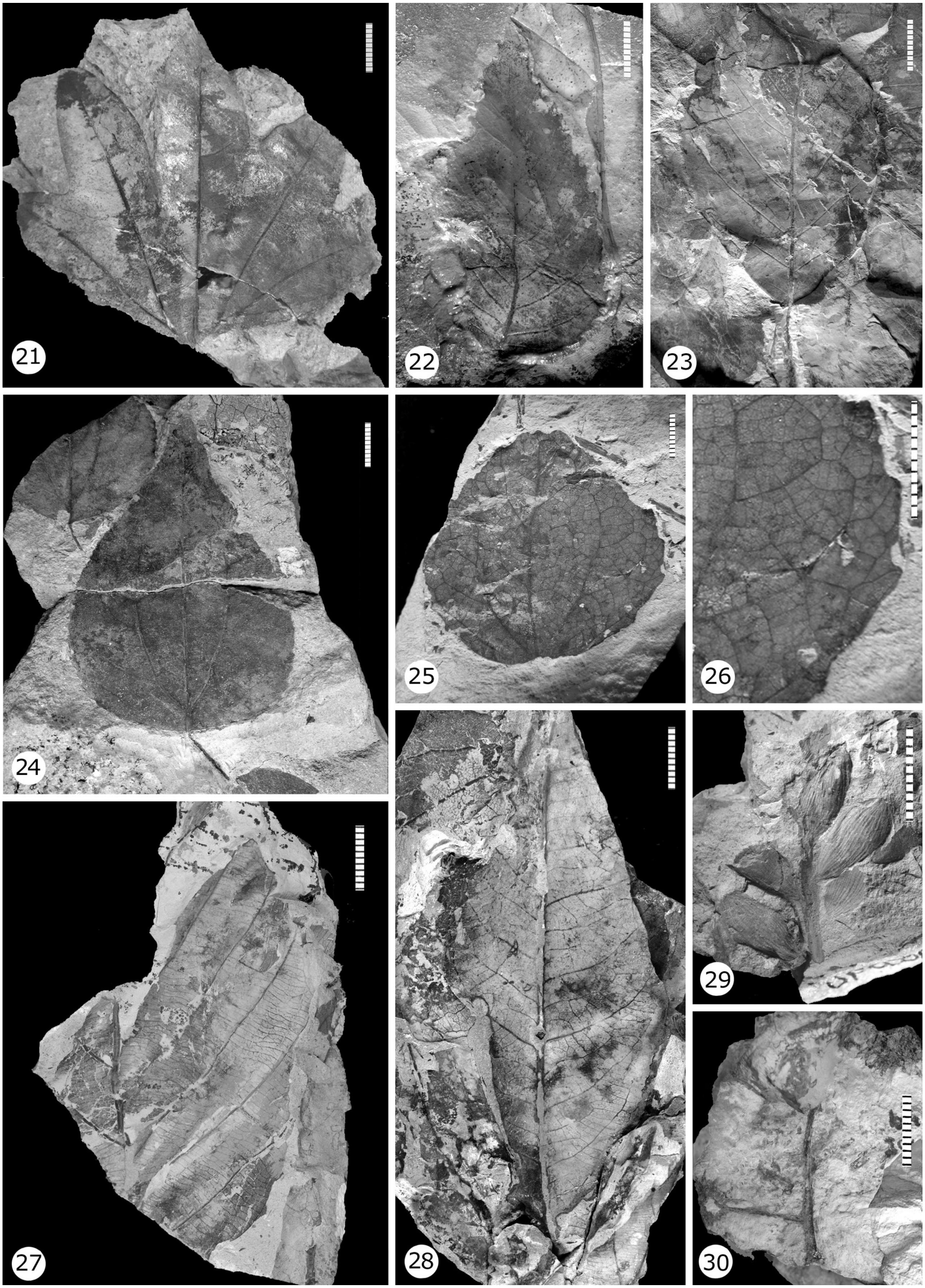
A ledge-forming siltstone about 15 to 20 cm thick at the base of the lahar in which the Hancock Tree and other stumps are embedded contains moderately well preserved leaf impressions that we consider to be approximately coeval with the stumps and logs, possibly representing the forest litter layer that was inundated by the lahar. Although specimens are difficult to excavate due to the overlying lahar, several specimens were obtained during the 1970s that bring additional insight to the Hancock Canyon fossil flora. The most common remains are *Macginitiea* Wolfe & Wehr (Fig. 21), *Platimeliphyllum* N. Maslova (Figs. 22, 23), and *Trochodendroides* Berry (Figs. 24–26). The first two are extinct members of the Platanaceae, while the latter is considered to be an extinct member of the Saxifragales with similarities to *Cercidiphyllum* Sieb. & Zucc. The same layer includes fruiting remains of *Macginicarpa* Manchester (Fig. 30, likely corresponding to *Macginitiea*; Manchester 1986) and *Nyssidium* Heer (Fig. 29, likely the corresponding to *Trochodendroides* (Crane and Stockey 1985). *Trochodendroides* leaves have a similar pattern of venation to those of the extinct leaf type known as *Zizyphoides* Seward & Conway (Crane 1984), but the serrations are closer and more regularly spaced in the former. *Zizyphoides* and the commonly associated extinct fruit type *Nordenskioeldia* J. Sahlberg, are not known from the Clarno Formation, although both are found in the Eocene of Republic Washington (Pigg et al 2001). Although fossil leaves occur elsewhere in Hancock Canyon, the specimens illustrated here were all collected from the same side canyon as the Hancock Tree (UF loc. 69). Other fragmentary leaf types encountered include probable Fagaceae (Fig. 27) and Theaceae (Fig. 28).

DISCUSSION

The correspondence of leaf types with wood types remains somewhat speculative, as we have no instances of physical attachment. However, the occurrence of both woods and leaves of Platanaceae supports the likelihood that the same extinct genus may be represented by *Macginitiea* and *Platanoxylon*, both of which also occur in the Nut Beds and at Yellowstone. The botanical affinities of the *Trochodendroides*-*Nyssidium* plant (closely related and possibly equivalent to *Joffrea* Crane & Stockey at the Paleocene locality of Joffre Bridge, Alberta, Canada; Crane and Stockey 1985) have been considered likely to belong with Cercidiphyllaceae Sieb. & Zucc., but none of the associated woods correspond to modern *Cercidiphyllum*. Wood anatomy of the present-day woody Saxifragales overlap in their features, and it is possible [probable] that this wood with features of the Exbucklandoideae represents the trunk of the *Trochodendroides*-*Nyssidium* plant.

The low diversity and the sizes of the Hancock Canyon trees argue against them representing an old growth, well-established forest. The average diameters of the Exbucklandoideae woods (29 cm, n=15) and *Platanoxylon* (20 cm, n=15) fall in the category of small tree and sapling respectively (http://ecoplexity.org/node/236). Some species of *Exbucklandia* are pioneers at disturbed sites (Whitmore 1973,

► **Figures 21–30.** Fossil leaves and fruits from tuff bed immediately below the silicified wood horizon at outcrop E (UF loc.69). **21**. Platanaceae: *Macginitiea angustiloba*. UF69-56182. **22**. Platanaceae: *Platimeliphyllum* sp. UF69-56194. **23**. *Platimeliphyllum* sp. UF69-56181, **24**. Cercidiphyllaceae: *Trochodendroides* sp. with finely serrate margin, UF 69-56193. **25, 26.** *Trochodendroides* sp. with glandular-toothed margin, UF 69-56199. **27**. Probable fagaceous leaf with craspedodromous secondary veins closely spaced percurrent tertiary veins and spinose teeth. UF69-56194. **28**. Probable theaceous leaf with semicraspedodromous secondary veins, intersecondary veins and finely serrate margin, UF56193. **29**. Cercidiphyllaceae: *Nyssidium* fruits UF 69-56187. **30**. Platanaceae: Globose infructescences of *Macginicarpa*, indicated by arrows; lower left head is attached on peduncle UF69-56192. Scale bars = 1 cm.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Ohsawa 1991) and the Hancock Canyon flora may represent such a site. In contrast, average trunk diameters of the 8 wood types of the middle Miocene Vantage fossil wood flora (Wheeler and Dillhoff 2009) ranged from 20 (sapling) to 84 (giant tree) cm, with averages of four types being those of medium-sized trees and two types of large trees (Wheeler and Dillhoff 2009).

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