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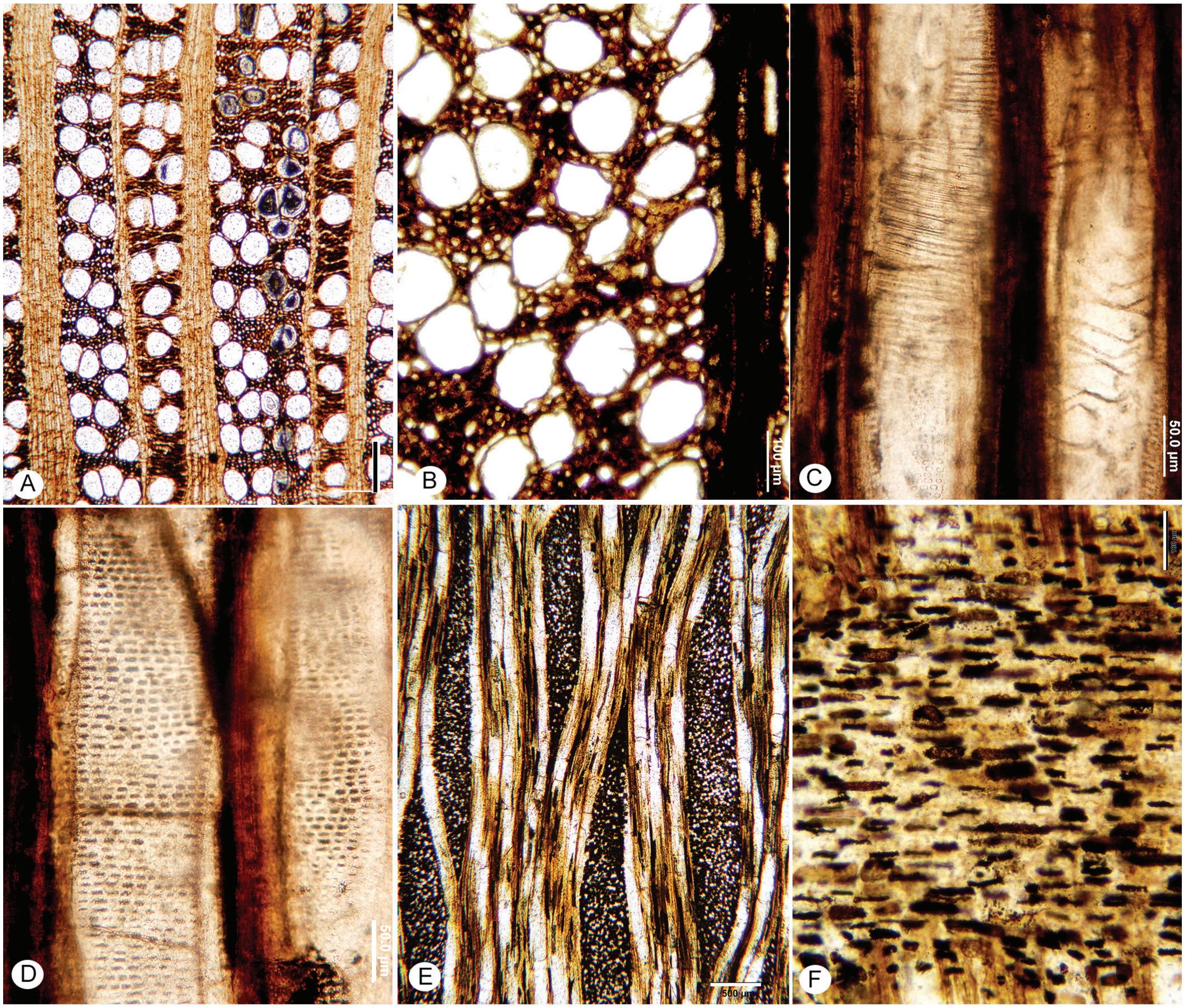

Elisabeth A. WHEELER, Steven R. MANCHESTER, & Pieter BAAS (2023). A late Eocene wood assemblage from the Crooked River Basin, Oregon, USA.

Cover: Sectional views of the wood of *Platanoxylon haydenii* from the late Eocene Crooked River Basin in Oregon, USA. See Figure 6 for the detailed descriptions.

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A late Eocene wood assemblage from the Crooked River Basin, Oregon, USA

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Well-preserved silicified woods are common in the Pacific Northwest, USA. Localities near the town of Post, Oregon, provide insights into the late Eocene vegetation and climate ca. 36 million years ago and data for comparing both older and younger wood floras of the region. New investigations of the late Eocene Dietz Hill locality (UF 278) revealed woods belonging to the families Pinaceae (*Keteleeria farjonii* sp. nov.), Cupressaceae (*Taxodioxylon* sp.), Magnoliaceae (*Magnolia hansnooteboomii* sp. nov.), Lauraceae (*Laurinoxylon* sp. A and B), Platanaceae (*Platanoxylon haydenii* (Felix) Süss and Müller-Stoll, 1977), Fabaceae (cf. *Styphonolobium* sp.), Fagaceae (*Fagus dodgei* Wheeler and Manchester, 2021*, Quercus* sp., Red Oak type), Juglandaceae (*Carya leroyii* sp. nov.), Ulmaceae (*Ulmus woodii* Wheeler and Manchester, 2007), Sapindaceae (*Aesculus constabularisii* sp. nov., *Klaassenoxylon wilkinsonii* gen. et sp. nov.), and Araliaceae (*Plerandreoxylon oskolskii* sp. nov.). Some woods could be assigned to order, but not to family, Rosales (*Urticaleoxylon stevensii* gen. et sp. nov., and two unnamed woods with features of Cannabaceae and Moraceae), Sapindales (cf. *Fagaroxylon* sp.). There also is a *Hamamelidoxylon* sp., which has features found in both the Theaceae and Hamamelidaceae. These woods, together with taxa identified from co-occurring silicified fruits and seeds represent a diverse assemblage of warm temperate to subtropical woody plants, some with East Asian affinities. Comparing the wood functional traits of the Dietz Hill assemblage to the older Clarno Nut Beds (mid-Eocene) woods and to the younger woods associated with Oligocene Bridge Creek flora attests to increased seasonality and cooling climate.

Keywords: fossil wood, late Eocene, Sapindaceae, Urticalean rosids, secondary xylem

INTRODUCTION

The John Day and Crooked River Basins in Oregon, USA, are notable for having localities where silicified woods, fruits, and seeds co-occur as well as sites with abundant leaf impressions. Different plant parts differ in their likelihood of entering the fossil record because of factors such as variation in resistance to decay, ease of transport to sites of deposition, and abundance in the original vegetation. Thus, the most complete understanding of ancient vegetation comes from studying more than one type of plant remain (see discussion in Poole 2000). The middle Eocene Nut Beds locality in the John Day Basin near the town of Clarno has exceptionally diverse wood and fruit/seed assemblages (Manchester 1994, Wheeler and Manchester 2002). Some taxa are represented by both woods and reproductive structures (e.g., Juglandaceae DC ex Perleb, 1818; *Magnolia* Plum ex L., 1753*;* Vitaceae Juss., 1789; and others as only one or the other (e.g., Malvaceae Juss., 1789, as wood; Burseraceae Kunth, 1824, and Sapotaceae Juss., 1789, as fruits/seeds).

The objective of this paper is to describe well preserved petrified woods from the late Eocene Dietz Hill locality (UF 278) in the Crooked River Basin near the town of Post, Oregon. Previously, we described woods from the nearby Post Hammer locality UF 279 (Wheeler et al. 2006, Wheeler and Manchester 2021). These woods, together with impressions of leaves, fruits, and flowers from the contemporaneous and nearby Teater Road site (e.g., Manchester 1992, McClain and Manchester 2001, Corbett and Manchester 2004, Manchester and Lott in press) provide new insights into late Eocene vegetation for comparison with younger floras in the same region including the Oligocene Gray Ranch leaf and wood floras (Chaney 1927, Beck 1942, Meyer and Manchester 1997).

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We compare the Dietz Hill (UF 278) and Post Hammer (UF 279) assemblages (John Day Formation, late Eocene) to the older Clarno Nut Beds wood assemblage (Clarno Formation, middle Eocene) to assess whether there are differences in the incidence of wood anatomical features that are consistent with changes in climate, particularly the increase in seasonality from the mid-Eocene to the late Eocene (e.g., Zachos et al. 2001).

MATERIALS AND METHODS

Locality—The Dietz Hill site (UF 278) is situated about three km east of the town of Post, Oregon, USA, and is named informally for Dewey Dietz, a devoted fossil collector who brought the site to our attention and donated some of the fossil fruits and seeds that we investigated (Manchester and McIntosh 2007). The silicified woods are found along with fruits and seeds weathering out of a tuff in the lower part of the John Day Formation (Figure 1C) as mapped by Waters (1968). A minimum age for these wood sites is provided by a white tuff overlying the fossiliferous tuff at the site (Figure 1A). Sanidine crystals from this white tuff yielded an age of 36.21+/-0.26 MA (n = 26) by the ^{40}Ar/^{39}Ar method (Manchester and McIntosh 2007). There are no datable tuffs at or immediately below the fossiliferous horizon to provide a maximum age. However, this late Eocene date may be a reasonable approximation of the age of the Post woods, contrasting with the middle Eocene age of the Clarno Nut Beds.

Sample preparation—A diamond lapidary saw was used to cut thick sections (wafers) exposing transverse (TS), tangential longitudinal (TLS), and radial longitudinal (RLS) surfaces. Sections were prepared by two methods, grinding and peeling. For the grinding method, 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 until they were thin enough (ca. 30 µm) to transmit light for microscopy. Initial grinding was done using a Buehler petrographic thin section grinding machine. Final thinning was done by hand, using a glass plate and a slurry of carborundum grit. Cover slips were mounted using Canada Balsam. For the peel method, the desired cut surfaces were etched for 60 to 90 seconds in 48% hydrofluoric acid. After washing in water to neutralize, the dried etched surfaces were squirted with acetone and a piece of acetate sheet was applied by hand and allowed to fuse with the etched surface as the acetone evaporated. After 30 minutes, the sheet was gently peeled from the sample, trimmed with scissors, and mounted on a glass slide with Canada Balsam and a coverslip. Samples are deposited in the paleobotanical collections of the Florida Museum of Natural History, University of Florida, Gainesville (specimen numbers prefixed UF).

Affinities—Initially, we used the InsideWood (IW) database to search for taxa with the combination of features of the fossil wood (InsideWood 2004-onwards). We used some of the strategies described by Wheeler (2011) and Wheeler et al. (2020). The search criteria used are given, i.e., IAWA hardwood list feature numbers (IAWA Committee 1989) followed by the codes "**p**" for present, “**r**” for required present; "**a**" for absent, “**e**” for required absent. Subsequently, descriptions in the literature and available slides of the taxa (genera and families) were compared to the fossil. Samples of extant woods are referred to by their wood collection numbers, most abbreviations as given by Index Xylariorum 4.1 (Lynch and Gasson 2010). The descriptions are presented following the APG IV classification (Angiosperm Phylogeny Group 2016).

The text-figures illustrating the features used to establish relationships show transverse (TS), tangential longitudinal (TLS), and radial longitudinal (RLS) sections. For quantitative features, we mostly report average (standard deviation), range; if three values are given, this is minimum–average–maximum.

SYSTEMATIC PALEONTOLOGY

PINACEAE Spreng. ex F. Rudolphi, 1830

KETELEERIA Carrière, 1866

KETELEERIA FARJONII sp. nov.

Fig. 2A–G

Diagnosis—Growth rings distinct. Gradual transition from earlywood to latewood. Intertracheary bordered pits primarily uniseriate, occasionally biseriate, on radial walls. Axial parenchyma absent to rare. Rays exclusively uniseriate, average ray height medium (*sensu* IAWA Committee 2004, 5–15 cells), ray tracheids absent to rare, cross-field pits cupressoid to taxodioid, 2–4 pits per cross-field, horizontal end walls of ray parenchyma pitted. Axial canals with thick-walled epithelial cells present; radial canals absent.

Holotype—UF 278-84891, estimated maximum diameter 4 cm.

Occurrence—Dietz Hill (UF 278).

Etymology—Named for Aljos Farjon, THE expert on all things coniferous.

Description—Growth rings distinct. Gradual transition from earlywood to latewood (Fig. 2A–C). Average tangential diameter of longitudinal tracheids 24 (SD=4.7), range 13–33 µm; intertracheary bordered pits

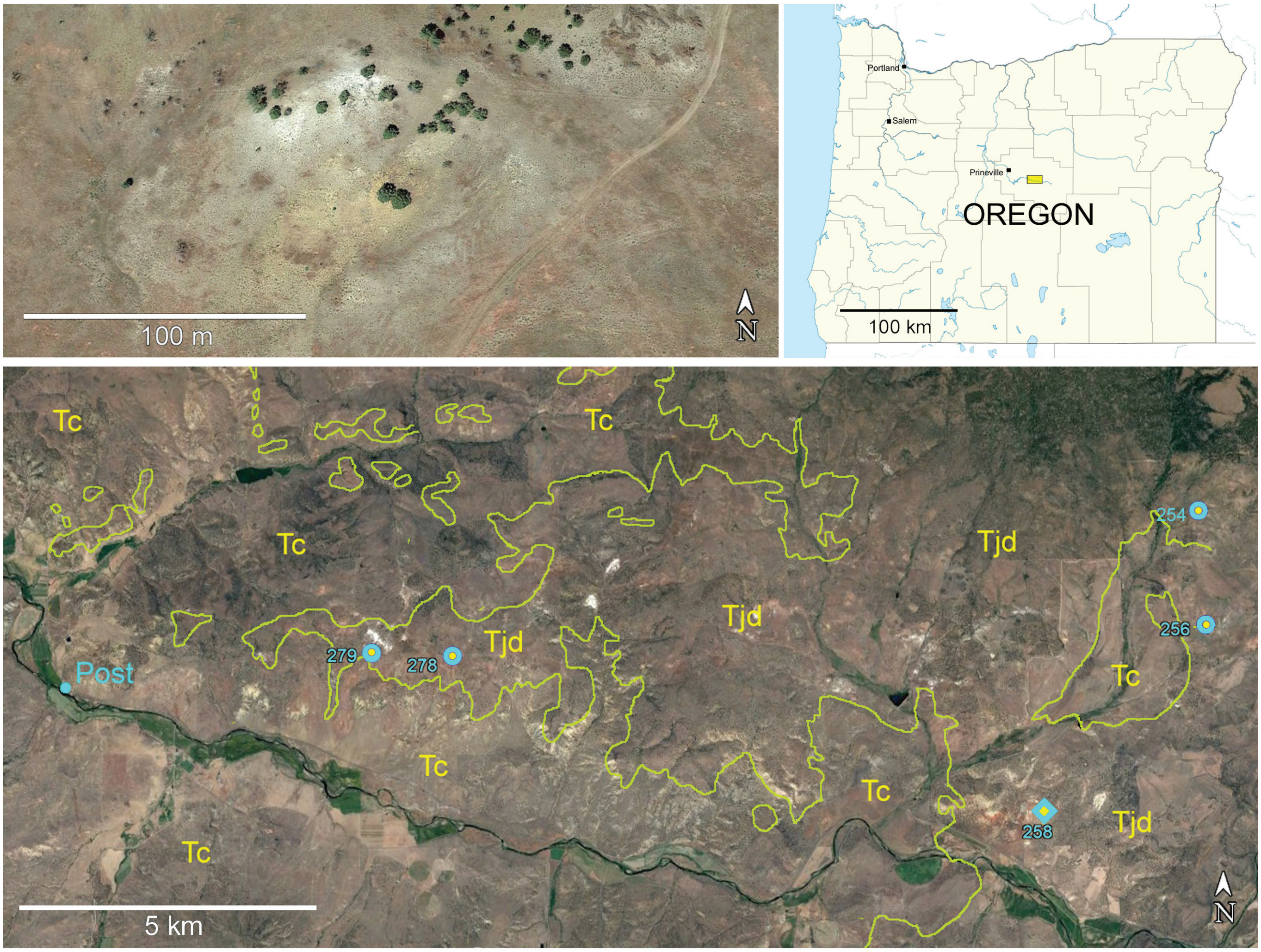

Figure 1. A. Oblique northerly view of Dietz Hill, site UF278. White tuff capping the hill yielded radiometric age of 36.21±0.26 Ma (n=26) (Manchester and McIntosh 2007). Woods and fruits and seeds derive from the same tuff. Google Earth imagery. **B.** Index map of Oregon. Yellow rectangle showing the location of satellite image in C. **C**. Paleobotanical localities in the vicinity of Post, Oregon, in the Crooked River valley. Yellow line marks the approximate contact between the Clarno Formation (Tc) and overlying John Day Formation (Tjd) based on the geologic mapping of Waters (1968). Quaternary deposits in the Crooked River floodplain and localized Plio-Pleistocene igneous intrusions not shown (see Waters 1968 for detail). Late Eocene localities: UF279 Post Hammer site; UF278 Dietz Hill (subject of this treatment), UF254 Brummers Spring, UF256 Teater Road leaf locality. Early Oligocene locality: UF258. Crooked River leaf site (Chaney 1927, Meyer and Manchester 1997).

primarily uniseriate, occasionally biseriate, on radial walls (Fig. 2E, F).

Axial parenchyma not observed with certainty (Fig. 2A–C).

Rays uniseriate (Fig. 2D); 2–18 cells, average 8 (SD=4) cells; 176 (SD=87) µm high, 67–358 µm; only ray parenchyma observed (Fig. 2E–G); end walls of ray parenchyma nodular (Fig. 2G); horizontal walls of ray parenchyma apparently pitted (Fig. 2G); cupressoid/taxodioid pits, 2–4 pits per cross field, mostly two. (Fig. 2E–G).

Ray tracheids apparently absent. Normal and traumatic axial canals present with rather thick-walled epithelial cells (Fig. 2A–C). Radial canals absent.

Comparisons with extant and fossil woods—The only extant conifer with axial resin canals (normal and traumatic), but without radial resin canals is *Keteleeria.* Other features we observed in UF 278-84891 are consistent with its assignment to this genus: cupressoid-taxodioid cross-field pits, nodular end walls of ray parenchyma (e.g., Phillips 1948, Lin et al. 2000, Lin et al. 2002, Itoh et al. 2022).

Today, *Keteleeria* (three to five species) is native to the broadleaved evergreen forests of Central and South China, Laos, Vietnam, and Taiwan (Farjon 1990, Shu 1999, POWO 2023). It is another example of an Asian endemic that had a more extensive range in the past. Its

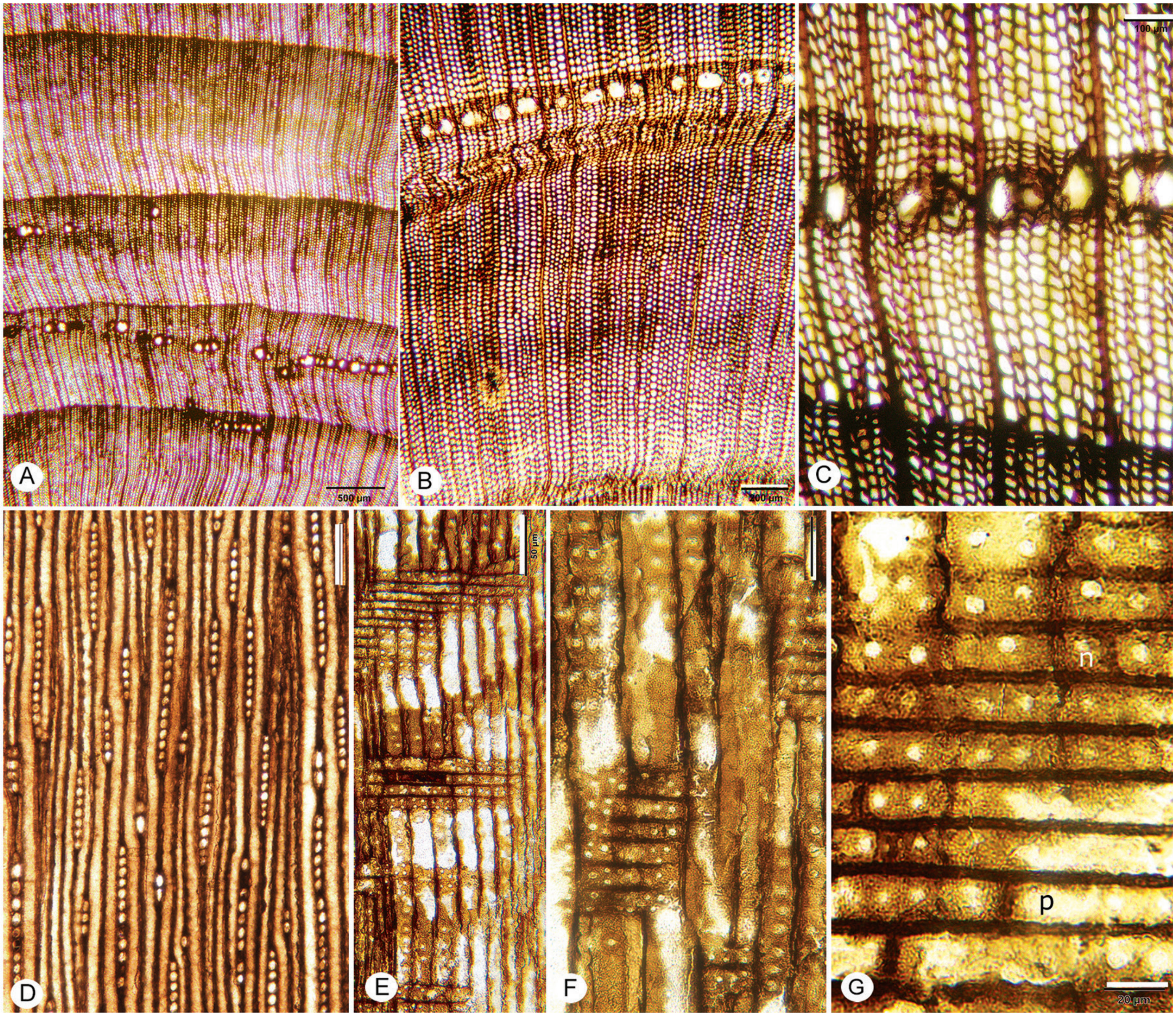

Figure 2. Pinaceae. *Keteleeria farjonii,* UF 278-84891. **A–C.** Distinct growth rings, gradual transition from earlywood to latewood, traumatic resin canals, TS. **D**. Uniseriate rays, TLS. **E, F**. Intertracheary pitting mostly uniseriate, rays composed of ray parenchyma cells, RLS. **G**. Mostly two pits per cross-field, difficult to determine if taxodioid or cupressoid; n to left of nodular end wall; p above pitted horizontal walls, RLS. Scale bars=500 µm in A; 200 µm in B; 100 µm in C, D; E; 50 µm in F; 20 µm in G.

distinctive seeds are known from the Eocene and Oligocene of North America (Meyer and Manchester 1997, Manchester et al. 2009), as well as the Oligocene-Miocene of Europe (Manchester et al. 2009).

Shi et al. (2022) reviewed the record of fossil woods resembling *Keteleeria* and described a new species *Keteleerioxylon changchunense* Shi, Sun, Meng et Yu (2022) from the early Cretaceous of China. There are three other reports of *Keteleerioxylon* I.A. Shilkina (1960) from the Cretaceous, Oligocene, Pliocene, Miocene of Russia (Shilkina 1960, Blokhina and Bondarenko 2005, Blokhina et al. 2006). However, those woods and the Miocene *Keteleeria* wood described from the Miocene of Japan (Choi et al. 2010) differ from UF 278-84891 in having cells that resemble ray tracheids. Such cells appear absent from this Dietz Hill wood. Given that it has a combination of features only seen in extant *Keteleeria,* we are assigning it to the genus.

CUPRESSALES Link, 1829

CUPRESSACEAE Gray, 1821

TAXODIOXYLON (Hartig) Emend. Gothan, 1905

TAXODIOXYLON SP.

FIG. 3A–I

Description—Growth ring boundaries distinct (Fig. 3A–C). In rings without compression woods, latewood narrow with 1–3 rows of radially narrow longitudinal tracheids. Average tangential diameter of earlywood tracheids 32 (SD=7) in UF 278-84886, 30 (SD=7) µm in UF278-84889. Intertracheary pitting occasionally biseriate (Fig. 3G). Transition from earlywood to latewood gradual.

Axial parenchyma abundant, diffuse and in short lines (3A, B), end walls smooth (Fig. 3F).

Rays homocellular, all ray parenchyma (Fig. 3G–I), very rarely with some marginal ray cells possibly ray tracheids (Fig. 3G), uniseriate (Fig. 3D–F), rarely with a biseriate portion one cell high; cross-field pits taxodioid, 2–4 (occasionally more) per cross field (Fig. 3I); horizontal and end walls of ray parenchyma smooth (Fig. H). Ray height 2–7–18 cells, average 146 (SD=77) µm in UF 278–84886, 2–7–24 cells, 153 (SD=115) µm in UF 278-84889.

Specimens—UF 278-84886, UF 278-84889, estimated maximum diameters 8 cm, 16 cm.

Occurrence—Dietz Hill (UF 278).

Comments—Ring width is quite variable in UF 278-84886. Some growth rings have compression wood, indicated by longitudinal tracheids tending to be circular in outline with thickened walls in a broad latewood zone (Fig. 3C).

Comparisons with extant woods—A search for the IAWA softwood features: 40p, 43p, 61e, 72p, 73p, 76p, 80r, 85p, 87p, 94p, 98p, 99p, 103p, 107p, 109a, 110a, 118a with zero mismatches yields the following Cupressaceae: *Chamaecyparis pisifer* (Siebold and Zucc.) Endl. (1847), *Cryptomeria japonica* (Thunb. ex L.f) D. Don (1839), *Cunninghamia konishii* Hayata (1908), *Cunninghamia lanceolata* (Lamb.) Hook. (1827), *Glyptostrobus pensilis* (Staunton ex D. Don) K. Koch (1873), *Platycladus orientalis* (L.) Franco (1949), and *Taiwania cryptomerioides* Hayata (1906). *Taxodium distichum* (L.) Rich. (1810) is among many other Cupressaceae having just one mismatch with the fossil: smooth instead of irregularly thickened or beaded transverse end wall of axial parenchyma (IAWA Softwood Feature 76), which often is of variable occurrence (Richter et al. 2004).

Comparisons with fossil woods—*Taxodioxylon* has long been used for fossil woods with distinct growth rings, abundant axial parenchyma, and predominantly taxodioid cross-field pits (e.g., Kraüsel 1949). *Taxodioxylon's* features and variability have been reviewed multiple times (e.g., van der Burgh and Meijer 1996, Dolezych 2011) and the overlap between the different species noted. It is common in the Northern Hemisphere (e.g., Elliott and Foster 2014, Akkemik and Acarca Bayam 2019) and has been used for fossil woods resembling not just *Taxodium* Richard (1810), but also *Cryptomeria* Don (1838) and *Cunninghamia* R. Br. Ex Rich. (1826a) (Yi et al. 2003, Miocene China), two of the genera returned in our search of the InsideWood conifer database. Given that this Dietz Hill wood conforms to van der Burgh and Meijer's concept of the genus, we assign it to *Taxodioxylon*, but not to a particular species.

ANGIOSPERMS

MAGNOLIALES BROMHEAD 1838
MAGNOLIACEAE JUSS. 1789
MAGNOLIA L. 1753
MAGNOLIA HANSNOOTEBOOMII SP. NOV.

FIG. 4A–G

Diagnosis—Wood diffuse-porous. Vessels solitary and in radial multiples; vessels very narrow to narrow. Perforation plates exclusively scalariform with fewer than 20 bars; intervessel pits predominantly scalariform. Vessel-ray parenchyma pits horizontally elongate. Fine helical thickenings present throughout the body of each vessel element. Thin-walled tyloses present.

Fibers non-septate.

Axial parenchyma marginal.

Rays mostly 3–4 cells wide, uniseriate rays rare. Oil/mucilage cells absent.

Holotype—UF 278-84871, estimated maximum diameter 7 cm

Etymology—In recognition of the late Hans Peter Nooteboom (1934–2022) and his many years of study of the Magnoliaceae.

Description—Growth rings present, marked by radially narrow fibers and marginal parenchyma.

Wood diffuse-porous; vessels solitary and predominantly in radial multiples of 2–4 (Fig. 4A); mean tangential diameter 45 (9) µm, 28–68 µm; 75–100 per mm^2. Perforation plates exclusively scalariform with 4–11–17 bars (n=23) (Fig. 4B, C, F); intervessel pits predominantly scalariform (Fig. 4D). Vessel-ray parenchyma pits horizontally elongate and throughout the ray (Fig. 4E). Fine helical thickenings present throughout the body of the vessel element (Fig. 4B, C). Vessel element lengths average 609 (92) µm, range 407–746 (n=24). Thin-walled tyloses present (Fig. 4G).

Fibers non-septate.

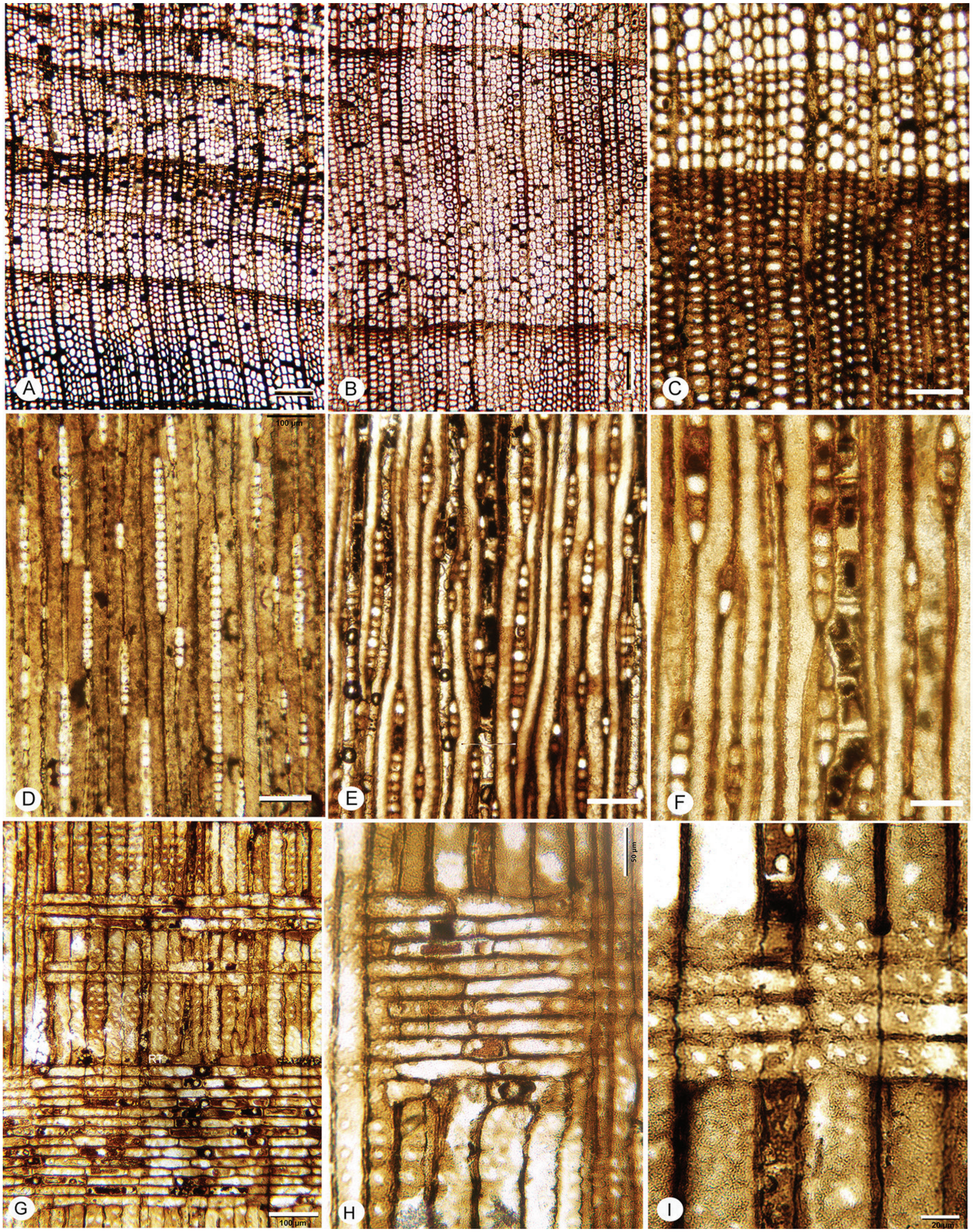

Figure 3. Cupressaceae. *Taxodioxylon* sp. **A, C, E–I**. UF 278-84886. **B, D**. UF 278-84889. **A, B.** Narrow latewood zone, axial parenchyma diffuse and in short tangential lines, TS. **C.** Latewood with compression wood, TS. **D, E**. Uniseriate rays, TLS. **F**. End walls of axial parenchyma smooth, TLS. **G.** Circular bordered pits on radial walls of longitudinal tracheids, occasionally biseriate; most rays homocellular composed of ray parenchyma, bottom ray with top marginal row possibly composed of ray tracheids (RT) RLS. **H.** Ray composed of ray parenchyma, horizontal and end walls smooth, RLS. **I**. Taxodioid cross-field pits, RLS. Scale bars=200 µm in A, B; 100 µm in C, D, E, G; 50 µm in F, H; 20 µm in I.

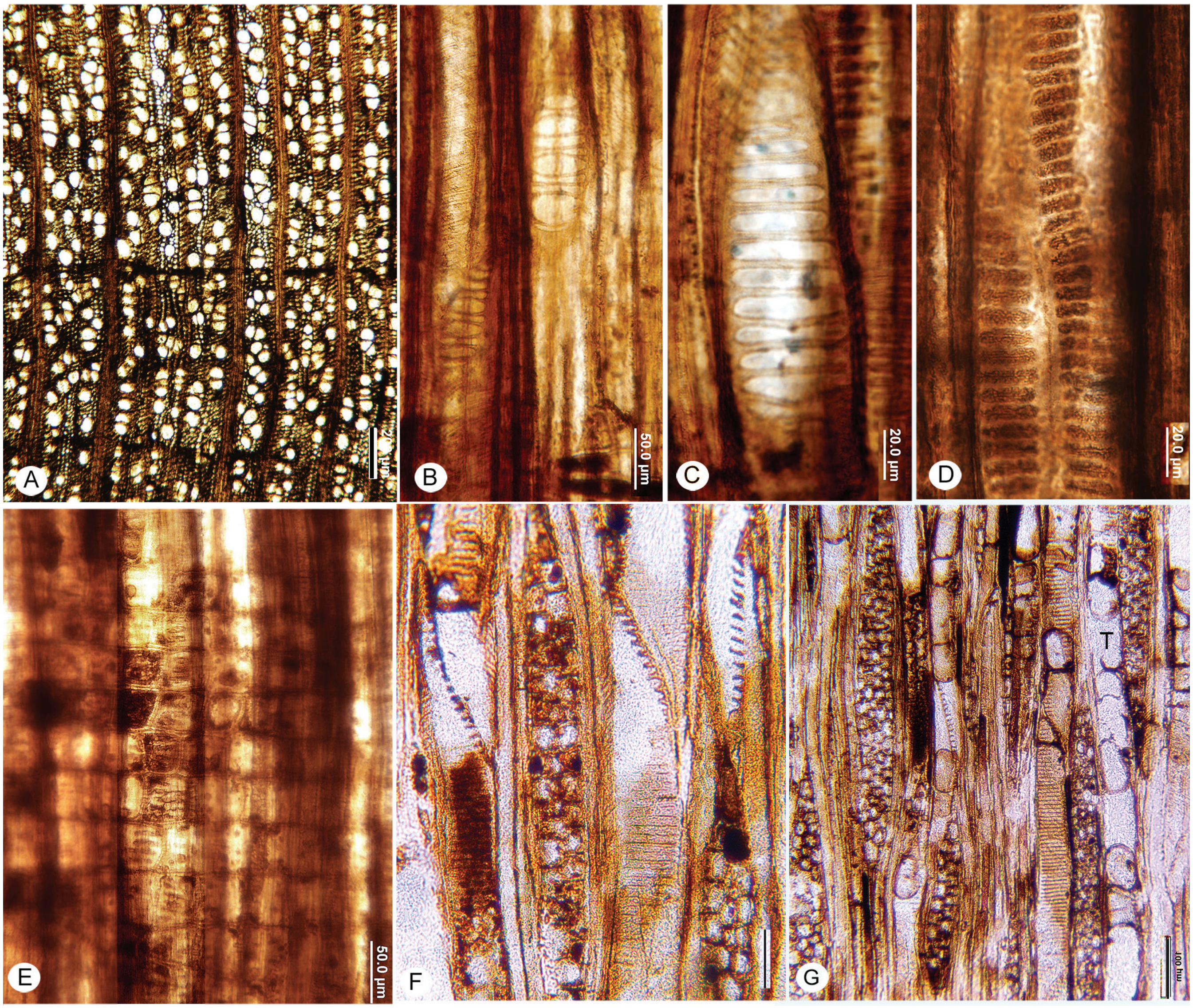

Figure 4. Magnoliaceae. *Magnolia hansnooteboomii*, UF 278-84871. **A**. Diffuse-porous wood, vessels predominantly in radial multiples, T.S. **B, C.** Scalariform perforation plates with fewer than 20 bars, helical thickenings in vessel elements, RLS. **D**. Scalariform intervessel pitting, TLS. **E**. Vessel-ray parenchyma pits with reduced borders, horizontally elongate in outline, RLS. **F, G**. Rays mostly 3–4 cells wide, scalariform perforation plates, non-septate fibers, note scalariform intervessel pits in F and tyloses (T) in G, TLS. Scale bars=200 µm in A; 100 µm in G; 50 µm in B, E, F; 20 µm in C, D.

Axial parenchyma marginal.

Rays mostly 3–4 cells wide, uniseriate rays not common (Fig. 4F, G). Weakly heterocellular. Average multiseriate ray height 583 (212) µm, range 271–1243 µm; 5–8 per mm. Oil/mucilage cells and crystals not observed.

Comparisons with extant woods—Affinities with *Magnolia* are indicated by this combination of features: diffuse-porous wood with distinct growth rings (1p, 5p), vessels solitary and in radial multiples but without a distinctly patterned arrangement (6a, 7a, 8a, 9a), exclusively scalariform perforation plates with less than 20 bars (13a, 14p, 18a), scalariform intervessel pitting (20p), vessel-ray parenchyma horizontally elongate and with reduced borders (30a), helical thickenings throughout the body of the vessel element (36p, 37p), non-septate fibers (66p), marginal parenchyma (89p), rays not markedly heterocellular (108a, 109a), and oil/mucilage cells in rays absent (124a), although many tropical *Magnolia* species have oil/mucilage cells. In addition to the descriptions provided by Metcalfe and Chalk (1950) and Metcalfe (1987), descriptions of Magnoliaceae woods have been presented in publications devoted to the family: Stark (1954), Canright (1955), Chen et al (1993), as well as in wood anatomical atlases: Kribs (1968), Détienne and

Jacquet (1983), Sosef et al. (1998), Carreras and Dechamps (1995), Lemmens et al. (1995), Carreras et al. (2012), Aguilar-Alcantara (2014), Sonsin et al. (2014), Eom (2015) and Itoh et al. (2022). Data from most of these publications are in the InsideWood database and were consulted.

The wood anatomy of *Magnolia* in the broad modern sense of the genus as well as in its earlier, more narrow circumscription is diverse with variation in these features: perforation plates simple and/or scalariform; intervessel pits opposite and/or scalariform; helical vessel wall thickenings present or absent; rays ranging from narrow (1—2-seriate) to medium width (2—5)-seriate, and secretory cells (oil/mucilage cells) present or absent. The full range of this diversity was described in detail by Chen et al. (1993) for the Magnoliaceae of China—*the* center of diversity of the family. Chen et al. (1993) provided a dichotomous key to the genera that were recognized at the time and this fossil from Dietz Hill keys to *Michelia* L. (1753) with 25 species studied, all now subsumed into *Magnolia*. Of those species, only *Magnolia compressa* Maxim. (1872) was returned in the search of InsideWood. Although Chen et al. (1993) concluded that the old paraphyletic genera could mostly be recognized by their wood anatomy, they also showed considerable overlap.

Different authors estimate different numbers of genera and species in the Magnoliaceae; Figlar and Nooteboom (2004) and Wang et al. (2020) recognize only two genera of Magnoliaceae (*Liriodendron* L.,1753*, Magnolia*), while Xia et al. (2008) and Sima and Lu (2012) divided *Magnolia* into 16 genera. Estimates of the number of species vary: Stevens (2001–onwards) ca. 225 species of *Magnolia;* the Flora of China ca. 300 species; Mabberley (2017) 221 species.

Only 60 extant *Magnolia* species are represented in InsideWood by descriptions and/or images. Six match the combination of features of the fossil: the Asian *Magnolia compressa* Maxim. (1872)*, M. fordiana* (Oliv.) Hu (1924)*, M. kwangsiensis* Figlar and Noot. (2004)*,* and *M. sieboldii* Koch (1853); the North American *M. grandiflora* L. (1759) and *M. virginiana* L. (1753). No Neotropical *Magnolia* species match UF 278-84871's features. Not all of the aforementioned species have been included in phylogenetic analyses. Figlar and Nooteboom (2004), as did Wang et al. (2020), placed *M. grandiflora* and *M. virginiana* in subgenus *Magnolia* sect. *Magnolia*: *M. grandiflora* is the better match for the fossil as its helical thickenings are distinct*.* Wang et al. (2020) placed *M. fordiana* (S. China to Vietnam) in sect. *Manglietia; M. kwangsiensis* (S. China) in sect. *Kmeria* (Pierre) Dandy (1927) and the temperate Asian *M. sieboldii* in sect. Oyama. A review of the Leiden wood slide collection and a new atlas for Chinese woods (Itoh et al. 2022) showed that *M. foveolata* (Merr.ex Dandy) Figlar (2000) and *Ma. martini* H. Lév. (1904) also are close matches for this Dietz Hill wood.

Given the overlap in wood anatomy within *Magnolia* and there being over 100 species whose wood anatomy is unknown, it is highly likely that *M. hansnooteboomii* is a close match of more species than the ones discussed above.

Comparisons to fossil woods—Fossil woods of Magnoliaceae date back to the late Cretaceous (Campanian). Among the 18 fossil Magnoliaceae woods in the InsideWood database (Table 1), two species share the aforementioned features with *M. hansnooteboomii*: *M. nanningensis* Huang, Jin and Okolski (2019) from the upper Oligocene, China, and *Magnolioxylon parenchymatosum* van der Burgh (1973) from the Miocene of western Europe,

Although today Magnoliaceae are no longer native in western North America, fossil woods confirm its former presence, including three representatives from the middle Eocene Clarno Nut Beds of Oregon: *M. pageae* Wheeler and Manchester (2002)*, Magnoliaceoxylon angulata* (Scott and Wheeler) Wheeler and Manchester (2002), and *Ma. cutleri* Wheeler and Manchester (2002). All differ from *M. hansnooteboomii* (Table 1). Seed casts of *Magnolia* also occur at the Dietz Hill locality (Manchester and McIntosh 2007).

The wood that Huard (1967) described as *Laurinoxylon intermedium* from the Neogene of southwest France is not Lauraceae, but Magnoliaceae. That species had exclusively scalariform perforation plates and scalariform intervessel pitting, which do not occur in the Lauraceae. It seems probable that he used the occurrence of idioblasts to assign the sample to Lauraceae and was unaware that secretory idioblasts also occur in *Magnolia* wood. Additionally, Huard's wood does not have paratracheal parenchyma, only widely spaced apotracheal parenchyma bands, yet another feature consistent with magnoliaceous affinities. Accordingly, we hereby propose a new combination, *Magnolia intemedia* (Huard) comb. nov. Wheeler, Manchester, and Baas.

A comparison with fossil *Magnolia s.l.* species described in the literature, including *M. intermedia,* (Table 1) reveals that UF 278-84871differs in its combination of intervessel pits predominantly scalariform; helical vessel wall thickenings present; oil/mucilage cells absent. This

Table 1. Comparison of fossil Magnoliaceae woods in chronological order. **K**=Cretaceous, (**C**)=Campanian, (**M**)=Maastrichtian, **Eo**=Eocene, **Olig**=Oligocene; **Mio**=Miocene, **e**=early, **m**=middle, **up**=upper; **IVP**=intervessel pitting, **S**=scalariform, **O**=opposite; **Bars/PP**=number of bars per scalariform perforation plate; **Si**=simple perforation plates present; **HT**=helical thickenings in vessel elements; **O/M**= oil/mucilage cells; **Y**=present; **N**=absent; *****=small axis, **( )**=not as common. **References**. **1**=Cevallos-Ferriz and Stockey (1990); **2**=Huang et al. (2020; **3**=Huard (1967); **4**=Iamandei et al. (2011); **5**=Iamandei et al. (2020); **6**=Page (1970); **7**=Prakash et al. (1971); **8**=Sakala et al. (2010); **9**=Srivastava and Suzuki (2001); **10**=Suzuki (1976); **11**=Takahashi and Suzuki (2003); **12**=van der Burgh (1973); **13**=Wheeler et al. (1977); **14**=Wheeler and Manchester (2002).

Species	**Age**	**IVP**	**Bars/PP**	**Si**	**HT**	**OM**	**Reference**
Magnoliaceoxylon hokkaidoense	K(C-M)	S, O	12–47	N	N	N	11
Magnoliaceoxylon panochensis	K (C)	S, O	up to 10	N	N	N	6
Magnoliaceoxylon wetmorei	e m Eo	S, (O)	8–26	N	N	Y	13
Liriodendroxylon mutltiporosum	m Eo	O	2–10	N	N	(Y)	14
*Liriodendroxylon princetonensis **	m Eo	S, O	8–18	N	N	N	1
Magnolia pageae	m Eo	O	5–20	N	N	Y	14
Magnoliaceoxylon angulata	m Eo	S, O	15–18	N	N	N	14
Magnoliaceoxylon cutleri	m Eo	S, (O)	8–20	N	N	Y	14
Magnoliaceoxylon longiradiata	m Eo	S, (O)	6–20	N	N	(Y)	14
Magnolia hansnooteboomii sp. nov.	l Eo	S	8–16	N	Y	N	This paper
Magnoliaceoxylon palaeogenica	e Olig	S	4–15	N	N	N	9
Michelia oleifera	Olig	S, O	7–15	N	Y	Y	10
Liriodendroxylon tulipiferum	Olig	O	~10	N	N	N	7, 8
Magnolia nanningensis	up Olig	S, O	2–11	N	Y	Y	2
Magnolioxylon cf. transilvanicum	m Mio	S, O	short	Y	N	N	4
Magnolioxylon kräuselli	m Mio	(S), O	10–12	N	N	N	5
Magnolia intermedia	Mio	S	15–20	N	N	Y	3
Magnolioxylon parenchymatosum	Mio	S	3–12	N	N	N	12

justified its recognition as a new species.

LAURALES Juss es Berchtold & J.Presl., 1820

LAURACEAE Jussieu, 1789

LAURINOXYLON Felix emend Dupéron, Dupéron-Laudoueireix, Sakala, De Franceschi, 2008

LAURINOXYLON sp. A of Dietz hill

Fig. 5A–F

Description—Growth ring boundaries distinct, marked by radially flattened fibers (Fig. 5A, B). Diffuse-porous; vessels solitary (56%) and in radial pairs (Fig. 5A, B); mean tangential diameter 84 (SD=14), range 62–110 µm. Simple perforation plates; intervessel pits crowded alternate (Fig. 5C), polygonal in outline, 6–7–9 µm in horizontal diameter; coarse vessel-ray parenchyma pits with reduced borders, horizontally enlarged (Fig. 5D); vessel element length averages 339 (SD=82), range 158–497 µm; tyloses present, thick-walled.

Axial parenchyma scanty paratracheal parenchyma, 4–6 cells per strand.

Fibers without obvious pits; non-septate, rarely septate; thin-to-thick-walled (Fig. 5E, F).

Rays 1–3-seriate (Fig. 5F), multiseriate rays heterocellular with 1–3 rows of marginal square/upright cells (Fig. 5E); average ray height 338 µm (SD=141) µm, range 132–662 µm; 6–8 rays per mm.

Oil/mucilage cells present, but not common (Fig. 5B, E, F), isolated among fibers and possibly in ray margins.

Specimen—UF 278-84868, estimated maximum diameter 6 cm.

Occurrence—Dietz Hill (UF 278).

Comments—The cross sections give the impression that axial parenchyma is abundant, but the longitudinal sections show that it is scanty paratracheal.

Comparison with modern woods—A search for diffuse-porous woods with randomly distributed vessels that are solitary and in short multiples (1p 5p 6a 7a 8a

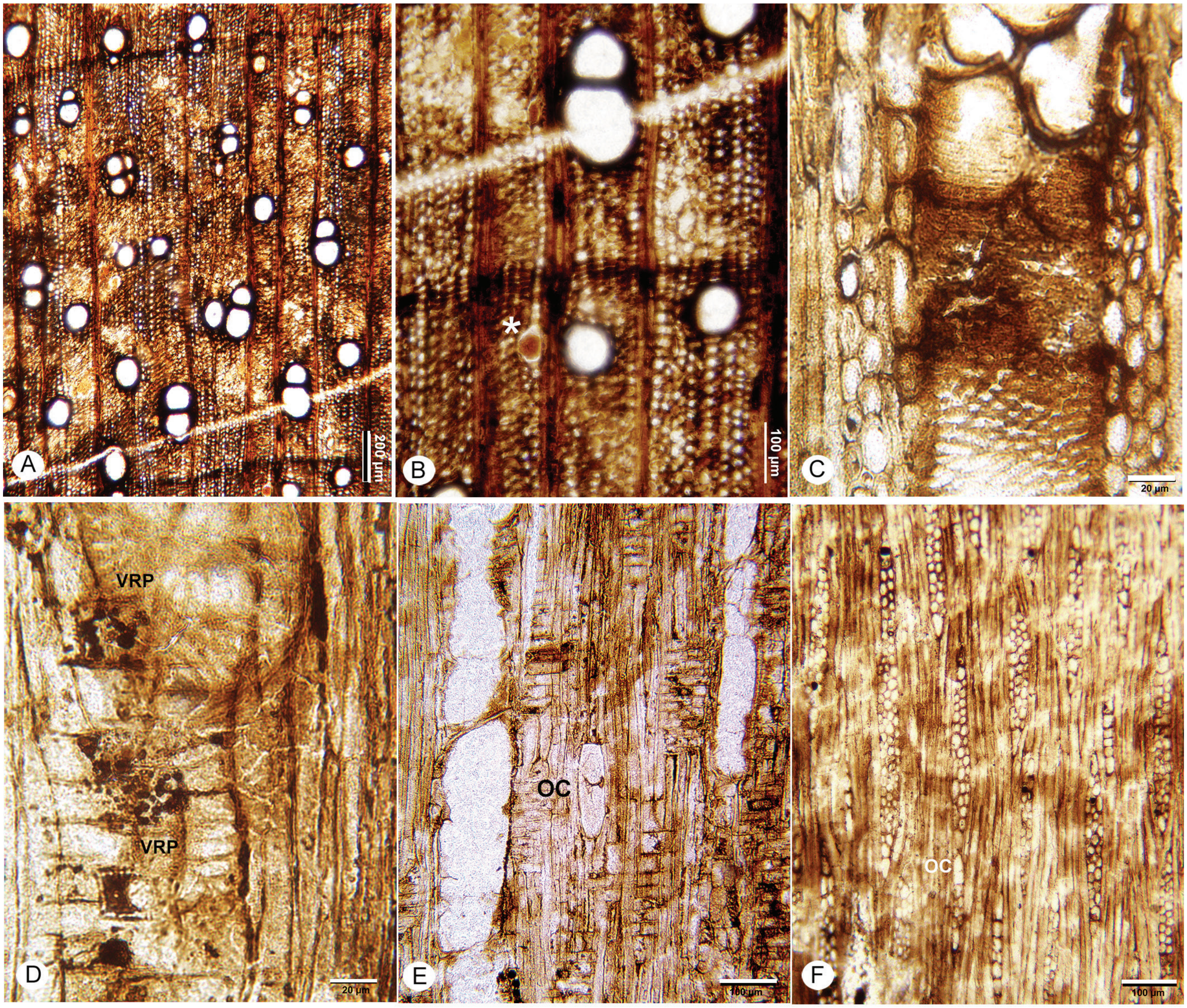

Figure 5. Lauraceae. *Laurinoxylon* sp., UF 278-84868. **A, B**. Diffuse-porous wood with distinct growth ring boundaries; vessels solitary and in radial pairs, * to the left of an oil cell., TS. **C**. Crowded alternate intervessel pits, polygonal in outline, tyloses, TLS. **D**. Vessel-ray parenchyma pits (VRP) with reduced borders to simple, RLS. **E**. Oil/mucilage cell (OC), RLS. **F**. Rays 1-3-seriate with marginal rows of 1–3 upright/square cells; likely oil/mucilage cell (OC), mostly non-septate fibers, TLS. Scale bars=200 µm in A; 100 µm in B; E, F; 20 µm in C, D.

9a 10a 11a), simple perforation plates (13p), alternate intervessel pits that are not minute (22p 24a), vessel-ray parenchyma pits with reduced borders to apparently simple, horizontally elongate (32p), non-septate fibers with simple pits (61p 66p), scanty paratracheal not accompanied by obvious axial parenchyma (78p 80a 83a 85a 86a), rays 1–3 seriate (97p), not homocellular (104a 105a), and oil/mucilage cells among fibers (126p) yields only members of the Lauraceae. The IW search for these features returned species of the genera *Beilschmiedia* Nees (1831), *Cryptocarya* R. Br. (1810), *Lindera* Thunb. (1783), *Litsea* Lam. (1792), and *Ocotea* Aubl. (1775). The inclusion of oil/mucilage cells in rays (124p) yielded the same genera. We did not observe any scalariform perforation plates in this wood, but given that there is only one small sample, we cannot exclude the possibility of them being a rare occurrence in the original tree.

Richter's work on the family is the most comprehensive and he noted that there is overlap in the anatomical features of some genera making it difficult in some cases to identify an isolated piece of lauraceous wood to a single genus (Richter 1981, 1987). Reviewing images in wood anatomical atlases (e.g., the FFPRI on-line database and Itoh et al. 2022) confirms this. There is also considerable intraspecific variation as shown by the image database of FFPRI that includes multiple samples of single species. For example, the 27 samples of *Lindera erythrocarpa* Makino (1897) vary markedly in abundance of oil/mucilage cells and axial parenchyma abundance as do 14 samples of *Litsea acuminata* (Blume) Kurata (1968).

Comparisons with fossil woods—The diagnosis of *Laurinoxylon* Felix as emended by Dupéron et al. (2008) is broad enough to accommodate this Dietz Hill wood—vessels solitary and in radial multiples, perforation plates simple and sometimes scalariform (we interpret that to mean that perforation plates can be exclusively simple), intervessel pits alternate and moderately large, tyloses present, paratracheal parenchyma (type and abundance not specified), 1–5-seriate rays (rays 1–3 fall within this range), slightly heterocellular and less than 1.0 mm high, ray-vessel pits large and often stretched, libriform fibers, oil or mucilage cells (idioblasts) present (no mention of location).

A search of InsideWood's 'Fossil Hardwood' database for the same features used for modern hardwoods yielded two reports of *Cinnamomoxylon* (Huard) Gottwald (1997), three of *Cryptocaryoxylon* Leisman (1986), ten of *Laurinoxylon* and one of *Litseoxylon* Huang et al. (2018). Of these the most similar is the Paleocene *Laurinoxylon* sp. B from the Denver Basin, Colorado, because oil/mucilage cells are not common and are amongst the fibers and ray parenchyma, however, the Paleocene wood has wider rays (Wheeler et al. 2019).

The literature is awash with reports of fossil Lauraceae dating back to mid-1800s with woods ranging in age from the late Cretaceous through the Cenozoic (see list in Gregory et al., 2009). Of those, among the most important is the critical review and summary by Dupéron-Laudoueneix and Dupéron (2005). Subsequent publications describing Lauraceae woods include those by Boonchai and Manchester (2012), Franco (2012), Shukla et al. (2013), Brea et al. (2015), Franco et al. (2015), Koutecký and Sakala (2015), Mantzouka et al. (2016), Cevallos-Ferriz et al. (2016, 2021), Jud and Dunham (2017), Estrada-Ruiz et al. (2018), Huang et al. (2018), Mantzouka (2018), Akkemik et al. (2019, 2021); Güngör et al. (2019), Parrott (2019), Pérez-Lara and Estrada-Ruiz (2019), Wheeler et al. (2019), Ruiz et al. (2020), and Vasquez-Loranca and Cevallos-Ferriz (2022). Lauraceae fossil woods are common and relatively diverse (seven species) in the nearby middle Eocene Clarno Nut Beds (Wheeler and Manchester 2002). These more recent publications all include comparisons of the new species described therein with those previously described.

Because of the variation within Lauraceae, we prefer not to create a new species based on a single sample, but to refer to it as *Laurinoxylon* sp. A of Dietz Hill.

PROTEALES Juss. Ex Berchtold & J. Presl. 1820
PLATANACEAE T. Lestib. 1826
PLATANOXYLON Andreánszky emend. Süss & Müller-Stoll, 1977
PLATANOXYLON HAYDENII (Felix) Süss & Müller-Stoll, 1977

Fig. 6A–F

Description—Wood diffuse-porous (Fig. 6A, B). Growth rings present, marked by slightly noded rays (Fig. 6B) and 1–2 rows of radially narrow fibers. Vessels solitary and in short multiples, some tangentially arranged (Fig. 6A, B); average tangential diameters range from 68 (14)–80 (12) µm; average number of vessels per mm^2 ranges from 40–63. Perforation plates exclusively scalariform (Fig. 6D), 4–40 bars per plate observed; intervessel pits opposite (Fig. 6E), vessel-ray parenchyma pits not observed. Fibers non-septate, pits not observed. Axial parenchyma diffuse, diffuse-in-aggregates, and in interrupted short uniseriate lines (Fig. 6A–C). Rays of two distinct sizes, larger rays typically over 1 mm and more than 10–seriate (6F), maximum ray widths 20–30 cells, composed of procumbent cells, sometimes with 1–2 marginal rows of square cells.

Specimens—UF 278-84874, 84879, 84881, 84885, estimated maximum diameters 12 cm, 4 cm, 2.3 cm, 12 cm.

Comments—As was the case for the platanaceous wood from the Post Hammer locality (UF.279) (Wheeler and Manchester 2021), we were not able to clearly see the vessel-ray parenchyma pits in the Dietz Hill Platanaceae. However, their other features indicate they are *Platanoxylon*: diffuse-porous wood; narrow numerous vessels, predominantly solitary vessels, with occasional tangential multiples; scalariform perforation plates; intervessel pits predominantly opposite; diffuse and diffuse-in-aggregates parenchyma; tall and wide rays composed mostly of procumbent cells. There was variation in the ray sizes. In the samples that were small entire axes (UF 278-84881, UF 278-84879), rays more than 10-seriate were less common. The characteristics that distinguish Platanaceae woods from other woods with wide rays (e.g., *Fagus* L., 1753, and *Euptelea* Siebold and Zucc., 1840) were detailed by Scott and Wheeler (1982) and Wheeler and Manchester (2002, 2014, 2021) and

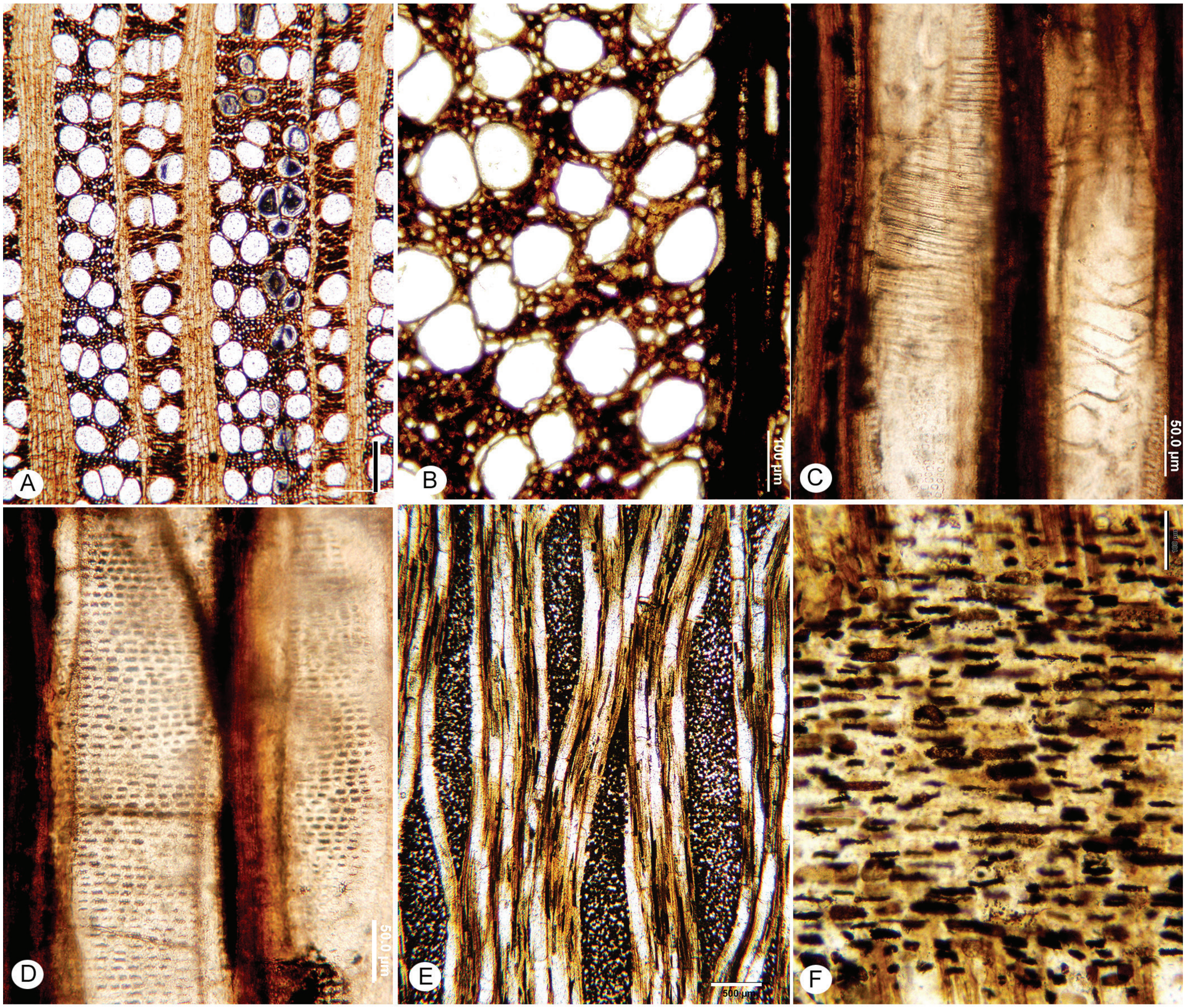

Figure 6. Platanaceae. *Platanoxylon haydenii.* **A, B**. Diffuse-porous wood, vessels mostly solitary, a few tangential multiples; diffuse and diffuse-in-aggregates axial parenchyma; fiber walls of medium thickness, TS, UF 278-84881(**A**), UF 278-84874 (**B**). **C**. Scalariform perforation plates, UF 278-84874, RLS. **D**. Opposite intervessel pitting, UF 278-84874, TLS. **E**. Wide (>10-seriate) and tall (>1 mm) rays, UF 278-.84874, TLS. **F.** Rays composed predominantly of procumbent cells, UF 278-84879, RLS. Scale bars=500 µm in E; 200 µm in A; 100 µm in B, F; 50 µm in C, D.

are repeated in detail in our discussion of *Fagus* herein.

We also searched the InsideWood database for modern and fossil woods with the following suite of features: 1p, 5p, 10a, 13a, 14p, 21p, 41p, 46a, 50a, 66p, 76p, 77p, 79a, 80a, 83a, 84a, 85a, 99p, 102p, 103p, and allowing no mismatches. This yielded four species of modern woods: three *Ilex* Tourn. ex L. (Aquifoliaceae), in which radial multiples are of regular occurrence and rays are more heterocellular, and *Carpodetus serratus* J.R. Forst. and G.Forst. (1776) (Rousseaceae), which has rays with a high proportion of square and upright cells. The rays of the Dietz Hill (UF 278) platanaceous woods have predominantly procumbent cells with one to only a few marginal rows of square cells (Fig. 6E, F). Of the six fossil species returned, four can be dismissed because they lack information on critical diagnostic features, leaving only reports of *Platanoxylon haydenii* from the early middle Eocene of Yellowstone National Park, USA (Wheeler et al. 1977) and the middle Eocene Nut Beds flora, Oregon, USA (Wheeler and Manchester 2002).

Almost all western North America's Eocene fossil wood localities have Platanaceae woods. The nearby Post Hammer locality (UF 279) had both *Platanoxylon* with exclusively scalariform perforation plates and *Platanus*

L. (1753) with both simple and scalariform perforation plates (Wheeler and Manchester 2021). Woods similar to *P. haydenii* are common in the older Clarno Formation, with multiple samples occurring at both the Nut Beds (Wheeler and Manchester 2002) and Hancock Canyon (Wheeler and Manchester 2014). A single infructescence of Platanaceae was recovered at UF 278 (Dietz Hill), it could not be determined if it was *Platanus* or the extinct genus *Macginicarpa* Manchester (1986*).*

FABALES Bromhead, 1838
FABACEAE Lindley, 1836
STYPHNOLOBIUM Schott, 1830
cf. *STYPHONOLOBIUM* sp.
Fig. 7A–I

Description**—**Growth rings distinct. Wood ring-porous. Earlywood vessels mostly solitary, rarely in radial multiples of two (Fig. 7A–C), average tangential diameter 99 (SD=21) µm, range 56–134 µm, earlywood zone 2–3 vessels deep with an abrupt transition to latewood with vessels solitary and in short radial multiples (Fig. 7A); perforation plates simple (Fig. 7D, H); intervessel pitting crowded alternate, polygonal in outline (Fig. 7D), 6–8.5 µm in horizontal diameter; vessel-ray parenchyma pits similar to intervessel pits (Fig. 7E); vessel elements short, average 213 µm (SD=53, n=7).

Fibers non-septate, pits not observed (Fig. 7F, G).

Axial parenchyma aliform-confluent-banded (Fig 7A, C); strands of 2–4 cells; non-storied. (Fig. 7F, G).

Rays 1–4 (-5)-seriate, heterocellular (Fig. 7F–H), in tangential view cells appear isodiametric and angular in outline, ray heights average 195 µm (SD=66), range 104–313 µm.; 5–8 per mm; non-storied.

Specimen—UF 278-84867, estimated maximum diameter 2.5 cm.

Occurrence—Dietz Hill (UF 278).

Comments—Rays near the pith had more upright cells than did the rays farther away. We are not sure what the ray cellular composition of an older stem would be, although the tangential section taken at the periphery suggests they will become homocellular and/or heterocellular with a single marginal row of square cells. This sample contained insect frass and invading roots and had a total of 16 growth rings. Also, in such a narrow stem, vessel diameters probably are narrower than would characterize mature wood of this wood type. We did not observe helical thickenings in this sample, which is unusual for ring-porous legume woods.

Comparisons to extant woods—One of our searches used 1p 3p (ring-porous wood), 7a 8a 9a 10a 11a (vessels randomly distributed, solitary and in short radial multiples), 13p 14a (perforation plates exclusively simple), 22p 26p (medium-sized alternate intervessel pitting), 30p (vessel-ray parenchyma pitting similar to intervessel pitting), 61p 66p (non-septate fibers with simple pits), 83p 85p (axial parenchyma confluent and in bands), 98p 105a (maximum ray width 4–10-seriate, and not composed exclusively of square/upright cells). This particular search only returned *Styphnolobium affine* (Torr. and A. Gray) Walp. (1842) (synonym *Sophora affinis* Torr. and A. Gray, 1840). The other searches we did, which were variations on the search given above, returned more legumes, as well as *Paulownia* Siebold and Zucc. (1835) and some Lamiaceae Mart. (1820), but invariably included *Styphnolobium* Schott (1830) in the results. This fossil has features in common with the *Sophora* A group of Fujii et al. (1994, Table 1), which includes *S. affine.* Gasson's 1994 review of the anatomy of the Sophoreae Spreng and DC. (1825) also indicates this fossil has a similarity with *Stypholobium.*

The LPWG (2017) proposed a new classification of the Fabaceae replacing the three traditional subfamilies: Caesalpinioideae DC. (1825), Mimosoideae DC. (1825), and Papilionoideae DC. (1825), which were based on floral characters, with six subfamilies: Caesalpinoideae, Cercidoideae LPWG (2017), Detarioideae Burmeister (1837), Dialioideae LPWG (2017), Duparquetioideae LPWG (2017), and Papilionoideae, as well as a mimosoid clade, based primarily on molecular work and supported by morphological data. *Styphnolobium* is one of 503 genera in Papilionoideae and includes nine species (POWO 2023). As best we can determine, there are wood anatomical descriptions for only two species: *S. japonicum* (L.) Schott (1830) (native to central and southern. China) and *S. affine* (native to Arkansas, Louisiana, Oklahoma, and Texas in the USA) (Fujii et al. 1994, Gasson 1994, Itoh et al. 2022); both are ring-porous. The other species of *Styphnolobium* are native to Central America, with one species extending into Columbia; some species grow in seasonally dry tropical biomes, some in wet tropics. The Chinese species belongs to Section *Oresbios* (Rudd) M. Sousa (1993)*;* the American species to Section *Styphnolobium.* Because of the relatively few samples available to us we are not sure whether there are wood anatomical differences between the two Sections.

Comparisons to fossil woods—The middle Eocene Clarno Nut Beds has three types of legume woods; all differ from the Dietz Hill wood as they are diffuse-porous (Wheeler and Manchester 2002). Müller-Stoll and Mädel (1967) reviewed the fossil wood record of

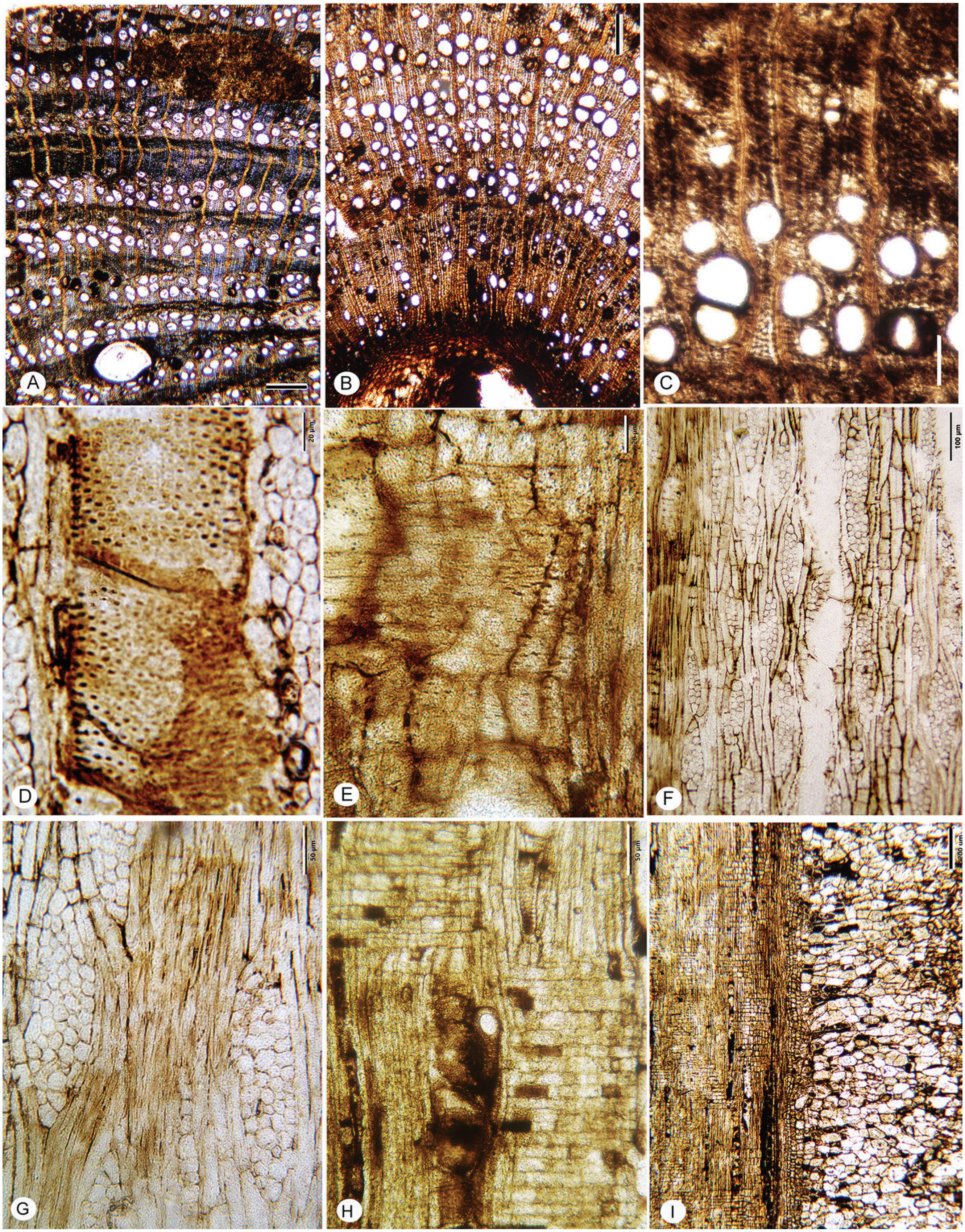

Figure 7. Caption on pg, 15

Figure 7. Fabaceae**.** cf. *Styphonolobium* sp., UF 278-84867. **A**. Ring-porous wood, with distinct earlywood zone 2–3 vessels deep, confluent-banded axial parenchyma, TS. **B**. Pith and first formed secondary xylem, first formed growth ring not ring-porous, pith with thin-walled parenchyma cells, TS. **C**. Earlywood vessels mostly solitary, one radial pair; latewood vessels in small multiples, confluent parenchyma, TS. **D**. Crowded alternate pits, TLS. **E**. Vessel-ray parenchyma pits similar to intervessel pits, RLS. **F**. Multiseriate rays; axial parenchyma strands of 2–4 cells, TLS. **G**. Multiseriate rays; non-septate fibers, TLS. **H**. Simple perforation plate in narrow vessel element; heterocellular rays with procumbent and square cells, RLS. **I**. Pith (at right) with thin-walled parenchyma cells, upright cells common in rays nearest to pith (at left), RLS. Scale bars=500 µm in A; 200 µm in B, I; 100 µm in C, F; 50 µm in G, H; 20 µm in D, E.

the Leguminosae and at that time recognized only 19 fossil genera. Because it is difficult to distinguish some present-day legume genera from one another, most of their genera accommodate more than one present-day genus. Their key to the genera included only two ring-porous genera: *Robinioxylon* Müller-Stoll and Mädel (1967) (differs in having latewood vessel clusters, storied axial parenchyma) and *Gleditsioxylon* Müller-Stoll and Mädel (1967) (rays often >10-seriate). Given that present-day Leguminosae comprises over 750 genera (LPWG 2017), it is not surprising that there are fossil legume woods that do not fit the 19 genera recognized in 1967.

More recently, the genus *Cercioxylon* Akkemik (2019) was created for a Pliocene wood considered to resemble *Cercis* L. (1753) and described as having_ring- to semi-ring-porous wood. It differs from this Dietz Hill wood because it does not have a well-defined narrow earlywood zone (Akkemik 2019, Plate V) and it is described as having vessel clusters common and storied axial parenchyma.

FAGALES Engl., 1892
FAGACEAE Dumort, 1829
FAGUS L., 1753
FAGUS DOGEI Wheeler & Manchester, 2021
Fig. 8A–K

We found five samples that have a combination of features indicating affinity with *Fagus.* There is variation in vessel frequency, ray size, and occurrence of compound rays. The abundant tyloses in some samples made it difficult to measure vessel element lengths and to clearly see perforation plates. A description of the features they share is given below. Table 2 gives information on each sample's vessel diameter and frequency, and ray width and height.

Description—Growth rings distinct, marked by radially flattened latewood fibers, and differences in vessel diameter between latewood and earlywood of subsequent rings (Fig. 8A, B).

Diffuse porous to semi-ring porous (Fig. 8A, B). Vessels predominantly solitary (Fig. 8B); vessels circular to oval to slightly angular in outline; vessels narrow. Perforation plates simple and scalariform with <10 bars (Fig. 8D–F); intervessel pitting scalariform to opposite (Fig. 8G), occasionally alternate; vessel-ray parenchyma pits oval to horizontally elongate with reduced borders (Fig. 8H). Vessel element lengths medium. Tyloses common, usually oriented horizontally across the vessel lumens (Fig. 8K).

Fibers non-septate, walls thick to very thick, with distinctly bordered pits in radial and tangential walls (Fig. 8G).

Axial parenchyma diffuse, less commonly diffuse-in-aggregates (Fig 8A, B), strands of 4–8 or more.

Rays of two distinct sizes, narrow rays 1–3 (-4) seriate and the wider rays more than 8-seriate (Fig. 8I–K). Homocellular, composed of procumbent cells or heterocellular with body of procumbent cells and 1–4 marginal rows of square/upright cells. Compound rays rare to common.

Specimens—UF 278-84869, 84873, 84888, 84896, estimated maximum diameters 15 cm, 18 cm, 26+ cm, 16+ cm.

Occurrence—Dietz Hill (UF 278).

Comparisons with extant woods—The combination of diffuse-porosity (5p), predominantly solitary vessels (9p), simple and scalariform perforation plates with few bars (13p, 14p, 15p), scalariform and opposite intervessel pitting (20p, 21p), vessel-ray parenchyma pits with reduced borders (31p), average tangential diameter less than 100 µm (42a, 43a), more than 40 vessels per mm^2 (46a–48a), non-septate fibers with bordered pits (62p, 66p), diffuse axial parenchyma unaccompanied by obvious paratracheal parenchyma (76p, 79–86a), rays more than 3-seriate, commonly more than 1.0 mm high, and of two distinct sizes (96a, 97a, 102p, 103p) occurs in *Fagus*. This combination of features also occurs in the Indian species *Vaccinium leschenautii* Wight which differs in having helical thickenings in its vessel elements and sheath cells in its rays.

A review of tangential sections of *Fagus* in the FFPRI Database of Japanese Woods (https://db.ffpri.go.jp) and the InsideWood image collection shows considerable variation in maximum ray width within the illustrated species: *Fagus crenata* Blume (1849)*, F. grandifolia* Ehrh. (1788)*, F. japonica* Maxim. (1887)*, F. orientalis* Lipsky

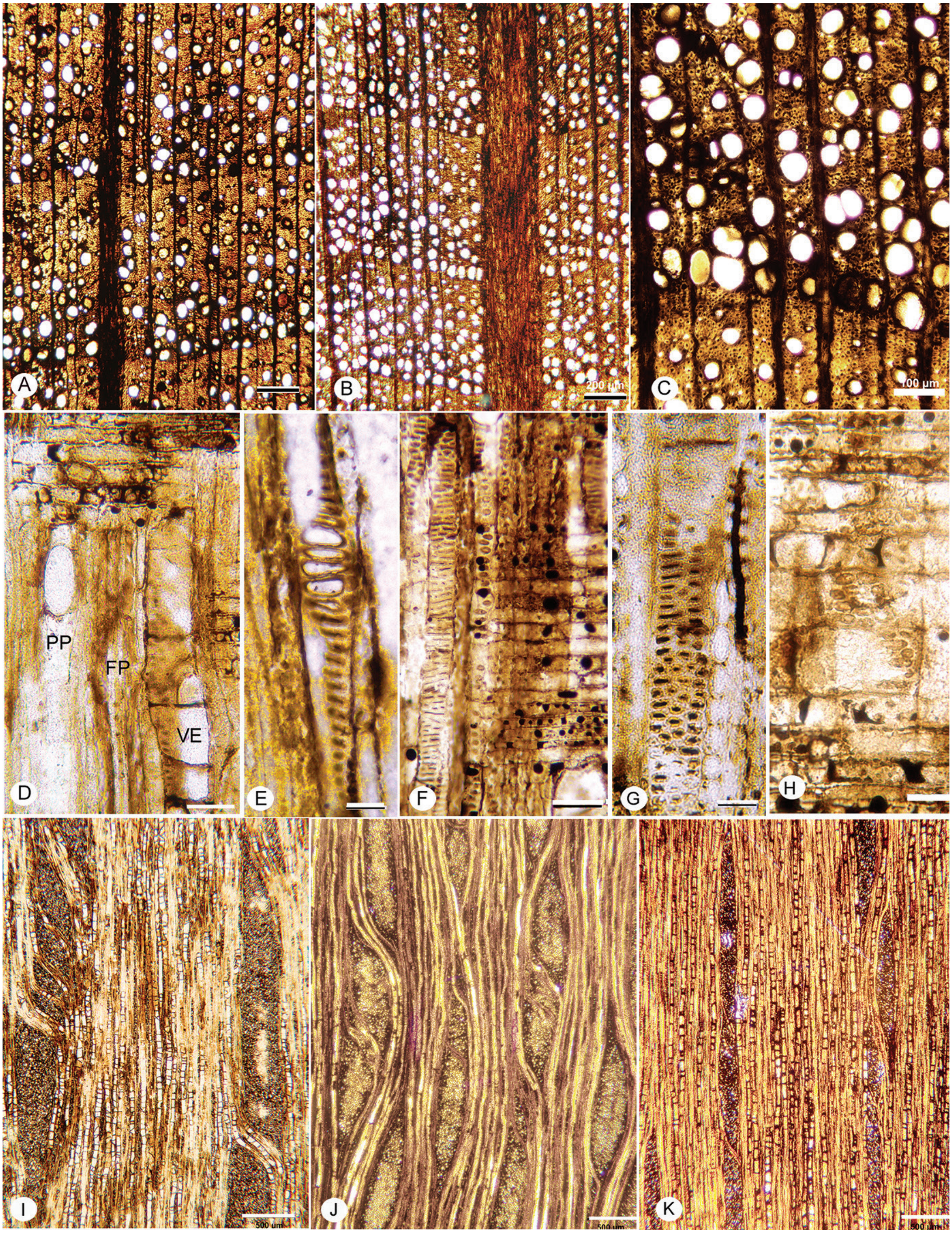

Figure 8. Caption on pg. 17.

Table 2. Comparison of fossil *Fagus* woods from Dietz Hill with *Fagus dodgei* from Post Hammer (UF 279, late Eocene, Wheeler and Manchester 2021) and *Fagus manosii* (mid-Miocene, Wheeler and Dillhoff 2009). **VTD**=vessel tangential diameter in µm, mean (SD); **V/mm^2**=number of vessels per square mm; **Lrg Ray**=large ray, number of cells wide; **Cmp**=compound ray; **Lrg Ray Ht.**=large ray height in µm, mean (SD, when known), range.

Sample	VTD	V/mm^2	Lrg Ray	Lrg Ray Ht.
UF 278-84869	59 (8)	39–53	6–9, Cmp	2214 (580), 1269–3102
UF 278-84903	49 (13)	67–82	7–12, Cmp	2566 (734), 1974–3948
UF 278-84873	44 (6)	86–103	to 22, Cmp common	1875 (500), 1356–2825
UF 278-84888	62 (12)	61–75	8–11, Cmp common	2358 (311), 1904–2744
UF 278-84896	53 (8)	87–117	to 20+, Cmp common	1967 (815), 705–3666
Fagus dodgei	55 (11)	39–79	18–20, Cmp	1560, 740–2690
Fagus manosii	52 (11)	110–130	to 16, Cmp absent	1700 (max)

(1898), and *F. sylvatica* L. (1753). Compound rays are more common in the Dietz Hill *Fagus* than in extant *Fagus,* although compound rays were observed in some samples of *F. grandifolia* and *F. orientalis.* Scalariform intervessel pitting is more common in the Dietz Hill *Fagus* than in modern *Fagus.*

Fagus and *Platanus* wood are superficially similar. Differences between them were reviewed by Panshin and DeZeeuw (1980), Hoadley (1990), and Wheeler and Manchester (2021). They include: 1) *Fagus* consistently has vessel-ray parenchyma pits with reduced borders, while *Platanus* has most vessel-ray parenchyma similar to intervessel pits, and only occasionally with reduced borders; 2) intervessel pits in *Fagus* are opposite-scalariform (transitional) to occasionally alternate, while in *Platanus* they are usually crowded opposite; 3) many samples of *Fagus* tend to be semi-ring-porous with a distinct latewood zone with narrower vessels, while *Platanus* is most commonly 'classic' diffuse-porous; 4) spacing and sizes of the wide rays is more variable in *Fagus* than in *Platanus;* 5) the ratio of narrow (1–3-seriate) rays to wide rays (>8-seriate) is higher in *Fagus* than in *Platanus,* e.g. , we observed ~9:1 in *F. grandifolia* and ~2:1 in *Platanus occidentalis* L. (1753).

Comparisons with fossil woods—The nearby Post Hammer locality (UF 279) has two samples of beech wood, both assigned to *Fagus dodgei* Wheeler and Manchester (2021) and which differed from the mid-Miocene *F. manosii* Wheeler and Dillhoff (2009) from the Vantage Fossil Forests of Washington State which has more scalariform intervessel pitting and shorter rays. Compound rays were not observed in *F. manosii.* We assign the Dietz Hill (UF 278) woods to *F. dodgei*; differences between these UF 278 samples and *F. dodgei* from the Post Hammer locality are comparable to the intraspecific variation seen within present-day *F. grandifolia* and *F. orientalis.*

The oldest well-documented occurrence of the beech genus is *F. langevinii* Manchester and Dillhoff (2004) from the early middle Eocene McAbee flora of British Colombia, based on cupules, nuts, foliage, and associated dispersed pollen, which was considered closest to the *Fagus* group that includes *F. grandifolia (*Manchester and Dillhoff 2005). Other Cenozoic North America *Fagus* megafossil occurrences include *F. pacifica* Chaney (1925) from the Oligocene Bridge Creek flora of Oregon (cupules and leaves; Chaney 1927, Meyer and Manchester 1997), *F. idahoensis* Chaney and Axelrod (1959), and *F. washoensis* LaMotte (1936) from the Miocene of Idaho and Oregon (Chaney and Axelrod 1959). The Eurasian fossil record of *Fagus* based on leaves and cupules, has been reviewed previously (Kvacek and Walther 1991, Tanai 1974, Denk et al 2002). The tricolporate pollen of *Fagus*, which is distinctive in its ornamentation as viewed in SEM, has been recognized in the Paleocene of Greenland (Grimsson et al 2016), early Eocene of China (Hofmann et al. 2019) and various sites in the Miocene of Europe (e.g.,

Figure 8. Fagaceae. *Fagus dodgei*. **A–C.** Diffuse- to semi-ring-porous wood; vessels predominantly solitary; rays of two size classes; diffuse axial parenchyma, thick- to very thick-walled fibers, TS, UF 278-84888 (**A**), UF 278-84873 (**B, C**). **D**. Simple perforation plate (pp); fiber with distinctly bordered pits (FP); tyloses segmenting a vessel element (VE), RLS, UF 278-84896. **E**. Scalariform perforation plate; scalariform intervessel pitting, RLS, UF 278-84896. **F**. Scalariform intervessel pitting; procumbent ray cells, RLS, UF 278-84896. **G**. Intervessel pitting, TLS, UF 278-84896. **H**. Vessel-ray parenchyma pitting with reduced borders, UF 278-84896. **I–K**. Two size classes of rays, TLS, UF 278-84896 (**I**), UF 278-84873 (**J**), UF 278-84888 (**K**). Scale bars=500 µm in I, J, K; 200 µm in A, B; 100 µm in C; 50 µm in D, F; 20 µm in E, G, H.

Denk and Bouchal 2021).

Today, *F. grandifolia* is North America's only species of *Fagus.* It has an extensive range in the eastern half of the continent. Renner et al. (2016) reviewed the biogeographic history of the genus. They proposed that there was a Pacific-North American lineage that diverged from a Eurasian lineage by the Middle Eocene. The beech woods from UF 278 and UF 279 are likely part of that Pacific-North American lineage.

QUERCINIUM UNGER, 1842

QUERCINIUM SP.

FIG. 9A–F

Description—Growth rings boundaries present but not well-defined (Fig. 9A), marked by radially flattened latewood fibers, and differences in vessel diameter between latewood and earlywood of subsequent rings.

Diffuse porous to semi-ring porous. Vessels with a very slight tendency to diagonal arrangement; exclusively solitary; vessels circular in outline (Fig. 9A); vessel tangential diameters average 88 (SD=17) µm, range 53–133 µm; perforation plates exclusively simple (Fig. 9B); pits to vasicentric tracheids circular bordered, alternate (Fig. 9C); vessel-ray parenchyma pits enlarged with reduced borders and vertical to diagonal (Fig. 9D). Tyloses present.

Vasicentric tracheids present (Fig. 9C). Fibers nonseptate, most commonly without distinctly bordered pits.

Axial parenchyma diffuse and probably diffuse-in-aggregates, difficult to see in transverse section, but visible in longitudinal sections, 4–8 or more cells per strand (Fig. 9E, F).

Rays of two distinct sizes, uniseriate and multiseriate rays to 15+ cells wide (Fig. 9E, F); wide rays quite rare. Uniseriate rays usually less than 12 cells high (Fig. E, F). Mainly composed of procumbent cells.

Crystals not observed.

Specimen—UF 278-84878, estimated maximum diameter 8+ cm.

Occurrence—Dietz Hill (UF 278).

Comparisons with extant plants—The combination of exclusively solitary vessels, simple perforation plates, vasicentric tracheids, vertically oriented vessel-ray parenchyma pits with reduced borders, and two size classes of rays (not aggregate rays) indicates that this wood belongs to the Fagaceae, subfamily Quercoideae Oersted (1753) (Wheeler, et al. 2022). The diffuse- to semi-ring-porosity suggests an evergreen *Quercus* L. (1753) or *Lithocarpus* Blume (1825), but they typically have aggregate rays according to Suzuki and Ohba (1991), as does the western U.S. endemic *Notholithocarpus* Manos, Cannon and S.H.Oh (2008) (Wheeler et al. 2022). However, one (TWTw 20973) of the twelve *Lithocarpus* samples in the FFPRI image database appears to have rays similar to UF 278-14 as do multiple samples of diffuse-porous to semi-ring-porous *Quercus* spp. (e.g., TWTw 19013, 19097, 25282, 22654, FFPRI Wood Identification Database Team, 2002). In the Naturalis slide collection (Lw), two *Lithocarpus* species (*Lithocarpus ewyckii* (Korth.) Rehder (1929), *L. solerianus* (Vidal) Rehder (1919) and numerous species of diffuse- to semi-ring-porous *Quercus* (e.g., *Quercus agrifolia* Née, 1801; *Q. gilva* Blume, 1850; *Q. ilex* L., 1753; *Q. phellos* L., 1753) have rays similar to this fossil.

Comparisons with fossil woods—Probably because of a combination of original abundance in ancient landscapes, resistance to decay, and ease of recognition, reports of fossil Quercoideae woods, especially oaks, are common (see Gregory et al. 2009). At the nearby Post Hammer locality (UF 279), there are three Quercoideae woods, two *Lithocarpoxylon* (Petrescu) emend. Suzuki and Ohba (1991) and a *Quercus* of the Red Oak Group (Wheeler and Manchester 2021), and one at the middle Eocene Clarno Nut Beds, *Quercinium crystallifera* Scott and Wheeler (1982).

Because this wood has features found in both *Quercus* and *Lithocarpus,* we are not assigning it to *Quercus.* The emended diagnosis and discussion of *Lithocarpoxylon* indicate that this genus is for Quercoideae woods with aggregate rays (Petrescu 1978, Suzuki and Ohba1991), and because this wood does not have aggregate rays we do not assign it to *Lithocarpoxylon*.

***Quercinium vs Quercoxylon*—**The history of generic names for woods resembling *Lithocarpus* and *Quercus* is complex and has been discussed at length by Müller-Stoll and Mädel (1957), Brett (1960), Mädel-Angeliewa (1968), and Gros (1988). Relying on these publications, the best we can sort out is as follows. The oldest name applied to such woods is *Kladenia* used by Göppert in 1839, but Müller-Stoll and Mädel (1957) argued against using this name. Unger (1842) proposed the name *Quercinium* for fossil wood resembling *Quercus.* The name *Quercoxylon was* first used by Hoffman (1929), but it was not designated as gen. nov. and *Quercoxylon* Hoffman seems to have been mostly ignored. Subsequently, Kraüsel (1939) again proposed the genus *Quercoxylon* Kräusel and later Müller-Stoll and Mädel (1957, p. 125) provided a formal diagnosis for *Quercoxylon* (Kräusel) emend. Müller-Stoll and Mädel (1957). In their discussion, Müller-Stoll and Mädel note that *Quercoxylon* and

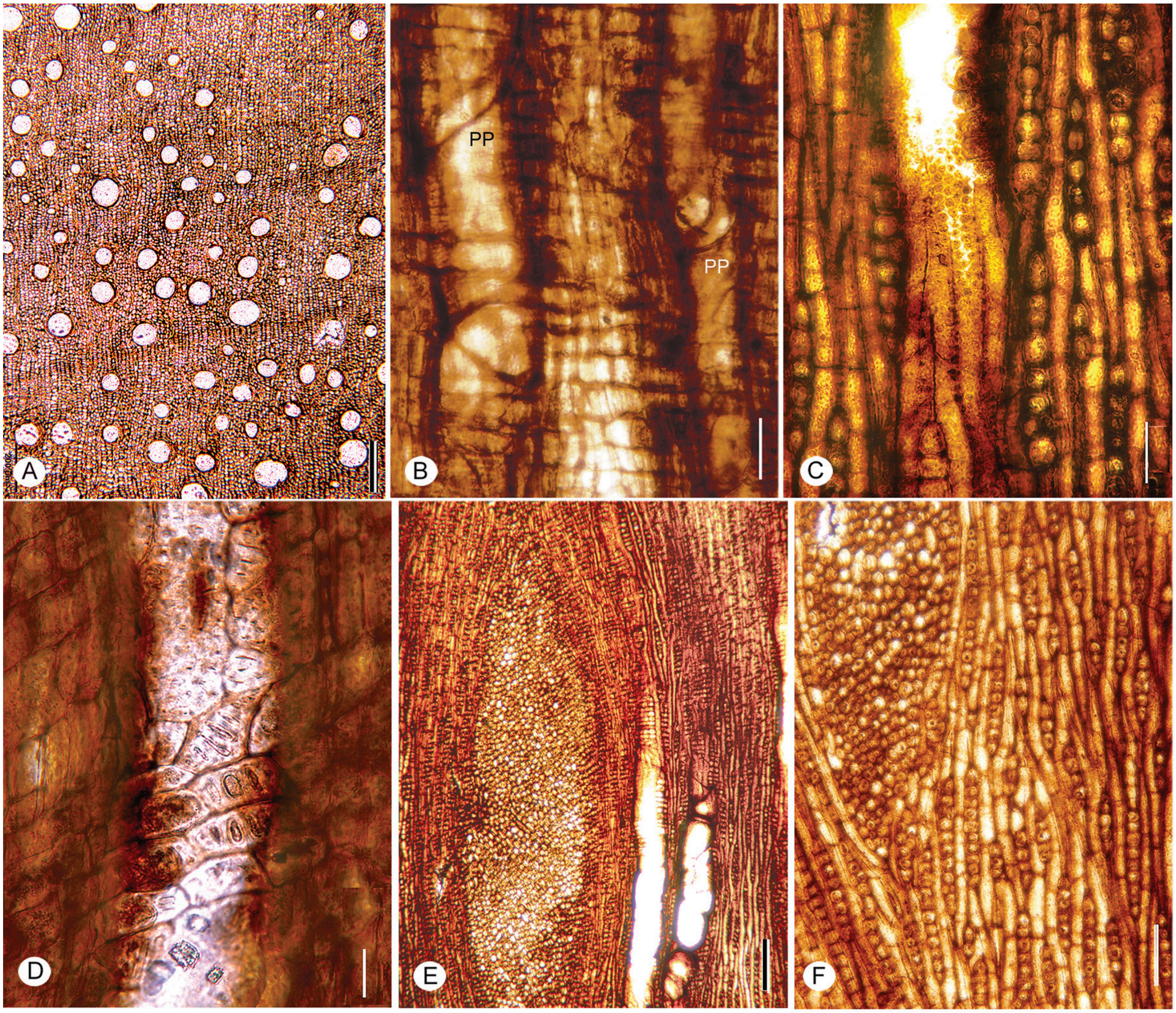

Figure 9. Fagaceae. *Quercinium* sp, UF 278-84878. A. Diffuse- to semi-ring-porous wood; vessels exclusively solitary, very slight tendency to diagonal arrangement, TS. **B**. Simple perforation plates (PP), RLS. **C**. Vasicentric tracheids, uniseriate rays, axial parenchyma strands, TLS. **D**. Vessel-ray parenchyma pits with reduced borders to simple, tyloses, RLS**. E, F**. Rays of two distinct sizes, TLS. Scale bars=200 µm in A, E; 100 µm in B, C, F; 50 µm in C; 20 µm in D.

Quercinium are completely identical in content [“*Quercoxylon* Kraüsel and *Quercinium* Unger stimmen inhaltlich völlig überein”]. Although *Quercinium* has priority (Unger 1842), they stated that *Quercoxylon* Kraüsel (1939) should be used because most authors are of the opinion that fossil woods named after a modern genus should use -*oxylon* (Müller-Stoll and Mädel 1957, p. 125–126). There is no formal requirement to use -*oxylon* in a generic name for a fossil wood. Consequently, we are assigning this wood to *Quercinium* Unger because that name has priority.

A noteworthy feature of this Dietz Hill *Quercinium* is that it does not have a distinct radial, diagonal, or dendritic vessel arrangement. This feature also characterizes *Quercinium porosum* Brett (1960) from the British Eocene, which has markedly wider vessels which average 237 µm in tangential diameter. We do not know whether this Dietz Hill sample might be root wood which could explain the lack of a distinct vessel arrangement pattern (Cutler et al. 1987). We are not creating a new species for this small, single sample of Quercoideae wood, and think it is sufficient to report its occurrence at the Dietz Hill (UF 278) locality.

JUGLANDACEAE DC EX PERLEB, 1818

CARYA NUTTALL, 1818

Carya leroyii sp. nov.

Fig. 10A–I

Diagnosis—Growth rings present. Wood semi-ring-porous. Vessels solitary and in radial multiples of 2–3. Perforations simple, intervessel pits crowded alternate medium to large; vessel-ray parenchyma pits similar in size and shape to intervessel pits. Non-septate fibers. Axial parenchyma scanty paratracheal and in narrow bands throughout the growth rings. Rays 1–3-seriate, heterocellular with procumbent body cells and 1–3 marginal rows of square-upright cells. Crystals in chambered axial parenchyma strands, some crystal containing cells enlarged.

Holotype—UF 278-84908.

Occurence—Dietz Hill (UF 278).

Etymology—Named in honor of J.F. Leroy in recognition of the importance of his studies of extant and fossil Juglandaceae.

Description—Growth rings present, marked by radially flattened fibers and differences in latewood and earlywood vessel diameters of successive growth rings (Fig. 10A–C). Semi-ring-porous, a slight tendency to diagonal arrangement in some regions (Fig. 10A) .

Vessels solitary and in radial multiples of 2–3, average tangential diameter of earlywood vessels 229 (44) µm, range 136–294 µm; perforations exclusively simple (Fig. 10H), intervessel pits alternate (Fig. 10D), ca. 10–12 µm; vessel-parenchyma pits similar in shape and size to intervessel pits (Fig. 10E); vessel element length averages for 451 (SD=70) µm, range 339–565 µm; thin-walled tyloses present (Fig. 10B, C, F, G, I).

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

Axial parenchyma scanty paratracheal, in tangential bands one to two cells wide throughout the growth ring, bands more closely spaced in the latewood than in the earlywood (Fig. 10A, B); strands without crystals of 4–8 cells (Fig. 10G, H).

Rays 1–3-seriate (Fig. 10 G–H). Multiseriate rays heterocellular, with procumbent body cells and mostly with 1–3 marginal rows of square to upright cells, occasionally more (Fig. 10E, F); uniseriate rays composed of mostly upright cells, total multiseriate ray height averages 438 (SD=92) µm, range 283–544 µm; 4–6 per mm.

Crystals common, in chambered axial parenchyma strands, sometimes in much enlarged axial parenchyma cells within an axial parenchyma strand (Fig. 10G–I).

Comparisons with extant woods—Affinities with Juglandaceae are indicated by the combination of semi-ring-porosity, vessels solitary and in short radial multiples, narrow continuous lines of axial parenchyma, medium-sized alternate intervessel pits, vessel-ray parenchyma pits similar in size to intervessel pits.

Its combination of features, including absence of scalariform perforations (a characteristic of Engelhardieae Mann., 1978), is consistent with placement in the Juglandoideae Eaton (1836) (Wheeler, et al. 2022). Our sample is missing the pith, so we cannot confirm that it was solid, as expected in *Carya* Nuttall (1818), or septate which characterizes *Juglans* L. (1753)*, Pterocarya* Kunth (1824) and *Cyclocarya* Iljinsk. (1953).

Whether crystals are present and their location are useful features in distinguishing genera and species groups in the Juglandoideae. Crystals are common in this wood so it differs from *Pterocarya* and the butternut group of *Juglans* (Asian species of Section *Cardiocaryon* Dode, 1909*,* and the American *Juglans cinerea* L., 1759*,* traditionally placed in section *Trachycaryon* Klotzsch, 1845). The tropical black walnuts have crystalliferous axial parenchyma strands, but not in enlarged cells; the north temperate black walnuts have crystals in enlarged axial parenchyma cells, but not in long chains (Miller 1976). Consequently, *Juglans* does not seem a good match for UF 278-84908.

The presence of crystals in chambered axial parenchyma and in enlarged axial parenchyma cells suggests affinities with *Carya,* but not with the North American species of sect. *Carya* which are ring-porous and have thick-walled fibers (Stark 1953). Heimsch and Wetmore (1939) noted that crystals in swollen axial parenchyma cells were most common in *Carya tonkinensis* Lecomte (1921). Leroy (1950) described the evergreen species *Carya sinensis* Dode (1912) (synonym: *Annamocarya sinensis* (Dode) J.-F. Leroy (1950) and compared it to *C. tonkinensis.* Based on what he acknowledged as limited material, he suggested the two species had similar anatomy. He also noted that the rays in these two species are more heterocellular than in the American species. Müller-Stoll and Mädel (1960) reported another difference for these two species, i.e., they do not have thick-walled vessel elements. However, neither species has crystals in chambered axial parenchyma similar to UF 278-84908.

Neither Heimsch and Wetmore (1939) nor Leroy (1953) gave details about intervessel pitting. The one sample of *C. sinensis* we had access to has minute-small intervessel pitting (3–5 µm, Wheeler et al 2022); the only other juglandaceous wood with minute intervessel pitting is *Rhoiptelea* Diels and Hand.-Mazz. (Hand.-Mazz., 1932) (Withner 1941). *Carya cathayensis* Sarg. (1916) has crystals in enlarged axial parenchyma cells, but not

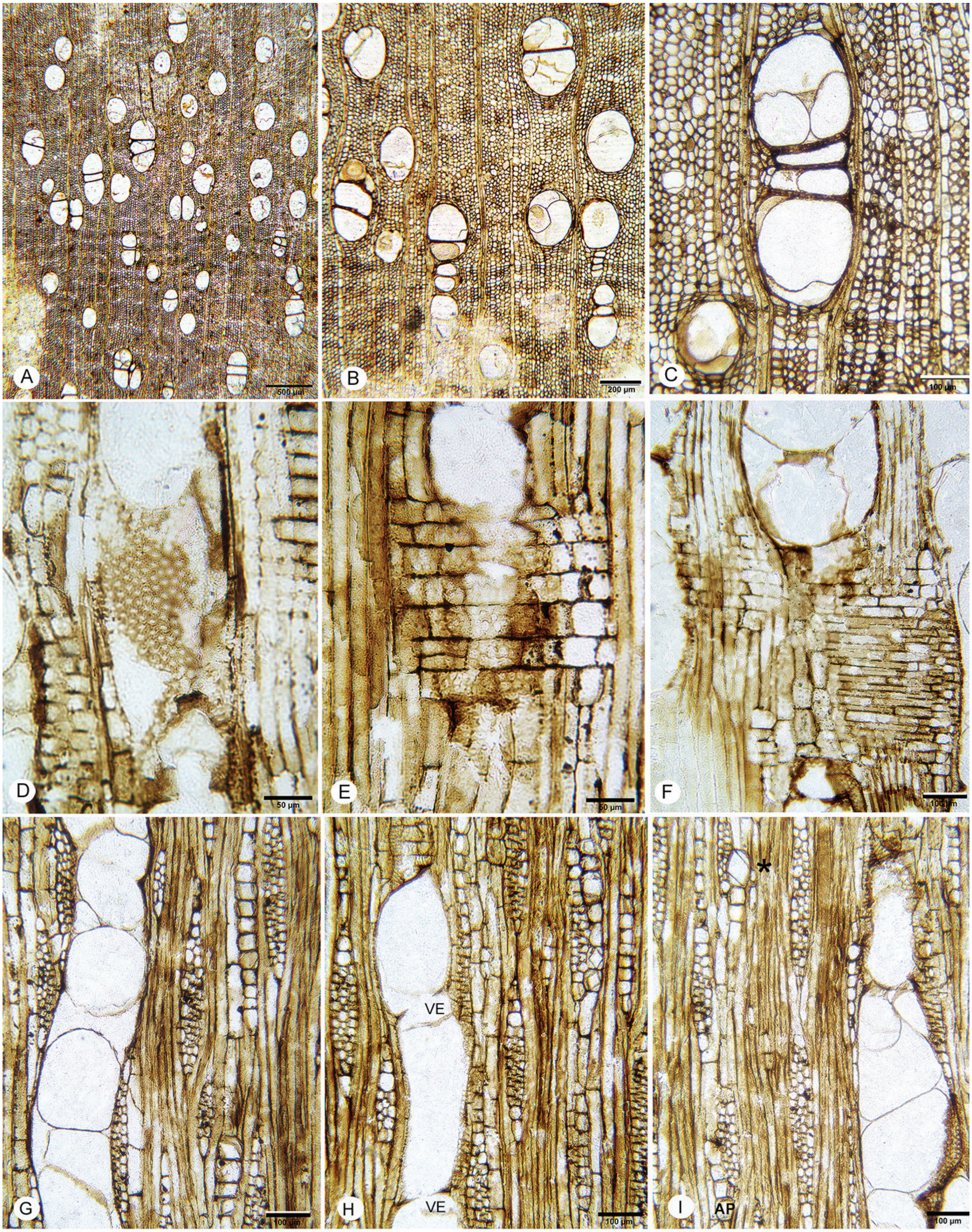

Figure 10. Caption on pg. 22.

Figure 10. Juglandaceae. *Carya leroyii* sp. nov., UF 278-84908. **A, B.** Semi-ring-porous wood with vessels solitary and in radial multiples, axial parenchyma in narrow bands throughout the growth ring, thin-walled tyloses, TS. **C**. Radial multiple of 4, thin-walled tyloses, marginal axial parenchyma, crystal-containing idioblasts, TS. **D**. Crowded alternate intervessel pits, RLS. **E**, Vessel-ray parenchyma pitting of similar size as intervessel pits, RLS. **F**. Body of ray composed of procumbent cells, RLS. **G**. Thin-walled tyloses in vessel, rays 2–3 (-4) seriate, crystals in chambered axial parenchyma cells, TLS. **H**. Oblique end walls of vessel elements (VE), rays 1–3 (-4) seriate, axial parenchyma strands with crystals. **I**. Crystals in enlarged axial parenchyma cell (*) and in chambered axial parenchyma (AP). Scale bars=500 µm in A; 200 µm in B; 100 µm in C, F, G. H, I; 50 µm in D, E.

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in chambered axial parenchyma; its heterocellular rays are consistent with earlier observations of Asian species (Itoh et al. 2022). Unfortunately, we do not have information on the Asian *C. hunanensis,* C.C. Cheng and R.H. Chang (1979) or *C. kweichowensis* Kuang and A.M. Lu (1979). Because of its heterocellular rays and abundant crystals, we suggest that UF 278-84908 is most similar to Asian *Carya* species.

Comparisons with fossil woods—The two juglandaceous woods of the nearby middle Eocene Nut Beds differ: *Clarnoxylon blanchardii* Wheeler and Manchester (2002) has prismatic crystals commonly occurring in enlarged ray parenchyma cells; *Engelhardioxylon nutbedensis* Wheeler and Manchester (2002) has both simple and scalariform perforation plates and prismatic crystals in ray parenchyma. *Pterocaryoxylon* Müller-Stoll and Mädel (1960) at the nearby Post Hammer locality (UF 279) lacks crystals entirely (Wheeler and Manchester 2021). There is at least one species of *Carya,* possibly two, in the Dietz Hill locality's carpoflora (Manchester and McIntosh 2007).

The classic treatment of fossil juglandaceous woods is Müller-Stoll and Mädel's 1960 paper, *Juglandaceen-Hölzer aus dem ungarischen Tertiär des pannonischen Becken*, which reviewed the anatomy of the family and all fossil woods assigned to the family by that time. None of the woods they described had the combination of features of UF 278-84908.

ROSALES Berchtold & J. Presl, 1820

URTICALEAN ROSIDS

Previously, the Cannabaceae Martinov (1820), Moraceae Gaudich. (1835), and Ulmaceae Mirbel (1815) were placed in the Order Urticales Juss. ex Bercht. and J. Presl (1820); they are now part of the Rosales (APG III) and informally referred to as urticalean Rosids. Three woods of this informal group, not assignable to family were found in the middle Eocene Clarno Nut Beds (Wheeler and Manchester 2002). The nearby Post Hammer locality (UF 279) has multiple samples of *Ulmus* L. (1753) (Wheeler and Manchester 2007) and one species of *Celtis* L. (1753) (Cannabaceae) (Wheeler and Manchester 2021). The Cannabaceae are represented in the fruit and seed flora of Dietz Hill (UF 278) by endocarps of *Aphananthe* Planchon (1848) (Manchester and McIntosh 2007).

At Dietz Hill, there are three samples (UF 278-84866, UF 278-84883, UF 278-62702) with features similar to *Ulmus woodii* Wheeler and Manchester (2007) from Post Hammer (UF 279). Additionally, we have found Dietz Hill (UF 278) woods with features found in the Cannabaceae and Moraceae. These are described below and compared in Table 3.

ULMACEAE Mirbel, 1815

Ulmus L. (1753)

cf. *Ulmus woodii* Wheeler and Manchester, 2007

Fig. 11A–F

Description—Growth ring boundaries distinct (1p). Wood semi-ring-porous to ring-porous (3p, 4p). Latewood vessels in radial multiples and clusters (11p) arranged in wavy tangential bands (6p) (Fig.11A–C). Mean tangential diameters of earlywood vessels 70 (SD=13) µm, range 48–87 µm. Perforation plates exclusively simple (13p, 14a). Intervessel pits crowded alternate (22p), polygonal in outline (23p), not vestured (29a), 7–11 µm in horizontal diameter (26p 27p); vessel-ray parenchyma pits similar in size to intervessel pits with borders somewhat reduced (31p) (Fig. 11D). Vessel element lengths 139–214 µm (n=7). Widely spaced thin-walled tyloses present.

Fibers non-septate (66p), pits not observed (62a).

Axial parenchyma paratracheal, non-crystalliferous strands usually 4 cells.

Rays mostly 3–5-seriate (98p), uniseriate rays not common (Fig. 11E,F); homocellular composed of procumbent cells (104p) (Fig. 11D); multiseriate ray heights average 267 µm (SD=95), range 146–444 µm.

Solitary prismatic crystals in chambered axial parenchyma strands, not in ray parenchyma (136p 138a 142p) (Fig. 11D,F).

Pith composed of thin-walled isodiametric parenchyma.

Specimens—UF 278-62702, 84866, 84880, 84883, estimated maximum diameters of 4 cm, 2 cm with pith, 1.1 cm with pith.

Comments—Because of the tyloses, we could only

Table 3. Comparison of urticalean woods. **POR**=porosity, **DP**=diffuse-porous, **SRP**=semi-ring-porous, **RP**=ring-porous; **V Grp**=vessel grouping, **S**=solitary, **Rm**=radiatl multiples; **V Arr**=vessel arrangement, **Ran**=random, **Diag**=diagonal; **IVP**=horizontal diameter of intervessel pits in µm; **VRP**=vessel-ray parenchyma pits, **Sim**=similar to intervssel pitting, **Red**=reduced borders to simple; **RW**=ray width in cell number; **Rcp**=ray cellular comosition, **Ho**=homocellular, **He**=heterocellular rays, number of marginal rows of upright/square cells in parentheses; **ShC**=sheath cells, **Ab**=absent, **Occ**=occasional; **Ax Par**=axial parenchyma distribution, **Sc**=scanty paratracheal, **V**=vasicentric, **Al**=aliform, **Cf**=confluent, **Bnd**=banded, **M**=marginal; **Cry**=crystals, **AB**=absent, **RP**=present in ray parenchyma, **A**=present in axial parenchyma; **?**=no information; *****=small axis.

UF.278 WOODS	POR	V Grp	V Arr	IVP	VRP	RW	Rcp	ShC	Ax Par	Cry
Urticaleoxylon stevensii/ UF 278-84893	SRP	S-Rm (2–3)	Ran	8–11	Sim/ Red	1–6	Ho, He (1)	Ab	Sc, V, Al, Cf, M	RP
Moroxylon?/UF 278-84899	RP	S-Rms (Cl)	Diag	8–11	Sim/ Red	1–3 (–4)	Ho, He (1–2)	Ab	Cf, M	Ab
Cannabaceae/Moraceae Wood Type 1UF 278-84894	DP	S-Rm (2–3)	Ran	8 –12	Sim/ Red	1–6	Ho, He	Occ	Sc, V, M	Ab
Cannabaceae/Moraceae Wood Type 2UF 278-84906	? *	S-Rm (2–3)	Ran	8–13	Red	to 6	He	Occ	Vc, Cf ?	RP
NUT BEDS										
Scottoxylon eocenicum	DP	S-Rm	Ran	5 –12	Red	1–7	Ho, He	Occ	V, Al, Cf, M	Ab
Clarno Urticalean Wood I	DP	S-Rm	Ran	8–12	Red	1–8	Het	Ab	Bnd	RP
Clarno Urticalean Wood 2	DP	S-Rm	Ran	5–8	Sim/ Red	1–4	Het	Ab	V, Al, Cf	RP (A)

measure seven vessel element lengths.

Comparisons with extant and fossil woods—These Dietz Hill (UF 278) specimens are small axes so we did not use quantitative features in our searches of InsideWood. We used the IAWA features given in the description above to search InsideWood, varying porosity type.

The search of the modern wood database using ring-porosity (3p) yielded *Maclura pomifera* (rays consistently narrower, latewood clusters not as discrete as in this wood, tyloses closely spaced and bubble-like) and eight species of *Ulmus.* Results of a search of the IW fossil wood database, excluding incomplete descriptions, returned one species of *Ulmoxylon* and two species of *Ulmus.* When semi-porosity is used, only two fossil wood species are returned *U. danielii* Wheeler and Manchester (2007) and *U. woodii* Wheeler and Manchester (2007), both from the nearby Post Hammer (UF 279) locality. *Ulmus danielii* varies from diffuse-porous to semi-ring-porous, while *U. woodii* varies from semi-ring-porous to ring-porous. Thus, we consider UF 278-84866, 84883, and 62702 to belong to *U. woodii.*

MORACEAE Dumort, 1829

cf. *Moroxylon* Selmeier, 1933

Fig. 12A–F

Description—Growth rings present, marked by radially narrow fibers, and marginal axial parenchyma (Fig. 12A, B).

Wood ring-porous; earlywood zone narrow with 1–2 rows of earlywood vessels that are rounded in outline (Fig. 12A–C); mean tangential diameter of earlywood vessels 91 µm (SD=16), range 67–132 µm; latewood vessels often in a diagonal arrangement, solitary and in radial multiples (Fig. 12B), vessel clusters uncommon. Perforation plates simple (Fig. 12D–F); intervessel pits alternate, polygonal in outline (Fig. 12D), horizontal diameter 8–11 µm. Vessel-ray parenchyma pits similar in size to intervessel pits (Fig. 12F). Vessel elements short, typically less than 200 µm. Thin-walled tyloses. Helical thickenings not observed.

Fibers thin- to thick-walled, mostly non-septate, occasionally septate (Fig. 14D, E), pitting not observed. Vasicentric/vascular tracheids absent.

Axial parenchyma marginal and confluent (Fig. 12A–C); strands of 2–4 cells (Fig. 14D, E).

Rays 1–3 (-4) seriate; uniseriate rays rare, average multiseriate ray height 263 (SD=65) µm, 166–432 µm. Rays homocellular, composed of procumbent cells, and heterocellular with 1-2 marginal rows of square/upright cells (Fig. 12D–F), rarely more, 4–6 per mm.

Storied structure and oil/mucilage cells not observed.

Specimen—UF 278-84899, estimated maximum diameter 4 cm.

Occurrence—Dietz Hill (UF 278).

Comments—The intervessel pits and most of the vessel-ray parenchyma pits have a similar size, but we

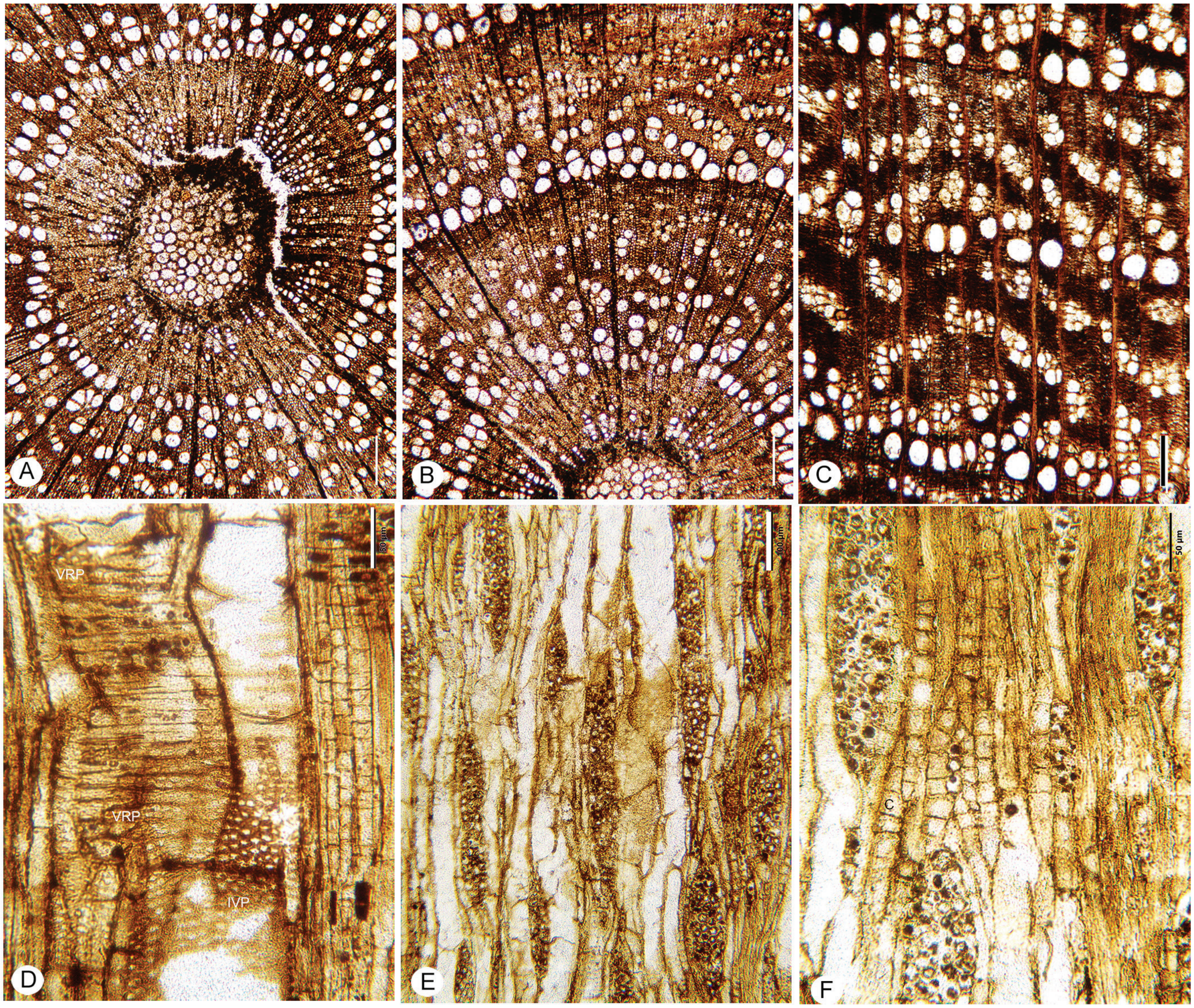

Figure 11. Ulmaceae. *Ulmus woodii.* **A.** Pith composed of isodiameteric parenchymatous cells, first ring of wood with vessels mostly solitary and in radial alignment, TS, UF 278-84883. **B.** Rings 2 and 3 semi-ring-porous, TS, UF 278-84883. **C.** Outermost rings of the sample, latewood vessels in radial multiples and clusters in a ulmiform pattern, UF 278-84866. **D–F.** Rays composed of procumbent cells, crowded alternate intervessel pits (IVP), vessel-ray parenchyma pits (VRP) of similar size to intervessel pits, crystalliferous axial parenchyma strands (C), RLS, UF 278-62702. **E**. Ray mostly 3–5-seriate, uniseriate rays rare, TLS. **F**. Multiseriate rays, and crystalliferous axial parenchyma strands (C), TLS. Scale bars=200 µm in A–C; 100 µm in E; 50 µm in D, F.

found it difficult to determine whether the vessel-ray parenchyma pits did or did not have reduced borders. The occurrence of tyloses suggests that they have reduced borders (Chattaway 1949, Bonsen and Kucera 1990, Wheeler et al. 2007).

Comparisons with modern woods—We searched InsideWood for ring-porous woods (3p) with vessels solitary and in short radial multiples (9a 10a), latewood with a diagonal pattern (7p), simple perforation plates (13p), alternate intervessel pitting that is not minute (22p 24a), vessel-ray parenchyma pitting both similar to intervessel pits (30p) and with reduced borders to apparently simple (31p), non-septate fibers with simple pits (61p 66p), confluent axial parenchyma (83p), rays not exclusively uniseriate or >10-seriate (96a 99a), rays not comprised of all upright cells (105a) and not markedly heterocellular (108a), storied structure absent (118a 120a), oil/mucilage cells absent (124–126a), and radial canals absent (130a).

This search with 30p and 31p gave two exact matches: *Celtis australis* L. (1753) and *Broussonetia papyrifera* (L.) l'Hér. ex Vent (1799). If only 30p is used, the results also include *Catalpa bignonioides* Walter., *Ca. speciosa* Teas (1875; Bignoniaceae), *Celtis tournefortii* Lam. (1797;

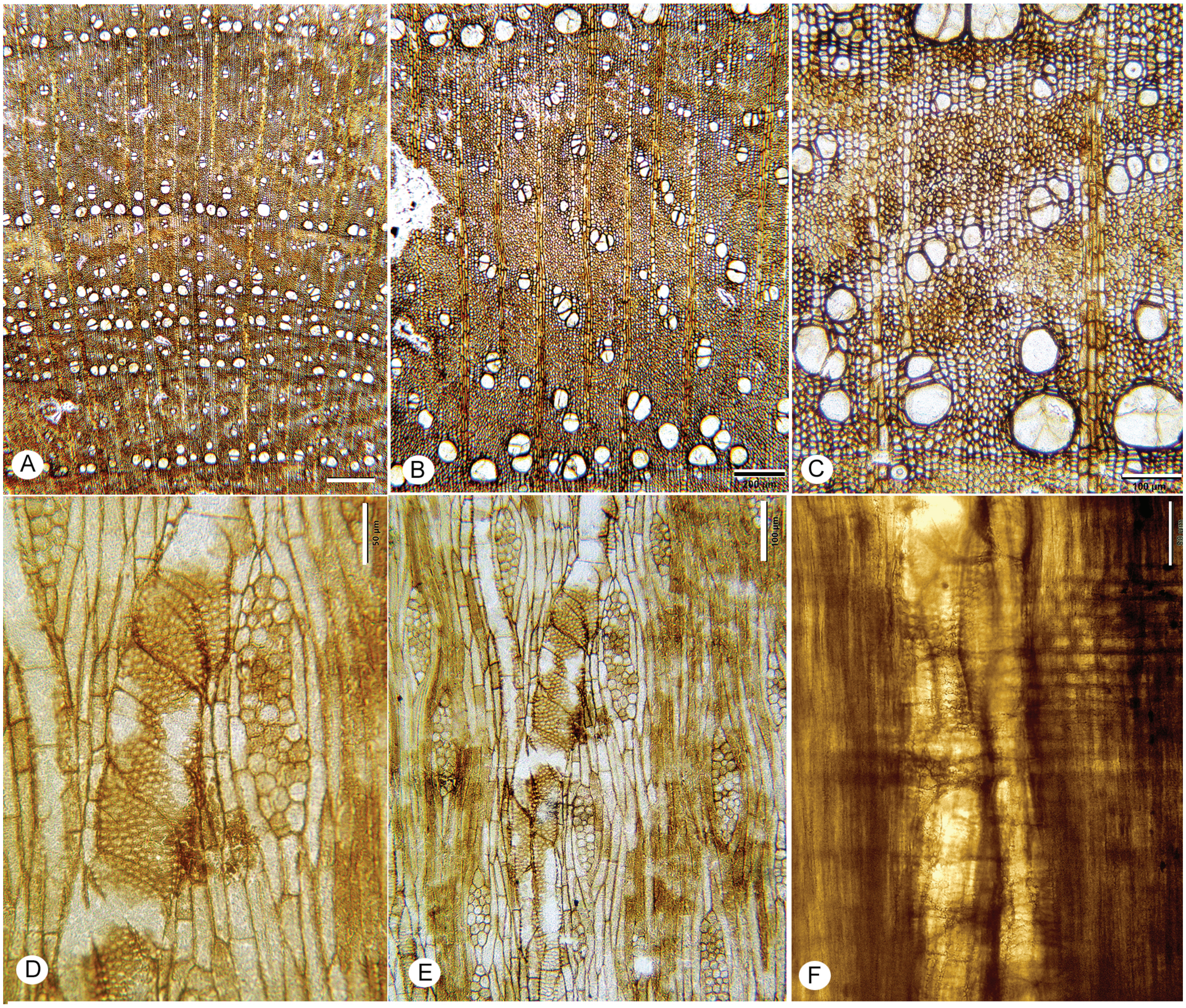

Figure 12. Urticales. cf. *Moroxylon* sp., UF 278-84899. **A–C**. Ring-porous wood, with distinct earlywood zone 1–2 vessels deep, latewood vessels solitary and in radial multiples in a diagonal pattern, TS. **D**. Crowded alternate pits, axial parenchyma strands of 2–4 cells. TLS. **E**. Vessel elements with inclined end walls, rays predominantly 3-seriate, axial parenchyma strands of 2–3 cells, TLS. **F**. Simple perforation plates, crowded alternate intervessel pits, vessel-parenchyma pits of similar size to intervessel pits; ray parenchyma cells square and weakly procumbent, RLS. Scale bars=500 µm in A; 200 µm in B; 100 µm in C, E; 50 µm in D, F.

Cannabaceae), *Ehretia acuminata* R.Br. (1810; Boraginaceae Juss.,1789), *Gymnocladus dioicus* (L.) K. Koch (1869), *Platyosprion platycarpum* Maxim. (1877; Fabaceae), *Melia azedarach* L. (1753; Meliaceae), *Phellodendron chinense* C.K. Schneid. (1907), *Ptelea trifoliata* L. (1753; Rutaceae Juss., 1789). If only 31p is used, the results also include *Rhus chinensis* Mill. (1768; Anacardiaceae) and *R. virens* Lindh. ex A. Gray (1850), *Ce. biondi* Pamp. (1910; Cannabaceae), *Ce. bungeana* Blume (1852), *Ce. jessoensis* Koidz., *Morus alba* (Moraceae), *Mo. cathayana* Hemsl. (Forbes and Hemsley, 1894), and *Mo. serrata* Roxb. (1832). It seems most probable that this wood belongs to the Urticales group.

Narrow earlywood zones as seen in this wood are fairly common in *Celtis* as shown by a review of images in the Chinese Wood Atlas (Itoh et al. 2022), e.g., *Ce. biondi, Ce. bungeana, Ce. sinensis* Pers. (1805), *Ce. tetrandra* Roxb. (1832), *Ce. vandervoetiana* C.K. Schneid. (Sargent 1917). InsideWood's image collection shows this feature also occurs in *Ce. australis. Ce. laevigata* Willd. (1814), and *Ce. occidentalis* L. (1753). However, these species usually have obvious vessel clusters in latewood, unlike this fossil, and wider rays, usually with obvious sheath cells. Also, prismatic crystals occur in all *Celtis* woods described to date. Septate fibers do not occur in the Cannabaceae.

Earlywood zones with 1–2 rows of wide vessels also occur in some samples of ring-porous *Morus,* e.g., *Mo. alba, Mo. australis* Poiret (1796)*, Mo. bombycis* Koidz. (1915a)*, Mo. cathayana, Mo. kagayamae* Koidz. (1915b) (FFPRI's Wood Database, https://db.ffpri.go.jp/WoodDB/index-E.html). Vessel clusters and prismatic crystals are not constant features of *Morus*. Consequently, we suggest this wood's affinities are most likely with the Moraceae.

Comparison with fossil woods—We used InsideWood's fossil wood menu to search the fossil wood database and used the features: wood ring-porous (3p), vessels not in dendritic arrangement or exclusively solitary or commonly in radial multiples of four or more (8–10a); simple perforation plates (13p); intervessel pits alternate and not minute (22p, 24a); fibers with simple pits (61p); confluent axial parenchyma (83p), rays between 2–10 cells wide (96a, 99a) and not composed of all upright/square cells or markedly heterocellular (105a, 108a); tile cells, storied structure, radial canals, and oil/mucilage cells all absent (111a, 303a, 120a, 130a, 304a). Ignoring the fossil wood descriptions with a majority of features coded as unknown (?), a search allowing no mismatches returned two Cannabaceae, one Moraceae, one legume, one Rutaceae, and an Ulmaceae. The Cannabaceae, the legume, the Rutaceae, and the Ulmaceae are not good matches as they commonly have vessels in clusters and vessels in wavy tangential bands.

Moroxylon Selmeier (1993) is diagnosed as having latewood vessels commonly in clusters and in ulmiform tangential bands. However, vessel clusters do not look common in Selmeier's figures 3, 4, and 13 and the vessel arrangement appears as much diagonal/oblique as tangential. *Moroxylon sturmii* Selmeier (1993) differs from this Dietz Hill wood in having an earlywood zone more than 1–2 vessels deep, occasional sheath cells and prismatic crystals in upright/square ray cells (Table 3). We think that the similarities between them are such that we are referring this wood to cf. *Moroxylon.*

FAMILY INDET.

URTICALEOXYLON GEN. NOV.

Diagnosis—Growth ring boundaries marked by marginal parenchyma. Wood semi-ring-porous to diffuse porous, vessels solitary and in radial multiples of 2–3, rarely more. Perforation plates exclusively simple. Intervessel pits alternate, medium to large in horizontal diameter; vessel-ray parenchyma pits oval to horizontally elongate, simple or with reduced borders. Non-septate and septate fibers present. Axial parenchyma marginal, scanty paratracheal, vasicentric, and in latewood some aliform-confluent. Rays homocellular composed of procumbent cells to heterocellular with one (rarely more) marginal row of upright to square cells. Crystals, if present, in marginal ray cells.

Etymology—Name to indicate a wood with features found in urticalean families.

URTICALEOXYLON STEVENSII SP. NOV.

FIG. 13A–I

Diagnosis—Same as genus.

Holotype—UF 278-84893, estimated maximum diameter 8 cm.

Occurrence—Dietz Hill (UF 278).

Etymology—Named for Peter F. Stevens in thanks for the creation and maintenance of Angiosperm Phylogeny Website.

Description—Growth rings present, marked by radially narrow fibers, and marginal axial parenchyma (Fig. 13A–C). Wood semi-ring-porous; vessels solitary and in radial multiples of 2–3 (rarely 4) (Fig. 13A); mean tangential diameter of earlywood vessels 119 µm (SD=18), range 78–150 µm. Perforation plates simple (Fig. 13E, F, H, I); intervessel pits alternate (Fig. 13D), horizontal diameter 8–11 µm. Vessel-ray parenchyma pits horizontally elongate, simple or with reduced borders (Fig. 13E). Mean vessel element length 377 (SD=148) µm; range 153–594 µm vessel element end walls inclined to nearly horizontal. Thin-walled tyloses (Fig. 13D, I).

Fibers thin- to thick-walled, mostly non-septate, occasionally septate, pitting not observed (Fig. 13H, I).

Axial parenchyma marginal, scanty paratracheal, vasicentric, more abundant in the latest latewood with some aliform-confluent (Fig. 13B, C); strands of 2–4 cells (Fig. 13H, I).

Rays 1–6 seriate, mostly 4–5-seriate; uniseriate rays short, usually less than five cells high (Fig. 12G–I); average multiseriate ray height 448 (SD=199) µm, 216–878 µm. Rays homocellular, composed of procumbent cells, and heterocellular with 1–2 marginal rows of square/upright cells, rarely more; 4–6 per mm.

Occasional solitary prismatic crystals in upright marginal ray cells (Fig. 13H, I).

Storied structure and oil/mucilage cells not observed.

Comments—Fine fungal hyphae are common in the sample and can be confused with septate fibers. Most fibers appear non-septate, but there are a few septate fibers as well.

Comparisons with extant plants—We searched

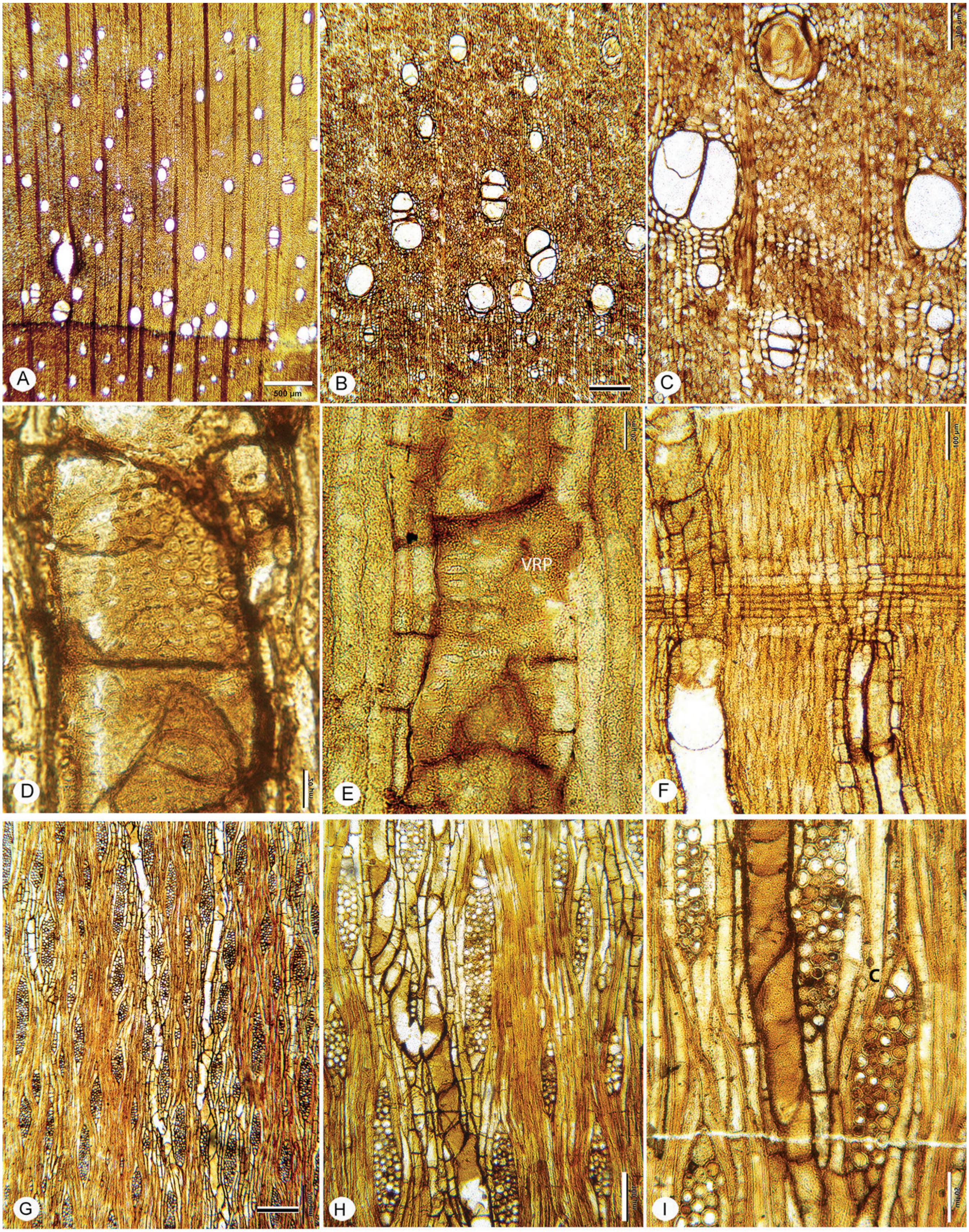

Figure 13. Caption on pg. 28.

Figure 13. Urticales. *Urticaleoxylon stevensii,* sp. nov., UF 278-84893. **A**. Wood semi-ring-porous, vessels solitary and in radial multiples. **B, C.** Vessels solitary and radial multiples of 2–3; marginal, scanty paratracheal, and vasicentric axial parenchyma. **D**. Alternate intervessel pitting, oval to slightly angular in outline, thin-walled tyloses. **E**. Vessel-ray parenchyma pits (VRP) horizontally elongated. **F**. Ray composed of procumbent body cells and square to upright marginal cells, simple perforation plates, axial parenchyma strands adjacent to vessels. **G, H.** Rays 1 to 4–5-seriate, multiseriate rays usually with one marginal square/upright cell; uniseriate rays not common, axial parenchyma strands of four cells. **I.** Solitary prismatic crystal (C) in marginal ray cell, widely spaced thin-walled tyloses. Scale bars=500 µm in A; 200 µm in B, G; 100 µm in C, F, H; 50 µm in I; 20 µm in D, E.

InsideWood multiple times using slightly different combinations of features. In all searches we used: presence of distinct growth ring boundaries (1p), wood semi-ring-porous (4p), absence of exclusively solitary vessels, distinct vessel arrangement, and radial multiples of 10 or more common (6a, 7a, 8a, 9a, 10a), presence of simple perforation plates and alternate intervessel pits that are not minute (13p, 22p, 24a), vessel-ray parenchyma pits with reduced borders and horizontally elongate (32p), non-septate fibers with simple pits (61p, 66p), vasicentric axial parenchyma (79p), maximum ray width 4-10-seriate (98p), rays not composed of all upright cells or markedly heterocellular or with intermixed procumbent and square/upright cells (105a, 108a 109a), storied structure and oil/mucilage cells absent (118a, 120a, 124a 125a 126a), radial canals absent (130a), prismatic crystals in square/upright ray cells (136p, 137p).

A search using the features listed above and not allowing mismatches returned only Cannabaceae (*Celtis*) and Moraceae (*Morus* L., 1753; *Maclura* Nutt., 1818). Semi-ring-porous *Celtis* commonly have vessel clusters and the diffuse-porous species have more axial parenchyma. Axial parenchyma is much more abundant and there are more vessel multiples in *Maclura* (ter Welle et al., 1986). A search allowing a single mismatch returned *Antiaris* Lesch. (1810) and *Helicostylis* Trécul (1847), both Moraceae. When we added presence of both septate and non-septate fibers (65p 66p), there were no matches, but allowing one mismatch also returned Cannabaceae (*Celtis*) and Moraceae (*Antiaris, Morus,* and *Maclura*) as well as a *Toxicodendron* Mill. (1754; Anacardiaceae R. Brown, 1818a) differing in ray size and appearance of vessel-ray parenchyma pits; *Vitex* L. (1753) spp. (Verbenaceae J. Saint-Hilaire, 1805), which only has septate fibers; *Cedrela* P. Browne (1756) (Meliaceae Jussieu , 1789)), which can be excluded because of its small intervessel pits and vessel-ray parenchyma pits being similar to the intervessel pits.

Porosity in present-day *Celtis* and *Morus* woods varies, with temperate zone species being ring-porous, subtropical species semi-ring-porous to diffuse-porous, and tropical species diffuse-porous. There is also variation within species. The FFPRI's Database of Japanese Woods (https://db.ffpri.go.jp/WoodDB/JWDB-E/home.php) has images of multiple samples of *Morus alba* L. (1753), *M. boninensis* Koidz. (1917) and *Broussonetia papyrifera* (L.) L'Hér. ex Vent. (1799). Most are ring-porous with latewood vessels in clusters tending to be arranged in wavy tangential bands, but some samples have porosity, vessel grouping and arrangement similar to UF 278-84893: *Mo. alba* (TWTw 17381); *B. papyrifera* (TWTw 19291, TWTw 23325). One of the two FFPRI samples of *Mo. bonienesis* (TWTw 10933) also is similar.

Kew's Plants of the World accepts 19 species of *Morus* (POWO 2023)*;* ter Welle et al (1986) described the wood anatomy of seven species; InsideWood has descriptions and/or images of eleven species.

We infer that this Dietz Hill (UF 278) wood belongs to the group of families once placed in the Urticales, but now considered to belong to the Rosales and informally referred to as the urticalean rosids.

Consequently, we propose the genus *Urticaleoxylon* to accommodate such woods.

Comparisons with fossil plants—There are no fossil woods in the InsideWood database that exactly match the criteria used to search the modern wood database.

Celtis popsii Wheeler and Manchester (2021) occurs at the Post Hammer location (UF 279). It differs from this Dietz Hill (UF 278) wood because its latewood vessels are in clusters arranged in wavy tangential bands, rays are of two size classes, and sheath cells are present.

At the older middle Eocene Nut Beds locality, there were three woods placed in the Urticales (Wheeler and Manchester 2002). *Scottoxylon eocenicum* Wheeler and Manchester (2002) was one of the most common Clarno Nut Beds woods with more that 50 samples. It differs from this Dietz Hill (UF 278) woods as axial parenchyma is more common, rays are larger, and none of the samples had crystals. Doweld (2021) proposed that *Scottoxylon* be replaced because it was a homonym of an earlier genus name, *Scotoxylon* Vogellehner (1968); unfortunately, the name he proposed, *Alloceltidoxylon* Doweld (2021), implies affinities with *Celtis.* We retain *Scottoxylon* because it was validly published (note this spelling differs from *Scotoxylon* Vogellehner; the botanical code of nomenclature recommends against, but does not prohibit, similar spelling. Clarno Urticalean Wood Types I and II also had more abundant axial parenchyma than is known for *Celtis*.

CANNABACEAE/MORACEAE WOOD TYPE 1

Fig. 14A–F

Description—Growth rings present, marked by radially narrow fibers, and marginal axial parenchyma. Narrow latewood vessels in the marginal parenchyma bands (Fig. 14A, B).

Wood diffuse-porous; vessels solitary and in radial multiples of 2–3 (Fig. 14A, B); mean tangential diameter of vessels 164 µm (SD=27), range 118–218 µm; 6–10 vessels per mm². Perforation plates simple; intervessel pits alternate (Fig. 14C), horizontal diameter 9–12 µm. Vessel-ray parenchyma pits similar in size to the intervessel pits, simple or with reduced borders (Fig. 14D). Vessel element lengths short, <350 µm; vessel element end walls slightly inclined. Thin-walled tyloses present.

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

Axial parenchyma marginal, scanty paratracheal to vasicentric (Fig. 14A, B); strands of 4–8 cells.

Rays (1–2) 3–6 seriate, mostly 4–5-seriate; uniseriate rays rare; average multiseriate ray height 489 (SD=180) µm, range 191–842 µm. Rays homocellular, composed of procumbent cells, and heterocellular with 1-2 marginal rows of square/upright cells, rarely more (Fig. 14F); sheath cells in some rays (Fig. 14C); 4–7 per mm.

Storied structure, oil/mucilage cells, and crystals not observed.

Specimen—UF 278-84894, estimated maximum diameter 20+ cm.

Occurrence—Dietz Hill (UF 278).

Comparisons with extant woods—Our initial search of InsideWood used: presence of distinct growth ring boundaries (1p), wood diffuse-porous (5p), absence of exclusively solitary vessels, distinct vessel arrangement, and radial multiples of ten or more common (6a, 7a, 8a, 9a, 10a), presence of simple perforation plates and alternate intervessel pits that are not minute or small (13p, 22p, 24a 25a), vessel-ray parenchyma pits with reduced borders (31p), non-septate fibers with simple pits (61p, 66p), scanty paratracheal, vasicentric axial parenchyma and marginal parenchyma present (78p, 79p. 89p), maximum ray width 4–10-seriate (98p), rays not >1mm or of two sizes (102, 103a), rays not composed of all upright cells or markedly heterocellular or with intermixed procumbent and square/upright cells (105a, 108a 109a), sheath cells present (110p), storied structure and oil/mucilage cells absent (118a, 119a, 120a, 124a 125a 126a), radial canals required absent (130e). If no mismatches are allowed, this particular search only returns *Morus* spp.

Allowing one mismatch returns *Morus* spp. again, two species of *Celtis* (Cannabaceae), and *Petersianthus* Merrill (1916) (Lecythidaceae A. Rich. (1826b). The last genus can be excluded because its parenchyma is aliform-confluent and diffuse-in-aggregates to narrow bands. According to Kew’s Plants of the World (POWO 2023), there are 17 accepted species of *Morus* and 66 accepted species of *Celtis.*

Of the images of diffuse-porous woods of Moraceae in InsideWood, it looked as if only *Morus insignis* Bureau (1873) (Uw 24976) had axial parenchyma distribution similar to this Dietz Hill wood, all others had more abundant axial parenchyma. In the Chinese Atlas (Itoh et al. 2022), diffuse-porous *Morus* also appear to have more abundant axial parenchyma. The diffuse-porous *Mo. macroura* Miq. (1851) (TWTw 13642) and *Celtis africana* Burm. f. (FPAw 31962, Kw IND.845) both appear to have narrow vessel elements embedded in seemingly marginal parenchyma. has narrow vessel elements embedded in seemingly marginal parenchyma.

This wood has a combination of features found in *Celtis* and *Morus.*

Comparisons with fossil woods—When no mismatches are allowed, the only matches in the fossil wood database were two descriptions with most features coded as unknowns. If one mismatch is allowed, *Scottoxylon eocenicum* (Urticales, family unknown) from the middle Eocene Clarno Nut Beds is returned (Wheeler and Manchester 2002), but it has more axial parenchyma as does the other result, *Dracontomeloxylon palaeomangiferum* Prakash (1979) from the Deccan Intertrappean Beds. There does not appear to be a previously described fossil wood that is a good match for this Dietz Hill wood. Because of this wood's resemblance to both *Celtis* (Cannabaceae) and *Morus* (Moraceae) we refer to it as Cannabaceae/Moraceae Wood Type 1.

CANNABACEAE/MORACEAE WOOD TYPE 2

Fig. 15A–I

Description—Growth rings distinct (Fig. 15A, B), ring width 0.2–0.9 mm. Wood ring-porous or semi-ring porous. Wide vessels in earlywood solitary and in pairs, tangential diameters average 182 (SD 29) µm, range 123–247 µm; narrow vessels solitary, in radial multiples, and occasionally in clusters (Fig. 15A, B). Perforation plates exclusively simple (Fig. 15C); intervessel pitting crowded alternate, oval to polygonal (Fig. 15D, E), 8–11–13 µm in horizontal diameter; vessel-ray parenchyma pits with

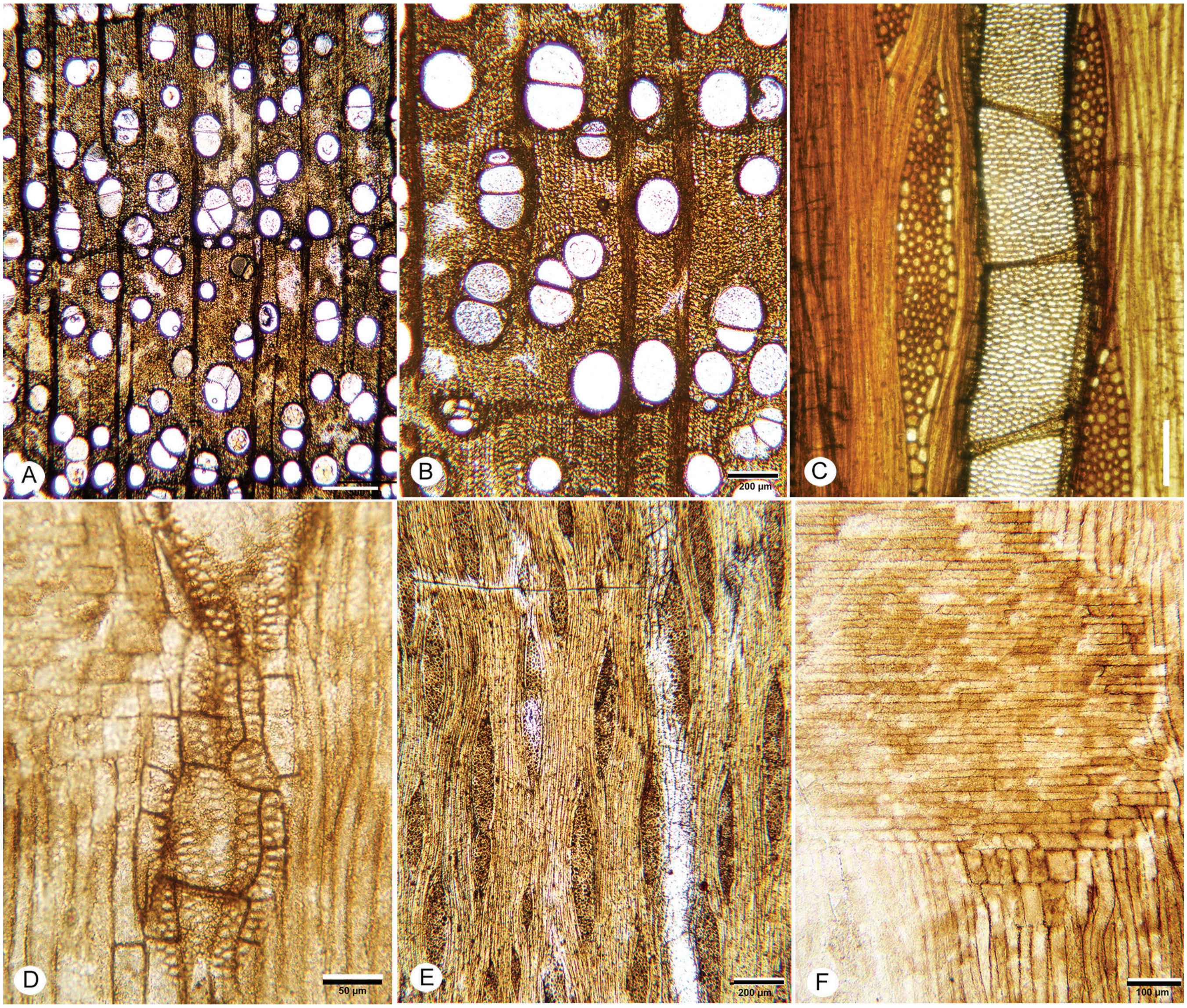

Figure 14. Urticales. Cannabaceae/Moraceae Wood Type 1. UF 278-87894. **A, B**. Wood diffuse-porous, vessels solitary and in radial multiples; marginal parenchyma, TS. **C.** Alternate intervessel pitting, polygonal in outline, simple perforation plates, ray with sheath cells, TLS. **D**. Vessel to parenchyma pits, similar in size to intervessel pitting with reduced borders, RLS. **E**. Rays predominantly multiseriate, 1-2-seriate rays rare, TLS. **F**. Ray body cells procumbent, marginal row of upright/square cells, RLS. Scale bars–500 µm in A; 200 µm in B, E; 100 µm in F; 50 µm in C, D.

reduced borders, oval in outline (Fig. 15F). Helical thickenings observed in some of the narrowest vessels (Fig. 15C). Vessel element lengths difficult to measure because of the abundant tyloses (Fig. 15G), 205–333 µm (n=3).

Axial parenchyma hard to distinguish in cross sections, probably vasicentric, confluent, and marginal (initial) bands, commonly in strands of 2–4 (Fig. 15D).

Rays commonly 4–5 (–6)-seriate, uniseriate rays rare (Fig. 15G); multiseriate rays heterocellular with procumbent body cells and usually 1–3 (-4) marginal rows of square to upright cells (Fig. 15H), weakly defined sheath cells in a few rays (Fig. 15G); average multiseriate ray height 295 (SD=99) µm, range 128–539 µm; ~4-5 rays per mm. Non-storied.

Solitary prismatic crystals occasional in upright ray cells (Fig. 15I)

Specimen—UF 278-84906, estimated maximum diameter 11 cm.

Occurrence—Dietz Hill (UF 278).

Comments—It is difficult to determine if this is a vine or a ring-porous wood (shrub, sapling, or tree branch) with very narrow growth rings. The cross-sectional areas of woody vines typically have a high proportion of vessels (e.g., Carlquist 1991, Baas et al. 2004, Angyalossy

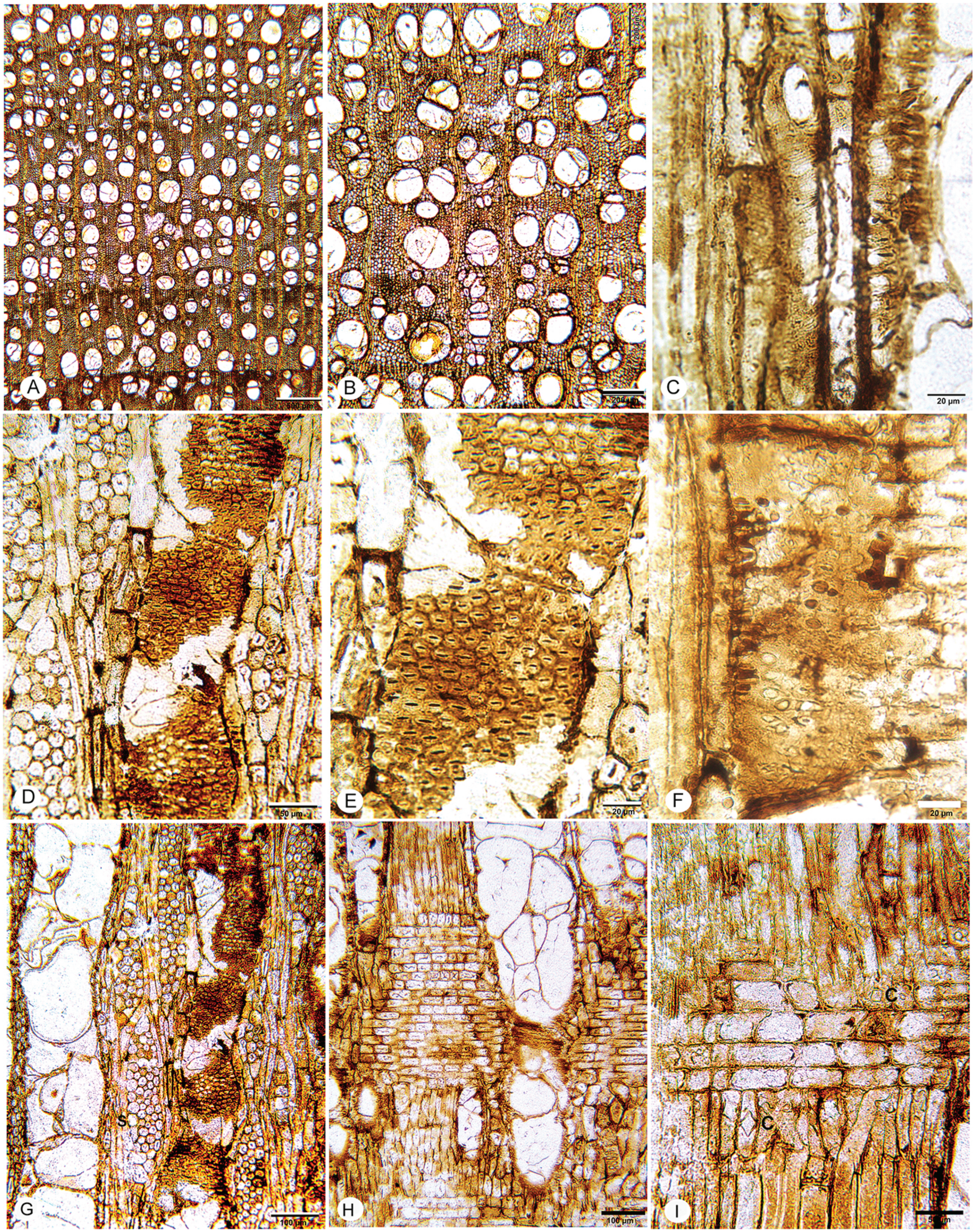

Figure 15. Caption on pg. 32.

Figure 15. Urticales, Cannabaceae/Moraceae Wood Type 2. UF 278-84906. **A, B**. Distinct growth rings, vessels solitary and in short radial multiples, occasional clusters; thin-walled tyloses, TS. **C.** Simple perforation plate in narrow vessel element with helical thickenings, RLS. **D**. Series of vessel elements with crowded alternate intervessel pitting, angular in outline, TLS. **E**. Crowded alternate intervessel pitting, TLS. **F.** Vessel-ray parenchyma pitting with reduced borders, round to oval in outline, RLS. **G**. Thin-walled tyloses, rays predominantly multiseriate, weakly differentiated sheath cells (S), ray cells polygonal in outline, TLS. **H**. Heterocellular rays with procumbent body cells; thin-walled tyloses, RLS. **I**. Heterocellular ray, crystals (C) in square and upright ray cells, RLS. Scale bars=500 µm in A; 200 µm in B; 100 µm in G, H; 50 µm in D, I; 20 µm in C, E, F.

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et al. 2015), as is seen in this fossil. When ring-porous arborescent plants have narrow growth rings, those rings will consist mostly of earlywood and have a high proportion of vessels; consequently, samples from such areas can resemble woody vines (see Fig. 8 in IAWA Committee 1989).

Moreover, because of the narrow rings the porosity type is not obvious. Other difficulties with this sample include: 1) determining latewood vessel arrangement because of the narrow growth rings, and 2) differences between fibers and axial parenchyma in transverse section are not obvious, so axial parenchyma distribution is difficult to determine, but given the parenchyma strands visible in longitudinal sections, we suspect marginal (wide initial bands) as well as vasicentric and confluent are present.

Comparisons with modern woods—We began by searching InsideWood's modern wood database for this combination of features: 1p (growth rings distinct), vessels not exclusively solitary (9a), exclusively simple perforation plates (13p 14a), intervessel pits alternate, polygonal in outline and medium- to large-sized (22p, 23p, 24a, 25a), vessel-ray parenchyma pits with reduced borders (30a), helical thickenings in narrower vessel elements (39p), tangential vessel diameter not narrow (40a, 41a), tyloses common (56p), non-septate fibers with simple pits (61p, 66p), larger rays 4–10-seriate (98p), less than 1 mm high (102a), not of two distinct sizes (103a), heterocellular with procumbent body cells (104a, 105a, 109a), tile cells absent (111a), storied structure, radial canals, and oil/mucilage cells absent (118–121a, 124–126a, 130a). This search returned six matches: *Rhus chinensis* Mill. (1768) (Anacardiaceae), *Celtis laevigata* (Cannabaceae), *Maclura pomifera* (Raf.) C.K. Schneid. (1906), *Morus alba, Mo. nigra* L. (1753), *Mo. rubra,* and *Mo. serrata* Roxb. (Moracee). We think it unlikely that this fossil has affinities with *Rhus* because ray structure and appearance are quite different. Both *Celtis* and *Maclura* include species that are ring-porous or vines. Consequently, we suggest that this wood has affinities with the urticalean group, and most probably with Moraceae. According to ter Welle et al. (1986), the climber *Maclura cochinchinensis* (Lour.) Corner (1962) ranges from Sri Lanka and India to China and Japan, and throughout the Malesian Archipelago; it has variable anatomy and includes samples that are semi-ring- to ring-porous and that have helical thickenings.

Comparison with fossil woods—When we searched the Fossil Hardwood database using equivalent features in the Fossil Hardwood menu for that database, the results only included descriptions with most diagnostic features coded as unknown. Allowing one mismatch, returned 17 matches, 12 of which lack information on vessel-ray parenchyma pitting. Among the results were two reports of *Moroxylon xinhuanensis* Yin, Liu, and Cheng (2013), a distinctly ring-porous wood from the Neogene of China (Yin et al. 2013, Cheng et al. 2018). It is possible that UF 278-84906 is a ring-porous wood with narrow rings, but the diagnosis of *Moroxylon* Selmeier (1993) includes "groups of small vessels, especially in the latewood, forming a pattern of tangential or discontinuous oblique bands" and in this wood with its narrow rings that is not visible. Although it is likely this wood is Moraceae, we think it better to refer to it as Cannabaceae/Moraceae Wood Type 2 because of the possibility of a relationship with *Celtis.*

SAPINDALES

SAPINDACEAE Jussieu, 1789

AESCULUS L., 1753

AESCULUS CONSTABULARISII SP. NOV.

Fig. 16A–L

Diagnosis—Wood diffuse-porous to semi-ring-porous. Vessels solitary and in short radial multiples. Mean tangential diameters <100 µm. Perforation plates simple, intervessel pits alternate, small to medium; vessel-ray parenchyma pits similar to intervessel pits. Widely spaced helical thickenings throughout the vessel elements.

Fibers non-septate.

Axial parenchyma not common, some scanty paratracheal and marginal.

Rays exclusively uniseriate; homocellular, composed of procumbent cells, non-storied.

Holotype—UF 278-84887, estimated maximum diameter 10+ cm.

Etymology—Named for Adam Constabularis, NC State Library IT guru, who watches over the InsideWood web site.

Occurrence—Dietz Hill (UF 278).

Description—Growth rings present, marked by radially narrow fibers.

Wood diffuse-porous to semi-ring-porous with a concentration of vessels at the beginning of a growth ring (Fig. 16A–C); vessels solitary and in radial multiples of 2–3 (rarely 4–5); mean tangential diameter 83 (17) µm, range 44–105 µm; 61–74 vessels/mm^2. Perforation plates simple (Fig. 16E–F, J, K); intervessel pits alternate (Fig. 16G), horizontal diameter 5.5–7.5 µm. Vessel-ray parenchyma pits slightly smaller than intervessel pits (Fig. 16H). Vessel element lengths 302–438–588 µm; vessel element end walls inclined. Widely spaced inclusions present (Fig. 16J). Helical thickenings throughout vessel elements (Fig. 16K, L).

Fibers thin-thick-walled, non-septate, pitting not observed (Fig. 16K).

Axial parenchyma not common, some scanty paratracheal, and some in growth ring margins.

Rays exclusively uniseriate (Fig. 16I–K). Average ray height 11 cells, range 4–26. Homocellular, composed of procumbent cells (Fig. 16L), 8–12 per mm, non-storied.

Oil/mucilage cells and crystals not observed.

Comparisons with modern woods—In the InsideWood database, only genera of Sapindaceae have this combination of features: wood not ring-porous (3a), vessels solitary and in short multiples with a random arrangement (6a 7a 8a 9a 10a), simple perforation plates (13p), alternate intervessel pit small-medium (22p 24a 27a), vessel-ray parenchyma pitting similar to intervessel pitting (30p), helical thickenings throughout vessel elements (36p 37p), vessel diameter not large (43a), non-septate fibers without obvious pits (61p 66p), axial parenchyma not conspicuous (77a 79a 80a 83a 84a 85a 86a), exclusively uniseriate homocellular rays (96p 104p). Of the eleven matching genera, only *Aesculus* has exclusively non-septate fibers, the other genera have predominantly septate fibers.

Consequently, we consider this wood to belong to the Sapindaceae, Tribe Hippocastaneae, a tribe with a disjunct distribution (Stevens, 2001-onwards). Kew's Plants of the World (POWO 2023) recognizes 12 accepted species of *Aesculus.* Wood anatomical differences between the species include vessel-ray parenchyma pitting type, diameter and abundance of vessels, presence/absence of storied rays or marginal parenchyma. Klaassen (1999) noted that *Handeliodendron* Rehder (1935) wood is nearly identical to *Aesculus,* but it has only heterocellular rays. Both genera have widely spaced helical thickenings in the vessels, a unique feature within the Sapindaceae; in other sapindaceous genera with helical thickenings the thickenings are closely spaced (Klaassen 1999, Itoh et al. 2022).

The clades recovered by phylogenetic analyses of the Sapindaceae (e.g., Xiang et al. 1998, Harris et al., 2009, Du et al., 2020) generally align with the five groups recognized on the basis of morphology by Hardin (1957). The exception is the position of *Aesculus californica* (Spach) Nutt. (1838)*,* which was recovered as belonging Section *Calothyrsus* Spach (1834) along with the Asian species, *A. chinensis* Bunge (1833)*, A. assamica* Griff. (1854), *A. indica* (Wall. ex Cambess.) Hook*.* (1859). All the aforementioned species have vessel-ray parenchyma pits similar to the intervessel pits (IAWA feature 30). There are no wood anatomical descriptions for species in Sections *Macrothyrsus* Spach (1834) or *Parryana.* Available information on Section *Pavia* indicates its species differ as they have horizontally elongate vessel-ray parenchyma pits with reduced borders. Section *Aesculus* species (*A. turbinata* Blume, 1847*, A. hippocastanum* L., 1753) have storied structure or a tendency to it as do *A. chinensis* and *A. indica* of Section *Calothyrsus* Spach (1834).

The concentration of vessels at the beginning of a growth ring is unusual for *Aesculus*, but a tendency to this feature occurs in some samples of *A. turbinata* and *A. chinensis.* In most extant *Aesculus* the vessels are more crowded than in this fossil, but in some *A. indica* and *A. californica* samples the vessels are as widely spaced as in this late Eocene wood. Available information on present-day *Aesculus* wood anatomy suggests that *A. klaassenii* belongs to Section *Calothyrsus* because it has vessel-ray parenchyma pitting similar to intervessel pitting and is closest to *A. californica* because it lacks storied structure.

Comparisons with fossil woods—We only know of five reports of fossil woods suggested to be related to *Aesculus* (Gregory et al. 2009). There are three Miocene woods that we consider reliably assigned to *Aesculus: A. hankinsii* Prakash and Barghoorn (1961) from Washington, USA; *A. mioxyla* Suzuki and Terada (1996) from Japan; *Aesculus* sp. from Korea (Jeong et al. 2004). All three are strictly diffuse-porous with vessels more crowded than this Eocene wood. *Aesculus hankinsii* differs as its numerous vessels are evenly distributed throughout the growth ring and rays show a tendency to storied structure. *Aesculus mioxyla* also has evenly distributed vessels as well as weakly storied rays. Two reports are questionable as their descriptions lack the details (e.g., vessel-ray parenchyma pits) necessary to confirm relationships with *Aesculus* or the Sapindaceae: *Aesculoxylon deccanense* Trivedi and Srivastava (1982)

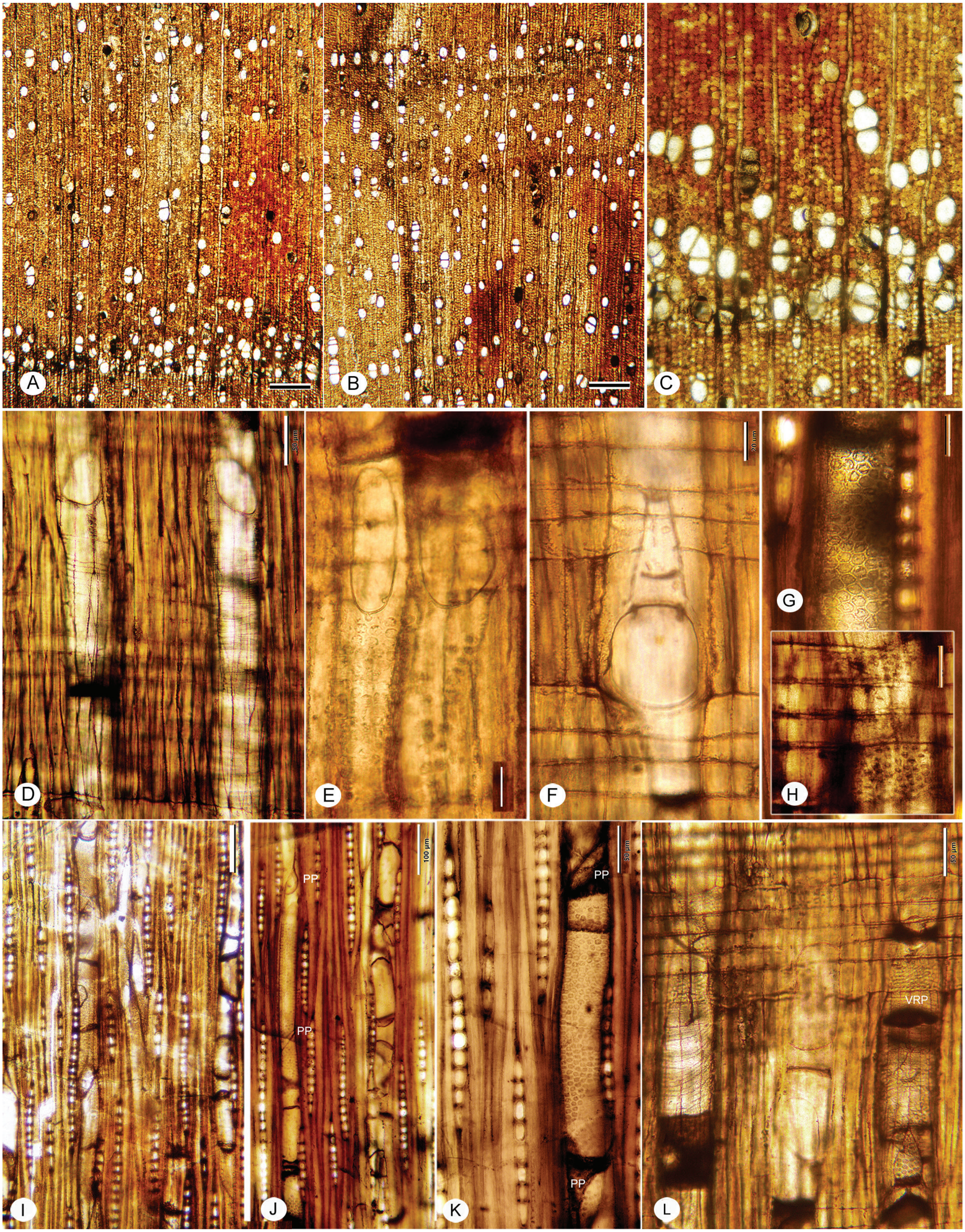

Figure 16. Caption on pg. 35.

Figure 16. Sapindaceae. *Aesculus constabularisii* sp. nov., UF 278-84887. **A–C**. Vessels concentrated at the beginning of the growth ring, vessels solitary and in short radial multiples, TS. **D**. Simple perforation plates; fine fairly widely spaced helical thickenings throughout the vessel element, RLS. **E, F.** Simple perforation plates, procumbent ray cells, RLS. **G**. Crowded alternate intervessel pitting, TLS. **H.** Vessel-ray parenchyma pitting, RLS. **I, J**. Uniseriate rays, simple perforation plates (PP), widely spaced tyloses. **K**. Uniseriate rays, simple perforation plates (PP), crowded alternate intervessel pitting. **L**. Helical thickenings in vessel element at left, procumbent ray cells, small vessel-ray parenchyma pits (VRP). Scale bars=200 µm in A, B; 100 µm in C, I, J; 50 µm in D, K, L; 20 µm in E, F, G, H.

from the Deccan Intertrappean Beds and *Aesculus* sp. from the Eocene of Montana (Yamamoto and Chadwick 1982). Since this Dietz Hill wood is assignable to *Aesculus,* but does not match any extant or fossil species*,* we have assigned it to the new species, *A. klaassenii*.

KLAASSENOXYLON GEN. NOV.

Diagnosis—Growth rings distinct to indistinct. Wood diffuse-porous. Vessels solitary and in short radial multiples. Perforation plates exclusively simple; intervessel pits alternate, minute to small; vessel-ray parenchyma pits similar to intervessel pits. Axial parenchyma rare, scanty paratracheal. Fibers with simple pits, septate and non-septate. Rays uniseriate (rarely biseriate), heterocellular. Crystals, if present, in chambered fibers

Etymology—For René Klaassen, whose monograph on the wood anatomy of the Sapindaceae was a major contribution to our understanding of this family.

KLAASSENOXYLON WILKINSONII SP. NOV.

FIG. 17A–K

Diagnosis—Growth rings distinct to indistinct. Wood diffuse-porous. Narrow vessels solitary and in short radial multiples. Perforation plates exclusively solitary; intervessel pits alternate, minute to small; vessel-ray parenchyma pits similar to intervessel pits. Fibers with simple pits, septate and non-septate. Axial parenchyma rare, scanty paratracheal. Rays uniseriate (rarely biseriate), heterocellular, less than 1 mm tall. Long chains of crystals in fibers,

Holotype—UF 278-84877, estimated maximum diameter 12 cm.

Paratypes—UF 278-84882, 84897, estimated maximum diameters 2.2 cm (with pith), 4 cm.

Etymology—Named for Hazel Wilkinson (1932-2019), a devoted plant anatomist with a long career at the Jodrell Laboratory, Kew, U.K.

Occurrence—Dietz Hill (UF 278).

Description—Growth rings present, marked by radially narrow fibers (Fig. 17A, B).

Wood diffuse-porous; vessels solitary 29% in UF 278-84877, 64% in UF 278-84897 and in radial multiples of 2–3(-4), solitary vessels round to oval in outline (Fig. 17A, B); mean tangential diameters 74 (16) µm in UF 278-84877, 67 (12) µm in UF 278-83897, total range of both specimens 45–106 µm; 18–23–33 vessels/mm^2. Perforation plates exclusively simple (Fig. 17C, F); intervessel pits alternate, minute to small (Fig. 17C); vessel-ray parenchyma pits similar to intervessel pits (Fig. 17D). Average vessel element length 350 (SD=71) µm, range 249–452 µm.

Axial parenchyma rare, scanty paratracheal, in 3–4-celled strands as viewed in radial section.

Fibers thin- to thick-walled, pitting not observed, septate and non-septate (Fig. 17F, G).

Rays uniseriate (Fig. 17F, G), with intermixed weakly procumbent to square cells to weakly upright cells; in others a tendency for square to upright cells to be restricted to ray margins; average ray height 346 (SD=154) µm in UF.84877; 284 (127) µm in UF 278-84897; 10–14 rays per mm.

Prismatic crystals in chambered fibrous elements.

Description of pith—Pith complex, surrounded by a sheath of small cells with dark contents and clusters and strands of fiber-sclereids and sclereids (Fig. 17I). Pith proper composed of two types of parenchyma cells: 1) large “empty” rectangular cells that are in radial rows towards the periphery and clusters of isodiametric cells in the center, and 2) small cells with dark contents (tannins?) forming a three-dimensional network throughout the pith and partly segmenting it by concave arches as seen in cross section (Fig. 17G). There are isodiametric empty cells and dark cells resembling irregular “rosettes” as described by Poole and Wilkinson (1992) for *Sapindoxylon guioaoides* Poole and Wilkinson (1992), *Guioa* Cav. (1797), and *Alectryon* Gaertn. (1788). However, UF 278-84882’s pith differs significantly in having a distinct sheath of small-cells including some sclereids bordering the protoxylem. Prismatic crystals present in peripheral pith parenchyma (Fig. 17J, K).

Comparison to extant woods—We initially searched the InsideWood database for diffuse-porous wood (5p), vessels solitary and in short multiples and not arranged in an obvious pattern (6–11a), simple perforation plates (13r), minute to small alternate intervessel pitting (22p, 26a, 27a), vessel-ray parenchyma pits similar to intervessel pits (30p), vessel tangential diameter averaging less than 200 µm (43a), vessel frequency between 5–40 per

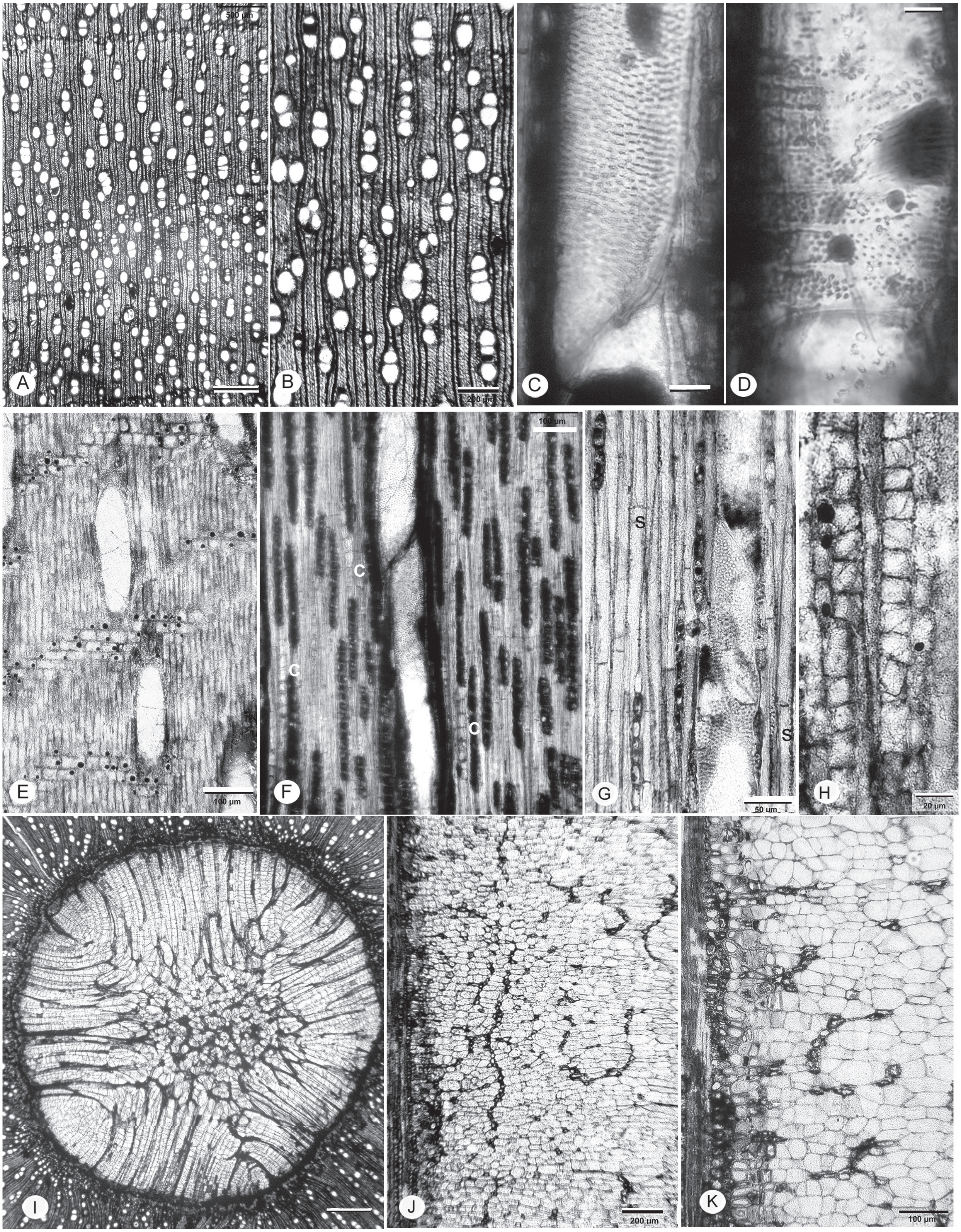

Figure 17. Caption on pg. 37.

Figure 17. Sapindaceae. *Klaassenoxylon wilkinsonae* sp. nov. **A, B**. Diffuse-porous wood. Vessels solitary and in short radial multiples, UF 278-84877, TS. **C**. Crowded alternate intervessel pitting, some coalescent apertures, UF 278-84877, TLS. **D**. Vessel-ray parenchyma pitting similar to intervessel pitting, procumbent ray cells, UF 278-84877, RLS. **E**. Rays with barely procumbent and square cells, UF 278-84897, RLS. **F**. Uniseriate rays, crystals in chambered fibers (C), UF 278-84877, TLS. **G**. Uniseriate rays, septate fibers (S= septae), TLS. **H**. Chambered crystals in fibers, UF 278-84897, TLS. **I**. Complex pith, UF 278-84882, TS. **J, K**. Longitudinal sections ofpith, UF 278-84882. Scale bars=500 µm in A, I; 200 µm in B, J; 100 µm in E. F, K; 50 µm in G; 20 µm in C, D, H.

mm^2 (46a, 49a, 50a), fibers with simple pits (61p), axial parenchyma not obvious (77a, 79–86a), rays exclusively uniseriate (96p), storied structure absent (118a, 120a), and prismatic crystals present in fibers (143p). This first search returned two Lythraceae J. St.-Hil. (1805) records and 37 Sapindaceae.

Search 2 included presence of both septate and non-septate fibers and yielded one Lythraceae and 32 Sapindaceae.

Search 3 added presence of rays with procumbent, square, and upright cells intermixed throughout the ray (109p) and absence of dimorphic fibers (67a) this narrowed the possibilities to seven sapindaceous genera, one of which, *Lecaniodiscus* Planch. ex Benth. (1849) has crystals in ray cells as a constant and so does not match the Dietz Hill (UF 278) woods. Consequently, we consider that these woods are allied with the Sapindaceae.

Klaassen (1999: p. 174–175) surveyed the wood anatomy of the Sapindaceae and recognized four wood anatomical types. These Dietz Hill (UF 278) woods fit his Type IVa, which includes 26 genera that have intervessel pits of 3–6 µm, septate fibers, scanty paratracheal parenchyma, heterocellular uniseriate rays, and crystals in fibrous elements. *Cnesmocarpon* Adema (1993) New Guinea, Australia)*,* *Delavaya* Franch. (1886) (China)*,* *Gereaua* Buerki and Callm. (2010) (syn. *Haplocoelum* Radlk., 1878*;* Africa)*,* *Macphersonia* Blume (1848) (Tropical E. Africa, Madagascar), *Pseudopteris* Baill. (1874) (Madagascar)*,* *Ungnadia* Endl. (1833[1835]; Mexico, sw USA). Klaassen's synoptical key with twenty-six features is slightly awkward to use. We excluded genera that have as constant features ones not observed in these fossils (vessels in a radial pattern, mean intervessel pit diameter >7 µm, mean vessel diameter >120 µm, fiber dimorphism present, apotracheal parenchyma abundant, complete sheaths of vasicentric parenchyma, aliform to confluent parenchyma, banded non-marginal parenchyma, idioblastic axial cells, bi- and tri-seriate rays common, mean ray height >1 mm, rays all homocellular, rays of two distinct sizes, crystals in ray cells). In addition to the six genera listed above as sharing features with UF 278-84887, Klaassen's key indicates the following genera also have similarity: *Arytera* Blume (1847)*,* *Beguea* Capuron (1969)*,* *Cupania* L. (1753)*,* *Cupaniopsis* Radlk. (1879/1880)*,* *Diploglottis* Hook.f. (Bentham and Hooker, 1862)*,* *Neotina* Capuron (1969)*,* *Thouinia* Poit. (1804), and *Toechima* Radlk. (1877[1879]) of Type IVa; *Alectryon* Gaertn. (1788)*,* *Matayba* Aubl. (1775)*,* *Schleichera* Willd. (1805) of Type IVb; and *Handeliodendron* Rehder (1935), which did not fit in any of Klaassen's wood type groups.

Buerki et al.'s (2021) recent analysis of Sapindaceae recognized four subfamilies and twenty tribes. All six genera from InsideWood Search 3 belong to subfamily Sapindoideae Burnett (1835), but to three different tribes: Ungnadieae Buerki and Callm. (2021) (*Delavaya, Ungnadia*)*,* Stadmanieae Buerki and Callm. (2021) (*Gereaua* Buerki and Callm. (2010)*, Macphersonia, Pseudopteris*)*,* and Cupanieae Blume (*Cnesmocarpon*).

It is tempting to suggest, based on present day geographic distribution as well as shared anatomical features, that these Dietz Hill sapindaceous woods might be related to tribe Ungnadieae. However, as pointed out by Klaassen (1999), wood anatomical differences between the genera of groups IVa and IVb are small and could easily break down upon examination of more species per genus and more specimens per species. The main conclusion of the searches reported above and assorted alternative searches we did consistently yielded multiple Sapindaceae. We consider the similarity in the complex pith anatomy with some modern and fossil Sapindaceae as strong support for the family assignment.

Comparison to fossil woods—The diagnosis of *Sapindoxylon* as adapted by Poole and Wilkinson (1992) from a translation of Kraüsel's work (1922) follows: "*Wood*: Diffuse porous. *Growth rin*gs: lacking. *Vessels*: 2–8 per mm^2, mostly solitary or paired, seldom in threes, when abutting tangentially flattened, otherwise circular or elliptical. Perforation plates simple with mainly horizontal or slightly oblique end walls. *Fibres*: Libriform, forming the groundmass in regularly arranged rows; occasionally septate. *Wood parenchyma:* Surrounding the vessels in one or two layers [vasicentric], sometimes also scattered. *Rays:* Uniseriate, occasionally biseriate, 3–30 cells high, consisting of one cell type; the marginal cells occasionally contain a crystal."

It is unfortunate that the vessel frequency was so narrowly defined. Some *Sapindoxylon* species do not conform to the diagnosis in that feature, e.g., *Sapindoxylon guioaoides* (average of 40 vessels mm^2), *S. elattostachyoides* Grambast-Fessard (1966), (20–40 vessels per mm^2), *S.*

koelreuteroides Poole and Wilkinson (1992) (average of 43 vessels mm^2). These Dietz Hill (UF 278) samples have double the number of vessels per mm^2 of *Sapindoxylon* Kraüsel. They also differ in 1) not having vasicentric axial parenchyma, but just scanty paratracheal; 2) heterocellular rays, rather than homocellular; 3) crystals in fibers/chambered axial parenchyma, rather than in marginal ray parenchyma cells. These three features were used in Klaassen's (1999) synoptic key and so were considered important in recognizing genera. *Sapindoxylon klaassenii* Wheeler and Manchester (2002) from the middle Eocene Clarno Nut Beds differs from the Kraüsel's (1922) diagnosis in having rare axial parenchyma and heterocellular rays.

Consequently, we choose not to assign UF 278-84887 to *Sapindoxylon* Kraüsel and propose the genus *Klaassenoxylon* to accommodate these Eocene sapindaceous woods from Oregon. We also propose the new combination:

KLAASSENOXYLON KLAASSENII (WHEELER AND MANCHESTER) COMB. NOV.

Basionym—*Sapindoxylon klaassenii* Wheeler et Manchester (2002, p. 132)

The complex pith of UF 278-84882 resembles the piths described by Poole and Wilkinson (1992) for extant *Allectryon* and *Guioa* and the fossil *Sapindoxylon guioaoides* Poole and Wilkinson (1992). The wood of *Guioa* also resembles this fossil (Klaassen 1999). Pith anatomy remains an underexplored field, which is unfortunate because in the Sapindaceae pith features are highly diagnostic (Wilkinson 1988, Poole and Wilkinson 1992).

SAPINDALES FAMILY INDET.

FAGAROXYLON VAN DER BURGH, 1964

CF. *FAGAROXYLON* SP.

FIG. 18A–I

Description—Growth rings present, marked by radially narrow fibers, (probably also marginal parenchyma) (Fig 18A, B).

Wood diffuse-porous (Fig 18A, B). Vessels solitary (14%) and in radial multiples mostly 2–4 (-7), clusters rare; mean tangential diameter 63 (SD=15) µm, range 28–90 µm; 36–42–50 vessels/mm^2. Perforation plates simple (Fig. 18E, F); intervessel pits crowded alternate (Fig. 18C), horizontal diameters small to medium 5–8.5 µm. Vessel-ray parenchyma similar to intervessel pits (Fig. 18D). Vessel element lengths 235–277–353 µm (n=12); vessel element end walls obliquely inclined. Helical sculpturing (grooves) in some narrow vessel elements (Fig. 18E, F). Gum-like deposits common.

Fibers thin-walled, non-septate, pitting not observed (Fig. 18E–H).

Axial parenchyma not common, scanty paratracheal (hard to distinguish from thin-walled fibers) and probably also marginal (Fig. 18H).

Rays 1–4 (-5)-seriate (Fig. 17E, G). Average ray height 497 (SD=203) µm, range 181–1062 µm. Homocellular, composed of procumbent cells (Fig. 18D, F, I), 6–9 per mm, non-storied.

Crystals common in chambered axial cells (fibers), strands sometimes adjacent to rays, one crystal per chamber, numerous (10+) crystalliferous chambers per strand (Fig. 18E, G, I).

Specimen—UF 278-84907, estimated maximum diameter 10 cm.

Occurrence—Dietz Hill (UF 278).

Comparisons with extant woods—We searched the InsideWood database multiple times. One search used diffuse porosity (5p), absence of vessel patterning and exclusively solitary vessels (6-9a), exclusively simple perforation plates (13p 14a), alternate intervessel pitting that is neither minute nor large (22p, 24a, 27a), vessel-ray parenchyma pits similar to intervessel pits (30p), average vessel diameter less than 200 µm (43a), vessels per mm^2 between five and 100 (46a, 50a), non-septate fibers with simple to minutely bordered pits (61p 66p), axial parenchyma scanty paratracheal and marginal, but not accompanied by more obvious axial parenchyma (78p, 89p, 80-88a), homocellular rays not exclusively uniseriate or greater than 10-seriate (96a, 99a, 104p), storied structure absent (118–122a), oil/mucilage cells and intercellular canals absent (124–130a), prismatic crystals present in fibers (136p 143p). When not allowing any mismatches, this search yielded only Meliaceae (*Capuronianthus* J.-F.Leroy, 1958*; Quivisianthe* Baill., 1893, from Madagascar (Rutaceae); *Aeglopsis* Swingle, 1912*; Afraegle* (Swingle) Engl., 1915, from Africa; and Sapindaceae (one Asian *Acer* L., 1753).

When one mismatch was allowed, results again included Meliaceae (three species), Rutaceae (12 species), Sapindaceae (19 species, including 11 of *Acer*). Other families retrieved were Combretaceae R.Br. (1810) (three *Terminalia* L. (1767) species), which differ in having crystals in idioblasts or in having more abundant axial parenchyma), Lamiaceae (one *Vitex* species with mostly septate fibers and crystals of other shapes), Fabaceae (five species, none have crystals in fibers, although there is the possibility crystals in fibers might have been

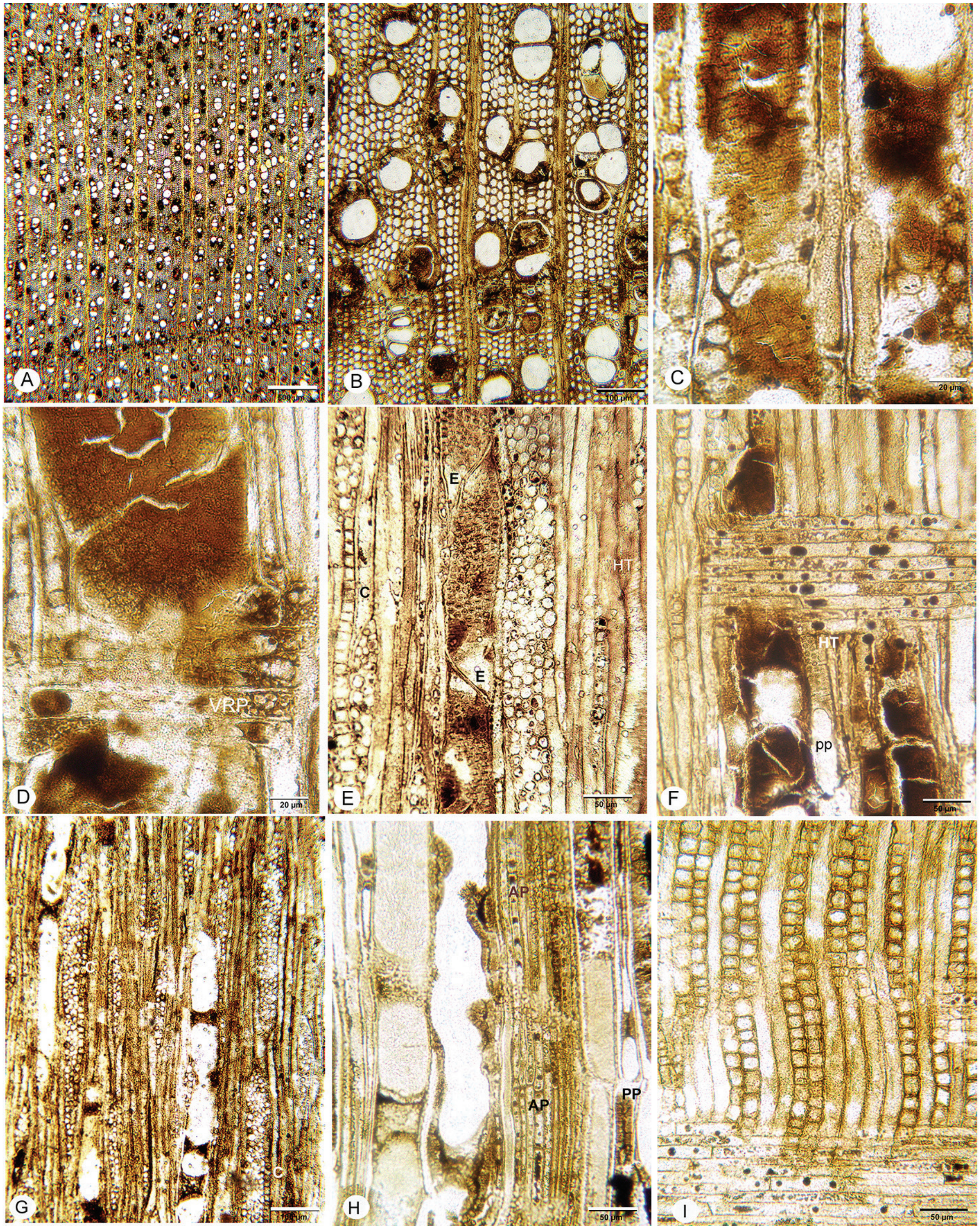

Figure 18. Caption on pg. 40.

Figure 18. Sapindales. *Fagaroxylon* sp., UF 278-84907. **A, B**. Diffuse-porous wood; vessels solitary and in radial multiples, thin-walled fibers, growth ring boundary marked by radially narrow fibers, and axial parenchyma, TS. **C.** Crowded alternate intervessel pitting, TLS. **D.** Vessel-ray parenchyma pits (VRP) similar to intervessel pits, procumbent ray cells, RLS. **E.** Multiseriate rays; crystalliferous strand (C); crowded alternate intervessel pitting, vessel element end walls (E), helical thickenings (HT) in narrow vessel elements, TLS. **F**. Ray composed of procumbent cells; narrow vessel element with simple perforation plate (PP) and helical thickenings (HT), RLS. **G**. Rays 1–4-seriate, crystalliferous strands adjacent to rays (C), TLS. **H**. Marginal axial parenchyma (AP); simple perforation plate (PP), RLS. **I**. Crystals in fibers, RLS. Scale bars=500 µm in A; 100 µm in B, G, 50 µm in E, F, H, I; 20 µm in C, D.

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interpreted as crystals in chambered axial parenchyma as reported for four of them).

We tried other searches using slightly different combinations of features, and all of them consistently returned members of the Sapindalean families Meliaceae, Rutaceae, and Sapindaceae. We are confident that this wood belongs to the Sapindales and are inclined to think that it is most likely related to Sapindaceae, which is noted as the Sapindalean family most commonly having crystals in fibers (Pace et al. 2022). It resembles *Acer* most closely, but all present-day *Acer* consistently have helical thickenings in vessel elements, so this wood is not assigned to *Acer.* The fruit and seed flora of Dietz Hill has an endocarp that might have affinities with *Acer* (Manchester and McIntosh 2007).

Dipteronia Oliv. (1889) is closely related to *Acer* and fruits of it occur in the Teater Road shales that we infer to be of similar age to the Dietz Hill (UF 278) locality (McClain and Manchester 2001). Itoh et al. (2022) described *Dipteronia sinensis* Oliv. (1889) (under the name *Acer dielsii* H. Lév. (1912). That description differs somewhat from the descriptions and observations of *D. dyeriana* A. Henry (1903) and *D. sinensis* made by Peter Gasson (Royal Botanic Gardens, Kew) and Michael Wiemann (Center for Wood Anatomy Research, Madison) and available on InsideWood (insidewood.lib.ncsu.edu). Itoh et al. (2022) report helical thickenings in narrow vessel elements and rays commonly more than 1 mm high, features not seen by Gasson or Wiemann. Crystals are not reported for *Dipteronia.*

Comparisons with fossil woods—Excluding fossil wood descriptions with most features coded as unknown, the results of our searches of InsideWood's fossil wood database returned two species of *Fagaroxylon* Van der Burgh (1964) from the Miocene of Europe. *Fagaroxylon* is a genus created for woods with features of both *Fagara* L. (1759), which is now subsumed into *Zanthoxylum* L. (1753). Its diagnosis (Van der Burgh 1964) and later descriptions of *Fagaroxylon bavaricum* (Selmeier 1975) and *Fa. limburgense* (Van der Burgh 1973) are remarkably similar to this Dietz Hill (UF 278) wood. Similarities include most vessel features, axial parenchyma distribution, chambered crystals, ray width and cellular composition, and even the occasional occurrence of helical vessel wall thickenings. Vessel frequency is lower in *Fa. limburgense*, but this likely is because in the past vessel multiples (groups) were counted as one unit (Wheeler 1986). *Fagaroxylon limburgense,* the type species, is reported to have fibers with distinctly bordered pits (diameter 3 µm) in their radial walls, a feature we did not observe in UF 278-84907. Because variations in preservation and the effects thereof can make it difficult to determine whether fiber pits are >3 µm across, we choose to assign UF 278-84907 to *Fagaroxylon.*

Fagaroxylon's combination of features occurs in other genera of Rutaceae, as well as the Meliaceae and Sapindaceae and is not unique to *Zanthoxylum*. It should be noted that seeds that correspond closely to the extant genus *Zanthoxylum* occur at Dietz Hill (UF 278).

Other Sapindalean fruit and seed remains in the Teater Road shales include *Koelreuteria* Laxm (1771) (Wang et al 2013), *Dipteronia* (McClain and Manchester 2001), and several species of *Acer* leaves and fruits (Wolfe and Tanai, 1987, indicated as "Sheep Rock Creek").

APIALES NAKAI, 1930

ARALIACEAE JUSS., 1789

PLERANDREOXYLON WHEELER & MANCHESTER 2002 EMEND WHEELER, MANCHESTER, BAAS

Emended diagnosis—Wood semi-ring-porous to ring-porous. Earlywood vessels in multiple rows, usually less than 100 µm in tangential diameter; latewood vessels in discontinuous wavy tangential bands or diagonal to oblique arrangement. Perforations simple or simple and scalariform with fewer than 20 bars; intervessel pits alternate to scalariform, medium to large in horizontal diameter; vessel-ray parenchyma pits with reduced borders to simple.

Fibers septate or septate and non-septate.

Axial parenchyma rare to scanty paratracheal.

Rays multiseriate, less than 10-seriate and averaging less than 700 µm high, heterocellular, sheath cells occasionally present; uniseriate rays not common; fewer than 10 rays per mm.

Crystals, oil/mucilage cells, storied structure, and radial canals absent.

PLERANDREOXYLON OSKOLSKII SP. NOV.

FIG. 19A–G

Diagnosis—Growth rings distinct, marked by radially flattened latewood fibers, and differences in vessel diameter between latewood and earlywood of subsequent rings.

Semi-ring-porous to ring-porous. Vessels solitary and in radial multiples, small clusters in the latewood. Earlywood with multiple rows of vessels, latewood vessels arranged in a tangential to diagonal pattern in narrower rings. Perforation plates simple, intervessel pits alternate, medium to large; vessel-ray parenchyma pits with reduced borders to simple, oval to slightly horizontally elongate. Tyloses present.

Fibers with simple to minutely bordered pits; thin to thick-walled; septate.

Axial parenchyma extremely rare.

Rays predominantly multiseriate, sheath cells occasional, average ray height <1 mm. Rays homocellular, composed of procumbent body cells, or heterocellular with a single marginal row of square cells and weakly procumbent cells. Rays per mm few.

Holotype—UF 278-84872, estimated maximum diameter 8–9 cm.

Paratype—UF 278-84905.

Occurrence—Dietz Hill, UF 278.

Etymology—Named for our good colleague and friend Alexei Oskolski who has studied Araliaceae wood and done much to further the field of wood anatomy in general.

Description—Growth rings distinct, marked by radially flattened latewood fibers. Ring-porous to semi-ring-porous. Vessels solitary and in short radial multiples, small clusters in the latewood. Earlywood with multiple rows of vessels; latewood vessels arranged in a tangential to diagonal pattern in narrower rings, mostly in radial multiples, solitary vessels not common (Fig. 19A, B.). Earlywood vessels 97 (SD=22) µm, range 48–137 µm. Vessel element lengths commonly 350–500 µm. Perforation plates simple (Fig. 19C). Intervessel pits alternate, 8–10 µm in horizontal diameter, tending to be angular in outline (Fig. 19D); vessel-ray parenchyma pits with reduced borders and oval to slightly horizontally elongate (Fig. 19E). Tyloses present (Fig. 19C, E, G).

Fibers with simple to minutely bordered pits, septate (Fig. 19F), thin to thick-walled.

Axial parenchyma extremely rare.

Rays homocellular, composed of procumbent body cells, or heterocellular with a single marginal row of square cells and barely procumbent cells; sheath cells occasional; 3–7 cells wide, mostly 5–6 cells (Fig. 19F, G). Ray height averages 449 (126) µm, range 126–728 µm; 3–4 rays per mm.

Crystals, oil/mucilage cells, storied structure, and radial canals absent.

Comparisons to extant and fossil woods—We searched the InsideWood database multiple times. One search used: distinct growth ring boundaries (1p); wood ring-porous to semi-ring porous (5a, not diffuse-porous); vessels in wavy tangential bands (6p); simple perforation plates (13p); intervessel pits alternate and not minute (22p 24a); vessel-ray parenchyma pits rounded with much reduced borders (30a, 31p); septate fibers (65p); axial parenchyma rare (75p); rays more than 4-seriate, <1 mm high and with one row of square marginal cells (98p 102a 106p); storied structure, oil/mucilage cells, and radial canals absent (118a 120a 124a 125a 126a 130a). The IW matches only included Araliaceae (order Apiales): two modern (*Aralia elata* var. *ryukyuensis* J.Wen (1994) and *Kalopanax septemlobus* (Thunb.) Koidz. (1925), both East Asian) and two fossil woods (*Plerandreoxylon oregonensis* Wheeler and Manchester, 2002, and *Aralinium excellens* Platen, 1908), both from the Eocene of the USA. These two Dietz Hill woods' absence of uniseriate rays and the occasional occurrence of sheath cells are additional features that are consistent with the Araliaceae. Unfortunately, Platen's *Aralinium excellens* cannot be placed with certainty in the Araliaceae and reasonably compared with this Dietz Hill (UF 278) wood because its description lacks details on ray cellular composition and height and whether fibers are septate or non-septate (Platen 1908). Moreover, it was described as having crystals in enlarged cells, a feature not reported for the Araliaceae.

Another search used absence of vessel-ray parenchyma pits similar to intervessel pits (30a) rather than 31p and absence of obvious axial parenchyma features (77a, 79–86a) rather than 75p. This search returned an additional two modern woods (*Aralia spinosa* L., 1753; *Gamblea ciliata* C.B. Clarke, 1879; Araliaceae) and an additional fossil wood (*Evodia gadjirian* Gregory, 1976, from an unspecified Eocene site in the vicinity of Post, Oregon, USA). Unfortunately, the description of the putative *Evodia* Forst. and Forst. (1775) lacked information on intervessel and vessel-ray parenchyma pitting and ray cellular composition; the accompanying images were at too low of a magnification to determine those details. Whether or not this wood truly is *Evodia* (Rutaceae) or might be Araliaceae is impossible to determine because the location of Gregory's material is unknown and so it cannot be reexamined.

Alternative searches, e.g., 1p, 4p, 9a, 10a, 13p, 26p,

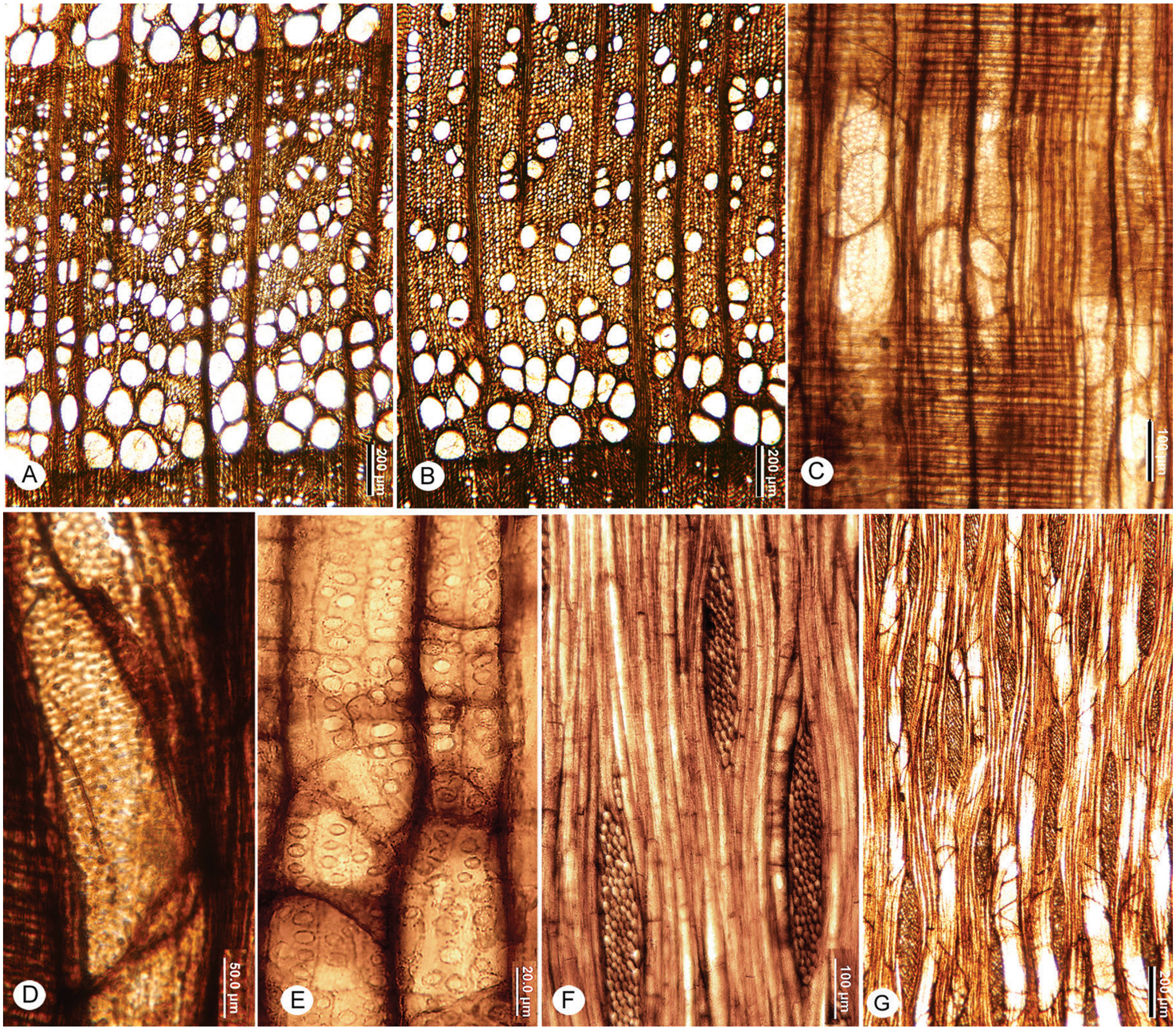

Figure 19. Araliaceae. *Plerandreoxylon oskolski* sp. nov., UF 278-84906. **A**. Semi-ring-porous wood with latewood vessels arranged in wavy tangential bands/diagonal arrangement, vessel clusters in latest latewood, axial parenchyma rare, T.S. **B**. Semi-ring-porous wood, vessels solitary and in short radial multiples, axial parenchyma rare, TS. **C**. Simple perforation plates, rays with procumbent body cells, RLS. **D**. Crowded alternate intervessel pitting, TLS. **E**. Vessel-ray parenchyma pits with reduced borders, oval to slightly horizontally elongate in outline, tyloses, RLS. **F.** Rays 5-6 cells wide, septate fibers, TLS. **G**. Rays predominantly multiseriate, TLS. Scale bars: 200 µm in A, B, G; 100 µm in C, F. 50 µm in E; 20 µm in D.

30a, 31p, 56p, 61p, 65p, 98p, 106p, in addition to Araliaceae, also retrieved two extant species of *Toricellia* DC (1830) (Toricelliaceae Hu 1934), also in the Apiales. Adams (1949, p. 239) remarked "[the] overall character of the wood is suggestive of araliaceaeous affinities." *Toricellia* differs from the fossil in having helical vessel wall thickenings, taller rays (to 1.8 mm), slightly more rays per mm, scanty paratracheal parenchyma more obvious, and conspicuous tyloses (Noshiro and Baas 1998). *Toricellia* DC, is known by fruits from the Clarno Nut Beds (Manchester et al. 2017) but is not known from any Post locality.

There are araliaceous fruits (*Paleopanax oregonensis* Manchester, 1994) and two species of fossil wood, *Plerandreoxylon nutbedensis* Wheeler and Manchester (2002) and *Pl. oregonensis* Wheeler and Manchester (2002), known from the middle Eocene Clarno Formation. This Dietz Hill wood agrees with the diagnosis of *Plerandreoxylon*, aside from "rays usually less than 4-seriate" and so we have emended the diagnosis to rays less than 10-seriate. *Plerandreoxylon nutbedensis* differs in having some scalariform perforation plates, some scalariform intervessel pitting, with uniseriate rays more common; *Pl. oregonensis* has mostly non-septate fibers and some scalariform intervessel pitting (Wheeler and Manchester 2002). We consider these differences sufficient to warrant assigning this wood to a new species of *Plerandreoxylon*.

? MALPIGHIALES Juss. ex Bercht. & J. Presl, 1820

Fig. 20A–L

Description—Growth rings present, marked by radially narrow fibers (Fig. 20A, B).

Wood diffuse-porous; solitary vessels rare, 8% solitary vessels, vessels predominantly in radial multiples of 2–6 (-9) (Fig. 20A–C); mean tangential diameter 52 µm (SD=11), range 26–76 µm; 90–121 vessels per mm^2. Perforation plates simple and scalariform with fewer than 10 bars (Fig. 20D–F); intervessel pits alternate (Fig. 20G), horizontal diameter 6–8–10 µm. Vessel-ray parenchyma pits similar in size to intervessel pits, generally oval in outline, with reduced borders (Fig. 20H). Vessel elements short, <350 µm. Thin-walled tyloses abundant (Fig. 20I).

Fibers thin- to thick-walled, apparently non-septate, pitting not observed.

Axial parenchyma not obvious in transverse sections, but visible in longitudinal section, strands of 4–8 cells.

Rays 1–2 seriate, mostly uniseriate (Fig. 20J, K); average biseriate ray height 227 (SD=52) µm, 131–315 µm. Rays composed primarily of procumbent cells (Fig. 20I, L); 12–15 per linear mm.

Storied structure, radial canals, and oil/mucilage cells absent.

Specimen—UF 278-84892, estimated maximum diameter 10 cm.

Occurrence—Dietz Hill (UF 278).

Comments—Specimen UF 278-84892 was problematic because it was highly compressed. The longitudinal sections provided a combination of radial and tangential views, measuring the quantitative vessel features and rays per mm were affected by the compression. The tyloses made it difficult to measure vessel element lengths.

Comparison with modern and fossil woods—We searched InsideWood's modern and fossil wood database multiple times using various combinations of features, with almost all searches including wood diffuse-porous (5p), vessels in radial multiples of four or more common (10p), perforation plates simple (13p), intervessel pits alternate and not minute (22p 24a), fibers non-septate (66p), narrow rays (searching for rays 1–3 seriate - 97p or rays uniseriate - 96p). Although scalariform perforation plates are rare, we used their presence (14p). Most searches returned *Nothofagaceae* Kuprian (1962) (Fagales), which is an unlikely match because no macro- or microfossils of this Southern Hemisphere family have ever been found in the Northern Hemisphere (Pujana et al. 2021). Members of the Salicaceae sensu APG were also returned as well as other malpighialean families (e.g., Achariaceae Harms, 1925; Euphorbiaceae Juss., 1789; Peraceae Klotzch, 1859; Phyllanthaceae Martinov, 1820; Putranjivaceae Endl., 1841). Results of other searches included Elaeocarpaceae Juss. (1816, Oxalidales Bercht. and J. Presl, 1820). No fossil wood in the InsideWood database was a good match. In spite of reviewing the family descriptions in Metcalfe and Chalk (1950) and reviewing the literature on the aforementioned families, at this time, we are not able to assign it to family. We suggest it belongs to the Malpighiales Martius, but we cannot confirm that placement.

Populus L. (1753) and *Salix* L. (1753) (Salicaceae Mirbel (1815)) are common in the compression floras of the U.S.A., although woods of those genera are rare, which is probably because they readily decay making them less likely to enter the fossil record. Initially, we thought this sample might be *Populus* or *Salix* because the transverse section of this diffuse-porous wood shows narrow and abundant vessels that are commonly in radial multiples, abundant narrow rays, and axial parenchyma looked to be rare. However, this first impression was incorrect because this wood has some scalariform perforation plates, a feature that does not occur in present-day *Salix* or *Populus.* Moreover, strands of axial parenchyma are visible in the longitudinal sections. This sample serves as a cautionary tale that generally wood identification needs to be based on microscopic examination of longitudinal sections, not just transverse section.

INCERTAE SEDIS
?THEACEAE Mirb., 1816
?HAMAMELIDACEAE R. Brown, 1818
HAMAMELIDOXYLON Lignier, 1907
cf. *HAMAMELIDOXYLON* sp.

Fig. 21A–H

Description—Wood diffuse-porous, narrow growth increments, boundaries of 1–3 radially narrow fibers (Fig. 21A, B). Vessels predominantly solitary, overlapping end walls of vessel elements appearing as tangential or oblique pairs; vessels angular in outline (Fig. 21A, B); very narrow to narrow, average tangential diameter 43 (9) µm; very numerous, >100 mm^2. Perforation plates

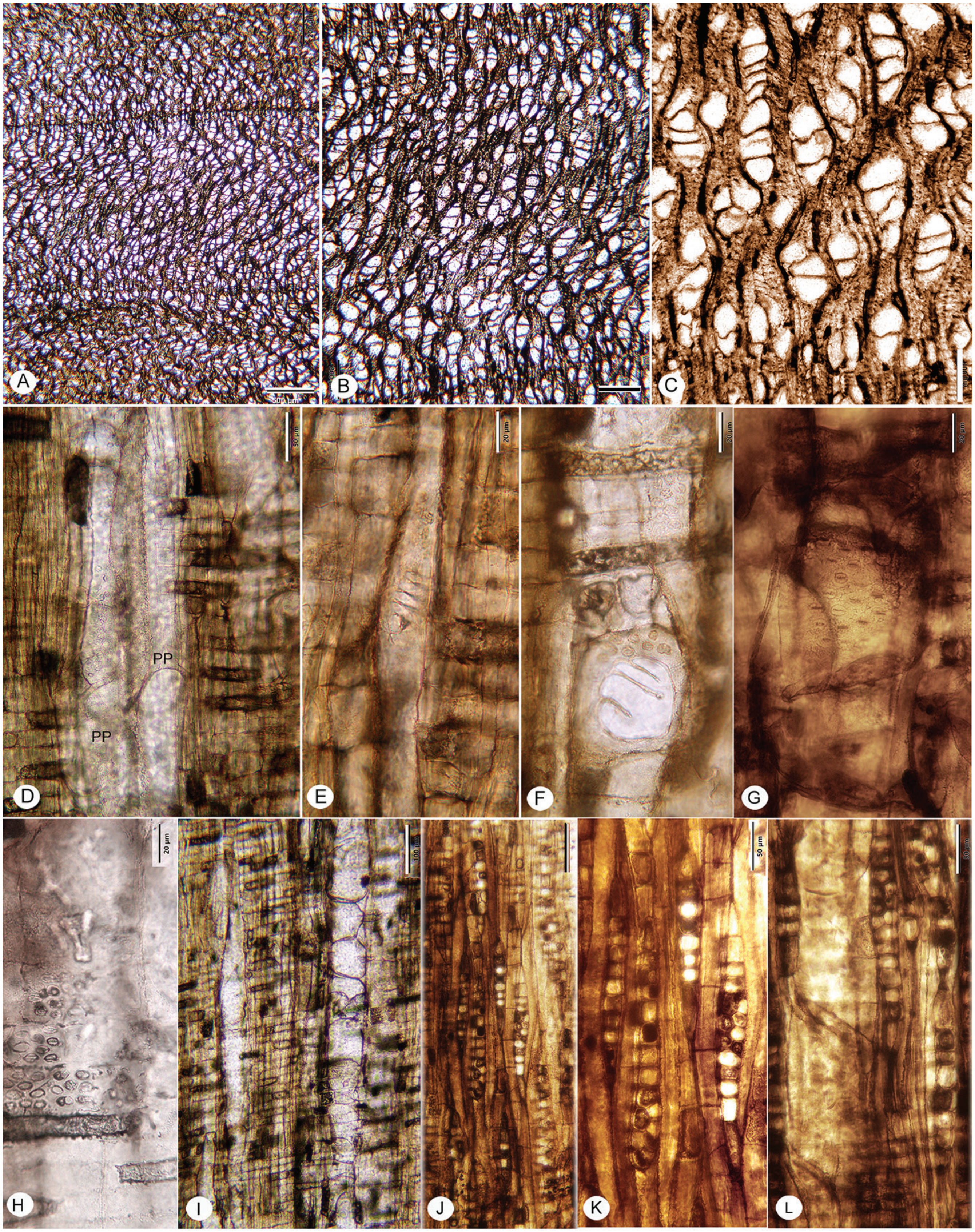

Figure 20. Caption on pg. 45.

Figure 20. Malpighiaceae?. UF 278-84892. **A–C**. Distinct growth ring boundaries, wood diffuse-porous, vessels predominantly in radial multiples, TS. **D**. Simple perforation plates (PP), ray cells predominantly procumbent. RLS. **E**. Scalariform perforation plate with 5 bars, RLS. **F.** Perforation plate with partial bars, RLS. **G.** Crowded alternate intervessel pitting. RLS. **H.** Vessel-ray parenchyma pits. RLS? **I.** Tyloses in vessels, ray cells predominantly procumbent. RLS. **J, K**. Rays uniseriate and partially biseriate, axial parenchyma strands. TLS. **L**. Short vessel element, simple perforation plate (PP), rays partially biseriate. TLS. Scale bars=500 µm in A; 200 µm in B; 100 µm in C, I, J; 50 µm in D, K, L; 20 µm in E–H.

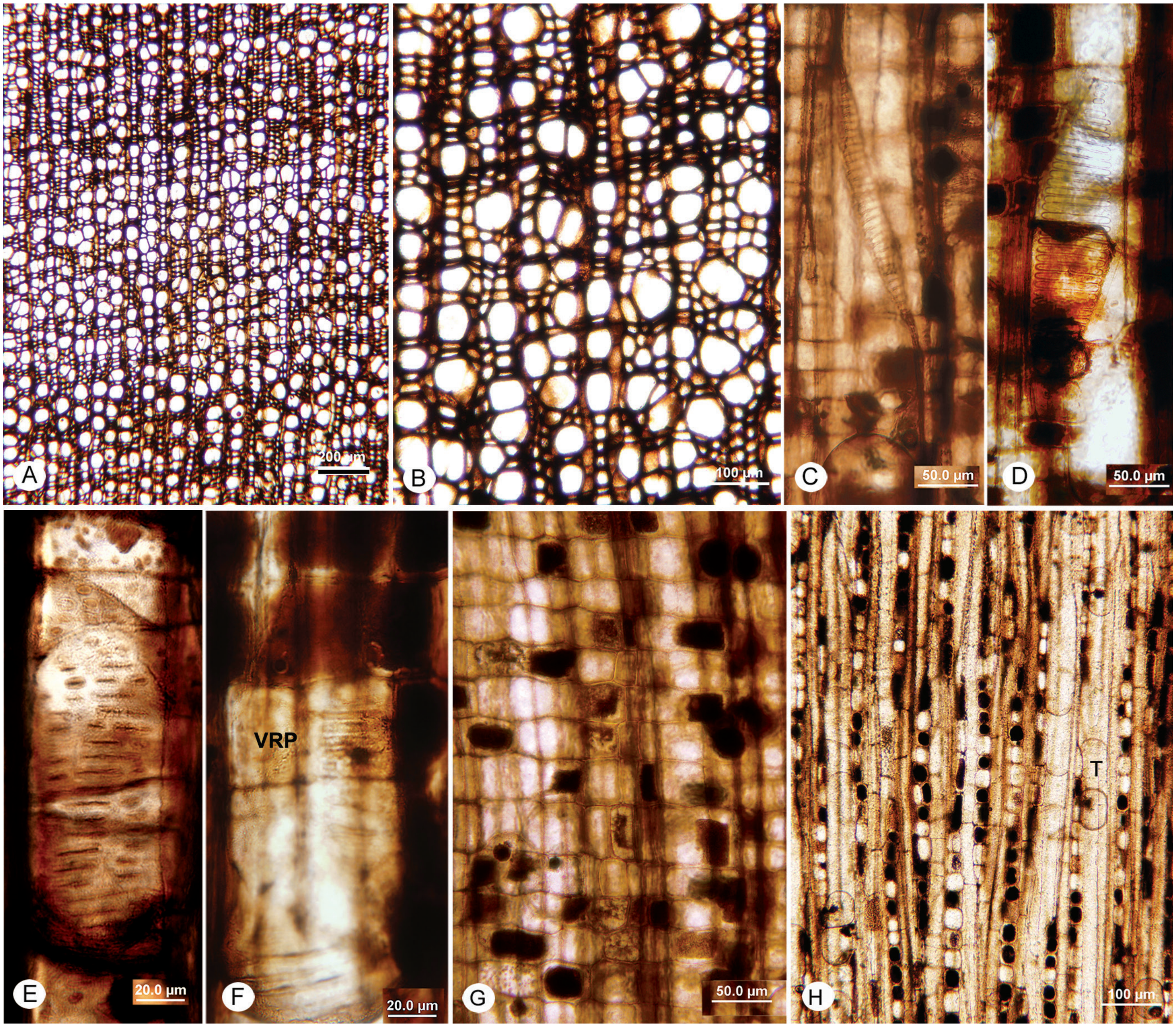

Figure 21. Incertae Sedis. cf. *Hamamelidoxylon* sp., UF 278-84876. **A, B**. Wood diffuse-porous, vessels solitary, angular in outline, TS. **C, D**. Scalariform perforation plates, RLS. **E**. Transitional intervessel pitting, ,scalariform to opposite, TLS. **F.** Vessel-ray parenchyma (VRP) pits horizontally elongate, RLS. **G**. Ray cellular composition, intermixed square, upright, and barely procumbent cells. **H.** Rays exclusively uniseriate, T next to beginning of tyloses formation, TLS. Scale bars=200 µm in A; 100 µm B, H; 50 µm in C; D, G; 20 µm in E, F.

exclusively scalariform with more than 20 bars (Fig. 21C, D), 34–42 bars counted. Intervessel pits scalariform to opposite. (Fig. 21E) Vessel-ray parenchyma pits horizontally elongate, half-bordered or with slightly reduced borders (Fig. 21F). Widely spaced tyloses common.

Fibers non-septate, thin-walled, bordered pits on radial walls.

Axial parenchyma diffuse and scanty paratracheal, in strands of 5 or more cells (Fig. 21H).

Rays uniseriate (Fig. 20H), heterocellular, composed of intermixed procumbent, square, and upright cells (Fig. 21G); 9–14 rays/mm.

Crystals and oil/mucilage cells not observed.

Specimen—UF 278-84876, estimated maximum diameter 4–5 cm.

Occurrence—Dietz Hill (UF 278).

Comparison to extant woods—We did multiple searches of the IW database for modern woods; all searches included diffuse-porous wood (5p), predominantly solitary vessels angular in outline (9p, 12p), exclusively scalariform perforation plates with more than 10 bars (13a, 14p, 15a), scalariform intervessel pits (20p), narrow numerous vessels (42a, 43a, 46a, 47a, 48a), non-septate fibers with bordered pits (62p, 66p) axial parenchyma not obvious (77a, 79–89a), exclusively uniseriate heterocellular rays (96p 104a, 105a). These searches returned Hamamelidaceae, usually *Chunia* H.T. Chang (1948), *Exbucklandia* R.W. Br. (1946), *Hamamelis* Gronov. ex L. (1753), and Theaceae Mirb. (1816), usually *Franklinia* W. Bartram ex Marshall (1785), *Gordonia* Ellis (1770), *Schima* Reinw. ex Blume (1823). Although in different orders, Saxifragales Bertchtold and J. Presl. (1820) and Ericales Bertchtold and J. Presl. (1820), respectively, these families have some genera with similar combinations of wood anatomical features, making it difficult, often impossible, to determine the familial affinities of small, isolated pieces of wood. The anatomy of the Theaceae has been reviewed by Liang and Baas (1990, 1991); the anatomy of the Hamamelidaceae has been reviewed by Tang (1943) and Wheeler et al. (2010). Descriptions of species of both families appear in wood anatomical atlases (e.g., Pearson and Brown 1932, Metcalfe and Chalk 1950, Suzuki, et al. 1991, Sosef et al. 1998, Itoh et al. 2022, and the online FFPRI Wood Database, https://db.ffpri.go.jp/WoodDB/index-E.html).

Comparison to fossil woods—A search of the IW fossil wood database using the same features given above returned species assigned to *Corylopsites* Mathiesen (1932) and *Hamamelidoxylon* Lignier (1907). The description of *Corylopsites groenlandicus* Mathiesen (1932) lacks details on vessel-ray parenchyma pitting, vessel element frequency; it differs in having crystals in both ray and axial parenchyma cells. Wheeler and Manchester (2021, Table 2) compared *Hamamelidoxylon* species with reasonably complete descriptions. Of those species, the most similar to this Dietz Hill (UF 278) wood is *H. uniseriatum* Wheeler and Manchester (2002) from the middle Eocene Clarno Nut Beds (but this species usually has rays with procumbent body cells, not intermixed procumbent, square, and upright cells.

One of the results, cf. *Hamamelidoxylon* sp. Terada et al. (2011), was considered "Family *incertae sedis"*. The authors noted that this wood type had features seen in the Hamamelidaceae and Theaceae, as well as Illiciaceae A.C. Sm. (1947). Illiciaceae wood has narrow rays, but not exclusively uniseriate rays and so is not similar to the Dietz Hill (UF 278) fossil. We follow Terada et al.'s example and note that while UF 278-84876 has a combination of features that are consistent with *Hamamelidoxylon,* we cannot assign it to family. We suggest that some other *Hamamelidoxylon* species need reassessment to determine whether or not they have combinations of features unique to the Hamamelidaceae.

DISCUSSION

To date, we have recognized two species of conifers and 18 species of angiosperms among the woods from Dietz Hill (UF 278) (Table 4). These woods indicate a diverse temperate to subtropical forest, based on the present-day distribution of the genera.

Paleoclimate

Table 5 gives the percentage of porosity and perforation plate types in the woods from Dietz Hill (UF 278), Post Hammer (UF 279) (Wheeler and Manchester 2021), and the Clarno Nut Beds (Wheeler and Manchester 2002). Ring-porosity is a feature correlated with seasonal climates and deciduousness (Bailey 1924, Gilbert 1940, Boura and DeFranceschi 2007). It is predominantly a feature of north temperate zone woods today, with low incidences in the Cretaceous, Paleocene, and early–middle Eocene (e.g., Wheeler and Baas 2019). Given that seasonality increased from the middle to late Eocene in western North America (e.g., Prothero and Berggen 1992, Wolfe 1994), it was expected there would be differences in porosity between the middle Eocene Nut Beds woods(UF 225) and the late Eocene woods of Post Hammer (UF 279) and Dietz Hill (UF 278) woods. Ring-porosity is rarer in the Nut Beds assemblage than it is in either UF 278 or UF 279. The percentages for perforation plates fall within the range of modern warm to cool temperate regional floras (Baas 1976, Wheeler et al. 2007).

There was a pronounced change in climate from the late Eocene to the early Oligocene (e.g., Zanazzi, et al. 2007). Well preserved silicified woods were collected in 1932 about 9 km to the east of Dietz Hill (UF 278) from the Gray Ranch site associated with the Oligocene Crooked River fossil leaf locality of the Bridge Creek flora (Fig. 1C; Chaney 1927, Meyer and Manchester 1997). Beck (1942) investigated those woods and recognized

Table 4. Comparison of the composition of UF 278 and UF 279 wood assemblages.

TAXA	UF 278 - Dietz Hill	UF 279 - Post Hammer
PINALES		
Pinaceae	*Keteleeria farionii*	not found
CUPRESSALES		
Cupressaceae	*Taxodioxylon* sp.	not found
CONIFER INCERTAE SEDIS	not found	Family indet.
MAGNOLIALES		
Magnoliaceae	*Magnolia hansnooteboomii*	not found
Lauraceae	*Laurinoxylon* sp. A	not found
Lauraceae	*Laurinoxylon* sp. B	not found
PROTEALES		
Platanaceae	*Platanoxylon haydenii*	*Platanoxylon haydenii*
Platanaceae	not found	*Platanus* sp.
TROCHODENDRALES		
Trochodendraceae	not found	*Trochodendron beckii*
SAXIFRAGALES		
Hamamelidaceae	Possibly present	*Hamamelidoxylon crystalliferum*
Cercidiphyllaceae	not found	*Cercidiphyllum alalongum*
FABALES		
Fabaceae	cf. *Styphonolobium* sp.	not found
ROSALES		
Ulmaceae	*Ulmus woodii*	*Ulmus danielii, U. woodii*
Cannabaceae	Possibly present	*Celtis popsii*
Uricalean Rosids	*Urticaleoxylon stevensii*	not found
Uricalean Rosids	*cf. Moroxylon*	not found
Uricalean Rosids	Cannabaceae/Moraceae Wood Type 1	not found
Uricalean Rosids	Cannabaceae/Moraceae Wood Type 2	not found
FAGALES		
Fagaceae	*Fagus dodgei*	*Fagus dodgei*
Fagaceae	*Quercus* sp. (Red Oak type)	not found
Fagaceae	not found	*Quercinium* sp. (evergreen oak)
Fagaceae	not found	*Lithocarpoxylon ashwillii.*
Fagaceae	not found	*Lithocarpoxyon* sp
Juglandaceae	*Carya leroyii*	not found
Juglandaceae	not found	*Pterocaryoxylon* sp.
SAPINDALES		
Anacardiaceae	not found	*Pistacia terrazasae*
Sapindaceae	not found	*Acer* (2 spp.)
Sapindaceae	*Aesculus klaassenii*	not found
Sapindaceae	*Klaassenoxylon wilkinsonii*	not found

Table 4 (cont.). Comparison of the composition of UF 278 and UF 279 wood assemblages.

TAXA	UF 278 - Dietz Hill	UF 279 - Post Hammer
SAPINDALES		
Rutaceae?, Sapindaceae?	*cf. Fagaroxylon* sp.	not found
MALVALES		
Malvaceae	not found	*Wataria kvacekii*
APIALES		
Araliaceae	*Plerandreoxylon oskoslkii*	not found
?MALPIGHIALES		
Salicaceae?	Unnamed	not found
INCERTAE SEDIS		
Theaceae?, Hamamelidaceae?	*Hamamelidoxylon* sp.	*Hamamelidoxylon suzukii*

Table 5. Comparison of the incidence of porosity and perforation plate types at the middle Eocene Clarno Nut Beds and the late Eocene Post Hammer (UF 279) and Dietz Hill (UF 278) localities.

POROSITY	Nut Beds n=65	UF 279 n=15	UF 278 n=16
Ring-porous	1 %	13 %	13 %
Semi-ring-porous	28 %	37 %	22 %
Diffuse-porous	71 %	50 %	65.%
PERFORATION PLATES			
Simple	78 %	69 %	76%
Scalariform	22 %	31 %	24%

a temperate association including *Sequoia* Endl. (1847), *Platanus, Quercus, Corylus* L. (1753), *Celtis, Zelkova* Spach (1841), and *Tilia* L. (1753). Comparing the Oligocene Gray Ranch woods with the older woods from Dietz Hill (UF 278) and Post Hammer (UF 279) sites also reflects changes in wood features correlated with change in paleoclimate; the Oligocene *Celtis* and *Zelkova* woods are distinctly ring-porous.

Locality UF 278 vs. UF 279

It is noteworthy that although the Post Hammer (UF 279) and the Dietz Hill (UF 278) localities are only 1.6 km apart (Fig. 1C) and believed to be of similar age they have few species in common, only *Platanoxylon haydenii*, *Fagus dodgei,* and *Ulmus woodii* (Table 4). In fact, there are relatively few families in common: Pinaceae, Cupressaceae, Magnoliaceae, Lauraceae, Fabaceae, and Araliaceae were found at Dietz Hill and not at Post Hammer; conversely, Trochodendraceae Eichler (1865), Cercidiphyllaceae Engl. (1907), Cannabaceae, Anacardiaceae, and Malvaceae were found at Post Hammer and not at Dietz Hill. Juglandaceae and Sapindaceae were found at both localities, but the genera are different.

We consider it likely that these differences reflect lateral variation and different subenvironments. If we treat them collectively, the diversity increases, but the wood assemblage is still less diverse than the contemporaneous Teater Road compression flora some 11.5 km to the east (Fig. 1C). This compression flora is preserved in lacustrine shale and has about 51 genera of leaves and 57 of flowers, fruits, and seeds (Manchester and Lott, in progress). It includes only a few broadleaved evergreens (*Mahonia* Nutt. (1818), and perhaps Lauraceae), and a variety of deciduous angiosperms including Ulmaceae (*Ulmus*, *Cedrelospermum* Saporta emend. Manchester 1987), Fagaceae (*Quercus*), Betulaceae Gray, 1821 (*Carpinus* L., 1753*; Alnus* Mill., 1754), Malvaceae (*Florissantia* Manchester, 1992*; Craigia* W.W. Sm. and W.E. Evans, 1921), Sapindaceae (*Koelreuteria, Dipteronia, Acer* spp.), Simaroubaceae DC., 1811 (*Ailanthus* Desf., 1786*; Chaneya* Wang and Manchester, 2000), Fabaceae (*Cercis* and other genera), Rhamnaceae Juss., 1789 (*Paliurus* Mill., 1754), and Hydrangeaceae Dumort., 1829 (*Hydrangea* L., 1753).

Our understanding of the composition of Dietz Hill (UF 278) vegetation comes from silicified fruits and seeds as well as woods from the same site. Disseminules that co-occur with the Dietz Hill woods include *Magnolia*, Menispermaceae Juss. (1789), *Meliosma* Blume (1823), *Sabia* Colebr. (1819), Platanaceae, *Ampelopsis* A.Rich. ex Michx. (1803), *Aphananthe, Carya*, Burseraceae, *Cedrela*, Rutaceae, *Acer*, and *Alangium* Lam. (1783), as illustrated and described by Manchester and McIntosh (2007). Other fruits that have been identified subsequently from the same site (Manchester personal observation) include *Hydrangea* and *Juglans*. Once again, this shows the importance of utilizing multiple plant parts to gain a fuller picture of the taxonomic composition, as was also the case for the Clarno nut beds flora. The extent of overlap between the wood and fruit genera at Dietz Hill (*Magnolia, Carya*) is minimal. Some of the fruits and seeds may represent non-arborescent taxa that would not be expected among the woods (*Ampelopsis*, Menispermaceae, *Hydrangea*), but most of the other disseminules likely represent trees.

CONCLUSIONS

The middle to late Eocene fossil plant localities of Central Oregon document changes in woody vegetation and anatomical features correlated with climate change, which are changes in the incidences of temperate vs subtropical genera and ring-porous and semi-ring-porous vs. diffuse-porous wood. They also provide an excellent example of how a better understanding of the diversity of ancient floras comes from the study of multiple plant parts with some genera only occurring as wood and others occurring only as fruits and seeds.

The Dietz Hill (UF 278) fossil wood assemblage includes North America's first known wood of *Keteleeria* (Pinaceae); its oldest known wood of *Aesculus* (Sapindaceae); two new genera: *Urticaleoxylon* (family indet., order Rosales, Urticalean Rosids) and *Klaasenxoylon* (Sapindaceae); new species of *Plerandreoxylon* (Araliaceae), *Magnolia* (Magnoliaceae), and *Carya* (Juglandaceae). There are also genera that are of common occurrence in the Eocene of North America: *Taxodioxylon* (Cupressaceae), *Laurinoxylon* (Lauraceae), *Platanoxylon* (Platanaceae), *Quercus* (Fagaceae). Some woods resemble east Asian species rather than any American or European species: *Magnolia hansnooteboomi,* and *Carya leroyii*. The Urticalean Rosids are the most diverse group at the locality. However, the multiple samples of beech (*Fagus*) and sycamore (*Platanus*) that are more than 10 cm in diameter suggest they were dominants in the vegetation. Given that the Eocene to Oligocene is a critical time in the evolution of the Northern Hemisphere flora, we encourage future work on both Eocene and Oligocene woods.

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