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Late Eocene woods from central Oregon, western USA

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ABSTRACT. Brummer Spring is one of several late Eocene wood localities near the town of Post, Oregon, western USA. This locality includes four conifer wood types (one *Pinus* and three probable Cupressaceae) and 16 angiosperm woods, 13 of which can be assigned to family and three that cannot be reliably placed in an order. Angiosperm families recognized include Lauraceae, Platanaceae, Cercidiphyllaceae, and Fagaceae (common at Eocene localities in North America), as well as Salicaceae (common in compression floras, but rare in wood assemblages), Rosaceae, which has the most specimens at this locality, Meliaceae, and Malvaceae. The affinities of these woods are primarily with warm temperate to subtropical vegetation of eastern Asia and eastern North America. Only *Platanoxylon* and *Fagus* occur at the two other Post localities. There also are fruits at Brummer Spring with the only overlap between the fruits and woods being one poorly preserved "*Prunus*-like" endocarp. Other fruits and seeds are *Juglans*, *Nyssa*, possible *Magnolia* and Taxaceae, and an Incertae Sedis. As was true for the other two Post wood localities, the higher incidence of ring-porosity here as compared to the older middle Eocene Clarno Nut Beds wood assemblage attests to increased seasonality from middle to late Eocene in western North America.

KEYWORDS: John Day Formation, fossil wood, Lauraceae, Rosaceae, *Prunus*, Malvaceae, Platanaceae

INTRODUCTION

The Pacific Northwest of the USA has many Tertiary plant and vertebrate localities. Amongst them are Eocene localities in the John Day and Crooked River Basins of Central Oregon that have co-occurring woods, leaves, fruits and seeds providing a better visage of the diversity of the ancient flora than would a single type of plant remain. A view of climate change is provided by comparing ecologically significant wood anatomical features of the diverse middle Eocene Clarno Nut Beds wood assemblage of the John Day Basin (Wheeler and Manchester, 2002) with the late Eocene Post wood assemblages of the Crooked River Basin. Earlier, we described woods from the Post Hammer locality (UF279, Wheeler and Manchester, 2021) and the Post Dietz Hill locality (UF278, Wheeler et al., 2023). Herein, we present woods from the Post Brummer Spring (UF254) and Red Hill (UF305) localities and continue our comparisons of these Eocene localities to one another. These woods augment studies of the leaf, flower and fruit remains preserved in nearby shales of the same formation (Manchester and Lott, 2024) to provide additional information on late Eocene floristic diversity and paleoclimate and provide data that can be used in biogeographic and phylogenetic studies.

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MATERIALS AND METHODS

LOCALITY

The Brummer Spring site (UF254) is situated on private land in the Sheep Rock Creek Drainage, about 19 km east and 3 km north of the town of Post, Oregon. The silicified woods are found along with fruits and seeds free from matrix weathering out of a tuff attributed to the John Day Formation (Fig. 1C) as mapped by Waters (1968). We also include woods from a site rich in petriified woods dubbed Red Hill 2 (UF 305; fig. 1A, C). In our estimation, the floristic content of these sites is consistent with a late Eocene age. There are no dated tuffs adjacent to the fossiliferous horizon to provide radiometric age estimates. However, the local stratigraphy indicates that these sites should be older than 36 million years, the date for an ash layer immediately overlying the Dietz Hill silicified wood and fruit locality (13 km to the west) (Fig. 1; Manchester and McIntosh, 2007; Wheeler et al., 2023).

Specimens were collected mostly at the soil surface and in the dry creek bed, but also amateur collectors had dug and screened topsoil at the site to recover more specimens. Silicified *Juglans* nuts and a boat-shaped endocarp probably related to *Chandlera*, were observed by SRM in the private collection of Fred Rohner, of Albany, Oregon, in the mid 1970s, but that collection has been lost. Several additional fruit and seed specimens, and the woods treated here, were collected from the Brummer Spring site by S.R. Manchester and high school students of the OMSI paleobotany summer field program during visits in the 1980s, following directions provided by Mr. Rohner. These specimens are now housed at the Florida Museum of Natural History at University of Florida, Gainesville, Florida, USA, with catalog numbers prefixed by "UF."

SAMPLE PREPARATION

A diamond lapidary saw was used to cut thick sections (wafers) of transverse (TS), tangential (TLS), and radial (RLS) surfaces. Sections were prepared by the grinding method. One side of the wafer was smoothed to remove saw marks and then affixed to a glass side

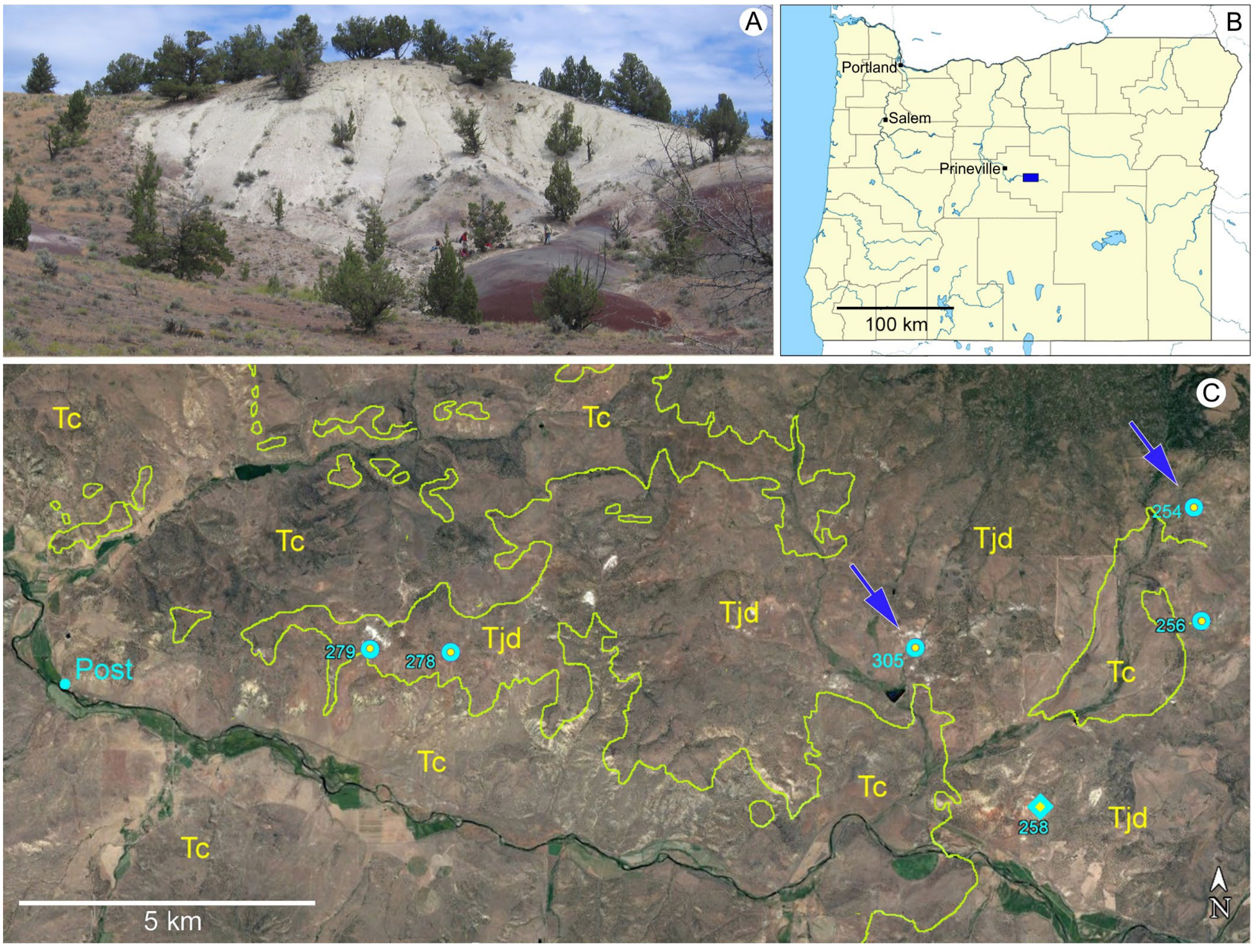

Figure 1. **A**. Red Hill 2 locality (UF305) in the Lost Creek drainage, where numerous woods are preserved. Google Earth imagery; **B**. Index map of Oregon. Yellow rectangle showing the location of satellite image in C; **C**. Paleobotanical localities in the vicinity of Post, Oregon in the Crooked River valley with blue arrows indicating the two sites treated herein. 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). Localities: 279 – Post Hammer site; 278 – Dietz Hill; 254 – Brummer Spring; 305 – Red Hill 2; 256 – Teater Road leaf locality (Manchester and Lott, 2024); 258 – Crooked River leaf site, Oligocene (Chaney, 1927; Meyer and Manchester, 1997)

using 24-hour transparent epoxy. The sections were then ground until they were thin enough (~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.

AFFINITIES AND NAMES

Initially, we used the InsideWood (IW) database to search for taxa with the combination of features observed in each of the fossil wood types (InsideWood 2004-onwards). We used some of the search strategies described by Wheeler (2011) and Wheeler et al. (2020). The search criteria used are given in the form of a list of numbers corresponding to the 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 taxonomic treatments herein follow the APG IV classification (Angiosperm Phylogeny Group, 2016) and the descriptions use the terminology of the IAWA Hardwood List of Microscopic Features for Hardwood Identification (IAWA Committee, 1989). When the woods have a combination of features unique to a present-day genus, we assign the fossil woods to that genus; if not we assign them to a fossil genus, generally with the suffix -oxylon, e.g. *Pterocaryoxylon*, whose features are found in both *Pterocarya* and some *Juglans* (see discussions in Collinson, 1986; Wheeler and Manchester, 2002, 2021).

Figure captions use the abbreviations: TS for transverse section, RLS for radial longitudinal section, and TLS for tangential longitudinal section. For quantitative features we indicate the average followed by standard deviation (SD), and then the range; when three values are given, they are presented in the sequence minimum – average – maximum.

SYSTEMATICS

CONIFERS

There are four types of conifers in the Brummer wood assemblage. One (UF254-25205) is a pine based on the presence of axial resin canals with thin-walled epithelial cells (Fig. 2A). Unfortunately, it is contorted and not well enough preserved to see cross-field pitting. The radial sections of this pine (UF254-25205) and samples UF254-24691 and 24692 were not informative and are not figured.

UF254-25203, 24691, and 24696 most probably are Cupressaceae, but we found it impossible to see their cross-field pits clearly. These woods differ in ray size and axial parenchyma presence. Brief descriptions of each type are given below. Biseriate rays are common in UF254-24696, which is unusual for conifers. Figures 36 and 37 of Bailey and Faull's (1934) classic paper on variation in *Sequoia sempervirens* show tangential sections in which biseriate rays are common. Consequently, it seems probable that this sample belongs to the subfamily Taxodioideae, which includes *Sequoia*.

? CUPRESSALES Link

? CUPRESSACEAE Gray

UF254 CONIFER 1

Fig. 2B–E

Material. UF254-25203.

Description. Growth rings distinct. Gradual transition from earlywood to latewood. Latewood narrow, only 1–3 rows (Fig. 2B, C). Average tangential diameter of longitudinal tracheids 37 (SD = 8), range 21–43 µm; intertracheary bordered pits on radial walls 1–2-seriate (Fig. 2E).

Axial parenchyma present, perhaps marginal, as radial section shows a strand near a growth ring boundary; transverse end walls smooth (Fig. 2E).

Rays uniseriate (Fig. 2D). Ray height in cell number averages 5 (SD = 2), range 2–11 cells; ray height averages 124 µm (SD = 55), range 60–276 µm. Cross-field pits probably cupressoid. End walls and horizontal walls of ray parenchyma apparently smooth (Fig. 2E). Ray tracheids absent.

UF254 CONIFER 2

Fig. 2F, G

Material. UF254-24691.

Description. Growth rings distinct. Gradual transition from earlywood to latewood. Latewood narrow, only 1–3 rows (Fig. 2F). Average tangential diameter of longitudinal tracheids 37 µm (SD = 8), range 23–53 µm.

Axial parenchyma diffuse (Fig. 2F).

Rays predominantly uniseriate, occasionally biseriate (Fig. 2G). Ray height in cell

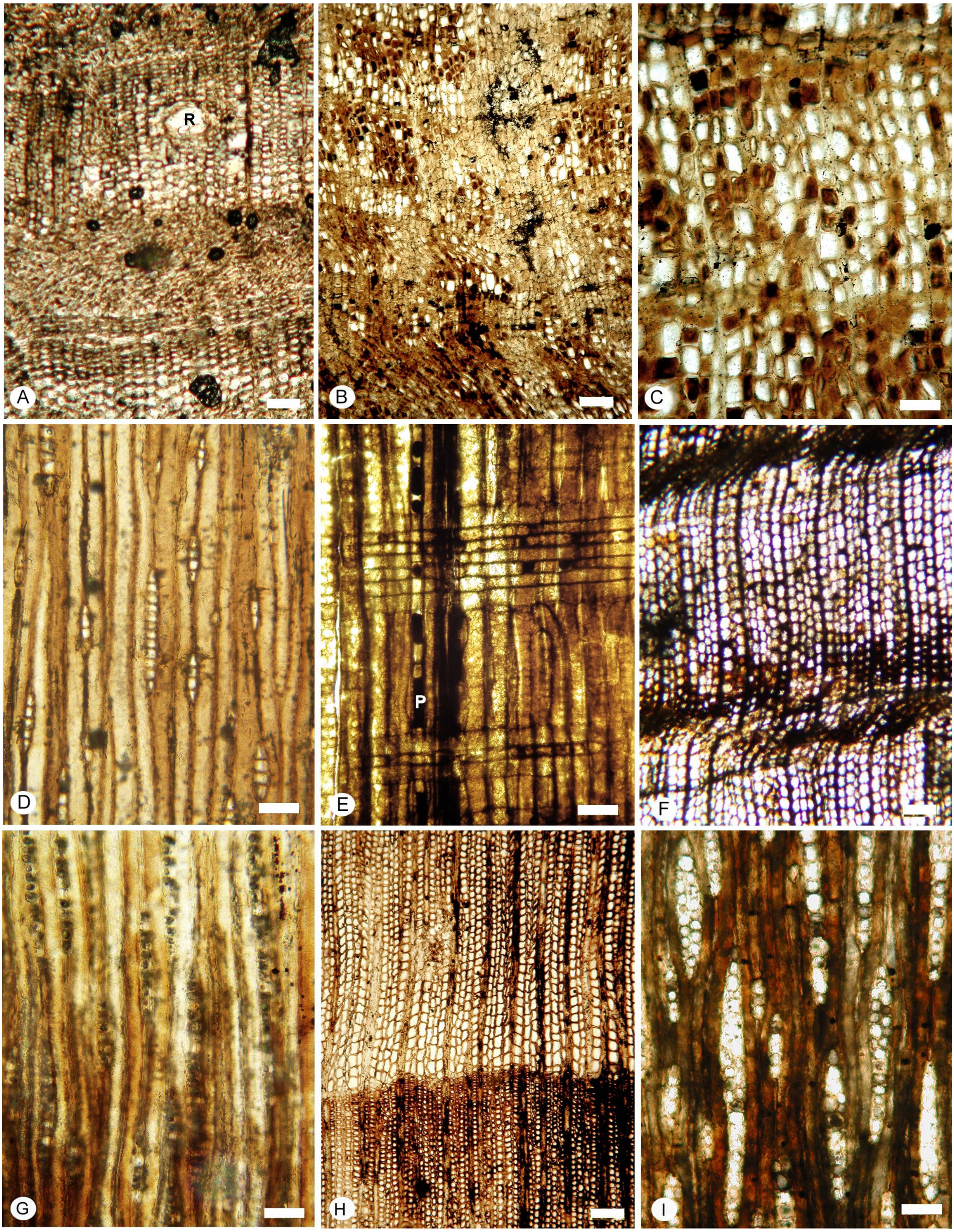

Figure 2. **A**. Pinaceae, UF254-25205, resin canal (R) with thin-walled epithelial cell, distinct growth rings, TS. **B–I**. Cupressaceae?; **B–E**. Conifer 1, UF254-25203; **B**, **C**. Distinct growth rings, gradual transition from earlywood to latewood, TS; **D**. Uniseriate rays, TLS; **E**. Rays composed exclusively of ray parenchyma; axial parenchyma strand (P), end walls smooth, TLS; **F**, **G**. Conifer 2, UF254-24691; **F**. Distinct growth rings, gradual transition to a narrow latewood zone; diffuse axial parenchyma, TS; **G**. Rays predominantly uniseriate, occasionally biseriate, TLS; **H**, **I**. Conifer 3, UF254-24696; **H**. Distinct growth rings, gradual transition to a broad latewood, TS; **I**. Rays commonly biseriate, TLS. Scale = 200 μm in A, B, F, H; 100 μm in C, D, E, G, I

number averages 12 (SD = 6), range 3–23 cells; ray height averages 304 µm (SD = 144), range 141–625 µm. Cross-field pitting not observed.

UF254 CONIFER 3

Fig. 2H

Material. UF254-24696.

Description. Growth rings distinct. Gradual transition from earlywood to latewood, wide zone of thicker-walled cells, possibly compression wood, as some tracheids with circular lumens (Fig. 2H). Average tangential diameter of earlywood longitudinal tracheids 27 µm (SD = 3.5), range 20–34 µm.

Axial parenchyma possibly rare diffuse.

Rays 1–2(–3)-seriate (Fig. 2I). Ray height in cell number averages 12 (SD = 5), range 3–21 cells; ray height averages 400 µm (SD = 180), range 107–849 µm.

ANGIOSPERMS

LAURALES Jus es Berchtold et Japers

LAURACEAE Jussieu

Laurinoxylon Felix emend Dupéron, Dupéron-Laudouereix, Sakala et De Franceschi

Laurinoxylon sp. A

Fig. 3A–F

Material. UF305-25300.

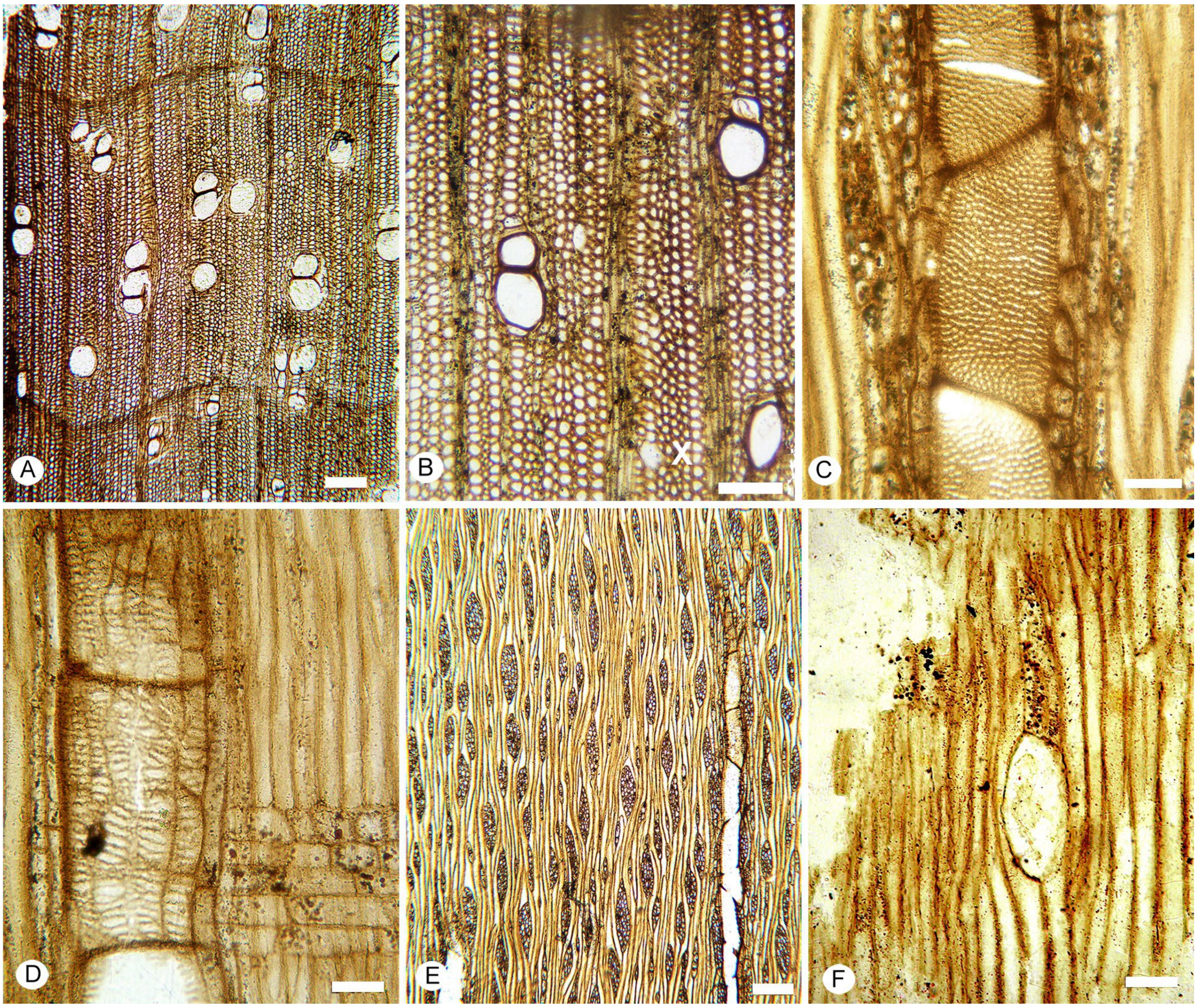

Figure 3. *Laurinoxylon* sp. A UF305-25300. **A**. Distinct growth rings, wood diffuse porous, vessels solitary and in radial multiple, TS; **B**. Detail of growth ring boundary, vessels solitary and in radial multiples, thin-thick-walled fibers, X next to an idioblast among the fibers, TS; **C**. Crowded alternate intervessel pits, axial parenchyma strands adjacent to the vessel, non-septate fibers, TLS; **D**. Parenchyma strands adjacent to the vessel, simple perforation plates, vessel-ray-parenchyma pits with reduced borders, marginal row of square cray parenchyma cells, non-septate fibers, RLS; **E**. Rays commonly 3-4-seriate, TLS; **F**. Idioblast among the fibers, TLS. Scale = 200 µm in A, E; 100 µm in B; 50 µm in C, D, F

Description. Growth rings distinct. Wood diffuse-porous.

Vessels solitary and in radial multiples of 2–3; mean tangential diameter 97 µm (SD = 19), range 56–134 µm; 7–9 vessels per mm^2; solitary vessels round to oval in outline; perforations simple; intervessel pits crowded alternate, angular in outline, medium to large in horizontal diameter; vessel-ray parenchyma pits with much reduced borders, horizontal to vertical; vessel element lengths average 283 (43) µm, range 207–420 µm; tyloses occasional, widely spaced.

Fibers non-septate; thin- to thick-walled, fiber pits not distinct on either radial or tangential walls.

Axial parenchyma scanty paratracheal; strands mostly of 4 cells.

Rays 1–4(5)-seriate, multiseriate ray heights average 224 µm (58), range 134–392 µm; multiseriate rays heterocellular, usually with one marginal row of square / upright cells; uniseriate rays not common, less than 10 cells high.

Idioblasts (oil/mucilage cells) rare, axially oriented, isolated amongst the fibrous elements.

Storied structure absent.

Comparisons with present-day woods. The combination of vessels solitary and in short radial multiples, simple perforation plates, crowded alternate intervessel pitting, vessel-ray parenchyma pits with reduced borders, scanty paratracheal to narrow vasicentric axial parenchyma, heterocellular rays with one marginal row, and idioblasts (oil cells) indicates that this wood belongs to the Lauraceae. The non-septate fibers suggest a relationship with the Northern Hemisphere Laureae (Richter, 1981, 1987). Idioblasts are rare in this wood and were only found isolated amongst the fibers as in Dietz Hill sample.

Comparisons with fossil woods. This sample differs from the Nut Beds lauraceous woods because none of them have idioblasts among the fibers (Wheeler and Manchester, 2002), but there is similarity with *Laurinoxylon* sp. A (UF278-84869) from the nearby Post Dietz Hill locality. In this Dietz Hill sample idioblasts are rare and isolated amongst the fibers and most fibers are non-septate, however, its rays are narrower (1–3-seriate) and more heterocellular with 1–3 marginal rows of square/upright cells than in the Brummer Spring sample.

There is a rather overwhelming number of fossil woods of Lauraceae, most assigned to *Laurinoxylon* (see list in Gregory et al., 2009); fossil lauraceous woods continue to be described (e.g. Vasquez-Loranca and Cevallos-Ferriz, 2022). Mantzouka et al. (2016) grouped Oligocene-Miocene European *Laurinoxylon* according to idioblast location; none of the groups were for idioblasts only amongst the fibers. As best we can determine, this late Eocene sample differs from all previously described *Laurinoxylon* species and including the *Laurinoxylon* from the Dietz Hill locality.

Laurinoxylon sp. B

Fig. 4A–H

Material. UF305-25302, UF254-25217.

Note. In the following description, quantitative values for UF305-25302 are given first, followed by those for UF254-25217.

Description. Growth rings distinct. Diffuse porous, with a slight tendency to semi-ring porosity.

Vessels solitary and in radial multiples of 2–3; average tangential diameter 156 (21) µm and 128 (25) µm; 6–7 per mm^2; solitary vessels round to oval in outline; perforations simple, scalariform perforation plates not seen; intervessel pits crowded alternate, angular in outline, 7.5–10 µm in horizontal diameter; vessel-ray parenchyma pits with much reduced borders, mostly horizontally elongate (class B of Richter, 1987); tyloses occasional, widely spaced; vessel element length ranges 405–551 µm and 474–627 µm.

Fibers non-septate; thin- to thick-walled, pits not distinct on either radial or tangential walls.

Axial parenchyma scanty paratracheal; strands mostly of 4 cells.

Rays 1–4 (6)-seriate. Multiseriate rays heterocellular, usually with one marginal row of square / upright cells; ray height averages 582 (125) µm and 422 (113) µm.

Idioblasts (oil/mucilage cells) rare, associated with axial parenchyma.

Storied structure absent.

Comments. Although there are differences in quantitative features between UF305-25302 and UF254-25217, we do not consider those differences significant and are considering them to be the same wood type.

Comparisons with present-day woods. As was the case for *Laurinoxylon* sp. A treated

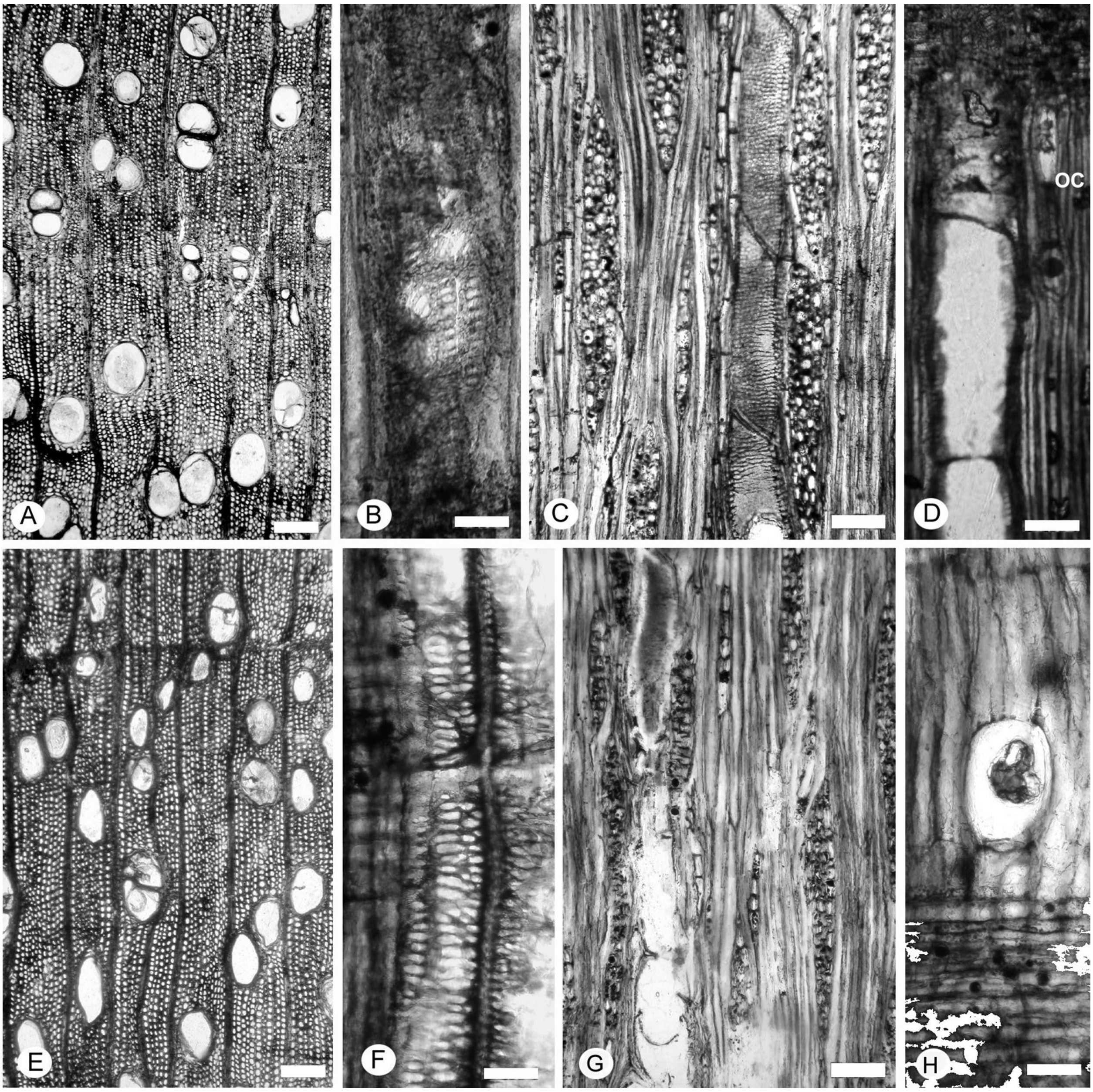

Figure 4. *Laurinoxylon* sp. B of Brummer Spring. **A–D**. UF305-25302; **E–H**. UF254-25217; **A**, **E**. Diffuse-porous wood with vessels solitary and in short radial multiples, TS; **B**, **F**. Vessel-ray parenchyma pits with simple to reduced borders and horizontally elongate, RLS; **C**, **G**. Rays 1–4-seriate, non-septate fibers, TLS; **D**, **H**. Idioblasts / oil cells (OC) in axial parenchyma strand, RLS. Scale = 200 µm in A, E; 50 µm in B, D, F, H

above (UF305-25300), the combination of vessels solitary and in short radial multiples, simple perforation plates, crowded alternate intervessel pitting, vessel-ray parenchyma pits with reduced borders, heterocellular rays with one marginal row, and idioblasts (oil cells) indicates that these woods are Lauraceae. Idioblasts also are rare in these two samples, but look to be associated with axial parenchyma strands, rather than isolated amongst the fibers. There is, of course, the possibility that these two samples and UF305-25300 might represent different locations in the same tree or represent other individuals of the same species showing infraspecific variation.

Of the 203 descriptions of present-day Lauraceae in InsideWood, the genera with species that have idioblasts only associated with axial parenchyma, lack abundant axial parenchyma, and have mostly non-septate fibers are *Beilschmiedia*, *Cryptocarya* and *Endiandra.* These three genera are placed in Cryptocaryeae Nees, a pantropical group, which includes some subtropical members (Stevens, 2001-onwards).

Comparisons with fossil woods. Because the idioblasts of these two samples are only associated with axial parenchyma, they differ from *Laurinoxylon* sp. A of Red Hill, (UF305-25300), as well as from *Laurinoxylon* sp. A of the nearby Dietz Hill locality, and all Clarno Nut Beds Lauraceae. We are only aware of one well-detailed published description of a fossil Lauraceae wood with idioblasts only associated with axial parenchyma, *Ulminium kokubunii* Takahashi and Suzuki (2003) from the late Cretaceous of Japan. It differs, however, from these Brummer Spring woods in being semi-ring-porous and having septate fibers and some scalariform perforation plates.

PROTEALES
Juss. ex Berchtold et J. Presl.

PLATANACEAE T. Lestib.

Platanoxylon
Andreánszky emend. Süss et Müller-Stoll

Platanoxylon haydenii
(Felix) Süss et Müller-Stoll 1977

Fig. 5A–F

Materials. UF254-24705, 25175, 25206; UF305-25295, 25298, 25299, 25301.

Description. Wood diffuse-porous. Growth rings indistinct to distinct, if present, marked by slightly noded rays and 1–2 rows of radially narrow fibers (Fig. 5A, B).

Vessels mostly solitary and in short multiples, some tangentially arranged (Fig. 5A, B); average tangential diameters range from 54 (11)–71 (12) µm; 40–100 vessels/mm^2. Perforation plates exclusively scalariform (Fig. 5C, D, J), 4–30 bars per plate observed; intervessel pits opposite (Fig. 5D, J), vessel-ray parenchyma pits generally similar to intervessel pits, sometimes horizontally elongate (Fig. 5E).

Fibers non-septate, pits not observed.

Axial parenchyma diffuse, diffuse-in-aggregates, and in interrupted short uniseriate tangential lines (Fig. 5A, B, H, I).

Rays of two distinct sizes, rays sometimes compound, larger rays typically over 1 mm with maximum ray widths of 15–30+ cells (Fig. 5F, L), composed of procumbent cells, sometimes with 1–2 marginal rows of square cells (Fig. 5G, K). Occasionally prismatic crystals in radial alignment in procumbent ray cells present (Fig. 5K – UF305-25298).

Comments. Fossil woods with features consistent with the Platanaceae are common at Cenozoic localities in the Northern Hemisphere. Present-day Platanaceae have both simple and scalariform perforation plates, while most Paleogene platanoid woods have exclusively scalariform perforation plates. These latter woods are assigned to the fossil wood genus *Platanoxylon* to indicate they differ from the present-day *Platanus*.

Comparisons with present-day and fossil woods. The combination of diffuse-porous woods, with mostly solitary vessels with some tangential to oblique pairs, diffuse and diffuse-in-aggregates axial parenchyma, scalariform perforation plates, opposite intervessel pits, vessel-ray parenchyma mostly similar to intervessel pits, rays that are wider than 10-seriate and taller than 1 mm and are not markedly heterocellular indicates affinities with *Platanoxylon* of the Platanaceae. Woods of this type also occur at the nearby Post Hammer locality (UF279, two samples, Wheeler and Manchester, 2021) and Post Dietz Hill locality (UF278, four samples, Wheeler et al., 2023). As was the case at the Dietz Hill locality, there was variation in ray sizes and occurrence of compound rays. This type of variation is similar to intraspecific variation in present-day *Platanus* species, so we infer that there would be similar variation within *Platanoxylon* species. Thus, we assign them to *Platanoxylon haydenii*, which occurs at the other Post localities.

SAXIFRAGALES Berchtold et Pres.

CERCIDIPHYLLACEAE Engl.

Cercidiphyllum Siebold et Zucc.

cf. ***Cercidiphyllum alalongum***
Scott et Wheeler 1982

Fig. 6A–G

Material. UF254-24687.

Description. Growth rings distinct (1p) marked by 1–3 rows of radially narrow fibers,

Wood diffuse-porous (5p).

Vessels predominantly solitary, radial and oblique pairs rare; absence of a tangential or radial pattern (6a, 7a,); somewhat angular in outline, mean tangential diameter 67 (11) µm,

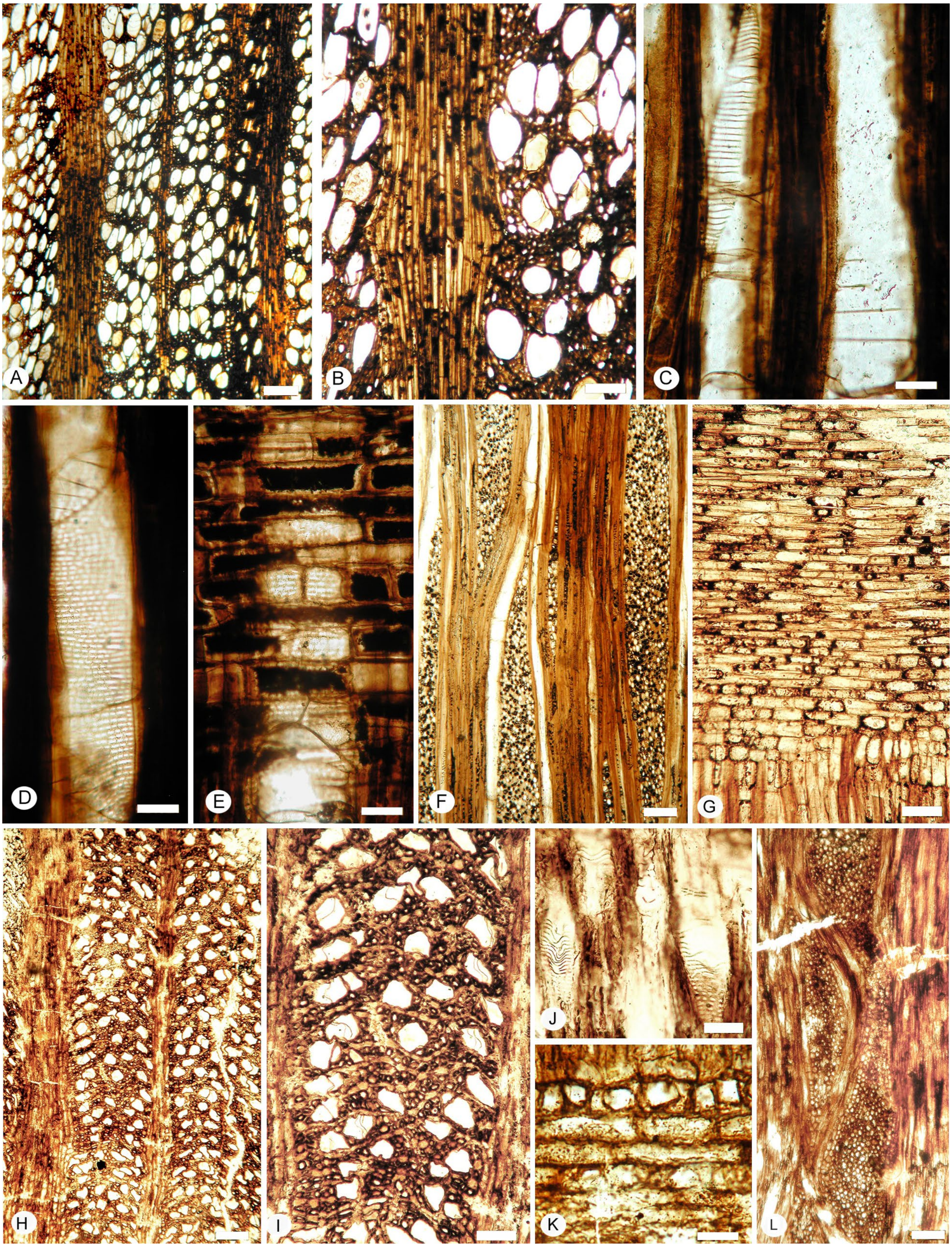

Figure 5. *Platanoxylon haydenii*. **A**, **B**. Wood diffuse-porous, growth ring boundaries marked with noded rays, vessels mostly solitary with occasional multiples, axial parenchyma diffuse and diffuse-in-aggregates, UF305-25295, TS; **C**. Scalariform perforation plates, UF254-25206, RLS; **D**. Opposite intervessel pitting, scalariform perforation plates with less than 10 bars, UF254-25206, TLS; **E**. Vessel-ray parenchyma pits, UF254-25206, RLS; **F**. Wider rays more than 10-seriate, UF305-25299, TLS; **G**. Procumbent body cells, UF305-25295, RLS; **H–L**. UF305-25298; **H**, **I**. Wood diffuse-sporous, growth rings indistinct, axial parenchyma diffuse-in-aggregates, in 1-seriate lines, TS; **J**. Scalariform perforation plates and opposite intervessel pitting, RLS; **K**. Prismatic crystals in radial alignment, RLS; **L**. Rays more than 10-seriate, TLS. Scale = 200 μm in A, F, H, L; 100 μm in B, G, I, J; 50 μm in C, D, E, K

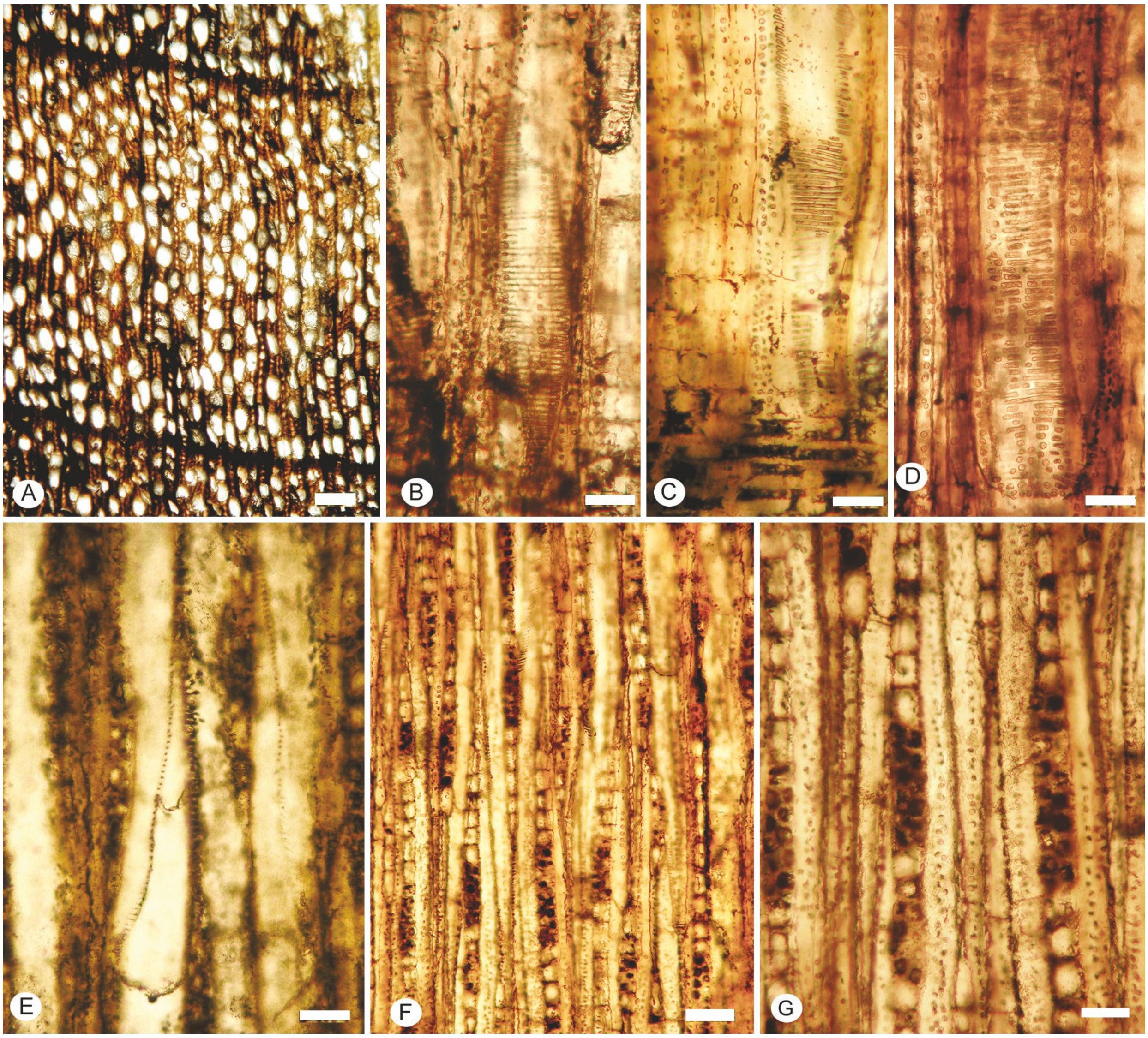

Figure 6. cf. *Cercidiphyllum alalongum*. UF278-24687. **A**. Distinct growth ring boundaries, wood diffuse-porous, vessels predominantly in solitary, TS; **B**. Scalariform perforation plate, RLS; **C**, **D**. Scalariform intervessel pitting, fibers with distinctly bordered pits, RLS; **E**. Scalariform perforation plates with many bars, TLS; **F**, **G**. Rays 1–2-seriate, some rays with alternating uniseriate and biseriate portions, some with a tendency for the uniseriate and biseriate portions to be of similar width, TLS. Scale = 200 µm in A; 100 µm in F; 50 µm in B, C, D, E; 20 µm in G

44–86 µm (average vessel diameter <100 µm: 42a, 43a); >69–87 vessels per mm^2 (49p); perforations exclusively scalariform with 24–48 bars (14p, 17p); intervessel pits scalariform (20p); vessel-ray parenchyma pits similar to intervessel pits (30p); vessel element lengths 950–1500 µm (54p); occasional widely spaced tyloses. [Possibly helical thickenings in vessel element tips.]

Fibers with distinctly bordered pits on radial and tangential walls (62p, 63p), walls of thin to medium thickness, septate fibers absent (65a), all fibers non-septate (66p).

Parenchyma rare (75p), apotracheal diffuse (76p), with ~10 cells per strand (94p).

Rays 1–2 seriate (97p), some rays with alternating uniseriate and biseriate parts, sometimes with a tendency for the width of uniseriate portions to be equal to biseriate portions (100p).

Comparisons with present-day woods. We searched the InsideWood database multiple times using various combinations of the features given in the description, either allowing none or one mismatch. In some searches we used 9p for vessels exclusively solitary and in others 10a and 11a for absence of radial multiples of 4 or more and absence of vessel clusters. Results of the searches included Altingiaceae (*Liquidambar*), Cercidiphyllaceae (*Cercidiphyllum*), Cornaceae (*Cornus oblonga*), Daphniphyllaceae (*Daphniphyllum*), Ericaceae (*Kalmia*), Hamamelidaceae (*Corylopsis*, *Disanthus*, *Mytilaria*), Nyssaceae (*Davidia*), Pentaphylacaceae (*Adinandra*, *Cleyera*, *Ternstroemia*), Schisandraceae (*Illicium*), Theaceae (*Apterosperma*, *Camellia*, *Polysporas*), Viburnaceae (*Viburnum*).

Cornus, *Nyssa* and Pentaphyllaceae do not have horizontally elongate vessel-ray parenchyma pitting and so can be eliminated. Only *Liquidambar*, *Cercidiphyllum*, and *Corylopsis* have helical thickenings in vessel element tails. Alternating uniseriate and biseriate portions of rays with a tendency to be of the same width have been reported for *Cercidiphyllum* (Scott and Wheeler, 1982; Wheeler and Manchester, 2002). We reviewed descriptions and images of *Cercidiphyllum* in the Anatomical Database and Atlas of Chinese woods (Itoh et al., 2022) and FFPRI's Database of Japanese Woods (FFPRI 2002). There are differences between these two databases' descriptions of *Cercidiphyllum* and this fossil; they both report a vessel frequency of >100 per sq. mm and crystals in upright ray cells.

Comparisons with fossil woods. We consider this wood to be similar to *Cercidiphyllum alalongum* from the middle Eocene Clarno Nut Beds, Oregon (Scott and Wheeler, 1982; Wheeler and Manchester, 2002) and the nearby late Eocene Post Hammer locality (Wheeler and Manchester, 2021). The occurrence of helical thickenings in vessel element tips and the alternating uniseriate and biseriate portions of rays with a tendency for the uniseriate and biseriate portions to be of the same width were used to distinguish *Cercidiphyllum alalongum* from the European and Asian species: *Cercidiphylloxylon kadanense* (Sakala and Privé-Gill, 2004) and *Cercidiphyllum spenceri* Brett (1956). The occurrences of *Cercidiphyllum*-like fossil woods were reviewed by Sakala and Privé-Gill (2004) and Guo et al. (2010).

MALPIGHIALES Martius

SALICACEAE Mirbel

Populus L.

Populus sp.

Fig. 7A–C

Material. UF254-24704.

Description. Growth rings distinct, marked by radially flattened fibers, differences in latewood and earlywood vessel diameters, and possibly marginal parenchyma. Wood semi-ring porous to diffuse-porous (Fig. 7A).

Vessels solitary and in radial multiples of 2–4, occasionally more (Fig. 7A); average tangential diameters 53 (SD = 8) µm, range 36–67 µm; vessel frequency 53–83 per mm^2; solitary vessels round to oval in outline; perforations exclusively simple; intervessel pits crowded alternate, 7–9 µm in horizontal diameter; angular in outline (Fig. 7C); vessel-ray parenchyma pits with reduced borders to

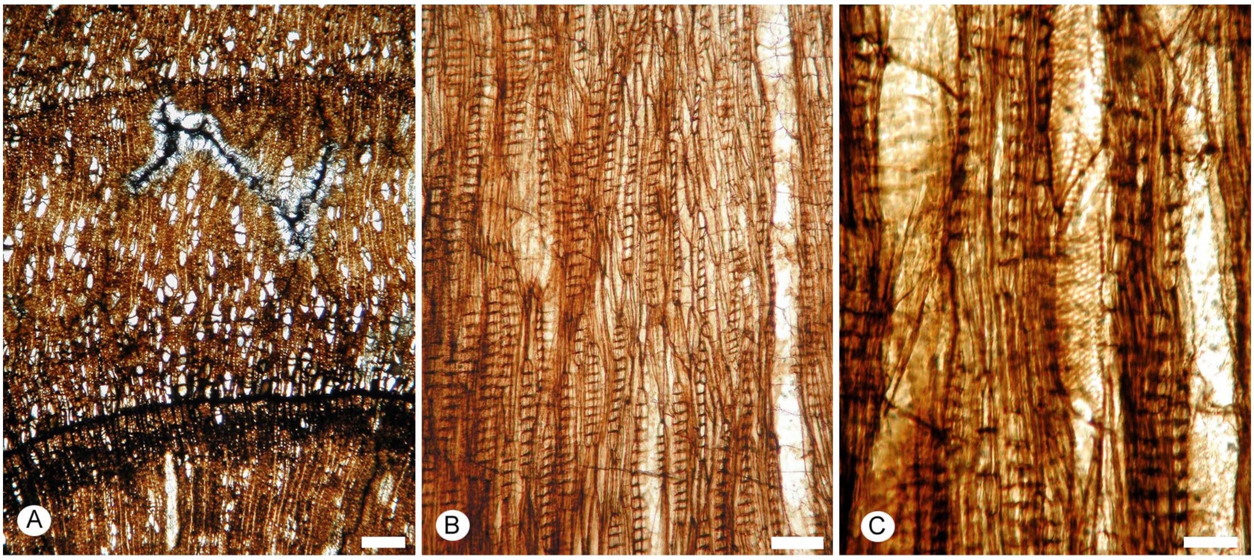

Figure 7. *Populus* sp. UF254-24704. **A**. Growth rings distinct, vessels solitary and in radial multiples, TS; **B**. Rays exclusively uniseriate, thin-walled tyloses in vessels; **C**. Intervessel and vessel-ray parenchyma pits, the latter with reduced borders. Scale = 200 µm in A, 100 µm in B; 50 µm in C

simple, shape similar to intervessel pits; vessel element lengths <350 µm; thin-walled tyloses present.

Fibers non-septate; thin-walled, fiber pits not seen.

Axial parenchyma rare, marginal parenchyma possibly present.

Rays exclusively uniseriate (Fig. 7B); apparently homocellular [or heterocellular ??]; ray height averages 10 (SD = 4) cells, range 4–19 cells; >12 per mm.

Storied structure absent. Crystals not observed.

Comments. Fine fungal hyphae are common in this sample and when they cross fibers they are easy to confuse with septa. Tyloses and contortion of the fossil interfered with measuring vessel element lengths. Compressed vessels were not included in vessel diameter measurements. Because of the compression and contortion of the samples longitudinal sections were intermediate between radial and tangential.

Comparisons with present-day woods. We searched the InsideWood database for distinct growth rings (1p), diffuse-porous to semi-ring porous woods (3a), vessels solitary and in radial multiples (9a, 11a), simple perforation plates (13p), alternate intervessel pitting angular in outline and medium-to large (21a, 22p, 23p, 24a, 25a), vessel-ray parenchyma pitting with reduced borders, rounded to angular in outline (31p), fiber pits not obvious (61p), non-septate fibers (66p), axial parenchyma rare (75p), rays exclusively uniseriate and homocellular (96p, 104p), storied rays and radial canals absent (118a, 130a). This search returned multiple species of *Populus* (Salicaceae). A second search used presence of marginal parenchyma (89p) and absence of obvious axial parenchyma (77a, 79–83a, 86a, 87a) instead of using axial parenchyma rare (75p). The results were the same as for the first search.

References for present-day *Populus* usually do not offer means to distinguish individual species (e.g. Brazier and Franklin, 1961; Panshin and DeZeeuw, 1980; Schweingruber, 1990).

Comparisons with fossil woods. Mädel-Angeliewa (1968) reviewed reports of *Populus*-like fossil woods and only recognized four as legitimate and placed them in her genus *Populoxylon*. There have been subsequent reports of European *Populoxylon* (see lists in Gregory et al., 2009 and Iamandei et al., 2023). Asian and American paleobotanists are less likely to use -oxylon endings than European paleobotanists, e.g. *Populus soyaensis* Terada and Suzuki from the Miocene of Japan (Choi et al., 2010). *Populus* leaves and fruits are common in Tertiary compression floras, but we have not been able to find any detailed description of a North American fossil wood with features unique to *Populus*. *Populus* wood has a reputation for being non-durable and rapidly decaying, as would be expected given its low specific gravity and few extractives (e.g. Panshin and DeZeeuw, 1980). Consequently, it has a low residence time and may rot away before being silicified, which likely explains its rarity in the fossil record. Given the difficulty in distinguishing present-day *Populus* species from one another, we choose not to create a new species for this single sample, but to refer to it simply as *Populus* sp.

ROSALES
Berchtold. et J.Presl

ROSACEAE Jussieu

There are nine samples possessing a combination of features diagnostic of the Rosaceae (e.g. Metcalfe and Chalk, 1950; Zhang, 1992). All have vessels solitary and in radial multiples, simple perforation plates, alternate intervessel pitting, vessel-ray parenchyma pitting smaller than the intervessel pitting, widely spaced helical thickenings along the length of the vessel element, non-septate fibers, axial parenchyma that is not common, rays 1–3 (–4)-seriate composed predominantly of procumbent cells and less than 1 mm in height. There is variation in growth ring boundary distinctiveness, presence of a distinct row of earlywood vessels, porosity type, how common radial multiples are, and how crowded vessels appear. The FFPRI Database includes multiple samples of *Prunus*, usually more than five samples per species, and some species show similar variation in the aforementioned features, e.g. *Prunus grayana* Maxim. (albeit distinct in having wider rays), *P. jamasakura* Sieb. Ex Koldz., *P. maximowiczii* Rupr., *P. nipponica* Matsumura, and *P. ssiori* Fr. Schm. (FFPRI 2002),

Given the variation within present-day species of *Prunus*, it is possible that these nine samples are fragments from different parts of the same plant or from different individuals of the same species; nonetheless we recognize four groupings based on appearance of the transverse sections, particularly the vessel grouping and vessel density.

Group 1 of the rosaceous woods considered here has a high percentage of vessel multiples and vessels appear crowded. It has distinct growth rings and is semi-ring-porous (UF305-25293). It is distinctive and we recognize it as a new species, *Prunus tonyzhangii*.

Group 2 also has a high percentage of vessel multiples and vessels appear crowded, but it has indistinct growth rings boundaries and is diffuse-porous (UF254-34475).

Group 3 includes six samples with vessels solitary and in short radial multiples, vessels do not appear crowded, three have a distinct row of earlywood vessels (UF254-86831, 25201, 25207), and three do not (UF254-25176, 34474; UF305-25297).

Group 4 includes only one sample (UF254-86812). Radial multiples are rare and there are tangential and oblique pairs instead. Vessels appear crowded.

Prunus L.

***Prunus tonyzhangii* sp. nov.**

Wheeler, Manchester et Baas

Fig. 8A–F

Diagnosis. Growth rings distinct. Wood semi-ring-porous. Solitary vessels rare, vessel multiples of 4 or more relatively common. Simple perforation plates. Intervessel pitting alternate, minute to small, vessel-ray parenchyma pits similar, but smaller than intervessel pits. Widely spaced helical thickenings extending along the entire vessel element length. Non-septate fibers with distinctly bordered pits on radial walls. Axial parenchyma not common. Rays 1–3-seriate and heterocellular.

Holotype. UF305-25293.

Repository. Florida Museum of Natural History at University of Florida, Gainesville, Florida, USA.

Type Locality. UF305, Red Hill 2.

Strata. John Day Formation, late Eocene.

Etymology. Named for Tony Zhang recognizing his comprehensive study of Rosaceae wood anatomy.

Description. Growth rings distinct, marked by radially flattened fibers, and differences in vessel diameters between latewood and earlywood of subsequent growth rings. Wood semi-ring-porous.

Vessels rarely solitary and commonly in radial multiples of 2–6 or more; average tangential diameters of the early-wood 76 (SD = 17 µm) with a range of 43–111 µm; vessel frequency 37–46 per mm^2 in earlywood, solitary vessels round to oval in outline; perforations simple, no scalariform perforation plates observed; intervessel pits alternate, 5–7 µm in horizontal diameter; vessel-ray parenchyma pits similar to but smaller than intervessel pits, ~3–4.5 µm; vessel element lengths average 839 (SD = 97) µm; range 712–983 µm (n = 7); helical thickenings present along the whole length of the vessel elements, spacing between helices about 10–15 µm.

Fibers non-septate; medium-thick walls, distinctly bordered pits on radial walls.

Axial parenchyma not common, likely diffuse.

Rays mostly 1–2-seriate, rarely 3-seriate. Multiseriate rays heterocellular, 2–4 or more marginal rows of square and upright cells; uniseriate rays composed of upright cells; 2–3-seriate ray height averages 795 (SD = 199) µm (n = 16); rays 6–7 per mm.

Storied structure absent; crystals not observed.

Comparisons with present-day woods. We searched the InsideWood Database using the *presence* of these features 1p (growth rings distinct), 4p (wood semi-ring-porous), 10p (radial multiples of four or more common), 13p (simple perforation plates), 22p, 25p (intervessel pitting alternate and small), 30p (vessel-ray parenchyma pits similar to intervessel pits), 36p, 37p (helical thickenings present along the entire vessel element length), 62p, 66p (non-septate fibers with distinctly bordered pits), 97p (rays 1–3 seriate), and the *absence* of these features 12a (vessels angular in outline), 42a, 43a (average vessel tangential diameters >100 µm), 79a, 80a, 83a, 85a, 86 (axial parenchyma not obvious), and 104a, 105a (rays not homocellular). This returned two species of *Prunus*: *P. avium* and *P. cerasus* as exact matches.

Zhang carried out an extensive study of Rosaceae wood anatomy (Zhang, 1992; Zhang and Baas, 1992; Zhang et al., 1992). This fossil wood has features consistent with

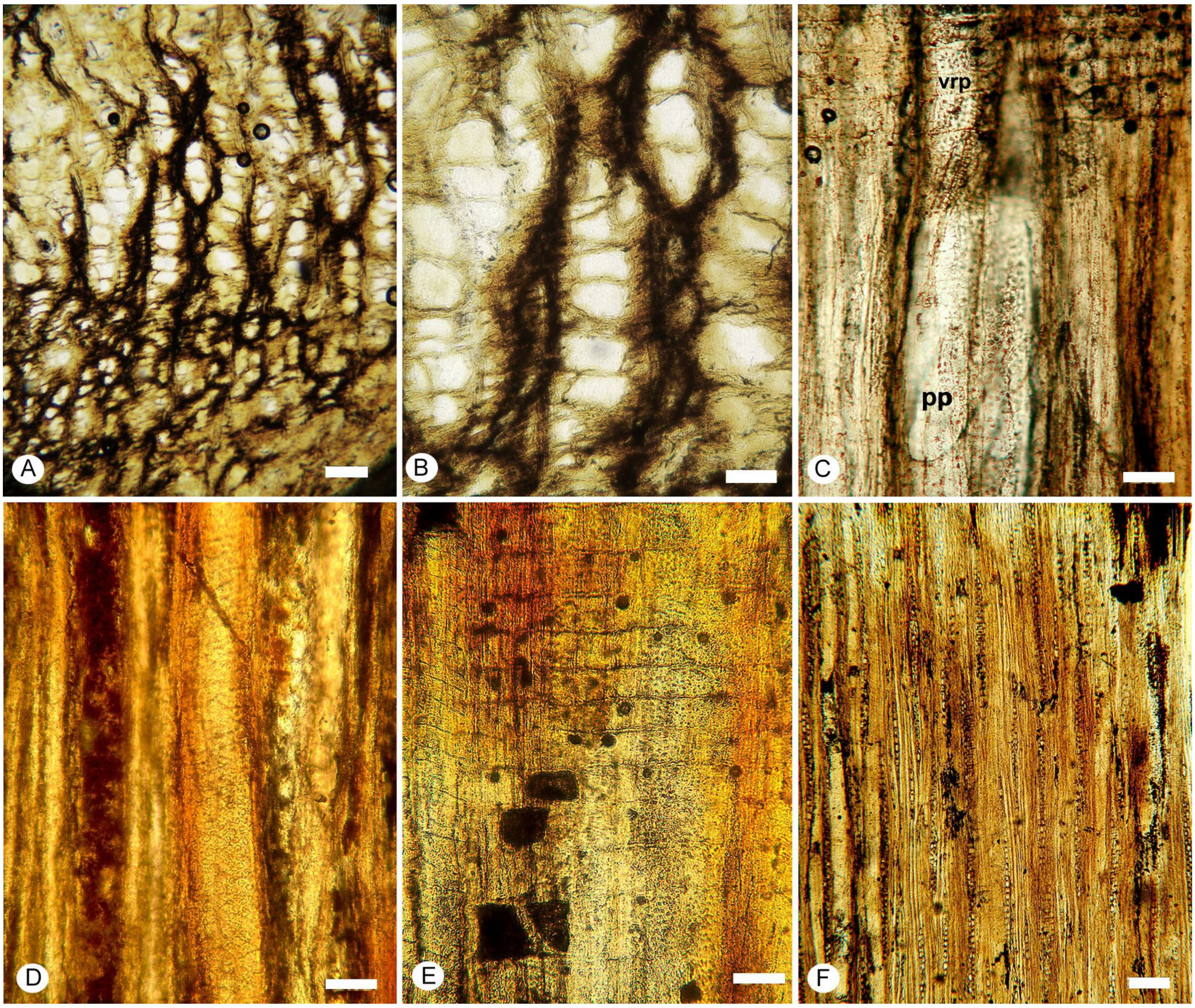

Figure 8. *Prunus tonyzhangii*. UF305-25293. **A**. Semi-ring-porous wood, with radial multiples common, TS; **B**. Earlywood vessels in radial multiples, TS; **C**. Simple perforation plates (PP), vessel-ray parenchyma pits (vrp) similar to intervessel pits, RLS; **D**. Alternate intervessel pits, helical thickenings in vessel elements, 2–3-seriate ray, TLS; **E**. Vessel-ray parenchyma pits, RLS; **F**. Rays mostly 1–2 seriate, TLS. Scale = 200 µm in A, F; 100 µm in B; 50 µm in C, D, E

his Group XII, which includes *Prunus* s. str. and the *Cerasus* group. Zhang's Group XII is uniquely characterized by vessel-ray parenchyma pits that are markedly smaller than the intervessel pits (total ranges typically 2–5 versus 4–11 µm). This strengthens UF305-25293's identity as *Prunus.* Most, but not all, *Prunus* species have wider rays, 4-seriate or more, and at times rays are of two distinct size classes. In the Chinese Wood Atlas (Itoh et al., 2022), there are three species with rays only 1–3-seriate: *Prunus maackii*, *P. patentipila* and *Prunus spinulosa* Siebold and Zuccarini 1845.

According to Mabberley (2017), there are more than 200 present-day species of *Prunus*; according to POW (2024), there are as many as 342 species. InsideWood has coded descriptions for only 40 species with images only for an additional 13 species. Zhang's PhD study of the Rosaceae is the most comprehensive study of the family with information on 69 species of *Prunus* s.l. including 9 species of *Prunus* s.str. (Zhang, 1992; Zhang and Baas, 1992).

Comparisons with fossil woods. Fossil woods with relatively complete descriptions and considered related to *Prunus* are compared in Table 1 and arranged by age. This Brummer Spring wood is the only one to have the combination of semi-ring-porous wood, vessels commonly in radial multiples of 4 or more, rays <4-seriate. Consequently, we propose a new species *Prunus tonyzhangii.*

Additional evidence for *Prunus* in the Eocene of western North America comes from distinctive endocarps of the Princeton Chert of British Columbia (Cevallos-Ferriz and Stockey, 1991) and the Clarno Nut Beds (Manchester,

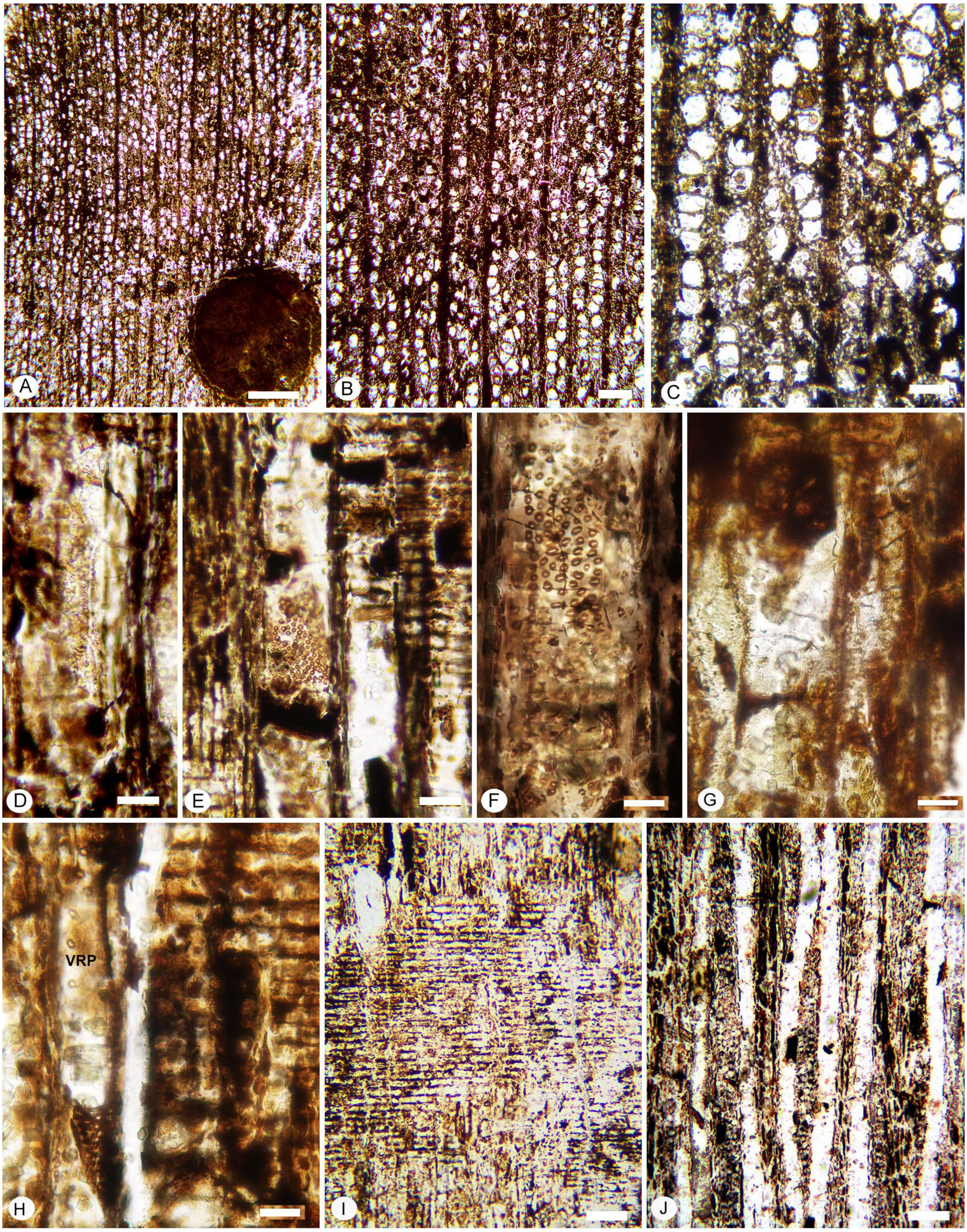

Figure 9. *Prunus* Group 2. UF254-34475. **A**. Diffuse-porous wood, vessels solitary and in radial multiples; circular frass / insect damage at right, TS; **B**, **C**. Indistinct growth ring boundaries; diffuse-porous; vessels solitary and in radial multiples of 2–3, TS; **D**. Simple perforation plate, RLS; **E**. Alternate intervessel pits, ray with procumbent cells, RLS; **F**. Alternate intervessel pits, helical thickenings in vessel element, RLS; **G**. Widely spaced helical thickenings in vessel elements, RLS; **H**. Vessel-ray parenchyma pits (VRP) similar to intervessel pits, RLS; **I**. Ray composed of procumbent cells, RLS; **J**. Rays to 4–6 cells wide, TLS. Scale = 500 µm in A; 200 µm in B; 100 µm in C, I, J; 50 µm in D, E; 25 µm F, G, H

Table 1. Comparison of fossil woods resembling Prunus. DP = diffuse-porous, SRP = semi-ring-porous; EW row = row of vessels in earlywood; RMs = radial multiples of 4 or more common; VTD = mean vessel tangential diameter, * for earlywood; IVP = intervessel pit diameter in μm or in IAWA category of min = minute, sm = small; AP = axial parenchyma, R = rare; D = diffuse, DA = diffuse-in-aggregates; SC = scanty paratracheal, Mg = marginal; RW = ray width in cell number; RC = ray cellular composition, Ho = homocellular, He = heterocellular, number of marginal rows with square to upright marginal cells, if given; MRH = multicellular ray height; Cry = crystals present; Eo = Eocene, Olig = Oligocene, Mio = Miocene; Coding: Y = Yes, N = No, V = variable occurrence; r = for range, if no average given

Group	Porosity	EW row	RMs-4	VTD	Vessels/ mm^2	IVP	AP	RW	RC	MRH	Cry	Age	Locality	Reference
Group 1 – *Prunus tonyzhangii*														
UF305-25293	SRP	N	Y	76 (17)	37–46	5–7	R, D	1–3	He, 2–3 (–4)	839 (97)	N	late Eo	OR, USA	This paper
Group 2 – *Prunus* sp.														
UF254-34475	DP	N	Y	47 (7)	71–100	5–6–8	R	1–4 (–6)	He, 2–3 (–4)	618–1120	N	late Eo	OR, USA	This paper
Group 3 – *Prunus* sp.														
UF254-25176, 25201, 25207, 25276, 34474, 86831, UF305-25297	DP, SRP	Y/N	N	52–58	30–54	5–10	R, D, (Mg)	1–4 (6)	He, 1–4	297 (102) – 658 (133)	N	late Eo	OR, USA	This paper
Group 4														
UF254-86812	DP	N	N	61 (13)	47–58	6–10	R?	1–3	He, 1–2?	335 (81)	N	late Eo	OR, USA	This paper
Species sorted by age – youngest – oldest														
Pruninium sp.	(DP), SRP	N	N	r=30–70	82–125	5–7	R, D	1–4 (–5)	He, 2–4	to 565	Y	late Mio	Germany	Selmeier, 1984
Prunus rodgersae	DP	N	N	52 (9.5)	100–130	6.5–8	SC, Mg	1–6	Ho, He, 1–2	528 (196)	N	mid Mio	WA, USA	Wheeler and Dillhoff, 2009
Prunus barnetti	DP	N	N	41 (10)	62–94	6.5–8	R, SC	1–4 (–5)	He, 1	320 (102)	N	mid Mio	WA, USA	Wheeler and Manchester, 2002
Prunus wadiai	DP	N	N	r=32–120	?	min	D	4+	He	r=600–1200	N	mid Mio	India	Guleria et al., 1983
Prunus iwatense	DP	N	N	r=60–100	18–40	?	R, D	1–7	He, 1	?	Y	early Mio	Japan	Watari, 1941; Takahashi and Suzuki, 1988
Prunoidoxylon prunoiides	SRP	N	N	55	40–100	5–8*	SC, Mg	two sizes; 5–8	He, 1+	to > 1 mm	Y	early Mio	Turkey	Akkemik, 2021
Prunoidoxylon aytugii	DP, SRP	N	N	52	40–100	?	R?	two sizes; 6–8	He, 1–4+	to > 1 mm	N	early Mio	Turkey	Akkemik et al., 2019
Prunidoxylon multiporosum	SRP	N	N	r=20–70	100–195	5–6	R	1–5	He	to > 1 mm	N	Olig, late Mio	France, Romania	Duperon, 1976; Iamandei et al., 2023
Prunus ascendentiporulosa	DP, (SRP)	N	V	r=20–100	80–140	5–10	R, D	1–4 (–5)	He, 1–2	650	Y	Olig	Japan	Suzuki, 1984
Prunus palaeozippeliana	DP, (SRP)	V	Y	r=30–75	160–200	4–7	R, D	1–5 (–6)	He	636	N	Olig	Japan	Suzuki, 1984
Prunus polyporulosa	DP	N	Y	r=25–55	240–300	4–7	R, D	1–6	He	554	N	Olig	Japan	Suzuki, 1984
Prunus uviporulosa	DP	N	Y	r=20–75	175–270	4–8	R	1–5 (–6)	He	661	N	Olig	Japan	Suzuki, 1984
Prunoidoxylon eocenicum	DP	N	N	38 (8)	120–190	6–8	D, DA, SC	two sizes; 6–8	He	460 (132)	N	late Eo	NE, USA	Wheeler and Landon, 1992
cf. *Prunus gummosa*	DP	N	N	46	103–203	6–8	D, SC	1–3 (–4)	He, 1	313 (46)	Y	mid Eo	OR, USA	Wheeler and Manchester, 2002
Prunus allenbyensis (twig)	SRP	N	N	28	283	4–6	D	1–8	He, 1–2	370	N	mid Eo	BC, Canada	Cevallos-Ferriz and Stockey, 1990
Prunus sp.	SRP	N	N	117 (21)*	?	4–6	D, DA, SC	1–8	He, 1	472 (168)	Y	mid Eo	OR, USA	Wheeler and Manchester, 2002
Prunus gummosa	DP, SRP	N	N	47	78–98	min-sm	R, D	1–4	He, 1	r=105–763	N	e. mid Eo	WY, USA	Wheeler et al., 1978

1994), and flowers from the Eocene of Republic, Washington (Benedict et al., 2011).

ROSACEAE

Prunus Group 2

Fig. 9A–J

Material. UF254-34475.

Description. Growth rings indistinct (Fig. 9B, C). Wood diffuse-porous.

Vessels solitary and in radial multiples of 2–3 (Fig. 9A, B, C); average tangential diameter 47 µm (SD = 7 µm); range of 35–62 µm; vessel frequency 71–100 per mm^2; solitary vessels oval in outline; perforations simple (Fig. 9D), no scalariform perforation plates observed; intervessel pits alternate, round to oval in outline (Fig. 9E, F), 5–6–8 µm in horizontal diameter; vessel-ray parenchyma pits similar to intervessel pits (Fig. 9H); helical thickenings present, along whole length of the vessel elements (Fig. 8F, G).

Fibers non-septate; medium-thick walls, distinctly bordered pits likely on radial walls.

Axial parenchyma not common.

Larger rays 4–5-seriate, heterocellular with procumbent body cells and marginal rows of square and upright cells; multiseriate ray heights 616–1120 µm (n = 8); rays 5–7 per mm.

Storied structure absent; crystals not observed.

Comparisons with present-day woods. The rationale for assigning this sample to the Rosaceae was given in the introductory paragraph about the UF254 Rosaceae woods.

Comparisons with fossil woods. Table 1 compares the characteristics of *Prunus* Group 2 with the other UF254 samples assigned to *Prunus*. Its vessel frequency and ray heights are higher than the other UF254 Rosaceae.

Prunus Group 3

Fig. 10A–I

Material. UF254-86831, 25201, 25207, 25176, 34474; UF305-25297.

Description. Growth rings distinct, marked by radially flattened fibers and occasionally by marginal parenchyma. Wood diffuse-porous to semi-ring-porous with a near-continuous row of earlywood vessels (Fig. 10A, G, H).

Vessels solitary (>50%) and in radial multiples of 2 (–3); mean tangential diameters vary from 52 (10) to 58 (10) µm; 30–54 vessels per mm^2; perforations exclusively simple (Fig. 10B); intervessel pits crowded alternate, slightly angular in outline, 6–11 µm in horizontal diameter; vessel-ray parenchyma pits smaller than intervessel pits (5–6 µm) (Fig. 10D, E); helical thickenings along length of vessel elements (Fig. 10D, I), spacing between helices 11–17 µm.

Fibers non-septate; medium-thick walls, pitting not observed.

Axial parenchyma not common, diffuse, probably also marginal in some samples.

Rays 1–4 seriate (Fig. 10F); mean height of 3–4-seriate rays 297 (102)–658 (133); heterocellular with procumbent body cells and 1–4 marginal rows of square cells; 4–6 rays per mm.

Storied structure absent; crystals not observed.

Comments. Preservation of the samples in this group was not good. It was not possible to measure many vessel element lengths or to measure ray heights because of uncertainty of where the ends of the rays were.

Comparisons with present-day woods. InsideWood searches indicate that *Prunus* s.l. is the best match for these woods' combination of features: distinct growth rings, diffuse-porous to semi-ring-porous wood with vessels solitary and in short radial multiples not arranged in a particular pattern, simple perforation plates, alternate intervessel pitting, vessel-ray parenchyma pits smaller than intervessel pits, widely spaced helical thickenings throughout the vessel elements, non-septate fibers, 1–4-seriate heterocellular rays that are <1 mm high.

Zhang (1992: table 2: 94–96) recognized 12 wood anatomical groups within the Rosaceae. Because this wood has marginal parenchyma and vessel-ray parenchyma pits similar in size to the intervessel pits it has characteristics of his Group XI. However, Group XI has a high degree of vessel grouping unlike this wood. Group XII has vessel-ray parenchyma pits clearly smaller than intervessel pits and well-developed and widely spaced helical thickenings. This fossil has the latter characteristic, but the vessel-ray parenchyma pits are only slightly smaller than the intervessel pits.

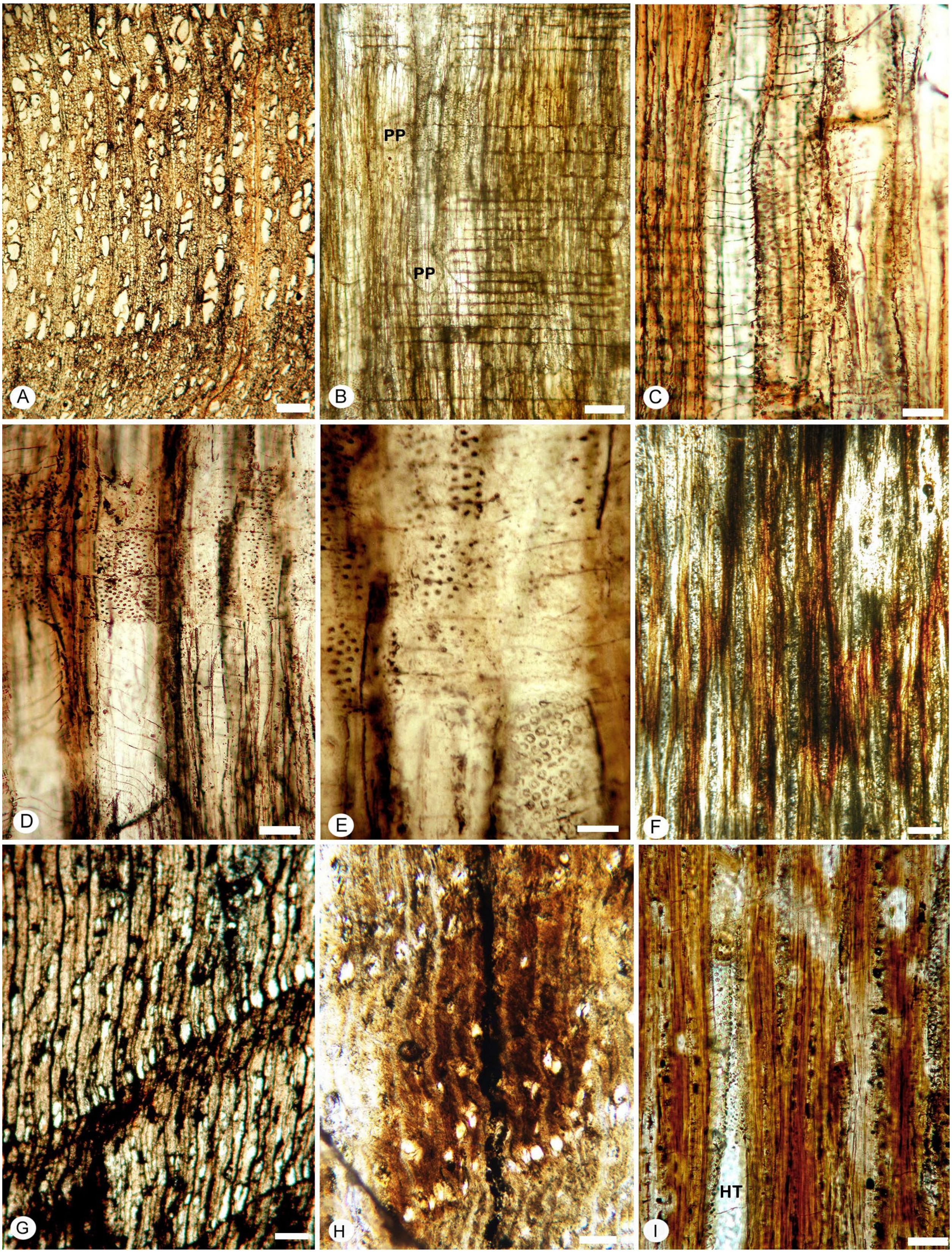

Figure 10. *Prunus* Group 3. **A–F**. UF305-25297; **A**. Diffuse-porous to slightly semi-ring porous wood, with vessels solitary and in radial multiples of 2–4, TS; **B**. Simple perforation plates (pp), heterocellular rays with procumbent body cells, and marginal row of upright cells, RLS; **C**. Helical thickenings throughout the vessel elements, RLS; **D**. Small vessel-ray parenchyma pits, helical thickenings in vessel elements, RLS; **E**. Vessel-ray parenchyma pits smaller than intervessel pits, RLS; **F**. Rays commonly 4–6-seriate, TLS; **G**. UF254-25201. Solitary near-continuous row of earlywood vessels, TS; **H**. UF254-25207. Solitary near-continuous row of earlywood vessels, TS; **I**. UF254-25201. Multiseriate rays, helical thickenings (HT) in vessel elements, TLS. Scale = 200 µm in A, F, G, H; 100 µm in B, I; 50 µm in C, D; 25 µm in E

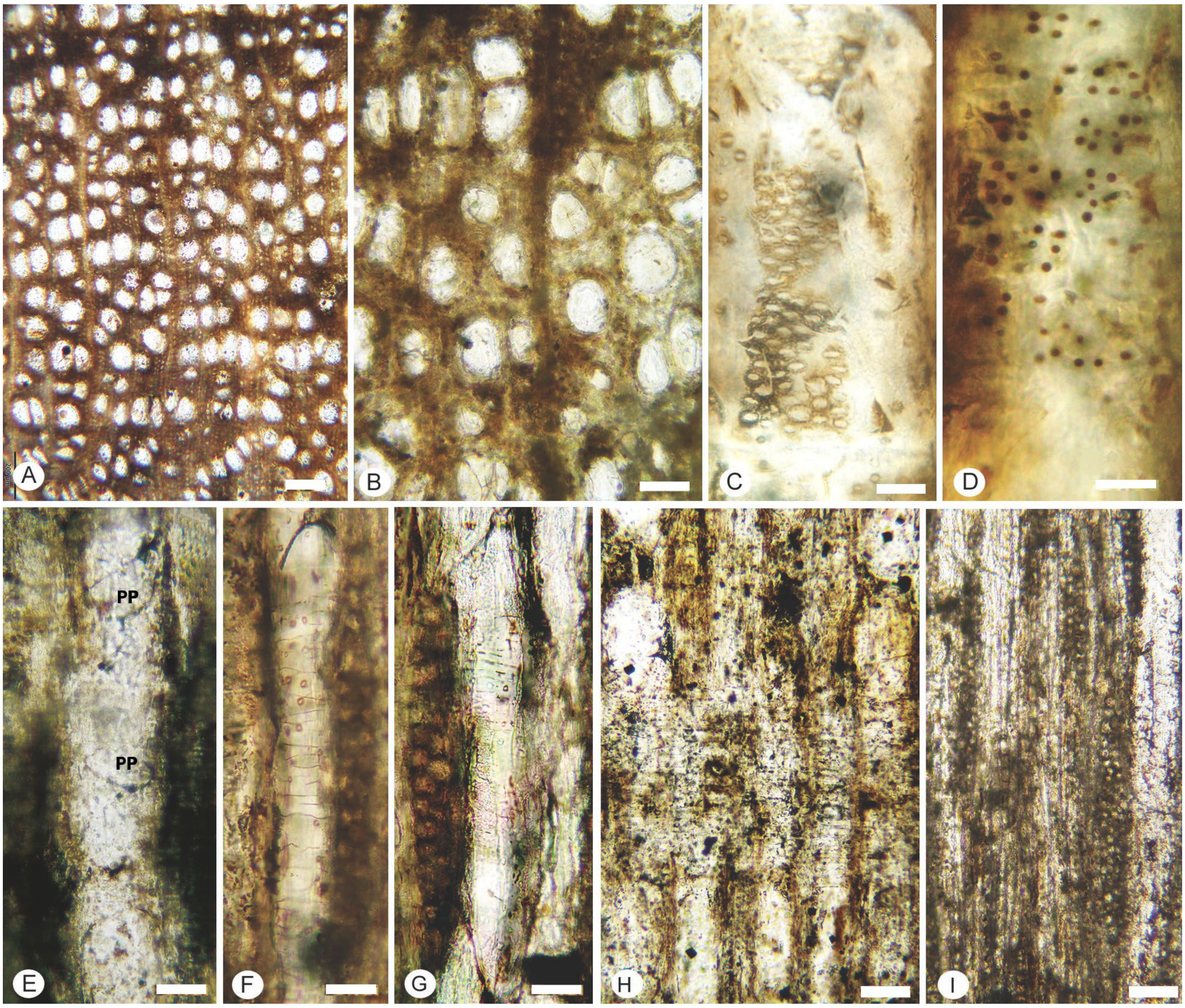

Figure 11. *Prunus* Group 4. UF254-86812. **A**, **B**. Diffuse-porous wood, vessels solitary and in tangential multiples, TS; **C**. Crowded alternate intervessel pits, RLS; **D**. Vessel-ray parenchyma pits, RLS; **E**. Simple perforation plates (PP), RLS; **F**, **G**. Helical thickenings in vessel elements with simple perforation plates, rays 3-seriate, TLS; **H**. Rays with procumbent body cells; **I**. Rays 1–3(–4) cells wide. Scale bars: 200 µm in A; 100 µm in B, H, I; 50 µm in E, F, G; 20 µm in C, D

Comparisons with fossil woods. Table 1 shows that Group 3 woods are not an exact match for any previously described in detail fossil considered related to *Prunus*.

Prunus Group 4

Fig. 11A–I

Material. UF254-86812.

Description. Growth rings present, marked by radially flattened fibers. Wood diffuse-porous.

Vessels solitary and in tangential multiples (Fig. 11A, B); mean tangential diameter 61 µm (SD = 13), range 32–94 µm; 47–58 vessels per mm^2; perforations simple (Fig. 11E, F, G); intervessel pits crowded alternate, occasionally slightly angular in outline (Fig. 11C), 6–10 µm in horizontal diameter; vessel-ray parenchyma pits smaller than intervessel pits (Fig. 11D), 5–7 µm in horizontal diameter; helical thickenings along length of vessel elements (Fig. 11F, G), spacing between helices 9–13 µm. Vessel element lengths average 475 (SD = 94) µm, range 260–621 µm.

Axial parenchyma not observed.

Fibers non-septate; medium-thick walls, pitting not observed.

Rays 1–3(–4) seriate (Fig. 11I); average height of multiseriate rays 335 (SD = 81) µm, range 188–526 µm; heterocellular with procumbent body cells and a few marginal rows of square cells; 4–6 rays per mm.

Storied structure absent; crystals not observed.

Comments. Preservation of this sample was poor. Growth rings in this sample were narrow (Fig. 11A), so there is a possibility that this is a semi-ring-porous wood in which only the earlywood is visible. This phenomenon was seen in the Paleogene *Paradiospyroxylon kvacekii* (Koutecky et al., 2022). It was difficult to determine ray cellular composition other than to see that ray body cells were procumbent. We think that axial parenchyma is not common and were unable to see it in cross section, in longitudinal sections it seemed possible that there were a few strands.

Comparisons with present-day woods. This wood's combination of features: diffuse-porous (slightly semi-ring-porous) wood with vessels solitary and in small multiples, simple perforation plates, alternate intervessel pitting, vessel-ray parenchyma pits smaller than intervessel pits, helical thickenings throughout the vessel elements, non-septate fibers, 1–3(–4)seriate heterocellular rays that are <1 mm high are diagnostic of the Rosaceae. Because the vessel-ray parenchyma pits are clearly smaller than the intervessel pits this sample fits Zhang's Group XII, which he wrote included "*Amygdalus*, *Armeniaca*, *Cerasus*, *Laurocerasus* A, *Padus*, and *Prunus*" (Zhang, 1992). The first five genera in his list are now considered synonyms of *Prunus* (POWO 2024).

Comparisons with fossil woods. Table 1 shows UF254-86812 differs from the other UF254 samples assigned to the *Prunus* by having tangential multiples rather than just radial multiples.

FAGALES Engl.

FAGACEAE Dumort

Fagus L.

Fagus dodgei
Wheeler et Manchester 2021

Fig. 12A–H

Material. UF305-25304.

Description. Growth rings distinct, marked by radially flattened fibers, and noded rays, and by differences between latewood and earlywood vessel diameters in successive rings. Wood diffuse-porous.

Vessels predominantly solitary, rarely in tangential to radial pairs; average tangential diameter 56 (11), range 41–84 µm; vessel frequency 32–46 /mm^2, round to oval in outline; perforations simple and scalariform with up to 20 bars, some reticulate or meshlike; intervessel pits rare, opposite to scalariform, at ends of vessel elements scalariform; vessel-ray parenchyma pits with reduced borders, rounded in outline or horizontally enlarged; vessel element lengths medium; tyloses rare, appearing as widely spaced.

Fibers non-septate; medium-thick to thick walls, distinctly bordered pits on radial walls, some on tangential walls, especially prominent on the imperforate elements adjacent to vessels.

Axial parenchyma diffuse-in-aggregates, in irregular uniseriate lines, common; strands of mostly 4 cells.

Rays of two distinct sizes, 1–3-seriate, and rays more than 20-seriate, sometimes compound, the wide rays widely spaced. Multiseriate rays heterocellular, 1–8 marginal rows of square and upright cells, sheath cells not observed; in tangential section, the cells in the center of the largest multiseriate rays appearing larger than those at the sides; upright and square marginal ray cells of the narrow rays with distinctly pitted end walls; wide rays commonly more than 1 mm high; 6–10 rays per mm.

Storied structure absent.

Comparisons with present-day woods. We searched InsideWood for the following features: 1p 5p 6a 7a 8a 9p (presence of distinct growth rings and diffuse-porosity; absence of tangential, radial or dendritic arrangement of vessels), 13p 14p (simple and scalariform perforation plates present), 32p (vessel-ray parenchyma pits with reduced borders and horizontally elongate), 42a 43a 46a (vessel tangential diameter <100 µm and more than 5 vessels per mm^2), 62p 66p (non-septate fibers with bordered pits), 76p 77p 79a 80a 83a 85a (axial parenchyma diffuse to diffuse-in-aggregates present, obvious paratracheal parenchyma and axial parenchyma bands >3 cells wide absent), 99p 103p (larger rays commonly >10-seriate and rays of two distinct sizes present), rays not homocellular (104a 105a). No modern wood entries in the InsideWood database were an exact match but allowing one mismatch returned three entries for *Fagus* species.

Fagus and *Platanus* woods can be confused with one another. Differences between them include: 1) *Fagus* consistently has vessel-ray parenchyma pits with reduced borders, while

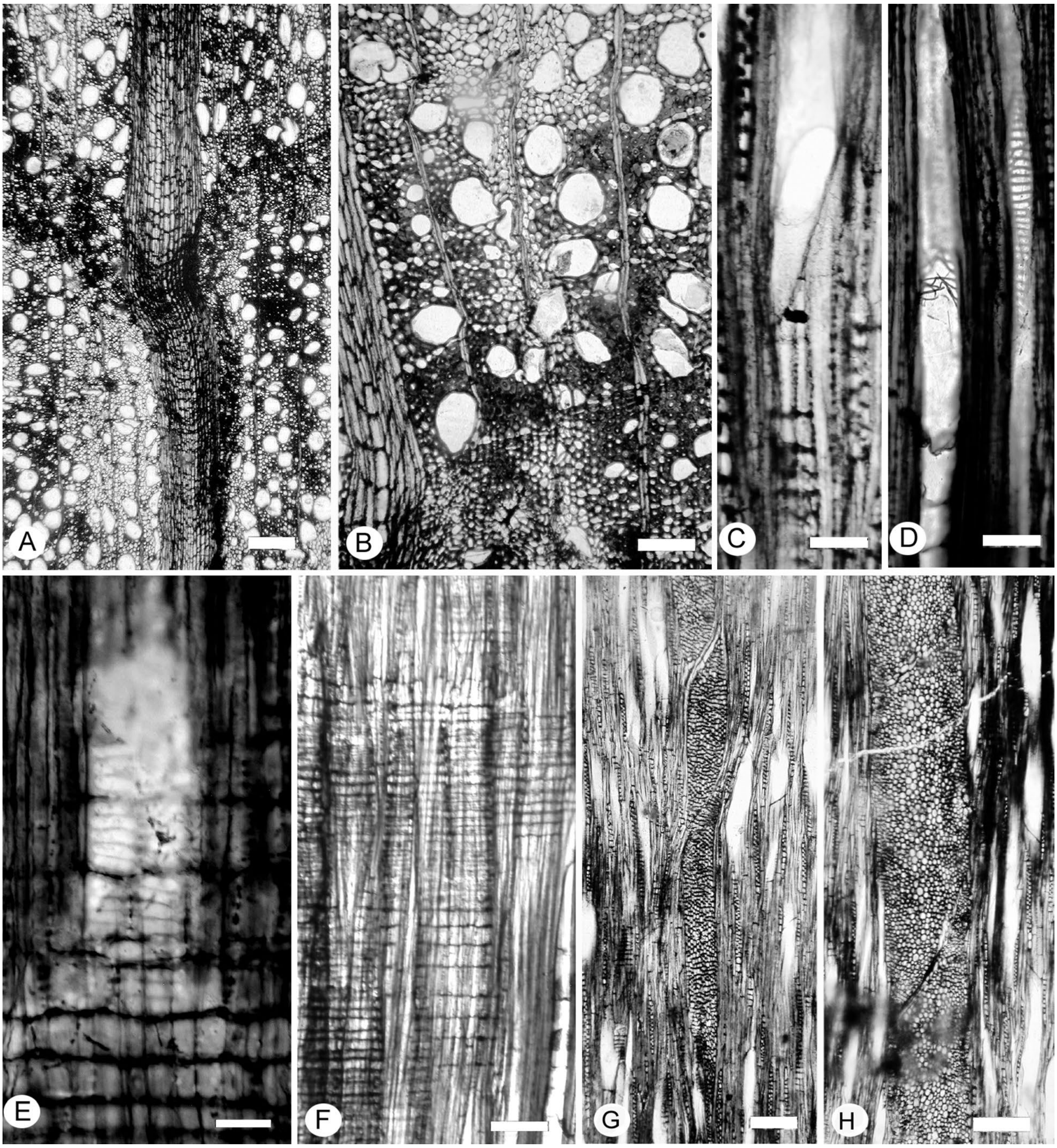

Figure 12. Fagaceae. *Fagus dodgei.* UF305-25304. **A**, **B**. Growth rings distinct, diffuse-porous, vessels solitary, diffuse and diffuse-in-aggregates parenchyma, TS; **C**. Simple perforation plate, TLS; **D**. Scalariform perforation plate, RLS; **E**. Vessel-ray parenchyma pits with reduced borders and horizontally elongate RLS; **F**. Heterocellular rays, RLS; **G**, **H**. Rays of two distinct sizes, TLS. Scale = 200 µm in A, G; 100 µm in B, F, H; 50 µm in C, D; 20 µm in E

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 *Fagus grandifolia* and ~2:1 in *Platanus occidentalis* (Panshin and DeZeeuw, 1980; Hoadley, 1990; Wheeler and Manchester, 2021).

Comparisons with fossil woods. We repeated the above search for fossil woods. Results included *Fagus dodgei* from another locality in the John Day Formation (Wheeler and Manchester, 2021), three species of *Fagoxylon* (a name used by Europeans for fossil woods resembling *Fagus*) with all differing in having some homocellular rays, *Fagus grandiporosa* Beyer (1954) whose description lacks details needed to confirm affinity with *Fagus*, and four other records with most IAWA features unknown (*Fagus* sp. from the Pliocene of Holland, Slijper, 1932; *Icacinoxylon* sp. from the Oligocene of Romania, Petrescu and Dragastan, 1972; *Platanoxylon* sp. from the Miocene of Hungary, Andreánszky, 1951; *Platanus* sp., Slijper, 1932).

This UF254 wood conforms well with *Fagus dodgei*, which was first described from the nearby Post Hammer Locality, UF279 (Wheeler and Manchester, 2021). Five additional samples were found at nearby Dietz Hill, UF278, the Dietz Hill locality (Wheeler et al., 2023). In our study of the *Fagus* woods from that locality, we remarked on the variation in extant *Fagus*. This sample differs from the other *Fagus dodgei* samples, however, in not showing any tendency to semi-ring-porosity and in having more abundant diffuse-in-aggregates parenchyma; differences that likely are intraspecific.

SAPINDALES Berchtold et J. Presl

MELIACEAE Jussieu

Cedreloxylon Selmeier

Cedreloxylon sp.

Fig. 13A–F

Material. UF254-24702.

Description. Growth rings distinct, marked by radially flattened fibers, and a pronounced difference in vessel diameter from latewood to earlywood of successive rings.

Ring-porous. Vessels solitary and in radial multiples of 2 (rarely 3); average earlywood tangential diameters 121 (26), range 78–200 µm; solitary vessels round to oval in outline; perforations simple; intervessel pits crowded alternate, 3–5 µm in horizontal diameter; vessel-ray parenchyma pits similar to intervessel pits; vessel element lengths average 303 (51) µm; range 188–363 µm; dark deposits (representing gum) common near perforation plates.

Fibers non-septate; medium thick walls, fiber pits not distinct on either radial or tangential walls.

Axial parenchyma scanty paratracheal to vasicentric to aliform with a tendency to aliform, and marginal; strands mostly 4 cells.

Rays 1–3-seriate, Multiseriate rays heterocellular, usually with one marginal row of upright cells; ray heights average 254 (74) µm, range 174–389 µm; 5–7 rays per mm.

Storied structure absent.

Traumatic gum canals present, in long tangential lines.

Comparisons with present-day woods. The combination of semi-ring-porous to ring-porous wood without distinctive latewood vessel arrangement patterns, simple perforations, minute-small intervessel pits, vessel-ray parenchyma pits similar to intervessel pits, scanty paratracheal to vasicentric axial parenchyma, and traumatic canals indicates affinities with *Cedrela* or *Toona*, the sole members of tribe Cedreleae DC. of the Meliaceae.

Cedrela as now circumscribed is restricted to species of the subtropical and tropical Americas. The closely related *Toona* has a wide geographic range including Afghanistan, India, Tropical Asia, and China (e.g. Mabberley, 2017; POWO, 2024). Both genera include valued timber species. The semi-ring-porosity to ring-porosity in today's *Cedrela odorata* L. has been linked to marked dry seasons (Dünisch et al., 2002). The preservation of this sample is mediocre, we did not clearly observe septate fibers. Nonseptate fibers are more common in *Toona* and the porosity and vessel arrangement of *Toona sinensis* resemble this fossil (e.g. Itoh et al., 2022, ID0882). Consequently, we are inclined to think it more closely related to the "Old World" *Toona*, rather than the "New World" *Cedrela*.

However, more samples of *Cedrela* and *Toona* need to be examined to establish whether they can be distinguished wood anatomically. Earlier, when what are now considered *Toona* species were treated as part of *Cedrela*, Brazier and Franklin (1961) had but one description for all species. They did note that they observed druses only in *Cedrela toona*, a synonym of *Toona ciliata*. We did not see druses, but they did not occur in all samples of *Toona*.

Rays and vessels are narrower in this fossil, which likely is related to its small diameter and being juvenile wood.

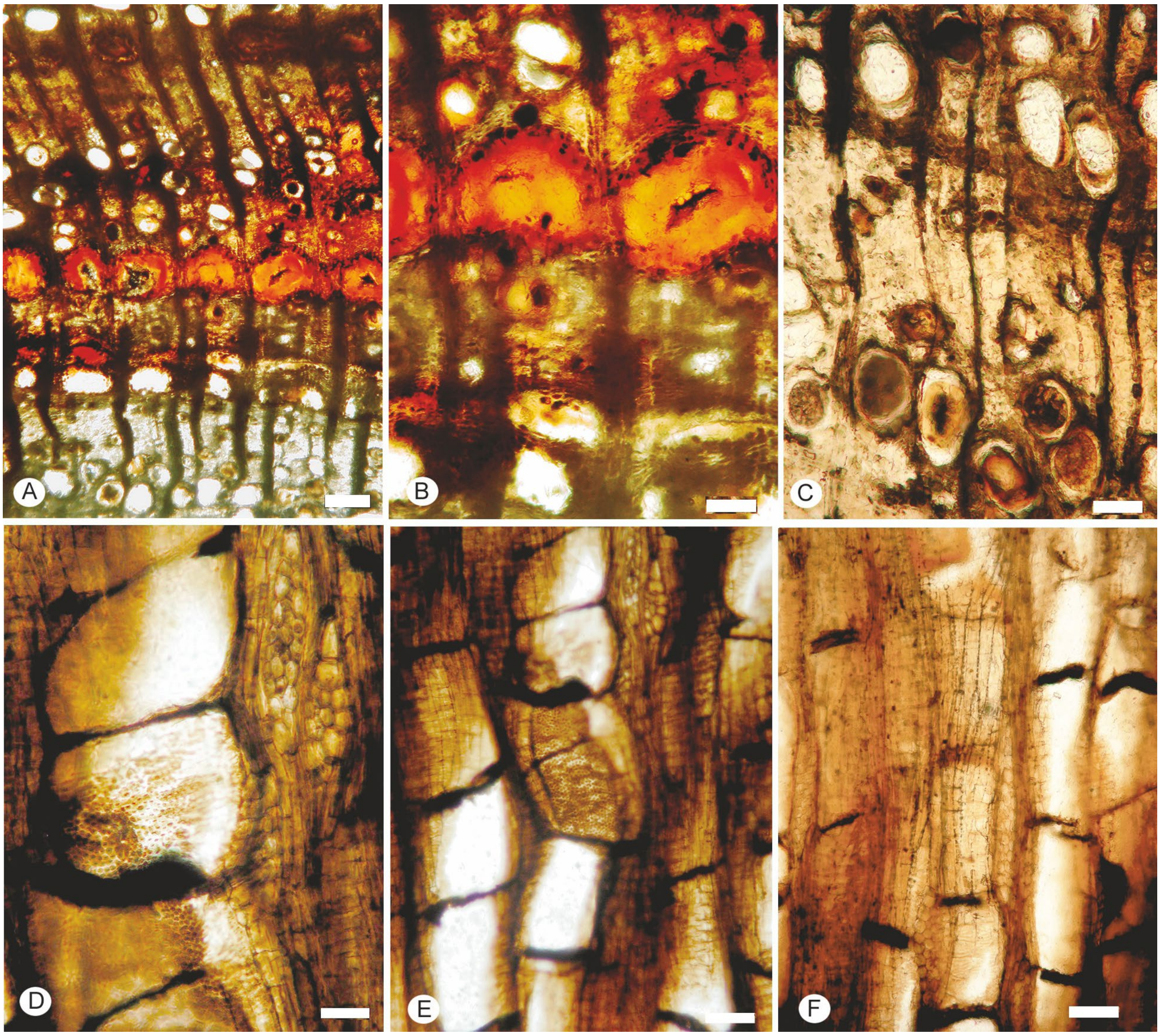

Figure 13. *Cedreloxylon* sp., UF254-24702. **A–C**. Wood ring-porous to semi-ring-porous. Vessels solitary and in short multiples, axial parenchyma scanty paratracheal to vasicentric and marginal. Traumatic canals, TS; **D**, **E**. Rays 2–3-seriate with 1–2 marginal rows of upright/square cells. Minute-small alternate intervessel pits, vessel-axial parenchyma pits similar to intervessel pits, dark deposits at vessel end walls, TLS; **F**. Axial parenchyma strands adjacent to vessel elements, TLS. Scale = 200 µm in A; 100 µm in B, C, E, F; 50 µm in D

Comparisons with fossil woods. There are reports of *Cedreloxylon cristalliferum* Selmeier (1987) from Europe (Miocene, Gottwald, 1997, 2002; Eocene, Gottwald, 1992) and Asia (Miocene and Pliocene of China, Cheng et al., 2006, 2018; Pliocene of Japan, Choi et al., 2010). Gottwald (1997) suggested that European *Cedreloxylon cristalliferum* was most similar to *Toona*. *Cedreloxylon tlaxcaliensis* Castañeda-Posadas, Calvillo-Canadell, and Cevallos-Ferriz (2009) occurs in the Miocene of Mexico. There are two samples of *Cedreloxylon* sp. in the middle Eocene Clarno Nut Beds wood assemblage of Oregon, USA (Wheeler and Manchester, 2002). The tendency to ring-porosity is more pronounced in this late Eocene Post wood than in the middle Eocene Nut Beds *Cedreloxylon*.

MALVALES Berchtold. et J.Presl

MALVACEAE Jussieu

cf. ***Grewia*** L

Fig. 14A–H

Material. UF254-25218.

Description. Growth rings distinct, marked by radially flattened fibers, and differences in vessel diameters between latewood and earlywood of subsequent growth rings, and marginal parenchyma.

Semi-ring-porous. Vessels solitary and occasionally in radial pairs; average tangential diameters of the first two rows of earlywood

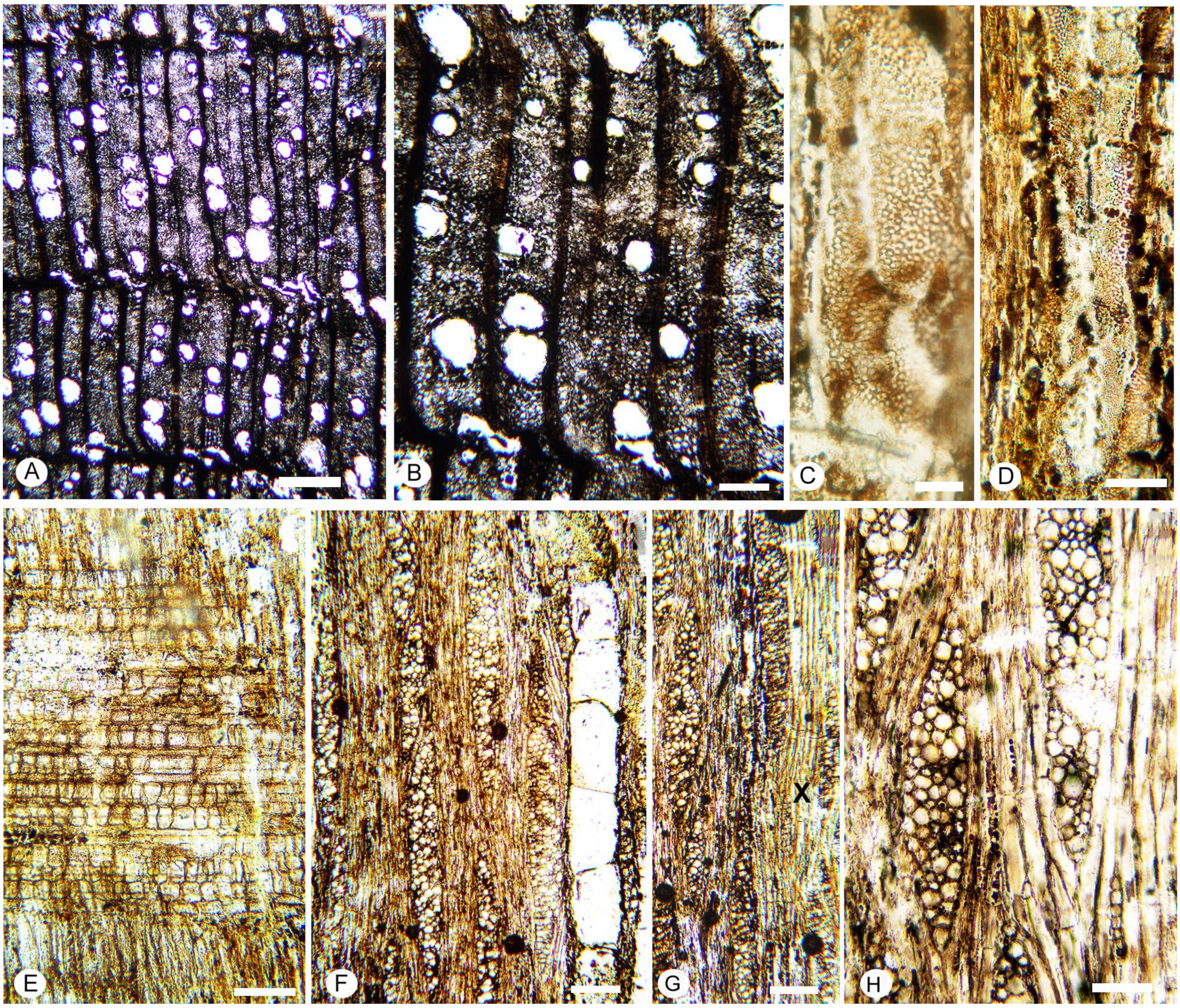

Figure 14. Malvaceae. UF254-25218. **A**, **B**. Semi-ring-porous wood, vessels solitary and occasionally in radial pairs, TS; **C**. Alternate intervessel pitting, TLS; **D**. Vessel-axial parenchyma pits, TLS; **E**. Ray with tile cells, RLS; **F**. Multiseriate rays common, tile cells, vessel elements with end walls slightly inclined, TLS; **G**. Multiseriate rays with tile cells, fusiform elements storied (above X), TLS; **H**. Detail of multiseriate rays with tile cells and storied fusiform elements, TLS. Scale = 500 µm in A; 200 µm in B, F, G; 100 µm in E, H; 50 µm in D; 20 µm in C

159 (SD = 24) µm, range 115–210 µm; average tangential diameters of the latewood 77 (SD = 15) µm, range 44–99 µm; solitary vessels rounded to weakly angular in outline; perforations simple; intervessel pits alternate, 3–4 µm in horizontal diameter; vessel-parenchyma pits similar to intervessel pits; vessel element lengths average 389 (SD = 61) µm, range 271–486 µm; helical thickenings not observed.

Fibers with medium-thick walls, pitting not observed. Possibly some septate, but septa hard to distinguish from thin fungal hyphae.

Axial parenchyma difficult to detect arrangement in transverse section; but longitudinal sections suggest axial parenchyma is diffuse and diffuse-in-aggregates; in tangential section strands of 4–7+ cells occur adjacent to vessels suggesting scanty paratracheal or narrow vasicentric also present. Some fusiform to two-celled apotracheal strands that are storied also present.

Rays 1–8-seriate, rays < 3-seriate rare, most rays 4–6-seriate. Ray height averages 917 (SD = 393) µm, range 260–1,718 µm; rays 6–7 per mm. Tile cells present, probably the intermediate between *Durio* and *Pterospermum* type (Manchester and Miller, 1978: IAWA Committee 1989).

Crystals not observed.

Comparisons with present-day woods. The occurrence of well-defined tile cells is unique to the Malvaceae. In the InsideWood database for present-day woods, there are three genera of Malvaceae with semi-ring-porous to ring porous species: *Grewia* (Grewioideae), which today is widespread in the Old World; *Reevesia* (Helicteroideae), with a disjunct distribution, occurring from Assam through IndoChina and in Mexico and Nicaragua; *Craigia yunnanensis* (Tilioideae), native to Tibet, Vietnam, and S China (POWO 2024). *Craigia* differs in having prominent sheath cells, larger rays, wider vessels, helical thickenings in vessel elements, and more pronounced storied structure (Manchester et al., 2006). Today, ring-porous species of *Grewia* and *Reevesia* typically have latewood vessels in clusters, but in semi-ring-porous *Grewia tiliifoli*a (RBHw 17481), *Reevesia clarkii* (MADw 44043) and *R. wallichii* (SJRw 30221) clusters are rare. Information available to date is that all *Reevesia* species have helical thickenings in their latewood vessel elements unlike UF254-25218 and *Grewia*.

This Brummer Spring wood can be confidently assigned to the Malvaceae. Of the present-day Malvaceae, *Grewia* is the best match.

Comparisons with fossil woods. A search of the fossil wood database for semi-ring-porous to ring porous woods without distinct vessel arrangement patterns of groupings (1p 5a 6a 7a 8a 9a 10a 11a), simple perforation plates (13p), alternate and minute intervessel pitting (22p 24p), vessel-ray parenchyma pits similar to intervessel pits (30p), mean vessel diameters of 100–200 µm (42p) fibers with simple to minutely bordered pits (61p), absence of broad axial parenchyma bands (85a), larger rays commonly 4-to 10-seriate (98p), and tile cells (111p) with 0 allowable mismatches returned only *Wataria kvacekii* from the nearby Post Hammer Location (Wheeler and Manchester, 2021). However, *Wataria kvacekii* is distinctly ring-porous with more obvious storied axial parenchyma. Two malvalean woods, *Chattawaya paliforme* (Manchester, 1980) and *Triplochitioxylon oregonense* (Manchester, 1979) occur in the middle Eocene Clarno Nut Beds. *Chattawaya* has wider (to 14-seriate) and taller (to 2.2 mm) rays with well-defined *Pterospermum*-type tile cells and crystals are common. This Post wood has some similarity with *Triplochitioxylon*, which is diffuse-porous to semi-ring-porous with intermediate-type tile cells; it differs in having obviously storied fibers, commonly occurring rays <3-seriate, sheath cells, and crystals.

The fossil wood genus *Wataria* was created for woods from the Oligocene and Miocene of Japan, which were originally assigned to *Reevesia* (Watari, 1952). *Wataria* was diagnosed as being distinctly ring-porous wood and with distinctly storied axial parenchyma (Terada and Suzuki, 1998). There is a recent remarkable report of a monodominant stand (130 stumps) of *Wataria* associated with a forest floor covered by the leaf fossil *Byttneriophyllum tiliifolium* (Nishino et al., 2023). *Wataria* has also been reported from the Miocene of Korea (Jeong et al., 2003). *Wataria* species vary in earlywood vessel diameter, number of rows of earlywood vessels, vessel element length, ray width and height (Wheeler and Manchester, 2021: tab. 4). Given that *Wataria* is distinctly ring-porous, this UF254 wood does not fit the diagnosis of the genus.

Grewioxylon Schuster emend. Prakash and Dayal (1965) was diagnosed as having diffuse-porous wood. So again, this UF254 wood does not match the diagnosis. However, Selmeier (2000) illustrated variation within the European *Grewioxylon ortenburgenxe*, with some samples appearing to have semi-ring-porous wood. NB: *Grewioxylon* Schuster was shown to be an illegitimate genus and *Grewioxylon* Shallom, a later homonym of *Grewioxylon* Schuster, is considered a synonym of *Grewinium* Srivastava et Guleria (Srivastava and Guleria, 2000). *Grewia americana* Woodcock, Meyer, et Prado (2019) from the Eocene of Peru was described as diffuse- to semi-ring porous and having intermediate-type tile cells. It differs in having radial multiples common, narrower vessel elements, larger intervessel pits (5–7.5 µm), narrower rays (2–3-seriate), and storied rays.

On balance we prefer to consider UF254-25218 as cf. *Grewia* sp., but note its similarities with *Wataria*, *Triplochitioxylon* and *Reveesia*.

INCERTAE SEDIS

cf. ***Ubiquitoxylon raynoldsii***
Wheeler 2019

Fig. 15A–K

There are three samples (UF254-25215, UF305-25296, UF305-25303) whose vessel arrangement, intervessel and vessel-ray parenchyma pitting, axial parenchyma distribution, and ray features are similar to the UF254 and UF305 Lauraceae woods described previously. However, we did not find any oil cells in them, so they cannot be assigned to *Laurinoxylon*. Oil

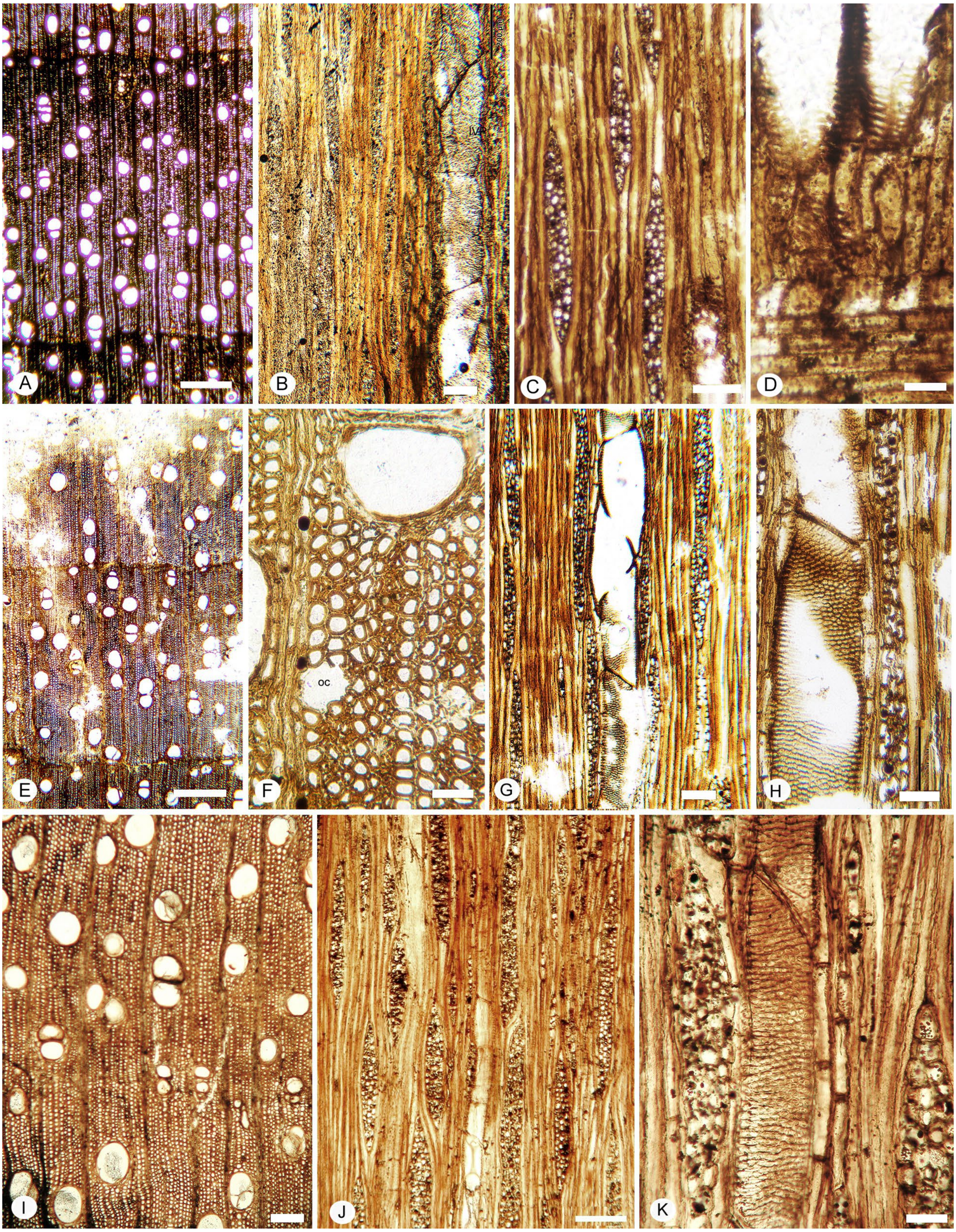

Figure 15. cf. *Ubiquitoxylon raynoldsii.* **A–D**. UF254-25215; **A**. Wood diffuse-porous, vessels solitary and in radial multiples of two, rarely three, TS; **B**. Rays mostly 3-seriate, uniseriate rays rare, crowded alternate intervessel pitting, TLS; **C**. Rays 3-seriate, non-septate fibers, TLS; **D**. Vessel-ray parenchyma pits with much reduced borders and horizontally elongate, marginal row of square ray parenchyma cells, RLS; **E–H**. UF305-25296; **E**. Wood diffuse-porous, vessels solitary and in radial multiples of two, TS; **F**. Possible oil/mucilage cell (oc), TS; **G**. Rays mostly 3-seriate, TLS; **H**. Rays 3-seriate, crowded alternate intervessel pitting, fibers non-septate, TLS; **I–K**. UF305-25303; **I**. Wood diffuse-porous, vessels solitary and in radial multiples of two, TS; **J**. Rays 1–6-seriate, uniseriate rays present, TLS; **K**. Crowded alternate intervessel pitting, axial parenchyma strand to right of vessel, TLS. Scale = 500 μm in A, E; 200 μm in B, G; 100 μm in C; 50 μm in D, F, K

Table 2. Comparison of cf. *Ubiquitoxylon raynoldsii* samples. TD = vessel tangential diameter, mean (SD), range; V/MM^2 = vessels per sq. mm; VEL = vessel element length; RH = multiseriate ray height; RW = ray width in cell number

	TD (µm)	V/MM2	VEL (µm)	RH (µm)	RW
UF254-25215	129 (24) 76–182	7–8	356–422 n=3	486 (186) 234–830	(2–) 3 (–4), 1s rare
UF305-25296	150 (23) 74–186	6–7	645 (224) 279–983	645 (224) 279–983	1–3 (4)
UF305-25303	147 (23) 109–188	6–8	400–556 n=7	559 (175) 297–927	1–4 (–6)

cells are rare in these samples, therefore it is possible the cuts of these three woods missed the rare oil cells. Below we provide a general description with Table 2 giving details of the quantitative features.

Description. Growth rings present, marked by radially flattened fibers and some narrow widely spaced vessels. Diffuse-porous.

Vessels solitary and in radial multiples of 2–3; solitary vessels round to slightly oval in outline; perforations simple; intervessel pits crowded alternate, angular in outline, 9–12 µm in horizontal diameter; vessel-ray parenchyma pits with much reduced borders, horizontally enlarged; tyloses occasional, widely spaced.

Fibers all non-septate or with rare septate fibers; thin walls, fiber pits not distinct on either radial or tangential walls.

Axial parenchyma rare, scanty paratracheal; strands mostly of 4 cells.

Multiseriate rays heterocellular, mostly 3–4-seriate, usually with one marginal row of upright / square cells.

Storied structure absent. Crystals and oil/mucilage cells not observed in longitudinal sections. Possible oil cell isolated amongst fibers in UF305-25296 (Fig. 15F).

Comparisons with present-day woods. This wood can be described by the presence of IAWA Hardwood Features – 1 5 13 22 23 26 27 32 42 47 53 61 66 69 78 92 97v 98v 106 115. Our different searches of InsideWood for matches for this wood indicated that its combination of the aforementioned features occurs in more than one family of more than one order, notably the Lauraceae (Laurales), as well as the Anacardiaceae and Burseraceae (Sapindales), Lamiaceae and Verbenaceae (Lamiales).

Comparisons with fossil woods. In InsideWood's fossil wood database the best match is with *Ubiquitoxylon raynoldsii* from the Paleocene of the Denver Basin (Wheeler et al., 2019). This genus was established to accommodate fossil woods that could not be assigned with certainty to a single family or order and have these features: vessels solitary and in short radial multiples, simple perforation plates, alternate intervessel pits to over 10 µm; non-septate or mostly non-septate fibers, axial parenchyma rare to scanty paratracheal, larger rays usually >4-seriate, rays with 1–2 rows of upright /square marginal ray cells, but lack storied structure, canals, and oil / mucilage cells. The average ray heights of the Paleocene *Ubiquitoxylon* (5 samples) are shorter, 289 (SD = 67) to 354 (SD = 82) µm and the vessel frequencies higher, 9–12 to 30, than of these Brummer Springs and Red Hill woods.

There are also similarities to *Carlquistoxylon* Wheeler, McClammer et LaPasha (1995), but this genus has narrower, more numerous vessels and rays, and growth ring boundaries are absent or indistinct (Wheeler et al. 1995; Nunes et al. 2018). Quantitative features of vessels and rays are well-known to be variable features, and we consider UF254-25215, UF305-25296 and UF305-25303 to be similar to *Ubiquitoxylon raynoldsii*.

? SAPINDACEAE Jussieu

Brummer Spring Unknown 1

Fig. 16A–H

Material. UF254-25178.

Description. Growth rings distinct, marked by radially flattened fibers. Wood diffuse-porous to weakly semi-ring-porous.

Vessels solitary and commonly in radial multiples of 2–3 (–4); average tangential diameter 78 (SD = 14) µm; range of 55–120 µm; 23–26 vessels per mm^2; solitary vessels oval in outline; perforations simple, no scalariform perforation plates observed; intervessel pits crowded alternate, 7–10 µm in horizontal diameter; vessel-ray parenchyma pits probably similar to intervessel pits; vessel element lengths average 472 (SD = 84) µm, range 362–746 µm; helical thickenings not observed; widely spaced thin-walled tyloses occasional.

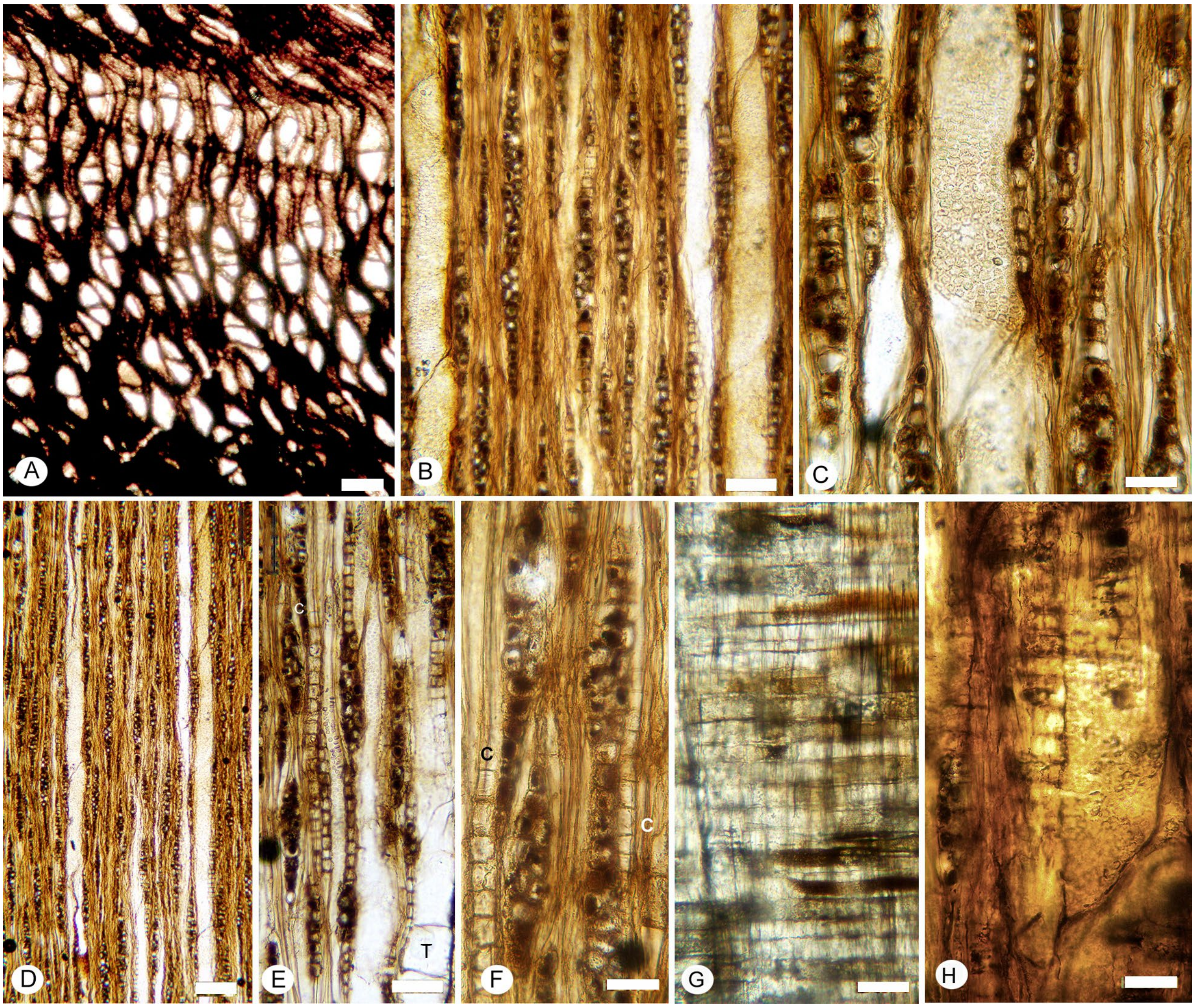

Figure 16. Brummer Spring Unknown 1. Sapindales? Sapindaceae? UF254-25178. **A**. Diffuse-porous to slightly semi-ring porous wood, with vessels solitary and in radial multiples of 2–4, TS; **B**, **C**. Vessel elements with simple perforation plates and crowded alternate intervessel pits, TLS; **D**. Rays 1–2-seriate, TLS; **E**. Narrow rays, horizontal tylosis (T), TLS; **F**. Crystals in chambered fibers, c adjacent to crystalliferous strand, TLS; **G**. Procumbent ray cells, RLS; **H**. Vessel-ray parenchyma pits, RLS. Scale = 200 μm in A, D; 100 μm in B, E; 50 μm in C, F, G, H

Fibers non-septate; medium-thick walls, no pitting observed; some crystalliferous, difficult to distinguish from crystals in chambered axial parenchyma.

Axial parenchyma rare.

Rays 1–2-seriate; rays with uniseriate margins of 1–8 cells, but in radial section, only procumbent cells seen; biseriate ray height 261 (56) μm, range 167–409 μm; 10–12 rays per mm.

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

Comments. Because this sample is contorted, true radial sections were difficult to make, making it difficult to determine with certainty ray cellular composition, vessel-ray parenchyma pitting, and whether the vessels originally were in a diagonal arrangement.

Comparisons with present-day plants. We tried various searches of InsideWood, sometimes allowing one or two mismatches. Features in bold were included in all searches: diffuse-porous wood with vessels solitary and in radial multiples not arranged in a tangential or dendritic pattern (5p 6a 8a 9a 11a), exclusively simple perforation plates (13p 14a), alternate intervessel pitting that is not minute (22p 24a), vessel-ray parenchyma pits similar to intervessel pits (30p) helical thickenings absent (36a), non-septate fibers with simple to minutely bordered pits (61p 66p), axial parenchyma rare (75p), ray width 1 to 3 cells (97p), ray <1 mm high (102a), rays per mm >4 per mm (114a), storied structure absent (118a 119a 120a 121a), oil and/or mucilage cells absent (124a 125a 126a), radial canals absent (130a), crystals present (136p).

Because it can be difficult to distinguish crystals in fibers from crystals in chambered axial parenchyma and it is possible that in the literature crystals in fibers were described as crystals in chambered axial parenchyma we searched two options: crystals in fibers (143p) or crystals not in ray cells or non-chambered axial parenchyma cells (137a 138a 139a 140a 141a).

Most of the suggested matches possess septate fibers; we are not sure if there might be a few septate fibers in addition to the mostly non-septate fibers in this sample. The matching taxa included the Sapindaceae (*Allophylus*, *Eriocoelum*, *Lecaniodiscus*, *Lychnodiscus*, *Schleichera*, *Tina*, *Toechima*), Meliaceae (*Quivisianthe*), and Rutaceae (*Zanthoxylum*), all of which are members of the Sapindales, and Lythraceae (*Pehria*) of the Myrtales.

Reasons for considering some genera to not be good matches: *Eriocoelum*, *Lecaniodiscus* and *Tina* have smaller intervessel pits (4–7 µm); *Quivisanthe* also has smaller intervessel pits, as well as more axial parenchyma; *Zanthoxylum* has more axial parenchyma; *Pehria* has exclusively septate fibers and smaller intervessel pitting.

It seems most probable that this wood has affinities with the Sapindales (see review by Pace et al., 2022), in particular with the Sapindaceae, a family whose anatomy was reviewed by Klaassen (1999). However, it is extremely unusual for Sapindaceae woods to have tyloses. Metcalfe and Chalk (1950) and Moll and Janssonius (1911) reported their occasional presence in *Schleichera*, one of the genera with similarity to this fossil. Klaassen considered those tyloses to be traumatic.

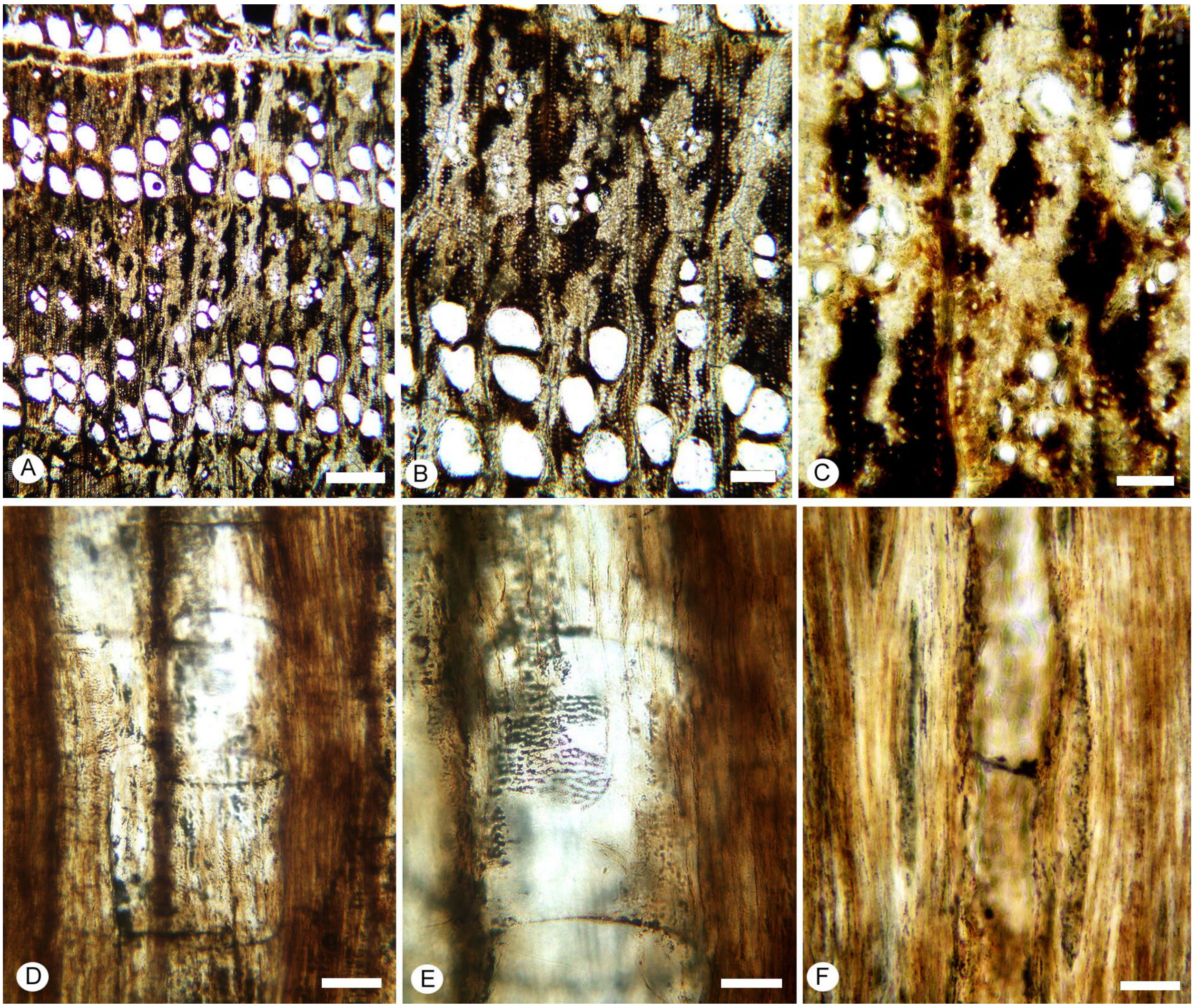

Figure 17. Brummer Spring Unknown Ring-Porous Wood. UF254-25209. **A–C**. Wood ring-porous, earlywood vessels solitary and in radial multiples of two, rarely three, latewood vessels in radial multiples and small clusters in which vessels tend to be rounded in outline. TS; **D**. Simple perforation plates, RLS; **E**. Alternate intervessel pitting, TLS; **F**. Rays 1–3 (–4)-seriate, uniseriate rays, TLS. Scale = 500 µm in A; 200 µm in B; 100 µm in C, D, F; 50 µm in E

Comparisons with fossil woods. There was no good match in InsideWood's fossil wood database. Most descriptions had too many features coded as unknowns to allow reasonable comparisons. The most similar were in the Salicaceae (*Flacourtioxylon mohgaonense* Trivedi and Srivastava 1988 and *Homalioxylon assamicum* Prakash and Tripathi 1972).

Brummer Spring Unknown Ring-Porous Wood

Fig. 17A–F

Material. UF254-25209.

Description. Growth rings distinct, marked by radially flattened fibers, and pronounced differences in latewood and earlywood vessel diameter within a growth ring. Ring-porous, earlywood zone 2–4 vessels deep.

Vessels solitary and in radial multiples of 2 (rarely 3), latewood vessels rounded, occasionally in small groups (clusters), but individual vessels retaining a circular to oval outline, sometimes in short tangential lines, average earlywood tangential diameter 180 (27) µm, range 134–226 µm; solitary vessels round to oval in outline; perforations simple; intervessel pits crowded alternate, angular in outline, 7–10 µm; vessel-ray parenchyma pits similar to intervessel pits; vessel element lengths average 297 µm (n = 8); range 226–339 µm.

Fibers medium thick walls, fiber pits not observed.

Axial parenchyma not observed, possibly scanty paratracheal to vasicentric.

Rays 1–4-seriate. Multiseriate rays heterocellular, probably with procumbent body cells and one marginal row of square / upright cells; multiseriate ray heights average 559 (SD = 192) µm, range 192–881 µm, 3–7 rays per mm.

Storied structure and crystals not observed.

Comments. The preservation of this sample did not allow us to determine the type of fiber pitting, whether fibers were septate or non-septate, whether intervessel pits were vestured or non-vestured, and we could not resolve the outlines of individual ray parenchyma cells in tangential section to accurately determine maximum ray seriation. It was also difficult to be sure of axial parenchyma distribution.

Comparisons with extant and fossil woods. We did multiple searches of InsideWood, using no or a few mismatches, and various combinations of *presence* of distinct ring-porosity; latewood vessels in groups; simple perforation plates; medium-sized alternate intervessel pitting; vessel-ray parenchyma pits similar to intervessel pits; mean vessel diameter >100 µm; and *absence* of exclusively solitary vessels; latewood vessels in tangential, diagonal, or dendritic arrangement; vessels in radial multiples of four or more; rays exclusively uniseriate or >10-seriate or of two distinct size classes; storied structure.

Among the families that included matches were the Bignoniaceae (e.g. *Catalpa*, *Chilopsis*), Meliaceae (*Toona*), Moraceae (*Morus*), Rhamnaceae (*Frangula*, *Zizyphus*), Rutaceae (*Phellodendron*) and Fabaceae. We reviewed images in InsideWood, the Chinese Wood Atlas (Itoh et al., 2022), the CSIRO Atlas (Ilic, 1991), the FFPRI Database of Japanese Woods (FFPRI 2002), and publications on the systematic wood anatomy of these families (Gregory, 1980). One of the characteristics of this sample is that the latewood vessels in groups have a rounded outline; unlike most of the aforementioned taxa, *Styphnolobium* (Fabaceae/Papilionoideae) is somewhat similar. One of the Post Dietz Hill (UF278) woods has some resemblance to this genus.

The most similar wood in InsideWood's Fossil Hardwood database is Selmeier's (2015) "Taxa Indet. 13", but it does not have similar vessel clusters and its vessels tend to a tangential arrangement.

Although this single sample seems unique, we prefer not to create a new taxon for it.

Brummer Spring Unknown Tall Ray Wood

Fig. 18A–F

Material. UF254-25220.

Description. Growth ring boundaries marked by radially flattened fibers. Wood diffuse-porous.

Vessels predominantly solitary; average tangential diameter 31 (6) µm; range of 22–39 µm; vessel frequency 83–118 per mm^2; perforations exclusively scalariform, 35–67 bars, averaging 49 (10); vessel-ray parenchyma pitting opposite, sometimes appearing scalariform because of coalescent apertures, 3–5.5 µm in horizontal diameter; vessel element lengths >800 µm.

Fibers non-septate; medium-thick walls, distinctly bordered pits on radial walls.

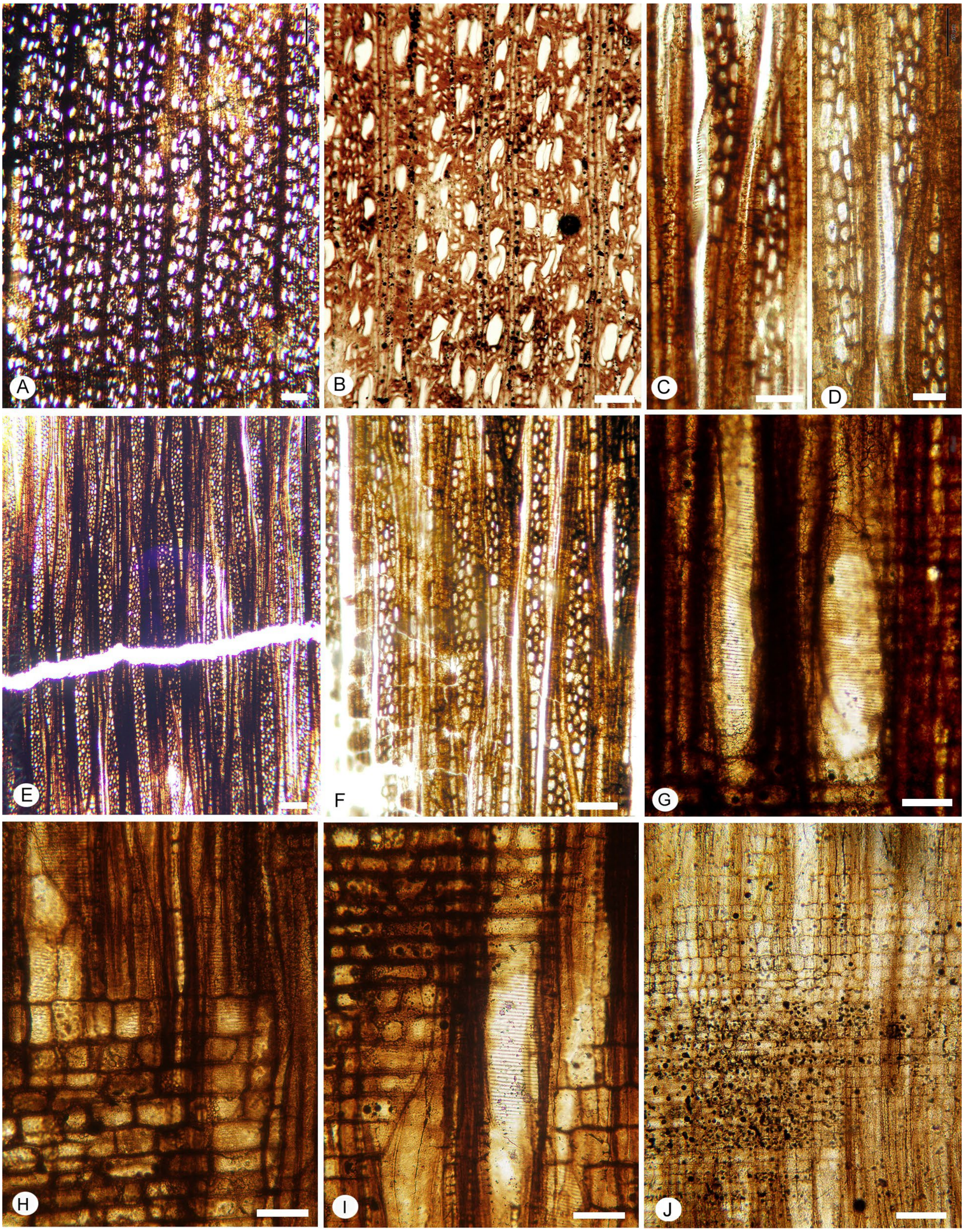

Figure 18. Brummer Spring Unknown Tall Ray Wood. UF254-25220. **A**. Diffuse-porous wood, vessels predominantly solitary TS; **B**. Vessels mostly solitary, diffuse to diffuse-in-aggregates axial parenchyma, TS; **C**, **D**. Scalariform perforation plates with more than 20 bars, TLS; **E**, **F**. Heterocellular rays, rays mostly 3–4 seriate, TLS; **G**. Scalariform perforation plates with many bars, RLS; **H**, **I**. Heterocellular rays, vessel-ray parenchyma pits, scalariform perforation plates, RLS; **J**. Heterocellular ray, predominance of upright / square cells. Scale = 200 µm in A, E; 100 µm in B, F, J; 50 µm in C, D, G, H, I

Axial parenchyma diffuse to diffuse-in aggregates, in long (>5-celled) strands.

Rays 1–3(–4)-seriate, body of intermixed square/upright cells and occasional procumbent cells, ray margins of 4 or more upright cells; multiseriate ray height averages 1122 (276) µm, range 746–1,808 µm; 7–9/mm.

Helical thickenings and crystals not observed.

Comments. Because of the predominantly solitary vessels, we were unable to find intervessel pitting, but we think it likely it is similar in size to the vessel-ray parenchyma pitting and so we used absence of medium-large intervessel pits (26a 27a) in our searches of the InsideWood database. The vessel elements were tangentially compressed, so the vessel diameter measurements are narrower than the original dimensions. The steeply inclined vessel element end walls made it difficult to measure the entire vessel element lengths, but it appears they belong to IAWA Feature 54 / Mean vessel element length >800 µm.

Comparisons with present-day woods. We searched InsideWood's modern wood database for these features in various combinations: diffuse-porous wood with vessels exclusively solitary and not arranged in a radial / diagonal or tangential pattern (5p 6a 7a 9p), exclusively scalariform perforation plates with more than 40 bars (13a 14p 18p), intervessel pits not medium or large (26a 27a), absence of vessel-ray parenchyma pits with much reduced border to apparently simple: pits horizontal (scalariform, gash-like) to vertical (palisade) (32a); vessel diameters <100 µm (42a 43a) and more than 40 vessels per mm^2 (46a 47a 48a), vessel elements >800 µm long (54p); non-septate fibers (66p); diffuse axial parenchyma not accompanied by well-defined paratracheal or banded axial parenchyma (76p 79a 80a 82a 83a 84a 85a 86a) with more than 5 cells per strand (91a 92a); rays not of two distinct sizes (103a), commonly >1 mm high (102p), and not composed exclusively of procumbent cells (104a).

The larger rays are mostly 3-seriate, at times 4-seriate, thus we searched for rays not exclusively uniseriate or >10-seriate (96a 99a) or for larger rays commonly 4- to 10-seriate (98p). We searched for exact matches and also allowed one mismatch. This wood has features found in more than one family or order and cannot be placed with confidence in any of them, although we think it most likely it is an Asterid.

The orders and families of Asterids with similarities in wood anatomy are listed below by their placement in APG IV, as presented by Stevens (2001-onwards). We are not listing here the families that mismatched in having markedly shorter rays, vessel-ray parenchyma pits enlarged and with reduced borders; rays with two distinct diameter classes, or well defined-sheath cells.

ROSID II – Crossomatales–Stachyuraceae (*Stachyurus*).

ASTERIDS – Cornales: Cornaceae (*Cornus*), Curtisiaceae (*Curtisia*), Hydrangeaceae (*Deutzia*). Ericales: Clethraceae (*Clethra*), Pentaphylacaceae (*Cleyera*, *Eurya*, *Ternstroemia*), Styracaceae (*Huodendron*), Symplocaceae (*Symplocos*).

CAMPANULID/ASTERID II – Dipsacales: Viburnaceae (*Viburnum*).

Comparisons with fossil woods. When we searched InsideWood's modern wood database, we also searched IW's fossil wood database. Results included 1) *Mastixioxylon microporosum* Gottwald (2000) and *Mastixioxylon symplocoides* Meijer (2000) (Cornaceae or Symplocaceae), both from the Late Cretaceous of Belgium, but not good matches because intervessel and vessel-ray parenchyma pits are enlarged; 2) *Frutecoxylon yubariense* Takahashi and Suzuki (2003) (possibly Cornaceae), has rays that are too wide; 3) *Chaloneroxylon pagei* Falcon-Lang et al. (2012) from the Late Cretaceous of Georgia, USA, has scalariform and unilaterally compound vessel-ray parenchyma pits; 4) Nut Beds Xylotype 1-A.2 (UF225-33245) from the middle Eocene Clarno Nut Beds, Oregon, USA (Wheeler and Manchester, 2002). This last wood type was represented by a single 10 mm diameter sample with pith. Intervessel and vessel-ray parenchyma pitting were not observed in this sample, thus we cannot determine if it and UF254-25220 are the same wood type.

Fruits and Seeds

Fig. 19A–K

The Brummer Spring flora also includes silicified fruits and seeds. Although found along with the petrified wood, they are mostly casts rather than permineralized. Many

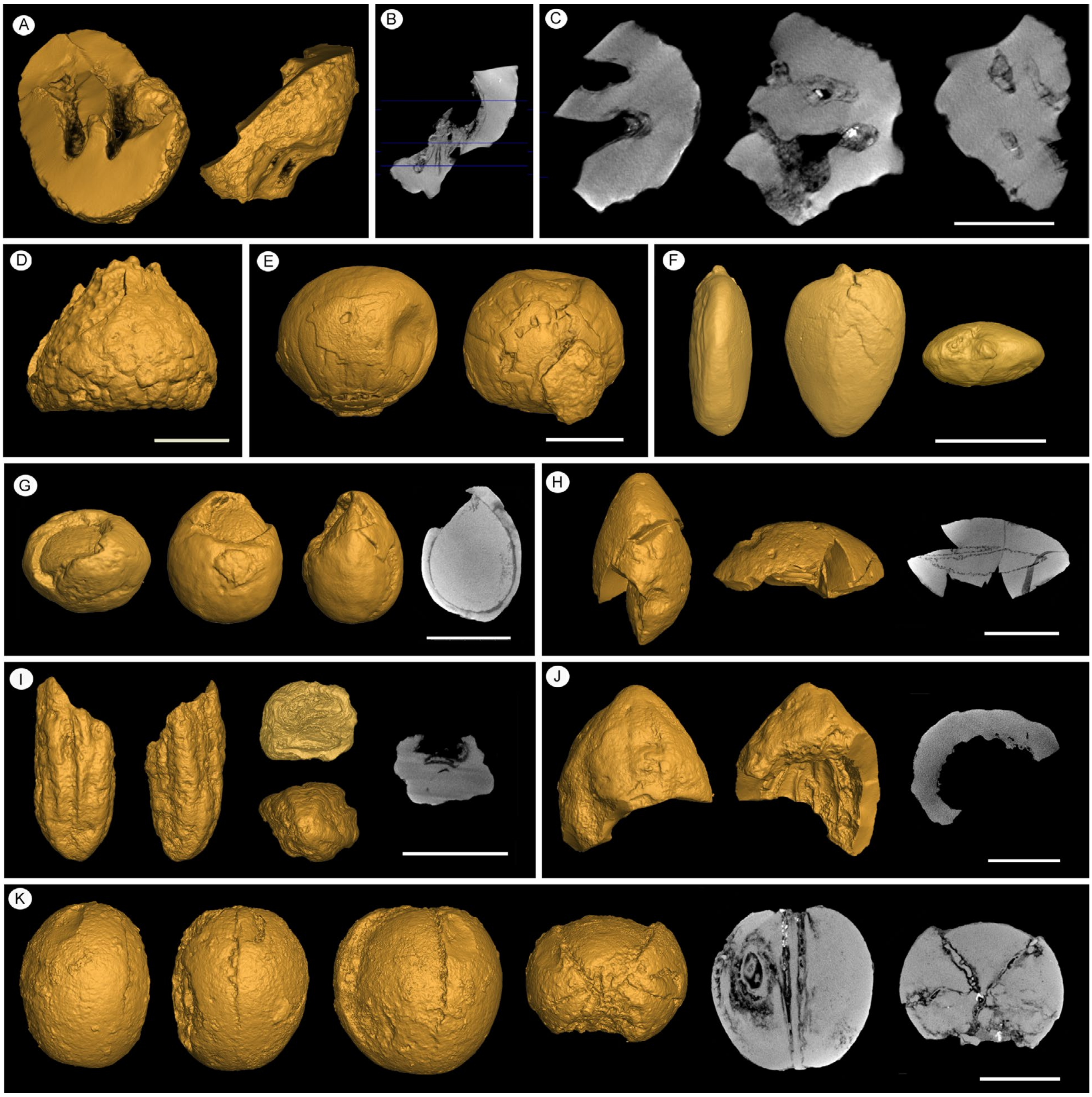

Figure 19. Fruits and seeds of the Brummer Spring flora imaged by micro-CT scanning. **A–C**. *Juglans* sp., UF254-62730; **A**. Surface rendering of the fractured nut, showing thick nutshell and two lobes of the cotyledons; **B**. Virtual longitudinal section, with horizontal lines indicating the levels of transverse sections shown in C; **C**. Successive virtual transverse sections from equator (left) to basal portion. Note that the right hand image indicates that the base of the locule is divided into four lobes by the intervening primary and secondary septa; **D**, **E**. *Quercus* sp.; **D**. Cupule in lateral view, UF254-72892; **E**. Isolated nut in lateral and basal view, 254-62728; **F**. Unidentified seed, UF254-62729; **G**. Bisymmetrical, unilocular fruit with keel in the plane of symmetry; apical and lateral views, and virtual longitudinal section. Cf. *Prunus*, UF254-62726; **H**. Incomplete, thick-walled unilocular fruit in apical and lateral views and virtual transverse section. Cf. *Prunus*, UF254-62723; **I**. *Nyssa* sp. Endocarp surface rendering in lateral, transverse fracture, and basal views. Right hand image is a virtual transverse section apparently showing two locules, 254-62727; **J**. Unidentified thick-walled endocarp with about ten longitudinal inner ribs, UF254-62724; **K**. Unidentified pentalocular eudicot fruit. Rotated through lateral and basal views, followed by a virtual longitudinal section showing single seed within locule and axile placentation, UF254-62725. Scale bars = 5 mm

specimens collected by amateurs in the 1960s and 70s have been lost, but a small collection is archived at Florida Museum of Natural History. They are shown in Figure 19. They include *Juglans* (Fig. 19A–C), *Quercus* (Fig. 19D, E), *Nyssa* (Fig. 19I), and some unidentified taxa. Two of those unidentified (Fig. 19G, H) show similarities with *Prunus*, but they are preserved without sufficient anatomical details to confirm their identity.

DISCUSSION

We found 20 distinct wood types at Brummer Spring (UF254). Among them are four

Table 3. Comparison of the composition of Post wood assemblages

Taxa	UF278 – Dietz Hill	UF279 – Post Hammer	This study
PINALES			
Pinaceae	*Keteleeria farionii*	not found	*Pinus* sp.
CUPRESSALES			
Cupressaceae	*Taxodioxylon* sp.	not found	Conifers 1, 2, 3
CONIFER INCERTAE SEDIS	not found	Family indet.	not found
MAGNOLIALES			
Magnoliaceae	*Magnolia hansnooteboomii*	not found	not found
LAURALES			
Lauraceae	*Laurinoxylon* 2 species	not found	*Laurinoxylon* 2 species
PROTEALES			
Platanaceae	*Platanoxylon haydenii*	*Platanoxylon haydenii*	*Platanoxylon haydenii*
	not found	*Platanus* sp.	not found
TROCHODENDRALES			
Trochodendraceae	not found	*Trochodendron beckii*	not found
SAXIFRAGALES			
Hamamelidaceae	Possibly present	*Hamamelidoxylon crystalliferum*	not found
Cercidiphyllaceae	not found	*Cercidiphyllum alalongum*	*Cercidiphyllum alalongum*
FABALES			
Fabaceae	cf. *Styphnolobium* sp.	not found	possibly present
MALPIGHIALES			
Salicaceae	not found	not found	*Populus* sp.
ROSALES			
Rosaceae	not found	not found	*Prunus* 4 spp.
Ulmaceae	*Ulmus woodii*	*Ulmus danielii*, *U. woodii*	not found
Cannabaceae	Possibly present	*Celtis popsii*	not found
Uricalean Rosids	*Urticaleoxylon stevensii*	not found	not found
	cf. *Moroxylon*	not found	not found
	Cannabaceae/Moraceae Wood Type 1, Type 2	not found	not found
FAGALES			
Fagaceae	*Fagus dodgei*	*Fagus dodgei*	*Fagus dodgei*
	Quercus sp. (Red Oak type)	*Quercinium* sp. (evergreen oak)	not found
	not found	*Lithocarpoxylon* 2 spp.	not found
Juglandaceae	*Carya leroyii*	*Pterocaryoxylon* sp.	not found
SAPINDALES			
Anacardiaceae	not found	*Pistacia terrazasae*	not found
Meliaceae	not found	not found	*Cedreloxylon* sp.
Sapindaceae	not found	*Acer* (2 spp.)	not found
	Aesculus klaassenii	not found	not found
	Klaassenoxylon wilkinsonii	not found	not found
Rutaceae?, Sapindaceae?	cf. *Fagaroxylon* sp.	not found	not found
MALVALES			
Malvaceae	not found	*Wataria kvacekii*	cf. *Grewia*
APIALES			
Araliaceae	*Plerandreoxylon oskoslkii*	not found	not found
? MALPIGHIALES			
Salicaceae?	*Populus* sp.	not found	not found
INCERTAE SEDIS			
Theaceae?, Hamamelidaceae?	*Hamamelidoxylon* sp.	*Hamamelidoxylon suzukii*	not found
Sapindaceae ?	not found	not found	Brummers Spring Unknown 1
	not found	not found	cf. *Ubiquitoxylon raynoldsii*
	not found	not found	Brummers Spring Unknown Ring-Porous Wood
	not found	not found	Brummers Spring Unknown Tall Ray Wood

Table 4. Comparison of the incidence of porosity and perforation plate (PP) types at the middle Eocene Clarno Nut Beds and the late Eocene Post localities: Brummer Spring (UF254), Hammer (UF279) and Dietz Hill (UF278)

Porosity	Nut Beds n=65	UF254 n=16	UF279 n=15	UF278 n=16
Ring-porous	1%	13%	13%	13%
Semi-ring-porous	28%	19%	37%	22%
Diffuse-porous	71%	68%	50%	65%
PP				
Simple	78%	72%	69%	76%
Scalariform	22%	22%	31%	24%

types of conifers, including one *Pinus* and three probable Cupressaceae. The preservation of these conifers was not good, therefore we were unable to distinguish with certainty critical diagnostic features such as cross-field pitting. Most abundant of the angiosperm woods are Rosaceae with a combination of features found in *Prunus* (four species). Although *Populus* is common in Tertiary compression floras of the western USA, it is generally not known in wood assemblages, most likely because *Populus* wood decays readily and does not have a long resident time minimizing the time available for petrification. To the best of our knowledge, the *Populus* sp. at Brummer Spring is the only reliable record of fossil *Populus* wood in the North American Paleogene. Other woods in the Brummer assemblage include two species of *Laurinoxylon* (but differing from those at Post Dietz Hill and the Nut Beds), *Cercidiphyllum alalongum* (first described from the Clarno Nut Beds, and also present at the Post Hammer Locality), one Malvaceae with some resemblance to *Grewia*, and four distinctive wood types that we are unable to assign to order or family. One of these unknowns has a suite of characters that matches the fossil wood genus *Ubiquitoxylon*, previously described from the Paleocene of Colorado (Wheeler et al., 2019).

Although the Post localities are relatively close geographically (Fig. 1) and believed to be similar in age, there is little overlap in their composition (Table 3). The only species found at all three localities are *Platanoxylon haydenii* and *Fagus dodgeii*. These three Post wood assemblages are markedly smaller and less diverse than the middle Eocene Clarno Nut Beds. Each Post locality has less than one-third of the number of species of the Nut Beds; Dietz Hill (UF278) with 22 species; Post Hammer (UF279) with 19 species; Brummer Spring (UF254) with 20 species; Clarno Nut Beds with 76 species.

PALEOCLIMATE

It is well established that ring-porosity is a feature correlated with seasonal climates and deciduousness (Bailey, 1924; Gilbert, 1940; Boura and DeFranceschi, 2007). It is also well established that there was increased seasonality from the middle to late Eocene in western North America (e.g. Prothero and Berggen, 1992; Wolfe, 1994). Thus, it is reasonable to hypothesize that there would be differences in the incidence of porosity types between the middle Eocene Nut Beds wood assemblage and late Eocene Post woods. Table 4 shows that ring-porosity is rarer in the Nut Beds assemblage than it is in the Post wood assemblages, reflecting the increase in seasonality. In contrast, the incidences of perforation plate type are not notably different between the Nut Beds and Post. The incidences of perforation plates fall within the range of modern warm to cool temperate regional floras (Baas, 1976; Wheeler et al., 2007). Because it has woods of Lauraceae, Meliaceae, and Malvaceae, we suggest that the Brummer Spring fossil assemblage, like the other Post localities, represents warm temperate to subtropical vegetation.

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ADDITIONAL INFORMATION

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