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A DIVERSE ASSEMBLAGE OF LATE EOCENE WOODS FROM OREGON, WESTERN USA

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Abstract: Well-preserved silicified woods from a site near the town of Post, Oregon, western USA, provide insights into the late Eocene vegetation and climate ca. 36 million years and data for comparing with both older and younger wood floras regionally and globally. The composition of this wood flora, taken into consideration along with taxa identified from silicified fruits and seeds of the same locality, provides a more complete picture of the former vegetation. We recognize woods belonging to the families Anacardiaceae (*Pistacia terrazasae* sp. nov.), Cannabaceae (*Celtis popsii* sp. nov.), Cercidiphyllaceae (*Cercidiphyllum* cf. *alalongum* R.A.Scott et E.A.Wheeler), Fagaceae (*Fagus dodgeii* sp. nov., *Lithocarpoxylon ashwillii* sp. nov., *Lithocarpoxylon* sp., *Quercus* sp.), Hamamelidaceae (*Hamamelidoxylon crystalliferum* sp. nov., *H.* cf. *suzukii* E.A.Wheeler et T.A.Dillhoff), Juglandaceae (*Pterocaryoxylon* sp.), Malvaceae (*Wataria kvacekii* n. sp.), Platanaceae (*Platanoxylon* cf. *haydenii* (Felix) Süss et Müll.-Stoll, *Platanus* sp.), Sapindaceae (*Acer*, 2 spp.), Trochodendraceae (*Trochodendron beckii* (Hergert et H.K.Phinney) R.A.Scott et E.A.Wheeler). This assemblage, which we refer to as the Post Hammer flora (UF 279), is comparable in age to the nearby Teater Road flora known mainly from fossil leaf impressions. Comparing the functional traits of the Hammer woods to the older Clarno Nut Beds woods attests to changing climate in the region, including an increase in seasonality.

Key words: John Day Formation, fossil wood, Anacardiaceae, Cannabaceae, Cercidiphyllaceae, Fagaceae, Hamamelidaceae, Juglandaceae, Malvaceae, Platanaceae, Sapindaceae, Trochodendraceae

Introduction

Central Oregon in the west-coastal United States is home to a sequence of middle Eocene to Early Oligocene terrestrial sediments that contain abundant and diverse fossil woods, leaves, fruits and seeds, and vertebrates (Chaney 1948, Hanson 1996, Retallack et al. 2000, Dillhoff et al. 2009). The middle Eocene Clarno Nut Beds deposit includes a rich fossil fruit and seed assemblage (Scott 1954, Manchester 1994) as well as the world's single most diverse assemblage of fossil woods (Wheeler and Manchester 2002). The fossil woods described herein are ca. 8 million years younger from a late Eocene deposit of the John Day Formation near the community of Post, Oregon. These were investigated as part of an ongoing treatment of the flora at the Post Hammer locality (UF locality 279), which includes at least ten fruit types (Manchester and McIntosh 2007). Twelve woods were introduced previously, representing the families Aceraceae, Anacardiaceae, Cercidiphyllaceae,

Fagaceae, Hamamelidaceae, Juglandaceae, Malvaceae, Ulmaceae, and Cupressaceae (Wheeler et al. 2006). Woods referable to *Trochodendron beckii*, *Cercidiphyllum alalongum*, and *Liriodendroxylon multiporosum* were described earlier (Scott and Wheeler 1982; see Wheeler and Manchester 2002 for locality clarification) and a more detailed treatment of the ulmaceous woods from the same flora was presented by Wheeler and Manchester (2007). Three assemblages from sites east of Post are currently under study: Brummers Spring (UF 254), Dietz (UF 278), and Hammer (UF 279).

In this article we focus on woods of the Post Hammer site and discuss their significance for understanding past floristic diversity, providing data for biogeographic and phylogenetic studies, and providing insights into woody plants' responses to changing climates. We describe the woods in alphabetical sequence by family and compare the incidence of features considered of ecological significance to the older Nut Beds wood assemblage.

Materials and methods

Locality

The Post Hammer locality (UF 279) is situated about three km east of the town of Post, Oregon, and is named informally for Michael Hammer, a devoted fossil collector who brought it to our attention. The silicified woods are found loose in eroded tuffs that are situated in the upper part of the Clarno Formation near the transition to the John Day Formation. A minimum age for these wood sites is provided by a white tuff overlying the fossiliferous tuff at UF locality 278. Sanidine crystals from this white tuff give an ^{40}Ar/^{39}Ar date of 36.21 ± 0.26 MA (n = 26; Manchester and McIntosh 2007). There are no datable tuffs in or immediately below the fossiliferous horizon to provide a maximum age. However, this late Eocene date may be a reasonable approximation of the age of the Post woods, contrasting with the middle Eocene age of the Clarno Nut Beds.

Sample preparation

The University of Florida (UF) collections at the Florida Museum of Natural History include more than 80 specimens of silicified wood from the Hammer locality. After examining them with a handlens and/or dissecting microscope, we selected examples of what appeared to be different wood types for thin sectioning. This paper describes 16 wood types. Eight additional angiosperms represented by secondary xylem, a palm, and one conifer from the same collection remain undescribed.

A diamond lapidary saw was used to cut thick sections (wafers) of transverse (TS), tangential (TLS), and radial (RLS) surfaces. One side of the wafer was smoothed to remove saw marks, and then affixed to a glass side using 24-hour transparent epoxy. The sections were then ground until they were thin enough (ca. 30 µm) to allow seeing anatomical details with transmitted light 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 to improve clarity for light microscopy. Samples are deposited in the palaeobotanical collections of the Florida Museum of Natural History, University of Florida, Gainesville; in this paper individual samples are referred to by their UF specimen numbers.

Affinities

Possible relationships of the fossils to modern woods were determined by searching the InsideWood database (InsideWood 2004-onwards), using some of the strategies described by Wheeler (2011) and Wheeler et al. (2020). The search criteria used are given, i.e., IAWA hardwood list feature numbers (IAWA Committee 1989) followed by the codes "p" for present, "r" for required present; "a" for absent, "e" for required absent. Subsequently, descriptions and slides of the suggested matches 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 text-figures illustrating the features used to establish relationships show TS = transverse section, RLS = radial

longitudinal section, and TLS = tangential longitudinal section.

For quantitative features, we mostly report average (standard deviation), range; if three values are given, this is minimum – average – maximum.

The minimum diameters of the samples were estimated from the growth ring curvature and/or divergence of the rays. Although our fragmentary samples do not allow for providing information on dbh (diameter breast height, a common forestry measurement), we consider this crude estimate to be useful for indicating whether the sample came from juvenile or mature wood. There can be differences between juvenile and mature wood anatomy, especially in quantitative features and ray structure (e.g., Carlquist 2001). Most of the descriptions in InsideWood are for mature wood samples, so this needs to be kept in mind when making comparisons.

We refer to images of modern wood samples by Index Xylariorum 4.1 numbers (Lynch and Gasson 2010).

Nomenclature

There is a tradition among some Indian and European palaeobotanists that fossil woods should be assigned to a genus ending in -*oxylon* or -*inium*, even when the fossil wood has a combination of characters unique to an extant genus, e.g., *Cistoxylon* for a wood with features unique to *Cistus* (Gottwald 1992), *Evodinium* for woods thought to resemble *Evodia* (Bande and Prakash 1984). The International Code of Botanical Nomenclature does not require or recommend that fossil wood names have these endings. In our monograph on woods from the middle Eocene Nut Beds flora, our approach to naming was: "When a fossil wood has a suite of anatomical features characteristic of an extant genus, we assign it to that genus. Collinson (1986) provided rationale for this approach. This does not preclude the possibility that the wood may have belonged to a plant that had leaves and/or reproductive structures different from the specified extant genus" (Wheeler and Manchester 2002: 11). We continue this approach here as well because we think that doing so provides information on mosaic evolution and variation in how different plant parts change through time.

New names of fossil plants and other nomenclatural acts are registered in the Plant Fossil Names Registry, which is hosted and operated by the National Museum, Prague for the International Organisation of Palaeobotany, each with a unique PFN number.

Systematic palaeobotany

Family Anacardiaceae R.Br., 1818 nom. cons.

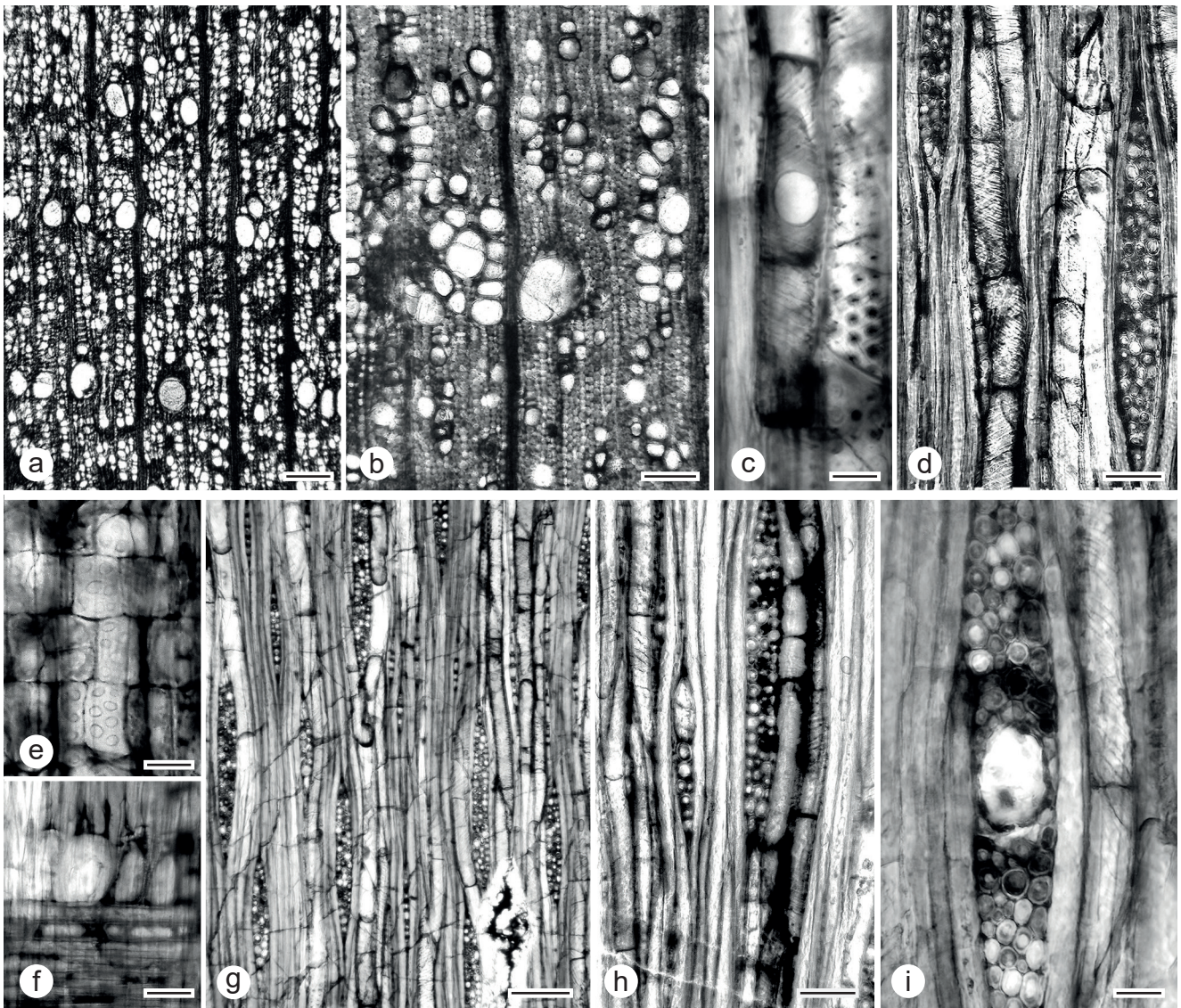### Genus *Pistacia* L., 1753

Pistacia terrazasae sp. nov.
Text-fig. 1a–i

Holotype. Designated here. UF 279-24545 (Text-fig. 1b–i).

Paratype. Designated here. UF 279-85025 (Text-fig. 1a).

Plant Fossil Names Registry Number. PFN002712 (for new species).

Text-fig. 1. *Pistacia terrazasae* sp. nov., a: UF 279-85025; b–i: UF 279-24545. a: Ring-porous wood with widely spaced solitary earlywood vessels; latewood vessels in radial multiples of 4 or more and in clusters, TS. b: Growth ring boundary, fiber walls thin to thick, TS. c: Simple perforation plates, alternate intervessel pits, helical thickenings in vessels, TLS. d: Multiseriate rays to 4-seriate, tyloses in vessels, helical thickenings throughout body of vessel element, and alternate intervessel pitting, TLS. e: Vessel-ray parenchyma pitting with reduced borders, oval in outline, RLS. f: Marginal row of upright cells, one inflated and crystalliferous, procumbent body cells, RLS. g: Multiseriate rays mostly 3-seriate, occasionally 4-seriate, uniseriate rays usually <10 cells tall, TLS. h: Ray with enlarged crystalliferous marginal cell, to left of C, TLS. i: Ray with canal, TLS. Scale bars: 200 µm in a, g; 100 µm in b, d, h; 50 µm in c, i; 20 µm in e, f.

Table 1. Comparison of *Pistacioxylon* (arranged by age, oldest to youngest) and *Pistacia terrazasae*. EW VTD = earlywood vessel tangential diameter in µm; EW row = number of rows of wide earlywood vessels; IVP = horizontal diameter of intervessel pits in µm; Cry = crystals, Ab = absent, UpR – in upright ray parenchyma cells, Tyl = in tyloses; RW = width in cell number of rays without canals; C = common, U = Uncommon; Eo = Eocene, Ol = Oligocene, Mio = Miocene, l = late, e = early.

Taxon (Reference)	EW VTD	EW row	IVP	Cry	RW	Canals	Age, Location
Pistacioxylon muticoides (1)	75–188	1	6–8	Ab	1–3(–4)	C, 1–3 per ray	Ol, France
P. hollieisii (2)	117 (105–165)	4–5	7–10	Tyl	1–3	U, 1 per ray	l Mio, Germany
P. leiloensis (3)	170 (109–265)	1	5–8	Ab	1–5*	U, 1 per ray	l Mio, China
P. praeterebinthus (4)	80–105	2–3	6–8	?	1–5*	1 per ray	Mio?, Germany
P. sp. (4)	120–150	2–3	7–19	?	1–5*	1–2 per ray	Mio?, Germany
P. ufuki (5)	81 (42–130)	1	5–7	Ab	1–3	C, 1–3 per ray	e Mio, Turkey
Pistacia terrazasae sp. nov. (this paper)	89 (57–139)	1	7–9	UpR	1–3(–4)	U, 1 per ray	l Eo, USA

1. Dupéron (1973), 2. Selmeier (2000a), 3. Cheng et al. (2012), 4. Gottwald (2004), 5. Akkemik et al. (2018)

* Ray width described as to 5 cells wide, however, it seems probable that is the width of rays with canals.

Etymology. Named for Teresa Terrazas to acknowledge her comprehensive treatment of the wood anatomy of the Anacardiaceae

Type locality. UF 279. About 3 km east of Post, Crook County, Oregon, USA.

Type stratum and age. John Day Formation, Eocene.

Diagnosis. Growth rings distinct. Wood ring-porous with a narrow earlywood zone, mostly 1 pore deep, earlywood vessels not contiguous; latewood vessels predominantly in radial multiples, some in clusters. Helical thickenings present. Perforation plates exclusively simple. Intervessel pitting alternate. Vessel-ray parenchyma pits with reduced borders, rounded to oval in outline. Fibers non-septate. Axial parenchyma not common, scanty paratracheal. Radial canals present. Rays heterocellular with a few marginal rows of square to upright cells. Crystals in marginal ray parenchyma cells.

Description. Growth rings present, marked by radially flattened latewood fibers, and differences in vessel diameter and density between latewood and earlywood of subsequent rings. Ring-porous.

Earlywood vessels solitary and rounded to slightly oval in outline, earlywood pore zone 1(–2) pores deep, not contiguous; latewood vessels mostly in radial multiples and clusters, solitary latewood vessels angular in outline (Text-fig. 1a, b); average tangential diameter of earlywood vessels 89 (22) μm, range 57–139 μm; perforations exclusively simple (Text-fig. 1c); intervessel pits alternate (not angular in outline) (Text-fig. 1c, d), 7–9 μm in horizontal width; vessel-ray parenchyma pits with reduced borders and rounded to oval in outline (Text-fig. 1e), occasionally irregular in shape, most commonly in upright/square ray cells; prominent helical thickenings along the full length of narrow vessel elements (Text-fig. 1c, d); mean vessel element length 354 (38), range 275–435 μm; tyloses abundant, bubble-like in earlywood vessels, more widely spaced in latewood vessels.

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

Axial parenchyma rare, scanty paratracheal.

Rays 1–3(–4)-seriate, uniseriates low, usually less than 10 cells high (Text-fig. 1d, g, h). Multiseriate rays heterocellular, body of procumbent cells, with 1–2(–4) marginal rows of upright cells (Text-fig. 1e); total multiseriate ray height average 308 (100), range 135–555 μm; 4–5/mm. Solitary crystals occasional in upright/square marginal ray cells (Text-fig. 1f, h), some crystalliferous cells enlarged, rarely chambered. Radial canals present (Text-fig. 1i), oval in outline, canal size – width by height ranging from 40 × 70 μm to 60 × 110 μm, with thin-walled walled epithelial cells.
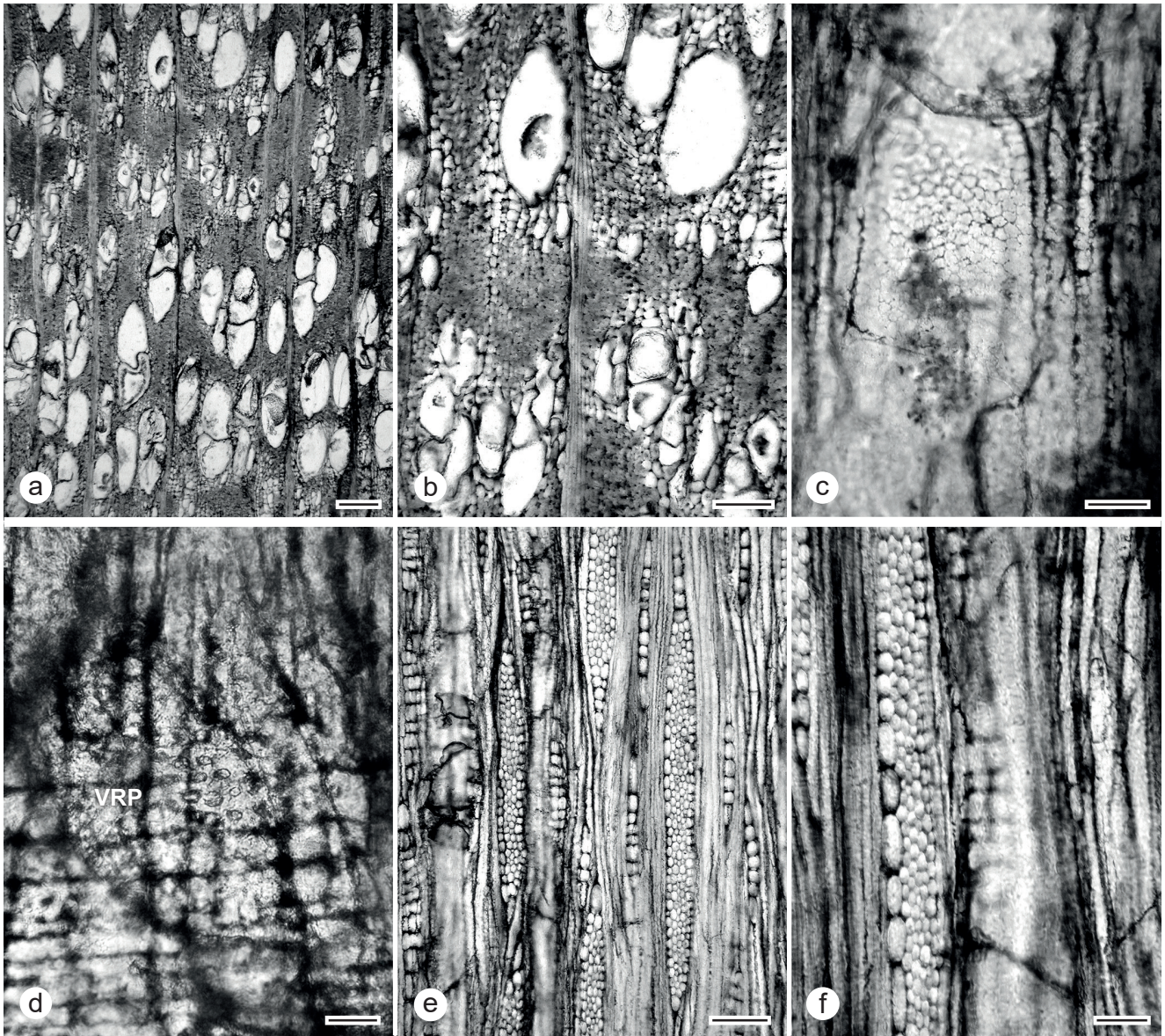
Comparisons with extant woods. A search of InsideWood for ring-porous wood (3p), vessels in radial multiples of four or more common (10p), simple perforation plates (13p), alternate intervessel pits (22p), vessel-ray parenchyma pits with reduced borders (31p), helical thickenings along the length of the vessel elements (36p 37p), and radial canals (130p) returned five species of *Pistacia* and *Rhus microphylla* ENGELM. in the Anacardiaceae. *Rhus microphylla* has a broad earlywood zone, while *Pistacia* species have narrow earlywood zones, usually with one discontinuous row (more rarely two rows) of enlarged solitary earlywood pores (Fahn et al. 1986, Terrazas 1994, Abundiz-Bonilla et al. 2004). Consequently, we assign these Post Hammer woods to *Pistacia*.

Pistacia is a genus of shrubs to small trees with a disjunct distribution (Mabberley 2017). Seven species occur from the Mediterranean basin to Central Asia (*P. atlantica* DESF., *P. integerrima* J.L.STEWART, *P. khinjuk* STOCKS, *P. lentiscus* L., *P. palaestina* BOISS., *P. terebinthus* L., *P. vera*) L., two species occur in eastern Asia (*P. chinensis* BUNGE, *P. weinmannifolia* J.POISS. ex FRANCH.), two species are distributed from the southwestern United States to Central America (*P. mexicana* KUNTH, *P. texana* SWINGLE) (Yi et al. 2008). InsideWood has reference images of *Pistacia chinensis* (FRI 547, CAFw 8636). *P. khinjuk* (Lw s.n.), *P. lentiscus* (SJRw 14465), *P. mexicana* (FPAw 27837, MADw 12256), and *P. palaestina* (MADw 26695). The latewood of *Pistacia terrazasae* does not have a pronounced diagonal or tangential arrangement and thus resembles the latewood of *P. lentiscus* (SJRw 14465) and *P. mexicana* (MADw 12256) more than the other species which usually have a pronounced tangential to diagonal-dendritic arrangement. Ray widths in this new species also are similar to *P. lentiscus* and *P. mexicana*. According to Terrazas (1994), who examined wood of 10 extant *Pistacia* species, multiseriate rays in *P. mexicana* and *P. lentiscus* were "most commonly 2–3" cells wide, implying that in other species multiseriate rays usually are 3–5. Appendix I of her dissertation (p. 308) shows the quantitative ray and vessel element features of these two species are similar.

Pistacia lentiscus is found from the Canary Islands across southern Europe from Portugal to Greece and Turkey, across North Africa from Morocco to Egypt and the Middle East; *P. mexicana* is found in southern Texas, Mexico, Guatemala, and Honduras (AL-Saghir 2010). Both species are evergreen, which is unusual for ring-porous species because ring-porous species almost always are deciduous (Boura and De Franceschi 2007). Yi et al. (2008), using molecular data, placed these two species in section *Lentiscus*, while AL-Saghir (2010, 2012), using morphological data (almost exclusively leaf characters), placed them in section *Lentiscella*. Earlier phylogenetic analyses also placed these two widely separated geographically species in the same section (Parfitt and Baldenes 1997).

Comparisons with fossil woods. Dupéron (1973) created the genus *Pistacioxylon* DUPÉRON to accommodate a late Eocene/Oligocene wood with features found in ring-porous species of *Pistacia*. Selected features of the *Pistacioxylon* species described to date are compared with *Pistacia terrazasae* (Tab. 1). This Post Hammer wood type and the other species assigned to *Pistacioxylon* have a combination of wood anatomical features unique to *Pistacia*. We suggest all could be assigned to *Pistacia* to indicate that their anatomy is indistinguishable from that of the extant genus.

Text-fig. 2. *Celtis popsii* sp. nov., UF 279-34460. **a:** Growth ring with earlywood of multiple rows of vessels solitary and in radial multiples; latewood vessels in wavy tangential bands, TS. **b:** Growth ring boundary, latewood vessels in multiples with axial parenchyma confluent, TS. **c:** Simple perforation plates, alternate intervessel pits, polygonal in outline, TLS. **d:** Vessel-ray parenchyma pits to right of VRP, oval in outline, with slightly reduced borders, RLS. **e:** Rays tending to two sizes, some multiseriate rays with distinct sheath cells, multiseriate rays usually with 1 marginal row of square to upright cells, occasionally with 4 or more; uniseriate rays less than 10 cells high, TLS. **f:** Detail of multiseriate ray with distinct sheath cells, vessel element end walls, TLS. Scale bars: 200 μm in a, e; 100 μm in b; 50 μm in c, f; 20 μm in d.

Co-occurring fruits/seeds. Manchester and McIntosh (2007) illustrated a silica fruit cast with characters similar to those of extant *Anacardium* L., *Cyrtocarpa* KUNTH, and *Pistacia* from the same locality (UF 279). It is possible that this wood and that fruit came from the same source plant, given they are the only Anacardiaceae known at locality UF 279. However, without direct attachment between them or repeated co-occurrences this cannot be established. The Nut Beds flora included a fossil fruit, *Pistachioides striata* MANCHESTER (Manchester 1994), which shares many features with pistachio nuts, but it was not assigned to the modern genus because of insufficient preservation of anatomical details. Although numerous silicified woods are preserved at the Nut Beds, including some Anacardiaceae, none of them resemble *Pistacia*.

Remarks. Xie et al. (2014) hypothesized that *Pistacia* originated near the Eocene-Oligocene boundary at 37.60 Ma. The minimum age for the Post sites is 36.21 ± 0.26 Ma (Manchester and McIntosh 2007), which places *Pistacia terrazasae* near this hypothesized time of origin. It is the oldest known occurrence of a wood with features of *Pistacia* and the only one known from the USA. Ramírez and Cevallos-Ferriz (2002) described *Pistacia marquezii* J.L.RAM. et CEV.-FERRIZ, based on Oligocene leaves (Pie de Vaca Formation, Mexico) and that they thought most similar to present-day *P. chinensis*. They used this similarity to support the concept of exchange between low-latitude North America and Asia. The question remains whether this Oregon fossil wood is evidence for a migration of *Pistacia* from Asia to Mexico and the American Southwest via the Pacific Northwest.

Family Cannabaceae MARTINOV, 1820 nom. cons.

Genus *Celtis* TOURN. ex L., 1753

Celtis popsii sp. nov.
Text-fig. 2a–f

H o l o t y p e . Designated here. UF 279-34460 (Text-fig. 2a–f). Minimum estimated axis diameter 28 cm.

P l a n t   F o s s i l   N a m e s   R e g i s t r y   N u m b e r . PFN002695 (for new species).

R e p o s i t o r y . Paleobotany Collections, Florida Museum of Natural History, Gainesville, Florida, USA.

E t y m o l o g y . Named in honor of Raymond "Pops" Shepherd, who loved and respected the natural beauty of our earth, father of Mark Shepherd, generous supporter of the J. C. Raulston Arboretum.

T y p e   l o c a l i t y . UF 279. About 3 km east of Post, Crook County, Oregon, USA.

Type stratum and age. John Day Formation, Eocene.

D i a g n o s i s . Growth rings distinct, wood ring-porous to semi-ring-porous, earlywood zone with multiple rows of earlywood vessels, latewood vessels in diagonal-tangential arrangement. Perforations simple. Intervessel pitting crowded alternate; vessel-ray pitting oval with reduced borders. Axial parenchyma paratracheal, vasicentric to confluent. Rays <10-seriate, heterocellular, sheath cells present.

D e s c r i p t i o n . Growth rings distinct. Wood ring-porous to semi-ring-porous.

Earlywood zone 2–4(4+) rows deep with vessels solitary and in radial multiples of 2–3. Latewood vessels in radial multiples and clusters arranged diagonally and in tangential bands (Text-fig. 2a, b). Tangential diameter of earlywood vessels 126 (18), 88–166 μm; perforations exclusively simple; intervessel pits crowded alternate, mostly polygonal in outline (Text-fig. 2c), medium-large, 7–11; vessel-ray parenchyma pits oval in outline, not crowded, borders slightly reduced (Text-fig. 2d); vessel element lengths average 380 (141) μm; thin-walled bubble-shaped tyloses present.

Fibers mostly non-septate, possibly a few septate, pits not observed, likely thick-walled.

Axial parenchyma vasicentric-confluent (Text-fig. 2a, b), strands mostly of 4 cells.

Rays 1–5(–6) cells wide; tendency to two size classes as 2–3-seriate rays are rare, sheath cells present in most of the wider rays (Text-fig. 2e, f); heterocellular with procumbent body cells and 1–2(–5) marginal rows of square and upright cells. Multiseriate ray height average 737 (169) μm; 4–6/mm. Possibly crystals in somewhat enlarged upright marginal ray parenchyma cells.

C o m p a r i s o n s   w i t h   e x t a n t   w o o d s . A search of InsideWood for the combination: wood not diffuse-porous (5e), tangential bands of vessels (6p), simple perforation plates (13p), alternate intervessel pitting that is not small to minute (22p 24a 25a), non-septate fibers (66p), vasicentric parenchyma (79p), heterocellular rays of two size classes (103p 104a 105a) with sheath cells (110p) only returned

species of *Celtis* (Cannabaceae). If vessels in a diagonal arrangement (7p) is used instead of vessels in a tangential arrangement, again only *Celtis* has that combination of features.
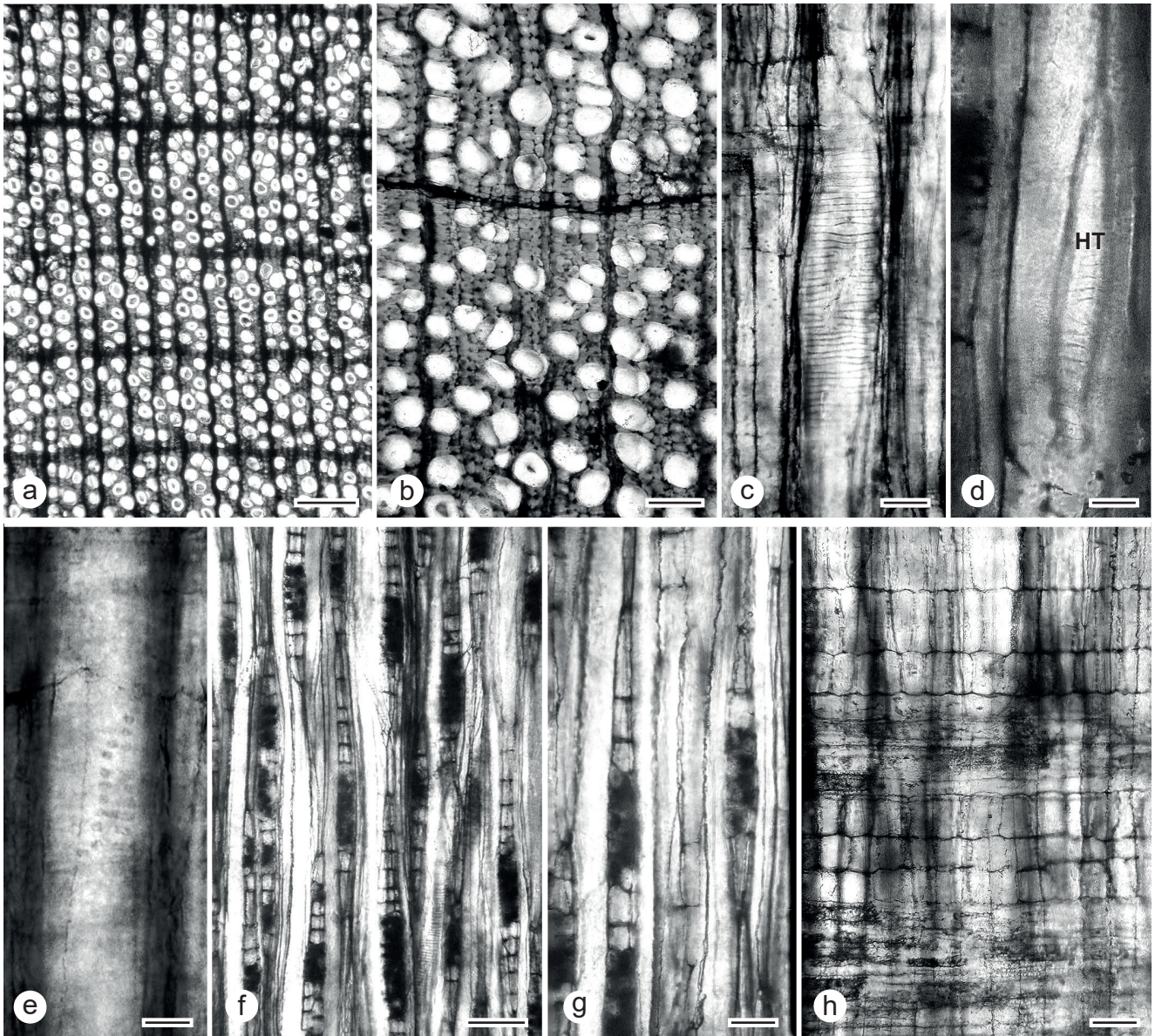
Celtis is a widespread genus with ca. 60 species, mostly trees, that occurs in temperate and tropical regions (Africa, Asia, Central and South America, North America, Southern Europe; Sattarian 2006, Mabberley 2017). InsideWood includes coded descriptions of 25 species and images of 22 species.

There is variation in porosity within the genus, and sometimes within a species, related to geography, climate, and leaf retention. Typically, tropical species are diffuse-porous, e.g., *C. africana* BURM.F., *C. gomphophylla* BAKER, and *C. mildbraedii* ENGL. (Africa) and *C. schippii* STANDL. (Central and South America), while temperate species are ring-porous, e.g., *C. laevigata* WILLD., *C. occidentalis* L. (North America), *C. bungeana* BLUME, *C. sinensis* PERS. (temperate Asia), as well as *C. australis* L. (Mediterranean region). *Celtis pallida* TORR., a shrub to small tree native to dry regions of southwest North America, extending to Central and South America, is semi-evergreen and diffuse-porous to somewhat semi-ring-porous (Sweitzer 1971, Wheeler et al. 1988, Zhong et al. 1992, Wood Identification Database Team, FFPRI accessed 2020–2021, InsideWood 2004-onwards). The Asian *C. philippensis* BLANCO is diffuse-porous in tropical regions and semi-ring- to ring-porous in more seasonal environments (Zhong et al. 1992). One sample each of *C. laevigata* (BWCw 8303, Florida, USA), *C. laevigata* var. *reticulata* (TORR.) L.D.BENSON (SJRw 40228, Texas, USA), and *C. biondii* PAMP. (CAFw 20246, Jiangxi, southeast China) were semi-ring-porous, rather than ring-porous.

Present-day ring-porous *Celtis* species usually have only 1–2 rows of earlywood vessels. However, some samples of *C. occidentalis* (BWCw 8272; BWCw 8456; FPAw 9598), and *C. sinensis* (TWTw 23448) have multiple rows of earlywood vessels. Ring-porous *Celtis* generally have wider rays (to 12-seriate) than diffuse-porous species (to 8-seriate, but mostly 1–5-seriate). The anatomy of this Post Hammer wood with its tendency to semi-ring-porosity and rays to 5–6-seriate suggests it grew in a seasonal environment, but one not as pronounced as North Temperate *Celtis* species experience today.

C o m p a r i s o n s   w i t h   f o s s i l   w o o d s . Apparently, the three generic names – *Celtisoxylon* T.TRIVEDI (Trivedi 1971), *Celtixylon* GREGUSS (Greguss 1943), *Celtoxylon* WURZINGER (Wurzinger 1953) – created for fossil woods thought to resemble *Celtis* – were not properly diagnosed (Gregory et al. 2009). *Celtisoxylon* was applied to a wood from Deccan Intertrappean beds of India but was only mentioned in an abstract without diagnosis or designation of holotype, *Celtixylon* was never formally diagnosed, and *Celtoxylon* was used in a thesis, but not formally published.

Woods thought to have affinities with *Celtis* have been reported from the Miocene of temperate Europe and Asia. Selmeier (1989, 2015) described *Celtixylon cristalliferum* A.SELM. from the lower and middle Miocene of Germany and compared it to *C. palaeohungaricum* GREGUSS and

Text-fig. 3. *Cercidiphyllum* cf. *alalongum* R.A.Scott et E.A.Wheeler, UF 279-24543. a, b: Diffuse-porous wood, exclusively solitary vessels, axial parenchyma rare, thick-walled fibers, TS. c: Scalariform perforation plate with more than 30 bars, RLS. d: Helical thickenings (HT) in vessel element tip, RLS. e: Opposite to scalariform intervessel pits, RLS. f, g: Heterocellular rays 1–2 cells wide, occasionally uniseriate and biseriate portions of similar width, TLS. h: Ray with alternating rows of procumbent and upright (-square) cells, RLS. Scale bars: 200 µm in a; 100 µm in b, f; 50 µm in c, g, h; 20 µm in d, e.

C. campestre (E.Hofm.) Greguss from the Miocene of Hungary. These latter two species had rays up to 10–12 cells wide, while the widest rays of *C. cristalliferum* were 6–7-seriate. *Celtixylon cristalliferum* differs from *Celtis popsii* because it has a narrower earlywood pore zone with 1–2 (3) rows of large vessels, less well-defined sheath cells in the rays, and not as obvious a tendency to two size classes of rays. The illustration of the *Celtixylon* sp. (probable Miocene age) that Gottwald (2004) described also shows only 1–2 rows of large earlywood pores.

As detailed above, *Celtis popsii* differs from other fossil wood species thought related to *Celtis* and has wood anatomical features that fall within the range of and are unique to *Celtis*, so we assign it to the genus. To the best of our knowledge, this is the only fossil *Celtis* wood known from North America.

Co-occurring fruits/seeds. To date, there is no record of *Celtis* in the fruit/seed assemblage of locality UF 279.

Family Cercidiphyllaceae Engl., 1907 nom. cons.

Genus *Cercidiphyllum* Siebold et Zucc., 1846

***Cercidiphyllum alalongum* R.A.Scott
et E.A.Wheeler, 1982**
Text-fig. 3a–h

Material. A single specimen (UF 279-24543) with an estimated minimum diameter of 8.8 cm.

Description. Growth rings distinct, marked by bands of radially narrow fibers, difference in vessel diameter between latewood and earlywood vessels of successive rings (Text-fig. 3a, b). Wood diffuse-porous.

Vessels predominantly solitary (Text-fig. 3a, b), mean tangential diameter 59 (12) μm, 32–86 μm; 82–95–102/mm^2; perforations all scalariform, 28–47 fine bars (Text-fig. 3c); intervessel pits rare, opposite to scalariform (Text-fig. 3e); vessel-ray parenchyma pits scalariform; vessel element lengths 980–1,400 μm; tyloses not observed. Faint helical thickenings occasionally observed in vessel element tips (Text-fig. 3d).

Fibers non-septate, thick-walled, small (2–3 μm) bordered pits observed on radial walls of some fibers.

Axial parenchyma rare.

Rays 1–2(–3)-seriate, uniseriate portions frequently alternating with multiseriate portions, occasionally width of the uniseriate and multiseriate portions similar (Text-fig. 3f, g), markedly heterocellular with upright cells often 2× the height of the procumbent cells (Text-fig. 3h), procumbent cells with relatively thick walls and richly pitted, upright and square cells with relatively thin walls; uniseriate rays exclusively of upright and square cells, usually less than 10 cells high; ~12 rays per mm.

Crystals not observed.

C o m p a r i s o n s   w i t h   e x t a n t   w o o d s . The combination of diffuse-porous wood (5p), exclusively solitary vessels (9p), scalariform perforation plates with more than 20 bars (17p), opposite-scalariform pits (22a – alternate pits absent), narrow numerous vessels (42a 43a 46a 47a 48a – absence of both medium-wide vessels and fewer than 40 vessels per mm^2), long vessel elements (54p), fibers with bordered pits (62p), axial parenchyma rare-absent (75p), rays 1–3-seriate (97p) and heterocellular rays (104a 105a) occurs in the saxifragalean families Altingiaceae (*Liquidambar* L.), Cercidiphyllaceae (*Cercidiphyllum*), and Hamamelidaceae (*Corylopsis* Siebold et Zucc.). Sakala and Privé-Gill (2004) discussed how to distinguish woods of these three genera and concluded that *Cercidiphyllum* consistently had more bars per perforation plate (to >40 bars) than the other two genera. Based on their criteria this wood has affinities with the Cercidiphyllaceae. Scott and Wheeler (1982) detailed differences between the ray structure of *Cercidiphyllum* and *Corylopsis*: rays in *Cercidiphyllum* have more than two alternating 1-seriate and 2–3-seriate portions and in some rays the 1-seriate and 2–3-seriate portions are of equal width.

C o m p a r i s o n s   w i t h   f o s s i l   w o o d s . Sakala and Privé-Gill (2004) reviewed the occurrences of *Cercidiphyllum*-like wood and recognized only two species: *Cercidiphylloxylon kadanense* U.Prakash, Březinová et Bůžek (Prakash et al. 1971) from the Czech Republic, and *Cercidiphylloxylon spenceri* (D.W.Brett) H.L.Pearson from the Paleocene of Scotland and the Eocene London Clay (Brett 1956, Pearson 1987). Subsequently, Guo et al. (2010) assigned a sample from the Paleocene of China to *Cercidiphylloxylon spenceri*, and again reviewed the occurrences and criteria for recognizing wood of Cercidiphyllaceae.

Pearson (1987) and Crawley (1989) suggested the Clarno Nut Beds wood *Cercidiphyllum alalongum* R.A.Scott et E.A.Wheeler (Scott and Wheeler 1982) should be included in *Cercidiphylloxylon spenceri* (Pearson 1987). Ray structure is notorious for its variability, especially differences between

juvenile wood and mature wood. Nonetheless, we consider the Nut Beds *Cercidiphyllum* distinct from the European *Cercidiphyllum*-like woods, which do not have alternating uniseriate and multiseriate parts. The Chinese sample does, but the parts are not of equal width. Helical thickenings in vessel element tails were not reported for the European or Chinese woods. Admittedly, the preservation of those specimens does not appear to be as good as the Oregon specimens, so helical thickenings might have been difficult to observe.

R e m a r k s . Leaves and fruits with features unique to *Cercidiphyllum* are not known prior to the Oligocene, although extinct genera attributed to the family are widespread in the Paleocene and Eocene (e.g., Crane and Stockey 1985). This was a major part of the rationale Sakala and Privé-Gill (2004) used for assigning the Nut Beds and London Clay *Cercidiphyllum*-like woods to *Cercidiphylloxylon*, i.e., these Eocene woods predate the occurrence of "real" *Cercidiphyllum*. However, the Oligocene *Cercidiphyllum*-like woods, which are of an age when there is "real" *Cercidiphyllum* also were placed in *Cercidiphylloxylon*. It is a matter of opinion, but we do not think there are significant anatomical differences between the Paleocene, Eocene, or Oligocene *Cercidiphyllum*-like woods and present-day *Cercidiphyllum* and do not think it necessary to assign the Paleogene woods to *Cercidiphylloxylon* rather than *Cercidiphyllum*. This "disconnect" between fossil woods resembling the present-day *Cercidiphyllum* and fruits that do not may be an example of mosaic evolution within the Cercidiphyllaceae.

C o - o c c u r r i n g   f r u i t s / s e e d s . By "real" *Cercidiphyllum*, we refer to occurrences of fruits with follicles borne in sessile clusters, in association with leaves closely resembling those of extant *Cercidphyllum japonicum*. Such fossils occur only a few km from the UF 279 wood locality, but in overlying strata considered to be lower Oligocene (Meyer and Manchester 1997). Brown (1935) used a broader concept of the genus *Cercidiphyllum*, incorporating fossil infructescences with fruits borne in racemes rather than clusters, associated with *Trochodendroides* E.W.Berry leaves which are similar to the leaves of extant *Cercidiphyllum*. Today such infructescences are usually placed in the extinct genus *Jenkinsella* E.Reid et M.Chandler (syn. *Nyssidium* auct non Heer) (Golovneva and Alekseev 2017). In Central Oregon, *Jenkinsella* infructescences are known from the Hancock Canyon site (Wheeler and Manchester 2014).

Fagaceae Dumort., 1829
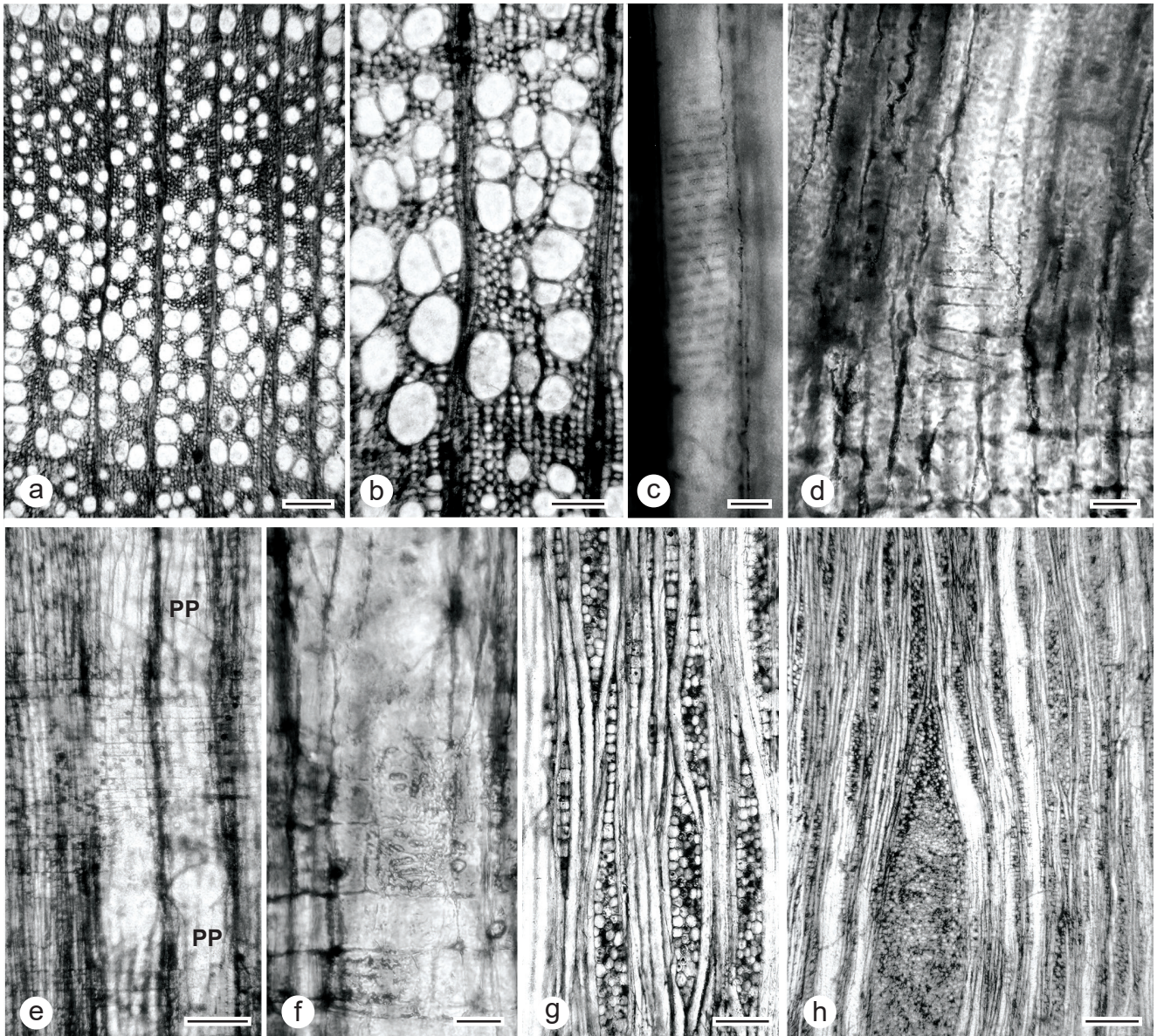
Genus *Fagus* Tourn. ex L., 1753

Fagus dodgei sp. nov.
Text-fig. 4a–h

H o l o t y p e . Designated here. UF 279-34468 (Text-fig. 4a, b, d–h). Minimum estimated axis diameter 10 cm.

A d d i t i o n a l   m a t e r i a l . UF 279-30165 (Text-fig. 4c).

P l a n t   F o s s i l   N a m e s   R e g i s t r y   N u m b e r . PFN 002679 (for new species).

Text-fig. 4. *Fagus dodgei* sp. nov., a, b, d–h: UF 279-34468; c: UF 279-30165. a: Wood diffuse-porous to semi-ring-porous with distinct latewood zone with narrower vessels; vessels solitary and in short multiples; diffuse, diffuse-in-aggregates axial parenchyma visible in latewood, TS. b: Growth ring boundary, TS. c: Opposite intervessel pitting, TLS. d: Scalariform perforation plate with fewer than 10 bars, RLS. e: Simple perforation plates (PP), RLS. f: Vessel-ray parenchyma pitting with reduced borders and frequently oval in outline, RLS. g: Rays 1–4(–5)-seriate with variable numbers of marginal rows, TLS. h: Rays of two distinct sizes, widest rays >10-seriate, TLS. Scale bars: 200 μm in a, h; 100 μm in b, e, g; 50 μm in d, f.

Etymology. Named for William W. Dodge IV, who made sure paleoxylotomy in North Carolina was alive and well during the Covid-19 pandemic.

Type locality. UF 279. About 3 km east of Post, Crook County, Oregon, USA.

Type stratum and age. John Day Formation, Eocene.

Diagnosis. Growth rings distinct. Diffuse-porous to semi-ring-porous. Vessels mostly solitary, but also in occasional radial, oblique, or tangential pairs; tangential diameters average <100 μm; perforations simple and scalariform; intervessel pits opposite, transitional to scalariform; pits to ray parenchyma oval to horizontally elongate, with reduced borders. Non-septate fibers with distinctly bordered pits on radial walls. Axial parenchyma diffuse and diffuse-in-aggregates as short uniseriate bands. Rays uniseriate and multiseriate, tending to be of two sizes, wider multiseriate rays >10-seriate; wide rays irregularly spaced; average multiseriate ray height >1 mm; homocellular to heterocellular, body composed of procumbent cells with marginal rows of square and upright cells. Solitary rhomboidal crystals occasional in procumbent ray cells. Storied structure absent.

Description. Growth rings distinct, marked by radially narrow fibers, and differences between latewood and earlywood vessels of subsequent rings (latewood vessels are narrower and not as crowded as earlywood vessels) (Text-fig. 4a, b). Diffuse-porous to semi-ring-porous (Text-fig. 4a).

Vessels mostly solitary, but also occasional radial, oblique and tangential pairs; average earlywood tangential diameter 55 (11), range 39–79 µm; vessel frequency in first half of growth ring ca. 90/mm^2; perforations simple and scalariform with 4-24 bars, mostly 8–12 bars (Text-fig. 4d, e); intervessel pits opposite (5–7 µm), transitional to scalariform (Text-fig. 4c); pits to ray parenchyma oval to horizontally elongate, with reduced borders (Text-fig. 4f); vessel element lengths 450–520 µm.

Non-septate fibers with distinctly bordered pits on radial walls.

Axial parenchyma apotracheal, diffuse as isolated cells and diffuse-in-aggregates as short uniseriate bands, more easily seen in latewood (Text-fig. 4a).

Rays uniseriate and multiseriate, tending to be of two sizes, with rays 1–5(–6)-seriate common, and wider multiseriate rays to 18–20-seriate, with few intermediate widths; wide rays irregularly spaced (Text-fig. 4g, h); average multiseriate ray height 1.56 mm, range 0.74–2.69 mm; homocellular to heterocellular, body composed of procumbent cells usually with 1–4 (up to 8) marginal rows of square and upright cells.

Solitary rhomboidal crystals occasional in procumbent ray cells. Storied structure absent.

C o m p a r i s o n s   w i t h   e x t a n t   w o o d s . The following combination of features indicates affinities with *Fagus* (Fagaceae): distinct growth rings (1p), simple and scalariform perforation plates (13p 14p), opposite intervessel pitting (21p), vessel-ray parenchyma pits with reduced borders (30a), narrow numerous vessels (42a 43a 46a 47a), non-septate fibers with distinctly bordered pits on radial walls (62p 66p), diffuse and diffuse-in-aggregates axial parenchyma (76p 77p), wide rays >10 cells wide and >1 mm high (99p 102p). To the best of our knowledge, there is not a reliable means of distinguishing present-day *Fagus* species based on wood anatomy alone (Brazier and Franklin 1961, Wheeler and Dillhoff 2009).

Woods of the Platanaceae are common in the Paleogene of the western USA. and superficially resemble *Fagus*. However, there are features useful in distinguishing them (e.g., Panshin and DeZeeuw 1980, Hoadley 1990). *Fagus* consistently has vessel-ray parenchyma pits with reduced borders that are somewhat horizontally elongate, while *Platanus* L. has vessel-ray parenchyma pits similar to intervessel pits. Vessel multiples are rare in both, but *Platanus* has some tangential multiples and a tendency to vessels being tangentially arranged; consequently, intervessel pits are more common in *Platanus* than in *Fagus*. Intervessel pits are consistently opposite in *Platanus;* while *Fagus* usually has transitional (opposite- scalariform) intervessel pitting. Spacing of and size of the wide rays is more uniform in *Platanus* than in *Fagus*. All these features can be reviewed in the InsideWood image collection (InsideWood 2004-onwards).

C o m p a r i s o n s   w i t h   f o s s i l   w o o d s . *Fagus*-like woods have been described as species of *Fagus*, *Fagoxylon* STOPES et FUJII, and *Fegonium* UNGER (Süss 1986). Descriptions of most lack details that would permit confirming their relationships with *Fagus*. There are at least ten *Fagus*-like woods reported from the Mio-Pliocene of Europe (Gregory et al. 2009), but their descriptions are brief,

so it is not possible to do detailed comparisons of them with this late Eocene wood.

There are differences between *Fagus dodgei* and the mid-Miocene *Fagus manosii* E.A.WHEELER et T.A.DILLHOFF from Washington State, USA (Wheeler and Dillhoff 2009), which had more scalariform intervessel pits and larger opposite intervessel pits, narrower and shorter rays (to 16-seriate and 1.7 mm high), less axial parenchyma, and lacked crystals. Thus, although there is no reliable way to distinguish between extant species of *Fagus*, we are choosing to recognize *Fagus dodgei* as a new species to emphasize that it differs from the mid-Miocene Vantage *Fagus* wood.

R e m a r k s . Denk and Grimm (2009) proposed that *Fagus* evolved in the Northern Pacific Region. Fossil species of *Fagus*, based on fruits and leaves, are known from the Paleogene of the Pacific Northwest. The middle Eocene *Fagus langevinii* MANCHESTER et R.M.DILLHOFF from McAbee, British Columbia, and Republic, Washington, differs from the early Oligocene *Fagus pacifica* R.W.CHANEY from the Bridge Creek flora of Oregon (Manchester and Dillhoff 2004).

C o - o c c u r r i n g   f r u i t s . A single silicified *Fagus* nut was recovered from the same locality, UF 279 (Manchester and McIntosh 2007).

Genus *Lithocarpoxylon* IUST.PETRESCU, 1978 emend. by Suzuki and Ohba (1991)

Lithocarpoxylon ashwillii sp. nov.
Text-fig. 5a–g

H o l o t y p e . Designated here. UF 279-24559 (Text-fig. 5a–g).

P l a n t   F o s s i l   N a m e s   R e g i s t r y   N u m b e r . PFN 002680 (for new species).

R e p o s i t o r y . Paleobotany Collections, Florida Museum of Natural History, Gainesville, Florida, USA.

T y p e   l o c a l i t y . UF 279. About 3 km east of Post, Crook County, Oregon, USA.

T y p e   s t r a t u m   a n d   a g e . John Day Formation, Eocene.
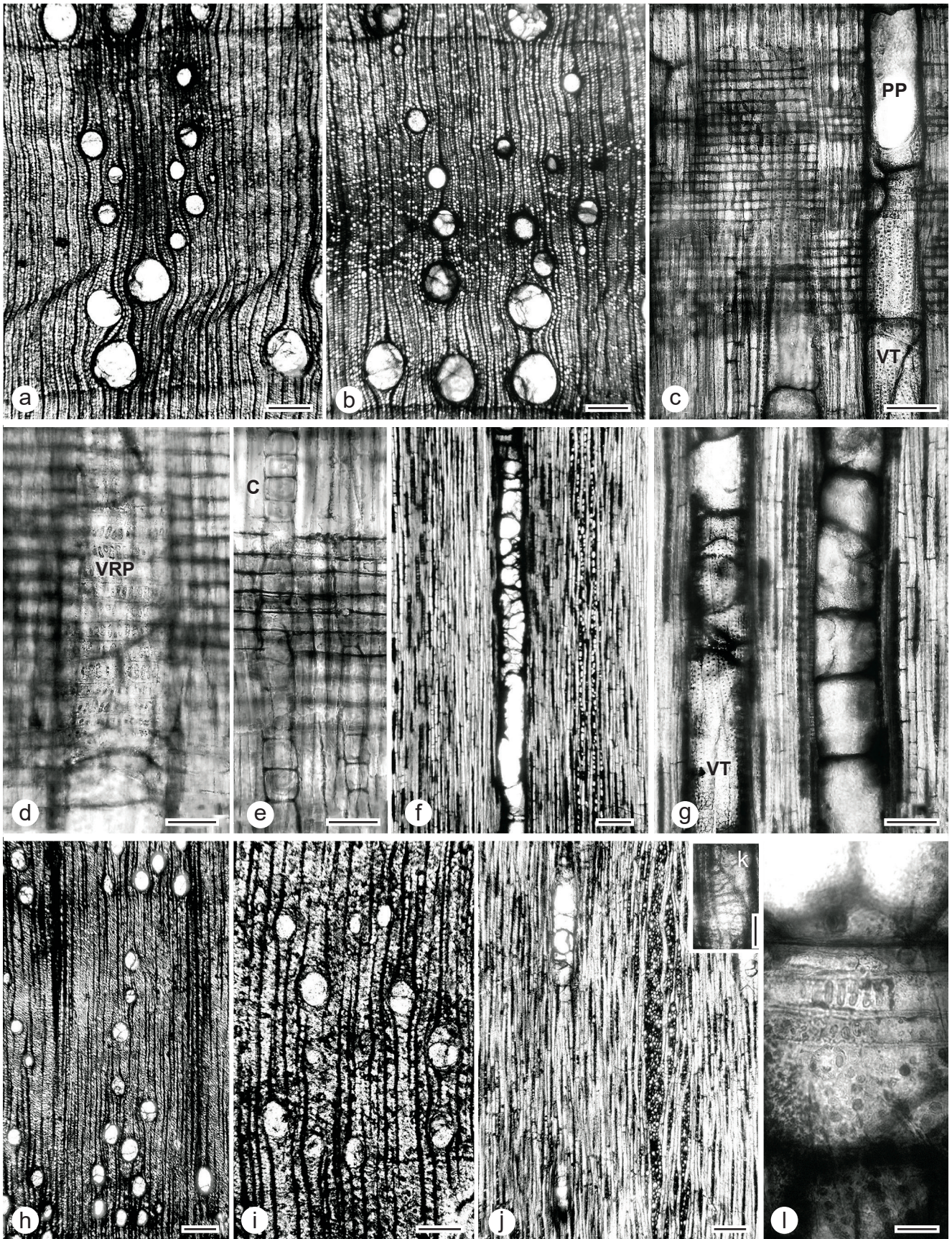
E t y m o l o g y . Named for Melvin Ashwill, who alerted S. R. Manchester to these woods.

D i a g n o s i s . Growth rings distinct. Semi-ring-porous to diffuse-porous. Exclusively solitary vessels in a diagonal to radial arrangement. Simple perforation plates. Vessel-ray parenchyma pits with reduced borders, often vertically elongate. Vasicentric tracheids present. Axial parenchyma diffuse, diffuse-in-aggregates and in uniseriate lines. Non-septate fibers. Uniseriate rays and aggregate rays composed of loosely associated narrow rays.

D e s c r i p t i o n . Minimum estimated diameter of 30 cm.

Growth rings distinct. Semi-ring-porous.

Vessels in diagonal to radial alignment; exclusively solitary, round to oval in outline (Text-fig. 5a, b), mean tangential diameter of the earlywood vessels (first three rows) 208 (28)–215 (39) µm, 160–260 µm. Simple perforation

Text-fig. 5. *Lithocarpoxylon ashwillii* sp. nov., UF 279-24544. a, b: Semi-ring porous wood, exclusively solitary vessels in a radial/ diagonal arrangement, diffuse axial parenchyma, TS. c: Homocellular rays composed of procumbent cells; vasicentric tracheids; vessel elements with simple perforation plates (PP), TLS. d: Vessel-ray parenchyma pits (VRP) with reduced borders, vertical, RLS. e: Crystalliferous axial parenchyma strand (C) with a single crystal per chamber; ray with procumbent cells, RLS. f: Aggregate ray (right) composed of loosely associated 1–2-seriate rays, TLS. g: Uniseriate rays, thin-walled tyloses in vessels, vasicentric tracheids (VT). *Lithocarpoxylon* sp., UF 279-84864. h, i: Semi-ring porous wood, exclusively solitary vessels in radial arrangement. j: Aggregate ray and uniseriate rays. k: Scalariform perforation plate with fewer than 10 bars. l: Vessel-ray parenchyma pits with reduced borders to simple, vertical. Scale bars: 200 µm in a, b, f, h, j; 100 µm in c, i; 50 µm in d. e; 20 µm in k, l.

plates (Text-fig. 5c, d), end walls of vessel elements usually horizontal (Text-fig. 5g). Vessel-ray parenchyma pits with reduced borders and commonly vertically elongated (Text-fig. 5d). Thin-walled tyloses common in wider vessels.

Non-septate fibers of medium wall thickness. Some with small (ca. 3 µm) bordered pits on radial walls. Vasicentric tracheids present (Text-fig. 5c, g).

Axial parenchyma apotracheal diffuse, diffuse-in-aggregates, and in 1-seriate lines (Text-fig. 5a, b), 4–8 cells per strand.

Rays uniseriate (Text-fig. 5f, g), homocellular composed of procumbent cells and heterocellular with some square and upright cells; upright and square cells more common in region of vessels. Some loosely aggregate rays composed of 1–2(–3)-seriate rays (Text-fig. 5f). Rays 2–15–47 cells high; uniseriate rays 12–15–18/mm.

Solitary prismatic crystals occasional in chambered axial parenchyma, 1 crystal per chamber, number of chambers 2–10 (Text-fig. 5e).

C o m p a r i s o n s   w i t h   e x t a n t   w o o d s . The affinities of this wood are clearly with the Fagaceae because of the combination of semi-ring-porosity (4p), exclusively solitary vessels that are in a radial to diagonal arrangement (7p 9p), vertical vessel-ray parenchyma pits with reduced borders (32p), vasicentric tracheids (60p), and aggregate rays (101p).

Aggregate rays are rare in this fossil and comprised of loosely associated narrow ray*s*, similar to rays of *Notholithocarpus densiflorus* (Hook. et Arn.) Manos, Cannon et S.H.Oh (synonym: *Lithocarpus densiflorus* (Hook. et Arn.) Rehder) (BWCw 8593). Images in InsideWood, the on-line FFPRI Database of Japanese Woods (Wood Identification Database Team, FFPRI accessed 2020–2021), and wood anatomical atlases (Ilic 1991, Ogata et al. 2008) indicate that aggregate rays in the evergreen oaks and *Lithocarpus* Blume species are more common and composed of considerably wider individual rays. Two samples of *Castanopsis* (D.Don) Spach (TWTw 22503, TWTw 15003) have aggregate rays composed of 1–3-seriate rays, but they were more closely associated than in this fossil. It is tempting to consider that this fossil might have affinities with *Notholithocarpus* Manos, Cannon et S.H.Oh, a western North America endemic, found to be more closely related to *Castanopsis* than to *Lithocarpus* (Manos et al. 2008). However, we only saw a small sampling of the hundreds of extant species of evergreen oaks, *Castanopsis*, and *Lithocarpus*, so we cannot be certain of that relationship.

C o m p a r i s o n s   w i t h   f o s s i l   w o o d s . In their useful overview of *Quercus* L. and *Quercus*-like fossil woods, Suzuki and Ohba (1991) emended the diagnosis of *Lithocarpoxylon* (Petrescu 1978) and indicated that this name should be applied to fagaceous woods that are diffuse to semi-ring-porous, with radially arranged pores, and aggregate rays. They noted that this combination occurred not only in *Lithocarpus*, but in evergreen species of *Quercus* and tropical species of *Castanopsis*. We are following Suzuki and Ohba's recommendation and assigning this Post Hammer wood to *Lithocarpoxylon*. To the best of our knowledge, no other *Lithocarpoxylon* has aggregate rays composed of such loosely associated 1–2-seriate rays, so we

designate it a new species. Selmeier and Velitzelos (2000) described evergreen oak types; transverse sections of two of their samples (15 and 20) suggest the possibility of similar aggregate rays, but, unfortunately, there were no tangential sections provided for verification.

Lithocarpoxylon sp.
Text-fig. 5h–l

M a t e r i a l . UF 279-84864.

D e s c r i p t i o n . Growth rings indistinct to distinct. Semi-ring-porous to diffuse-porous.

Vessels in radial to slightly diagonal alignment; exclusively solitary, round to oval in outline (Text-fig. 5h, i), mean tangential diameter of the vessels in the first half of the growth ring 122 (22) µm, 67–166 µm. Predominantly simple perforation plates, one scalariform perforation plate with fewer than 10 bars observed (Text-fig. 5k). Vessel-ray parenchyma pits with reduced borders and commonly vertically elongated (Text-fig. 5l). Thin-walled tyloses common.

Axial parenchyma apotracheal diffuse, diffuse-in-aggregates (Text-fig. 5h, i), 4–8 cells per strand.

Vasicentric tracheids present (Text-fig. 5j, l).

Rays uniseriate and aggregate (Text-fig. 5j), homocellular composed of procumbent cells. Aggregate rays composed of 1–8-seriate rays, loosely associated (Text-fig. 5j). Uniseriate rays 3–11–16 cells high; uniseriate rays >12 per mm.

Crystals not observed.

C o m p a r i s o n s   w i t h   e x t a n t   w o o d s . The rationale for assigning this sample to *Lithocarpoxylon* is the same as that for UF 279-24559 described above. This sample differs in having more frequent aggregate rays composed of wider individual rays and narrower vessels.

C o m p a r i s o n s   w i t h   f o s s i l   w o o d s . Most other species of *Lithocarpoxylon*, with the notable exception of *Lithocarpoxylon microporosum* Y.M.Cheng, Y.F.Wang, F.X.Liu, R.C.Mehrotra, X. M.Jiang, C.S.Li et Y.G.Jin from the Pliocene of Yunnan, China (Cheng et al. 2018), have wider vessels than this Post Hammer wood; most also have rays greater than 10 cells wide or compound rays. For now, we are hesitant to assign this wood to a new species based on differences in quantitative features.
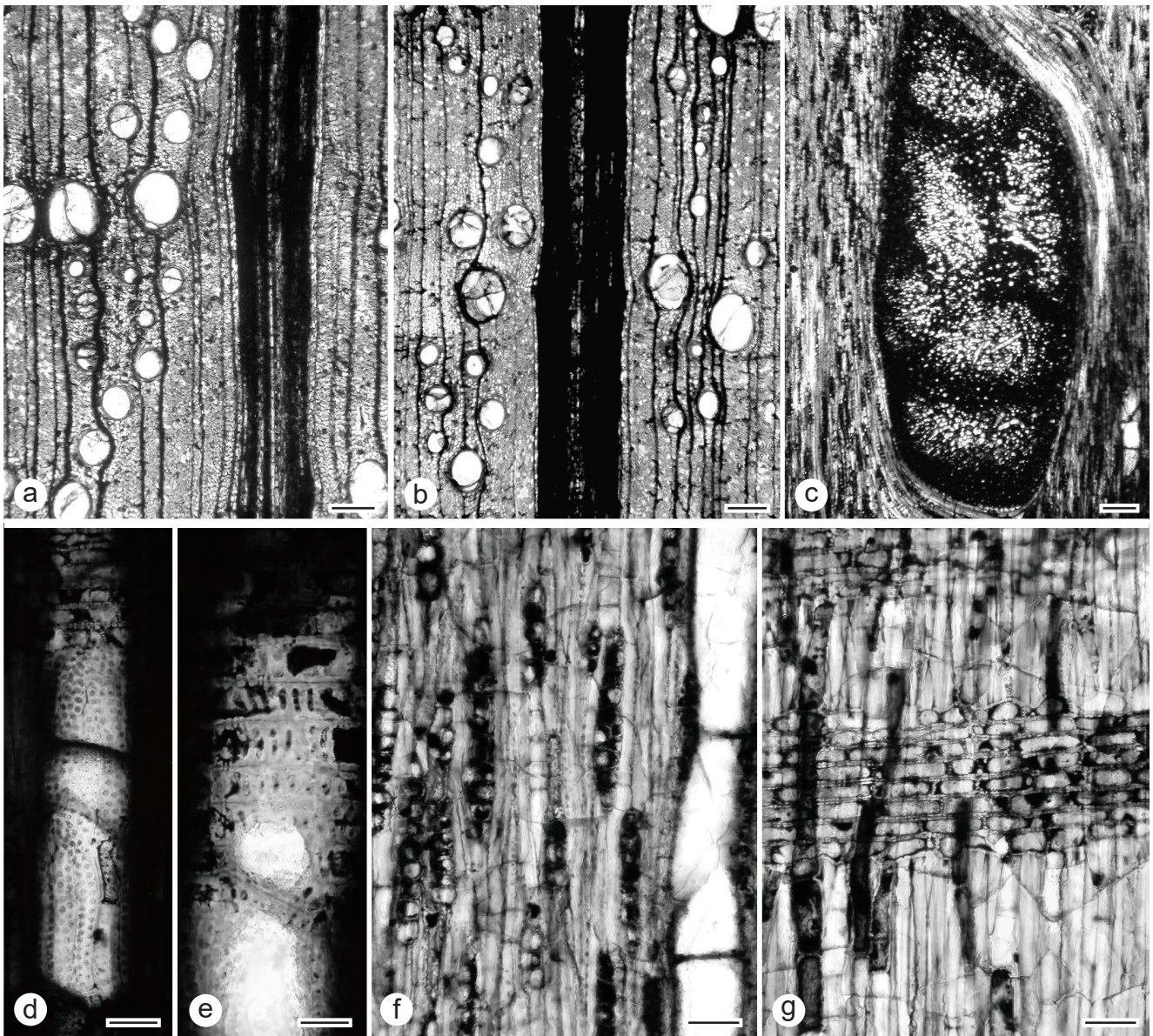
Genus *Quercus* L., 1753

Quercus sp. Red oak group
Text fig. 6a–g

M a t e r i a l . UF 279-24550.

D e s c r i p t i o n . Growth rings distinct. Ring-porous to semi-ring-porous.

Vessels exclusively solitary, latewood vessels in diagonal to radial alignment (Text-fig. 6a, b), round to occasionally oval in outline, mean tangential diameter of earlywood vessels 199 (28), 124–244 µm; perforations simple (Text-fig. 6e); vessel-vasicentric pits alternate, rounded in outline (Text-fig. 6d), ~9–10 µm; vessel-ray parenchyma pits with reduced borders, horizontally to vertically elongate, variable (Text-fig. 6e); vessel element lengths 275–325 µm. Thin-walled tyloses present.

Text-fig. 6. *Quercus* sp. Red Oak, UF 279-24550. a, b: Wood semi-ring-porous to diffuse-porous; vessels exclusively solitary; thin-walled tyloses in wide vessels; diffuse, diffuse-in-aggregates axial parenchyma; rays of two distinct sizes. TS. c: Rays of two distinct sizes, TLS. d: Vessel-vasicentric tracheid pitting, RLS. e: Vessel-ray parenchyma pitting with reduced borders, vertically elongate, RLS. f: Narrow rays 1-2 cells wide, TLS. g: Ray composed of procumbent cells, RLS. Scale bars: 200 μm in a, b, c; 50 μm in d, f, g; 20 μm in e.

Imperforate tracheary elements include vasicentric tracheids (Text-fig. 6d), and non-septate fibers with thick walls.

Axial parenchyma apotracheal, relatively abundant, diffuse, diffuse-in-aggregates, and in 1-seriate lines (Text-fig. 6a, b); strands of 4 cells.

Rays of two distinct sizes (Text-fig. 6a, b, c), uniseriate (rarely with biseriate portions) (Text-fig. 6f) and wide rays 38–62 cells wide, 0.49–1.1 mm; some wide rays with areas of cells of differing wall thicknesses and some with imperforate elements, probably beginning of ray dissection; homocellular, composed of procumbent cells (Text-fig. 6g); uniseriate rays 2–7–15 cells high; numerous 8–12–14 per mm.

Crystals occasional in chambered axial parenchyma strand, usually less than 4-chambers.

Comparisons with extant woods. This wood has features of the Castaneioideae (e.g., Wheeler et al. 2022): vessels exclusively solitary in radial/diagonal, vasicentric tracheids, vessel-ray parenchyma pits with reduced borders, homocellular rays of two distinct sizes, apotracheal parenchyma. Because the latewood vessels are rounded in outline, this wood is assigned to the Red Oak group, *Quercus* sect. *Lobatae* LOUDON; latewood vessels in the White Oak group are angular in outline (e.g., Brazier and Franklin 1961, Panshin and DeZeeuw 1980). Distinguishing species in the Red Oak Group based on wood anatomy is not feasible, so we are only designating it as *Quercus* sp. Red Oak Group.

Comparisons with other fossil woods. This ring-porous to semi-ring-porous wood differs from the Nut Beds *Quercinium crystallifera* R.A.SCOTT et

E.A.Wheeler, which is diffuse to semi-ring-porous. Other differences are that UF 279-24550 has exceptionally wide rays, its rays are not typically aggregate, and crystals are not common. Reports of fossil oak woods are quite common in the literature, with different species reflecting differences in age and locality as much as differences in anatomy (e.g., Müller-Stoll and Mädel 1957, Suzuki and Ohba 1991).

C o - o c c u r r i n g   f r u i t s . Manchester and McIntosh (2007) illustrated an oblate nut covered in whorls of scales and preserved as a silica cast lacking internal anatomy from locality UF 279 (figs 37–39) that was interpreted as representing an acorn of *Quercus* with the nut fully enclosed by the cupule.

Family Hamamelidaceae R. Br., 1818 nom. cons.

Genus *Hamamelidoxylon* Lign., 1907

Hamamelidoxylon crystalliferum sp. nov.
Text-fig. 7a–i

H o l o t y p e . Designated here. UF 279-34464 (Text-fig. 7a–i). Minimum estimated axis diameter 15 cm.

P a r a t y p e . UF 279-24555 (minimum estimated diameter 30 cm).

P l a n t   F o s s i l   N a m e s   R e g i s t r y   N u m b e r . PFN002681 (for new species).

R e p o s i t o r y . Paleobotany Collections, Florida Museum of Natural History, Gainesville, Florida, USA.

T y p e   l o c a l i t y . UF 279. About 3 km east of Post, Crook County, Oregon, USA.

T y p e   s t r a t u m   a n d   a g e . John Day Formation, Eocene.

E t y m o l o g y . Named for crystals in this wood.

D i a g n o s i s . Growth rings distinct to indistinct. Wood diffuse-porous. Vessels predominantly solitary, narrow, and numerous. Perforation plates exclusively scalariform, fewer than 20 bars per perforation plate. Intervessel pitting scalariform. Vessel-ray parenchyma pits with reduced borders and horizontally elongate. Fibers non-septate, with bordered pits on radial walls. Axial parenchyma rare. Heterocellular rays, 1–2 cells wide. Solitary prismatic crystals in chambered and non-chambered square to upright ray cells, crystal-containing cells somewhat inflated.

D e s c r i p t i o n . Growth rings boundaries distinct to indistinct, marked by a few rows of radially narrow fibers, with latest latewood vessels narrower than the first earlywood vessels (Text-fig. 7a, b). Wood diffuse-porous.

Vessels predominantly solitary, angular in outline (Text-fig. 7a, b), mean tangential diameter 43 (8)–47(6); 104–149 mm^2; perforations all scalariform, 11–15 bars (Text-fig. 7e); intervessel pits scalariform (Text-fig. 7c); vessel-ray parenchyma pits horizontally elongated (Text-fig. 7f), vessel element lengths 690–950 μm.

Fibers non-septate, medium-thick to thick walled; distinctly bordered pits on radial walls and tangential walls (Text-fig. 7c, f).

Axial parenchyma rare.

Rays 1–2(–3)-seriate, heterocellular, uniseriate and biseriate portions occasionally alternating, but not commonly (Text-fig. 7f, g); width of uniseriate portions usually not the same as the biseriate portions; uniseriate rays composed of upright cells, biseriate portions of rays composed of procumbent cells, with uniseriate portions of 1–4 (or more) rows of upright cells, upright cells at least 4× higher than the procumbent cells (Text-fig. 7h).
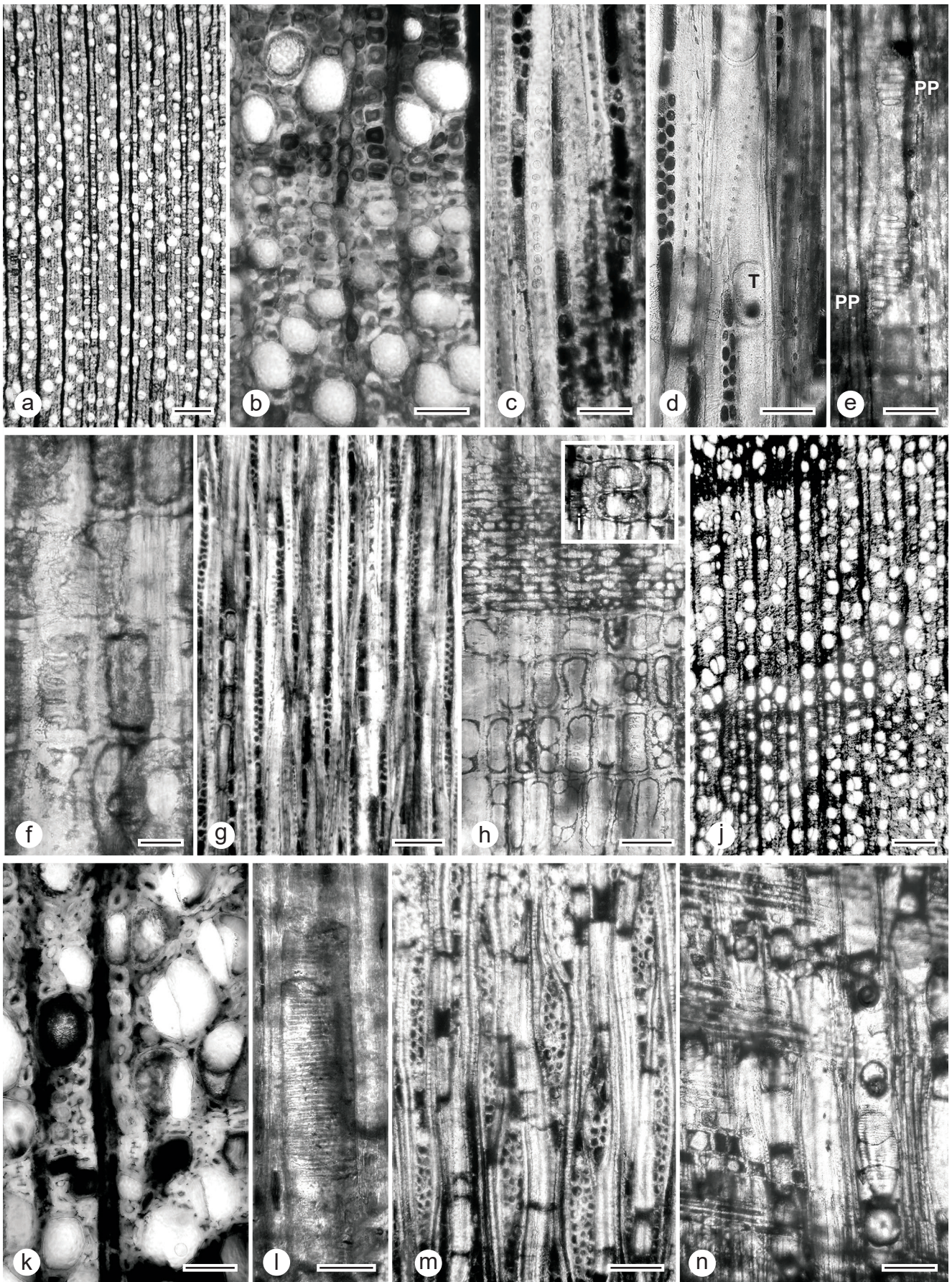
Solitary crystals occasional in chambered (2–3) upright ray cells, crystalliferous cells usually inflated (Text-fig. 7i).

C o m p a r i s o n s   w i t h   e x t a n t   w o o d s . In InsideWood, the combination of diffuse-porous woods (5p), narrow, numerous vessels (42a 43a 47a 48a) that are predominantly solitary (9p), exclusively scalariform perforation plates (13a 14p), scalariform intervessel pits (20p), vessel-ray parenchyma pits horizontally elongate with reduced borders (32p), axial parenchyma rare (75p), fibers with distinctly bordered pits (62p), heterocellular 1–2-seriate rays (97p 104a 105a), and crystals in chambered upright ray cells (140p) is unique to the Hamamelidaceae, occurring in *Corylopsis*, *Eustigma* Gardner et Champ., *Sinowilsonia* Hemsl. (subfamily Hamamelidoidieae), and *Mytilaria* Lecomte (subfamily Mytilariodeae). Of these, *Sinowilsonia* is the most similar because of its lower number of bars per perforation plate (<20) compared to the three other genera.

The anatomy of extant Hamamelidaceae has been reviewed by Tang (1943), Skvortsova (1975), and Wheeler et al. (2010). The growth ring boundaries resemble those seen in evergreen Asian species of the family (e.g., *Chunia* H.T.Chang, *Exbucklandia* R.W.Br.) more than those of deciduous species.

C o m p a r i s o n s   w i t h   f o s s i l   w o o d s . Lignier's (1907) diagnosis of the genus *Hamamelidoxylon* includes these features: rays numerous, rays uniseriate, rarely biseriate, vessels predominantly solitary, scalariform perforation plates, axial parenchyma rare. His plate XX (line drawings of *H. renaulti* Lign.) shows a perforation plate with over 25 bars, horizontally elongate vessel-ray parenchyma pitting, ray cell walls with abundant pitting as seen in radial sections, and thick-walled fibers. Subsequently, woods with rays 1–2(–3) cells wide were assigned to the genus, e.g., the European species: *H. castellanense* Grambast-Fessard (Grambast-Fessard 1969), *H. daphniphylloides* H.Gottwald (Gottwald 1992), and *H. rhenamum* Burgh (van der Burgh 1973). The genus has been used for woods that have characteristics of the family, but not necessarily of the genus *Hamamelis* L.

Three species of *Hamamelidoxylon* have been described from the Pacific Northwest of North America: *H. uniseriatum* E.A.Wheeler et Manchester from the middle Eocene Clarno Formation (Wheeler and Manchester 2002, 2014) whose characteristics best fit the Tribe Exbucklandiodeae, and *H. beckii* E.A.Wheeler et T.A.Dillhoff and *H. suzukii* E.A.Wheeler et T.A.Dillhoff from the middle Miocene Vantage Forests, Washington (Wheeler and Dillhoff 2009). Table 2 compares *H. crystalliferum* to them and to the European and Asian *Hamamelidoxylon* species that have reasonably complete descriptions. The data in the table show that *H. crystalliferum*'s combination of 15 or fewer bars per perforation plate, rays 1–2(–3) cells wide, and crystals in

Text-fig. 7. *Hamamelidoxylon crystalliferum* sp. nov., UF 279-34464. a: Diffuse porous wood with exclusively solitary vessels, tending to be angular in outline, TS. b: Growth ring boundary, marked by radially narrowed fibers, latewood vessels narrower than earlywood vessels of the next ring, fibers thick-walled, no axial parenchyma visible, TS. c: Scalariform intervessel pits in narrow vessel (left), fibers with distinctly bordered pits, TLS. d: Scalariform perforation plate, tyloses (T) formation from marginal ray cell, TLS. e: Scalariform perforation plates with fewer than 15 bars (PP), RLS. f: Vessel-ray parenchyma pits with

Table 2. Comparison of *Hamamelidoxylon* species. Arranged by age, oldest to youngest. GR = Growth ring boundaries, I = indistinct, D = distinct; VTD = vessel tangential diameter in μm, standard deviation in parentheses when known; V/mm² = vessels per mm²; Bars/PP = number of bars per perforation plate; RW = ray width in cell number; Cry = crystals, Rch = crystals in chambered square / upright cells, I = crystalliferous cells inflated; K = Cretaceous, Pal = Paleocene, Eo = Eocene, Mio = Miocene, e = early, m = middle, l = late; OR = Oregon, WA = Washington.

Taxon (Reference)	GR	VTD (μm)	V/mm2	Bars/PP	RW	Cry	Age	Locality
Hamamelidoxylon crystalliferum sp. nov. (UF 279-24555) (this paper)	D / I	47 (6)	122–149	11–15	1–3	Rch, I	l Eo	OR, USA
Hamamelidoxylon crystalliferum sp. nov. (UF 279-34464) (this paper)	D / I	43 (8)	104–131	11–15	1–2(–3)	Rch, I	l Eo	OR, USA
Hamamelidoxylon cf. *suzukii* (UF 279-34465) (this paper)	D	58 (11)	85–117	18–32	1–2(–3)	R	l Eo	OR, USA
H. obiraense (1)	D	52	83–120	22–56	1(–2)	no	l K	Japan
H. uniseriatum (2)	D	58 (13)	72–133	24–40	1(–2)	no	m Eo	OR, USA
cf. *H. uniseriatum* (3)	D	55 (11)	50–82	20–36	1	no	m Eo	OR, USA
H. daphniphylloides (4)	D	45	?	30–58	1–2(–3)	no	Eo	Germany
H. renaultii (5, 6)	D	36	119–200	32	1(–2)	no	Mio, Pal/Eo	France, UK
H. beckii (7)	D / I	54 (7)	77–94	14–24	1(–2)	R	m Mio	WA, USA
H. suzukii (7)	D	53 (7)	60–86	16–27	1–2	R	m Mio	WA, USA
H. rhenanum (8)	I	30–50 μm	?	20–25	1–2(–3)	no	Mio	Germany
H. castellanense (9)	I	40–60	80–100	ca. 16–20	1–2(–3)	Rch, I	Mio	France

1. Takahashi and Suzuki (2003), 2. Wheeler and Manchester (2002), 3. Wheeler and Manchester (2007), 4. Gottwald (1992), 5. Lignier (1907), 6. Crawley (2001), 7. Wheeler and Dillhoff (2009), 8. van der Burgh (1973), 9. Grambast–Fessard (1969)

chambered upright ray cells does not match any of the other species and indicates it is appropriate to create a new species.

Liquidambaroxylon and all Altingiaceae never possess crystals in chambered upright ray cells.

C o - o c c u r r i n g f r u i t s / s e e d s. The fossil genus *Fortunearites* MANCHESTER, known from infructescence in the middle Eocene Clarno Nut Beds, Oregon, has a combination of characters found only in *Fortunearia* and *Sinowilsonia* (Manchester 1994, Manchester et al. 2009). It is possible that these two late Eocene wood samples might be related to the plant that produced *Fortunearites*. However, present-day *Fortunearia* wood has banded axial parenchyma, so is distinct from *Sinowilsonia* and these Post Hammer woods.

Hamamelidoxylon cf. *suzukii* E.A.WHEELER et T.A.DILLHOFF, 2009
Text-fig. 7j–n

M a t e r i a l. UF 279-34465. Minimum estimated axis diameter 30 cm.

D e s c r i p t i o n. Growth rings boundaries distinct, marked by a few rows of radially narrow fibers, with latest latewood vessels narrower than the first earlywood vessels (Text-fig. 7j, k). Wood diffuse-porous.

Vessels predominantly solitary, angular in outline (Text-fig. 7j, k), mean tangential diameter 58 (11), range 45–90 μm; 85–117/mm²; perforations all scalariform, 18–41 bars (Text-fig. 7l); vessel element lengths average 997 (146) μm.

Fibers non-septate, thick walled; distinctly bordered pits on radial walls and tangential walls (Text-fig. 7k, m, n).

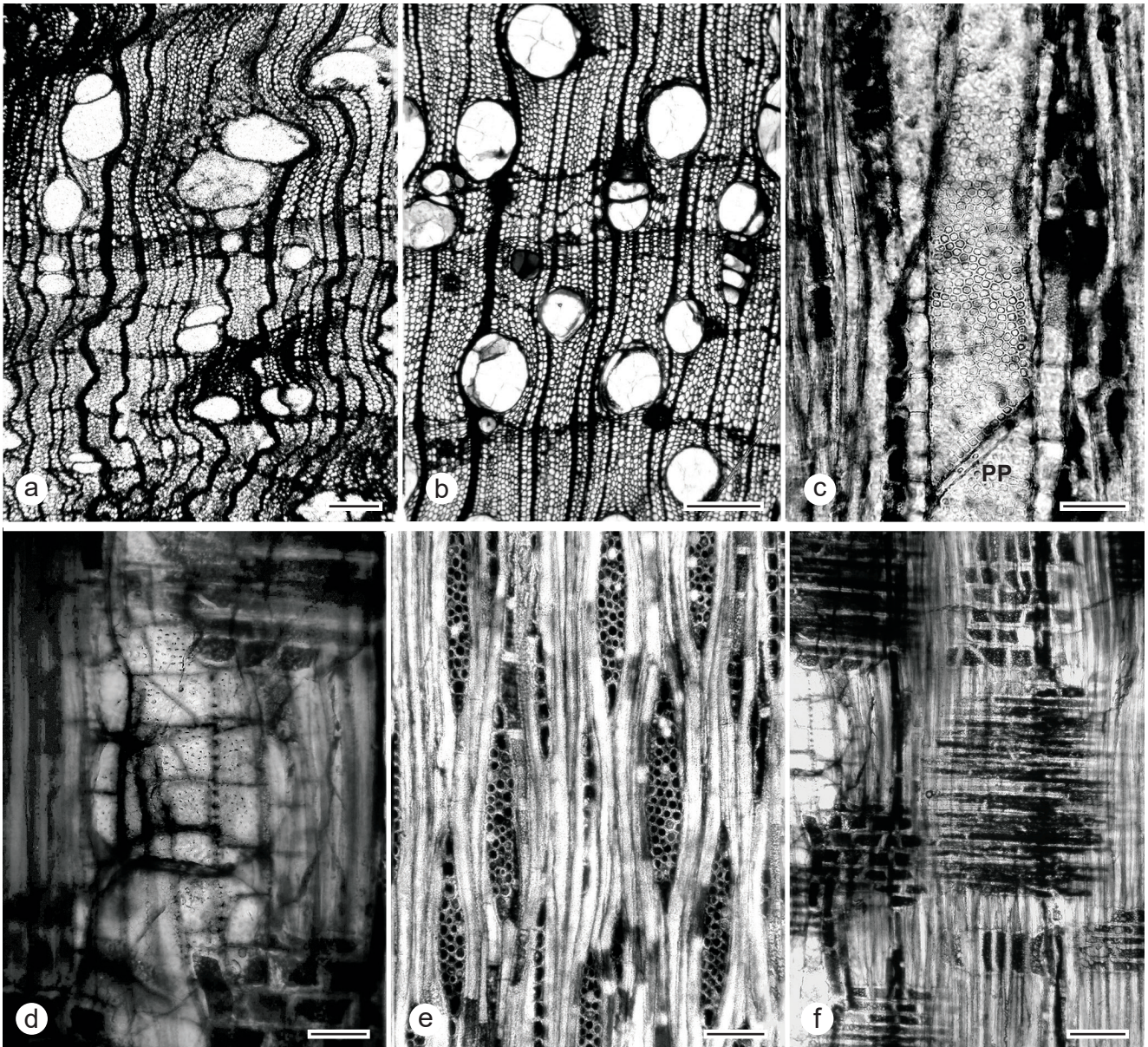Axial parenchyma rare, diffuse (Text-fig. 7k).

Rays 1–2(–3)-seriate (Text-fig. 7m), heterocellular (Text-fig. 7m); ray body composed of procumbent cells, with marginal rows of square cells, (Text-fig. 7n).

Solitary crystals occasional in upright/square ray cells (Text-fig. 7n).

C o m p a r i s o n s w i t h e x t a n t w o o d s. The combination of features used to search InsideWood for this sample's affinities was similar to that used for the sample designated *Hamamelidoxylon crystalliferum*, except that we used crystals in upright/square ray parenchyma cells (137p) as a search criterion, not crystals in chambered upright ray parenchyma cells (140p). Results of this search returned Hamamelidaceae (*Corylopsis*, *Mytilaria*, *Sinowilsonia*), Altingiaceae (*Liquidambar*), and *Cercidiphyllum*. As we did for *Cercidiphyllum*, we used the work of Sakala and Privé-Gill (2004) on distinguishing between these families, and, in this case, conclude that this wood has affinities with the Hamamelidaceae.

C o m p a r i s o n s w i t h f o s s i l w o o d s. Table 2 compares features of the *Hamamelidoxylon* species with relatively complete descriptions. Although there are differences in quantitative features (higher vessel frequency, rays more frequently 3-seriate), we suggest this late Eocene wood is similar to *Hamamelidoxylon suzukii* (Wheeler and Dillhoff 2009) from the middle Miocene, Ginkgo Petrified Forest State Park, Washington, USA.

reduced borders and horizontally elongate, RLS. g: Rays 1–2-seriate, TLS. h: Upright cells approximately 4× higher than procumbent cells, RLS. i: Inflated chambered crystalliferous ray cell, RLS. *Hamamelidoxylon* cf. *suzukii*, UF 279-34465. j, k: Diffuse-porous wood with exclusively solitary vessels, angular in outline, thick-walled fibers, axial parenchyma not common, apotracheal diffuse, TS. l: Scalariform perforation plate with >20 bars, RLS. m: Rays mostly 2–3-seriate, TLS. n: Rays with procumbent body cells and square marginal cells. Scale bars: 200 μm in a, j; 100 μm in g, m, n; 50 μm in b, c, d, e, g, h, I, k, l; 20 μm in f.

Text-fig. 8. *Pterocaryoxylon* sp., a–c, e: UF 279-85024; d, f: UF 279-24551. a, b: Wood semi-ring-porous, vessels solitary and in short radial multiples, axial parenchyma scanty vasicentric, marginal, and in narrow lines, TS. c: Crowded alternate intervessel pitting, simple perforation plate (PP), TLS. d: Vessel-axial parenchyma pitting similar to intervessel pitting, RLS. e: Rays mostly 1–3 cells wide, occasionally 4 cells, uniseriate rays probably mostly square to upright cells, TLS. f: Rays heterocellular, body cells procumbent. Scale bars: 200 μm in a, b; 100 μm in e, f; 50 μm in c; 20 μm in d.

Family Juglandaceae DC. ex PERLEB, 1818 nom. cons.

Genus *Pterocaryoxylon* sensu Müller-Stoll and Mädel (1960)

***Pterocaryoxylon* sp.**
Text-fig. 8a–f

Material. UF 279-24551 (minimum estimated diameter 11.8 cm), UF 279-24557 (minimum estimated diameter 13 cm), UF 279-85024.

Description. Growth rings present, marked by radially flattened fibers and differences in latewood and earlywood vessel diameters of successive growth rings (Text-fig. 8a, b). Semi-ring-porous.

Vessels solitary and in radial multiples of 2, average tangential diameter of earlywood 206 (28) μm, range

124–294 μm; perforations simple, intervessel pits alternate (Text-fig. 8c), ca. 7 μm; vessel-parenchyma pits similar to intervessel pits (Text-fig. 8d); vessel element lengths averages 460 (73)–486 (88) μm; thin-walled tyloses occasional.

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

Axial parenchyma scanty paratracheal to vasicentric, marginal, and in tangential bands one to two cells wide throughout the growth ring, lines more closely spaced in the latewood than in the earlywood (Text-fig. 8a, b); strands usually of eight cells.

Rays 1–3(4)-seriate (Text-fig. 8e). Multiseriate rays heterocellular, with procumbent body cells and usually with 1–2 marginal rows of square to upright cells; uniseriate rays composed of mostly upright cells (Text-fig. 8f), total multiseriate ray height averages 382 (91) μm, range 225–625 μm. 10–12/mm.

Table 3. Comparison of *Pterocaryoxylon knowltonii* and UF 279 *Pterocaryoxylon* sp. EW VTD = earlywood vessel tangential diameter in µm; LW = latewood; IV = intervessel; VE = vessel element length.

Feature	*Pterocaryoxylon knowltonii*	UF 279 *Pterocaryoxylon* sp.
EW VTD (µm)	160-215-310	124-206-294
LW vessel arrangement	Diagonal	Tending to diagonal
IV pit size (µm)	10–12	ca. 7
VE length (µm)	460–850 (range)	460 (73) – 486 (88)
Ray width (cell number)	1–3	1–3(–4)
Ray height (µm)	155–315 (range)	222-382-625

Crystals not observed. Storied structure absent.

R e m a r k s . These juglandaceous woods were compressed and contorted, especially their earlywood. For measuring vessel diameters, we selected vessels that were oval to circular in outline and that we considered to be close to their original outline in the living tree.

C o m p a r i s o n s   w i t h   e x t a n t   w o o d s . Affinities with Juglandaceae are indicated by the combination of semi-ring-porosity, vessels solitary and in short radial multiples, narrow continuous lines of axial parenchyma, medium-sized alternate intervessel pits, vessel-ray parenchyma pits similar in size to intervessel pits. Because these woods have exclusively simple perforations and lack crystals, they are most similar to *Pterocarya* KUNTH and the butternut group of *Juglans* L. (Asian species of Section *Cardiocaryon*, and the American *J. cinerea* L., traditionally placed in section *Trachycaryon*). Phylogenetic analyses confirm a close relationship between *Pterocarya* and *Juglans* (Stanford et al. 2000, Manos et al. 2007). Sometimes *Pterocarya* woods can be distinguished from the butternuts because latewood vessels in *Pterocarya* can be in a pronounced diagonal pattern (Müller-Stoll and Mädel 1960, Miller 1976, Wheeler et al. 1978). A difference between these Post Hammer woods and woods of extant *Pterocarya* and the *Juglans* butternut group is that rays in the recent woods typically are homocellular with all procumbent cells. However, some extant juglandaceous species have heterocellular rays (e.g., *Juglans californica* S.WATSON of section *Rhysocaryon*, BWCw 8695).

C o m p a r i s o n s   w i t h   f o s s i l   w o o d s . Because of the similarity of woods of *Pterocarya* and the butternut group of *Juglans*, Müller-Stoll and Mädel (1960) created the genus *Pterocaryoxylon*. One species is known from North America; *Pterocaryoxylon knowltonii* E.A.WHEELER, R.A.SCOTT et BARGH. (Wheeler et al. 1978) from the early middle Eocene of Yellowstone National Park, Wyoming. Table 3 compares this older species to the Post Hammer *Pterocaryoxylon* and shows the latter differ in having smaller intervessel pits and taller rays. Growth rings of the Post *Pterocaryoxylon* are narrower than those of the Yellowstone wood. When growth rings are narrow, latewood vessel arrangement patterns may not be obvious (IAWA Committee 1989). It is possible that if this Post wood had wider growth rings, a diagonal latewood vessel arrangement would have been observed. We are hesitant to create a new species based on differences in quantitative features and are choosing to refer to these Post Hammer woods as *Pterocaryoxylon* sp. The Yellowstone *Pterocaryoxylon* also has heterocellular rays. These western North America *Pterocaryoxylon* are the oldest known species of the genus. *Pterocaryoxylon* and *Pterocarya* have been reported from the Miocene-Pliocene of central and eastern Asia (e.g., Rajput and Khan 1982, Choi et al. 2010, Cheng et al. 2018), and Europe (e.g., Müller-Stoll and Mädel 1960, Privé 1974, Dupéron 1988). Müller-Stoll and Mädel (1960) cited another character of the type species of *Pterocaryoxylon*, not strictly a wood character, but useful to confirm affinity with the *Pterocarya-Juglans-Cyclocarya* group and distinguishing it from all other extant genera of the Juglandaceae: septate pith. The center of the stem is not known for these Eocene species.

The two juglandaceous woods of the nearby older middle Eocene Nut Beds, Oregon, differ: *Clarnoxylon blanchardii* MANCHESTER et E.A.WHEELER (which has solid pith rather than septate) has prismatic crystals commonly occurring in enlarged ray parenchyma cells; *Engelhardioxylon nutbedensis* MANCHESTER has both simple and scalariform perforation plates and prismatic crystals in ray parenchyma (Wheeler and Manchester 2002).

C o - o c c u r r i n g   f r u i t s / s e e d s . The bi-winged fruits of *Pterocarya* have not been confirmed prior to the Oligocene. However, the extinct 4-winged genus *Cruciptera* known from the middle to late Eocene of Oregon (Manchester 1991), the early middle Eocene of Yellowstone (pers. obs.), and middle Eocene of Germany (Manchester et al. 1994), seems to have been rather common. We speculate that *Cruciptera* may have been produced on trees with wood similar to that of *Pterocarya*, and it may have corresponded to *Pterocaryoxylon*.

Family Malvaceae JUSS., 1789 nom. cons.

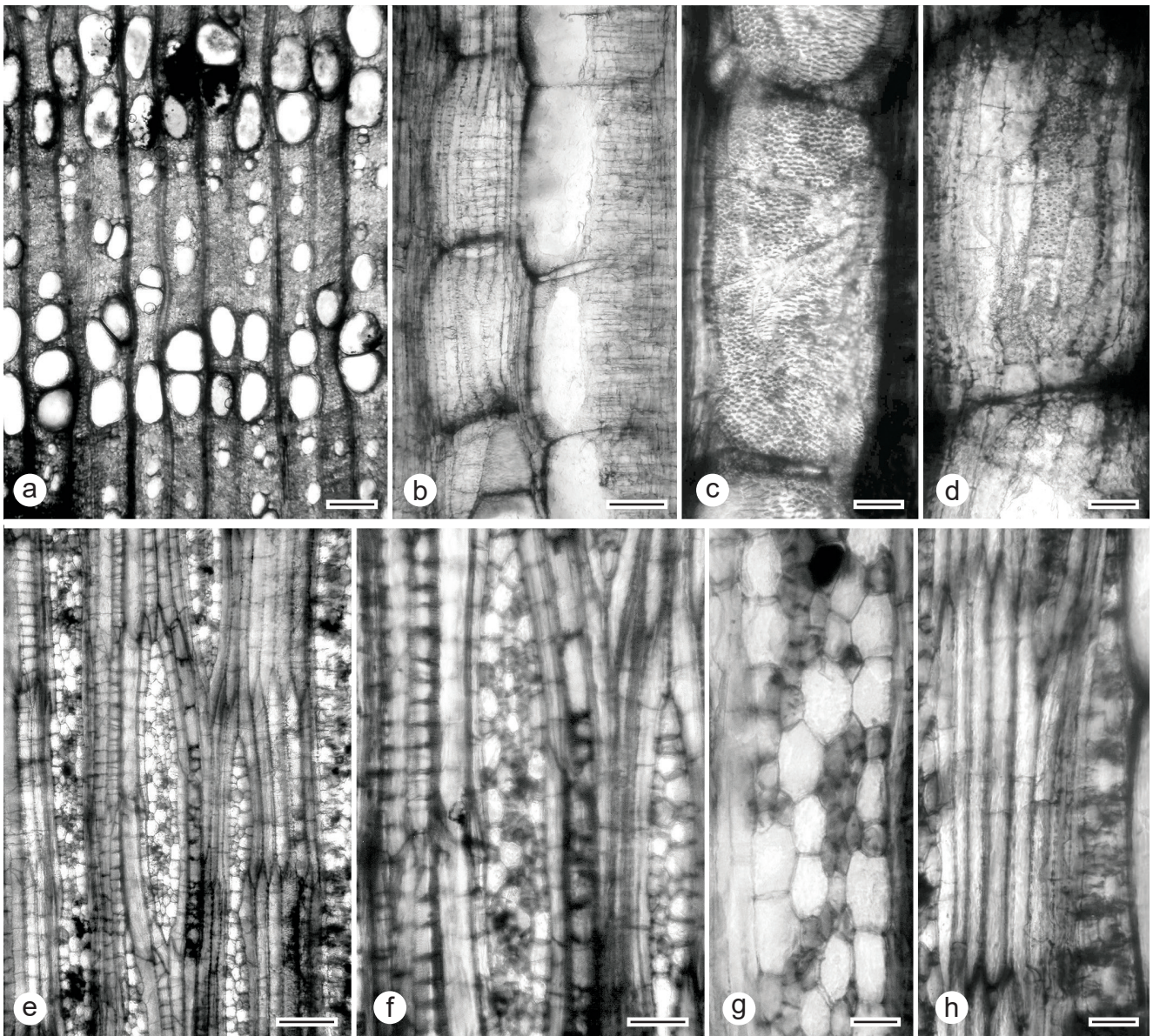**Genus *Wataria* K.TERADA et MITS.SUZUKI, 1998**

***Wataria kvacekii* sp. nov.**
Text-fig. 9a–h

H o l o t y p e . Here designated. UF 279-24546 (Text-fig. 9a–h).

P l a n t   F o s s i l   N a m e s   R e g i s t r y   N u m b e r . PFN002682 (for new species).

R e p o s i t o r y . Paleobotany Collections, Florida Museum of Natural History, Gainesville, Florida, USA.

E t y m o l o g y . Species name to honor Zlatko Kvaček, a kind man, who was and will continue to be an inspiration for those who study Tertiary floras.

T y p e   l o c a l i t y . UF 279. About 3 km east of Post, Crook County, Oregon, USA.

Text-fig. 9. *Wataria kvacekii* sp. nov., UF 279-24556. **a:** Wood ring-porous, earlywood with 2–3 rows of wide pores, vessels solitary and in radial multiples of 2, axial parenchyma scanty vasicentric and some apotracheal diffuse-in-aggregates, TS. **b:** Series of vessel elements with simple perforations, axial parenchyma strands adjacent to vessels, RLS. **c:** Alternate intervessel pitting, vessel element end walls horizontal, RLS. **d:** Vessel-axial parenchyma pitting similar to intervessel pitting, RLS. **e, f:** Rays with tile cells, storied axial parenchyma, some strands chambered crystalliferous, TLS. **g:** Detail of ray, TLS. **h:** Storied imperforate elements. Scale bars: 200 μm in a; 100 μm in b, e; 50 μm in c, d, f, h; 20 μm in g.

Type stratum and age. John Day Formation, Eocene.

Diagnosis. Wood ring-porous. Earlywood zone with more than 1 row of earlywood vessels. Vessels solitary and in short radial multiples. Perforation plates exclusively simple. Intervessel pits alternate, small; vessel-ray parenchyma pits similar to intervessel pits. Vessel elements and imperforate elements regularly or irregularly storied. Axial parenchyma scanty paratracheal to vasicentric and diffuse-in-aggregates. Rays typically less than 10-seriate; heterocellular; commonly >1 mm high. Tile cells present, *Pterospermum*-type.

Description. Growth rings present, marked by radially flattened fibers, and differences in diameters of latewood and earlywood vessels of subsequent rings (Text-

fig. 9a). Wood distinctly ring-porous, earlywood pore zone usually 3 vessels deep.

Vessels predominantly solitary and in occasional radial multiples of 2 in both earlywood and latewood (Text-fig. 9a); average tangential diameter of earlywood vessels 143 (33) μm; perforations simple (Text-fig. 9b); intervessel pits alternate (Text-fig. 9c), 3–5 μm in horizontal diameter; vessel-parenchyma pits similar to intervessel pits (Text-fig. 9d); vessel element length averages 346 (26), range 310–410 μm; widely spaced thin-walled tyloses present; helical thickenings not observed.

Fibers thin to medium-thick-walled, storied, without distinctly bordered pits; non-septate, tending to be storied structure (Text-fig. 9e, h).

Axial parenchyma scanty paratracheal to vasicentric, (diffuse-) diffuse-in-aggregates, strands of 4–8 (Text-

Table 4. Comparison of *Wataria* species and *Triplochitioxylon*. EW VTD = earlywood vessel tangential diameter in µm; EW row = number of rows of wide earlywood vessels; IVP = horizontal diameter of intervessel pits in µm; VEL = vessel element lengths in µm; RW = width in cell number; R Ht = ray height in µm; Cry = Crystal location, APc = chambered axial parenchyma, R = ray parenchyma; Eo = Eocene, Ol = Oligocene, Mio = Miocene, e = early, m = middle, l = late; OR = Oregon.

Taxon (Reference)	EW VTD	EW row	IVP	VEL (µm)	RW	R Ht (µm)	Cry	Age, Country
Wataria kvacekii sp. nov. (this paper)	143	(1–)2–3	3–5	310-346-410	1–6	320-1075-2600	APc	l Eo, OR, USA
Wataria miocenica (1, 2)	257–294	(1–)2–3	2–4	70-234-350	1–10(–12)	621, 870, 1280*	APc, R	Mio, Japan
Wataria miocenica (3)	252	1–3	?	200-257-345	est. to 8	140-985-1900	R	Mio, Korea
Wataria oligocenica (2)	210	3–5	ca. 3	75-219-325	1–10+	200-688-1000	APc	Ol, Japan
Wataria parvipora (2)	150–181	1–2(–3)	ca. 5	65-185-290	(1–)3–5(–7)	550-803-1200	R	e Mio, Japan
Wataria parvipora (3)	181	1–2(–3)	?	125-178-250	1–7	120-558-900	R	e Mio, Korea
Wataria yunnanica (4)	270	1 (–2–3)	ca. 3	144-280-569	1–12	193-873-2037	APc, R	m Mio, China
Triplochitioxylon oregonense (5)	185	n/a	3–5	400-440-600	(1–)4–6(–10)	?-1267-2100	R	m Eo, OR, USA

1. Watari (1952), 2. Terada and Suzuki (1998), 3. Jeong et al. (2003), 4. Li et al. (2015), 5. Manchester (1979)

* mean ray heights

fig. 9a, b), also chambered with solitary prismatic crystals (Text-fig. 9e, f). Rays 1–6-seriate (Text-fig. 9e).

Multiseriate rays heterocellular with uniseriate rows of 1–3 cells; *Pterospermum*-type tile cells present; (Text-fig. 9f, g) some rays the same height as the vessel elements and axial parenchyma strands, most rays extending over multiple tiers of the storied parenchyma. Total multiseriate ray height averages 1,075 (634) µm, 320–2,600 µm. 5–8 mm.

Axial parenchyma and vessel elements storied (Text-fig. 9e).

C o m p a r i s o n s   w i t h   e x t a n t   w o o d s . Tile cells are unique to the Malvales. A search of the InsideWood database for the combination of tile cells (111p) and ring-porosity (3p) only returned species of the present-day genera *Grewia* L. (Malvaceae/Grewioideae) and *Reevesia* Lindl. (Malvaceae/Helicteroideae), and the fossil wood genus *Wataria* from the Oligocene – Miocene of Asia, whose species were originally assigned to *Reevesia* (Terada and Suzuki 1998).
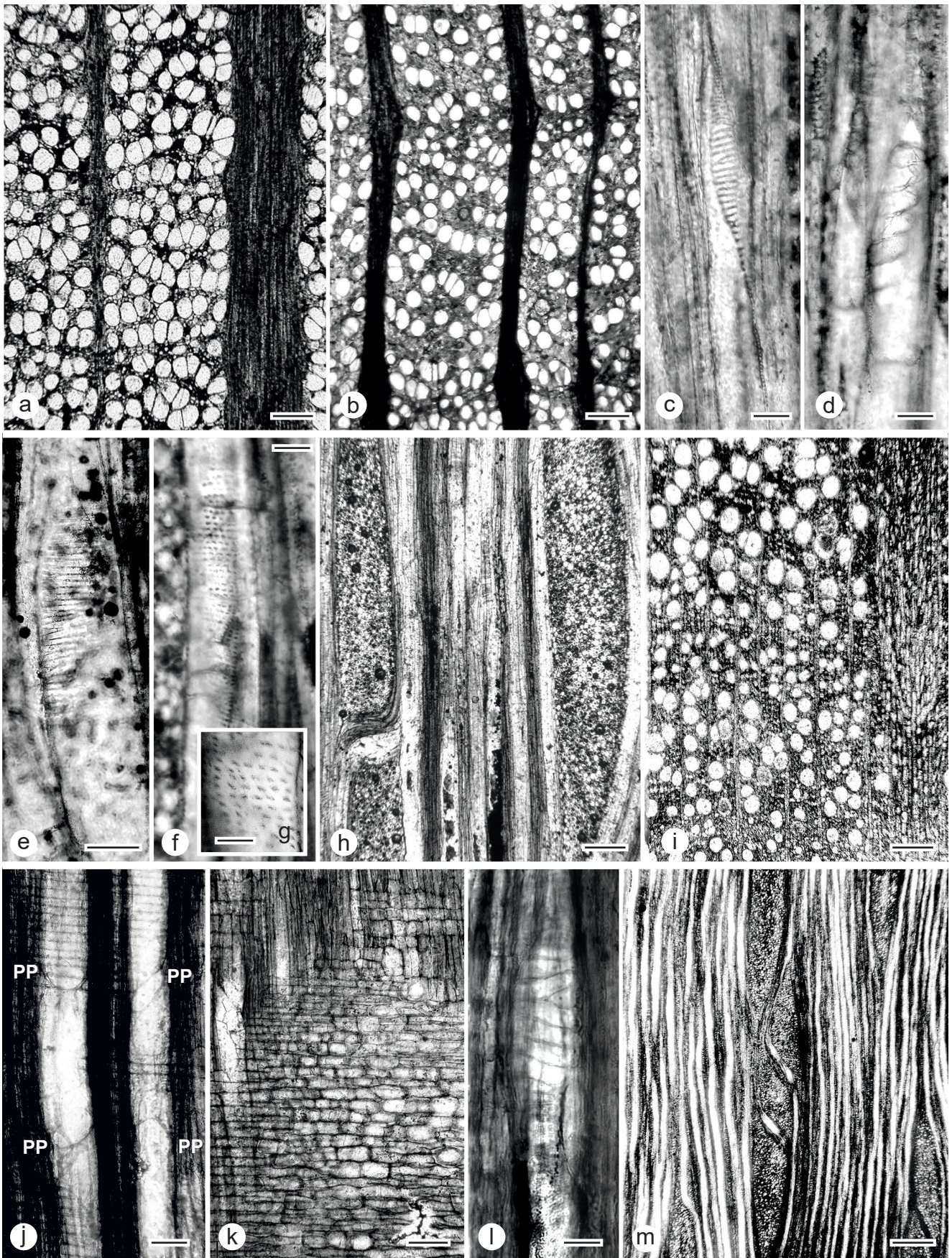
Ring-porous species of *Grewia* and *Reevesia* differ from *Wataria kvacekii* because their latewood vessels are in clusters.

C o m p a r i s o n s   w i t h   f o s s i l   w o o d s . Rodríguez-Reyes et al. (2014) reviewed the characteristics of fossil malvaceous woods and noted only two genera with distinctly ring-porous species: *Reevesia* and *Wataria*. Selmeier (2000b) described semi-ring-porous *Grewioxylon* with a transition from earlywood to latewood that is gradual. This Post Hammer wood generally conforms to the genus *Wataria* K.Terada et Mits.Suzuki (Terada and Suzuki 1998), diagnosed as having distinctly ring-porous woods, earlywood vessels mostly solitary with latewood vessels mostly solitary, not in clusters; perforation plates simple; alternate intervessel pitting; helical thickenings absent; storied axial parenchyma, heterocellular multiseriate rays with tile cells. To date, four species of *Wataria* have been described *W. miocenica* K.Terada et Mits.Suzuki, *W. oligocenica* K.Terada et Mits. Suzuki, *W. parvipora* K.Terada et Mits.Suzuki, and *W. yunnanica* Yan-Jie Li et Oskolski (Tab. 4). Species have been distinguished based on number of rows of wide earlywood vessels, latewood vessel grouping, and crystal occurrence

(e.g., Li et al. 2015). There also are differences in quantitative features (earlywood vessel diameter, vessel element length, axial parenchyma strand length, ray width and height). Table 4 indicates that this *Wataria kvacekii*'s combination of the aforementioned features differs from previously described *Wataria* species and so consider it a new species. Axial parenchyma is not as easy to see in the Post *Wataria* wood as it is in the Asian species, but as best we can determine its distribution is similar to other species.

Two types of malvaceous woods were reported from the nearby middle Eocene Nut Beds flora, Clarno Formation, Oregon, both are semi-ring-porous to diffuse-porous, without a well-defined earlywood pore zone (Manchester and Miller 1978, Manchester 1979, 1980, Wheeler and Manchester 2002). *Chattawaya paliforme* Manchester also differs because it lacks storied structure and its rays are wider (to 14-seriate). Although not distinctly ring-porous, *Triplochitioxylon oregonensis* Manchester shares many features with this Post Hammer wood: storied structure, intervessel pit size, vessel-ray parenchyma pit type, ray heights, crystals in chambered axial parenchyma. Terada and Suzuki (1998) commented on the similarities between *Triplochitioxylon* Manchester and *Wataria*. *Triplochitioxylon* has longer vessel elements; averages of 440–487 µm vs. average of 346 µm with a maximum of 410 µm for *Wataria kvacekii*. This difference likely is related to most measurements for the Post *Wataria* being of the barrel-shaped earlywood vessel elements. Wide earlywood vessel elements are shorter than the narrow latewood vessels (e.g., Süss 1967, Kitin et al. 1999); it's been suggested that the widening of earlywood vessel elements in ring-porous woods results in their shortening (Chalk and Chattaway 1935). It is tempting to hypothesize that *Wataria kvacekii* belongs to the same lineage as *Triplochitioxylon* and that the differences in porosity between them are associated with the increasing seasonality in the transition from the middle Eocene to the late Eocene.

C o - o c c u r r i n g   f r u i t s / s e e d s . Malvaceae recognized from fruits from the Teater Road locality include *Craigia* W.W.Sm. et W.E.Evans and the extinct genus *Florissantia* Knowlt. (Manchester 1992: figs 34,

Text-fig. 10. *Platanoxylon* cf. *haydenii*, a, e, h: UF 279-34470; b, c, d, f g: UF 279-34469. a, b: Diffuse porous wood with vessels solitary and in small multiples, which are mostly tangential or oblique, diffuse and diffuse-in-aggregates axial parenchyma., TS. c–e: Scalariform perforation plates. f, g: Opposite intervessel pits, TLS. h: Two size classes of rays, TLS. *Platanus* sp., UF 279-24552. i: Predominantly solitary vessels, diffuse and diffuse-in-aggregates parenchyma, growth ring boundary distinct, noded rays, TS. j: Simple perforation plates (PP), RLS. k: Body of ray with procumbent ray cells, RLS. l: Scalariform perforation plate, RLS. m: Rays of two sizes, wide rays >10-seriate, TLS. Scale bars: 200 μm in a, b, h, i, m; 100 μm in j, k: 50 μm in c, d, e, f, l.

35, 37–40). Extant *Craigia* wood is distinguished from the fossil wood treated here by its helically thickened vessel elements, wider rays (>10-seriate), and lack of storied structure (Manchester et al. 2006). Fossils of flowers and fruits with the distinctive persistent calyx of *Florissantia* occur in eastern Asia (Manchester 1999: fig. 7B) as well as at various localities in North America. Pollen from the anthers of *Florissantia* flowers is similar to that of *Tilia* L. and *Craigia* (Manchester 1992, Kvaček et al. 2005). Based on circumstantial evidence of co-occurrence, it is possible that *Wataria/Triplochitioxylon* trees may have borne flowers corresponding to the genus *Florissantia*.

Family Platanaceae T.Lestib., 1826 nom. cons.

Genus *Platanoxylon* Andr., 1952 emend. by Süss and Müller-Stoll (1977)

Platanoxylon cf. *haydenii* (Felix) Süss et Müll.-Stoll, 1977
Text-fig. 10a–h

Material. UF279-34469; UF 279-34470, minimum estimated axis diameter 30 cm.

Description. Growth rings present, marked by slightly noded rays and 1–2 rows of radially narrow fibers. Wood diffuse-porous.

Vessels solitary and in short multiples, some tangentially arranged (Text-fig. 10a, b); average tangential diameter 76 (11) µm, range 59–96 µm; average 45/mm². Perforation plates exclusively scalariform, generally with fewer than 20 bars (Text-fig. 10c, d); intervessel pits opposite (Text-fig. 10f, g), vessel-ray parenchyma pits not observed.

Fibers non-septate, pits not observed.

Axial parenchyma diffuse-in-aggregates, in interrupted short uniseriate lines (Text-fig. 10a, b, f).

Rays of two distinct sizes, larger rays often >20 cells wide (Text-fig. 10a, b, h), composed of procumbent cells, sometimes with 1–2 marginal rows of square cells; multiseriate ray height averages 3.05 mm, range 1.1–5.53 mm.

Remarks. Although vessel-ray parenchyma pits were not observed in these samples, their other characteristics indicate they are *Platanoxylon* (narrow numerous vessels, some in tangential multiples (Text-fig. 10a, b); scalariform perforation plates (Text-fig. 10c, d, e); opposite intervessel pits (Text-fig. 10f, g); diffuse-in-aggregates parenchyma; tall and wide rays composed mostly of procumbent cells (Text-fig. 10h). The characteristics that distinguish them from other woods with wide rays (e.g., *Fagus* and *Euptelea*) were detailed by Scott and Wheeler (1982) and discussed earlier with reference to *Fagus dodgei*. Platanoid woods are common in the Paleogene of western North America. Woods similar to *Platanoxylon haydenii* are common in the older Clarno Formation, with multiple samples occurring at both the Nut Beds (Wheeler and Manchester 2002) and Hancock Canyon (Wheeler and Manchester 2014). These Post Hammer woods with their exclusively scalariform perforation plates are similar to other Eocene platanoid woods and differ from present-day *Platanus* woods that have both simple and scalariform perforation plates.

Genus *Platanus* L., 1753

Platanus sp.
Text-fig. 10i–m

Material. UF 279-24552, minimum estimated axis diameter 30 cm.

Description. Growth rings present, marked by noded rays, rows of radially narrow latewood fibers, and differences between vessel diameters between latest latewood and earliest earlywood. Wood diffuse-porous (Text-fig. 10i).

Vessels predominantly solitary, occasionally in oblique or tangential multiples; average tangential diameter 58 (9) µm, range 42–77 µm; 82–102 vessels/mm². Perforation plates predominantly simple (Text-fig. 10j), rare scalariform perforation plates with fewer than 15 bars (Text-fig. 10l); scalariform intervessel pits observed at ends of vessel elements, vessel-ray parenchyma pits horizontally elongated. Vessel element lengths average 499 (100) µm, range 260–740 µm.

Fibers non-septate, thick-walled.

Axial parenchyma diffuse, diffuse-in-aggregates, and in interrupted short uniseriate lines (Text-fig. 10i).

Rays of two distinct sizes, narrow rays 1–3-seriate (Text-fig. 10m), larger rays to 24 cells wide and 6.6 mm high; heterocellular, body of procumbent cells with 1–4 marginal rows of square to upright cells. In radial section, some ray cells appear enlarged and possibly crystalliferous (Text-fig. 10k).

Remarks. We place this wood in *Platanus*, rather than *Platanoxylon*, because it has predominantly simple perforation plates like the extant genus, in contrast with woods of *Platanoxylon/Plataninium*, which have exclusively or predominantly scalariform perforation plates. The horizontally elongate vessel-ray parenchyma pits are not typical of extant *Platanus* but occasionally occur in the Vietnamese species *P. kerrii* Gagnep. The occurrence of multiple types of Platanaceae woods agrees with the leaf and fruit record.
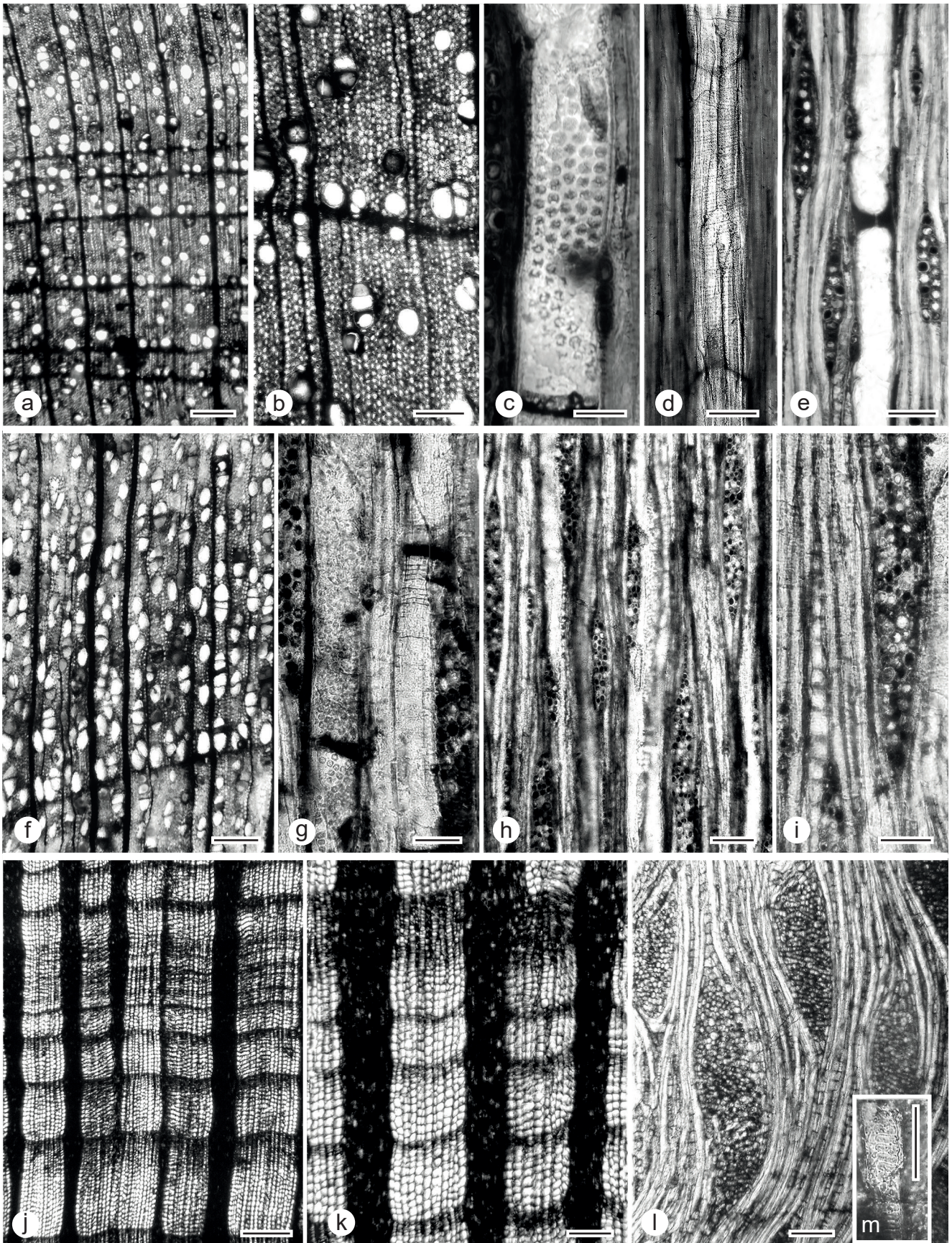
Coeval megafossils of Platanaceae from the late Eocene of Oregon include dispersed fruits with the distinctive basal tuff of hairs diagnostic of extant *Platanus* from the Teater Road locality (Manchester and Lott, pers. obs.). Also present in the region during the late Eocene are leaves of the extinct genera *Macginitiea* J.A.Wolfe et Wehr (and associated fruits of *Macginicarpa* which lack dispersal hairs, late Eocene of Gray Butte and middle Eocene Clarno Formation sites), *Platameliphyllum* N.Maslova (Clarno Formation sites; Huegele et al. 2022) *Platanites* E.Forbes (John Day Gulch locality of the Clarno Formation) as well as extant *Platanus* leaves (Clarno Formation sites).

Family Sapindaceae Juss., 1789 nom. cons.

Genus *Acer* L., 1753

Acer Post Hammer sp. 1
Text-fig. 11a–e

Material. UF 279-34456 (minimum estimated diameter 12.5 cm).

Text-fig. 11. *Acer* Post Hammer species 1, UF 279-34456. **a, b:** Diffuse-porous wood with distinct growth rings, marked by marginal parenchyma, vessels solitary and in short radial multiples, TS. **c:** Crowded alternate intervessel pits, TLS. **d:** Simple perforation plates, helical thickenings in vessel elements, TLS. **e:** Rays 2–3-seriate, gum deposit in vessel element, TLS. *Acer* Post Hammer species 2. UF 279-34466. **f:** Diffuse-porous wood with distinct growth rings, marked by marginal parenchyma, vessels solitary and in short radial multiples, TS. **g:** Alternate intervessel pits, helical thickenings in vessel elements, TLS. **h:** Rays 1–4(–5)-seriate, TLS. **i:** Crystalliferous strand, multiseriate ray, TLS. *Trochodendron beckii*, UF 279-24558. **j, k:** Distinct growth rings, abrupt transition from earlywood to latewood, vesselless, wide rays noded at growth ring boundaries, TS. **l:** Rays of two distinct sizes, uniseriate and multiseriates >10-seriate, TLS. **m.** Scalariform intertracheary pits. RLS. Scale bars: 500 μm in j; 200 μm in a, f, k, l; 100 μm in b, h; 50 μm in c, d, e, g, i, m.

Description. Growth rings distinct, marked by radially flattened fibers. Diffuse-porous (Text-fig. 11a, b). Vessels solitary (57 %) and in radial multiples of 2(–3); average tangential diameters 40 (SD = 10), range 24–63 μm; vessel frequency 50–56/mm²; perforations exclusively simple (Text-fig. 11d); gum deposits appear accumulated at ends of vessel elements (Text-fig. 11e); intervessel pits crowded alternate, mostly polygonal in outline with included apertures (Text-fig. 11c), small to medium; vessel-ray parenchyma pits similar in size and shape to intervessel pits; helical thickenings present along entire length of the vessel element (Text-fig. 11d).

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

Axial parenchyma marginal. (Text-fig. 11a, b).

Rays 1–3(–4)-seriate (Text-fig. 11e). Homocellular, composed of procumbent cells; multiseriate ray height averages 238 (69) μm; 8–10 /mm.

Storied structure absent; crystals not observed.

Acer Post Hammer sp. 2
Text-fig. 11f–i

Material. UF 279-34466.

Description. Growth rings distinct, marked by radially flattened fibers. Diffuse-porous (Text-fig. 11f). Vessels solitary (48 %) and in radial multiples of 2–4; average tangential diameter 55 (11), range 39–73 μm; vessel frequency 64–78/mm²; perforations simple; intervessel pits crowded alternate (Text-fig. 11g), rounded to polygonal in outline with included apertures, 8–10 μm; vessel-ray parenchyma pits similar in size and shape to intervessel pits; helical thickenings present along entire length of the vessel element; (Text-fig. 11g) vessel element lengths 275–495 μm; mean 390 μm (n = 12); tyloses absent. Fibers non-septate, walls of thin to medium thickness, pitting not observed. Axial parenchyma marginal (Text-fig. 11f), apparently diffuse; strands of chambered crystalliferous cells with more than 16 chambers per strand (Text-fig. 11i); one crystal per chamber. Rays 1–4(–5)-seriate (Text-fig. 11h). Multiseriate rays homocellular, composed of procumbent cells; multiseriate ray height averages 512 (206) μm, range 175–850 μm; 5–7/mm. Chambered crystalliferous cells, occasional, more than 16 chambers per strand; one crystal per chamber. Storied structure absent.

Comparisons with extant woods. Woods of *Acer* are relatively easy to identify to genus because of their distinctive combination of features: diffuse-porosity (5p), vessels solitary and in short radial multiples (6a 7a 8a 9a 10a 11a), exclusively simple perforation plates (13p 14a), alternate intervessel pits that are neither minute nor large (22p 24a 27a), vessel-ray parenchyma pits similar in size and shape to the intervessel pits (30p), spiral thickenings throughout the vessel elements (36p 37p), vessels not wide or few (42a 43a 46a), non-septate fibers with simple to minutely bordered pits (61p 65a 66p), non-storied homocellular rays that are not exclusively uniseriate or >10-seriate (96a 99a 104p 118a), axial parenchyma not abundant and marginal parenchyma present (77a 79a 80a 83a 86a 89p) and in some species crystals in chambered axial parenchyma cells (e.g., Brazier and Franklin 1961, Panshin and DeZeeuw 1980).

Dipteronia Oliv. wood differs from *Acer* wood in that helical thickenings are uncommon and faint in the narrower vessel elements; it also differs from these Post maple woods as its rays are wider (to 6-seriate) and commonly >1 mm high (T. Itoh, personal communication).

Today there are ~125 *Acer* species (Mabberley 2017). It is not easy to identify an isolated piece of maple wood of unknown geographic origin to a species or section. In Ogata's (1967) monograph of the genus, he suggested ray shape, ray width in cell number, and crystal occurrence are useful for distinguishing sections in *Acer*. Based on these features we recognize two species of *Acer* in the UF 279 assemblage.

Comparisons with fossil woods. The oldest known wood with features unique to *Acer* occurs in the middle Eocene Clarno Nut Beds (Wheeler and Manchester 2002). Takahashi and Suzuki (1988) reviewed the record for fossil *Acer* woods. More recently, fossil *Acer* woods have been reported from Asia (Jeong et al. 2009) and Turkey (Akkemik et al. 2016, 2018, Bayam et al. 2018). Table 5 compares their features; this table only includes reports for stem wood with reasonably complete anatomical descriptions and images. The Turkish Miocene woods are distinct from all other *Acer* fossil woods because of their markedly higher vessel frequency. *Acer* PH sp. 1, which lacks crystals, is similar to *A. minokamoensis* E.K.Jeong, Kyung.Kim et Mits.Suzuki in vessel diameter and ray size, but its description only notes that the vessels are numerous. Thus, it is not clear whether or not they are similar in vessel frequency. *Acer* PH sp. 2 differs from other crystal-bearing fossil *Acer* woods in vessel frequency and ray height. We are hesitant to provide diagnoses that rely heavily on differences in quantitative features for distinguishing species.

Co-occurring fruits/seeds or leaves. Wolfe and Tanai (1987) described seven species of *Acer* based on leaf and fruit remains from the Teater Road locality, which they referred to as Sheep Rock Creek. *Dipteronia* fruits are also recognized there (McClain and Manchester 2001).

Family Trochodendraceae Eichler, 1865 nom. cons.

Genus *Trochodendron* Siebold et Zucc., 1839

Trochodendron beckii (Hergert et H.K.Phinney) R.A.Scott et E.A.Wheeler, 1982
Text-fig. 11j–m

Material. UF279-24558 (estimated minimum diameter of stem 15 cm), USNM 326709 (holotype, estimated minimum diameter 18 cm).

Description. Growth rings distinct, marked by noded rays and abrupt transition in radial diameters of latewood tracheids to the subsequent ring's earlywood tracheids. Vessels absent. Transition from earlywood to latewood abrupt. Tangential diameter of earlywood tracheids 29 (7), 15–51 μm; tangential diameter of latewood tracheids 26 (5) μm, 17–42; scalariform intertracheary pitting observed on radial walls; axial parenchyma rare, occasional isolated cells; rays of two distinct sizes: uniseriates and multiseriates up to 15 cells wide; uniseriates numerous, composed

Table 5. Comparison of *Acer* species. Arranged by age, oldest to youngest. VTD = vessel tangential diameter in µm, mean (standard deviation) or minimum-average-maximum; V/mm² = vessels per mm², range or average as a single number; RW = ray width in cell number; MsRH = multiseriate ray height in µm, mean (standard deviation) or minimum-average-maximum; Cry = crystals present in long chambered strands; Eo = Eocene, Mio = Miocene, e = early, m = middle, l = late; OR = Oregon, WA = Washington.

Taxon (reference)	VTD (µm)	V/mm2	RW	MsRH (µm)	Cry	Age	Country
Acer integrifolioxylon (3)	48 (5)–50 (7)	88–97	1–3(–4)	297 (137)–546 (159)	Yes	m Eo	OR, USA
Acer Post Hammer sp. 1 (this paper)	24-40-63	50–56	1–3(–4)	238 (69)	No	l Eo	OR, USA
Acer Post Hammer sp. 2 (this paper)	39-55-73	64–78	1–4(–5)	512 (206)	Yes	l Eo	OR, USA
A. momijiyamense (2, 5)	20–75 (range)	20–70	1–4(–5)	50–600(–750)*	Rare	Ol	Japan
	24-50-79	numerous	1–4	47-500-932	No	e Mio	Korea
A. cf. *amoenum* (1)	up to 75 µm	?	1–6(–9)	up to 1200	Yes	e Mio	Japan
Acer spp. (7)	37	132	1–5	214	No	e Mio	Turkey
Acer spp (6)	55	206	1–5	220	No	e Mio	Turkey
A. minokamoensis (5)	24-43-55	numerous	1–3	79-290-505	No	e Mio	Korea
A. pohangensis (5)	24-39-55	numerous	1–4	32-600-1185	No	e Mio	Korea
A. watarianum (2)	30–90 (range)	15-35	1–5(–6)	70–460 (range)	Yes	e Mio	Japan
A. beckianum (4)	31-60-82	23–35	1–3	237 (65)	Yes	m Mio	WA, USA
A. berkhoffii (4)	35-65-90	17–24	1–3	365 (135)	No	m Mio	WA, USA
A. olearyii (4)	30-59-80	52–71	1–7	437 (239)	No	m Mio	WA, USA
A. puratanum (4)	30-53-72	18–26	1–4(–5)	230 (60)	Yes	m Mio	WA, USA

1. Watari (1952), 2.Takahashi and Suzuki (1988), 3.Wheeler and Manchester (2002), 4.Wheeler and Dillhoff (2008), 5. Jeong et al. (2009), 6. Bayam et al. (2018), 7. Akkemik et al. (2016)

* 50–600 reported as range, with 750 µm given as outlier.

exclusively of upright cells; central cells of multiseriate rays procumbent, with up to 10 marginal rows of upright cells, heights of multiseriate portions of the rays 0.7–1.56 mm.

Note: We did not measure total ray height including the uniseriate margins because it was difficult to be sure of where the uniseriate margins ended.

R e m a r k s . Vesselless woods are rare among angiosperms, and this specimen with its wide heterocellular rays and scalariform bordered pits has features of Trochodendraceae (Bailey and Nast 1945, Hergert and Phinney 1954). This specimen from the Post Hammer locality (UF 279) further documents the occurrence of *Trochodendron* wood in the Eocene of Oregon (Scott and Wheeler 1982). This species was previously recognized from the Miocene of Oregon (Hergert and Phinney 1954) from the same formation where fossil trochodendraceous infructescences and leaves have been recognized (Manchester et al. 2018). There are differences in the quantitative features (tracheid diameters, ray width) between the woods from these separate occurrences, but we don't consider them to be great enough to treat them as different species. Although the two extant genera of this family, *Trochodendron* and *Tetracentron*, are confined to eastern Asia, the family is well represented in the Cenozoic of western North America and known from leaves and fruits of both modern and extinct genera ranging from Paleocene to Miocene (Manchester et al. 2018, Manchester et al. 2021).

Conclusions

The wood assemblage from the late Eocene Post Hammer locality is smaller and less diverse than the middle Eocene Clarno Nut Beds wood assemblage. It includes woods with anatomy similar to extant genera: *Pistacia* (Anacardiaceae); *Celtis* (Cannabaceae), *Cercidiphyllum* (Cercidiphyllaceae), *Fagus*, *Quercus* of the red oak group (Fagaceae), *Acer* (Sapindaceae), *Ulmus* (Ulmaceae; Wheeler and Manchester 2007), and *Trochodendron* (Trochodendraceae).

To the best of our knowledge, the *Pistacia*, *Celtis*, and *Trochodendron* woods are the oldest occurrences of woods with characteristics unique to these genera. There is also a permineralized palm stem (UF 279-24547) from the same site. Angiosperm woods that can be identified to family but have a combination of features found in more than one extant genus of that family are *Lithocarpoxylon*, resembling *Lithocarpus*, *Notholithocarpus*, and the evergreen *Quercus* species (Fagaceae); *Hamamelidoxylon* (Hamamelidaceae); and *Pterocaryoxylon*, with features shared with *Juglans* (butternut group) and *Pterocarya* (Juglandaceae). Two genera are likely extinct because they can be identified to family but have a combination of features that does not conform to a modern genus: *Wataria* (Malvaceae), which also occurs in Japan, and *Platanoxylon* (Platanaceae), one of the most commonly occurring fossil woods in the Paleogene of the Northern Hemisphere. Study of this wood assemblage is an example of how studying coeval fruit and seed assemblages, leaf compressions, and woods provides a better understanding of the vegetation (Tab. 6).

These taxa are consistent with warm temperate possibly to subtropical vegetation. Differences between the Post Hammer assemblage and the Clarno Nut Bed assemblage document changes in vegetation and functional traits as would be expected as a result of the middle to late Eocene climatic change, increased seasonality and decreased mean annual temperature. All Post Hammer woods have distinct growth ring boundaries, whereas one-third of the Nut Beds have indistinct growth ring boundaries (Wheeler and

Table 6. Taxonomic composition of the Post Hammer locality.

Family	Wood taxa	Reproductive structures[2]
Taxaceae		*Diploporus torreyoides* seed
Conifer	Indet. wood	
Palmae	Indet. stem	*Sabal* seed
Trochodendraceae	*Trochodendron beckii* (HERGERT et H.K.PHINNEY) R.A.SCOTT et E.A.WHEELER	
Platanaceae	*Platanoxylon haydenii* (FELIX) SÜSS et MÜLL.-STOLL	
	Platanus sp.	
Cercidiphyllaceae	*Cercidiphyllum alalongum* R.A.SCOTT et E.A.WHEELER	
Hamamelidaceae	*Hamamelidoxylon crystalliferum* sp. nov.	
	H. suzukii E.A.WHEELER et T.A.DILLHOFF	
Betulaceae		*Alnus* sp. infructescence
Fagaceae	*Fagus dodgeii* sp. nov.	*Fagus* sp. nut
	Quercus sp.	*Quercus* sp. nut
	Lithocarpoxylon ashwillii sp. nov.	
	Lithocarpoxylon sp.	
Juglandaceae	*Pterocaryoxylon* sp.	
		Carya sp. nut
Malvaceae	*Wataria kvacekii* sp. nov.	
Anacardiaceae	*Pistacia terrazasae* sp. nov.	Indet. fruit similar to *Pistacia*
Cannabaceae	*Celtis popsii* sp. nov.	
Ulmaceae	*Ulmus danielii* E.A.WHEELER et MANCHESTER[1]	
	Ulmus woodii E.A.WHEELER et MANCHESTER	
Sapindaceae	*Acer*, 2 spp.	
Alangiaceae		*Alangium* sp. fruit
Davidiaceae		*Davidia* fruit
Mastixiaceae		*Tectocarya* sp. (misidentified as *Mastixicarpum* by Manchester 2006) fruit

[1]presented by Wheeler and Manchester 2007
[2]presented in Manchester and McIntosh 2006

Manchester 2002). Moreover, two of the Post Hammer woods are distinctly ring-porous, a trait not seen in any of the Nut Beds woods; ring-porosity is correlated with the deciduous habit and distinct seasonality.

As research continues, we will compare this assemblage with other wood localities in the region. The Dietz locality (UF 278), situated a few km east of the Hammer locality, has also yielded well preserved woods in association with silicified fruits and seeds. Although we have encountered some of the same woods at UF 278 (Platanaceae, Ulmaceae), there are differences, including the presence of Magnoliaceae, Araliaceae, and more conifers.

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