

## Early angiosperm woods from the mid-Cretaceous (Turonian) of New Mexico, USA: *Paraphyllanthoxylon*, two new taxa, and unusual preservation

Karen Chin <sup>a,\*</sup>, Emilio Estrada-Ruiz <sup>b</sup>, Elisabeth A. Wheeler <sup>c,d</sup>, Garland R. Upchurch Jr. <sup>e</sup>, Douglas G. Wolfe <sup>f</sup>

<sup>a</sup> Department of Geological Sciences and Museum of Natural History, University of Colorado Boulder, 265 UCB, Boulder, CO 80309, USA

<sup>b</sup> Departamento de Zoología, Laboratorio de Ecología, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, 11340 Ciudad de México, Mexico

<sup>c</sup> Department of Forest Biomaterials, North Carolina State University, Raleigh, NC 27695, USA

<sup>d</sup> North Carolina Museum of Natural Sciences, Raleigh, NC 27601, USA

<sup>e</sup> Department of Biology, Texas State University, San Marcos, TX 78666, USA

<sup>f</sup> Zuni Dinosaur Institute for Geosciences, 224 East Main Street, Springerville, AZ 85938, USA



### ARTICLE INFO

#### Article history:

Received 9 August 2018

Received in revised form

19 December 2018

Accepted in revised form 24 January 2019

Available online 4 February 2019

#### Keywords:

Fossil wood

Angiosperms

Cretaceous

Turonian

Moreno Hill Formation

*Paraphyllanthoxylon*

Phosphatized wood

### ABSTRACT

The fossil record of Cretaceous angiosperm wood is skewed toward the latest part of the period; most described taxa are based on specimens from Campanian or Maastrichtian sediments. The low percentage of pre-Campanian angiosperm woods relative to other flowering plant organs may reflect a taphonomic bias or the existence of relatively few woody angiosperm taxa until the last part of the Cretaceous. The discovery of three fossil angiosperm wood taxa in the Turonian Moreno Hill Formation of New Mexico offers additional data on the occurrence of secondary xylem in early angiosperms. These wood fossils represent a common Cretaceous wood taxon plus two new angiosperm wood types, and increase the number of known pre-Campanian wood types by 10–20%.

Analyses of thin sections from a large (>50 cm diameter) silicified log at a locality in the lower Moreno Hill Formation reveal it is *Paraphyllanthoxylon arizonicense* Bailey, a wood taxon known from Cenomanian and Maastrichtian to Paleocene sites in the American Southwest. *Paraphyllanthoxylon arizonicense* represents large trees that may belong to Laurales. Several other sizeable logs in the same area are also likely to be *P. arizonicense*. In contrast, two taxa from a stratigraphically higher site in the Moreno Hill have not been previously described and are each represented by only one specimen. These two new wood types, based upon small, phosphatic axes (5–7 cm in diameter), differ from *Paraphyllanthoxylon* in their smaller diameter vessels and scalariform perforation plates. The unique combinations of character states of these phosphatic specimens indicate that they are new genera. Although the taxonomic affinities of *Herendeenoxyylon zuniense* gen. et sp. nov. are uncertain, it is possible that it belongs to the Ericales. The affinities of the other new wood type, *Vasunum cretaceum* gen. et sp. nov. are unknown.

The presence of three angiosperm wood taxa in the Moreno Hill Formation is noteworthy because exposures of terrestrial Turonian deposits are uncommon. The large diameter and apparent abundance of *P. arizonicense* in the lower member of the Moreno Hill Formation suggest that these trees were dominant members of woodland or forest habitats of the ancient coastal lowlands. The small diameters and scarcity of the other two wood types suggest that they came from shrubs or small trees that were not common.

© 2019 Elsevier Ltd. All rights reserved.

\* Corresponding author.

E-mail addresses: [karen.chin@colorado.edu](mailto:karen.chin@colorado.edu) (K. Chin), [emilkpaleobot@yahoo.com.mx](mailto:emilkpaleobot@yahoo.com.mx) (E. Estrada-Ruiz), [xylem@ncsu.edu](mailto:xylem@ncsu.edu) (E.A. Wheeler), [gu01@txstate.edu](mailto:gu01@txstate.edu) (G.R. Upchurch), [dhcwolfe@aol.com](mailto:dhcwolfe@aol.com) (D.G. Wolfe).

## 1. Introduction

Most unequivocal records of Cretaceous angiosperm woods (75% of <250 records) are from the Campanian and Maastrichtian stages (83.6–66.0 Ma) (InsideWood, 2004 onwards; Wheeler and Lehman, 2009; Jud et al., 2017). This is notable because angiosperm leaves are common in pre-Campanian rocks and occur worldwide, ranging from the equator to the Arctic and Antarctic (e.g., Upchurch et al., 1994; Cantrill, 2000). Some authors have suggested that this poor record for wood reflects a mostly herbaceous to shrubby growth habit for Early Cretaceous angiosperms (Wing and Boucher, 1998; Philippe et al., 2008; Coiffard and Gómez, 2012). However, it also might indicate that Cretaceous angiosperm woods are poorly sampled relative to other plant parts—or that many were low density woods with few secondary compounds and were thus readily decayed and unlikely to enter the fossil record (wood extractives can enhance wood durability; Kirker et al., 2013). These competing hypotheses demonstrate why the discovery of new pre-Campanian angiosperm woods have particular value for broadening our understanding of early angiosperms (Wheeler and Baas, 1991).

We here describe the characteristics of three dicot wood types in a fossil wood assemblage from the Turonian Moreno Hill Formation of New Mexico (Sweeney et al., 2009) and discuss their possible affinities. These fossils add to the growing number of reports of Cretaceous angiosperm woods worldwide and increase our understanding of the taxonomic diversity of woody Cretaceous angiosperms. Two of the specimens also provide rare examples of wood preserved through phosphatization.

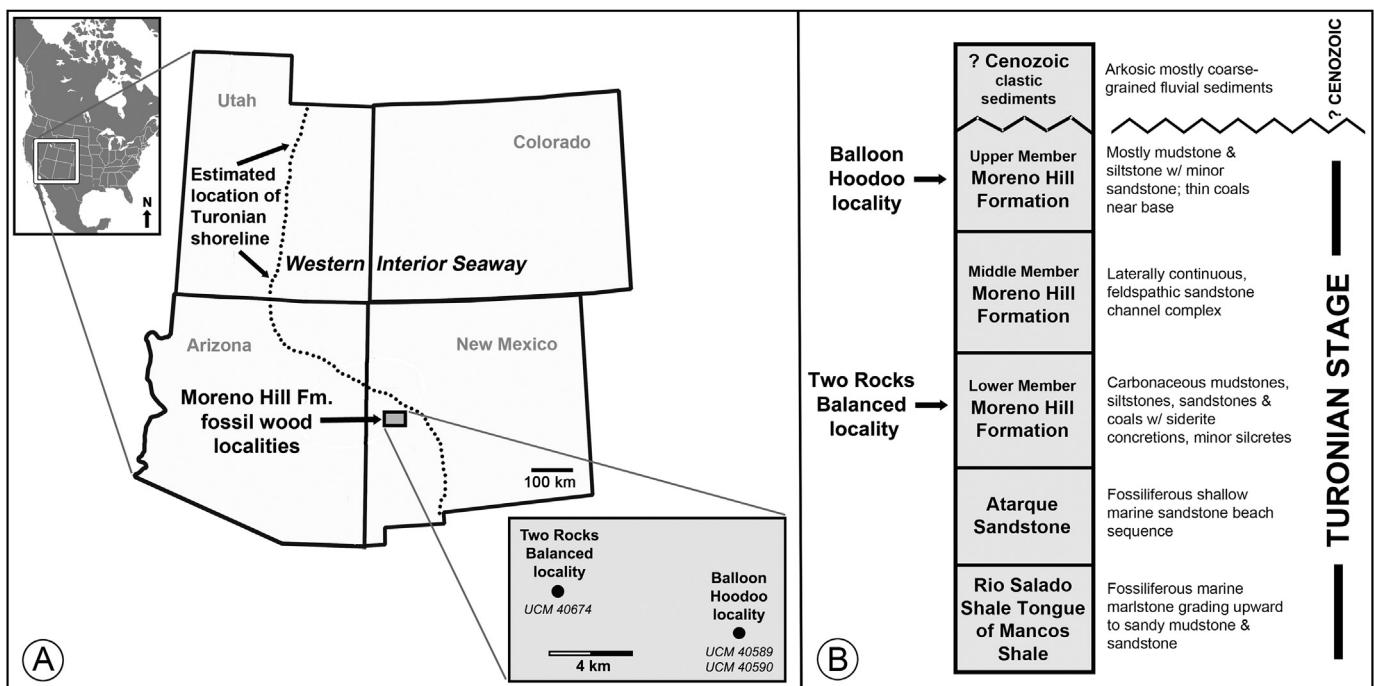
## 2. Geological setting

Among the Upper Cretaceous strata of the San Juan Basin, the Turonian Moreno Hill Formation presents a rare example of a well-preserved, regressive, coastal-terrestrial sequence deposited

during a generally transgressive phase of the Western Interior Seaway (Molenaar et al., 2002). Non-marine deposits of Turonian age are uncommon (Wolfe and Kirkland, 1998), thus the Moreno Hill Formation offers a rare window on terrestrial environments of the early Late Cretaceous. Sediments in this formation were deposited along the southwestern coastline of the Western Interior Seaway and inter-finger northeastward with fossiliferous marine strata of the Mancos Shale, which provide biostratigraphic control on age (Molenaar et al., 2002 and references therein).

Moreno Hill Formation outcrops are limited by definition and geographic extent to the southern portion of the San Juan Basin–Colorado Plateau near the Arizona–New Mexico Border (Fig. 1A). McLellan et al. (1983) recognized three members in this formation. The lower member comprises fluvial facies including sandstone, siltstone, mudstone and coal. The middle member is a prominent, arkosic sandstone channel complex, and the upper member is primarily mudstone and siltstone, with minor sandstones and thin coals in the lower portion (Fig. 1B).

South of the Zuni Plateau, the Moreno Hill Formation lies above mostly marine sediments of the inter-tonguing Dakota Group and Mancos Shale. North of the Zuni Plateau, the Moreno Hill loses its identity where the marine Pescado Tongue of the Mancos Shale divides terrestrial strata into the (lower) Tres Hermanos Formation and the (upper) Crevasse Canyon Formation. The Pescado Tongue is correlative with the middle–upper Turonian index fossil *Lopha lugubris* (Molenaar et al., 2002). At its type section and our study area, the Moreno Hill lies directly above the Atarque Sandstone which contains abundant near-shore marine fossils, shallow-water ichnofossils, and sedimentary structures indicative of a prograding beach sequence. The Atarque Sandstone conformably overlies the fully marine Rio Salado Shale Tongue of the Mancos. Both the upper portion of the Rio Salado Shale and the Atarque Sandstone are considered early–middle Turonian in age based on biostratigraphic index fossils (Wolfe, 1989; Molenaar et al., 2002). Although the age



**Fig. 1.** Locality and stratigraphic context of the Moreno Hill Formation study areas. **A**, Maps showing the study area in North America (left), the Four Corners area (center), and the proximity of the two described fossil wood localities (right). Dotted line indicates the approximate location of the shoreline of the Western Interior Seaway in the Turonian, based upon reconstructions of Wolfe and Kirkland (1998) and Blakey (2014). **B**, Column showing the generalized stratigraphic context of the Moreno Hill Formation and describing the sediments of its upper, middle, and lower members. Approximate stratigraphic levels of the Balloon Hoodoo and Two Rocks Balanced localities are shown.

of the upper portion of the Moreno Hill Formation is poorly constrained in the study area, correlative strata north-eastward contain upper Turonian index fossils. Thus the upper member of the Moreno Hill appears to be middle–upper Turonian—possibly younger near the top.

The prevalence of carbonaceous shales and coal in the Moreno Hill Formation is consistent with a lowland coastal plain setting. Moreover, the absence of pedogenic carbonates and other paleosol features suggest that the Turonian Moreno Hill and Tres Hermanos formations were deposited in humid to sub-humid paleoclimates (Mack, 1992). Both coalified and permineralized fossil wood are common in the Moreno Hill Formation (Sweeney et al., 2009). This study examines fossil angiosperm wood from two sites in the Moreno Hill Formation which are approximately 9 km apart, the Two Rocks Balanced and Balloon Hoodoo localities.

The Two-Rocks Balanced locality (Fig. 1A, B) is located in the middle third of the lower member of the Moreno Hill Formation, based on structural projection of the contact between the Atarque Sandstone and Moreno Hill Formation at nearby outcrops (Wolfe and Kirkland, 1998). Thus, taxa from this site are middle Turonian in age. This site yielded diverse fossil vertebrates, including dinosaurs that have not been found elsewhere: the ceratopsian *Zuniceratops christopheri* (Wolfe and Kirkland, 1998); a therizinosaur, *Nothronychus mckinleyi* (Kirkland and Wolfe, 2001; Hedrick et al., 2015); and a hadrosaur, *Jeyawati rugoculus* (McDonald et al., 2010). The locality also contains terrestrial elements (mammal teeth, *in situ* tree stumps and tracks) in close association with aquatic elements (crocodilomorphs, turtles, amiid and gar fish, plus crocodilomorph swim tracks and localized silcrete layers interpreted as pond deposits). *Nothronychus* has affinities to therizosaurs previously thought to be restricted to Asia (Kirkland and Wolfe, 2001).

The Balloon Hoodoo locality is separated by volcanic cover from the Two Rocks Balanced locality, and its stratigraphic position is not as well constrained. However, barring significant structural displacement, projection of the prominent middle Moreno Hill sandstones indicates that the Balloon Hoodoo site is in the upper member of the Moreno Hill. The sediments at this site show less lignite and appear more oxidized, suggesting drier conditions. Vertebrate fossils are less common than at the Two Rocks Balanced site. An unconformable upper contact between the Moreno Hill and clastic sediments mapped as early Cenozoic in age lies a few tens of meters up-section from the Balloon Hoodoo locality, which is likely middle–late Turonian in age.

### 3. Materials and methods

#### 3.1. Sample collection

Fossilized wood samples were collected in the Moreno Hill Formation from the Balloon Hoodoo site in 2005 (under BLM Free Use Permit NM-120-05-01) and from the Two Rocks Balanced locality in 2000 and 2001. Collected samples are reposed at the University of Colorado Museum of Natural History (UCM). The fossil wood specimens are often highly fractured, so localized accumulations are assumed to have derived from one woody plant, and were assigned one field and catalog number.

The smaller ~0.04 km<sup>2</sup> Balloon Hoodoo locality was thoroughly searched for coalified, permineralized, and charcoalfied wood, and fragments with axes as small as ~3 cm in diameter were documented: eleven coal inclusions, two silicified stumps, three phosphatic specimens, and two charcoalfied wood samples were recovered from the vicinity of Balloon Hoodoo (Sweeney et al., 2009).

The search for fossil wood at the larger (~0.4 km<sup>2</sup>) Two Rocks Balanced exposure focused on mapping larger, permineralized logs,

and did not record all small diameter wood fossils. Eleven silicified wood specimens (or accumulations of wood) were found at this locality, and at least seven of these were derived from sizeable angiosperms. These include six angiosperm logs with minimum estimated diameters ranging from 21 to 52 cm, and an *in situ* coalified and silicified stump ~59 cm across at the base of the tree (fig. 3B in Sweeney et al., 2009). The large log from which the UCM 40674 (ML) specimens were taken (described in this study) was located within 2 m of the *in situ* stump, so it is possible that it came from the same tree.

#### 3.2. Thin sections and mineral identification

Transverse (TS), tangential longitudinal (TLS), and radial longitudinal (RLS) surfaces of three specimens were analyzed for this study: silicified specimen UCM 40674 (ML), phosphatized specimen UCM 40589 (PA) and phosphatized specimen UCM 40590 (PB). Orientation abbreviations are indicated in the figure captions. The thin sections had been previously prepared and were examined to study the taphonomy of the wood at this locality (Sweeney et al., 2009). Photomicrographs of the sections were made with two microscope systems: a Leica DMRX microscope with an RT SPOT Diagnostic Instruments Inc. camera at the University of Colorado Boulder, and a Zeiss Photoscope I with a Canon EOS Digital Rebel XSi camera at Texas State University. The mineralogy of the wood samples was previously determined by X-ray diffraction, electron microprobe, and cathodoluminescence (Sweeney et al., 2009).

#### 3.3. IAWA feature coding and identification

Descriptions generally follow the International Association of Wood Anatomists (IAWA) list of features for hardwood identification (IAWA Committee, 1989). For quantitative features, the values are presented as minimum–mean–maximum. Each description is preceded by a list of the IAWA Hardwood List feature numbers (IAWA Committee, 1989) we observed in the specimen. A “?” after a feature number indicates we are uncertain if that feature is present or absent in the sample, a “v” after a feature number indicates that the feature is variable in occurrence or that there is a tendency towards showing the feature, e.g., 22v indicates a tendency to alternate intervessel pitting. We subsequently used the multiple entry key of the *InsideWood* website (<http://insidewood.lib.ncsu.edu>; Wheeler, 2011) to search for present-day and fossil woods with the combinations of features observed in the Moreno Hill woods. The search criteria we used are listed at the beginning of the discussion of affinities, with IAWA feature numbers followed by these codes: “p” for present and “a” for absent.

Once we had a list of taxa with shared features, we compared the features of the genera and families on those lists with descriptions found in Metcalfe and Chalk (1950) and in recent publications from the Plant Micromorphology section of the Kew Bibliographic Database <http://kbd.kew.org/kbd/searchpage.do>.

#### 3.4. Calculation of axis diameters

When possible, the radius or diameter of wood axes or stumps was measured directly. For fragmentary specimens, minimum axis diameter was estimated by calculating minimum radius and multiplying by 2.

Specimens UCM 40589 and 40590 are very fragile and were recovered in numerous fragments. Where feasible, pieces were glued together with acryloid B-72 in acetone in order to get a sense of the original size of the wood axes.

#### 4. Systematic paleobotany

##### Genus *Paraphyllanthoxylon* Bailey 1924

Type species: *Paraphyllanthoxylon arizonense* Bailey

##### *Paraphyllanthoxylon arizonense* (Figs. 2A, B; 3A–H)

**Material.** UCM 40674 taken from silicified log ML (Fig. 2A, B), at least 52 cm in diameter and 286 cm in length (minimum dimensions measured in the field).

**Locality and horizon.** Two Rocks Balanced locality of Sweeney et al. (2009). Upper Cretaceous, Turonian, Moreno Hill Formation, New Mexico, USA.

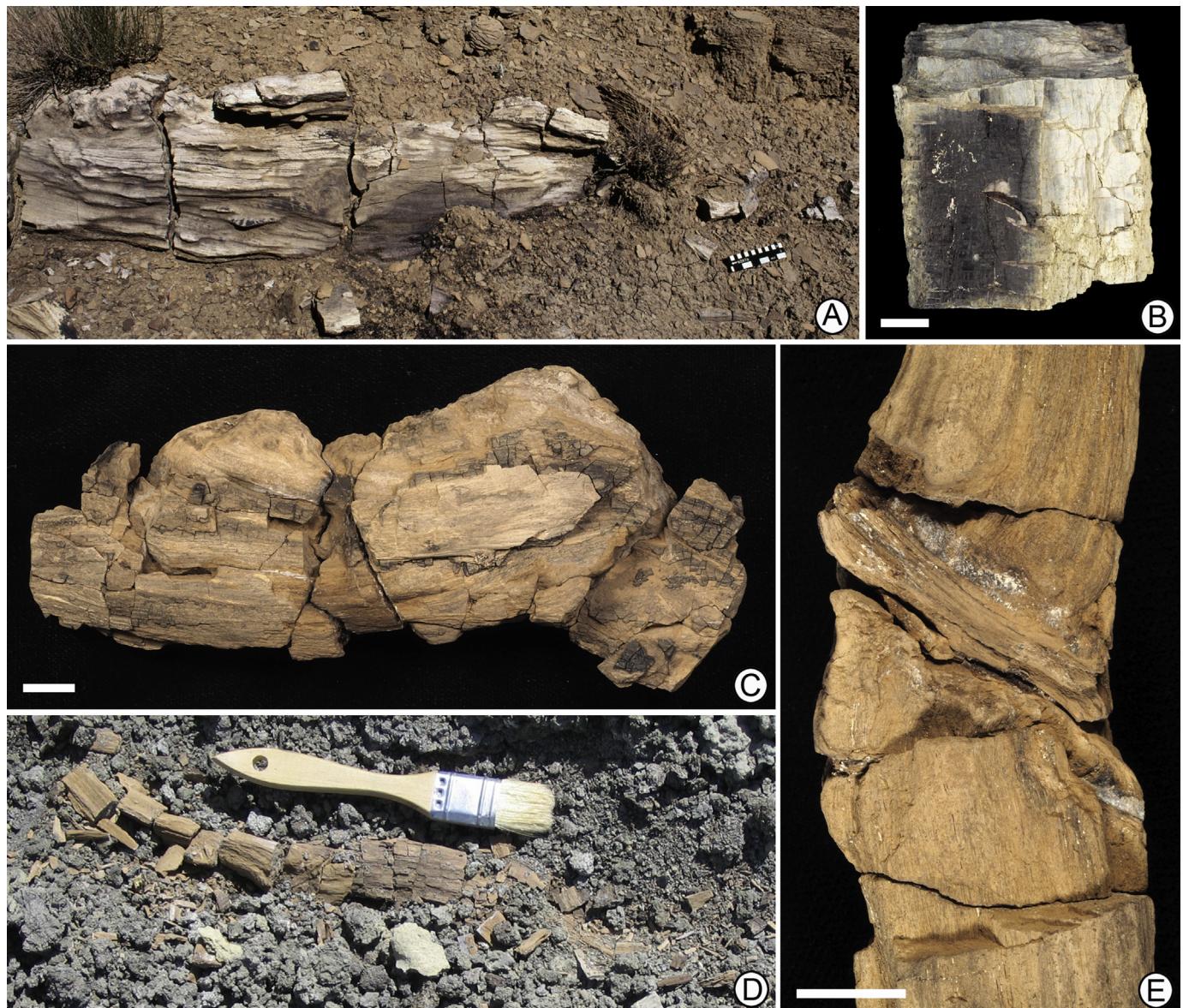
**Repository.** University of Colorado Museum of Natural History, Boulder, Colorado, USA

**IAWA features observed.** 2, 5, 13, 22, 23, 31, 42, 47, 56, 61, 65, 66, 69, 75, 78, 98, 107, 115.

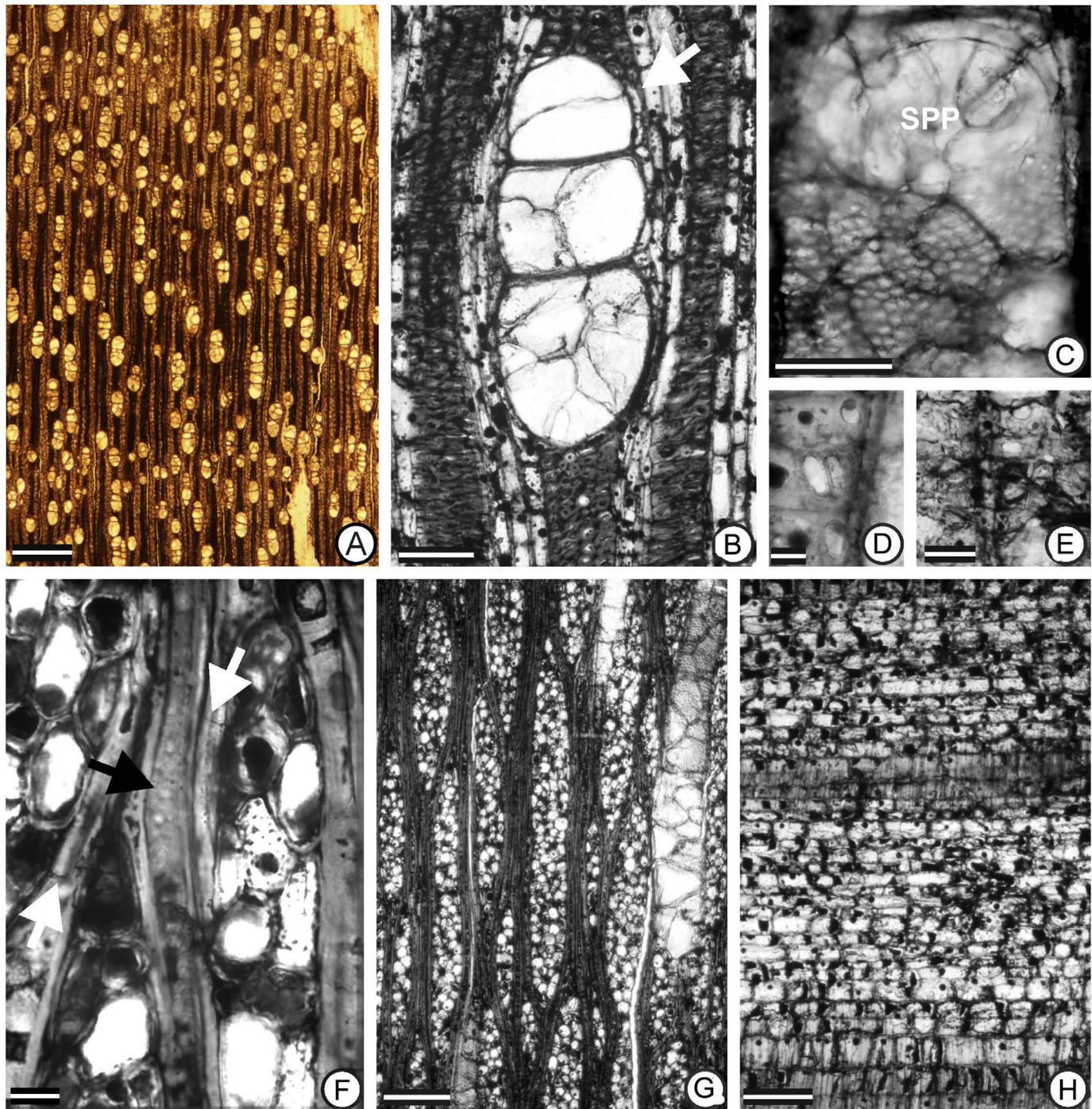
**Description.** Growth rings indistinct, diffuse porous wood; vessels solitary (22%) and in radial multiples of 2–3 (up to 6) (Fig. 3A, B); solitary vessels circular to oval in outline in transverse section (Fig. 3A), tangential vessel diameter 50–150–224  $\mu\text{m}$ ; vessels per  $\text{mm}^2$  3–7–12; exclusively simple perforation plates (Fig. 3C), intervessel pitting alternate, large ~10  $\mu\text{m}$ , polygonal in outline (Fig. 3C); vessel–ray parenchyma pitting with reduced borders, pits mostly round in outline (Fig. 3D, E); abundant tyloses present, thin-walled, bubble-like (Fig. 3B, C, G).

Axial parenchyma rare, some scanty paratracheal (Fig. 3A, B).

Rays predominantly multiseriate, mostly 3 to 4 (up to 6) cells wide (Fig. 3G), uniseriate rays rare; multiseriate rays heterocellular with procumbent body cells and usually one marginal row of square cells; some body cells with a radial length ~2–3 times their height (Fig. 3H); multiseriate ray heights 6–48 cells, 232–872–1600  $\mu\text{m}$ ; 5–10 rays per mm.



**Fig. 2.** Angiosperm wood specimens from the Moreno Hill Formation. **A**, *Paraphyllanthoxylon arizonense* Bailey log associated with UCM 40674. **B**, Radial view of a chunk of UCM 40674 showing light-colored weathered surfaces (right) and dark recently exposed wood (left). **C**, Largest reconstructed piece of UCM 40589, *Herendeenoxylon zuniiense* gen. et sp. nov. Note somewhat straight grain at the bottom of photo and burl-like texture of wood at top of image. **D**, UCM 40590, *Vasunum cretaceum* gen. et sp. nov., as discovered in the field. **E**, Close-up view of UCM 40590. Note 1 cm diameter branch emerging from the axis. Scale bars in **B**, **C**, and **E** represent 1 cm.



**Fig. 3.** *Paraphyllanthoxylon arizoneense* UCM 40674. **A**, Diffuse porous wood with indistinct growth rings, vessels solitary and in radial multiples, variable vessel density, TS. Scale bar = 920  $\mu$ m. **B**, Scanty paratracheal parenchyma (arrow); fibers with medium thick to thick walls, TS. Scale bar = 100  $\mu$ m. **C**, Simple perforation plate (SPP) and alternate intervessel pits, RLS. Scale bar = 108  $\mu$ m. **D**, Vessel–ray parenchyma pits, mostly oval shape with reduced borders, RLS. Scale bar = 32  $\mu$ m. **E**, Vessel–ray parenchyma pits, round with reduced borders, RLS. Scale bar = 50  $\mu$ m. **F**, Pits on the fibers (black arrow) and septate fibers (white arrows), TLS. Scale bar = 16  $\mu$ m. **G**, Multiseriate rays with thin-walled ray cells: abundant tyloses in vessel elements, TLS. Scale bar = 200  $\mu$ m. **H**, Heterocellular rays with procumbent and square ray cells, RLS. Scale bar = 145  $\mu$ m.

Fibers mostly septate (Fig. 3F, white arrows) and some non-septate, with medium-thick walls, fiber pits simple and very rare (Fig. 3F, black arrow).

**Affinities.** This Moreno Hill Formation wood has a combination of features (listed above) found in *Paraphyllanthoxylon* Bailey (1924). More than ten species of *Paraphyllanthoxylon* have been described from the Cretaceous. The characteristics and possible affinities have

been reviewed multiple times (e.g., Mädel, 1962; Thayn and Tidwell, 1984; Herendeen, 1991; Takahashi and Suzuki, 2003; Gryc et al., 2009; Wheeler and Lehman, 2009; Jud et al., 2017).

*Paraphyllanthoxylon arizoneense* (Bailey, 1924) was initially described from the Cenomanian of Arizona, USA, and subsequently described from the Maastrichtian–Paleocene of the San Juan Basin, New Mexico (Wheeler et al., 1995). The combination of features of

UCM 40674 indicates it is another occurrence of *Paraphyllanthoxylon arizone*nse in the American Southwest. The minimum diameter of the ML Moreno Hill log (52 cm diameter) is comparable to logs from Bailey's locality (>60 cm diameter) (Wheeler and Lehman, 2009) and broader than the San Juan Basin *P. arizone*nse logs (20 cm, 25 cm, 30 cm). Table 1 compares quantitative features of *P. arizone*nse samples.

Although Bailey (1924) noted that "similar structural complexes occur in the section Phylanthoideae of the Euphorbiaceae" [now family Phylanthaceae], he warned that "sufficient data are not at present available for hazarding the statement that it [*Paraphyllanthoxylon arizone*nse] is actually confined to the Euphorbiaceae." One of us (EAW) recently examined slides of the holotype (USNM 42263) and sections of woods collected from near the original locality (images available in *InsideWood*). The tangential sections show that uniserial rays are not common, ray cells are thin-walled, and the ray body contains some barely procumbent to square cells. In contrast, uniserial rays are common in Phylanthaceae wood and the ray cells do not appear thin-walled. Thus, it seems unlikely that *Paraphyllanthoxylon arizone*nse has affinities with the Phylanthaceae. One North American *Paraphyllanthoxylon* species represents Laurales: a charcoaled twig with *Paraphyllanthoxylon* type wood is attached to a reproductive structure (Herendeen, 1991) that represents either Lauraceae (Drinnan et al., 1990) or the sister lineage to Lauraceae + Hernandiaceae (Doyle and Endress, 2010). Tangential sections of a large diameter *Paraphyllanthoxylon* from British Columbia (Jud et al., 2017) show some inflated cells resembling oil cells, also suggesting that this wood may represent Laurales.

As noted by Jud et al. (2017) some of the woods assigned to *Paraphyllanthoxylon* should be removed from the genus because their anatomy differs. For example, *Paraphyllanthoxylon illinoense* (Wheeler et al., 1987) differs in having commonly occurring uniserial rays, multiseriate rays with obvious marginal rows of upright cells, and thick-walled ray cells. Additional work is needed to resolve the placement of this wood type, but it probably belongs to the Malpighiales (Wheeler, personal observation).

??? ERICALES  
Incertae sedis

Genus *Herendeenoxyylon* gen. nov.

**Etymology.** In honor of Dr. Patrick S. Herendeen, in recognition of his contributions to the paleobotany of North America.

Type species: *Herendeenoxyylon zuniense* sp. nov.

**Diagnosis.** Diffuse porous wood; predominantly solitary vessels, scalariform perforation plates, predominantly opposite intervessel pits with a tendency to alternate; some vessel-ray parenchyma pits elongated with reduced and indistinct borders, some similar to intervessel pits; non-septate fibers with distinctly bordered pits on

radial and tangential walls; apotracheal diffuse parenchyma; heterocellular rays, mostly 1–2 cells wide.

***Herendeenoxyylon zuniense* sp. nov. (Fig. 4A–H)**

**Etymology.** The specific epithet refers to the Zuni Basin, where the material was collected.

**Type material.** Holotype UCM 40589 (field identification PA), phosphatized, sample PA.

**Locality and horizon.** Balloon Hoodoo locality, Upper Cretaceous, Turonian, Moreno Hill Formation, New Mexico, USA.

**Repository.** University of Colorado Museum of Natural History, Boulder, Colorado, USA

**Diagnosis.** As for the genus.

**IAWA features observed.** 2, 5, 9, 14, 17, 21, 22v, 30, 32, 41, 48, 49, 53, 54, 60?, 62, 63, 66, 69, 76, 97, 108, 115.

**Description.** This highly fractured sample is phosphatized (predominantly fluorapatite; Sweeney et al., 2009) but includes some coalified tissues. The largest reconstructed piece is 13.5 cm long, with a minimum diameter of 4.8 cm (Fig. 2C). However, the inferred radius is 3.3 cm (based on the apparent location of the pith), suggesting a minimum diameter of 6.6 cm. The center of the wood axis (the inner 1.5 cm) has somewhat straight grain, but the exterior has more twisted grain and shows a burl-like configuration.

Growth rings indistinct to absent, diffuse porous wood; predominantly solitary vessels, round to slightly angular in outline in transverse section (Fig. 4A, B), tangential diameter 38–62–87 (sd = 11.4)  $\mu$ m; vessels per mm<sup>2</sup> 26–40–52, some vessels with dark contents; scalariform perforation plates with 14–21–32 bars per perforation plate, bars sometimes forked (Fig. 4C); intervessel pits opposite, in some areas tending toward alternate (Fig. 4F), vessel-ray parenchyma pits with reduced borders and horizontally elongate (Fig. 4G), some similar to intervessel pits (Fig. 4H); vessel element length 452–856–1491  $\mu$ m (sd = 268)  $\mu$ m. Tyloses not observed (Fig. 4D).

Axial parenchyma apotracheal diffuse (Fig. 4A, B).

Rays heterocellular, 1–2 (–3) cells wide (Fig. 4D, E); uniserial rays composed of square and erect cells, 4–14–42 cells (sd = 9), 225–643–2000  $\mu$ m (sd = 460  $\mu$ m) high; biserial and triserial rays with procumbent body cells, 6–60 cells, 280–943–2300  $\mu$ m high (sd = 584)  $\mu$ m; with a variable number, 2–5–13, marginal rows of square/upright cells (Fig. 4D, J); 8–12 rays per mm.

Fibers non-septate (Fig. 4D, E); walls thin to medium-thick; distinctly bordered pits on both radial and tangential walls; some cells adjacent to the vessels with over two rows of distinctly bordered pits (Fig. 4I), interpreted as vasicentric tracheids.

**Comparison with modern woods.** *InsideWood* was searched for this combination of features: diffuse porous wood (5p), randomly arranged exclusively solitary vessels (6a 7a 8a 9p), exclusively scalariform perforation plates with fewer than 40 bars (13a 14p 18a), opposite intervessel pits (21p), vessel-ray parenchyma pits with reduced borders and horizontally elongate (32p), non-septate fibers with distinctly bordered pits on radial and tangential walls (62p 63p 66p), diffuse axial parenchyma only (76p 77a 79a 80a 83a 84a 85a 89a), 1–3 seriate markedly heterocellular rays (97p 108p).

According to *InsideWood*, this combination of features occurs in some species of Altingiaceae, Hamamelidaceae (Saxifragales), Pentaphylacaceae, Symplocaceae, Theaceae (Ericales), Cunoniaceae (Oxalidales), and Olacaceae (Santalales).

Crystals are consistently present in all genera of Olacaceae with exclusively solitary vessels. Crystals often, but not always, occur in the Altingiaceae and Hamamelidaceae. Alternate pitting has not been reported in Altingiaceae and Hamamelidaceae wood. These

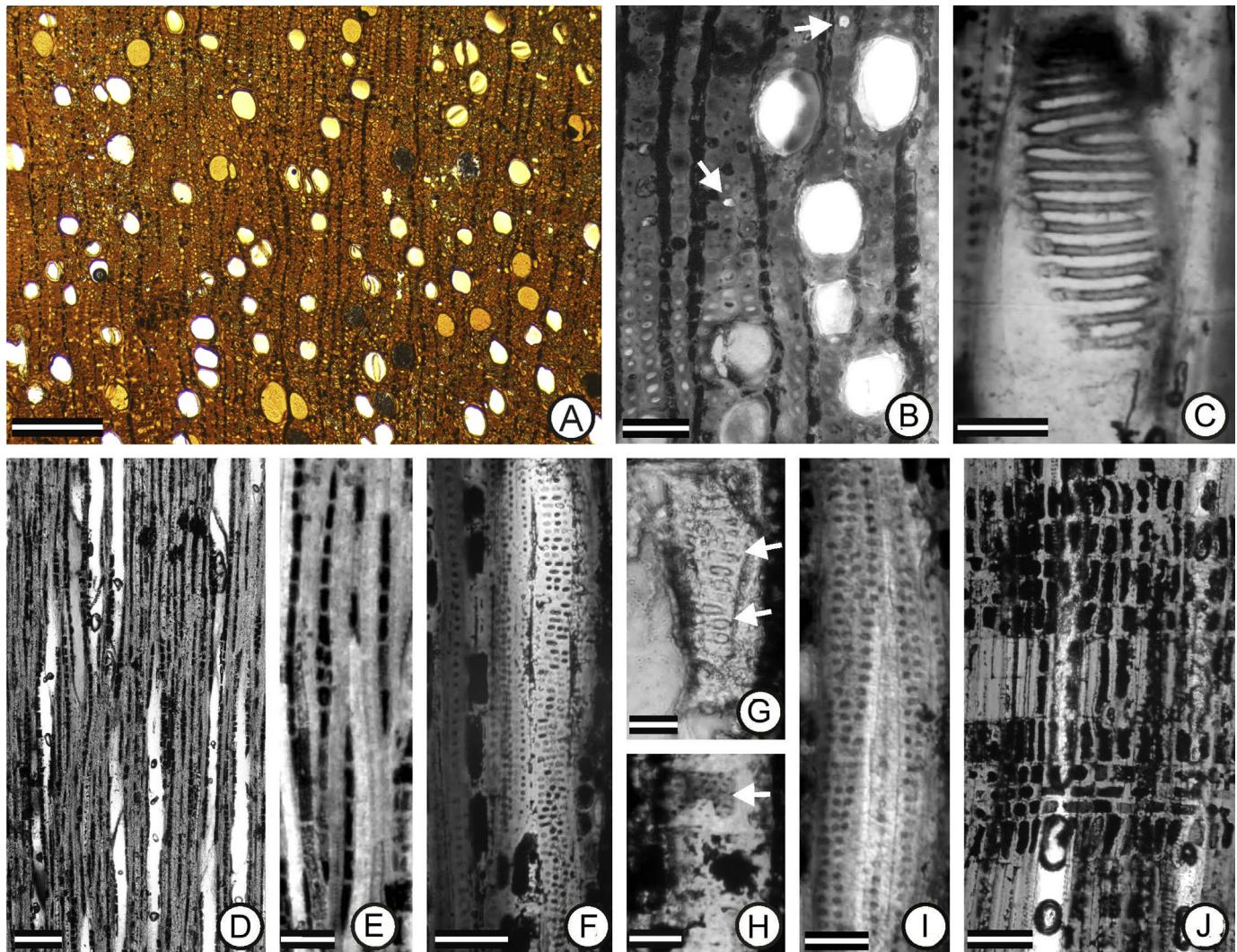
**Table 1**

Quantitative features of *Paraphyllanthoxylon arizone*nse samples. MTD = mean tangential diameter of vessel lumina (range); V/mm<sup>2</sup> = vessels per square mm; RW = ray width in cells (maximum ray width in cells); MsRH = multiseriate ray height, minimum–mean–maximum. YPM = Yale Peabody Museum.

Sample	MTD ( $\mu$ m)	V/mm <sup>2</sup>	RW	MsRH ( $\mu$ m)
Holotype <sup>a</sup>	177 (sd = 42)	5–14	3–4 (–7)	364–857–1515
Kirtland Fm <sup>b</sup>				
YPM 30155	143 (sd = 26)	3–6–10	2–3 (–4)	169–809–1692
YPM 30156	180 (sd = 37)	6–14–28	3–4	273–679–1808
YPM 30151	184 (sd = 38)	3–5–6	2–3 (–4)	248–680–1495
UCM 49674	150 (50–224)	3–7–12	3–4 (–6)	232–872–1600

<sup>a</sup> Bailey, 1924, Wheeler, personal observations.

<sup>b</sup> Wheeler et al., 1995.



**Fig. 4.** *Herendeenoxylon zunense* gen. et sp. nov., UCM 40589. **A**, Diffuse porous wood; exclusively solitary vessels, TS. Scale bar = 300  $\mu$ m. **B**, Solitary vessels, diffuse axial parenchyma (arrows); fibers with medium-thick to thick walls, TS. Scale bar = 90  $\mu$ m. **C**, Scalariform perforation plate, with a forked bar, TLS. Scale bar = 75  $\mu$ m. **D**, Vessel elements with steeply inclined end walls; narrow rays, TLS. Scale bar = 200  $\mu$ m. **E**, Uniseriate and biserrate rays, TLS. Scale bar = 75  $\mu$ m. **F**, Predominantly opposite intervessel pits, in some areas tending to alternate; fibers with distinctly bordered pits, TLS. Scale bar = 75  $\mu$ m. **G**, Vessel-ray parenchyma pits with reduced borders and round to elongated in outline (arrows), RLS. Scale bar = 55  $\mu$ m. **H**, Vessel-ray parenchyma pits with distinct borders (arrow), RLS. Scale bar = 25  $\mu$ m. **I**, Vasicentric tracheids, RLS. Scale bar = 35  $\mu$ m. **J**, Heterocellular rays with upright cells at least twice the height of the procumbent cells, RLS. Scale bar = 100  $\mu$ m.

differences argue against UCM 40589 having an affinity with these three families.

There is overlap in the anatomy of the Pentaphylacaceae, Symplocaceae, Theaceae (Ericales), and Cunoniaceae (Oxalidales). Because of this we cannot confidently assign this new wood type to a family. It is tempting to consider it to belong to the Ericales because the order is well-represented in the Northern Hemisphere Cretaceous, with reports of leaves, woods, fruits, seeds, and flowers (e.g., Knobloch and Mai, 1984, 1986; Nixon and Crepet, 1993; Keller et al., 1996; Estrada-Ruiz et al., 2007; Wheeler and Lehman, 2009; Schönenberger et al., 2012; Crepet et al., 2013).

**Comparison with fossil woods.** The combination of exclusively (predominantly) solitary vessels, exclusively scalariform perforation plates, vessel-ray parenchyma pits with reduced borders, opposite intervessel pits, fibers with distinctly bordered pits, apotracheal parenchyma, and narrow (1–3 seriate) rays occurs in other Cretaceous woods. Table 2 presents a comparison of these woods; the Moreno Hill wood is most similar to Baileyan Big Bend Type I from the Campanian Aguja Formation, Texas. There are differences with

the other woods in vessel outline in transverse section, quantitative vessel element features, and whether there are only opposite intervessel pits or if there are also scalariform or alternate pits.

We did not find any formally described and named Cretaceous wood with all the features of this Moreno Hill wood. Because its preservation is good enough to show important diagnostic features (e.g., pitting, perforation plates, axial parenchyma distribution, ray type) and its combination of features is distinctive, we propose a new genus here, *Herendeenoxylon*. It is likely that Baileyan Big Bend Type I is another occurrence of this genus.

#### Incertae sedis

Genus ***Vasunum*** gen. nov.

**Etymology.** Named for the exclusively solitary vessels of the wood.

**Type species:** *Vasunum cretaceum* sp. nov.

**Diagnosis.** Diffuse porous wood; predominantly solitary vessels, oval in outline in transverse section; exclusively scalariform

**Table 2**

Cretaceous woods with predominantly solitary vessels, scalariform perforation plates, opposite intervessel pits, vessel–ray parenchyma pits with reduced borders, fibers with bordered pits, apotracheal parenchyma and narrow heterocellular rays. MTD = mean tangential diameter of vessel lumina (range); V/mm<sup>2</sup> = vessels per square mm (range); B/PP = bars per perforation plate (maximum bars per plate); IVP = intervessel pitting type; S = scalariform; O = opposite; A = alternate; V Shape = vessel outline in transverse section; Ang = angular; Ov = oval; C = circular; RW = ray width in cells (maximum ray width in cells); Unk = unknown; \* = charcoalfied samples, MTD and V/mm<sup>2</sup> estimated.

Taxon	MTD	V/mm <sup>2</sup>	B/PP	IVP	V Shape	RW
<i>Illicioxylon antarcticum</i> <sup>a</sup>	50 (16–91)	124 (95–204)	35–80	S–O	Ov (Ang)	1–2 (–3)
<i>Illicioxylon tenuiradiatum</i> <sup>a</sup>	36 (29–46)	56–156	43–64	S–O	Ang	1–2
Baileyan Big Bend Type I <sup>b</sup>	42 (8)–68 (12)	21–35	12–24	O	Ov–Ang	1–3
Potomac Group Type II <sup>c</sup>	Unk	Unk	7–15	O–S	C	1–2
Upatoi Wood Type 7 <sup>d</sup> *	60 (9)–167 (21)	21–72	<10 (–15)	A–O	C–Ov	1–2
<i>Herendeenoxyylon zuniente</i>	62 (11)	26–40–52	14–21–32	O (A)	Ov (Ang)	1–2 (–3)

<sup>a</sup> Poole et al., 2000.

<sup>b</sup> Wheeler and Lehman, 2000.

<sup>c</sup> Herendeen, 1991.

<sup>d</sup> Falcon-Lang et al., 2012.

perforation plates, often >40 bars; intervessel pits opposite; vessel–ray parenchyma pits differ from intervessel pits; vessel elements long, > 800 µm; fibers with bordered pits; axial parenchyma uncommon; heterocellular multiseriate rays >1 mm high.

#### *Vasunum cretaceum* sp. nov. (Fig. 5A–I)

**Etymology.** The specific epithet refers to its Cretaceous age

**Type material.** UCM 40590 (field identification PB).

**Locality and horizon.** Balloon Hoodoo locality, Upper Cretaceous, Turonian, Moreno Hill Formation, New Mexico, USA

**Repository.** University of Colorado Museum of Natural History, Boulder, Colorado, USA

**Diagnosis.** As for the genus.

**IAWA features observed.** 2, 5, 9, 14, 18, 21, 31, 41, 48, 54, 62, 63, 66, 69, 75, 98, 102, 107, 108.

**Description.** Description based on one fractured phosphatized sample (predominantly fluorapatite; Sweeney et al., 2009) representing a fragment of an axis that includes a branch axis emerging from the center of the wood. In the field, the fragment appears to be at least 25 cm long (Fig. 2D), but the largest reconstructed piece is 14 cm long. The wood axis has a minimum diameter of 2.8 cm, but this is also the minimum inferred radius based on the position of the emerging branch (Fig. 2E). The minimum diameter of the wood axis is thus approximately 5.6 cm.

Growth rings indistinct to absent, diffuse porous wood; vessels predominantly solitary, round to oval in outline in transverse section (Fig. 5A, B), vessel tangential diameter 32–61–90 µm, (sd = 17 µm); vessels per mm<sup>2</sup> 13–25–41; some vessels with dark or yellow contents; scalariform perforation plates with over 50 bars per plate (Fig. 5C, arrow); intervessel pits opposite to scalariform (Fig. 5D), vessel–ray parenchyma pits with reduced borders (Fig. 5E, arrows); vessel elements over 1000 µm long.

Axial parenchyma rare, possibly some apotracheal diffuse (Fig. 5A, B).

Rays heterocellular, 1–5, mostly 3–4 cells wide (Fig. 5F); multiseriate rays with procumbent body cells and generally 2–4 marginal rows of upright/square cells (Fig. 5I); 12–55 cells, 408–1200–2248 µm high, (sd = 434 µm); 5–8 per mm.

Fiber walls of thin to medium thickness, fibers with distinctly bordered pits on both radial and tangential walls, it could not be determined with certainty whether the fibers were septate and/or non-septate (Fig. 5G, H).

**Comparison with modern woods.** This sample came from a small axis and it is unknown whether it represents a tree or shrub, or a stem or a branch. If it came from the main axis of a tree, then it is probable that there are differences in vessel quantitative features and ray cellular composition and sizes between this juvenile wood

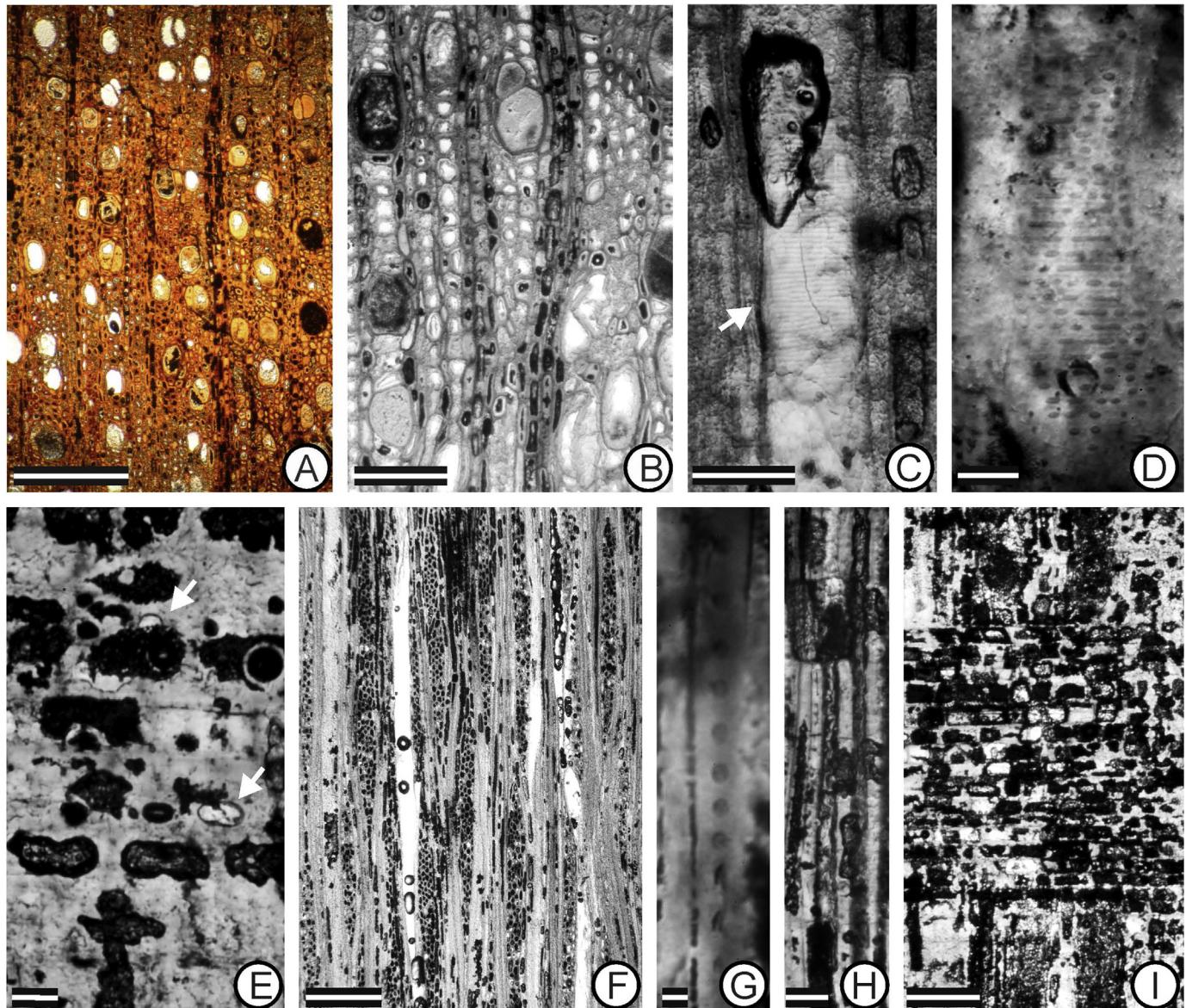
sample and mature wood of any present-day relative. Consequently, our search used mostly qualitative features: We searched *InsideWood* for diffuse porous wood (5p), predominantly solitary randomly arranged vessels (6a 7a 8a 9p), scalariform perforation plates with more than 10 bars (14p 15a), opposite intervessel pits (21p), vessel–ray parenchyma pits not similar to intervessel pits (30a), vessel elements not short (52a), non-septate fibers (66p), rare axial parenchyma (75p), and 1–4 (–5) seriate heterocellular rays that are commonly > 1 mm tall (96a, 99a, 102p, 104a 105a). This combination of features occurs in the Dilleniaceae (Dilleniales), Eupteleaceae (Ranunculales), Grubbiaceae (Cornales), Olacaceae (Santalales), Staphyleaceae (Crossosomatales), Symplocaceae and Theaceae (Ericales), and Violaceae (Malpighiales).

Of these, Dilleniaceae and Eupteleaceae are unlikely matches because they usually have wider rays and a tendency toward two distinct ray sizes; Grubbiaceae has predominantly scalariform intervessel pits and vessel–ray parenchyma pits are horizontally elongate (scalariform). The remaining families cannot be excluded confidently as “matches” for this wood.

We did another more specific search using the presence of features observed in this wood: vessels exclusively solitary (9p), scalariform perforation plates with more than 40 bars (14p 20p), opposite intervessel pitting (21p), vessel–ray parenchyma pits with reduced borders and rounded (31p), non-septate fibers with distinctly bordered pits (62p 66p), axial parenchyma absent/extremely rare (75p), and wider rays > 4-seriate and >1 mm high (98p 102p). This search returned matches with genera of Ericaceae, Symplocaceae (Ericales), Staphyleaceae (Crossosomatales), Dilleniaceae (Dilleniales), and Eupteleaceae (Ranunculales). Again, the Dilleniaceae and Eupteleaceae can be eliminated for the reasons given above.

The preceding text serves to indicate that this wood has the same “problems” that Page (1979) encountered when working with a suite of small diameter Late Cretaceous woods. Because most systematic wood anatomical descriptions are based on mature wood samples, and since there are differences between juvenile wood (wood formed by a young cambium) and mature wood, it is often difficult to determine the modern affinities of small-diameter fossil woods.

**Comparison with fossil woods.** We searched the fossil wood database of *InsideWood* for this combination of features: 9p (exclusively scalariform perforation plates), 14p (scalariform perforation plates), 21p (opposite intervessel pits), 30a (vessel–ray parenchyma pits not like intervessel pits), 62p (fiber pits bordered), 75p (axial parenchyma rare), 98p (larger rays > 4 cells wide), and 102p (rays > 1 mm high). Only four matches were found, and only one had a relatively complete description. That wood is DB.D1



**Fig. 5.** *Vasunum cretaceum* gen. et sp. nov. UCM 40590. **A**, Diffuse porous wood; solitary vessels rounded to oval in outline, TS. Scale bar = 190  $\mu$ m. **B**, Solitary vessels, some with dark contents; fiber walls medium-thick, TS. Scale bar = 95  $\mu$ m. **C**, Scalariform perforation plate (arrow), RLS. Scale bar = 80  $\mu$ m. **D**, Opposite intervessel pits, TLS. Scale bar = 35  $\mu$ m. **E**, Vessel-ray parenchyma pits with reduced borders and round to oval in outline (arrows), RLS. Scale bar = 32  $\mu$ m. **F**, Multiseriate rays, TLS. Scale bar = 300  $\mu$ m. **G**, Pits on the fibers, RLS. Scale bar = 6  $\mu$ m. **H**, Possible septate fibers, TLS. Scale bar = 60  $\mu$ m. **I**, Heterocellular rays with procumbent body cells and square to upright marginal cells, RLS. Scale bar = 120  $\mu$ m.

Xylotype 2 from the Paleocene of the Denver Basin (Wheeler and Michalski, 2003), but it has two distinct sizes of rays and sheath cells in the rays—features that do not occur in *Vasunum cretaceum*. As best as we can determine, this Moreno Hill wood has a distinct combination of features that has not been described before for fossil wood of any geological age. Thus, although its affinities are unknown, we are describing it here as a new genus and species.

## 5. Discussion

The woods described and illustrated here add to a growing number of reports of angiosperm woods from the mid-Cretaceous. The Moreno Hill woods are noteworthy because the terrestrial record for the Turonian is sparse. Moreover, the fact that two of the wood types are phosphatized suggests that further investigation between anatomy and mode of preservation is warranted.

### 5.1. Affinities of the Moreno Hill woods

*Paraphyllanthoxylon* has been assigned to various families (e.g., Thayn and Tidwell, 1984; Oakley and Falcon-Lang, 2009), but many members of this wood taxon probably represent the order Laurales. Leaves of Laurales are common in the mid-Cretaceous record. By the latest Albian, some have the advanced features of embedded guard cells and scale-shaped thickenings on paracytic stomatal complexes that are diagnostic of Lauraceae, while others have a mosaic of venational and epidermal features found in multiple extant families of Laurales (e.g., Upchurch and Dilcher, 1990; Coiffard et al., 2009). Flowers fully comparable to those of extant Lauraceae are present by the Cenomanian, and trimerous flowers comparable to those of Lauraceae, but lacking staminodia are present in the lower–middle Albian Puddledock locality, Virginia, USA (Crane et al., 1994; von Balthazar et al., 2007, 2011).

The most compelling evidence linking this wood taxon with Laurales was the discovery of a fruit attached to an axis with *Paraphyllanthoxylon* wood (Herendeen, 1991). This fruit was initially interpreted as lauraceous (Drinnan et al., 1990; Herendeen, 1991), but was subsequently assigned to the sister clade of Lauraceae + Hernandiaceae based on a detailed phylogenetic analysis of the reconstructed whole plant (Doyle and Endress, 2010).

*Paraphyllanthoxylon* woods are present by the middle Albian (Edwards Limestone of Texas; Serlin, 1982; Wheeler, 1991) and are common during the Late Cretaceous (Wheeler et al., 1995; Estrada-Ruiz et al., 2012; Jud et al., 2017). Woods assigned to *Paraphyllanthoxylon* have been reported from the Upper Cretaceous of the San Juan and Cutler Sag/Love Ranch basins in New Mexico (Wheeler et al., 1995; Estrada-Ruiz et al., 2012), Big Bend National Park in Texas (Wheeler and Lehman, 2000), and, most recently, from the San Carlos Formation in Chihuahua, Mexico (García-Hernández et al., 2016).

The wood anatomical features of the new genus *Herendeenoxyylon* can place it in one of several different families or orders, but the widespread distribution of Ericales in the Cretaceous of North America suggests its affinity with this order. If *Herendeenoxyylon* proves to be Ericales, it would offer additional support for the proposal that the considerable morphological variation in Ericales (relative to other orders) might be related to early diversification of the group during the Late Cretaceous (Lens et al., 2007).

## 5.2. Preservation

Fossil wood in the Moreno Hill Formation has been preserved through silicification, phosphatization, coalification, and charcoalification (Sweeney et al., 2009). Both coalified and mineralized specimens are common in the Moreno Hill Formation, and two of the specimens described in this report have both coalified and mineralized tissues. Sweeney et al. (2009) suggest that coalification and mineralization of wood are competitive taphonomic processes that are affected by both intrinsic properties of the wood (e.g., permeability and chemical composition) and characteristics of the depositional environment (sedimentology and microbial degradation). Whatever the mechanisms of preservation, the prevalence of associated mineralized and coalified tissues in fossil wood from the Moreno Hill Formation appears to reflect reducing conditions that prevented oxidation of coalified tissues. We note that coal was not evident on sub-aerially exposed surfaces of the *P. arizonense* log, UCM 40674 (ML), even though buried portions of the log retained considerable coalified wood. Moreover, the dark-colored wood tissues evident in thin sections of all three specimens and in recently exposed surfaces of UCM 40674 (ML) (Fig. 2B) suggest that some original organic matter is retained in the wood tissues.

Most of the lithified wood fossils in the Moreno Hill Formation are primarily mineralized with silica, and their completely-filled cell lumina indicate that these specimens were fossilized through permineralization. Many of these silicified wood specimens retain good cellular structure, including the UCM 40674 (ML) specimen of *P. arizonense* (Fig. 2). Even so, some silicified wood from the Moreno Hill Formation is so poorly preserved that cell structure is not recognizable (see fig. 5N in Sweeney et al., 2009). Indeed, the diagenetic history of these specimens can be complex. Silica is predominant in these woods, but Sweeney et al. (2009) observed minor phosphate concentrations in some vessel lumina of UCM 40674 (ML) with an electron microprobe. They inferred that partial phosphate precipitation preceded silicification.

Although silicified wood is common in the fossil record, primarily phosphatized wood specimens are rare (Reolid et al., 2010).

Thus, the discovery of phosphatized woods at the Balloon Hoodoo locality of the Moreno Hill Formation is highly unusual. These fossils are much smaller than the large silicified logs and stumps from the formation; the type specimen of the new dicot wood taxon *Herendeenoxyylon zuniense* has a minimum diameter of 6.6 cm, and *Vasunum cretaceum* was at least 5.6 cm in diameter. A much smaller piece of phosphatic wood (~2.8 cm diameter) from an unidentified angiosperm was also found about one km from the Balloon Hoodoo locality. The incompletely-filled cell lumina of the phosphatized wood specimens suggest that the dominant mode of fossilization was through authigenic mineralization (replacement) of the wood tissues rather than through permineralization. This helps explain why the primarily phosphatic wood tissues are considerably more fragile than the silicified UCM 40674 *P. arizonense* wood.

Many animal fossils have been preserved through phosphatization, but the source of phosphorus for this process usually appears to have originated in the tissues of the animal carcasses (Briggs, 2003). Phosphatized woods are uncommon because phosphorus generally occurs in very low concentrations in both plant tissues (Allen, 1989) and in sedimentary rocks (less than 0.2%; Yaroshevsky, 2006). Phosphatization of wood thus requires a supply of allochthonous phosphate. Several possible phosphorus sources have been proposed for the origin of phosphorus in phosphatized wood: guano or feces (Arena, 2008), vertebrate tissues (Pailler et al., 2000; Viney et al., 2017), decaying marine life (Reolid et al., 2010), phosphorus-rich bedrock (Viney et al., 2017), volcanic influences on groundwater (Jefferson, 1987), and/or extensive microbial activity (Pailler et al., 2000; Reolid et al., 2010). Regardless of the source of phosphorus, it appears that microbial exploitation of organic matter is necessary to create chemical gradients that can facilitate phosphate precipitation (Briggs, 2003).

The source of phosphorus for the phosphatized wood specimens preserved at the Balloon Hoodoo locality is unknown. Nor is it clear why the larger *Paraphyllanthoxylon* logs were primarily silicified and the smaller pieces of *Herendeenoxyylon zuniense* and *Vasunum cretaceum* were phosphatized. The depositional context of these wood fossils is relevant to this enigma. Sweeney et al. (2009) noted that the phosphatic *Herendeenoxyylon zuniense* and *Vasunum cretaceum* specimens both occurred in clay-rich sediments, whereas the siliceous conifer stump (UCM 40591) at the Balloon Hoodoo locality was preserved in a more permeable sandstone. This sedimentary context is consistent with their respective modes of fossilization because permeable sediments would have exposed wood to the flow of silica-rich groundwater, whereas claystones would have created conditions that were conducive to authigenic mineralization of smaller pieces of wood—that is, anaerobic microbial activity in a closed microenvironment (Briggs, 2003).

Differences in wood anatomy may have also played a role by affecting permeability or susceptibility of the wood to microbial attack. It is notable that the silicified *Paraphyllanthoxylon* specimen UCM 40674 has wide vessels and simple perforation plates, in contrast to the narrow vessels and scalariform perforation plates of the two identified phosphatized woods. On the other hand, examples of silicified conifer wood are also present in the Moreno Hill Formation.

The influence of wood biochemistry on mineral type is suggested by the observation that a phosphatized wood fragment near the Balloon Hoodoo locality was found in the same sedimentary layer as a piece of charcoalized wood that was permineralized with calcite. If wood chemistry played no role in wood mineralization and both wood fragments were exposed to the same diagenetic history, we would expect both wood fossils to be permineralized with the same mineral. However, charcoal is relatively inert

(Schmidt and Noack, 2000), so the differences in mineralization between these wood pieces might reflect that the phosphatized wood was more susceptible to microbial decay, which in turn facilitated phosphate precipitation (Sweeney et al., 2009).

These considerations raise the possibility that the unusual phosphatic preservation of *Herendeenoxylon zuniense* and *Vasunum cretaceum* offer rare glimpses of angiosperm wood taxa that were not easily preserved by silicification. Nevertheless, addressing the feasibility of correspondence between taxonomy and wood taphonomy will require examination of more phosphatic wood specimens. Whether or not a correlation exists, differences in wood fossilization remind us that it is important to examine all modes of preservation in order to better understand the original wood diversity of an ancient environment.

### 5.3. Turonian angiosperm woods

Turonian records of fossil wood are rare. Indeed, no more than 10 wood types had been described before this report (InsideWood, 2004 onwards; Wheeler and Lehman, 2009). A search of InsideWood found that more than 50% of Cenomanian–Turonian wood types have features considered plesiomorphic within angiosperms (see Bailey and Tupper, 1918; Baas et al., 2004), e.g., solitary and long vessel elements, exclusively scalariform perforation plates, opposite intervessel pits, and heterocellular rays. Two of the three samples studied here have those characteristics, in particular *Vasunum cretaceum*, which has >50 bars per perforation plate and long (>800 µm) vessel elements. In contrast, exclusively simple perforation plates and alternate intervessel pits occur in Cenomanian–Turonian *Paraphyllanthoxylon* (Bailey, 1924; Cahoon, 1972; Jud et al., 2017).

### 5.4. Woody angiosperms in the Turonian Moreno Hill Formation

Wood fossils are common at the Two Rocks Balanced and Balloon Hoodoo sites of the Moreno Hill Formation, and approximately thirty deposits of fossil wood have been observed. As previously noted, the search parameters for fossil wood at the two sites were somewhat different: all sizes of coalified, mineralized, and charcoalfied wood axes were documented at Balloon Hoodoo whereas larger permineralized logs were recorded at the Two Rock Balanced site. Despite the potential collection bias, the surveys reveal a noticeable difference in the diameters of preserved wood sections at these sites. Eleven of the wood deposits at the stratigraphically lower Two Rocks Balanced locality are logs or stumps from sizeable trees with minimum diameters ranging from 21 to 76 cm. At least seven of these are angiosperms, and we infer that they, like UCM 40674, are *P. arizone*. Only two wood fossils from the Balloon Hoodoo site are within this size range and they are both *in situ* conifer stumps; UCM 40591-GS is approximately 33 cm in diameter at the base (see fig. 5A in Sweeney et al., 2009).

The Moreno Hill Formation fossil wood assemblages must be interpreted with care since many of the fossil wood specimens occurred at different stratigraphic layers. Moreover, some scattered collections of fossil wood fragments could have come from a single tree. Nevertheless, the abundance, sizes, and spatial distribution of fossil wood at different stratigraphic levels offer some insights on the ancient Moreno Hill environments.

The inferred abundance of *Paraphyllanthoxylon arizone* at the Two Rocks Balanced locality, and its apparent absence at Balloon Hoodoo reinforces that these two sites represent different habitats. Sedimentological and paleontological evidence suggests that the stratigraphically lower Two Rocks Balanced locality was a wetter paleoenvironment than the Balloon Hoodoo site. Structurally

prominent *P. arizone* trees would have served as physical ecosystem engineers (Jones et al., 1997) that modulated the availability of resources for other plants and animals in the ancient Two Rocks Balanced environment.

We do not know the mature sizes of *Herendeenoxylon zuniense* or *Vasunum cretaceum* from Balloon Hoodoo and whether they were trees or shrubs. Both taxa are each represented by a single specimen, and it is not clear whether their scarcity reflects poor preservation potential, less than optimal habitat, or naturally low frequency in Moreno Hill paleoenvironments. However, they do demonstrate that the Turonian hosted a greater diversity of woody angiosperms beyond the sizeable *Paraphyllanthoxylon* trees that are already known from other mid-Cretaceous localities (Bailey, 1924; Spackman, 1948; Cahoon, 1972).

Fossil wood specimens at Balloon Hoodoo are dominated by coal inclusions (isolated pieces of coalified wood). Their abundance and scattered distributions suggest that coarse woody debris was prevalent in the ancient environment. Coarse woody debris provides important ecological functions in modern forests, such as hosting robust fungal and detritivore communities that support larger animals (Maser et al., 1979; Carpenter et al., 1988). Several of the large pieces of wood from the Two Rocks Balanced locality show patterns of degradation that resemble decay by pocket rot.

## 6. Conclusions

The discovery of three angiosperm wood taxa in the Moreno Hill Formation improves our perceptions of Turonian vegetation and the diversity of pre-Campanian angiosperm wood taxa. The wood taxon, *Paraphyllanthoxylon arizone*, has already been reported from Cenomanian and Maastrichtian to Paleocene sites in Arizona and New Mexico. Its presence in the Moreno Hill Formation underscores that large flowering trees played prominent roles in structuring and modulating environmental conditions in mid-Cretaceous woodlands or forests. This study also describes two new angiosperm wood taxa. Both *Herendeenoxylon zuniense* and *Vasunum cretaceum* are each represented by a single piece of phosphatized wood. Their small-diameter woody axes may indicate that these plants were shrubs or small trees; it is not clear whether their rarity reflects taphonomic bias or naturally low density.

Features of some *Paraphyllanthoxylon* woods indicate that this genus may represent trees within the order Laurales. The systematic affinities of *Herendeenoxylon* are still ambiguous, but paleogeography and histological features suggest that this taxon might belong to the Ericales. These fossil woods suggest that the Moreno Hill paleoenvironment hosted a mosaic of woody angiosperms and conifers in woodland or forest habitats.

## Acknowledgments

We thank Ian J. Sweeney and Justin S. Tweet for discovering the *Herendeenoxylon zuniense* and *Vasunum cretaceum* fossil wood specimens. We also thank Kevin Carson, Phil Gensler, and the Bureau of Land Management for facilitating the fieldwork on this project, as well as Bobby McKinley and his family for giving us access to the Two Rocks Balanced field site. We appreciate the assistance of Toni Culver, James Kirkland, and Hazel Wolfe for helping with different stages of this research. Portions of this work were funded by a National Science Foundation postdoctoral fellowship to K. Chin (EAR-9901708), a National Science Foundation grant to G. Upchurch (DEB-1655885), and student grants to I. Sweeney from the Geological Society of America, the University of Colorado and Shell. Finally, we thank Laureen S. R. Alves, two

anonymous reviewers, and Editor Eduardo Koutsoukos for constructive comments.

## References

Allen, S.E. (Ed.), 1989. Chemical Analysis of Ecological Materials, second ed. Blackwell Scientific Publications, Oxford. 368 pp.

Arena, D.A., 2008. Exceptional preservation of plants and invertebrates by phosphatization. *Riversleigh*, Australia. *PALAIOS* 23, 495–502. <https://doi.org/10.2110/palo.2006.p06-142r>.

Baas, P., Ewers, F.W., Davis, S.D., Wheeler, E.A., 2004. The evolution of xylem physiology. In: Hemsley, A.R., Poole, I. (Eds.), *Evolution of plant physiology. From whole plants to ecosystems. Linnaean Society Symposium Series No. 21*. Elsevier Academic Press, pp. 273–296.

Bailey, I.W., 1924. The problem of identifying the wood of Cretaceous and later dicotyledons. *Paraphyllanthoxylon arizonicense*. *Annals of Botany* 38, 439–451.

Bailey, I.W., Tupper, W.W., 1918. Size variation in tracheary cells. I. A comparison between the secondary xylems of vascular cryptograms, gymnosperms and angiosperms. *Proceedings of the American Academy of Arts and Sciences* 54, 149–204. <https://doi.org/10.2307/20025747>.

Blakely, R.C., 2014. Paleogeography and paleotectonics of the Western Interior Seaway, Jurassic–Cretaceous of North America. *AAPG Search and Discovery Article #30392*, pp. 1–72.

Briggs, D.E.G., 2003. The role of decay and mineralization in the preservation of soft-bodied fossils. *Annual Review of Earth and Planetary Sciences* 31, 275–301. <https://doi.org/10.1146/annurev.earth.31.100901.144746>.

Cahoon, E.J., 1972. *Paraphyllanthoxylon alabamense*—a new species of fossil dicotyledonous wood. *American Journal of Botany* 59, 5–11. <https://doi.org/10.1002/j.1537-2197.1972.tb10057.x>.

Cantrill, D., 2000. Cretaceous (Aptian) flora from President Head, Snow Island, Antarctica. *Palaeontographica Abteilung B* 253, 153–191.

Carpenter, S.E., Harmon, M.E., Ingham, E.R., Kelsey, R.G., Lattin, J.D., Schowalter, T.D., 1988. Early patterns of heterotrophy activity in conifer logs. *Proceedings of the Royal Society of Edinburgh* 94B, 33–43.

Coiffard, C., Gómez, B., 2012. Influence of latitude and climate on spread, radiation and rise to dominance of early angiosperms during the Cretaceous in the Northern Hemisphere. *Geologica Acta* 10, 181–188. <https://doi.org/10.1344/105.000001701>.

Coiffard, C., Gómez, B., Thiébaut, M., Kváček, J., Thévenard, F., Néraudeau, D., 2009. Intramarginal veined Lauraceae leaves from the Albian-Cenomanian of Charente Maritime (Western France). *Palaeontology* 52, 323–336. <https://doi.org/10.1111/j.1475-4983.2009.00845.x>.

Crane, P.R., Friis, E.M., Pedersen, K.R., 1994. Palaeobotanical evidence on the early radiation of magnoliid angiosperms. *Plant Systematics and Evolution [Supplement]* 8, 51–72.

Crepet, W.L., Nixon, K.C., Daghlian, C.P., 2013. Fossil Ericales from the Upper Cretaceous of New Jersey. *International Journal of Plant Sciences* 174, 572–584. <https://doi.org/10.1086/668689>.

Doyle, J.A., Endress, P.K., 2010. Integrating Early Cretaceous fossils into the phylogeny of living angiosperms: Magnoliidae and eudicots. *Journal of Systematics and Evolution* 48, 1–35. <https://doi.org/10.1111/j.1759-6831.2009.00058.x>.

Drinnan, A.N., Crane, P.R., Friis, E.M., Pedersen, K.R., 1990. Lauraceous flowers from the Potomac Group (mid-Cretaceous) of eastern North America. *Botanical Gazette* 151, 370–384.

Estrada-Ruiz, E., Martínez-Cabrera, H.I., Cevallos-Ferriz, S.R.S., 2007. Fossil wood from the late Campanian–early Maastrichtian Olmos Formation, Coahuila, Mexico. *Review of Palaeobotany and Palynology* 145, 123–133. <https://doi.org/10.1016/j.revpalbo.2006.09003>.

Estrada-Ruiz, E., Upchurch, G.R., Wheeler, E.A., Mack, G.H., 2012. Late Cretaceous angiosperm woods from the Crevasse Canyon and McRae Formations, New Mexico, USA: Part 1. *International Journal of Plant Sciences* 173, 412–428. <https://doi.org/10.1086/664714>.

Falcon-Lang, H.J., Wheeler, E., Baas, P., Herendeen, P.S., 2012. A diverse charcoalfi ed assemblage of Cretaceous (Santonian) angiosperm woods from Upatoi Creek, Georgia, USA. Part 1: Wood types with scalariform perforation plates. *Review of Palaeobotany and Palynology* 184, 49–73. <https://doi.org/10.1016/j.revpalbo.2012.03.016>.

García-Hernández, P., Estrada-Ruiz, E., Martínez-Cabrera, H.I., 2016. Maderas fósiles de la Formación San Carlos (Cretácico Superior), Chihuahua, México. *Botanical Sciences* 94, 269–280. <https://doi.org/10.17129/botsci.438>.

Gryc, V., Vavrik, H., Sakala, J., 2009. Cenomanian angiosperm wood from the Bohemian Cretaceous Basin, Czech Republic. *International Association of Wood Anatomists Journal* 30, 319–329.

Hedrick, B.P., Zanno, L.E., Wolfe, D.G., Dodson, P., 2015. The slothful claw: osteology and taphonomy of *Nothronychus mckinleyi* and *N. graffami* (Dinosauria: Theropoda) and anatomical considerations for derived therizinosaurids. *PLoS One* 10 (6), e0129449. <https://doi.org/10.1371/journal.pone.0129449>.

Herendeen, P.S., 1991. Charcoalfi ed angiosperm wood from the Cretaceous of eastern North America and Europe. *Review of Palaeobotany and Palynology* 70, 225–239. [https://doi.org/10.1016/0034-6667\(91\)90032-X](https://doi.org/10.1016/0034-6667(91)90032-X).

IAWA Committee, 1989. IAWA list of microscopic features for hardwood identification. *International Association of Wood Anatomists Bulletin New Series* 10, 219–332.

InsideWood, 2004 onwards. <http://insidewood/lib.ncsu.edu/search>. Accessed August 2018.

Jefferson, T.H., 1987. The preservation of conifer wood: examples from the Lower Cretaceous of Antarctica. *Palaeontology* 30, 233–249.

Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78, 1946–1957.

Jud, N.A., Wheeler, E.A., Rothwell, G.W., Stockey, R.A., 2017. Angiosperm wood from the Upper Cretaceous (Coniacian) of British Columbia, Canada. *International Association of Wood Anatomists Journal* 38, 141–161. <https://doi.org/10.1163/22941932-20170164>.

Keller, J.A., Herendeen, P.S., Crane, P.R., 1996. Fossil flowers of the Actinidiaceae from the Campanian (Late Cretaceous) of Georgia. *American Journal of Botany* 83, 528–541.

Kew Bibliographic Database <http://kbd.kew.org/kbd/searchpage.do>.

Kirker, G.T., Blodgett, A.B., Arango, R.A., Lebow, P.K., Clausen, C.A., 2013. The role of extractives in naturally durable wood species. *International Biodeterioration & Biodegradation* 82, 53–58.

Kirkland, J.I., Wolfe, D.G., 2001. First definitive therizinosaurid (Dinosauria; Theropoda) from North America. *Journal of Vertebrate Paleontology* 21, 410–414.

Knobloch, E., Mai, D.H., 1984. Neue Gattungen nach Früchten und Samen aus dem Cenoman bis Maastricht (Kreide) von Mitteleuropa. *Feddes Repertorium* 95, 3–41.

Knobloch, E., Mai, D.H., 1986. Monographie der Früchte und Samen in der Kreide von Mitteleuropa, 47. *Rozpravy ústředního ústavu geologického*, Praha, pp. 1–219.

Lens, F., Schönenberger, J., Baas, P., Jansen, S., Smets, E., 2007. The role of wood anatomy in phylogeny reconstruction of Ericales. *Cladistics* 23, 229–254. <https://doi.org/10.1111/j.1096-0031.2006.00142.x>.

Mack, G.H., 1992. Paleosols as an indicator of climatic change at the Early–Late Cretaceous boundary, southwestern New Mexico. *Journal of Sedimentary Petrology* 62, 483–494.

Mädel, E., 1962. Die fossilen Euphorbiaceen-Hölzer mit besonderer Berücksichtigung neuer Funde aus der Oberkreide Süd-Afrikas. *Senckenbergiana Lethaea* 43, 283–321.

Maser, C., Anderson, R.G., Cromack Jr., K., Williams, J.T., Martin, R.E., 1979. Dead and down woody material. In: Thomas, J.W. (Ed.), *Wildlife Habitats in Managed Forests; the Blue Mountains of Oregon and Washington*. USDA Forest Service, Washington, D.C, pp. 78–95.

McDonald, A.T., Wolfe, D.G., Kirkland, J.I., 2010. A new basal hadrosauroid (Dinosauria: Ornithopoda) from the Turonian of New Mexico. *Journal of Vertebrate Paleontology* 30, 799–812. <https://doi.org/10.1080/0272463>.

McLellan, M., Haschke, L., Robinson, L., Carter, M.D., Medlin, A., 1983. Middle Turonian and younger Cretaceous rocks, northern Salt Lake Coal Field, Cibola and Catron Counties, New Mexico. In: Hook (compiler), J.W. (Ed.), *Contributions to Mid-Cretaceous Paleontology and Stratigraphy of New Mexico, Part II: New Mexico Bureau of Mines and Mineral Resources Circular*, no. 185, pp. 41–47.

Metcalfe, C.R., Chalk, L., 1950. Anatomy of the Dicotyledons. 2 Vols. Clarendon Press, Oxford.

Molenaar, C.M., Cobban, W.A., Merewether, E.A., Pillmore, C.L., Wolfe, D.G., Holbrook, J.M., 2002. Regional stratigraphic cross sections of Cretaceous rocks from east–central Arizona to the Oklahoma panhandle. *U.S. Geological Survey Miscellaneous Field Studies Map MF-2382*, 3 sheets.

Nixon, K.C., Crepet, W.L., 1993. Late Cretaceous fossil flowers of ericalean affinity. *American Journal of Botany* 80, 616–623.

Oakley, D., Falcon-Lang, H.J., 2009. Morphometric analysis of Cretaceous (Cenomanian) angiosperm woods from the Czech Republic. *Review of Palaeobotany and Palynology* 153, 375–385.

Page, V.M., 1979. Dicotyledonous wood from the Upper Cretaceous of central California. *Journal of the Arnold Arboretum* 60, 323–349.

Paillet, D., Flicoteaux, R., Ambrosi, J.-P., Médus, J., 2000. Les bois fossiles miopliocènes de Nkondo (lac Albert, Ouganda), composition minéralogique et mode de formation. The Mio-Pliocene fossil woods from Nkondo (Lake Albert, Uganda), mineralogical composition and formation. *Comptes Rendus de l'Académie des Sciences - Series IIa - Earth and Planetary Science* 331, 279–286.

Philippe, M., Gomez, B., Girard, V., Coiffard, C., Daviero-Gomez, V., Thevenard, F., Billon-Bruyat, J.-P., Guiomar, M., Latil, J.-L., Le loeuff, J., Néraudeau, D., Olivero, D., Schiögl, J., 2008. Woody or not woody? Evidence for early angiosperm habit from the Early Cretaceous fossil wood record of Europe. *Paleoworld* 17, 142–152. <https://doi.org/10.1016/j.palwor.2008.06.001>.

Poole, I., Gottwald, H., Francis, J.E., 2000. *Illicioxylon*, an element of Gondwanan Polar Forests? Late Cretaceous and Early Tertiary wood in Antarctica. *Annals of Botany* 86, 421–432.

Reolid, M., Philippe, M., Nagy, J., Abad, I., 2010. Preservation of phosphatic wood remains of the Brentskaardhaugen (Middle Jurassic) from Svalbard (Boreal Realm). *Facies* 56, 549–566.

Schmidt, M.W.I., Noack, A.G., 2000. Black carbon in soils and sediments: analysis, distribution, implications, and current challenges. *Global Biogeochemical Cycles* 14, 777–793.

Schönenberger, J., von Balthazar, M., Takahashi, M., Xiao, X., Crane, P.R., Herendeen, P.S., 2012. *Glandulocalyx upatoiensis*, a fossil flower of Ericales (Actinidiaceae/Clethraceae) from the Late Cretaceous (Santonian) of Georgia, USA. *Annals of Botany* 109, 921–936.

Serlin, B.S., 1982. An Early Cretaceous fossil flora from northwest Texas, USA: its composition and implications. *Palaeontographica* 182B, 52–86.

Spackman Jr., W., 1948. A dicotyledonous wood found associated with the Idaho Tempskyas. *Annals of the Missouri Botanical Garden* 35, 107–116.

Sweeney, I.J., Chin, K., Hower, J.C., Budd, D.A., Wolfe, D.G., 2009. Fossil wood from the middle Cretaceous Moreno Hill Formation: unique expressions of wood mineralization and implications for the processes of wood preservation. *International Journal of Coal Geology* 79, 1–17. <https://doi.org/10.1016/j.coal.2009.04.001>.

Takahashi, K., Suzuki, M., 2003. Dicotyledonous fossil wood flora and early evolution of wood characters in the Cretaceous of Hokkaido, Japan. *International Association of Wood Anatomists Journal* 24, 269–309. <https://doi.org/10.1163/22941932-90001597>.

Thayn, G.F., Tidwell, W.D., 1984. A review of the genus *Paraphyllanthoxylon*. *Review of Palaeobotany and Palynology* 43, 321–335.

Upchurch Jr., G.R., Dilcher, D.L., 1990. Cenomanian angiosperm leaf megafossils, Dakota Formation, Rose Creek locality, Jefferson County, southeastern Nebraska. *U.S. Geological Survey Bulletin* 1915, 55 pp.

Upchurch Jr., G.R., Crane, P.R., Drinnan, A.N., 1994. The megaflora from the Quantico locality (Middle to Upper Albian), Lower Cretaceous Potomac Group of Virginia. *Virginia Museum of Natural History Memoir* 4, 58 pp.

Viney, M., Mustoe, G.E., Dillhoff, T.A., Link, P.K., 2017. The Bruneau Woodpile: a Miocene phosphatized fossil wood locality in southwestern Idaho, USA. *Geosciences* 7, 82. <https://doi.org/10.3390/geosciences7030082>.

von Balthazar, M., Pedersen, K.R., Crane, P.R., Stampanoni, M., Friis, E.M., 2007. *Potomacanthus lobatus* gen. et sp. nov., a new flower of probable Lauraceae from the Early Cretaceous (Early to Middle Albian) of eastern North America. *American Journal of Botany* 94, 2041–2053.

von Balthazar, M., Crane, P.R., Pedersen, K.R., Friis, E.M., 2011. New flowers of Laurales from the Early Cretaceous (Early to Middle Albian) of eastern North America. In: Wanntorp, L., DeCraene, L.P.R. (Eds.), *Flowers on the Tree of Life*. Cambridge University Press, pp. 49–87.

Wheeler, E.A., 1991. Paleocene dicotyledonous trees from Big Bend National Park, Texas. Variability in wood types common in the Late Cretaceous and Early Tertiary, and ecological inferences. *American Journal of Botany* 78, 658–671.

Wheeler, E.A., 2011. InsideWood—A web resource for hardwood anatomy. *International Association of Wood Anatomists Journal* 32, 199–211. <https://doi.org/10.1163/22941932-90000051>.

Wheeler, E.A., Baas, P., 1991. A survey of the fossil record for dicotyledonous wood and its significance for evolutionary and ecological wood anatomy. *IAWA Bulletin* 12, 275–332. <https://doi.org/10.1163/22941932-90001256>.

Wheeler, E.A., Lehman, T.M., 2000. Late Cretaceous woody dicots from the Agua and Javelina Formations, Big Bend National Park, Texas, USA. *International Association of Wood Anatomists Journal* 21, 83–120.

Wheeler, E.A., Lehman, T.M., 2009. New late Cretaceous and Paleocene dicot woods of Big Bend National Park, Texas, and review of Cretaceous wood characteristics. *International Association of Wood Anatomists Journal* 30, 293–318. <https://doi.org/10.1163/22941932-90000220>.

Wheeler, E.A., Michalski, T., 2003. Paleocene and early Eocene woods of the Denver Basin, Colorado. *Rocky Mountain Geology* 38, 29–43.

Wheeler, E.A., McClammer, J., LaPasha, C.A., 1995. Similarities and differences in dicotyledonous woods of the Cretaceous and Paleocene, San Juan Basin, New Mexico, USA. *International Association of Wood Anatomists Journal* 16, 223–254.

Wheeler, E.F., Lee, M., Matten, L.C., 1987. Dicotyledonous woods from the Upper Cretaceous of southern Illinois. *Botanical Journal of the Linnean Society* 95, 77–100.

Wing, S.L., Boucher, L.D., 1998. Ecological aspects of the Cretaceous flowering plant radiation. *Annual Review of Earth and Planetary Sciences* 26, 379–421.

Wolfe, D.G., 1989. The stratigraphy and paleoenvironments of middle Cretaceous strata along the central Arizona–New Mexico border. Unpublished Masters thesis, University of Colorado, Boulder, 222 pp.

Wolfe, D.G., Kirkland, J.I., 1998. *Zuniceratops christopheri* n. gen. & sp., a ceratopsian dinosaur from the Moreno Hill Formation (Cretaceous, Turonian) of west–central New Mexico. *New Mexico Museum of Natural History and Science Bulletin* 14, 303–317.

Yaroshevsky, A.A., 2006. Abundances of chemical elements in the Earth's Crust. *Geochemistry International* 44, 48–55.