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SYSTEMATIC AFFINITIES OF EARLY EOCENE PETRIFIED WOODS FROM BIG SANDY RESERVOIR, SOUTHWESTERN WYOMING

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Petrified woods from the Eocene Bridger Formation of Big Sandy Reservoir, southwestern Wyoming, were examined to assess their diversity and systematic affinities. They are assigned to *Palmoxylon macginitiei* Tidwell, Simper, & Medlyn (Arecaceae), *Edenoxylon parviareolatum* Kruse (Anacardiaceae), *Laurinoxylon stichkai* sp. nov. (Lauraceae), *Wilsonoxylon edenense* gen. et sp. nov. (Canellaceae), and one unnamed dicotyledonous species of uncertain familial affinity. *Edenoxylon* and *Palmoxylon* are represented by multiple samples and appear to have been dominant in the local vegetation at the time of deposition. Although the floristic diversity from this locality is low, the affinities of these plants are consistent with other evidence that the climate in the late Early Eocene of this region was subtropical, in contrast with the present arid, temperate conditions.

Keywords: petrified woods, Eocene, Bridger Formation, southwestern Wyoming.

Introduction

Eocene sediments of western and central Wyoming are rich in fossil plant remains that have played an important role in the reconstruction of vegetation and climate (e.g., Berry 1930; MacGinitie 1969, 1974; Wing 1988; Wilf 2000). Most of the paleobotanical studies on this region have dealt with leaf impressions from lacustrine sediments. Well-preserved petrified woods are also abundant but have rarely been analyzed. The best-studied example of petrified woods in this region is the succession of fossil forests at Yellowstone National Park from the Sepulcher and Lamar River formations (late Early Eocene to early Middle Eocene) in northwestern Wyoming (Wheeler et al. 1977, 1978).

About a century ago, early rock hunters reported petrified stumps ~1.8–2.4 m high and up to ~1 m in diameter in Eden Valley, southwestern Wyoming (Hausel 2004). The Eden Valley area is well known among hobbyist collectors for the intrinsic beauty and gemstone-like preservation of petrified woods found there (Alexander 2009). Despite public interest, only a few taxonomic investigations have been performed on these woods (Kruse 1954; Tidwell et al. 1971, 1973), and the systematic affinity of most specimens has remained a mystery. A detailed examination of these woods is therefore necessary to generate a more complete understanding of the paleovegetation of this region, which to date is known mostly from fossil leaves. Furthermore, a study of these petrified woods will allow comparison with fossil woods from other regions, leading to a more complete understanding of the diversity and distribution of woody plants in the Early Eocene of the Northern Hemisphere.

In this article, we describe woods recovered from Big Sandy Reservoir, one of the petrified-wood sites in Eden Valley, including wood of Anacardiaceae, Canellaceae, Lauraceae, and an unidentified dicotyledonous species of uncertain familial affinity, and we provide additional information on co-occurring palm stems. We discuss the significance of these findings in relation to other data on the composition of late Early Eocene vegetation in the region.

Locality and Geology

We investigated the anatomy of silicified woods from immediately east of Big Sandy Reservoir (fig. 1), one of the most popular collecting sites for petrified wood in Eden Valley, part of the Greater Green River Basin in southwestern Wyoming. This site is ~30 km west of the Hay Ranch site, from which wood samples of similar age from the Green River Formation were described by Kruse (1954). The locality is at the base of the Bridger Formation, near the contact with the Laney Member of the Green River Formation, on the geologic map of Bradley (1961). This indicates a late Early Eocene age of ~49 Myr, according to the correlations of Smith et al. (2008). Sediments of the Bridger Formation are varied, including white to pale greenish-gray, mixed clastic tuffaceous sandstone, siltstone, mudstone, claystone, and shale, and are interpreted to represent fluvial, lacustrine, playa, paludal, marginal mudflat, basin margin, and volcanic-ash deposition (Roehler 1993; Buchheim et al. 2000; Smith et al. 2008; Murphey et al. 2011). Traditionally, the Bridger has been considered to represent a transition from a lacustrine depositional environment to one that was more fluvial as the lake began to regress (Buchheim et al. 2000).

In 2010, we collected fragments of petrified wood that were scattered on the surface as a result of previous excava-
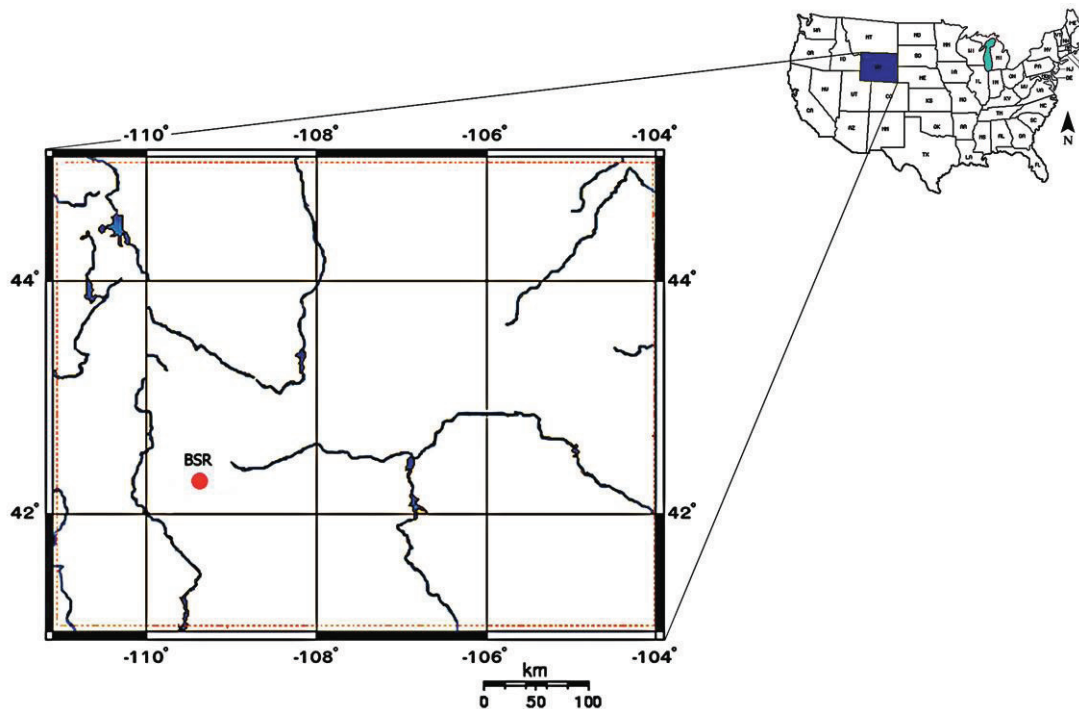

Fig. 1 Map showing location of Big Sandy Reservoir (BSR) fossil wood site in southwestern Wyoming.

tions by hobbyists. Many of the hand-dug excavations for individual logs or stumps were about a half-meter deep, exposing shale with some iron staining and grayish mudstone beneath the surface soil. The stems are typically mantled with a thick rim of poorly preserved algae that appears to have accumulated before deposition, indicating that specimens were probably deposited in a shallow lake (Roehler 1993). Besides the wood, two specimens of *Knightia* fish and some snail shells were found at the same site. The gastropods are very small (~2–3 mm in diameter) and are similar to the modern freshwater snails of the Planorbidae that usually live in slow-moving streams, marshes, or lakes (John Slapcinsky, personal communication, 2010). An undetermined dicot leaf impression (specimen UF327-54538) and part of a pinna impression of *Lygodium kaulfussi* (UF327-54541) were also collected.

This site contains abundant anatomically preserved stems of *Palmoxylon macginitiei*, which range from 20 to 30 cm in basal diameter (Tidwell et al. 1971). In their treatment of the palm, Tidwell et al. (1971) did not mention any other types of stems; however, subsequent collecting by Stichka et al. (see below) has revealed many dicotyledonous logs and/or stumps. We studied the anatomy of dicotyledonous woods, along with that of the palm stems, to learn more about the component trees of the original vegetation.

Material and Methods

The specimens used in this study are from a site east of Big Sandy Reservoir, in Sublette County, Wyoming (fig. 1). Fifty-one samples were studied, 12 of which were collected by James B. Stichka from 1966 to 1984 and donated to the Paleobotanical Collection of the Florida Museum of Natural History in December 2009. With Stichka's guidance, we revisited the site in June 2010 to record the geographic coordinates, study the geology, and collect additional specimens. The collections from this site, covering an area of ~2 km² (UF locality 327; 42°17.0′N, 109°21.9′W), are deposited at the Florida Museum of Natural History. The samples are believed to represent different individuals because the pieces were found in separate excavations.

Most of the slides for anatomical study were prepared by the acetate peel method (Galtier and Phillips 1999) because this method gave quick results similar in quality to the standard ground-thin-section method traditionally used for such fossil woods. Other sections were prepared by standard petrographic grinding methods with a Buehler thin-sectioning machine.

For comparison with previously described Eocene woods from Hay Ranch, also in Eden Valley, we borrowed the original specimens of Kruse (1954) from the Cleveland Museum of Natural History (CMNH). In some cases, the original thin sections had been lost, so we prepared new sections from the original samples, following the procedures indicated above, for curation at CMNH. We used a paper-thin diamond blade on a Microslice II annular saw to minimize kerf loss when cutting wafers from smaller samples.

The slides were examined and photographed by transmitted-light microscopy with a Zeiss Axiophot microscope. Identifications were made with reference to the InsideWood Web site (InsideWood 2004–; Wheeler 2011) and through comparison with descriptions and illustrations of other fossil and extant

woods and study of modern wood slides at the Smithsonian Institution, Washington, DC.

At least five areas were counted for the calculation of vessels per square millimeter, and at least 25 cells were measured for quantitative values, except where we have indicated a smaller number of measurements because of patchy preservation. For species represented by multiple samples, we provide the mean and standard deviation (SD) for the samples with the lowest and highest means. Anatomical descriptions follow the terminology and definitions of Wheeler et al. (1989).

Results: Systematic Descriptions and Affinities of Fossil Wood

Family—Anacardiaceae Lindl.

*Genus—*Edenoxylon *Kruse*

*Species—*Edenoxylon parviareolatum *Kruse*

Specimens studied. UF327-53954, 53956 (fig. 2), 53958–53961, 54501, 54506, 54519, 54523, 54526, 54528, 54529, and 54537.

Description. Growth ring boundaries intermediate between distinct and indistinct, marked by a change in fiber radial diameter and marginal parenchyma. Wood semi-ring-porous to diffuse-porous, with a distinct ring of closely spaced early-wood vessels that are not markedly larger than the latewood vessels. Vessel frequency 56–70/mm^2. Vessels solitary (23%–25%) and more commonly in radial multiples of 2–6, occasionally in clusters of 2–4; round to slightly oval in outline, mean tangential diameters of samples 56 ($n = 12$; SD $= 14$) to 101 (SD $= 19$) μm, with a total range of 35–130 μm; mean vessel element length 224 ($n = 14$, SD $= 66$) to 362 (SD $= 106$) μm, with a total range of (88–) 150–500 μm; perforation plates simple. Intervessel pitting crowded alternate (fig. 2E), small to medium, 4–6 μm (occasionally 7 μm; mean 5 μm). Vessel-ray pits with much-reduced borders to apparently simple, usually horizontally elongate (fig. 2J, 2K). Tyloses abundant. Black deposits fill the lumina of some vessel elements. Axial parenchyma scanty paratracheal to vasicentric and occasionally in marginal or seemingly marginal bands (fig. 2A, 2B, 2I); at least seven cells per parenchyma strand (fig. 2I). Rays commonly 1- (2- or 3-)seriate, or up to 5-seriate when containing gum ducts; a portion of one specimen shows an unusual area of wound tissue. Gum ducts common, 1 or 2 (4)/ray, oval to elliptical (rarely round) in tangential view, and varying in size (fig. 2D). The size of gum ducts typically ranges from (25) 30 to 50 (80) μm wide (mean 38 μm) and from (30) 50 to 100 (200) μm high (mean 68 μm).

Mean multiseriate ray heights 362 (SD $= 118$) to 393 (SD $= 111$) μm. Mean height of rays without gum ducts 285 (SD $= 109$) to 423 (SD $= 195$) μm, rays 14–21/mm. Mean width of rays without gum ducts 16 (SD $= 7$) to 23 (SD $= 9$) μm. Rays heterocellular, consisting of two types, the first having procumbent body cells and one to four rows of upright/square marginal cells (fig. 2G, 2H) and often including gum ducts, and the second consisting of procumbent, square, and upright cells mixed throughout the body (fig. 2L). Rays not storied. Prismatic crystals present in some of the upright

ray cells (fig. 2K, 2L). Fibers septate (seen more clearly in radial section; fig. 2F), with thin to medium-thick walls. Helical thickenings absent.

Comments. This species, represented by at least 16 samples, appears to have been dominant among the dicotyledons recovered from the Big Sandy Reservoir site. The estimated diameter of the stems ranges from at least 6 to 20 cm.

Affinities. We consider these specimens to represent *E. parviareolatum*, which was originally described from the Hay Ranch site of similar age ~30 km to the east of our site (Kruse 1954). The woods correspond in the density and composition of rays, vessels, gum ducts, and crystals. However, there are some differences that could indicate that they are distinct taxa. (1) Axial parenchyma is rare in Kruse's holotype from Hay Ranch, but it ranges from scanty paratracheal to vasicentric and occasionally occurs in marginal bands in the Big Sandy Reservoir samples. (2) Rays in Kruse's specimen (fig. 3C) are almost exclusively uniseriate (rarely biseriate), but in the Big Sandy specimens they are more varied, from uniseriate to occasionally 2- or 3-seriate. (3) Vessels in the holotype are smaller (mean tangential diameter 50 μm) than those in our samples (56–101 μm). It is probable, however, that these differences relate to xylem maturity. Kruse's samples were from small-diameter axes (a twig or small stem 3.7 cm in diameter and a root 1.7 cm in diameter) and would be juvenile rather than mature stem wood.

The fossil genus *Edenoxylon* was erected by Kruse (1954) with a detailed description and images but without a formal diagnosis. A generic diagnosis was provided later, with the report of *Edenoxylon aemulum* from the Eocene of Herne Bay, Kent, England (Brett 1966; Gregory et al. 2009). Subsequently, another specimen, from the Eocene of Sheppey, ~20 km west of Herne Bay, was named *Edenoxylon? atkinsoniae* (Crawley 1989); however, that sample lacks the gum ducts present in the type species of the genus. Crawley (1989) emended *Edenoxylon* to include species that lacked gum ducts (radial canals), but we retain the genus in the narrower concept of Kruse (1954) and Brett (1966).

We reexamined Kruse's original slides of *E. parviareolatum* (CMNH B 3280) and made some new slides from the holotype specimen, and we provide new figures here (fig. 3) for direct comparison with the Big Sandy samples. We found that axial parenchyma is not absent in *E. parviareolatum*, as indicated in Kruse's description, but rare, with scanty paratracheal distribution (fig. 3D). The intervessel pits (fig. 3D) were remeasured horizontally, including the borders, and found to range from (3) 4 to 5 (6) μm, confirming the small size described by Kruse. Rays in the holotype range from 12 to 20/mm, similar to their size in our specimens from Big Sandy Reservoir, and are commonly composed of procumbent cells and one marginal row of upright and/or square cells (fig. 3F), occasionally with procumbent and square cells mixed throughout (fig. 3E). The small diameter of the holotype stem (or twig) presents some challenges for the identification of woods from larger-diameter stems, because wood anatomical features can vary with maturation.

Among the *Edenoxylon* specimens described in this study, specimen UF327-53961 (~14 cm in diameter) is the most similar to Kruse's holotype in being mostly uniseriate. However, 2–3-seriate rays were observed in a tangential-section
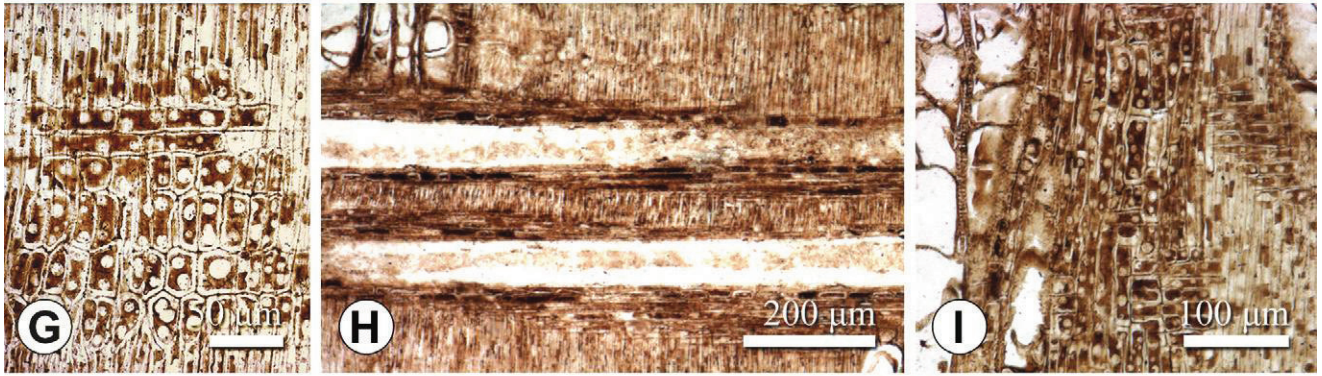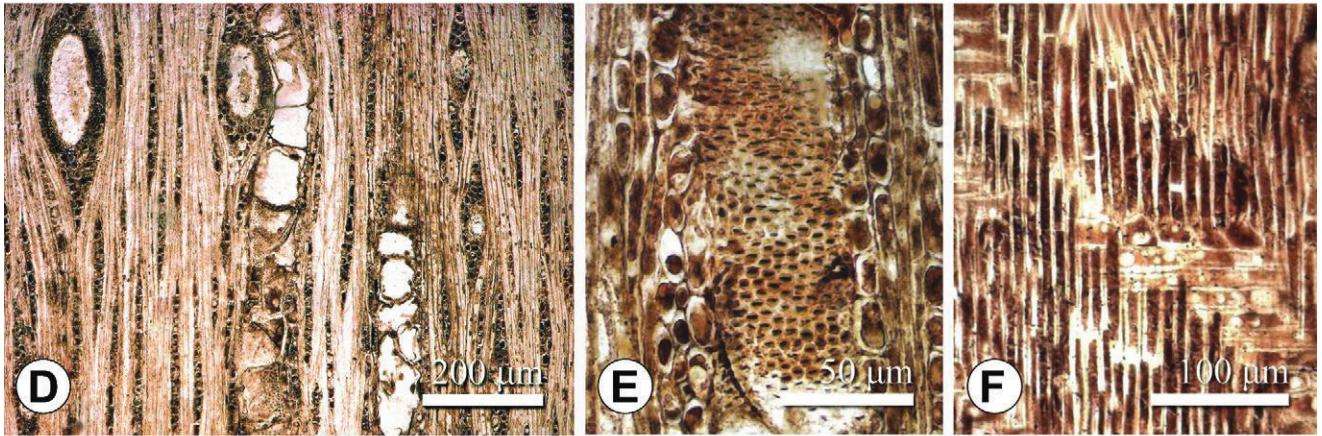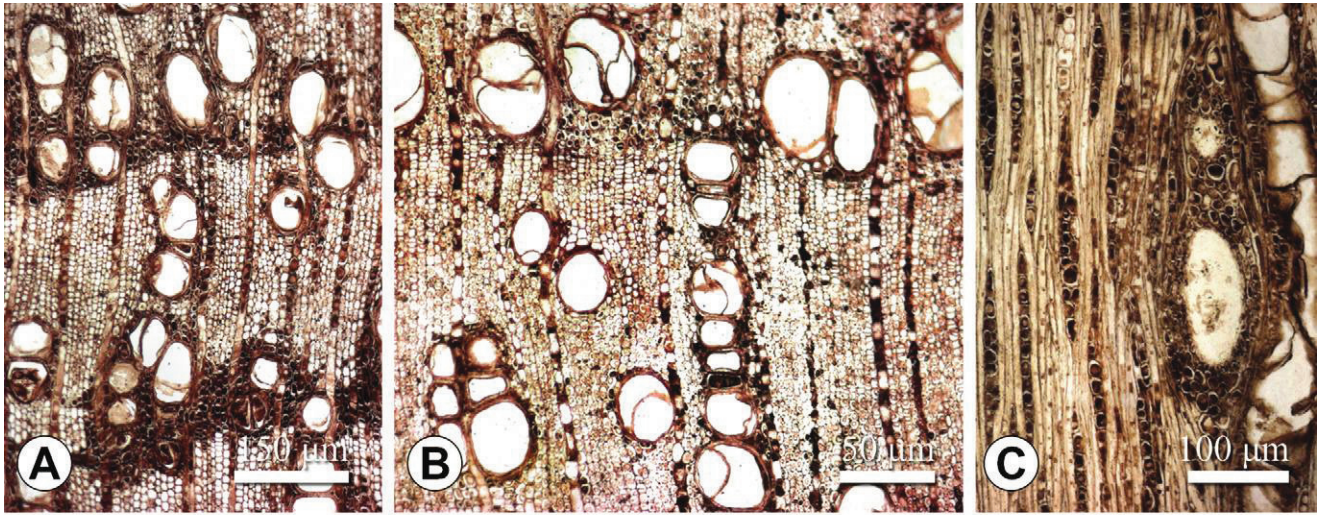
slide in the area of a branch collar, where the wood was cut through a very small attached branch, showing the pith and xylem in cross section (~3 mm in diameter, excluding bark). In the branch area, vessels are solitary and in radial multiples, fibers are thin walled, and axial parenchyma was not observed.

In specimen UF327-53960 (~8 cm in diameter), axial parenchyma cells are rare near the pith but gradually increase in abundance away from the pith. Rays close to the pith are exclusively uniseriate, but biseriate as well as uniseriate rays occur farther from the pith. Hence, parenchyma and ray seriation varies within the wood of an individual tree, depending on maturity and the region examined. Therefore, on the basis of wood anatomy alone, there are not enough differences between Kruse's sample and the Big Sandy Reservoir specimens to justify placing them in different species.

The anatomical features of *E. parviareolatum* show similarities to those of modern wood of the families Anarcardiaceae and Burseraceae. These similarities include radial gum ducts, simple perforation plates, alternate intervessel pitting, vessel-ray parenchyma pits with reduced borders, and scanty paratracheal to vasicentric axial parenchyma. Brett (1966) made a table comparing wood of five anacardiaceous tribes with that of Burseraceae and *Edenoxylon*. He indicated that burseraceous woods uniformly possess unilaterally compound vessel-ray pits, as a distinction from *Edenoxylon*. However, vessel-ray pitting in Burseraceae is generally described as pits with much-reduced borders to apparently simple; the pits are rounded or angular and may be elongated horizontally or vertically (InsideWood 2004–; Ogata et al. 2008), as in Anacardiaceae and *Edenoxylon*. Among burseraceous woods, similar anatomy can be found in *Protium*; however, this genus is distinguished by much lower vessel density (~5–20, occasionally 20–40/mm^2) and typically larger intervessel pits ($\geq$10 μm; Metcalfe and Chalk 1950; InsideWood 2004–). The larger intervessel-pit size applies to many other Burseraceae, indicating that *Edenoxylon* probably does not represent that family. The full suite of characters observed in *Edenoxylon* is best accommodated within Anacardiaceae, as concluded by previous authors (Kruse 1954; Brett 1966). One of the differences between *Edenoxylon* and most extant anacardiaceous wood is the minute to small intervessel pit size (4–6 μm), which is unusual compared to the usual mean diameter of ~7 to at least 10 μm for the Anacardiaceae (Terrazas 1996; Ogata 2008). There are, however, some examples of woods with smaller pits (see below).

The summary tables of modern-wood characters in the tribes of Anacardiaceae provided by Brett (1966) and Terrazas (1994) allow us to distinguish *Edenoxylon* from the Dobineae because of the absence of radial canals in wood of this tribe. Species of tribe Mangiferae (Anacardieae) tend to have homocellular rays and banded parenchyma (Metcalfe and Chalk 1950) and differ from *Edenoxylon* in the larger intervessel pits (mean 11 μm; Terrazas 1994). Semecarpeae

are distinguished from *Edenoxylon* by the absence of septate fibers (Brett 1966; Terrazas 1994). Although the precise relationship of *Edenoxylon* to extant genera of Anacardiaceae remains uncertain, the tribes Rhoideae (Rhoeae) and Spondiae (Spondiadeae), both of which can have septate fibers (Terrazas 1994) and gum ducts in rays, are the most likely tribes to which this fossil might belong. Very small (*Faguetia* and *Trichoscypha*) and small (*Lithraea*, *Protorhus*, and *Rhus*) intervessel pits are known in the Rhoideae (Metcalfe and Chalk 1950; Brett 1966).

Worldwide, at least 27 genera of fossil anacardiaceous wood have been reported (Gregory et al. 2009). Many of them were reported from Asia, especially India; others are from the Americas, Europe, and Africa. Fossil anacardiaceous woods previously reported from North America include *Anacardioxylon*, *Maureoxylon*, *Rhus*, *Schinoxylon*, *Tapirira*, and *Terrazoxylon* as well as *Edenoxylon* (Wheeler 1978; Wheeler and Manchester 2002; Gregory et al. 2009). *Anacardioxylon* differs from the *Edenoxylon* specimens described above in having either wider rays (often more than 4 cells wide, although some are 1–3-seriate) or a different arrangement of axial parenchyma (vasicentric, aliform, confluent) and usually having larger intervessel pits of at least 10 μm; gum ducts are common in *Edenoxylon* but are either absent or not common in the many species of *Anacardioxylon* (InsideWood 2004–). Some species of *Anacardioxylon* that have gum ducts, e.g., *Anacardioxylon shardai* Prakash & Tripathi, are still different from *Edenoxylon* in having large intervessel pits of at least 10 μm, axial parenchyma varying from scanty paratracheal to vasicentric, aliform, confluent, or banded. *Anacardioxylon sorindeoides* Lemoigne differs in having only one row of upright and/or square marginal cells (InsideWood 2004–).

Although fossil leaves (Brown 1934; MacGinitie 1969) and woods (Wheeler et al. 1978, 2006) of *Rhus* have been reported from the Middle Eocene elsewhere in Wyoming, *Edenoxylon* is readily distinguished from that genus. *Rhus* wood is typically ring-porous, unlike the diffuse-porous wood of *Edenoxylon*. Some *Rhus* species, e.g., *Rhus taitensis*, have diffuse-porous wood, but the vessels (mean tangential diameter 502 ± 118 μm) and intervessel pits (10 μm) are larger in *R. taitensis* than in *Edenoxylon* (Kruse 1954; Brett 1966; Terrazas 1994; InsideWood 2004–). In addition, the Eocene wood *Rhus crystallifera* Wheeler, Scott & Barghoorn from Yellowstone has mostly solitary pores and intervessel pits up to 10 μm in size, whereas *Edenoxylon* woods commonly have pores in radial multiples of 2–6 and smaller intervessel pits (Wheeler et al. 1978).

The other Eden Valley wood assigned to Anacardiaceae, *Schinoxylon actinoporosum* Kruse (1954), also has gum ducts and minute to small intervessel pit sizes of (3) 4–6 μm, but its vessels are arranged in radial rows, a characteristic of *Schinus* and the fossil genus *Schinoxylon*. *Schinoxylon actinoporosum*

Fig. 2 *Edenoxylon parviareolatum* Kruse (UF327-53956). *A, B,* Growth rings intermediate between distinct and indistinct, vessels solitary and in radial multiples of 2–6, wood diffuse-porous. *C, D,* Narrow rays 1–2-seriate, plus wider rays 3–5-seriate, containing gum ducts of various sizes; vessels with tyloses. *E,* Alternate intervessel pits. *F,* Septate fibers. *G,* Heterocellular ray. *H,* Gum ducts among the ray cells. *I,* Axial parenchyma strands. *J, K,* Horizontally elongate vessel-ray pits. *L,* Ray with both procumbent and square cells; prismatic crystals in square ray cells. In all figures, XS, TLS, and RLS denote cross, tangential, and radial sections, respectively. *A, B* = XS; *C–E* = TLS; *F–L* = RLS.
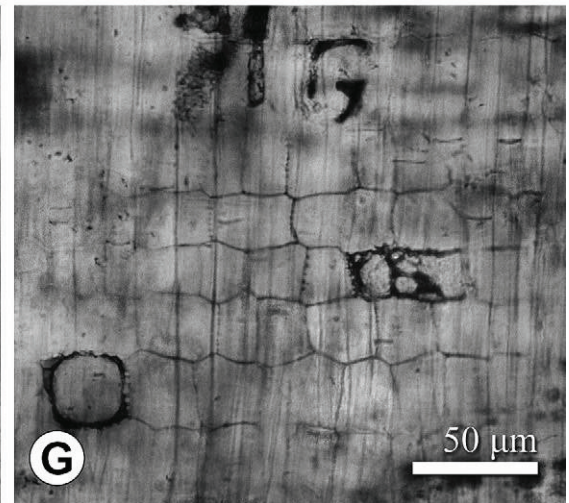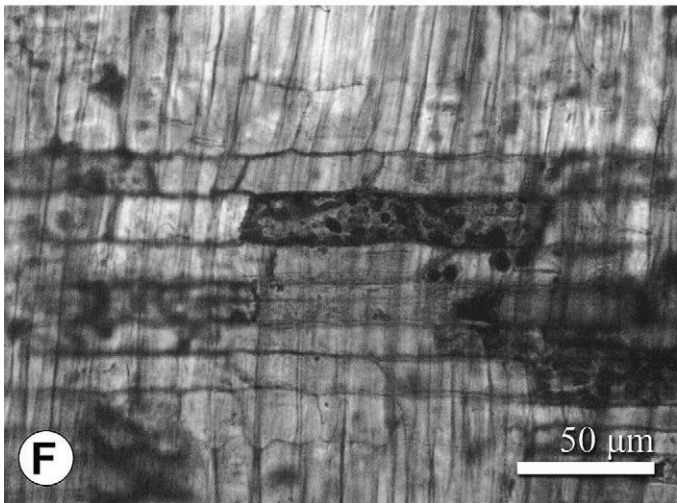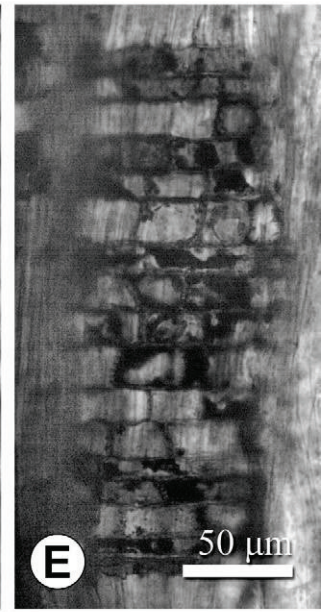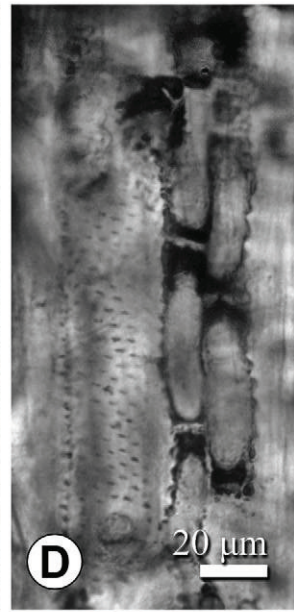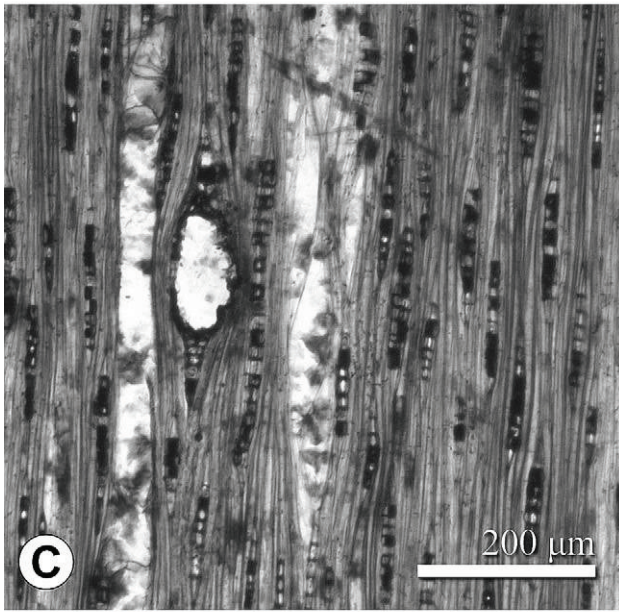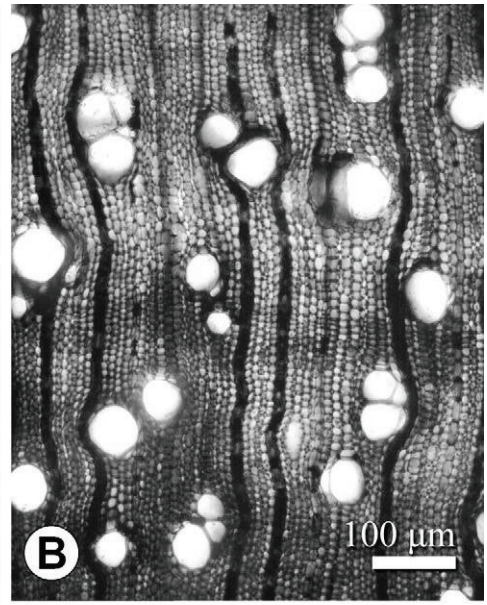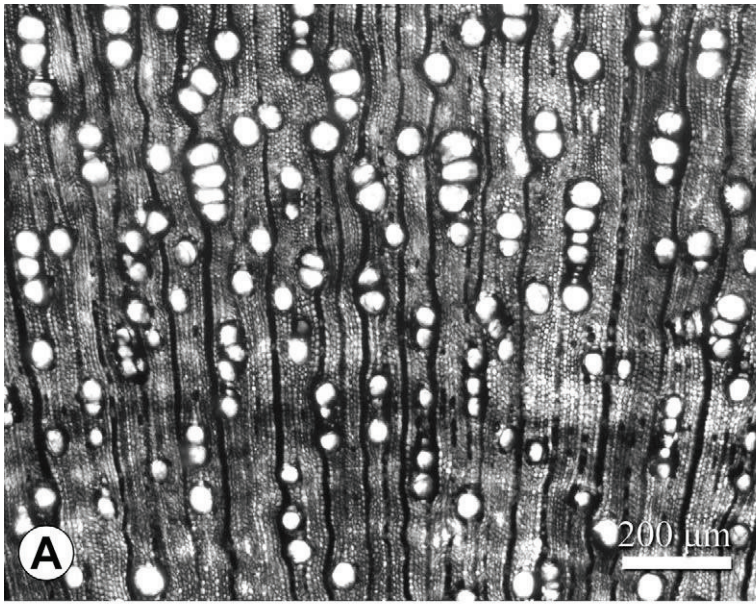
has two kinds of vessels: large ones, which are commonly solitary but occasionally in radial multiples of 2–4, and smaller ones, which are mostly in radial multiples of 10–25 (Kruse 1954; H. O. Kruse, personal observation). In additional, helical thickenings present throughout the body of the vessel elements can be seen clearly in the narrower vessels of *S. actinoporosum*; this feature is absent in *Edenoxylon*. Axial parenchyma and septate fibers, which are apparently absent in *S. actinoporosum*, are present in *Edenoxylon*.

Other Eocene woods of Anacardiaceae from western North America include three species from the Middle Eocene Clarno Nut Beds of Oregon (Wheeler and Manchester 2002): *Maureroxylon crystalliphorum*, *Tapirira clarnoensis*, and *Terrazoxylon ductifera*. Of these, only the latter two have the combination of consistently diffuse-porous wood, gum ducts in rays, and septate fibers meriting close comparison with *Edenoxylon*. The number of rays per millimeter is ~2–4 times greater in *E. parviareolatum* than in *T. clarnoensis* and *T. ductifera*. *Terrazoxylon* has indistinct growth rings, intervessel pits 5–6 um in diameter, rays that often have more than four marginal rows of upright cells, and uniseriate rays composed of all upright cells, plus rays that are similar to those of *Edenoxylon*, consisting of upright and procumbent cells mixed throughout. However, the gum ducts are less prominent, and the upright ray cells in *Terrazoxylon* are 2–3 times higher than those in the procumbent cells, whereas in *Edenoxylon* they are only ~1.5–2 times higher. Compared to that in *T. clarnoensis*, the vessel density in our specimens is much higher (by 4–5 times) and the intervessel pits are smaller (4–6 vs. 7 μm), and the diffuse parenchyma that is occasionally present in *T. clarnoensis* (Wheeler and Manchester 2002) was not observed in our material (although Kruse indicated this condition for the type material of the genus). The anatomical comparison of our specimens with Kruse's type material of *E. parviareolatum* and with *E. aemulum*, *T. clarnoensis*, and *T. ductifera* is shown in table 1. Fossil fruits from the Eocene confirm the presence of both extinct and extant genera (Manchester 1994), and it is possible that *Edenoxylon* corresponds to one of the extinct fruit genera, e.g., *Pentoperculum*, which is known from both the Clarno Nut Beds and the Bridger Formation at Blue Rim, Wyoming.

Family—Lauraceae Juss.

Genus—Laurinoxylon *Felix*

Species—Laurinoxylon stichkai *N. Boonchai et Manchester sp. nov.*

Holotype. UF 327-53955, here designated (fig. 4).

Etymology. We take pleasure in naming this species in honor of James B. Stichka, who collected and donated the specimens analyzed in this study.

Description. Growth ring boundaries weakly developed. Wood diffuse-porous. Vessels solitary (28%), more commonly in radial multiples of 2–4 (rarely 5), occasionally in clusters of 3–4 (6). Vessels 8–19/mm^2 (mean 14.4/mm^2). Solitary vessels oval in outline. Vessels small to medium in tangential diameter, 70–170 μm (mean 117 μm; SD = 31). Vessel element length (199–) 231–501 μm (mean ~310 μm); perforation plates simple (fig. 4F), intervessel pits alternate (fig. 4E) and medium to large, 8–12 μm. Vessel-ray pits with much reduced borders to apparently simple, pits rounded or angular and horizontal (scalariform, gashlike) to occasionally oblique (fig. 4G). Axial parenchyma scanty paratracheal to vasicentric; strands 4–8 (–12) cells long, commonly including oil cells (fig. 4C). Rays 28–63 μm wide (avg. 44 μm), 2–3-seriate, (150–) 220–400 (–460) μm high (avg. 285 μm). Rays heterocellular, consisting of procumbent body cells and a marginal row of upright/square cells. Rays nonstoried. Crystals not observed. Oil cells barrel shaped to oval, thin walled, and very common as isolated cells in ray margins (fig. 4C, 4D) or occasionally in the body of the ray, plus sometimes isolated or in small chains of 2–4 (rarely 6) cells in parenchyma strands. The oil cells range from 38 to 69 μm wide (average 54 μm) and from 56 to 125 μm high (average 86 μm), measured from tangential section. The density of oil cells ranges from 11 to 36 cells/mm^2 (mean 23 cells/mm^2) in cross section and 10–29 cells/mm^2 (mean 24 cells/mm^2) in tangential section. Fibers septate, very thin walled.

Comments. This species is represented by one sample, estimated diameter 60 cm, collected from the Big Sandy Reservoir site in 1984 by James Stichka.

Affinities. *Laurinoxylon stichkai* shares numerous features with modern lauraceous woods, including oil cells occurring in rays and axial parenchyma (fig. 4A–4C); alternate intervessel pitting; vessel-ray parenchyma pits with reduced borders; paratracheal axial parenchyma; vessels of medium diameter; and narrow heterocellular rays (Metcalfe and Chalk 1950; Richter 1981; Metcalfe 1987; Wheeler and Manchester 2002). Although this family is easily identified by their wood anatomical characters, distinguishing individual genera of Lauraceae by means of wood anatomy is difficult and cannot always be done (Edwards 1931; Metcalfe and Chalk 1950; Stern 1954; Richter 1981; Ogata et al. 2008). Nevertheless, *L. stichkai* is easily distinguished from *Sassafras*, which has ring-porous wood, and from *Cinnamomum*, which typically has diffuse, vasicentric, aliform, and confluent axial parenchyma. *Cryptocarya* species commonly have oil and/or mucilage cells associated with the axial parenchyma rather than in the ray cells (Kribs 1968; Metcalfe 1987; Ilic 1991; InsideWood 2004–), whereas the oil cells of *L. stichkai* are common in both rays and axial parenchyma.

Laurinoxylon stichkai resembles extant wood of the genera *Actinodaphne*, *Aniba*, *Endlicheria*, *Laurus*, *Licaria*,

Fig. 3 *Edenoxylon parviareolatum* Kruse holotype of Kruse (1954) from Hay Ranch, CMNH B 3280 and B2818. *A*, *B*, Indistinct growth rings, marked by a change in fiber radial diameter; vessels solitary and in radial multiples of 2–6 (–8); diffuse-porous wood; fiber walls thin. *C*, Narrow rays, 1- (2-)seriate, plus wider rays with a central gum duct. *D*, Alternate intervessel pits and scanty paratracheal parenchyma. *E*, Ray with procumbent and square cells mixed throughout the ray. *F*, Body ray cells procumbent with a row of upright/square marginal cells. *G*, Body ray cells square with some upright marginal cells. *A*, *B* = XS; *C* = TLS; *D–G* = RLS.

Table 1

Anatomical Comparison of *Edenoxylon parviareolatum* (from Big Sandy Reservoir [BSR] and Hay Ranch [HR]), *Edenoxylon aemulum*, *Tapirira clarnoensis*, and *Terrazoxylon ductifera* (Kruse 1954; Manchester 1977; Brett 1996)

	E. parviareolatum (BSR)	*E. parviareolatum* (HR)	*E. aemulum*	*T. clarnoensis*	*T. ductifera*
Locality	Big Sandy Reservoir, Wyoming	Hay Ranch, Wyoming	Herne Bay, Kent, England	Clarno Nut Beds, Oregon	Clarno Nut Beds, Oregon
Epoch	Early Eocene	Early Eocene	Early Eocene	Middle Eocene	Middle Eocene
Diameter (cm)	9–20 (stem)	3.7 (stem)	Not indicated	1.5–3 (stem)	≤20
Porosity	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse
Vessel density (per mm²)	56–70	~100	44 (mean)	8–13	18–48
Vessel arrangement	Solitary and radial, multiples of 2–6	Solitary and radial, multiples of 2–3 (–9)	Solitary and radial, multiples of 2–6 (–8)	Solitary and radial, multiples of 2–3 (–5)	Solitary and radial, multiples of 2–6
Mean (range) vessel tangential diameter (μm)	56–101[a] (35–130)	50 (not described)	95 (30–140)	121–138 (not described)	100–108 (not described)
Mean (range) vessel element length (μm)	224–362 (88–500)	(100–300)	Not indicated	165 (425–544)	377–457 (not described)
Perforations	Simple	Simple	Simple	Simple	Simple
Intervessel pits, size (μm)	Alternate, 4–6 (–7)	Alternate, (3–) 4–5 (–6)	Alternate, ~5	Alternate, ~7	Alternate, 5–6
Vessel-ray pitting	Pits with much-reduced border to apparently simple	Pits with much-reduced border to apparently simple	Pits with much-reduced border to apparently simple	Pits with much-reduced border to apparently simple	Pits large with much-reduced border to apparently simple
Axial parenchyma	Scanty, paratracheal to vasicentric, occasional marginal bands	Rare, scanty, paratracheal to vasicentric	Scanty, paratracheal	Uniseriate vasicentric, usually incomplete sheath, occasionally diffuse	Uniseriate, vasicentric
Fibers	Thin to medium-thick walls (2–3.5 μm), septate	Thin to slightly thick walls (2–3 μm), septate	Thin walls, septate	Very thin to thin walls (2–2.5 μm), septate	Thin to medium-thick walls (2–3.5 μm), septate
Ray type	Heterocellular	Heterocellular	Heterocellular	Heterocellular	Heterocellular
Ray seriation	1 (2–3), 3–5 in wide rays	1–3, mostly 1	Almost all 1 near the pith; almost all 2, plus some 3–5 in mature wood	(1–) 2 (–5)	1–2 (–4)
Mean ray height (μm)	With duct, 362–393; without ducts, 304–423	Range 70–450	With duct, up to 1000	Without ducts, 350 (range, 140–500)	Without ducts, 344–360
Rays/mm	14–21	12–20	6–12	6–8	5–9
Width of gum ducts (μm)	(25–) 30–50 (–80)	28–70	Not described	20–50	20–30

[a] Mean of the specimen with narrowest diameter and mean of the specimen with largest diameter, after measurements of many specimens of the same species.

Litsea, *Nectandra*, *Neolitsea*, *Nothaphoebe*, *Ocotea*, and *Systemonodaphne* in having oil cells associated with both rays and axial parenchyma, simple perforation plates, and heterocellular rays with a row of upright/square marginal cells. Janssonius (1926) investigated the occurrence of oil cells in almost every genus of lauraceous wood and found that the oil cells are widely variable in different species of the family as to size, shape, and distribution. He noted that the oil cells tend to occur in three main places: at the margins of parenchyma, diffuse among the libriform fibers, and often among the upright cells of the rays (Janssonius 1926).

Wheeler et al. (1977) emphasized that the presence or absence, distribution, and abundance of idioblasts varies greatly within a genus and noted that some species of *Ocotea* are without idioblasts, that some have idioblasts in ray tissues, and that others may have idioblasts only isolated among the fibrous elements. Although Richter (1981) cautioned that any quantitative statement on the presence of oil or mucilage cells in a single wood sample cannot be considered represen-

tative of the entire genus or even of a species among extant Lauraceae, he showed that the oil cells in wood of *Ocotea* spp. are apparently more crowded than those in other genera, a feature shared with the fossil species described here. *Ocoteoxylon*, a form genus for fossil woods believed to have affinities with *Ocotea*, was proposed by Schuster (1907). Two species of *Ocoteoxylon*, *Ocoteoxylon algovicum* Schuster (1909) from the Upper Oligocene and *Ocoteoxylon tigurinum* Schuster (1907) from the Cretaceous and Eocene of Germany (Bavaria), were described, but subsequently the species were reassigned to genus *Laurinium* because of Gothan's (1908) belief that the separation of *Ocoteoxylon* from *Laurinium* was unjustified (Edwards 1931). Later, they were transferred to the form genus *Laurinoxylon* as *Laurinoxylon algovicum* and *Laurinoxylon tigurinum*, respectively (Berger 1950; Gregory et al. 2009).

Thus far, fossil woods of Lauraceae from around the world have been attributed to ~22 genera (Gregory et al. 2009), including both modern and fossil wood genera. Some that had been assigned to extant genera were reinvestigated and merged in synonymy with fossil wood morphogenera (Gregory et al. 2009). The genus with the most species (at least 119) is *Laurinoxylon* Felix (Gregory et al. 2009). *Laurinoxylon* is widely accepted as a genus for lauraceous fossil woods, although it is actually a junior synonym of *Ulminium* (Dupéron-Laudoueneix and Dupéron 2005, pp. 135–136). The diagnosis of *Laurinoxylon* was recently emended by Dupéron et al. (2008) as fossil wood with vessels of medium diameter, both solitary and in radial multiples; simple and sometimes scalariform perforation plates; alternate, moderately large intervessel pits; tyloses; paratracheal axial parenchyma; 1–5-seriate, slightly heterocellular rays usually less than 1 mm high; vessel-ray pits large, often elongate; fibers libriform or with pits on radial walls; and oil or mucilage cells (idioblasts) present.

Wheeler et al. (1977) described three species of Lauraceae from Yellowstone National Park, *Ulminium eocenicum*, *Ulminium parenchymatosum*, and *Ulminium porosum*, which were later treated as *Laurinoxylon eocenicum*, *Laurinoxylon parenchymatosum*, and *Laurinoxylon porosum* (Dupéron-Laudoueneix and Dupéron 2005; Gregory et al. 2009), respectively. *Ulminium eocenicum* has predominantly solitary (70%) vessels occasionally in pairs but rarely in radial multiples, in contrast to *L. stichkai*, which has a lower proportion of solitary vessels (28%) and more common radial multiples of 2–5. Banded parenchyma (3–8 cells wide) is present in *U. eocenicum* but absent in *L. stichkai*. The density of oil cells in *U. eocenicum* (1–2 cells/mm^2) is only ~5% that of *L. stichkai*.

Although idioblasts are similarly abundant in *U. parenchymatosum* (15–35 cells/mm^2), their shape, size, and distribution are completely different from those in *L. stichkai*. For example, the idioblasts in *U. parenchymatosum* are very elongated (height ~8 times greater than the tangential width), unlike the barrel-shaped to oval oil cells in *L. stichkai*. In addition, idioblasts in *U. parenchymatosum* are scattered among the fibrous elements or to the side of a ray, but in *L. stichkai* idioblasts are confined to the ray and axial parenchyma. In addition, *U. parenchymatosum* has vasicentric, aliform, and aliform-confluent axial parenchyma rather than the scanty paratracheal to vasicentric condition seen in *L. stichkai*.

Rays in the three species of *Ulminium* discussed above are larger than those of *L. stichkai*, in both height (up to 1 mm)

and width. *Laurinoxylon porosum* has multiseriate rays up to 5-seriate with uniseriate margins of one to three rows of square and upright cells, but rays of *L. stichkai* are 2–3-seriate, with only one row of upright/square marginal cells. The highest ray measured in *L. stichkai* is ~500 μm; no rays reaching 1 mm in height were observed.

Other genera of lauraceous woods previously described from the Eocene of North America include *Cinnamomoxylon*, *Cryptocaryoxylon*, *Mezilaurinoxylon*, *Paraperseoxylon*, and *Ulminium* (Wheeler and Manchester 2002; Gregory et al. 2009). Five of these were recognized from the Middle Eocene Nut Beds flora of the Clarno Formation in Oregon (Wheeler and Manchester 2002). Both simple and scalariform perforation plates occur in *Cinnamomoxylon oleiforum* (4–8 bars/plate) and *Paraperseoxylon scalariforme* (4–12 bars/plate; Wheeler and Manchester 2002), but only simple perforations were observed in *L. stichkai*. In the described species of *Cryptocaryoxylon*, the range of radial multiples for vessels is either much greater (2–10 adjacent vessels in *Cryptocaryoxylon radiporosum* and 2–11 in *Cryptocaryoxylon hancockii*) or less (2, rarely 3, in *Cryptocaryoxylon meeksii*) than that in *L. stichkai* (Wheeler and Manchester 2002). Rays in *C. meeksii* are commonly 1–2 cells wide, which is narrower than those in *L. stichkai*. *Laurinoxylon stichkai* is also unlike *Ulminium magnioleiferum*, which has aliform-confluent axial parenchyma, wider rays (1–4-seriate), and 1–8 rows of square/upright ray cells. Only one of the previously described Eocene North American species, *Mezilaurinoxylon eiporosum* Wheeler and Manchester (2002), has septate fibers, a feature shared with *L. stichkai*. *Laurinoxylon stichkai* differs from *M. eiporosum*, however, in lower vessel density, shorter vessel elements, narrower, shorter rays, more abundant oil cells, and thinner fiber walls.

The features of the fossil wood described above fit well with the emended diagnosis of the fossil genus *Laurinoxylon* (Dupéron et al. 2008). *Laurinoxylon stichkai* appears to be unique among previously described fossil lauraceous woods in having extraordinarily abundant oil cells in the rays and axial parenchyma (10–36 oil cells/mm^2, based on counts in 18 areas of the specimen) scattered over the specimen in both transverse and longitudinal sections (Wheeler et al. 1977; Wheeler and Manchester 2002; Dupéron-Laudoueneix and Dupéron 2005; Dupéron et al. 2008; Wheeler and Dillhoff 2009).

Today, Lauraceae contains at least 45 genera and more than 2200 species worldwide, mostly from warm and tropical regions, especially Southeast Asia and Central and South America (Stern 1954; Mabberley 1987). Most plants in this family are aromatic evergreen trees and shrubs, usually with spherical ethereal oil cells in parenchymatous tissues (Mabberley 1987).

Family—Canellaceae Mart.

Genus—Wilsonoxylon gen. nov.

Etymology. The generic name honors Thomas K. Wilson, whose treatment of extant canellaceous woods was important for the comparative analysis of this fossil.

Generic diagnosis. Wood with indistinct growth rings, wood diffuse-porous. Vessels very small to small, exclusively
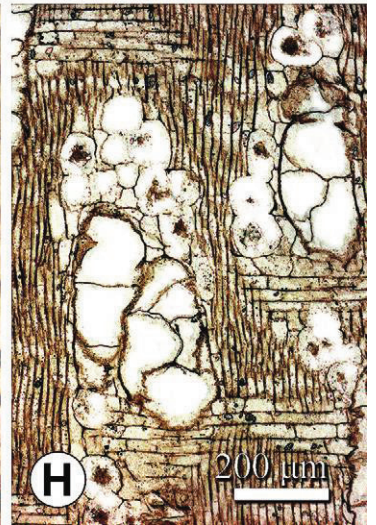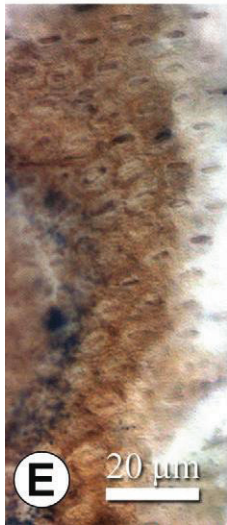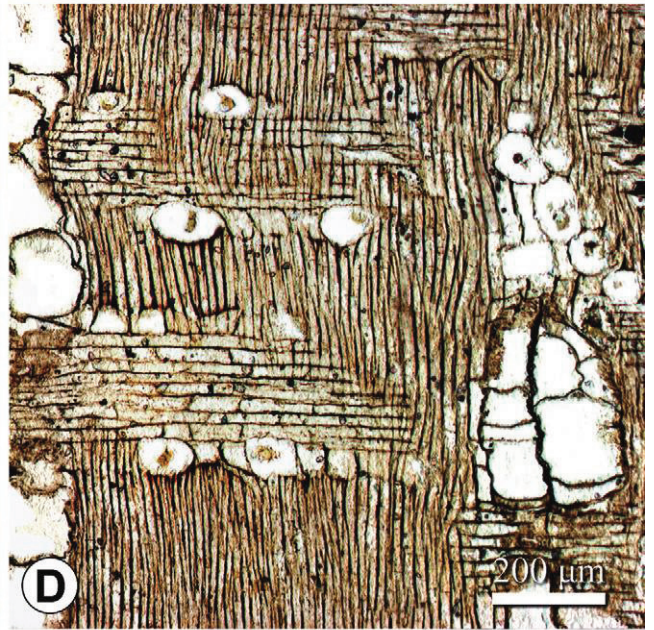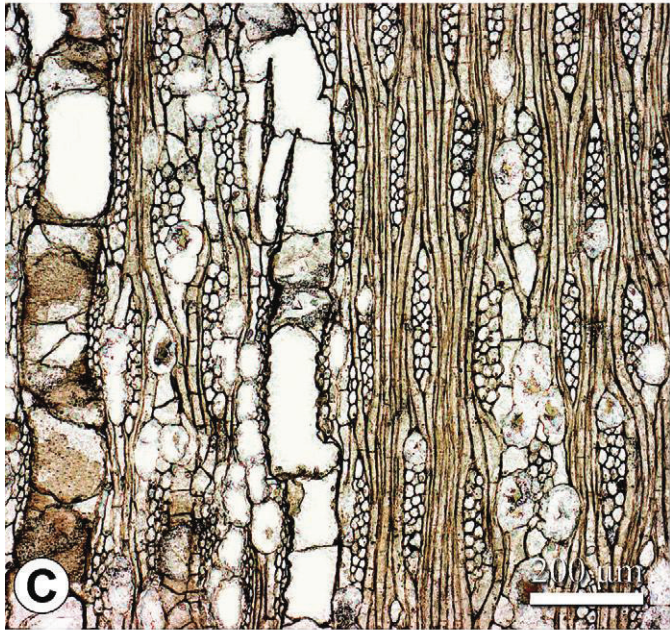
solitary, with mean tangential diameter less than 100 μm; perforations scalariform; parenchyma diffuse; vessel-ray pits with distinct borders, mostly circular to slightly horizontally elongate; rays 2–3-seriate, heterocellular; idioblastic cells (oil cells) in axial and ray parenchyma. Fibers with numerous, conspicuous bordered pits on tangential and radial walls; nonseptate, thin to thick walled.

Type species. *Wilsonoxylon edenense* N. Boonchai et Manchester sp. nov. (fig. 5).

Etymology. The epithet *edenense* refers to Eden Valley, Wyoming.

Holotype. UF 327-54507, here designated (fig. 5A–5D, 5F, 5G, 5J).

Paratypes. UF 327-54515 (fig. 5E, 5H, 5I), UF 327-54518.

Specific diagnosis. Same as for genus.

Description. Growth ring boundaries usually indistinct but visible in some areas, demarcated by radially narrower fibers in a tangential line. Wood semi-ring-porous to diffuse-porous, the earlywood vessels noticeably wider than the preceding year's latewood vessels. Vessels exclusively solitary, occasionally in oblique pairs because of overlapping end walls. Vessel density ~40–60/mm^2, but as low as 22/mm^2 in latewood. Pores oval, mean tangential diameter of the samples ranging from 35 (SD = 7) to 40 (SD = 6) μm; total range of vessel tangential diameters is 25–56 μm. Perforation plates exclusively scalariform, with ~10–20 bars/plate (fig. 5D, 5E); mean vessel element length 442 (SD = 144) to 488 (SD = 171) μm, total range (217–) 310–663 μm; vessel-ray pits with distinct borders, mostly circular to slightly horizontally elongate throughout the ray cell (fig. 5J). Intervessel pits not observed because the vessels are exclusively solitary. Axial parenchyma diffuse, difficult to distinguish in transverse section but observed in tangential section (fig. 5C). Rays 2–3-seriate, heterocellular; body ray cells procumbent with one or two marginal rows of square and/or upright cells. Mean ray height 315 (SD = 122) to 371 (SD = 121) μm. Rays nonstoried. Idioblasts (interpreted as oil cells) more common in axial parenchyma than in ray parenchyma, 20–35 μm wide, and (55–) 80–116 μm high. Fibers nonseptate, medium-thin to very thick walled (mostly thick to very thick walled), with distinct circular bordered pits on tangential and radial walls.

Affinities. The combination of exclusively small and solitary vessels (fig. 5A) with scalariform perforation plates (fig. 5D, 5E) and fibers with distinctly bordered pits (fig. 5F) occurs in many families, e.g., Canellaceae, Fagaceae, Monimiaceae, Atherospermataceae (which was previously considered a subfamily of Monimiaceae), and Hamamelidaceae (Metcalfe and Chalk 1950; InsideWood 2004–; Wheeler and Dillhoff 2009; Wheeler et al. 2010). Numerous other features, however, distinguish this fossil wood from all these families except Canellaceae.

The enlarged cells described as idioblasts (fig. 5C) could be interpreted as crystalliferous cells in which the crystals were not preserved, but we interpret them as oil cells because no distinct rhomboidal crystal outlines were seen in this sample, although we know that they have been preserved in other woods (*Edenoxylon*) from the same locality. Considering these idioblasts to be oil cells suggests lauralean affinities at first glance, but fibers with distinctly bordered pits and the combination of exclusively solitary vessels and exclusively scalariform perforation plates does not occur in extant Magnoliaceae or Lauraceae. Woods of Fagaceae and Hamamelidaceae differ in the absence of idioblasts (Metcalfe and Chalk 1950; InsideWood 2004–). In addition, fagaceous woods commonly have either exclusively uniseriate rays or rays of two distinct sizes (Metcalfe and Chalk 1950; InsideWood 2004–).

Although the lauralean families Monimiaceae and Atherospermataceae have many characters in common with this fossil, including the presence of oil cells in a few species, rays in these two families are distinctly different from those in *Wilsonoxylon*. In both families, the rays are consistently larger (up to 3–4-seriate and 1 mm high in Atherospermataceae and 7-seriate and 1–15 mm high in Monimioideae of Monimiaceae; Metcalfe and Chalk 1950; Carlquist 2001).

The closest affinities of *Wilsonoxylon* appear to be with Canellaceae, which shares the occurrence of exclusively solitary vessels, small size, exclusively scalariform perforation plates with many bars, circular to elliptical vessel-ray pits with distinct borders, fibers with distinctly bordered pits, and oil cells in ray and axial parenchyma (Solereder 1908; Wilson 1960; Metcalfe 1987; InsideWood 2004–). Wilson (1960) and Metcalfe (1987) summarized the anatomical characters of six genera of extant Canellaceous wood: *Canella*, *Capsicodendron*, *Cinnamodendron*, *Cinnamosma*, *Pleodendron*, and *Warburgia*. There are a few differences between our samples and these extant genera (table 2), e.g., longer vessel elements in most of the extant genera and the presence of a larger number of bars in the scalariform plates of some of them. Unlike the fossil specimens, which have 1–3-seriate rays, the rays of these extant genera are generally 1- (2-)seriate, with the exception of *Cinnamodendron* and *Warburgia*, whose rays are 1–4-seriate (commonly 2–3-seriate in *Warburgia*; Metcalfe and Chalk 1950; Wilson 1960, 1965; Metcalfe 1987; InsideWood 2004–). However, we consider these differences to be minor for comparison at the family level, because vessel element length and the number of bars in scalariform perforation plates are influenced by differences in ecology, latitude, altitude, and temperature (Carlquist 2001; Baas and Wheeler 2011). Of the six genera mentioned above, our specimens are more similar to *Capsicodendron*, *Cinnamodendron*, and *Warburgia* than to *Canella*, *Cinnamosma*, and *Pleodendron*. Unlike our specimens, the latter three

Fig. 4 *Laurinoxylon stichkai* sp. nov. holotype, UF327-53955. *A*, *B*, Vessels solitary and in radial multiples of 2–4; diffuse-porous wood; oil cells common in rays; very thin fiber walls. *C*, Nonstoried 2–3-seriate rays; oil cells common in both rays and axial parenchyma strands. *D*, Procumbent body ray cells with one row of upright/square marginal cells; oil cells common in ray margins. *E*, Alternate intervessel pits. *F*, Simple perforation plate. *G*, Vessel-ray pits with much-reduced borders to apparently simple. *H*, Crowded oil cells in radial section. *A*, *B* = XS; *C*, *E* = TLS; *D*, *F*–*H* = RLS.
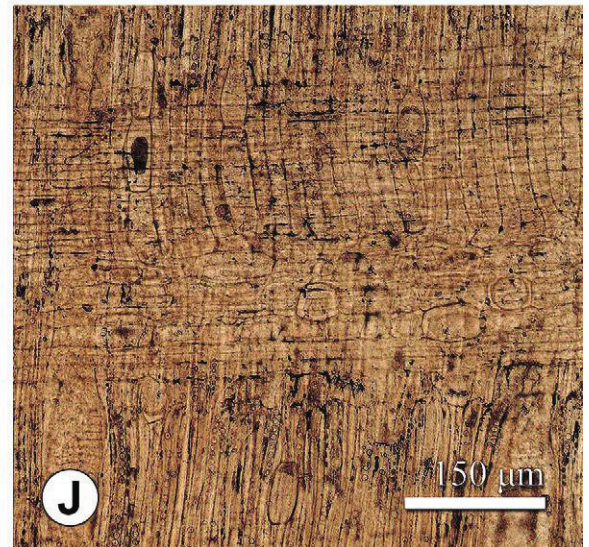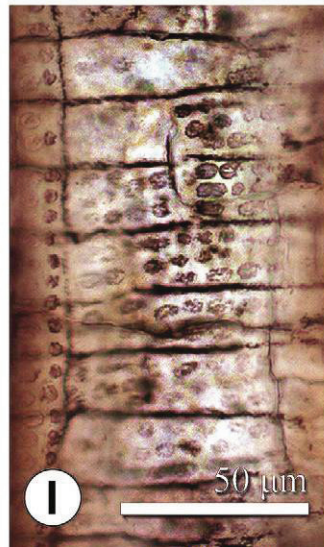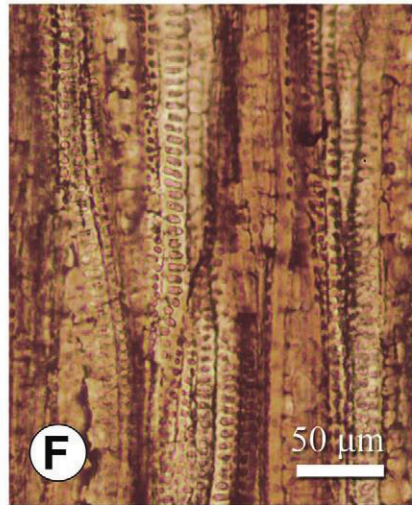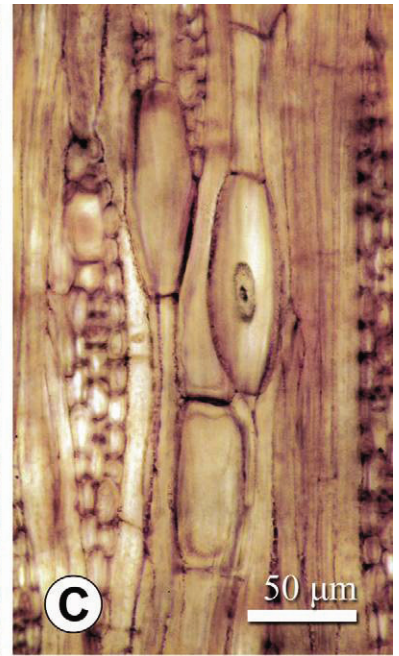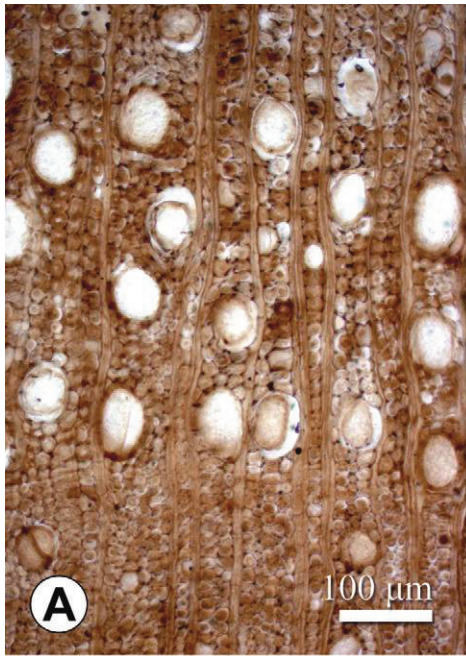
genera have axial parenchyma ranging from diffuse to vasicentric to aliform and confluent and rays 1–2-seriate (mostly uniseriate) and usually homocellular (Wilson 1960, 1965; InsideWood 2004–; Roque et al. 2007). Of the three more-similar genera, it is possible that the fossil has the closest affinity with *Warburgia*, because the other two differ from our specimens in the following features: *Cinnamodendron* has thin fiber walls (Wilson 1960, 1965; Metcalfe 1987), and rays in *Capsicodendron* are commonly homocellular and 1–2-seriate rather than 3-seriate and heterocellular (Wilson 1960, 1965; Metcalfe 1987). However, we cannot conclusively align our specimens with a single genus of these three genera, because some anatomical features vary among species and might overlap between genera (Wilson 1960, 1965; Metcalfe 1987; Ilic 1991; InsideWood 2004–; Roque et al. 2007).

The fossil record of Canellaceae is limited to two genera reported from Tertiary deposits of Latin America (Hammel and Zamora 2005). Leaves of *Canella* from beds in Bahia, Brazil, estimated as Pliocene, were described in 1924 by Hollick and Berry, and Oligocene pollen of *Pleodendron* has been reported from Puerto Rico (Graham and Jarzen 1969). Fossil wood of Canellaceae has not been reported previously (Gregory et al. 2009). Consequently, we erect the morphogenus *Wilsonoxylon* for fossil wood with anatomical similarities to the genera of the Canellaceae and propose the new species name as *W. edenense*.

Family, Genus, and Species—incertae sedis

Specimen studied. UF327-54503 (fig. 6).

Description. Growth rings indistinct, with a change in fiber wall thickness in some regions that might be boundaries between growth increments. Wood diffuse-porous, vessels solitary (41%–53%) and in radial multiples of 2 (3); tangential walls of vessels in radial multiples occasionally overlapping; vessel frequency 14–23/mm^2; vessels oval in outline; tangential diameter 40–95 μm (mean 59 μm, SD = 20); perforation plates simple, oblique; vessel element lengths (120–) 175–453 μm (mean 255 μm, SD = 88); intervessel pits alternate, of medium size (7–10 μm) measured horizontally, polygonal, angular in outline; vessel-ray parenchyma pits with reduced borders and variable in outline, rounded, horizontally or vertically enlarged; tyloses not common. Axial parenchyma absent or extremely rare, apparently in scanty paratracheal arrangement. Fibers nonseptate, with no pits observed on either tangential or radial walls, very thin to thick walled. Rays (2–) 3–4-seriate, heterocellular, body procumbent with a single marginal row of upright and/or square cells, occasionally with square cells present in the body, nonstoried. Ray height (120–) 262–960 μm (mean 430 μm, SD = 215); ~17 rays/mm.

Comments. This species is represented by a small specimen ~7 cm wide, partially compressed and distorted in some areas.

Affinities. The combination of characters, including wood diffuse-porous with vessels solitary and in multiples; simple perforation plates; alternate intervessel pitting; medium, nonseptate fibers without distinctly bordered pits; paratracheal parenchyma; and rays that are not exclusively uniseriate or commonly more than 10-seriate, is widespread among extant angiosperms of many families, such as Anacardiaceae, Asteraceae, Barbeyaceae, Bignoniaceae, Cannabaceae, Capparaceae, Euphorbiaceae, Fabaceae, Lythraceae, Malpighiaceae, Melastomataceae, Moraceae, Myrsinaceae, Ochnaceae, Oleaceae, Rhamnaceae, Verbenaceae, and Salicaceae (Metcalfe and Chalk 1950; InsideWood 2004–; Wheeler and Lehman 2009). Previously described fossil woods with similar characters include "Big Bend Small Axis Campanian Wood" from Big Bend National Park (Wheeler and Lehman 2009), *Carlquistoxylon*, and *Paraphyllanthoxylon* (InsideWood 2004–; E. Wheeler, personal communication, 2011).

Carlquistoxylon nacimientense was described as a new genus and species from the Late Cretaceous and Early Paleocene of the San Juan Basin, New Mexico (Wheeler et al. 1995). Our fossil is similar to the diagnosis of *Carlquistoxylon*, but with a few minor differences: *Carlquistoxylon* has a higher mean vessel element length (between 500 and 800 μm) and narrower rays (less than 4-seriate, rarely uniseriate) than does this specimen. The size of intervessel pits is large (11–14 μm), in contrast to the medium-sized pits in our fossil.

Paraphyllanthoxylon, known from the Cretaceous to Tertiary, was first described by Bailey (1924). *Paraphyllanthoxylon*, whose generic diagnosis was emended by Mädel in 1962 (Thayn and Tidwell 1984), also has many of the characters shown by this fossil. However, *Paraphyllanthoxylon* usually has septate fibers, which are absent from the fossil described here (Thayn and Tidwell 1984; Wheeler et al. 1995; InsideWood 2004–). In addition, *Paraphyllanthoxylon* has large ($\geq$10 μm) or rarely minute ($\leq$4 μm) intervessel pits (InsideWood 2004–), in contrast to the medium-sized intervessel pits of the fossil described here.

Because the set of features shown by this fossil can also be found among species of at least 27 families of 12 orders of core eudicots (InsideWood 2004–; Wheeler and Lehman 2009), we cannot match it precisely to any nearest relative.

Family—Palmae Juss.

Genus—Palmoxylon Schenk

Species—Palmoxylon macginitiei Tidwell

Specimens. UF 327-53962 (fig. 7), 54500, 54505, 54530–54536, 54539.

Fig. 5 *Wilsonoxylon edenense* gen. et sp. nov. holotype (UF327-54507; *A–D, F, G, J*) and paratype (UF327-54515; *E, H, I, K*). *A*, Diffuse porous wood with exclusively solitary pores. *B*, Nonstoried 1–3-seriate rays and scattered idioblasts in axial parenchyma. *C*, Idioblasts in ray and axial parenchyma. *D, E*, Scalariform perforation plate. *F*, Fibers with horizontal elongate and circular bordered pits. *G*, Half-bordered pits in side view at the junction of parenchyma with vessel. *H*, Circular bordered pits on imperforate elements and opposite parenchyma vessel pitting. *I*, Vessel-ray pits with distinct borders, mostly circular to slightly horizontally elongate throughout the ray cell. *J*, Idioblasts solitary and in vertical rows of axial parenchyma and scattered in ray parenchyma. *A* = XS; *B–H* = TLS; *I, J* = RLS.

Table 2

Comparison of Fossil and Extant Wood of Canellaceae (Modified from Metcalfe 1987) with Additional Data from Metcalfe and Chalk (1950), Wilson (1960), InsideWood (2004–)

	Wilsonoxylon gen. n.	Canella Browne	Capsicodendron Hoehne	Cinnamodendron Endlicher	Cinnamosma Baillon	Pleodendron Tieghem	Warburgia Engler
Vessels:							
Diameter (μm)	25–56	50–100	25–50	50–73 (24–122)[a]	50–100	52–94	42–136
Element length (μm)	310–663	500–1500	1100–1500	1600–2400	Long–very long	900–1300	1100–2300
Bars/perforation plate	~10–20	5–28	46–64	50–100	11–49 (15–30)	15–40	13–52
Exclusively solitary, occasionally oblique paired[b]	+	+	+	+	+	+	+
Vessels in small multiples or clusters	−	(+)	−	−, (+)[c]	+	−	(+)
Parenchyma:							
Paratracheal	−	(Vasicentric, unilateral[d])	(Occasional)	−	Vasicentric	+	(+)
Apotracheal in short lines or diffuse	Diffuse, short lines?	(Diffuse)	(Diffuse)	Diffuse, short lines	−	(Diffuse)	Diffuse, short lines
Rays:							
Seriation	2–3	1 (2)	1–2 (–3)	1–2 (1–4)	1–2	1–2	(1–) 2–3 (–4)
Homocellular	(+)	+	+	(+)	+	(+)	(+)
Heterocellular	+	+	+	+	(+)	(+)	(+)
Fibers:							
Wall thickness	Medium-thin to very thick	Thick	Thick or thin	Thin	Thick to very thick	No record	Thick

Note. A plus sign denotes present; a minus sign denotes absent; "(+)" denotes occasionally present.
[a] Recorded in *Cinnamodendron sampaioanum* (Occhioni 1948; Metcalfe 1987).
[b] The appearance of vessels in pairs is due to oblique overlapping end walls of two vessel elements of the same vessel (Wilson 1960).
[c] Reported in only one species. Groups of 3–4 vessels are recorded in *Cinnamodendron sampaioanum* (Occhioni 1949; Metcalfe 1987).
[d] Described by Wilson (1960) as confined to one side, which is feature 84 of IAWA hardwood feature list (Wheeler et al. 1989): axial parenchyma unilateral paratracheal.
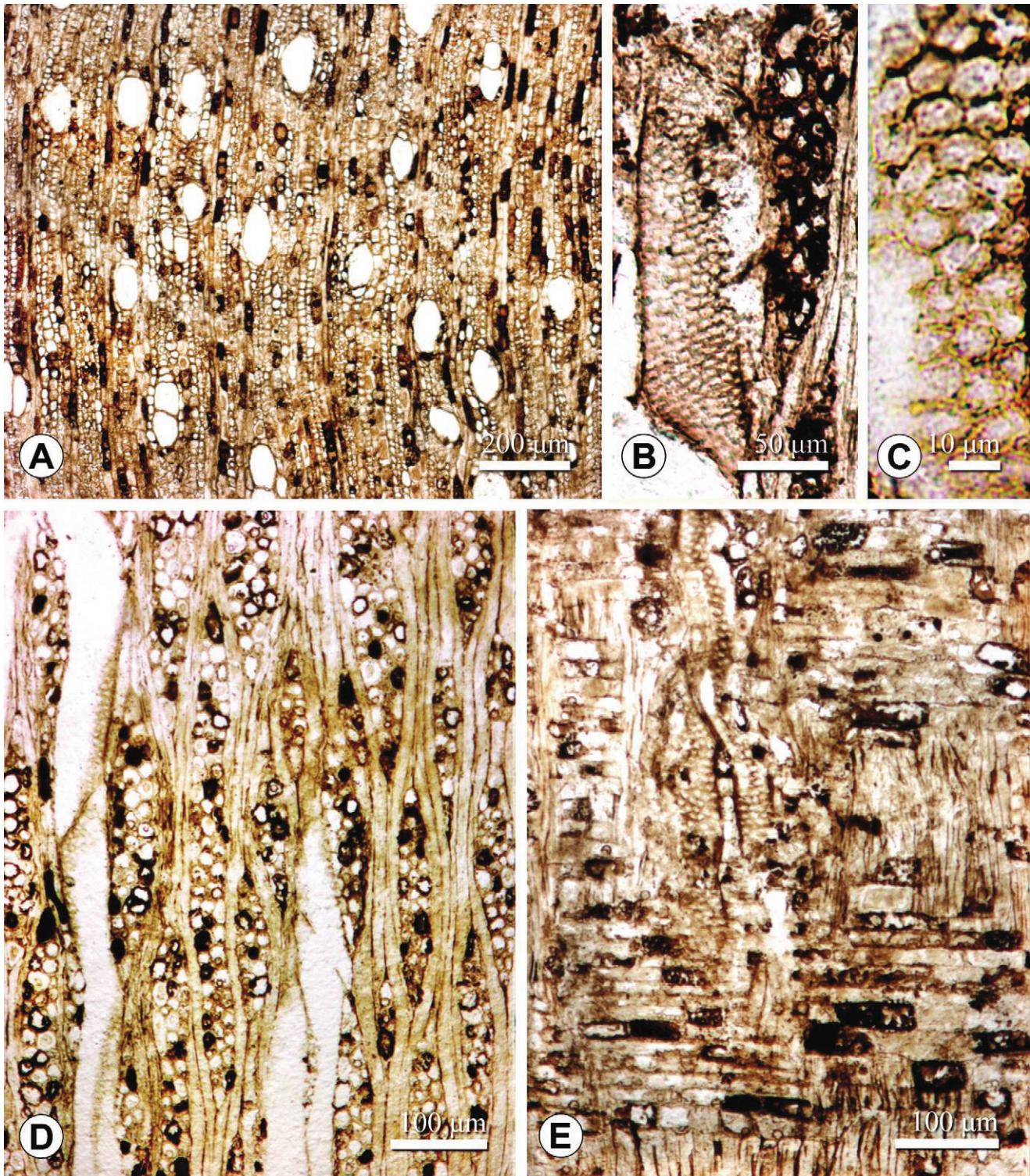
Fig. 6 Unknown dicotyledonous species (UF327-54503). *A*, Diffuse porous wood; vessels solitary and in radial multiples of 2. *B*, Alternate intervessel pits. *C*, Polygon-shaped intervessel pits. *D*, Ray 3–4-seriate; nonseptate fibers. *E*, Vessel-ray pits with much-reduced borders to apparently simple; procumbent body ray cells with one row of upright/square marginal cells. *A* = XS; *B–D* = TLS; *E* = RLS.
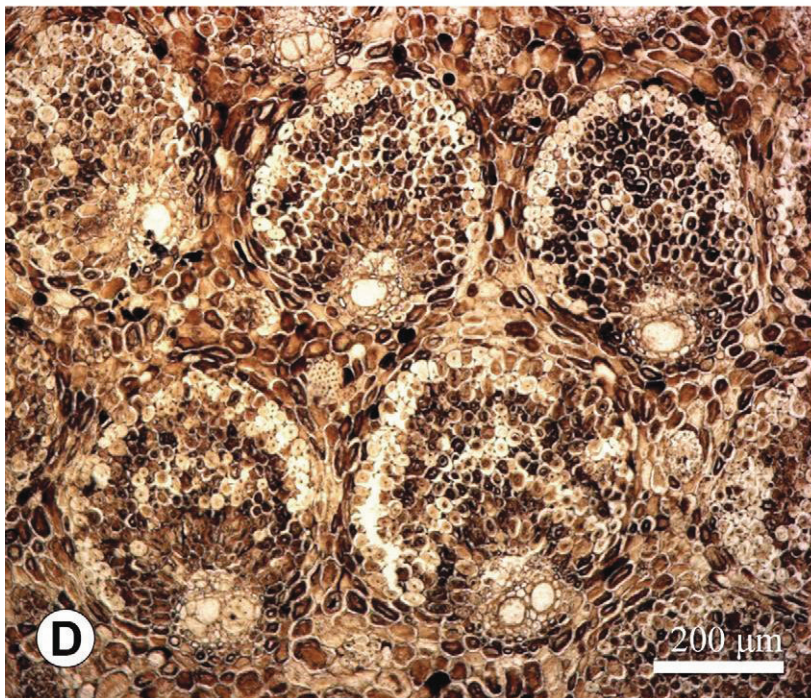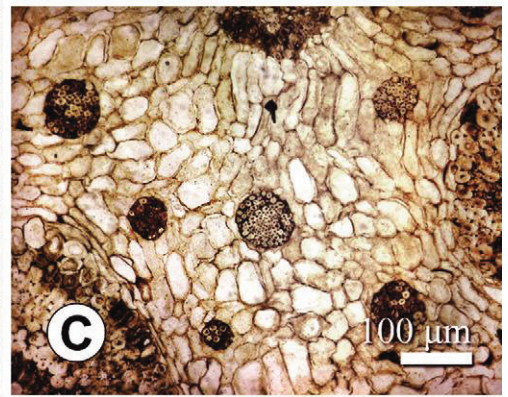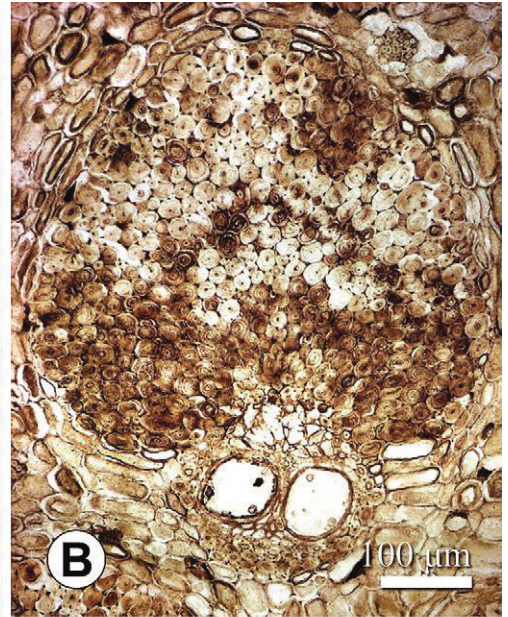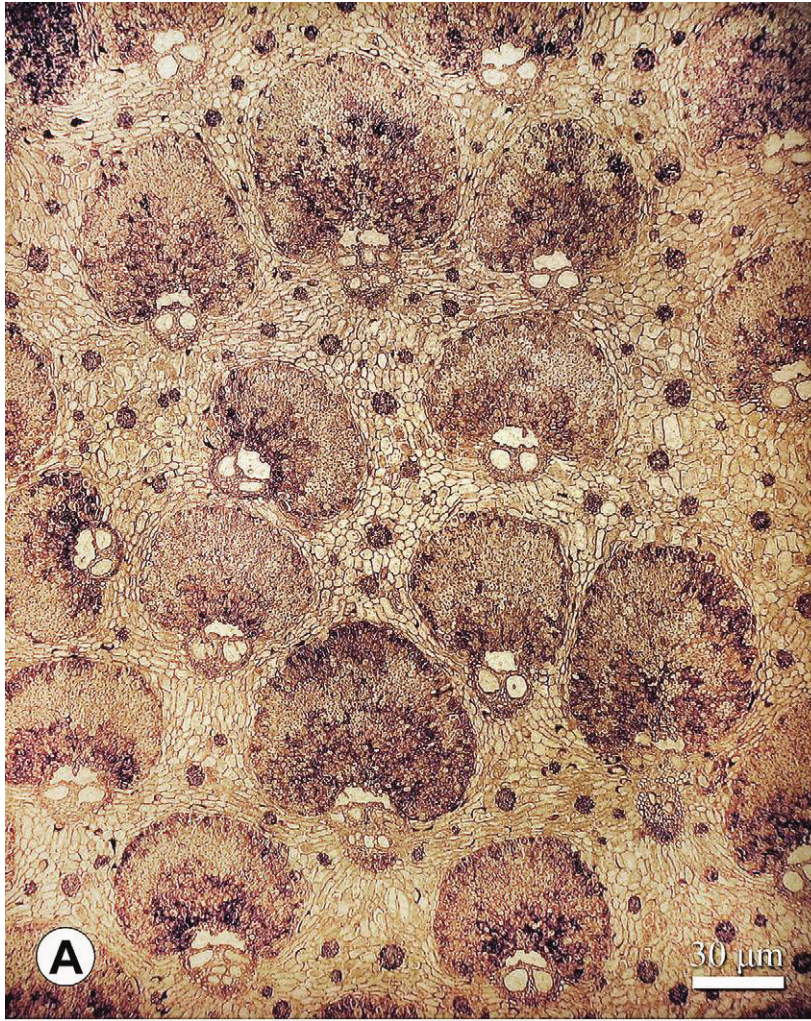
Affinities. This species was already described from the same locality by Tidwell et al. (1971). Although the specimens we recovered were small fragments, Tidwell's more complete specimens were 15–30 cm in diameter and are generally 2–3 ft long (~61–91 cm; Tidwell et al. 1973). Our material appears to be better preserved, such that the acetate peels show the anatomy much more clearly than the illustrations published previously. Although there are some minor differences in the number, size, and density of the bundles, these features are known to vary within individuals of the same species because of factors such as the size and age of the palm (Tomlinson et al. 2011). Tomlinson et al. (2011) concluded that a small sample of any vegetative palm organ cannot represent its anatomical variation in the same way that a small wood sample gives a good overview of the overall image of the secondary xylem of a dicotyledonous tree. In the Early Tertiary of western North America, palms were distributed in the areas surrounding the Green River lake system, which covered vast areas of the Eocene landscape in of Colorado, Wyoming, and Utah (MacGinitie 1969; Nambudiri and Tidwell 1998). *Palmoxylon* and palm roots, *Rhizopalmoxylon*, have been described from the Eocene Dipping Vat Formation of central Utah (Tidwell et al. 1972), and four species of *Palmoxylon* recognized from the Eocene Green River Formation, Eden Valley, Wyoming were identified as *P. macginitiei*, *Palmoxylon edenese*, *Palmoxylon contortum*, and *Palmoxylon colei* (Tidwell et al. 1973).

Discussion and Conclusion

Diversity, Abundance, and Stature

Only angiosperms were recovered, including four kinds of dicotyledonous wood plus the palm stems. No gymnosperm woods were observed in the field or in the collections. Of the 51 sampled individuals, 11 (22%) are palm stems, and the rest are dicotyledonous woods. Of the 40 dicotyledonous woods, at least 16 specimens represent the anacardiaceous taxon *Edenoxylon* (~31% of all collected samples including palms, or ~40% of the dicots). Other dicotyledonous woods include representatives of the Lauraceae (*Laurinoxylon stichkai*, represented by one specimen), Canellaceae (*Wilsonoxylon edenense*, three specimens), and the unidentifed taxon (one specimen). We have not identified the remaining 18 samples; although not as well preserved, they are clearly not *Palmoxylon*, and they appear likely to be additional examples of the dicotyledonous taxa mentioned above.

The dicotyledonous woods were collected only as fragments, not in place, so we are uncertain where along the full length of the stems our diameter estimates are taken. Nevertheless, the recovered dimensions and growth ring counts indicate that these were trees but not giant ones. Most samples are relatively young stems with attached branches. Judging from the size of collected fragments and growth ring curva-

ture, the stems are estimated to have ranged from 6 to 60 cm or more in diameter. The largest stem observed belongs to *L. stichkai*, with a diameter ~60 cm. It is possible that these woody stems were part of young forest vegetation close to the lake.

Comparison of Fossil Woods with Other Plant Organs

With respect to taxa known from adjacent fossil leaf assemblages, we did not find any wood samples of *Populus*, which is common in the leaf and fruit flora of the Bridger and Green River Formations in this region, or any wood of Platanaceae, although this family is well represented by leaves of *Macginitiea* from the Green River strata (MacGinitie 1969; Manchester 1986). MacGinitie (1969) recognized four lauraceous leaf types in the Green River flora, which he assigned to modern genera: *Beilschmiedia eocenica* (Brown) MacGinitie, *Lindera varifolia* MacGinitie, *Ocotea coloradensis* (Brown) LaMotte, and *Persea coriacea* MacGinitie. Leaves of Lauraceae are widely variable, such that the same morphological types can be produced by different genera, so the assignment to particular modern genera may be questioned. Nevertheless, MacGinitie's work indicates that the family was well represented in the leaf record by both lobed and unlobed species, some having simple pinnate venation and others distinguished by a strongly ascending basal pair of secondary veins. The growth habit of Lauraceae, which includes shrubs as well as trees, cannot be determined from leaf impressions alone, but size of the *L. stichkai* specimen indicates that it was a tree.

The identification of *Edenoxylon* as a member of Anacardiaceae augments leaf and fruit data showing the importance of this family in the late Early to early Middle Eocene of the region. MacGinitie (1969) recognized four genera of this family on the basis of impression fossils from the Green River Formation: winged fruits of *Anacardites schinoloxus* Brown (said to be similar to extant *Schinopsis*) and leaves of *Astronium truncatum* (Lesq.) MacGinitie, *Toxicodendron winchesteri* (Knowlton) MacGinitie, and *Rhus nigricans* (Lesq.) Knowlton. The isolated winged fruits that had been attributed to *A. truncatum* by MacGinitie (1969) have since been shown to represent an extinct genus of simaroubaceous affinity (Wang and Manchester 2000). The leaves that MacGinitie assigned to *A. truncatum* show features characteristic of Anacardiaceae but cannot be considered as exclusively matching those of *Astronium*. Fruits of the extinct anacardiaceous genus *Pentoperculum* Manchester (Manchester 1994) have also been identified from the Bridger Formation collections from Blue Rim, Wyoming (S. R. Manchester, personal observation). We do not yet know which, if any, of these dispersed fruit and leaf types might have been produced by the trees bearing *Edenoxylon* wood, but this study indicates that the tree was an important component of the local plant community.

Fig. 7 Stem of *Palmoxylon macginitiei* Tidwell (UF327-53962). *A*, *B*, Vascular bundles in subdermal zone with two (sometimes three) metaxylem elements and one or two layers of tabular parenchyma around the bundle sheath. *C*, Fibrous bundles. *D*, Dermal-zone vascular bundles with one or two metaxylem elements. *E*, Longitudinal section through vessel elements showing scalariform wall thickening. *A–D* = XS; *E* = RLS.

Ecological Considerations

Anacardiaceae, Canellaceae, Lauraceae, and Palmae today are mainly distributed in tropical to subtropical regions of the world (Wilson 1960; Elias 1980; Mabberley 1987; Ogata et al. 2008). The dicotyledonous woods recovered so far, including the unidentified taxon as well as the three families mentioned above, are diffuse-porous to semi-ring-porous. The lack of ring-porous woods might be an indication of limited seasonality; however, drawing conclusions about the climate based on wood structural characteristics from only four dicotyledonous taxa may be questionable, so we have not applied the methods of Wiemann et al. (1999). The presence of palms, however, suggests relatively frost-free conditions. The paleoflora from this study is consistent with other evidence (Roehler 1993) for subtropical conditions during the Early to Middle Eocene in southwestern Wyoming.

Kruse (1954) examined ~100 specimens of Eocene fossil dicotyledonous wood from Hay's Ranch, ~30 km east of the Big Sandy Reservoir site. The site also lies within Eden Valley, but it is in the underlying Green River Formation and is perhaps a few million years older. The geological strata consist of interbedded sandstone, siltstone, and shale, but most of the fossil wood occurred in sandstone (Kruse 1954). Eleven species, distributed among 10 genera and eight families, were described by Kruse (1954). The species were identified as *Myrica scalariformis* (syn. *Myricoxylon scalariforme*; Myricaceae); *Talauma multiperforata* (Magnoliaceae, but later inferred to be Lauraceae; Wheeler et al. 1977); *Forchhammerioxylon scleroticum* (Capparidaceae); *Amyridoxylon ordinatum*, *Fagara monophylloides* (stem and root), and *Fagara biseriata* (Rutaceae); *Suriana inordinata* (Simaroubaceae; this genus was moved to family Surianaceae; Gregory et al. 2009); *Heveoxylon microporosum* (Euphorbiaceae); *Schinoxylon actinoporosum* and *Edenoxylon parviareolatum*

(Anacardiaceae); and *Aspidospermoxylon uniseriatum* (Apocynaceae). Collectively, these woods are also suggestive of subtropical conditions. The families Lauraceae and Anacardiaceae are represented at both Hay Ranch and Big Sandy Reservoir, but the Hay Ranch forest was apparently more diverse, including several dicotyledonous taxa not known from the Big Sandy Reservoir site. More investigations of fossil woods from Hay Ranch, Parnell Draw, and other localities in Eden Valley area of southwestern Wyoming are in progress to gain a regional perspective on the plant communities and for comparison with other plant organs, including leaves and pollen, to form a more complete reconstruction of the paleoclimate and paleoenvironment from the Early and Middle Eocene of Wyoming.

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