Fossil woods of Yellowstone National Park

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INTRODUCTION

Among the wonders of Yellowstone National Park are the spectacular fossil forests of Amethyst Mountain and Specimen Ridge in the northeastern section of the park and the Gallatin Fossil Forests in the northwestern section. In 1898, John Muir, who was instrumental in establishing the US National Park System, wrote: "Yonder is Amethyst Mountain … beneath the living trees the edges of petrified forests are exposed to view … standing on ledges tier above tier where they grew, solemnly silent in rigid crystalline beauty after swaying in the wind thousands of centuries ago, opening marvelous views back into the years and climates and life of the past time." Muir's visit to Amethyst Mountain was no doubt prompted by the early descriptions and diagrams showing multiple layers of fossil forests there (Figure 1A) (Holmes 1878, 1879). Specimen Ridge and the Gallatin Fossil Forests also have successive tiers of fossil forests. Erling Dorf's 1964 *Scientific American* article "The Petrified Forests of Yellowstone Park" includes an illustration of Specimen Ridge with more than 20 layers of fossil forests within a vertical section of some 2,000 feet of volcanics. It is unclear how many different volcanic eruptions were involved in creating these massive accumulations of petrified stumps and logs and the time span represented, as well as how long-lived were the individual forests. The classic paper on the geology of the region is by Smedes and Prostka (1972), who concluded that the Lamar River Formation in which Amethyst Mountain and Specimen Ridge occur and the Sepulcher Formation in which the Gallatin Fossil Forests occur are comparable in age, approximately 50 million years old.

USING WOOD FEATURES TO INTERPRET PALEOENVIRONMENTS

Some wood anatomical features are correlated with environment (e.g., Carlquist 1975, 2001; Baas 1976, 1986), and so fossil woods help in interpreting paleoenvironments. Distinctiveness of growth ring boundaries gives information about seasonality. The transition between wood formed early in the growing season (earlywood) and the wood formed later in the season (latewood) is another important indicator of climate. Questions about Yellowstone's fossil forests: (1) do these early Middle Eocene dicot woods reflect the increased seasonality inferred for the change from early Eocene to middle Eocene; and 2) are their characteristics consistent with the possibly higher elevation and cooler climate inferred for them compared to the like-aged compression floras to the south (Wing 1987)?

PRESERVATION

Different plant parts differ in their likelihood of entering the fossil record because of factors such as variation in resistance to decay, ease of transport to sites of deposition, and original abundance (e.g.., Poole 2000). Fossil wood assemblages invariably are less diverse than contemporaneous compression floras with leaves, fruits, and seeds, but they often contain families and genera not found in the compression floras. For example, this is true of the late early Eocene Bridger Formation, Wyoming, with the Canellaceae (Canella or wild-cinnamon family) unique to the wood assemblage (Boonchai and Manchester 2012; Allen 2017). Thus, fossil woods contribute to a fuller knowledge of past biodiversity and provide data useful for biogeographic studies and reconstructing the history of different plant groups.

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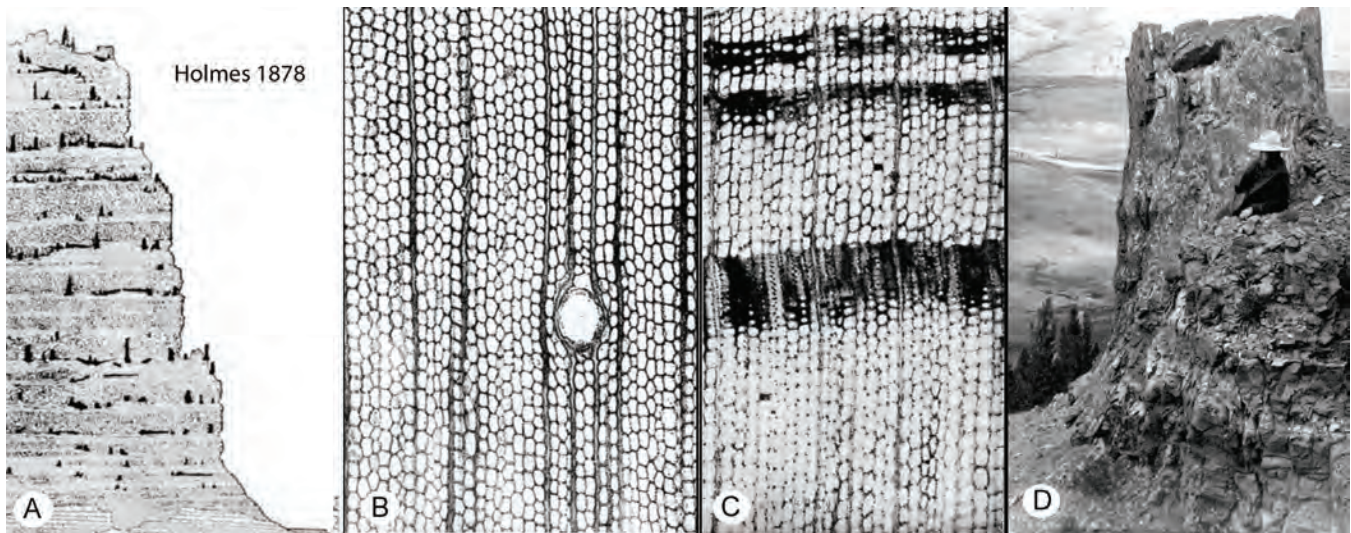710 Dixie Trail
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FIGURE 1. Figure 1. (A) Holmes' 1878 diagram of Amethyst Mountain showing a mixture of upright and prone logs in multiple tiers. (B–D) Specimen Ridge conifer woods; images from Knowlton's 1899 monograph. US GEOLOGICAL SURVEY PHOTO ARCHIVES (B) *Pinus fallax;* the hole is a resin canal, a feature of the pine family, TS. (C, D) *Sequoia magnifica.* (C) Wood with distinct latewood bands, TS. (D) Sequoia stump on Specimen Ridge.

Yellowstone's fossil woods are noteworthy not only for their abundance, but for their exquisite preservation and the anatomical details they possess (Figures 1B, 1C). They are silicified, with the numerous volcanic eruptions in the region being a source of abundant silica. The conducting cells in wood are hollow and serve as pathways for liquids, including silica-rich solutions. Moreover, wood cell walls are porous and have an affinity for silica, which can infiltrate and bind to the cell walls. The woods of Arizona's Petrified Forest awe visitors with the range of colors they display. In contrast, the majority of the Yellowstone woods are dark brown to black and awe paleobotanists because this coloration indicates some original cell wall material is present and minute anatomical details probably are preserved. The photomicrographs of the Yellowstone fossil angiosperm woods in this paper are unstained, the brown color being from the residual cell walls.

Fritz's (1980a, 1982) studies of Amethyst Mountain led to the conclusion that although many upright trees were preserved *in situ*, there were also upright logs and stumps that had been transported, so that some layers might contain a mixture of plants from different elevations and different habitats. The effects of the 1980 Mount St. Helens eruption in Washington state, which swept trees down the mountain, was key to this conclusion (Fritz 1980b). There are but two studies of Yellowstone's fossil forests that inventoried the composition of individual layers: (1) one unit of Amethyst Mountain (Fritz and Fisk 1978), and (2) three units of the Gallatin Fossil Forests that have differences in composition (Chadwick and Yamamoto 1984). The Specimen Ridge forests have been interpreted as being preserved in relatively low-energy depositional environments with most of the upright stumps *in situ* (e.g., Retallack 1981; Fritz 1982; Yuretich 1984). In one 10-meter interval at Specimen Ridge, four of ten stumps of *Sequoia magnifica* were suitable for growth ring analyses; the other stumps had surfaces too rough for measuring growth rings. The growth ring signatures of these four stumps indicated they were contemporaries (Ammons et al. 1987). The logistics of sampling woods from individual layers is challenging given the precipitous cliff faces, but future studies doing so would help answer questions about how long-lived each forest layer was, whether there are variations in tree age within the layers, whether different tiers represent different stages in forest succession, different climates, and whether there were changes in forest composition through time.

PREVIOUS STUDIES

The earliest publications devoted to describing and naming Yellowstone's fossil woods are two German papers on Amethyst Mountain woods (Felix 1896; Platen 1908). F.H. Knowlton's 1899 monograph "Fossil Flora of Yellowstone National Park" concentrated on Specimen Ridge's compression flora (mostly leaves) and briefly described seven wood species. Although there was some updating of the compression flora's composition by Dorf (1960), it needs restudy using modern criteria for identifying fossil leaves, and until that happens his identifications should be considered suspect. Unfortunately, Knowlton's misidentifications of leaves led to some misidentifications of fossil woods because it was assumed that the woods should belong to the same genera as the leaves.

In his overview of Eocene and Oligocene vegetation of the Rocky Mountains, Wing (1987) noted that the Yellowstone compression flora differs from contemporaneous (early Bridgerian, approximately 50 Ma) compression floras, including the Little Mountain flora (Green River Formation, Wyoming; MacGinitie 1969) and Kisinger Lakes–Tipperary flora (Aycross Formation, Wyoming; MacGinitie 1974). The characteristics of the dicot leaves (leaf margins and leaf sizes) in the US National Museum's collections suggest that the Yellowstone assemblages were derived from "a variety of broad-leaved evergreen forests that included a substantial element of conifers" and "grew under a somewhat cooler" climate than the contemporaneous floras (Wing 1987). The Yellowstone fossil woods provide support for that interpretation, as all studies of the woods show that conifers are common.

CONIFER WOODS

Subsequent to his 1899 monograph, Knowlton (1914) wrote a shorter account of Yellowstone's fossil forests and noted that 95% of the trunks on Specimen Ridge were conifers: pines (*Pinus,* family Pinaceae) (Figure 1B) and a redwood (*Sequoia magnifica;* Figures 1C, 1D). Another pine species (*Pinus,* family Pinaceae) and a member of the cypress or cedar family (Cupressaceae) were found at Amethyst Mountain (Felix 1896; Platen 1908). Read's (1930) collections of Specimen Ridge woods also showed conifer dominance. Read provided more detailed anatomical descriptions than did Knowlton and created the new species combination *Pinus fallax* (Felix) and transferred into it the two pines Knowlton described using an older generic name for pine woods (*Pityoxylon aldersoni* and *Pityoxylon amethystianum*). In addition to *Pinus fallax,* a soft pine, and more examples of *Sequoia magnifica,* Read described two new species, *Pinus baumani* Read in the hard pine group and *Cupressinoxylon lamarense* Read (Cupressaceae). In 1941, Beyer collected woods from Specimen Ridge, but a publication on those woods did not appear until well after the end of World War II. He also found *Sequoia magnifica* and *Pinus fallax* abundant and described woods resembling *Abies* (fir) and *Picea* (spruce) of the Pinaceae (pine family), and *Thuja* and *Libocedrus* of the Cupressaceae (cedar family) (Beyer 1954). Fritz and Fisk (1978) inventoried the woods in their unit 10 of Amethyst Mountain and, once again, conifers dominated (83%), represented by *Sequoia magnifica, Pinus fallax, Picea* (spruce) or *Larix* (larch) species, and a wood thought to resemble the Southern Hemisphere *Podocarpus,* but not placed therein with confidence. This last wood most probably is another member of the cedar family. Andrews' (1939) study of the Gallatin Fossil Forests documented the dominance of *Sequoia magnifca, Cupressinoxylon lamarense,* and *Pinus* spp. there.

It puzzled Knowlton (1914) that conifers dominated the wood assemblages, but angiosperms (dicots or hardwoods) dominated the compression floras. One part of the answer to that puzzle may be that conifer woods (softwoods), especially redwood and cedars, generally are more resistant to decay than dicot woods (e.g., Panshin and DeZeeuw 1980). Consequently, they would have a longer time in which to become silicified. It is telling that *Populus* (cottonwood, poplar) and *Salix* (willow) leaves are common in compression floras, but fossil woods of them are rare, likely because their low-density woods decay so readily.

WHAT IS IT? IDENTIFYING FOSSIL WOODS AND BASICS OF WOOD
"Problems"
Isolated samples of modern woods cannot always be identified to genus because some genera within a family share similar anatomical features. Consequently, some woods can only be identified to family, which is especially true for the laurel and legume families. With present-day woods it is rare to be able to identify an isolated piece of wood to an individual species, especially when its exact geographic source is unknown. There even are instances where genera in different families (e.g., Theaceae, tea family; Hamamelidaceae, witch hazel family) have similar wood anatomy.

The petrified woods at Yellowstone, like other Eocene plants, vary in the degree to which they can be related to present-day plants. Some fossil Yellowstone woods have a combination of characters unique to a single modern genus, e.g., *Prunus gummosa* (Rosaceae), with features similar to black cherries. Others can be identified to family, but not to a single genus, e.g., *Pterocaryoxylon knowltonii* (Juglandaceae—walnut family) with features of the Eurasian *Pterocarya* (wingnut) and *Juglans* (soft walnut group). Nearest living relatives of Eocene plants may no longer occur in North America, but are extant on other continents, especially Asia (e.g., Manchester 1989; Manchester et al. 2009). This adds to the challenges of identifying Eocene woods because information is needed on woods from different continents. Thankfully, there are now online databases useful for wood identification (e.g., Wheeler 2011; Wheeler et al. 2021; Itoh et al. 2022).

Cell Types

For most woody plants, microscopic features are needed to identify them. Wood (secondary xylem) is a complex plant tissue with dead hollow cells for water conduction and for support. Support and conducting cells are oriented parallel to the long axis of a plant (i.e., an axial or longitudinal orientation). Rays are aggregations of ray parenchyma cells and extend from the bark towards the center of the tree; ray heights vary from less than 0.1 mm (0.04 in) to 1 cm (0.4 in) or more. Parenchyma cell functions include: 1) food storage so that energy is available during the growing season, 2) wound responses to form callus-like tissue to isolate damage and pathogens, and 3) manufacture of chemicals that inhibit fungal, bacterial, and insect attack. Most dicot trees also have some axial parenchyma, aligned parallel to the long axis of the trunk. Ray and axial parenchyma cells are living in the sapwood of a tree. As parenchyma cells die and the tree forms heartwood, these cells produce secondary metabolites that are responsible for adding color to the wood and may inhibit wood decay, as in redwoods and cedars. The sizes, proportions, arrangements, and interconnections between these cell types vary among plant families and genera and are important for wood identification (e.g., Wheeler and Baas 1998).

Wood Surfaces

Because wood is an ordered tissue composed of longitudinally oriented and horizontally oriented cells (ray cells), making sections useful for seeing features important for wood identification requires precise cuts in three different planes: cross or transverse (cut across the longitudinal axis, equivalent to providing the end view of a log), tangential longitudinal (cut down parallel to outside surface of a tree, equivalent to flat-sawn lumber), and radial longitudinal (cut down parallel to the rays' orientation, from outside of tree toward its center, equivalent to quarter-sawn lumber). These three different cuts expose different diagnostic features. Transverse sections (TS) show growth ring boundaries and diameters and distribution of the conducting cells (Figures 2A–D); tangential sections (TLS) show ray height and width (Figure 2E); radial sections (RLS) show ray cellular composition and details of the interconnections between the conducting cells and the ray cells (Figure 2F).

Conifer Anatomy and Identification

A single cell type, the longitudinal tracheid, comprises more than 90% of the volume of conifer wood. These hollow pipe-like cells have closed ends and typically are 2–3 mm long, but there are breaks (pits) in their walls for water to move upward from tracheid to tracheid. Most, but not all, conifers have distinct growth rings, but there is variation in how well-defined the differences are between earlywood (wood formed at the beginning of a growing season) and latewood (wood formed later in growing season); compare Figures 1B and 1C. Resin canals (Figure 1B) regularly occur only in about half of the Pinaceae genera (*Pinus*—pine, *Picea*—spruce, *Larix*—larch, *Pseudotsuga*—Douglas fir, *Keteeleria*—native to southern China, Laos, and Vietnam, a genus without an anglicized common name), making these genera's woods the easiest of all conifer woods to recognize. It is especially challenging to identify fossil Cupressaceae (cypress or cedar family) woods to genus because doing so usually relies on the minute feature of cross-field pitting (interconnections between longitudinal tracheids and ray parenchyma). Unfortunately,
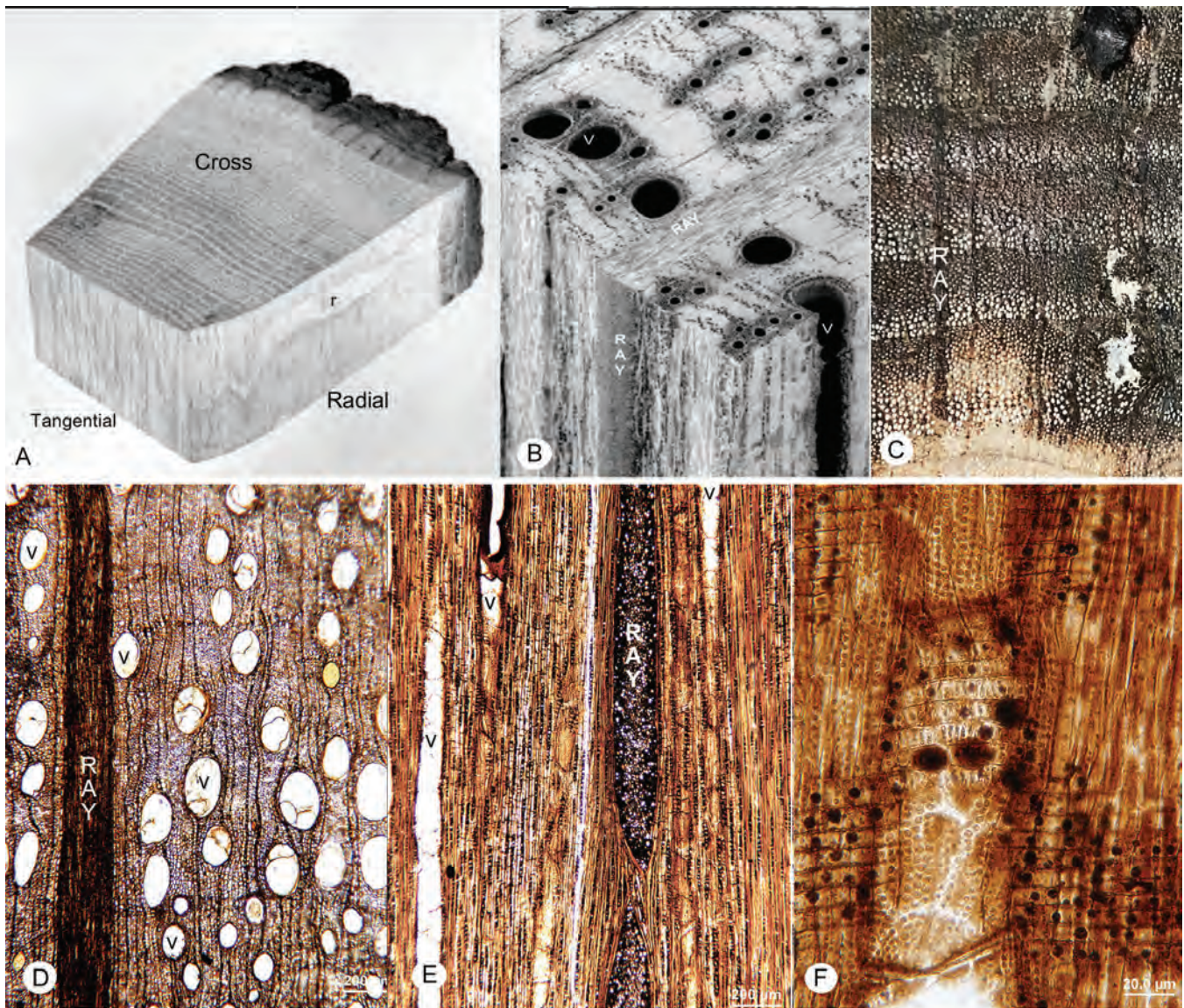
FIGURE 2. (A) Block of present-day *Quercus falcata*, southern red oak, cut to show the transverse (cross), radial, and tangential sections; a large ray (r) in radial section. (B) Scanning electron microscope view of a red oak wood with an orientation similar to that shown in A. Vs are in vessels and a large ray is labeled. PHOTOGRAPH COURTESY OF SUNY (C) *Quercinium lamarense*, an evergreen oak from Specimen Ridge, TS. (D–F) *Quercinium amethystianum*, an evergreen oak from Amethyst Mountain. (D) Exclusively solitary vessels (V), with vessel diameters gradually decreasing within a growth ring, one wide ray and numerous narrow rays, TS. (E) Rays of two distinct sizes: more than 10 cells wide and only one cell wide, V in the vessels, TLS. (F) Detail of a radial section showing interconnections (pits) between the cells, RLS.

wood must be exceptionally well-preserved to show this feature. The phrase "If you've seen one, you've seen them all" rather fits most Cupressaceae fossil wood because of the uniformity of wood structure in this family.

DICOT WOOD ANATOMY AND IDENTIFICATION

Although most of the large erect stumps and large logs in Yellowstone are conifers (Figure 1D), there is a variety of fossil dicot woods at Amethyst Mountain, Specimen Ridge, and the Gallatin Fossil Forests (Felix 1896; Platen 1908, 1909; Beyer 1954; Fritz 1977; Wheeler et al. 1977, 1978; Fritz and Fisk 1978; Yamamoto and Chadwick 1982). Information on systematic wood anatomy has increased markedly since these studies were published and some of the identifications in these early papers need re-evaluation (Table 1).

There is much work left to do on the fossil dicot woods of Yellowstone. Some were easy to assign to family or genus and have been described in the literature (see Table 1), but many others are not easy to identify. Oaks are probably the easiest angiosperm woods to identify to genus, but an isolated piece of oak wood cannot be identified to species, but rather to one of three broad groups: white oaks, red oaks, or evergreen oaks. Oaks have a distinctive combination of

TABLE 1. Angiosperm woods in the Yellowstone Fossil Forests. AM=Amethyst Mountain, GFF = Gallatin Fossil Forests; SR = Specimen Ridge

Family	Species	Location	Reference
Identification Seems Correct			
Anacardiaceae	*Rhus crystallifera*	AM, SR	Wheeler et al 1978
Araliaceae	Genus indet.	AM	Fritz and Fisk 1979
Betulaceae	*Alnus latissima*	GFF	Wheeler et al. 1977
Betulaceae	*Carpinus absarokensis*	SR	Wheeler et al. 1977
Betulaceae	*Carpinus saximontana*	GFF	Wheeler et al. 1977
Betulaceae	*Betula* ?	AM	Fritz and Fisk 1979;
Cyrillaceae	*Cyrilloxylon eocenicum*	SR	Wheeler et al. 1978
Fagaceae	*Quercinium amethystianum*	AM	Wheeler et al. 1978
Fagaceae	*Quercinium lamarense*	SR	Wheeler et al. 1978
Fagaceae	*Quercinium knowltonii*	AM	Felix 1896
Fagaceae	*Quercus rubida*	SR	Beyer 1954
Juglandaceae	*Pterocaryoxylon knowltonii*	SR	Wheeler et al. 1978
Lauraceae	*Laurinoxylon eocenicum*	SR	Wheeler et al. 1977
Lauraceae	*Laurinoxylon porosum*	AM	Wheeler et al. 1977
Lauraceae	*Laurinoxylon wheelerae*	SR	Wheeler et al. 1977; Dupéron-Laudoueneix and Dupéron 2005
Lauraceae	Genus indet.	AM	Fritz and Fisk 1979
Lauraceae	*Perseoxylon aromaticum*	AM	Felix 1896
Leguminosae	"*Laurinoxylon*" *pulchrum*	AM, SR	Knowlton 1896; Platen 1906
Magnoliaceae	*Magnoliaceoxylon wetmorei*	GFF	Wheeler et al. 1977
Magnoliaceae	Genus indet.	AM	Fritz and Fisk 1979
Myricaceae	*Myrica absarokensis*	SR	Wheeler et al. 1978
Nyssaceae	*Nyssa saximontana*	SR	Wheeler et al. 1978
Platanaceae	*Platanoxylon haydenii*	AM, SR	Felix 1896; Platen 1908; Wheeler et al. 1978
Rosaceae	*Prunus gummosa*	AM	Platen 1908; Wheeler et al. 1978
Salicaceae	*Populus* ?	AM	Fritz and Fisk 1979
Ulmaceae	*Zelkovoxylon occidentale*	SR	Wheeler et al. 1978
Questionable Identification			
? Altingiaceae	*Liquidambar* sp.—probably Hamamelidaceae	GFF	Yamamoto and Chadwick
? Celastraceae	*Elaeodendroxylon polymorphum*	AM	Platen 1908
? Cornaceae	*Cornus* sp.	GFF	Yamamoto and Chadwick 1982
? Fagaceae	*Fagus grandiporosa, Fagus* sp.	SR, GFF	Beyer 1954
? Nyssaceae	*Nyssa* sp.	GFF	Yamamoto and Chadwick 1982
? Rhamnaceae	*Rhamnacinium radiatum*	AM	Felix 1896
? Staphyleaceae	*Turpinia lamarense*	SR	Wheeler et al. 1978
Incorrect Identification	Betulaceae—*Alnus* sp., *Betula* sp; Ebenaceae—*Diospyros* sp.; Fagaceae—*Fagus* sp.; Magnoliaceae—*Liriodendron* sp., *Magnolia* sp.; Oleaceae—*Fraxinus* sp.; Platanaceae—*Platanus* sp.; Salicaceae—*Salix* sp.; Sapindaceae—*Acer* sp., *Aesculus* sp.	GFF	Yamamoto and Chadwick 1982

wood anatomical features, including the wide water-conducting vessels being exclusively solitary, rays of two distinct size classes (rays more than 10 cells wide and rays only one cell wide), and large vessel-ray parenchyma pits (Figures 2A–F). Present-day red and white oaks are ring-porous with a distinct earlywood zone with wide vessels and an abrupt change to a latewood zone with much narrower vessels (Figure 2B). The vessel widths of Amethyst Mountain oaks gradually decrease within a growth ring (semi-ring-porous), indicating they belong to the evergreen oak group (Figures 2C–D).

The side-by-side interconnections between cells (pits) are among the key features for wood identification; pits are visible in longitudinal sections. Radial longitudinal sections (RLS) are best for seeing the end-to-end connections (perforation plates) between the individual open-ended vessel elements (Figures 2F, 3A). Vessel elements usually are <1 mm (<.04 in) long, but they align end to end to form vessels, which range in length from a few centimeters to more than 10 m (33 ft). Vessel-ray parenchyma pits are observed in radial sections (Figure 3B). Tangential longitudinal sections (TLS) expose ray width and height and usually are best for seeing the intervessel pits (Figure 3C).

Knowlton (1899) greatly admired the anatomical details of one of the woods he collected and sectioned and named it *Laurinoxylon pulchrum*. He thought it belonged to the laurel family (Lauraceae), hence the genus name *Laurinoxylon*, with *pulchrum*, Latin for beauty, as the specific epithet. The thin sections of this wood were prepared in the late

FIGURE 3. (A) Block cut to reveal interconnections between vessels and ray parenchyma (vrp), between adjacent vessels (ivp = intervessel pits), and locations of perforation plates (PP) between vessel elements (VEL), *Acer palmatum* (Japanese maple). **(B)** Enlarged vessel-ray parenchyma pits (vrp) in longitudinal section, *Cinnamomum camphora* (Lauraceae). **(C)** Rays, mostly two cells wide; outgrowths of ray parenchyma (tyloses) into the vessel (V), *Cinnamomum camphora* (Lauraceae), TLS. (A–C) SEMS COURTESY OF FFPRI, TSUKUBA, JAPAN **(D–F)**. Photomicrographs of Knowlton's *Laurinoxylon pulchrum*. **(D)** Distinct growth ring boundaries, vessels gradually decrease in width within a growth ring, latewood vessels surrounded by axial parenchyma (arrow points to light colored cells forming wings around the vessels), TS. **(E)** Rays, mostly two cells wide; arrow points to axial parenchyma strands, TLS. **(F)** Parenchyma strands (p) next to the vessels, vessel-parenchyma pits (VP) small, RLS.
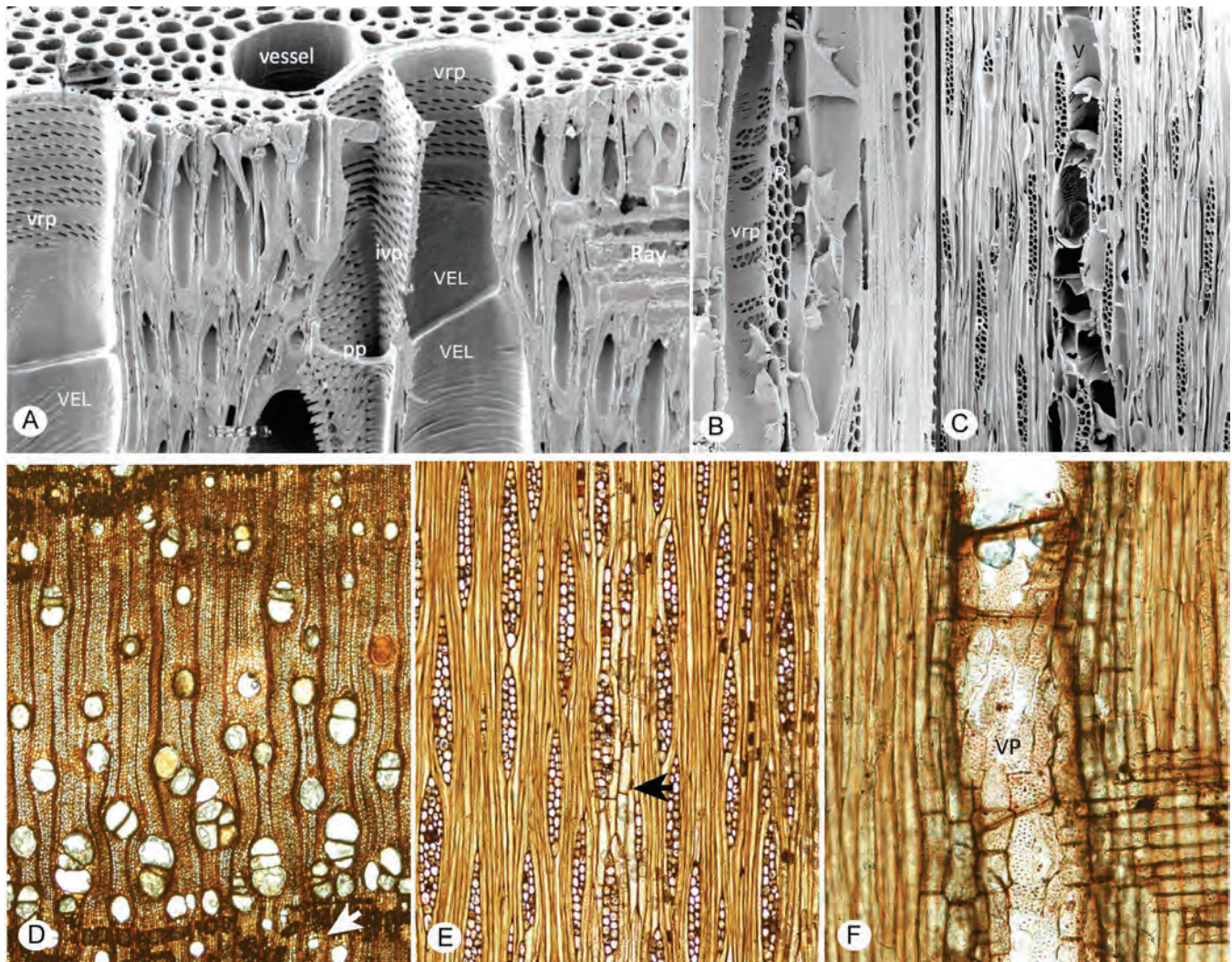
1800s and are still in excellent condition; Figures 3D–F are recent photomicrographs of them. This wood has distinct growth rings, with vessels gradually decreasing in diameter throughout the growth ring (Figure 3D), narrow rays that are mostly two cells wide (Figure 3E), and axial parenchyma associated with the vessels (Figures 3D, 3F). While deserving of the epithet *pulchrum,* it has a combination of characters that are not diagnostic of the Lauraceae but indicate that it is more likely related to the legume family. In the Lauraceae, the interconnections between vessels and parenchyma cells generally are enlarged and differ from the interconnections between vessel elements (Figure 3B). In *Laurinoxylon pulchrum* those interconnections are small (Figure 3F). An impetus for Knowlton assigning this wood to Lauraceae is that leaves of the family are common in the compression flora.

Nonetheless, lauraceous woods are common in the Eocene and are present at Yellowstone. These include *Perseoxylon aromaticum* (Felix 1896) and *Laurinoxylon porosum* from Amethyst Mountain (Figures 4A–C), and *L. eocenicum* and *L. wheelerae* from Specimen Ridge (Wheeler et al. 1977). Fritz and Fisk (1979) found, but did not name, a Lauraceae wood in their Unit 10 of Amethyst Mountain. The Gallatin Fossil Forests also have Lauraceae woods, with at least one type in Yamamoto and Chadwick's (1982) collections and another in R.A. Scott's collection that need description. The Gallatin lauraceous woods differ from those of Amethyst Mountain and Specimen Ridge. Many, but not all, Lauraceae have a distinctive feature in their wood—inflated oil cells—that helps to identify them (Figures 4B–C). The woods mentioned in this paragraph all have that feature.

One of the most common of the angiosperm woods is *Platanoxylon*, belonging to the sycamore or plane tree family (Platanaceae). This complements an 1860s story about Specimen Ridge (Figure 5A), attributed to Jim Bridger: "I looked up the petrified tree, and out on a petrified limb saw a petrified bird singing; a petrified song sticking out his mouth about ten petrified feet. Looking down, I saw that the ground was covered with petrified balls like sycamore balls, and from these a considerable forest was growing up and stretching away to the east" (Haines 1974: 38–39). Bridger was a famous fabulist, but this observation foretold what Felix (1898), Platen (1909), Beyer (1954), and Wheeler et al (1977) observed—sycamore-like fossil woods (*Platanoxylon*) are common at Yellowstone. The sycamore-like woods of Yellowstone have a combination of features, i.e., narrow, numerous vessels evenly distributed throughout a growth ring (diffuse-porous) (Figure 5B), and rays that are wide and tall (Figure 5C), telling of a relationship with modern sycamore/plane trees (*Platanus*). These Eocene sycamore-like woods differ from present-day ones because all the end walls of the water-conducting cells (vessel elements) have bars across them (scalariform

FIGURE 4. *Laurinoxylon porosum* from Amethyst Mountain. (A) Growth ring boundaries not well defined, vessels solitary and in multiples, of similar size throughout a growth ring (diffuse-porous), TS. (B) Rays, mostly 3–4 cells wide; oil cell (OC) at the margin of one ray, tangential section, TLS. (C) Oil cell (oc) in a ray; most of the ray cells (rc) are horizontally elongate, RLS.
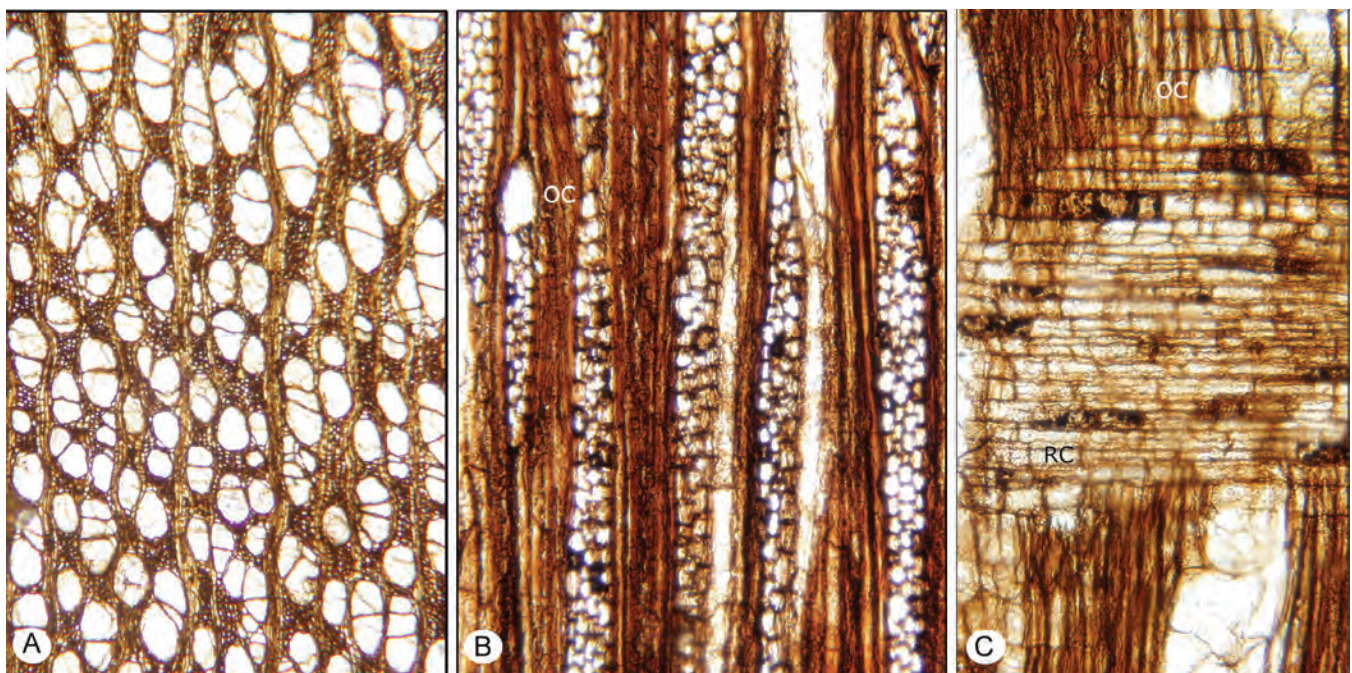
FIGURE 5. (A) Erling Dorf in 1976 next to what was the trailhead marker for the trail to Specimen Ridge, Lamar River Valley. (B–C) *Platanoxylon haydenii*. (B) Growth rings present, wood diffuse-porous, narrow and numerous vessels, wide rays, TS. (C) Tall and wide rays; insert showing a scalariform perforation plate, with bars across the opening, TLS. (D–F) *Spiroplatanoxylon* sp., Gallatin, Yamamoto and Chadwick specimen 05045. (D) Narrow and numerous vessels, wide rays, TS. (E) Tall and wide rays. TLS. (F) Spiral thickenings in a vessel element (arrow), RLS.

perforation plates) (insert in Figure 5C), while all present-day sycamores have some water-conducting cells with completely open ends (simple perforation plates). Wood anatomists have long considered scalariform perforation plates to be more primitive than simple perforation plates.

GALLATIN FOSSIL FOREST DICOTS

Chadwick, Yamamoto, and I are re-evaluating the affinities of the dicot woods they earlier described (Yamamoto and Chadwick 1982). We've had some surprises. Among their collections are woods with narrow, numerous vessels fairly evenly distributed throughout a growth ring (diffuse-porous) and tall and wide rays (Figures 5D–E); these woods initially were thought to be *Platanoxylon* but have proved not to be. One has helical thickenings in its vessel elements (Figure 5F); this feature does not occur in present-day sycamores. *Spiroplatanoxylon* is a generic name created for Oligocene–Miocene European *Platanus*-like woods with helical thickenings (Süss 2007). This Gallatin wood is the first report of the genus in North America, as well as the oldest known. To date, there are some 12 distinct dicot woods in Yamamoto and Chadwick's collections, ten of which seem to deserve being named new species. Two are shown in Figures 6A–D. One (Figures 6C–D) is not a surprise because it has characteristics of the witch hazel family (Hamamelidaceae), a family commonly found in Northern Hemisphere fossil floras.
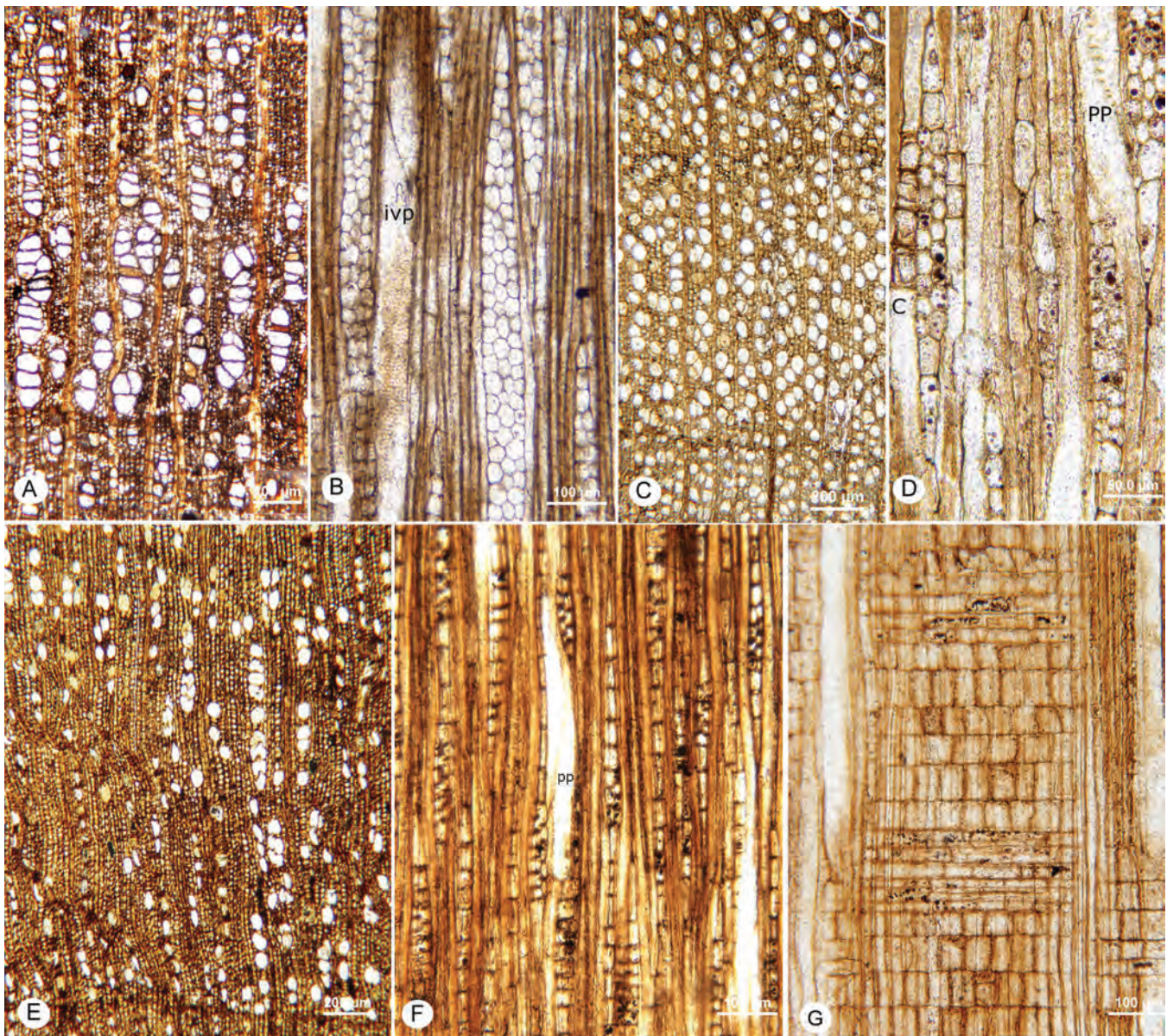
FIGURE 6. (A, B) Gallatin, Yamamoto and Chadwick specimen 05065. (A) Vessels commonly in multiples aligned parallel to the rays, TS. (B) Rays, mostly three cells wide; intervessel pits (ivp), TLS. (C, D) Gallatin, specimen Yamamoto and Chadwick specimen 05026. (C) Diffuse-porous wood, vessels mostly solitary, TS. (D) Narrow rays, perforation plate (PP) in side view, crystals in axial parenchyma strand (C), TLS. (E–G) USGS Sample D2089-3. (E) Growth ring boundaries weakly defined, wood diffuse-porous, vessel groups aligned parallel to the rays, TS. (F) Narrow rays, steeply inclined vessel element end wall/ scalariform perforation plate (pp), TLS. (G) Ray composed of procumbent, square, and upright ray parenchyma cells, RLS.

There were three easy-to-identify wood types in R.A. Scott's collection of Gallatin woods, and these have been described in the literature: *Alnus latissima,* an alder, and *Carpinus saximontana,* a hornbeam, both of the birch family (Betulaceae); and *Magnoliaceoxylon wetmorei,* a magnolia, but not similar to the southeastern US species. However, there are at least eight other distinct wood types left to describe; Figures 6E–G show one of them.

WORK IN PROGRESS, USGS COLLECTIONS

In the late 1950s, 1960s, and early 1970s, R.A. Scott of the US Geological Survey collected woods from (1) USGS Paleobot. Loc. No. D2054A, Amethyst Mountain, Lamar River Formation; (2) USGS Paleobot. Loc. No. D2054B. Specimen Ridge, Lamar River Formation; and (3) USGS Paleobot. Loc. No. D2089, Gallatin Fossil Forest, Fortress Mountain Member of the Sepulcher Formation. Scott's objective was to collect angiosperm woods that appeared well preserved. Because he wanted to avoid harming the integrity of the standing trees and stumps he only collected detached pieces. These collections were made prior to the advent of GPS units, so the samples' exact positions within the fossil forest levels are not known.

After the 1977 and 1978 papers on Scott's collections (Wheeler et al. 1977, 1978, Table 1), the intention was to publish a third paper because there are additional distinctive wood types from all three of Scott's localities. That third paper is a still a work in progress, reflecting the reality that relatively easy-to-identify fossil plants will be the first published, while the difficult-to-identify taxa may languish for years.

Figure 7 shows two examples of Scott's woods that await formal descriptions. Figures 7A–C show a Specimen Ridge wood that probably is a legume. Figures 7D–F show an Amethyst Mountain wood that most certainly is a legume; the preservation of this wood is exceptional and shows a minute anatomical feature important for confirming affinities with the legumes—vestured intervessel pits (Figure 7F). Photomicrographs of the Yellowstone woods that Scott collected, including most of the unidentified ones, are archived on the North Carolina State University library servers associated with InsideWood and can be found by doing a keyword search for Yellowstone AND (in caps) Wheeler (InsideWood 2004–onwards; Wheeler 2011; Wheeler et al. 2020).

CONCLUSIONS

Because Scott's collections are a composite of woods from different layers, their use in paleoenvironmental and

FIGURE 7. (A–C) Probable legume from Specimen Ridge, USGS Sample D2054B-4. A) Distinct growth rings, semi-ring-porous wood, axial parenchyma (light colored tissue) associated with the vessels, TS. (B) Rays, mostly two cells wide, TLS. (C) Procumbent ray cells with their long axis oriented perpendicular to the longitudinal cells, simple perforation plate in bottom third of the photomicrograph, RLS. (D, E) Legume wood from Amethyst Mountain, USGS Sample D2054-1. (D) Diffuse-porous wood with abundant axial parenchyma, TS. (E) Rays, mostly three cells wide; axial parenchyma strands mostly of two cells, TLS. (F) Crowded intervessel pits with vestures, TLS.
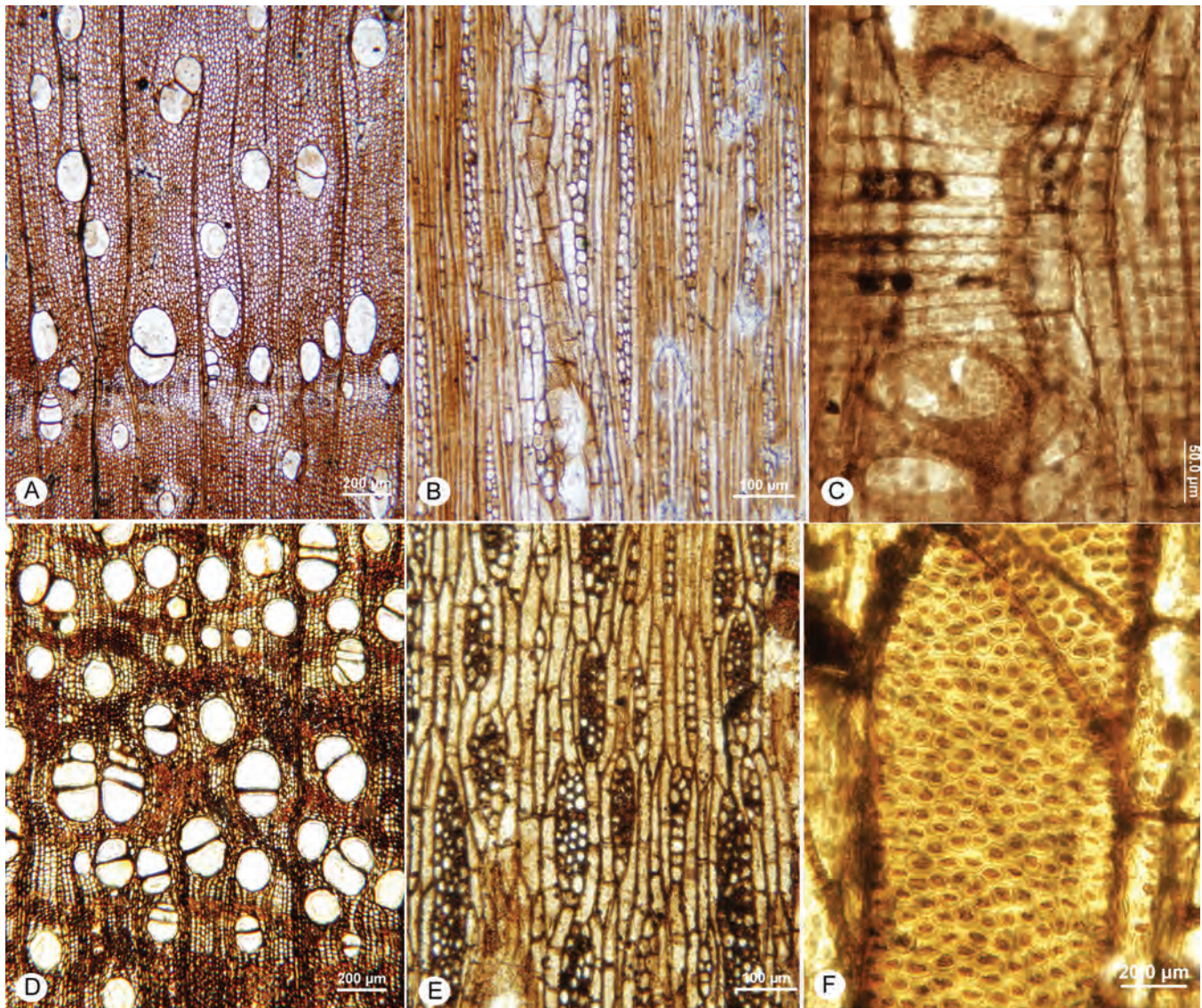
TABLE 2. Comparison of growth ring distinctiveness, porosity, and perforation plate type.

Feature	Specimen Ridge (n=16)	Amethyst Mountain (n=14)	Gallatin (n=20)
Distinct Growth Rings	72%	90%	75%
Indistinct Growth Rings	28%	10%	25%
Ring-porous	4%	0	0
Semi-ring-porous	31%	46%	10%
Diffuse-porous	63%	54%	90%
Simple Perforations	56%	64%	39%
Scalariform Perforations	44%	36%	61%

paleoecological interpretations is compromised. However, none of the woods have the combination of diffuse-porosity with few, wide vessels as occurs in trees of lowland aseasonal tropical forests. The nearest living relatives of most woods listed in Table 1 are warm temperate to subtropical, and some seemingly have relationships with eastern Asia (e.g., *Zelkovoxylon* of the elm family, *Magnoliaceoxylon wetmorei, Nyssa saximontana*) or the southeastern US (e.g., *Cyrilloxylon eocenicum*). Somewhat unexpectedly, based on collections to date, Specimen Ridge and Amethyst Mountain (Lamar River Formation) have few dicot woods in common: only *Rhus crystallifera,* the legume *Laurinoxylon pulchrum,* and *Platanoxylon haydenii.* No dicot woods are shared between the Lamar River Formation and the Sepulcher Formation (Gallatin Fossil Forests). Table 2 (above) shows some environmentally significant dicot wood features that also differ.

Computing the incidences of growth ring distinctiveness, porosity, and perforation plate types for the Yellowstone dicot woods can only give an extremely generalized picture of their early middle Eocene environment (Table 2). The unidentified woods were included in this exercise. Woods with distinct growth rings are more common than woods with indistinct growth rings. Ring-porous woods are associated with pronounced seasonal climates and deciduousness. In all the years that Yellowstone woods have been studied, the sole report of a ring-porous wood is a red oak from Specimen Ridge, *Quercus rubida* (Beyer 1954). There are obvious differences between the Lamar River Formation woods (Specimen Ridge and Amethyst Mountain) and the Sepulcher Formation woods (Gallatin Fossil Forests) in the incidences of porosity and perforation plate types. The higher incidence of semi-ring-porous woods and simple perforation plate types in the Specimen Ridge and Amethyst Mountain woods compared to the Gallatin woods suggests they lived in more seasonal climates with increased selection for efficient water conduction. Experimental work has demonstrated that scalariform perforation plates impede water flow (e.g., Christman and Sperry 2010). The incidence of this feature at Yellowstone is considerably higher than for the younger Neogene fossil woods of the Northern Hemisphere (Wheeler and Baas 2019). Scalariform perforation plates are relatively common (up to 40%) in subtropical–warm temperate woody plants growing at higher elevations (Baas 1976). Perhaps the relatively high incidence of this feature in the Yellowstone woods is consistent with Wing's (1987) suggestion that Yellowstone's fossil flora grew in a cooler environment than contemporary fossil floras.

The obvious closing remarks to make are there is considerable work left to be done and the Yellowstone fossil woods need to be conserved in a manner that allows that to happen. There are three mountains composed of forests entombed in volcanics and much to be learned about the forests' composition and growth dynamics, and the similarities and differences in the composition of the different tiers of fossil forests. Further study will lead to a better understanding of the ancient vegetation of Yellowstone, in particular, and, more generally, the responses of woody plants to changing climate and the history of the Northern Hemisphere flora. For the future, one can only hope that there will be agile paleobotanists and geologists who can meet the challenges needed to make additional surveys and collections of the Yellowstone forests and have the support to do so.

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