

Eocene woods of central Oregon

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Eocene terrestrial strata of central Oregon contain abundant and well-preserved fossil woods that are important for understanding past floristic diversity, forest structure, and climate. In addition to the remarkably diverse and well-preserved Middle Eocene wood assemblage of the Clarno Nut Beds in the type area of the Clarno Formation in the John Day basin, there are well-preserved diverse Late Eocene wood assemblages from the vicinity of Post in the Crooked River Basin. The Post assemblages discussed herein share some genera with the Nut Beds flora (*Acer*, *Cercidiphyllum*, *Quercinium*, *Ulmus*), but also include some new elements that remain to be described in detail, including woods referable to the families Anacardiaceae, Fagaceae, Hamamelidaceae, and Juglandaceae. Comparison of the middle Eocene Nut Beds woods to the younger Post woods documents changes in climate, with the Post assemblages indicating increasing seasonality and an increase in deciduousness.

INTRODUCTION

Fossil wood occurs throughout North America and is especially common in the Tertiary of the western United States. The middle Eocene Clarno Nut Beds of the Clarno Formation in the John Day Basin yields the world's most diverse assemblage of fossil woods (Wheeler and Manchester 2002). The Nut Beds assemblage is a reference point for studies of other Eocene wood assemblages from central Oregon, as well as those from Eocene localities elsewhere in North America, Europe, and eastern Asia. It is particularly relevant in assessing the relationships between changes in climate and changes in vegetation or tree structure from the middle to late Eocene. Although late Eocene wood floras have been described from other parts of western North America (Wheeler and Landon 1992, Wheeler 2001), wood assemblages of late Eocene age in Oregon have received only limited attention.

Herein, we call attention to some prolific wood assemblages in the vicinity of Post, Oregon, in the Crooked River Basin. These sites also yield occasional silicified fruits and seeds reminiscent of those from the Nut Beds, providing the opportunity to examine both wood and reproductive organs from the same plant assemblage. Fossil woods from the Post area have long been collected by rockhounds because of their beauty. Their general anatomical characteristics have been described in informal publications, such as the Ore Bin (e.g., Gregory 1970) and George F. Beck's 1942 series "Fossil Woods of the Far West," and more rarely in the technical paleobotanical literature, as was done for a permineralized wood specimen from Crook County that Gregory (1971) interpreted as resembling modern *Acacia*.

In spite of fossil wood's relative abundance and over 100 years of study, there are surprisingly few detailed descriptions and discussions of North American Tertiary fossil wood in the scientific literature. For the North American Tertiary, there are fewer than 300 records of woods of flowering plants, and the Nut Beds wood assemblage accounts for the

bulk of those for the Eocene. Most paleobotanical studies of western North America have focused on leaves. In contrast, the biostratigraphic utility of fossil woods has received relatively little attention, probably because woods at some sites have been reworked and their exact provenance cannot be established. However, woods found in stratigraphic context merit detailed study for several reasons:

- 1) Sometimes wood is the only plant fossil at a locality, and thus may be the only data available for interpreting past vegetation and climate for that particular place and time.

- 2) Different plant parts differ in their likelihood of preservation, so even if other plant parts are present, woods contribute to a more complete interpretation of past vegetation and climate for a particular region and time.

- 3) When woods are associated with other plant parts, there can be opportunities for whole plant reconstructions.

- 4) Woods provide data on past plant diversity, may document the earliest occurrence of particular taxa, and are useful for addressing biogeographic questions.

- 5) Fossil woods provide the best or most direct estimate of plant stature, either through direct measurement of girth, or by occurrence of certain anatomical features that can be used to distinguish lianas from shrubs and trees, or that are known to only occur in large trees.

- 6) The incidence of some key wood anatomical characteristics within an assemblage is useful for general paleoclimatic interpretations.

In the context of these reasons, particularly 2 through 6, we give a short overview of the Nut Beds wood assemblage and one of three recently collected assemblages (UF 279) near Post, in the Crooked River Basin. Two of the three Post wood assemblages were combined as a dataset for a study investigating the use of selected wood anatomical characteristics for inferring MAT (Wiemann et al. 1999). This paper continues the study of the Post woods and their comparison to the Nut Beds woods, and begins the assessment of their relationships to extant plants.

MATERIALS AND METHODS

Three recently collected sites in the Post area (University of Florida Paleobotanical localities 254, 278, and 279) contain abundant silicified woods as well as silicified fruits and seeds. The Post specimens are found loose in eroded tuffs and are apparently from the lower part of the John Day Formation. A minimum age for these wood sites is provided by a white tuff overlying the fossiliferous tuff at UF locality 278. Sanidine crystals from this white tuff give an $^{40}\text{Ar}/^{39}\text{Ar}$ date of 36.21 ± 0.26 MA ($n = 26$) (Manchester and McIntosh, in press). There are no datable tuffs at or immediately below the fossiliferous horizon to provide a maximum age. The Post sites were previously referred to the Clarno Formation (Arnold 1952; Hergert (1961), but now are considered to be in the lower part of the John Day Formation (Manchester and McIntosh, in press).

A diamond lapidary saw was used to cut thick sections (wafers) of cross (transverse), tangential, and radial surfaces. After one side of each wafer was smoothed using a lap to remove saw marks, it was affixed to a glass slide using 24-hour transparent epoxy. The sections were then ground until they were thin enough ($\sim 30 \mu\text{m}$) so that anatomical details could be seen with transmitted light microscopy. Grinding was done either by hand, using a glass plate and a slurry of carborundum grit, or by using a Buehler petrographic thin-section grinding machine. Cover slips were mounted using Canada Balsam to improve clarity for light microscopy. All samples have been deposited in the paleobotanical collections of the University of Florida, Gainesville; in this paper, individual samples are referred to by their UF sample numbers. To date, we have examined thin-sections of 36 samples from UF 279 and 42 samples from UF 254. Relationships to extant plants were assessed by reference to North Carolina State University's InsideWood website (<http://insidewood.lib.ncsu.edu/search>).

RESULTS AND DISCUSSION

Systematic Information

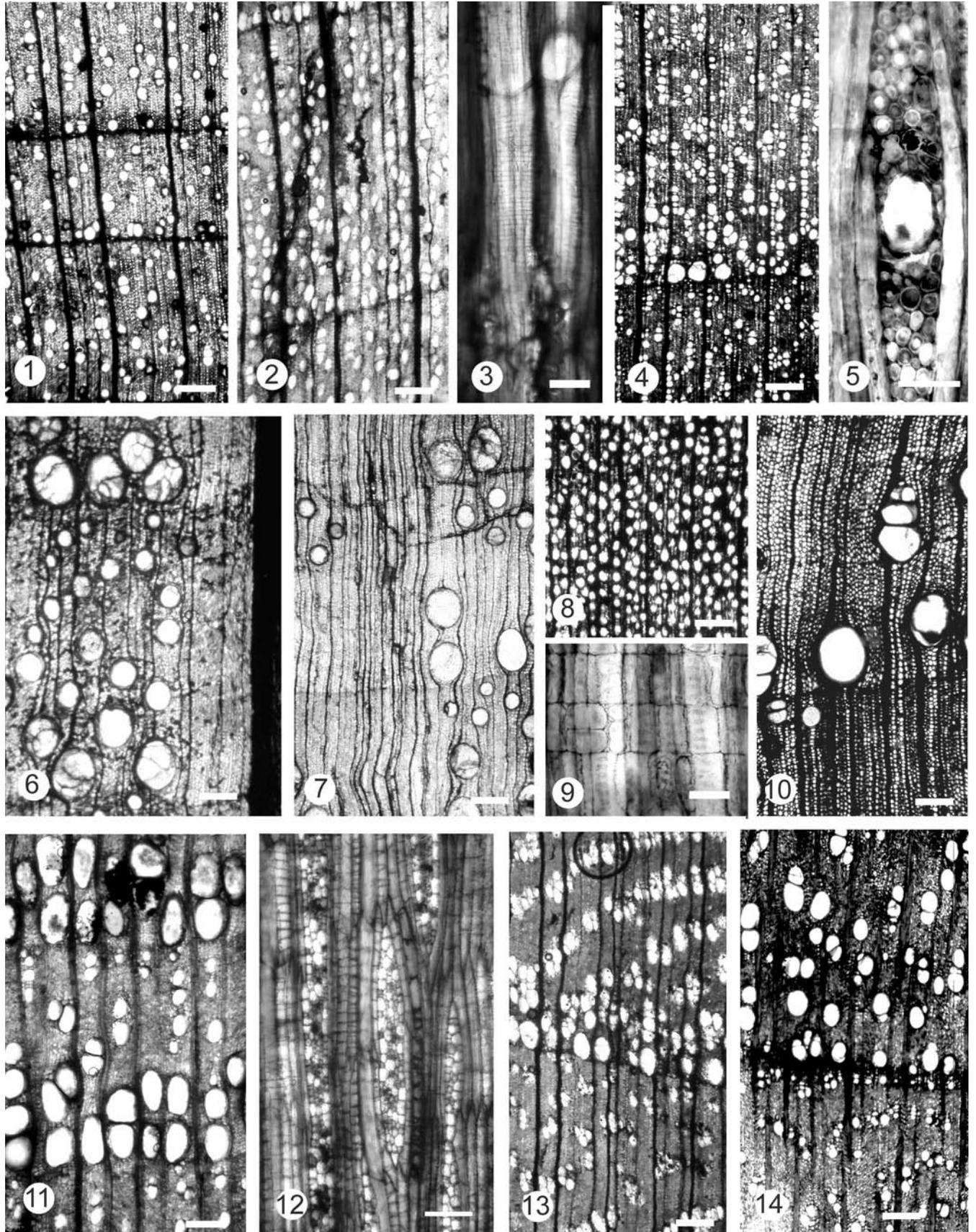
The middle Eocene Clarno Nut Beds flora is unusual because it preserves multiple plant parts including fruits,

seeds, woods, and leaves. The fruit and seed flora is especially diverse with over 170 species (Manchester 1994). The wood assemblage contains at least 76 species (Wheeler and Manchester 2002). Although the Nut Beds fruit and seed types outnumber the wood types more than 2:1, there are at least four families represented in the wood assemblage (i.e., Cercidiphyllaceae, Malvaceae *sensu lato*, Ginkgoaceae, taxodioid clade of the Cupressaceae) that do not occur in the fruit and seed assemblage. There are 19 families common to the fruit and seed and wood assemblages of the Nut Beds. In some families there is congruency in the information from the fruit and seed and wood assemblages; for example, in the Rosaceae (rose family) there are both woods and fruits and seeds similar to the modern genus *Prunus* (cherry) and to the subfamily Maloideae. However, in other families there is discrepancy. Woods structurally equivalent to the extant genera *Acer* (maple) and *Betula* (birch) occur, but the only fruits of the families Aceraceae and Betulaceae so far recovered belong to extinct genera. Conversely, in the Vitaceae (grape family), the Nut Beds woods do not resemble extant genera, but the fruits and seeds do. Such discrepancies should not be surprising because differential rates of evolution are expected for plant parts that serve different functions and are subject to different selective pressures. These discrepancies also suggest that if entire plants could be reconstructed with certainty, a higher percentage of extinct genera might be recognized, and that the characters of these genera would be especially useful in phylogenetic analyses based on morphological and anatomical features.

The localities in Post provide an opportunity for comparing the equivalencies of wood, fruit and seed, and leaf assemblages and their relationships to modern taxa. Our current observations reveal that there is little overlap in the woods and fruit and seed genera from UF 279 (Manchester and McIntosh, in press), although Juglandaceae are represented in both assemblages.

The diversity in the UF 279 wood assemblage is apparent in the selected cross-sectional views shown in Figs. 1, 2, 4, 6–8, 10, 11, and 13. There is variation in vessel distribution and size, as well as in ray size and spacing. There are

► **Figures 1–13.** Woods from UF locality 279. **Figure 14.** Nut Beds wood. **1.** *Acer* sp. 1, diffuse porous wood with narrow vessels that are solitary and in short multiples; cross section, UF 34456. **2.** *Acer* sp. 2, diffuse porous wood with narrow vessels that are solitary and in short multiples; cross section, UF 34466. **3.** *Acer* sp. 3, vessel element with simple perforation plate and helical thickenings; radial section, UF 24548. **4.** Anacardiaceae wood, ring porous with a solitary row of earlywood vessels and latewood zone with narrow vessels frequently in radial multiples; cross section, UF 24545. **5.** Anacardiaceae wood, ray with radial canal; tangential section, UF 24545. **6.** *Quercinium* sp., semi-ring porous to ring porous wood, solitary vessels, and rays of two distinct sizes; cross section, UF 24550. **7.** Semi-ring porous to ring porous Fagaceae wood showing solitary vessels and aggregate rays; cross section, UF 24559. **8.** Diffuse porous Hamamelidaceae wood showing solitary narrow vessels that are angular in outline; cross section, UF 24555. **9.** Hamamelidaceae wood with horizontally elongate vessel-ray parenchyma pits, and chambered crystalliferous ray parenchyma cell; radial section, UF 24555. **10.** Semi-ring-porous wood of cf. *Pterocaryoxylon* (soft walnut/Chinese walnut) showing gradual change in vessel diameter, and vessels solitary and in radial multiples; cross section, UF 24557. **11.** Ring porous Malvaceae wood; cross section, UF 24557. **12.** Malvaceae wood showing rays with tile cells, and storied axial parenchyma; tangential section, UF 24557. **13.** Ring porous wood of *Ulmus* sp. with solitary row of earlywood vessels, and latewood vessels in wavy tangential bands; cross section, UF 34457. **14.** Semi-ring-porous *Ulmus danielii* latewood with vessels in wavy tangential bands, USNM 507931. Scale bars: 200 μm in 1, 2, 4, 6, 7, 8, 10, 11, 13, 14; 100 μm in 12; 50 μm in 3 and 9; 25 μm in 5.



few woods, either fossil or modern, that can be identified to family based solely on their cross-sectional appearance. Some woods can be recognized as Fagaceae because they have exclusively solitary vessels, an obvious difference between earlywood and latewood vessel diameters, and rays of two distinct sizes (e.g., Fig. 6) or aggregate rays (e.g., Fig. 7). For most woods, features seen in other views (planes of section) are necessary for determining their relationships to extant plants. Radial sections are needed to view vessel elements with simple perforations and spiral thickenings, which are among the primary features used in determining that this wood is *Acer* (maple; Fig. 3). Tangential sections are needed to see rays with radial canals (Fig. 5), a feature found in only a few dicot families, and which indicates that this wood belongs to the Anacardiaceae (the cashew family). Figure 9 is a radial view that shows a chambered-ray cell with crystals, and elongated vessel-ray parenchyma pits, features indicating this wood belongs to the Hamamelidaceae (the witch hazel family) rather than the eight or more other families with genera that appear similar in cross-section. Tile cells in rays are unique to the Malvaceae *sensu lato*. Such cells can best be seen in longitudinal sections and Fig. 12, which shows ray cells of two distinct sizes that indicate the affinities of this UF 279 wood are with the Malvaceae.

To date, we have recognized 19 different wood types from UF 279; of these, 11 are identified to family: Aceraceae (maple family) (Figs. 1–3); Anacardiaceae (cashew family) (Figs. 4, 5); Cercidiphyllaceae; Fagaceae (oak family) (Figs. 6, 7); Cupressaceae (a taxodioid type conifer); Hamamelidaceae (witch hazel family) (Figs. 8, 9); Juglandaceae (walnut family) (Fig. 10); Malvaceae *sensu lato* (mallow family) (Figs. 11, 12); Ulmaceae (elm family) (Fig. 13); of these, seven can be assigned to genus (*Acer*, *Cercidiphyllum*, *Pterocaryoxylon*, *Quercinium*, *Ulmus*). Among the 19 wood types are 14 new species. Preliminary work indicates that the composition of UF 254 differs from UF 279, with at least 14 wood types recognized thus far, 10 of which are likely to be new species. Of the UF 254 woods, six can be assigned to family (Fagaceae, Lauraceae, Malvaceae, Platanaceae, Rosaceae, Pinaceae).

With additional work, we expect to clarify the affinities of most of these woods from these two Eocene localities. The woods of the families Aceraceae, Anacardiaceae, Juglandaceae, and Ulmaceae have particular utility in determining relationships between the eastern Asian and North American floras.

Table 1 lists the families that were identified with certainty in the Nut Beds and at UF 279. Given that many more Nut Beds samples were collected and studied than were UF 279 samples, it is not surprising that the Nut Beds assemblage is the more diverse of the two. The difference in their compositions reflects the modernization of the flora, as the families absent from the younger (UF 279) assemblage include the predominantly tropical families Araliaceae, Annonaceae, Lauraceae, Leguminosae, Magnoliaceae, Sabiaceae, and Sapindaceae. The families that are more speciose and more abundant

at UF 279 than at the Nut Beds today have a predominantly temperate distribution, Aceraceae (maple family; Figs. 1–3) and Ulmaceae (elm family; Fig. 13). Woods of *Acer* (maple), *Cercidiphyllum*, *Quercinium* (oak-like woods), and *Ulmus* (elm) occur in both the Nut Beds and UF 279 assemblages. Most temperate-zone Ulmaceae have latewood vessels in wavy tangential bands (Figs. 13, 14). The depth of the earlywood pore zone and the spacing of the wide earlywood vessels are considered important diagnostic features for distinguishing species of elm from one another. The single elm species in the Nut Beds has a broad earlywood zone and a gradual transition from earlywood to latewood (Fig. 14). UF 279 elms differ from the Nut Beds elm; for instance, UF 34457 shows an abrupt transition from earlywood to latewood, and displays a solitary row of wide earlywood vessels (Fig. 13).

The woods of the Aceraceae, Anacardiaceae, Fagaceae, Hamamelidaceae, Juglandaceae, and Malvaceae differ between the two assemblages. Moreover, the UF 279 woods of Anacardiaceae, Juglandaceae, and Malvaceae have more pronounced differences between earlywood and latewood than do the Nut Beds woods of these families. Extant hardwood trees that produce wood with such obvious differences between earlywood and latewood invariably are deciduous.

Ecological Wood Anatomy

It has long been known that various anatomical characteristics of wood, especially those related to the water-conducting vessels, correlate with latitude, altitude, ecology, and climate (see summaries of Baas 1986 and Carlquist 1988). For example, diffuse porous woods (defined as woods with nearly equal-sized vessels throughout a growth ring) that have very wide vessels (>200 μm) are relatively common in trees of the lowland moist tropics, but they do not occur in shrubs and trees of high latitudes or arid regions. Such woods are absent from the Post wood assemblages. Trees and shrubs of the temperate zone with diffuse porous woods have narrow vessels (Figs. 1, 2, 8). Ring porous woods with a distinct earlywood zone of very wide vessels and latewood with narrow vessels are typical of seasonal climates of the Northern Hemisphere (Gilbert 1940, Woodcock 1994, Woodcock and Ignas 1994, Baas et al. 2004) (Figs. 4, 11, 13). In addition, there are woods intermediate between diffuse porosity and ring porosity; these semi-ring porous woods have earlywood with wide vessels and a gradual transition to latewood with narrower vessels (Figs. 6, 7, 10, 14). Ring porous woods do not extend into high latitudes with short growing seasons and extreme cold (Woodcock and Ignas 1994). Consequently, their incidence has considerable potential in tracking the development of strongly seasonal climates. This includes following the transition from warm wet tropical and subtropical climates to temperate climates (appearance of and increase in ring porous woods), as well as the transition from warm or cool temperate to colder and more extreme climates (loss of ring porous woods) during the latest Tertiary (Wheeler and Baas 1991).

Table 1. Comparison of Nut Beds and UF 279 wood assemblages.

| Nut Beds | Post: UF 279 |
|---|---|
| ACERACEAE | |
| <i>Acer integrifolioxylon</i> Wheeler & Manchester | <i>Acer</i> , at least 2 species |
| ALANGIACEAE | |
| <i>Alangium oregonensis</i> Scott & Wheeler | Absent |
| ANACARDIACEAE | |
| 3 genera, 3 species | 1 species (cf. <i>Rhus</i>) |
| ANNONACEAE | |
| <i>Annonoxylon bonesii</i> Wheeler & Manchester | Absent |
| ARALIACEAE | |
| <i>Plerandroxylon oregonensis</i> Wheeler & Manchester | |
| <i>Plerandroxylon nutbedensis</i> Wheeler & Manchester | Absent |
| BETULACEAE | |
| <i>Betula clarnoensis</i> Scott & Wheeler | Absent |
| CERCIDIPHYLLACEAE | |
| <i>Cercidiphyllum alalongum</i> Scott & Wheeler | cf. <i>Cercidiphyllum</i> |
| FAGACEAE | |
| <i>Fagaceoxylon ostryopoides</i> Scott & Wheeler | <i>Lithocarpus</i> / <i>Castanopsis</i> |
| <i>Quercinium crystallifera</i> Scott & Wheeler | <i>Quercinium</i> sp. |
| HAMAMELIDACEAE | |
| <i>Hamamelidoxylon uniseriatum</i> Wheeler & Manchester | <i>Loropetalum</i> / <i>Sycopsis</i> |
| JUGLANDACEAE | |
| <i>Clarnoxylon blanchardii</i> Manchester & Wheeler | cf. <i>Pterocaryoxylon</i> |
| <i>Engelhardioxylon nutbedensis</i> Manchester | |
| LAURACEAE | |
| 5 genera, 6 species | Absent |
| LEGUMINOSAE | |
| 3 genera, 3 species | Absent |
| MAGNOLIACEAE | |
| 3 genera, 5 species | Absent |
| MALVACEAE | |
| <i>Chattawaya paliforme</i> Manchester | |
| <i>Triplochitioxylon oregonensis</i> Manchester | cf. <i>Triplochitioxylon</i> |
| PLATANACEAE | |
| <i>Platanoxylon haydenii</i> (Felix) Süss & Müller-Stoll 1977 | possible <i>Platanoxylon</i> ? |
| ROSACEAE | |
| 2 genera, 3 species | Absent |
| SABIACEAE | |
| 1 genus, 3 species | Absent |
| SAPINDACEAE | |
| 1 genus, 1 species | Absent |
| ULMACEAE | |
| <i>Ulmus danielii</i> Wheeler & Manchester | <i>Ulmus</i> , at least 2 species |
| VITACEAE | |
| 1 genus, 2 species | Absent |
| GYMNOSPERMAE | |
| GINKGOACEAE | |
| <i>Ginkgo bonesii</i> Scott, Barghoorn & Prakash | Absent |
| PINACEAE | |
| cf. <i>Pinus</i> , probably 2 species | Absent |
| CUPRESSACEAE | |
| cf. <i>Taxodioxylon</i> | cf. <i>Taxodioxylon</i> |

Ring porous and semi-ring porous woods (Figs. 4, 6, 7, 10, 11, 13) are more common at UF 279 (8 / 18 = 44%) and UF 254 (5 / 12 = 42%) than at the Nut Beds (13 / 76 = 17%). This is consistent with differences one would expect between middle Eocene and late Eocene woods, as markedly seasonal climates develop towards the end of the Eocene (e.g., Graham 1999). This change in porosity from the middle Eocene Nut Beds assemblage to the late Eocene Post localities also indicates an increase in deciduous species consistent with the postulate of somewhat cooler and more seasonal floras in the late Eocene than in the middle Eocene.

ACKNOWLEDGEMENTS

We are grateful to Jim Wood for giving permission to collect on his ranch where localities UF 278 and 279 are located, and to the summer 2004 OMSI student program for help with collecting.

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