Woods of the Eocene Nut Beds Flora

Clarno Formation, Oregon, USA

E.A. Wheeler
S.R. Manchester

IAWA Journal, Supplement 3

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by

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Cover: *Alangium oregonensis* Scott & Wheeler, cross section.

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CONTENTS

SUMMARY

The Nut Beds Flora of the Clarno Formation, dated at about 44 million years, is one of the most diverse fossil plant assemblages of North America, and contains fruits, seeds, woods, and leaves. The middle Eocene was a globally warm climatic interval and the diversity and composition of the Nut Beds fossil flora is considerably greater than that of the site's present-day arid semi-desert vegetation. Based upon examination of more than 600 samples of permineralized woods, 66 genera and 76 species are recognized, making the Nut Beds wood assemblage the most diverse fossil wood assemblage ever described from a single locality. The Nut Beds woods provide a dataset useful for systematic, evolutionary, biogeographic, and paleoecologic studies, and complement the data already provided by the rich co-occurring fruit and seed assemblage (145 genera, 173 species). Some families are known only from woods (Cercidiphyllaceae, Malvaceae s.l., Ginkgoaceae, Taxodiaceae). Others are known from both wood and fruits and seeds (Aceraceae, Alangiaceae, Anacardiaceae, Annonaceae, Araliaceae, Betulaceae, Fagaceae, Hamamelidaceae, Juglandaceae, Lauraceae, Leguminosae, Magnoliaceae, Platanaceae, Rosaceae, Sabiaceae, Sapindaceae, Ulmaceae s.l., Vitaceae, Palmae, Pinaceae). The discussion of Nut Beds *Meliosma* (Sabiaceae) woods includes new information on wood anatomical groups within extant *Meliosma*. Within these shared families, comparison of the fruits and seeds and wood shows: 1) similarity in relationships to modern genera (Hamamelidaceae, Rosaceae, Pinaceae); 2) woods are more diverse than fruits/seeds (Anacardiaceae, Araliaceae, Lauraceae, Leguminosae, Magnoliaceae); or 3) fruits and seeds are more diverse (Annonaceae, Juglandaceae, Palmae, Platanaceae, Sabiaceae, Ulmaceae s.l.). In some instances there is a mismatch between the wood and the reproductive structures in their relationships to extant genera and species, such that: a) woods resemble extant genera and the fruits and seeds do not (Aceraceae, Betulaceae), b) woods are assigned to extinct genera, yet the fruits/seeds resemble modern genera (Fagaceae, Vitaceae) or c) woods and fruits/seeds resemble different sections within the family or genus (Alangiaceae, Sapindaceae). Of the 38 wood genera assigned to family, some (34%) have anatomy corresponding to a single modern genus (e.g., *Acer, Alangium, Betula, Meliosma, Prunus*), others (16%) represent extinct genera (e.g., *Clarnoxylon*, Juglandaceae; *Triplochitioxylon*, Malvaceae s.l.), but most (50%) are stereotypic genera, woods that cannot be assigned to an extant genus, because their combination of features occurs in more than one extant genus (e.g., *Magnoliaceoxylon*, *Sapindoxylon*, *Maloidoxylon*). Seven genera are assigned to an order only (Malpighiales, Sapindales, Urticales); 21 are of unknown systematic affinities. Of the extant genera recognized, all now occur in eastern Asia. Some of these genera are also shared with eastern North America (50%) and/or Malesia (50%). The proportion of lianas or climbers represented in the Nut Beds woods (ca. 5%) is much lower than that for the fruits and seeds (43%), probably reflecting taphonomic differences between trees, shrubs, and vines. Leaf margin analyses of the Nut Beds flora, presence of Musaceae and high incidence of lianas in the fruit/seed assemblage suggest paratropical rainforest vegetation. One third of the wood types large enough to have growth rings have indistinct growth rings, suggesting relatively equable climates and weak seasonality. However, none of the Nut Beds woods have the syndrome of few, wide vessels associated with present-day tropical lowland trees. The relatively high incidence of scalariform perforation plates (22% in plants that were > 10 cm in diameter) and semi-ring porous woods (29%) is greater than that seen in tropical lowland rainforest trees today. These data indicate that the climatic conditions were probably in the range of warm temperate to subtropical, but not fully tropical.

Key words: Eocene, fossil wood, Tertiary, paleobotany, Clarno Formation, wood anatomy.

INTRODUCTION

The Eocene epoch (~55–34 million years ago) represents an intermediate point between the present-day and the initial radiation of the angiosperms in the lower Cretaceous, and was an important time in the evolution of modern angiosperm families and genera. In North America, the change from the warm, equable climates of the early Eocene to the cooler, more seasonal climates of the present day begins in the middle Eocene (see review in Graham 1999).

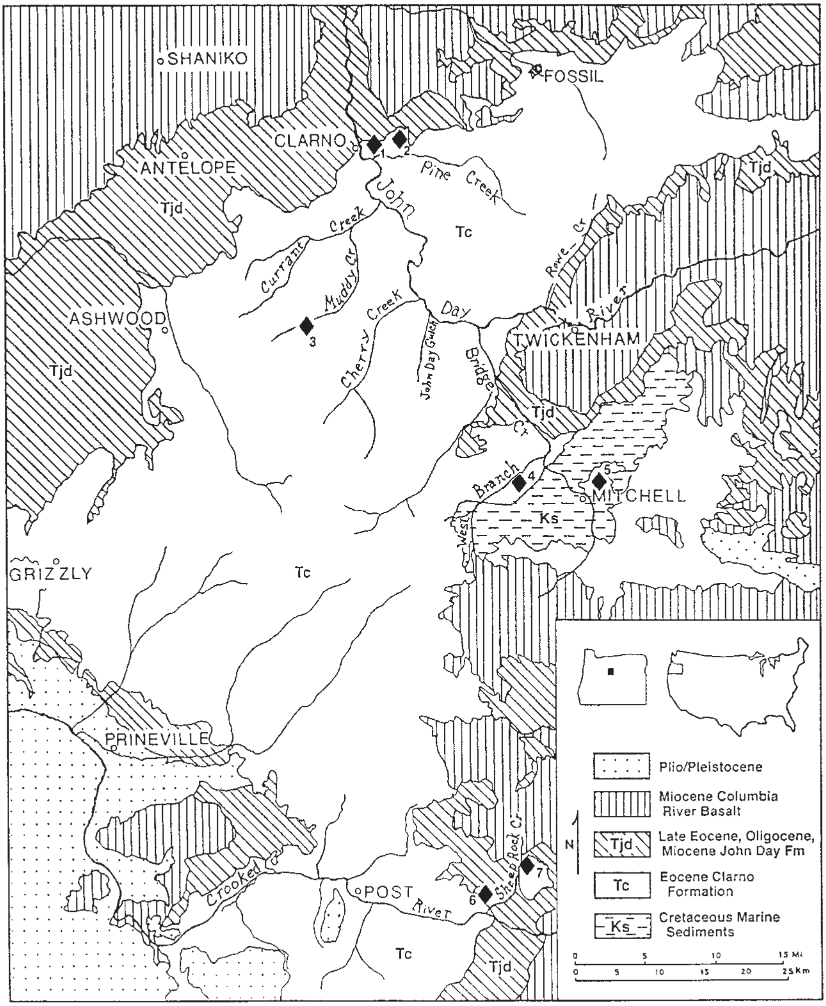

Fig. 1. Geologic map and index map (inset) of the John Day and Crooked River Basins, north-central Oregon, showing location of the Nut Beds (1), and other fossil wood localities in the Clarno Formation. Localities: 1: Nut Beds. 2: Hancock Quarry. 3: Muddy Creek. 4: West Branch Creek. 5: Mitchell, Fran Cherry Ranch. 6: Osmundites locality (Arnold). 7: Post. — Geologic map adapted from Walker (1977).

One of the most diverse assemblages of middle Eocene plant remains in western North America occurs in the type area of the Clarno Formation and is conserved within the John Day Fossil Beds National Monument in north-central Oregon, USA (Fig. 1). The Clarno Nut Beds Flora includes one of the most thoroughly documented and diverse fossil fruit and seed assemblages in North America (Scott 1954; Manchester 1994), with 173 species. The fruit and seed assemblage contains genera of

Fig. 2. A: Northwestern view to the Nut Beds locality. Silicified woods were recovered, along with silicified fruits and seeds, from each of the exposure faces numbered 1–4. – B: Students excavating for woods and fruits at the top of face 3 of the Nut Beds.

varied modern-day distribution, some with genera whose extant species are confined to temperate regions, and others with genera that are mainly confined to frost-free tropical regions (e.g., *Ensete*, *Sabal*, Menispermaceae). The present-day arid climate and vegetation of north-central Oregon and the Nut Beds locality (Fig. 2) contrast dramatically with the climate and vegetation indicated by the fossil flora, which has been interpreted as paratropical or subtropical forest with affinities primarily with southeast Asia (Manchester 1994). Today's mean annual temperature is 8.6 °C, with winter snows, and dry summers with daytime temperatures often over 35 °C. Vegetation is high desert grasslands, with scattered juniper (*Juniperus*) and sagebrush (*Artemisia tridentata*) as woody plants. It seems to fit best the *Juniperus occidentalis* Zone of Franklin and Dyrness (1973), which they describe as a savanna.

The Nut Beds locality is unusual because not only are fruits and seeds present, but also leaves and silicified woods. Because different plant parts differ in their likelihood of entering the fossil record, this locality provides an opportunity to more completely reconstruct an ancient flora than is usually the case, and to gain the broadest possible understanding of its systematic diversity. Eighteen types of wood have been described (Scott & Barghoorn 1955; Scott et al. 1962; Manchester 1979, 1980; Scott & Wheeler 1982; Manchester & Wheeler 1993; Wheeler & LaPasha 1994); an additional 58, including a palm, are described in this paper. This makes the Nut Beds fossil wood assemblage, with 76 entities, the most diverse wood assemblage ever recorded from a single locality.

The co-occurrence of woods, leaves, fruits, and seeds provides an opportunity to compare levels of 'modernization' of different plant parts during the middle Eocene and to expand our understanding of mosaic evolution in different families. Different plant parts are subject to different selective pressures and hence may evolve at different rates or vary in whether and to what degree they respond to various biotic, climatic or geologic changes that occurred at different times.

Numerous wood anatomical characters in the extant flora are correlated with climate, and, accordingly, altitude and latitude (Baas 1986; Baas & Schweingruber 1987; Carlquist 1988). An analysis of a database for fossil dicotyledonous woods (> 1200 records) showed there are differences between temperate and tropical regions throughout the Tertiary, particularly post-Eocene, in the incidences of wood anatomical features (Wheeler & Baas 1991, 1993). These differences are consistent with well-established ecological trends in the extant flora, e.g. wide vessels and low vessel densities are relatively common in the tropics and rare in the temperate zone. Also, incidences of selected features correlated with temperate climates, e.g., ring porosity, vessels in clusters, and helical thickenings, are rare in the early Tertiary when evidence from a variety of sources indicates the climate was warm and equable throughout most of the Northern Hemisphere. Characterizing the middle Eocene Nut Beds wood assemblage broadens our understanding of the extent of wood anatomical diversity at middle northern latitudes during this warm interval. The Clarno Nut Beds wood assemblage represents a dataset that can be compared to younger and older wood assemblages of western North America so as to further our understanding of the correlations of wood anatomy with climate, and the effects of climate on wood evolution.

We present descriptions of all wood types currently known from the Nut Beds locality, including those previously described and those of unknown affinities. The additional material examined for this monograph enabled us to refine the information for some of the species already described. Many of these wood taxa are new records that may be important for systematists tracing the early history of selected extant families and genera. We hope this publication will serve as a reference that can be used by others working on early Tertiary fossil woods of the Northern Hemisphere who wish to compare their material to the Nut Beds assemblage. Taxa of undetermined systematic affinity ("unknowns") are included in order to document the full diversity of the Nut Beds woods as currently understood. The affinities of these woods may be determined as additional information about the wood anatomy of extant plants is gathered, or if the same wood type is found at other localities and shows additional diagnostic features. Also, even if the affinities cannot be determined, the occurrence of similar wood types at other Tertiary fossil localities may provide useful biogeographic information, such as the timing of exchanges between different geographic areas.

MATERIALS AND METHODS

Geographic and geologic occurrence

The Clarno Formation of north-central Oregon is a terrestrial sequence of andesitic to basaltic lavas and intrusives, ash flows, volcanic mudflows or lahars, and tuffaceous sediments. Its geology is complex and details debated (e.g., Hanson 1996; Retallack et al. 2000). Although fossil woods occur at many locations within the Clarno Formation (Hergert 1961), we emphasize that all of the woods reviewed in this treatment are from the single locality known as the Nut Beds. This locality (UF loc. 225) is in the type area of the Clarno Formation, at 44° 56' 36" N latitude, 120° 25' 34" W longitude. Amateur fossil collectors named the locality the "Nut Beds" because of the abundant petrified walnuts that occur there. The Nut Beds have five outcrop faces, designated from south to north as Faces 1–5 (Fig. 2 shows faces 1–4).

Mammalian remains also occur, which are rare in Eocene strata of the Pacific Northwest and thus of considerable paleontological significance (Manchester 1994; Hanson 1996).

The Nut Beds consist of light colored, well-lithified siltstones, sandstones and conglomerates about 10 m thick. Silicified woods, along with fruits and seeds, occur throughout the vertical thickness of the deposit, but are most abundant in the upper half. The lower half of the sedimentary sequence consists mostly of alternating layers of siltstone and coarse sandstone, ranging from a few cm to 1.5 m in thickness, while the upper portion includes thicker layers of organic-rich siltstones, sandstones and conglomerates. The alternation of fine and coarse sediment layers suggests alternation of high-energy deposition, during times of flooding, with more quiet conditions. *Equisetum* stems are preserved in growth position in some of the thicker siltstone units (Scott 1954; Retallack 1981), indicating shallow water or moist surface conditions suitable for growth of these plants between flooding intervals. The lower siltstones sometimes contain leaf impressions (Manchester 1981) which are flat-lying, parallel to bedding of the sediments. Because the sediments are not fissile and fish remains are absent it seems unlikely that the Nut Beds sediments were lake-deposited. The Nut Beds sediments appear instead to represent levee and channel deposits (Bestland et al. 1999) of a stream that was periodically choked with volcanic ash.

Other important occurrences of silicified wood in the Clarno Formation include those of Hancock Canyon, Post, Muddy Creek, and Mitchell (Fig. 1). Although full analyses of these assemblages are beyond the scope of the present study, we note that they are worthy of future investigation.

In Hancock Canyon, Wheeler County, Oregon, about 2 km east of the Nut Beds there is a petrified forest preserved in a volcanic lahar deposit (Fig. 1, locality 2). The quantity and diversity of woods here is low compared to the Nut Beds, but these woods include large logs and standing trunks up to 60 cm in diameter. The most common woods here are *Platanoxylon* and cf. *Cercidiphyllum*. This assemblage has been inferred to represent early successional forest colonizing a prior volcanic ash deposit (Manchester 1986, p. 220). Bestland et al. (1999) place the Nut Beds and Hancock Canyon floras in the same geologic unit and consider them to be essentially coeval, although the beds cannot be physically traced from one to the other due to an inter vening dacite dome. Whereas the Hancock Canyon lahar deposits contain large tuffaceous clasts up to 12 inches in diameter, clasts in the Nut Beds deposits generally do not exceed 5 cm. The woods of the Nut Beds are highly abraded and evidently allochthonous (i.e., transported), whereas those of Hancock Canyon show minimal abrasion and may represent more or less *in situ* forest intercepted by a lahar.

The Mitchell fossil wood locality (Hergert 1961; UF loc. 257) is situated $1^1/_2$ miles north of Mitchell, Wheeler County, Oregon in sec. 15, T. 12 S., R. 21 E., on the east side of Nelson Creek. The resistant silicified woods are found scattered on the surface having eroded from tuffs and breccias of the Clarno Formation (Fran Cherry ranch; UF loc. 257). According to Hergert, more than half of the specimens from this area is pine, and there are at least 12 kinds of angiosperm woods.

Several locations with well preserved woods, and, sometimes also fruits and seeds, occur in the Clarno Formation east of Post, Crook County, Oregon. Richard Scott acquired from Thomas J. Bones a collection of woods from this area, which was informally referred to as the *Osmundites* locality because the same site also produced silicified fern stems of *Osmundites oregonensis* (Arnold 1945, 1952). Arnold (1952) gives the location as 8 miles due east of Post on Lost Creek, a tributary of the Crooked River, in the northwestern corner of sec. 27, R. 20 E., T. 16 S. Field numbers indicate that some of the woods described by Scott and Wheeler (1982) were actually from this *Osmundites* locality: *Cercidiphyllum alalongum*, *Liriodendroxylon multiporosum* and perhaps *Trochodendroxylon*. Locality data for the specimen of *Trochodendron beckii* described by Scott and Wheeler have been lost, but another sample of the same species (UF 24558) was recovered more recently from UF loc. 279, about 2 miles east of Post from a level believed to be stratigraphically equivalent to Arnold's locality.

Three recently collected sites in the Post area contain abundant silicified woods as well as occasional silicified fruits and seeds: UF localities 254, 278, and 279. Initial observations indicate they are all similar in composition. The specimens are found loose in eroded tuffs that are situated in the upper part of the Clarno Formation near the transition to the John Day Formation. A minimum age for these wood sites is provided by a white tuff overlying the fossiliferous tuff of locality 278. Sanadine crystals from this white tuff give an ^{40}Ar/^{39}Ar date of 36.21 ± 0.26 MA (n = 26; W. McIntosh pers. comm., 1995). There are no datable tuffs at or immediately below the fossiliferous horizon to provide a maximum age. However, this late Eocene date may be a reasonable approximation of the age of the Post woods, contrasting with the middle Eocene age of the Clarno Nut Beds. Ring porous and semi-ring porous woods are more common at Post than at the Nut Beds (Wiemann et al. 1999). This is consistent with expectations for differences between wood anatomical characteristics in the late Eocene and middle Eocene of western North America, as other evidence indicates development of markedly seasonal climates towards the end of the Eocene (Graham 1999).

Descriptions

Descriptions of the woods follow the format of the IAWA List of Features suitable for hardwood identification (IAWA Committee 1989). For vessel diameter, vessel element length, and multiseriate ray height, means and standard deviation (in parentheses) are given; for vessel density, if three numbers are given, e.g. 11–20–42/mm^2, the middle number represents the mean. For ray width, range of ray width is given; if the range is given as 1–3 (4), this indicates that 3-seriate rays are common, and that 4-seriate rays occur, but are not common. When multiple samples of a species have been studied, the range of the means is given, typically for vessel diameter, vessel density, vessel element length, and multiseriate ray height. Vessel element lengths were measured tip to tip from tangential sections. Ray height for rays with extended uniseriate margins of variable length is for the multiseriate portion of the ray; ray height for rays with relatively short uniseriate margins (1–3), exclusively uniseriate rays, and rays alternating between uniseriate and biseriate is for total ray height.

When fossil wood specimen diameters could be estimated or directly measured these diameters are given in parentheses after the anatomical descriptions.

Affinities

Affinities of the fossil woods initially were determined by consulting descriptions in “Anatomy of the Dicotyledons” (Metcalfe & Chalk 1950; Metcalfe 1987; Cutler & Gregory 1998), and searches of the computerized OPCN (Oxford/Princes Risborough/CTFT/NCSU) wood database that contains more than 5200 coded descriptions of dicotyledonous wood (Wheeler et al. 1986; LaPasha & Wheeler 1987). The Clarno woods were compared to other fossil woods of known provenance using a database prepared for a survey of changes in dicotyledonous wood structure through time (Wheeler & Baas 1991, 1993) and to extant woods in the Bailey-Wetmore Laboratory of Plant Anatomy and Morphology of Harvard University, Leiden and Utrecht University branches of the Nationaal Herbarium Nederland, the Jodrell Laboratory of the Royal

Botanic Gardens Kew, David A. Kribs (NC State University) wood collections, and illustrations and descriptions in standard references (Ilic 1991; and as listed in Gregory 1980, 1994). Sectioning blocks were provided by the Center for Wood Anatomy, USDA Forest Products Laboratory, Madison. Extant wood samples used for comparison are referenced by their wood collection numbers (Stern 1988).

Philosophy of naming

When a fossil wood has a suite of anatomical features characteristic of an extant genus, we assign it to that genus. We believe this is the most effective way to indicate the affinities indicated by analysis of isolated wood samples. This does not preclude the possibility that the wood may have belonged to a plant that had leaves and/or reproductive structures different from the specified extant genus. Thus, this approach might underestimate the number of extinct genera, yet the familial and intrafamilial positions assessed from the wood would probably still be correct.

For most of the woods whose affinities are uncertain, we have declined to assign them a formal generic name, but instead describe them with an informal designation indicating a characteristic feature or group of features. The use of such xylotypes follows Page (1979, 1980, 1981) who did not assign names to a large group of late Cretaceous woods of unknown affinities, but assigned them to wood types which were based primarily on vessel element features. However, the Nut Beds woods of uncertain affinities that are represented by a relatively large number of samples and have distinctive anatomical features are assigned names, e.g., *Anomalocentra*, *Scottoxylon*. We have followed the requirements of the International Code of Botanical Nomenclature when erecting these new generic and species names.

Collections

More than 700 permineralized wood samples were collected from the Nut Beds by Thomas J. Bones during the mid-1940s to the late 1970s. During the 1960s, Mr. Bones donated a large part of his collection to the U.S. Geological Survey where, under the care of Dr. Richard Scott, many were thin sectioned for analysis. This collection was subsequently loaned to the University of Florida (UF) for the present study with the provision that the samples be transferred to the National Museum of Natural History at the conclusion of the study. These samples are assigned USNM numbers and their collection numbers given in parentheses, i.e., numbers preceded by DEN or C4A are samples collected by Bones and Scott. Manchester made additional collections of about 600 specimens while in the field with Thomas Bones, and with the aid of student volunteers from the Oregon Museum of Science and Industry, during the mid 1970s to late 1980s when the site was still in private ownership. These samples are catalogued in the UF collection. The woods were recovered from throughout the Nut Beds exposure, from face 1 to face 5 (Manchester 1994), but the majority are from the top of face 3 (Fig. 2).

The silicified woods were recovered from the field by breaking the massive tuffaceous matrix with hammers and pry bars. One problem is that multiple wood fragments

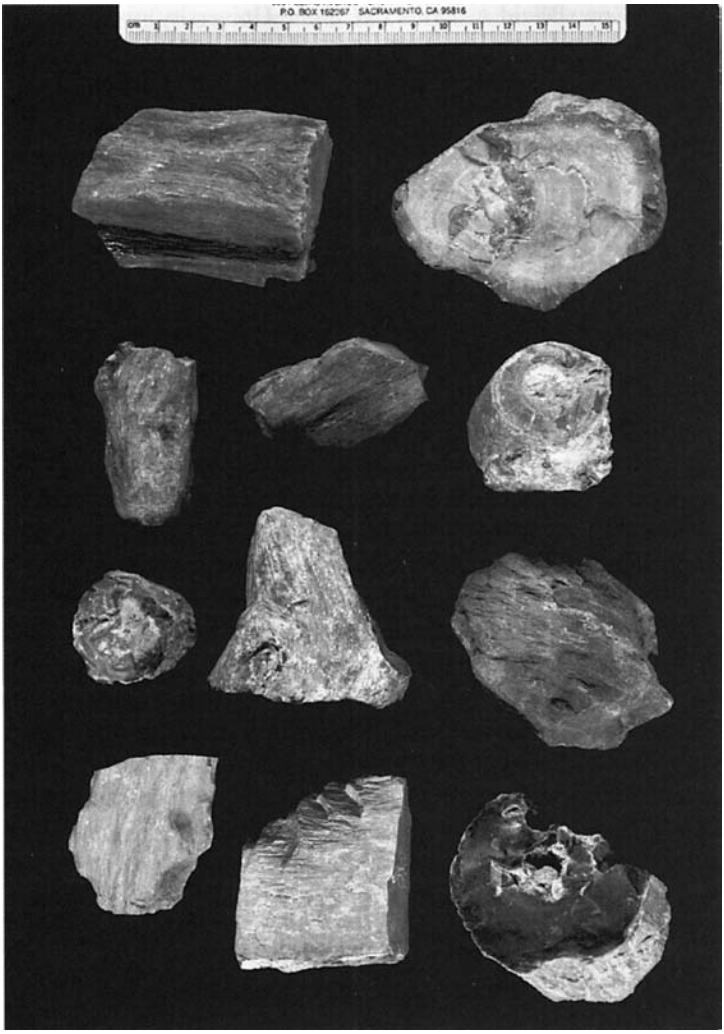

Fig. 3. Hand samples of the Nut Beds woods.

from one fossil plant may be collected at separate times, by the same or different collectors, and assigned separate catalog numbers giving the false impression of a greater number of sampled individuals. Only when specimens could be physically matched (fit together) in the lab were they assigned the same number. Many of the specimens represent stems of large diameter, judging from the growth ring curvature. Specimens are typically small irregular pieces one to several cm in diameter (Fig. 3).

Mode of fossilization

The Nut Beds woods are not oriented in growth position and do not represent *in situ* forest. Rather, the specimens are found as heavily abraded and jumbled pieces within poorly sorted conglomerates, siltstones and sandstones, likely indicating lahar deposition, and/or stream reworking of lahar deposits. Most woods are well preserved and some have secondary phloem and pith, all suggesting rapid silicification. Nearby hydrothermal springs may have supplied high concentrations of dissolved silica (Hanson 1996).

Most of the Clarno woods have fungal hyphae in them, and these likely are sap-staining fungi as hyphae are more common in parenchyma cells and in vessel lumens. This implies that many of the woods were sapwood because sap-staining fungi only invade living parenchyma cells with storage materials. The abundance of hyphae also implies that the woods were in moist, but not water-logged, aerobic conditions for some time before silicification, as fungi would not grow in anaerobic conditions. These samples likely were woody debris on the forest floor for some time before entering the fossil record. Some samples are penetrated by roots of other plants, also silicified. Most of the extremely well preserved woods we have observed have some fungal hyphae in them. It is possible that the increased permeability caused by the fungi may enable silica to more readily penetrate the cell walls.

A few Clarno woods show beginnings of tyloses formation, with bud-like outgrowths of parenchyma into the vessels (Figs. 7F, 15D, E) resembling the classical line drawings by Chattaway (1949) of tyloses formation. This suggests that these particular plants were not in a dormant phase when they entered the fossil record. What is known of tyloses formation (only a few species) indicates that tyloses formation occurs relatively quickly (24–48 hrs) in non-dormant plants after air enters the vessel (assuming large vessel-ray parenchyma pits of the type associated with tyloses formation). Silicification must have begun very soon after these samples were detached from the parent plant.

Some of the samples show evidence of insect damage and wounding and wound responses. The Nut Beds wood assemblage should be useful for studying plant/insect relationships during the Tertiary.

Preparation of samples

A diamond lapidary saw was used to cut thick sections (wafers) of transverse, tangential, and radial surfaces. One side of the wafer was smoothed to remove saw marks, and then affixed to a glass side using 24-hour transparent epoxy. The sections were then ground until they were thin enough (ca. 30 µm) to allow seeing anatomical details with transmitted light microscopy. 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. Permount was used for many of the early preparations; however, this proved unsatisfactory for archival purposes as this mounting medium crystallized and became opaque and obscured anatomical details. The acetate peel technique, using hydrofluoric acid, following the technique of Basinger and Rothwell worked well on some samples (see Fig. 28B). It is a quicker way to screen samples. However, we mostly used ground thin sections as they are preferable for viewing fine details and hydrofluoric acid is a hazardous material.

Table 1. List of the Clarno Nut Beds Woods.

This list includes genera with anatomy found in a single extant genus (LIV). — Extinct genera (EXT) with features of an extant family in which individual genera or groups of genera are well defined by distinctive wood anatomical features, but the fossil has a combination of characteristics that does not occur in those genera or groups of genera. — Stereotype genera (STE) with features of an extant family or order, but cannot be assigned to an extant genus because the same combination of features occurs in more than one extant genus within that family.

Dicotyledonous woods identified to family

Aceraceae
- *Acer integrifolioxylon* sp. nov. (LIV)

Alangiaceae
- *Alangium oregonensis* Scott et Wheeler (LIV)

Anacardiaceae
- *Maureroxylon crystalliphorum* gen. et sp. nov. (STE)
- *Tapirira clarnoensis* Manchester (LIV)
- *Terrazoxylon ductifera* gen. et. sp. nov. (STE)

Annonaceae
- *Annonoxylon bonesii* sp. nov. (STE)

Araliaceae
- *Plerandreoxylon oregonensis* gen. et sp. nov. (STE)
- *Plerandreoxylon nutbedensis* sp. nov. (STE)

Betulaceae
- *Betula clarnoensis* Scott & Wheeler (LIV)

Cercidiphyllaceae
- *Cercidiphyllum alalongum* Scott & Wheeler (LIV)

Fagaceae
- *Fagaceoxylon ostryopsoides* Scott & Wheeler (EXT)
- *Quercinium crystallifera* Scott & Wheeler (STE)

Hamamelidaceae
- *Hamamelidoxylon uniseriatum* sp. nov. (LIV)

Juglandaceae
- *Clarnoxylon blanchardii* Manchester & Wheeler (EXT)
- *Engelhardioxylon nutbedensis* Manchester (STE)

Lauraceae

Simple and scalariform plates

- *Cinnamomoxylon oleiferum* sp. nov. (STE)
- *Paraperseoxylon scalariforme* (Scott & Wheeler) gen. nov., comb. nov. (STE)

Simple perforations only

- *Cryptocaryoxylon hancockii* sp. nov. (STE)
- *Cryptocaryoxylon meeksii* sp. nov. (STE)
- *Cryptocaryoxylon radiporosum* sp. nov. (STE)
- *Mezilaurinoxylon eiporosum* gen. et sp. nov. (STE)
- *Ulminium magnioleiferum* sp. nov. (STE)

Leguminosae
- *Dichrostachyoxylon herendeenii* sp. nov. (STE)
- cf. *Euacacioxylon* (STE)
- cf. *Mimosoxylon* (STE)

Magnoliaceae
- *Liriodendroxylon multiporosum* Scott & Wheeler (LIV)
- *Magnolia pageae* sp. nov. (LIV)
- *Magnoliaceoxylon angulata* (Scott & Wheeler) comb. nov. (STE)
- *Magnoliaceoxylon cutleri* sp. nov. (STE)
- *Magnoliaceoxylon longiradiata* (Scott & Wheeler) comb. nov. (STE)

Malvaceae s.l.
- *Chattawaya paliforme* Manchester (EXT)
- *Triplochitioxylon oregonensis* Manchester (EXT)

Platanaceae
- *Platanoxylon haydenii* (Felix) Süss & Müller-Stoll 1977 (EXT)

Rosaceae
- *Maloidoxylon annae* sp. nov. (STE)
- cf. *Prunus gummosa* Wheeler, Scott, & Barghoorn (LIV)
- *Prunus* sp. (LIV)

Sabiaceae
- *Meliosma brehmii* sp. no. (LIV)
- *Meliosma deweyii* sp. nov. (LIV)
- *Meliosma dodsonii* sp. nov. (LIV)

cf. Sapindaceae
- *Sapindoxylon klaassenii* sp. nov. (STE)

Ulmaceae s.l.
  Ulmus danielii sp. nov. (LIV)

Vitaceae
  Vitaceoxylon carlquisti Wheeler & LaPasha (EXT)
  Vitaceoxylon tiffneyi Wheeler & LaPasha (EXT)

Dicotyledonous woods identified to Order

Malpighiales
  Clarno Malpighialean Wood I (Euphorbiaceae?) (STE)
  cf. *Hydnocarpoxylon* (STE)
  cf. *Paraphyllanthoxylon* (STE)

Sapindales
  cf. *Cedreloxylon*

Urticales
  Scottoxylon eocenicum gen. et sp. nov.
  Clarno Urticalean Wood I
  Clarno Urticalean Wood II

Dicotyledonous woods of uncertain affinities

Nut Beds Xylotype I-A:

Exclusively multiple perforations – Vessels solitary (over 80%), rays < 10-seriate

1) UF 12454 (Icacinaceae? Escalloniaceae?)
2) UF 00225-033245 (CC-32)
3) UF 00225-033246 (CC-13, Caprifoliaceae?)
4) USNM 507935 (C60-6), UF 12115

Nut Beds Xylotype I-B:

Exclusively multiple perforations – Vessels solitary and in radial multipes, rays < 10-seriate

1) USNM 508006 (C4A-31, Cornaceae s.l.?)
2) USNM 507900 (C4A-37)
3) UF 12380 (Malpighiales?)

Nut Beds Xylotype I-C:

Exclusively multiple perforations – Vessels solitary and in multiples, rays > 10-seriate

1) *Anomalocentra pseudoplatana* gen. et sp. nov.
2) *Euptelea baileyana* Scott & Barghoorn

Nut Beds Xylotype II:

Multiple and simple perforations

1) USNM 507942 (C4A-55), USNM 507823 (C4A-143), UF 12110 (Laurales? Magnoliales?)

Nut Beds Xylotype III-A-i:

Exclusively simple perforations – Vine-like anatomy – Interxylary phloem present

1) UF 00225-033247 (CC-35)

Nut Beds Xylotype III-A-ii:

Exclusively simple perforations – Vine-like anatomy – Interxylary phloem absent

1) USNM 507933 (DEN 108)

Nut Beds Xylotype III-B-i:

Exclusively simple perforations – Semi-ring porous to ring porous – Distinctive latewood vessel arrangements

1) USNM 507917 (DEN 34). Homocellular rays
2) USNM 507932 (DEN 43). Heterocellular rays Latewood vessels in diagonal to tangential arrangement

Nut Beds Xylotype III-B-ii:

Exclusively simple perforations – Semi-ring porous to ring porous – Latewood vessels randomly arranged

1) cf. *Fraxinoxylon* USNM 507930 (DEN 36)
2) UF 12378 (tends to diffuse porous)

Nut Beds Xylotype III-C-i:

Exclusively simple perforations – Diffuse porous – Distinctive vessel arrangement patterns

1) USNM 507830 (DEN 42). Tangential arrangement of vessels

Nut Beds Xylotype III-C-ii:

Exclusively simple perforations – Diffuse porous – Random vessel arrangement, rays ≤ 4-seriate

1) UF 12012, 12111
2) USNM 507827 (DEN 27)
3) Narrow Ray I
4) Narrow Ray II

Palmae
  Palmoxylon sp.

Gymnospermae
  Pinaceae — cf. *Pinus*
  Taxodiaceae — cf. *Taxodioxylon*
  Ginkgoaceae — *Ginkgo bonesii* Scott, Barghoorn & Prakash

  Unknown Conifer — ?Taxaceae

RESULTS AND DISCUSSION

Woods of the Clarno Nut Beds

We recognize 66 genera and 76 'species' of woods from the Nut Beds. Of these, 38 genera (including extant, stereotypic, and extinct genera) and 47 species are identified to the family level (34 dicots, 1 palm, *Ginkgo*, 2 conifers). Seven dicot genera (7 species) could not be identified to a particular family, but are assigned to order (Malpighiales, Sapindales, Urticales). Twenty-two 'species' are of unknown ordinal affinities (21 dicots, 1 gymnosperm).

Manchester (1994) divided the genera of Clarno fruits and seeds into four groups according to their relationships to extant plants. We use a similar approach for the woods, but are adding another group (see 3a below).

1) Extant genera (LIV) have anatomy found in a single extant genus. These woods are assigned names of the corresponding extant genus.
2) Extinct genera (EXT) have features of an extant family in which individual genera or groups of genera are well defined by distinctive wood anatomical features, but the fossil has a combination of characteristics that does not occur in those genera or groups of genera.
3) Stereotype genera (STE) have features of an extant family, but cannot be assigned to an extant genus because the same combination of features occurs in more than one extant genus within that family.
3a) Ordinal genera (ORD) have features that occur in genera of more than one family, but these families belong to the same monophyletic clade (order) as defined by recent phylogenetic analyses (APG 1998; Soltis et al. 2000).
4) Form genera (FRM), which also could be considered xylotypes, cannot be assigned to family or order. This category likely includes extant genera that we failed to identify, as they have features found in more than one family, as well as extinct genera or families.

Table 1 lists the woods in alphabetical order by family and genus, followed by the woods assigned to order, and finally the woods of unknown affinities. Table 2 groups the woods by selected anatomical features. Some Nut Beds woods are the oldest known with wood anatomical characteristics similar to an extant genus; these are *Acer, Alangium, Betula, Prunus, Meliosma,* and *Ulmus*. The most common wood types, in terms of number of fragments, include *Scottoxylon eocenicum* (order Urticales), *Platanoxylon haydenii* (Platanaceae), *Quercinium crystallifera* (Fagaceae), *Dichrostachyoxylon herendeenii* (Leguminosae), cf. *Hydnocarpoxylon* (order Malpighiales). Other common wood types are *Maureroxylon crystaliphorum* (Anacardiaceae), *Cryptocaryoxylon hancockii, Cryptocaryoxylon meeksii, Mezilaurinoxylon eiporosum* (Lauraceae), and cf. *Paraphyllanthoxylon* (order Malpighiales). The abundant species are the ones inferred to be trees, as would be expected, as one tree would produce more wood fragments than a shrub. The Lauraceae and Magnoliaceae are the most diverse families among the Nut Beds woods.

Comparisons of wood and fruit/seed assemblages

Dicots are the most abundant and most diverse elements of both the fruit and seed assemblage and the wood assemblage. Although the fossil woods are from the same horizon as the fruits and seeds, the familial and generic composition of the wood assemblage would not be expected to be identical to the fruit and seed assemblage. Different plant organs vary in their potential for fossilization, e.g., vary in resistance to decay, transportability, and initial relative abundance (see discussions in Page 1979; Poole 2000). Moreover, these differences are not consistent from one family or genus to another. It is probable that some of the Nut Beds woods and fruits and seeds represent the same plant, but without direct connection the species relationships can only be inferred.

(text continued on page 23)

Legends of Table 2: Summary of characteristics of the Nut Beds woods (pages 18–22).

GR	growth rings, + = present, – = absent, +/– = both, I = indistinct.
POR	porosity, D = diffuse porous, S = semi-ring porous, R = ring porous.
MTD	mean tangential diameter, VS = < 50 µm, S = 50–100 µm, M = 100–200 µm, L = > 200 µm.
VMM	vessels per sq.mm, 1 = < 5, 2 = 5–20, 3 = 20–40, 4 = 40–100, 5 = > 100, N/A = not applicable as wood ring porous or semi-ring porous.
PP	perforation plate, SI = simple, SC = scalariform, M = multiple, but not scalariform.
B	number of bars per scalariform perforation plate.
IVP	intervessel pit arrangement, A = alternate, O = opposite, S = scalariform, ? = not observed.
IVPS	intervessel pit size, in µm, individual pits measured in the horizontal direction; N/A = not measured if IVP opposite or scalariform, ? = not observed.
VRP	vessel-ray parenchyma pits, S = similar to intervessel pits, R = with reduced borders, C = unilaterally compound, ? = not observed.
HT	helical thickenings in vessel elements, + = present, – = not observed.
SF	septate fibers, + = present, – = absent, ? = not determinable.
AP	axial parenchyma, A = absent, R = rare, D = diffuse, DA = diffuse-in-aggregates, B = banded, M = marginal, SP = scanty paratracheal, V = vasicentric, AF = aliform, C = confluent.
RW	ray width in cell number; AGG = aggregate; 2S = two sizes.
RH	mean multiseriate ray height or mean height of uniseriate rays when rays exclusively uniseriate, 1 = mean height < 0.5 mm, 2 = mean height 0.5–1 mm, 3 = rays commonly > 1 mm.
RC	ray cellular composition, Ht = heterocellular, Ho = homocellular, US = all square and upright cells, M = mixed, upright, square, and procumbent cells throughout the ray.
SH	sheath cells, + = present, – = absent, +/– = not well defined.
I	idioblasts, – = absent, R = in rays, A = in axial parenchyma strands, F = isolated amongst fibers, ( ) indicates not common.
C	crystals, – = not observed, R = in rays, u = upright or square ray cells, p = in procumbent ray cells, A = in axial parenchyma strands, c = chambered axial parenchyma; I = idioblast.

Table 2. Summary of characteristics of the Nut Beds woods. — For legends, see previous page.

FAM *Species* or Xylotype	GR	POR	MTD	VMM	PP	B	IVP	IVPS	VRP	HT	SF	AP	RW	RH	RC	SH	I	C
I - VESSELS SOLITARY AND IN MULTIPLES																		
A - **Non–random vessel arrangement**																		
ARL *Plerandreoxylon nutbedensis*	+	S, D	S	NA	SI, SC	< 10	A, (S)	6–10	R	–	+	R	1–4	1, 2	Ht	+/–	–	–
ARL *Plerandreoxylon oregonensis*	+	S	S	NA	SI	–	A, O	12–14	R	–	+/–	R	1–4	1	Ht	+/–	–	–
ULM *Ulmus danielii*	+	S	S	NA	SI	–	A	7–8	S (R)	+	–	C	1–5	1	Ho, Ht	–	–	A
? III-B-i (2) USNM 507932	+	S	S	NA	SI	–	A, (O)	> 10	R?	–	–	R	1–3	2	Ht	–	–	–
? III-C-i USNM 507830	I	D	S	2	SI	–	A	4–5	S	–	–	C	1–5	1	Ht	–	–	–
Aggregate rays																		
FAG *Fagaceoxylon ostryopsoides*	+	D	S	3, 4	SI (SC)	4	A, O	5–10	R	–	–	D,DA,M	1–2	1	Ht	–	–	R:p
B - **Random vessel arrangement**																		
i - ***Scalariform perforation plates***																		
a - Marginal parenchyma																		
MAG *Liriodendroxylon multiporosum*	+	D	S	4	SC	2–10	O	NA	R,C	–	–	M	1–4	1	Ht	–	(R)	–
MAG *Magnoliaceoxylon angulata*	+	D	VS, S	4, 5	SC	15–18	O, S	NA	?	–	–	M	1–2 (3)	1	Ht	–	–	–
MAG *Magnoliaceoxylon longiradiata*	+	D	S	4	SC	6–26	S, (O)	NA	R	–	–	M	1–3	2, 3	Ht	–	(R)	–
MAG *Magnolia pageae*	+	D	S	3, 4	SC	5–20	O	NA	R, C	–	–	M	1–2 (3)	2	Ht	–	R	–
b - Diffuse, diffuse–in–aggregates parenchyma																		
Rays > 10-seriate																		
? I-C *Euptelea baileyana*	+	D	VS, S	4	SC	5–35	S, O	NA	R	–	–	D	to 18	3	Ht	–	–	–
PLT *Platanoxylon haydenii*	+	D	S, M	3, 4	SC	4–27	O	5–7	S	–	–	D, DA	2–27	3	Ht	–	–	R:p
? I-C *Anomalocentra pseudoplatana*	+	D	S	5	SC	8–15	O	5–7	?	–	–	D, DA	1–14	3	Ho, Ht	+	–	R:p

FAM	*Species* or Xylotype	GR	POR	MTD	VMM	PP	B	IVP	IVPS	VRP	HT	SF	AP	RW	RH	RC	SH	I	C
	Rays < 4-seriate																		
BET	*Betula clarnoensis*	+	D	S	3, 4	SC	10–25	A	2–4	S	–	–	D, DA, M	1–3	1	Ho (Ht)	–	–	–
c - Axial parenchyma rare																			
SAB	*Meliosma dodsonii*	+	D (S)	M	3	SC	4–24	A	4–6	?	–	–	R	1–4	3	M	–	–	–
SAB	*Meliosma deweyii*	+	D	S	3	SC	6–20	A	4–6	S	–	–	R	1–2	3	M	–	–	–
Ord: Mlp	cf. *Hydnocarpoxylon*	+/–	I, D	S	4	SC	8–24	A, O, S	> 10	R	–	+	R	1–8	2	Ht	–	–	R:u,c
? I-B	(1) USNM 508006	+	D	VS	5	SC	14–37	O	6–8	R	–	–	R	1–4	1,2	Ht	–	–	–
? I-B	(2) USNM 507900	+	D	S	4	SC	8–20	O, S	NA	R	–	–	R	1–3	2,3	Ht	–	–	–
? I-B	(3) UF 12380	–	D	VS	5	SC	12–15	A (O)	4–6	?	–	–	R	1–4	3	US, Ht	–	–	–
	Oil cells																		
MAG	*Magnoliaceoxylon cutleri*	I	D	S	1,2	SC	8–20	S, O	NA	R	–	–	R, SP	1–3 (4)	2, 3	Ht	–	R	–
ii - *Simple & scalariform plates*																			
a - Predominantly scalariform																			
SAB	*Meliosma brehmii*	+	D	S, M	3	SC (SI)	1–8	A	5–10	S (R)	–	–	SP, V, M	1–5	2, 3	M	–	–	–
ALG	*Alangium oregonensis*	I	D	S, M	3	SC (SI)	1–10	A	4–7	?	–	–	D, DA	1–6	3	Ht	–	–	–
b - Predominantly simple																			
	Banded parenchyma																		
JUG	*Engelhardioxylon nutbedensis*	+	D/S	M	2, 3	SI (SC)	3	A	7	?	–	–	B	1–4	1, 2	Ht	–	–	R:u:I
	Scanty paratracheal - rare parenchyma																		
LAU	*Cinnamomoxylon oleiferum*	+/–	D	S, M	3, 4	SI, SC	4–8	A	8–11	R	–	–	SP	1–4 (5)	1	Ht	–	R	–
LAU	*Paraperseoxylon scalariforme*	I	D	S	2	SI, SC	4–12	A	5	R	–	–	SP	1–2 (3)	1	Ht	–	R, F	–
? II	(1) USNM 507942	I	D	S	4	SI (M)	< 10	A	5–8	R	–	–	R	1–4	2	Ht	–	R, F	–
Ord: Mlp	Wood type I: USNM 507941	+/–	D	VS, S	4, 5	SI (M)	< 10	A	5–9	R, S	(+)	–	R	1–4	1	Ht	–	–	–

FAM	*Species* or Xylotype	GR	POR	MTD	VMM	PP	B	IVP	IVPS	VRP	HT	SF	AP	RW	RH	RC	SH	I	C
iii - *Simple perforation plates*																			
a - Axial parenchyma rare																			
Vessel–ray parenchyma pits similar to IV pits																			
ACE	*Acer integrifolioxylon*	+	D	VS, S	4 (5)	SI	–	A	5–6	S	+	–	R, D	1–3 (4)	1, 2	Ho	–	–	A:c
?	III-C-ii (2) USNM 507827	+	D	S	3	SI	–	A	3–5	S	–	–	R	1–4	1	Ht	–	–	–
?	III-C-ii (3) USNM 507937	+	D (S)	S, M	3	SI	–	A	3–5	S	–	–	R, M	1–2	2	Ht	–	–	–
SAP	*Sapindoxylon klaassenii*	+	D	S, M	2 (3)	SI	–	A	3–4	S	–	–/+	R	1	1	Ht	–	–	–
Vessel–ray parenchyma pits reduced borders																			
Ord: Mlp	cf. *Paraphyllanthoxylon*	I, –	D	S, M	2, 3	SI	–	A	8–14	?	–	+	–	1–4	2	Ht	–	–	R:u,c
?	III-C-ii (4) USNM 507928 Narrow Ray II	+/–	D	S	4	SI	–	?	?	R	?	–	R	1 (2)	2	M	–	–	–
b - Rare-scanty paratracheal																			
Rays < 1 mm																			
LEG	cf. *Mimosoxylon*	+	D	M	1	SI	–	A	10–12	S	–	–	SP (V)	1–4	1, 2	Ht	–	–	–
?	III-C-ii (1) UF 12012	+/–	D	S, M	3	SI	–	A	ca 5	S	–	–	R, SP	1–4	2	Ht	–	–	–
?	III-B-ii (2) UF 12378	+	S, D	S	2	SI	–	A	3–5	S	–	–	SP	1–2	1	Ht	–	–	–
LAU	*Mezilaurinoxylon eiporosum*	I	D	S, M	2, 3	SI	–	A	> 10	R	–	–	SP	1–4 (5)	1,2	Ht	–	R	–
Rays > 1 mm																			
VIT	*Vitaceoxylon carlquistii*	+	D	L	NA	SI	–	A	10–12	R	–	+	SP	1–8	3	Ht	–	R	–
VIT	*Vitaceoxylon tiffneyi*	+	D	M	NA	SI	–	A	10–12	R	–	+	SP	1–20	3	Ht	–	R	–
c - Scanty paratracheal-vasicentric																			
?	III-A-ii USNM 507933, Vine	+	S, R	L	NA	SI	–	A	6–8	S	–	–	SP, V	2S, 8	3	Ht	–	–	–
Ord: Urt	*Scottoxylon eocenicum*	+/–	D	M	2	SI	–	A	5–12	R	–	–	V, A, C,	1–7	2	Ht	–	–	–
ANA	*Maureroxylon crystalliphorum*	+	D, S	M	2, 3	SI	–	A	7–10	R	–	+	SP, V, D	1–3 (5)	1	Ht	–	–	R:u:I
LAU	*Cryptocaryoxylon meeksii*	+/–	D	S, M	2, 3	SI	–	A	6–10	R	–	–	SP, V	1–2	1	Ht	–	R	–

FAM	*Species* or Xylotype	GR	POR	MTD	VMM	PP	B	IVP	IVPS	VRP	HT	SF	AP	RW	RH	RC	SH	I	C
	Traumatic canals																		
Ord: Sap	cf. *Cedreloxylon*	+	S, R	M	NA	SI	–	A	4–6	S	–	–	SP, V	1–2	1	Ht	–	–	A:c
	Radial canals																		
ANA	*Tapirira clarnoensis*	+/–	D	M	2	SI	–	A	7	R	–	+	V	1–3	1	Ht	–	–	R:u,p
ANA	*Terrazoxylon ductifera*	I	D	M	3	SI	–	A	5–6	R	–	+	V	1–2 (4)	1	Ht	–	–	R:u
d - Aliform-confluent																			
	V-RP Pits similar																		
? III-B-ii	cf. *Fraxinoxylon*	+	S, D	S	2	SI	–	A	4–5	S	–	–	V, AF, C	1–3	1	Ho, Ht	–	–	–
LEG	*Dichrostachyoxylon herendeenii*	+/–	D	M	2	SI	–	A	8–10	S	–	–	V, AF, C	1–4	1	Ho, Ht	–	–	A:c
LEG	cf. *Euacacioxylon*	+	D	S, M	2	SI	–	A	4–6	S	–	–	V, AF,C (B)	1–4	1	Ho, Ht	–	–	A:c
? III-B-I	(1) USNM 507917	+	R	M	NA	SI	–	A	< 5	S	–	–	V, C	1–3	1	Ho, Ht	–	–	–
	V-RP Pits reduced borders																		
Urt	Urticalean Wood type II USNM 507918	+	D	M	2	SI	–	A	5–8	R	–	–	V, AF, C	1–4	1, 2	Ht	+/–	–	R:u,p (A)
	Oil cells																		
LAU	*Cryptocaryoxylon hancockii*	I	D	S	4	SI	–	A	3–5	R	–	–	V, AF, C	1–3 (4)	1	Ht	–	R, F	–
LAU	*Cryptocaryoxylon radiporosum*	I	D	S, M	(2) 3	SI	–	A	9–12	R	–	–	SP, M	1–3	1	Ht	–	R	–
LAU	*Ulminium magnioleiferum*	+	D	S	2	SI	–	A	6–10	?	–	–	V, AF, B	1–4	2	Ht			
e - Banded																			
ANN	*Annonoxylon bonesii*	I	D	M	2	SI	–	A	4–6	?	–	–	V, B	1–6	3	Ho,Ht	+	–	–
JUG	*Clarnoxylon blanchardii*	+	D, S	S,M	NA	SI	–	A	5–7	S	–	–	SP, V, B	1–3	1	Ht	–	–	R:u,p (I)
Ord:																			

FAM *Species* or Xylotype	GR	POR	MTD	VMM	PP	B	IVP	IVPS	VRP	HT	SF	AP	RW	RH	RC	SH	I	C
f - Apotracheal, diffuse, diffuse–in–aggregates																		
ROS cf. *Prunus gummosa*	+	D	S	5	SI	–	A	M	S	–	–	D	1–3	1	Ht	–	–	A:c
ROS *Prunus sp.*	+	S	M	NA	SI	–	A	M	S	–	–	D, DA	1–8	1, 2	Ht	–	–	A:c
Tile cells																		
MLV *Chattawaya paliforme*	+	S, D	M	2 (3)	SI	–	A	4–6	S	–	–	DA, V	1–14	3	Ht	+	–	R, A
MLV *Triplochitioxylon oregonensis*	+	S, D	M	1, 2	SI	–	A	3–5	S	–	–	DA, V	1–10	2, 3	Ht	+	–	R
II - EXCLUSIVELY SOLITARY VESSELS																		
A - Radial / diagonal arrangement of vessels																		
FAG *Quercinium crystallifera*	+, I	D, S	M, L	2	SI	–	A	5–8	R	–	–	D, DA	1, AGG	3	Ho	–	–	A:c
B - Randomly arranged vessels																		
i - *Scalariform perforations*																		
? I-A (1) UF 12454	I	D	S	(3) 4	SC	40–100	O (A, S)	NA	?	–	–	D, DA	1–5	3	US	+/–	–	–
? I-A (2) UF 00225-033245	–	D	VS	5	SC	to 80	?	?	?	–	–	D	1–3	3	Ht	–	–	–
? I-A (3) UF 00225-033246	–	D	VS	4 (5)	SC	> 50	A?	?	S	–	–	D?	1–3	3	US	–	–	–
CDP *Cercidiphyllum alalongum*	+	D	S	4 (5)	SC	20–40	S	NA	?	–	–	R	1–2	2	Ht	–	–	R:u
HAM *Hamamelidoxylon uniseriatum*	+	D	S	5	SC	20–40	O, S	NA	(R)	–	–	D	1 (2)	1	Ht	–	–	–
ia - *Multiple perforations?*																		
? I-A (4) USNM 507935	+	D	S	4	?	?	O (A)	3–5	S	–	–	D	1–5	2	Ht	–	–	–
ii - *Simple perforations*																		
ROS *Maloidoxylon annae*	+	D, S	VS	5	SI	–	A	6–8	S	+	–	D	1–3	1	Ht	–	–	A:c
Vine - Unlignified tissue																		
? III-A-i (1) UF 00225-033247	I	D	M, L	2	SI	–	A	3–5	?	–	?	?	1–3, 6–9	3	Ht	–	–	–

The criteria for defining a wood genus and a fruit/seed genus are not the same, or explicitly defined; rather they are based on comparisons to extant material and personal judgment (subjective). At present, and one would expect it to be true for the past, different plant parts differ in their systematic resolution, and this is not constant from family to family. An isolated wood fragment or an isolated fruit may have characteristics of only one or more than one genus. A single fossil wood type ("genus") could be associated with more than one fossil fruit/seed type ("genus"), or *vice versa*. Thus, it is unlikely that fossil wood genera and fossil fruit and seed genera represent equivalent entities. Nonetheless, we are comparing the relative proportions of genera identified to family, and, for those genera identified to family, the relative proportions of extant, stereotypic, and extinct genera.

A lower proportion of the wood genera (21 of 76, 29%) than fruit and seed genera (48%) have unknown affinities. This is in part because some wood genera (7 of 76, 9%) are assigned to order, as well as to family, but this situation might reflect differential organization and accessibility of modern reference material. Because wood is commercially important, there is considerable information on its anatomy and much of this information is organized and computerized to facilitate wood identification (Wheeler & Baas 1998). Information on fruits and seeds is more widely dispersed. Alternatively, fruits and seeds may evolve and diversify more rapidly than wood, and wood may be a conservative tissue with similar wood anatomical patterns shared by multiple extant and extinct species and genera.

Evidence suggesting that availability of modern reference material may influence the proportion of fossils identifiable to extant families may be obtained by comparing the statistics for trunk woods (well represented in modern reference collections) to those for twigs and smaller stems (poorly represented in reference collections). Diameter was estimated for samples of 65 of the Clarno dicot wood species. From these data, the woods are divided into two categories: those smaller than 10 cm in diameter and those larger than 10 cm in diameter. Of 36 species based on samples > 10 cm diameter, 89% are identified to family or order, 11% have unknown affinities. In contrast, of the 29 species based on samples < 10 cm, only 52% are identified to family or order, and 48% have unknown affinities. A higher proportion of the larger diameter woods could be placed in a family. Eventually, it would be useful to prepare reference slides of taxa known to occur in the early Tertiary of the Northern Hemisphere and whose modern relatives have limited secondary growth in order to determine whether they too are represented in the Nut Beds or other Tertiary wood assemblages.

Of the Nut Beds genera placed in extant families, a higher percentage of wood genera (19 of 38, 50%) than fruit and seed genera (15%) represent stereotypic genera. This is not surprising, because woods of closely related genera often share similar, sometimes overlapping, anatomical patterns. This may be one reason that we recognize fewer extinct genera of woods (16%) than there were extinct genera of fruits and seeds (35%) because the similar wood anatomical patterns shared by groups of extant genera also may have occurred in extinct genera. Half of the Nut Beds fruits and seeds assigned to family represented modern genera, 34% (13/38) of the woods assigned to family represent modern genera.

The extinct wood genera found at the Nut Beds are from

1) relatively small (in terms of genera) and well-studied families, the Fagaceae, Juglandaceae, and Platanaceae, in which the wood anatomical characteristics of individual genera and groups of genera are well documented. These are families known to have been more diverse in the early Tertiary (e.g., Manchester 1999);
2) a relatively large family, Malvaceae *sensu lato*, in which there are distinctive features, such as tile cells, whose appearance relative to extant plants can be evaluated. Tile cells are unique to the Malvaceae s.l. (Manchester & Miller 1978);
3) a medium-sized family, Vitaceae, in which some distinctive features associated with the liana habit may be of relatively recent origin.

Four families are known from woods, but not from fruits and seeds: Cercidiphyllaceae, Malvaceae s.l., Ginkgoaceae, Taxodiaceae.

Conversely, a larger number (14) of families are known from fruits and seeds, but not from woods (Table 3). It is possible some of the undetermined woods may belong to some of these families. Woods similar to *Mezilaurinoxylon eiporosum*, but which lack oil cells, a feature needed to confirm their lauraceous affinities, may be Bursera-

Table 3. Families in the Nut Beds represented by fruits/seeds, but not by woods. Names in bold type represent families definitely not present as woods. Number of genera and species in parentheses.

Actinidiaceae (1, 1)
Burseraceae (1, 2)
Hydrangeaceae (1, 1)
Icacinaceae (5, 8)
Lythraceae (1, 1)
Menispermaceae (13, 14)
Musaceae (1, 1)
Rubiaceae (1, 1)
Sapotaceae (1, 2)
Schisandraceae (1, 1)
Staphyleaceae (1, 1)
Symplocaceae (1, 1)
Theaceae (1, 1)
Taxaceae (3, 3)

Table 4. Families in the Nut Beds represented by fruits/seeds and woods (L = leaves present; ? = leaves possibly present, but not verified). Information on leaves based on Manchester 1981 and unpublished observations by Manchester.

Aceraceae
Anacardiaceae
Annonaceae (?)
Araliaceae (L)
Betulaceae
Fagaceae (L)
Hamamelidaceae
Juglandaceae (L)
Lauraceae (L)
Leguminosae (?)
Magnoliaceae (L)
Platanaceae (L)
Rosaceae (?)
Sabiaceae (L)
Sapindaceae
Ulmaceae s.l.
Vitaceae
Palmae (L)
Pinaceae

ceae. The wood originally assigned to Eupteleaceae possibly could be Icacinaceae. The unknown conifer is likely Taxaceae. Flacourtiaceae are not included in this list as it is probable at least one of the woods assigned to the Malpighiales is Flacourtiaceae. More information on each of these instances is presented in the discussion of those woods.

At the Nut Beds, nineteen families are common to the fruit and seed and wood assemblages, some of these families also are represented by leaves (Table 4).

Different families and genera differ in their representation by different plant parts. The Anacardiaceae are relatively common among the woods and the fruits/seeds, but are not known from leaves. For the Ulmaceae s.l. and Vitaceae, fruits/seeds are common, wood is occasional, but no leaves are known. Many of the fruits/seeds were drupes and likely bird-transported from some distance. The woods likely represent forest floor litter.

The families for which there is the greatest opportunity for reconstructing whole plants are the Araliaceae, Fagaceae, Juglandaceae, Lauraceae, Magnoliaceae, and Sabiaceae, as they are represented by fruits/seeds, woods, and leaves. Examining samples from other localities in the Clarno Formation to learn more about which entities repeatedly co-occur will help with this objective, as may sectioning and examining additional small diameter material from the Nut Beds. The Clarno Plane tree (*Macginitiea angustiloba*) is one of the few early Tertiary plants for which there is a 'whole plant' reconstruction (Manchester 1986).

Comparison within shared families

Comparing wood types to fruit and seed types within a family reveals both similarities and differences in the information content these plant parts provide. It is especially at this level of comparison the wood assemblage contributes to the diversity of the Nut Beds flora. In the following text these shared families are grouped according to whether

1) the woods and fruits and seeds are congruent in the information they provide,
2) woods are more diverse,
3) fruits and seeds are more diverse,
4) woods and fruits and seeds differ in apparent relationships to extant genera.

1) *Generally similar information:*

HAMAMELIDACEAE: 1 wood: *Hamamelis*-like; 1 fruit/seed: *Fortunearites* with characteristics of the Hamameloideae, also staminate inflorescences with pollen similar to *Hamamelis* and *Corylopsis*.

ROSACEAE: 2 *Prunus* woods; 2 *Prunus* fruits/seeds; 1 Maloideae wood, 1 Maloideae-like fruit/seed.

PINACEAE: *Pinus* as wood, seeds, pollen cones.

2) *Wood types more diverse than fruits/seeds:*

ANACARDIACEAE: 3 woods; 2 fruits.

ARALIACEAE: 2 woods; 1 fruit.

LEGUMINOSAE: 3 woods; 1 fruit.

LAURACEAE: 7 woods, at least one with characteristics of the *Lindera-Litsea* group; 5 fruit types, one assigned to *Lindera*.

MAGNOLIACEAE: 5 woods: 1 *Liriodendron*-like, 1 *Magnolia*, 3 *Magnoliaceoxylon* (stereotypic genus); 3 fruits/seeds: *Magnolia*.

3) *Fruits/seeds types more diverse than woods:*

ANNONACEAE: 1 wood; 3 seeds.

JUGLANDACEAE: 2 woods: *Engelhardioxylon, Clarnoxylon* (extinct, some characteristics of *Platycarya*); 4 fruits: *Cruciptera, Juglans*, cf. *Palaeocarya* (tribe Engelhardieae), *Paleoplatycarya?*.

PALMAE: 1 stem, 2 seeds.

PLATANACEAE: 1 wood: extinct genus *Platanoxylon* (abundant); 3 infructescences: *Macginicarpa* (abundant), *Platanus, Tanyoplatanus*.

SABIACEAE: 3 *Meliosma* woods: all similar to subgenus *Meliosma* sect. *Meliosma* [Asian distribution]; 5 *Meliosma* fruits/seed, 4 similar to subgenus *Meliosma* sect. *Meliosma*, 1 similar to subgenus *Kingsboroughia*.

ULMACEAE *sensu lato*: 1 wood: *Ulmus*; 4 fruits/seed: *Aphananthe, Celtis, Trema*, and an extinct genus of Ulmoideae (*Cedrelospermum*).

In the fruit and seed assemblage, *Juglans* (200+ samples of one species) and *Celtis* (260+ samples for two species) are among the most abundant genera. *Juglans* and *Celtis* would be expected to be common in a fruit and seed assemblage because their fruits are inherently resistant to decay. *Juglans* wood is also resistant to decay so the absence of wood with characteristics similar to extant *Juglans* is noteworthy. Extant diffuse porous *Celtis* wood is similar to other extant Urticalean woods, so isolated samples of diffuse porous *Celtis* wood may not be distinguishable as *Celtis*. One or more of the Urticalean woods may be from the same plant as produced the *Celtis* endocarps. Absence of *Celtis* wood may also be because it is not resistant to decay organisms.

4) *Mismatch in terms of resemblance to extant genera and species:*

ACERACEAE: 1 wood: *Acer*, resembles sect. *Integrifolia*; 1 extinct fruit/seed genus: *Deviacer.*

ALANGIACEAE: 1 wood: *Alangium*, resembles *A. javanicum* group, Sect. *Constigma*; 2 fruits: *Alangium*, both resemble *A. chinense* group.

BETULACEAE: 1 wood: *Betula,* similar to subsect. *Costatae*, sect. *Eubetula*; 1 fruit: extinct genus belonging to Coryloideae.

FAGACEAE: 2 woods: *Quercinium* (form genus includes woods similar to *Lithocarpus* and *Quercus*), *Fagaceoxylon* (extinct genus); 2 fruits: *Castanopsis, Quercus*.

SAPINDACEAE: 1 wood, generalized features seen in the Cupanieae alliance; 1 fruit/seed similar to extant *Allophylus*, which is not a member of the Cupanieae.

VITACEAE: 2 woods: *Vitaceoxylon* extinct genus, similar to *Vitis*; 7 seeds: 4 extant genera.

These discrepancies between the woods' and fruits' and seeds' resemblances to extant genera suggest that if whole plants could be reconstructed a higher percentage of extinct genera in the Nut Beds assemblage would be recognized. Some woods with features of extant genera could be part of a plant whose fruits and seeds are distinct from extant genera, or *vice versa*.

Comparison with other Eocene wood assemblages — The Nut Beds fruit and seed assemblage has long been compared to the early Eocene London Clay fruit and seed assemblage of southern England (e.g., Scott 1954). The shared genera (30%) and species (10%) of fruits and seeds of the London Clay and the Nut Beds are important corroborating evidence for the existence of land-connections between Europe and North America during the early Tertiary. In these two assemblages, the predominance of genera with affinities to Southeast Asian plants has contributed to the concept of an Eocene boreotropical forest (Wolfe 1975; Tiffney 1985). Woods also occur in the London Clay, but mostly as pyritized twigs (Poole 2000).

As is true for the Nut Beds, the London Clay contains more fruit and seed types (ca. 350 species, Collinson 1983) than wood types (ca. 15, as summarized in Poole 2000). Compared to the Nut Beds, a higher proportion of the London Clay wood types apparently does not have counterparts in the fruit and seed assemblage. This discrepancy may be because multiple localities were investigated for the London Clay, while we are comparing material from the same locality. The only record of Dipterocarpaceae in the London Clay is wood. There are London Clay woods described as resembling the genera *Catha* (Celastraceae), *Coscinium* (Menispermaceae), *Koelreuteria, Guioa* (Sapindaceae), *Rhoicissus* (Vitaceae); these families are reported from the London Clay fruit and seed assemblage, but not these particular genera.

Platanus-like and evergreen oak-*Lithocarpus*-like woods occur in both the London Clay and the Nut Beds. Further investigation of the *Platanus*-like woods from the London Clay would be warranted to see if the types recognized from the Nut Beds are comparable to those of the London Clay.

It is curious the only records for *Cercidiphyllum* for both the London Clay and for the Nut Beds are woods. Fruits and leaves similar to extant *Cercidiphyllum* are not known until the lower Oligocene (Manchester 1999). This leads us to hypothesize this wood type may be associated with the fossil genera *Trochodendroides* (leaf) and *Nyssidium* (fruit), which are widespread in the late Cretaceous and early Tertiary of the Northern Hemisphere.

The complete absence of growth rings in the dicot 'twigs' of the early Eocene London Clay (ca. 917 'twigs' representing 15 wood types; computed from data in Poole 1999) contrasts with the Nut Beds woods. Most of the woods from the early Eocene Yellowstone Fossil Forests, Wyoming (Wheeler et al. 1977, 1978, and unpub. data), and Eden Valley, Wyoming (Kruse 1954), have distinct growth rings. Of the hypotheses Poole proposed to explain the complete absence of growth rings in the London Clay woods, the suggestion "the dicot twigs might be too juvenile to exhibit clear growth rings" seems most plausible. Some of the large London Clay wood specimens Brett (1956, 1972) described have distinct growth rings. Seedlings of extant ring porous oak species sometimes do not have distinct growth rings (pers. observ.).

Fossil wood is abundant in western North America, particularly from the Eocene, a time when volcanic activity provided sources of silica for permineralization. However, the anatomy of fossil woods has been studied at relatively few sites. Kruse (1954) described 11 species from Eden Valley, Wyoming, all based on narrow diameter material. Two species with radial canals no doubt are Anacardiaceae, as Kruse indicated, but the affinities of the other woods need reevaluation. Examination of the woods assigned to *Talauma* (Magnoliaceae) revealed they did not have characteristics of Magnoliaceae (Wheeler et al. 1977). None of the wood types common in the Nut Beds were reported by Kruse; the absence of *Platanoxylon* and *Quercinium* from Eden Valley seems especially noteworthy.

The early Eocene Fossil Forests of Yellowstone National Park differ from the Nut Beds because conifers are common. The 31 dicot wood types from Yellowstone are from different fossil forest layers, not just a single fossil forest layer. The Nut Beds and Yellowstone species of *Quercinium, Platanoxylon*, and *Prunus* are similar, but there are no other shared species. For the families that occur at both the Nut Beds and Yellowstone, the genera at Yellowstone are different, e.g., Anacardiaceae (a semi-ring porous *Rhus*), Betulaceae (*Alnus, Carpinus*), Juglandaceae (*Pterocaryoxylon*), Ulmaceae (*Zelkovoxylon*). Woods of unknown affinities are different as well (unpub. data for Yellowstone).

The middle Eocene Princeton chert flora of southern British Columbia, Canada, has anatomically preserved fruits and seeds, as well as woods. This flora is still under study, but is apparently less diverse than the Nut Beds. It also differs as there are abundant *Metasequoia* remains and lianas are not common. *Prunus allenbyensis* (Cevallos-Ferriz & Stockey 1990b) and *Liriodendroxylon princetonensis* (Cevallos-Ferriz & Stockey 1990a) are similar to woods from the Nut Beds. If they had been recovered from the Clarno Formation, they would be considered as additional samples of *Prunus gummosa* and *Liriodendroxylon multiporosum*.

Late Eocene (Chadronian) woods from the Florissant Fossil Beds National Monument, Colorado (Wheeler 2001), and western Nebraska (Wheeler & Landon 1992) have characteristics that suggest seasonal climates. All woods have distinct growth rings; ring porous and semi-ring porous woods are common; and the diffuse porous woods have narrow vessels and a high vessel density.

There is considerable opportunity to further our knowledge of Eocene vegetation of western North America by additional studies of the fossil woods.

Biogeography — As is true for the extant genera represented by fruits and seeds, the majority of the extant genera represented by Nut Beds woods do not occur today in western North America (Table 5). All of the extant genera represented in the Nut Beds wood assemblage occur today in eastern/southeastern Asia and at least 50% occur in eastern North America and Malesia. The anatomical characteristics of the *Acer*, *Alangium*, *Liriodendron*, and *Meliosma* woods are those of species that today are Asian, further emphasizing the relationships of the Nut Beds woods to extant plants of eastern Asia.

Growth form — One characteristic of the Nut Beds fruit and seed assemblage is the abundance of vines as suggested by present-day habit of closest living relatives. Forty-four percent (31 of 71) of fruit and seed species for which growth form was inferred are vines. Only ~5% (4 of 76) of the wood species have anatomical features indicating they are vines. This discrepancy could be because:

1) as a group, vines generally have a high proportion of unlignified tissue (Carlquist 1991), so they would be less likely to enter the fossil record;
2) it may reflect bias in our sampling of material to study, as we chose to section the larger diameter material for microscopic examination, and the vines may be better represented among the small diameter material;
3) during the early Tertiary, some taxa that were vines may not have developed the suites of wood anatomical features that today are associated with the liana habit (e.g., cambial variant structure, two size classes of vessels but not ring porous, wide rays and a high proportion of the cross section occupied by vessels). Thus, woods of Eocene vines would not be recognized as vines based on their anatomy;
4) taxa that are vines today were not vines in the Middle Eocene.

If possibility 1 or 3 is correct and vines are underrepresented in the fossil wood record, or not recognizable as such, this would in part explain the greater diversity of the Nut Beds fruit and seed assemblage which includes a high proportion of vines. The Meni-

Table 5. Present geographic distribution of extant Nut Beds wood genera.

seAs = Southeast Asia, Mal = Malesia, wNA = western North America, eNA = eastern North America, cAM = Central America, sAM = South America, Eur = Eurasia, Afr = Africa.

Genus	seAS	Mal	wNA	eNA	cAM	sAM	Eur	Afr
Acer	+	+	+	+			+	
Alangium	+	+						+
Betula	+		+	+			+	
Cercidiphyllum	+							
Hamamelis	+			+				
Liriodendron	+			+				
Magnolia	+	+		+	+			
Meliosma	+	+			+	+		
Prunus	+	+	+	+			+	+
Ulmus	+			+			+	

spermaceae, which today is comprised of lianas, is the most diverse family in the Nut Beds fruit/seed flora, followed by the Icacinaceae, which includes many lianas.

Because many of the ca. 625 Clarno permineralized wood samples sectioned represent relatively narrow axes their quantitative features may differ from those of mature wood samples, which usually are examined for systematic wood anatomical studies. Generally, wood close to the pith has narrower more numerous vessels than does wood formed by an older cambium. It is also possible some of the Clarno woods represent small shrubs.

Root wood is not common in the Nut Beds wood assemblage. We surveyed 101 entire axes (unsectioned) less than 1 cm in diameter. Of these only 1 clearly lacked a pith and apparently is a root. Of the samples sectioned and examined microscopically, only three have characteristics that suggest they might be roots (see Figs. 29 D–F, 56 A–F), even though these samples did not include the center of the axis. Roots are relatively uncommon in the fossil records, probably because they are buried in the soil horizon and are unlikely to be transported into depositional basins.

Growth rings — Growth ring characteristics are often used for making generalizations about paleoclimates, especially in conifers. Three of the four Clarno gymnosperms have distinct growth ring boundaries; the dicotyledons vary in distinctiveness of the boundaries, sometimes within a single wood type.

Growth rings are usually less distinct in root wood than in stem wood. Individual growth rings in Eocene dicot woods and in fast-grown plantation trees of the present day can be more than 1 cm wide. If the Nut Beds wood types that might be roots or are based on axes less than 2 cm in diameter are excluded, this leaves 65 wood types. Of these 65, 44 (67%) have distinct growth rings; one is ring porous and 18 are semi-ring porous (Table 2). This incidence of semi-ring porous to ring porous woods (29% of the 65) is higher than would be expected for a tropical or paratropical forest. Semi-ring porous woods are not common in the tropics today (ca. 3%), even in seasonally dry or montane forests, but are relatively common in Northern Hemisphere woods (ca. 21%) (Wheeler & Baas 1991). Détienne (1989) found ca. 7% (2 of 30, both of which were non-native species grown on plantations) of the tree species he studied from tropical Africa and French Guiana were semi-ring porous. None of the 29 Amazonian tree species Vetter and Botosso (1989) studied and illustrate appear semi-ring porous. Ring porous and semi-ring porous woods today are deciduous indicating many of the Nut Beds woods were deciduous. The deciduousness could be correlated with seasonality in precipitation, temperature, or daylength. The earliest known ring porous wood is from the Cretaceous of Antarctica (Poole et al. 2000) suggesting this wood anatomical feature initially was an adaptation to pronounced seasonality in daylength.

Twenty-one wood types (33%) are represented by some samples that we describe as having vague, poorly defined growth rings. However, some of these woods have fine lines of radially flattened fibers (e.g. *Tapirira*, Fig. 7A) or changes in parenchyma spacing and frequency of parenchyma (e.g. *Alangium*, Fig. 5A). These structural features resemble regions that Lindorf (1994), Worbes (1989), Détienne (1989) and Vetter and Botosso (1989) label as growth ring boundaries in tropical trees, including those from forests with a dry season of 7–10 months, and inundation forests that are flooded for 8–9 months of the year. The range of growth ring types (distinct and ring porous to ill-defined) observed in the Nut Beds woods seems at present difficult to match with a single modern-day vegetation type. However, it is consistent with what might be expected for a flora described as comprised of plants whose affinities with extant genera range from those whose species are now confined to temperate regions to those whose species are now confined to frost-free tropical regions (Manchester 1994). Nut Beds woods that we consider to lack distinct growth rings include woods assigned to Anacardiaceae, Annonaceae, and Lauraceae. These families today are primarily tropical in distribution. The Nut Beds *Quercinium* is not ring porous, and has anatomy consistent with an evergreen oak.

A high proportion of woods with indistinct growth rings often is used to infer a climate that is not highly seasonal. However, some trees that grow in dry tropical forests with dry seasons of many months do not have growth ring boundaries as distinct as is characteristic of present-day trees of mid-latitudes (see Worbes 1989; Détienne 1989; Vetter & Botosso 1989; Lindorf 1994). Evidently, seasonality in precipitation alone is not associated with as high an incidence of distinct growth rings or as distinct growth rings as is associated with a cold season with temperatures below freezing, as occurs today above 42° N in the eastern United States (Woodcock 1994; Woodcock & Ignas 1994).

There are continua in growth ring boundary distinctiveness and porosity in extant and fossil woods. There are some woods for which there would be general agreement that they are ring porous vs. semi-ring porous vs. diffuse porous or whether growth rings are distinct or not. However, there are some woods that one observer might describe as semi-ring porous, another might describe as ring porous, and yet another as diffuse porous. What an observer trained in the tropics would describe as distinct growth rings is different than what an observer from the north temperate regions would describe as distinct growth rings. Thus, using growth rings and porosity for inferring specifics of climate or for phylogenetic analyses may be problematic, especially when using descriptors from various literature sources. Woodcock (1994) suggested using the incidence of a range of vessel diameter of 5× across a ring (graduated porous), rather than the categories ring porous or semi-ring porous. This approach may be useful for insuring consistency in describing and evaluating porosity, and image analysis systems may make this approach practical. However, there needs to be more sampling and characterization of extant woods from a variety of sites with detailed meteorological data.

Wood anatomical characteristics of the Nut Beds dicot woods — Baas and Schweingruber (1987) found some wood anatomical attributes are correlated with habit. Consequently, for comparison to data for modern forests, we are using only those woods from samples > 10 cm in diameter. Listed below is the incidence of a few selected anatomical features, ones that have featured prominently in discussions of ecological wood anatomy.

- Mean tangential diameters of vessels > 200 µm: 0%
- Exclusively scalariform perforations in vessel elements: 22%
- Helical thickenings in vessel elements: 6%

None of the Nut Beds woods have the syndrome of few (< 10 vessels per sq.mm) and wide vessels (> 200 µm) that is prevalent in modern tropical lowland rainforest trees. The only Nut Beds woods with vessel diameters typically greater than 200 µm are the four that we believe are vines and are characterized by two distinct vessel diameter classes or unlignified tissue. The incidence of scalariform perforations in the Nut Beds woods is higher than occurs in modern lowland rainforest trees (0–8%) or savannas and monsoon forests (1–5%), and within the range found in modern montane tropical forests (15–33%) and some subtropical to warm temperate woody floras (13–22%) (Baas 1976). Helical thickenings are common in modern woods of the temperate zone (ca. 45%) and rare in the tropics (4%); the incidence of helical thickenings in the Nut Beds woods is similar to that found in the tropics today.

MAT Inferences — Incidences of various wood anatomical features are correlated with climate (e.g., Baas 1986; Carlquist 1988); there is interest in describing ancient climates, especially estimating mean annual temperature. However, given that plants survive a range of temperatures, mean annual temperature (MAT) may not be the easiest of these parameters to estimate accurately (Wiemann et al. 1999). When Wiemann et al. (1998, 1999) computed MAT for the Nut Beds, they based their estimate on 66 wood types. Two of the many regression equations (Eq. 12, 15, given below) tested were considered best for estimating MAT because of how well they worked as MAT predictors at a range of present-day sites (Wiemann et al. 1999). Both equations are based on arcsine transformations of the relative proportions of species having the anatomical features: storied rays (stor), marginal parenchyma (marg), axial parenchyma absent (abs), and septate fibers (sept). On an individual basis, these particular features are not those that correlate best with MAT. As classic studies predict (e.g., Carlquist 1975; Baas 1986), vessel diameter and incidence of spiral thickenings are more highly correlated with MAT (Wiemann et al. 1999).

Eq. 12) $\text{MAT °C} = 24.78 + 36.57\,(\text{stor}) - 15.61\,(\text{marg}) - 16.41\,(\text{abs})$
Eq. 15) $\text{MAT °C} = 17.07 + 25.23\,(\text{stor}) - 23.17\,(\text{abs}) + 13.79\,(\text{sept})$

We have recomputed the MAT for the Nut Beds, using only those wood types represented by samples with a diameter 10 cm or more (n = 39). These equations use relatively few features, so if any one of these features is absent from a fossil wood assemblage the estimates of MAT are greatly affected. One of the Clarno woods has a tendency to storied rays; whether storied rays are considered absent (0/39) or intermediate (0.5/39) in occurrence in the Nut Beds assemblage affects the estimated MAT (see below).

Eq. 12: MAT = 9.2 °C (n = 66, Wiemann et al. 1999)
MAT = 14.6 °C (n = 39, incidence storied rays 0/39)
MAT = 18.8 °C (n = 39, incidence storied rays 0.5/39)

Eq. 15: MAT = 10.7 °C (n = 66, Wiemann et al. 1999)
MAT = 12.5 °C (n = 39, incidence storied rays 0/39)
MAT = 15.4 °C (n = 39, incidence storied rays 0.5/39)

The higher estimates of MAT are more consistent with the composition of the flora and with estimates of MAT based on leaf physiognomy, 16.8 °C and 17.0 °C (Wiemann et al. 1998). It is curious that removing the smaller diameter material from consideration affects the MAT estimates to such an extent. Differences in quantitative features (vessel diameter and density) between juvenile and mature wood are well documented (e.g., Panshin & DeZeeuw 1980), but differences between juvenile and mature woods in the incidences of storied structure, marginal parenchyma, rare parenchyma, and septate fibers are not.

The diversity of Lauraceae and Magnoliaceae woods, as well as the abundance of evergreen oak type and *Platanus*-like woods that are more like *P. kerrii,* the southeast Asian species, than any other extant *Platanus* species, is consistent with the generalization that the Nut Beds plants grew in a warm, moist, mostly equable climate (Manchester 1994). However, the relatively high incidence of semi-ring porous woods indicates some degree of seasonality.

While using wood anatomical features may not prove the best method for estimating MAT, wood can help reveal how variable the climate was during the lifetime of a tree, and should prove useful for inferring degree of seasonality and length of growing season. Also, if woods were collected from a series of localities in a restricted geographic locality, they would be useful for evaluating general climatic trends through time, by using incidence of such features as distinct growth rings, vessel diameter and density, and ring porosity.

DESCRIPTIONS
Dicotyledonous woods identified to family

ACERACEAE

Aceraceae (Sapindaceae s.l.) are represented in the Nut Beds by fruits of *Deviacer wolfei* Manchester (1994), an extinct genus that resembles *Acer*, but differs in its mode of attachment. *Dipteronia* fruits occur in other parts of the Clarno Formation (McClain & Manchester 2001). One wood with structure comparable to extant *Acer* is described below.

ACER L.

Acer integrifolioxylon sp. nov. (Fig. 4)

Growth rings distinct, marked by radially flattened fibers.

Diffuse porous. Vessels solitary and in radial multiples of 2–4; average tangential diameters 48 (5)–50 (7) µm; vessel frequency averages of 88–97/mm^2 (total range of 62–150/mm^2); perforations simple; intervessel pits crowded alternate, polygonal in outline with included apertures, 5–6 µm; vessel-ray parenchyma pits similar in size and shape to intervessel pits; helical thickenings present along entire length of the vessel element; vessel element lengths average 364 (123) µm; range 217–543 µm; tyloses absent.

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

Axial parenchyma apparently diffuse; chambered crystalliferous strands with over 16 chambers per strand; one crystal per chamber.

Rays 1–3-, rarely to 4–5-seriate. Multiseriate rays homocellular, composed of procumbent cells; multiseriate ray height averages of 297 (137)–546 (159) µm; 4–7/mm.

Storied structure absent.

Holotype: USNM 507832 (DEN 5, ≥ 40 cm).
Paratype: USNM 507831 (DEN 12, ≥ 22 cm).
Etymology: Specific epithet indicates this wood's anatomy is similar to section *Integrifolia* of *Acer*.

Similarities to extant woods — *Acer* is the only extant genus in the OPCN database with the combination of diffuse porosity, vessels solitary and in short radial multiples, simple perforation plates, alternate intervessel pits, vessel-ray parenchyma pits similar in size and shape to the intervessel pits, spiral thickenings in vessel elements, non-septate fibers without distinctly bordered pits, non-storied homocellular rays that are 3(–4)-seriate, scanty axial parenchyma, and crystals in chambered axial parenchyma. The vessel density is high for species of *Acer*, but within the range reported for the genus. The features of these woods do not differ from extant *Acer*, in contrast to the Nut Beds fruit, *Deviacer*.

According to Metcalfe and Chalk (1950) *Dipteronia* is distinct from *Acer* as it has vessel clusters and oblong vessel-ray parenchyma pits. We examined *D. dyeriana* (SJRw 29850) and *D. sinensis* (MADw 41703, Kw samples labeled cultivated at Wakehurst and MK 1966, and illustrations by Cheng 1980, Chang et al. 1992). The *D. dyeriana*

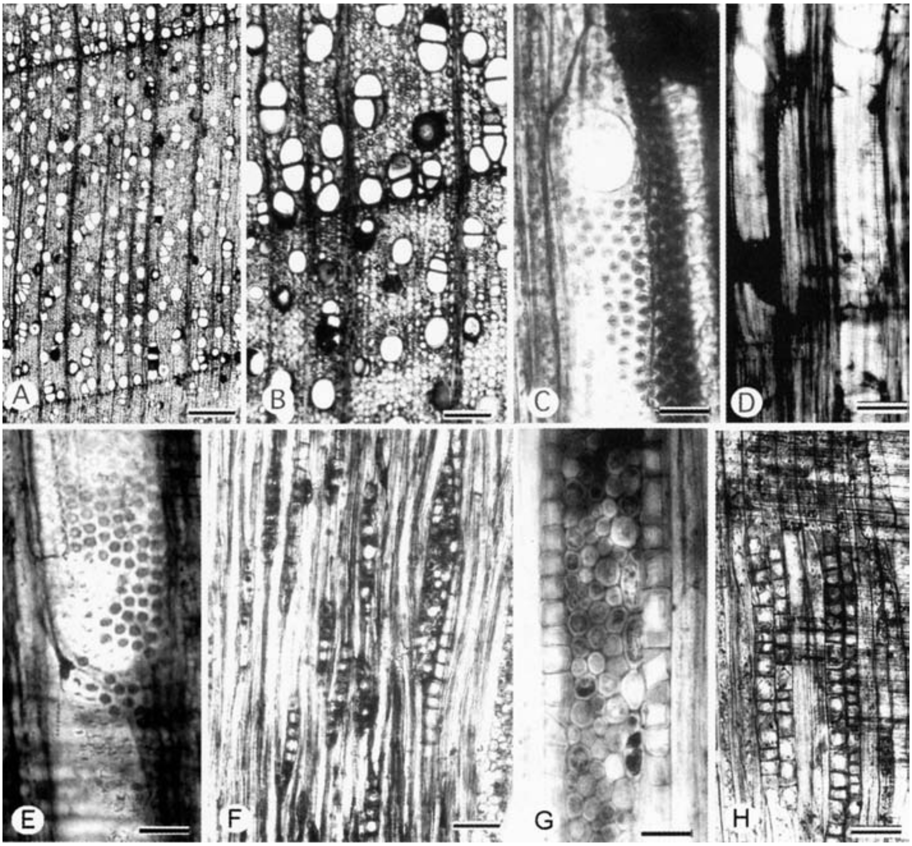

Fig. 4. *Acer integrifolioxylon* sp. nov. (USNM 507832). – A: Vessels solitary and in radial multiples, diffuse porous wood, XS. – B: Growth ring boundary, XS. – C: Simple perforation plate, crowded alternate intervessel pits. – D: Helical thickenings throughout vessel elements, simple perforation plates, RLS. – E: Vessel-ray parenchyma pits similar to intervessel pits, RLS. – F: Rays 1–3-seriate, TLS. – G: Multiseriate ray with crystalliferous strands on either side, TLS. – H: Ray composed of procumbent cells, crystalliferous strands of axial parenchyma , RLS. — Scale bars = 250 µm in A; 100 µm in B; 50 µm in D, F; 25 µm in C, E, G, H.

sample matched the description given by Metcalfe and Chalk (1950) because the vessel-ray parenchyma pits were horizontally enlarged and with reduced borders. However, we believe that the *D. dyeriana* SJRw 29850 sample is misidentified, as enlarged vessel-ray parenchyma pits are not characteristic of *Dipteronia sinensis* or the Sapindaceae s.l. *Dipteronia sinensis* wood is generally similar to *Acer* wood, with vessels solitary and in radial multiples, simple perforations, crowded alternate polygonal intervessel pits, vessel-ray parenchyma pits similar in size and shape to intervessel pits, libriform fibers, rare axial parenchyma, homocellular rays (to 4-seriate). *Dipteronia* differs as it lacks helical thickenings in the vessel elements and in MK 1966 and MADw 41703 radial multiples of 4 or more were relatively common. No crystals were observed and fibers were thin-walled. Tang (examined *D. dyeriana*, 1936) and Chang et al. (examined *D. sinensis*, 1992) did not observe crystals or spiral thickenings.

Although the differences between *Acer* and *Dipteronia* wood are slight, we consider this wood to be allied with *Acer* rather than *Dipteronia* because it has helical thickenings in the vessel elements and crystalliferous axial parenchyma.

Ogata (1967) examined the wood anatomy of 22 sections of *Acer*, and found that ray size was one of the most useful features for distinguishing sections of *Acer*. Of the sections that Ogata examined, the Clarno woods are similar to section *Integrifolia*, because only woods of this section normally have 3–4-seriate rays and crystalliferous axial parenchyma. Today this section occurs in southern China, southeast Asia, and Taiwan. The somewhat irregular ray shape of Clarno woods also suggests similarity to sections *Campestria* and *Trifoliata* (Suzuki, pers. comm. 2000).

Comparisons with other fossil woods — To our knowledge, this is the oldest report of fossil wood with characteristics of the genus *Acer*. *Acer beckianum, A. olearyi, A. puratanum*, and *Aceroxylon pennsylvanicum* occur in the Miocene Vantage Fossil Forests, Oregon, USA (Prakash & Barghoorn 1961a; Prakash 1968); *Acer watarianum, A.* cf. *amoenum* occur in the Miocene of Japan, *A. palmatoxylon* and *A. momijiyamense* occur in the Oligocene of Japan (Watari 1952; Suzuki 1982; Takahashi & Suzuki 1988; Suzuki & Hiraya 1989; Suzuki & Watari 1994). The Japanese *Acer* woods are considered closest to sections *Platanoidea*, *Palmata*, and *Macrantha* (Takahashi & Suzuki 1988). None of the Miocene Vantage *Acer* woods commonly have crystalliferous axial parenchyma and 3–4-seriate rays. Consequently, we are describing this Clarno wood as a new species of *Acer*.

ALANGIACEAE

This family contains the single genus *Alangium*, distributed today in Asia and Africa. Recent molecular data support the conclusion that *Alangium* is close to *Cornus* and should be placed in Cornaceae (Xiang & Soltis 1998). Two species of *Alangium* are recognized on the basis of fruits from the Nut Beds: *A. eydei* and *A. rotundicarpum*. These fruits fit section *Marlea* of *Alangium* and are morphologically similar to *A. chinense*.

ALANGIUM Lamarck

Alangium oregonensis Scott & Wheeler (Fig. 5)

Growth rings indistinct, but with zones with little or no parenchyma and smaller pores.

Diffuse porous. Vessels solitary and in radial multiples of 2–5; thin-walled; tangential diameter 70–140 µm, mean 104 µm; vessel frequency 22–31/mm^2, perforations scalariform with 1–10 thick bars, or rarely simple; intervessel alternate, small, 4.5–6.5 µm; vessel-ray parenchyma pits not preserved; helical thickenings absent; vessel elements long, mean 1200 µm; tyloses absent.

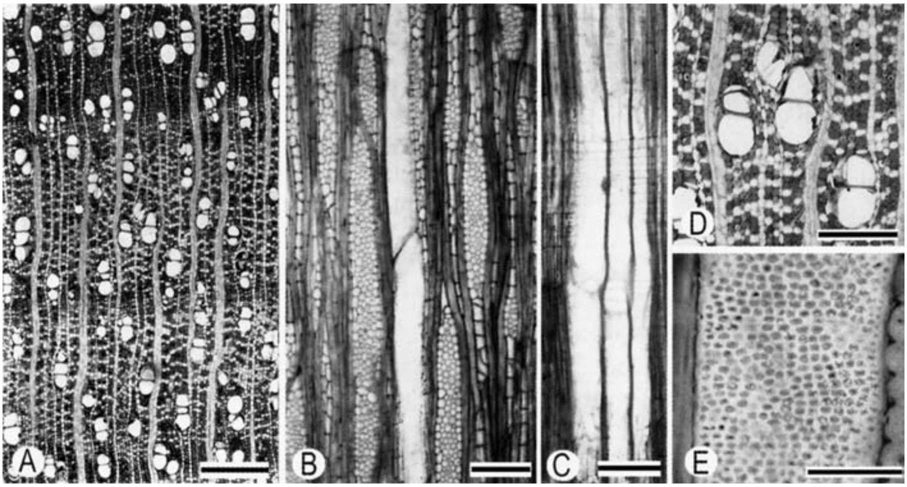

Fig. 5. *Alangium oregonensis* Scott & Wheeler (USNM 326699). – A: Diffuse porous wood with vessels commonly in radial multiples, XS. – B: Heterocellular rays with long tails of upright cells, TLS. – C: Scalariform perforation plates, RLS. – D: Diffuse-in-aggregates parenchyma, XS. – E: Alternate intervessel pitting, TLS. — Scale bars = 500 µm in A, 250 µm in D; 200 µm in B, C; 50 µm in E.

Fibers non-septate, thick-walled, pits simple.

Axial parenchyma apotracheal, diffuse, diffuse-in-aggregates in short uniseriate lines and as scattered cells, moderately abundant; more than 10 cells per strand.

Rays of two sizes. Uniseriate rays numerous, composed of upright cells. Multiseriate rays heterocellular, up to 6 cells wide with 1–10 rows of marginal upright cells, total ray height typically 1.5–3.0 mm. Occasional rays composed of alternating uniseriate and multiseriate portions; 4–7/mm.

Storied structure absent.

Holotype: USNM 326699 (C4A-50, > 10 cm).

Similarities to extant woods — The combination of pores in radial multiples, scalari form perforations, small alternate intervascular pitting, common apotracheal parenchyma and heterocellular rays more than 1 mm high indicates affinities with *Alangium* (Scott & Wheeler 1982). Metcalfe and Chalk (1950) recognized two wood anatomical groups of extant *Alangium*. The Clarno wood corresponds to the *A. javanicum* group (rather than the *A. chinense* group) on the basis of its scalariform perforation plates and small intervascular pits. However, the presence of some simple perforations in the Clarno wood is a difference from the *A. javanicum* type and suggests intermediacy with the *A. chinense* type. Because of the scalariform perforation plates, the key to woods of the Cornaceae alliance of Noshiro and Baas (1998) also indicates that this wood belongs to *Alangium* sect. *Constigma*, e.g., the *A. javanicum* group. Vessel element lengths of *A. oregonensis* are near the maximum and slightly longer than those reported for species of *Alangium* sect. *Marlea*, but are shorter than those reported for species of sect. *Constigma*, which are all > 1300 µm (Noshiro & Baas 1998).

Thus, it is possible that the wood of *A. oregonensis* corresponds to one of the fruit species, and that it represents a member of section *Marlea*, e.g. *A. chinense* type, but retaining scalariform perforations.

ANACARDIACEAE

The Anacardiaceae are represented in the Nut Beds fruit and seed assemblage unequivocally by at least two genera: *Pentoperculum* (an extinct genus of the Spondiadeae) and *Rhus* in the Rhoeae. In addition, Anacardiaceae is recognized in the Nut Beds wood flora by at least three kinds of wood: *Maureroxylon, Tapirira*, and *Terrazoxylon*.

Maureroxylon gen. nov.

Maureroxylon crystalliphorum gen. et sp. nov. (Fig. 6)

Growth rings present, marked by radially flattened fibers.

Wood semi-ring porous to diffuse porous. Vessels solitary and in radial multiples of 2–3, average tangential diameter 101 (20)–150 (14) µm, solitary vessels rounded in outline; vessel frequency averages of 16–28/mm^2 (total range of 11–43/mm^2); perforations exclusively simple, intervascular pits alternate, 7–10 µm; vessel-ray parenchyma pits enlarged; helical thickenings absent; vessel element length 300–460 µm; tyloses present.

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

Axial parenchyma scanty paratracheal to vasicentric, diffuse to diffuse-in-aggregates (usually in the earlywood), strands usually of 4 cells.

Rays 1–3(–5)-seriate. Multiseriate rays heterocellular, with 1–2 marginal rows of square and upright cells; ray height averages 295 µm, range 175–450 µm; sheath cells absent; 5–8/mm.

Storied structure absent.

Rhomboidal crystals present in idioblast ray cells or square or upright cells.

Holotype: UF 12500 (> 16 cm).

Additional samples: UF 12016, 12025 (2.5 cm), 12027 (1.5 cm fragment), 12034, 12036 (> 10 cm), 12037 (> 10 cm), 12041 (> 10 cm), 12062, 12063, 12065 (> 10 cm), 12069 (> 12 cm), 12072 (> 10 cm), 12085 (> 10 cm), 12097, 12101, 12129 (fragment 1.8 cm), USNM 507838 (DEN 179).

Etymology: This genus is named in memory of Katherine Maurer, on whose ranch the Nut Beds locality is situated. The specific epithet refers to the prominent crystals in idioblasts of the rays.

Comments — The distinctive features of this wood are idioblasts with rhomboidal crystals in rays, all septate fibers, vessel-ray parenchyma pits with reduced borders, and abundant tyloses. This is one of the most common woods at the Nut Beds site, known from more than 19 pieces.

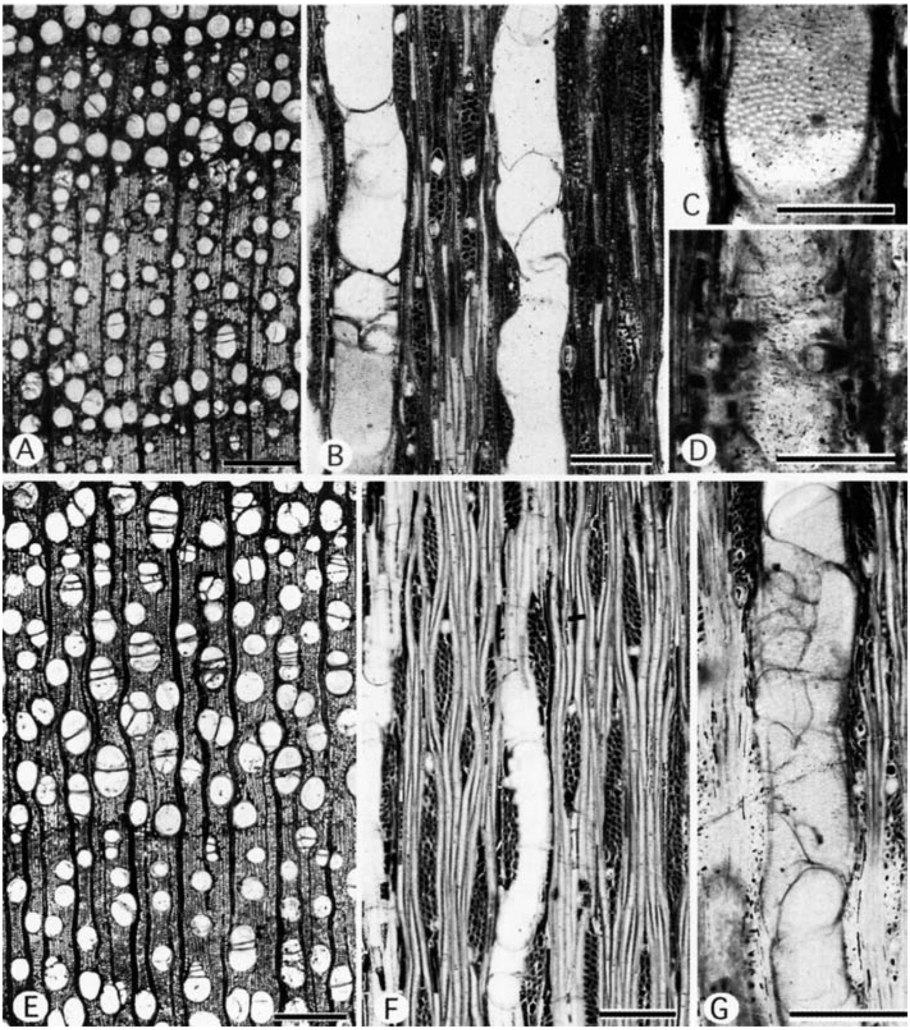

Fig. 6. *Maureroxylon crystalliphorum* gen. et sp. nov., A–D: UF 12097, E–G: UF 12500. – A: Semi-ring porous wood with vessels solitary and in radial multiples of 2–3, XS. – B: Rays commonly with crystalliferous idioblasts, occasional thin-walled tyloses, TLS. – C: Alternate intervessel pitting, TLS. – D: Vessel-ray parenchyma pits, RLS. – E: Diffuse porous wood with relatively wide vessels, XS. – F: Rays with crystal-bearing idioblasts, TLS. – G: Vessel with thin-walled tyloses, TLS. — Scale bars = 500 µm in A, E; 200 µm in B, F; 250 µm in C, D, G.

Some of the specimens are diffuse porous with almost no change in vessel diameter at the growth ring boundary (Fig. 6E); others are semi-ring porous (Fig. 6A). There is considerable variation in vessel diameter between samples. We excluded three samples [USNM 507833 (DEN 26, > 10 cm); UF 12110, ca. 6 cm; UF 12111, 3.5 cm] from the above description, because it is not certain whether these samples represent variation within the same species, or perhaps belong to a different species. They correspond in characters of the rays, idioblasts, septate fibers, intervascular pitting, and ray-vessel pitting, but are readily distinguished by their indistinct growth rings, diffuse porous wood, and wide vessels. For these samples, the mean tangential diameters of the vessels are 205 (30), 202 (27), and 218 (37) µm.

The tyloses in this wood precluded being able to measure more than 1 or 2 vessel element lengths per sample. UF 12053 shows evidence of wounding and it had more rays per mm, 6–10/mm.

Similarities to extant woods — A position within the Anacardiaceae is suggested by the occurrence of all septate fibers, vasicentric and scanty parenchyma, vessel-ray parenchyma pits with reduced borders, and rhomboidal crystals in the rays. In contrast to the other woods of this family in the Nut Beds, gum ducts were not observed. Some Burseraceae are similar; however, enlarged crystalliferous ray cells are not reported for this family (OPCN database).

This wood is strikingly similar to *Pleiogynium*, an extant genus of two species in the Philippines, Indonesia, New Guinea, Queensland, Fiji, and Samoa (Ilic 1991). However, the modern representatives have occasional gum ducts within the rays, which have not been observed in any of the Clarno specimens. *Pleiogynium* is a member of the Spondiadeae tribe of the Anacardiaceae, and has multilocular, operculate fruits somewhat similar to those of *Pentoperculum*, an extinct fruit genus common in the Nut Beds flora (Manchester 1994). This leads to the hypothesis that *Pentoperculum* and *Maureroxylon* may represent the same biological genus. A test of this hypothesis would be to determine if *Maureroxylon* wood can be found in the London Clay flora, the type area for *Pentoperculum*. Brett (1966) described an anacardiaceous wood from the Eocene of England, *Edenoxylon aeumulum*, but that wood differs from the Nut Beds taxa as 1) rays commonly have oval radial canals and are 0.25 mm wide at their widest part, 2) intervessel pits are small (5 µm), 3) only scanty paratracheal parenchyma is present, and 4) idioblasts are absent.

TAPIRIRA Aublet

Tapirira clarnoensis Manchester (Fig. 7A–C)

Growth rings delineated by 2–5 rows of radially flattened fibers, sometimes indistinct.

Diffuse porous. Vessels solitary and in radial multiples of 2–5 (mostly 2–3); average tangential diameters 121 (19)–138 (23) µm; average vessel frequency 11–14/mm^2, range 7–17/mm^2; perforations simple; intervessel pitting crowded alternate ca. 7 µm; vessel-ray parenchyma pits large and horizontally elongate; average vessel element lengths 425–544 (165) µm; tyloses common.

Fibers exclusively septate.

Axial parenchyma vasicentric, 1-cell-wide sheath; occasionally diffuse; 2–8 cells per strand.

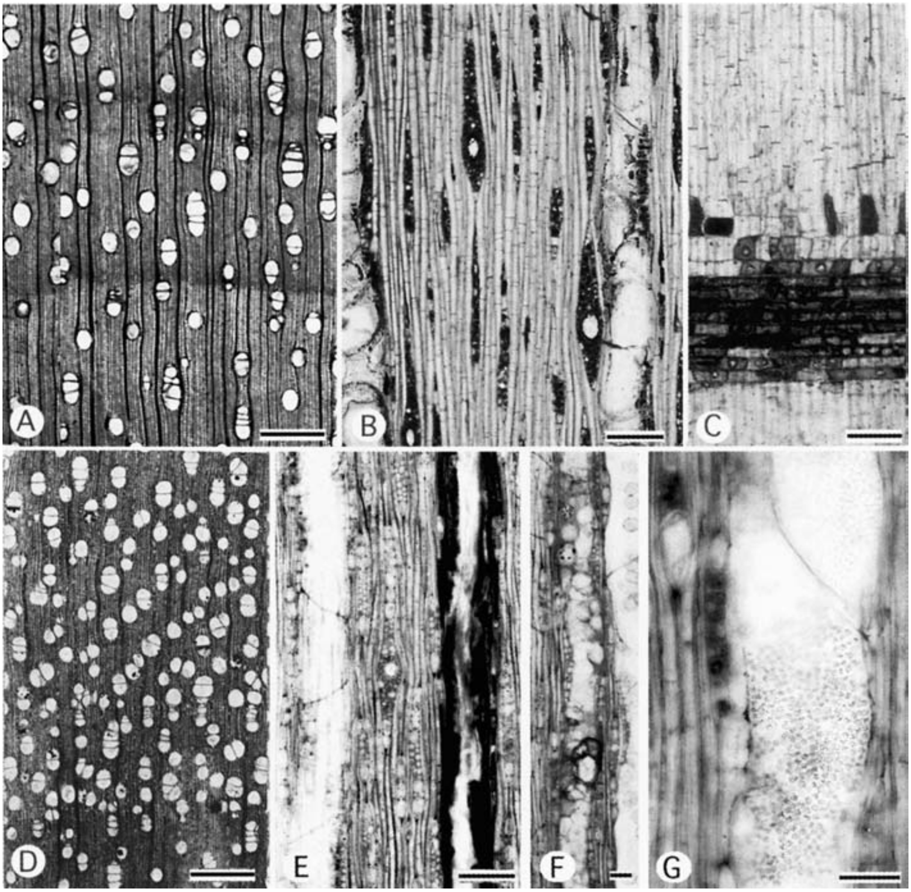

Fig. 7. A–C: *Tapirira clarnoensis* Manchester (USNM 507945). – A: Diffuse porous wood, XS. – B: Heterocellular biseriate rays and multiseriate rays with gum ducts; vessels with thin-walled tyloses, septate fibers, TLS. – C: Septate fibers, heterocellular ray with crystals in marginal square cells, RLS. — D–F: *Terrazoxylon ductifera* gen. et. sp. nov. (UF 12154). – D: Diffuse porous wood, XS. – E: Ray with radial duct, rays commonly with uniseriate portions equal in width to biseriate portion, TLS. – F: Vessels with tyloses, TLS. – G: Rhomboidal crystal in idioblast of ray, alternate intervessel pitting, TLS. — Scale bars = 500 μm in A; 200 μm in D; 150 μm in B; 100 μm in C, E, F; 50 μm in G.

Rays 1–2-seriate; or up to 5-seriate with oval radial gum ducts, ducts 20–50 μm in tangential diameter; rays mostly biseriate. Biseriate rays with uniseriate marginal rows of 1–6 cells; height 140–500 μm, average 350 μm; 6–8/mm.

Storied structure absent.

Solitary rhomboidal crystals in procumbent and upright ray cells.

Holotype: UF 12031 (> 10 cm).

Additional samples: UF 12167 (> 40 cm); USNM 507945 (ca. 10 cm), USNM 507943 (C 521, > 10 cm); USNM 507944 (C 524, > 20 cm).

Similarities to extant woods — This wood corresponds to the closely related families Anacardiaceae and Burseraceae in having diffuse porous wood, vasicentric and diffuse axial parenchyma, septate fibers, enlarged vessel-ray parenchyma pits, and narrow heterocellular rays with radial canals. Manchester (1977) assigned this wood type to the extant genus *Tapirira* based on the observation of an identical suite of anatomical characters in modern species of that genus. Similar wood occurs in some species of the burseraceous genus *Protium*. The fruit and seed assemblage of the Nut Beds flora includes fruits of burseraceous affinity, similar to *Protium* and other burseraceous genera, and fruits of Anacardiaceae. Molecular phylogenetic investigations indicate that Anacardiaceae and Burseraceae form a natural group (APG 1998; Soltis et al. 2000).

TERRAZOXYLON gen. nov.

Terrazoxylon ductifera gen. et sp. nov. (Fig. 7D–G)

Growth rings indistinct.

Diffuse porous. Vessels solitary and in radial multiples of 2–6; average tangential diameters 100 (21)–108 (29) µm; vessel frequency averages of 24–31/mm^2 (total range of 18–48/mm^2); perforations simple; intervessel pits alternate, 5–6 µm; vessel-ray parenchyma pits large and horizontally elongate with reduced borders; helical thickenings absent; average vessel element lengths 377 (65)–457 (92) µm; tyloses abundant.

Fibers septate. Pitting not observed.

Axial parenchyma vasicentric in uniseriate sheaths, 4 cells/strand.

Rays 1–2(–4)-seriate, with alternating uniseriate and biseriate sections, uniseriate portions similar in width to the biseriate portions. Heterocellular with body cells procumbent and 1–10, often > 4, marginal rows of upright cells, upright cells 2–3 times higher than procumbent cells; uniseriate rays composed entirely of upright cells; average total height of multiseriate rays without gum ducts 344 (99)–360 (155) µm; 5–9/mm.

Idioblasts with rhomboidal crystals common in the uniseriate portions.

Radial gum ducts occasional, ducts 20–30 µm in tangential diameter.

Holotype: UF 12154.

Paratype: UF 12026 (> 20 cm).

Etymology: The genus is named after Teresa Terrazas, in recognition of her work on extant Anacardiaceae. The specific epithet refers to the radial canals.

Similarities to extant woods — The combination of radial gum ducts (Fig. 7E), crystals in idioblasts of the rays (Fig. 7F), septate fibers, vessels with simple perforations and alternate intervascular pitting is compatible with placement of this wood in the family Anacardiaceae. Terrazas (1994) made a comprehensive study of the anatomy of extant anacardiaceous woods. She found that septate fibers were present in most genera, but missing in the tribe Semecarpeae, and some members of the Anacardieae and Rhoeae.

In some respects this wood is similar to that of *Astronium* from Central and South America. Both possess radial gum ducts and rays with biseriate and uniseriate regions of approximately equal width. It is likely that this same suite of characters may have occurred in other Anacardiaceae as well, including *Rhus* and other Rhoeae. Although *Astronium* has been reported before from the North American Tertiary based on foliage and flowers, none of these reports hold up well to closer scrutiny. In particular, the fruits that MacGinitie attributed to *Astronium* have been shown to be an extinct genus of Rutalean affinity (Wang & Manchester 2000).

Comparisons to other fossil woods — This wood is distinguished from the other canal-bearing anacardiaceous wood known from the Nut Beds, *Tapirira*, by the more common occurrence of idioblasts and the alternation in the rays of uniseriate and biseriate portions of similar width.

ANNONACEAE

The Annonaceae are represented in the Nut Beds by three species assigned to the stereotype genus *Annonaspermum* (Manchester 1994). In the Nut Beds wood assemblage, we recognize one wood type comfortably assigned to this family.

ANNONOXYLON Boureau

Annonoxylon bonesii sp. nov. (Fig. 8)

Growth rings indistinct, marked by marginal parenchyma of one or two rows.

Diffuse porous. Vessels solitary (about 50%) and in radial multiples of 2–5 and occasional clusters of 3–5; average tangential diameter 155 (22) µm; solitary vessels

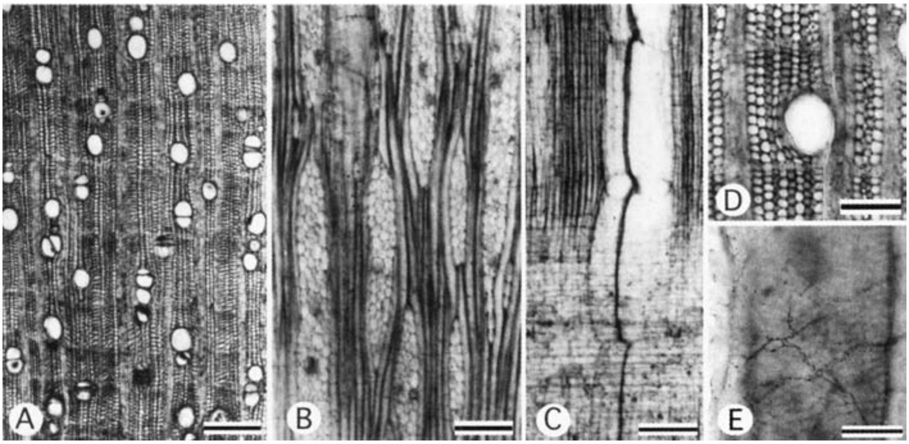

Fig. 8. *Annonoxylon bonesii* sp. nov. (UF 12020). – A: Diffuse porous wood with vessels solitary and in short radial multiples, XS. – B: Homocellular and slightly heterocellular rays, TLS. – C: Simple perforations, RLS. – D: Uniseriate lines of axial parenchyma, XS. – E: Alternate intervessel pitting, TLS. — Scale bars = 500 µm in A; 250 µm in C; 200 µm in B, D; 50 µm in E.

rounded in outline; vessel frequency 4–13, average 8/mm^2; perforations simple; intervessel pits crowded alternate, 4–6 µm, apertures slit-like, extending nearly to the outside of the border; vessel-ray parenchyma pits not observed (not preserved), helical thickenings absent; vessel element length 533 (144) µm; tyloses absent.

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

Axial parenchyma apotracheal in uni- and biseriate tangential lines that are relatively straight and continuous, and relatively closely spaced (separated from each other by 5 to 15 rows of fibers), and vasicentric in sheaths 1–2 cells wide; strands of 4–8 (mostly 8) cells.

Rays 1–6- (mostly 3–4-)seriate. Multiseriate rays homocellular to heterocellular, with up to 1–5 marginal rows of upright cells; sheath cells (up to three times as high as the procumbent cells) common; occasional ray cells slightly enlarged (idioblasts); ray cells relatively large; ray height 250–1750 µm; 2–6/mm, average 4/mm.

Storied structure absent. Crystals not observed.

Holotype: UF 12029 (> 10 cm).

Etymology: The species name is in honor of Thomas J. Bones.

Comments — Although represented by only a single sample, this wood is easily recognized as distinct by the thin discontinuous parenchyma bands, lack of well-defined growth rings, and rays with large cells.

Similarities to extant woods — The combination of vasicentric and thin parenchyma bands (Fig. 8A, D), simple perforations (Fig. 8C), small alternate intervessel pits (Fig. 8E), tall homocellular to heterocellular rays with variation in ray cell size (Fig. 8B) is characteristic of the Annonaceae (Metcalfe 1987). Also Annonaceae have few vessel-ray parenchyma pits (Metcalfe 1987), a feature of this Clarno wood type. The apparent absence or indistinctness of growth rings is a feature that is found in some Annonaceae, especially those of southeast Asia (Sosef et al. 1998).

Comparisons with other fossil woods — Other fossil woods attributed to Annonaceae include *Polyalthioxylon* from the Miocene of Thailand (Vozenin-Serra et al. 1989), and the early Tertiary and Miocene of India (e.g., Prakash 1976). *Polyalthioxylon*, like the extant *Polyalthia*, has secretory idioblasts in the rays which are apparently absent from the Nut Beds fossil wood.

The diagnosis of *Annonoxylon* Boureau emphasizes the regularly spaced narrow lines of axial parenchyma, relatively low vessel density, simple perforations, alternate intervessel pits, rays more than 4-seriate and to more than 1 mm high. This Clarno wood has those features and thus is assigned to *Annonoxylon*. It differs from Boureau's (1950, 1954) species (*A. striatum, A. edengense*) because it has more widely spaced parenchyma bands, more vessel multiples and a lower vessel frequency. However, it is possible that quantitative vessel descriptors might not be comparable as we counted each vessel as one, and Boureau may have counted a vessel multiple as one when computing vessel frequency and percentage of solitary vessels.

ARALIACEAE

Araliaceae are represented in the Nut Beds flora by compressions of the fruit type *Paleopanax oregonensis* Manchester (1994); similar fruits occur in the extant genus *Pseudopanax*. Two wood types with characteristics of Araliaceae are described below, they represent the oldest known occurrence of woods with characteristics of Araliaceae. A third wood type, in which critical diagnostic features are not visible, has generalized features seen in Araliaceae.

PLERANDREOXYLON gen. nov.

Wood semi-ring porous to ring porous. Latewood vessels in discontinuous wavy tangential to oblique arrangement, earlywood vessels usually less than 100 µm tangential diameter. Perforations simple or simple and scalariform with fewer than 20 bars; intervessel pits medium-large, alternate to scalariform; vessel-ray parenchyma pits horizontally enlarged and with reduced borders. Fibers septate and non-septate. Axial parenchyma rare to scanty paratracheal. Rays multiseriate, usually less than 4-seriate, and averaging less than 700 µm high; heterocellular, sheath cells sometimes present; uniseriate rays not common; fewer than 10 rays per mm. Storied structure and canals absent.

Type species: Plerandreoxylon oregonensis.

Etymology: Generic name indicates the wood has characteristics seen in members of the tribe Plerandreae.

Plerandreoxylon oregonensis sp. nov. (Fig. 9)

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

Semi-ring porous. Vessels solitary (not common) and in radial multiples and clusters, latewood vessels in oblique to tangential arrangement; vessels round to oval and slightly angular in outline; average tangential diameter of earlywood vessels 65 (11) µm, range 45–86 µm; perforations simple; intervessel pits crowded alternate to subopposite, large, 12–14 µm, sometimes near scalariform in narrower vessel elements; vessel-ray parenchyma pits seemingly with reduced borders and horizontally elongate; helical thickenings not observed; mean vessel element length 559 µm (n = 8), range 414–716 µm; tyloses not observed.

Fibers mostly non-septate, a few septate, walls thick, pitting not observed.

Axial parenchyma rare.

Rays 1–4-seriate, uniseriates rare. Multiseriate rays heterocellular, body of procumbent cells, with 1–2 marginal rows of upright cells; tendency to sheath cells; the total multiseriate ray height averages 485 (212) µm, range 155–986 µm; 4–5/mm.

Crystals not observed.

Storied structure and canals absent.

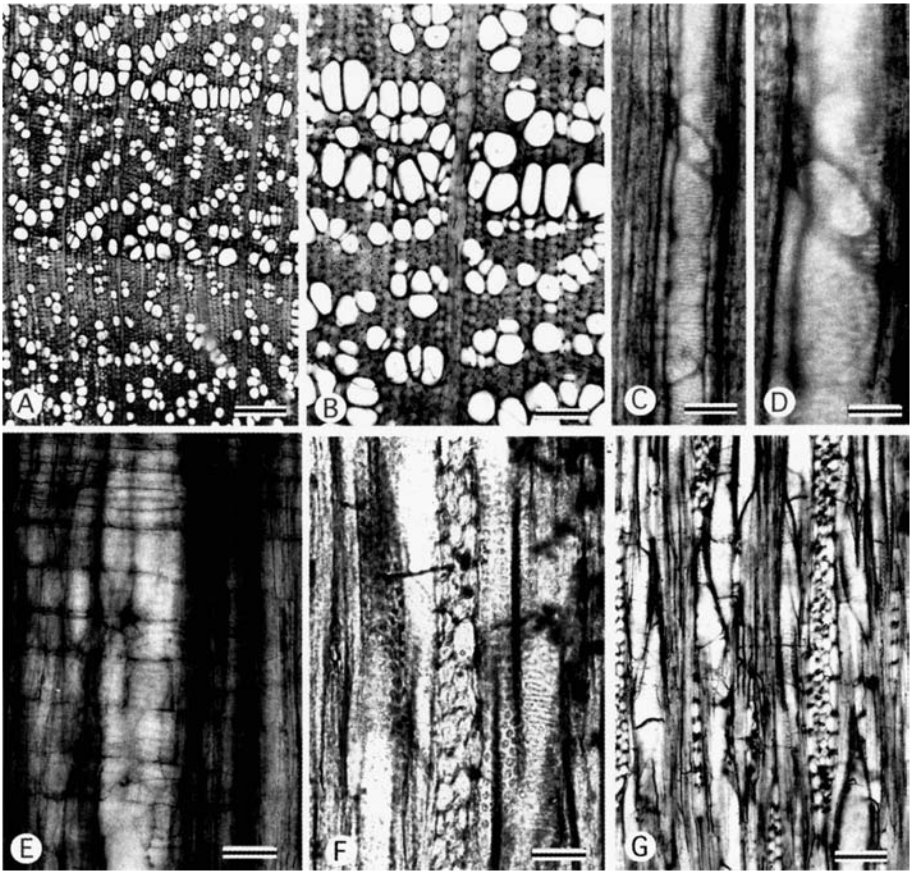

Fig. 9. *Plerandreoxylon oregonensis*. gen. et sp. nov. (UF 12406). – A: Portions of three growth rings, wood semi-ring porous with vessels in wavy tangential bands, XS. – B: Detail of growth ring boundary, showing latewood vessels in tangential groups and relatively thick-walled latewood fibers, XS. – C, D: Vessel element with simple perforation and large alternate intervessel pitting, TLS. – E: Vessel-ray parenchyma pitting, horizontally elongate, RLS. – F: Alternate to scalariform intervessel pits, TLS. – G: Multiseriate rays with sheath cells, widely spaced tyloses in vessel elements, TLS. — Scale bars = 250 μm in A; 100 μm in B, C, G; 50 μm in D, E, F.

Holotype: UF 12406 (2.3–6.0 cm).
Paratype: USNM 507834 (DEN 69, ≥ 6.0 cm).
Etymology: Specific epithet for the state of Oregon, where the Nut Beds locality is located.

Similarities to extant woods — Araliaceae are the only extant family in which the following features co-occur: wood semi-ring porous to ring porous, tangential arrangement of vessels, simple perforations, alternate and some scalariform intervessel pits, septate fibers, sheath cells, scanty–rare axial parenchyma. Ulmaceae s.l. (including Celtidaceae) also have semi-ring porous to ring porous woods, sheath cells, and tangential arrangement of vessels, but Ulmaceae woods do not have scalariform intervessel pits, rarely have septate fibers, and axial parenchyma is usually more abundant. Consequently, this wood is considered a member of Araliaceae.

Oskolski's (1996) is the most recent study of the wood anatomy of Araliaceae (99 species from 37 of the 60 genera in the family examined). According to Oskolski, ring porous wood occurs in *Aralia*, *Dendropanax*, and *Kalopanax*, and semi-ring porous wood in *Acanthopanax, Oplopanax*, and *Tetrapanax*. In the OPCN database extant genera of Araliaceae that have tangential bands of vessels are *Acanthopanax*, *Aralia*, *Dendropanax, Hedera* (with large rays typical of woody climbers), *Kalopanax, Pseudopanax,* and *Schlefflera* (Wheeler et al. 1986). All of the aforementioned genera, except *Aralia* (tribe Aralieae), belong to the tribe Plerandreae of Tseng and Hoo (1982). *Hedera* is distinct from the Clarno wood because of its very large rays. According to Metcalfe and Chalk (1950) and Oskolski (1996), of the aforementioned genera *Aralia* and *Pseudopanax* have sheath cells and alternate intervessel pitting as does the fossil described here. Shrub species of *Acanthopanax* have a similar vessel arrangement, have occasional sheath cells, but have larger rays and scalariform plates are not common (Shuichi Noshiro, pers. comm. 2000). We observed similarity between the fossil and wood samples of extant *Aralia spinosa* (e.g., PACw 3196, PACw 7221) that have a broad earlywood zone and tend to be semi-ring porous rather than ring porous. Ray structure and vessel-ray pitting are similar to the fossil. *Pseudopanax* differs in having vascular tracheids and some scalariform perforation plates.

Comparisons with other fossil woods — The genus *Aralinium* Platen was diagnosed as having growth rings present, simple and occasionally scalariform perforation plates, large and simple vessel-ray parenchyma pits; broad rays composed of cells of varying sizes, and often containing crystals; axial parenchyma absent to rare; fibers with simple pits (Platen 1908, p. 59, translated from German). Platen considered the combination of large and simple vessel-ray parenchyma pits, mixed simple and scalariform pits, and scarcity of axial parenchyma diagnostic of Araliaceae. A type species was not designated; following the generic diagnosis are diagnoses of *Aralinium excellens, A. parenchymatosum, A. multiradiatum*, *A. lindgreni*, from the "auriferous gravels" of California. Because tangential vessel arrangement or clusters are not a diagnostic feature of *Aralinium*, and none of the Clarno woods have crystals, they are not referable to *Aralinium*. Species of *Aralinium* need to be reexamined to confirm that they are Araliaceae because the characteristics of *Aralinium* occur in Flacourtiaceae and Euphorbiaceae as well as Araliaceae.

Plerandreoxylon nutbedensis sp. nov. (Fig. 10)

Growth rings present, marked by radially flattened latewood fibers, and differences in vessel diameter between latewood and earlywood in subsequent rings.

Semi-ring porous to diffuse porous. Vessels solitary and in radial multiples, latewood vessels in oblique to tangential arrangement; average tangential diameter of earlywood vessels 60 (10) µm, range 36–74 µm; perforations simple in steeply inclined end walls and occasionally scalariform with fewer than 10 bars; intervessel pits alternate to sca-

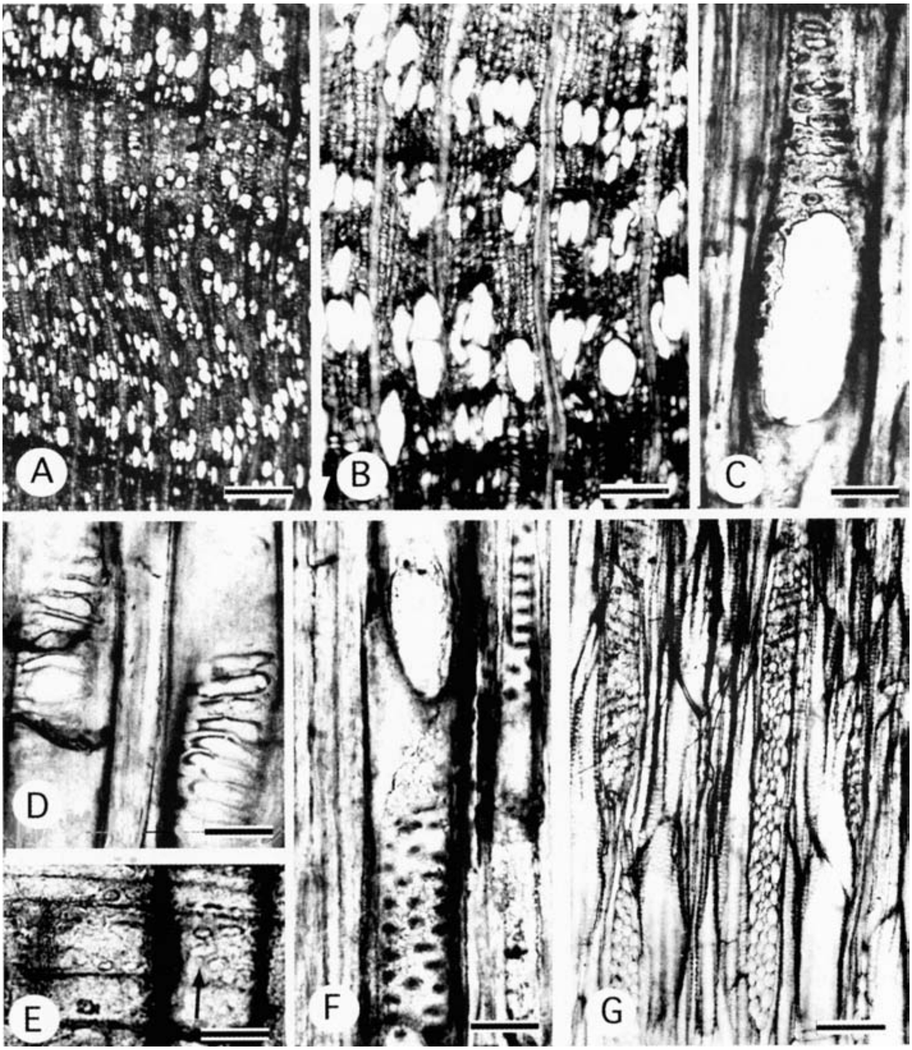

Fig. 10. *Plerandreoxylon nutbedensis* sp. nov. (USNM 507843). – A: Semi-ring porous wood with latewood vessels in diagonal to tangential arrangement, XS. – B: Latewood vessels in tangential arrangement, XS. – C: Simple perforation and scalariform intervessel pits in vessel element tip, TLS. – D: Scalariform perforation plates, TLS. – E: Vessel-ray parenchyma pits horizontally elongate and with reduced borders (arrow), RLS. – F: Simple perforation plate and alternate intervessel pits rounded to oval in outline, TLS. – G: Multiseriate rays with tendency to sheath cells, and simple perforations, TLS. — Scale bars = 250 µm in A; 100 µm in B, G; 25 µm in C, D, E, F.

lariform (usually at end of the vessel elements), alternate pits 6–10 µm; vessel-ray parenchyma pits with reduced borders and horizontally elongate; helical thickenings not observed; vessel element length 441–633 µm; thin-walled tyloses present.

Fibers all septate, walls medium to thick, pitting not observed.

Axial parenchyma rare.

Rays 1–4-seriate. Multiseriate rays heterocellular, body composed of procumbent cells, usually with 1, but up to 3, marginal rows of square and upright cells; sheath cells occasional; uniseriate rays appear to be composed only of upright/square cells; total multiseriate ray height averages 507 (231) µm, range 165–933 µm; 4–7/mm.

Crystals not observed.

Storied structure and canals absent.

Holotype: USNM 507843 (DEN 78, ca. 3.5 cm).
Etymology: Species name for locality, the Nut Beds.

Similarities to extant woods — Only species of Araliaceae have the combination of semi-ring porosity, simple and scalariform perforation plates, tangential arrangement of vessels, mostly alternate intervessel pits with some opposite-scalariform pits, septate fibers, heterocellular rays, and scanty–rare axial parenchyma, a combination that also is consistent with the Plerandreae tribe. Data in Oskolski's (1996) generic table indicate none of the extant ring-porous to semi-ring porous genera have the combination of simple and scalariform perforation plates, sheath cells, and mostly alternate pitting that is rounded in outline. The steeply inclined simple perforation plates (Fig. 10C, F) are typical of East Asian Araliaceae (Shuichi Noshiro, pers. comm. 2000).

Comparisons with other fossil woods — This wood differs from the preceding wood because it has scalariform perforation plates and septate fibers are more common.

BETULACEAE

Betulaceae are represented by two fruit types: *Coryloides hancockii* with similarities to but not equivalencies with the extant genus *Corylus* and *Kardiasperma parvum* which is similar to locule casts of the Paleocene *Palaeocarpinus*, an extinct genus of the Coryleae. *Betula clarnoensis* was described by Scott and Wheeler (1982), and detailed comparisons of the Clarno *Betula* to extant and fossil *Betula* woods are in that paper.

BETULA L.

Betula clarnoensis Scott & Wheeler (Fig. 11A–F)

Growth rings present, marked by radially flattened latewood fibers.

Diffuse porous. Vessels solitary and in radial multiples of 2–8, mostly 2–5, occasional clusters in the latewood; average tangential diameter of 93 (15) µm, range 59–120 µm; vessel frequency 30–37–44/mm^2 perforations exclusively scalariform, 10–25 bars; intervessel pits alternate, 2–4 µm across; vessel-ray parenchyma pits similar to intervessel pits; helical thickenings not observed; mean vessel element length 832 (115) µm, range 667–1012 µm.

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

Axial parenchyma apotracheal diffuse, diffuse-in-aggregates, and marginal.

Rays 1–3-seriate. Multiseriate rays predominantly homocellular, composed of procumbent cells, occasionally with 1–2 marginal rows of square to upright cells; total multiseriate ray height 160–500 µm; 10–16/mm.

Crystals not observed.

Storied structure absent.

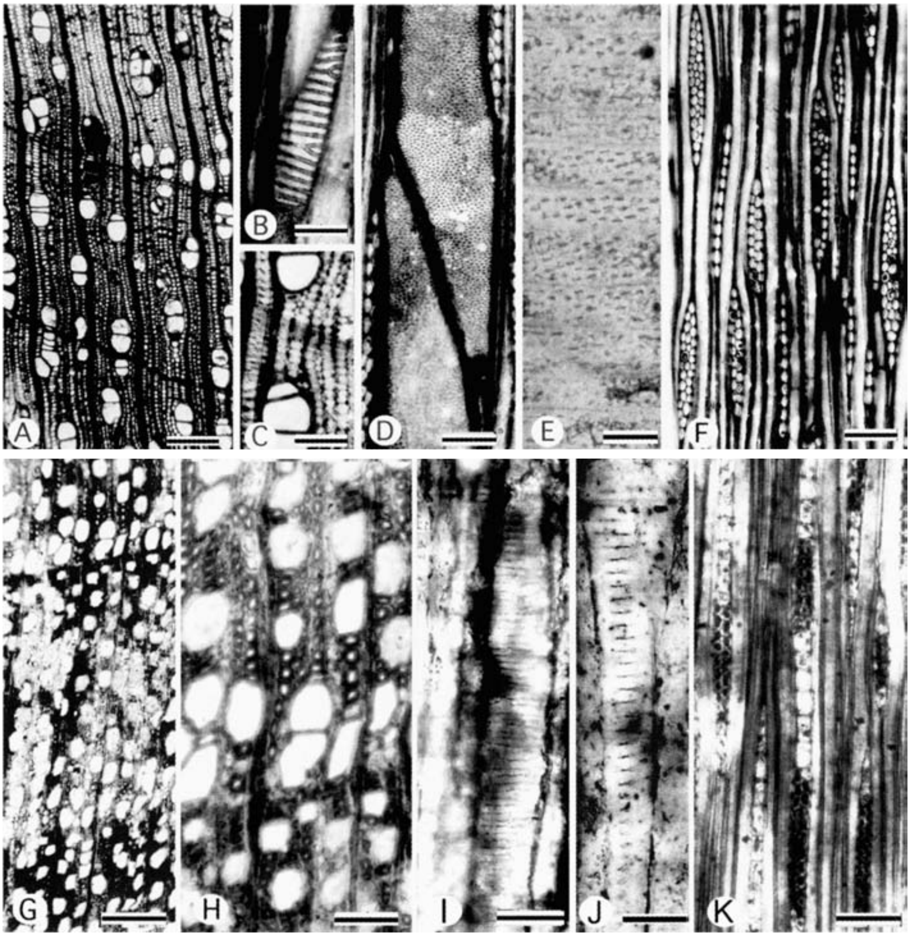

Fig. 11. A–F: *Betula clarnoensis* Scott & Wheeler (USNM 326700). – A: Diffuse porous wood, with vessels solitary and in short radial multiples, diffuse apotracheal parenchyma, XS. – B: Scalariform perforation plate, RLS. – C: Detail of growth ring boundary, marked by radially flattened fibers, XS. – D: Alternate intervessel pitting, TLS. – E: Vessel-ray parenchyma pits similar to intervessel pits, RLS. – F: Multiseriate homocellular rays, 1–3-seriate, TLS. — G–K: *Cercidiphyllum alalongum* Scott & Wheeler (USNM 507870). – G: Portions of three growth rings, wood diffuse porous with vessels predominantly solitary, XS. – H: Detail of growth ring boundary, solitary vessels tending to be angular in outline, XS. – I: Scalariform perforation plates with many fine bars, RLS. – J: Scalariform intervessel pitting, TLS. – K: Rays 1–2-seriate, alternating between uniseriate and biseriate, TLS. — Scale bars = 250 µm in A, G; 100 µm in B, C, F, H, K; 50 µm in D, I; 25 µm in E, J.

Holotype: USNM 326700 (C4A-63).

Similarities to extant woods — The combination of vessels solitary and in radial multiples, exclusively scalariform perforation plates, minute alternate intervessel pitting, diffuse axial parenchyma, and homocellular rays occurs only in *Betula*. The quantitative features of the Clarno wood, and of other fossil *Betula* woods, are similar to those found in subsection *Costatae* (section *Eubetula*) (see discussion in Scott & Wheeler 1982). The Clarno wood is the oldest known example of wood with structure comparable to *Betula*.

CERCIDIPHYLLACEAE

Cercidiphyllum fruits are not known from the Nut Beds. Fruits and seeds of *Cercidiphyllum* are not recognized until the lower Oligocene, with occurrences in both Europe and North America. However, the family is common in the Cretaceous and early Tertiary of North America, Europe, Asia, and Greenland; leaves have been assigned to the fossil genus *Trochodendroides* Berry, fruits to the fossil genus *Nyssidium*. Based on material from a Paleocene locality in Alberta, Canada, the fruits and leaves, together with seedlings and seeds were placed together in the genus *Joffraea* (review of occurrences in Manchester 1999).

CERCIDIPHYLLUM Siebold & Zucc.

Cercidiphyllum alalongum Scott & Wheeler (11G–K)

Growth rings distinct, marked by radially flattened latewood fibers.

Diffuse porous. Vessel predominantly solitary; tending to be angular in outline; average tangential diameter 59 (8) µm; average vessel frequency 92, range 72–118/mm^2; exclusively scalariform perforations, with more than 20 bars (22–45 bars counted); vessel elements at least 1 mm long; scalariform intervessel pits; vessel-ray parenchyma pits not observed; helical thickenings not observed; tyloses not observed.

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

Axial parenchyma absent–rare.

Rays 1–2(–3)-seriate, with alternating uniseriate and biseriate sections, occasionally the uniseriate and biseriate portions of similar width; heterocellular; average height 427 (108) µm, range 267–613 µm; 11–12/mm.

Solitary prismatic crystals in upright and square ray cells, occasionally in chambered upright ray cells.

Storied structure absent.

Holotype: USNM 326701 (Os 26).
Additional material: USNM 507870 (DEN 101, ≥ 10 cm).

Similarities to extant woods — Cercidiphyllaceae and Hamamelidaceae (particularly *Corylopsis*) have woods with the combination of diffuse porous wood, narrow, numerous vessels that are mostly solitary, scalariform perforation plates, scalariform intervessel pits, 1–2-seriate rays in which the uniseriate and biseriate portions are at times of similar width, rare axial parenchyma, and crystals in ray parenchyma. The type specimen of *Cercidiphyllum alalongum* (USNM 326701) has pith cells that are equidimensional indicating that this wood has affinities with Cercidiphyllaceae, rather than with Hamamelidaceae, which has vertically elongate pith cells (Scott & Wheeler 1982). The type of this species is from the younger Post, Oregon, Osmunda locality (USNM 326701, Os 26).

There are no marked differences between this Clarno wood and wood of extant *Cercidiphyllum*, although fruits and leaves directly comparable to *Cercidiphyllum* do not appear until a later epoch, the Oligocene.

FAGACEAE

The fruits of *Quercus* and *Castanopsis* that occur at the Nut Beds are the oldest known (Manchester 1994). Two fagaceous wood types occur: one is a stereotypic genus with characteristics of evergreen species of *Quercus* and *Lithocarpus*, the other an extinct genus, *Fagaceoxylon*.

FAGACEOXYLON Scott & Wheeler

Fagaceoxylon ostryopsoides Scott & Wheeler (Fig. 12A–D)

Growth rings present, distinct, marked by radially flattened fibers, marginal parenchyma, and noding of aggregate rays.

Diffuse porous. Vessels predominantly in radial multiples and clusters; arranged in a dendritic (flamelike) pattern, solitary vessels not common; average tangential diameters 75 (19)–84 (22) µm; mean vessel frequencies 38–53/mm^2; perforation plates predominantly simple, with one scalariform plate with 4 bars observed; intervessel pitting alternate to opposite, 5–10 µm; pits to ray parenchyma with reduced borders, horizontally and vertically elongated, and irregular in shape; vessel element lengths 300–760 µm, average 575 µm (n = 14); tyloses occasional.

Imperforate tracheary elements vasicentric tracheids, and non-septate fibers without obvious pits.

Axial parenchyma apotracheal diffuse, diffuse-in-aggregates, and marginal; strands of 4–8 cells.

Rays 1–2-seriate, aggregate rays occasional, composed of 10 or more rays across; biseriate rays homocellular and heterocellular with 1–4 marginal rows of square and upright cells; uniseriate portions of biseriate rays usually narrower, but sometimes as wide as the biseriate portions; average biseriate ray height 389 (143) µm; 10–13/mm.

Solitary rhomboidal crystals common in procumbent ray cells.

Holotype: USNM 326702 (C4a-4a).
Other samples: USNM 507876 (DEN 103, ca. 5 cm), USNM 507877 (DEN 50, > 50 cm).

Comments — *Fagaceoxylon* was the host plant for the fungal fruiting bodies described as *Cryptocolax* (Scott 1956). *Fagaceoxylon ostryopsoides* also occurs in the late Eocene assemblages from near Post, Oregon (pers. observ.).

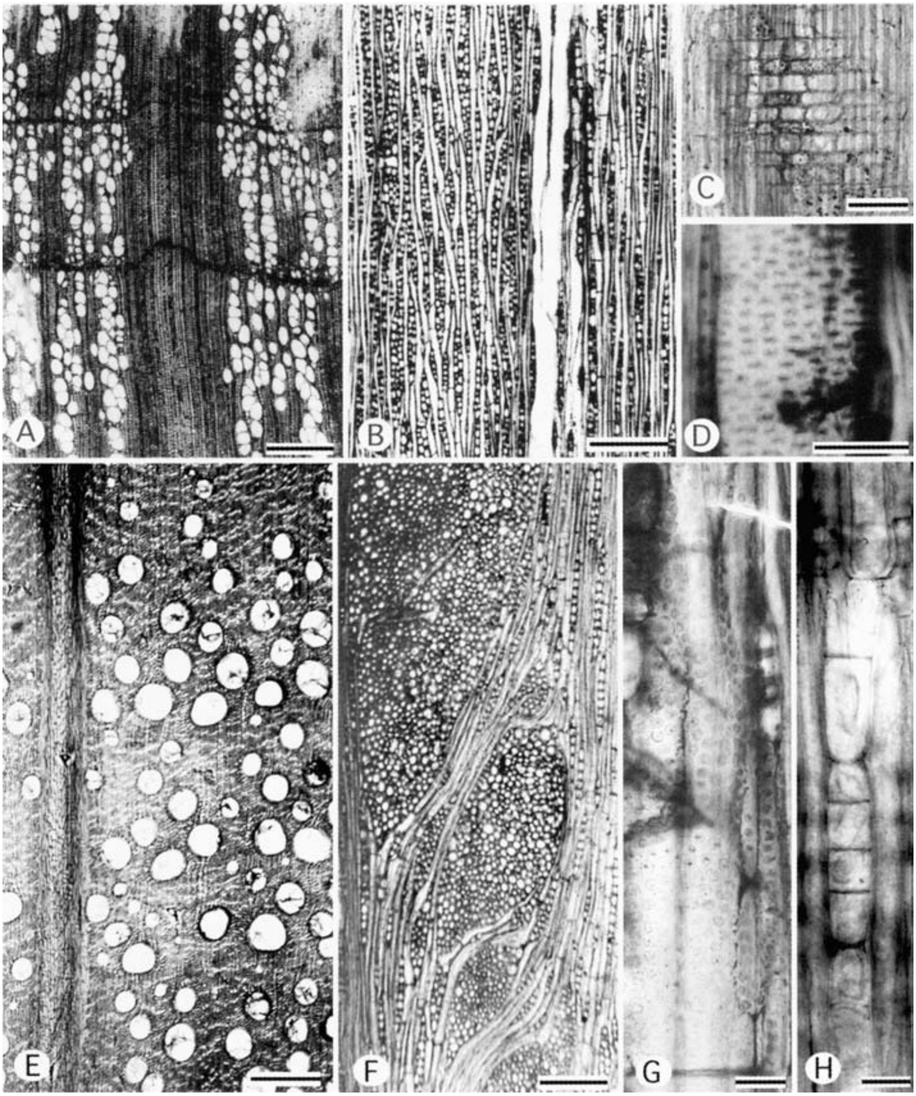

Fig. 12. A–D: *Fagaceoxylon ostryopsoides* Scott & Wheeler (USNM 326702). – A: Vessels both solitary and in radial multiples and clusters arranged in flame-like tracts, both narrow and aggregate rays, XS. – B: Uni- and biseriate rays, vessels with oblique endwalls, axial parenchyma, TLS. – C: Crystals in procumbent ray cells, RLS. – D: Opposite intervessel pits, TLS. — E–H: *Quercinium crystallifera* Scott & Wheeler (UF 12015). – E: Wood semi-ring porous, vessels exclusively solitary, XS. – F: Rays of two distinct sizes, uniseriate and large multiseriate rays, TLS. – G: Vasicentric tracheids, RLS. – H: Crystalliferous parenchyma strand, RLS. — Scale bars = 500 μm in A, E; 200 μm in B, F; 100 μm in C; 50 in D, G, H.

Similarities to extant woods — The combination of aggregate rays, opposite to alternate intervessel pits, and mostly simple vessel perforations are characteristic of the fagalean families Betulaceae and Fagaceae (Scott & Wheeler 1982). Although they noted that this fossil wood resembles the extant betulaceous genus *Ostryopsis* in cross-sectional appearance, Scott and Wheeler (1982) concluded that the affinities lie instead with the Fagaceae based on the presence of vasicentric tracheids and variable ray-vessel pits with reduced borders. The conspicuous flame-like distribution of pores, along with diffuse porosity, is also observed in some extant species of *Castanopsis, Lithocarpus*, and *Quercus*, but in the extant fagaceous species so far observed the vessels tend to be solitary rather than grouped or clustered as in this fossil. Accordingly, Scott and Wheeler established the extinct genus *Fagaceoxylon*.

Co-occurring fruits from the Nut Beds that could be considered candidates for corresponding with *Fagaceoxylon* include *Castanopsis* and the coryleoid betulaceous taxa *Coryloides hancocki* and *Kardiasperma parvum*. Although the extant species of *Castanopsis* for which wood anatomical data are available differ from *Fagaceoxylon* in the presence of mostly solitary vessels, the wood anatomy of the extant Vietnamese species *Castanopsis piriformis*, which has fruits most similar to the Nut Beds fruit *C. crepetii*, has not yet been examined. Its wood anatomy might possibly be found to match the wood of *Fagaceoxylon*. Fruit characters of both *Coryloides* and *Kardiasperma* indicate their affinities with the betulaceous subfamily Coryleae, and, in view of the above-mentioned similarities with wood of the extant coryleoid genus *Ostryopsis*, it is also possible that either of these fruit taxa might have been produced by the same plant as *Fagaceoxylon*.

QUERCINIUM Unger emend. Brett

Quercinium crystallifera Scott & Wheeler (Fig. 12E–H)

Growth rings present, distinct to indistinct.

Wood appearing diffuse porous in narrow rings, semi-ring porous in wider rings. Vessels solitary, circular to slightly oval in outline; mean tangential diameters 144 (43)–217 (37) µm; perforation plates simple, scalariform plates very rare, one observed, with 4 bars; vessel-vasicentric pits alternate circular in outline, 5–8 µm; vessel-ray parenchyma pits with reduced borders, horizontally to vertically elongate, variable; vessel element length 397 (112) µm; tyloses rare.

Imperforate elements vasicentric tracheids, and non-septate fibers without obvious pits.

Axial parenchyma apotracheal, relatively abundant, diffuse, diffuse-in-aggregates, and in uniseriate bands; strands of 8 cells or more.

Rays uniseriate and aggregate; uniseriate rays numerous > 15/mm; uniseriate ray height usually 6–30 cells high.

Crystalliferous chambered axial parenchyma strands.

Additional material: C4A-54, USNM 507982 (C4A-85, > 10 cm), USNM 507983 (C4A-90, > 16 cm), USNM 507984 (C4A-131, > 5 cm, branch?), UF 12015 (> 20 cm).

Comments — Although previously thought to have exclusively simple perforations, scalariform perforations with at least 8 bars were observed in these additional samples. Both scalariform and simple perforations are also present in a sample of this species from the "Osmundites locality" (Post, Oregon).

Similarities to extant woods — The solitary vessels, simple (to rarely scalariform) perforation plates, vasicentric tracheids, abundant apotracheal parenchyma, and uniseriate and aggregate rays indicate affinities with Fagaceae, especially with evergreen species of *Quercus* and *Lithocarpus*. Distinguishing the woods of these two genera is difficult. It is likely that *Quercinium crystallifera* is wood from the plant that pro duced the acorn *Quercus paleocarpa*. Characteristics of that acorn today occur in the strictly Asian subgenus *Cyclobalanopsis*, as well as in *Lithocarpus*.

Comparisons with other fossil woods — This wood has structure similar to that of *Quercinium haydenii*, which occurs in the early Eocene Yellowstone Fossil Forests (Wheeler et al. 1977). Crystals are more abundant in the Nut Beds woods.

HAMAMELIDACEAE

Hamamelidaceae are represented in the Nut Beds by *Fortunearites endressii* Manchester (1994), a genus with morphology similar to that found in subfamily Hamamelioideae, particularly the extant genera *Fortunearia* and *Sinowilsonia*. Two staminate inflorescences with characteristics of the Hamamelioideae have also been recovered, and, while similar in some respects to *Fortunearia* and *Sinowilsonia*, are not identical to either extant genus. Pollen from the stamens of *Fortunearites endressii* is more similar to *Hamamelis* and *Corylopsis* than to *Fortunearia*. The wood described below is similar to *Hamamelis*.

HAMAMELIDOXYLON Lignier

Hamamelidoxylon uniseriatum sp. nov. (Fig. 13)

Growth rings distinct, marked by radially flattened latewood fibers.

Diffuse porous. Vessels predominantly solitary, with an occasional radial or oblique pair; average tangential diameter 58 (13) µm, range 39–95 µm; average vessel frequency 106/mm^2; range 72–133/mm^2, scalariform perforations, mostly 24 to up to 30–40 thin bars; intervessel pits opposite to scalariform; vessel-ray parenchyma pits horizontally elongated, likely with reduced borders; helical thickenings not observed; tyloses few and widely spaced.

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

Axial parenchyma diffuse, 8–12 cells per strand.

Rays uniseriate, rarely biseriate. Heterocellular, with body of procumbent cells, and mostly square marginal cells, sometimes square cells intermixed with procumbent cells; average ray height 248 (79) µm, range 96–424 µm; 12–14/mm.

Crystals not observed.

Storied structure absent.

Holotype: UF 12381 (≥ 10 cm).
Etymology: Species name for the predominantly uniseriate rays.

Comments — Vessel element lengths could not be measured with confidence, likely the elements are long.

Similarities to extant woods — Theaceae and Hamamelidaceae have extant genera with the combination of diffuse porosity, vessels mostly solitary, more than 40 vessels/mm^2, scalariform perforations, non-septate fibers, exclusively uniseriate rays that are more than 12/mm, and diffuse axial parenchyma.

Schima (Theaceae) has exclusively uniseriate rays. Axial parenchyma, often with somewhat inflated crystalliferous cells, is common in the *Schima* species examined (*S. wallichii, S. notonhae*), as are markedly heterocellular rays (Deng Liang & Baas 1991). Because inflated crystalliferous cells are absent and the rays are composed mostly of procumbent cells this fossil wood is more likely related to the Hamamelidaceae than to the Theaceae.

Slides of extant Hamamelidaceae prepared for a study of the wood anatomy of the family (Lee & Baas 1998) were examined. *Fortunearia* has wider rays (up to 4-seriate), *Corylopsis* typically has biseriate rays. *Hamamelis* has exclusively uniseriate rays, e.g., *H. japonica* (TI-4852, Ox 1045, TWTw 2884), *H. mollis* (SJRw 32366), *H. vernalis* (MADw 18320), and *H. virginiana* (PACw 6078, 7167, 7215). The number of bars per perforation plate is higher and the bars are finer and more closely spaced in the fossil than in extant *Hamamelis*, which usually has fewer than 15 bars per perforation plate. Ray structure is similar to *H. virginiana*, which has more procumbent

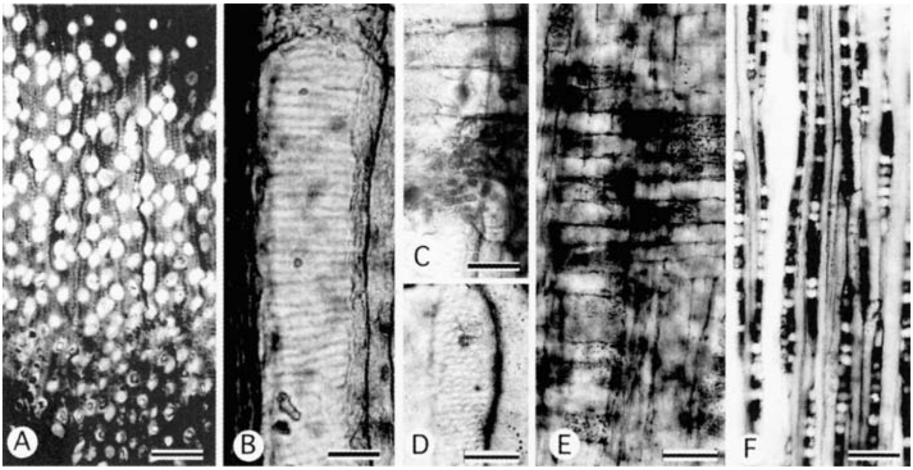

Fig. 13. *Hamamelidoxylon uniseriatum* sp. nov. (UF 12381). – A: Mostly solitary vessels, rare radial multiples, XS. – B: Scalariform perforation plate with more than 20 bars, RLS. – C: Vessel-ray parenchyma pits, RLS. – D: Opposite intervessel pits, TLS. – E: Ray composed mainly of procumbent cells, RLS. – F: Uniseriate rays, TLS. — Scale bars = 250 µm in A; 100 µm in F; 50 µm in D, E; 25 µm in B, C.

cells and fewer heterocellular rays than the other species. Although the fossil and *Hamamelis* have predominantly solitary vessels, both have occasional radial multiples. It was not possible to measure vessel element lengths in the fossil because of its relatively poor preservation, but it is likely that vessel elements are more than 1 mm long.

Comparisons with other fossil woods — Woods with similarities to *Hamamelis* have been assigned to *Hamamelidoxylon* Lignier (1907). Important diagnostic features of *Hamamelidoxylon* include: solitary vessels, scalariform perforation plates, apotracheal diffuse parenchyma, scalariform vessel-ray parenchyma pits, and exclusively uniseriate (very rarely biseriate) rays. Later authors have described species with multiseriate rays, e.g., the European Miocene *Hamamelidoxylon castellanse* Grambast-Fessard (1969) and *H. rhenamum* van der Burgh (1973), and the Eocene *H. daphniphylloides* (Gottwald 1992). The Eocene European *H. daphniphylloides* also has more bars per perforation (30–50) than the extant species and other *Hamamelidoxylon* species. *Hamamelidoxylon magdefrauii* (Greguss) van der Burgh (1973) is the most similar to the Clarno wood as both have mostly uniseriate rays, and up to 40 bars per perforation plate.

JUGLANDACEAE

Two types of juglandaceous wood have been recognized from the Clarno Nut Beds: *Engelhardioxylon* (Manchester 1983) and *Clarnoxylon* (Manchester & Wheeler 1993). Juglandaceous fruits from the same locality include both extant and extinct genera. They are *Cruciptera*, *Juglans*, cf. *Palaeocarya* and *Paleoplatycarya?*. In addition, the extinct playtcaryoid genus *Hooleya* occurs at other localities in the Clarno Formation.

CLARNOXYLON Manchester & Wheeler

Clarnoxylon blanchardii Manchester & Wheeler (Fig. 14A–C)

Growth rings present, distinct.

Diffuse porous to semi-ring porous. Vessels solitary and in radial multiples of 2–3 (up to 8 in last-formed latewood); tending to a diagonal arrangement; solitary vessels oval in outline, average tangential diameter 92 (20)–113 (13) µm; perforations simple; intervessel pits crowded alternate, 5–7 µm; vessel-ray parenchyma pits similar in size and shape to intervessel pits; helical thickenings not observed; average vessel element lengths 306 (78)–632 (109) µm; tyloses not observed.

Fibers non-septate, walls medium to thick, distinctly bordered pits not observed.

Axial parenchyma scanty paratracheal to vasicentric, and in apotracheal wavy tangential bands 1–3 cells wide, in both earlywood and latewood, less tangentially continuous and more widely spaced in the earlywood, spacing between bands 175–320 µm; 4–8 cells per strand.

Rays 1–3-seriate. Multiseriate rays heterocellular, body of procumbent cells, with up to 8 marginal rows of upright/square cells; total multiseriate ray height averages 293 (38)–320 (65) µm; 10–12/mm.

Prismatic crystals common in enlarged upright and procumbent ray cells.
Storied structure absent.
Pith solid.

Holotype: UF 12150, including numerous pieces from a log ca. 20 cm in diameter.
Additional samples: UF 12045, UF 12486.

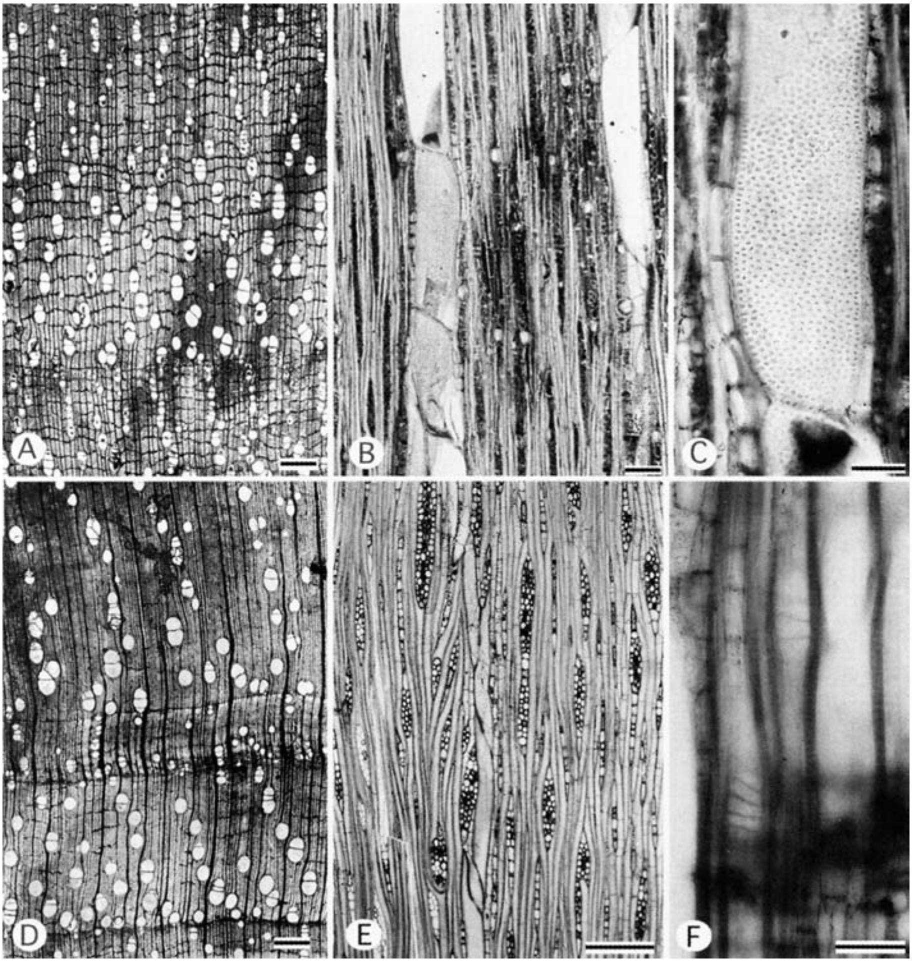

Fig. 14. A–C: *Clarnoxylon blanchardii* Manchester & Wheeler (UF 12486). – A: Wood diffuse porous to slightly semi-ring porous, vessels solitary and in radial multiples and tending to diagonal arrangement, dark wavy tangential lines of parenchyma, weak growth ring boundary, XS. – B: Narrow rays with idioblasts, TLS. – C: Alternate intervessel pitting, TLS. — D–F: *Engelhardioxylon nutbedensis* Manchester (USNM 507885). – D: Diffuse porous wood with vessels solitary and in radial multiples, tendency to diagonal arrangement, wavy tangential lines of parenchyma, growth rings, XS. – E: Narrow heterocellular rays, TLS. – F: Scalariform and simple perforations, RLS. — Scale bars = 500 µm in A, D; 250 µm in B, E; 200 µm in F; 100 µm in C.

Similarities to extant woods — *Clarnoxylon* has a suite of characters that led Manchester and Wheeler (1993) to infer juglandaceous affinity: diagonal vessel arrangement, vessels solitary and in short radial multiples, axial parenchyma both vasicentric and in narrow apotracheal bands, semi-ring porosity, medium-sized alternate pitting, vessel-ray parenchyma pits generally similar in size and shape to intervessel pits, and narrow heterocellular rays. They considered *Clarnoxylon* an extinct genus because the only extant Juglandaceae that has crystal-bearing idioblasts is *Platycarya*; and that genus has well-defined ring porosity, latewood vessels and vasicentric tracheids in a diagonal to dendritic pattern, and helical thickenings in its narrow vessel elements and tracheids. These characteristics are ones that today are associated with markedly seasonal climates, which the Nut Beds flora would not have experienced.

Clarnoxylon has a solid pith, not a chambered pith as occurs in *Juglans, Pterocarya,* and *Cyclocarya*. As an extinct kind of juglandaceous wood, it is of interest to deduce the kind of fruit it would be associated with. Generic distinctions among the extant Juglandaceae are based mainly on fruits. In addition to nuts resembling extant *Juglans*, the Nut Beds flora includes fruits of three other genera (at least two of which are extinct): *Cruciptera* (tribe Juglandeae), *Palaeocarya* (tribe Engelhardieae), and *Paleoplatycarya?* (tribe Platycaryeae). *Cruciptera* would be expected to have septate pith in conformity with other members of Juglandeae. Likewise, *Palaeocarya* would be expected to possess some scalariform perforations and lack idioblasts in the rays. *Paleoplatycarya* seems the most likely candidate for the type of fruit produced by *Clarnoxylon* wood, because the surviving modern genus (*Platycarya*) also has solid pith, no scalariform perforations and idioblasts in the rays.

Comparisons with other fossil woods — *Clarnoxylon* is similar to *Engelhardioxylon macrocrystallosum* Gottwald (1992) from the upper Eocene of Helmstedt, Germany, including having a solid pith and similar arrangement of parenchyma and vessels as seen in transverse section. However, Gottwald reported that in addition to predominantly simple perforation plates, there were occasional scalariform perforations. We found only simple perforations in *Clarnoxylon*.

ENGELHARDIOXYLON Manchester

Engelhardioxylon nutbedensis Manchester (Fig. 14D–F)

Growth rings present, marked by radially flattened fibers.

Semi-ring porous to diffuse porous. Vessels solitary and in radial multiples of 2–4; average tangential diameter 151 µm, range 44–242 µm; vessel frequency 11–43/mm^2; perforations mostly simple, but with occasional scalariform plates of up to 3 bars in narrower elements; intervessel pits alternate, ca. 7 µm; vessel element lengths average 411 (57)–602 (161) µm; thin-walled tyloses present.

Fibers non-septate, thin–thick-walled.

Axial parenchyma in wavy tangential lines one to two cells wide, strands usually of 8 cells.

Rays 1–4-seriate. Multiseriate rays heterocellular with uniseriate rows of up to 7 cells; total multiseriate ray height averages 471 (131)–453 (182) µm, range 230–950 µm; 5–8/mm.

Rhomboidal crystals in idioblasts or square and upright cells of rays.

Storied structure absent.

Samples: UF 32345 (DEN 90, > 10 cm), USNM 507885 (DEN 46, ca. 6 cm).

Comments — Vessel element lengths were measured from tangential sections, and a tangential section only represents one part of the growth ring. Vessel element lengths usually are shorter in earlywood than in latewood. Thus, vessel element lengths measured from different tangential sections of different samples may vary, especially in semi-ring porous woods, as is this wood.

Similarities to extant woods — *Engelhardioxylon* has the same suite of juglandaceous characters mentioned in the discussion of *Clarnoxylon*, above, but lacks idioblasts in the rays and has occasional scalariform vessel perforations. The only extant juglandaceous genera known to have scalariform as well as simple perforations are *Engelhardia*, *Oreomunnea* and *Alfaroa* – all of the tribe Engelhardieae. The only fruits of Engelhardieae known from the Nut Beds assemblage are closest to *Engelhardia* (*Palaeocarya clarnensis*; Manchester 1987, 1994). We find it interesting that we were unable to identify wood identical to extant *Juglans*, although *Juglans* fruits are abundant at the Nut Beds. It is possible that early woods of *Juglans* might have retained scalariform perforations, and would therefore be classified as *Engelhardioxylon*.

Comparisons with other fossil woods — In addition to the generic features mentioned above, *Engelhardioxylon nutbedensis* is distinguished from *Clarnoxylon blanchardii* by less thoroughly distributed axial parenchyma lines. It also resembles *Pterocaryoxylon*, but that genus lacks scalariform perforations.

LAURACEAE

Lauraceae are represented in the Nut Beds flora by five fruit types; one assigned to the extant genus *Lindera*, one to the stereotypic genus *Laurocalyx* and three to the stereotypic genus *Laurocarpum*. One species of Lauraceae wood has been previously described from Clarno: *Ulminium scalariforme* (Scott & Wheeler 1982). Lauraceae woods are common at Clarno, at least seven types, and easy to recognize because of the combination of vessels solitary and in radial multiples, simple perforation plates, which sometimes co-occur with scalariform perforation plates, alternate intervessel pits, vessel-ray parenchyma pits with reduced borders, predominantly paratracheal parenchyma and idioblasts (“oil cells”). Table 6 compares the salient features of the Clarno lauraceous woods.

Reports of fossil Lauraceae woods are relatively common (e.g. Süss 1958; Gottwald 1992; Brea 1995; Yang Jianmin et al. 1995; Poole et al. 2000). They are known from the Cretaceous and Tertiary of the northern (Europe, North America, Asia) and southern hemispheres (Antarctica, Australia, South America). The number of Lauraceae

Table 6. Comparison of Lauraceae woods from the Clarno Nut Beds.

Species	RM	MTD	V/MM2	PP	IVP	VRP	MVEL	SEP	AP	RW	MRH	IDIO	R/MM
Paraperseoxylon scalariforme	2–3	70–87	14	SI, SC	5	a	280	–	scp	1–2 (3)	340–387	c, R, F	6–7
Cinnamomoxylon oleiferum	2 (3)	98–114	44–48	SI, SC	8–11	b	447	–	scp	1–4 (5)	227–446	o, R	5–9
Cryptocaryoxylon hancockii	2–11	56–67	47–62	SI	3–5	b (a)	345–375	–	vc, alf, con	1–3 (4)	330–382	o, R, F	7–10
Cryptocaryoxylon radiporosum	2–10	101	34	SI	9–12	b	393	–	scp, mg	1–3	302	o, R	5–7
Cryptocaryoxylon meeksii	2 (3)	87–136	7–26	SI	6–10	b	294–381	–	scp, vc	1–2 (3)	214–387	c, R	5–7
Mezilaurinoxylon eiporosum	2–3 (4)	84–125	16–38	SI	> 10	c	494–500	+	scp	1–4 (5)	437–615	o, R	6–7
Ulminium magnioleiferum	2 (3)	89	5–19	SI	6–10	?	200–488	?	vc,, alf, mg	1–4	596	c, R, F	5–8

Legends: RM = number of vessels per radial multiple — MTD = mean tangential diameters in µm — V/MM2 = mean number of vessels per sq.mm — PP = perforation plate type; SI = simple, SC = scalariform — IVP = width of intervessel pits — VRP = type of vessel-ray parenchyma pits, according to Richter (1987) — MVEL = mean vessel element length in µm, numbers in brackets are ranges of vessel element lengths when less than 25 vessel elements could be measured — SEP = septate fibers, + = present, – = absent (not observed) — AP = axial parenchyma distribution, scp = scanty paratracheal, vc = vasicentric, alf = aliform, con = confluent, mg = marginal — RW = ray width — MRH = mean multiseriate ray height — IDIO = idioblasts, o = occasional, c = common, R = in ray, F = isolated amongst fibers — R/MM = rays per mm.

fossil wood types known (> 60) ranks third in abundance behind the Leguminosae (> 200) and Fagaceae (> 90) (information from database for Wheeler & Baas 1991). This abundance of Lauraceae fossil woods may be due not just to original abundance. Lauraceous woods are easy to recognize as such when idioblasts are present, and so are more likely to be described in the literature. Also, heartwood of many lauraceous woods is resistant to decay, so these woods are more likely to enter the fossil record because they have an extended time to be 'captured' by silicification.

The Lauraceae wood types described below differ from one another in features considered taxonomically significant by Richter (1981, 1987):

- presence or absence of scalariform perforation plates,
- intervessel pit size in combination with vessel-ray parenchyma pit appearance,
- presence or absence of septate fibers,

and by the number of vessels per radial multiple, ray size, and presence of and location of oil cells (see Table 6).

Richter (1981, 1987) found three classes of vessel-ray parenchyma pits in the Lauraceae, which correlated with diameter classes of intervessel pits. These correlations existed by the middle Eocene as similar correlations between intervessel pit size and vessel-ray pits occur in the Clarno woods. These are:

- Class a) intervessel pits from 3–7 (8) μm and vessel-ray parenchyma pits of similar size and shape as intervessel pits, sometimes opening into compound pits that are horizontally or vertically enlarged, or are curved (e.g., *Paraperseoxylon scalariforme*);
- Class b) intervessel pits 8–12 μm with vessel-ray pits variable in shape, round to oval, to elongated horizontally, vertically or diagonally (e.g., *Cinnamomoxylon oleiferum, Cryptocaryoxylon radiporosum*);
- Class c) intervessel pits 10–15 μm diameter, vessel-ray pits very large and windowlike (e.g., *Mezilaurinoxylon eiporosum*).

Differences in vessel diameter and density, parenchyma abundance, and oil cell frequency between eight wood specimens of *Cinnamomum camphorum* in the Bailey-Wetmore Laboratory are such that if they were found as isolated samples of fossil wood it is likely they would be assigned to different wood types (Wheeler et al. 1977). Conversely, different extant Lauraceae genera have similar wood anatomy (Richter 1987), and so it is possible that isolated pieces of fossil woods that represent different genera would be assigned to the same fossil wood type. Thus, the correlation between Lauraceae fossil wood types and the number of biological genera and species they represent is difficult to establish (Gottwald 1992).

It is unfortunate, but *Ulminium* Unger 1842 has priority over *Laurinoxylon* Felix 1883 as the name for fossil woods with characteristics of the Lauraceae (see discussions by Page 1967, Romero 1970). Gottwald (1992, 1997) follows a European tradition and uses *Laurinoxylon* for woods with characteristics of Lauraceae, rather than *Ulminium*. Subsequent to Richter's work on woods of extant Lauraceae, Gottwald (1992, 1997) began reevaluating fossil Lauraceae wood, characterizing them according to categories for vessel diameter (< 100 µm, < 150 µm, and > 150 µm), intervessel pit size (< 5 µm, 5–7 µm, > 7 µm), axial parenchyma type (vasicentric, aliform, confluent, and marginal), and vessel-ray parenchyma pit appearance (similar size to intervessel pits, round and large, variable in form and size). Gottwald also established two genera for lauraceous woods that have combinations of characteristics shared by some groups of genera: *Caryodaphnoxylon* Gottwald (1992) and *Cinnamomoxylon* Gottwald (1997). Another genus of lauraceous fossil woods is *Cryptocaryoxylon* Leisman (1986) of probable late Eocene–early Oligocene age from Australia.

It seems sensible to emulate Gottwald and establish additional genera for fossil lauraceous woods. The genera *Laurinoxylon* and *Ulminium* contain a variety of wood types that differ in features that Richter determined useful for distinguishing groups of extant genera. Continuing to assign well-preserved fossil lauraceous wood only to *Ulminium* or *Laurinoxylon* hides the diversity of ancient Lauraceae wood, and confounds attempts to follow changes in diversity through time, as such studies often count genera.

Lauraceae today are comprised of at least 52 genera, and contain distinctive wood anatomical types. Consequently assigning distinctive wood anatomical types to genera other than *Laurinoxylon* or *Ulminium* seems warranted. At the very least, five distinct genera for fossil woods of Lauraceae should be recognized, four corresponding to the four groupings of intervessel pit sizes and vessel-ray parenchyma pit types that Richter recognized, plus *Sassafrasoxylon* Brezinova et Süss 1988, which is distinctive because it is ring porous. Gottwald advocated using *Laurinoxylon* Felix for woods clearly referable to Lauraceae, but in which features critical for determining relationships to extant genera cannot be observed, e.g. vessel-ray parenchyma pits. We are adopting that concept, except for using *Ulminium*, which has priority (ICBN), rather than *Laurinoxylon* for the wood in which we were unable to observe vessel-ray parenchyma pits, or determine whether the septate fibers were present.

CINNAMOMOXYLON Gottwald

Cinnamomoxylon oleiferum sp. nov. (Fig. 15)

Growth rings indistinct (UF 12028) to distinct (UF 12017), marked by radially flattened latewood fibers.

Diffuse porous. Vessels solitary and in radial multiples of 2 (3), average tangential diameters of 98 (20)–114 (17) µm; average vessel frequencies of 44–48/mm^2, range 32–69/mm^2; simple and scalariform (4–8 bars) perforations; intervessel pits crowded alternate with angular outline, 8–11 µm; vessel-ray parenchyma pits enlarged and with reduced borders, generally oval to horizontally elongated (Richter Class b); helical thickenings absent; average vessel element length 447 (77) µm, range 336–616 µm; abundant thin-walled tyloses present.

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

Axial parenchyma scanty paratracheal, strands of 4–9 cells.

Rays 1–4(–5)-seriate. Multiseriate rays heterocellular, body composed of procumbent cells, with one row of square/upright cells; ray cells often with colored contents;

mean total height of multiseriate rays 227 (53)–446 (73) µm, total range of 226–587 µm, 300-460 µm; 5–9/mm.

Oil cells common in margins of rays, in radial section series of 4–5 oil cells found.

Crystals not observed.

Storied structure absent.

Holotype: UF 12017 (≥ 15 cm).

Paratypes: UF 12028 (3 cm fragment), UF 12482 (≥ 17 cm), USNM 507897 (DEN 76, 2 cm fragment).

Etymology: Specific epithet is for the prominent secretory idioblasts.

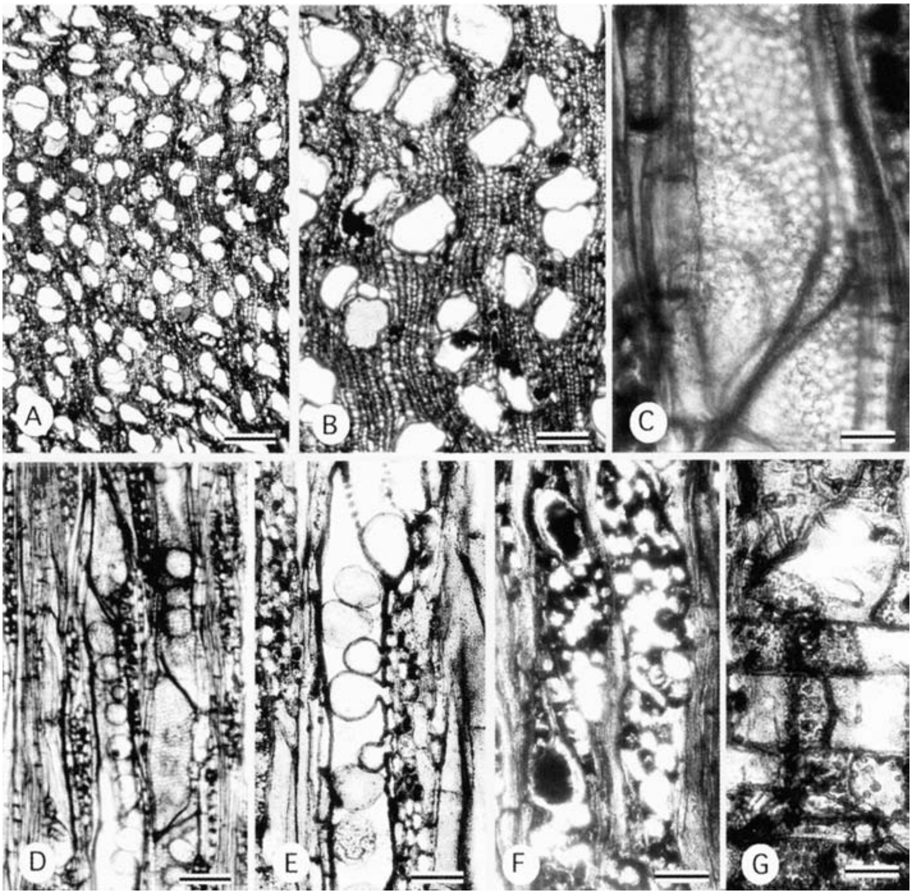

Fig. 15. *Cinnamomoxylon oleiferum* sp. nov. (UF 12017). – A: Vessels solitary and in radial multiples of 2, XS. – B: Scanty paratracheal to narrow vasicentric axial parenchyma, thin-walled fibers, XS. – C: Crowded alternate pitting, TLS. – D: Multiseriate rays, alternate intervessel pitting, tyloses, TLS. – E: Scalariform perforation plates, and tyloses formation, TLS. – F: Multiseriate rays with marginal idioblasts filled with dark contents, TLS. – G: Horizontally enlarged vessel-ray parenchyma pits with reduced borders, RLS. — Scale bars = 250 µm in A, D; 100 µm in B, E; 50 µm in C, F, G.

Similarities to extant woods — Lauraceae genera that include species with both simple and scalariform perforation plates, intervessel pits approximately 8–11 µm, class b vessel-ray parenchyma pits, and only scanty paratracheal parenchyma are *Persea, Phoebe, Dehaasia*, *Cryptocarya,* and *Apollonias* (Richter 1981: Table 11). Extant Asian species of *Cinnamomum* usually have idioblasts associated with axial parenchyma, and infrequently with rays, while South American species have idioblasts almost exclusively associated with the rays (Richter 1987).

Comparisons with other fossil woods — This wood is tentatively assigned to *Cinnamomoxylon* Gottwald with which it shares occurrence of both simple and scalariform perforations, class b vessel-ray parenchyma pits, medium to large alternate pits, non-septate fibers, and similar vessel diameters and ray sizes. This Clarno wood differs from the *Cinnamomoxylon* species Gottwald described and from Asian species of extant *Cinnamomum* because the Clarno wood has idioblasts associated only with the rays, as observed in the South American species of *Cinnamomum*.

The other United States fossil lauraceous wood, *Ulminium eocenicum* (early Eocene, Yellowstone National Park, Wheeler et al. 1977), with both simple and scalariform perforation plates, differs because it has banded parenchyma. *Paraperseoxylon scalariforme* (see below) is distinct because it has relatively small intervessel pits (5 µm).

PARAPERSEOXYLON gen. nov.

Wood diffuse porous. Vessels solitary and in short radial multiples; mean tangential diameter less than 100 µm; perforations simple and scalariform; intervessel pits crowded alternate, approximately 5 µm across; vessel-ray parenchyma pits (Richter class a) with reduced borders, horizontally elongate and curved, and small and rounded. Fibers non-septate, thin- to thick-walled. Axial parenchyma scanty paratracheal to vasicentric to confluent. Rays 1–4-seriate, weakly heterocellular; idioblastic secretory cells (“oil cells”) common in ray margins, and scattered among fibers.

Type species: Paraperseoxylon scalariforme (Scott & Wheeler). — *Ulminium scalariforme* Scott & Wheeler 1982.

Etymology: Generic name indicates that the wood has characteristics that occur in a group of genera that includes the genus *Persea*.

An additional sample of the wood type originally described as *Ulminium scalariforme* (USNM 507899, DEN 63, 4 cm estimated diameter) provides additional information on this wood type; vessel element lengths could not be measured in the type (USNM 326704).

Paraperseoxylon scalariforme (Scott & Wheeler) comb. nov. (Fig. 16)

Growth rings indistinct.

Diffuse porous. Vessels solitary and in radial multiples of 2–3; average tangential diameters of 70 (14)–87 (15) µm; vessel frequency averages 14/mm^2; range of 7–28/mm^2; perforations simple and scalariform with 4–12 bars; intervessel pits crowded

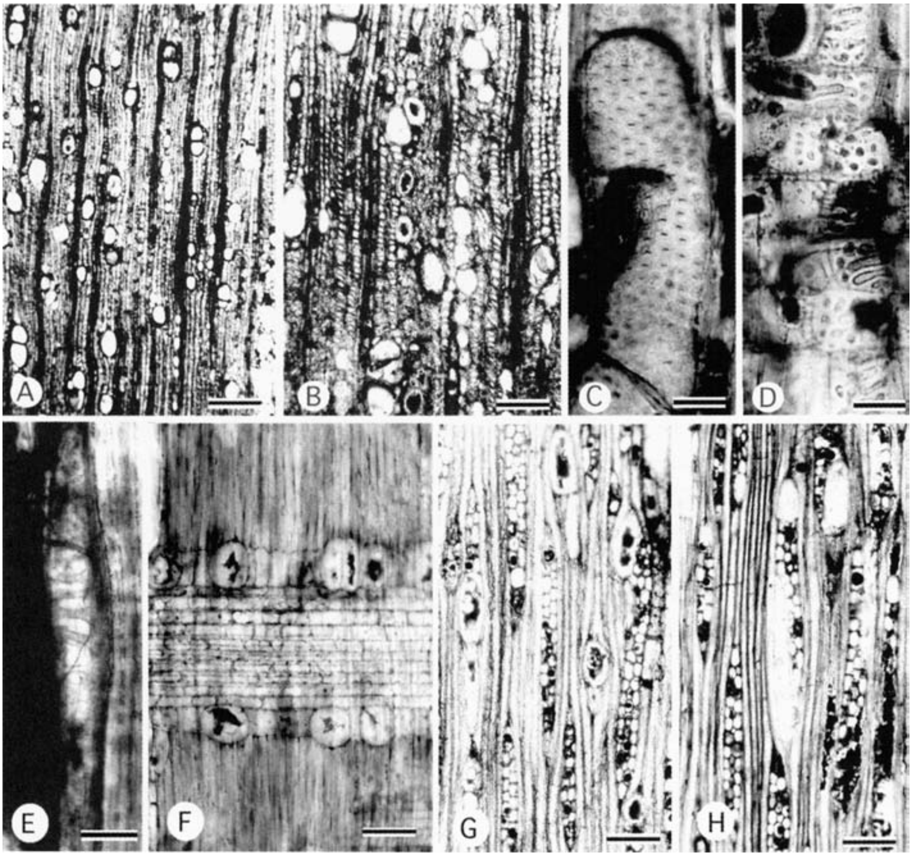

Fig. 16. *Paraperseoxylon scalariforme* (Scott & Wheeler) gen. nov., comb. nov. (USNM 507899). – A: Diffuse porous wood, vessels solitary and in radial multiples, XS. – B: Oil cells visible in cross section, vessels solitary and in short radial multiples, XS. – C: Crowded alternate intervessel pitting, TLS. – D: Vessel-ray parenchyma pits with reduced borders, some horizontally elongate to slightly irregular in shape, RLS. – E: Scalariform perforation plates with thick-walled bars, RLS. – F: Idioblasts in ray margins, RLS. – G: 1–3-seriate rays, idioblasts with dark contents, TLS. – H: Elongate idioblast located to side of the ray, TLS. — Scale bars = 250 µm in A; 100 µm in B, F, G, H; 25 µm in C, D, E.

alternate with angular outline, ~5 µm across; vessel-ray parenchyma pits with reduced borders, elongate horizontally and curved and also small and rounded; helical thickenings absent; vessel element lengths 280 (101) µm; thin-walled tyloses present.

Fibers non-septate, walls thin to thick, pits not observed.

Axial parenchyma scanty paratracheal.

Rays 1–2(–3)-seriate. Multiseriate rays heterocellular, body composed of procumbent cells with a single marginal row of square/upright cells; mean ray heights of 340 (135)–387 (150) µm; 6–7/mm.

Oil cells common in margins of rays and interspersed among the fibers.

Crystals not observed.

Storied structure absent.

Holotype: USNM 326705.

Additional material: USNM 507899 (DEN 63).

Similarities to extant woods — Extant Lauraceae genera that include species with both simple and scalariform perforation plates, intervessel pits approximately 5 μm, class a vessel-ray parenchyma pits, scanty paratracheal parenchyma, and non-septate fibers are *Actinodaphne, Laurus, Lindera* Group A, *Persea* p.p., and *Neolitsea* (Richter 1981: Table 11).

Comparisons with other fossil woods — This wood is distinct from other well-preserved lauraceous fossil woods as its intervessel pits are relatively small, ca. 5 μm. Intervessel pit size is one of the features that both Richter (1981, 1987) and Gottwald (1992, 1997) consider important in delimiting wood groups within the Lauraceae. Consequently, this wood is assigned to a new genus. This wood differs from *Cinnamomoxylon* Gottwald which has intervessel pits 8–12 μm across, significantly larger than this Clarno wood.

CRYPTOCARYOXYLON Leisman

Cryptocaryoxylon hancockii sp. nov. (Fig. 17)

Growth rings indistinct.

Diffuse porous. Vessels solitary (about 10%) and in radial multiples of 2–11 (mostly 2–6); average tangential diameters 56 (8)–67 (11) μm; vessel frequency averages 47–62/mm^2, total range of 29–83/mm^2; perforations simple; intervessel pits alternate, 3–5 μm; vessel-ray parenchyma pits similar to size to intervessel pits in multiple rows and also horizontally elongate, Richter class a; helical thickenings absent; vessel element length averages 345–375 (53) μm, range 279–500 μm; tyloses not observed.

Fibers non-septate, walls medium-thick to thick, no pits observed.

Axial parenchyma vasicentric, aliform to confluent; sometimes also in diffuse strands and in uniseriate terminal bands; strands usually of 4 cells.

Rays 1–4- (mostly 2–3-)seriate. Multiseriate rays heterocellular with 1–9 (mostly 1–4) marginal rows of upright cells; height averages 330 (134)–382 (139) μm, range 130–720 μm; 7–10/mm.

Oil cells occasional at margins of rays and sometimes scattered amongst the fibers.

Storied structure absent.

Holotype: UF 12046.

Additional material: USNM 508007 (C4A-87, > 14 cm diam.), USNM 508008 (C4A-99, > 15 cm), UF 12047, UF 12224 (> 10 cm).

Etymology: This species is named in memory of amateur paleontologist Alonzo W. Hancock, who was among the first to bring the Nut Beds locality and its well-preserved flora to the attention of the scientific community and general public.

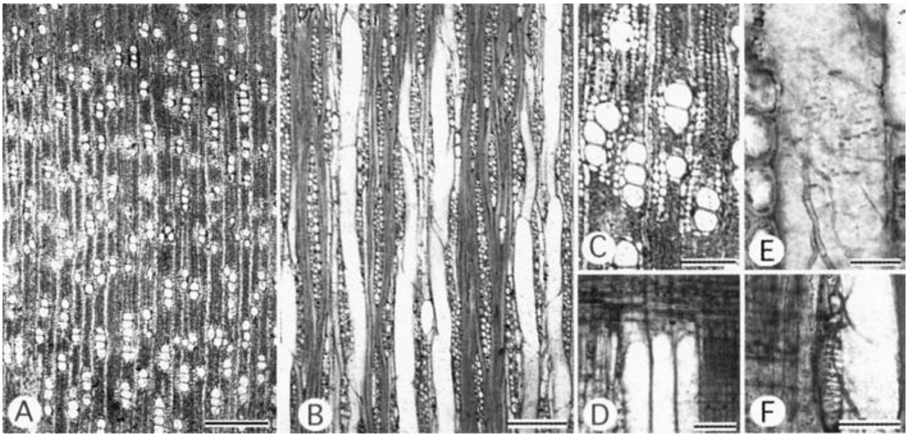

Fig. 17. *Cryptocaryoxylon hancockii* sp. nov. (UF 12046). – A: Diffuse porous wood, growth rings indistinct to absent, vessels commonly in radial multiples, vasicentric to aliform parenchyma-confluent parenchyma, XS. – B: Uni- to triseriate heterocellular rays, enlarged oil cells in axial parenchyma, TLS. – C: Pores solitary and in radial multiples, vasicentric to confluent parenchyma, XS. – D: Simple perforations, RLS. – E: Crowded alternate intervessel pits, TLS. – F: Horizontally elongate vessel-ray parenchyma pits, RLS. — Scale bars = 500 µm in A; 200 µm in B; 150 µm in C, D; 100 µm in F; 50 µm in E.

Similarities to extant woods — This wood corresponds to the Lauraceae in the presence of oil cells in rays and axial parenchyma and occurrence of some enlarged vessel-ray parenchyma pits, simple perforations and paratracheal parenchyma. The common occurrence of vessels in radial chains is unusual for Lauraceae, but does occur (e.g. *Cryptocarya kurzii*).

Comparisons with other fossil woods — Among the lauraceous woods from the Nut Beds, this wood is distinctive by the high proportion of radial multiples of vessels and well-developed aliform to confluent parenchyma. It is tentatively assigned to *Cryptocaryoxylon*. However, in *C. hancockii* vessel-ray parenchyma pits sometimes are similar to intervessel pits (Richter class a) and intervessel pits are relatively small (4–6 µm).

Cryptocaryoxylon meeksii sp. nov. (Fig. 18)

Growth rings indistinct to distinct and marked by radially flattened latewood fibers.

Diffuse porous. Vessels solitary and in radial multiples of 2 (rarely 3), average tangential diameters of 87 (15)–136 (19) µm; average vessel frequencies of 7–26/mm^2, range 4–37/mm^2, simple perforations; intervessel pits crowded alternate with angular outline, 6–10 µm; vessel-ray parenchyma pits elongated horizontally and with reduced borders; helical thickenings absent; average vessel element length 294 (73)–381 (55) µm; thin-walled tyloses present, widely spaced.

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

Axial parenchyma scanty paratracheal to narrow vasicentric, 4–8 cells per strand.

Rays 1–2(–3)-seriate. Multiseriate rays heterocellular, body composed of procumbent cell, with one marginal row of square and/or upright cells; mean height of multiseriate rays 214 (44)–387 (250) µm, total range of 145–847 µm; 5–7/mm.

Oil cells common in margins of rays.

Crystals not observed.

Distinct storied structure absent, but with a tendency to storied rays, the rays "en echelon".

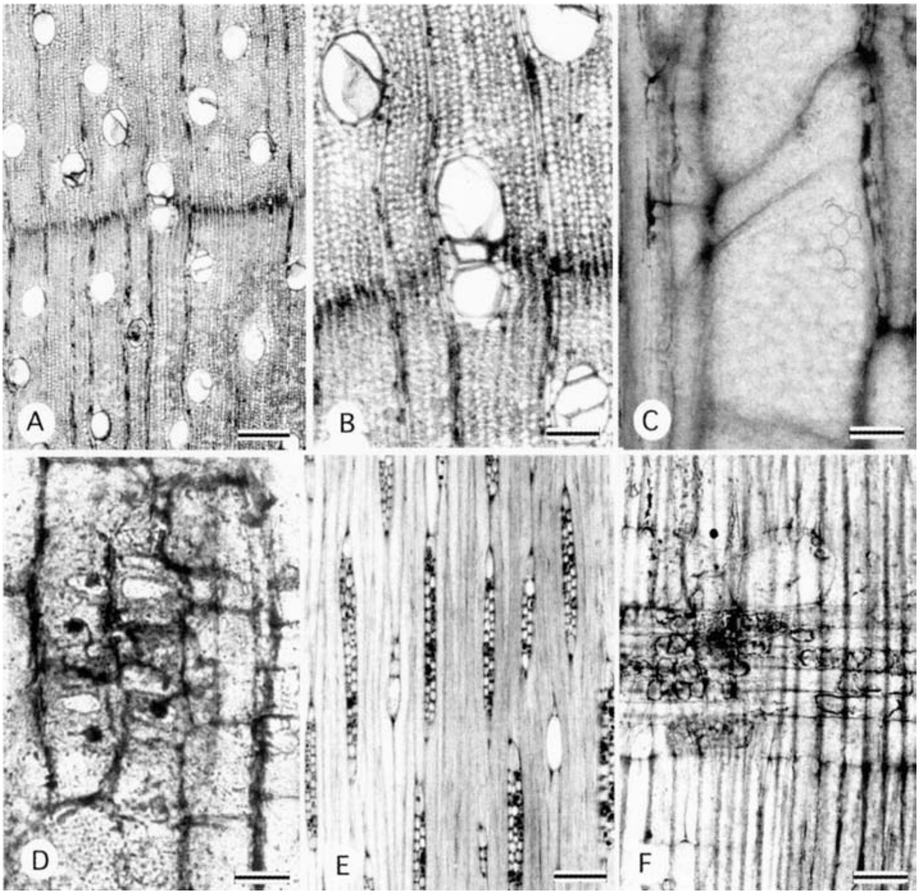

Fig. 18. *Cryptocaryoxylon meeksii* sp. nov. (UF 12240). – A: Diffuse porous wood, with vessels solitary and in short radial multiples, XS. – B: Detail of growth ring boundary with radially narrower fibers, XS. – C: Crowded alternate intervessel pitting, TLS. – D: Horizontally elongate vessel-ray parenchyma pits, RLS. – E: Rays to 3-seriate, idioblasts in margins of rays, TLS. – F: Ray with procumbent body cells, and idioblasts in the marginal rows, RLS. — Scale bars = 250 µm in A; 100 µm in B, E; 50 µm in C, D, F.

Holotype: UF 12240 (estimated minimum diam. ≥ 20 cm).

Paratypes: USNM 507893 (DEN 28, ≥ 10 cm), USNM 507894 (DEN 64, ≥ 10 cm), USNM 507895 (DEN 65, large > 1 m), USNM 507896 (DEN 126), USNM 507994 (C4A-66, sample 4 cm), UF 12020 (≥ 10 cm), UF 12067, UF 12236 (≥ 14 cm), UF 12459 (≥ 10 cm).

Etymology: Specific epithet for Hal Meeks, for many years of help with stubborn computers.

Similarities to extant woods — The horizontally elongated vessel-ray pits are the most commonly occurring of the three categories of vessel-ray pits Richter (1981, 1987) recognizes for the Lauraceae. A tendency to storied rays is rare in the Lauraceae, occurring in some species of five genera. *Beilschmiedia, Endiandra,* and *Potameia* all differ from this Clarno wood as they have marginal parenchyma bands. *Mezilaurus* differs as it has septate fibers and class c vessel-ray parenchyma pits. *Aspidostemon*, segregated from *Cryptocarya* and native to Madagascar, differs as it has septate fibers, regular storied structure, occasional scalariform perforations, and only scanty paratracheal parenchyma (Richter 1990).

Comparisons with other fossil woods — This wood is distinguished from other Lauraceae fossil woods by its relatively small rays (mostly 2 cells wide and averaging < 350 µm high) that tend to be arranged in echelon, in combination with scanty paratracheal to vasicentric parenchyma, non-septate fibers, and oil cells in the rays.

Cryptocaryoxylon radiporosum sp. nov. (Fig. 19)

Growth rings indistinct, tendency for radially narrower latewood fibers.

Diffuse porous; occasionally solitary (7%) and mostly in radial multiples of 2–10 or more; average tangential diameter 101 (22) µm; vessel frequencies 16–34–43/mm^2; exclusively simple perforations; intervessel pits crowded alternate, 9–12 µm horizontal diameter; vessel-ray parenchyma pits with reduced borders, and mostly horizontally elongate (class b); vessel element lengths average 393 (75) µm.

Fibers non-septate; walls medium-thick; pits not observed.

Axial parenchyma scanty paratracheal and marginal, strands 4–8 cells.

Rays 1–3-seriate. Multiseriate rays heterocellular with one row of square to upright marginal cells; mean ray height 302 (91) µm, range 203–610 µm; 5–7/mm.

Idioblasts (“oil cells”) occasional in ray margins, and rarely at sides of rays.

Holotype: UF 12383 (≥ 8 cm).

Etymology: Specific epithet is for the numerous radial multiples.

Similarities to extant woods — A high proportion of vessels in radial multiples is not common in the Lauraceae. Richter (1981) observed this characteristic in some species of *Mezilaurus, Cryptocarya,* and *Litsea*. *Mezilaurus* differs from this Clarno wood as it has class c vessel-ray parenchyma pits and septate fibers. *Litsea* and *Cryptocarya* have class b vessel-ray parenchyma pits. *Litsea* does not have marginal parenchyma, but *Cryptocarya* does. Idioblasts in extant *Cryptocarya* usually are diffuse, while in some species of *Litsea* (e.g. *L. chinensis*) they are almost exclusively associated with the rays. *Cryptocarya* includes some 200 species of warm and tropical regions, *Litsea* some 400 species, also of warm and tropical regions, especially Asia and Australia (Mabberley 1997).

Comparisons with other fossil woods — This wood is assigned to *Cryptocaryoxylon* Leisman because of similarity in intervessel pit size, type of vessel-ray parenchyma pits (class b, horizontally elongate), and non-septate fibers. The Clarno wood differs from *Cryptocaryoxylon gippslandicum* Leisman because the Clarno wood has a higher proportion of its vessel in radial multiples, idioblasts are associated with the rays, rather than diffuse, and rays are shorter. The Australian *Cryptocaryoxylon gippslandicum*, of probable Eocene–Oligocene age, has some similarity to extant *Cryptocarya oblata* Bailey, which occurs in the rainforests of northern Queensland (Leisman 1986).

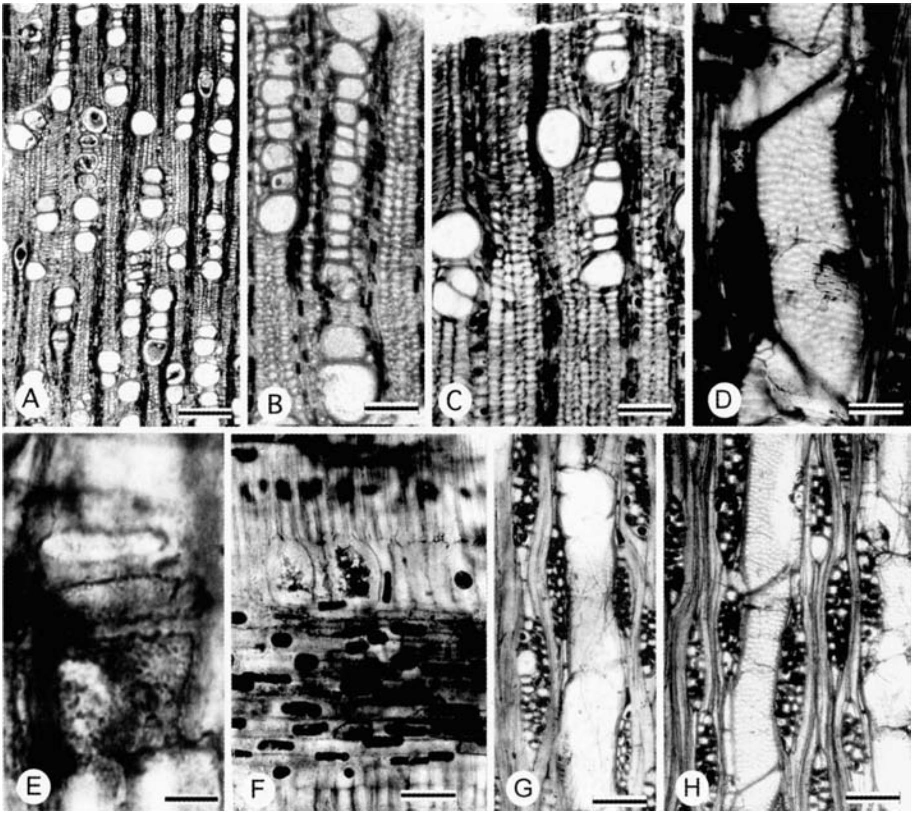

Fig. 19. *Cryptocaryoxylon radiporosum* sp. nov. (UF 12383). – A: Diffuse porous wood, with vessels mostly in radial multiples, XS. – B: Long radial multiple, XS. – C: Marginal parenchyma (?) at growth ring boundary, XS. – D: Crowded alternate intervessel pits, TLS. – E: Horizontally elongate vessel-ray parenchyma pits with reduced borders, RLS. – F: Inflated cells (?oil cells) in marginal row of ray, RLS. – G: Ray with idioblast at side rather than at margin, TLS. – H: Multiseriate rays 3–4-seriate, vessels with thin-walled tyloses, ray cell with marginal idioblast (upper right), TLS. — Scale bars = 250 µm in A; 100 µm in B, C, G, H; 50 µm in D, F; 12 µm in E.

Mezilaurinoxylon gen. nov.

Diffuse porous. Vessels solitary and in short radial multiples, mean tangential diameters small to medium (50–150 µm); simple perforations; intervessel pits alternate, > 10 µm, vessel-ray parenchyma pits enlarged and with reduced borders, oval to window-like. Fibers all septate. Axial parenchyma scanty paratracheal to vasicentric. Rays 1–5-seriate, heterocellular, usually with one row of marginal square to upright cells; idioblasts ("oil cells") occasional in ray margins.

Type species: Mezilaurinoxylon eiporosum.

Etymology: Name indicates the wood has a suite of characters seen in the extant genus *Mezilaurus*.

Mezilaurinoxylon eiporosum sp. nov. (Fig. 20A–F)

Growth rings generally indistinct, sometimes marked by radially flattened latewood fibers.

Diffuse porous. Vessels solitary and in radial multiples of 3 (rarely 4); average tangential diameters 84 (14)–125 (30) µm; vessel frequency averages of 16–38/mm^2, range of 10–45/mm^2, simple perforations; intervessel pits crowded alternate with angular outline, large, > 10 µm; vessel-ray parenchyma pits enlarged and with reduced borders (Richter type c), generally oval to horizontally elongate and tending to be window-like; helical thickenings absent; average vessel element lengths 494 (27)–500 (92) µm, total range 339–678 µm; abundant thin-walled tyloses present.

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

Axial parenchyma scanty paratracheal, 4 cells per strand.

Rays 1–4(–5)-seriate. Multiseriate rays heterocellular, body composed of procumbent cells, with 1 row of square/upright cells; ray cells often with colored contents; mean heights of multiseriate rays 437 (194)–615 (235) µm, total range of 259–1423 µm; 6–7/mm.

Oil cells occasional in margins of rays, not common, in radial view appearing only slightly enlarged relative to other marginal ray cells.

Crystals not observed.

Storied structure absent.

Holotype: UF 12397 (≥ 10 cm).

Paratypes: USNM 507866 (DEN 62, 4 cm), USNM 507892 (DEN 81, ≥ 50 cm), UF 12068, UF 12308 (≥ 7 cm), possibly USNM 507868 (DEN 79).

Etymology: The specific epithet refers to the occurrence of fenestriform (window-like, "eiporous") vessel-ray parenchyma pits.

Fig. 20. A–F: *Mezilaurinoxylon eiporosum* gen. et sp. nov. (UF 12397). – A: Diffuse porous wood, with vessels solitary and in short radial multiples, XS. – B: Indistinct growth rings, with a few radially narrower fibers, XS. – C: Crowded alternate intervessel pits, TLS. – D: Vessel-ray parenchyma pits with reduced borders and rounded to box-shaped, RLS. – E: Vessels with thin-walled widely spaced tyloses, septate fibers, multiseriate rays, oil cell in margin of biseriate ray, TLS. – F: Rays with procumbent body cells and marginal row of square-upright cells, dark contents common in rays, RLS.

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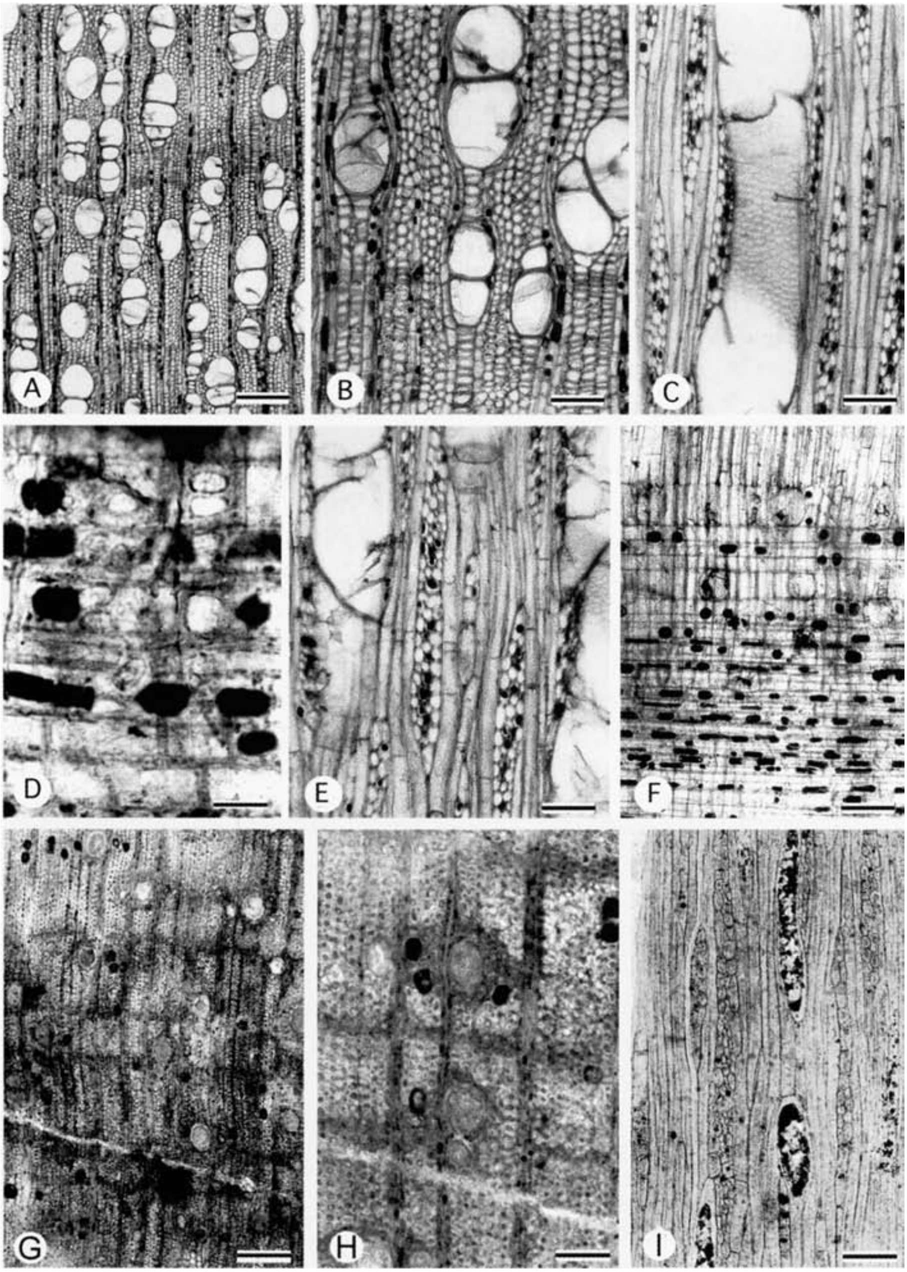


(Fig. 20) G–I: *Ulminium magnioleiferum* sp. nov. (USNM 507946). – G, H: Diffuse porous wood, with vessels solitary and in short radial multiples, vasicentric to aliform parenchyma, and narrow parenchyma bands, idioblasts with dark contents. – I: Heterocellular multiseriate rays, idioblasts with axial orientation and dark contents. — Scale bars = 250 μm in A, G; 100 μm in B, C, E, F, H, I; 50 μm in D.

Similarities to extant woods — According to Richter (1981), large, window-like vessel-ray pits (class c) occur in: *Anaueria, Clinostemon, Mezilaurus*, *Sextonia* (formerly *Ocotea rubra*), and some species of *Nothaphoebe*. *Anaueria* differs from this Clarno wood as it has aliform-confluent parenchyma and non-septate fibers; *Mezilaurus* includes species with scanty paratracheal parenchyma. There are ca. 20 species of extant *Mezilaurus*, ranging from tropical South America to Costa Rica (Mabberley 1997). Rohwer (2000) recognized the neotropical clade of *Mezilaurus* and its segregate *Williamodendron*, and considered it distinct from a large sister group, which includes the Laureae and most of the *Ocotea* group.

Comparisons with other fossil woods — This wood resembles *Ulminium porosum* from the Eocene Yellowstone Fossil Forests (Wheeler et al. 1977). Vessel diameter, ray width and height, parenchyma distribution and abundance, and frequency and location of oil cells are similar. However, *U. porosum* has a higher vessel density (32–85/mm^2) and its vessel-ray parenchyma pits are usually rounded or oval-elongate, and not fenestriform (window-like) as is common in this Clarno wood type. Richter (1981, 1987) considered vessel-ray parenchyma pits an important character for distinguishing extant Lauraceae woods. Consequently, we are considering these woods distinct from the early Eocene *U. porosum*.

The samples listed below are similar to *Mezilaurinoxylon eiporosum*, except they lack oil cells. Without oil cells they cannot with certainty be assigned to the Lauraceae, and might represent a separate wood type. However, given that oil cells are of variable occurrence within some species of Lauraceae, present in some samples, absent in others, these woods may represent the same plant as the *M. eiporosum* wood. The characteristics of these woods that lack oil cells occur in the Anacardiaceae and Burseraceae, families represented in the fruit and seed flora; the abundance of septate fibers suggests Burseraceae, rather than Anacardiaceae. Moreover, the large window-like pits are not documented for Anacardiaceae (Terrazas 1994). The two Nut Beds species of *Bursericarpum* most closely resemble the extant genera *Protium, Tetragastris* and *Bursera*. There are two genera of Anacardiaceae fruits: *Rhus* (tribe Rhoeae) and the extinct genus *Pentoperculum* (tribe Spondiadeae).

Samples: USNM 507864 (DEN 13, 4 cm), USNM 507867 (DEN 67, 4.5 cm), USNM 507869 (DEN 87, 2.5 cm), USNM 507902 (DEN 58, ≥ 10 cm), UF 12022, UF 12051, UF 12309 (≥ 25 cm).

ULMINIUM Unger

Ulminium magnioleiferum sp. nov. (Fig. 20 G–I)

Growth rings present, marked by radially flattened latewood fibers and marginal/zonate parenchyma.

Diffuse porous. Vessels solitary and in radial multiples of 2 (rarely 3), average tangential diameter of 89 (17) µm; vessel frequency 5–19/mm^2, simple perforations; crowded alternate intervessel pitting, 6–10 µm; vessel-ray parenchyma pits not observed; vessel element lengths 200–448 µm (n = 9).

Fibers non-septate (?), walls thin to medium-thick, pitting not observed.

Axial parenchyma vasicentric, aliform-confluent; banded (marginal/zonate?), usually 2 cells deep; 1–4 cells per strand.

Rays 1–4-seriate. Multiseriate rays heterocellular, body of procumbent cells, with 1–8 rows of square/upright cells, often asymmetric, marginal cells usually considerlably vertically enlarged relative to body cells; mean of total height of multiseriate rays 596 (249) µm, range of 200–1,100 µm; uniseriate rays composed exclusively of upright cells; 5–8/mm.

Enlarged oil cells, ~ 50 µm wide, 300–400 µm long, isolated among fibers or to side of rays, 5–10/mm^2 in cross section.

Storied structure absent.

Crystals not observed.

Holotype: USNM 507946 (C4A-139, ≥ 10 cm).
Etymology: Specific epithet is for the large idioblasts in this wood type.

Comments — The idioblasts, paratracheal parenchyma, simple perforations, and alternate intervessel pitting indicate this wood belongs to the Lauraceae. Unfortunately, the sample's preservation is poor, and vessel-ray parenchyma pits were not observed and presence of septate fibers could not be determined. Therefore, it is assigned to *Ulminium*, as its characteristics indicate it is Lauraceae, but features important for determining affinities to extant genera are not observable.

Comparison with extant woods — Some *Beilschmiedia* species have banded parenchyma and isolated idioblasts (cf. Ilic 1991: photo 1954 and personal observations of *B. mannii* PACw 1048), others have rays 4 or more cells wide and are markedly heterocellular as is this Clarno wood (cf. Ilic 1991: photo 1955 and *B. fordiana* A164 in PACw collection).

Comparisons with other fossil woods — This wood is distinct from the other Clarno Lauraceae woods because of the relatively abundant paratracheal parenchyma, narrow axial parenchyma bands and large idioblasts positioned either next to the rays or isolated amongst the fibers.

LEGUMINOSAE

Only one type of legume fruit is known from the Nut Beds locality, with three additional undescribed fruit types known from other localities in the Clarno Formation. The preservation of the one fruit type, based on one specimen, was such that it was not possible to determine intrafamilial relationships. There are three wood types in the Nut Beds that have characteristics indicating affinities with the Leguminosae. Another wood type, described as Nut Beds Xylotype III-B-i (USNM 507917, DEN 34), has characteristics seen in the Leguminosae and other families.

There are more fossil woods of the Leguminosae described in the literature than any other dicot family. Determining intrafamilial affinities for isolated legume woods is problematic because of the great diversity and variability of the wood types and the occurrence of similar characteristics in more than one extant genus, tribe, or even subfamily (Wheeler & Baas 1992). Müller-Stoll and Mädel (1967) critically reviewed the fossil record of legume wood and recognized 19 form genera (names all ending in -oxylon). Subsequently, Gros (1992, 1994) listed and compared types of Mimosoideae fossil woods (18 genera, 67 species), Awasthi (1992) summarized Indian fossil legume woods (mentioning 22 fossil wood genera with names ending in -oxylon, and 65 species assigned to some 30 extant genera), and Wheeler and Baas (1992) presented an overview of the fossil record for legume woods (more than 200 records). As best we could determine, none of the Clarno legume woods have anatomy diagnostic of a single extant genus, so we are choosing to use the genera established by Müller-Stoll and Mädel. It would be worthwhile to reassess the entire fossil wood record of the legumes, especially of woods resembling Papilionoideae, as there is additional comparative information on extant woods of this group (e.g., Fujii et al. 1994, Gasson 1999, and references cited therein).

DICHROSTACHYOXYLON Müller-Stoll & Mädel

Dichrostachyoxylon herendeenii sp. nov. (Fig. 21)

Growth rings distinct to indistinct, marked by radially flattened fibers.

Diffuse porous. Vessels solitary and in radial multiples of 2–3 (6); average tangential diameters of 123 (28)–186 (30) µm; some radial multiples including a vessel half the width of other vessels in the multiples; average vessel frequencies of 6–18/mm^2, total range 3–25/mm^2; perforations exclusively simple; intervessel pits crowded alternate, 8–10 µm; vessel-ray parenchyma pits similar to intervessel pits; helical thickenings absent; average vessel element lengths of 234 (87)–379 (71) µm, total range 217–621 µm; tyloses absent.

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

Axial parenchyma predominantly paratracheal, vasicentric, aliform, and at times confluent; 2–8 cells per strand, most frequently 8.

Rays 1–4-seriate. Multiseriate rays homocellular with procumbent cells and weakly heterocellular with 1(–2) marginal rows of square/upright cells; mean multiseriate ray heights range from 166 (35)–297 (59) µm, total range of 92–420 µm; 6–8/mm.

Solitary prismatic crystals present in chambered axial parenchyma, more than 16 chambers.

Storied structure absent.

Holotype: USNM 507909 (DEN 56, > 50 cm).

Samples: USNM 507907 (DEN 29, 2 cm), USNM 507908 (DEN 55, poor preservation, 6.5 cm), USNM 507911 (DEN 73, > 10 cm), USNM 507912 (DEN 74, 3–5 cm, possibly complete axis), USNM 507913 (DEN 77, 4.5 cm, possibly complete axis), USNM 507914 (DEN 84, 3 cm across), USNM 507915 (DEN 92, 7 cm), USNM 507916 (DEN 112, 3 cm), USNM 507906 (DEN 124), UF 12061.

Etymology: Named for Patrick Herendeen, who has done much to illuminate the history of the Leguminosae.

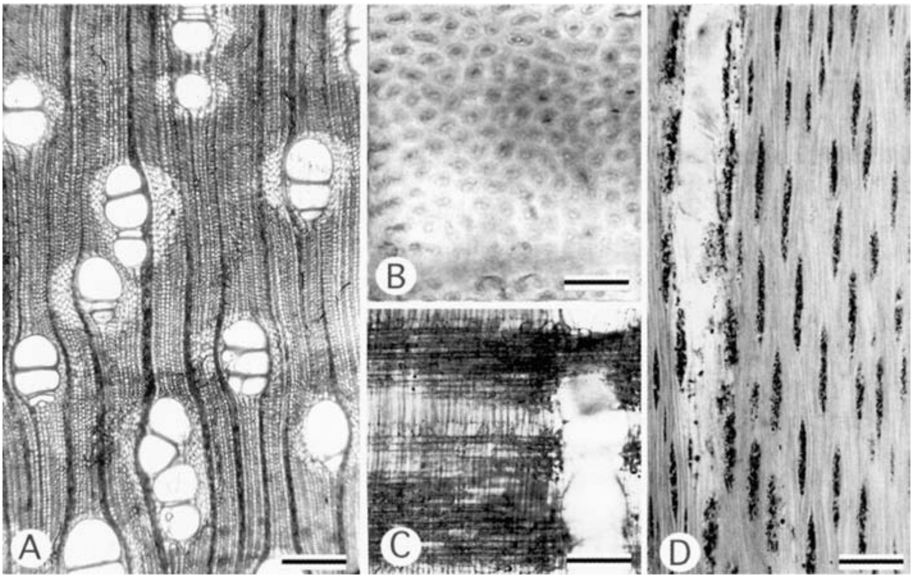


Fig. 21. *Dichrostachyoxylon herendeenii* sp. nov. (USNM 507909) – A: Diffuse porous wood, vessels solitary and in short radial multiples, some multiples with tendency to two size classes of vessels, vasicentric to lozenge-type aliform parenchyma, XS. – B: Crowded alternate intervessel pitting, TLS. – C: Rays with procumbent body cells and one marginal row of square and radially shorted procumbent cells, RLS. – D: Multiseriate rays, tending to be homocellular, uniseriate rays rare, TLS. — Scale bars = 250 µm in A, C, D; 25 µm in B.

Comments — USNM 507908 (DEN 55) differs in some features from other samples assigned to *Dichrostachyoxylon herendeenii*. Axial parenchyma more often appears broad vasicentric than lozenge aliform, vessels in radial multiples have a uniform diameter, and crystals are in unchambered axial parenchyma. This sample was compressed, and not as well preserved as many of the Clarno woods. It could very well represent yet another type of legume wood.

Similarities to extant woods — Families that include diffuse porous woods with vessels solitary and in short radial multiples, simple perforation plates, alternate intervessel pits, vessel-ray parenchyma pits not enlarged, non-septate fibers, vasicentric and aliform parenchyma, non-storied homocellular rays, and crystals in chambered parenchyma are: Combretaceae, Leguminosae (all three subfamilies, but most commonly Caesalpinioideae), Meliaceae, Rhamnaceae, Rutaceae, and Vochysiaceae. The pits in this fossil appear vestured; vestured pits occur in Combretaceae, Leguminosae, and Vochysiaceae, but not in Meliaceae, Rhamnaceae, or Rutaceae.

Comparisons with other fossil woods — This wood type has some similarities to a wood called *Acacia gregorii*, which came from an outcrop in Crook County, Oregon, once mapped as in the Clarno Formation (Gregory 1970, 1971). This wood was described as having diffuse porous wood, medium-sized vessels, 4–11 vessels/mm^2, vessels solitary and in radial multiples of 2 (3), simple perforations, vessel elements 200–400 µm long, mostly vasicentric to aliform (occasionally confluent) parenchyma, libriform fibers, homogeneous rays to 4–6-seriate, and 30–40 cells high, and vertical traumatic gum canals. *Acacia gregorii* is not a validly described species because no type was designated for this species; slides and samples of it cannot be located. Although not mentioned in the description, long crystalliferous parenchyma strands are visible in the illustration of the radial section. Intervessel and vessel-ray parenchyma pits were not described and are not visible in the illustrations. Characteristics of this wood are not restricted to the genus *Acacia*. This wood differs from the Nut Beds wood described here as it has wider rays, less aliform parenchyma, marginal parenchyma, and traumatic gum canals are common.

Of the 19 form genera Müller-Stoll and Mädel (1967) recognized, this wood conforms best to the diagnosis for *Dichrostachyoxylon*: wood diffuse porous, vessels solitary and in short radial multiples, simple perforations, medium-sized alternate pitting, vessel-ray parenchyma and vessel-axial parenchyma pitting similar to intervessel pitting; non-septate libriform fibers; axial parenchyma vasicentric, aliform, and occasionally confluent, marginal parenchyma often present; rays 1–10 cells wide, usually more than 3 cells wide, homogeneous to weakly heterogeneous [translated from the German].

Gros (1991, 1992) compared the critical diagnostic features of 15 genera of fossil mimosoid wood. Gros (1992) noted that the genera *Dichrostachyoxylon* and *Tetrapleuroxylon* are very similar. However, diffuse axial parenchyma is common in *Tetrapleuroxylon*, and is not mentioned in the diagnosis of *Dichrostachyoxylon* (Müller-Stoll & Mädel 1967). The name *Dichrostachyoxylon* suggests affinities with the genus *Dichrostachys*. However, since the time *Dichrostachyoxylon* was established it has been recognized that its characteristics also occur in *Acacia* (Müller-Stoll & Mädel 1967; Selmeier 1990; Gros 1994).

Compared to other species of *Dichrostachyoxylon,* the Clarno wood has more aliform parenchyma, larger intervessel pits, and smaller rays. It also does not have marginal parenchyma, a feature that is described as often present, but is absent from *D. prambachense* (Hoffmann) Müller-Stoll & Mädel (1967), one of the older *Dichrostachyoxylon* wood types described to date (Oligocene of Austria). We consider these differences sufficient to recognize this wood as a distinct species. The larger intervessel pits and generally narrower rays could be considered justification for establishing a separate genus. However, as this wood conforms to the general diagnosis of *Dichrostachyoxylon*, we choose to assign it to that genus, at the same time emphasizing that it is not equivalent to the extant genus *Dichrostachys*.

Woods assigned to *Dichrostachyoxylon* are known from the Oligocene and Miocene of Europe (e.g., Müller-Stoll & Mädel 1967; Privé 1969; Selmeier 1990), Miocene of Africa (e.g., Lakhanpal & Prakash 1970), and the United States (e.g., wood originally described as *Leguminoxylon occidentale* Prakash & Barghoorn 1961).

EUACACIOXYLON Müller-Stoll & Mädel

cf. ***Euacacioxylon*** (Fig. 22)

Growth rings present, marked by radially flattened fibers.

Diffuse porous. Vessels solitary, and in radial multiples of 2–4 (8), sometimes occasional tangential groups, some clusters; average tangential diameters 98 (23)–147 (27) µm; vessel frequency 5–20/mm^2; perforations simple; intervessel pits crowded

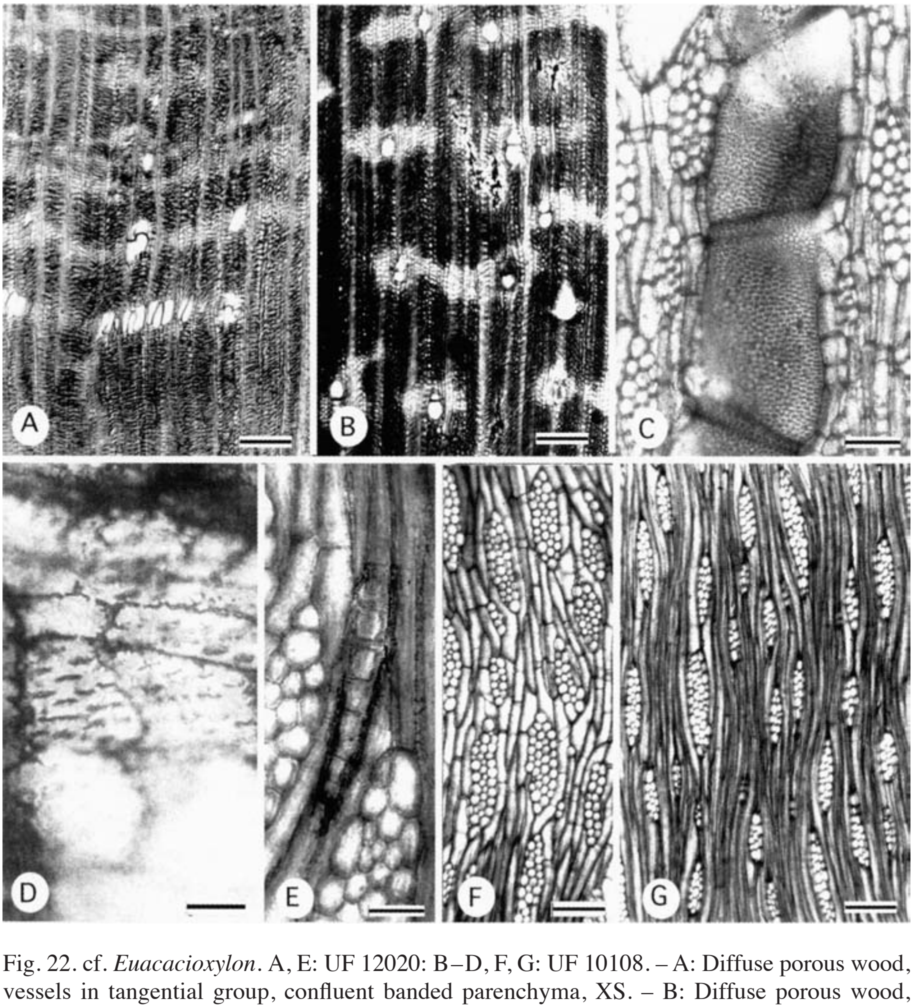


Fig. 22. cf. *Euacacioxylon*. A, E: UF 12020: B–D, F, G: UF 10108. – A: Diffuse porous wood, vessels in tangential group, confluent banded parenchyma, XS. – B: Diffuse porous wood, vessels solitary and in radial multiples, confluent parenchyma, XS. – C: Vessel elements with simple perforations and crowded alternate intervessel pitting, TLS. – D: Vessel-ray parenchyma pits similar to intervessel pits, RLS. – E: Crystalliferous strand, single crystal per chamber, TLS. – F: Multiseriate rays, and 2–4-celled parenchyma strands, TLS. – G: Multiseriate rays, tending to be homocellular, uniseriate rays rare, TLS. — Scale bars = 250 µm in A, B; 100 µm in F, G; 50 µm in C; 25 µm in D, E.

alternate, 4–6 µm; vessel-ray parenchyma pits similar in size and shape to intervessel pits; average vessel element lengths of 227 (51)–260 (35) µm.

Fibers apparently non-septate, walls medium to thick, pits not obvious.

Axial parenchyma paratracheal, vasicentric, aliform, to confluent-banded; 2–6 cells per strand; solitary crystals in chambered axial parenchyma strands (4–8 chambers).

Rays mostly 3–4-seriate (to 6-seriate), uniseriate rays present, but not common and very low (usually less than 5 cells high). Rays homocellular and heterocellular, body of procumbent cells, some rays with one row of square/upright cells; mean height of the multiseriate rays 282 (40)–311 (61) µm, total range of 203–441 µm; 6–10/mm.

Storied structure not observed.

Samples: UF 12010 (probably greater than 10 cm, incomplete 1.5 cm), UF 12108 (3.5–5 cm, complete).

Comments — The wider vessel elements of UF 12010 (147 µm) are consistent with this sample being a larger axis than UF 12108.

Similarities to extant woods — The combination of diffuse porosity, exclusively simple perforation plates, crowded alternate intervessel pitting, vessel-ray parenchyma pits similar to intervessel pits, homocellular rays that are 4-seriate or more, confluent parenchyma, non-septate fibers without distinctly bordered pits, absence of storied structure, and chambered crystalliferous axial parenchyma occurs most commonly in the Leguminosae (all three subfamilies), and also in the Meliaceae and Rutaceae. The outlines of the pit borders do not appear smooth at high magnification, so it is likely that they are vestured, which indicates affinities with the Leguminosae.

Tangentially arranged vessels occur in some genera of Leguminosae, although usually in species that are semi-ring porous to ring porous and have vessel clusters. Scarcity of uniseriate rays is seen in the Mimosoideae / Leguminosae.

Comparisons with other fossil woods — Of the genera that Müller-Stoll and Mädel (1967) and Gros (1992, 1994) recognized, these Clarno woods are similar to *Euacacioxylon* as they share aliform to banded axial parenchyma and non-septate fibers. They differ as *Euacacioxylon* has homocellular rays that usually are wider than 3-seriate, and can be up to 10-seriate. Most of the rays in the Clarno wood are composed only of procumbent cells, and rays three or more cells wide are common (though not wider than 6-seriate). For now, we are tentatively assigning this wood to *Euacacioxylon* and choose not to establish a new genus based on these differences, as ray width and ray cellular composition (homocellular to weakly heterocellular) is variable within extant Leguminosae.

MIMOSOXYLON Müller-Stoll & Mädel

cf. ***Mimosoxylon*** (Fig. 23)

Growth rings present, marked by radially flattened latewood fibers.

Diffuse porous. Vessels mostly solitary, and in radial multiples of 2(–3), near some growth ring boundaries some multiples of over 4 vessels, and with some very narrow vessels near the boundary; average tangential diameter 162 (21) µm; 1–4/mm^2; perforations simple; intervessel pits alternate, crowded and polygonal in outline, 10–12 µm; vessel-ray parenchyma pits similar in size and shape to intervessel pits; vessel element lengths of 226–361 µm; tyloses not observed.

Fibers likely non-septate, walls thin to medium, pits not obvious.

Axial parenchyma scanty paratracheal to narrow vasicentric, strands of 4–8 cells.

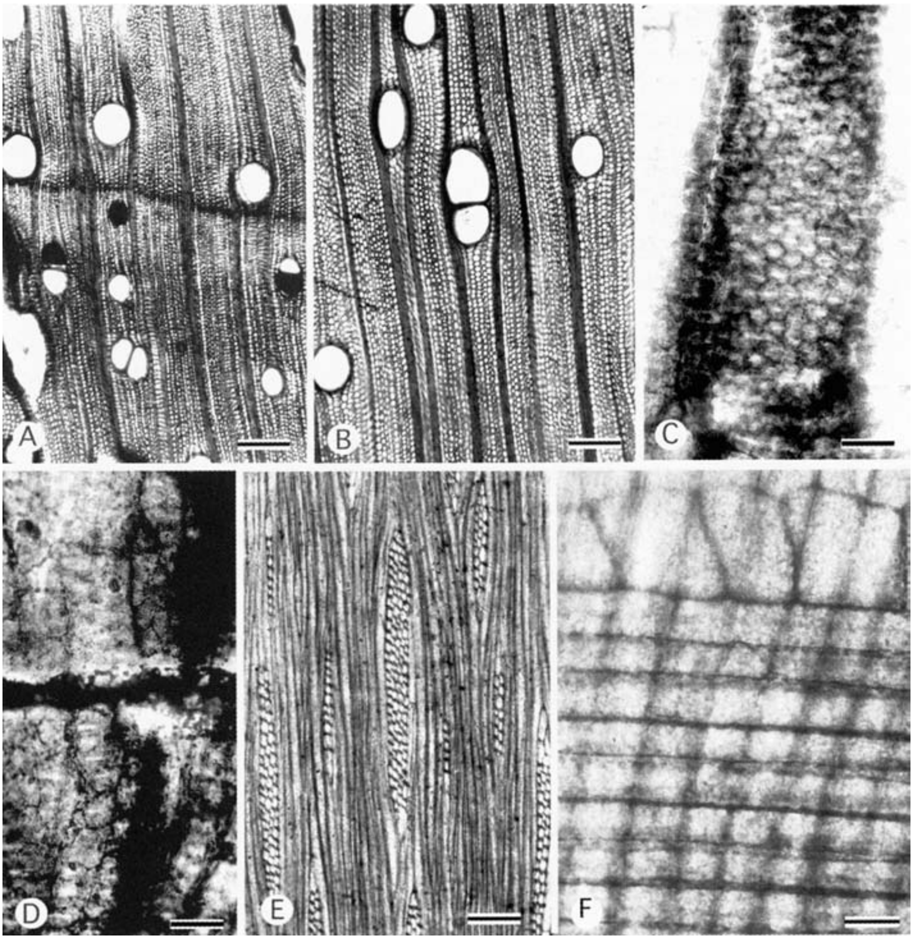


Fig. 23. cf. *Mimosoxylon*. (UF 12082). – A: Growth ring boundary, vessels widely spaced, XS. – B: Vessels solitary and one radial multiple of 2, narrow vasicentric parenchyma, XS. – C: Crowded alternate intervessel pits, TLS. – D: Vessel-parenchyma pits similar in size to the intervessel pits, RLS. – E: Multiseriate rays, TLS. – F: Ray with body of procumbent cells, and one marginal row of upright cells, RLS. — Scale bars = 250 µm in A, B; 100 µm in E; 50 µm in F; 25 µm in C, D.

Rays 1–4-seriate. Multiseriate rays heterocellular, body of procumbent cells, with 1(–2) rows of square/upright cells; mean height of multiseriate rays 476 (192) µm, total range of 191–878 µm; 3–6/mm.

Crystals not observed.

Storied structure absent.

Sample: UF 12082.

Comments — UF 12088 is poorly preserved, but its cross section resembles UF 12082 and so it may represent another example of this wood type.

Similarities to extant woods — The combination of diffuse porosity, vessels solitary and in radial multiples, mean vessel diameter greater than 100 µm, vessel density less than 20/mm^2, simple perforation plates, non-minute alternate intervessel pitting, vessel-ray parenchyma pitting similar to intervessel pitting, non-septate fibers, axial parenchyma scanty paratracheal to vasicentric, slightly heterocellular rays that can be up to 4 or more cells wide and fewer than 12 per mm suggests affinities with the Leguminosae, especially subfamilies Caesalpinioideae and Mimosoideae.

This wood type has the lowest vessel density of any of the Clarno dicot woods, and a relatively large mean vessel diameter.

Comparisons with other fossil woods — Of the genera that Müller-Stoll and Mädel (1967) recognized, this matches the diagnosis of *Mimosoxylon*, which has non-septate fibers, no storied structure, weakly heterocellular rays, and axial parenchyma that is mostly narrow vasicentric. Rays are somewhat wider in this Clarno wood (1–4 cells wide) than in the two Cretaceous species Müller-Stoll and Mädel transferred to *Mimosoxylon* (1–3 cells wide). Intervessel pits are also larger in the Clarno wood than described for the two original species of *Mimosoxylon*. For now we are tentatively assigning this wood to *Mimosoxylon* because the general features of this Nut Beds wood are those of this form genus.

Cevallos-Ferriz and Barajas-Morales (1994) listed the distinctive features of woods assigned to *Mimosoxylon*. The relatively large intervessel pits, lower vessel density, and lack of aliform-confluent parenchyma distinguish this Clarno wood from all other woods assigned to *Mimosoxylon*.

MAGNOLIACEAE

Three variable species of *Magnolia* seeds are recognized from the Nut Beds (Manchester 1994). Manchester noted that more species of *Magnolia* might be recognized if the criteria used for the London Clay magnoliaceous seeds were applied. Two species of Magnoliaceae wood previously have been reported from the Nut Beds, as has a *Liriodendron*-like wood from the Post locality (Scott & Wheeler 1982). Additional samples of the magnoliaceous wood types described previously provide information on the variability of these wood types. Two additional species of Magnoliaceae wood are described below, and two new combinations proposed (Table 7).

Table 7. Comparison of Clarno Magnoliaceae woods.

Species	TD	V/MM2	IVP	B/PP	MP	IDIO
Liriodendroxylon multiporosum	54–67 (13)	44–100	o	2–10	+	(+)
Magnolia pageae	75 (11)	21–42	o	5–20	+	+
Magnoliaceoxylon						
angulata	40 (8)–66 (10)	59–112	o, s	15–18	+	–
cutleri	64 (13)	5–10	s (o)	8–20	–	+
longiradiata	69 (10)–70 (9)	44–83	s (o)	6–26	+	(+)

Legend: TD = mean tangential diameter, standard deviation in parentheses, in µm; V/MM2 = vessels per sq. mm; IVP = intervessel pit arrangement, o: opposite, s: scalariform, ( ) indicates not common; B/PP = bars per perforation plate; MP = marginal parenchyma, + = present, – = absent; IDIO = idioblasts (oil cells?), + = present, (+) = present, but not common, – = absent.

LIRIODENDROXYLON Prakash, Brezinová, & Buzek

Liriodendroxylon multiporosum Scott & Wheeler (Fig. 24)

An additional sample of *L. multiporosum* recovered from the Nut Beds proper provides more information about variation in quantitative features, and values for both samples are given below.

Growth rings distinct, marked by marginal parenchyma.

Diffuse porous. Vessels mostly in multiples, up to 7 pores per radial multiple, and in clusters, average tangential diameters 54 (10)–67 (13) µm; average vessel frequency

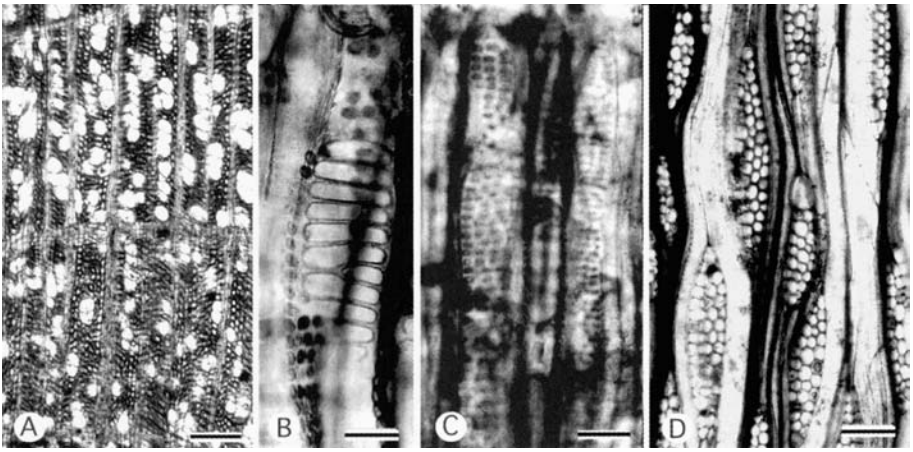


Fig. 24. *Liriodendroxylon multiporosum* Scott & Wheeler (USNM 507919). – A: Diffuse porous wood, with numerous multiples, marginal parenchyma, XS. – B: Scalariform perforation plate, RLS. – C: Opposite intervessel pits, TLS. – D: Multiseriate rays, tending to homocellular, idioblast at margin of central multiseriate ray, TLS. — Scale bars = 250 µm in A; 100 µm in C, D; 50 µm in B.

44–84, to more than 100/mm^2; exclusively scalariform perforations with 2–10 bars; intervessel pitting opposite; vessel-ray parenchyma pits oval in outline, at times unilaterally compound; vessel element lengths average 590 (122)–697 (97) μm, total range 425–904 μm.

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

Axial parenchyma marginal, 3–6 rows of parenchyma, 8–10 cells per strand.

Rays 1–4-seriate, usually wider in zones of marginal parenchyma. Heterocellular, with 1 (2–3) marginal rows of upright/square cells to homocellular with all procumbent cells; uniseriates rare; mean total ray height 333 (112) μm, 90–900 μm; 6–9/mm. Inflated marginal cells (idioblasts) rare.

Additional material: USNM 507919 (DEN 30, > 10 cm).

Comments — USNM 507919 closely resembles the holotype material from the Osmunda locality near Post, Oregon (USNM 326705, Os 31).

Similarities to extant woods — The combination of numerous narrow vessels that are solitary and in multiples, exclusively scalariform perforation plates, opposite intervessel pitting, marginal parenchyma, and rare uniseriate rays are characteristics of the Magnoliaceae. Predominantly opposite pits characterize *Liriodendron* and *Magnolia* section *Rhytidospermum*. Stark (1954) was unable to find reliable features to distinguish *Liriodendron tulipifera* and *Magnolia fraseri* and *M. tripetala*, all native to the United States. Although this wood has characteristics of extant *Liriodendron*, its characteristics also occur in *Magnolia*. Consequently, this wood is assigned to *Liriodendroxylon*, rather than *Liriodendron* to indicate that it cannot be equated only with the genus *Liriodendron*. One feature observed in USNM 507919 and not seen in the type of *Liriodendroxylon multiporosum* is the rare occurrence of enlarged marginal ray cells ("oil cells") (Fig. 24D). Chen et al. (1993) noted the rare occurrence of oil cells in extant *Liriodendron chinense*, this feature is also illustrated by Cheng (1980). Oil cells are not reported for *L. tulipifera* (Stark 1954; pers. observ.).

Comparisons with other fossil woods — *Liriodendroxylon tulipiferum* from the Oligocene of Bohemia was considered to closely resemble wood of extant *Liriodendron tulipifera*, and to be distinct from *Magnolia* because the Oligocene wood had opposite pits and *Magnolia* wood has "interversal [sic] pits [that] are predominantly linear" (Prakash et al. 1971). These authors were unaware of the extant *Magnolia* species that have predominantly opposite pits. The European *Liriodendroxylon tulipiferum* has wider (60–150 μm), fewer (25–45/mm^2) vessels, lower ray density (4–7/mm), and lacks oil cells. The sample *Liriodendroxylon tulipiferum* is based on measures 2 cm in diameter, but it is not mentioned whether this is an entire axis or mature wood, so it is unclear whether the quantitative differences between it and the North American *Liriodendroxylon* woods are related to ontogenetic differences. Also, it is possible that Prakash et al. (1971) computed vessel density by counting vessel multiples as one vessel unit, thus resulting in a lower vessel density.

Liriodendroxylon princetonensis Cevallos-Ferriz & Stockey (1990a) from the Middle Eocene of British Columbia differs only slightly from *Liriodendroxylon* *multiporosum*, having a lower vessel density, and in that regard is intermediate between the Clarno and Bohemian wood. However, if the samples of *L. princetonensis* had been found in Europe or in the Clarno Formation, they probably would not have been recognized as a distinct entity, and would have been assigned to *Liriodendroxylon tulipiferum* or *L. multiporosum*. Species of fossil wood sometimes reflect differences in provenance or authorship rather than significant anatomical differences.

We choose to keep the Clarno *Liriodendroxylon* as a separate species from *Liriodendroxylon tulipiferum* because of the occasional occurrence of oil cells, its geographic origin and its age. The oil cells indicate this wood is more likely to have affinities with present-day *Liriodendron chinense* rather than with *Liriodendron tulipiferum*.

MAGNOLIA L.

Magnolia pageae sp. nov. (Fig. 25)

Growth rings distinct, marked by radially narrower fibers, and marginal parenchyma.

Diffuse porous. Vessels solitary and in radial multiples of 2–3, vessels tend to be angular in outline, average tangential diameters 75 (11) µm; vessel frequency 21–42/mm^2; scalariform perforations, with 5–20 bars, usually 8–10 bars; opposite intervessel pits; vessel-ray parenchyma pits horizontally enlarged, with reduced borders, some unilaterally compound; average vessel element length 793 (140) µm, range 610–1017 µm; helical thickenings not observed; tyloses occasional, widely spaced, some appear as individual "bubbles".

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

Axial parenchyma marginal, 2–4 cells wide, strands 6–8 cells.

Rays 1–2(–3)-seriate. Heterocellular, with uniseriate margins of 1–4 (up to 6) cells; uniseriate rays composed of upright cells; total multiseriate ray height averages 864 (280) µm, range 463–1751 µm; 4–6/mm. Idioblasts in rays, in uniseriate margins of the multiseriate rays, and in uniseriate rays, rarely in body of ray.

Crystals not observed.

Storied structure absent.

Holotype: UF 12490 (4.5 cm across).

Etymology: Named in honor of Virginia Page, and her contributions to the study of fossil wood.

Similarities to extant woods — The combination of exclusively scalariform perforation plates, opposite intervessel pits, "oil cells", marginal parenchyma, and narrow rays is unique to the Magnoliaceae. Predominantly opposite pitting and commonly occurring oil cells indicate affinities with *Magnolia*, rather than other magnoliaceous genera (Chen et al. 1993; Canright 1955).

Comparisons with other fossil woods — This wood is distinct from the other Clarno magnoliaceous woods because of the combination of predominantly opposite pitting, commonly occurring idioblasts, and narrow rays (Table 7). There are three late Tertiary European wood types that were assigned to *Magnolioxylon* Hofmann (1952) and

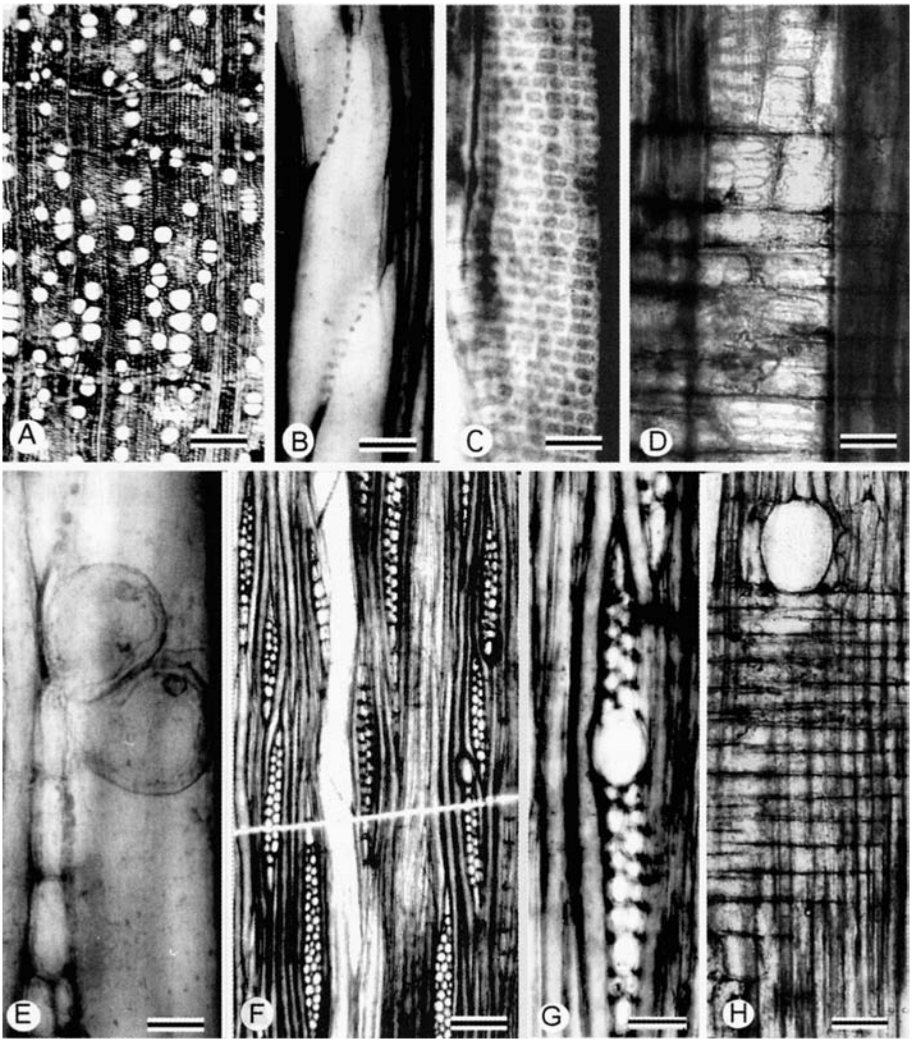


Fig. 25. *Magnolia pageae* sp. nov. (UF 12490). – A: Diffuse porous wood with vessels solitary and in short radial multiples, marginal parenchyma, XS. – B: Scalariform perforation plates, TLS. – C: Opposite intervessel pitting, TLS. – D: Horizontally elongate vessel-ray parenchyma pits, RLS. – E: Tyloses formation from marginal ray parenchyma cell, TLS. – F: Multiseriate rays 2–3 cells wide, uniseriate rays rare, TLS. – G: Ray with idioblast ("oil cell") in body of ray, TLS. – H: Body ray cells procumbent with marginal rows of square to upright cells, and one idioblast, RLS. — Scale bars = 250 µm in A; 100 µm in F; 50 µm in B, G, H; 25 µm in C, D, E.

are likely to be Magnoliaceae. Unfortunately, the genus *Magnolioxylon* is based on a sample that was later determined not to be Magnoliaceae (Kramer 1974). Their affinities with extant magnoliaceous genera need reassessment. All three differ from the Clarno fossil woods: *Magnolioxylon parenchymatosum* van der Burgh has spiral thickenings in its vessel elements and few bars per perforation plate, *M. krauselii* (Greguss) van der Burgh (1973) and *M. scandens* Schönfeld (1958) have some simple perforation plates, a feature suggesting they are most likely *Magnolia*.

MAGNOLIACEOXYLON Wheeler, Scott, & Barghoorn

Magnoliaceoxylon angulata (Scott & Wheeler) comb. nov. (Fig. 26)

Magnolia angulata Scott & Wheeler 1982, p. 142, figs. 38–42.

Growth rings distinct, marked by radially narrower fibers, and marginal parenchyma.

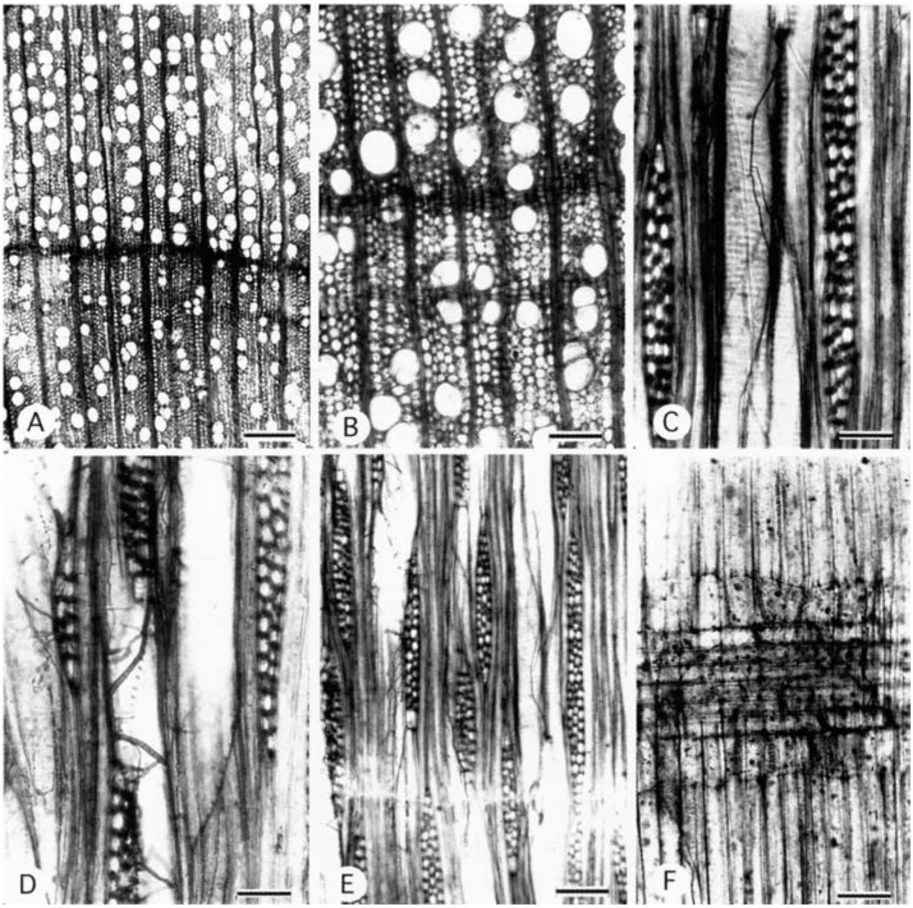


Fig. 26. *Magnoliaceoxylon angulata* (Scott & Wheeler) comb. nov. (UF 12461). – A: Diffuse porous wood with vessels solitary and in short radial multiples, XS. – B: Detail of growth ring boundary, XS. – C: Scalariform intervessel pitting, TLS. – D: Scalariform perforation plate, TLS. – E: Multiseriate rays 2–3 cells wide, TLS. – F: Body ray cells procumbent with marginal rows of square to upright cells, RLS. — Scale bars = 250 µm in A; 100 µm in B, E; 50 µm in C, D, F.

Diffuse porous. Vessels solitary and in radial multiples of 2–3 (rarely to 5), vessels tend to be angular in outline, average tangential diameters 40 (8)–66 (10) µm; average vessel frequency 59–112/mm^2, range 37–135/mm^2; scalariform perforations, with 15–18 bars; opposite to scalariform intervessel pits; vessel-ray parenchyma pits not observed; average vessel element length 423 (201) µm; helical thickenings and tyloses not observed.

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

Axial parenchyma marginal.

Rays 1–2(–3)-seriate. Heterocellular, with uniseriate margins of 1–2 cells; uniseriate rays rare, and composed of upright cells; total multiseriate ray height averages 495 (225) µm, range 250–1,200 µm; 5–7/mm.

Crystals not observed.

Storied structure absent.

Additional material: UF 12461 (specimen 8 cm across).

Comments — Vessels are more numerous and narrower in the type specimen (USNM 326707) than in UF 12461, which is consistent with the type specimen being a smaller axis including a pith (ca. 2.5 cm diameter), as vessels are narrower and more numerous closer to the pith. Scalariform intervessel pits are more common in UF 12461 than in the type. When this Clarno wood type was first described (Scott & Wheeler 1982), information available on extant Magnoliaceae wood suggested that the occurrence of some opposite intervessel pits in combination with scalariform intervessel pits indicated affinities with *Magnolia*, rather than with *Michelia*. However, subsequent examination of additional samples shows this not to be a reliable distinction as *Michelia* species can have opposite and scalariform intervessel pits (Chen et al. 1993). Consequently, we are transferring this species to *Magnoliaceoxylon* with which it shares the characteristics given below.

Similarities to extant woods — The combination of narrow vessels that are solitary and in short radial multiples, scalariform and opposite pits, marginal parenchyma, 2–3-seriate heterocellular multiseriate rays, and rare uniseriate rays indicates affinities with the Magnoliaceae. There are occasional opposite intervessel pits; according to Chen's key this feature suggests affinities are more likely to be with evergreen species of *Magnolia*, rather than with *Manglietia*. However, the features (vessel-ray parenchyma pits, and small crystals) used to distinguish *Magnolia* from *Michelia* and *Knemeria* were not observed. Consequently, it is not possible to say with certainty which genus this Clarno wood most closely resembles (Chen et al. 1993).

Magnoliaceoxylon cutleri sp. nov. (Fig. 27A–H)

Growth rings indistinct, with latewood fibers slightly flattened radially.

Diffuse porous. Vessels solitary and in radial multiples of 2–3, solitary vessels tend to be angular in outline, average tangential diameter 64 (13) µm; 5–10/mm^2, scalariform perforations, with 8–20 bars; opposite to mostly scalariform intervessel pits; vessel-ray parenchyma pits horizontally elongate and with reduced borders; helical thickenings not observed; vessel elements 1161 (157) µm long; tyloses not observed.

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

Axial parenchyma rare, scanty paratracheal, 9–12 cells per strand.

Rays 1–3(–4)-seriate. Multiseriate rays heterocellular, with 1–2 marginal rows of square/upright cells, uniseriate rays not common and composed of upright cells; total height of multiseriate rays 960 (200), 565–1,240 µm high; idioblasts present in ray margins; 8–12/mm.

Crystals not observed.

Storied structure absent.

Holotype: USNM 507999 (C4A-140 / DEN 38, > 9 cm).

Paratype: USNM 508002 (C4A-40, 6.5 cm).

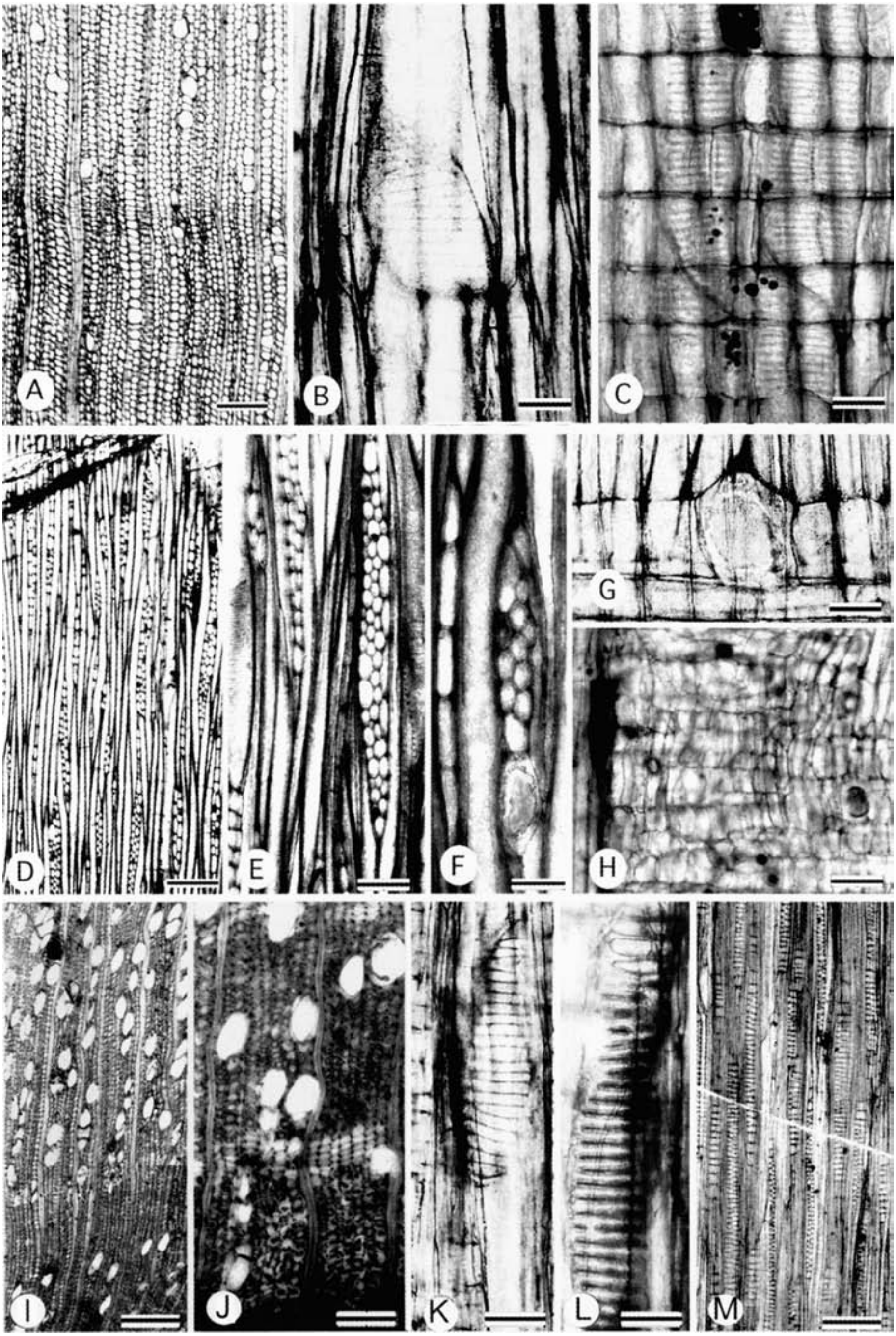
Etymology: Named for David F. Cutler, who in 1999 retired as Head of the Anatomy Section, Jodrell Laboratory, Kew, and has studied root wood anatomy.

Comments — It is possible that this wood could be root wood, as fibers are very thin-walled. The absence of distinct growth rings and marginal parenchyma also is consistent with this sample being root wood. Although vessels are sometimes wider in roots than in stems, there are examples of narrower, fewer vessels in root wood (Carlquist 1961). No pith is present so it is not possible to determine whether it is stem or root wood. Inflated cells filled with orange-brown contents ("oil cells"?) are common in this wood, and the distorted tissue indicates wounding (Fig. 27H).

Similarities to extant woods — The combination of exclusively scalariform perforation plates, predominantly scalariform with some opposite intervessel pits, "oil cells", and 1–3(–4)-seriate rays is unique to the Magnoliaceae. Wood of Chinese Magnoliaceae has been studied by Chen et al. (1993), and the family's wood anatomy reviewed by Canright (1955) and Metcalfe (1987). This Clarno magnoliaceous wood is not similar to present-day temperate *Magnolia*, all of which lack oil cells, have distinct growth rings marked by radially flattened fibers and marginal parenchyma, and often have some simple perforations. Exclusively scalariform perforation plates, predominantly scalariform intervessel pits, and rays with oil cells occur in *Elmerillia* and some *Michelia* (tribe Micheliodeae of subfamily Magnolioideae), and some evergreen tropical to sub-tropical *Magnolia* (including *Aromadendron* and *Talauma*, tribe Magnolieae of Magnolioideae).

According to Chen et al.'s (1993) key to Chinese Magnoliaceae, the lack of helical thickenings suggests affinities with evergreen species of *Magnolia* which lack helical thickenings, rather than with *Michelia* which has helical thickenings. However, helical thickenings are extremely fine and barely visible using phase contrast in four of the extant *Michelia* species. The preservation of this fossil is good, but we doubt that it is good enough to allow determining whether weakly developed helical thickenings are present or absent. The low vessel density (5–10/mm^2) is more consistent with the Michelioideae than the Magnolioideae (Metcalfe 1987; Lemmens et al. 1995; Sosef et al. 1998). Using quantitative features for determining affinities of Middle Eocene woods, especially samples of small diameter axes, is questionable. It is not clear whether *Michelia* and *Elmerillia* can be distinguished by their wood anatomy.

Because this wood has features occurring only in the Magnoliaceae, but not within a single extant genus, it is assigned to *Magnoliaceoxylon*.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Comparisons with other fossil woods — This wood has a lower vessel density than any other *Magnoliaceoxylon* species (Table 7). Also, the combination of mostly scalariform pits, frequent oil cells, and lack of obvious marginal parenchyma distinguishes it from other *Magnoliaceoxylon*. Consequently, it is recognized as a separate species. *Michelia oleifera* Suzuki (1976) from the Oligocene of Japan has helical thickenings in its vessel elements and vessel density > 100/mm^2.

Magnoliaceoxylon longiradiata (Scott & Wheeler) comb. nov. (Fig. 27 I–M)

Magnolia longiradiata Scott & Wheeler 1982, p. 141–142, figs. 32–37.

Growth rings distinct, marked by radially narrower fibers and marginal (zonate) parenchyma bands that are 2–4 cells wide.

Diffuse porous. Vessels solitary and in radial multiples of 2–3 (rarely 4), average tangential diameter 69 (10)–70 (9.5) µm, range 50–85 µm; vessel frequency 44–83/mm^2; scalariform perforations, with 6–26 bars, mostly 12–15; 3–5 µm between bars; mostly scalariform intervessel pits, some opposite and transitional; vessel-ray parenchyma pits with narrow borders and horizontally elongate; mean vessel element lengths 875 (143)–1,090 (153) µm; helical thickenings and tyloses not observed.

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

Axial parenchyma marginal to zonate, 8–12 cells per strand.

Rays 1–3-seriate. Heterocellular, with uniseriate margins of 1–3, up to 10, marginal rows of square and upright cells; uniseriate rays composed of upright cells; idioblasts rare (one observed in ray margin); total multiseriate ray height 0.2–2 mm; 5–11/mm.

Crystals not observed.

Storied structure absent.

Additional material: UF 12011 (7 cm).

Comments — UF 12011 is similar to the type of *Magnoliaceoxylon longiradiata*, except it lacks idioblasts and has shorter rays (maximum ray height of 1300 µm). We consider these differences comparable to those found within a single species of magnoliaceous wood and that this sample is another representative of the *M. longiradiata* wood type.

←

Fig. 27. A–H: *Magnoliaceoxylon cutleri* sp. nov. (USNM 507999). – A: Few widely spaced narrow vessels, thin-walled fibers, indistinct growth rings, XS. – B: Scalariform perforation plate, < 20 bars, RLS. – C: Horizontally elongate vessel-ray parenchyma pits, RLS. – D: Multiseriate heterocellular rays, mostly 2–3 cells wide, TLS. – D, E: Multiseriate rays and scalariform intervessel pits, TLS. – F: Ray with marginal idioblast, TLS. – G: Idioblast in marginal row of ray, RLS. – H: Probable wound area with distorted cells, and some ray cells with contents, RLS. — I–M: *Magnoliaceoxylon longiradiata* comb. nov. (UF 12011) – I: Diffuse porous wood, with vessels solitary and in radial multiples, marginal parenchyma, XS. – J: Growth ring boundary marked by marginal parenchyma, XS. – K: Scalariform perforation plate ca. 20 bars, RLS. – L: Scalariform intervessel pits, TLS. – M. Narrow multiseriate heterocellular rays, TLS. — Scale bars = 250 µm in A, D, I, M; 100 µm in E, H, J; 50 µm in K, L; 25 µm in B, C, F, G.

Similarities to extant woods — The combination of marginal parenchyma, scalariform perforation plates, scalariform-opposite intervessel pits, non-septate fibers, and rays less than 4-seriate only occurs in the Magnoliaceae, mostly commonly in the genus *Magnolia*, but also in *Kmeria, Manglietia*, *Elmerillia* and *Michelia* (Chen et al. 1993). On the basis of quantitative features, this fossil is more likely to be related to *Magnolia* or *Manglietia* than to *Elmerillia* (< 5 vessels/mm^2 and < 10 bars per perforation plate) or *Michelia* (2–5 bars per perforation plate). Because this wood type has a combination of features diagnostic of Magnoliaceae, but not only of the genus *Magnolia*, we propose that *Magnolia longiradiata* be transferred to *Magnoliaceoxylon*.

Comparisons with other fossil woods — This wood was recognized as a distinct species of Magnoliaceae fossil wood because some perforations have more than 20 bars and there are tall (> 1 mm) rays (Scott & Wheeler 1982).

MALVACEAE *sensu lato*

Genera previously attributed to the Sterculiaceae are now attributed to the broadly circumscribed Malvaceae which includes former Sterculiaceae, Tiliaceae, Bombacaceae, and Malvaceae (Beyer et al. 1999; Judd & Manchester 1998).

CHATTAWAYA Manchester

Chattawaya paliforme Manchester (Fig. 28)

Growth rings distinct, delineated by a broadening of the rays and by the abrupt transition from small latewood vessels to larger earlywood vessels of the succeeding ring.

Wood semi-ring porous to diffuse porous; vessels solitary and in radial multiples of 2–4; average tangential diameter 111 (26) µm in UF 12352, 151 (32) µm in UF 12071, vessel frequency 10–18/mm^2 (UF 12071), 12–30/mm^2 (UF 12352); perforations simple; intervessel pits alternate, 4–6 µm; vessel-parenchyma pits similar to intervessel pits; helical thickenings absent; average vessel element length 422 (123) µm; thin-walled tyloses present.

Fibres non-septate, no pits observed.

Axial parenchyma reticulate, in uniseriate tangential aggregates separated by 2–4 rows of fibers, diffuse, and in vasicentric sheaths; strands of 4–8 cells.

Rays 1–14-seriate, in some areas tending to be aggregate, and tending to be of two sizes. Multiseriate rays heterocellular; sheath and tile cells abundant; tile cells about 1/3 as wide radially as the procumbent; average height of rays with obvious differences in ray cell size 1,002 (496)–1,036 (524) µm, range 330–2,240; uniseriate rays less than 10 cells high; 2–6/mm.

Rhomboidal crystals in axial parenchyma strands, common in the tile cells.

Storied structure absent.

Holotype: UF 12071 (> 9 cm).
Additional material: UF 12352 (> 30 cm).

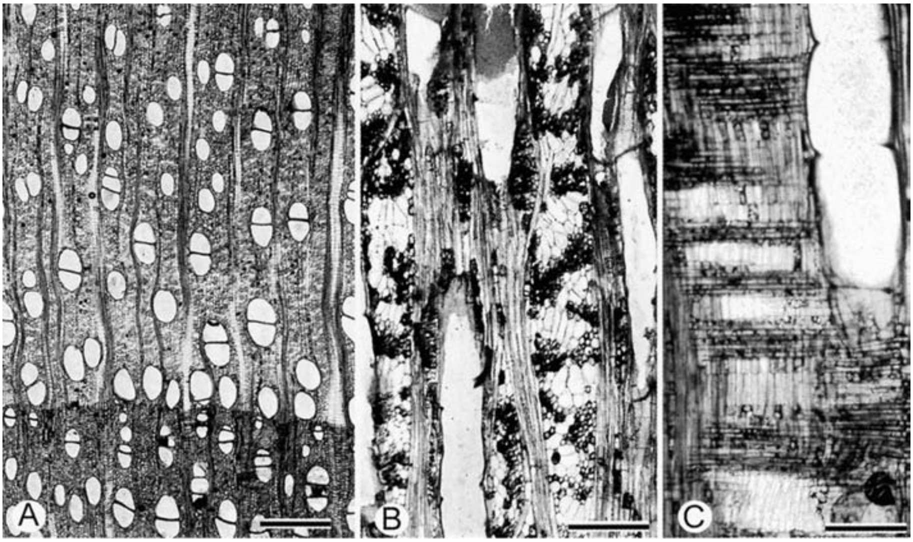

Fig. 28. *Chattawaya paliforme* Manchester (UF 12071). – A: Diffuse to semi-ring porous wood with vessels solitary and in radial multiples, XS. – B: Rays with prominent tile cells, TLS. – C: Short vessel elements and tile cells in the rays. — Scale bars = 500 µm in A; 250 µm in B, C.

Similarities to extant woods — Features of the axial parenchyma distribution, and the occurrence of tile cells indicate that this wood belongs to the Malvales. Manchester (1980) found the closest resemblance to some species of the extant *Pterospermum*, although the characteristic winged seeds of that modern genus have not been found as fossils.

TRIPLOCHITIOXYLON Manchester

Triplochitioxylon oregonensis Manchester (Fig. 29)

Growth rings distinct, semi-ring porous to diffuse porous (the latter probably representing root wood).

Vessels solitary and in radial multiples of 2–3; average tangential diameter 185 µm (85 µm in suspected root wood); vessel frequency averages 1–9 (mean 5) mm^2 (3–6–15/ mm^2 in suspected root wood), perforations simple; intervessel pits alternate, 3–5 µm; vessel-parenchyma pits similar to intervascular; helical thickenings absent; vessel elements 400–600 µm, average 440 (50) µm in UF 12050, 487 (59) µm in USNM 508023 (n = 7); thin-walled tyloses present (Manchester 1979: fig. 13).

Fibres non-septate, storied, lengths 517 (46)–535 (55) µm, 430–640 µm.

Axial parenchyma in uniseriate to biseriate tangential bands separated by 1–3 rows of fibers, and in vasicentric sheaths 1–3 cells wide; strands of 2–12 cells. Distinctly to indistinctly storied.

Rays 1–10-seriate (4–6). Heterocellular; sheath and tile cells abundant. Tile cells of the intermediate type, 2–3 times wider tangentially and 2–3 times higher than the procumbent cells but half to 1/8 as wide radially; multiseriate ray height 780 (295) µm, maximum 1400 µm in USNM 508023, 1267 (595) µm, maximum 2100 µm in UF 12050 (n = 18); 4–8 / mm in USNM 508023, 3–4 / mm in UF 12050.

Rhomboidal crystals present in some of the tile cells (Manchester 1979: fig. 6).

Holotype: UF 12050.
Paratype: USNM 508023 (C4A-8, > 10 cm).

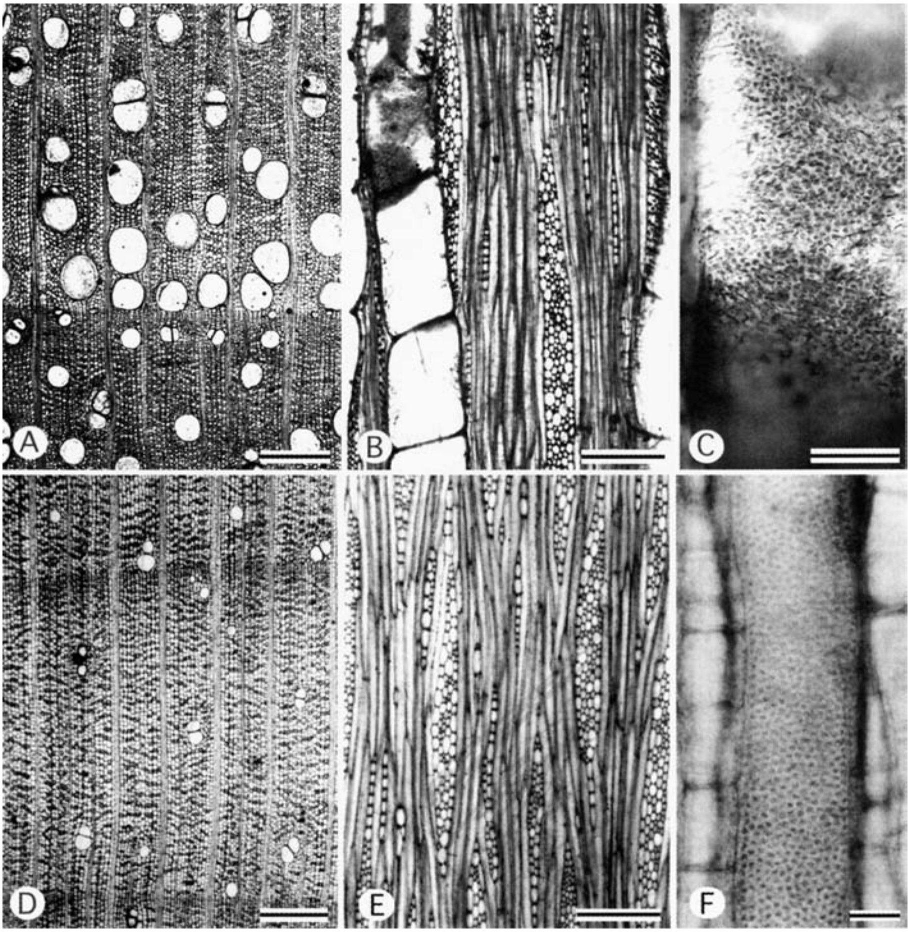

Fig. 29. *Triplochitioxylon oregonensis* Manchester, A–C: Holotype, stem wood (UF 12050), D–F: Root? (USNM 508023). – A: Transition from narrow latewood vessels to wide early-wood vessels at growth ring boundary, reticulate parenchyma, XS. – B: Vessel elements with slightly inclined end walls, storied parenchyma, and rays interspersed with tile cells, TLS. – C: Crowded alternate intervascular pits. – D: Diffuse porous wood; narrow few vessels, and reticulate paren-chyma, XS. – E: Storied parenchyma strands; rays with tile cells, TLS. – F: Alternate intervascular pits, TLS. — Scale bars = 500 µm in A, D; 250 µm in B, E; 50 µm in C, F.

Comments — Of the two *Triplochitioxylon* samples observed from the Nut Beds, one (UF 12050) is semi-ring porous (Fig. 29A) and believed to represent aerial stem wood, while the other (USNM 508023) is diffuse porous (Fig. 29D), with narrower, more scattered vessels and thought to represent root wood. Vessel element and fiber lengths are similar in the two samples. USNM 508023 (root?) has shorter, narrower, and more frequent rays than UF 12050.

Similarities to extant woods — The pattern of axial parenchyma distribution, coupled with the occurrence of tile cells confirms that this wood belongs within the order Malvales. Manchester (1979) established the genus *Triplochitioxylon* for this wood based on striking similarities to the African genus *Triplochiton*. He also observed differences particularly in length of elements and degree of storying, that led him to recognize the fossil as an extinct genus. Extant *Triplochiton* has distinctive *Acer*-like winged fruits that have not been observed in the fossil record, although they would be needed to confirm the presence of that genus.

Triplochitioxylon oregonensis is also known from some samples from upper Eocene localities in Oregon, indicating that its occurrence was not limited to the middle Eocene: at Post, Oregon (UF loc. 279, sample 24546), and "Clarno flats" (UF loc. 18309, specimen UF 25233). Based on co-occurrence at these other localities, *Triplochitioxylon* wood might correspond to the extinct Malvalean genus *Florissantia* known from flowers and fruits (Manchester 1992). Both *Florissantia* and *Triplochitioxylon* extend from the middle to the late Eocene of Oregon. Fruits of *Florissantia* even continue into the Oligocene; *Triplochitioxylon* wood has not yet been confirmed from the lower Oligocene.

Terada and Suzuki (1998) recognized a very similar extinct genus of fossil wood from the Oligocene and Miocene of Japan, which they named *Wataria*. They consider that it is most similar to *Triplochiton* and *Triplochitioxylon*, but noted *Wataria* had more pronounced ring porosity, shorter vessel elements, more cells per parenchyma strand, and lacked crystals in ray and axial parenchyma. The more pronounced ring porosity of *Wateria* is consistent with its younger age, an age when seasonal climates were more common.

PLATANACEAE

The Platanaceae is represented in the Nut Beds by three genera of fruits (Manchester 1994), one of leaves (Manchester 1986), and at least one of wood (Scott & Wheeler 1982).

PLATANOXYLON Andreansky emend. Süss & Müller-Stoll

Platanoxylon haydenii (Felix) Süss & Müller-Stoll (Fig. 30)

Platanus haydenii Felix 1896. Zeitschr. Deut. Geol. Ges. 48: 251.

Plataninium haydenii Felix emend. Wheeler, Scott & Barghoorn 1977, p. 295 (and other references cited therein).

Platanoxylon haydenii (Felix) Süss & Müller-Stoll 1977.

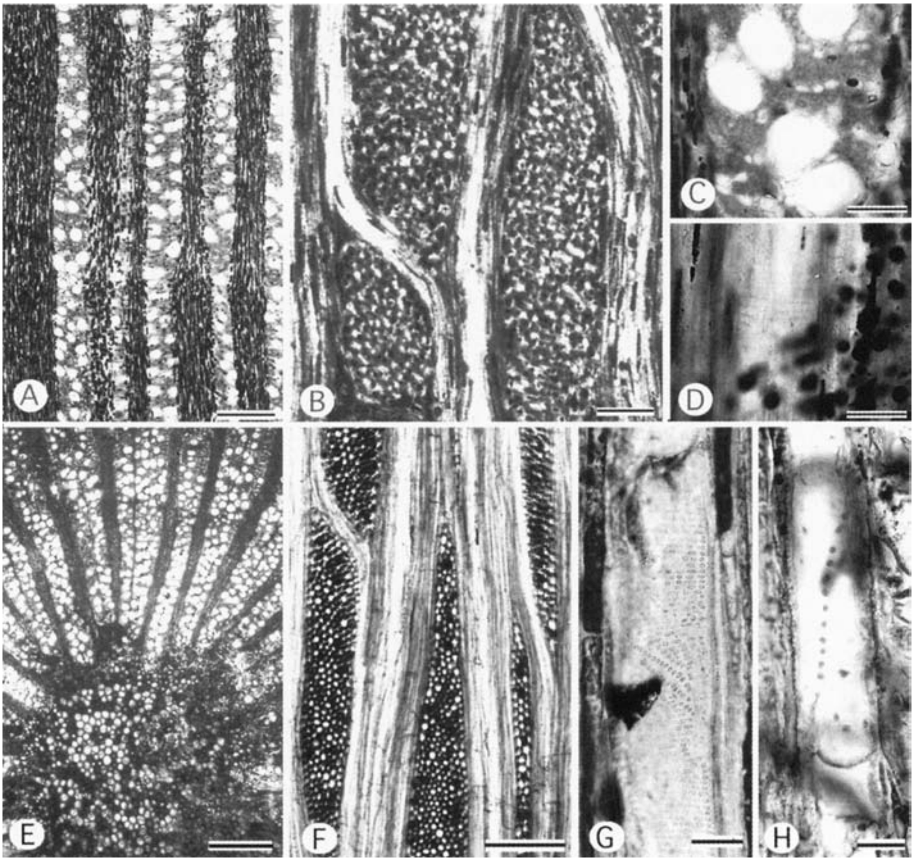

Fig. 30. *Platanoxylon haydenii* (Felix) Süss & Müller-Stoll, A–D: UF 6738; E, F: UF 32875; G, H: USNM 508014. – A: Diffuse porous wood with solitary vessels, and occasional multiples, XS. – B: Wide multiseriate rays, > 15 cells wide, TLS. – C: Diffuse-in-aggregates axial parenchyma, XS. – D: Scalariform perforation plate, RLS. – E: Pith composed of isodiametric parenchymatous cells, multiseriate ray width increasing with distance from pith, XS. – F: Multiseriate rays > 10-seriate common, uniseriate rays rare. – G: Opposite intervessel pits, TLS. – H: Scalariform perforation plates, TLS. — Scale bars = 500 µm in A, E; 250 µm in B, F; 100 µm in C, D; 50 µm in G, H.

Growth rings distinct, marked by an abrupt transition to somewhat smaller pores, and dilation of the rays.

Diffuse porous. Earlywood pores somewhat larger than latewood pores; solitary, and in multiples of 2–5 (often tangentially arranged) average tangential diameter 68–117, mean 91 µm; vessel frequency averages of 25–67/mm^2 (total range of 15–80/mm^2), perforations exclusively scalariform, with 4–27 bars, generally less than 10 bars; intervessel pits (rarely preserved) opposite, 5–7 µm; pits to parenchyma opposite and scalariform; vessel element lengths average 732; range 500–990 µm; tyloses common to abundant.

Fibres non-septate, pitting not observed.

Axial parenchyma apotracheal, diffuse as isolated cells and diffuse-in-aggregates as short uniseriate bands.

Rays 2–27-seriate and up to 500 µm wide, rarely uniseriate. Homocellular to heterocellular with 2–3 rows of square and upright cells, composed of procumbent cells; multiseriate ray height up to 5 mm; 3–4/mm. Height of procumbent cells in center of multiseriate rays average 30–62 µm.

Rhomboidal crystals occasional to common in procumbent ray cells.

Storied structure absent.

Pith 2–4 mm diameter, composed of parenchyma cells 37–62 µm in diameter, without fibrovascular bundles (cf. *Anomalocentra pseudoplatana*).

Samples: USNM 326708 (Scott & Wheeler 1982); USNM 508010 (C61-19, 1.6 cm, complete with pith), USNM 508012 (C4A-9, > 10 cm), USNM 508013 (C4A-17, 4.5 cm), USNM 508014 (C4A-21, > 10 cm), USNM 508015 (C4A-52, > 28 cm, complete), USNM 508016 (C4A-102, > 10 cm), USNM 508017 (C4A-118, 9 cm), USNM 508018 (C4A-142, > 14 cm), USNM 508019 (C4A-143A, > 8 cm); UF 6738 (23 cm diam.), UF 12438 (> 20 cm), UF 32874 (2 cm), UF 32875 (1.2 cm), UF 32876 (1 cm).

Scott and Wheeler (1982) recognized this species from the Nut Beds as conspecific with the Yellowstone platanoid species, *Plataninium haydenii* Felix emend. Wheeler, Scott & Barghoorn (1977). Their generic assignment was based on the broad concept of *Plataninium* Felix as emended by Page (1968) to accommodate a wide range of generally *Platanus*-like fossil woods. However, Süss and Müller-Stoll (1977) advocated a much narrower circumscription of *Plataninium*, noting that Unger's original diagnosis of the genus mentions spirally thickened elements – which do not occur in extant *Platanus*, for example. Thus, in the scheme of Süss and Müller-Stoll, *Platanus*-like woods with spiral thickening belong in *Plataninium* (e.g., Süss 1971), while the other *Platanus*-like fossil woods should be placed in *Platanoxylon*. Accordingly, Süss and Müller-Stoll (1977) transferred many species formerly placed in *Plataninium* to *Platanoxylon* and, in the process, created the new combination *Platanoxylon haydenii* (Felix) Süss & Müller-Stoll. We accept this interpretation, and use that binomial for the Nut Beds species.

Although wood similar to that of *Platanus* occurs in genera of some unrelated families, e.g., *Citronella* (Icacinaceae), *Euptelea* (Eupteleaceae), *Fagus* (Fagaceae), Scott and Wheeler (1982) summarized criteria that can be used to distinguish them. The rays of *Platanus* are homocellular and range from very large to medium, with only rare uni- and biseriate rays. In the other genera uniseriate rays are more common. In *Euptelea* and Icacinaceae, the rays are heterocellular. In addition, Süss indicated that the modern genera *Fagus* and *Platanus* can be separated by the height of the procumbent cells in the center of large multiseriate rays: less than 20 µm in *Fagus*, 20–30 µm in *Platanus*, and more than 30 µm in *Euptelea* and Icacinaceae. In *Platanoxylon haydenii* these cells measure 30–60 µm; however, the similarity to *Platanus* remains very striking in the other characters. As already emphasized (Scott & Wheeler 1982), *P. haydenii* differs from all of the modern species of *Platanus*, with both simple and scalariform vessel perforations, because this fossil has only scalariform perforations.

It is possible that *Platanoxylon haydenii* represents the living genus *Platanus*; however, the apparent lack of simple vessel element perforations in the fossil species is an important difference, suggesting either that the wood retains this as a primitive feature now lost from the extant species, or that the fossil wood may indeed represent an extinct genus of the family. Among the fruiting remains at the Nut Beds, the extinct platanaceous genus *Macginicarpa* (Manchester 1986, 1994) is one of the most abundant taxa. Based on co-occurrence at multiple localities, *Macginicarpa* is considered likely to correspond to the extinct leaf genus, *Macginitiea* (Manchester 1986). *Macginitiea* and *Macginicarpa* occur together not only at the Nut Beds, but at many localities elsewhere in the Clarno Formation and in the lower part of the John Day formation, as well as at Yellowstone. *Macginitiea* and *Macginicarpa* are missing from the Tertiary of Europe, and the fossil platanaceous woods found in Europe differ from *Platanoxylon haydenii*, and resemble extant species of *Platanus*, in possessing both scalariform and simple vessel perforations. *Platanus* leaves were not found in the Nut Beds, although they are known from other localities of the Clarno Formation. Leaves of both *Macginitiea* and *Platanus* occur in the tuffs at Yellowstone where the original collection of *Platanoxylon haydenii* wood was made.

Platanoxylon haydenii is represented in the Nut Beds by both roots and aerial parts of the tree. Some of the pieces are fragments from axes of large diameter but lack the central portion needed to determine whether they are roots or aril parts. Stems and branches, verifiable by the presence of a central pith, range from about one cm to more than 23 cm diameter**.** The largest root, lacking pith (C4A-2A), is 8 cm in diameter. The wood of these two are shown for comparison in Figure 30. In the axis with pith, the rays are crowded with relatively little space for intervening fiber and vessels. In the root, the rays are spaced more widely.

ROSACEAE

Two species of *Prunus* were recognized in the Nut Beds flora on the basis of fruit types. The shape and anatomy of one species resemble the domesticated cherry, *Prunus avium* (L.) L. *Quintacava velosida* Manchester, whose affinities could not be established with certainty, has characteristics consistent with fruits of the Maloideae. The rosaceous woods are consistent with fruit types; one wood has characteristics of the Maloideae, two have characteristics of *Prunus*.

MALOIDOXYLON Grambast-Fessard

Maloidoxylon annae sp. nov. (Fig. 31)

Growth rings distinct, marked by radially flattened fibers, and a differences in vessel diameter between the latewood and earlywood of successive rings.

Diffuse porous to semi-ring porous. Vessels almost exclusively solitary; tending to be angular in outline, average tangential diameter 45 (9) µm; vessel frequency 114–140/mm^2; perforations simple; intervessel pits alternate, round to irregular in outline, 6–8 µm; vessel-ray parenchyma pits similar in size and shape to intervessel pits;

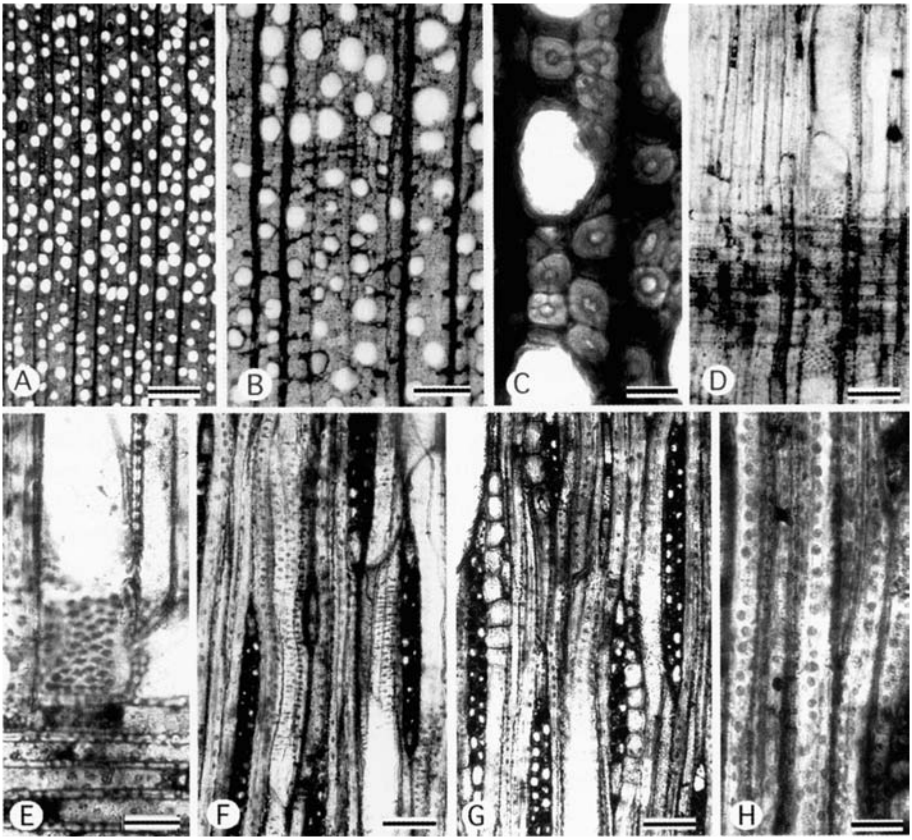

Fig. 31. *Maloidoxylon annae* sp. nov. (USNM 507927). – A: Diffuse porous wood with vessels almost exclusively solitary, XS. – B: Growth ring boundary, last formed latewood vessels narrower than next year's earlywood vessels, apotracheal diffuse and scanty paratracheal parenchyma, XS. – C: Medium-thick to thick-walled fibers, with pits in both radial and tangential walls, XS. – D: Simple perforation and heterocellular rays with square marginal cells, RLS. – E: Vessel-ray parenchyma pitting, ray parenchyma cells with many simple pits, RLS. – F: Helical thickenings throughout length of vessel element, TLS. – G: Rays 1–3-seriate, crystalliferous axial parenchyma strands, TLS. – H: Fiber pits distinctly bordered, RLS. — Scale bars = 250 µm in A; 100 µm in B, D; 50 µm in F, G; 25 µm in C, E, H.

helical thickenings present throughout the length of the vessel elements; average vessel element length 437 (188) µm; tyloses not observed.

Fibers non-septate, walls medium to thick, distinctly bordered pits on both radial and tangential walls.

Axial parenchyma apotracheal, diffuse, and with a few cells touching the vessels, 4–8 cells per strand.

Rays 1–3-seriate. Multiseriate rays heterocellular, body of procumbent cells, and usually with one row of marginal square/upright cells; total multiseriate ray height averages 441 (51), range 339–520 µm; 8–12/mm.

Prismatic crystals in inflated crystalliferous strands of axial parenchyma, crystalliferous strands usually adjacent to the rays, 4–8 chambers.

Storied structure absent.

Holotype: USNM 507927 (DEN 40, fragment 3 cm across).
Etymology: Named for Anna Wheeler.

Similarities to extant woods — Only genera of the Rosaceae have the combination of exclusively solitary, narrow (< 100 μm) vessels, simple perforations, alternate intervessel pits, spiral thickenings on vessel element walls, fibers with distinctly bordered pits, diffuse axial parenchyma, and crystals in chambered axial parenchyma. The Maloideae are characterized by having distinctly bordered pits on both radial and tangential walls (Zhang & Baas 1992; Zhang 1992).

Zhang (1992) developed a key to extant genera of Rosaceae. According to that key, this wood has characteristics of his wood group VII, which includes the genera *Amelanchier, Crataegus, Cydonia* p.p., *Docynia, Malus* p.p., *Mespilus, Peraphyllum, Polylepis, Pyrus* p.p., and *Sorbus*, all Maloideae, plus *Cercocarpus*, tentatively assigned to the Rosidae. Extant genera of Maloideae are difficult to distinguish wood anatomically. Because the Clarno wood has characteristics of the Maloideae and these characteristics are consistent with the diagnosis of *Maloidoxylon*, it is assigned to that genus.

Comparisons with other fossil woods — The Clarno wood differs from previously described *Maloidoxylon* species because it has helical thickenings throughout the vessel elements. The two European species, *M. castellanense* (Miocene, Grambast-Fessard 1966) and *M. lutetianium* (Eocene, Privé-Gill 1981) have both simple and scalariform perforation plates, and their rays usually have more than one marginal row of upright cells. The two species from the Miocene of the United States are based on roots with wider rays and shorter vessel elements (Wheeler & Matten 1977).

Prunus L.

cf. ***Prunus gummosa*** (Platen) Wheeler, Scott, & Barghoorn (Fig. 32A–E)

Growth rings present, distinct, marked by 2–3 rows of radially flattened fibers.

Diffuse porous. Vessels solitary (48%) and in radial multiples of 2–5, with a few clusters; solitary vessels round to oval in outline; average tangential diameter 46 μm; vessel frequency 103–168–213/mm^2; perforations simple; intervessel pits alternate, round to irregular in outline, 6–8 μm; vessel-ray parenchyma pits similar to intervessel pits or slightly smaller; helical thickenings not observed; vessel element lengths 203–372 μm; tyloses not observed, gum deposits appear to be in some vessels.

Fibers non-septate, walls medium-thick, distinct pitting on radial walls, especially on fibers near vessels.

Axial parenchyma apotracheal diffuse, and with a few cells touching the vessels, 4–8 cells per strand.

Rays 1–3(–4)-seriate. Multiseriate rays heterocellular, body composed of procumbent cells, usually with one row of marginal square/upright cells; uniseriate rays com-

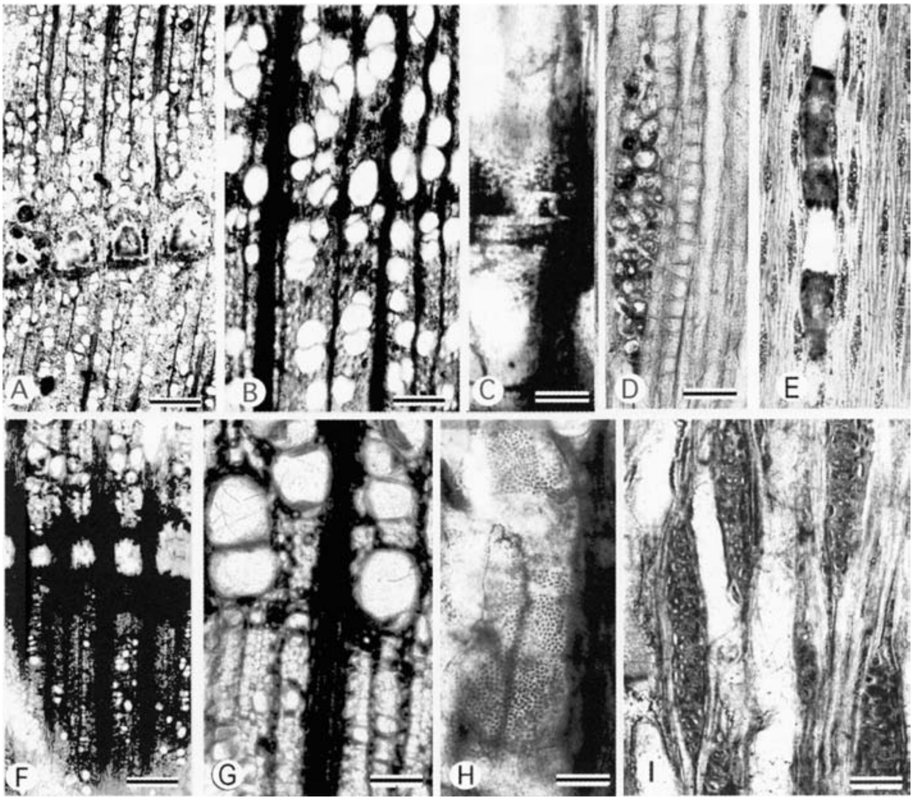

Fig. 32. A–E: cf. *Prunus gummosa* (Platen) Wheeler, Scott, & Barghoorn (USNM 507926). – A: Diffuse porous wood with traumatic gum canals at the beginning of the growth ring, XS. – B: Detail of growth ring boundary, XS. – C: Intervessel pits and vessel-ray parenchyma pits, RLS. – D: Multiseriate ray and chambered axial parenchyma with one crystal per chamber, TLS. – E: Multiseriate rays, 3–4 cells wide, TLS. — F–I: *Prunus* sp. (UF 32328). – F: Earlywood zone with traumatic canals, latewood zone with vessels in radial multiples and clusters, XS. – G: Growth ring boundary, earlywood vessels markedly wider than latewood vessels, diffuse parenchyma, XS. – H: Crowded alternate intervessel pits, TLS. – I: Rays tending to be of two sizes, wide multiseriate rays up to 8 cells across, and narrow rays mostly 1–3-seriate, TLS. — Scale bars = 250 μm in A, E, F; 100 μm in B, G, I; 50 μm in C, D, H.

posed of upright cells, 5–8 cells, 120–200 μm high; multiseriate ray height averages 313 (46) μm, 249–452 μm; 5–8/mm.

Prismatic crystals present in chambered axial parenchyma, not enlarged to slightly enlarged, up to 17 chambers.

Storied structure absent.

Traumatic canals present, in tangential lines at growth ring boundaries.

Sample: USNM 507926 (DEN 33, > 13 cm across).

Similarities to extant woods — *Prunus* s.l. (Rosaceae) is the only extant genus in the OPCN database that has the combination of narrow (< 100 µm), numerous vessels (> 40 /mm^2) that are solitary and in multiples, simple perforations, alternate intervessel pits, heterocellular rays, fibers with distinctly bordered pits, diffuse parenchyma, and traumatic axial canals. The characteristics listed here are consistent with the data for *Prunus* s.l. (Zhang 1992; Zhang & Baas 1992). Zhang uses ray size in his key to Rosaceae: ray height > 1 mm vs. height < 1 mm; rays 1–3(–4)-seriate or narrower vs. widest rays not narrower than 4-seriate. It is questionable whether these quantitative ray features would be reliable diagnostic features for relatively small diameter material of the Rosaceae, such as the Clarno material. According to Zhang's key to extant genera of the Rosaceae, the Clarno wood closely resembles *Padus* p.p., which is included in *Prunus* s.l. Zhang observed crystals only in the Chinese species of the *Padus* group of *Prunus* s.l. According to Zhang's (1992) key, the *Cerasus* group (which includes *Prunus avium*) differs from this Clarno wood because the *Cerasus* group has rays higher than 1 mm, libriform fibers, and less than 30 % of the vessels are solitary.

Comparisons with other fossil woods — Woods with characteristics of the Prunoideae have been described from the Eocene of North America (Wheeler et al. 1978; Süss & Müller-Stoll 1980; Cevallos-Ferriz & Stockey 1990b; Wheeler & Landon 1992), Oligocene of Europe (Dupéron 1976), and Oligocene and Miocene of Asia (Suzuki 1984; Takahashi & Suzuki 1988; Suzuki & Watari 1994; Suzuki & Terada 1996). The four species of Oligocene Japanese *Prunus* woods have a higher proportion of vessel multiples and longer radial multiples than the Eocene Prunoideae woods. The Miocene *Prunus iwatense* (Watari) Takahashi & Suzuki has relatively few vessel multiples and wider rays (3–7-seriate). The French Oligocene *Prunus* wood and some of the Japanese species have a dendritic to diagonal vessel arrangement. A late Eocene *Prunus*-like wood from Nebraska differs because it has rays tending to two distinct sizes, with the larger rays typically 6–8-seriate (sometimes to 10-seriate). The middle Eocene *Prunus allenbyensis* (Cevallos-Ferriz & Stockey 1990b) from the Princeton Chert, British Columbia, is similar to *Prunus gummosa* but was considered distinct on the basis of small quantitative features (mainly vessel element features); wider rays (to 8-seriate) also distinguish *P. allenbyensis*.

Vessel element dimensions (diameter and length) are remarkably similar in the Clarno *Prunus* and the early Eocene Yellowstone *Prunus gummosa* (mean tangential diameter 47 µm, lengths to 370 µm). Rays of the Clarno *Prunus* wood are shorter and slightly narrower than the Yellowstone *Prunus gummosa* (105–763 µm, 4-seriate). The Clarno *Prunus* wood and the Yellowstone *Prunus* wood may represent different species, but they are as similar to one another as are five different samples of extant *Prunus serotina* (BWCw 8022, 8061, 8199, 8263, 8284, 8623). These extant woods vary in whether the multiseriate rays are commonly 3-seriate or 4-seriate (a difference between the Yellowstone and Clarno *Prunus* woods), whether vessels are randomly arranged or tend to a diagonal to tangential arrangement, and whether they are diffuse porous or tend to be semi-ring porous. Multiseriate ray width also varies within *Prunus avium* (Süss & Müller-Stoll 1980). Crystals were not observed in the Yellowstone wood, but crystal abundance varies within a species, so this does not seem a valid reason to consider the Clarno wood a separate species. Thus, the Clarno wood is assigned to *Prunus gummosa*.

Prunus sp. (Fig. 32F–I)

Growth rings present, distinct, marked by 2–3 rows of radially flattened fibers, and by differences in latewood-earlywood vessel diameter.

Semi-ring porous. Vessels solitary and in radial multiples of 2–5, also clusters, especially in the latewood; solitary vessels round to oval in outline; average tangential diameter of earlywood vessels 117 (21) µm, 84–140 µm; perforations simple; intervessel pits crowded alternate, round to irregular in outline, 4–6 µm; vessel-ray parenchyma pits similar to intervessel pits or slightly smaller; helical thickenings not observed; vessel element lengths 258–448 µm; tyloses not observed.

Fibers non-septate, walls medium-thick, distinctly bordered pits on radial walls.

Axial parenchyma apotracheal diffuse and diffuse-in-aggregates, and with a few cells touching the vessels.

Rays 1–8-seriate. Multiseriate rays heterocellular, body composed of procumbent cells, and usually with one row of marginal of upright cells; uniseriate rays composed mostly of square and upright cells, with some procumbent cells, multiseriate ray height averages 472 (168) µm, 203–825 µm; 6–9/mm.

Prismatic crystals present in chambered axial parenchyma, chambers not enlarged, up to over 20 chambers in a strand.

Storied structure absent.

Traumatic canals present, in tangential lines at growth ring boundaries.

Sample: UF 32328 (> 10 cm).

Comments — There is only one small fragment of this wood type. Traumatic gum canals are common. Wounded woods often have larger rays than unwounded woods. The distinctiveness of the growth rings may also be related to the wounding.

Similarities to extant woods — The general characteristics of this wood are the same as extant *Prunus* s.l. Suzuki and Terada (1996) discussed similarities between *Prunus* and *Elaeagnus* wood, which share heterocellular rays, traumatic gum-canals, and rather large rays and ray cells. This Clarno wood is similar to *Prunus,* not *Elaeagnus*, which commonly has solitary vessels, fibers with distinctly bordered pits on both radial and tangential walls, moderately abundant axial parenchyma, and lacks crystalliferous strands of axial parenchyma (Metcalfe & Chalk 1950; pers. observ.).

Comparisons with other fossil woods — This wood is distinct from *P. gummosa* because it has larger multiseriate rays, fewer uniseriate rays and is distinctly semi-ring porous to almost ring porous. We are choosing not to assign this wood a name, as the extensive wounding may have altered some of its characteristics, relative to normal wood. If further collections from the Nut Beds or other parts of the Clarno Formation yield additional samples similar to this one, but without extensive wounding, then it would be appropriate to assign a specific epithet.

SABIACEAE

The Nut Beds assemblage includes five species of *Meliosma* based upon fruits and seeds (Manchester 1994); there are leaves as well (Manchester 1981). The endocarp species correspond most closely to subgenus *Kingsboroughia* (one species) and subgenus *Meliosma* section *Meliosma* (four species), a section which today is exclusively Asian and Malesian. There are 55 extant species of *Meliosma*, 15 tropical Asian and 40 American (Mabberley 1997).

There are three types of *Meliosma* wood in the Nut Beds assemblage, distinguished by variation in porosity, ray size and ray cellular composition. Six wood anatomical groups can be distinguished in extant *Meliosma* subgenus *Meliosma*. Descriptions of these six wood groups follow the descriptions of the three Clarno *Meliosma*. For each extant wood anatomical group, its similarities to the Clarno woods is discussed.

All Clarno *Meliosma* woods have characteristics of subgenus *Meliosma* section *Meliosma*. *Meliosma brehmii* and *M. deweyii* have characteristics of Wood Group IV which includes species of subsection *Simplices*. Characteristics of *Meliosma deweyii* also occur in Wood Group VI, which includes species of subsection *Pinnatae*. *Meliosma dodsonii* does not match any of the extant wood groups, semi-ring porous wood occurs in Wood Group V, but Group V has predominantly simple perforations.

It is possible that, with additional collections of both extant and fossil wood, it will be determined that there are fewer than three *Meliosma* wood types at Clarno, as there may be samples with anatomy intermediate between the types now recognized.

MELIOSMA Blume

Meliosma brehmii sp. nov. (Fig. 33)

Growth rings distinct, marked by radially flattened fibers, and by marginal parenchyma.

Diffuse porous. Vessels solitary (47%) and in radial multiples of 2–4, average grouping 1.39; solitary vessels oval to slightly angular in outline; average tangential diameters of 104 (27) µm; vessel frequencies of 16–25–37/mm^2; scalariform perforations with 1–8 widely spaced bars, average 5 bars, occasionally bars forked, bars ca. 5 µm thick, spacing between bars 15–27 µm, one simple perforation observed; crowded alternate intervessel pits, 5–10 µm; most vessel-ray parenchyma pits generally similar to intervessel pits, but with slightly reduced borders, some with moderately reduced borders and horizontally elongate; helical thickenings not observed; average vessel element length 691 (165) µm; tyloses present.

Fibers non-septate, walls thin, generally appearing to be in regular radial rows, rectangular in cross-sectional outline; pits not observed; tangential diameter 29 (5) µm.

Axial parenchyma scanty paratracheal to vasicentric, and marginal, at least 8 cells per strand.

Rays 1–5-seriate. Body of multiseriate rays apparently with some square to barely procumbent cells, upright cells very common, uniseriate rays common and composed exclusively of upright cells, often less than 10 cells high; multiseriates 767 (106) µm, to 2.3 mm high; 6–7/mm.

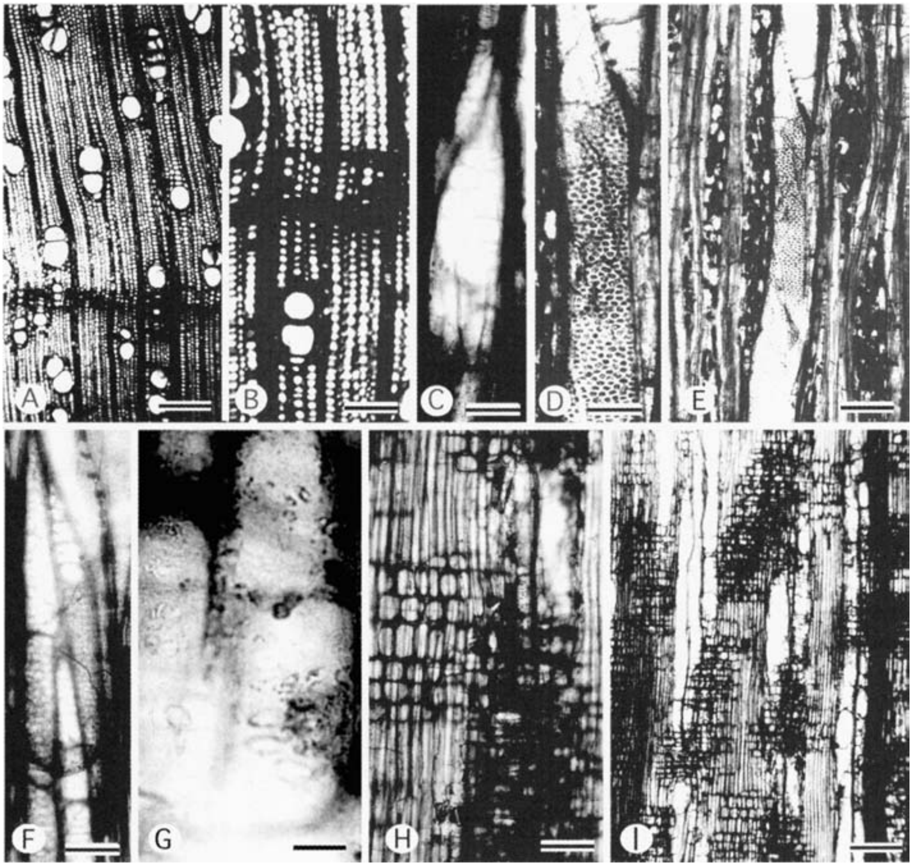

Fig. 33. *Meliosma brehmii* sp. nov. (USNM 507929). – A: Diffuse porous wood, vessels solitary and in radial multiples of 2–3, XS. – B: Thin-walled fibers; growth ring boundary, XS. – C: Scalariform perforation plate with 5 bars, RLS. – D: Crowded alternate to subopposite pits, TLS. – E: Alternate intervessel pits, scalariform perforation, tall multiseriate rays, TLS. – F: Scalariform perforation, TLS. – G: Vessel-ray parenchyma pits horizontally enlarged and with reduced borders, RLS. – H, I: Rays composed mostly of upright and square cells, RLS. — Scale bars = 250 µm in A, I; 100 µm in B, E, H; 50 µm in C, D, F; 12 µm in G.

Prismatic crystals not observed.

Storied structure absent.

Holotype: USNM 507929 (DEN 116, > 5 cm).

Etymology: Named for Bert Brehm, biology professor at Reed College, Portland, Oregon.

Meliosma deweyii sp. nov. (Fig. 34A–H)

Growth rings distinct, marked by radially flattened fibers.

Diffuse porous. Vessels solitary (38%) and in radial multiples of 2 (rarely 3), 1.53 vessel grouping; solitary vessels usually oval in outline; average tangential diameter

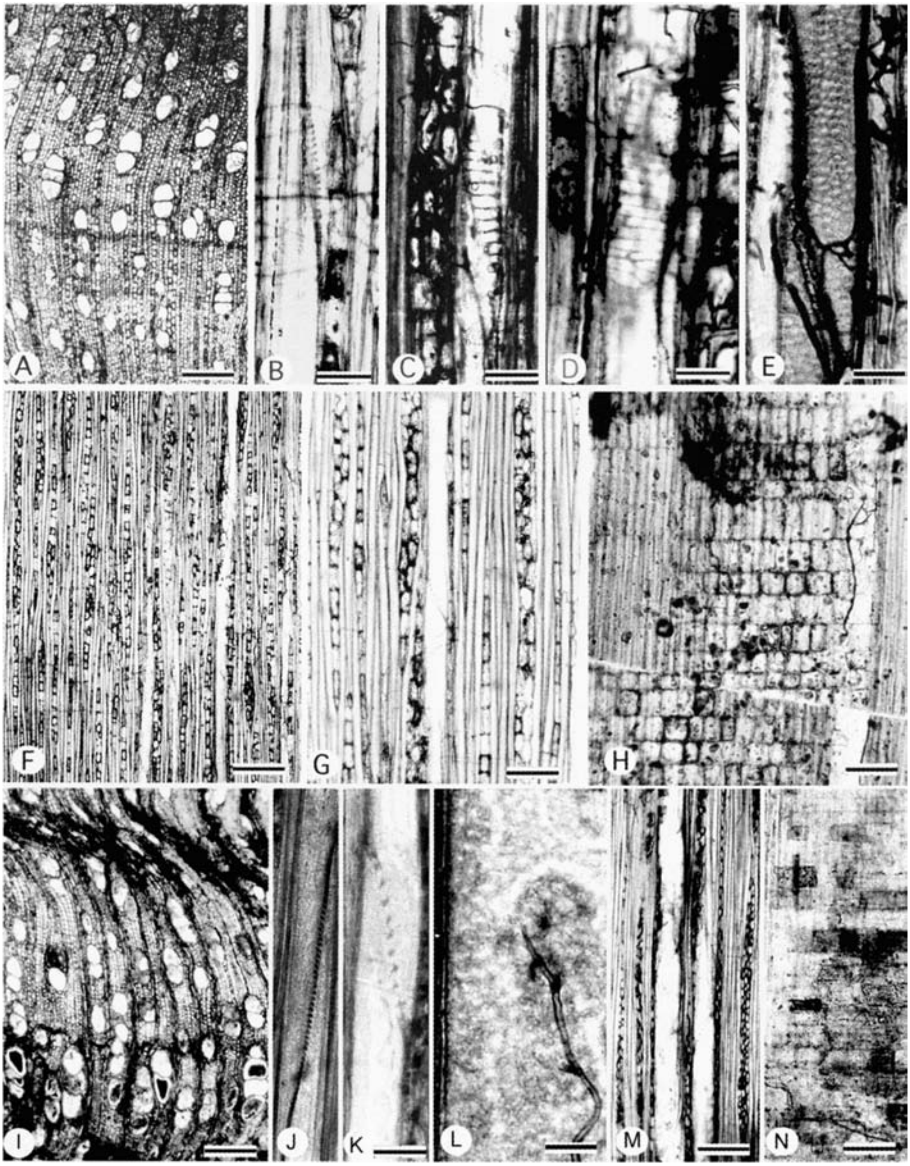

Fig. 34. A–H: *Meliosma deweyii* sp. nov. (UF 12488). – A: Diffuse porous wood with vessels solitary and in radial multiples of 2–3, XS. – B, C, D: Scalariform perforation plates, TLS. – E: Crowded alternate intervessel pits, TLS. – F: Tall, narrow rays with multiseriate and uniseriate rays both common, TLS. – G: Non-septate fibers, and vertically elongated ray cells, TLS. – H: Heterocellular ray mostly of upright and square cells, RLS. — I–N: *Meliosma dodsonii* sp. nov. (UF 12363). – I: Tendency to semi-ring porosity, XS. – J: Scalariform perforation in narrow vessel element, with > 20 bars, TLS. – K: Scalariform perforation with < 10 bars, TLS. – L: Alternate intervessel pitting, TLS. – M: High multiseriate rays, TLS. – N: Ray composed mostly of square cells, RLS. — Scale bars = 250 µm in A, F, I, M; 100 µm in G, H, J, K, N; 50 µm in B, C, D; 25 µm in E, L.

81 (18) µm; vessel frequency 19–31–52/mm^2; scalariform perforations, averaging 10 bars, range 6–20; crowded alternate intervessel pits, 4–6 µm; vessel-ray parenchyma pits similar in size to intervessel pits; helical thickenings not observed; average vessel element length of 829 (107) µm.

Fibers non-septate, thin-walled.

Axial parenchyma rare.

Rays 1–2- (rarely 3-)seriate, uniseriate rays very common. Rays composed mostly of square and upright cell, procumbent cells present, but not common; total multiseriate ray height 1,475 (245) µm, to 2 mm; 7–12 per mm.

Prismatic crystals not observed.

Storied structure absent.

Holotype: UF 12488 (9 cm).

Etymology: Named for David Dewey Johnson, in thanks for his years of teaching wood anatomy labs.

Comments — Compared to *Meliosma brehmii*, this wood has less parenchyma, shorter vessel multiples, more bars per perforation, longer vessel elements, and narrower rays. Consequently, we are recognizing it as a distinct entity.

Meliosma dodsonii sp. nov. (Fig. 34 I–N)

Growth rings distinct, marked by radially flattened fibers.

Diffuse porous, tending to semi-ring porous. Vessels solitary (34–42%) and in radial multiples of 2 (rarely 3), 1.46–1.56 vessel grouping; solitary vessels usually oval in outline; average tangential diameter 112 (23)–129 (18) µm; average vessel frequency 22–31/mm^2; total range of 15–45; scalariform perforations, averaging 8–9 bars, range 4–24; crowded alternate intervessel pits, 4–6 µm; vessel-ray parenchyma pits not observed; helical thickenings not observed; average vessel element length of 886 (146)–953 (140) µm.

Fibers non-septate, walls mostly thin, sometimes medium-thick, pits not observed.

Axial parenchyma rare.

Rays 1–4-seriate, uniseriate rays common; rays tending to be of two sizes; composed of intermixed square, upright, and procumbent cells; to 7 mm high; 6–10/mm, mostly 7/mm.

Prismatic crystals not observed.

Storied structure absent.

Holotype: UF 12363 (> 10 cm).

Paratype: UF 32217 (5–8 cm).

Etymology: Named for James Dodson.

Comments — This wood differs from the other Clarno *Meliosma* wood types as it is semi-ring porous and has markedly taller rays.

There is an additional wood (UF 12453) that resembles *Meliosma* in appearance, but has poor preservation, and intervessel and vessel-ray parenchyma pits were not observed. This wood's characteristics are:

Growth rings faintly marked by radially flattened fibers.

Diffuse porous. Vessels solitary (14%), usually oval in outline, and in radial multiples of 2–4 (6), 1.94 vessel grouping; average tangential diameter 102 (23) µm; vessel frequency 17–24–38/mm^2; scalariform perforations, averaging 7 bars, range 5–10; average vessel element length of 1,011 (70) µm.

Fibers non-septate, thin-walled.

Axial parenchyma rare.

Rays 1–3-seriate, uniseriate rays very common. Rays composed of square, upright and procumbent cells; total multiseriate ray height to 2.3 mm high; usually 5 per mm.

Prismatic crystals not observed.

Storied structure absent.

Sample: UF 12453 (6 cm).

Comments — The vessel distribution pattern, long vessel element lengths, scalariform perforation plates, thin fiber walls, and ray structure are consistent with *Meliosma*. However, because neither intervessel nor vessel-ray parenchyma pits were observed this wood cannot with certainty be assigned to family or genus. Radial multiples are more common in this wood than in the Nut Beds woods assigned to *Meliosma*.

Similarities to extant woods — The combination of scalariform perforation plates and alternate intervessel pits is not a common one among extant dicotyledons; in the OPCN database *Meliosma* is the only genus with these two characters in combination with rays commonly > 1 mm high, and predominantly paratracheal parenchyma. Carlquist et al. (1993) examined 30 species of *Meliosma* (one sample each). This study emphasized the potential ecological implications of variations in wood anatomy (especially of vessel characteristics), and briefly discussed systematic implications. They recorded variation between species in whether perforations were exclusively simple or scalariform, number of bars per perforation plate, ray composition (whether rays were composed predominantly of upright, square, or procumbent, or a mixture), abundance of uniseriate rays, vessel grouping, diameter, frequency, and vessel element length.

Meliosma was monographed by Van Beusekom (1971), who used morphological features, particularly endocarp features. We have examined slides of extant *Meliosma* (prepared by SRM) to investigate further whether the infrageneric groups within *Meliosma* have distinctive wood anatomy. Species examined and wood anatomical features are listed below according to Van Beusekom's infrageneric classification scheme. Species names are those associated with the wood samples, with Van Beusekom's synonymies in parentheses. The wood anatomical groupings are assigned numbers.

Subgenus Meliosma

Section Lorenzanea: [New World] *M.* cf. *allenii*, *M. dentata* (SJRw 55354), *M. glabrata* (SJRw 35418), *M. glossophylla* (SJRw 43275: Type), *M. herbertii, M. occidentalis* (SJRw 42851: Type), *M. panamaensis* (SJRw 11972, 35519), *M. pittieriana* (SJRw 23984), *M. sinuata* (U 12587).

MELIOSMA WOOD GROUP I — Growth rings indistinct to absent, distinct growth rings only observed in *M. pittieriana* and there marked by distinct bands of radially narrower, thick-walled fibers. Wood diffuse porous. Vessels solitary and in radial multiples of 2 (rarely 3); mean tangential diameters of 77–127 µm; mean vessel element lengths 762–1,052 µm, mostly > 900 µm; perforations almost exclusively reticulate to foraminate with some scalariform in *M. occidentalis* and *M. panamaensis*, almost exclusively scalariform with less than 10 bars (usually less than 5) in *M. dentata* and *M. herbertii*, and mixed scalariform and foraminate-reticulate in others; alternate intervessel pits, 6–12 µm; vessel-ray parenchyma pits with reduced borders, and often enlarged and irregularly shaped, vertically elongated or narrow kidney-shaped. Fibers without distinctly bordered pits, walls thin to medium. Axial parenchyma rare, scanty paratracheal. Rays 1–4(–5)-seriate, composed of intermixed square, upright, and procumbent cells, procumbent cells not common; uniseriate rays few to common. No crystals observed.

Comments — Perforation type varies within this section, but otherwise it is wood anatomically homogeneous. More samples per species should be examined before determining whether species or species groups can be distinguished by type of multiperforate plate.

Similarities to Nut Beds woods — None of the Nut Beds *Meliosma* woods are likely to be related to this New World section. *Meliosma brehmii* differs because it has a simple perforation, vessel-ray parenchyma pits have reduced borders, but they are not enlarged relative to the intervessel pits and not irregular in shape. *Meliosma deweyii* differs because it has vessel-ray parenchyma pits similar to the intervessel pits, perforation plates have up to 20 bars, and no foraminate-reticulate plates were observed. *Meliosma dodsonii* has distinct growth rings and is semi-ring porous.

Section Meliosma

Subsection Simplices: *M. cuneifolia* (SJRw 21732; = *M. dilleniifolia* subsp. *cuneifolia* (Franch.) Beus.), *M. fischeriana* (SJRw 21735; = *M. simplicifolia* subsp. *yunnanensis* (Franch.) Beus.), *M. lepidota* subsp. *lepidota* (DeWilde & DeWilde-Duyfjes 15058, 14115), *M. myriantha* (OSU 2848, PRFw 1498), *M. nitida* (SJRw 30615, = *M. sumatrana* (Jack) Walp.), *M. parviflora* (PFRw 14719), *M. simplicifolia* (SJRw 12564, 35520), *M. simplicifolia* subsp. *simplicifolia* (Beusekom & Geesink 2662, 3768), *M. squamulata* (SJRw 6524, 24932, = *M. lepidota* Blume subsp. *squamulata*).

MELIOSMA WOOD GROUP II — *Meliosma myriantha/M. parviflora* — Growth rings distinct, marked by radially narrower latewood fibers. Diffuse porous. Vessels solitary and in radial multiples of 2; average tangential vessel diameters of 63–95 µm; vessel element lengths < 700 µm; alternate intervessel pits minute to small, 2–4 µm; vessel-ray parenchyma pits are similar to intervessel pits; rays are 1–4-seriate, and composed of procumbent (common), and square and upright cells. Fibers without distinctly bordered pits, walls thin to medium. Vasicentric parenchyma is distinct, strands typically more than 8 cells. Crystals observed in the ray cells of *M. parviflora* (both samples), but not in *M. myriantha*.

Comments — *Meliosma myriantha* and *M. parviflora* form a distinct group as they have both simple and scalariform perforation plates and mostly solitary vessels surrounded by vasicentric parenchyma; in *M. myriantha*, some vessels are in short radial chains separated by a single parenchyma cell, and at low magnification appear to be vessel multiples.

Similarities to Nut Beds woods — All the Nut Beds woods differ from this group as they have predominantly or exclusively scalariform plates, larger intervessel pits, and the rays do not commonly have procumbent cells.

MELIOSMA WOOD GROUP III — *Meliosma fordii* — Growth rings absent to indistinct. Diffuse porous. Vessels solitary, and mostly in radial multiples; perforations scalariform, mostly 5–12 bars, alternate intervessel pits, vessel-ray parenchyma pits usually similar to intervessel pits, but some with reduced borders and somewhat enlarged. Fibers without distinctly bordered pits, thin- to medium-thin-walled. Parenchyma scanty paratracheal, usually 4 cells per strand. Rays mostly > 4-seriate, to 8-seriate, uniseriate rays rare; rays composed of intermixed square, procumbent, and upright cells. Crystals in ray parenchyma.

Comments — Carlquist et al. (1993) questioned whether *M. fordii* should be reduced to a subspecies of *M. simplicifolia* because the sample they examined had distinctive wood anatomy. Another wood sample of *M. fordii* that we examined also suggests that *M. fordii* is distinct wood anatomically within subsection *Simplices* because it commonly has radial multiples, its multiseriate rays are typically more than 4-seriate and up to 8-seriate, and uniseriate rays are rare.

Similarities to Nut Beds woods — The Nut Beds woods differ from this wood group as they commonly have solitary vessels, multiseriate rays are narrower and uniseriate rays are common.

The remainder of the samples of subsection *Simplices* are similar and intergrade in their anatomical features.

MELIOSMA WOOD GROUP IV — Growth rings distinct, marked by radially flattened fibers, or by zonate parenchyma. Diffuse porous. Vessels solitary and in radial multiples of 2–3; average tangential diameters of 75–124 µm, perforations scalariform with 5–20 bars, occasional reticulate and multiperforate perforations in *M. lepidota* subsp. *lepidota*; alternate intervessel pits 5–11 µm; vessel-ray parenchyma pits similar to intervessel pits, or with reduced borders but not much enlarged, some narrow horizontal; average vessel element lengths 682–946 µm. Fibers without distinctly bordered pits, walls thin to medium. Parenchyma scanty paratracheal, to narrow vasicentric (no more than 1 cell wide sheath), 4–8 cells per strand. Rays tending to be of two distinct sizes; 1–4-seriate (to 6 in *M. cuneifolia*), uniseriate rays common to abundant; rays composed of intermixed square, procumbent, and upright cells. Crystals (solitary or in groups) in ray parenchyma of *M. simplicifolia*.

Similarities to Nut Beds woods — The general features of both *Meliosma brehmii* and *M. deweyii* occur in Meliosma Wood Group IV, except that the Nut Beds woods' rays do not tend to be of two sizes.

> ***Subsection Pinnatae:*** *M. arnottiana* (= *M. pinnata* subsp. *arnottiana*), *M. kirkii* (= *M. pinnata* subsp. *arnottiana*, PRFw 14718), *M. macrophylla* (= *M. pinnata* subsp. *macrophylla*, MADw 5740, MADw 37811, Kostermans 6911), *M. oldhami* (= *M. pinnata* subsp. *arnottiana*, SJRw 24931), *M. pinnata* (SAN 79851, R. Schodde 2409), *M. rhoifolia* (= *M. pinnata* subsp. *arnottiana*, SJRw 9412), *M. sumatrana* (SJRw 35521), *M. wallichii* (= *M. pinnata* subsp. *arnottiana*, SJRw 46612).

Meliosma Wood Group V — Growth rings distinct, marked by rays widened at growth rings, radially narrower latewood fibers, and more abundant vessels in the earlywood (pronounced in *M. kirkii*), diffuse porous to semi-ring porous. Vessels solitary, in radial multiples, and in groups (the groups often being circular in outline). Perforations predominantly simple, some scalariform usually with less than 5 widely spaced bars. Intervessel pits alternate. Vessel-ray parenchyma pits similar to intervessel pits. *Meliosma rhoifolia* with helical thickenings throughout the body of the vessel elements. Axial parenchyma rare, a few strands adjacent to vessels. Fiber walls thin. Rays usually of two distinct sizes, uniseriate rays common, multiseriate rays to 6–10-seriate, procumbent cells common in body of ray. No crystals observed.

Comments — Carlquist et al. (1993) noted that wood anatomy supported the placing of *M. kirkii, M. oldhami, M. rhoifolia*, and *M. wallichii* in the same taxon, and merging *M. pinnata* subsp. *arnottiana* with *M. arnottiana*. The samples we studied also supports this conclusion, and indicates the wood anatomy of these species is similar, and constitute a distinct wood group.

Similarities to Nut Beds woods — None of the Nut Beds woods are referable to this wood group because they have exclusively scalariform perforations, lack circular groups of vessels, and typically have narrower rays.

The remainder of woods of subsection *Pinnatae* intergrade.

Meliosma Wood Group VI — Growth rings indistinct to distinct (*M. macrophylla*), diffuse porous. Vessels mostly solitary with occasional radial multiples of 2, perforations exclusively to predominantly scalariform, usually less than 10 bars, occasional foraminate plates (*M. nitida, M. ferruginea*), intervessel pits alternate, vessel-ray parenchyma pits mostly similar in size to intervessel pits, sometimes with reduced borders, axial parenchyma scanty paratracheal with 4–8 cells per strand. Fiber walls thin, fibers square to rectangular in outline, rarely polygonal. Rays 1–3-seriate, uniseriate rays very common in *M. sumatrana*, *M. pinnata* with mixed procumbent, square, and upright cells; rays 1–6-seriate in *M. ferruginea* and *M. macrophylla*, with uniseriates not common in *M. ferruginea*, obviously procumbent cells present. Crystals observed in rays of one sample of *M. sumatrana* (MADw 35521).

Comments — *Meliosma deweyii* is similar to this Wood Group VI. They share exclusively scalariform perforations, vessel-ray parenchyma pitting similar to intervessel pitting, thin-walled fibers that are rectangular in outline, narrow rays with intermixed procumbent, square, and upright cells.

SUBGENUS KINGSBOROUGHIA is distinct wood anatomically because it has exclusively or predominantly simple perforations, and homocellular rays. No Clarno *Meliosma* woods have these characteristics.

Comparisons with other fossil woods — *Meliosma mio-oldhami* (Watari 1949; Suzuki & Watari 1994) from the Miocene of Japan is similar to the extant *Meliosma oldhami*. It commonly has vessel clusters and very wide (to 9-seriate) rays, and so is distinct from the Clarno *Meliosma* woods. *Meliosma mio-oldhami* has characteristics of Wood Group V, a group that none of the Clarno woods match.

SAPINDACEAE

Two species of *Palaeoallophylus* are recognized in the Nut Beds fruit and seed flora (Manchester 1994), which have some characteristics of the extant genus *Allophylus*; *Koelreuteria* (unpub.) occurs in other parts of the Clarno Formation.

SAPINDOXYLON Kräusel

Sapindoxylon klaassenii sp. nov. (Fig. 35)

Growth rings distinct, marked by radially flattened latewood fibers.

Diffuse porous. Vessels solitary and in radial multiples of 2–3; average tangential diameters of 51 (11)–114 (30) µm; average vessel frequencies of 15–22, total range of 8–34/mm^2; perforations exclusively simple; intervessel pits crowded alternate, 3–4 µm; vessel-ray parenchyma pits similar to intervessel pits; helical thickenings not observed; average vessel element lengths of 363–440 µm, total range 217–621 µm; tyloses absent.

Fibers non-septate and septate, possibility of septate fibers in bands; walls thin to medium; pits not obvious.

Axial parenchyma rare to absent, occasional strand of parenchyma adjacent to vessel in some samples, with 8 or more cells in the strand.

Rays exclusively uniseriate. Heterocellular with 1–3 rows of marginal rows of square cells, some rays with square cells in the body of the ray; mean ray heights of 263 (117)–350 (160) µm, total range of 95–824 µm; 10–13/mm.

Crystals not observed.

Storied structure absent.

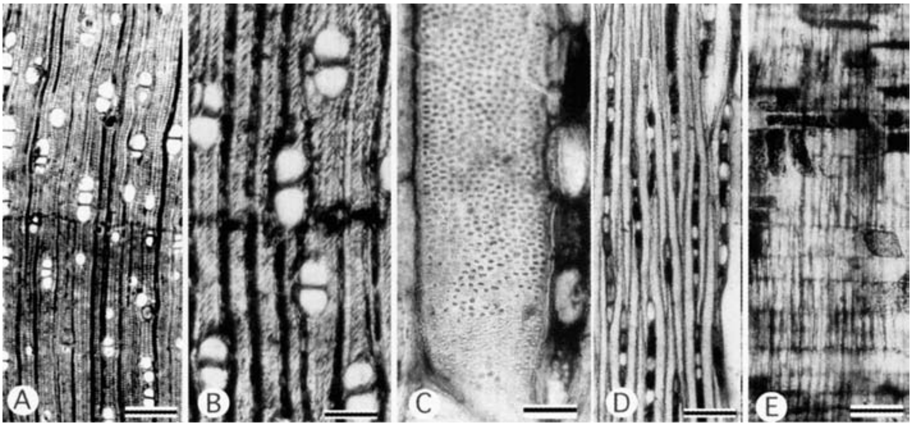

Fig. 35. *Sapindoxylon klaassenii* sp. nov. (UF 12005). – A: Diffuse porous wood with vessels solitary and in short radial multiples, XS. – B–E (UF 12003). – B: Detail of growth ring, marked by some radially flattened fibers, XS. – C: Crowded alternate intervessel pits, TLS. – D: Exclusively uniseriate rays, TLS. – E: Rays with procumbent and square/upright cells of similar height, square and procumbent cells sometimes intermixed, RLS. — Scale bars = 250 µm in A; 100 µm in B, D; 50 µm in E; 25 µm in C.

Holotype: UF 12003 (ca. 2 cm).

Paratypes: UF 12002 (> 14 cm), UF 12005 (> 10 cm), UF 12080, UF 12102.

Etymology: Named for René Klaassen, in recognition of his monographic treatment of the wood anatomy of the Sapindaceae.

Similarities to extant woods — Extant genera with the combination of vessels solitary and in short radial multiples, simple perforations, small-minute alternate intervessel pits, vessel-ray parenchyma pits similar to intervessel pits, indistinct fiber pits, heterocellular uniseriate rays that have a few marginal rows of upright/square cells, and rare axial parenchyma occur in the families Loganiaceae, Lythraceae, Punicaceae, and Sapindaceae. In *Neubergia* (Loganiaceae), solitary vessels are rare and rays reach 1 mm in height, in *Adenaria* and *Punica* (Lythraceae) vessel density is high (more than 40/mm^2), and in samples of *Adenaria* available for comparison rays were markedly more heterocellular. On the basis of quantitative vessel features, the fossil described above shares more features with the Sapindaceae than with the other aforementioned families.

Klaassen (1999) surveyed the wood anatomy of the Sapindaceae, examining 103 of the 133 genera, including representatives of all 13 tribes of the family. It is possible that this wood represents the same plant as the *Palaeoallophylus* recognized in the fruit and seed flora. However, extant *Allophylus* wood differs as it has mostly septate fibers, intervessel pits are 5–8 µm, and crystals in fibrous elements are a constant character (Klaassen 1999). The general pattern of extant *Allophylus* wood is similar to the Clarno fossil. However, Klaassen found that intervessel pit size, which he considered a useful diagnostic feature, was a stable character and not affected by stem diameter.

There are four wood anatomical types in extant Sapindaceae (Klaassen 1999). The Clarno wood is most similar to Group IV because of having intervessel pit sizes of 3–6 µm, scanty paratracheal parenchyma, and uniseriate rays. The Clarno wood lacks the abundant septate fibers and crystalliferous fibers that are characteristic of Group IV. However, crystal occurrence is variable within some sapindaceous genera and species. Group IV wood anatomy is particularly common in the Cupanieae alliance. In extant Sapindaceae, all deciduous species have obvious vessel wall sculpturing, and often have marginal parenchyma. Neither feature characterizes this Clarno wood, suggesting it is from an evergreen tree, rather than a deciduous tree.

Comparisons with other fossil woods — *Sapindoxylon* Kräusel 1922 is based on fossil wood from the ?Miocene of south Sumatra. The Clarno wood described above shares with *Sapindoxylon* the features: diffuse porous wood, vessels solitary and in short radial multiples, simple perforation plates, small alternate intervessel pits, vessel-ray parenchyma pits similar to intervessel pits, libriform fibers that are occasionally septate, paratracheal axial parenchyma that is not abundant, and predominantly uniseriate rays. *Sapindoxylon jansonnii* differs from the Clarno wood as its vessel density is 2–8/mm^2, vessel tangential diameters reach 200 µm, and marginal cells occasionally contain crystals. The material Kräusel studied was mature wood, the Clarno samples are relatively small fragments and probably are juvenile wood. It is not unusual for juvenile wood to have higher vessel frequencies and narrow vessels than mature wood, and to have heterocellular rays, while the mature wood has homocellular rays. Consequently, although the Clarno wood does not strictly conform to the genus *Sapindoxylon*, the differences are those associated with differences between juvenile and mature wood and we have chosen to assign the wood to *Sapindoxylon*. Klaassen (1999) found differences between juvenile and mature wood samples of Cupaniodeae in vessel frequency and diameter.

Other fossil woods with relatively high vessel densities and heterocellular rays have been assigned to *Sapindoxylon* (e.g., *S. koelreuterioides* Poole & Wilkinson 1992 based on small axes from the Eocene London Clay, England, and which had 43 vessels/mm^2). *Sapindoxylon* has become a variable construct, used for a variety of fossil woods with a combination of characteristics found in the Sapindaceae. It includes some species with only scanty paratracheal parenchyma (e.g., *S. chhindwarensis* Chitaley & Shallom 1969), and some species with aliform-confluent parenchyma (e.g., *S. haile-sellassiei* Lemoigne 1970).

Two species of *Sapindoxylon* were described from the London Clay (Eocene) of southeast England (Poole & Wilkinson 1992). The affinities of these twigs were determined not only on wood characteristics, but on pith cell characteristics. *Sapindoxylon guioaoides* pith cell characteristics are similar to those of extant *Alectryon* and *Guioa*; *S. koelreuterioides* pith cell characteristics are similar to those of extant *Nephelium* and *Koelreuteria*. Although *S. koelreuterioides* is named to suggest affinities with *Koelreuteria*, it is not ring porous as is extant *Koelreuteria*. The diffuse porosity of this twig might not reflect the porosity of the mature wood of this plant, as in extant woods sometimes wood near the pith is not ring porous while wood produced by an older cambium is. Also, an Eocene relative of *Koelreuteria* might have diffuse porous, rather than ring porous wood, as ring porosity is a feature most often expressed in seasonal climates. Axial parenchyma distribution could not be determined, so whether the London Clay twig has aliform-confluent parenchyma as does extant *Nephelium* is indeterminable.

ULMACEAE *sensu lato*

There are at least three members of the Celtidoideae (*Aphananthe, Celtis, Trema*), and one member of the Ulmoideae (the extinct genus *Cedrelospermum*) in the Nut Beds fruit and seed flora; fruits and foliage of *Ulmus* occur elsewhere in the Clarno Formation. There is one wood with characteristics of *Ulmus*; another wood resembles *Celtis*, but it has characteristics also seen in the Moraceae, so is described later as a member of the order Urticales, rather than assigned to family.

ULMUS L.

Ulmus danielii sp. nov. (Fig. 36)

Growth rings distinct, marked by radially flattened latewood fibers and differences in vessel diameter and arrangement between earlywood and latewood.

Semi-ring porous. Vessels solitary and in radial multiples, latewood vessels in tangential arrangement; average tangential diameter of earlywood vessels 87 (14) µm, range 61–101 µm; perforations simple; intervessel pits crowded alternate, 7–8 µm; vessel-ray parenchyma pits similar in size to intervessel pits, some with reduced borders; helical thickenings in narrowest vessel elements; average vessel element length 192 (33) µm, 129–246 µm; thin-walled, uncrowded tyloses in wider vessel elements.

Fibers non-septate, walls medium to thick, pits not observed.

Axial parenchyma paratracheal, interconnecting latewood vessel groups, 2–4 cells per strand.

Rays 1–5-seriate. Multiseriate rays homocellular to heterocellular, body composed of procumbent cells, heterocellular with 1 (2–4) rows of marginal square/upright cells; uniseriates low, mostly 3–4 cells high, up to 10 cells; average total multiseriate ray height 214 (72) µm, range 120–405 µm; 5–8/mm. Sheath cells not observed.

Solitary prismatic crystals in non-chambered axial parenchyma strands, possibly present in marginal upright cells of the rays.

Storied structure absent.

Holotype: USNM 507931 (DEN 4, > 14 cm).
Etymology: Named for Daniel Wheeler.

Comments — *Cedrelospermum* is known from twigs with attached leaves, fruits, and flowers (Manchester 1989) and is common at both Clarno and Florissant. However, the wood structure of *Cedrelospermum* twigs is not known, Ulmaceae wood at Clarno is not similar to Ulmaceae wood at Florissant, so it is not possible to infer the wood structure of this common Eocene plant.

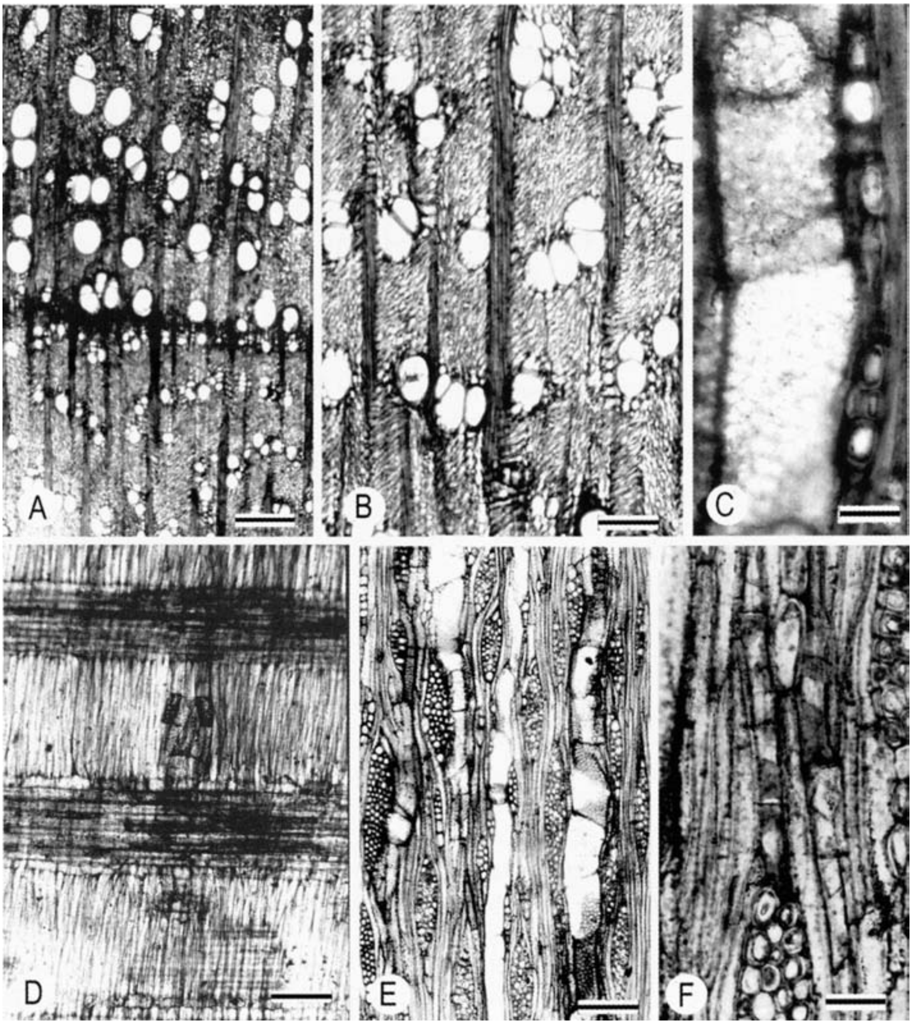

Fig. 36. *Ulmus danielii* sp. nov. (USNM 507931). – A: Semi-ring porous wood with latewood vessels in tangential arrangement, XS. – B: Latewood vessels, solitary and in multiples, with paratracheal parenchyma, XS. – C: Crowded alternate intervessel pitting, TLS. – D: Body of ray composed of procumbent cells, RLS. – E: Multiseriate rays, occasional thin-walled tyloses, side view of simple perforations, TLS. – F: Solitary prismatic crystals in axial parenchyma strand, TLS. — Scale bars = 250 µm in A; 100 µm in B, D, E; 50 µm in F; 25 µm in C.

Similarities to extant woods — The combination of semi-ring porosity (to ring porous), vessels in tangential arrangement, medium-sized to large intervessel pits, helical thickenings in vessel elements, vessel-ray parenchyma pits that are not enlarged, non-septate fibers, predominantly paratracheal parenchyma that is not banded, at least some homocellular rays, absence of storied structure, and crystals in ordinary cells occurs in the Ulmaceae.

There is considerable information about wood of the Ulmaceae (e.g., Sweitzer 1971; Wheeler et al. 1989; Zhong et al. 1992). The occurrence of mostly homocellular rays and crystals in axial parenchyma, rather than in ray parenchyma, suggests this wood belongs to the Ulmoideae. *Zelkova* is distinctive because of the enlarged crystalliferous ray cells; *Hemiptelea* usually has sheath cells and lacks crystals; *Planera*, which ranges from diffuse to ring porous, has more frequent clusters and helical thickenings, and obvious storied structure. Therefore, this wood is most similar to *Ulmus*. There are both ring porous and diffuse porous species of extant elms. Ring porous *Ulmus* are deciduous trees (rarely shrubs) from temperate to subtropical (rarely tropical) regions; diffuse porous *Ulmus* are evergreen or deciduous trees from subtropical to tropical regions (Zhong et al. 1992).

Comparisons with other fossil woods — Fossil woods of Ulmaceae are known from the early and late Eocene of the western United States, and the Tertiary of Japan and Europe. *Zelkova*-like woods, with their characteristic inflated crystalliferous marginal ray parenchyma cells, occur in the early Eocene Yellowstone Fossil Forests, Wyoming (Wheeler et al. 1978) and the late Eocene Florissant Fossil Beds, Colorado (Wheeler 2001). The Yellowstone *Zelkovoxylon* is semi-ring porous rather than ring porous as is extant *Zelkova*.

Fossil woods attributed to *Ulmus* occur in the Miocene Vantage Fossil Forests, Washington (Prakash & Barghoorn 1961a, 1961b); they differ from this Eocene wood as they are distinctly ring porous. Late Tertiary European and Japanese woods assigned to *Ulmus* or *Ulmoxylon* also are distinctly ring porous (e.g., *Ulmoxylon* sp. Hofmann 1944; *Ulmus* sp. Van der Burgh 1978, *Ulmus crystallophora* Watari 1952).

VITACEAE

Four genera of Vitaceae seeds are reported from the Nut Beds, *Ampelocissus* (2 spp.), *Ampelopsis, Parthenocissus* (2 spp.), and *Vitis* (2 spp.). Two vitaceous woods occur (Wheeler & LaPasha 1994). In contrast to the Clarno seeds whose combination of characteristics can be accommodated within extant genera, the wood's combination of characters cannot be accommodated within extant genera.

VITACEOXYLON Wheeler & LaPasha

Vitaceoxylon carlquistii Wheeler & LaPasha (Fig. 37A–D)

Growth rings distinct, marked by radially flattened latewood fibers.

Diffuse porous. Vessels tending to be of two diameter classes, solitary and in radial multiples of up to 16; average tangential diameter of solitary vessels 215 µm, range 50–325 µm; average radial diameter of solitary vessels 230 µm, range 50–365 µm; vessel frequency 8–15/mm^2; perforations simple; intervessel pits crowded alternate, 10–12 µm; vessel-ray parenchyma pits with reduced borders and horizontally enlarged; helical thickenings not observed; average vessel element length 654 µm, range 576–757 µm; tyloses present in some vessels.

Fibers septate, usually 3–4 septa per fiber, up to 6 septa; walls medium to thick, numerous simple pits on radial walls; storied; 667–904 µm long.

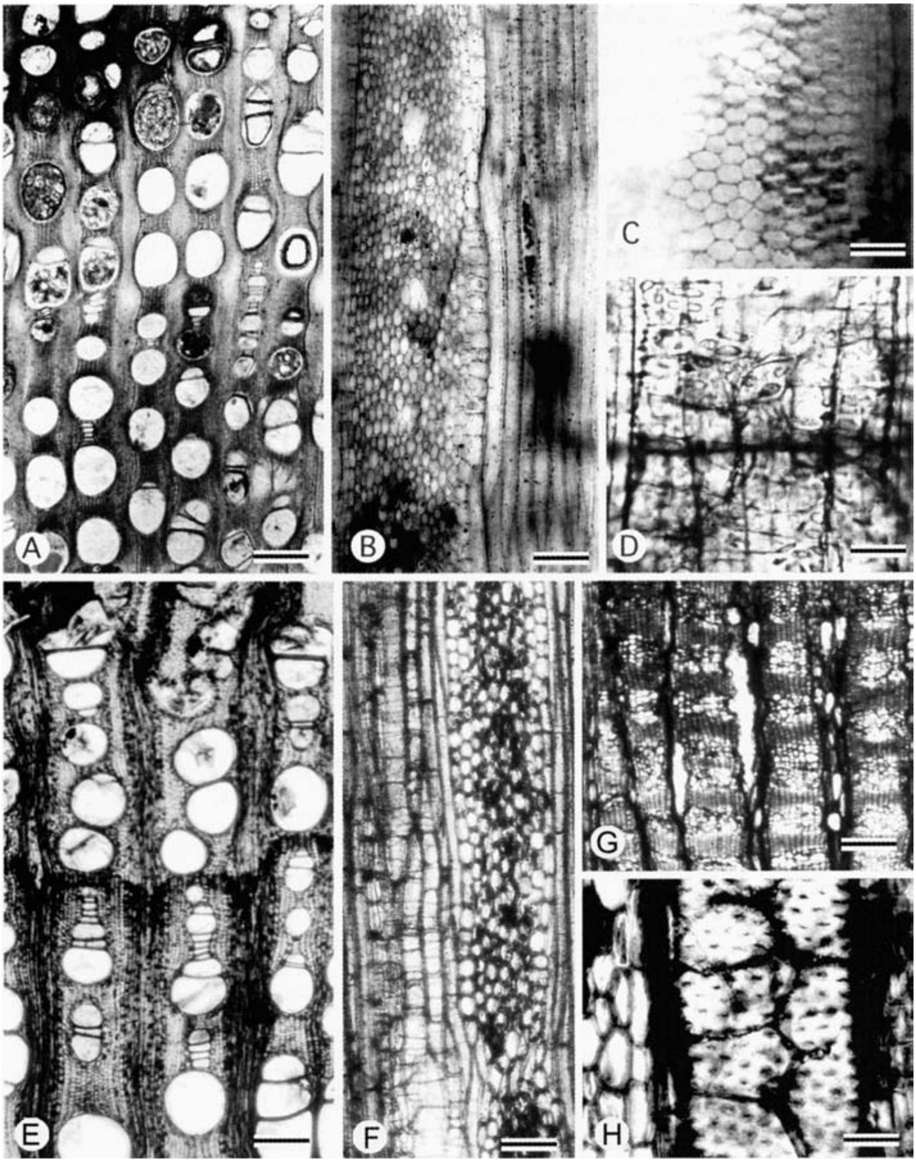

Fig. 37. *Vitaceoxylon*. – A–D: *V. carlquistii* Wheeler & LaPasha. – A: Vessels tending to two distinct widths, narrow vessels in radial multiples, XS. – B: Multiseriate ray, with "idioblasts" in center of ray. Storied imperforate elements, TLS. – C: Crowded alternate intervessel pits, TLS. – D: Vessel-ray parenchyma pits with reduced borders and horizontally enlarged, RLS. — E–H: *V. tiffneyi* Wheeler & LaPasha. – E: Vessels tending to two distinct widths, growth ring boundary distinct, XS. – F: Multiseriate ray and storied imperforate elements, TLS. – G: Secondary phloem with alternating zones of conducting elements and fibers, rays with idioblasts, XS. – H: Crowded alternate pitting, thin-walled tyloses. — Scale bars = 250 µm in A, G; 200 µm in E; 100 µm B, F; 50 µm in D, H; 25 µm in C.

Axial parenchyma scanty paratracheal, up to 12 cells per strand, storied.

Rays up to 8 cells wide. Multiseriate rays heterocellular, body composed of procumbent cells, with a few marginal rows of square/upright cells; idioblasts present in wider rays; uniseriates rare, less than 15 cells high; total multiseriate ray height in excess of 1 cm.

Holotype: USNM 458561 (C4WA-13).

Vitaceoxylon tiffneyi Wheeler & LaPasha (Fig. 37E–H)

Growth rings distinct, marked by radially flattened latewood fibers and ray cells ending at the growth ring boundaries.

Diffuse porous. Vessels tending to be of two diameter classes, wider ones usually solitary, narrower vessels in radial multiples of up to 12 vessels; average tangential diameter of solitary vessels 175 μm, range 50–320 μm; average radial diameter of solitary vessels 192 μm, range 50–340 μm; vessel frequency 8–14–25/mm^2; perforations simple; intervessel pits crowded alternate, 10–12 μm; vessel-ray parenchyma pits with reduced borders and horizontally enlarged; helical thickenings not observed; average vessel element length 445 μm, range 350–600 μm; tyloses present in some vessels, likely associated with wounds.

Fibers septate, 4–8 septa per fiber; walls medium to thick, pits not observed; tendency to storied structure.

Axial parenchyma scanty paratracheal, up to 20 cells per strand, with a tendency to storied structure.

Rays up to 20 cells wide, mostly 8–10 cells wide. Multiseriate rays heterocellular, body composed of procumbent cells, heterocellular with up to 8 marginal rows of square/upright cells; idioblasts present in wider rays; uniseriates rare; total multiseriate ray height in excess of 5 mm; occasional perforated ray cells with simple perforation.

Secondary phloem with alternating zones of thick-walled fibers and thin-walled cells (sieve tube elements, companion cells, and parenchyma); fibers rectangular in outline in cross section, zones of fibers 4–8 cells deep. Rays with enlarged cells containing raphides.

Holotype: USNM 458560 (C4A-70).

Comments — *Vitaceoxylon carlquistii* and *V. tiffneyi* share features (two width classes of vessels with small vessels in radial multiples, simple perforation plates, storied parenchyma, vessel-ray parenchyma pits with reduced borders, scanty paratracheal parenchyma, septate imperforate elements with abundant simple pits, broad high rays with idioblasts) that indicate they are Vitaceae. *Vitaceoxylon tiffneyi* has secondary phloem, and its structure, alternating layers of thick-walled fibers and thin-walled conducting cells, occurs in extant *Vitis*. Both species of *Vitaceoxylon* resemble *Vitis* in vessel arrangement, ray structure, and imperforate element characteristics. However, extant *Vitis* species have scalariform intervessel pits, rather than alternate pits as occurs in *Vitaceoxylon*. Thus, *Vitaceoxylon* woods have a combination of features not seen in any of the extant Vitaceae woods available for study and were considered to represent an extinct genus (Wheeler & LaPasha 1994).

DICOTYLEDONOUS WOODS REFERABLE TO ORDERS

MALPIGHIALES *sensu* APG (1998)

Numerous permineralized specimens and occasional casts of fruits of an extinct genus of Flacourtiaceae (*Saxifragispermum* Reid & Chandler) are known from the Nut Beds (Manchester 1994). There also are genera that resemble Flacourtiaceae (*Polygrana, Pyrisemen*) and Euphorbiaceae (*Durocarpus*), but cannot with certainty be assigned to those families. Among the Clarno woods are three types that have characteristics seen in families that belong to the Malpighiales *sensu* APG (1998), Euphorbiaceae and Flacourtiaceae. A fourth wood type has characteristics that occur in Flacourtiaceae and Violaceae (also Malpighiales), but this wood is a small axis so its alliance with Malpighiales is less certain and it is described as a form genus of uncertain affinities.

Clarno Malpighialean Wood Type I (?Euphorbiaceae) (Fig. 38)

Growth rings indistinct to barely distinct marked by radially flattened latewood fibers.

Diffuse porous. Vessels solitary (24–30%) and in radial multiples of 2–8 (up to 16); average tangential diameters 44 (8)–49 (8) µm; mean vessel frequency 99–115/mm^2, range 64–176/mm^2; predominantly simple perforations, occasional multiple perforation plates, scalariform with less than 10 bars and reticulate; intervessel pits crowded alternate with angular outline or not crowded and oval in outline, 5–9 µm; some vessel-ray parenchyma pits slightly enlarged relative to intervessel pitting and with borders somewhat reduced, rounded to slightly oval in outline, others horizontally elongate and with reduced borders and appearing simple; mean vessel element lengths 796 (159)–821 (142) µm, range 452–1,085 µm, end walls very tapered and oblique; tyloses occasional, widely spaced, and segmenting vessels.

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

Axial parenchyma rare, occasional strands seen near vessels, 8 or more cells/strand.

Rays 1–4-seriate. Multiseriate rays heterocellular, body composed of procumbent cells, with 1–10 or more rows of square/upright cells, often very asymmetric, with one margin having 1–2 rows of upright cells and the other with 8–10; mean height

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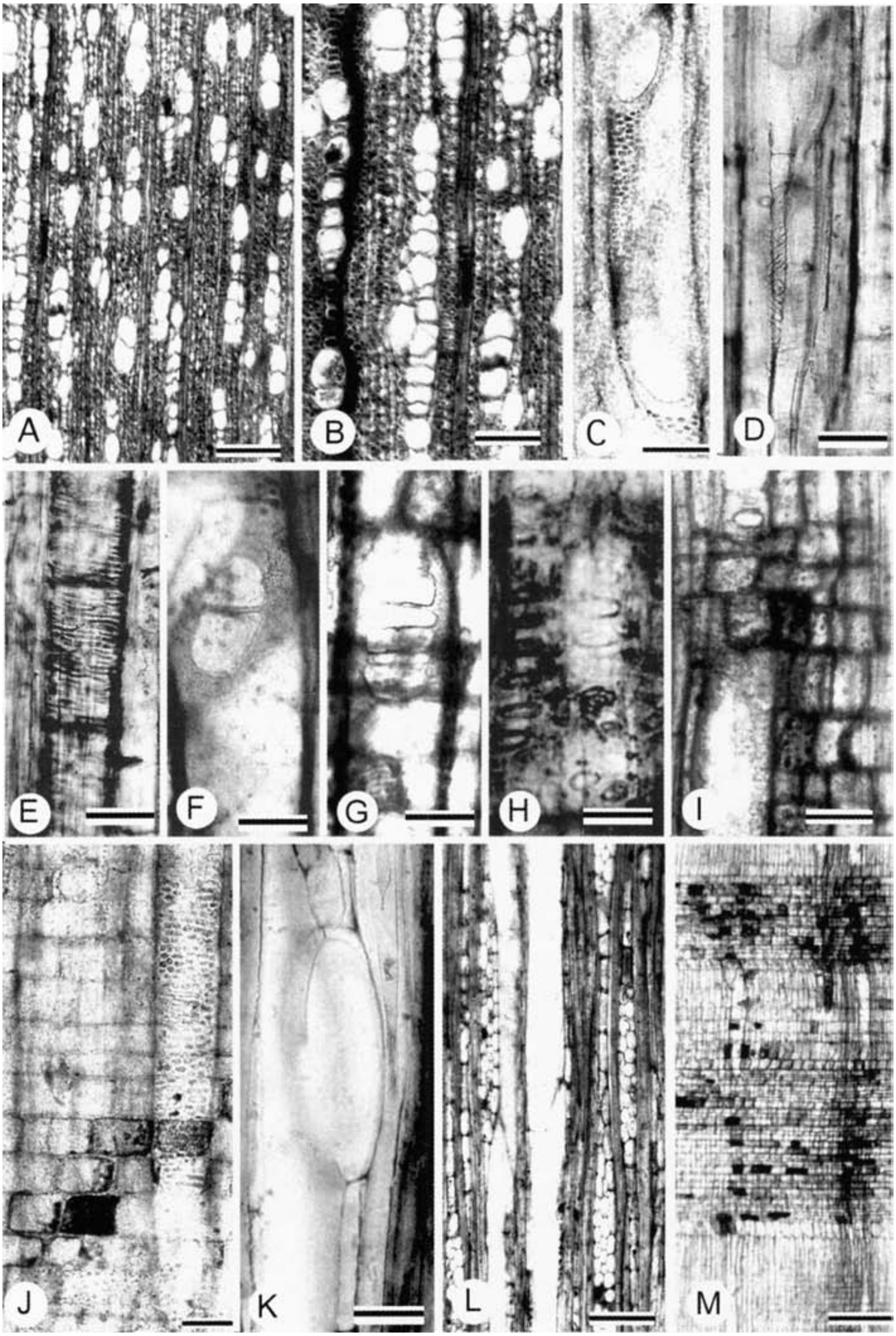
Fig. 38. Nut Beds Malpighialean wood, ?Euphorbiaceae, A–D, F–M: USNM 507941 (C4A-41); E: USNM 507940 (C4A-34). – A: Diffuse porous wood with vessels mostly in radial multiples, indistinct growth ring boundaries, XS. – B: Long radial multiples, XS. – C: Simple perforations, alternate intervessel pitting, TLS. – D, E: Helical thickenings in vessel elements, TLS. – F, G: Scalariform perforation plates, RLS. – H: Vessel-ray parenchyma pits horizontally elongate and with reduced borders, RLS. – I: Upright and square ray parenchyma cells, possible perforated ray cells, RLS. – J: Square and procumbent cells, vessel-ray parenchyma pitting, RLS. – K: Perforated ray cell, TLS. – L: Narrow 1–3-seriate rays with uniseriate margins of upright cells, TLS. – M: Heterocellular rays, procumbent and square cells of similar height, RLS. — Scale bars = 250 µm in A, M; 100 µm in B, L; 50 µm in C, D, I, J; 25 µm in E, F, G, H, K.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of multiseriate portion of the rays 256 (144)–475 (214), total range of 89–980 µm; in radial section, parenchyma-parenchyma pits obvious on all walls; uniseriate rays common and composed of upright cells; 7–12/mm.

Crystals not observed.

Storied structure absent.

Samples: USNM 507940 (C4A-34, 8 cm), USNM 507941 (C4A-41, 7 cm).

Comments — Some ray cells appear enlarged relative to other ray cells, and might represent perforated ray cells (Fig. 38K). Fungi are common in the vessel elements and ray parenchyma, some fibers have the S_2 wall layer eroded and the S_3 layer appears “collapsed”. Although there appear to be coarse spiral thickenings in some of the narrower vessel elements, these structures might represent cavities formed as a result of fungal activity. However, these “spirals” are more obvious in narrow vessel elements (Fig. 39E) and towards the ends of vessel elements (Fig. 39D). This distribution is more consistent with these structures being spiral thickenings, rather than fungal degradation.

Similarities to extant woods — Families with some members that have radial multiples of 4 or more, both simple and scalariform perforation plates, alternate intervessel pitting, non-septate fibers without distinctly bordered pits and heterocellular rays are Apocynaceae and Rubiaceae of the Gentianales, and Euphorbiaceae of the Malpighiales. Only Rubiaceae (*Emmenopterys*) occur in the Clarno fruit and seed flora, although Apocynaceae and Euphorbiaceae are reported from elsewhere in western North America (Taylor 1990; Manchester 1999).

The vessel-ray parenchyma pits of Apocynaceae and Rubiaceae usually are similar to the intervessel pitting, with the exception of some species of Psychotrieae in the Rubiaceae (Jansen et al. 1997). Within the Psychotrieae, subtribe Psychotriinae and the Clarno wood share rare axial parenchyma and vessels predominantly in radial multiples. The vessel-ray parenchyma pits of this fossil are more elongate than those we observed or are figured for the Psychotrieae. The intervessel pits are larger than is typical for Rubiaceae, but of a size that occurs in Euphorbiaceae. Pits in Rubiaceae are vestured. Although the pits of this Clarno wood appear non-vestured, this cannot be stated with certainty.

We consider this wood’s affinities most likely to be with Euphorbiaceae, but do not consider this relationship established. In Euphorbiaceae, many genera have markedly heterocellular rays, and horizontally enlarged vessel-ray parenchyma pits with reduced borders are common. Spiral thickenings in vessels have been reported for some genera within the Phyllanthoideae and the Crotonoideae. This Clarno wood is unlikely to be related to the Aporosa Type of the Phyllanthoideae or Crotonoideae Type (*sensu* Metcalfe & Chalk 1950) as these groups have abundant apotracheal parenchyma, and the Aporosa group has rays of two distinct sizes. This fossil has similarity to the Glochidion Type of the Phyllanthoideae (Metcalfe & Chalk 1950; Mennega 1987). However, this group has septate fibers, and this Clarno wood does not. It is possible that the apparent absence of septate fibers could be related to the abundant occurrence of fungal hyphae, and the removal of septa by fungal degradation.

cf. ***Hydnocarpoxylon*** Bande & Khatri (Fig. 39)

Growth rings indistinct to distinct, marked by radially narrower fibers.

Diffuse porous. Vessels solitary (17–37%) and in radial multiples of 2–4 (8); average tangential diameters range from 60 (12)–98 (19) µm; vessel frequency averages 46–67/mm^2, total range of 29–85/mm^2, perforations scalariform, with 8–24 bars, occasionally reticulate to near foraminate; intervessel pits alternate, opposite, and scalariform (in narrower vessels, and at ends of vessel elements); vessel-ray parenchyma pits simple or with much reduced borders, round to somewhat horizontally oval in outline; helical thickenings absent; average vessel element lengths of 713–914 µm; thin-walled bubble-like tyloses common.

Fibers septate; walls medium to thick (not clear whether some fibers are gelatinous, or have swollen walls because of decay); pitting not observed.

Axial parenchyma absent–rare.

Rays 1–8-seriate, maximum ray width narrower in small diameter specimens (1–3); multiseriate rays heterocellular, composed of procumbent body cells, and marginal rows of 1–6 (or more); sheath cells absent; average multiseriate ray heights range from 408 (175)–656 (223) µm; 6–8/mm to 10–16/mm.

Solitary prismatic crystals in upright and square ray cells observed in some samples (e.g., UF 12314, UF 12319), occasionally in 2-chambered upright cells.

Storied structure absent.

Samples: USNM 507845 (DEN 49, ca. 4 cm, branch), USNM 507878 (DEN 125), USNM 507879 (DEN 19, ≥ 10 cm), USNM 507880 (DEN 20, ≥ 10 cm); UF 12064, UF 12078 (≥ 10 cm), UF 12311 (≥ 10 cm), UF 12314 (4.5 cm, branch), UF 12319 (ca. 2–3 cm), UF 12322 (ca. 2.5 cm).

Similarities to extant woods — In the OPCN database, genera with the combination of vessels solitary and in multiples and not few or wide (i.e., neither less than 5 per sq.mm nor greater than 200 µm average tangential diameter), exclusively scalariform perforation plates, vessel-ray parenchyma pits with reduced borders, septate fibers, heterocellular rays that are more than 4 cells wide, and rare/absent axial parenchyma occur in the families Atherospermataceae (*Laurelia*) and Monimiaceae (*Daphnandra, Xylamos*) of the Laurales, Flacourtiaceae (*Dasylepis, Erythrospermum, Rawsonia, Scottellia*, tribe Berberidopsideae; *Carpotroche*, tribe Oncobeae; and *Tetrathylacium*, tribe Casearieae; Miller 1975) of the Malpighiales, and Tapisciaceae (formerly in Staphyleaceae), placed in the Rosids (*Huertea, Tapiscia*; Carlquist & Hoekman 1985). The combination of features of these Clarno woods is more consistent with the Flacourtiaceae than the other families mentioned.

Radial multiples are uncommon and there are few vessels per multiple in *Laurelia* and *Daphnandra* (Metcalfe 1987), although radial multiples of four or more occur in *Xylamos*. Chambered crystalliferous cells are not reported for either Atherospermataceae or Monimiaceae.

Although *Tapiscia* is confirmed from seeds in the Nut Beds, vessel multiples are more common in the Clarno woods than in *Tapiscia* and *Huertea* (Tapisciaceae). Carlquist and Hoekman did not observe crystals in *Tapiscia*, but did in subdivided

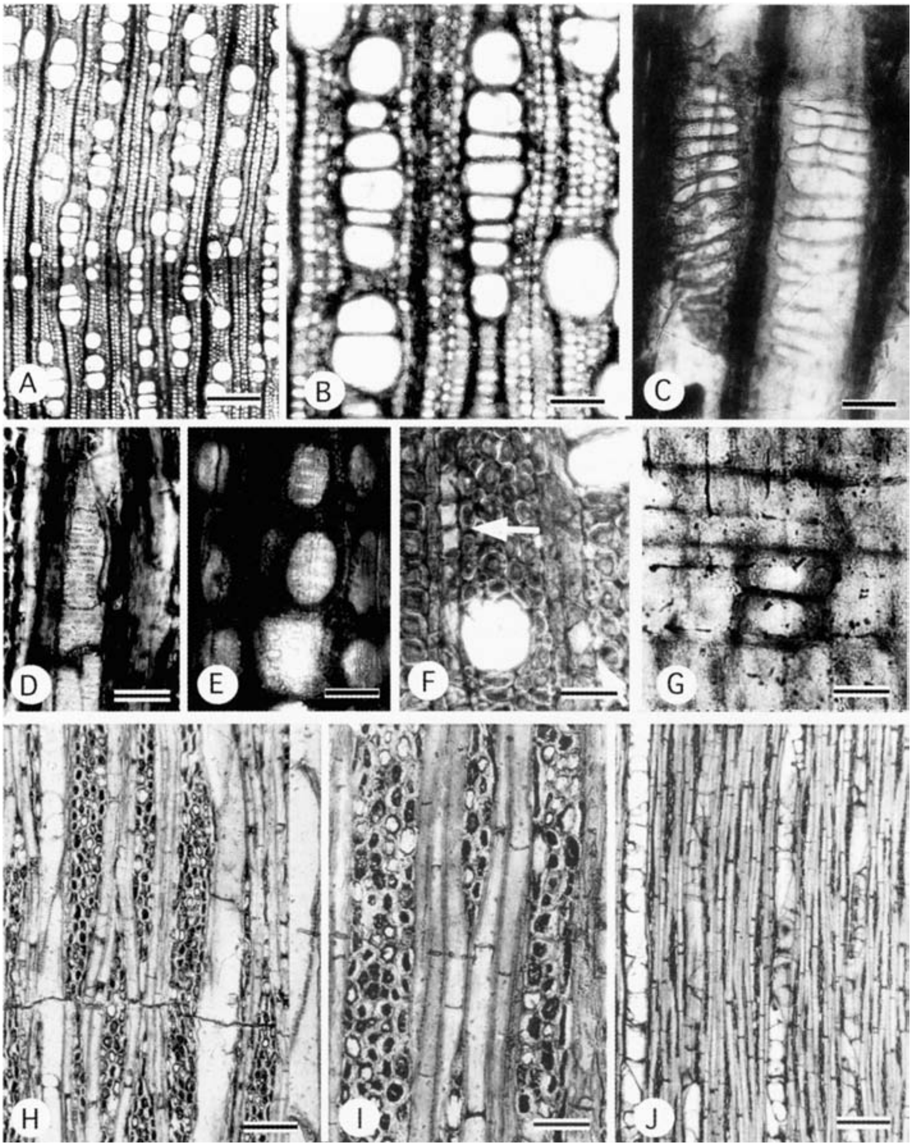


Fig. 39. Malpighiales. cf. *Hydnocarpoxylon* Bande & Khatri, A–E, J: USNM 507879; F, G: UF 12314; H, I: UF 12322. – A: Diffuse porous wood, with many radial multiples of vessels, XS. – B: Radial multiples, fiber thin- to thick-walled, XS. – C: Scalariform perforations, RLS. – D: Scalariform intervessel pitting, TLS. – E: Vessel-ray parenchyma pits, RLS. – F: Crystals (arrow) in ray parenchyma, XS. – G: Chambered ray parenchyma, with one crystal per chamber (arrow), RLS. – H, I: Heterocellular multiseriate rays, septate fibers, fungal hyphae, TLS. – J: Heterocellular multiseriate rays, and uniseriate rays composed of upright cells. — Scale bars = 250 µm in A, H, J; 100 µm in B, I; 50 µm in D, F, G; 25 µm in C, E.

ray cells of *Huertea* (also pers. observ. *H. granadina* U 10997), but this species lacks septate fibers and vessels are rarely in multiples. Quantitative features (vessel element length, tangential diameter, and vessels per sq.mm) for the Clarno woods are similar to those reported for these two genera of Staphyleaceae, but quantitative features should not be given priority when determining affinities.

This Clarno wood type has a combination of wood anatomical features that puts it in Group I of the Flacourtiaceae wood anatomical types recognized by Miller (1975). This type was considered primitive and occurs in 5 of the 9 tribes Miller studied.

Comparisons with slides and descriptions of *Erythrospermum*, *Rawsonia*, *Scottellia*, and *Tetrathylacium* showed them to be similar to the fossil, although chambered upright ray parenchyma cells were not observed in the samples available of these genera. Crystals in chambered upright cells occur in some Group I Flacourtiaceae woods (Miller 1975).

Comparisons with other fossil woods — Woods believed to have relationship to Flacourtiaceae have been described from Africa and India and assigned to the genera *Casearioxylon* (Dupéron-Loudoueneix 1977), *Flacourtioxylon* (*sensu* Louvet 1970; *sensu* Trivedi & Srivastava 1986), *Homalioxylon* (Prakash & Tripathi 1972), *Hydnocarpoxylon* (Bande & Khatri 1980), and *Pangioxylon* (Trivedi & Srivastava 1982). *Flacourtioxylon mohgaonense* "gen. et sp. nov." as designated by Trivedi and Srivastava is not valid, as no type was designated, and the name *Flacourtioxylon* was used earlier by Louvet (1970).

The general features of this Clarno wood (vessels solitary and in radial multiples, scalariform perforation plates, vessel-ray parenchyma pits with reduced borders, septate fibers, rare–absent parenchyma, heterocellular multiseriate rays) occur in *Hydnocarpoxylon indicum* (Deccan Intertraps of India; Bande & Khatri 1980) and *Flacourtioxylon* (*Monimioxylon*) *gifaense* (Eocene of Europe; Louvet 1970).

The diagnosis of *Hydnocarpoxylon* is a general one: "Wood diffuse porous. Growth rings indistinct or absent. Vessels small to medium, solitary and in radial multiples forming fine radial lines on the cross-surface, rarely in small clusters; perforations scalariform; intervessel pit-pairs bordered, alternate to opposite to scalariform. Parenchyma absent. Xylem rays heterogeneous. Fibers moderately thick-walled, septate." The general structure of the Clarno wood is consistent with this general diagnosis. Bande and Khatri (1980) indicated that the structure of *Hydnocarpoxylon indicum* is not only close to *Hydnocarpus* but very similar to the species now occurring in India. Rays of *Hydnocarpoxylon indicum* typically are smaller (1–3-seriate) than this Clarno wood. *Flacourtioxylon gifaense* Louvet has fewer bars per perforation plate, rays of two distinct sizes with the multiseriate rays being more than 1 mm high; intervessel pitting and vessel-ray parenchyma pits were not described.

Because this Clarno wood type has features of Flacourtiaceae and conforms to the diagnosis for *Hydnocarpoxylon*, we tentatively assign it to *Hydnocarpoxylon*, recognizing, however, that this Clarno wood's characteristics are not restricted to a single modern genus as implied by the name.

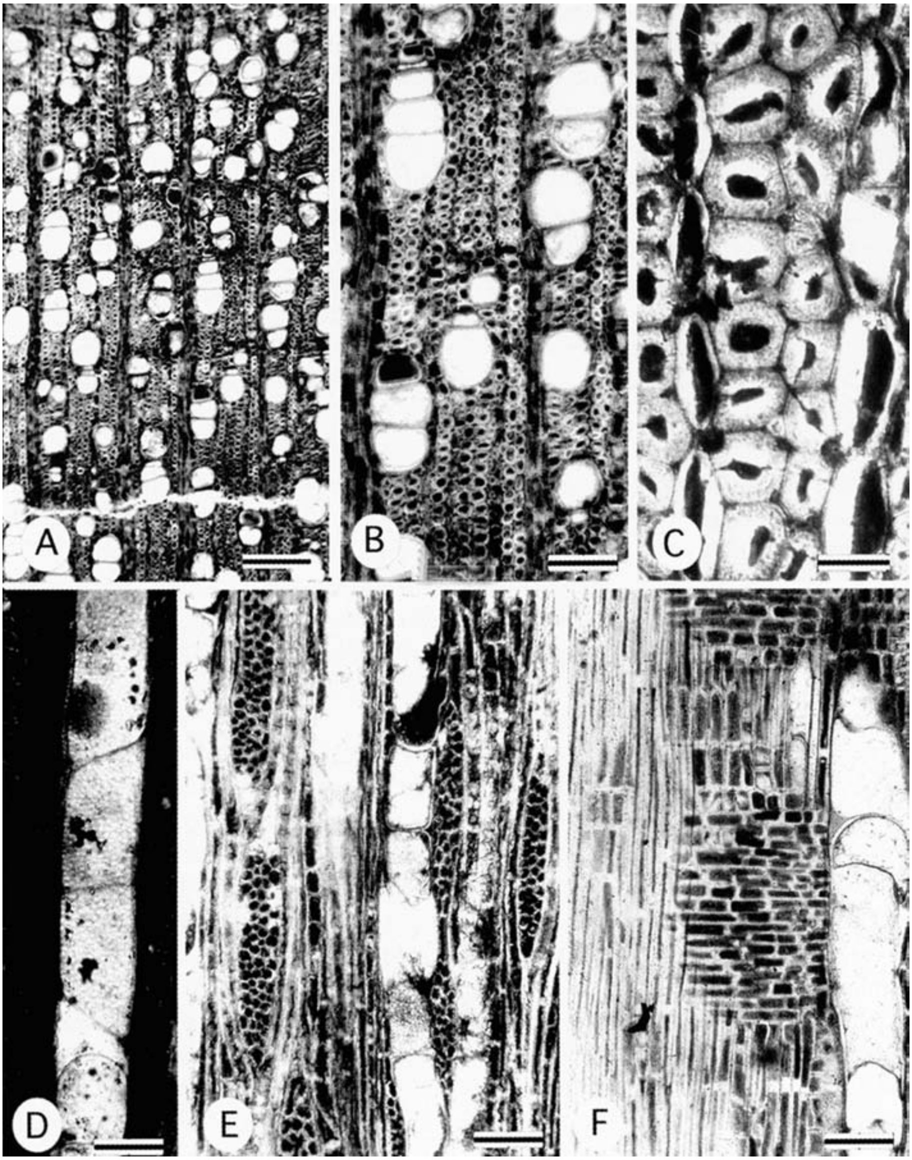


Fig. 40. Malpighiales. cf. *Paraphyllanthoxylon* Bailey, A, B, D–F: UF 12204; C: USNM 507881 – A, B: Diffuse porous wood, indistinct growth rings, vessels solitary and in radial multiples, XS. – C: Fibers with medium-thick walls, crystal in ray parenchyma cell, XS. – D: Series of vessel elements, crowded alternate intervessel pits, TLS. – E: Heterocellular multiseriate rays, septate fibers, tyloses, TLS. – F: Heterocellular rays, with marginal upright cells 2 times the height of procumbent body cells, crystals in chambered upright ray parenchyma cell, RLS. — Scale bars = 250 μm in A; 100 μm in B, D, E, F; 50 μm in C.

cf. ***Paraphyllanthoxylon*** Bailey (Fig. 40)

Growth rings absent, to indistinct with some radially flattened latewood fibers.

Diffuse porous. Vessels solitary (20–25%) and in radial multiples of 2–5; average tangential diameters of 86 (16)–104 (17) µm; vessel frequency averages of 14–24/mm^2, total range of 9–37/mm^2; simple perforations; intervessel pits crowded alternate, at times sub-opposite, 8–14 µm; vessel-ray parenchyma pits not observed; helical thickenings absent; total range of vessel element lengths 406–689 µm; tyloses present, thick-walled and abundant to widely spaced and thinner-walled.

Fibers all septate, medium-thick to thick walls, pitting in radial walls (visible in cross section).

Axial parenchyma absent.

Rays 1–4-seriate. Multiseriate rays heterocellular, with 1–10 (mostly 1–3) marginal rows of markedly upright cells; rays often vertically fused, uniseriate rays composed of all upright cells; multiseriate portion of the multiseriate rays averages 454 (136)–549 (184) µm high; solitary prismatic crystals common in upright/square ray cells, crystalliferous ray cells sometimes chambered; 6–9/mm.

Storied structure absent.

Samples: USNM 507881 (DEN 1, ≥ 50 cm), USNM 507882 (DEN 21, ≥ 10 cm), UF 12204 (≥ 10 cm), UF 12446 (ca. 4 cm), USNM 507986 (C 517).

Comments — The preservation of this wood type is generally good. However, vessel-ray parenchyma pits were not observed with certainty as the ray cells often have abundant dark-colored contents which obscured viewing the pits. The common occurrence of colored compounds likely indicates that this wood originally had a high extractive content. Fungal hyphae are not common, compared to many of the Clarno samples.

Similarities to extant woods — Genera with the combination of vessels solitary and in radial multiples, simple perforations, large alternate pitting, septate fibers, markedly heterocellular rays, absence of axial parenchyma, and crystals in chambered ray parenchyma occur in the families Euphorbiaceae (e.g. *Acalypha* and *Bischofia*, both of Group B, Glochidion type of Metcalfe & Chalk), and Flacourtiaceae (*Ahernia*, tribe Berberidopsideae; *Caloncoba*, *Carpotroche, Lindackeria*, tribe Oncobeae; *Dovyalis, Itoa*, tribe Flacourtiaeae; *Eleutherandra*, *Trichadenia*, tribe Pangieae; *Hasseltia*, tribe Prockieae; *Homalium*, tribe Homalieae; *Scolopia*, tribe Scolopieae) (Miller 1975).

Great similarity exists between the woods of some genera in the *Glochidion* group of the Euphorbiaceae, subfamily Phyllanthoideae, and some genera of Flacourtiaceae (Metcalfe & Chalk 1950). Mennega (1987) has most recently studied wood anatomy of the Phyllanthoideae. The Clarno wood's intervessel pit size and absence of parenchyma occur in the extant genera *Bischofia* (which frequently has colored contents in its ray cells, Ilic 1991: p. 194) and *Bridelia* (Mennega 1987). *Bischofia javanica* (Ilic

1991: p. 194; Lemmens et al. 1995: p. 85) appears similar to this Clarno wood, although the Clarno wood has shorter vessel elements. Vessel element lengths reported for fossil wood, which are measured from tangential sections, are likely shorter than lengths determined from macerations, where it is easier to measure the entire length of the vessel element.

Of the extant Flacourtiaceae mentioned above, chambered crystalliferous ray cells occur in *Ahernia, Hasseltia, Homalium*, and *Scolopia* (rarely). *Scolopia* and *Homalium* have small intervessel and vessel-ray parenchyma pits. *Hasseltia* usually has some, often predominantly, scalariform pits. This wood is similar to *Ahernia*, based on the literature (Miller 1975), slides (*Ahernia glandulosa* BF 126183) and illustrations (Ilic 1991: p. 217). *Ahernia* has two species (1 Hainan, 1 Philippines, Mabberley 1997).

However, the large intervessel pits and inclusions in the wood suggest its affinities are more likely with the Euphorbiaceae than with the Flacourtiaceae. However, without being able to determine the vessel-ray parenchyma pits, it is not possible to confirm the affinities of this wood.

Comparisons with other fossil woods — This wood type has a combination of characters (vessels solitary and in radial multiples, simple perforations, large alternate intervessel pits, rare axial parenchyma, septate fibers, heterocellular rays) that occurs in *Paraphyllanthoxylon* Bailey (1924), a genus based on a Cretaceous fossil wood said to resemble the extant genus *Phyllanthus*. None of the Cretaceous *Paraphyllanthoxylon* species have crystals, and crystals are not mentioned in Bailey's diagnosis, nor are visible in the type specimen (pers. observ.). However, one European wood with crystals in ray cells was assigned to *Paraphyllanthoxylon, P. lignitum* Daniou & Dupéron-Laudoueneix (1978).

A review of the genus *Paraphyllanthoxylon* seems warranted; it is likely that it should be further subdivided based on ray characteristics. Some species have marked heterocellular rays; others do not.

SAPINDALES

cf. ***Cedreloxylon*** Selmeier (Fig. 41)

Growth rings distinct, marked by radially flattened fibers, a marked change in vessel diameter from last formed latewood to the first formed earlywood, and thin-walled ground tissue in the earlywood.

Ring porous to semi-ring porous. Earlywood vessels solitary, and in radial multiples of 2, latewood vessels solitary and in short radial multiples of 2–4 (5); average tangential diameter of the earlywood 115 (34)–117 (31) µm; perforations simple; intervessel pits alternate, 4–6 µm, crowded and polygonal in outline; vessel-ray parenchyma pits similar to intervessel pits; helical thickenings not observed; average vessel element lengths of 427 (67) µm; tyloses not observed, dark deposits common near perforation plates.

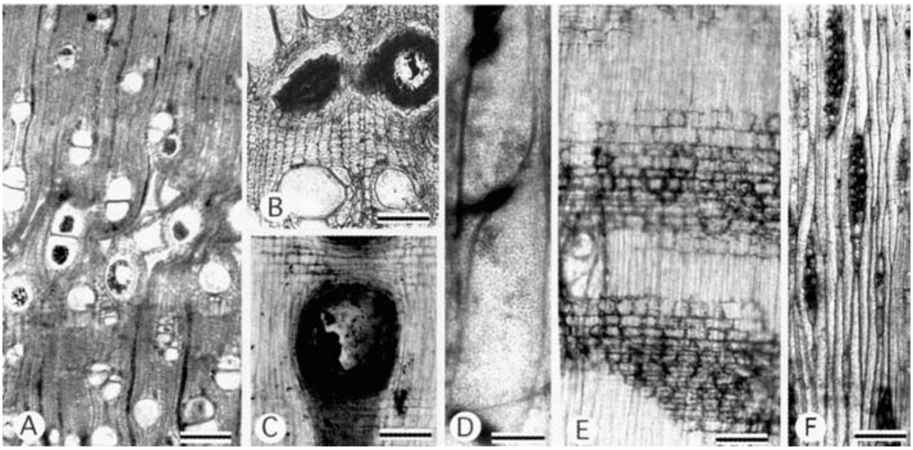


Fig. 41. Sapindales. cf. *Cedreloxylon* Selmeier (UF 12373). – A: Ring porous to semi-ring porous wood, with earlywood zone 3 or more vessels deep, vessels solitary and in short radial multiples, XS. – B: Traumatic canals at growth ring boundary, XS. – C: Traumatic canal, RLS. – D: Alternate intervessel pitting, TLS. – E: Heterocellular rays, simple perforation to left of center, RLS. – F: Multiseriate rays, with short uniseriate margins, possible septate fibers, TLS. — Scale bars = 250 µm in A; 100 µm in B, C, E, F; 50 µm in D.

Septate fibers not observed, walls thin in earlywood, walls thin to medium-thick in rest of growth ring, pits not obvious.

Axial parenchyma predominantly scanty paratracheal, some narrow vasicentric, 4–8 cells/strand.

Rays 1–2(–3)-seriate. Rays heterocellular, with 1–3 marginal rows of square cells, and intermixed square, upright and procumbent cells. Mean height of multiseriate rays 301 (47)–325 (60) µm, total range of 203–429 µm; 6–8/mm.

Prismatic crystals occasional in chambered axial parenchyma, one crystal per chamber, rare in ray parenchyma.

Storied structure absent.

Traumatic axial canals present, some isolated and similar in size to vessels, to tangentially fused for more than 2 mm.

Samples: UF 12373 (> 10 cm), UF 12445 (> 10 cm).

Similarities to extant woods — Traumatic canals, a tendency to semi-ring porosity, randomly arranged latewood vessels that are solitary and in short radial multiples and rarely in clusters, small alternate intervessel pits, vessel-ray parenchyma pits similar to intervessel pits, thin-walled fibers that do not have obvious bordered pits, non-storied wood, and paratracheal parenchyma suggest affinities with Meliaceae (*Cedrela* or *Toona*), Rutaceae, or Simaroubaceae, all members of the Sapindales. The genera of Rutaceae (*Balfourodendron*) and Simaroubaceae (*Picrasma*) with the aforementioned feature differ from this Clarno wood in vessel grouping and arrangement (more radial multiples), and ray appearance.

Comparisons with other fossil woods — The general features of this wood conform to *Cedreloxylon* Selmeier (1987), a fossil wood genus intended to encompass fossil woods with characteristics of the extant genera *Cedrela* (New World Tropics) and *Toona* (Old World Tropics). The European Miocene *Cedreloxylon cristalliferum* has wider vessels (earlywood vessels averaging more than 200 µm), larger intervessel pits (6–7 µm), and wider rays (usually 3-seriate) (Selmeier 1987; Gottwald 1992, 1997). *Cedreloxylon cristalliferum* appeared most similar to the extant *Toona sinensis* (Gottwald 1997). No Meliaceae have been reported from the Nut Beds. However, there are reports of leaves and pollen of *Cedrela* from the Middle Eocene through Oligocene of western North America (Taylor 1990).

URTICALES

The three woods described below have characteristics that suggest affinities with either the Moraceae or Ulmaceae s.l., especially tropical to subtropical species of *Celtis*. Moraceae are not represented in the fruit/seed or leaf assemblages of the Nut Beds; *Celtis* endocarps are common in the Nut Beds. Consequently, it is tempting to suggest that one or more of the three woods described below represent *Celtis*.

Scottoxylon eocenicum gen. et sp. nov. (Fig. 42)

Growth rings indistinct to distinct, delineated by 2–4 rows of terminal parenchyma.

Wood diffuse porous; vessels solitary and in radial multiples of 2–4; average tangential diameter 107 (23)–183 (27) µm; vessel frequency averages 9–21/mm^2 (total

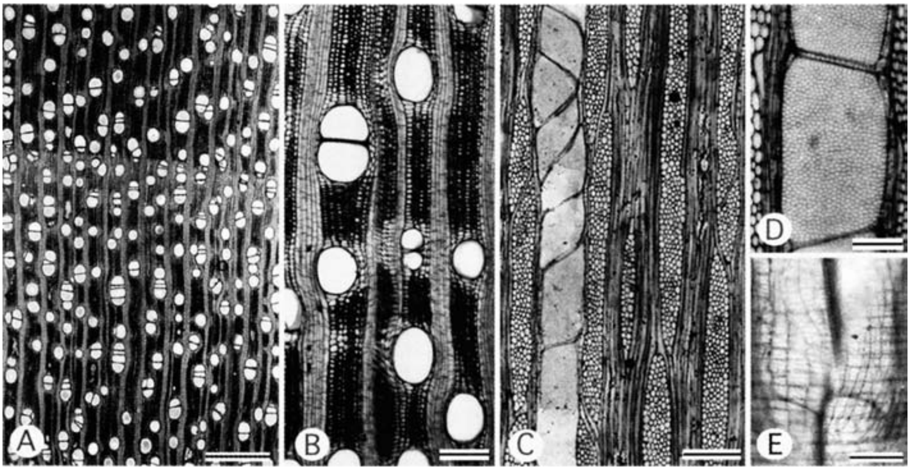


Fig. 42. *Scottoxylon eocenicum* gen. et sp. nov. (USNM 507952, C4A-56). – A: Diffuse porous wood, vessels solitary and in radial multiples, XS. – B: Vasicentric, aliform, and confluent parenchyma, XS. – C: Medium to short vessel elements, large multiseriate rays, TLS. – D: Alternate intervascular pits, TLS. – E: Vessel-ray parenchyma pits, RLS. — Scale bars = 500 µm in A; 200 in B; 250 µm in C; 100 µm in D; 50 µm in E.

range of 5–29/mm^2), perforations simple; intervessel pits alternate, 5–12 µm; vessel-parenchyma pits round to elliptical, with reduced borders and horizontally elongated, ca. 15 µm across, larger than the intervascular pits; helical thickenings absent; vessel element lengths average 325 (67)–407 (91) µm; tyloses present in some samples.

Fibres non-septate, pits not observed, walls medium-thick.

Axial parenchyma vasicentric, aliform, confluent, and terminal. Strands 4–8 cells long.

Rays 1–7- (mostly 5–6-)seriate, mostly homocellular, but multiseriate rays rarely with uniseriate 1–7 (mostly 1–3) marginal rows of upright cells; sheath cells present. Uniseriates rare, composed mainly of upright cells; multiseriate ray height averages 650 (276)–806 (369) µm, range 200–1,760 µm. Rays 3–5 per mm.

Crystals absent.

Storied structure absent.

Holotype: USNM 507952 (C4A-56, > 50 cm).

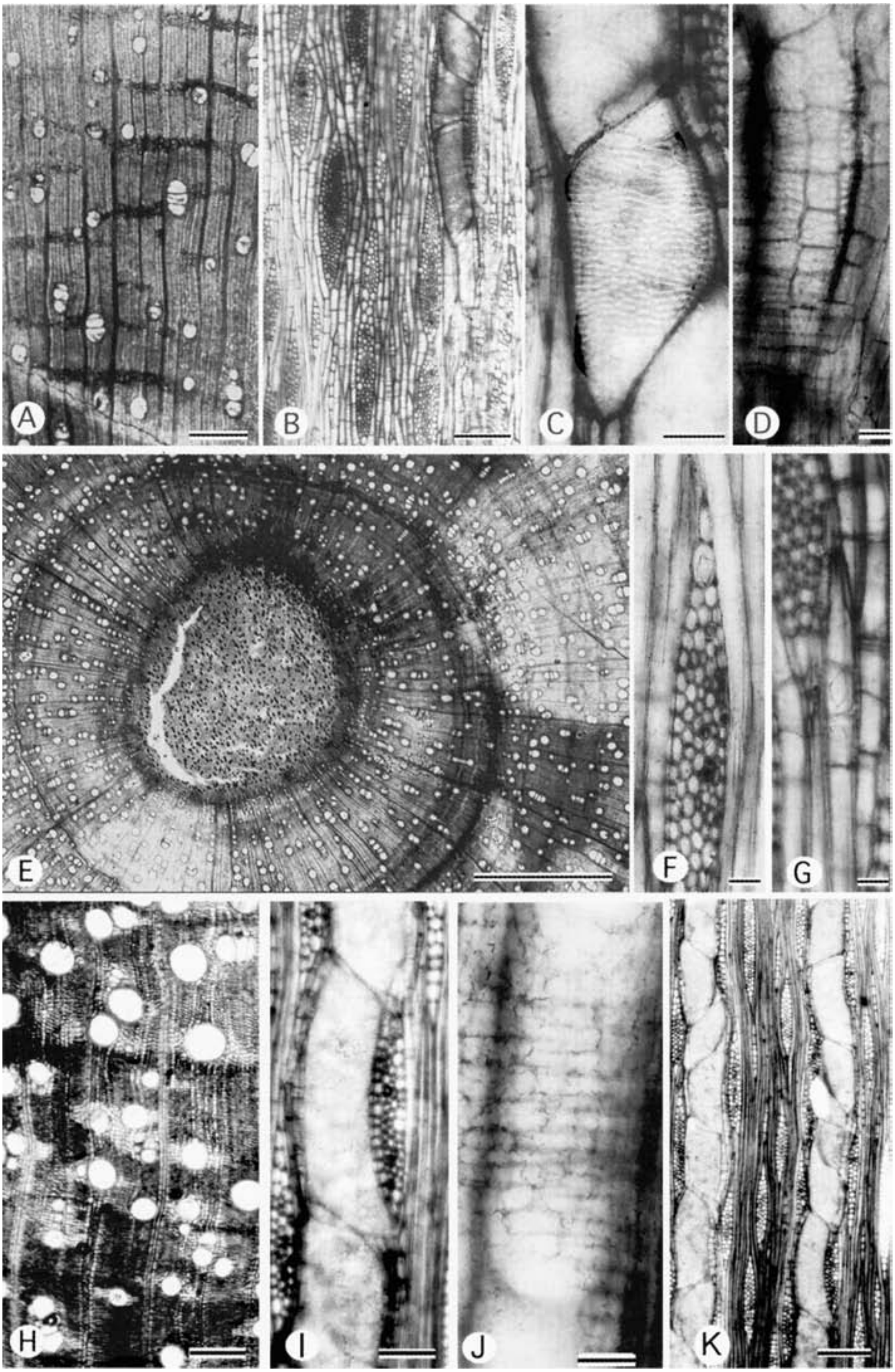
Samples: UF 12006, 12013, 12021, 12023, 12030, 12032, 12040, 12043, 12055, 12056, 12058, 12059, 12066, 12074, 12077, 12123, 12128, 12139, 12153, 12165, 12238, 12245, 12249, 12268, 12310, 12312, 12410, 12442, 12501, 12572; USNM 507847 (C4A-83, 3 cm fragment), 507848 (C4A-98, 3.5 cm), 507849 (C4A-170), 507850 (C4A-171), 507851 (C4A-175), 507852 (DEN 14, 3 cm fragment), 507853 (C4A-54, > 50 cm), 507854 (C4A-109, > 12 cm), 507855 (DEN 10, > 10 cm), 507856 (DEN 23, > 10 cm), 507857 (C4A-52, 4 cm fragment), 507858 (C4A-59, > 10 cm), 507859 (C4A-72, 4 cm fragment), 507860 (C4A-93, 5 cm, near complete), 507861 (C4A-95, 5 cm, near complete), 507862 (C4A-99, 3 cm, complete), USNM 507863 (DEN 18), 507947 (C4A-11, > 7 cm), 507948 (C4A-58, > 10 cm), 507949 (C4A-59, > 18 cm, complete), 507950 (C4A-15, > 50 cm), 507951 (C4A-53, > 16 cm), 507954 (C4A-74, > 15 cm), 507955 (C4A-96, > 12 cm), 507056 (C4A-121), 507957 (C4A-57, 3 cm, complete), 507960 (C4A-6, 10 cm), USNM 507962 (C 529, > 15 cm), 507892 (C4A-82, > 17 cm).

Etymology: The generic name is in honor of Richard A. Scott and his work on fossil plants of the Clarno Formation. The specific epithet refers to the age of the fossil.

Comments — This is one of the most common wood types in the Nut Beds locality.

Similarities to extant woods — Predominantly paratracheal axial parenchyma, simple vessel element perforations, large alternate intervessel pits, vessel-ray parenchyma pits with reduced borders, relatively wide heterocellular rays with sheath cells suggest that this wood type's affinities are with the Moraceae or Ulmaceae s.l. (*Celtis*). Some species of extant *Cordia* (Boraginaceae) are similar in general appearance. However, the vessel-ray parenchyma pits in extant *Cordia* are similar to the intervessel pits.

Comparisons with other fossil woods — Awasthi (1984) and Süss (1987) both created *Cordioxylon* to accommodate a Paleogene wood from Egypt. *Cordioxylon* Awasthi, which has priority, has vessels in clusters as is seen in some extant *Cordia*. Vessel features of the wood Süss described are similar to this Nut Beds wood, however; it, like the extant *Cordia*, differs in having vessel-ray parenchyma pits similar to the intervessel pits.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Clarno Urticalean Wood Type I (Fig. 43A–G)

Growth rings indistinct to distinct.

Wood diffuse porous; vessels solitary and in radial multiples of 2–3; average tangential diameter 114 (17)–117 (18) µm; average vessel frequency 9–10/mm^2 (total range of 5–17/mm^2), perforations simple; intervessel pits alternate, 8–12 µm; vessel-parenchyma pits round to oval to horizontally elongate with reduced borders; helical thickenings absent; vessel element lengths 338 (54)–319 (153) µm; tyloses present, thin-walled.

Fibres non-septate, walls thin-medium, no pits observed.

Axial parenchyma in irregularly spaced tangential bands 8–10 cells wide that are largely apotracheal, but sometimes intercept vessels. Strands 4–8 cells long. Rhomboidal solitary crystals occasional.

Rays 1–8-seriate. Multiseriate rays heterocellular with up to 5 rows of upright cells, procumbent cells decrease in width toward the center of multiseriate rays, sheath cells present; uniseriates of upright cell. Mean height of multiseriate rays 483 µm, range 350–675 µm; 4–6/mm**.**

Rhomboidal crystals occasional in upright ray cells.

Storied structure absent.

Pith solid, composed of globose parenchyma cells 12.5–50 µm diameter (larger cells in center, decreasing in size peripherally) with intracellular spaces.

Samples: USNM 508004 (DEN 44 = C4A-46, ca. 8 cm, with pith), USNM 507920 (DEN 16, 4 cm).

Similarities to extant woods — Among the Nut Beds woods, this species is the only one with axial parenchyma distributed in broad bands. This feature, in combination with short vessel elements, medium-large alternate intervascular pits, vessel-ray parenchyma pits with reduced borders, and large rays with sheath cells, suggest affinities with the Moraceae or Ulmaceae. A survey of modern moraceous woods was conducted by Ter Welle et al. (1986a, b). The anatomy of this fossil wood resembles the genus *Broussonetia*. Although species of section *Broussonetia* have ring porosity and spirally thickened vessels, Ter Welle et al. (1986a) point out that species of the other section, *Allaeanthus*, are diffuse porous and lack spiral thickening. The Nut Beds wood corresponds to extant woods of *Broussonetia* section *Allaeanthus* in: diffuse

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Fig. 43. Nut Beds Urticalean Woods. – A–G: Type I: A, E: USNM 508004 (C4A-46); B–D, F, G: USNM 507920. – A: Diffuse porous wood, vessels solitary and in short radial multiples, tangential bands of parenchyma, XS. – B: Multiseriate rays, tendency to sheath cells, 4–8-celled parenchyma strands, TLS. – C: Vessel elements with alternate intervascular pitting, TLS. – D: Vessel to parenchyma pits, RLS. – E: Center of axis showing pith, XS. – F: Ray with rhomboidal crystal, TLS. – G: Crystals in axial parenchyma, TLS. — H–K: Type II: USNM 507918 (DEN 6). – H: Diffuse porous wood, growth rings marked by radially flattened fibers, aliform-confluent parenchyma, XS. – I: Crowded alternate intervessel pitting, simple perforations, TLS. – J: Body of ray composed of procumbent cells, RLS. – K: Non-storied multiseriate rays, vessel elements with simple perforations, TLS. — Scale bars = 2000 µm in E; 500 µm in A, B; 250 µm in H, K; 100 µm in I; 50 µm in C, D, F, G, J.

porosity, vessel frequency, vessel member length, intervascular pit size, banded parenchyma, and rhomboidal crystals in the axial parenchyma, although the vessels themselves are narrower. The suite of features also characterizes other members of Moraceae, such as *Pachytrophe*, *Streblus*, *Trophis*, *Olmedia* (Ter Welle et al. 1986a).

Clarno Urticalean Wood Type II (Fig. 43H–K)

Growth rings distinct, marked by radially flattened latewood fibers (possible marginal parenchyma).

Diffuse porous. Vessels solitary (60%), and in short radial multiples, usually of 2; solitary vessels round in outline; mean tangential diameter 146 (19) µm; vessel frequency 5–10–16/mm^2; perforations simple; intervessel pits crowded alternate, 5–8 µm; vessel-ray parenchyma pits rounded in outline, not crowded; mean vessel element length 370 (83) µm.

Fibers likely non-septate, walls medium to thick, pits not obvious.

Axial parenchyma paratracheal, vasicentric, aliform to confluent; usually 8 cells per strand.

Rays 1–4-seriate, uniseriate rays present, usually more than 4 cells and less than 10 cells high. Rays mostly heterocellular, body of procumbent cells, marginal rows 1–4, of square to slightly upright cells; mean total height of multiseriate rays 458 (93) µm, range 270–610 µm; 3–5/mm.

Storied structure not observed.

Solitary rhomboidal crystals common in square and procumbent ray cells, usually filling the cell, occasional in axial parenchyma.

Samples: USNM 507918 (DEN 6, ≥ 4 cm), UF 12301 (fragment 4.5–7 cm across).

Comments — Outlines of the pit apertures appear smooth, so it is unlikely the pits are vestured. There is a tendency for some of the cells along the sides of the rays to appear different from the interior cells (Fig. 43 I, K) and, thus, resemble sheath cells, but this is not well-defined.

UF 12301 is similar to USNM 507918, but it has fewer solitary vessels (46%), narrower (125 µm), more numerous (mean of 23/mm^2) vessels, shorter vessel elements (ca. 300 µm), and more confluent parenchyma. Crystals were not observed in UF 12301. However, we consider these differences in quantitative features and crystal occurrence to be of the type that occur within extant species, and for now are considering them to be the same wood type.

Similarities to extant woods — Diffuse porous woods with vessel elements with simple perforations, medium-sized alternate intervessel pits, non-septate libriform fibers, aliform-confluent axial parenchyma, heterocellular rays, and crystals in ray parenchyma cells occur in the families: Bignoniaceae, Combretaceae (*Terminalia*), Leguminosae (all three subfamilies), Moraceae, and Ulmaceae *sensu lato* (especially *Celtis*). Rays with well-defined uniseriate margins of upright cells, and a tendency to sheath cells suggest relationships with the Moraceae and *Celtis*, as would non-vestured pits.

DICOTYLEDONOUS WOODS OF UNCERTAIN AFFINITIES (XYLOTYPES)

The affinities of the woods described below are unknown. Some likely represent extant genera that we failed to identify; it is quite possible (likely even) that with additional comparative work the familial and generic affinities of some of these woods can be discovered. Many extant families share similar wood anatomy, and our work to date has not determined that any of these woods has a combination of features uniquely diagnostic of a single family. Others may represent extinct genera. Because some of these axes are small, and include pith, they may represent small trees or shrubs, or barely woody plants. Because of their limited value to the timber industry, the wood anatomy of such plants is less well documented in the literature. The anatomy of small branches and, especially, roots may differ from that of mature stem wood (Carlquist 1961; Cutler et al. 1987), so some of the small axes might represent lateral branches or roots of species already known from mature stem wood.

We are describing the woods of unknown affinities in sequence by selected wood anatomical features, as given below. Those woods that are not assigned generic names will be referred to by these general categories (xylotypes).

I. Exclusively Multiple Perforation Plates
    A: Vessels solitary (over 80%), rays < 10-seriate
    B: Vessels solitary and in radial multiples, rays < 10-seriate
    C: Vessels solitary and in multiples, rays > 10-seriate
II. Multiple and Simple Perforation Plates
III. Exclusively Simple Perforation Plates
    A: Vine-like anatomy
        i. *Interxylary phloem present*
        ii. *Interxylary phloem absent*
    B: Semi-ring porous to ring porous
        i. *Distinctive latewood vessel arrangement patterns*
        ii. *Latewood vessels randomly arranged*
    C: Diffuse porous
        i. *Distinctive vessel arrangement patterns*
        ii. *Vessels solitary and in radial multiples, random vessel arrangement, rays ≤ 4-seriate*

NUT BEDS XYLOTYPE I – EXCLUSIVELY MULTIPLE PERFORATION PLATES

A: Vessels solitary (over 80%), rays < 10-seriate

1) **UF 12454** (Icacinaceae? Escalloniaceae?) (Fig. 44)

Growth rings indistinct, with some radially flattened fibers.

Diffuse porous. Vessels mostly solitary (86%), with occasional radial and oblique multiples, angular in outline; average tangential diameter 56 (10) µm, range of 35–78 µm; average vessel frequency 48/mm^2, range 27–67/mm^2; perforations scalariform, usually with more than 40 bars, up to 100; intervessel pits rare, alternate, mostly opposite, and scalariform; vessel-ray parenchyma pits not observed with certainty; heli cal thickening absent; average vessel element length 1121 (152) μm, 915–1,413 μm (n = 9); tyloses not observed.

Fibers non-septate, walls medium to thick, some elements with distinctly bordered pits on both radial and tangential walls.

Axial parenchyma diffuse and diffuse-in-aggregates, relatively abundant.

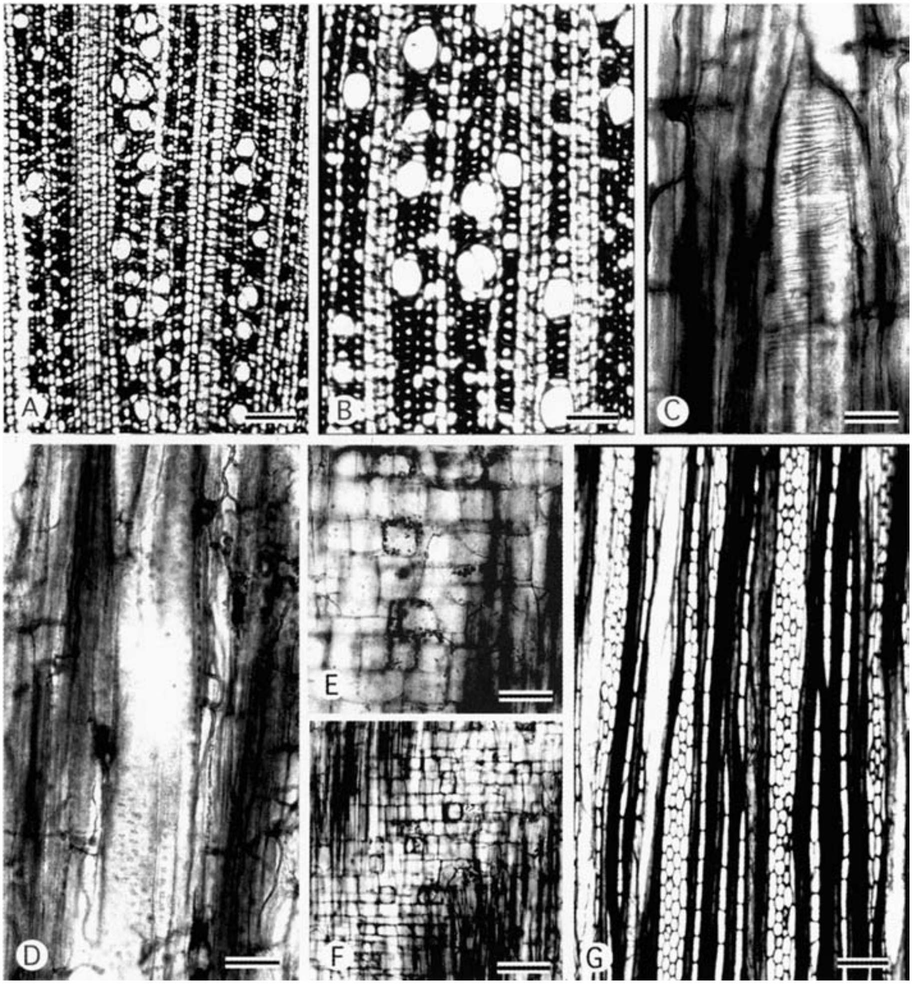

Fig. 44. Nut Beds Xylotype I-A: UF 12454. – A: Diffuse porous wood, solitary vessels angular in outline, XS. – B: Solitary vessels, thick-walled fibers, diffuse axial parenchyma, XS. – C: Scalariform perforation plates with more than 20 fine bars, RLS. – D: Sub-opposite to alternate intervessel pitting, RLS. – E, F: Rays composed predominantly of square and upright cells, RLS. – G: Multiseriate rays with long uniseriate margins, and uniseriate rays of all upright cells, TLS. — Scale bars = 250 μm in A, G; 100 μm in B, F; 50 μm in C, D, E.

Rays 1–5-seriate, mostly 3-seriate, uniseriate rays common. Multiseriate rays composed of square and upright cells; rays very high, with long uniseriate margins (in some more than 15 cells); uniseriate rays 3–29 cells tall; ray cells very thin-walled; some rays with what appear to be sheath cells, average height 3.1 mm µm, up to 5.9 mm; 7–12/mm.

Crystals not observed.

Storied structure absent.

Sample: UF 12454 (2 cm).

Comments — This wood type is represented by only one sample of 2 cm diameter. In this sample, the secondary xylem adjacent to the pith has more axial parenchyma than subsequently formed secondary xylem. Ray structure varies considerably with cambial age (Carlquist 1988), so it is questionable whether the ray cellular structure of this wood should be used to determine affinities. This plant's broad rays are composed predominantly of square and upright cells. Fiber pits were rarely observed with certainty in longitudinal sections, although in some places distinctly bordered pits were present in elements adjacent to vessels. In cross section there appeared to be "channels" in the fiber walls, but it was difficult to determine if these were fiber pits or bore holes made by wood decaying fungi.

Fungi are abundant in this wood, being particularly common in vessel lumens and in the ray parenchyma.

Vessel-ray parenchyma pits were not observed with certainty, but in some areas there were features that could be interpreted as vessel-ray parenchyma pits and which were small, alternately arranged and had only slightly reduced borders.

Similarities to extant woods — Families with the combination of features: exclusively solitary vessels, vessel diameter < 100 µm, scalariform perforation plates with many bars, opposite intervessel pits, diffuse axial parenchyma, and tall rays between 4–10-seriate include the Caprifoliaceae, Chloranthaceae (*Ascarina*), Clethraceae, Cornaceae, Dilleniaceae, Escalloniaceae, Icacinaceae, Saurauiaceae, Symplocaceae, and Theaceae. This Clarno wood tends to have two size classes of rays. Families with the above combination and two size classes of rays include: Chloranthaceae, Clethraceae, Cornaceae, Escalloniaceae, Icacinaceae, and Theaceae. The vessel-ray parenchyma pits in the fossil appear small, of the families just listed, those with some members that do not have large vessel-ray parenchyma pits include: Clethraceae, Cornaceae, Escalloniaceae, Icacinaceae, and Theaceae. Abundant diffuse and diffuse-in-aggregates axial parenchyma and rays up to 5 mm high with thin-walled cells were not observed in the Clethraceae, Cornaceae, or Theaceae (pers. observ. of slides used for Noshiro & Baas 1998, Deng & Baas 1991).

Woods of *Carpodetus, Escallonia, Polyosma* (Escalloniaceae) were examined. *Carpodetus* wood is generally similar to the fossil, sharing similar vessel grouping, parenchyma arrangement, rays of two sizes, vessel-ray parenchyma pits, and thin-walled ray parenchyma cells.

It is tempting to consider this wood to be Icacinaceae, as this family is well represented in the Nut Beds fruit and seed assemblage. Twig wood of some Icacinaceae is characterized by rays with mostly square and upright cells (pers. observ., Leiden collections). However, this ray structure is often seen in plants that are barely woody, or secondarily woody (Carlquist 1988). The ray structure of this wood is not that of the "highly specialized climbing plants of the Iodeae, Sarcostigmateae, and Phytocreneae" because multiseriate rays tend to be absent from the first formed secondary xylem (Metcalfe & Chalk 1950).

We do not believe it appropriate at this time to assign this wood a name suggesting affinities with a single genus or family because its characteristics occur in at least two extant families: Escalloniaceae and Icacinaceae.

2) **UF 00225-033245** (Fig. 45A–E)

Growth rings absent.

Diffuse porous. Vessels predominantly solitary, some local tendencies to radial chains, vessels angular in outline; average tangential diameter 39 (5) μm; average vessel frequency 230/mm^2, 140–300/mm^2; perforations exclusively scalariform, with numerous (50–80) fine, closely spaced (1–2 μm) bars in steeply inclined end walls; intervessel and vessel-ray parenchyma pits not observed; vessel element lengths 920–1,000 μm.

Fibers non-septate, medium-thick walls.

Axial parenchyma diffuse, 12 or more cells per strand.

Rays 1–3-seriate. Multiseriate rays markedly heterocellular, with long uniseriate margins; uniseriate rays composed exclusively of upright cells; rays mostly > 1 mm high, some taller than the section; 7–10/mm.

Crystals not observed.

Pith of thin-walled isodiametric cells.

Sample: UF 00225-033245 (CC-32, 10 mm with 2 mm wide pith).

Comments — This sample has a small diameter, and we were not able to observe intervessel or vessel-pitting, so it is difficult to suggest affinities with any degree of certainty. Families which have members with predominantly solitary vessels, scalariform perforations with more than 20 bars, vessels that are not wide (> 200 μm) or few (< 5/mm^2), non-septate fibers, narrow heterocellular rays, and diffuse parenchyma include: Buxaceae, Caprifoliaceae, Chloranthaceae, Clethraceae, Cornaceae, Cunoniaceae, Daphniphyllaceae, Dilleniaceae, Eucryphiaceae, Grubbiaceae, Hamamelidaceae, Icacinaceae, Myricaceae, Symplocaceae, Theaceae. Of these, Cornaceae, Hamamelidaceae, Icacinaceae, Symplocaceae, and Theaceae occur in the fruit and seed assemblage at the Nut Beds.

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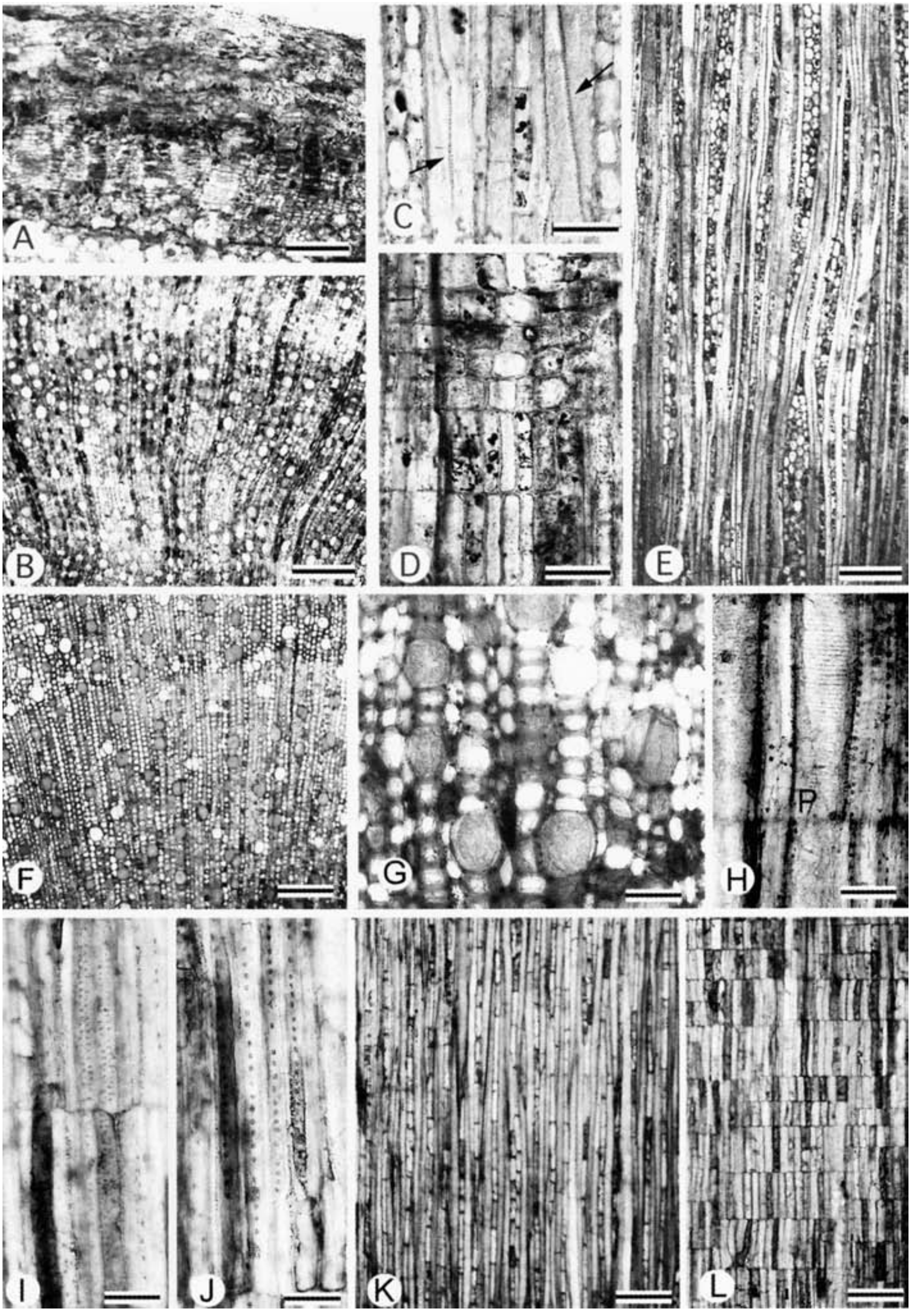
Fig. 45. Nut Beds Xylotype I-A: woods with solitary vessels, scalariform perforations, rays < 10-seriate. A–E: UF 00225-033245 (CC-32). – A: Bark, XS. – B: Numerous narrow angular vessels, XS. – C: Scalariform perforation plates in steeply inclined end walls (arrows), TLS. – D: Square body cells, markedly upright marginal cells, RLS. – E: Heterocellular multiseriate and uniseriate rays of markedly upright marginal cells, TLS. — F–L: UF 00225-033246 (CC-13). – F: Solitary angular vessels, diffuse porous wood, XS. – G: Narrow angular vessels, XS.



(Fig. 45) H: Scalariform perforation plates with many, closely spaced bars (above P), RLS. – I: Vessel-ray parenchyma pits, RLS. – J: Fiber pits with distinct borders, RLS. – K: Narrow rays with markedly upright cells, TLS. – L: Upright ray cells, RLS. — Scale bars = 250 µm in A, B, E, F; 100 µm in K, L; 50 µm in C, D, G, H, I, J.

3) **UF 00225-033246** (Caprifoliaceae? *Dipelta*? *Viburnum*?) (Fig. 45F–L)

Growth rings absent.

Diffuse porous. Vessels predominantly solitary, angular in outline; average tangential diameter 45 (7) µm; average vessel frequency 75/mm^2, range 40–110/mm^2; perforations exclusively scalariform, with numerous (> 50) bars in steeply inclined end walls; intervessel pits apparently small and alternate to subopposite; vessel-ray parenchyma pits small, similar in size to the intervessel pits, oval in outline, crowded opposite; vessel element lengths 0.86–1.2 mm long.

Fibers non-septate, walls thin to medium; distinctly bordered pits on both radial and tangential walls.

Axial parenchyma likely diffuse and scanty paratracheal.

Rays 1–3-seriate. Rays composed exclusively of upright cells, usually 3 times taller than wide; rays mostly > 1 mm high, some taller than the section; 7–10/mm.

Crystals not observed.

Pith “hollow.”

Sample: UF 00225-033246 (CC-13, 9 mm with 2.7 mm wide pith).

Similarities to extant woods — Metcalfe and Chalk’s descriptions (1950) indicate that only three families include genera with predominantly solitary vessels, scalariform perforation plates, alternate to opposite intervessel pits, vessel-ray parenchyma pits similar to intervessel pits, fibers with bordered pits on both walls, and rays composed entirely of upright and square cells: Caprifoliaceae, Ericaceae, and Canellaceae. The Caprifoliaceae are more similar to this wood than Ericaceae, in which only the woods with exclusively uniseriate rays lack procumbent cells, or Canellaceae, which have large intervessel pits, oil cells, and commonly have crystals. The characteristics of *Viburnum* (more than 20 bars per perforation plate, and rays with few procumbent cells) and *Dipelta* (rays composed entirely of square to upright cells) are consistent with this Clarno wood.

Caprifoliaceae are not reported from the Nut Beds fruit and seed assemblage. However, the extinct fruit genus *Diplodipelta* occurs from the Eocene to Miocene in the western United States (Manchester & Donoghue 1995).

4) **USNM 507935** (Fig. 46)

Growth rings present, marked by radially flattened fibers.

Diffuse porous, but with latewood vessels tending to be narrower than the earlywood vessels. Exclusively solitary, tending to be angular in outline; average tangential diameters 72 (12)–73 (11) µm; vessel frequency averages of 58–70 vessels/mm^2, total range of 32–123/mm^2; in tangential section appearing to be scalariform perforations with many bars in steeply inclined end walls, but in radial section only crowded opposite pits observed; intervessel pits crowded, predominantly opposite to locally alternate, small, 3–5 µm; vessel-ray parenchyma pits similar to intervessel pits; helical thickenings not observed; mean vessel element length of 996 µm, range 788–1266 µm; tyloses absent.

Fibers non-septate, walls thick, distinctly bordered pits on radial and tangential walls.

Axial parenchyma diffuse, scanty, strands of 8–12 cells.

Rays 1–5(–6)-seriate. Multiseriate rays heterocellular, body ray cells procumbent with 1–2 rows (usually) of marginal rows of upright and square cells, up to 8 marginal rows, upright cells markedly taller (2–3 times) than the procumbent cells; uniseriate

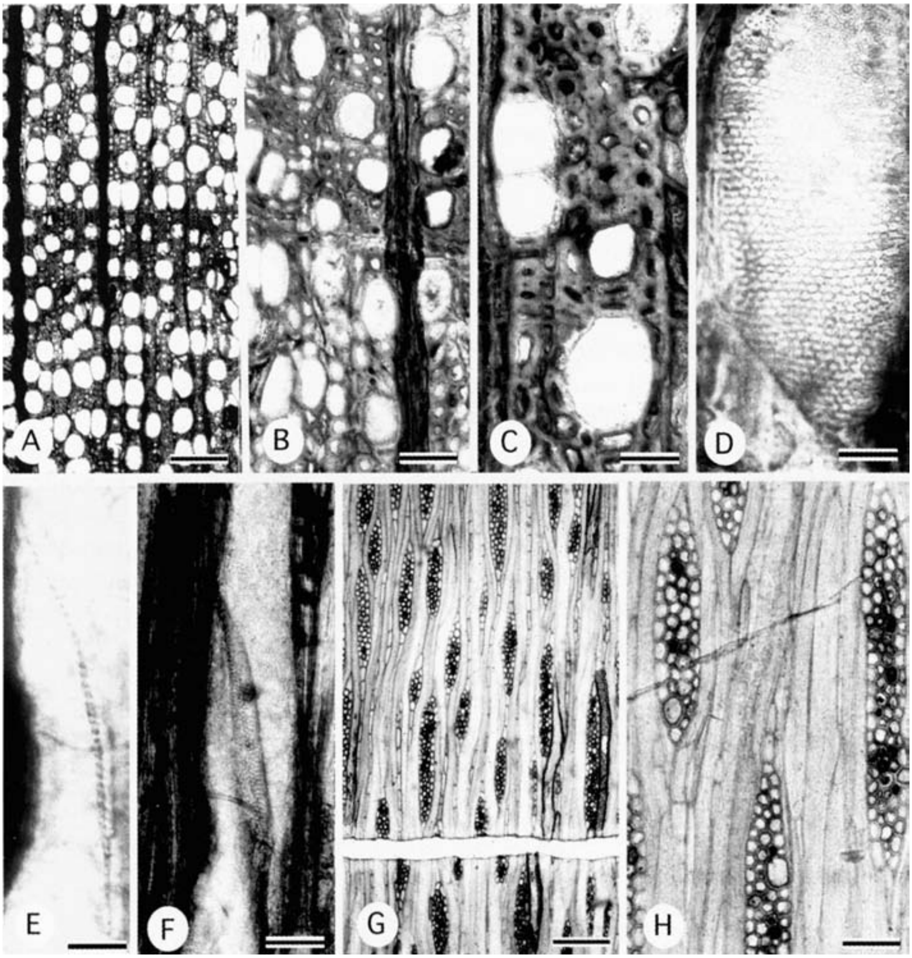


Fig. 46. Nut Beds Xylotype I-A: wood type with solitary vessels and multiple perforation plates, not scalariform. A–E: USNM 507935; F–H: USNM 507936. – A: Diffuse porous wood, growth ring boundaries distinct, XS. – B: Detail of growth ring boundary, XS. – C: Fibers with medium-thick walls, pits on both radial and tangential walls, XS. – D: Vessel element end wall, TLS. – E: End wall of vessel element, steeply inclined, TLS. – F: Oblique view of vessel element end wall, TLS. – G: Multiseriate rays with marginal rows of upright cells, TLS. – H: Multiseriate rays, two with idioblasts, TLS. — Scale bars = 250 μm in A, G; 100 μm in B, H; 50 μm in C, E, F; 25 μm in D.

rays all upright and square cells, usually less than 10 cells high; some rays with idioblasts, larger cells with thicker walls; multiseriate portion of the ray with an average height of 637 (79) μm, range 520–848; 7–10/mm.

Crystals not observed.

Storied structure absent.

Samples: USNM 507935 (C60-6), USNM 507936 (C60-10, >10 cm), UF 12115 (5 cm).

Comments — A distinctive feature of this wood is the appearance of the vessel element end walls. Initially we thought this wood type had scalariform perforation plates with many bars because of the appearance of the end walls in tangential section (Fig. 46E). However, in oblique and radial sections we never observed bars, but rather what appears to be small crowded opposite pitting (Fig. 46D, F). Foraminate perforation plates typically have wider openings than observed in this wood.

Similarities to extant woods — Families that have genera with diffuse porous woods that have exclusively solitary vessels, multiple perforation plates, numerous and narrow vessels, fibers with distinctly bordered pits, vessel-ray parenchyma pits not enlarged and similar to the intervessel pits, rays that are between 4–10-seriate, and diffuse parenchyma include Clethraceae, Ericaceae, Symplocaceae, Theaceae (all Ericales *sensu* APG); Cornaceae (Cornales *sensu* APG), Garryaceae (Garryales *sensu* APG), Myricaceae (Fagales), Escalloniaceae, Icacinaceae.

Some Ericaceae, in addition to scalariform perforations and/or simple perforation plates, have bordered pits mixed with the perforations (e.g., *Vaccinium*, Metcalfe & Chalk 1950), or areas where it appears that there are groups of pits rather than perforations (pers. observ.). The pits are larger and less crowded than in this wood. Moreover, extant Ericaceae usually have alternate pitting in addition to opposite pitting. Slides of 16 genera of Ericaceae were examined. In *Meisteria* aggregations of pits at end walls were fairly common, and a few had small opposite pits aggregated at the ends of vessel elements. However, the vessels in this genus are in well-defined straight tangential bands and rays are of two distinct size classes. Some *Gaylussacia* and *Lyonia* samples also had some end-wall aggregations of opposite pits, although not as crowded or numerous.

To our knowledge, such commonly occurring aggregations of crowded small opposite pitting at the ends of vessel elements have not been reported for the other families listed above.

NUT BEDS XYLOTYPE I – EXCLUSIVELY MULTIPLE PERFORATION PLATES

B: Vessels solitary and in radial multiples, rays < 10-seriate

1) **USNM 508006** (Cornaceae s.l.?) (Fig. 47A–G)

Growth rings present, marked by radially flattened latewood fibers, and by earlywood vessels wider than preceding ring's latewood vessels.

Diffuse porous. Vessels solitary (ca. 37%) and in radial multiples of 2–8, with a tendency to radial chains and a radial alignment; average tangential diameter 38 (6) µm; average vessel frequency 256/mm^2, range 165–350/mm^2, perforations exclusively scalariform, with 14–37 fine bars, average 20, distance between bars ca. 5–8 µm, bars occasionally forked; intervessel pits opposite, 6–8 µm, in narrower vessels scalariform, vessel-ray parenchyma pits horizontally elongate; helical thickenings not observed; vessel element lengths 486–1,032 µm; tyloses not observed.

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

Axial parenchyma rare, occasional isolated strands.

Rays 1–4-seriate. Multiseriate rays heterocellular, composed of procumbent body cells, with 1–2 (up to 8) rows of uniseriate marginal cells, marginal cells sometimes > 3 times the height of procumbent cells; some tendency to sheath cells; mean height of multiseriate portion of ray 496 (209) µm, range 226–927 µm; uniseriate rays composed of upright cells; 6–8/mm.

Crystals not observed.

Storied structure absent.

Pith composed of isodiametric parenchymatous cells.

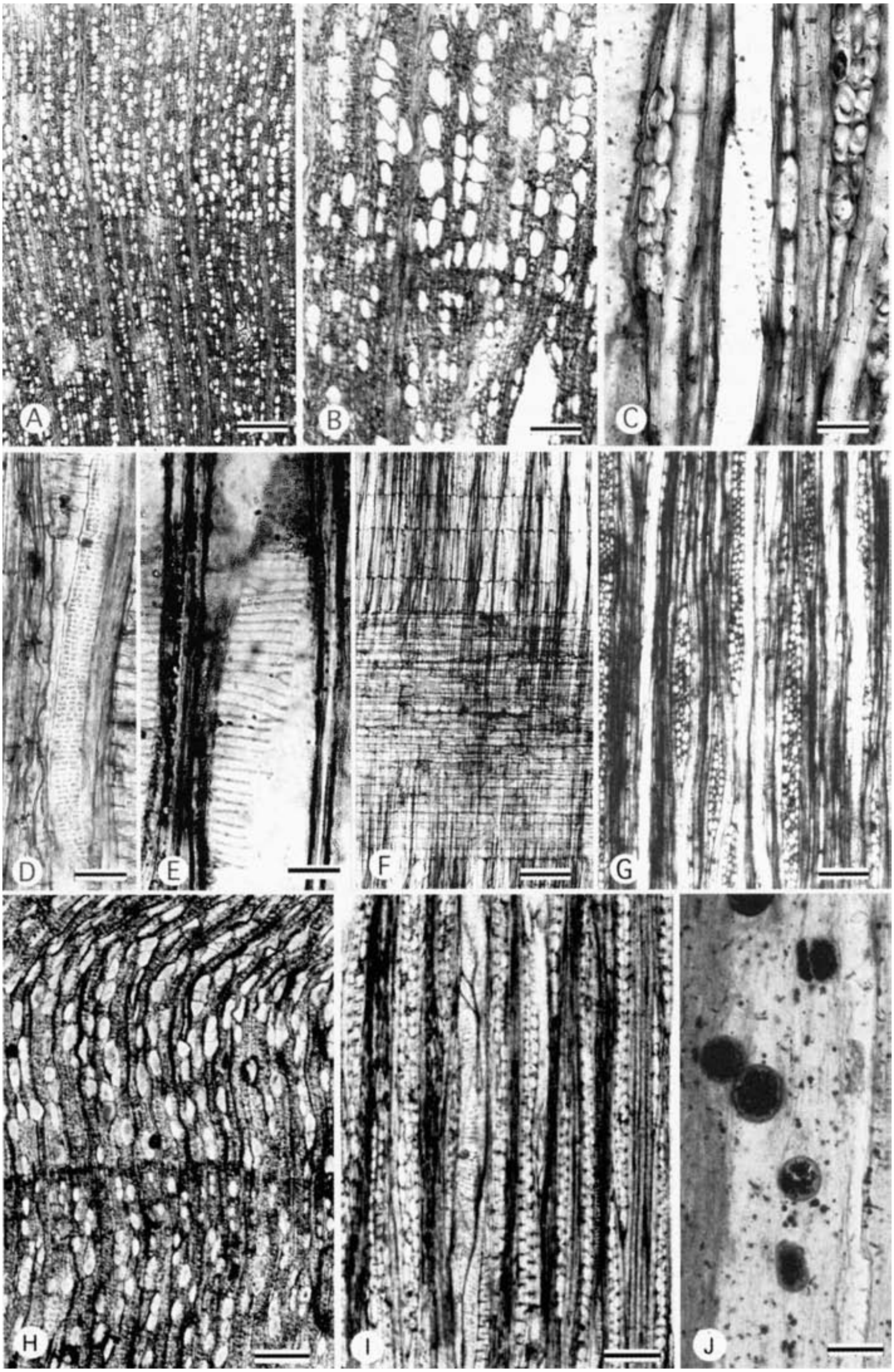
Sample: USNM 508006 (C4A-31, ≥ 3.5 cm).

Comments — Most of the pith cells are filled with fungal hyphae and fungal spores. Hyphae also are common in the vessels and ray parenchyma, and in many fibers the S_2 layer has been eroded away. The vessel-ray parenchyma pits appear horizontally elongate, but it is not clear if they have reduced borders or not. Also, it cannot not be determined with certainty whether spiral thickenings are present in the elongated tips of the vessel elements.

Similarities to extant woods — Families that include diffuse porous woods with the combination of radial multiples and solitary pores, with either a tendency to a radial arrangement or vessels commonly in radial multiples of 4 or more, scalariform perforations, opposite-scalariform intervessel pits, and heterocellular multiseriate rays include the Aquifoliaceae, Cornaceae s.l. (including Nyssaceae), Olacaceae, and Styracaceae. Apotracheal parenchyma is more abundant, usually diffuse-in-aggregates, in the Aquifoliaceae and Olacaceae, in contrast to this wood in which axial parenchyma is not common. Styracaceae have small and round vessel-ray parenchyma pits.

There is some similarity to those species of *Turpinia* (Staphyleaceae) that commonly have radial multiples. The ray structure (4-seriate or more) and vessel-ray parenchyma pits (horizontally elongate) of *Turpinia* are consistent with this Clarno wood. However, in *Turpinia* vessel multiples are not as common, there are fewer vessels per multiple, and there is scanty paratracheal axial parenchyma rather than diffuse apotracheal parenchyma.

It is tempting to consider this wood to be Cornaceae because of that family's occurrence in the fruit and seed record at Clarno and its excellent record in the early Tertiary of the western United States (Manchester 1999). The Nut Beds fruit and seed assemblage includes both extant and extinct genera of Cornaceae: *Cornus, Mastixia, Mastixioidiocarpus, Mastixicarpum, Langtonia,* and *Nyssa*.


A
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However, the anatomy of this wood does not conform to any one genus within the Cornaceae, so we cannot exclude the possibility that this wood has affinities with the other families mentioned above. Additional work on these families may help to resolve this Clarno wood's affinities. In *Nyssa* vessel-ray parenchyma pits usually are small and round, only rarely being horizontally elongate (Noshiro & Baas 1998; pers. observ.), which is unlike this Clarno wood. Horizontally enlarged vessel-ray parenchyma pits occur in *Mastixia*, but radial multiples of vessels are not common in *Mastixia*.

Given that there are extinct genera of Cornaceae in the fruit and seed assemblage, it would not be surprising if there were also extinct genera of Cornaceae in the wood assemblage. Analyses of rbcL sequences revealed four lineages within the cornaceous clade, and suggested monophyly for the Nyssoid-Mastixioid group. However, analyses of wood anatomical data did not place *Nyssa* and *Mastixia* in the same group within the Cornaceae (Noshiro & Baas 1998). This Clarno wood has characteristics that would be consistent with a Nyssoid-Mastixioid group.

Noshiro and Baas (1998) found differences in quantitative features between the temperate-subtropical species of *Nyssa* and the tropical *N. javanica*; vessel density 26–150/mm^2 vs. 11–23/mm^2, vessel tangential diameter 33–66 μm vs. 77–109 μm, ray width 1–3 cells vs. 1–6 cells, respectively. This Clarno wood has a vessel density and diameter that matches temperate-subtropical species, but has wider rays consistent with the tropical *N. javanica*.

Comparisons with other fossil woods — Woods assigned to Nyssaceae occur in the Cretaceous and Tertiary of Europe, North America, and Asia (Mädel 1959; Prakash & Barghoorn 1961b; Van der Burgh 1964; Petrescu 1970, 1978; Suzuki 1975; Wheeler et al. 1978; Gottwald 1992; Meijer 2000). Although generally similar to them, this wood differs as its vessel-ray parenchyma pits are not similar to intervessel pits. *Mastixioxylon* Gottwald (1992) has predominantly solitary vessels, as do most of the woods assigned to *Cornoxylon* or *Cornus* (e.g., *Cornoxylon latiporosum* Kräusel & Schönfeld 1924, *Cornus simanensis* (Watari) Watari 1948, 1952), except for *Cornus tsuyazakiensis* Suzuki (1982), which has alternate pits.

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Fig. 47. Nut Beds Xylotype I-B: woods with vessels solitary and in radial multiples, scalariform perforations, rays, < 10-seriate. – A–G: USNM 508006 (C4A-31) ?Cornaceae s.l. – A: Diffuse porous wood, vessels mostly in radial multiples, XS. – B: Detail of growth ring boundary, XS. – C: Scalariform perforation plate, TLS. – D: Opposite intervessel pits, TLS. – E: Scalariform perforation plate with thin bars, occasional forking, RLS. – F: Heterocellular multiseriate rays, body of procumbent cells and markedly upright marginal cells, RLS. – G: Multiseriate heterocellular rays, TLS. — H–J: USNM 507900 (C4A-37). H: Distinct growth rings marked by radially narrower fibers; vessels solitary and in radial multiples, XS. – I: Narrow rays, scalariform intervessel pitting, TLS. – J: Spores? in vessels, TLS. — Scale bars = 250 μm in A, H; 100 μm in B, F, G, I; 50 μm in C, D; = 25 μm in E, J.

2) **USNM 507900** (Fig. 47H–J)

Growth rings present, marked by radially narrower latewood fibers.

Diffuse porous. Solitary and in radial multiples of 2 (3), solitary vessels tend to be oval in outline; average tangential diameter 72 (16) µm; average vessel frequency 44, range 32–59/mm^2, perforations exclusively scalariform, with 8–20 bars; intervessel pits opposite, and scalariform, vessel-ray parenchyma pits with reduced borders and oval and somewhat horizontally elongate; helical thickenings not observed; vessel element lengths 610–790 µm; tyloses not observed.

Fibers non-septate, walls medium-thick; pits not observed.

Axial parenchyma absent–rare.

Rays 1–3-seriate, mostly 2–3-seriate. Multiseriate rays heterocellular, composed of procumbent body cells, mostly 2–4 rows of uniseriate marginal cells; 598–1130 µm high; 12–15/mm.

Crystals not observed.

Storied structure absent.

Sample: USNM 507900 (C4A-37, > 6 cm).

Comments — This wood was not well preserved; some areas were badly crushed. There is also evidence of considerable wood degradation by insects and fungi.

Similarities to extant woods — Families that include diffuse porous woods with the combination of radial multiples and solitary pores, scalariform perforations, opposite-scalariform intervessel pits, rare axial parenchyma, 1-3-seriate heterocellular rays, and non-septate fibers include the Atherospermataceae, Caprifoliaceae, Cercidiphyllaceae, Cornaceae, Epacridaceae, Eucryphiaceae, Hamamelidaceae, and Staphyleaceae. *Cercidiphyllum* has alternating uniseriate and biseriate rays and so differs from this wood.

3) **UF 12380** (Malpighiales?) (Fig. 48)

Growth rings indistinct.

Diffuse porous. Vessels solitary (ca. 22%) and in radial multiples of 2–7, solitary pores rounded in outline, tending to a radial alignment; average tangential diameter 47 (12) µm; average vessel frequency 114, range 93–133/mm^2; perforations scalariform with 12–15 widely spaced (ca. 8–15 µm) bars, sometimes bars relatively thick (ca. 3 µm); intervessel pits mostly alternate, usually rounded in outline, sometimes tending to opposite and transitional in the narrower vessel elements, 4–6 µm; vessel-ray parenchyma pits not observed; helical thickenings not observed; possible to measure only one vessel element length, 600 µm; tyloses present, thin-walled, in tangential section appearing to subdivide vessels, as well as appearing more bubble-like.

Fibers appear non-septate, walls thin, pitting not observed.

Axial parenchyma rare, occasional isolated strands of more than 12 cells.

Rays 1–4(–6)-seriate. Multiseriate rays homocellular composed entirely of upright and square cells, and heterocellular, composed predominantly of upright and square cells with some intermixed procumbent cells; averaging 2.8 mm high, up to 4.5 mm; uniseriates composed exclusively of upright cells; 4–6/mm.

Crystals not observed.

Storied structure absent.

Sample: UF 12380 (1.4–2.2 cm).

Comments — The sample has a hollow pith, but the hollowness may be due to the decay of thin-walled parenchymatous cells by fungi. Fungal hyphae are abundant in vessels, ray parenchyma, and fibers. There is considerable infilling of the cells with

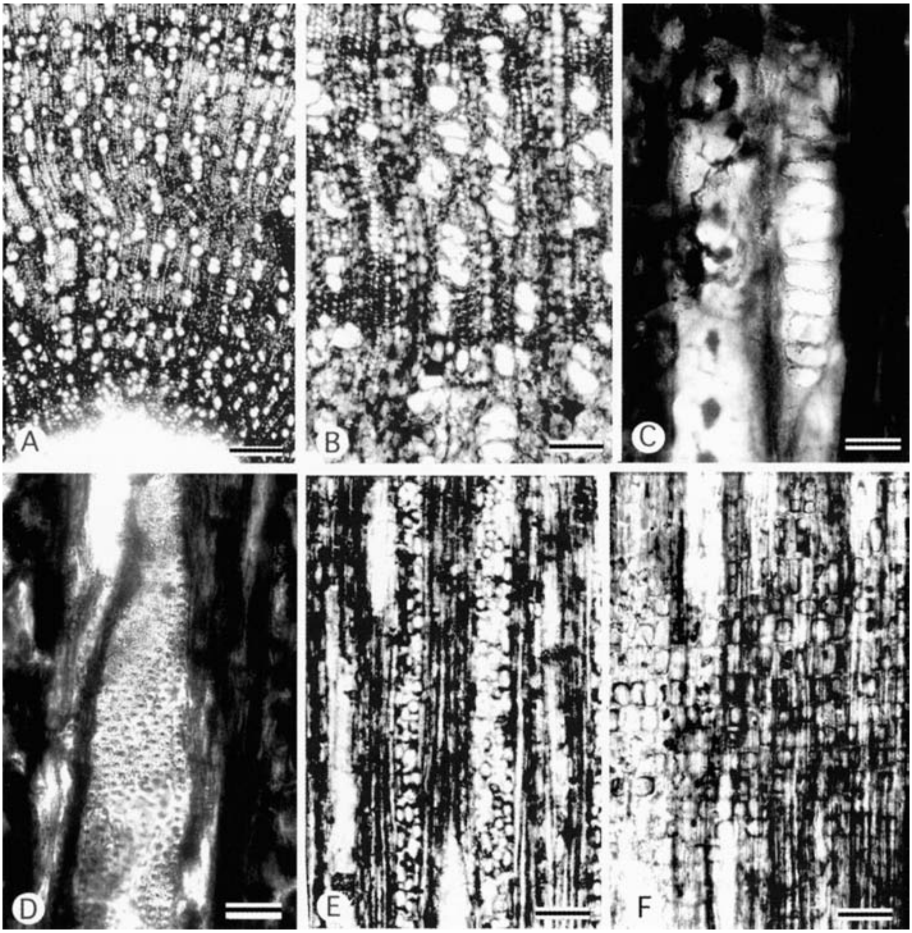


Fig. 48. Nut Beds Xylotype I-B: UF 12380 (Malpighiales?). – A: Vessels solitary and commonly in radial multiples, XS. – B: Indistinct growth ring boundary, vessels in radial multiples, XS. – C: Scalariform perforation with widely spaced bars, RLS. – D: Intervascular pits, TLS. – E: Tall multiseriate rays, TLS. – F: Ray composed mostly of square to upright cells, RLS. — Scale bars = 250 µm in A; 100 µm in B, E, F; 50 µm in C; 25 µm in D.

colored compounds, possibly byproducts from fungal degradation. Septa were not observed, but these may have been removed by fungal decay. The abundance of dark-colored compounds in the ray cells makes it difficult to clearly view vessel-ray parenchyma pits. In some areas where rays contacted vessels the pits appear similar in size and shape to the intervessel pits, but we cannot state with certainty that this is the case.

Similarities to extant woods — The combination of vessels commonly in radial multiples, scalariform perforations, alternate and opposite intervessel pitting, rare axial parenchyma, and rays taller than 1 mm suggests affinities with Flacourtiaceae and Violaceae, both in the Malpighiales *sensu* APG (1998). Rays composed entirely of upright and square cells are reported for both these families (Metcalfe & Chalk 1950). Crystals are nearly always present in ray cells in Flacourtiaceae and common in Violaceae; septate fibers are usually present in both families; neither feature was observed in this fossil. Whether this absence is due to original absence or preservational effects is unclear. Crystals often are in chambered cells in Flacourtiaceae, but no chambered cells were observed in the fossil. In both Flacourtiaceae and Violaceae rays are more abundant than in the fossil, but ray features change pith to bark. Because the vessel-ray parenchyma pits were not observed and it is not clear whether this wood had septate fibers, it is not possible to determine its affinities.

NUT BEDS XYLOTYPE I – EXCLUSIVELY MULTIPLE PERFORATION PLATES

C: Vessels solitary and in multiples, rays > 10-seriate

ANOMALOCENTRA gen. nov.

Anomalocentra pseudoplatana gen. et sp. nov. (Fig. 49)

Axes usually small, < 5 cm, with pith containing vertical fibrovascular bundles, 120 to 270 µm in diameter scattered among the parenchyma tissue. Parenchyma cells of the ground tissue rounded in transverse section, square to rectangular in longitudinal section, 40–60 µm in diameter. Tracheary elements of the bundles 20 to 31 µm in horizontal diameter, helically to annularly thickened, accompanied by elongate axial parenchyma strands similar to those of the secondary xylem, with cells ca. 95–120 µm long.

Growth rings distinct, marked by radially flattened fibers and dilation of rays.

Diffuse porous. Pores solitary, and in multiples of 2–5 (tangentially or radially arranged, or in clusters); tangential diameter 32–90 (average 60) µm; vessel frequency range of 136–300/mm^2, perforations exclusively scalariform with 8–15 bars; intervessel pits opposite, 5–7.5 µm; pits to parenchyma not observed; vessel element lengths 450–680, average 590 µm; tyloses not observed.

Fibres non-septate, pitting usually not apparent. Vasicentric tracheids occasionally present with pits on tangential and radial walls.

Axial parenchyma apotracheal, diffuse, as isolated cells and diffuse-in-aggregate, in short uniseriate bands.

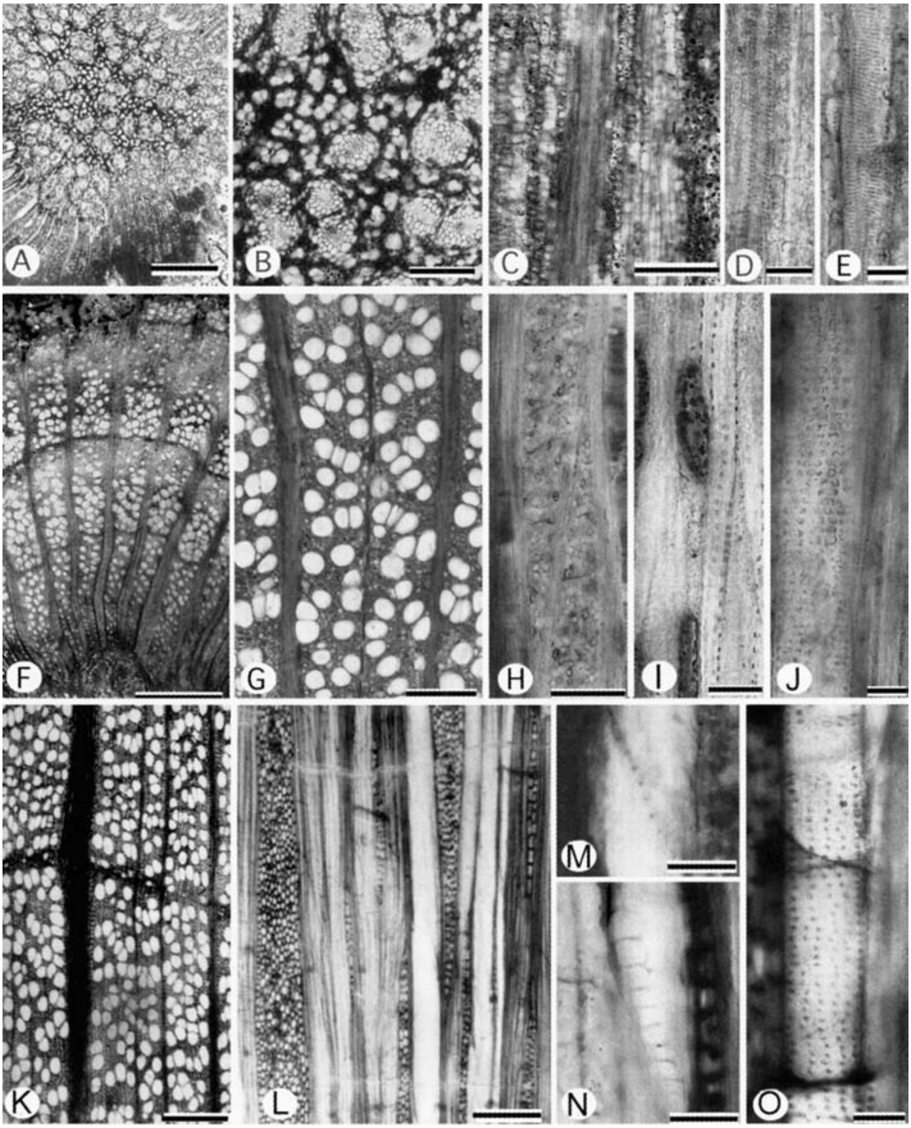


Fig. 49. Nut Beds Xylotype I-C: *Anomalocentra pseudoplatana* gen. et sp. nov. A–F: UF 32867; G–I: UF 32873; J–N: USNM (C4A-143A). – A: Center of small axis showing pith and wide rays, XS. – B: Detail of pith, showing fibrovascular strands scattered through the parenchyma, XS. – C: Fibrovascular strands in the pith, RLS. – D, E: Helical to annular thickenings of tracheary elements in pith, RLS. – F: Growth rings near pith, XS. – G: Vessels solitary and in multiples, wide rays, XS. – H: Multiseriate rays, TLS. – I: Imperforate tracheary elements with distinctly bordered pits on tangential and radial walls, TLS. – J: Opposite intervessel pits, TLS. – K: Diffuse porous wood, distinct growth rings, large rays, tendency for tangential multiples, XS. – L: Heterocellular multiseriate rays, TLS. – M, N: Scalariform perforations, TLS. – O: Vessel to imperforate tracheary element pitting, opposite arrangement, TLS. — Scale bars = 1000 μm in A; 500 μm in F, K; 250 μm in G; 200 μm in B, C, L; 100 μm in H; 50 μm in D, E, M, N, O; 25 μm in I, J.

Rays 1–14-seriate, homocellular to heterocellular with 1–5 rows of square or upright cells; multiseriate rays composed of procumbent cells except for the margins which include one or more rows of square or upright cells, sheath cells common; uniseriate rays composed of upright cells; multiseriate ray height up to 3 mm; 3–5/mm.

Occasional rhomboidal crystals in the procumbent cells in the rays.

Storied structure absent.

Holotype: UF 32873 (32 mm).

Additional specimens: USNM 507898 (C4A-2, not C4A-2a), USNM 507820 (C4A-143A, not C4A-143, > 50 mm), UF 32867 (11 mm diam.), UF 32868 (20 mm diam.), UF 32869 (34 mm), UF 32870 (16 mm), UF 32871 (23 mm), UF 32872 (10 mm).

Etymology: The generic name refers to the anomalous pith anatomy of these stems. The specific epithet refers to the topographic similarities of the secondary xylem to that of *Platanus* and *Platanoxylon*.

Comments — Based on the general topology of this wood, including vessel and parenchyma distribution patterns and wide rays, opposite intervessel pitting and scalariform perforation plates, we first thought that these specimens belonged to *Platanoxylon*, perhaps even the Nut Beds *P. haydenii*. However, examination of the smaller diameter axes reveals highly distinctive pith. The pith of this fossil contains abundant scattered fibrovascular bundles composed of annularly and helically thickened tracheary elements. This kind of pith is not found in *P. haydenii*, nor in any extant Platanaceae, *Euptelea*, or *Fagus*. It is not reported for the Icacinaceae, but that family needs more thorough investigation for pith characters. The recognition of anomalous pith in this fossil species prompted a more detailed scrutiny of the secondary xylem, to facilitate the recognition of specimens when the pith is not available. We also checked axes of *P. haydenii* with intact pith to verify that the pith was normal in that species. In most characters the wood of *Anomalocentra* is similar to *Platanoxylon haydenii*, but *Anomalocentra* tends to have more uniseriate rays and more heterogeneous multiseriate rays than *P. haydenii*. Tyloses are rare or absent in *Anomalocentra*, but can be common in *P. haydenii*. Pits to parenchyma are rarely if at all preserved in *Anomalocentra*, but common and often scalariform in *P. haydenii*. Most importantly, perhaps, is the presence of patches of fiber-tracheids with prominent circular pits on tangential and radial walls seen in well-preserved samples of *Anomalocentra*, but not in *Platanoxylon*.

Euptelea baileyana Scott & Barghoorn 1955 (Fig. 50)

Euptelea has not been confirmed in the Tertiary record by its diagnostic fruits. Nevertheless, the report of its wood in the Cenozoic of North America, based on the sample from the Nut Beds identified by Scott and Barghoorn (1955) has been regarded as evidence for a broader distribution of this genus in the early Tertiary. There are, however, some differences already cited by Scott and Barghoorn (1955) that cause us to question this assignment (see below).

Description:

Growth rings present, marked by the transition from radially flattened fibers and narrow vessels of the latewood to inflated fibers and wider vessels of earlywood.

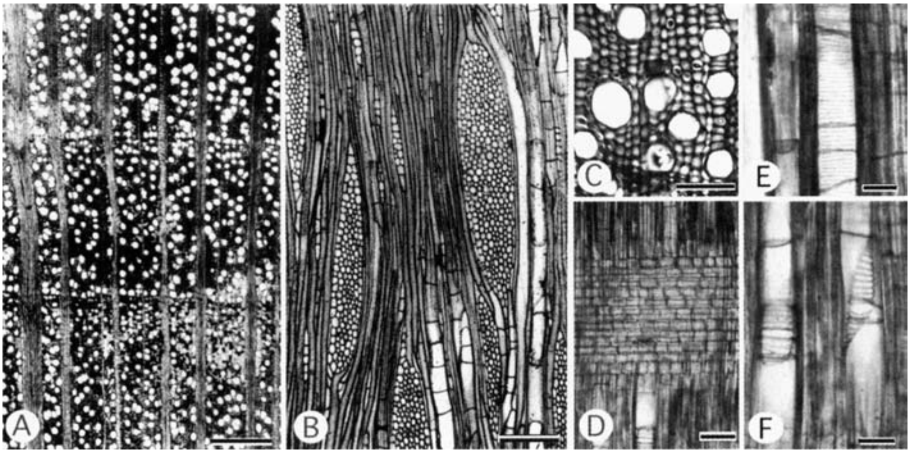


Fig. 50. Nut Beds Xylotype I-C: *Euptelea baileyana* Scott & Barghoorn (UM 32338). – A: Diffuse porous wood with predominantly solitary vessels, distinct growth rings, XS. – B: Tall a nd wide multiseriate rays, and uniseriate rays, tyloses segmenting vessels, TLS. – C: Detail of growth ring boundary, absence of axial parenchyma. – D: Heterocellular rays, scalariform perforation plates, RLS. – E: Opposite to scalariform intervessel pits, TLS. – F: Scalariform perforation plates, RLS. — Scale bars = 500 μm in A; 200 μm in B; 100 μm in C, D; 50 μm in E, F.

Wood diffuse porous ca. 85 per mm^2, slightly more abundant in earlywood than in latewood; vessels solitary and occasionally in radial multiples of 2–4; thin-walled, oval in outline; tangential diameter 25–70, average 50 μm, slightly angular in cross section; elements up to 850 μm long; perforations oblique, exclusively scalariform; 5–35 bars, average 15, bars mostly narrow and widely spaced; intervessel pits scalariform to opposite; vessel-ray parenchyma pits scalariform, the apertures wider than those of the intervascular pits; helical thickenings absent; thin-walled tyloses common.

Fibers thick-walled, with small pits. Pits prominent on radial walls.

Axial parenchyma very scanty diffuse.

Rays heterocellular (Kribs Type IIA): multiseriate rays up to 18-seriate and 2 mm high with 1–6 marginal rows of enlarged square or upright cells; uniseriate rays 2–7 cells high, composed chiefly of upright cells, but occasionally with one or more almost procumbent cells, up to 8 per mm. Sheath cells absent.

Storied structure absent.

Holotype: University of Michigan Museum of Paleontology 32338; duplicate slides at Harvard University, No. 55572.

Comments — If truly representative of extant *Euptelea*, this wood would be the only indication of the genus from the Tertiary. The distinctive winged fruits have never been found, though they might be expected if the genus were really present in the Clarno Formation.

Similarities to extant woods — Scott and Barghoorn (1955) assigned this species to the extant genus *Euptelea*, based on close similarities of the wood anatomical topology including vessel and parenchyma distribution and ray type. They did, however, summarize some important differences between this fossil and the two modern species of *Euptelea*. The intervascular pitting is transitional (opposite-scalariform) in extant species, but chiefly scalariform in the fossil; the extant species has numerous (20–90) fine bars per perforation plates, whereas the fossil has 5–15 (usually 15) bars. The largest rays observed in the fossil (18-seriate) are wider than the largest observed in the extant species (13-seriate). If the differences were simply due to advancement within the same lineage, it might be expected that the Eocene representative would have perforations with more (not less) numerous bars.

The wood is somewhat similar to that of *Platanoxylon* but differs by the lack of diffuse-in-aggregates axial parenchyma. Similar woods occur among extant *Fagus* (Fagaceae), *Citronella* and *Ottoschultzia* (Icacinaceae), *Platanus*, as well as *Euptelea* (Scott & Wheeler 1982). However, *Platanus* is distinguishable by its tendency for few uniseriate rays, and for rays that are not markedly heterogeneous.

NUT BEDS XYLOTYPE II – MULTIPLE AND SIMPLE PERFORATION PLATES

Wood with idioblasts (Laurales / Magnoliales?) (Fig. 51)

Growth rings indistinct.

Diffuse porous. Vessels solitary and in radial multiples of 2–4 (6), average tangential diameters 58 (7)–64 (7) µm; mean vessel frequencies of 49–56/mm^2, range 29–80 / mm^2; perforations predominantly simple, occasional multiple perforations, some visible in cross section as horizontally inclined plates, some with partial bars; intervessel pits alternate, 5–8 µm, vessel-ray parenchyma pits with reduced borders and horizontally enlarged in upright cells, extending almost the whole width of the ray cell, smaller, and at times appearing similar to intervessel pits in procumbent cells; helical thickenings not observed; vessel element lengths 283–554 µm; widely spaced tyloses common in vessels, sometimes appearing as isolated sacs.

Fibers non-septate, walls thin-medium, pits not observed.

Axial parenchyma rare.

Rays 1–4-seriate. Multiseriate rays heterocellular, intermixed square, upright, and procumbent cells in some rays, procumbent body cells in others; uniseriate rays not common, low, less than 10 cells high; ray cell walls abundantly pitted, total multiseriate ray height 528 (222)–539 (231) µm high; 10–12/mm.

Crystals not observed.

Storied structure absent.

Occasional idioblasts present in rays or isolated amongst ground tissue fibers.

Samples: USNM 507942 (C4A-55, 3 cm), UF 12110 (3 cm), USNM 507823 (C4A-143, ≥ 8 cm).

Similarities to extant woods — The idioblasts in this wood did not appear crystalliferous, and we are interpreting them as oil or mucilage cells. Such cells are reported for Annonaceae, Aristolochiaceae, Burseraceae, Canellaceae, Dilleniaceae, Hernan-

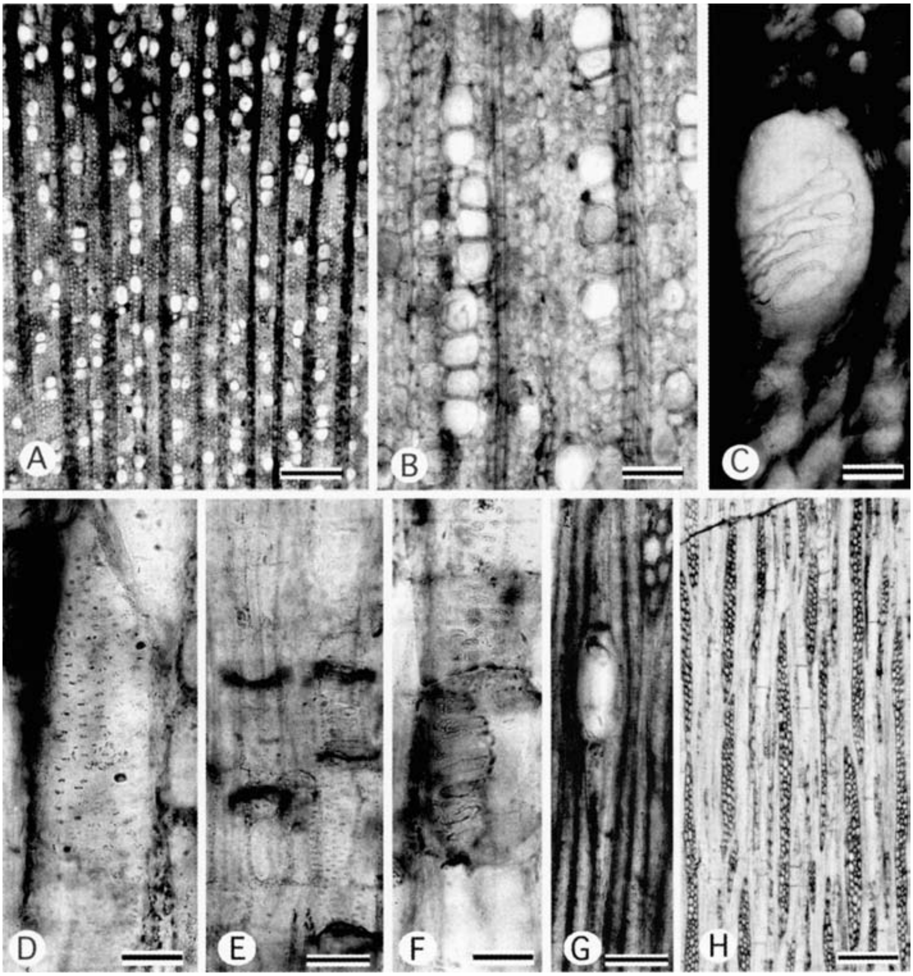


Fig. 51. Nut Beds Xylotype II: wood with idioblasts, Laurales/Magnoliales? A, B, D–F, H: USNM 507942 (C4A-55). C, G: USNM 507823 (C4A-143). – A, B: Diffuse porous wood, vessels solitary and in radial multiples, XS. – C: Multiple perforation plate, XS. – D: Crowded alternate intervessel pits, TLS. – E: Vessel-ray parenchyma pits, similar to intervessel pits, RLS. – F: Vessel-ray parenchyma pits horizontally enlarged, to left of P, RLS. – G: Idioblast (i) in ray, TLS. – H: Multiseriate rays. — Scale bars = 250 µm in A, H; 100 µm in B; 50 µm in E, G; 25 µm in C, D, F.

diaceae, Lauraceae, Magnoliaceae, Monimiaceae, Myristicaceae, Piperaceae, Rutaceae, Saurauiaceae, Schisandraceae, and Winteraceae (Metcalfe & Chalk 1950). Of these, Dilleniaceae (opposite-scalariform intervessel pits, fibers with distinctly bordered pits), Hernandiaceae (parenchyma moderately abundant), Lauraceae, Magnoliaceae, Monimiaceae, Myristicaceae, Piperaceae, Saurauiaceae, Schisandraceae have both simple and scalariform perforations.

The combination of idioblasts, simple and occasional multiple perforations, alternate intervessel pitting, and some horizontally enlarged vessel-ray parenchyma pits suggests affinities with Lauraceae. However, the scarcity of axial parenchyma and transversely oriented multiple perforation plates are not consistent with this assignment. Thus, we hesitate to assign this wood to Lauraceae. It likely belongs in the Magnoliales or Laurales, based on the occurrence of idioblasts and some scalariform perforation plates.

Extant genera of Lauraceae that include species with both simple and scalariform perforation plates, intervessel pits in the range of 5–8 µm, class a or b vessel-ray parenchyma pits, non-septate fibers and scanty axial parenchyma are *Actinodaphne, Laurus, Lindera* Group A, *Persea* p.p., and *Neolitsea* (with Type a vessel-ray parenchyma pits), and *Cryptocarya* and *Apollonias* (with Types a and b) (Richter 1981).

NUT BEDS XYLOTYPE III – EXCLUSIVELY SIMPLE PERFORATION PLATES

A: Vine-like anatomy

i: *Interxylary phloem present*

"Clarno vine with unlignified tissue present" (Fig. 52A–G)

Growth rings indistinct.

Diffuse porous. Vessels exclusively solitary, circular in outline; mean tangential diameter 198 (70) µm, range 90–282 µm, tendency to two width classes of vessels; vessel frequency 6–10/mm^2; simple perforations, with near horizontal end walls; "intervessel" pits crowded alternate, 3–5 µm; mean vessel element length 270 (102) µm, range 158–510 µm.

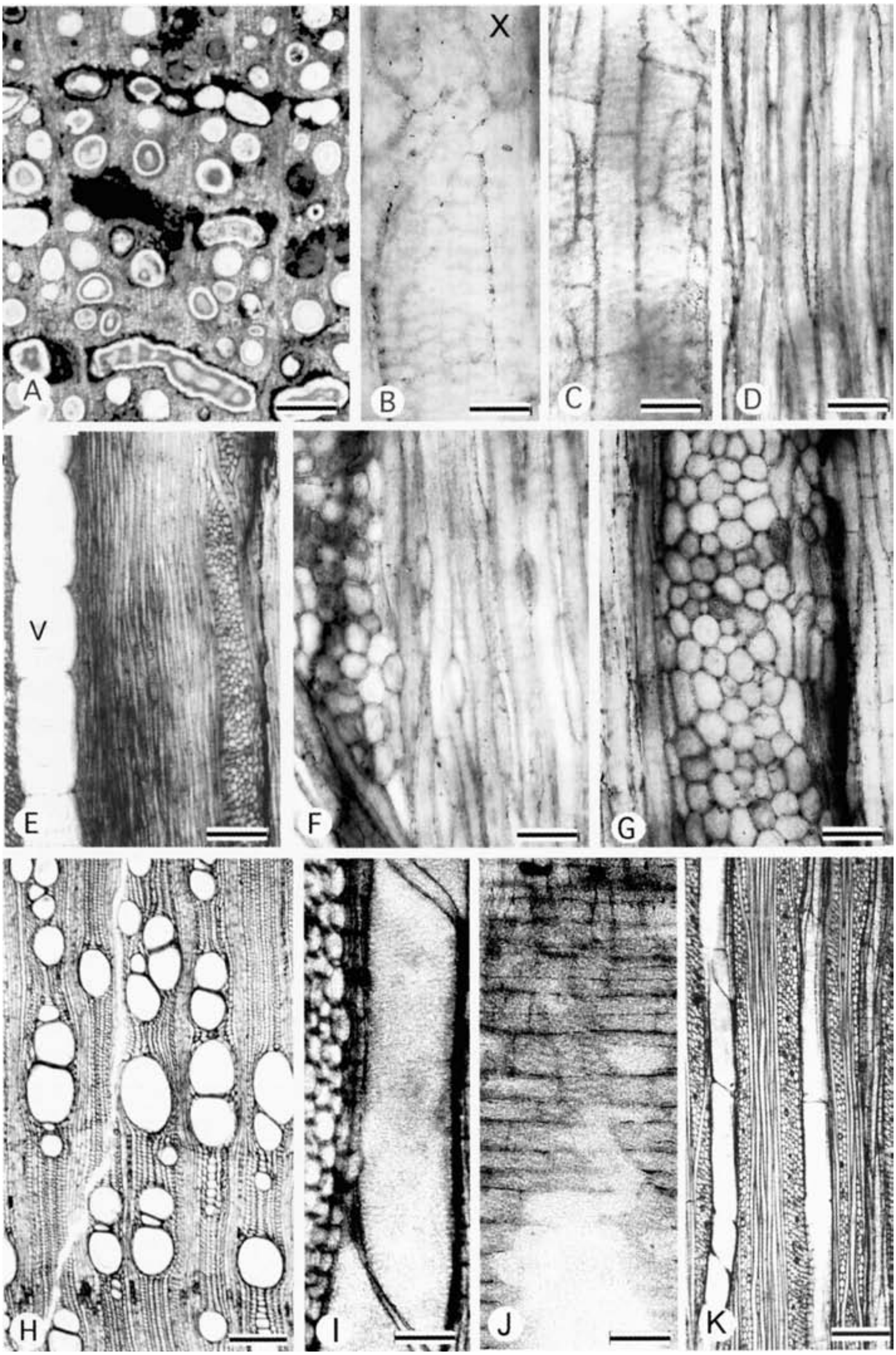
Imperforate elements intergrade between axial parenchyma and fibers, some with abundant simple pits as viewed in tangential section, some without obvious pits on side walls and more fiber-like; 2–4 cells per strand, or 2–4 septa per cell; vasicentric tracheids likely present.

Rays of two sizes, uniseriate rays 1–3 cells tall, multiseriate rays 6–9 cells wide, 735–3400 µm high; ray cells of multiseriate rays thin-walled and variable in size.

Regions of unlignifed tissue, perhaps representing interxylary (included phloem) of the island (foraminate) type, with the "islands" tangentially elongated, ratio tan-

→

Fig. 52. Nut Beds Xylotype III-A: woods with vine-like anatomy. – A–G: Nut Beds Xylotype III-A-i. UF 00225-033247 (CC-35). – A: Solitary vessels, included phloem or unlignifed areas, XS. – B: Crowded alternate intervessel pits, possible tracheid at X, TLS. – C: Vessel-axial parenchyma pits small and crowded, TLS. – D: Imperforate elements, TLS. – E: Tall multiseriate ray, series of vessel elements with transverse end walls, TLS. – F: End of multiseriate ray, 1–2-cell high uniseriate rays, TLS. – G: Ray with cells of variable size, TLS. — H–K: Nut Beds Xylotype III-A-ii. USNM 507933. – H: Vessels tending to be of two distinct sizes, narrow vessels in radial multiples, especially at growth ring boundaries, XS. – I: Simple perforations and small alternate intervessel pits, TLS. – J: Vessel-ray parenchyma pits similar to intervessel pits, TLS. – K: Tall multiseriate rays, non-septate fibers, TLS. — Scale bars = 500 µm in A; 250 µm in E, G, H, K; 50 µm in C, D, F, I, J; 25 µm in B.


X
A
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gential:radial width of bundles averages 2, range 1.5–2.7; mean tangential width of bundles 550 (170) µm, mean radial width of 270 (42) µm.

Sample: UF 00225-033247 (CC-35, 16 mm, center with insect frass).

Similarities to extant woods — There are relatively few families that have interxylary phloem produced by a single cambium (foraminate or island-type included phloem) (see Metcalfe & Chalk 1950; Carlquist 1988; IAWA Committee 1989). Of the families listed as having this feature, this wood has some similarities to the Melastomataceae and Combretaceae, both members of the Myrtales (Van Vliet 1979, 1981) because these two families contain genera with exclusively solitary vessels. Metcalfe and Chalk note that in *Memecylon* uniseriate rays are often only 1 cell high, a feature of this Clarno wood.

Comparisons with other fossil woods — There are at least two other fossil woods with island-type interxylary phloem or unlignifed areas resembling that feature known: *Mennegoxylon jonesii* (Nyctaginaceae), a tree, from the Eocene of Texas and Louisiana (Hueber et al. 1991) and *Memecyloxylon germanicum* (Memecylaceae/ Melastomataceae) Gottwald (1992) from the late Eocene of Germany. *Mennegoxylon* has many radial multiples and exclusively uniseriate rays and so differs from this Clarno wood. *Memecyloxylon* was diagnosed as having rays of two shapes, uniseriate and 2–4-seriate, and vessel diameters of 50–150 µm. The type species, *M. germanicum,* has vessel diameters of 60–75 µm, narrower than the narrowest vessels of the Clarno wood. This Clarno wood has markedly larger rays and wider vessels than *Memecyloxylon*.

ii: *Interxylary phloem absent*

"Clarno vine with radial multiples, no interxylary phloem" (Fig. 52H–K)

Growth rings distinct, marked by radially flattened latewood fibers, a marked change in vessel diameter from last formed latewood and first formed earlywood, and somewhat inflated rays.

Ring porous to semi-ring porous. Earlywood vessels solitary and in radial multiples of 2–3; latewood vessels mostly in radial multiples, frequently more than 4 per multiple, some multiples extending through growth ring boundaries; average tangential diameters of the earlywood vessels 229 (21)–236 (20) µm, total range 170–283 µm; perforations simple; intervessel pits alternate, 6–8 µm, crowded and polygonal in outline, vessel-ray parenchyma pits similar in size and shape to intervessel pits; average vessel element lengths 585 (55)–618 (74) µm; tyloses not observed.

Fibers non-septate, walls thin, pits not obvious.

Axial parenchyma scanty paratracheal to narrow vasicentric, 8–12 cells per strand.

Rays of two distinct size classes, short uniseriate rays usually less than 10 cells high, and tall multiseriate rays up to 8 cells wide. Rays heterocellular, with body of procumbent cells, and usually one marginal row of square/upright cells; multiseriate rays frequently more than 3 mm high, up to 7 mm; 6–8/mm.

Prismatic crystals not observed.
Storied structure not observed.

Samples: USNM 507933 (DEN 108, 2 cm across), USNM 508027 (C4A-94, 7 cm), USNM 508026 (C4A-71, 5 cm, bark present).

Similarities to extant woods — The combination of two size classes of vessels, with the narrower vessels arranged in radial multiples, and tall and wide rays is a syndrome of characters that today is common in vines of different families (Carlquist 1991). Unlike many extant vines, these samples do not exhibit cambial variant structure or included phloem. The Leguminosae, Sapindaceae, and Bignoniaceae are families that include many vines, and have vessel-ray parenchyma pits similar to intervessel pits, and paratracheal parenchyma. The outlines of the pit apertures appear smooth, so it is likely vestured pits are not present and that these woods are not Leguminosae. The intervessel pits are medium-sized and the fibers are non-septate. Sapindaceae usually have small to minute intervessel pits and septate fibers. Thus, these woods appear most similar to the Bignoniaceae. However, information on vine anatomy is not compiled to the same extent as it is for other woody plants, so we are hesitant to assign these woods to the Bignoniaceae at this time.

Comparisons with other fossil woods — *Vitaceoxylon tiffneyi* and *V. carlquistii* Wheeler & LaPasha (1994) differ from the vine wood described above because the Vitaceae woods have wider rays with idioblasts, septate fibers, storied structure, and vessel-ray parenchyma pits that are horizontally elongated with much reduced borders.

NUT BEDS XYLOTYPE III – EXCLUSIVELY SIMPLE PERFORATION PLATES

B: Semi-ring porous to ring porous

i: *Distinctive latewood vessel arrangement patterns*

Ring porous wood with latewood clusters, homocellular rays (Fig. 53A–G)

Growth rings distinct, marked by radially flattened latewood fibers, a marked change in vessel diameter from last formed latewood and first formed earlywood, and by marginal parenchyma.

Ring porous. Earlywood vessels mostly solitary, occasionally in radial multiples, latewood vessels in radial multiples of more than four, or in clusters; average tangential diameter of the earlywood 132 (25) µm; perforations simple; intervessel pits alternate, crowded and polygonal in outline, small, less than 5 µm; pits to parenchyma generally similar to intervessel pits, slightly smaller and more rounded in outline; fine helical thickenings present throughout some of the narrower vessel elements; vessel element lengths 174–202 µm; tyloses not observed.

Fibers non-septate, walls medium-thick, pits not obvious, none seen on tangential walls.

Axial parenchyma paratracheal, vasicentric and confluent, 2–8 cells per strand.

Rays 1–3-seriate. Rays homocellular, composed exclusively of procumbent cells, and heterocellular with body composed of procumbent cells with one row of square/upright cells; average total height of multiseriate rays 205 (77), total range of 92–410 µm; 6–8/mm; simple pits numerous and well-defined on all walls.

Crystals not observed.

Storied structure absent.

Sample: USNM 507917 (DEN 34, 6 cm).

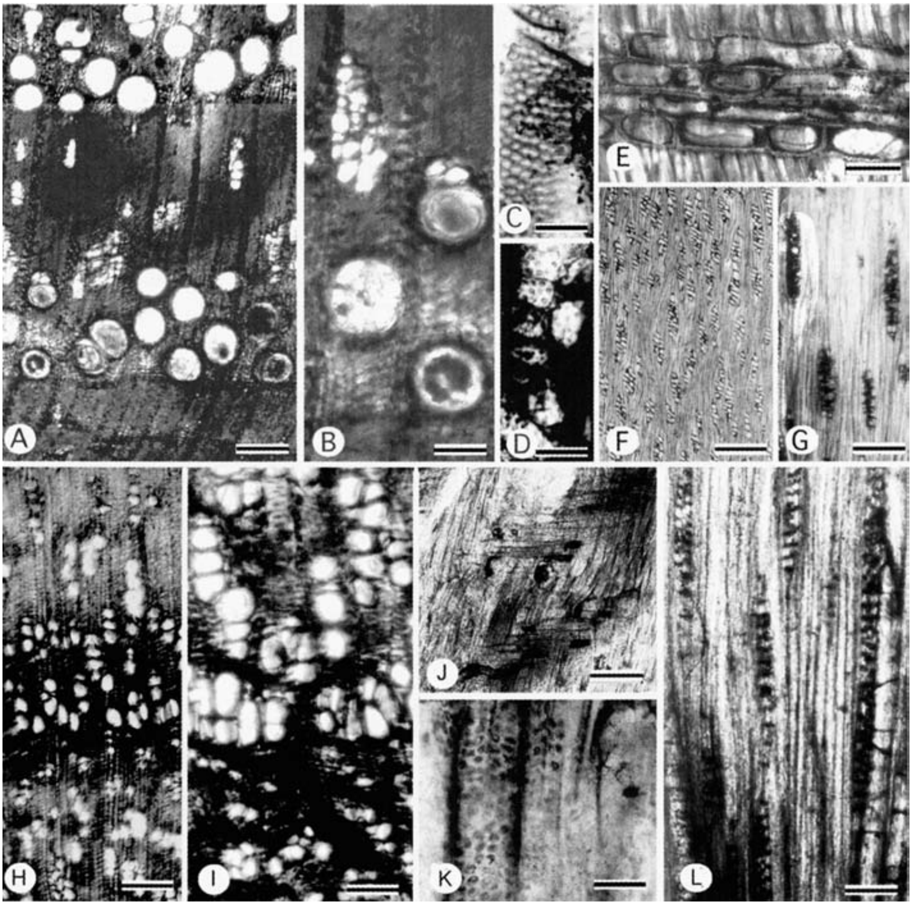


Fig. 53. Nut Beds Xylotype III-B-i: semi-ring porous to ring porous woods of unknown affinities – A–G: USNM 507917 (DEN 34). – A: Ring porous wood, with rounded solitary earlywood vessels, and latewood vessels in clusters, XS. – B: Growth ring boundary, vessels in clusters in latewood, XS. – C: Crowded alternate intervessel pitting, TLS. – D: Vessel-ray parenchyma pitting similar to intervessel pitting, RLS. – E: Ray composed of procumbent cells, RLS. – F, G: Short multiseriate rays, TLS. — H–L: USNM 507932 (DEN 43). – H: Semi-ring porous wood with latewood vessels in radial-diagonal arrangement, XS. – I: Growth ring boundary, XS. – J: Rays mostly of procumbent cells, RLS. – K: Crowded alternate intervessel pitting, TLS. – L: Narrow multiseriate rays, TLS. — Scale bars = 250 µm in A, F, H; 100 µm in B, G, I, J, L; 25 µm in C, D, E, K.

Similarities to extant woods — The combination of ring porosity, latewood vessels in clusters, but no obvious tangential arrangement, vessel-ray parenchyma pits similar to intervessel pits, non-septate fibers, predominantly paratracheal parenchyma, and homocellular 1–3-seriate rays occurs in species of the Bignoniaceae, Leguminosae (all three subfamilies), Meliaceae, and Oleaceae. In some parts of the radial sections, where it was possible to get a relatively "flat" view of the pitting, some pits appear "punctate" and so may be vestured, which would suggest this wood is a legume.

Semi-ring porous wood with latewood vessels in diagonal to tangential arrangement, heterocellular rays (Fig. 53 H–L)

Growth rings distinct.

Semi-ring porous, with crowded earlywood vessels forming a band in the first formed earlywood. Vessels rarely solitary, in radial multiples, often more than 4 per multiple, and clusters; latewood vessels with a radial, diagonal, or tangential orientation; average tangential diameter of the earlywood vessels 75 (18) µm; perforations simple; intervessel pitting mostly crowded alternate (> 10 µm), also opposite to scalariform; vessel-ray parenchyma pits not observed with certainty, possibly with reduced borders, but similar in size to intervessel pits; helical thickenings not observed; vessel element lengths of 723–927 µm; widely spaced thin-walled tyloses present, bubble-like to appearing to segment vessels.

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

Axial parenchyma rare or scanty paratracheal, more than 8 cells per strand.

Rays 1–3-seriate, uniseriates not common. Multiseriate rays heterocellular; range multiseriate ray height 320–820 µm, average 538 (n = 11); ca. 4/mm.

Sample: USNM 507932 (DEN 43, fragment 2 cm).

Comments — The longitudinal sections produced from this fragment did not allow 25 measurements of vessel element lengths and ray heights, or 5 measurements for rays per mm. Because the sample is contorted longitudinal sections are mostly oblique. Preservation of this sample is irregular with some areas highly opalized, and others showing reasonable anatomical detail.

Similarities to extant woods — The combination of a radial/oblique to tangential vessel arrangement, vessels commonly in long radial multiples, simple perforations, large alternate to scalariform intervessel pits, heterocellular rays that are not exclusively uniseriate or more than 10-seriate, low ray frequency, scanty paratracheal parenchyma, and semi-ring porosity occurs in the Araliaceae. Similar vessel arrangement patterns also occur in the Rhamnaceae.

Comparisons with other fossil woods — This wood's general characteristics are consistent with the diagnosis of *Plerandreoxylon*. This wood differs from the two *Plerandreoxylon* species, as its radial multiples are more common, and the tangential arrangement is not as pronounced. Although this wood generally conforms to *Plerandreoxylon* and to the Araliaceae in general, we are not assigning it a specific epithet because the preservation precluded determining important diagnostic characters such as presence of septate fibers and some scalariform perforation plates, and the type of vessel-ray parenchyma pits. Moreover, the possibility that this wood might have relationships with the Rhamnaceae cannot be excluded. Rhamnaceae do not occur among the Nut Beds fruits, but there are leaves that seem to represent Rhamnaceae (unpublished data). Fruits of *Paliurus* occur from the early Eocene through Miocene in western North America (Manchester 1999). Extant *Paliurus* wood examined to date has latewood vessels with a diagonal to tangential arrangement, but has exclusively uniseriate rays.

ii: *Latewood vessels randomly arranged*

cf. "***Fraxinoxylon***" Hofmann (Fig. 54)

Growth rings distinct, marked by differences between latewood vessel diameter and subsequent earlywood vessel diameter and by radially flattened fibers.

Diffuse porous to tending to semi-ring porous. Vessels solitary (22%) and in radial multiples of 2–3(–4); multiples 8-shaped, rather than 0-shaped; at the end of growth rings longer radial multiples and occasional clusters; average tangential diameter of 74 (14) µm; vessel frequencies 12–16/mm^2 in latewood; perforations exclusively simple; intervessel pits crowded alternate, 4–5 µm, with apertures extending to edges of borders; vessel-ray parenchyma pits similar to intervessel pits; helical thickenings absent; average vessel element length 278 (57) µm, 190–403 µm; tyloses absent.

Fibers non-septate; walls thin; pits not observed.

Axial parenchyma paratracheal, vasicentric, in latewood aliform to confluent, marginal-zonate, usually 4 cells wide; 4–8 cells per strand.

Rays 1–3-seriate. Homocellular rays composed of procumbent cells, and heterocellular with body of procumbent cells and one marginal row of square cells; uniseriates mostly 2–3 cells high; total multiseriate ray height 112–390 µm, average 183 (50) µm; 7–12/mm.

Crystals not observed.

Storied structure absent.

Sample: USNM 507930 (DEN 36, ca. 7 cm).

Comments — This wood type appears to have non-vestured pits because the outlines of the intervessel pit borders appear smooth at high magnification. Therefore, we used non-vestured pits as a diagnostic feature. Vasicentric-aliform-confluent parenchyma is more obvious in the last formed latewood of the relatively wide growth rings.

Secondary phloem is present, with clusters of fiber-sclereids, at times appearing to alternate with zones of sieve tubes, which appear crushed. No periderm was observed.

Similarities to extant woods — The combination of vessels solitary and in radial multiples, simple perforations, minute-small alternate intervessel pits, vessel-ray parenchyma pits similar to intervessel pits, non-septate fibers, paratracheal parenchyma, marginal parenchyma, and narrow homocellular rays suggests affinities with the Oleaceae, particularly *Fraxinus*. Secondary phloem structure also is consistent with that of extant *Fraxinus*, which has clusters of fiber-sclereids (Nanko & Côté 1980).

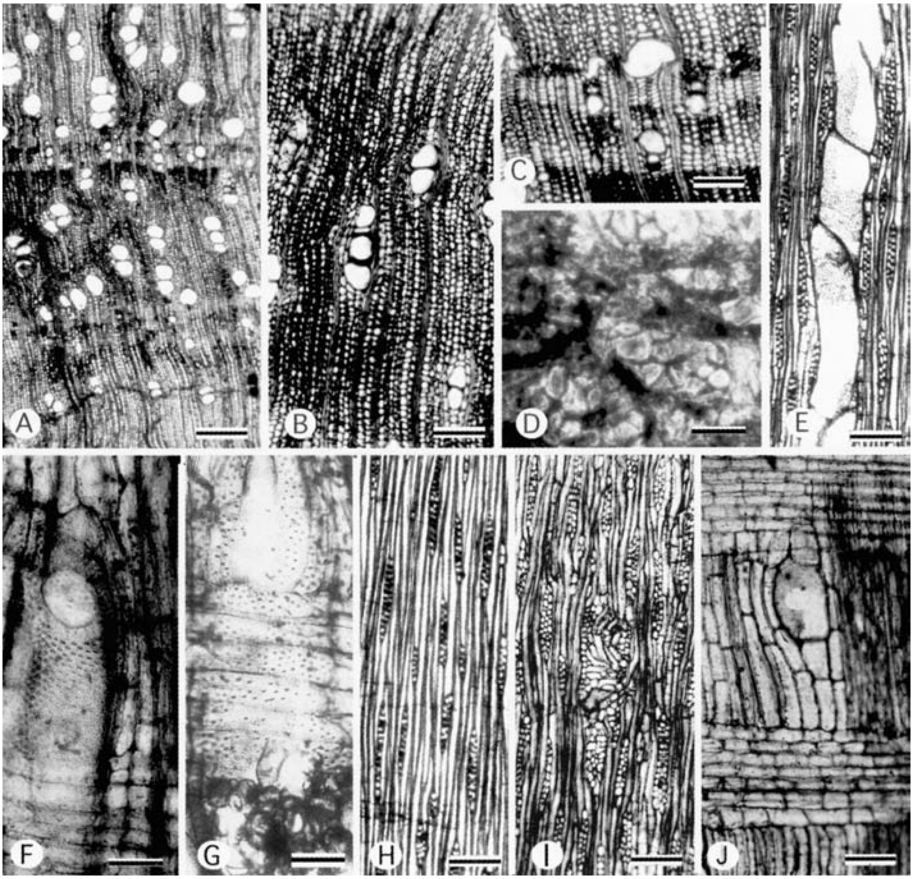


Fig. 54. Nut Beds Xylotype III-B-ii: cf. *Fraxinoxylon* Hofmann (USNM 507930, DEN 36). – A: Vessels solitary and in radial multiples, semi-ring porous, XS. – B: Latewood vessel elements in radial multiples, vasicentric to aliform parenchyma, XS. – C: Growth ring boundary, confluent-banded parenchyma, XS. – D: Secondary phloem with groups of thick-walled cells, XS. – E: Vessel elements with simple perforations and inclined end walls, TLS. – F: Crowded alternate intervessel pits, simple perforation, RLS. – G: Vessel-ray parenchyma pits similar to intervessel pits, RLS. – H: Rays mostly 2-seriate, homocellular, fibers non-septate, TLS. – I: Localized disorientation of radial and axial elements, TLS. – J: Rays composed of procumbent cells, axial parenchyma strands, possible growth ring boundary and initial parenchyma, RLS. — Scale bars = 250 µm in A; 100 µm in B, C, E, H, I; 50 µm in J; 25 µm in D, F, G.

The Clarno wood is not distinctly ring porous, but tends to be semi-ring porous. Samples of present-day *Fraxinus* available for study (those used by Baas et al. 1988) are either distinctly ring porous or less frequently diffuse porous (*F. greggii, F. griffithii*, and *F. malacophylla* from Mexico, Taiwan, and China, respectively), and none tend to be semi-ring porous. During the middle Eocene, when climates were more equable, ring porosity was not as common as at present (Wheeler & Baas 1991, 1993). This Clarno wood may be related to a plant whose wood at the present day is obviously ring porous. Fruits of *Fraxinus* do not occur at the Nut Beds, but are present at other Clarno Formation localities (e.g., West Branch Creek, Clarno lacustrine shales of the Cherry Creek drainage).

Some Bignoniaceae, Rutaceae, and Sapindaceae also have a similar combination of characteristics, but based on available information no one genus within these families has this Clarno wood's particular combination of features. *Catalpa bignonioides* (BWCw 8663), *C. ovata* (268-Hankins) and *C. speciosa* (PACw 6230, 6232, and 6233) (Bignoniaceae) are more obviously ring porous, with latewood vessels in clusters, rather than just in radial multiples, and in tangential bands, and have larger and less crowded intervessel pits. *Cybistax* (Bignoniaceae) is predominantly diffuse porous, although *C. chrisae* SJRw 1244 has some rings that tend to be semi-ring porous; 3-seriate rays in this genus are not slender as in the Nut Beds wood described above. Rutaceae seem less likely to have affinities with this Clarno wood than do Oleaceae as Rutaceae often have crystals, usually in somewhat enlarged cells, and some diffuse parenchyma, and these features were not observed in this Clarno wood. Moreover, the semi-ring porous and ring porous Rutaceae woods we observed have a pronounced tangential arrangement of latewood vessels (e.g. *Phellodendron japonicum* Kw 3428, *P. sachalinense* Kw 3429, *Ptelea trifoliata* PACw 5882). Sapindaceae usually do not have 8-shaped vessel multiples, 1–3-seriate heterocellular rays, or exclusively non-septate fibers (Klaassen, pers. comm.) as occur in this wood.

Comparisons with other fossil woods — Fossil woods assigned to *Fraxinoxylon* are known from the Oligocene of Europe and Japan (e.g. Suzuki 1982; Privé-Gill 1990), and Miocene of Europe (e.g. Andreanszky 1951). All are ring porous.

Semi-ring porous to diffuse porous wood, rays < 4-seriate and heterocellular

(Fig. 55)

Growth rings distinct, marked by radially flattened fibers and differences between latewood and earlywood of subsequent rings.

Semi-ring porous to diffuse porous. Vessels solitary and in radial multiples of 2–4, some clusters; average tangential diameter 77 (17) µm, 56–118 µm; average vessel frequency 17/mm^2, range of 14–24/mm^2; simple perforations; intervessel pits crowded alternate with angular outline, 3–5 µm, aperture linear extending to edge of the border; vessel-ray parenchyma pits appear similar to and slightly smaller than intervessel pitting; helical thickenings not observed; mean vessel element length 409 (48), range 316–474 µm (n = 11); tyloses only observed in a few vessels that had abundant fungal hyphae in them.

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

Axial parenchyma paratracheal, 8 or occasionally more cells per strand.

Rays 1- to mostly 2-seriate. Multiseriate rays heterocellular, body composed of procumbent cells, with more than 4 rows of square/upright cells; mean height of multiseriate portion of multiseriate rays 248 (79) µm, total range of 96–424 µm; 9–13/mm.

Crystals not observed.

Storied structure absent.

Sample: UF 12378 (fragment 1.4 cm across).

Comments — Fungal hyphae are abundant in ray parenchyma (sap-staining fungi?). It is possible that vascular or vasicentric tracheids are present, as in cross section cells associated with the vessels are markedly narrower than them, but wider than surrounding fibers. In radial section there are narrow cells with pitting similar to intervessel pitting.

This specimen is badly compressed and fibers are thin-walled, thus it was difficult to determine parenchyma distribution in cross section. In both tangential and radial sections, parenchyma strands were adjacent to vessels, so it is likely that parenchyma

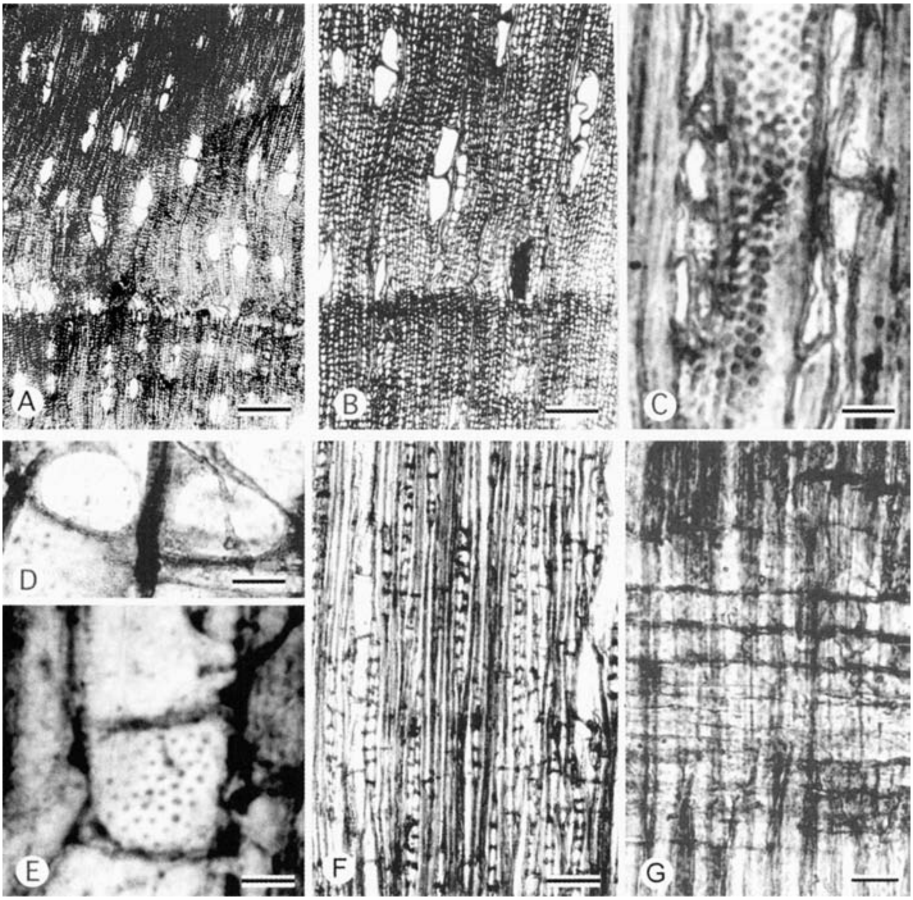


Fig. 55. Nut Beds Xylotype III-B-ii: semi-ring porous to diffuse porous wood, rays < 4-seriate and heterocellular (UF 12378). – A: Wood tending to be semi-ring porous, vessels solitary and in short radial multiples, XS. – B: Growth ring boundary, XS. – C: Crowded alternate intervessel pits, TLS. – D: Simple perforations, RLS. – E: Vessel-ray parenchyma pits, RLS. – F: Uniseriate and biseriate heterocellular rays, TLS. – G: Ray with procumbent body cells and upright marginal cells, RLS. — Scale bars = 250 µm in A; 100 µm in B, F; 50 µm in G; 25 µm in C, D, E.

is at least vasicentric. In some regions of the latewood, there appears to be aliform-confluent parenchyma. Hyphae were abundant in vessel lumens and in ray parenchyma.

Comparisons with other fossil woods — This wood type has some similarities to the Clarno wood called cf. *Fraxinoxylon*, as both tend to be semi-ring porous with vessels solitary and in radial multiples, and have simple perforations, small alternate intervessel pitting, vessel-ray parenchyma pits similar to intervessel pits, narrow rays, and paratracheal parenchyma. However, this wood has more clusters in the latewood, less paratracheal parenchyma and heterocellular rays. The *Fraxinoxylon* wood is based on a larger sample (ca. 7 cm) than this wood (ca. 4 cm). It is possible the difference in ray structure could be related to differences between mature and juvenile wood, rather than representing species differences.

NUT BEDS XYLOTYPE III – EXCLUSIVELY SIMPLE PERFORATION PLATES

C: Diffuse porous

i: *Distinctive vessel arrangement patterns*

USNM 507830: Tangential arrangement of vessels (Fig. 56)

Growth rings indistinct, in some areas marked by radially flattened fibers.

Diffuse porous. Vessels solitary, in radial multiples of 2–3, oblique pairs, and rarely clusters, mostly with a tangential pattern, vessels appearing aligned tangentially with interconnecting axial parenchyma; vessels tending to be angular in outline; average tangential diameter 83 (14) µm, range 50–112 µm; vessel density low, less than 20/mm^2; perforations simple; intervessel pits crowded alternate, 4–5 µm; vessel-ray parenchyma pits similar to intervessel pits; helical thickenings not observed; vessel element lengths 136–362 µm; thin-walled tyloses present, usually bubble-like.

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

Axial parenchyma paratracheal, confluent, 2–6 cells per strand.

Rays 1–5-seriate, mostly 3–4-seriate, uniseriates not common, very low, less than 5 cells high. Multiseriate rays heterocellular, body of procumbent cells, usually with 1–2 marginal rows of upright cells; total multiseriate ray height averages 254 (48) µm, range 350–599 µm; 7–11/mm.

Crystals not observed.

Storied structure absent.

Sample: USNM 507830 (DEN 42, ca. 5 cm).

Comments — Because of the widely spaced tangential vessel arrangement of the vessels, some areas do not have vessels. Vessel density in the sample is low, certainly less than 20/mm^2.

Low vessel density, and extensive vesselless areas are more common in root wood than in stem wood (Carlquist 1961; P. Baas, R.B. Miller pers. comm.). The center of this axis is not present, so it is not possible to see if a pith is present. The thin-walled fibers are consistent with this axis being a root.

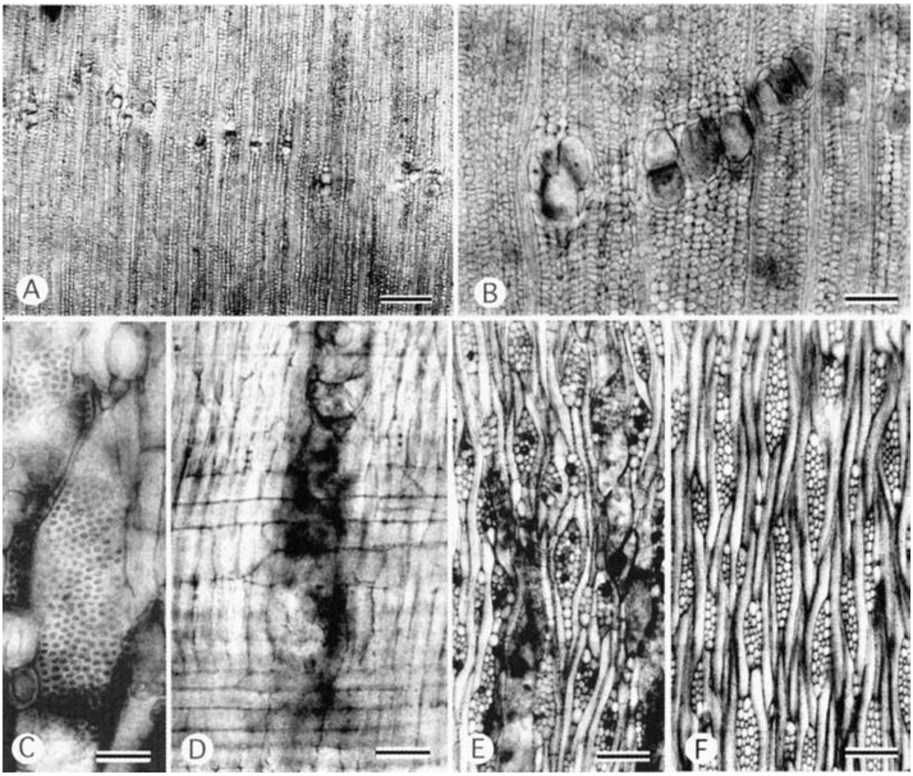


Fig. 56. Nut Beds Xylotype III-C-i: diffuse porous wood with tangentially arranged vessels (USNM 507830, DEN 42). – A, B: Tangentially arranged vessels, with paratracheal parenchyma, XS. – C: Alternate intervessel pitting, TLS. – D: Heterocellular rays, with procumbent body cells, tyloses in vessels, RLS. – E: Series of vessel elements with inclined end walls, heterocellular rays, some with obvious marginal rows, TLS. – F: Multiseriate rays with 1–2 marginal rows of cells, non-septate fibers, TLS. — Scale bars = 250 µm in A; 100 µm in B, E, F; 50 µm in D; 25 µm in C.

Similarities to extant woods — Tangentially arranged vessels are uncommon in diffuse porous woods. In the OPCN database families that have members with diffuse porous woods with tangentially arranged vessels, simple perforations, alternate intervessel pits, vessel-ray parenchyma pits similar to intervessel pits and lack storied structure, include the Boraginaceae and Solanaceae (Solanales), Buddlejaceae (Lamiales), and Leguminosae (all three subfamilies). Because it is likely that this axis represents a root and because it is relatively small it would be necessary to prepare considerable comparative material to be able to determine its affinities with some degree of certainty. This represents an investment of time we consider beyond the scope of this study. The Clarno seed *Nephrosemen reticulatus* resembled seeds of the Solanaceae.

ii: *Random vessel arrangement; rays ≤ 4-seriate*

The next four woods share a similar pattern: distinct growth rings, diffuse porosity, vessels solitary and in radial multiples, simple perforations, alternate intervessel pitting, narrow (≤ 4-seriate) heterocellular rays, and scanty-rare axial parenchyma. These woods do not have any unique feature or combination of features that allows assigning them to a single extant family. Someday it may be possible to determine affinities of some of these woods by using characteristics that usually are not reported in systematic wood anatomical studies and whose value as diagnostic features is not generally established, e.g. ray cell sizes. It is questionable whether it is appropriate to count these four woods as separate genera for purposes of comparing the wood assemblage to the fruit and seed assemblage. These four woods are more similar to one another than the other woods that were assigned to the broad xylotype categories already described.

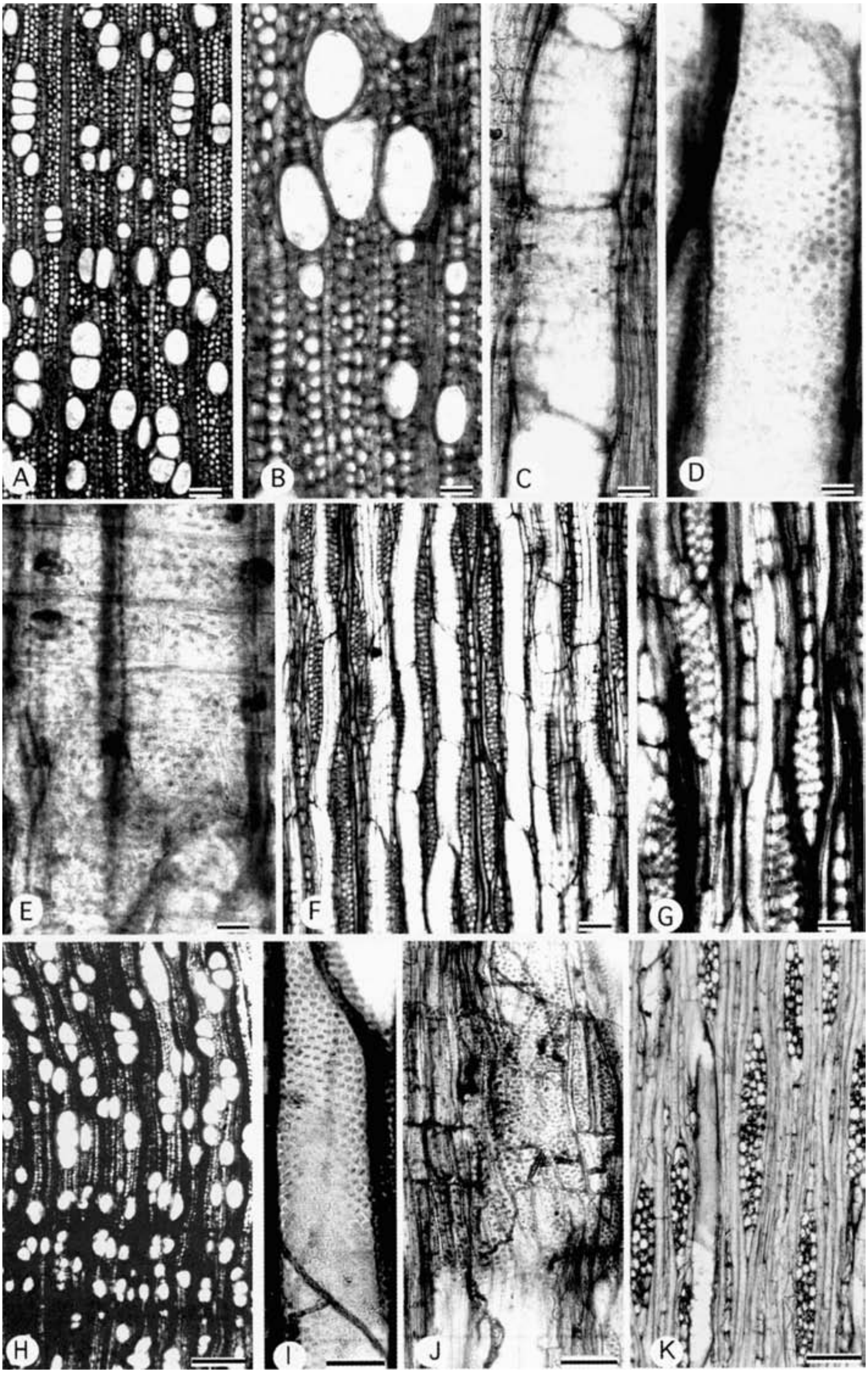
1) **UF 12012** (Fig. 57A–G)

Growth rings distinct to indistinct, marked by radially flattened latewood fibers, marginal parenchyma, and vessel diameter differences between latewood and earlywood of subsequent rings, sometimes small diameter vessels in the growth ring boundary.

Diffuse porous, but with vessels gradually narrowing throughout the growth ring, sometimes with tendency to diagonal arrangement. Vessels solitary (34%) and in radial multiples of 2–4 (6), vessel grouping of 1.58; average tangential diameters of 68 (10) to 111 (15) µm; average vessel frequency 28–38/mm^2, range 11–67/mm^2, solitary vessels generally oval in outline; simple perforations; intervessel pits crowded alternate with angular outline, approximately 5 µm; possibly vestured; vessel-ray parenchyma pits appear similar to intervessel pitting; helical thickenings not observed; average vessel element length 647 (120) µm; some widely spaced tyloses, appearing to segment vessels, and some bubble-like tyloses.

→

Fig. 57. Nut Beds Xylotype III-C-ii: diffuse porous woods, vessels solitary and in radial multiples, axial parenchyma rare, simple perforations, alternate intervessel pits, vessel-ray parenchyma pits similar to intervessel pits. ?Gentianales: Apocynaceae/Rubiaceae?. – A–E: UF 12012 – A: Vessels solitary and in radial multiples, XS. – B: Detail of growth ring boundary, marked by changes in vessel diameter, with narrow vessels in the growth ring boundary, thin-walled fibers, XS. – C: Simple perforation plates, RLS. – D: Alternate intervessel pits, TLS. – E: Vessel-ray parenchyma pits similar to intervessel pits, RLS. – F: Markedly heterocellular rays, parenchyma strands adjacent to vessels, TLS. – G: Uniseriate rays composed of high upright cells, asymmetric multiseriate rays with marginal cells approximately 2 times the height of the body cells, TLS. — H–K: USNM 507827 (DEN 27). – H: Diffuse porous wood with vessels solitary and in radial multiples, XS. – I: Crowded alternate intervessel pitting, TLS. – J: Vessel-ray parenchyma pitting similar to intervessel pitting, RLS. – K: Heterocellular multiseriate rays, usually < 3 marginal rows, TLS. — Scale bars = 250 µm in H; 100 µm in K; 50 µm in A, F, I, J; 25 µm in B, C, G; 12 µm in D, E.


A
B
C
D
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K

Fiber walls thin to medium-thick, very fine slit-like pits observed in earlywood imperforate elements.

Axial parenchyma scanty paratracheal, and occasionally marginal (?), 6–8 cells per strand.

Rays 1–4-seriate. Multiseriate rays heterocellular, body composed of procumbent cells, with 1–12 rows of square/upright cells, rays often asymmetric with one margin with one row of upright/square cells, other margin with 3–4 (or more), marginal cells 2–3 times taller than procumbent cells; uniseriate rays common, composed exclusively of upright cells; mean height of multiseriate portion of multiseriate rays 626 (67) µm, total range of 497–802 µm; 7–9/mm.

Crystals not observed.

Storied structure absent.

Samples: UF 12012 (≥ 10–20 cm), UF 12111.

Comments — Very fine fungal hyphae occur throughout this wood, making it difficult to determine whether there are septate fibers. Sometimes what initially were thought to be septa were found to be hyphae which extended from one fiber to the next. However, some fibers look septate, especially some of the earlywood fibers.

Axial parenchyma is not obvious in cross section, but in both radial and tangential sections parenchyma strands associated with vessels are visible.

Similarities to extant woods — Woods that are diffuse porous, and have vessels solitary and in radial multiples that are neither extremely narrow or wide, simple perforations, small intervessel pits, vessel-ray parenchyma pits similar to intervessel pits, non-septate fibers, rays 1–4 cells wide, and lack storied structure, occur in the families Apocynaceae and Rubiaceae of the Gentianales, Euphorbiaceae, Flacourtiaceae and Malpighiaceae of the Malpighiales, and Meliaceae and Rutaceae of the Sapindales. The preservation of this wood is good; the pitting appears to be vestured as the outlines of the apertures do not look smooth but crenulated. However, even in well preserved woods it can be difficult to establish with certainty the presence of vestures. Of the aforementioned families, vestures occur in Apocynaceae, Rubiaceae, and Malpighiaceae.

We examined slides and illustrations of woods of 19 genera of Apocynaceae and 56 genera of Rubiaceae. This represents but a small sampling of these two large families. No one genus examined has the particular combination of features of this Clarno wood, although both families have woods with vessel grouping and ray structure similar to this fossil. There does not appear to be a reliable way to distinguish woods of the two families. Among the Rubiaceae, this wood is most similar to the tribe Psychotrieae because of the rare axial parenchyma and relatively narrow rays. The Psychotrieae are a very large tribe and most genera in this tribe do not have distinctive wood anatomy (Steven Jansen, pers. comm. 2000). While these Clarno woods resemble these two families of the Gentianales (Apocynaceae and Rubiaceae), we are unable to exclude the possibility that they belong to the Malpighiaceae.

Comparisons with other fossil woods — *Grangeonixylon apocynorubioides* Privé-Gill (1983) is another fossil wood that has characteristics of both the Apocynaceae and Rubiaceae. This genus has mostly solitary vessels and so is distinct from this Clarno wood. *Grangeonixylon danguense* occurs in the lower Eocene of France (Sakala et al. 1999). Fossil woods assigned to the Apocynaceae or Rubiaceae, and with some age assignment, are not common. Some records may need reevaluation, as some descriptions do not mention useful diagnostic features, such as vessel-ray parenchyma pits. Two woods assigned to the Apocynaceae are known from the Eocene of Europe and the United States, respectively: *Apocynoxylon sylvestris* Gazeau & Koeniguer (1975) which commonly has radial multiples of 4 or more and *Aspidospermoxylon uniseriatum* Kruse (1954) which has radial canals; vessel-ray parenchyma pits were not described for either species. With one exception, woods assigned to the Rubiaceae and with an age assignment are from the late Tertiary of Africa. *Rubioxylon* has been used for woods with solitary vessels (Hofmann 1952, the one European report), as well as for woods that commonly have radial multiples of four (e.g. Lemoigne 1978). It would be appropriate to revise this genus as currently it includes more than one distinct wood anatomical type and assigning distinct wood anatomical types to the same genus obscures the diversity of rubiaceous-like woods in the fossil record.

2) **USNM 507827** (DEN 27) (Fig. 57H–K)

Growth rings distinct, marked by radially flattened latewood fibers and differences between latewood and earlywood of subsequent rings.

Diffuse porous. Vessels solitary (ca. 33%) and in radial multiples of 2–4 (8), average tangential diameter of 76 (15) µm; vessel frequency 27–34–43/mm^2; exclusively simple perforations; intervessel pits crowded alternate with angular outline, 3–5 µm, vestured (?); vessel-ray parenchyma pits similar to intervessel pitting; helical thickenings not observed; average vessel element length 468 (68) µm, 339–610 µm; tyloses not observed.

Fiber walls thin to medium-thick, small slit-like pits on radial walls.

Axial parenchyma rare, occasional solitary strands adjacent to vessels.

Rays 1–4(–5)-seriate. Multiseriate rays heterocellular, body of procumbent cells, usually with 1–2 (up to 8) rows of square/upright cells, rays often asymmetric with one margin with one row of upright/square cells, other margin with 3–4 (or more); uniseriate rays composed exclusively of upright cells and less than 10 cells high; in radial section ray cells with pits on all walls; mean height of multiseriate rays 419 (125) µm, total range of 179–721 µm; 5–7/mm.

Crystals not observed.

Storied structure absent.

Sample: USNM 507827 (DEN 27, > 10 cm).

Comments — Hyphae occur throughout this wood, so that it is difficult to be sure of the presence or absence of septa in fibers. In radial section, it is apparent that the fungi preferred the ray parenchyma, and so are likely sapstaining fungi. The common occurrence of hyphae in the fibers may indicate the presence of living fibers (which are often septate). The outline of the pit apertures consistently appears irregular and bumpy, so it is likely that this wood has vestured pits.

No septate fibers were observed, but, as explained above, it is not clear whether this represents original absence.

Similarities to extant and fossil woods — This wood is similar to the wood type represented by UF 12012, except that its rays are somewhat wider and there is less difference between body and marginal ray cells. The same combination of features as the wood above suggests possible relationships to the families Apocynaceae and Rubiaceae (especially Psychotrieae because of the rare occurrence of axial parenchyma) of the Gentianales, and Malpighiaceae of the Malpighiales.

3) **Narrow Ray I** (Fig. 58A–E)

Growth rings distinct, marked by radially flattened latewood fibers and differences between latewood and earlywood vessel diameters of subsequent rings, and marginal parenchyma.

Diffuse porous to slightly semi-ring porous. Vessels solitary (ca. 32–41%) and in radial multiples of 2–8, average tangential diameters of 74 (20)–101 (20) µm; average vessel frequencies of 25–27/mm^2, total range of 16–37/mm^2; simple perforations; intervessel pits crowded alternate with angular outline, 3–5 µm; vessel-ray parenchyma pits similar to intervessel pitting; helical thickenings absent; average vessel element lengths of 383 (72) to 469 (82) µm; tyloses observed in a few vessels that had abundant fungal hyphae in them.

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

Axial parenchyma sometimes present as marginal parenchyma bands 2–4 cells wide.

Rays 1–2-seriate, mostly uniseriate. Multiseriate rays heterocellular, body composed of procumbent cells, with more than 4 rows of square/very high upright cells; uniseriate rays composed of high upright cells; total mean height of multiseriate rays 504 (60) to 590 (232) µm, total range of 250–1110 µm; 9–13/mm.

Crystals not observed.

Storied structure absent.

Samples: USNM 507937 (C4A-133, > 20 cm), USNM 507938 (C4A-7, > 14 cm); USNM 507825 (DEN 100, ca. 10 cm); USNM 507826 (DEN 102, sample 3 cm across).

Comments — USNM 507938 has evidence of insect damage, as there are oval areas (as viewed in cross section) composed of groups of cell fragments. The amount of fungal decay in all four samples is similar; fungal hyphae are common in all samples, in vessels, ray parenchyma, and imperforate axial elements. The outlines of pit borders do not appear smooth, it is likely that the intervessel and vessel-ray parenchyma pits are vestured.

Marginal parenchyma was observed in USNM 507937 and 507938, but not in 507825 and 507826. All other features are similar. The two samples without marginal parenchyma have smaller estimated diameters than those with marginal parenchyma. It is possible that the presence or absence of marginal parenchyma might vary with cambial age, not being present in wood closer to the pith.

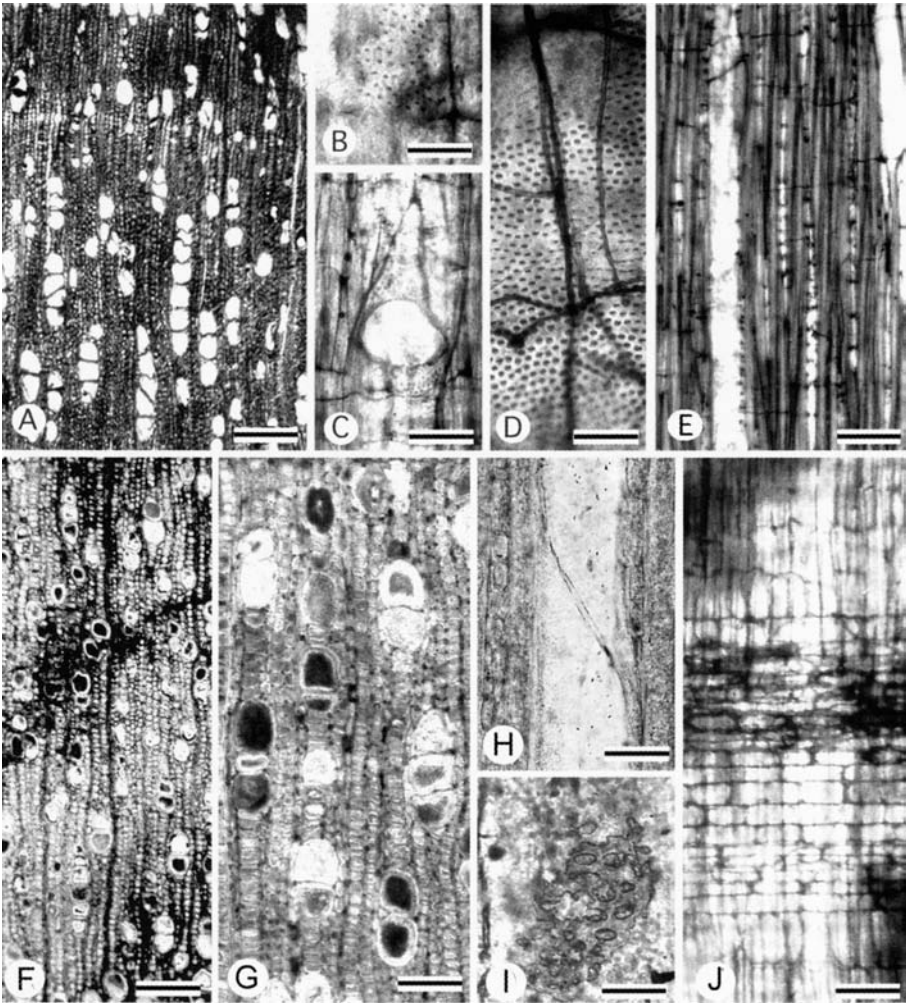

Fig. 58. Nut Beds Xylotype III-C-ii: Narrow Ray I: A–E: USNM 507937 (C4A-133) ?Oleaceae/ Rubiaceae. – A: Diffuse porous wood, vessels solitary and in radial multiples of up to 8, marginal parenchyma, XS. – B: Vessel-ray parenchyma pits. – C: Simple perforation. – D: Small crowded alternate intervessel pits. – E: Narrow rays with upright cells. — F–J: Narrow Ray II: USNM 507928 (EN 113) – F: Vessels solitary and in radial multiples, XS. – G: Vessels in radial multiples, fibers in radial alignment, XS. – H: Simple perforation plate, TLS. – I: Vessel-ray parenchyma pits horizontally enlarged and with reduced borders, RLS. – J: Heterocellular rays, RLS. — Scale bars = 250 µm in A, F; 100 µm in E, G, J; 50 µm in C, H; 25 µm in B, D, I.

Another alternative is that there are two “species” represented, one with and one without marginal parenchyma.

Similarities to extant woods — The families Lythraceae (Myrtales), Oleaceae (Lamiales), and Rubiaceae (Gentianales) have genera with vessels in radial multiples, minute to small alternate intervessel pits, vessel-ray parenchyma pits similar to intervessel pits, simple perforations, narrow heterocellular rays, marginal parenchyma and no vasicentric-aliform-confluent parenchyma. Vestured pits routinely are present in the Lythraceae and Rubiaceae, and in some Oleaceae. The simplified wood anatomical key to the genera of the Oleaceae (Baas et al. 1988) indicates this Clarno wood has structure similar to *Forestiera*, *Noronhia*, and some *Olea* species.

4) **Narrow Ray II** (Fig. 58F–J)

Growth rings indistinct to distinct, marked by radially flattened fibers and differences between latewood and earlywood of subsequent rings.

Diffuse porous. Vessels solitary (19%) and in radial multiples of 2–4 (8), tending to a radial alignment, as fibers rather wide and narrow vessels intergrading with fibers; average tangential diameter of 59 (11) µm, 49–103 µm; vessel frequency of 50–65–80/mm^2; simple perforations in rather steeply inclined end wall; intervessel pits not observed, vessel-ray parenchyma pits with reduced borders and horizontally enlarged; helical thickenings not observed; vessel element lengths of 550–820 µm (n = 5); tyloses not observed.

Fibers non-septate, thin-walled, in radial alignment, and retaining rectangular outline in cross section; pitting not observed.

Axial parenchyma rare.

Rays 1(–2)-seriate, mostly uniseriate, with biseriate portion being less than 10 cells high, usually less than 5 cells high. Multiseriate rays heterocellular, body composed of procumbent cells, with long uniseriate portions of upright cells; uniseriate rays composed of upright cells; total mean height of multiseriate rays 651 (173) µm, total range of 550–820 µm; 5–11/mm.

Crystals not observed.

Storied structure absent.

Sample: USNM 507928 (DEN 113, 1 narrow fragment 1.5 cm across).

Comments — The preservation of this sample was poor, and we were not able to see intervessel pits, and only rarely saw perforations. This wood is distinct from other diffuse porous Clarno woods with simple perforations as it has a high proportion of vessel multiples, high vessel density, vessel-ray parenchyma pits with reduced borders, rare axial parenchyma, and predominantly uniseriate rays. This wood has some similarities to *Salix*, but biseriate rays are more common in this wood than is usual for that genus, and we could not see whether the intervessel pits are crowded alternate and large as is characteristic of *Salix*.

PALMAE

Palms are represented in the Nut Beds by two species of *Sabal* seeds. In addition, silicified petioles are common and occasionally stem material is found. Examples are UF 12019 (3 cm diam.) and UF 12394 (2 cm across). They show numerous scattered fibrovascular bundles in a parenchymatous ground tissue (Fig. 59). The anatomy is consistent with that of *Sabal*. However, it is difficult to distinguish different extant genera of palms by stem anatomy, and so the Clarno palms are placed in the genus *Palmoxylon*.

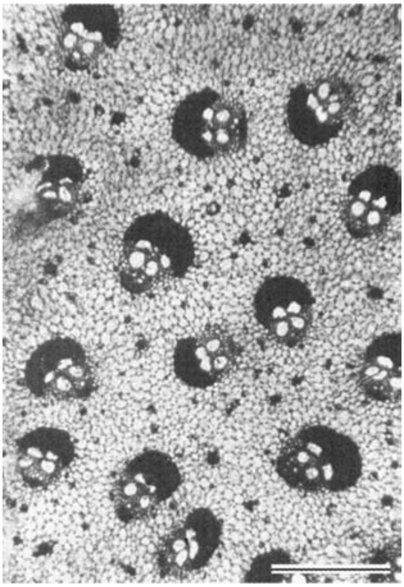

Fig. 59. *Palmoxylon* sp. (UF 12019). – Scattered fibrovascular bundles.

GYMNOSPERMAE

There are at least four types of gymnospermous wood present at the Nut Beds: *Pinus* (Pinaceae), *Sequoia*-like (Taxodiaceae), *Ginkgo* (Ginkgoaceae), and an unknown (likely Taxaceae). Although cycad fronds similar to *Dioon* are preserved (Manchester 1981) we have not found silicified cycad xylem.

PINACEAE

The Pinaceae are represented in the Nut Beds flora by seed and pollen cones of *Pinus*, and at the Clarno West Branch Creek locality by 5–7-needled fascicles and seeds (Manchester 1994).

cf. ***Pinus*** L. (Fig. 60A–C)

Growth rings distinct.

Longitudinal tracheids 19–55 μm, average 40 μm tangential diameter; bordered pits circular 14 μm diameter, uniseriate on radial walls; cross field pits not preserved; axial parenchyma not visible.

Rays of two kinds: a) short uniseriate, often < 10 cells high, and b) wider fusiform rays up to 4-seriate in the central portion containing resin canals.

Resin canals present, both axial and radial. Epithelial cells thin-walled. Axial canals 80–220 μm, average 170 μm diameter; radial ducts much smaller, 30–50 μm diameter.

Samples: UF 12100, UF 12116, USNM 507871 (DEN 11, > 20 cm), USNM 507968 (3/61-7, > 10 cm), USNM 507922 (DEN 3, 9–10 cm).

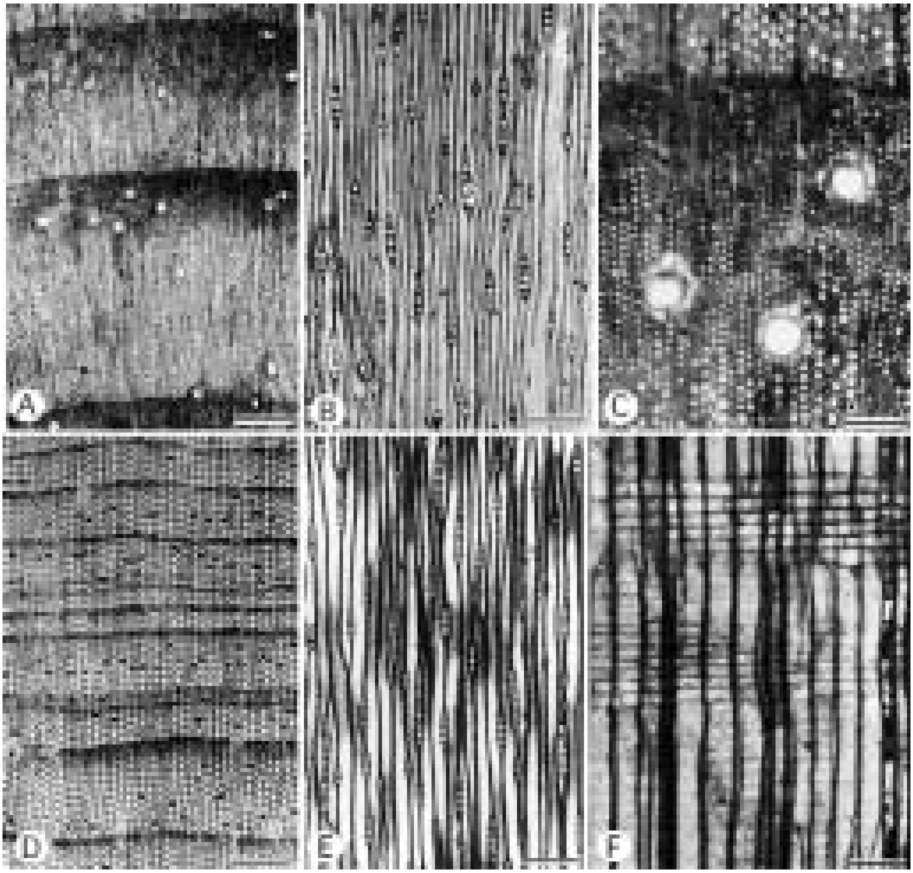

Fig. 60. A–C: *Pinus* sp. (USNM 507922, DEN 3). – A: Growth ring with weakly defined latewood, XS. – B: Uniseriate and fusiform rays, TLS. – C: Axial resin canals in latewood, XS. – D–F: cf. *Taxodioxylon* sp. (UF 12060). – D: Scattered parenchyma cells with dark contents, XS. – E: Uniseriate rays, TLS. – F: Biseriate intertracheary pits, axial parenchyma strand at right, RLS. — Scale bars = 1000 µm in A; 500 µm in D, 200 µm in B, C, E; 100 µm in F.

Similarities to extant woods — Because of the presence of axial and radial resin canals, this wood can be attributed to the Pinaceae. Within Pinaceae, both axial and radial canals occur in *Pinus, Picea, Larix* and *Pseudotsuga* (Phillips 1948). This wood is distinguished from *Larix*, *Picea* and *Pseudotsuga* by its thin-walled epithelial cells.

Specimens UF 12116 and USNM 507871 resemble hard pines because of an abrupt transition to a well-defined dense latewood zone within each growth ring (Panshin & DeZeeuw 1980). USNM 507922 (DEN 3), on the other hand, has a more gradual transition from earlywood to latewood and may represent a soft pine, or compression wood of a hard pine. The transition from earlywood to latewood is less abrupt in the compression wood of hard pines (Panshin & DeZeeuw 1980). Details of ray tracheids and cross field pitting are poorly preserved in all these specimens. Whether these differences in growth ring appearance indicate two or more taxa, or variability within a single species is uncertain, because we cannot determine whether these samples have similar or different types of ray tracheids (e.g., dentate vs. smooth) and cross field pits (e.g., window-like vs. pinoid).

TAXODIACEAE

cf. ***Taxodioxylon*** (Fig. 60 D–F)

Growth rings distinct. Abrupt transition from earlywood to latewood within one growth ring. Tangential diameter of longitudinal tracheids 25–58 µm, averages 35–43 µm; intertracheary bordered pits usually biseriate, but also uniseriate and triseriate on radial walls.

Scattered axial parenchyma strands with dark contents, smooth end walls.

Rays uniseriate and biseriate, 2–55 cells, 28–1100 µm high; homocellular (no ray tracheids observed), smooth end walls, vertical and horizontal walls unpitted; taxodioid cross field pits, 2–4 per cross field.

Samples: UF 12060 (ca. 10 cm, preservation good), UF 12408 (7 cm, best preserved), UF 12411 (> 10 cm), UF 12462 (> 20 cm), USNM 507925 (DEN 107, ca. 7 cm, bark preserved), USNM 507872 (DEN 51, > 12 cm), USNM 507968 (3/61-8, > 10 cm), USNM 507971 (3/61-10, 3–4.5 cm), possibly UF 12338.

Comments — There is considerable variation in growth ring width in these samples. Growth rings are relatively narrow in UF 12060, 0.12–0.86 mm, sometimes with only 4–10 tracheids per increment, including one row of latewood tracheids. In contrast, USNM 507872 (DEN 51) has growth rings 2.3–3.5 mm wide and with latewood zones 0.2–1.0 mm wide.

Similarities to extant woods — This wood type is anatomically similar to wood of the Taxodiaceae and Cupressaceae in the lack of resin ducts, presence of scattered axial parenchyma. The biseriate intertracheary pitting and large taxodioid pits suggest affinities with *Sequoia*, *Sequoiadendron, Metasequoia*, or *Taxodium*.

Taxodiaceae are not known from seeds or foliage at the Clarno Nut Beds, so this wood adds a new record. At the West Branch Creek locality of the Clarno Formation, foliage and cones of *Sequoia* are present. Since no other taxodiaceous genera have been confirmed from the Clarno Formation (*Metasequoia* is not known prior to the Oligocene in the John Day Basin), it is likely that this wood belongs to *Sequoia*. However, it is difficult to confirm a generic determination within the Taxodiaceae based only upon wood anatomy.

GINKGOACEAE

Ginkgo is known from a few fragmentary leaf specimens from the Nut Beds flora (Manchester 1981: fig. 6), although it is not known from other Clarno localities, and has not been identified from seeds in the Nut Beds.

Ginkgo bonesii Scott, Barghoorn & Prakash (Fig. 61A–C)

Growth rings "inconspicuous, their boundaries marked by 1–2 rows of small tracheids; small tracheids more numerous in the latewood."

Tracheids of two sizes and irregularly arranged as seen in transverse section: a) large tracheids up to 50 µm in tangential diameter, rectangular to oval or irregular in outline, walls about 6 µm thick, 8–10 µm bordered pits on radial walls opposite, 1–3-seriate; apertures mostly circular; scattered bordered pits on tangential walls of some tracheids; b) small tracheids 20 to 40 µm in diameter scattered among the large tracheids or arranged in short tangential or oblique bands 1 cell wide, oval to irregular in outline; walls about 10 µm thick; bordered pits about 10 µm in a single row on radial walls, apertures circular.

Axial parenchyma diffuse, in strands of up to 8 cells or, more commonly, in strands of up to 16 with greatly inflated cells that presumably contained crystals; some strands containing both normal and inflated cells.

Rays uniseriate or rarely with short biseriate parts, 1–12 cells high, pits in cross field half-bordered, oval, 8–10 µm in diam., apertures slit-like, 2–8 pits per cross field.

Holotype: USGS Wood Coll. No. W-593 as cited in Scott et al. 1962 (> 30 cm).
Additional material: USNM 507970 (3/61-9, 7 cm wide fragment).

Similarities to extant woods — According to Scott et al (1962), wood of *Ginkgo* is readily distinguished from conifer wood by the occurrence of two sizes of tracheids – bigger (both longer and wider) and smaller (shorter and narrower). This results in a distinctive appearance of the wood as viewed in transverse section: in *Ginkgo* each radial row of tracheids includes both small and large diameter cells, whereas in conifers the tracheids of each radial row are uniform in their tangential diameters. Another conspicuous feature is the presence of axial chains of inflated parenchyma cells, usually crystalliferous. The occurrence of both these features in the Nut Beds fossil, together with the corresponding ray and pit characters, indicate that this wood is reliably identified to *Ginkgo* (Scott et al. 1962). The same authors noted that the fossil species differs from the living *Ginkgo biloba*. In *Ginkgo bonesii,* the smaller tracheids tend to be arranged in tangential lines; in the extant species they are more randomly distributed.

Comparisons with other fossil woods — Another species of *Ginkgo* wood was identified from the Miocene of Vantage, Washington. This wood more closely resembles the modern species in the more scattered arrangement of small tracheids within the xylem (Scott et al. 1962).

Conifer wood of unknown affinities

?**Taxaceae** (Fig. 61D–G)

Growth rings absent. Average tangential diameter of longitudinal tracheids 52 (11) µm, range 27.5–75 µm; single wall thickness 12–13 µm; intertracheary pits circular bordered and primarily uniseriate.

Axial parenchyma absent.

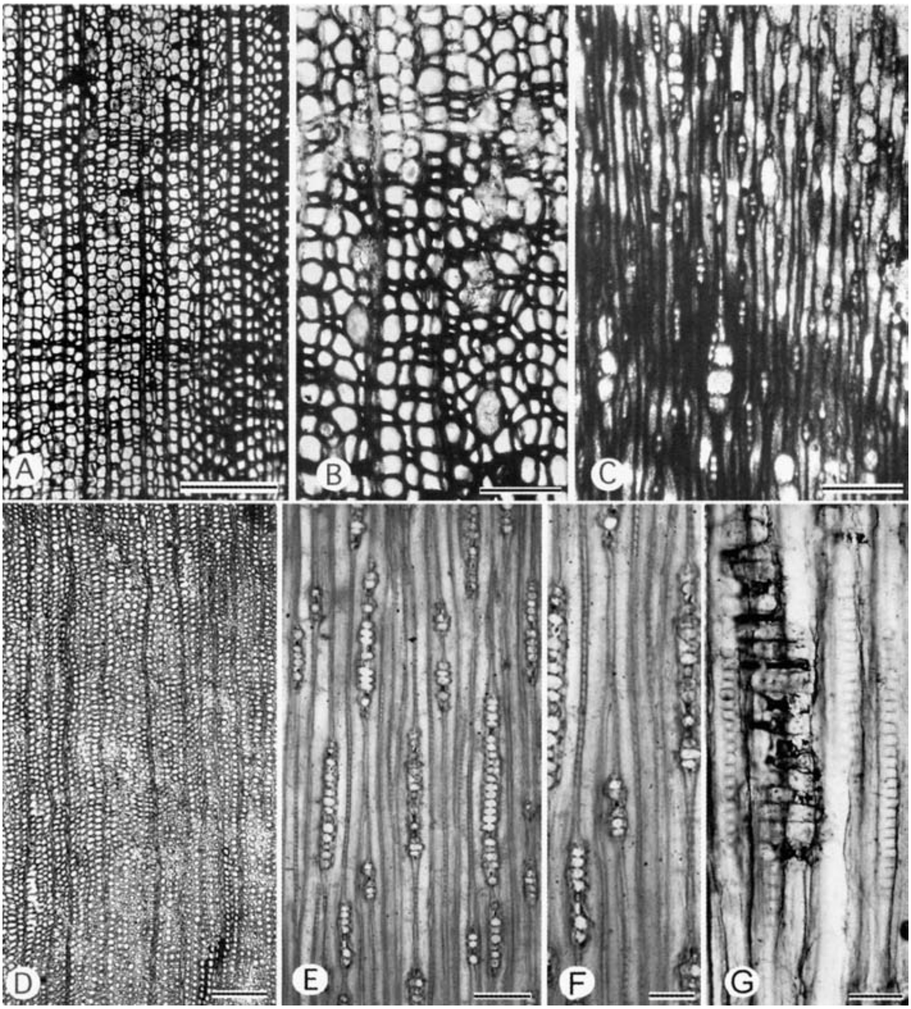

Fig. 61. A–C: *Ginkgo bonesii* Scott, Barghoorn & Prakash (USNM 507970). – A: Indistinct growth ring boundaries, XS. – B: Tracheids of two sizes, XS. – C: Short uniseriate rays and inflated cells, in axial parenchyma strand, TLS. — D–G: Taxaceae? USNM 507873 (DEN 86). – D: Longitudinal tracheids of uniform radial diameter, XS. – E: Uniseriate rays of variable height, TLS. – F: Possible helical thickenings in longitudinal tracheids. – G: Uniseriate intertracheary pitting and homocellular rays, near RLS. — Scale bars = 500 µm in A, D, 200 µm in B, C, E; 100 µm in F, G.

Rays uniseriate and of variable height, usually 20–500(–1400) µm, averaging 264 (272) µm; 2–16(–33) cells high, averaging 8 cells. Cross field pits apparently cupressoid and fewer than 4 per cross field.

Axial and horizontal resin canals absent.

Sample: USNM 507873 (DEN 86, 3.5 cm).

Similarities to extant woods — The absence of axial parenchyma and resin canals and presence of cupressoid cross field pits suggests Taxaceae (Phillips 1948). Taxaceae are characterized by helical thickenings in the longitudinal tracheids. We observed some very faint lines oriented horizontally to the axial walls of the longitudinal tracheids (Fig. 62F), but cannot with certainty say that these are remnants of helical thickenings.

Extant Taxaceae typically have distinct growth rings, this sample does not. Longitudinal tracheids are wide, averaging > 50 µm high, wider than typical of extant Taxaceae. One possibility is that this wood may represent a root. Root wood usually has wider tracheids and less distinct growth rings than stem wood.

Taxus, *Torreya* and an extinct genus of Taxaceae are known from Nut Beds seeds (Manchester 1994).

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