IAWA Journal, Vol. 21 (1), 2000: 83–120

LATE CRETACEOUS WOODY DICOTS FROM THE AGUJA AND JAVELINA FORMATIONS, BIG BEND NATIONAL PARK, TEXAS, USA

by

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SUMMARY

Angiosperm woods occur throughout Upper Cretaceous (84–66 million years old) continental strata of Big Bend National Park, Texas, USA. Vertebrate remains occur along the same stratigraphic levels, providing a rare opportunity to reconstruct associations of sedimentary facies, wood remains, and vertebrate remains. The wood collection sites span a vertical stratigraphic succession that corresponds to an environmental transect from poorly-drained coastal salt- or brackish water swamps to progressively better drained freshwater flood-plains lying at increasingly greater distance from the shoreline of the inland Cretaceous sea and at higher elevations. The eight dicot wood types of the Aguja Formation differ from the five types of the Javelina Formation, paralleling a change from a fauna dominated by duckbill and horned dinosaurs to a fauna dominated by the large sauropod, *Alamosaurus*. These woods increase the known diversity of Cretaceous woods, and include the earliest example of wood with characteristics of the Malvales. The lower part of the upper shale member of the Aguja contains numerous narrow axes, some seemingly in growth position, of the platanoid/icacinoid type, and of another wood that has a suite of features considered primitive in the Baileyan sense. Duckbill dinosaur remains are common in the facies with these woods. In contrast to other Cretaceous localities with dicot wood, *Paraphyllanthoxylon* is not common. Dicotyledonous trees are most abundant at the top of the Aguja and the lower part of the Javelina Formations in sediments indicating well-drained inland fluvial flood-plain environments. One locality has logs and *in-situ* stumps, with an average spacing of 12–13 metres between each tree, and trees nearly 1 metre in diameter. To our knowledge this is the first report of anatomically preserved *in situ* Cretaceous dicot trees. *Javelinoxylon* wood occurs at all levels where remains of the giant sauropod *Alamosaurus* occur. The vertebrate faunas of the late Cretaceous of New Mexico and Texas are said to comprise a 'southern' fauna distinct from the 'northern fauna' of Alberta and Montana. The wood remains are consistent with such provincialism. It has been suggested that dicots were not commonly trees in the late Cretaceous of the northern part of

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the western interior of North America. The Big Bend woods provide direct evidence for dicot trees having more than a subordinate role in Cretaceous vegetation at lower latitudes. Most of the dicot wood types of Big Bend are characterized by high proportions of parenchyma, over 50% in one type. Whether these high proportions of parenchyma are correlated with the higher CO_2 levels of the Cretaceous and/or the pressures exerted by aggressive browsing by large dinosaur herbivores is unknown.

Key words: Paleobotany, fossil wood, wood anatomy, Cretaceous, Aguja Formation, Javelina Formation, Big Bend National Park, Malvales.

INTRODUCTION

A continuous sequence of Upper Cretaceous (Campanian–Maastrichtian) through Lower Tertiary (Paleocene) continental strata is exposed in Big Bend National Park of southwestern Texas (Fig. 1). These deposits have yielded vertebrate faunas including dinosaurs (*Alamosaurus*, the last of the giant sauropods), pterosaurs (*Quetzalcoatlus*, with a 12 metre wing span that was the largest flying animal ever), crocodilians (*Deinosuchus*, a 20 ton crocodile with a skull over 2 metres long), and a variety of smaller turtles, fish and mammals (Lawson 1975, 1976; Lehman 1987, 1997; Rowe et al. 1992). These are North America's most southerly well-studied Late Cretaceous vertebrate faunas. Preserved in the same deposits are petrified woods of conifers and angiosperms.

This paper is part of a continuing study documenting the types of fossil woods that occur in Big Bend National Park, and their associations with sedimentary facies and vertebrate faunas. Because woods and vertebrate remains are found together along the same stratigraphic levels, the Big Bend fossils provide a rare opportunity to reconstruct such associations. This paper describes dicotyledonous woods from the Aguja Formation (middle Campanian–early Maastrichtian, approximately 84–74 million years ago) and the Javelina Formation (early–late Maastrichtian, approximately 74–66 million years ago). Previous reports described the dicot woods *Javelinoxylon*, the most common wood in the Javelina Formation (Wheeler et al. 1994), and *Paraphyllanthoxylon* (abundant, hundreds of logs) and *Plataninium* (rare, 1 sample) from the overlying Paleocene Black Peaks Formation (Wheeler 1991).

For the whole world, most samples of mature Cretaceous dicotyledonous woods (trunk wood some distance from the pith) conform to the phyllanthoid or platanoid/icacinoid type. These two wood types are the earliest known dicot wood types (Herendeen 1991a, 1991b; Thayn et al. 1983, 1985); the phyllanthoid wood type is particularly common at late Cretaceous localities in the northern hemisphere. Phyllanthoid and platanoid/icacinoid types occur at Big Bend, but are not the most common Cretaceous wood types. This report documents additional diversity among Late Cretaceous dicotyledonous wood types. The distinctive anatomy of some of these woods may reflect a response to elevated Cretaceous atmospheric CO_2 levels, or to intense dinosaur herbivory.

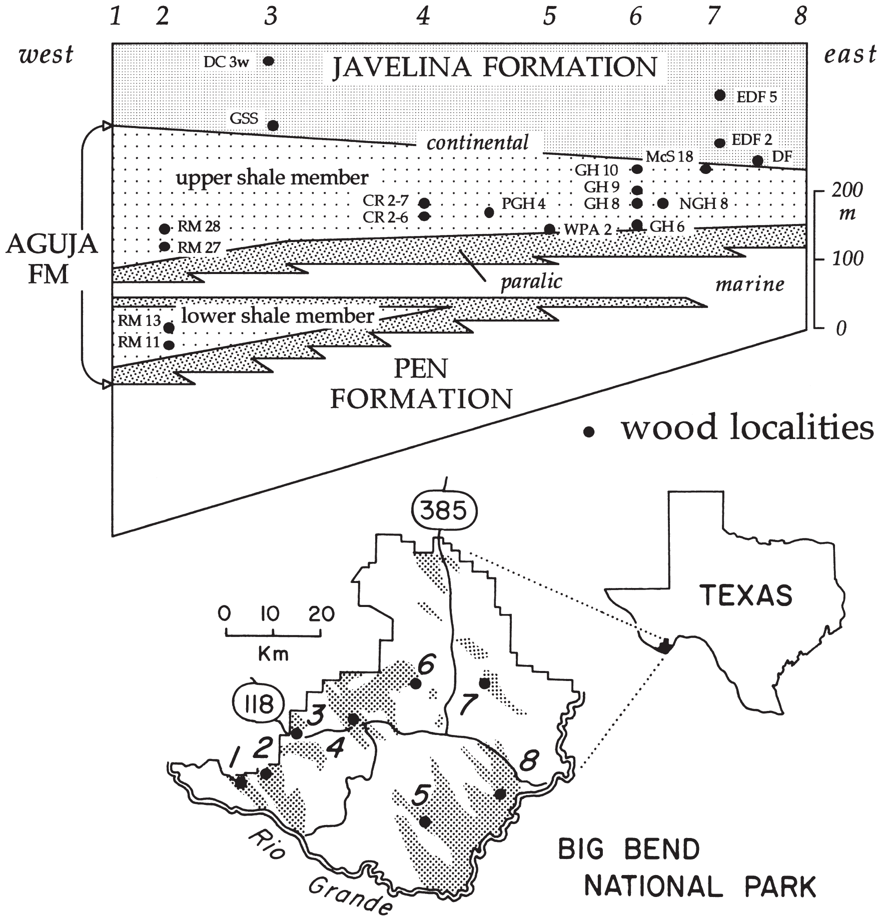

Fig. 1. Map showing location of wood collection sites and exposures of Upper Cretaceous sedimentary rocks (stippled) in Big Bend National Park, Texas. Shown above is a cross section indicating the general stratigraphic relationships of the Aguja and Javelina Formations, and the relative stratigraphic positions of wood collection sites discussed in the text.

The wood collection sites in the Aguja and Javelina Formation span a vertical stratigraphic succession that corresponds to an environmental transect from poorly-drained coastal salt- or brackish water swamps, to progressively better drained freshwater flood-plains lying at increasingly greater distance from the shoreline and at higher elevation. The restricted stratigraphic and facies distribution of wood types strongly suggests preservation *in situ* of characteristic vegetational associations. Some sedimentary facies have only conifer and palm wood, while others have only dicotyledons. It is also apparent that some of the Big Bend dicot trees grew on relatively stable substrates, a preference not yet demonstrated for more northerly Cretaceous floras (Wing & Boucher 1998).

There is considerable uncertainty regarding exactly which plants comprised the typical fodder for dinosaurian herbivores. There have been inferences about the significance of dicotyledonous trees in dinosaur diets, e.g., “Late Cretaceous angiosperm tree trunks were mainly less than 10 cm in diameter and thus were of a size that they could have easily been knocked over by ceratopsids [horned dinosaurs]” (Dodson 1993: 230). Putative dinosaur stomach contents and coprolites (which are few) suggest that Late Cretaceous dinosaur herbivores fed primarily on conifers, although angiosperms were common in many environments by that time (review by Taggart & Cross 1997). The Big Bend dinosaur faunas are dominated by large herbivores; in the Aguja Formation the ‘duck-billed’ hadrosaur *Kritosaurus* and horned ceratopsian *Chasmosaurus*, in the Javelina Formation the sauropod *Alamosaurus* (Lehman 1987). The repeated spatial association of herbivorous dinosaur remains with specific angiosperm wood types in Big Bend suggests an ecological relationship.

Late Cretaceous faunas of the Big Bend region are distinct from correlative faunas known from the northern Great Plains region of Wyoming, Montana, and Alberta. The latitudinal separation between these faunas corresponds to the transition from the northern *Aquilapollinites* to the southern *Normapolles* palynofloral provinces (Lehman 1987, 1997). Although Late Cretaceous angiosperms were diverse and dominated palynofloras and compression floras (Crane 1987; Wolfe & Upchurch 1987; Upchurch & Wolfe 1987, 1993), it has been suggested that Cretaceous dicotyledonous trees were ‘weedy’ and restricted to disturbed habitats (Wing et al. 1993; Wing & Boucher 1998). Such inferences are, however, based primarily on evidence from the northern floras.

Direct evidence for the stature of fossil dicotyledons comes from fossil woods. Large dicotyledonous logs, over 1 meter in diameter, are locally abundant at some Cretaceous localities in the United States, e.g., Alabama (Cenomanian: Cahoon 1972), southern Illinois (Maastrichtian: Wheeler et al. 1987). Logs of *Javelinoxylon* from Big Bend exceeded 70 cm in diameter (Wheeler et al. 1994). Additional Big Bend woods described in this report show that dicotyledonous trees with large diameter trunks were not only present, but locally dominated some Cretaceous forests in this region.

STRATIGRAPHY

Upper Cretaceous strata are well exposed in the Big Bend region of Texas, and consist of a gradational series of marine, paralic, and terrestrial deposits (Fig. 1). Marine shale of the Pen Formation grades upward into coastal sandstone, shale, and coal of the Aguja Formation, which grades upward into inland fluvial flood-plain deposits of the Javelina Formation (Maxwell et al. 1967). These deposits record the gradual retreat of the Cretaceous Interior Seaway from North America at the end of Cretaceous time, and offer an excellent opportunity to document changes in dicotyledonous wood types in a conformable sequence through the Late Cretaceous and Early Tertiary.

Marine and paralic strata in the Pen and Aguja Formations preserve a molluscan fauna with ammonites, ostreid bivalves, and inoceramid bivalves that allow for biostratigraphic correlation with Upper Cretaceous strata in the Western Interior and Gulf Coast provinces of North America (Lehman 1985). Similarly, continental strata in the Aguja and Javelina Formations preserve a diverse terrestrial vertebrate fauna with a wide variety of dinosaurs, crocodilians, turtles, and mammals (Lawson 1975, 1976; Lehman 1985; Rowe et al. 1992). These vertebrate faunas allow for biostratigraphic correlation of the non-marine section. Hence, the ages of dicotyledonous wood types described herein are fairly well constrained with biostratigraphic data.

Aguja Formation

Lehman (1985) subdivided the Aguja Formation into several informal members (Fig. 2). Wood samples were collected from terrestrial deposits in both the lower shale member and upper shale member of the Aguja Formation.

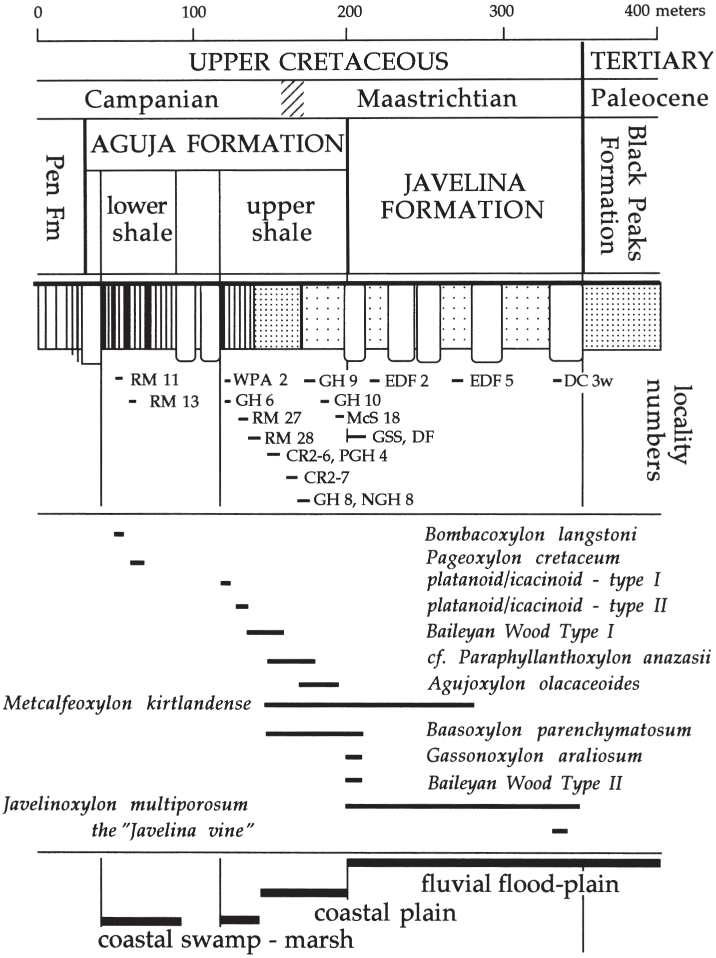

Fig. 2. Generalized stratigraphic column of the Aguja and Javelina Formations, showing the inferred depositional environments, relative positions of wood collection localities, and the distribution of wood types described in the text.

Lower shale member — The lower shale member of the Aguja Formation consists primarily of dark organic-rich shale, lignite, and coal. These sediments accumulated in poorly-drained coastal marshes and swamps immediately adjacent to the shoreline. The associated invertebrate faunas suggest that these environments were subject to saline or brackish water conditions, at least periodically (Lehman 1985). Although wood is common in these lignite shales, it is typically carbonized and poorly preserved. Two well-preserved dicotyledonous wood types (*Bombacoxylon*, at locality RM-11, and *Pageoxylon*, at locality RM-13) are represented, however. This interval is middle Campanian in age.

Upper shale member — The upper shale member of the Aguja Formation consists primarily of drab olive, yellow, and tan shale with lenticular beds of sandstone. These sediments accumulated in coastal plain environments progressively farther removed from the shoreline. Wood samples were collected from three successive intervals in the upper shale member.

The lowermost part of the upper shale member (lower 10 to 20 m, Fig. 2) consists of dark, organic-rich shale similar to that found in the lower shale member. These sediments likewise accumulated in a poorly drained coastal swamp environment very near the shoreline, although evidence for saline conditions is not as pronounced here as in the lower shale member. Several wood samples of platanoid/icacinoid types, and 'Baileyan Big Bend Wood Type I' were collected from this part of the section (localities: GH-6, GH-6a, WPA-2, RM-27, RM-28). This interval is early late Campanian in age.

The central part of the upper shale member (20 to 50 m from base, Fig. 2) consists of olive, yellow, and tan shale with prominent thick lenses of sandstone. These sediments accumulated in a moderately well-drained fluvial flood-plain environment, at least several kilometers from the shoreline. Exclusively freshwater conditions prevailed in this setting. Soils are immature and poorly developed in these flood-plain deposits. Several wood samples were collected from this part of the section (localities: CR2-6, CR2-6b, CR2-6c). This interval is late Campanian in age.

The uppermost part of the upper shale member (50 to 80 m from base, Fig. 2) consists of banded purple, gray, and olive shale with thick sandstone beds. These sediments accumulated in a very well-drained inland fluvial flood-plain environment at great distance from the shoreline. These flood-plains experienced extended periods of soil formation which resulted in well-differentiated soils (Lehman 1989, 1990). Wood is particularly abundant in this interval, and numerous specimens were collected here (localities: GH-9, GH-10, MCS 18), some with trunk diameters of 60–100 cm. This interval is latest Campanian to early Maastrichtian in age.

Javelina Formation

The Javelina Formation consists of an alternating series of purple and gray shales with abundant calcium carbonate nodules, and thick lenticular conglomeratic sandstone beds. These sediments are gradational with the underlying upper shale member of the Aguja Formation, and likewise accumulated in a very well-drained fluvial flood-plain environment. Evidence for extended periods of flood-plain soil development are particularly striking in the Javelina Formation, where mature well-differentiated soil profiles are preserved (Lehman 1989). Sedimentological and isotopic data suggest that a warm, dry climate prevailed during deposition of the Javelina Formation (Ferguson et al. 1991). *Javelinoxylon multiporosum*, a wood type described in an earlier paper (Wheeler et al. 1994), occurs throughout the Javelina Formation. At one locality (Dagger Flats, DF), there is a log jam dominated by this species. Two additional wood types ('The Javelina Vine', from the DC 3w locality, and 'Baileyan Big Bend Wood Type II', GSS locality) were collected from the Javelina, which is middle to late Maastrichtian in age.

MATERIALS AND METHODS

The woods described in this paper are from localities that are relatively accessible and were visited during 1989–1995. Thin sections of cross, radial, and tangential faces were prepared. Quantitative data and descriptive terminology follow recommendations of an IAWA Committee (1989). For quantitative features sample means are given followed by standard deviations in parentheses. When a wood type is represented by multiple samples, the range of sample means and those sample's individual standard deviations are given. In cases where it was not possible to obtain as many measurements as recommended for computing a mean for a sample, the range is given. If a mean was computed using fewer than the recommended number of measurements, then the number of measurements is given. Samples are deposited at the Smithsonian Institution (USNM).

Comparative work — Affinities of the fossils initially were assessed by consulting descriptions in 'Anatomy of the Dicotyledons' (Metcalfe & Chalk 1950), and through searches of the computerized OPCN wood database that contains more than 5000 coded descriptions of extant dicotyledonous wood (Pearson & Wheeler 1981; Wheeler et al. 1986; LaPasha & Wheeler 1987). Subsequently, the material was compared with slides of extant genera from the wood collections at Kew, Leiden, North Carolina State University, and the Bailey-Wetmore Laboratory of Anatomy and Morphology, Harvard, more recent literature as listed by Gregory (1994) and wood anatomical atlases (e.g. Ilic 1991). Initial comparisons to other fossil dicotyledonous woods were done by reference to a database for fossil dicotyledonous woods prepared in 1991 (Wheeler & Baas 1991), and subsequently enlarged using more recent literature.

Because Cretaceous dicotyledonous woods often have a generalized structure that is seen in more than one extant family, order, or even subclass, their classification and naming has prompted some debate. Page (1979, 1980, 1981) classified a large suite of Late Cretaceous woods from California into structural types, based mainly on vessel characteristics and axial parenchyma type. Suzuki et al. (1996) also classified Japanese and Russian Cretaceous woods into types, using ray features as well as vessel and parenchyma features. We are assigning binomials to some of the woods, but not to the platanoid/icacinoid types, the two woods that have a suite of primitive features as defined by the Baileyan trends and whose characteristics fit three or more fossil wood genera, and the vine-like wood, in which critical diagnostic features are not preserved. We are also indicating to which of Page's structural types the woods belong. Woods are described in a sequence generally corresponding to the stratigraphic level they are first encountered.

DESCRIPTIONS

Bombacoxylon (Carr.) Gottwald 1969

Bombacoxylon langstoni sp. nov. (Fig. 3)

Growth rings indistinct, marked by radially flattened fibres.

Diffuse-porous; vessels solitary and in short radial multiples of 2–4; 17–31% solitary; mean tangential diameters 95 (18)–119 (27) µm; 8–16 per mm^2; mean vessel element lengths 337 (34)–575 (126) µm; exclusively simple perforations; crowded alternate intervessel pits, 8–11 µm across; vessel-ray parenchyma pits of similar size as intervessel pits and throughout the ray, not restricted to the marginal rows; thin-walled bubble-like tyloses common.

Axial parenchyma abundant diffuse and diffuse-in-aggregates, up to 8 cells per strand.

Rays: multiseriate rays 2–5, mostly 3, cells wide, 33 (8)–57 (15) µm; heterocellular with body of multiseriate rays composed entirely of procumbent cells with 1–2 rows of square to slightly upright cells to sub-homocellular composed entirely of procumbent cells with ill-defined marginal rows; in tangential view some rays tending to have two distinct sizes of ray cells, but in radial view no obvious tile cells visible; multiseriate ray heights 319 (93)–383 (226) µm; uniseriate rays extremely rare; rays not storied; 6–13, mostly 9–11 per mm.

Fibres: pits not distinguishable; walls medium-thick.

Inclusions: solitary prismatic crystals sometimes present, rare in marginal ray cells (USNM 507018).

Holotype: USNM 507018 (RM 11-4).
Paratypes: USNM 507019 (RM 11-2), USNM 507020 (RM 11-3), USNM 507021 (RM 11-8).
Stratum: Upper Cretaceous, Aguja Formation / Lower Shale Member.
Derivation of name: The specific name recognizes Wann Langston Jr. for his many contributions to the vertebrate paleontology of the Big Bend region.

Comments — The combination of vessels solitary and in radial multiples (Fig. 3a, b), simple perforations (Fig. 3c), alternate pits (Fig. 3c), abundant diffuse-in-aggregates parenchyma (Fig. 3a, b), fibres without distinctly bordered pits, multiseriate rays (Fig. 3f, g) that are not markedly heterocellular or homocellular, rare uniseriate rays, and crystals in non-chambered cells (Fig. 3g) suggests affinities with the Bombacaceae or Malvaceae s.l. The presence of two size classes of ray cells is consistent with this suggestion. The anatomy of these woods is similar to other fossil woods that have been assigned to the genus *Bombacoxylon* Gottwald (1969) (syn. *Dombeyoxylon* Carruthers). These Big Bend woods represent the oldest known occurrence of woods of this type as well as the first report for the western United States. *Bombacoxylon* woods have been reported from the Paleogene (epoch unknown), Oligocene, and Miocene of north Africa (Koeniguer 1967; Gevin et al. 1971; Beauchamp et al. 1973; Beauchamp & Lemoigne 1973; Lemoigne 1978), and the Eocene, Oligocene and Miocene of Europe (Hofmann 1952; Privé-Gill & Pelletier 1981; Selmeier 1985).

These samples fit Page's (1979) Group XA (vessels present, solitary and in groups, perforations simple, alternate intervessel pits, apotracheal parenchyma present).

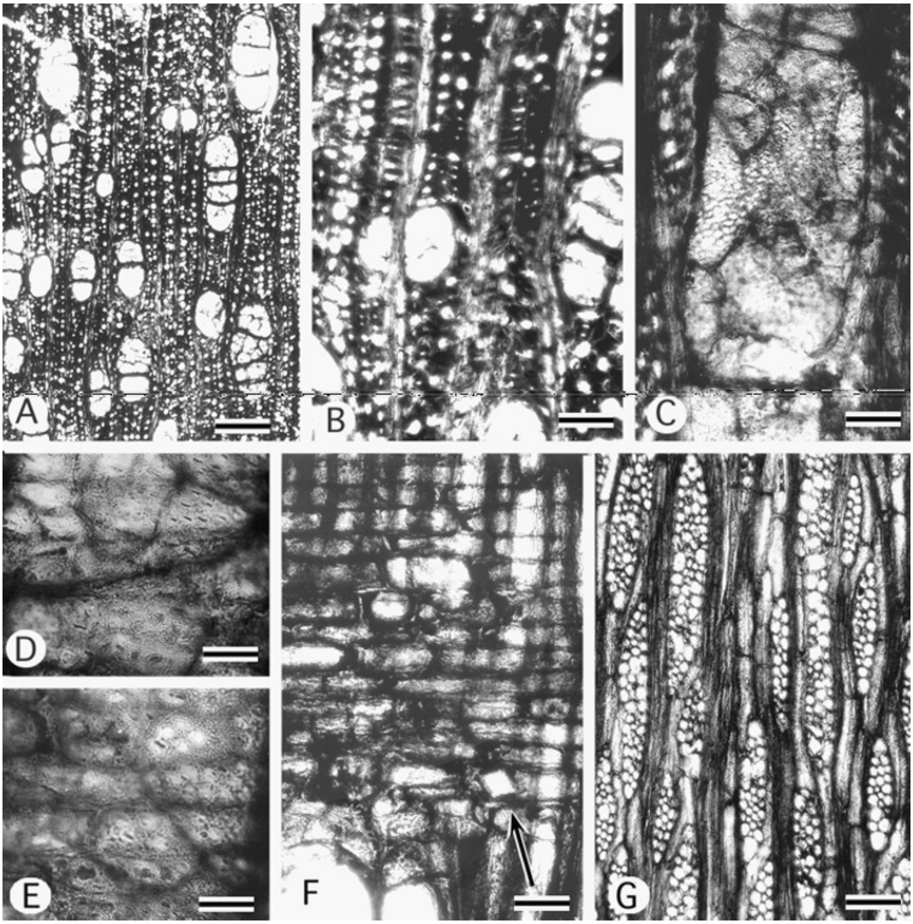

Fig. 3. *Bombacoxylon langstoni* sp. nov. (USNM 507018) — A: Vessels solitary and in radial multiples. XS. – B: Diffuse and diffuse-in-aggregates axial parenchyma. XS. – C: Crowded alternate intervessel pits. Thin-walled tyloses. Simple perforation plates. TLS. – D, E: Vessel-ray parenchyma pits. RLS. – F: Prismatic crystal (arrow) in procumbent ray parenchyma cell. RLS. – G: Ray cells tending to be of two sizes. TLS. — Scale bar = 250 µm for A; 100 µm for B, G; 50 µm for C, F; 25 µm for D, E.

Legends for Fig. 3–13: RLS = radial section; TLS = tangential section; XS = cross section.

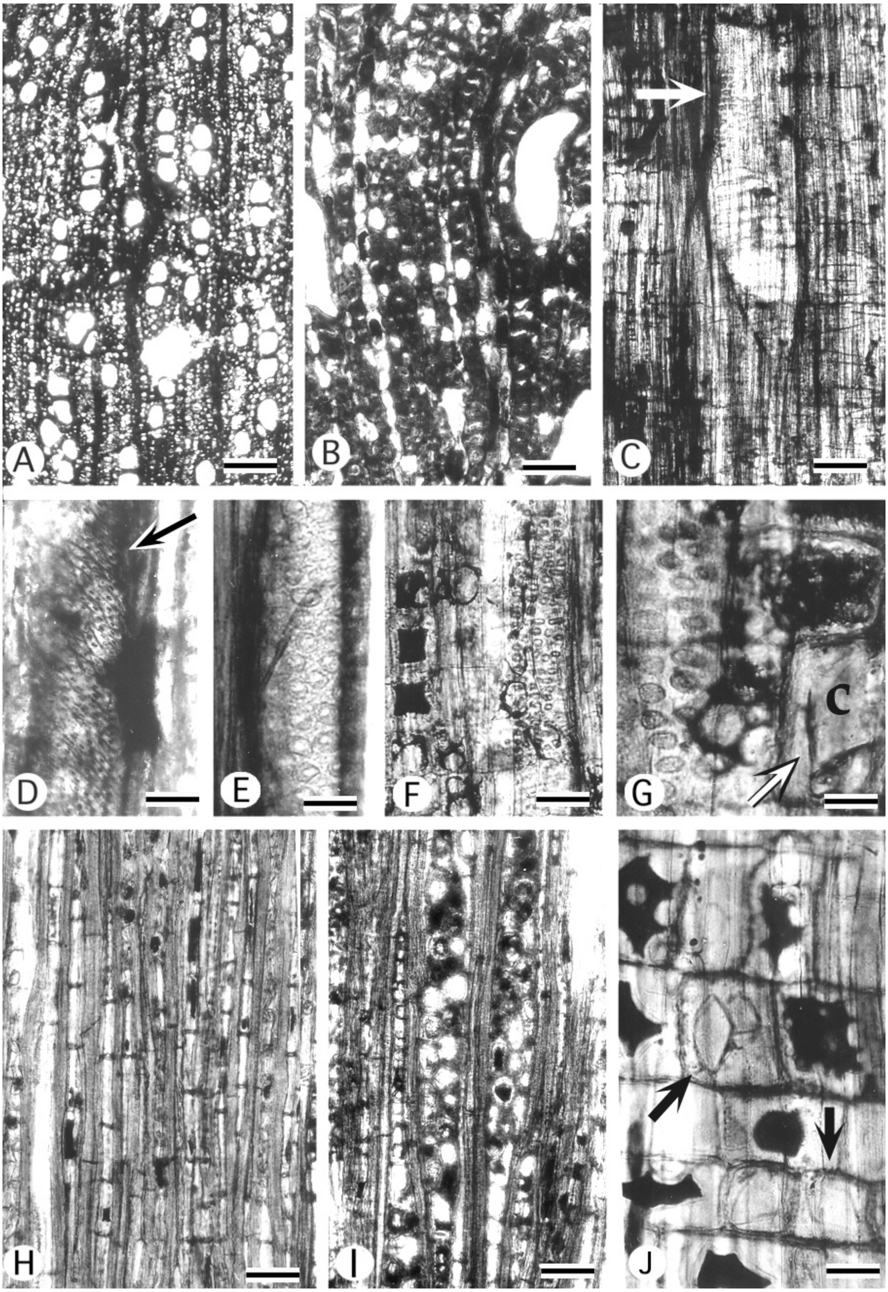

Fig. 4. *Pageoxylon cretaceum* gen. et sp. nov. (USNM 507022) — A: Vessels solitary and in radial multiples. XS. – B: Diffuse axial parenchyma. XS. – C: Scalariform perforation plate, opposite pitting (arrow). RLS. – D: Wall markings suggesting helical thickenings (arrow) in vessel element. TLS. – E: Alternate intervessel pitting. TLS. – F: Square/upright ray parenchyma cells (left). Vessel-ray parenchyma pits (right). RLS. – G: Vessel-ray parenchyma pits

Pageoxylon cretaceum gen. et sp. nov. (Fig. 4)

Generic diagnosis:

Wood diffuse-porous; vessels solitary and in short radial multiples; tendency to radial chains; perforation plates exclusively scalariform, less than 25 bars; intervessel pitting alternate-opposite; vessel-ray parenchyma pits with reduced borders, but similar in size to intervessel pits. Axial parenchyma apotracheal, diffuse-in-aggregates. Rays less than 4 cells wide and markedly heterocellular, with a few procumbent cells.

Specific diagnosis:

Growth rings faint, marked by radially flattened fibres.

Diffuse-porous; vessels solitary and in radial multiples of 2–4; with a tendency to form radial chains; mean tangential diameter 86 (13) µm, range 62–106 µm; 17–38 per mm^2; mean vessel element length 1089 (234) µm, range 746–1424 µm; scalariform perforation plates, 4–16, mostly 8–12 bars, 5–9 µm between bars; alternate to opposite intervessel pits, crowded and polygonal and also not crowded, usually 8 µm across; vessel-ray parenchyma pits of similar size as intervessel pits, but with reduced borders; occasional thin-walled tyloses.

Axial parenchyma diffuse and diffuse-in-aggregates, abundant, 6–8 cells per strand.

Rays 1–3 cells wide, procumbent ray cells rare, mostly upright cells twice as high as wide, multiseriate rays only 2–3-seriate for a short distance and markedly heterocellular with few procumbent cells and many rows of square to upright cells; uniseriate rays common, and composed exclusively of upright cells; not storied; 8–15 per mm.

Fibres: pits not distinguishable; thick walls.

Inclusions: solitary prismatic crystals common in ray cells, 1–3 per cell.

Holotype: USNM 507022 (RM 13-6).

Stratum: Upper Cretaceous, Aguja Formation / Lower Shale Member.

Derivation of name: The generic name recognizes V.M. Page, whose study of a large suite of Cretaceous woods greatly increased our knowledge and appreciation of the generalized characteristics of Cretaceous dicot woods. The specific epithet is for the age of the wood.

Comments — This sample was very badly compressed; measurements could only be obtained from a few portions. In one isolated region there appear to be helical thickenings in the vessel elements (Fig. 4d). These apparent helical thickenings might represent cracks in the vessel walls. Helical thickenings are uncommon in Cretaceous and Early Tertiary woods (Wheeler & Baas 1991, 1993).

Extant species that have vessels solitary and in multiples (Fig. 4a, b), scalariform perforation plates (Fig. 4c), diffuse parenchyma (Fig. 4a, b), heterocellular multiseriate rays that are not exclusively uniseriate or 10-seriate or more (Fig. 4h, i), and crystals (Fig. 4j) occur in 16 families belonging to three of Cronquist's (1988) six subclasses

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with reduced borders, crystal (arrow, c) in ray cell. RLS. – H: Uniseriate portions of rays with high upright cells. TLS. – I: Multiseriate portion of ray. TLS. – J: Ray parenchyma cells with prismatic crystals (arrows). RLS. — Scale bar = 250 µm for A; 100 µm for H; 50 µm for B–D, F, I; 25 µm for J; 10 µm for E, G.

of Magnoliopsida: Hamamelidae (Hamamelidaceae, Juglandaceae, Betulaceae), Dilleniidae (Peridiscaceae, Styracaceae), Rosidae (Eucryphiaceae, Cunoniaceae, Rhizophoraceae, Nyssaceae, Olacaceae, Aquifoliaceae, Aextoxicaceae, Pandaceae, Euphorbiaceae). Of these families, ones that have species with vessels in a radial or oblique pattern include Aquifoliaceae, Betulaceae, Olacaceae, and Pandaceae; families with species that have some opposite or scalariform pits include Aextoxicaceae, Aquifoliaceae, Cunoniaceae, Eucryphiaceae, Euphorbiaceae, Hamamelidaceae, Nyssaceae, Olacaceae, Peridiscaceae, Rhizophoraceae, and Styracaceae. Some pollen from the Lower Shale Member of the Aguja Formation is said to represent hamamelid-like plants and Betulaceae (Baghai 1994). It is possible that this wood might represent one of those plants.

This sample has characteristics of Page's (1979) Group VB (vessels present, perforations scalariform, vessels solitary and in multiples, less than 50 bars per perforation, apotracheal parenchyma only).

Platanoid Types (Fig. 5)

This wood type (predominantly solitary vessels, scalariform perforation plates, tall and wide rays, and opposite-scalariform intervessel pits) is common in the Cretaceous and Early Tertiary, and is among the earliest known, occurring in the Albian (Thayn et al. 1985; Herendeen 1991a). Such woods with heterocellular rays usually are assigned to *Icacinoxylon*; woods with homocellular or near-homocellular rays usually are assigned to *Plataninium*. A comprehensive reevaluation is needed of all Cretaceous–Early Tertiary specimens with this pattern. Pending this work, no names are assigned to Big Bend Cretaceous woods of this pattern. There are at least two types of woods with the Platanoid pattern in the Aguja Formation; they are described separately below.

Platanoid Type I (USNM 507023, USNM 507024) is represented by small diameter axes. Platanoid Type II (USNM 507025) is represented by mature wood. The orientation of Type II's rays suggests it is a fragment some distance from the pith, and its minimum diameter (certainly an underestimate) is estimated to be 20 cm. The narrower, more numerous vessels in Type I compared to Type II are consistent with the different sized axes, vessel diameter typically increases with cambial age and distance from the pith. However, whether the differences in ray cell appearance are associated with cambial age or species differences is not known.

The woods from the WPA locality are not well preserved, but their cross-sectional anatomy is consistent with Type I. The WPA samples have small diameters and a pith, and in the field looked like roots (not likely because of the pith) or vines (not a habit of present-day Platanaceae, but found in the Icacinaceae). In the past the Platanaceae were more diverse than at present (e.g., Manchester 1986; Pigg & Stockey 1991; Magallon-Puebla et al. 1997), so it is conceivable that these narrow diameter axes could represent viny Platanaceae. Additional collections and better preserved material are needed to resolve the affinities and habit of these woods.

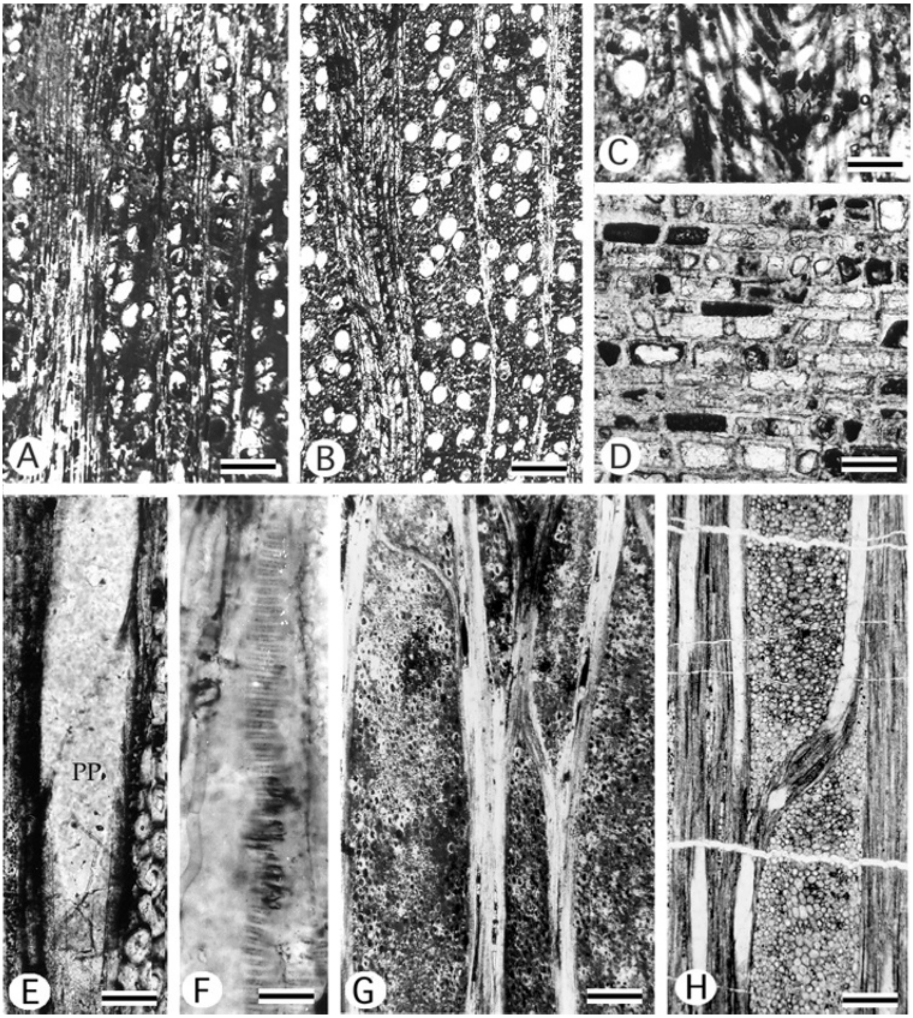


Fig. 5. Platanoid woods. Type 1 (USNM 507023): B, C, E, F, H; Type 2 (USNM 507025): A, D, G — A, B: Mostly solitary vessels, wide rays. XS. – C: Detail of ray cells with chevron pattern. XS. – D: Procumbent and square ray parenchyma cells. RLS. – E: Scalariform perforation plate. TLS. – F: Scalariform intervessel pitting, located near end of vessel element. TLS. – G, H: Broad and tall rays. TLS. — Scale bar = 250 μm for A, B, G, H; 100 μm for C, D; 50 μm for E; 25 μm for F.

Platanoid Type I (Fig. 5b, c, e, f, h)

Diffuse-porous. Vessels predominantly solitary, mean tangential diameter 55 (10), 39–81 μm; mean radial diameter 80 (12), 58–107 μm; 31–67 per mm^2; mean vessel element length 680 (80, n = 10), 520–768 μm; perforation plates exclusively scalariform with 8–26 bars; vessel pits rare and opposite-scalariform; vessel-ray parenchyma pits not observed.

Parenchyma diffuse-in-aggregates.

Rays: multiseriate rays very large and very variable in size, 3–19 cells, 45–493 µm wide, mean 255 µm; accounting for 33% of wood volume; mean ray height 2502 (1333) µm, 712–5424 µm; uniseriate rays absent. In cross section rays with chevron effect, cells oriented in such a way that the rays appear to point toward the pith. Ray cells predominantly procumbent; rays without extended uniseriate margins, uniseriate margins of upright and square cells short. Individual ray cells variable in size when viewed in tangential section.

Samples: USNM 507023 (GH 6a), USNM 507024 (WPA 2).
Stratum: Upper Cretaceous, Aguja Formation / base of Upper Shale Member.

Platanoid / Icacinoid Type II (Fig. 5a, d, g)

Diffuse-porous. Vessels predominantly solitary, mean tangential diameter 74 (10) µm; 38 per mm^2; perforation plates exclusively scalariform with 10–15 bars; vessel pits rare, scalariform; vessel-ray parenchyma pits not observed.

Parenchyma diffuse-in-aggregates.

Rays: multiseriate rays very large and very variable in size, 3–25 cells, 88–666 µm, mean 384 µm wide; accounting for 43% of wood volume; mean ray height 2582 (1399) µm; uniseriate rays absent. Rays without chevron effect, ray cells predominantly procumbent; rays without extended uniseriate margins, uniseriate margins of upright and square cells short. Individual ray cells appearing relatively uniform in size in tangential view.

Sample: USNM 507025 (RM 27).
Stratum: Upper Cretaceous, Aguja Formation / base of Upper Shale Member.

Comments — Platanoid wood occurs in the younger Paleocene Black Peaks Formation of Big Bend (Wheeler 1991), and in the Upper Cretaceous McRae Formation (Jose Creek Member), Texas (Upchurch & Mack 1998) and Kirtland Formation of New Mexico (Wheeler et al. 1995). The platanoid wood from the Upper Shale Member of the Kirtland Formation (correlative with the Upper Shale Member of the Aguja) has taller and narrower rays than the Big Bend platanoids. It has a few uniseriate rays, while the Big Bend Cretaceous platanoids do not. The platanoid in the McRae Formation is similar to Type II (EW, personal observation).

The number of bars per perforation plate in these Campanian Big Bend woods is lower than the Paleocene Big Bend platanoid and U.S. Eocene platanoid woods. However, only a few perforations (less than 5 per sample) were seen in these Campanian woods, so it is possible that there are perforations with more numerous and thinner bars, which may be less likely to be preserved. The shorter vessel elements of Type I are consistent with size of the sample, juvenile wood of extant *Platanus* (Baas 1969) has shorter vessel elements than mature wood (Wheeler 1991). On the basis of available samples, it cannot be determined if Type I and Type II represent the same type of plants. It is possible that juvenile wood of Type II would be similar to Type I wood.

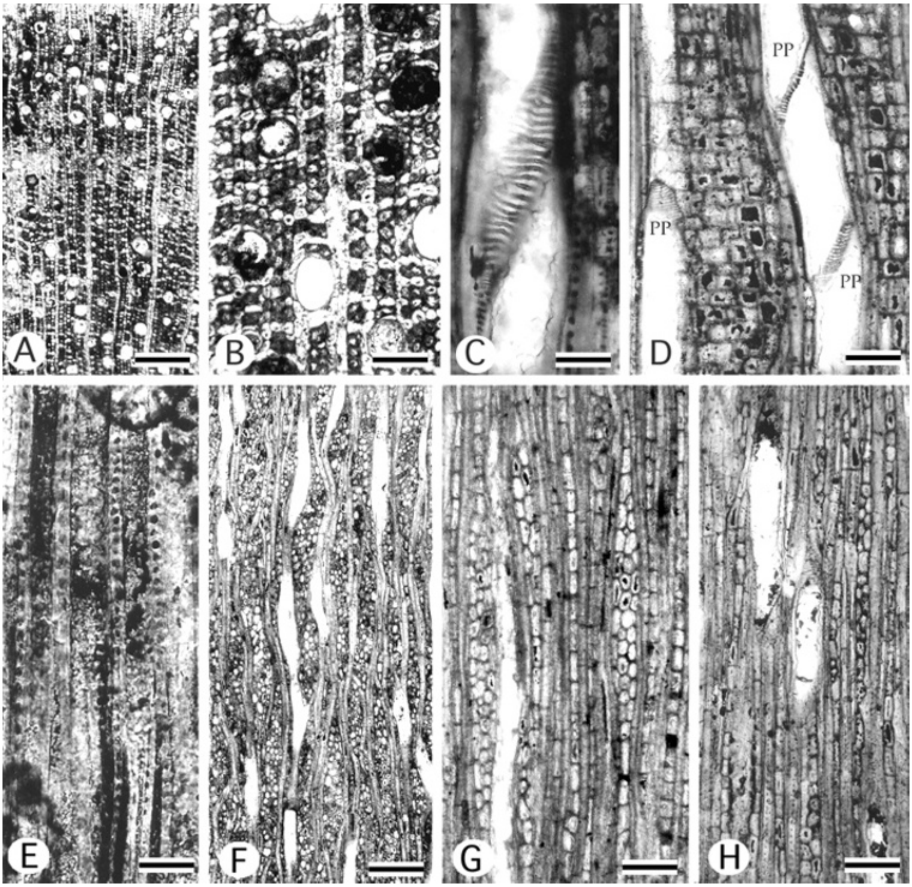


Fig. 6. 'Baileyan Big Bend Wood. Type I' — A, B: Vessels mostly solitary. Abundant diffuse and diffuse-in-aggregates parenchyma (USNM 507028). XS. – C: Scalariform perforation plate (USNM 507030). RLS. – D: Scalariform plates (PP). Rays with upright and square cells (USNM 507030). RLS – E: Fibres with distinctly bordered pits (USNM 507026). RLS. – F–H: Variation in ray width (USNM 507030 , USNM 507026, USNM 507027). TLS. — Scale bar = 250 µm for A, E, F; 100 µm for B, D, G, H; 50 µm for C; 25 µm for E.

'Baileyan Big Bend Wood, Type I' (Fig. 6)

Growth rings indistinct.

Diffuse-porous; vessels predominantly solitary, oval to slightly angular in outline; mean tangential diameters 42 (8)–68 (12) µm; mean radial diameters 66 (14)–115 (19) µm; mean vessel densities 21–35 per mm^2; mean vessel element lengths 574 (127)–834 (134) µm; exclusively scalariform perforation plates with 12–24 bars; inter-vessel pitting apparently opposite.

Axial parenchyma diffuse, rarely diffuse-in-aggregates, strands up to 14 cells long.

Rays: multiseriate rays 2–3-seriate, heterocellular, but with margins of less than 10 upright cells, procumbent cells barely rectangular, square, upright and procumbent cells intermixed within the body of the ray; mean multiseriate ray heights 499 (143)–718 (191) µm; not storied; 11–20 per mm.

Fibres: distinctly bordered pits in the radial walls.

Inclusions not observed.

Samples and Strata: Aguja Formation / Upper Shale Member / lower part: USNM 507026 (RM 28A), USNM 507027 (RM 28-2), USNM 507028 (RM 28-3), USNM 507029 (RM-nrP), USNM 507030 (RM 28-19). — Aguja Formation / Upper Shale Member / central part: USNM 507031 (CR2-6, vines).

Comments — The general pattern of these woods includes features considered primitive in the Baileyan sense: exclusively solitary vessels with a mean tangential diameter of less than 100 µm (Fig. 6a, b), exclusively scalariform perforation plates (Fig. 6c, d), fibres with distinctly bordered pits (Fig. 6e), narrow heterocellular rays (Fig. 6f, g, h), and relatively abundant apotracheal parenchyma (Fig. 6a, b). This combination of characters is widespread in extant angiosperms, occurring in 14 different families belonging to four of Cronquist's (1988) six subclasses of Magnoliopsida: Hamamelidae (Hamamelidaceae, Daphniphyllaceae, Myricaceae), Dilleniidae (Dilleniaceae, Epacridaceae, Symplocaceae, Theaceae), Rosidae (Buxaceae, Cornaceae, Cunoniaceae, Escalloniaceae, Icacinaceae, Olacaceae), Asteridae (Caprifoliaceae).

These woods fit Page's (1979) Group IIIB (vessels present, perforation plates scalariform, bars in perforation average fewer than 50, parenchyma mostly apotracheal).

Because these Big Bend woods' salient features are widespread among extant angiosperms, have the syndrome of features considered primitive in the Baileyan sense, and fit more than one genus for fossil wood, they are referred to in a general way as "Bailey's Big Bend Wood, Type I".

The samples of this wood were all small diameter axes, less than 2 cm across. This wood type was common throughout a hillside at one locality (CR2-6) where hadrosaur bones occur. With further excavation it should be possible to determine the spatial arrangement of these axes. Initial observations suggest they are scrambling vines.

Paraphyllanthoxylon Bailey 1924

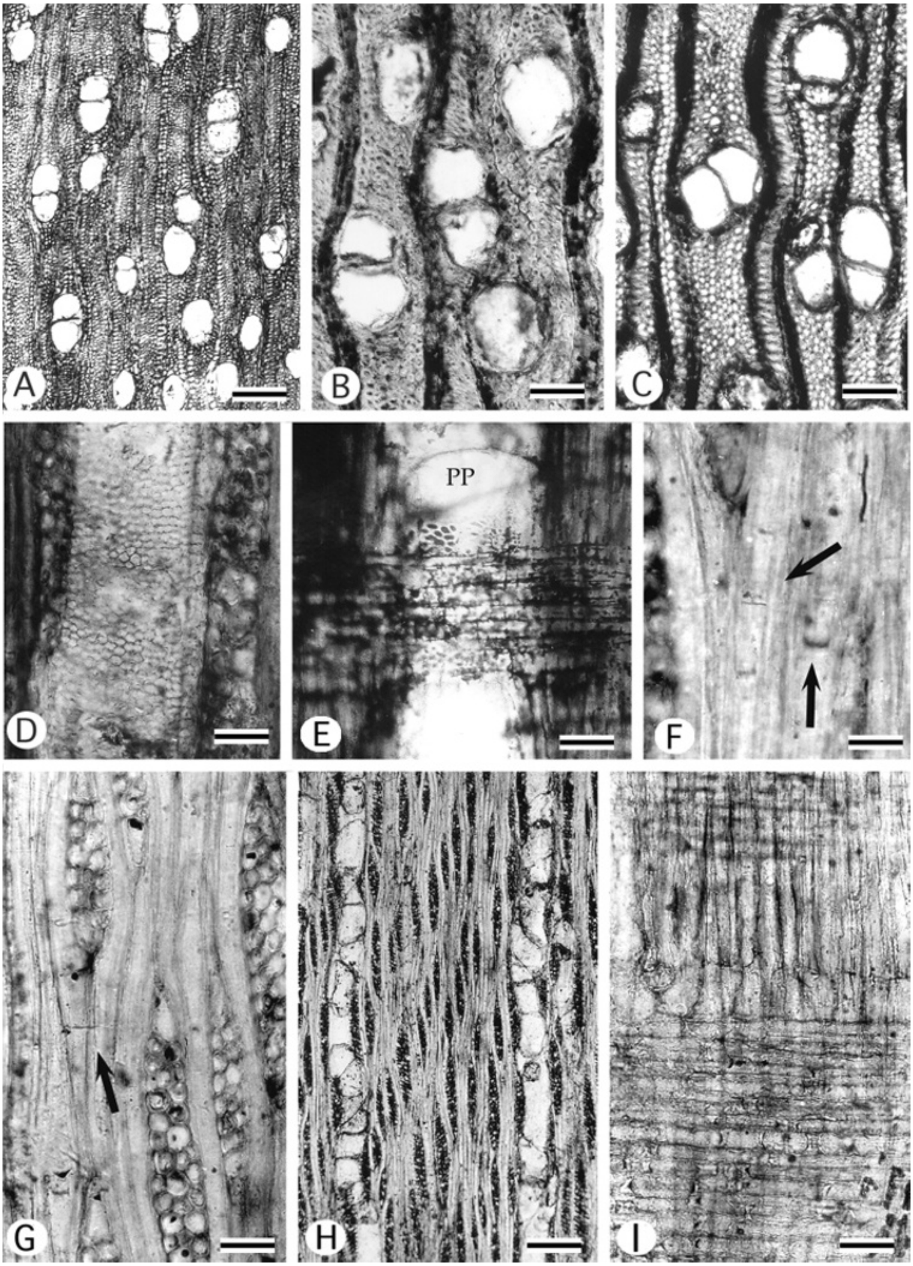
cf. ***Paraphyllanthoxylon anazasii*** Wheeler, McClammer, LaPasha (1995) (Fig. 7)

Growth rings indistinct, marked by radially flattened fibres.

Diffuse-porous; vessels solitary and in short radial multiples of 2–3; 40–64% solitary; mean tangential diameters 93 (18)–120 (14) µm; 10–20 per mm^2; mean vessel element lengths 396 (64)–440 (97) µm; exclusively simple perforations; crowded al-

→

Fig. 7. cf. *Paraphyllanthoxylon anazasii* Wheeler, McClammer & LaPasha — A: Vessels solitary and in radial multiples of 2 (USNM 507036). XS. – B: Relatively thick-walled fibres (USNM 507034). XS. – C: Scanty paratracheal to narrow vasicentric parenchyma, fibre walls of medium thickness (USNM 507037). XS. – D: Crowded alternate intervessel pits, polygonal in outline (USNM 507036). TLS. – E: Vessel-ray parenchyma pits with reduced borders and oval- to horizontally elongate, simple perforation plate (PP). RLS. – F: Possible septate (arrows)



fibres (USNM 507034). TLS. – G: Septae? or hyphae? (arrow) in fibre. Multiseriate rays (USNM 507034). TLS. – H: Rays with tendency to being arranged in echelon. Thin-walled tyloses in vessels (USNM 507034). TLS. – I: Rays with procumbent body cells and a single marginal row of upright cells (USNM 507036). RLS. — Scale bar = 250 µm for A, H; 100 µm for B, C, I; 50 µm for D–G.

ternate intervessel pits, angular in outline, 8–11 μm across; vessel-ray parenchyma pits of similar size as intervessel pits but with reduced borders, rounded in outline, and irregular in shape, not crowded, throughout the ray, not restricted to the marginal rows; thin-walled tyloses present, not filling vessels.

Axial parenchyma absent to rare, scanty paratracheal.

Rays: multiseriate rays 2–3 cells wide; heterocellular with body of multiseriate rays composed entirely of procumbent cells with 1–2 rows of square to slightly upright cells (with a clear distinction between the procumbent body cells and the marginal square/upright cells) to sub-homocellular composed entirely of procumbent cells with ill-defined marginal rows; mean heights multiseriate rays 311 (46)–377 (28) μm; uniseriate rays rare; not storied; 6–16, mostly 7–10 per mm.

Fibres: pits not distinguishable; walls medium-thick, predominantly non-septate, rarely septate.

Samples and Strata: Aguja Formation / Upper Shale / lower part: USNM 507032 (CR2-6b). — Aguja Formation / Upper Shale / upper part: USNM 507033 (CR2-7a), USNM 507034 (CR2-7b), USNM 507035 (CR2-7c), USNM 507036 (CR2-7d), USNM 507037 (GH9 3/95).

Comments — The spacing of samples USNM 507033, 507034, 507035, and 507036 in the field suggests they are four different trees; USNM 507033 and 507034 are too fragmented to estimate tree diameters, but judging by the abundance of wood fragments are at least as large as USNM 507035 and 507036, which have minimum estimated diameters of 36 cm and 56 cm, respectively.

The pattern of this wood is one that is common in a large number of extant families, and is that of *Paraphyllanthoxylon*, one of the two most common dicotyledonous wood types of the Cretaceous. These woods are similar to *Paraphyllanthoxylon anazasii* from the early Maastrichtian Kirtland Shale Formation of the San Juan Basin, New Mexico. There are some quantitative differences; the San Juan samples have narrower vessels (84 μm), more vessels per mm^2 (12–37 per mm^2), longer vessel elements (444–998 μm), and shorter multiseriate rays (234–294 μm) than the Big Bend samples. However the differences in these quantitative features are similar to those found within woods of a single extant species. Septate fibres are a defining feature of *Paraphyllanthoxylon*. This feature is visible in some Big Bend samples, but not in others that otherwise are similar and from the same locality. Thus, all specimens are tentatively assigned to *Paraphyllanthoxylon*. Presence or absence of septate fibres varies within some extant species, particularly members of the Lauraceae (Richter 1987), a family that some *Paraphyllanthoxylon* belong to (Herendeen 1991b).

These woods conform to Page's (1979) Group IX (simple perforation plates, alternate intervessel pits, sparse axial parenchyma).

Agujoxylon olacaceoides gen. et sp. nov. (Fig. 8)

Generic diagnosis:

Wood diffuse-porous. Vessels solitary and occasionally in radial multiples; tendency to radial alignment; perforation plates exclusively scalariform; intervessel pitting opposite-scalariform; vessel-ray parenchyma pits with reduced borders, appearing of two sizes, some enlarged and nearly filling the entire cross-field, other pits smaller. Axial parenchyma abundant, apotracheal, diffuse-in-aggregates. Rays uniseriate and multiseriate; multiseriate rays heterocellular, mixture of procumbent and square cells, without a marked distinction between the procumbent and square cells, multiseriate and uniseriate portions of the rays alternate. Imperforate elements with distinctly bordered pits in radial and tangential walls.

Specific diagnosis:

Growth rings absent.

Diffuse-porous; vessels solitary, occasionally in radial multiples; angular in outline, with a tendency to form radial files; mean tangential diameters 68 (13)–92 (16) µm; mean radial diameters 93 (18)–124 (18) µm; 14–35 per mm^2; mean vessel element lengths 1031 (212)–1192 (233) µm; perforation plates exclusively scalariform with more than 20 bars; intervessel pits opposite-scalariform; vessel-ray parenchyma pits with reduced borders, appearing of two sizes, some very enlarged nearly filling the entire cross-field, and other pits smaller; thin-walled tyloses present, appearing to segment the vessel elements, on occasion bubble-like.

Axial parenchyma abundant, apotracheal, diffuse-in-aggregates, of near equal abundance as the imperforate elements. In radial section, axial parenchyma and imperforate elements appear to alternate. Strand lengths of 12–14–19 cells.

Rays: multiseriate portions generally 4–6 cells wide; multiseriate and uniseriate portions of the rays alternate; heterocellular, mixture of procumbent and square cells, without much distinction between the procumbent and square cells; variable in height within samples, sample means 990 (467)–1201 (650) µm; not storied; 5–14, mostly 9–11 per mm.

Imperforate elements appearing to be fibre-tracheids (or tracheids *sensu* Carlquist 1988), bearing distinct bordered pits in both radial and tangential walls.

Inclusions: occasional 2- (rarely 4-)chambered crystalliferous cells within the longer axial parenchyma strands, each chamber containing a single prismatic crystal.

Holotype: USNM 507038 (GH 9/10-1).

Paratypes: USNM 507039 (GH9), USNM 507040 (GH9-1), USNM 507041 (GH9-11), USNM 507042 (GH9-20), USNM 507043 (GH9-21), USNM 507044 (GH9-23), USNM 507045 (GH9-25).

Stratum: Upper Cretaceous, from the Upper Aguja Formation, near boundary of Campanian–Maastrichtian.

Derivation of names: The generic name is derived from the Aguja Formation, and the specific epithet is for the woods' resemblance to members of the Olacaceae.

Comments — Rays are very abundant in this wood type. Rays typically alternated be-tween uniseriate and multiseriate (Fig. 8j), being of a type termed vertically fused rays by Mennega (1987), interconnected rays by Carlquist (1988), or polymerous by Hayden et al. (1993, cf. the "polymerer Holzstrahl" of Braun 1970). Moreover, there often was lateral fusing of rays, with portions of the rays extending to the side and

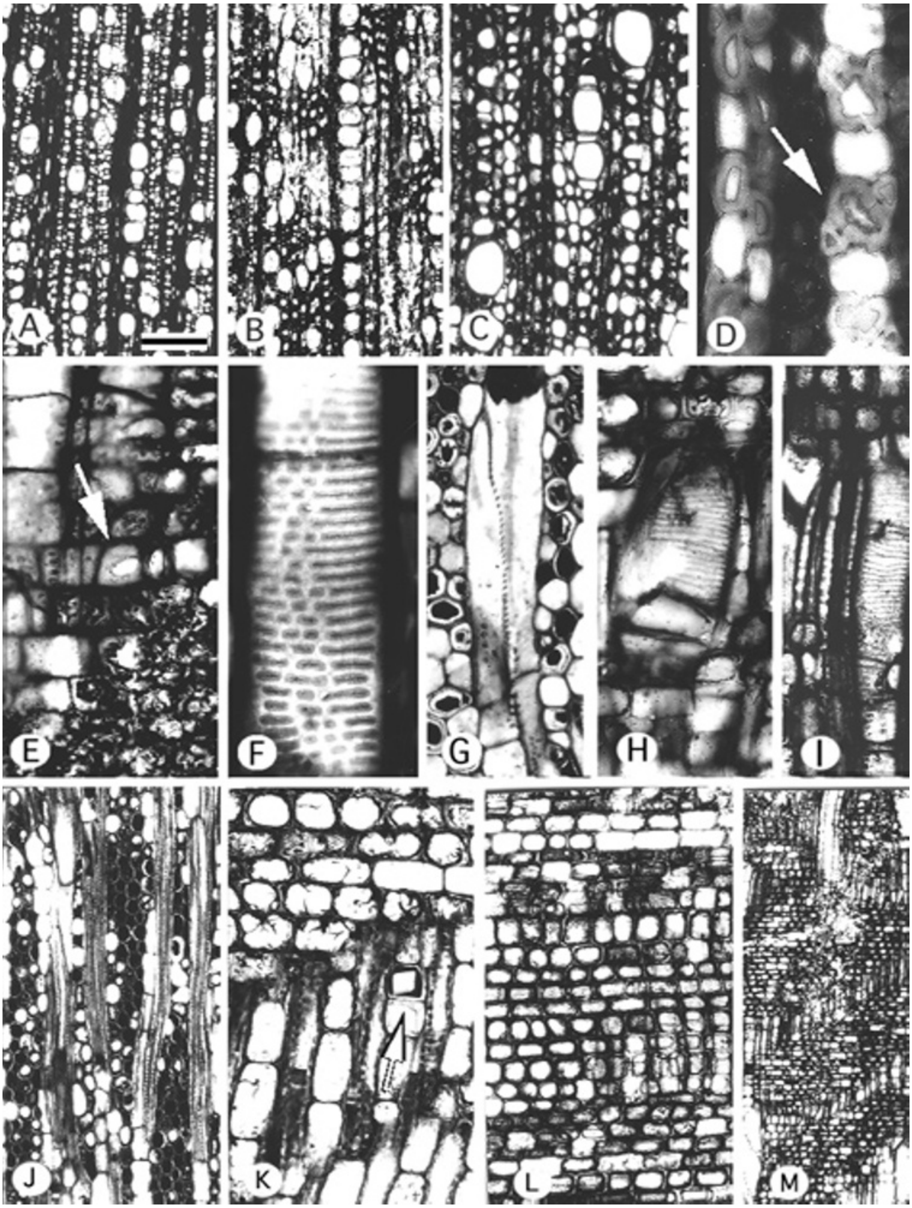


Fig. 8. *Agujoxylon olacaceoides* gen. et sp. nov. (USNM 507038: A, E, F, I, L; USNM 507045: C, G, H, J, K, M) — A, B: Vessels with tendency to radial alignment. XS. – C: Imperforate elements, narrow fibres and apotracheal parenchyma. XS. – D: Fibre wall pitting (arrow). XS. – E: Vessel-ray parenchyma pits. RLS. – F: Transitional intervessel pitting. TLS. – G: (TLS) & H & I: (RLS). Scalariform perforation plates. – J: Heterocellular rays and parenchyma strands. TLS. – K: Crystals (arrow) in chambered axial parenchyma. RLS. – L: Heterocellular ray with square, upright, and procumbent cells. RLS. — M: Heterocellular rays. RLS. — Scale bar (on A) = 250 μm for A, B, M; 100 μm for C, J, L; 50 μm for E, G–I, K; 25 μm for D, F.

fusing with other rays. It was particularly difficult to measure ray height in two of the samples because of these lateral interconnections. There is a gradation between procumbent and square to upright cells; the cells of the multiseriate portions of the rays do not differ significantly in shape and size from the cells of the uniseriate portions of the rays.

Imperforate elements (fibre-tracheids) occur in small groups alternating radially with apotracheal axial parenchyma (Fig. 8d). Because of the abundance of rays, sometimes these groups of imperforate elements are only 1–2 cells wide tangentially, and because of the abundance of apotracheal parenchyma, only 1–2 cells deep radially. Parenchyma is abundant, with ray and axial parenchyma combined, accounting for 37–59% of the wood volume, on average 46%.

The predominance of solitary vessels varies in these samples, some have mostly solitary vessels tending to a radial alignment, others have radial multiples. Vessels accounted for 15–25 % of the wood volume.

One of the distinctive features of this wood is the presence of two distinct sizes of vessel-ray parenchyma pits (Fig. 8e). This feature is not common in extant dicotyledons. Of the extant families that have exclusively scalariform perforation plates (Fig. 8g, h, i), opposite-scalariform intervessel pits (Fig. 8f), abundant apotracheal parenchyma, only the Olacaceae have large simple vessel-ray parenchyma pits accompanied by small vessel-ray parenchyma pits. Today the Olacaceae is a tropical to subtropical family of some 29 genera and 200 species (Mabberley 1997). To our knowledge, no other fossil woods with reliable age determinations have been assigned to the Olacaceae.

The fossil record of the Olacaceae in North America is mostly based on pollen records. Evidently the family was widespread in western North America in the Late Cretaceous and Early Tertiary, as there are Campanian–Maastrichtian records for the pollen genus *Anacolosidites* in California, the Northwest Territories, and South Dakota, and Eocene records for Arkansas, Texas, Virginia, Alabama, Tennessee, Mississippi (Taylor 1990). According to Muller (1981), *Anacolosidites* pollen is similar to that of the Old World tropical genus *Anacolosa* and the Neotropical genus *Cathedra* of the tribe Anacoloseae, and African members of *Ptychopetalum*. The wood of these extant genera differs from the fossil wood described above as all three have simple perforations and small alternate intervessel pits. Of the extant genera of Olacaceae, the fossil is most similar to members of the extant genus *Strombosia* which has vessels in radial chains and radial multiples, scalariform perforations and opposite-scalariform vessel pits, and abundant apotracheal parenchyma.

Because of the variation in whether vessels are predominantly solitary, or with some multiples, they conform to two of Page's (1979) groupings: IIIB (scalariform perforation plates, mostly solitary vessels, less than 50 bars per perforation, apotracheal parenchyma, transitional to opposite intervessel pits) and VIIB (scalariform perforation plates, vessels solitary and in multiples, less than 50 bars per perforation, apotracheal parenchyma).

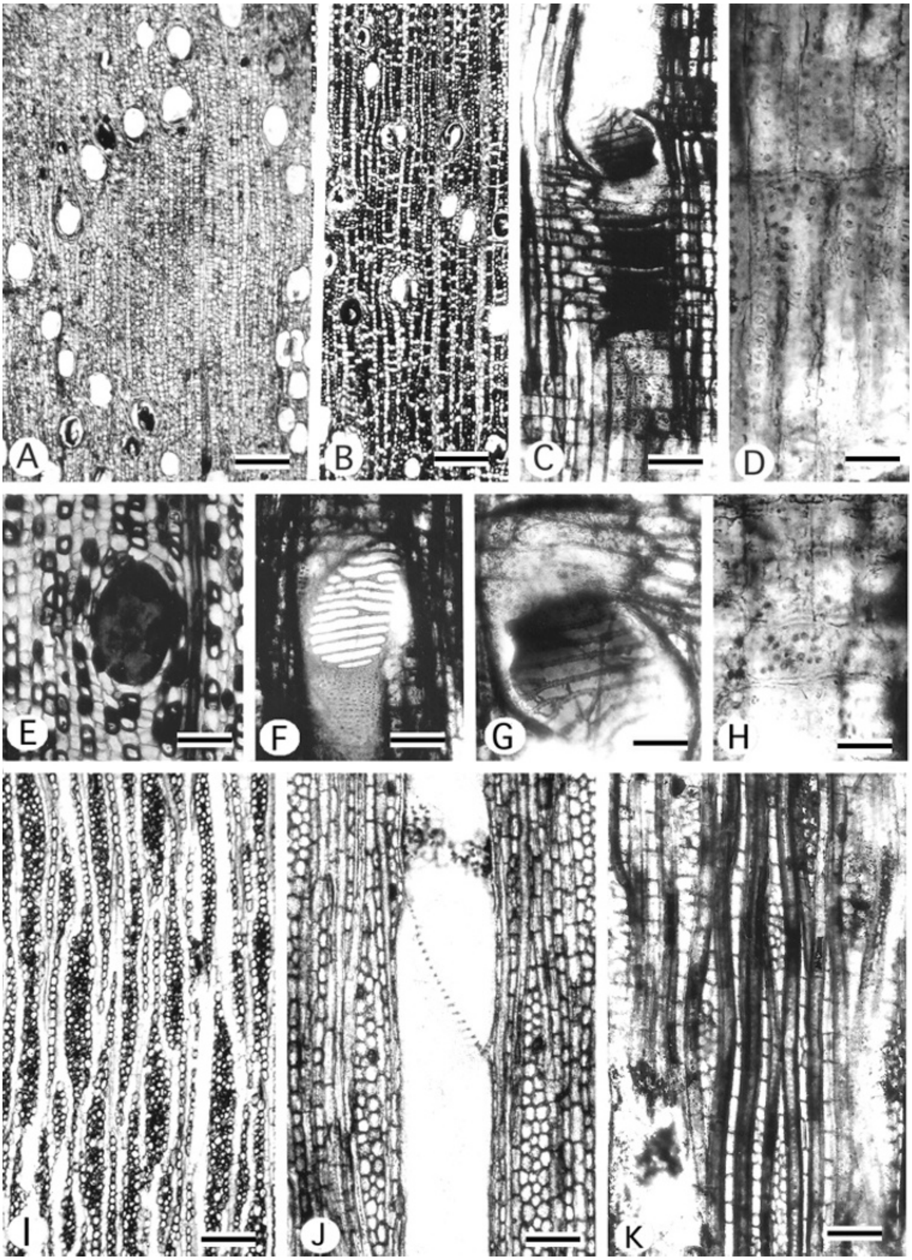


Fig. 9. *Metcalfeoxylon kirtlandense* Wheeler, McClammer & LaPasha — A: Tendency for solitary oval vessels to be in a diagonal pattern (USNM 507047). XS. – B: Solitary vessels and abundant diffuse parenchyma (USNM 507056). XS. – C: Scalariform perforation plate, vessel-ray parenchyma pits, ray structure (USNM 507051). RLS. – D: Imperforate element pitting, radial section (USNM 507048). RLS. – E: Fibre and axial parenchyma cell walls, vessel filled with dark contents (USNM 507051). XS. – F: Scalariform perforation plate and opposite inter-

Metcalfeoxylon Wheeler, McClammer, LaPasha (1995)

Metcalfeoxylon kirtlandense Wheeler, McClammer, LaPasha (1995) (Fig. 9)

Growth rings absent.

Diffuse-porous; vessels predominantly solitary, oval in outline, with a tendency to diagonal or radial arrangement; mean tangential diameters 115 (13)–183 (28) µm; mean radial diameters 139 (28)–209 (41) µm; mean vessel densities 2–15 per mm^2; mean vessel element lengths 1261 (296)–1566 (251) µm; perforation plates exclusively scalariform with 8–16, mostly 12–14 bars, generally 14 µm between bars of 3 µm thickness, most perforations with at least 1–2 reticulate (forked) bars; intervessel pits opposite to alternate; vessel-ray parenchyma pits similar to intervessel pits, 5–6 µm.

Axial parenchyma abundant apotracheal diffuse.

Rays: multiseriate rays 2–3-seriate, 29–40(–52) µm wide; markedly heterocellular with marginal rows of markedly upright cells, and body ray cells procumbent; uniseriate margins variable in length with 2–31 cells, frequently more than 10; average heights of the multiseriate portion of the ray ranging from 302 (76)–704≤(289) µm, total range 203–1390 µm; uniseriate rays common and composed exclusively of upright cells; not storied; 6–18 rays per mm.

Imperforate elements: distinctly bordered pits in both radial and tangential walls, thin to medium-thick walls; additionally there appear to be vasicentric tracheids, cells with more than 1 row of bordered pits encircling the vessels.

Samples and strata: Aguja Formation / Upper Shale / central part: USNM 507047 (CR2-6C) Croton Springs. USNM 507048 (GH8), USNM 507049 (NGH8). — Aguja Formation / Upper Shale / uppermost part: USNM 507050 (GH9-2), USNM 507051 (GH9?-10?-3); USNM 507052 (GH9-10-4), USNM 507046 (MCS18-Tree 1, 111 cm diameter), USNM 507053 (MCS18 TR4), USNM 507054 (MCS18 TR5), USNM 507055 (EDF2A), USNM 507056 (EDF5D).

Comments — The general pattern of these woods (exclusively solitary vessels that are not less than 50 µm or more than 200 µm wide, fewer than 40 vessels per mm^2, scalariform perforation plates (Fig. 9f, g), imperforate elements with distinctly bordered pits (Fig. 9d, k), rays usually less than 4-seriate and commonly with more than 10 marginal rows, vessel-ray parenchyma pits of similar size as the intervessel pits (Fig. 9h), and diffuse apotracheal parenchyma (Fig. 9b) occurs in extant species that belong to two of Cronquist's (1988) subclasses, the Rosidae (Order Celastrales: Celastraceae, Icacinaceae; Cornales: Cornaceae; Linales: Humiriaceae) and the Dilleniidae (Orders Dilleniales: Dilleniaceae, Violales: Stachyuraceae, and Theales: Theaceae).

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vessel pitting (USNM 507050). RLS. – G: Scalariform perforation plate and vessel-ray parenchyma pits similar in appearance to intervessel pits (USNM 507051). RLS. – H: Vessel-ray parenchyma pits (USNM 507051). – I: (USNM 507046), J: (USNM 507055) & K: (USNM 507051). Tangential sections. Variation in ray appearance, all samples have multiseriate rays with long uniseriate margins; uniseriate rays composed of high upright cells; parenchyma strands and scalariform plate in J, distinctly bordered imperforate elements in K. — Scale bar = 250 µm for A, B, I; 100 µm for C, E, F, J, K; 50 µm for D, G, H.

This wood conforms to Page's (1979) Group IIIB, sect. 4 (vessels present, scalariform perforations, less than 50 bars per perforation, apotracheal parenchyma, intervessel pits opposite-alternate). Of the fossil woods with some degree of dating, there is one Miocene wood with similar anatomy, *Goupioxylon stutzeri* from the Miocene of South America (Pons 1969).

Metcalfeoxylon kirtlandense was first described from the Late Cretaceous of the San Juan Basin (Wheeler et al. 1995). The species is based on sections from a trunk fragment with a 22 cm minimum diameter, recovered from the Lower Kirtland Formation of late Campanian age. The San Juan sample has fewer rays per mm (4–10) and less axial parenchyma than the Big Bend woods, but these differences are of the type that can be seen within extant species, and so the Big Bend woods tentatively are assigned to this species. There is variation in the appearance of the rays (Fig. 9i-k). In some samples the ray cells are more rounded to oval in outline, and ray width, usually 1–3-seriate, reaches 5-seriate in some samples. Ray structure is one of the more variable wood anatomical features. The variation seen in the Big Bend woods could be due to the location in the trunk or site conditions. The minimum diameters of the Big Bend *Metcalfeoxylon* specimens were from 40–100 cm.

Baasoxylon parenchymatosum gen. et sp. nov. (Fig. 10)

Generic diagnosis:

Wood diffuse-porous. Vessels mostly solitary with a tendency to form radial files, less than 100 µm in tangential diameter, fewer than 40 per mm^2; perforations exclusively scalariform, with fewer than 40 bars; intervessel pits mostly opposite, vessel-ray parenchyma pits similar to intervessel pits. Abundant diffuse-in-aggregates axial parenchyma. Multiseriate rays more than 4 cells wide, with a tendency to two sizes of ray cells. Wood with more than 50% parenchyma by volume. Imperforate elements with distinctly bordered pits in radial and tangential walls.

Specific diagnosis:

Growth rings indistinct.

Diffuse-porous; vessels solitary, rarely in radial multiples, with a tendency to form radial files; solitary vessels not angular in outline; oval in outline; range of mean tangential diameters 83 (15)–87 (14) µm; mean radial diameters 137 (23)–163 (27) µm; 15–39 (means 21–28) per mm^2; mean vessel element length 912 (154) µm, range 373–1243 µm; perforation plates exclusively scalariform with 15–30 bars, mostly 20–25, and 5–6 µm spacing between bars; intervessel pits opposite, 5–8 µm, with scalariform pits at the ends of some vessel elements; vessel-ray parenchyma pits similar to intervessel pits.

Axial parenchyma abundant apotracheal, diffuse-in-aggregates, of near equal abundance as the imperforate elements; strand lengths usually of 8 cells, up to 12 cells counted.

Rays: multiseriate rays generally 4–6(–8) cells, 141 (29)–205 (45) µm wide; heterocellular, in tangential section ray cells sometimes appearing to tend to two size classes, resembling tile cells; rays very variable in heights, averages range 631 (246)–1356 (520) µm; not storied; 4–10 per mm.

Imperforate elements appearing to be fibre-tracheids (or tracheids *sensu* Carlquist 1988), with distinctly bordered pits in both radial and tangential walls.

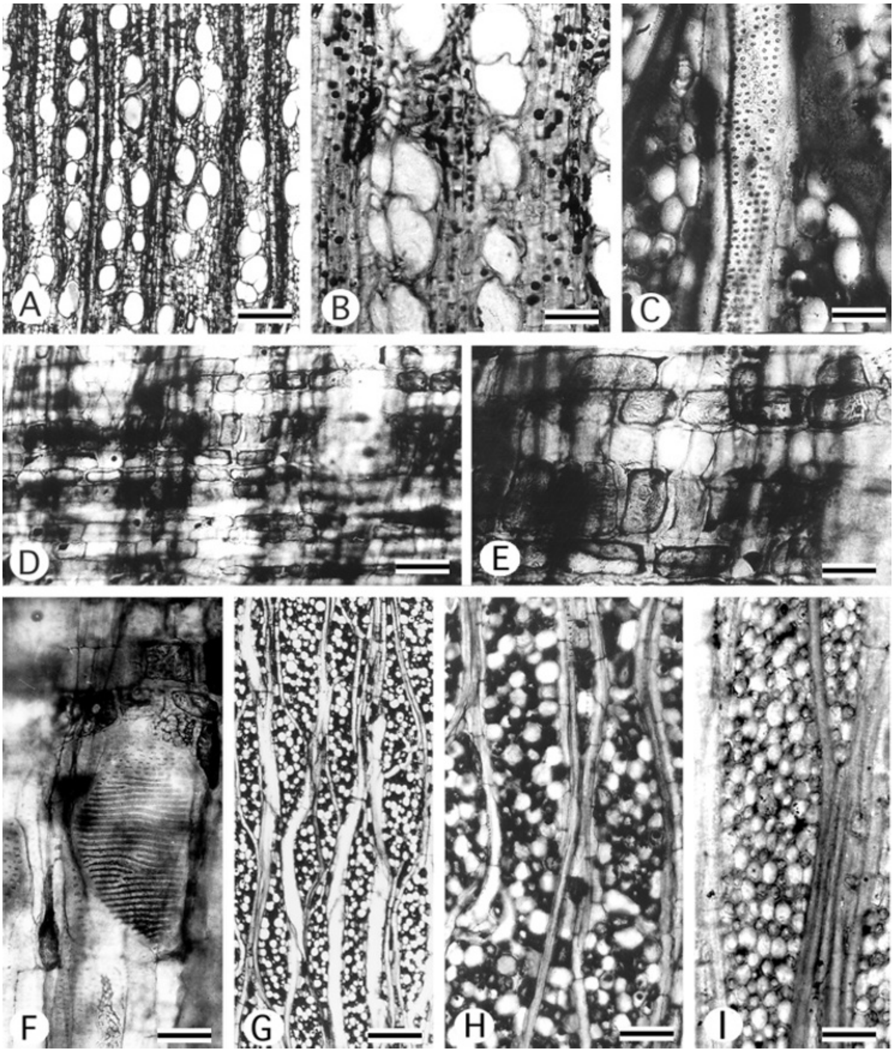

Fig. 10. *Baasoxylon parenchymatosum* gen. et sp. nov. (USNM 507057: A–H; USNM 507059: I) — A: Solitary oval vessels with a tendency to radial alignment. XS. – B: Vessels solitary and in radial multiples. XS. – C: Opposite intervessel pitting. XS. – D, E: Procumbent and upright cells. RLS. – F: Scalariform perforation plates and vessel-ray parenchyma pits. RLS. – G: Multiseriate rays with two sizes of ray cells, and differing in contents. TLS. – H: Rays with two sizes of ray cells. Imperforate elements with distinctly bordered pits. Parenchyma strands. TLS. – I: Ray with two sizes of ray cells. TLS. — Scale bar = 250 µm for A, G; 100 µm for B, D, H, I; 50 µm for C, E, F.

Holotype: USNM 507057 (PGH4a).
Paratypes: USNM 507058 (DF1-Stump 14), USNM 507059 (DF1-Stump 5, 70 cm diameter).
Stratum: Javelina Formation (lower part).
Derivation of names: The generic name is for Pieter Baas in recognition of his contributions to systematic and ecological wood anatomy; specific epithet for the abundant parenchyma in this wood type.

Comments — There are 16 families that have species with the combination of features: scalariform perforations, opposite pits, vessel-ray parenchyma pits similar to intervessel pits, imperforate elements with distinctly bordered pits, 4–10-seriate heterocellular rays, and apotracheal parenchyma. They belong to three of Cronquist's six (1988) subclasses of Magnoliopsida: Hamamelidae (Eupteleaceae, Myricaceae), Dilleniidae (Dilleniaceae, Epacridaceae, Clethraceae, Ericaceae, Symplocaceae, Theaceae, Saurauiaceae, Flacourtiaceae, Styracaceae), Rosidae (Buxaceae, Cornaceae, Escalloniaceae, Aquifoliaceae, Icacinaceae). Of these families, the following have species with exclusively solitary vessels: Buxaceae, Clethraceae, Cornaceae, Dilleniaceae, Epacridaceae, Ericaceae, Escalloniaceae, Eupteleaceae, Flacourtiaceae, Icacinaceae, Myricaceae, Saurauiaceae, Styracaceae, Symplocaceae, and Theaceae. Only the family Aquifoliaceae has vessels in a radial pattern.

These woods belong to Page's Group IIB, sect. 2 (vessels mostly solitary, scalariform perforation plates with less than 50 bars, apotracheal parenchyma, transitional/opposite pits).

A striking feature of these samples is their high proportion of parenchyma, over 50% of the wood volume is ray parenchyma. As is often true for wood, quantitative features of rays are variable; coefficients of variation for ray height are 38, 39, and 40%. Additionally, there is abundant axial parenchyma. Another distinctive feature is the presence of two size classes of ray cells, in tangential section resembling tile cells. Tile cells today are restricted to the Malvaceae s.l., but scalariform perforations do not occur in extant Malvales.

The size of the source wood samples, up to 70 cm in diameter, indicates this wood type belonged to a tree.

Gassonoxylon araliosum gen. et sp. nov. (Fig. 11)

Generic diagnosis:

Wood diffuse-porous. Vessels solitary and in short radial multiples, some tendency to vessels arranged in a tangential pattern, tangential diameter less than 100 µm, fewer than 20 per mm^2. Perforations simple, intervessel pits crowded alternate. Axial parenchyma scanty paratracheal to vasicentric. Heterocellular rays, less than 1 mm high, and mostly less than 4 cells wide.

Specific diagnosis:

Growth rings indistinct.

Diffuse-porous; vessels solitary and in radial multiples of 2–3, 47% solitary, in some regions vessels tend to be arranged in a tangential pattern; mean tangential diameter 57 (14) µm, range 36–92 µm; mean radial diameter of solitary vessels 114 (18) µm, range 87–149 µm; 4–8 per mm^2; vessel element lengths range 260–589 µm (mean 470 μm, n = 14); perforation plates simple; intervessel pits crowded alternate, ~10–11 μm; vessel-ray parenchyma pits not observed.

Axial parenchyma scanty paratracheal to vasicentric, 8 or more cells per strand.

Rays 1–3-seriate, mostly 3-seriate; heterocellular; multiseriate ray height 510 (207) μm; 7–14 per mm.

Imperforate elements: Pits not observed; thin-walled.

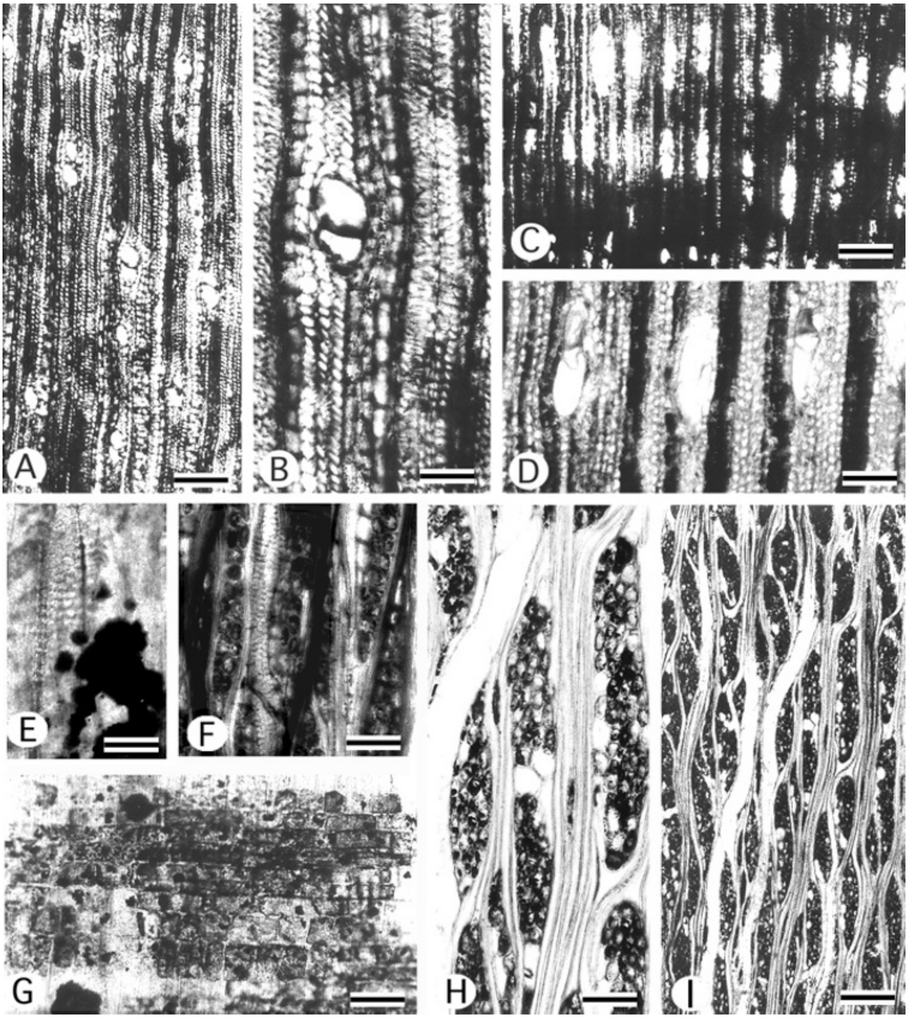

Fig. 11. *Gassonoxylon araliosum* gen. et sp. nov. (USNM 507060) — A: Widely spaced vessels, solitary and in short radial multiples. XS. – B: Radial multiple, fibres with thin to medium-thick walls. XS. – C, D: Vessels in tangential arrangement. XS. – E, F: Crowded alternate intervessel pitting. TLS. – G: Upright, square and procumbent cells, without pronounced difference between square and procumbent cells. RLS. – H: Multiseriate rays with enlarged cells. TLS. – I: Multiseriate rays, uniseriate rays rare. TLS. — Scale bar = 250 μm for A, C, I; 100 μm for B, D, F–H; 50 μm for E.

Holotype: USNM 507060 (DF1 10/18 4/4B).
Stratum: Javelina Formation (lower part).
Derivation of names: The generic name is for Peter Gasson in recognition of his many studies of legume woods and his help with collections of Big Bend fossil wood, and the specific epithet is for the presence of a wood pattern suggesting Araliaceae.

Comments — Families that have species with vessels in multiples, tangential arrangement of vessels, simple perforation plates, alternate pits, fewer than 20 vessels per mm^2, and no storied structure occur in two of Cronquist's (1988) six subclasses: Rosidae (Araliaceae, Leguminosae) and Asteridae (Solanaceae and Compositae). It is most likely that this Big Bend wood belongs to the Rosidae as fossils referable to the Solanaceae and Compositae are of more recent origin (Taylor 1990). Some rays have cells that resemble sheath cells, a characteristic suggesting Araliaceae rather than Leguminosae.

This wood conforms to Page's (1981) Group XIA (perforations simple, intervessel pits alternate, axial parenchyma vasicentric).

'Baileyan Big Bend Wood, Type II' (Fig. 12)

Growth rings absent.

Diffuse-porous; vessels mostly solitary; solitary vessels tend to be angular in outline; mean tangential diameters 74 (17) – 83 (13) µm; 16–53 (means 22–30) per mm^2; scalariform perforations with fewer than 10 bars; scalariform intervessel pits.

Axial parenchyma rare, occasional apotracheal strands.

Rays: multiseriate rays narrow, 2–3 cells wide, heterocellular with body of multiseriate rays composed entirely of procumbent cells with 4 or more marginal rows of upright cells; uniseriate rays composed of upright cells; rays not storied; 7–14 per mm.

Fibres with distinctly bordered pits in radial walls, wall thickness medium to thick.

Samples: USNM 507061-a (GSS 2-2), USNM 507061-b (GSS 2-13), USNM 507061-c (GSS 2-16).
Stratum: Javelina Formation (lower part).

Comments — Families of extant dicotyledons that have species with the combination of solitary vessels, scalariform perforations, fibres with distinctly bordered pits, heterocellular rays that are not exclusively uniseriate or more than 10-seriate, and rare axial parenchyma belong to three of Cronquist's (1988) subclasses: Magnoliidae (Trimeniaceae, Monimiaceae, Atherospermataceae), Dilleniidae (Grubbiaceae, Epacridaceae, Ericaceae), Rosidae (Hydrangeaceae, Celastraceae).

Vessel-ray parenchyma pits, a valuable diagnostic feature, were not observed in this fossil. Its general characteristics that are primitive in the Baileyan sense characterize more than one fossil wood genus (e.g., *Cornoxylon, Cyrilloxylon, Hamamelidoxylon, Liquidambaroxylon, Symplocoxylon*). Thus, it is referred to by a common name to indicate its anatomical characteristics and occurrence.

This wood belongs to Page's (1979, 1980, 1981) Group III (pores mostly solitary, perforations scalariform, bars averaging fewer than 50), B1 (axial parenchyma mostly apotracheal, vessel pits scalariform).

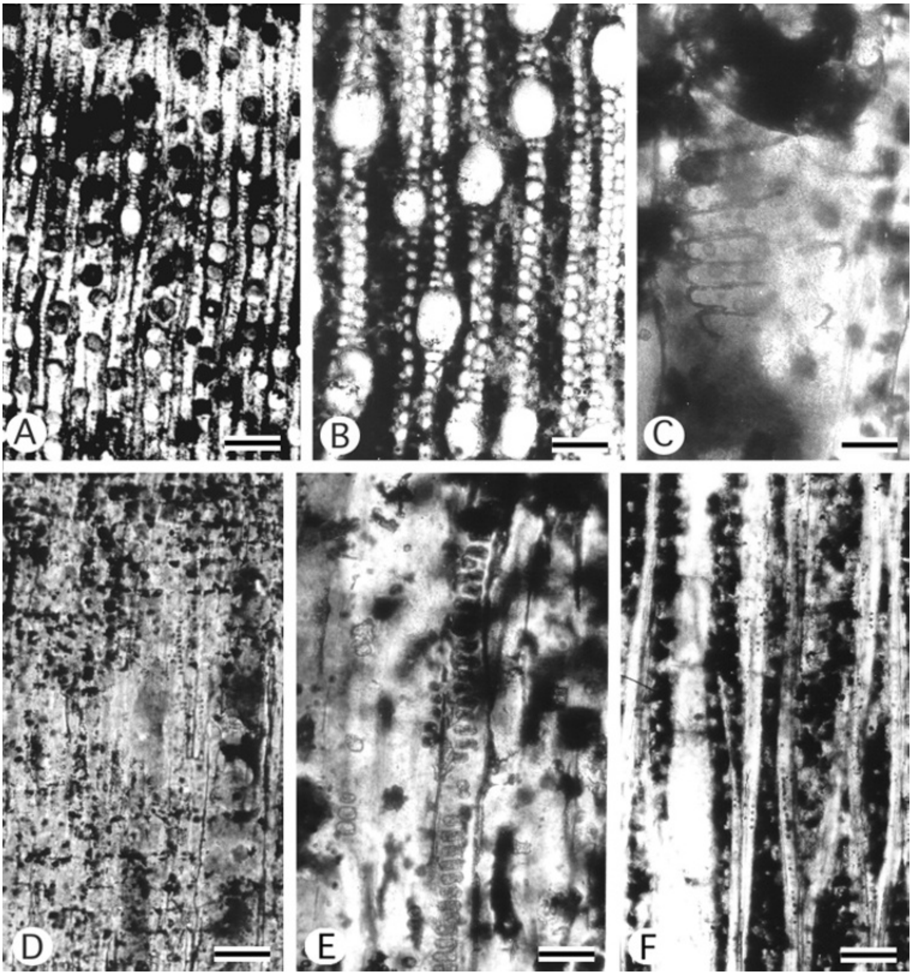

Fig. 12. 'Baileyan Big Bend Wood. Type II' (USNM 507061-c) — A: Diffuse-porous wood with solitary vessels. XS. – B: Solitary vessels tending to be angular in outline. XS. – C: Sca-lariform perforation plate. RLS. – D: Heterocellular rays, imperforate elements with distinctly bordered pits. RLS. – E: Scalariform intervessel pitting. RLS. – F: Heterocellular multiseriate rays (mostly 3-, rarely to 4-seriate) and imperforate elements with pits on tangential walls. TLS. — Scale bar = 250 μm for A, D; 100 μm for B, F; 50 μm for; 25 μm for C, E.

'The Javelina Vine' (Fig. 13)

Growth rings not observed.

Vessels solitary and mostly in radial multiples, with up to 10 vessels per multiple; mean tangential diameter 72 (21) μm, range 28–118 μm; 8–20 per mm^2; vessel element lengths not determinable; exclusively simple perforations probable; neither intervessel nor vessel-ray parenchyma pits observed.

Axial parenchyma apparently rare, scanty paratracheal.

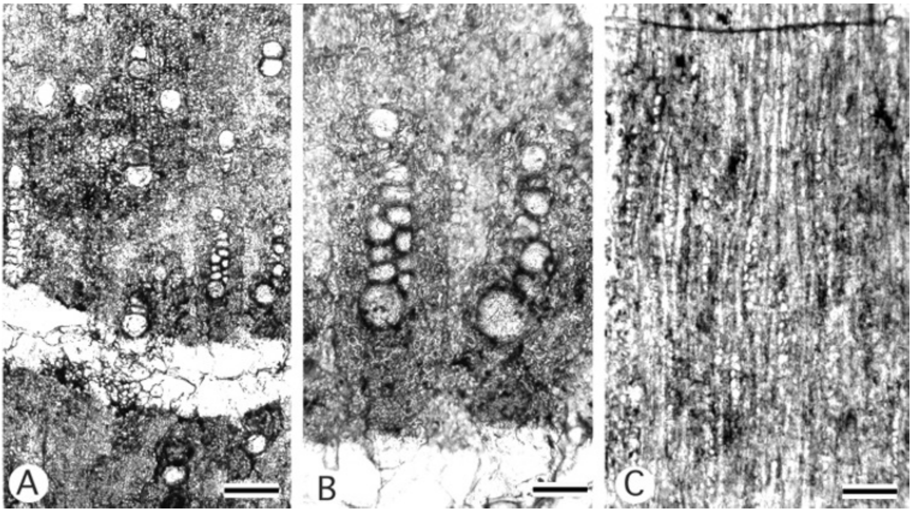

Fig. 13. 'The Javelina Vine' (USNM 507062) — A: Vessels solitary and in radial multiples. XS. – B: Pore multiples with tendency for two diameter classes of vessels. XS. – C: Heterocellular multiseriate rays, ray width usually 2–3-seriate. TLS. — Scale bar = 250 µm for A; 100 µm for B, C.

Rays: multiseriate rays 2–3 cells wide, heterocellular with body of multiseriate rays composed entirely of procumbent cells with 1–2 rows of square/upright cells; 373–506 µm high; not storied.

Fibres: pits not distinguishable; walls medium-thick.

Sample: USNM 507062 (DC 3w-SS).
Stratum: Javelina Formation (upper part).

Comments — Two distinct width classes of vessels and long radial multiples as observed in some regions of the sample is a syndrome that is usually associated with vines (Carlquist 1991). Vessel diameter values given above do not include the very narrow vessels in the longer radial multiples. This wood represents one of the earliest occurrences of two width classes of vessels. There is only one small sample of this wood type; its preservation is not good enough to allow determination of intervessel or vessel-ray parenchyma pits, important diagnostic features. Consequently, we chose not to assign a generic name to this wood, and are referring to it as 'The Javelina Vine' because its vessel characteristics suggest it was a vine.

DISCUSSION

Anatomy

As a group these woods agree with previous generalizations about Cretaceous dicotyledonous woods, namely that wood anatomical features considered primitive in the Baileyan sense are more common in the Cretaceous than in the Tertiary (Wheeler & Baas 1991, 1993). Eight of the 12 Big Bend dicot wood types have scalariform perforations, not simple; none have elaborate paratracheal parenchyma patterns. Suzuki et al. (1996) examined 41 dicot wood samples of Cenomanian–Maastrichtian age from Hokkaido (Japan) and Sakhalin (Russia); most of those woods also have scalariform perforation plates, scalariform intervessel pits, apotracheal parenchyma, and heterocellular rays.

One of the more striking features of the late Cretaceous Big Bend dicotyledonous woods is the abundance of apotracheal diffuse-in-aggregates parenchyma and/or ray parenchyma. Large amounts of parenchyma also characterize late Cretaceous (Maastrichtian) woods of southern Illinois (Wheeler et al. 1987). Some of the late Campanian–early Maastrichtian Big Bend woods with more than 50% parenchyma are from trunks 40–100 cm in diameter, a diameter certainly suggesting these were trees. Such large amounts of parenchyma invite speculation about the significance of this feature in Late Cretaceous trees.

Present-day tropical woods, as a group, have more parenchyma than temperate woods (Wheeler & Baas 1993). None of the Big Bend dicots have distinct growth rings, and so the high amounts of parenchyma would be consistent with an aseasonal tropical environment. Parenchyma is a storage tissue. CO_2 levels were higher in the Cretaceous atmosphere than at present (e.g., Cerling 1991). If the increased CO_2 levels resulted in an increase in photosynthate, this might be linked to the higher amounts of storage tissue volume.

In addition to photosynthate storage, it has been suggested, and for some extant trees demonstrated, that parenchyma is involved in water storage as well as photosynthate storage (Carlquist 1988; Holbrook 1995). Whether water storage would be correlated with indistinct growth rings by allowing continual growth during times of low water availability is unknown. If this were the case, it could reconcile the observed absence or indistinct character of growth rings in the Javelina Formation dicotyledonous woods with the sedimentological evidence suggesting arid conditions in their environments (Lehman 1989, 1990).

The large herbivorous dinosaurs of the Cretaceous likely fed on the foliage of these trees and may have routinely damaged or toppled them. Large amounts of stored photosynthate, presumably present in the large amount of parenchyma, may have been advantageous for replacing foliage and branches eaten by these herbivores. Large amounts of parenchyma might be effective in wound responses, and for enabling stump sprouting. Mattheck (1995) has pointed out that in addition to photosynthate storage, rays have a mechanical function. Larger or more abundant rays give greater strength to wood when pulled in the radial direction. It is possible that this would be advantageous for trees that had to survive aggressive browsing by large dinosaur herbivores. Apart from elephants, few modern herbivores can exert the physical pressure on trees that dinosaurs could.

Affinities

Most of the Big Bend Campanian and Maastrichtian woods are not assigned to an extant family or genus as their combination of characteristics occurs in more than one extant family, order, or subclass. *Bombacoxylon* is an exception as its characteristics are, to our knowledge, unique to the Malvales. The two size classes of ray cells in

Baasoxylon resemble tile cells, also suggesting Malvales. However, *Baasoxylon* has exclusively scalariform perforations and this characteristic does not occur in extant Malvales. One wood from the Maastrichtian of southern Illinois also resembles Malvales in every respect, except for scalariform perforations (Wheeler et al. 1987). Given the higher incidence of scalariform perforations in the Cretaceous relative to the Tertiary and present, it is possible that some early Malvales or allies of the Malvales may have been characterized by scalariform perforations. The Malvales have a fossil record extending back into the Cretaceous (Manchester 1999).

Agujoxylon has characteristics of the Olacaceae, a family previously reported from the Cretaceous. The in echelon rays of *Paraphyllanthoxylon anazasii* suggest that it is more likely to be allied with the Lauraceae than with the other families (Burseraceae, Anacardiaceae, Euphorbiaceae) that have wood anatomical patterns seen in *Paraphyllanthoxylon*. It is possible that *Pageoxylon* might represent the woody remains of the plants that produced the hamamelid-like or Betulaceae pollen reported from the lower shale member of the Aguja Formation (Baghai 1994).

Changes through time and with depositional environment

Well preserved dicot woods become more common and more often have large diameter axes when moving from the base (poorly drained soils near the shore) to the top (well-drained flood-plain environments many kilometres from the shoreline) of the Aguja Formation and into the Javelina. The wood types of the Aguja differ from those of the Javelina, paralleling the change from the *Kritosaurus-Chasmosaurus*-dominated fauna of the Aguja to the *Alamosaurus*-dominated fauna of the Javelina. The repeated spatial association of herbivorous dinosaur remains with specific angiosperm wood types suggests an ecological relationship (Fig. 14).

Aguja / Lower Shale Member — Two types of dicot woods, all represented by fragments, occur at this level: *Bombacoxylon* (likely Malvalean), and *Pageoxylon* of unknown affinities. Pollen recovered from the deposits where these woods occur is said to represent lowland, reducing, poorly drained coastal marsh and coastal swamps; 15–20% of the pollen and spores is said to represent wind-transported arborescent gymnosperms (*Parvisaccites*) and angiosperms (*Aercipites)* (Baghai 1994).

Aguja / Upper Shale Member / Lower Part — At this level two dicot wood types occur. One of the platanoid/icacinoid types represents at least a small tree, a growth form otherwise rare in these deposits, the other platanoid/icacinoid type and all samples of 'Baileyan Big Bend Wood, Type I' are slender axes. *Kritosaurus* and *Chasmosaurus* bone beds are common at this level. These two wood types were not recovered from the Lower Shale or upper portions of the Upper Shale. Samples taken from the horizons where the woods were recovered were almost barren of pollen and spores (Baghai 1994).

Aguja / Upper Shale Member / Central Part — At this interval, there occurs 'Baileyan Big Bend Wood, Type I', *Paraphyllanthoxylon anazasii*, and two wood types (*Agujoxylon* and *Metcalfeoxylon*) that also are present in the upper part of the Upper Shale Member. At one locality (CR2-6) 'Baileyan Big Bend Wood, Type I' axes are abundant and appear to be in growth position, resembling scrambling vines. This locality also has yielded hadrosaur (duckbill dinosaur) bones.

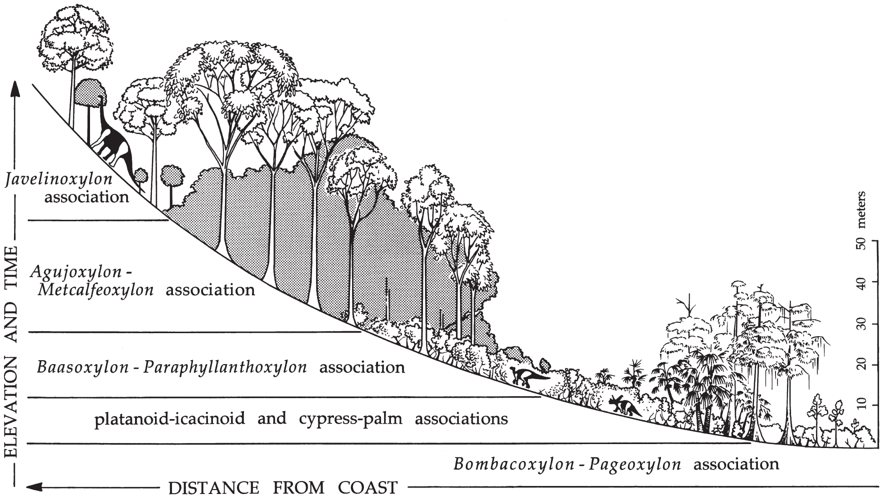

Fig. 14. Paleoenvironmental reconstruction showing a schematic transect from coastal environments (represented in the lower Aguja Formation) to inland environments (represented by the Javelina Formation) lying at progressively greater distance from the shoreline and at higher elevation. The woods suggest ecologically dominant trees in climax communities, associated browsing herbivorous dinosaurs are shown.

Aguja/Upper Shale Member/Uppermost Part — Stumps, logs, and large fragments of dicot woods are most common in this interval, with its well-drained soils at some distance from North America's interior Cretaceous sea. *Agujoxylon* and *Metcalfeoxylon* occur together at both the McKinney Springs and Grapevine Hills localities, and are the only two wood types found at these localities. The McKinney Springs stumps are still rooted in their original flood-plain soil, with strata suggesting a relatively low rate of sediment accumulation. The Grapevine Hill localities have fallen logs that likely were not transported and sediments here also suggest a relatively stable flood-plain environment.

Javelina Formation — Javelinoxylon multiporosum occurs throughout the Javelina Formation. The type and other described specimens each represent single trunks (Wheeler et al. 1994). A locality at Dagger Flats (lowermost Javelina) represents a major stream channel accumulation of transported trunks, i.e., a 'log jam'. Most of the logs at Dagger Flats are *Javelinoxylon* (sections of 15 well-preserved samples examined, and macroscopic examination of others), but at this locality *Baasoxylon* and *Gassonoxylon* also occur. 'Baileyan Big Bend Wood, Type II' was collected near the type sample of *Javelinoxylon* (lower Javelina). *Javelinoxylon* wood occurs at all levels where remains of the sauropod *Alamosaurus* occur. 'The Javelina Vine' is one of the oldest known examples of a diffuse-porous wood with two distinct diameter classes of vessels. This 'vine' is associated with aquatic channel-lake facies in the Javelina.

The anatomy of the Javelina Formation trees differs from the Aguja Formation trees in a fashion that may be consistent with the warmer, drier climate inferred for the Javelina. *Javelinoxylon* apparently was the most successful of the Javelina Formation trees; solitary vessels are rare in *Javelinoxylon*. Carlquist (1988) has suggested that vessel multiples become more common in more arid climates. However, growth rings are indistinct to absent in *Javelinoxylon* (Wheeler et al. 1994, and additional observations), and this absence does not suggest seasonal climates.

Cretaceous Trees

To our knowledge, the stumps at McKinney Springs represent the first report of anatomically preserved *in situ* Cretaceous dicot trees. Spacing between the 19 trees in 3 clusters averages 12–13 metres.

The stumps and logs of *Agujoxylon* that occur at Grapevine Hills are typically 40–60 cm in diameter; the *in-situ* stumps at McKinney Springs reached 111 cm in diameter. A linear relationship between diameter and height for logarithmically transformed data has been observed (McMahon 1973; Rich et al. 1986). Thus, it is possible to crudely estimate the height of these trees. However, the high proportion of parenchyma in these woods must surely affect their physical/mechanical properties, so it is questionable whether the same relationship between diameter and height would apply. Rich et al.'s study was based on mixed dicotyledonous trees in tropical wet forest of Costa Rica, and would be more applicable to the Big Bend trees than McMahon's data for record-sized North American trees. The heights of the Grapevine Hills trees are estimated to have been approximately 40 metres (based on a 60 cm diameter); the heights of the *in-situ* trees at McKinney Springs are estimated to have reached 50 metres (based on 111 cm diameter). *Javelinoxylon* trees (Maastrichtian age) which reached 70 cm diameter are estimated to also be over 40 metres high.

The sizes of the Big Bend late Campanian–Maastrichtian trees are inconsistent with the suggestion that most dicot trees were small and easily toppled (Dodson 1993). Also, logs and stumps occur in sediments representing well-developed, well-drained soils. This occurrence suggests that the Late Cretaceous vegetation in the southwestern interior of the United States would not fit generalizations for the more northerly western interior, which is characterized as having conifer- and fern-dominated vegetation in stable and low-nutrient environments (even though angiosperm pollen and leaves are common) (Wing & Boucher 1998). The Big Bend fossil dicot woods suggest that angiosperms had more than a subordinate role in Late Cretaceous vegetation at lower latitudes. Indeed, they appear to have been the dominant trees of the Normapolles province of the southwestern interior of the U.S.

ACKNOWLEDGMENTS

We thank Mark Ambrose, Tom Bevier, Fred Carter and C.A. LaPasha for help with specimen preparation, photographic processing, and obtaining some of the quantitative data, L. van den Oever for making available slides of the Olacaceae, staff of the wood collections of the Nationaal Herbarium Nederland/Leiden University branch, the Jodrell Laboratory of Kew, Royal Botanic Gardens, and the Bailey-Wetmore Laboratory of Plant Anatomy and Morphology of Harvard University for providing access to their wood collections, Susan Tomlinson and Bill Straight for help with collections, Peter Gasson for help with collections and comments on the RM28 and CR2-6c samples, and the staff of Big Bend National Park for their continued interest in paleobotanical work in the park. This work was supported by funds from the Big Bend Natural History Society.

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