FOSSIL WOODS FROM THE EL CIEN FORMATION
IN BAJA CALIFORNIA SUR: LEGUMINOSAE

by
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Summary
Three types of fossil woods with similarities to the Leguminosae are described, *Mimosoxylon tenax* (Felix) Müller-Stoll & Mädel, *Bajacaliforniaxylon cienense* Cevallos-Ferriz & Barajas-Morales, gen. et sp. nov., and *Copaiuroxylon matanzensis* Cevallos-Ferriz & Barajas-Morales, sp. nov. These woods are from the El Cien Formation in Baja California Sur, Mexico, which is dated as Zemorian-Saucesian, i.e., late Oligocene-early Miocene. Although two of the names of the fossil woods suggest affinity with a particular extant taxon, differences in some quantitative and qualitative features preclude their identification with a single extant taxon. The similarity among wood of some groups of extant Leguminosae and limited knowledge of character variability in woods of this family explains this taxonomic uncertainty. These fossil woods from Baja California underscore the need for an extensive systematic study of the wood anatomy of Leguminosae, add to the poorly known plant history of the Peninsula, suggest a tropical South American influence in the fossil flora of Baja California, and indicate that the climate during the Zemorian-Saucesian was different from the xeric conditions that prevail today in the area.

Key words: Wood anatomy, Leguminosae, fossil wood, Oligocene, Miocene, Baja California Sur, *Mimosoxylon*, *Bajacaliforniaxylon*, *Copaiuroxylon*.

Introduction
Over 100 Tertiary Leguminosae woods have been reported (e.g., Müller-Stoll & Mädel 1967; Awasthi 1992; Gros 1991, 1992; Wheeler & Baas 1991, 1992) from around the world. The confidence with which Leguminosae fossil wood can be identified to generic or specific levels contrasts with the confidence with which fossil reproductive organs or leaves of this family are compared to extant plants. While differentiation of the three sub-families (Caesalpinioideae, Papilionoideae, and Mimosoideae) in Leguminosae occurred by the Eocene (e.g., Herendeen & Dilcher 1991a, 1991b; Herendeen et al. 1992), the assignment of wood remains to a particular subfamily often is difficult. Even Pliocene or Pleistocene woods with affinities to the Leguminosae usually cannot be assigned to a single extant genus (e.g., Müller-Stoll & Mädel 1967; Gros 1991, 1992).

The first putative Leguminosae wood collected from the Tertiary of Mexico was *Haurea americana* Unger from sediments near Papantla, Veracruz (Unger 1845, 1857). However, its preservation is poor and its affinities are questionable, so it is considered a nomen nudum (Müller-Stoll & Mädel 1967). Later, *Mimosoxylon tenax* (Felix) Müller-Stoll & Mädel from Tertiary sediments near Tlalocula, Oaxaca, was described (Felix & Nathorst 1899; Müller-Stoll & Mädel 1967; Gros 1991, 1992; Wheeler & Baas 1991, 1992). Reproductive organs of fossil Leguminosae collected from Mexico include six different fruits from Tepexi de Rodríguez, Puebla, similar to *Lysiloma, Mimosa, Prosopis*, and *Sophora* (Magallón-Puebla & Cevallos-Ferriz 1993a, b) among others, and Oligocene-Miocene leaflets of *Acacia* included in amber have been reported from Simojovel, Chiapas (Miranda 1963).

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In the present study, three types of fossil legume woods, *Bajacalifornioxylon cienense* Cevallos-Ferriz & Barajas-Morales gen. et sp. nov., and *Copaijeroxylon matanzensis* Cevallos-Ferriz & Barajas-Morales sp. nov., and *Mimosoxylon tenax* (Felix) Müller-Stoll & Mädel, are described and compared to extant and fossil woods assigned to the Leguminosae.

**Materials and Methods**

The El Cien Formation outcrops around and to the east of the town of El Cien, Baja California Sur, and consists of alternating shales, sandstones, and limestones with tuffaceous and diatomaceous intercalations (Fig. 1). At least 15 different wood types are known from the El Cien Formation in Baja California Sur, Mexico. Of the over 50 wood samples collected so far, five have Leguminosae affinity. Several localities containing fossil wood are known. Woods reported here come from near ‘Rancho Matanzas’ and ‘Cañada El Canelo’ localities (Fig. 1). The former is about 5 km northeast from the town of El Cien, Baja California Sur, while the latter is approximately 3.5 km south (Fig. 1). The El Cien Formation has been dated as Zemorrian-Saucesian or late Oligocene—early Miocene (27–17 million years before present) based on paleontological, stratigraphical and radiometric data (Applegate 1985).

These fossil woods are preserved as silica permineralisations. All wood samples were cut into small slabs and transverse, tangential, and radial sections prepared using the standard thin section technique. Cell dimensions given in the descriptions are based on 25 measurements for each character, cell measurements include cell walls, and terminology follows the IAWA feature list (IAWA Committee 1989). All fossil specimens are
housed in the Museo de Paleontología of the Instituto de Geología, UNAM (IGU/NAM). Holotype numbers refer to slides produced from a single sample.

Extant Leguminosae woods (see Appendix) were compared anatomically with the fossil material. Sections 15–25 μm thick were cut on a sliding microtome and stained with safranin-fast green. Slides are deposited in the Instituto Nacional de Investigaciones Forestales y Agropecuarias (INIFAP), Mexico, and in the National Xilote in the Instituto de Biología, UNAM. For identification of the fossil woods, besides the direct comparison to woods of extant plants, the Guess program, OPCN database and a fossil angiosperm wood database (Wheeler et al. 1986; LaPasha & Wheeler 1987; Wheeler & Baas 1991) were used.

Systematic description

Class: Magnoliopsida
Order: Fabales
Family: LEGUMINOSAE
Subfamily: MIMOSOIDEAE

Genus: Mimosoxyylon Müller-Stoll & Mädel
Species: Mimosoxyylon tenax (Felix) Müller-Stoll & Mädel — Figs. 2–11


Material: Two small samples, 4 cm in diameter and 9 cm long are known.

Distinct growth rings marked by marginal parenchyma (Fig. 2). Diffuse-porous, on average 8 vessels/mm² (range 4–12). Vessels mainly solitary (77%) and in radial multiples of 2 to 4 (23%; Fig. 2), circular in outline, mean tangential diameter 152 μm (range 88–198 μm), mean radial diameter 138 μm (range 120–230 μm), mean vessel element length 213 μm (range 18–305 μm). End walls of vessel elements oblique (30°), simple perforation plates (Fig. 4); intervascular pits oval, alternate, minute (2–3 μm; Figs. 4, 5), and vestured. Thin-walled tyloses occasional in vessel elements. Non-septate thick-walled fibres, oval in transverse section, mean tangential and radial diameter 15 μm and 12 μm (range 6–18 μm and 7–15 μm) respectively.

Paratracheal parenchyma vasicentric to aliform and confluent, and in thin marginal bands (Figs. 2, 3), parenchyma cells with a mean tangential diameter of 17 μm (range 10–20 μm), mean radial diameter of 11 μm (range 6–15 μm), mean cell length of 60 μm (range 26–125 μm). Rays homocellular (Figs. 6–8), uniseriate rays short, up to 21 cells tall (Fig. 7), multiseriate rays 2–4-seriate (Figs. 6, 7), with a mean height of 403 μm (range 246–598 μm), all rays composed of procumbent cells (Fig. 8), 7 (range 5–10) rays per millimetre. Vessel to ray pits similar to intervacular pits (Figs. 10, 11). Chains up to 19 cells long of thin-walled parenchyma cells each containing a rhomboidal crystal, scattered among other parenchyma cells (Fig. 9). Wood without storied elements.

The second specimen is quantitatively and qualitatively very similar (Table 1). Their differences may reflect variation within a plant or between different plants.


Diagnosis: Diffuse-porous wood, growth rings indistinct; vessels mainly solitary, in radial multiples and clusters, intervacular pits medium, alternate and vestured, oblique simple perforation plates; non-septate libriform fibres; paratracheal parenchyma vasicentric, apotracheal parenchyma diffuse; homocellular rays 1–4-seriate, vessel element to ray parenchyma pits similar to intervacular pits; crystals in chambered axial parenchyma cells. Wood without storied elements.

Bajacalifornioxylon cienense Cevallos-Ferriz & Barajas-Morales, spec. nov. — Figs. 12–18

Holotype: IGM-LPB 1210–1213, IGM-LPB 1238.

Material: A small sample, 5 cm in diameter and 12 cm long.

Etymology: The generic name is after the Baja California Peninsula where the sample was found. The specific epithet cienense is after the nearby town of El Cien.
Figs. 9–11. *Mimosoxylon tenax*. – 9: Tangential section showing axial parenchyma cells where crystals were contained. IGM-LPB 971, × 400. – 10: Radial section showing vessel-ray pits. IGM-LPB 971, × 500. – 11: Radial section showing vessel-ray pits. IGM-LPB 979, × 350.

Diagnosis: Indistinct growth rings, diffuse-porous, on average 6 vessels/mm² (range 4–8). Vessels mainly (78%) solitary and in radial multiples of 2 (19%), occasionally in radial multiples of 3 or more (up to 7; Figs. 12, 13), oval in outline, mean tangential diameter 141 μm (range 93–210 μm), mean radial diameter 99 μm (range 40–190 μm), average vessel element length 320 μm (range 210–450 μm). End walls of vessel elements oblique (40º), with simple perforation plates (Fig. 16); intervacular pits oval, alternate, medium (4–7 μm), and vestured (Fig. 18). Fibres thick-walled (Fig. 13), oval in transverse section, non-septate, mean tangential and radial diameter 10 μm and 7 μm (range 9–12 μm and 6–9 μm), respectively. Up to four cells thick vasicentric parenchyma (Figs. 12, 13), some diffuse apotracheal parenchyma; parenchyma cells mean tangential diameter 12 μm (range 7–13 μm), mean radial diameter 6 μm (range 3–7.5 μm), mean cell length 78 μm (range 40–110 μm). Rays homocellular (Figs. 14, 17), uniseriate rays common, short, up to 12 cells tall; multiseriate rays 2–4-seriate, with a mean height of 383 μm (range 250–730 μm; Fig. 14) all rays composed of procumbent cells (Fig. 17), 10 (range 9–12) rays per millimetre. Vessel to ray parenchyma pits similar to intervacular pits. Chains up to 14 cells long of thin-walled parenchyma cells containing a rhomboidal crystal each scattered among fibres (Fig. 15).

Subfamily: CAESALPINIOIDEAE

Genus: *Copaieroxylon* Müller-Stoll & Mädel 1967

Species: *Copaieroxylon matanzensis* Cevallos-Ferriz & Barajas-Morales, spec. nov. — Figs. 19–29


Figs. 2–8. *Mimosoxylon tenax*. – 2: Transverse section showing vessel and parenchyma distribution. IGM-LPB 973, × 57. – 3: Transverse section showing detail of vasicentric parenchyma and thin-walled fibres. IGM-LPB 973, × 138. – 4: Radial section showing detail of vasicentric parenchyma and thin-walled fibres. IGM-LPB 973, × 138. – 5: Radial section showing alternate intervacular pits. IGM-LPB 981, × 885. – 6: Tangential section with uniseriate and multiseriate rays, vasicentric parenchyma, and vessel elements with alternate intervacular pits. IGM-LPB 974, × 138. – 7: Tangential section showing uniseriate and multiseriate rays. IGM-LPB 974, × 690. – 8: Radial section showing homocellular rays. IGM-LPB 971, × 126.
Material: Two small wood samples known, 18 cm long by 5 cm in diameter and 10 cm long by 4 cm in diameter, respectively, with the same anatomical pattern.

Etymology: The specific epithet *matanzensis* is after the nearby ranch Rancho Matanzas.

Diagnosis: Growth rings and axial parenchyma visible to the naked eye, limit between one growing season and the next one is marked by a band, 1–6 cells wide, of marginal parenchyma (Fig. 19). Around the axial canals the parenchyma bands are up to 10 cells wide (Fig. 19). Diffuse-porous, on average 5 vessels/mm² (range 2–6; Figs. 19, 20). Vessels solitary (84%; Fig. 19) accompanied by radial multiples of two (11%), and three (3%), or clusters (2%), almost circular in outline, mean tangential diameter 104 μm (range 87–128 μm), mean radial diameter 128 μm (range 70–150 μm); average vessel element length 291 μm (range 178–321 μm). End walls of vessel elements oblique (25°), simple perforation plates (Fig. 22); intervacular pits oval, small (5–7 μm), alternate and vented (Fig. 23). Non-septate, thin-walled fibres (Figs. 19, 20); many-sided in transverse section, mean tangential diameter 16 μm (range 5–20 μm), mean radial diameter 19 μm (range 13–25 μm), small simple pits in the radial walls (Figs. 27–29). Paratracheal parenchyma aliform to confluent and marginal, and apotracheal parenchyma diffuse (Figs. 19, 20). Aliform parenchyma winged, individual parenchyma cells 18 × 23 × 98 μm. Uniseriate rays common, up to 12 cells tall (Fig. 21), heterocellular rays (Figs. 25, 26) composed of procumbent cells in their main body and one row of upright cells in the margins. Multiseriate rays 2- or 3-seriate (Fig. 21), with a mean height of 528 μm (range 325–978 μm), heterocellular, composed of procumbent cells in their main body with up to 3 marginal rows of upright cells (Fig. 26), 7 (range 5–9) rays per millimetre. Vessel to ray parenchyma pits similar to intervacular pits (Figs. 24, 28). Chains up to 10 cells long of thin-walled parenchyma cells containing a rhomboidal crystal scattered among fibres (Fig. 29). Wood without storiad elements.

Discussion

Within the samples, there is little variation in the amount and type of axial parenchyma, ray structure, and dimensions and frequency of tracheary elements, all of which suggest mature wood structure (Carlquist 1975, 1988). However, it is not possible to say if the samples are trunk or branch wood, although their small diameter suggests that they are branches.

An important character in determining affinities of the fossil material is presence of vented pits. Although it is difficult to recognise vented pits in permineralised wood, intervacular pit apertures of nine undescribed woods from the same localities from which these Leguminosae woods were collected have smooth pit apertures in contrast with the tufted or verrucose pit apertures in the woods reported here. The presence of vented pits eliminates many families (e.g., Rhamnaceae, Rutaceae) from further comparisons. However, there were a few taxa in other families with vented pits (e.g., Vochysiaceae and Dipterocarpaceae) with anatomical structure similar to the Baja California Sur material.

The absence of marginal parenchyma distinguished *Vochysia* and *Qualea* (Vochysiaceae) from *Copaferoxylon matanzensis* (Metcalfe & Chalk 1950). *Shorea* (Dipterocarpaceae) is also characterized by the presence of vented pits but is readily distinguishable from *Bajacalifornioxylon* by the presence of much larger rays and fibres, as well as the absence of ray parenchyma.

Figs. 12–18. *Bajacalifornioxylon cienense*. – 12: Transverse section showing vessel and parenchyma distribution. IGM-LPB 1238, × 60. – 13: Transverse section showing detail of parenchyma and thin-walled fibres. IGM-LPB 1211, × 85. – 14: Tangential section with multiseriate rays, and vessel elements with simple perforation plates. IGM-LPB 1212, × 80. – 15: Tangential section with multiseriate rays, and crystals. IGM-LPB 1212, × 210. – 16: Tangential section showing vessel elements with simple perforation plates. IGM-LPB 1213, × 228. – 17: Radial section with multiseriate homocellular ray. IGM-LPB 1210, × 92. – 18: Tangential section showing detail of alternate pits. IGM-LPB 1213, × 428.
ceae) is also comparable to C. matanzensis and Bajacalifornioxylon cienense, but it has enlarged vessel element to ray parenchyma pits, while in the Mexican woods these pits are more or less the same size (Awasthi 1975 [1977]). The absence of apotracheal parenchyma in Qualea contrasts with the presence of diffuse parenchyma in Mimosoxylon tenax (Metcalfe & Chalk 1950).

Members of the three Leguminosae subfamilies (Caesalpinioideae, Mimosoideae, Papilionoideae) are comparable to the wood structure of the El Cien Formation plants (Metcalfe & Chalk 1950; Müller-Stoll & Mädel 1967; Baretta-Kuipers 1981; Wheeler & Baas 1992). However, each wood from Baja California Sur has a set of characters that relates them to a particular small number of Leguminosae taxa.

Figs. 19–25. Copaiferoxylon matanzensis. – 19: Transverse section showing vessel, axial canals and parenchyma distribution. IGM-LPB 179, x 50. – 20: Transverse section showing detail of aliform parenchyma, axial canals, and thin-walled fibres. IGM-LPB 181, x 110. – 21: Tangential section with uni- and multiseriate rays, and vessel with alternate intervacular pits. IGM-LPB 185, x 55. – 22: Radial section showing vessel element with simple perforation plate, alternate intervacular pits, and parenchyma cells with vessel element-parenchyma pits. IGM-LPB 191, x 180. – 23: Radial section showing detail of intervacular pits. IGM-LPB 191, x 1150. – 24: Radial section showing detail of vessel-ray pits. IGM-LPB 190, x 430. – 25: Radial section showing general view of heterocellular rays. IGM-LPB 186, x 90.
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<tr>
<th>Vessels per sq.mm</th>
<th>Vessel grouping</th>
<th>Mean vessel element length in μm</th>
<th>Mean tangential diameter of vessels in μm</th>
<th>Intervascular pit size in μm</th>
<th>Axial parenchyma arrangement</th>
<th>Rays per linear mm</th>
<th>Ray width in cell number</th>
<th>Mean ray height in μm</th>
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<td>IGM-LPB 148-177, 1202, 1203 (Baja California Sur)</td>
<td>189</td>
<td>160</td>
<td>4-5</td>
<td>vasicentric, confluent</td>
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<td>up to 4</td>
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<td>IGM-LPB 970-981 (Baja California Sur)</td>
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<td>up to 4</td>
<td>403</td>
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<td>Vessels per sq.mm</td>
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Table 1. Comparison of Mimoxoylex tenax from Baja California Sur and Oaxaca with extant Mimosa arenosa, Chlorophora and Haematoxylon.
Mimosoxylon

Mimosoxylon tenax Müller-Stoll & Mädel compares positively to some species of Piptadenia, Leucaena (Mimosoideae) and Caesalpinia (Caesalpinioidae; Wheeler et al. 1986; LaPasha & Wheeler 1987). The main difference among these taxa is the size of the intervascular pits, which are smaller in the woods of Baja California Sur. There is, however, a very close similarity of the fossil to Mimoso arenosa (Willd.) Poir., Chlorophora and Haematoxylon (Table 1; Chehaibar & Grether 1990). Although differences from Chlorophora and Haematoxylon are quantitative, it is clear from Table 1 that M. tenax is most similar to M. arenosa. Among extant Leguminosae, the absence of storied elements and the presence of homocellular rays (Baretta-Kuipers 1981) in Mimosoxylon tenax support a relationship to Mimosaideae. Within this subfamily, Mimosa appears most similar to the fossil plants (Chehaibar & Grether 1990). In the absence of other fossil organs supporting this relationship it would be premature to assign this fossil wood to M. arenosa; however, a close relationship to Mimosaideae, especially to Mimosa is well supported.

The El Cien Formation Mimosoxylon is quantitatively and qualitatively very similar to M. tenax supporting its identification as a member of this taxon, previously described from Tertiary sediments near Tlacolula, Oaxaca, Mexico (Felix & Nathorst 1899; Müller-Stoll & Mädel 1967; Table 1). The genus Mimosoxylon includes 9 species (Gros 1992). The main difference between Mimosoxylon tenax and other Mimosoxylon species is the absence in the Baja California Sur wood of a tendency to storied axial parenchyma (Müller-Stoll & Mädel 1967). However, in reviewing the descriptions of the species belonging to Mimosoxylon, this tendency is not always present, and Baretta-Kuipers (1981) suggests that storied wood is not typical of Mimosaideae. Large intervascular pits in M. ducis-aprutii (Chiarugi) Müller-Stoll & Mädel, heterogeneous rays in M. piptadenoides (Da Silva Curvello) Müller-Stoll & Mädel, 1- or 2-seriate rays in M. acacioides Kramer and M. krameri Lemohigne, well developed aliform parenchyma and numerous rays per millimetre in M. calpocalycoides Lemohigne, high rays in M. grandiporum Pons, very small pores and 2-seriate rays in M. mbaakouense Dupéron-Laudoueneix, and distinct growth rings, septate fibres and ray width in M. santamariensis Lutz distinguish them from the plants of Baja California Sur (Kramer 1974; Lemohigne 1978; Pons 1983; Lutz 1987).

Bajacalifornioxylon

Although woods of Melanoxylon brauna (Caesalpinioidae) and Myroxylon balsamum (Pipilionoideae) have some similarity with Bajacalifornioxylon ciense, the presence of storied elements (rays and axial parenchyma) in these extant species contrasts with the unstoried wood structure of the fossil plant (Wheeler et al. 1986; LaPasha & Wheeler 1987). The wood of Prioria copafera (Caesalpinioidae) is also similar to that of B. ciense, however, the presence of heterocellular rays and axial canals in the former contrast with the homocellular rays and the absence of axial canals in the wood of Baja California Sur. Among the wood of extant mimosoid plants that compare closely to B. ciense are: Ebenopsis flexicaulis, Havardia sp., Klugiodendron laetum, Marxoxylon sp., Pithecellubium sp. (Wheeler et al. 1986; LaPasha & Wheeler 1987), and Acacia melanoxyon (De la Paz Pérez-Olvera et al. 1980; Cevallos-Ferriz & Carmona-Valdivinos 1981). There is, however, a tendency in the wood of the first five plants to have either uniseriate rays and/or aliform parenchyma. In contrast, B. ciense has up to 4-seriate rays and one cell thick vasicentric parenchyma. Acacia melanoxyon is most similar to B. ciense, but the wood of the former has more abundant parenchyma and smaller vessel elements than the wood of El Cien Formation (De la Paz Pérez-Olvera et al. 1980; Cevallos-Ferriz & Carmona-Valdivinos 1981).

Some taxa of Leguminosae fossil woods are comparable to B. ciense. However, the presence of well developed marginal parenchyma (e.g., Albizia vantagensis Prakash & Barghoorn, Dichrostachyoxylon zirkelli (Felix) Müller-Stoll & Mädel, Paraalbizioxylon bavaricum (Selmeier) Gros, Isoberlini­oxylon congoense Lakhanpal & Prakash, and
Table 2. Leguminosae with axial canals. Data from Metcalfe & Chalk (1950), Baretta-Kuipers (1981), and Gasson (1994).

<table>
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<tr>
<th>Genus</th>
<th>Canals diffuse (D) / tangential (T)</th>
<th>Canals normal (N) or traumatic (T)</th>
<th>Parenchyma paratracheal (S) or aliform (A)</th>
<th>Rays uniseriate (U) and/or storied (S)</th>
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*Tetrapleuroxylon limagnense* Privé, as well as septate fibres, heterogeneous rays, and confluent parenchyma, contrasts with *B. cienense*.

*Acacioxylon* is the form-genus proposed by Schenk (1883) to include fossil woods similar to the secondary xylem of *Acacia*. However, reassignment of most fossil species in this taxon to *Euacacioxylon* and *Paracacioxylon* by Müller-Stoll & Mädel (1967) and its recent use to name some fossil woods from Chile (Nishida 1981, 1984) has created nomenclatural problems (Gros 1992). Both *Euacacioxylon* and *Paracacioxylon* have confluent and vasicentric parenchyma with a tendency to become aliform, their rays are 1–10-seriate, and the latter has septate fibres (Müller-Stoll & Mädel 1967). In contrast, *B. cienense* has only vasicentric parenchyma, 1–3 (–4)-seriate rays, and no septate fibres. *Baja­californiaoxylon cienense*, although similar to extant *Acacia*, differs from *Acacioxylon* and an Eocene *Acacia* in axial parenchyma distribution (Kräusel 1939; Navale 1962 [1963]; Gregory 1970; Gros 1992; Nishida 1984). While *Acacioxylon* and the Eocene *Acacia* have paratracheal (vasicentric, aliform and confluent) and uniseriate apotracheal bands, *B. cienense* typically has up to 4 cells thick vasicentric and some diffuse apotracheal parenchyma. *Metacacioxylon* was introduced by Gros (1981, 1984, 1988) to include woods similar to *Acacia* but with rays being (1–)7–12 (–18)-seriate. In contrast, rays in *B. cienense* are 1–3(–4)-seriate. While similarity of the wood of *Baja­californiaoxylon cienense* to that of extant *Acacia* is close, recognition of a new taxon is supported by the quantitative and qualitative differences found among wood form-genera comparable to the wood of *Acacia* and by the similarities shared by the El Cien wood and *Acacia melano­xylon*.

*Copaferoxylon*

The presence of axial canals in Leguminosae is a rare character, restricted to Caesal­pinioidae (Metcalfe & Chalk 1950; Baretta-Kuipers 1981; Gasson 1994; Table 2). These can be normal canals arranged in tangential bands, as in *Copaferoxylon matanzensis*, or scattered, or traumatic canals in tangential bands (Metcalfe & Chalk 1950; Gasson 1994). Five genera in Caesalpinioidae have normal axial canals in tangential bands, *Bathiaea, Copafera, Eperua, Sindora*, and *Sindoropsis* (Baretta-Kuipers 1981; Gasson 1994; Table 2). All of these genera, except *Detarium*, are characterised by having mostly scanty paratracheal parenchyma, although sometimes it tends to be aliform (Metcalfe & Chalk 1950;
Baretta-Kuipers (1981), in contrast with the mostly aliform and marginal parenchyma of the new fossil wood. Detarioxylon lacks uniseriate rays, but has vasicentric, mostly aliform, and also clearly demarcated lines of parenchyma on growth ring boundaries, while Pseudosindora further differs from the fossil plant in having uniseriate rays (Baretta-Kuipers 1981). Epierus is also distinct in having banded parenchyma (Metcalfe & Chalk 1950).

Distinction between the other genera, Bathiæa, Copaifera, Sindora, and Sindoras, with qualitative characters is difficult; however, there is a closer qualitative similarity of the fossil plant to Copaifera (Metcalfe & Chalk 1950; Moens 1955; Wheeler et al. 1986; LaPasta & Wheeler 1987).

Among the fossil Leguminosae genera known to the authors, eight species have axial canals and aliform and marginal parenchyma: Acacia gregorii Gregory, Caesalpinoxylon moragjonesiae Crawley, Copaiferoxylon copaiferoides Fessler Vrolant, C. miguirtinium (Chiarugi) Müller-Stoll & Mädel, Detarioxylon aegyphacum (Unger) Louvet, Erythrophloeoxylon scholleri (Boureau) Müller-Stoll & Mädel, Hopeoxylon indicum Navale, and Kingiodendron prebinnatum Awasthi & Prakash. However, axial canals in Acacia gregorii, Caesalpinoxylon moragjonesiae, and Erythrophloeoxylon scholleri are of the traumatic type (Gregory 1971 [1973]), while in Copaiferoxylon matanzensis they are normal. Kingiodendron prebinnatum has normal axial canals, but their diffuse arrangement contrasts with the banded pattern of C. matanzensis (Awasthi & Prakash 1986 [1987]). Detarioxylon aegyphacum differs in having broader rays (4–10-seriate vs 1–3-seriate), some enlarged vessel element to ray parenchyma pits (vs similar pits), and more vasicentric parenchyma than C. matanzensis. Hopeoxylon indicum also has some enlarged vessel element to ray parenchyma pits (vs similar pits), and more vasicentric parenchyma, but differs further from C. matanzensis in having more vessels per square millimetre (Awasthi 1975 [1977]).

Copaiferoxylon is known from two species, C. miguirtinium from the Miocene of Somalia (Müller-Stoll & Mädel 1967) and C. copaiferoides from the Oligocene of Tunisia (Fessler-Vrolant 1977). They are similar to C. matanzensis not only in the presence and distribution of axial canals, but also in the type of axial parenchyma, and vessel element distribution and grouping. There are, however, minor differences among them. Vasicentric parenchyma is more common in C. miguirtinium and C. copaiferoides (Fessler-Vrolant 1977); in contrast, aliform parenchyma is more common in C. matanzensis. Rays tend to be slightly wider in C. miguirtinium (1–5-seriate) than in the new species (1–3-seriate); ray parenchyma cells in the former are erect while in the latter these are mainly procumbent; rays are homocellular in the Somalian material and heterocellular in the Baja California Sur specimens (Müller-Stoll & Mädel 1967). Copaiferoxylon copaiferoides is also distinct from C. matanzensis by having radial canals and crystals in parenchyma cells (Fessler-Vrolant 1977). Similarity between these woods is close enough as to include the new wood in the same genus. However, differences in age and locality, as well as the qualitative and quantitative differences between the wood of the three plants, support the designation of a new species, C. matanzensis Cevallos-Ferriz & Barajas-Morales.

Subfamily affinities
Müller-Stoll and Mädel (1967) reviewed the problems of classifying fossil woods with affinity to the Leguminosae. Our study supports their idea of classifying Leguminosae fossil wood using taxa that compare to one or more extant taxa, sometimes even from different subfamilies. Reviews such as Gros’s (1991, 1992) for Mimosoideae are important in evaluating the status of fossil Leguminosae woods. However, new and more complete wood descriptions of extant plants will help in reviewing the limits of fossil taxa. Therefore, we suggest that there be more systematic studies of extant woods of Leguminosae.

Comparison of the generic diagnoses of Müller-Stoll and Mädel (1967) for fossil Leguminosae woods and the systematic review of Mimosoideae wood by Gros (1991, 1992) show little difference between some taxa. Both reviews suggest that the amount and distribution of axial parenchyma, the
relative size of vessel element to ray parenchyma pits, presence of septate fibres and storied elements are important characters in delimiting fossil Leguminosae genera. Although these characters may in fact be useful to identify fossil Leguminosae woods, caution is needed. The reviews of the family by Cozzo (1950), Reinders-Gouwentak (1955) and Baretta-Kuipers (1981) point out important differences between Mimosoideae and the combined Caesalpinioideae and Papilionoideae, suggesting that additional characters, like number of cells in a parenchyma strand and ray structure, may also be useful in determining relationships among fossil and extant woods of Leguminosae.

**Biogeography**

Extant plants with wood similar to *Mimosoxylon* (*Acacia, Mimosa, Hardwicchia, Bussea and Sesbania*) are mainly restricted to tropical South America, although some taxa are well represented in Mexico (e.g., *Acosmiun, Acacia*, and *Mimosa*), while others are found in India (e.g., *Hardwickia*) or tropical Africa (e.g., *Bussea*; Polhill & Raven 1981; Gros 1992). Presence of South American plants in the El Cien Formation is further suggested by the presence of *Copaiferoxylon* in Baja California Sur. Extant taxa with wood similar to *Copaiferoxylon* are restricted to tropical Africa, tropical South America and Asia; and *Copaifera*, which is most similar to *Copaiferoxylon matanzensis* grows in tropical South America and Africa (Polhill & Raven 1981). Although *Bajacaliforniouxylon* is similar to *Acacia*, a pantropical genus, it could be related to *Acaciella*, a group represented in Mexico, the Caribbean and South America, and whose wood anatomy remains to be studied. In this regard it is significant that the Oligocene flower from Simojovel, Chiapas, may be *Acaciella* rather than *Acacia* (Miranda 1963; Sousa & Delgado 1993).

These Leguminosae woods support the idea of an influence of the South American flora in the El Cien Formation; however, whole plant reconstructions are needed in order to fully understand the phylogenetic and phytogeographic importance of these woods. The functional-ecological significance of the fossil Leguminosae plants from Baja California Sur will be discussed in a later paper, along with other woods from the El Cien Formation. However, the inconspicuous growth rings, relatively abundant axial parenchyma, and relatively wide vessels suggest that the fossil flora inhabited a relatively humid environment without pronounced seasonality (cf. Barajas-Morales 1985).

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**References**


APPENDIX

List of extant taxa of Leguminosae compared with the fossil material.