Review of Palaeobotany and Palynology, 68 (1991): 257–267
Elsevier Science Publishers B.V., Amsterdam

An Eocene fossil tree with cambial variant wood structure*

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(Received August 30, 1990; revised and accepted March 14, 1991)

ABSTRACT

Hueber, F.M., Nambudiri, E.M.V., Tidwell, W.D. and Wheeler, E.F., 1991. An Eocene fossil tree with cambial variant wood structure. Rev. Palaeobot. Palynol., 68: 257–267.

Fossil wood with "anomalous structure" is reported from the Eocene of Louisiana and Texas. Superficially the wood appears to have diffuse (foraminate) included phloem, but what appear to be bundles of included phloem are bundles of parenchyma surrounding structures that resemble traumatic canals. These structures are of regular occurrence and distribution and, therefore, differ from traumatic canals which are irregular in distribution. Sieve elements and companion cells were not observed in the bundles. There appears to be no modern structural counterpart to this wood. Included phloem is considered a derived character and this type of Eocene tree might represent a "precursor" to diffuse included phloem. The wood has characteristics of both Nyctaginaceae and Loganiaceae.

Introduction

Included phloem in secondary xylem is of limited occurrence in dicotyledons. Some of the families with included phloem are not considered closely related so it is assumed that this type of cambial variant has arisen more than once (Carlquist, 1988). Even within one order, the Myrtales, included phloem has been suggested to have originated independently within the Memecyloideae, Combretoideae p.p., Onagraceae p.p. and Thymelaeaceae p.p. In this order it is considered an advanced feature (Van Vliet and Baas, 1985). To date, no fossil wood with diffuse (earlier referred to in the literature as foraminate) included phloem has been described from North America. The term included phloem, as used in this paper, does not have any developmental inferences, i.e., diffuse included phloem refers to the appearance of the mature wood and not to whether the axis was produced by the activity of a single cambium or successive cambia.

This paper describes permineralized wood from the Eocene of Louisiana and Texas that superficially appears to have diffuse included phloem. In the extant flora, included phloem is most frequent in lianas and desert shrubs and rare in trees. The type of fossil wood described herein is from trees, some samples are logs with diameters in excess of 120 cm. Locally, this type petrified wood is abundant and referred to as "snake wood" (R. Jones, pers. commun.).

Materials and methods

Thin sections of cross, radial and tangential surfaces were prepared and stained prior to placement on a slide (Bartholomew et al., 1970). All samples represent mature wood at least 5 cm from the center of the axis.

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*Paper No. 11488 of the Journal Series of the North Carolina Agricultural Research Service, Raleigh, NC 27695-7601, USA
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0034-6667/91/$03.50

The source of the Louisiana material is a locality in the Eocene Jackson Group within the Leesville, Louisiana Quadrangle (15 min Series, A.M.S. 7346-Series V785: SW 1/4, Section 14, T2N, R11W). The material from Texas was collected by Mr. Randy Jones of Brazoria, Texas and is from the Middle Eocene Yegua Formation, approximately 40 miles southeast of San Antonio and about 3 miles north of Falls City. The Yegua Formation, the uppermost unit of the Claiborne Group, is a massive crossbedded, fine-grained, mostly quartz sandstone containing well-laminated clay and lignite beds (Barnes, 1974, 1976).

Fossil plants reported from various localities in the Yegua Formation in Texas include four species of ferns, two species of coniferous wood and twenty-seven species of angiospermous leaves (Berry, 1924). One angiospermous wood described by Berry as *Laurinoxylon branneri* Knowlton was subsequently determined to be a member of the Juglandaceae and was assigned to *Engelhardioxylon texana* Manchester (1983). Other fossil plant remains from the Yegua Formation include *Laurinoxylon bakerii* Berry and numerous palynomorphs (Elsik, 1974, 1978).

Comparative material of extant dicotyledons with included phloem, particularly the Nyctaginaceae, was obtained from the Samuel J. Record collection (SJRw) housed at the USDA Forest Products Laboratory, Madison, Wisconsin; the Bailey-Wetmore Laboratory of Plant Anatomy and Morphology, Harvard University (Aw); and the David A. Kribs Wood Collection of N.C. State University (PACw). Wood samples of extant species are referenced by their xylariorum number (Stern, 1988). Slides of woods of the Loganiaceae, particularly *Strychnos*, and Nyctaginaceae were examined at the Rijksuniversiteit Utrecht, The Netherlands, courtesy of Dr. A.M.W. Mennega.

Means and standard deviations (s.d.) for vessel element diameter, vessel element lengths and ray height are based on twenty-five measurements; vessels per mm^2 and rays per mm are based on ten measurements. For vessels per mm^2, each vessel was counted individually (Wheeler, 1986; IAWA Committee, 1989).

Systematic description

Mennegoxylon gen. nov.

Diagnosis: Wood with parenchymatous bundles surrounding canals; bundles diffusely arranged; bundles wider tangentially than radially; vessels solitary and in radial pairs and oblique multiples of 2–4; vessels scattered and not always in association with the bundles; tangential diameter small-medium; perforations simple; intervessel pitting alternate, small; axial parenchyma scanty paratracheal; rays uniseriate, very numerous, composed exclusively of procumbent cells; vessel-ray parenchyma pits similar to intervessel pits.

Discussion: *Mennegoxylon* is an organ genus for fossil woods containing diffuse parenchymatous bundles with an arrangement similar to that of the diffuse included phloem of the Nyctaginaceae, but with the vessels generally not in association with the phloem bundles.

Generitype: *Mennegoxylon jonesii*

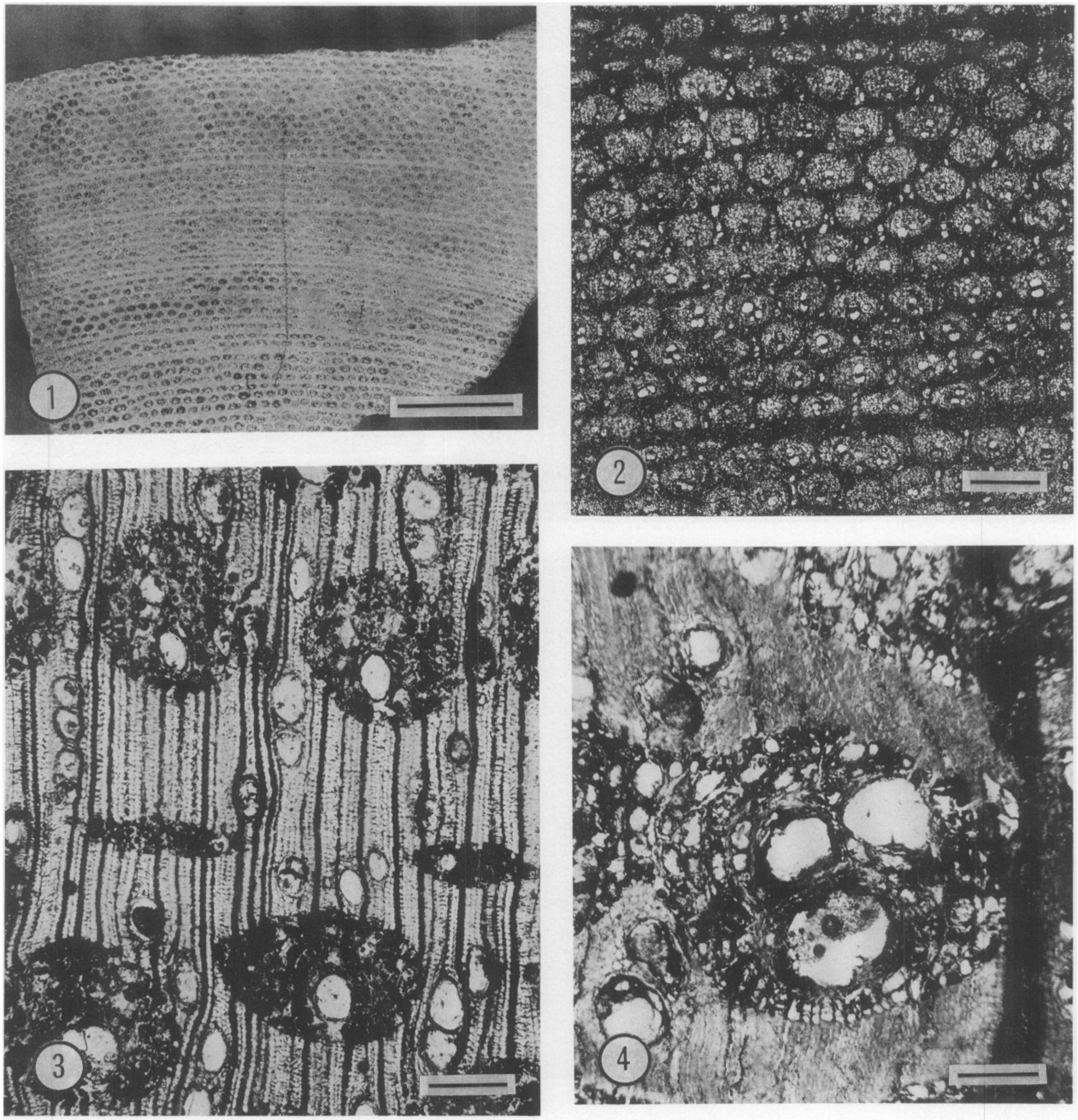
Source of name: The generic name is for Dr. Alberta Mennega in honour of her many contributions to the field of wood anatomy.

Mennegoxylon jonesii sp. nov. (Plates I, II)

Diagnosis: Growth increments: marked by zones with few bundles or zones with very small bundles that lack large openings.

Bundles: 13–20 per 10 mm^2; accounting for nearly half of the tissue in the stem, considerably larger than the vessels; shape of the individual bundles slightly circular, or oval and elliptical, wider tangentially than radially, with mean tangential diameters of 655 μm (s.d. = 130 μm) to 833 μm (s.d. = 168), range of 145–1183 μm and mean radial diameters of 515 μm (s.d. = 90 μm) to 537 μm (s.d. = 173 μm), range of 197–788 μm; with 1–3 large openings which in longitudinal sections appear to be unpartitioned canals; majority of the cells appear to be thin-walled parenchymatous cells which are not very longitudinally elongated and tend to be isodiametric; ray cells inflated and enlarged in the bundle, in longitudinal sections

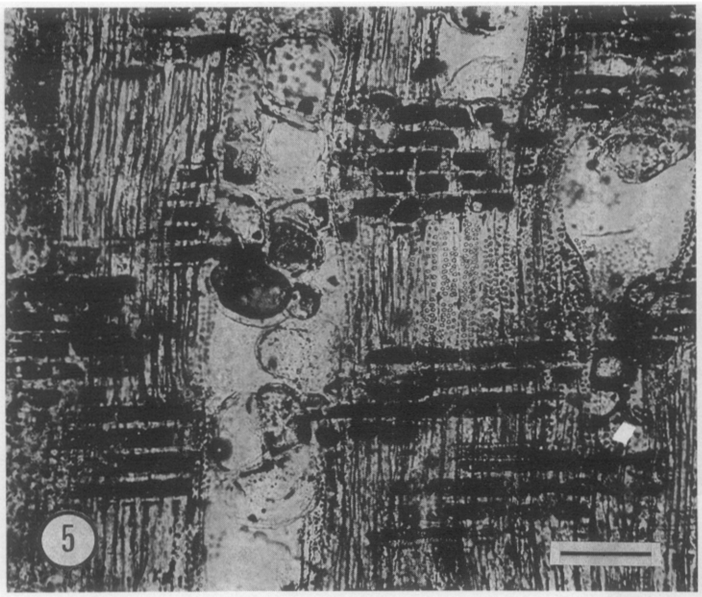
PLATE I

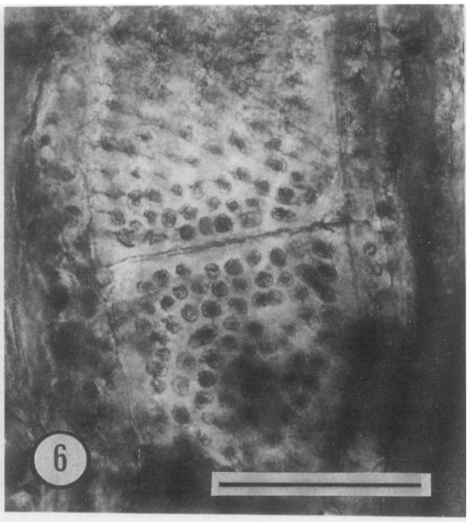


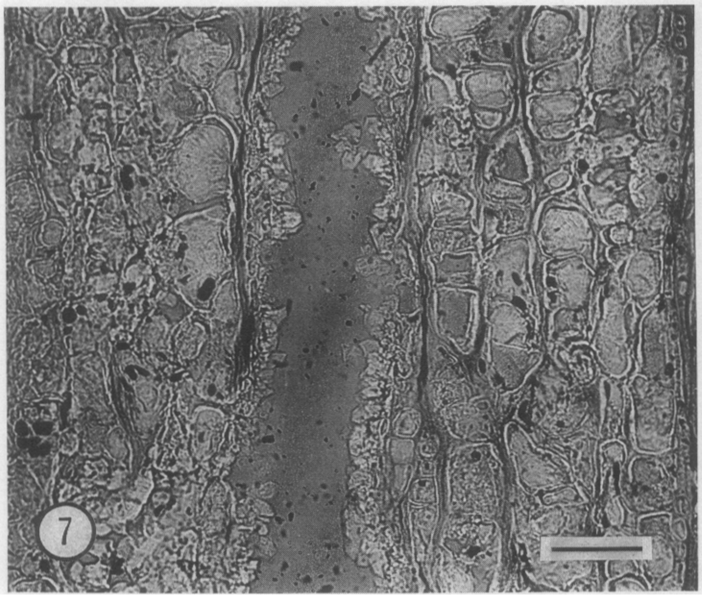
1–4. *Mennegoxylon jonesii*

1. Cross-sectional surface. Note numerous bundles and zones devoid of bundles that may represent growth ring boundaries. Scale bar = 1 cm.
2. Cross section showing abundant bundles and small vessels not in direct contact with the bundles. Scale bar = 1 mm.
3. Cross section showing small vessels that are solitary and in radial multiples. Scale bar = 250 μm.
4. Detail of "included phloem bundle" showing parenchymatous tissue and large openings in the bundle. Scale bar = 100 μm.

PLATE II







5–8 *Mennegoxylon jonesii*

5. Radial section showing rays composed of procumbent ray parenchyma cells, and imperforate elements with distinctly bordered pitting. Tyloses in vessels.
6. Crowded alternate intervessel pitting, and end wall of vessel element not much inclined from the horizontal. Tangential view.
7. Tangential section showing parenchymatous cells surrounding the "canal" in the bundle.
8. Tangential section showing short uniseriate rays and fusiform ray near phloem bundle. Scale bar in figs.5,7,8 = 100 μm; scale bar in fig.6 = 50 μm.

difficult to distinguish ray cells from other parenchymatous cells.

Vessels: solitary, in radial pairs and oblique multiples of 2–4 (rarely 5); not restricted to a position subtending the bundles, but at random in the fibrous tissue; mean tangential diameter 101 μm (s.d. = 20 μm)–105 μm, range 51–135 μm; 2–9 per mm^2; vessel element lengths range from 236 μm–397 μm; perforation plates exclusively simple, with end walls horizontal or only slightly inclined from the horizontal; intervessel pits small (3–4 μm) and alternate; vessel-ray parenchyma pits bordered and similar in size and shape to intervessel pits.

Rays: exclusively uniseriate; homocellular, composed entirely of procumbent cells; height in cell number from 2 to 16 cells, mean 7 to 8 cells; 88–323 μm, means of 172 μm (s.d. = 74 μm) to 194 μm (s.d. = 74 μm); non-storied; 9–17 per mm, means of 10.4 to 14.6 per mm. Rays in the vicinity of the bundles enlarged and multiseriate, with inflated central areas.

Parenchyma: scanty paratracheal, occasionally strands associated with the vessels, but not encircling them; and in bundles; non-storied.

Imperforate tracheary elements: fibers moderately thick-walled to thick-walled; non-storied; non-septate; near vessels elongated cells with distinctly bordered pits, possibly vasicentric tracheids; other imperforate elements without obvious bordered pits.

Specimens: *Holotype*: USNM 422619, other specimens studied USNM 455015, 455016.

Source of name: The specific epithet *jonesii* acknowledges Mr. Randy Jones who collected and donated the Texas material.

Discussion

This wood superficially appears to have diffuse (foraminate) included phloem, but no sieve tube elements or companion cells were observed in the bundles, only parenchyma. The phloem bundles of the diffuse type of included phloem have varying amounts of parenchyma associated with them, but there generally is more parenchyma than conducting elements in the bundles. Consequently, the apparent absence of conducting cells may just be due to the longitudinal sections not intersecting sieve tube elements or poor preservation. All of the larger parenchyma bundles have one to three large openings in them. But as illustrated in Plate II, 7 these openings are not vessels, but canals lined with irregularly shaped small cells. There is nothing to indicate that these openings are vessels, as no end walls are visible. The smaller parenchyma bundles generally lack canals. No extant wood is known to have similar regularly arranged parenchyma bundles containing canals.

Included phloem, both diffuse and concentric, is considered to be a derived character (Carlquist, 1988). If included phloem is indeed derived, then it would not be surprising to find intermediates between wood produced by a 'normal cambium' and diffuse included phloem, a cambial variant, in the fossil record. *Mennegoxylon jonesii* may represent such an intermediate.

Comparisons with extant plants with diffuse included phloem

Present day families with some species having diffuse included phloem are: Amaranthaceae, Apocynaceae, Asclepiadaceae, Chenopodiaceae, Combretaceae, Guttiferae, Hippocrateaceae, Icacinaceae, Loganiaceae, Melastomataceae, Nyctaginaceae, Onagraceae, Salvadoraceae, Thymeleaceae and Vochysiaceae (Metcalfe and Chalk, 1950; Carlquist, 1988). All members of the Amaranthaceae, Chenopodiaceae and Nyctaginaceae have either concentric or diffuse included phloem. In the other families included phloem is characteristic of only some genera. Characteristics of these families are summarized in Table I.

Chalk and Chattaway (1937) devised a dichotomous key to extant woods with included phloem. There are many "difficulties" in relying on dichotomous keys designed for genera of extant woods when determining affinities of fossil woods (Page, 1979), e.g., fossils may have a combination of characters not known in any extant genus. Because vessels are not restricted to a position subtending the bundles, *M. jonesii* keys out to the Loganiaceae or Thymeleaceae. But the combination of characters of the fossil indicates it resembles the Nyctaginaceae, as much as the former two families. In the

TABLE I Characteristics of woods with foraminate included phloem

	GR	VTD (μm)	V.ARR.	VSQMM	VEL(MM)	PP	IVP	Vest	VRPP	RW	RH
AMARANTHACEAE *Charpentiera* *Notrichtium*	–	s–m (40–140)	sol&rm 2–3	4–30	0.1–0.3	si	alt mod lrg.	–	>ivp	no rays or 10+	>1 mm
APOCYNACEAE *Lyonsia*	–	s	num.mult.	10–50	0.3–1	si	alt. vs-min	–	elng.&smp sim.	fam. 2–3s, sm spp all 1s	<1 mm
CHENOPODIACEAE	–	Vs-s	cls.-innr side phl.	?	0.075–0.1 mm	si	alt. sm-min	–	sim.	no rays	–
COMBRETACEAE *Calycopteris*	+,dp-srp	2d, 155 lrgr	lrg xsol sm cls & rm	lrg 2–5	lrg 0.3–0.5; sm 0.29–0.66	si	alt. 7–9	+	sim., $\frac{1}{2}$b	1,(2)	4–25–29 cells
Combretum, Afr. spp of sub Combretum	+(f–d)	64–302	sol&rare rm	3–40	0.2–0.44	si	alt 5–7(13)	+	sim.	–	–
Guiera (1 sp)	+(f)	vs.=57 lrgr=100–200	lrg-xsol; sm cls	21–27	0.18–0.19 (0.13–0.26)	si	alt. 5–8	+	sim.	1–2,(3)	160–175 μμ (80–330)
Thiloa	+(f)	49–61–73	sol&rare rm	33–45–80	–	si	alt, 5-7(10)	+	sim.(to elng)	1(2)	4–14–22 cells
CLUSIACEAE *Endodesmia* *Lubrunia*		2d;lrgr 100–200	xsol–pred sol	not rare	–	si	alt, lrg	–	enlg	1(2)	?
HIPPOCRATEACEAE 2 spp *Cheiloclinium* & *Salacia* (2 Afr. spp)		2 d; lrgr <100	nr xsol	6–15	0.3–0.8 (fam)	si	alt, sm, 3–5	–	sim.	1(2)	max. 1 mm
LOGANIACEAE *Antonia*	–	90 (40–120)	90% rm 2–6; cls	19 (12–27)	0.47 (0.3–0.67)	si	alt, 2.5	+	sim. $\frac{1}{2}$b	1	max 240 μm
Bonyunia	–	60–80 (36–100)	rm 2–9, files cls	32 (18–40)	0.425, 0.48	si	alt, sm	+	sm.crowded	1(2–4)	max 900 μm
Norrisia		90–100 (50–120)	mostly rm 2–5(14)	6–43	0.363 (0.2–0.5)	si	alt, 2–3	+	sim.	1	28–500 μm 1–12 cells
Strychnos	±	50–300	80–90% sol- 80% mult	8–200	0.35–0.65	si	alt, 3–9	+	sim.	2–10	>1mm, oft 2–4 mm
MELASTOMACEAE *Memecylon*	–	38–113 (25–153)	50–90% sol	9–126	0.26–0.44 (0.16–0.73)	si	alt, 3–5	+	$\frac{1}{2}$b,alt	1–3(4)	240–550 μm
Pternandra	±	64–112 (30–145)	70–100% sol	9–29	0.34–0.43	si	alt, 6–8	+	$\frac{1}{2}$b, elng. to 14 μm	1(2)	3–5(12) cells
NYTAGINACEAE	±	small	sol&rm's, cls		0.1–0.16	si	alt. sm	–	sim.	1(2–3)	low
ONAGRACEAE		40–110	rm freq		0.11–0.55	si	alt	+	$\frac{1}{2}$b	uni-mult	–
SALVADORACEAE *Salvadora* *Dobera*		vs-med	mult 2–4 & cls	2–10	0.13–0.2	si	alt sm-min	–	sim.	3–5	<1 mm
THYMELEACEAE 8 Genera		30–160	tend tang.		0.15–0.4	si	alt sm-vs	–	sim. $\frac{1}{2}$b	4 gen–1s; others 2–4 s	–
VOCHYSIACEAE *Erisma*	±	avg.200	pred sol, rm 2–4	2(1–5)	0.6	si	alt, 10	–	sim.	73% 1,2–4 8–31 cells	672 μm
Erismadelphus	±	avg.284	pred sol, rm 2–3	0–3	0.67	si	alt 10	–	sim.	586 μm, 13s	up to 400–700 μm, 12–15 cells

TABLE I (*continued*)

	Ray Type	SR	RPMM	Phloem in rays	PAR.	#C/PS	SP	Fibers	Phloem bundles	Habit
AMARANTHACEAE *Charpentiera* *Notrichtium*		–	?	–	sc pr, ali–cf	1–4,f	±	–b sep		sh
APOCYNACEAE *Lyonsia*	Typ. het.	–	8–23 (fam)	–	sm apo; sm para vc–ali, sc pr	typ to 8	–	–b/+b sep+	irreg. shaped	?
CHENOPODIACEAE		–			sc pr	f	+	–b		sh–sm tr
COMBRETACEAE *Calycopteris*	Het III–Homo	–	11–12	±	sc pr	2–4	–	si-min.b. septc	ovl to crstfm tang.flattened	li
Combretum, Afr. spp of sub *Combretum*	Het III–Homo	–	?	±	para sc–abund	?	–	sim-min.b. sep±		sh-tr
Guiera (1 sp)	ms-pro+ upr.marg	–	7–12	+in ms rays	–	1–3	–	sim-min.b. sep-	frequent	sm sh
Thiloa	Homo (pro)		11–13–15	+wide rays	sc pr	5&6	–	sim-min.b. sep-	frequent	
CLUSIACEAE *Endodesmia* *Lubrunia*		–	10–11	rare	sc pr	?	–	+b; vct	5/mm2; ovl-elng. tang; not assoc. w/vess.	tr
HIPPOCRATEACEAE 2 spp *Cheiloclinium* & *Salacia* (2 Afr. spp)	pred sq& upr cells	–	12–16	–	sc pr	4–8	–	+b; sep	300 μm wide irreg.tend.to concentric	tr
LOGANIACEAE *Antonia*	pro+occ row sq	–	8–9	–	sc apo, dif	·2–6	–	vstg.b sep-	small ovl;t pattern, 3–5/sq. mm, 100–340 μm td	sh–tr
Bonyunia	long ls wings	–	15(19–22)	–	sc apo	4,2–6	–	si/vstg,b sep-	nmbr,ovl-rnd islnds t.zones 5–8/sq.mm, 80–450 μm t.d.	sh
Norrisia	Homo (pro)	–	12(10–14)	–	sc pr	4–8	–	sm.b sep-	rnd.–ovl islnds. in t zns.2–3, 4–8/sq mm, 180–270 μm t.d.	tr
Strychnos	Het I-Het II	–	5–18	–	vc–ali–cf; +apo	2, 4–8	–	vt+ sep-	rnd–ovl, 0.05–5.5/sq.mm 250–2000 μm t.d.	sh,tr,li
MELASOMACEAE *Memecylon*	Het I–Het III	–	9–18	+1 sp	para–apo sc–abund	4–5 (3–7)	–	b+		sh-tr
Pternandra	upr. to wkly pro	–	12–18 (9–24)	+all	apo–dif para	2–3(4)	–	b+		sh–sm tr

TABLE I (*continued*)

	Ray Type	SR	RPMM	Phloem in rays	PAR.	#C/PS	SP	Fibers	Phloem bundles	Habit
NYTAGINACEAE	Het IIB& III;Homo.	±	5–12		sc pr	2–3,f	±	b−	widr.tang.than rad.	tr,sh,vine
ONAGRACEAE	pred.upr mstly wkly pro& sq.cls.	+ if low	−	−	sc pr; apo.wi.fp		−	b− + sep +		sub-sh, sm sh
SALVADORACEAE *Salvadora* *Dobera*	upr & sq.cells	−	8–14	−	sc pr–vc	1–4 f	+	b−	rnd-ovl; par.links	sh
THYMELEACEAE 8 Genera	Homo–HetIII	−	?		sc pr–vc– ali; sm apo bnds.	?	−	b+;		
VOCHYSIACEAE *Erisma*	Het III	−	?,45/mm2	+	apo, bnds 4–6 c.w	?	−	b− sep+	axl & in rays	
Erismadelphus	Het III	−	7,38/mm2	+	apo, bnds 4–6 c.w.	?	−	b− sep+	axl & in rays	

GR = Growth rings, − = absent, + = present, f = faint, dp = diffuse porous, srp = semi-ring porous. VTD = Tangential diameter of vessels; s = small, <100 μm; vs = very small, <50 μm; m = medium, 100–200 μm; 2d = with two distinct diameter classes. V.ARR = Vessel arrangement; sol = solitary; rm = radial multiples; cls = clusters; xsol = exclusively solitary. VSQMM = Vessel per square millimeter. VEL = Vessel element length. PP = Perforation plates; si = simple. IVP = Intervessel pit arrangement; alt = alternate; lrg = large >10 μm; vs = very small 4–5 μm; min = minute, <3 μm. Vest = Vestured pits, + = present; − = absent. VRPP = Vessel to ray parenchyma pits; >ivp = larger than intervessel pits; elng = elongate; smp = simple; sim = similar to intervessel pits; 1/2b = half-bordered. RW = Ray width in cell number. RH = Ray height. Ray Type; het = heterocellular; Het I, II, or III = Kribs Heterogeneous Types; ms = multiseriate; pro = procumbent; upr = upright; marg = marginal; sq = square. SR = Storied rays; + = present; − = absent. RPMM = Rays per millimeter. PAR = Parenchyma distribution; sc pr = scanty paratracheal; vc = vasicentric; ali = aliform; cf = confluent; apo = apotracheal; dif = diffuse; bnds. = bands. c.w. = cell width of bands. #C/PS = Number of cells per parenchyma strand. SP = Storied parenchyma; + = present; − = absent. Fibers; −b = without distinctly bordered pits; +b = with distinctly bordered pits; sep = septate; sim-min b = simple to minutely bordered; vstg. = vestigial; vt = tracheids present

The superscripts reference the sources of information, other than Metcalfe and Chalk (1950) and Chalk and Chattaway (1937). These are: 1 = Van Vliet (1979); 2 = Mennega (1972); 3 = Mennega (1980); 4 = Van Vliet (1981); 5 = Kato (1963); 6 = Carlquist (1975); 7 = Quirk (1980)

Thymeleaceae irregular clusters of vessels are common and the phloem bundles smaller, short vasicentric tracheids are present, but the ground tissue fibers have numerous bordered pits. The phloem strands in the Loganiaceae are smaller and more numerous than in the fossil (see Table 1). *Mennegoxyon jonesii* has thick-walled fibers rather than thin or moderately thick walls, the latter a key character of the Thymeleaceae or Loganiaceae. Dr. Alberta Mennega (pers. commun., 1989), who has monographed the wood anatomy of the Loganiaceae (Mennega, 1980), does not think the wood is equivalent to any extant genus in that family. *Antonia* differs in the size of its phloem bundles, vessel frequency, vessel element length, and parenchyma distribution. *Strychnos* rarely has large stems, rays are never exclusively uniseriate, and the ratio of phloem/vessel diameter observed in *M. jonesii* does not occur in any *Strychnos* species studied.

Table I lists the characteristics of the woods with diffuse included phloem. It shows that the wood structure of *M. jonesii* is similar to the Nyctaginaceae because of its exclusively uniseriate rays which are made up of predominatly procumbent cells, scanty parenchyma outside the phloem bundles, small diameter vessels with small intervessel pits and vessel-parenchyma pits similar to the intervessel pits. The Chalk and Chattaway key indicates that vessels in the Nyctaginaceae are restricted to a position subtending the phloem bundles, but in *Neea floribunda* (SJRw 18651) and *N. psychotrioides* (SJRw 10287, SJRw 12177), there are some solitary vessels to the side and not in contact with the bundles as well as vessels directly subtending the phloem bundles. In the Nyctaginaceae, rays are homogeneous in *Torrubia* and nearly so in *Neea* (Metcalfe and Chalk, 1950). On this basis, *M. jonesii* is more similar to these two genera than to *Pisonia* which is characterized by rays with both upright and square cells.

There is very little information on the anatomy of included phloem bundles. Most papers on included phloem only discuss cambial activity (e.g., Balfour, 1965; Studholme and Philipson, 1966) and do not describe the relative abundance, shape, or cellular structure of the bundles. Phloem is generally comprised of unlignified cells. Since most wood samples are dried and rarely embedded, the phloem cells collapse and thus during specimen preparation the delicate phloem tissue is torn and ripped out. Therefore, illustrations of woods with included phloem generally show holes where the phloem was located (e.g., Van Vliet, 1979, 1981; Détienne and Jacquet, 1983). Nonetheless, despite the limited information available on phloem bundles, our observations indicate the shape, size, and abundance of the bundles in *M. jonesii* are consistent with those in the extant Nyctaginaceae. According to Détienne and Jacquet (1983) 50% of the wood of *Rockia* (Nyctaginaceae) is phloem bundles. They reported the size of the individual bundles in *Neea* (Nyctaginaceae) to be 800 by 300 µm to 1500 by 800 µm, with the tangential dimension being the largest. Such characteristics are consistent with the structure of *M. jonesii.*

The growth increments in *M. jonesii* resemble those figured for *Pisonia grandis* from Heron Island off the coast of Queensland (Eckstein et al., 1981). There is an alternation between regions in which the anomalous lenses of parenchyma and phloem are confluent and regions in which they are smaller and discrete. This type of growth increment has not been observed in the Loganiaceae (A.M.W. Mennega, pers. commun.).

Raphides are characteristic of the Nyctaginaceae, but no inclusions were observed in this fossil. This apparent absence of inclusions may not reflect original absence, but dissolution of the crystals during permineralization. Other differences between *M. jonesii* and extant Nyctaginaceae include the occurrence of what appear to be some tracheids or fiber-tracheids with numerous distinctly bordered pits near the vessels and canals in the parenchymatous bundles in the fossil. This latter feature (canals) does not, to our knowledge, occur in any other family with included phloem. Imperforate tracheary elements with distinctly bordered pits are known from the Loganiceae and Thymeleaceae.

Vessel elements of *M. jonesii* are longer than those of extant Nyctaginaceae, shorter than those of extant Loganiaceae, and within the range of extant Thymeleaceae. Vessel elements in extant Nyctaginaceae are very short, 100–160 µm long. Extant Nyctaginaceae typically have some storied structure and this is not apparent in this fossil. The wood structure of extant Nyctaginaceae is more advanced than that of *M. jonesii* on the basis of these two characters.

Comments on the fossil record of the Nyctaginaceae and Loganiaceae

The earliest occurrence of pollen of the Nyctaginaceae is reported to be Eocene; the earliest record of *Pisonia* pollen is Miocene and fossil pollen of *Neea* and genera of Loganiaceae is not known (Muller, 1981). It is tempting to consider this wood as representing Nyctaginaceae, rather than Loganiaceae or Thymeleaceae, because pollen of the Nyctaginaceae is known from the Middle Eocene to Lower Oligocene of the southeast United States (Elsik and Dilcher, 1974; Frederiksen, 1980; Taylor, 1988). This pollen is described as similar to that found in the tribes Nyctagineae and Pisnieae of the Nyctaginaceae. Also, Berry (1924) reported leaves called *Pisonia claiborniana* from Middle Eocene strata in Louisiana. These leaves supposedly resembled those of the extant species *Pisonia floribunda* Britt of the Florida Keys and *P. longifolia* Sargent which extends from the Florida Keys to Brazil along the ocean beaches. How close the resemblance of these leaves is to extant *Pisonia* awaits reevaluation of this material.

The occurrence of this Eocene wood resembling both the Nyctaginaceae and Loganiaceae, but differing from both families in some characteristics, is further documentation of the occurrence of Paleogene plants with combinations of characters not known in extant plants. Concentric included phloem is known from the Eocene of the United States (*Forchhammerioxylon scleroticum* assigned to the Capparidaceae; Kruse, 1954) and (?) Miocene of Thailand (*Menispermoxylon circumballatum* assigned to the Menispermaceae; Vozenin-Serra et al., 1989).

Carlquist (1988) has discussed the phylogeny, habit and ecology of cambial variants. He stressed that cambial variants probably originated independently in most groups. Most of the interpretations of the function of included phloem and the associated parenchyma have been based on its value in lianas, not in trees. This wood unquestionably came from a tree so it seems unlikely that the suggestion that included phloem is of benefit in providing greater flexibility and thereby permitting more torsion would apply here. Another hypothesis is that abundant parenchyma in vines represents a site for regeneration in response to wounding, especially that suffered when the tree supporting the vine falls (Dobbins and Fisher, 1986; Carlquist, 1988), this also would not apply to this wood. Carlquist speculated that there may be advantages to having the phloem dispersed throughout a stem, and thereby provide a more effective three-dimensional dispersion of photosynthate throughout the stem. He suggested that such a system would be of particular advantage if the phloem and xylem functioned throughout the stem for a number of years as is known to occur in palms. With regard to this speculation there are no data on how long-lived the phloem strands are in the Nyctaginaceae, Loganiaceae, or Thymeleaceae. Reference to Table 1 shows over 50% of the genera with diffuse type included phloem have exclusively uniseriate rays or are rayless. In contrast, only 14% of the entries in OPCN Hardwood database have exclusively uniseriate rays (Wheeler et al., 1986). This indicates that although diffuse included phloem has originated separately in a number of families, it is often associated with similar features (raylessness or exclusively uniseriate rays), features which are related to the movement and storage of reserve photosynthate.

Acknowledgments

We would like to thank Dr. Alberta Mennega for examining photographs of the fossils and her most useful comments and for access to the slide collection at Utrecht; Dr. R.B. Miller of the USDA Forest Products Laboratory, Madison, WI for loaning slides and samples of the Nyctaginaceae; the curatorial staff of the Bailey-Wetmore Laboratory of Plant Anatomy and Morphology, Harvard University, for access to samples; and Dr. C.A. LaPasha and Dr. J. Mickle, N.C. State University, for comments on the manuscript. This research was supported in part by NSF Grant BSR 8708010 (EW).

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