Wood anatomy of major Bignoniaceae clades

Marcelo R. Pace, Lúcia G. Lohmann, Richard G. Olmstead & Veronica Angyalossy

Plant Systematics and Evolution

ISSN 0378-2697 Volume 301 Number 3

Plant Syst Evol (2015) 301:967-995 DOI 10.1007/s00606-014-1129-2





Your article is protected by copyright and all rights are held exclusively by Springer-Verlag Wien. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at link.springer.com".



Plant Syst Evol (2015) 301:967–995 DOI 10.1007/s00606-014-1129-2

ORIGINAL ARTICLE

Wood anatomy of major Bignoniaceae clades

Marcelo R. Pace · Lúcia G. Lohmann · Richard G. Olmstead · Veronica Angyalossy

Received: 24 March 2014/Accepted: 7 July 2014/Published online: 9 August 2014 © Springer-Verlag Wien 2014

Abstract The circumscription of Bignoniaceae genera and tribes has undergone major changes following an increased understanding of phylogenetic relationships within the family. While DNA sequence data have repeatedly reconstructed major clades within the family, some of the clades recovered still lack diagnostic morphoanatomical features, complicating their recognition. In this study we investigated the wood anatomy of all major lineages of Bignoniaceae (except Tourrettieae) in search for anatomical synapomorphies for clades. We sampled 158 species of Bignoniaceae, representing 67 out of the 82 genera currently recognized. Detailed descriptions of quantitative and qualitative wood anatomical features are presented for each clade and interpreted in the light of a molecular phylogeny for the family. Jacarandae are characterized by a paratracheal winged-aliform parenchyma, with the traditional subdivision of Jacaranda into sections Monolobos and Dilobos supported by the uniseriate and homocellular rays of Monolobos versus the wide and heterocellular rays of Dilobos. Tecomeae s.s. are characterized by scanty paratracheal parenchyma, septate fibers, and heterocellular rays, traits also found in Delostoma, a genus previously included in Tecomeae s.l., but recently shown to represent a separate lineage. Crescentiina includes two subclades, the Tabebuia alliance and the Paleotropical clade, which share abundant aliform parenchyma, short and

R. G. Olmstead Department of Biology, University of Washington, Seattle, WA 98195, USA mainly homocellular rays, less commonly with heterocellular rays with body procumbent and one row of marginal square cells. Members of the Tabebuia alliance and the Paleotropical clade can be distinguished from each other by the narrow vessels with a widespread storied structure found in members of the Tabebuia alliance, versus the vessels with medium to wide width and a non-storied structure found in members of the Paleotropical clade. Oroxyleae are characterized by a combination of simple and foraminate perforation plates and homocellular rays, while Catalpeae are characterized by scanty paratracheal parenchyma, abundant tyloses and vessel-ray pits simple to semi-bordered. Bignonieae differ from all other clades by a variant secondary growth and a typically lianoid wood anatomy. Overall, wood anatomical characters are not very labile within the family, being distributed across clades in a very predictive manner. Several anatomical characters represent good anatomical synapomorphies and provide further support to clades identified in molecular phylogenetic studies.

Keywords Tabebuia alliance · Coleeae · Bignonieae · Diversity · Liana · Secondary xylem · Neotropics · Paleotropics

Introduction

Bignoniaceae are a family of woody plants with approximately 860 species and 82 genera (Lohmann and Ulloa 2006 onwards). Most species are trees and lianas, although some members are shrubs and herbs (Gentry 1980; Lohmann 2004; Fischer et al. 2004; Olmstead et al. 2009). The family is pantropical and centered in tropical South America (Lohmann 2004; Fischer et al. 2004; Olmstead

M. R. Pace (⊠) · L. G. Lohmann · V. Angyalossy Departamento de Botânica, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, 277, Cidade Universitária, CEP 05508-090 São Paulo, SP, Brazil e-mail: marcelorpace@yahoo.com.br; marcelorpace@usp.br

et al. 2009; Olmstead 2013), with only a few genera reaching temperate climates (*Campsis*, *Catalpa*) or high mountains (*Argylia* in the Andes and *Incarvillea* in the Himalayas; Olmstead et al. 2009). Members of Bignoniaceae are generally recognizable by a woody habit, compound opposite leaves, tubular, zygomorphic and showy flowers, four didynamous stamens plus one staminode, and bi-valved dry capsular fruits (Gentry 1980; Lohmann 2004; Olmstead et al. 2009).

In the most recent angiosperm classifications, Bignoniaceae are placed in the order Lamiales (APG II 2003; APG III 2009), within which the family forms a well-supported lineage that is sister to a clade composed of Lamiaceae, Orobanchaceae, Rehmanniaceae, Paulowniaceae, Phrymaceae, Mazaceae, Verbenaceae, Thomandersiaceae, Lentibulariaceae and Schlegeliaceae (Refulio-Rodriguez and Olmstead 2014). Gentry (1980) recognized eight tribes in the family based on habit, fruit dehiscence, and geographical distribution: Bignonieae, Coleeae, Crescentieae, Eccremocarpeae, Oroxyleae, Tecomeae, Tourrettieae, and Schlegelieae (Gentry 1980, 1992; Fischer et al. 2004). However, Schlegelieae were shown to be distantly related from the rest of the family (Spangler and Olmstead 1999; Refulio-Rodriguez and Olmstead 2014) and were subsequently segregated into Schelegeliaceae Reveal. More recently, molecular phylogenetic studies (Spangler and Olmstead 1999; Zjhra et al. 2004; Olmstead et al. 2009) have indicated that some tribes were not monophyletic as traditionally circumscribed, suggesting that nine major clades should be recognized instead. Of these nine clades, two correspond to tribes previously recognized under Gentry's system (1980), i.e., Bignonieae and Oroxyleae. Two other tribes previously recognized under Gentry's system (1980), Crescentieae and Coleeae (minus Kigelia), also emerged as monophyletic but nested within more inclusive clades; Crescentieae emerged within the Neotropical Tabebuia alliance clade (Grose and Olmstead 2007a), and Coleeae emerged within the Paleotropical clade (Fig. 1; Zjhra et al. 2004; Olmstead et al. 2009). The large tribe Tecomeae, on the other hand, appeared scattered within six different clades: Catalpeae, the Tabebuia alliance, the Paleotropical clade, Delostoma, Tecomeae s.s., and Jacarandeae. While these clades are well supported by molecular characters, additional diagnostic morphological and anatomical traits are still desirable to characterize them. Indeed, Olmstead et al. (2009, page 1735) noted that: "Several of the large, prominent clades identified in this study lack evident diagnostic traits".

Stem anatomy is one of the most informative sources of diagnostic characters for Bignoniaceae. The wood anatomy of Bignoniaceae has been well studied, since the wood of several species are highly valuable, including that of *Handroanthus* (formerly included in a larger *Tabebuia*;

Grose and Olmstead 2007a, b), Tabebuia, Paratecoma, and Jacaranda (Record and Hess 1943; Chudnoff 1984; Dos Santos and Miller 1992, 1997). In addition, the lianas have called the attention of researchers because of the presence of a conspicuous type of cambial variant in their stems, with the formation of four, or multiples of four, phloem wedges that furrow the xylem, giving the stem an unmistakable cross-like shape in transverse section (Schenck 1893; Dobbins 1971; Dos Santos 1995; Pace et al. 2009; Angyalossy et al. 2012). Systematic wood anatomical studies were also successful in sorting lineages within the family. In the large genus Jacaranda, wood anatomical studies found differences between Jacaranda section Monolobos and Dilobos, with Jacaranda section Monolobos exhibiting uniseriate, homocellular rays only and Jacaranda section Dilobos exhibiting wide, heterocellular rays (Dos Santos and Miller 1997). The recent division of Tabebuia into three different genera (Grose and Olmstead 2007a, b), Handroanthus, Tabebuia, and Roseodendron matches perfectly a division long known by wood anatomists that divided *Tabebuia* s.l. in different groups, those of light woods, those of heavy woods, and some species that did not fit in one of these two major groups (Record and Hess 1943; Chudnoff 1984; Dos Santos and Miller 1992). In fact, the light woods are now recognized as Tabebuia s.s., the heavy woods with lapachol obstructing the vessels of the heartwood are now recognized as Handroanthus, and the wood anatomically unusual species are now recognized as Roseodendron (Grose and Olmstead 2007b). Given the importance of wood anatomical characters in the Bignoniaceae, our study aims to: i) describe the wood anatomy of all major woody clades of Bignoniaceae based in the new systematic arrangement of the family and, ii) search for commonalities on the wood anatomy and character that could represent anatomical synapomorphies of the clades delimited in phylogenetic studies of the family.

Materials and methods

Sampling

Altogether 158 species were sampled, belonging to 67 out of the 82 genera currently recognized in Bignoniaceae, and representing all major clades (Olmstead et al. 2009). Only Tourrettieae, a tribe of two monotypic genera of slenderstemmed vines from the Andes were not sampled. In most cases, two to three specimens were sampled per species. A complete list of species and specimens sampled, collecting numbers, and sampling localities are presented in "Appendix". Wood anatomical characters of the majority of arborescent and shrubby species were obtained from slides deposited at the Forest Products Laboratory Slide Wood anatomy of the Bignoniaceae

Collection (MADw and SJRw; Madison, Wisconsin, USA), with additional species/specimens from Calvino Mainieri Wood Collection (BCTw; São Paulo, Brazil). Anatomical characters from lianas were obtained from our private slide collection, which was prepared from specimens collected in natural populations or from the living collection of Plantarum Institute and Botanical Garden (Appendix 1). Samples were fixed in FAA 50–70 (50–70 % ethanol-formaldehyde-acetic acid; Berlyn and Miksche 1976) for a week, and subsequently stored in a solution of 50 % ethanol.

Anatomical procedures

Section for our slide collection was prepared according to Barbosa et al. (2010), following double staining in Astra Blue and Safranine (Bukatsch 1972) and mounted in a synthetic resin to obtain permanent slides. Scanning electron microscopy was done with thick sections of wood (ca. 1 mm), submitted to dehydration with acetone, placed on aluminium stubs, sputter-coated with gold, and subsequently analysed in a scanning electron microscope.

Wood description

Anatomical descriptions followed the IAWA list of microscopic features (IAWA Committee 1989) as a starting point, adjusting to the specificities of the Bignoniaceae according to the wood anatomical diversity encountered. Measurements of vessel grouping followed Carlquist (2001). Semi-ring to ring-porous woods have their earlywood and latewood measured separately, since vessels in latewood usually had a different grouping arrangement. In woods with vessels of two width classes (lianas and plants with ring-porous or semi-ring porous woods), both the wide and the narrow vessels were measure and their values expressed separately. All characters and character states examined are presented in Table 1. Measurements were performed using the free software ImageJ (ver. 1.45 s; Rasband 2012), with a minimum of 30 repetitions per specimen. Parameters for all types of xylem cells were measured, including vessel and axial parenchyma frequency, vessel diameter, number of vessels per group, axial parenchyma area, intervessel pit size, ray width and height. Quantitative results are presented as averages accompanied by their standard deviations.

Results

Some wood anatomical traits are common to most, if not all, species of Bignoniaceae. Most arborescent



Fig. 1 Phylogenetic relationship of the nine major clades of Bignoniaceae as proposed by Olmstead et al. (2009). *Number above branches* represent bootstrap support, followed by posterior probabilities (recovered from Olmstead et al. 2009); *Asterisk* indicates 100 % posterior probabilities

Bignoniaceae have diffuse porous woods (Fig. 2a), except for the species growing in subtropical and temperate regions, which are semi-ring porous (Fig. 2b) to ring-porous. Most lianas, on the other hand, have semi-ring porous woods (Fig. 2c). Growth rings are typically delimited by a line or band of marginal parenchyma (Fig. 2a, b), thickwalled and radially flattened fibers (Fig. 2c) and occasionally ray dilatation at the limits of the growth rings (Fig. 2c). Many species also have very narrow vessels associated with the marginal parenchyma (Fig. 2a). Vessel dimorphism (the association of very wide and very narrow vessels) is widespread in the lianas (Fig. 2c). Tyloses on the heartwood are only rarely encountered, but common in Catalpaeae (Fig. 2b), Spathodea campanulata, and occasionally sparsely present in the woods of other species, including the lianas. Most Bignoniaceae have a straight grain (Fig. 2d), but the grain may sometimes be wavy (Fig. 2e) or interlocked (as in some specimens of Handroanthus). Axial parenchyma is paratracheal (Fig. 2a-c), varying from scarce (Fig. 2c) to abundant (Fig. 2b), with confluences forming bands. Crystals are common in the family and generally confined to ray cells (Fig. 2i), silica is absent (except in Pachyptera kerere). All qualitative and quantitative traits analyzed are presented in Table 1, while a summary of the most conspicuous features is given in Table 2. Below we characterize the wood anatomy of each major clade of the Bignoniaceae currently recognized (Olmstead et al. 2009; Fig. 1).

M. R. Pace et al.

	Climate of occurrence	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Temperate	Tropical	Tropical	Tropical	Subtropical (Montame)	Subtropical (Montane)	Temperate (Montane)	Tropical	Subtropical	Tropical	Subtropical	Tropical	Tropical	Temperate	Subtropical	Temperate	Subtropical (arid)
	type of cambial variant	MA	NA	NA	NA	NA	NA	Perimedullar phibern	W	NA	NA	NA	NA	NA	NA	NA	NA	NA	W	MA	NA	W	MA	NA
	Crystals		Present in rays	Present in rays						•			,	Present in rays	Present in rays	•		Present in rays				Present in rays		
	Perforated ray cells							+		e	+		,	•	e-	+								
	sy Septate F fibers						. T	+	+	+	+		0.0	+	+	+		+ 6 0	. रू	+ 0 T		+		+
	lar Vessel-ri on pitting	1 Similar 1 1 intervess re pits	Similar 1 ar intervess	r to Similar t intervess ar rits	Similar 1 ar intervess cits	lar Simlar 1 ph intervess ls pits	lar Similar 1 pht intervess Is pits	lar Similar 1 ph1 intervess ls pits	1 Simlar 1 1 intervess re pits	lar Similar 1 intervess pits	lar Simlar 1 intervess pits	ber Similar 1 pht Intervess Is pits	ler Similar 1 phi Intervess Is pits	lar Similar 1 phi Intervess Is pits	lar Similar 1 intervess pits	er Intervess pits	Similar 1 ar intervess pits	1 Simlar 1 1 Intervess re pits	Simlar 1 ar intervess pits	Simlar 1 ar intervess pits	1 Simple 1 1 semi- re borderei	1 Simple 1 re borderei	1 Simple 1 re bordere	1 Simple 1 1 semi- re borderer
	Rays: cellu compositio	Homo and hetero with row of squa	Homosilu	Homocellula sightly heternoelul	Homosellul	Heterocellu with 2-4 square/upri marginal ce	Heterocellu with 2-4 square/upri marginal ce	Heterocellu with 2-4 square/upri marginal ce	Homo and hetero with row of sque cells	Heterocellu mixed	Heterocellu mixed	Heterocellu with 2-4 square/upri/ mercinal.ce	Heterocellu with 2-4 square/upri mercinal ce	Heterocellu with 2-4 square/upri marcinal ce	Heterocellu mixed	Heterocellu mixed	Homocellul	Homo and hetero with row of squa cells	Homocelul	Homoelu	Homo and hetero with row of squa cells	Homo and hetero with row of squa cells	Homo and hetero with row of squa cells	Homo and helero with row of squa cells
	er height	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Hgh >1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Hgh >1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm
Ray width	In numt of cell	2±1	±5 1±1	±4 3±1	1±0	±4 3±1	3#0	46 341	±6 2±1	49 341	±4 2±0	2±0	2±1	±7 2±0	~	±3 2±0	±7 3±0	48 3±1	46 3±0	3±0	±3 3±1	46 341	±5 3±1	±5 3±1
	ucture In I		- 20			- 24		8	- 21	. 32.	- 19			- 21		- 21	.8	- 33	8	8	- 28		- 25	. 35
	ands Strands	3-4) cells strand	3-4) cells strand	5-8) cells strand	5-4) cells strand	3-4) cells strand	8-4) cells strand	8-4) cells strand	3-4) cells strand	5-8) cells strand	5-8) cells strand	3-4) cells strand	3-4) cells strand	3-4) cells strand	3-4) cells strand	3-4) cells strand	3-4) cells strand	8-4) cells strand	5-4) cells strand	3-4) cells strand	3-4) cells strand	3-4) cells strand	3-4) cells strand	3-4) cells strand
	yma str	Four (Four (Eight (Four (Four (Four (Four (Four (Eight (Eight (Four (Four (Four (Four (Four (Four (Four (Four (Four (Four (Four (Four (Four (
	ma Diffu: trea parench	·		~	•				e9 -	•			•	5	·	•	•		9	•				-
Axial	cell mean a (µm2)	~	313 ± 15	685 ± 13	0	278±77	¢-	192 ± 61	361±11	80 ± 32	103±36	¢.	¢-	338 ± 13	٢	106 ± 40	374 ± 11	268 ± 60	221 ± 10	359 ± 4/	246±65	388 ± 23	567 ± 31	354 ± 16
	AXIBI parenchym: frequency	~	10%	36	~	2%	e-	12	4%	3%	4%	e-	0	%L	~	0.5%	7%	1%	8%	10%	2%	7%	7%	14%
	Confluence	Short	Long. forming	Long. forming framds	Long. forming bands	Short	Short	Absent	Long. forming bands	Absent	Absent	Absent	Absent	At short sectors	Absent	Absent	Long. forming bands	Absent	Short	Short	Absent	Short	Absent	Absent
	Patratracheal parenchyma	Alform	Alform	Aliform	Aliform	Alform	Alform	Scanty	Alform	Scanty	Scanty	Scanty	Scanty	Vasioentric	Scanty	Scanty	Vasiosntric	Scanty	Vasiontric	Alform	Scanty	Alform	Vasicentric	Scanty
	Helical thickening			•				+			•		,	+									•	٠
	Intervessel pit size (µm)	~	72±2	8,4 ± 4	10.9±2	10.3±2	10.2 ± 3	8.2 ± 1	9.4 ± 3	6	6.2 ± 3	e-	e-	4.3±1	~	5.6±4	9.0±2	4.0±1	3.1±3	5.3±2	11.1 ±3	6.3 ± 4	7.3 ±2	4.1±1
	Perforation plate	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Reticulate or foraminate plate present	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Reticulate or foraminate plate present	Reticulate or foraminate plate present	Smple	Simple	Simple	Simple
	w Tyloses	•		•	•	•			•	•		+	+	+	•	•					+	+	•	+
ssel diamete mean	de Narro sels vessel m) (µm)	AM 7	±7 NA	±40 MA	AN NA	±8 NA	2 NA	±36 26±0	±42 MA	t 14 ± 5	E 18 19 ± 1	AN VA	AN VA	E 13 NA	P NA	±4 NA	± 23 NA	e 12 NA	E 26 NA	± 18 NA	±17 32±8	± 10 MA	±36 26±	±16 31±1
*	ressel quency w sr mm2) ves (µ	e-	89 810	3±5 300	~	1±10 75	e-	50±91 158	6±5 125	35±17 83.	26±20 66	e-	e-	8±11 73	e-	12±38 30	8±11 70	6±20 70:	27 ± 8 80	4±4 179	10±3 204	6±4 131	4±11 200	4±10 142
	Vessel fre orphism (pr					. 2		*		+	+		,		+	÷								е •
	(group din	12	67.0	820	030	020		0.51	80	0.58	0.36			0.53		0.40	990	121	030	031	± 0.22 ± 3.18	90.36	± 0.18 ± 9.68	±0.75 ±2.43
	Vessels	×3 2.11±	×3 1.64±	3 1234	×3 1.37±	2091	2	3 5.32 ±	134±	3 222±	264±	2	2	×3 2.08±	2	ti 1,93±	×3 226±	×3 2.93 ±	-1.94 ±	x3 1.24±	EW 140	1.58 ±	EW 1.32	EW 2.00
	Vessel	Solitary to multiples of 2	Solitary to multiplies of 2	Solitary to multiples of 2	Solitary to multiples of 2	Solitary to multiples of 2	Solitary to multiples of 2	Solitary to multiples of 2	Solitary to multiples of 2	Solitary to multiples of 2	Solitary to multiples of 2	Solitary to multiples of 2	Solitary to multiples of 2	Softary to multiples of 2	Solitary to multiples of 2	Solitary to multiples of 2 or more, radii	Solitary to multiplies of 2	Softary to multiples of 2 & Radial multiples	Solitary to multiples of 2	Soltary to multiples of 2	Solitary to multiples of 2	Solitary to multiples of 2	Solitary to multiples of 2	Solitary to multiples of 2
	Vessel arrangement	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Tangential bands	Radial pattern	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse
Growth ring	marker: flattened fibers	+	+	+		•	÷	+	•	•	+		٠		~	٠	+		+	•	•		•	•
	rowtn ring irker.dilated rays					÷	÷			•		,	,	•	~	•	+			+				,
	orowtn ring k marker: ma parenchyma	+	+		÷	+	÷			÷	+	÷		+	e-		+	+	+	÷	+	÷		÷
	Porosity	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Porous	Diffuse	Semi-ring porous	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Semi-ring porous	Diffuse	Diffuse	Diffuse	Semi-ring porous	Diffuse	Semi-ring porous	Semi-ring porous
	Habit	Tree	Tree	Tree	Tree	Tree	Tree	Liana	Tree	Liana	Liana	Tree	Tree	Tree	Liana	Shrub/Lian a	Tree	Tree	Tree	Tree	Tree	Tree	Tree	Small tree
	Species	Dipomphia densicoma	lacaranda brasiliana	Arcaranda copaia	lacaranda obtusifolia	lacaranda puberuka	Jacarandia uter	Campais radicana	Deptenches bancare	Pandorea jasminoides	Podranea ricasoliana	Tecome cochabambensis	Tecome fulve	Tecome stans	Tecomentine dendrophila	Tecomania capenais	Tecomella undulata	Detostome integrifolie	Milingtonia hartensis	Droxyhum kralicum	Cataba bignoniories	Cataba longissime	Cataba spectosa	Chilopsis (hearis
	Tribe or clade		,	,	JACARANDEAE	÷	-		-		-	TECOMFAF						DELOSTOMA		OKOVILEAE		-	CATALPEAE	-

Table 1 Analyzed species, habit, xylem characters and climate of occurrence

Table 1 continued

	Climate of occurrence	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Temperate	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical
	type of cambial variant	Four phloem wedges	Four phloem wedges	lutiple of four phioem wedges	Four phloem wedges	Four phloem wedges	Four phicem wedges	Four phloem wedges	Four phloem wedges	phioem wedges	phioem wedges	phioem wedges	Included philoem wedges	Included phicem wedges	lultiple of four phloem wedges	fultiple of four phloem wedges	lultiple of four phloem wedges	luhiple of four phioem wedges	luhiple of four phinem wedges	Four phicem wedges	Four phloem wedges	Four phloem wedges	Multiple dissected phioem wedges	Multiple dissected phioem
	Crystals			Present in M rays	•		~								2	2	2 ~	2	2				,	
	Perforated ray cells	÷		~	•	~	~	~	+	÷	+			+	~	٠	÷	·		•		•	·	٠
	ay Septate F fibers	+	+ 0 10	0 10	*	~ p	~ 7	~ P	+	+	+	+	+	+	+ 9 ਵਿ	+		+ 0 ফ	+ 0 12	+ 0 12	+	• 1	+ 0 क	+ 0 ਵ
	ilar Vessel-n on pitting	liar Simple t semi- bordere	liar Simple I semi- bordere	liar Simple I semi- bordere	liar Simple t semi- bordere	liar Simple (semi- bordere	Simple t semi- bordere	itar Simple I semi- bordere	iar Simple I semi- bordere	ilar Similar 1 intervess	liar Similar I pits	itar Similar 1 pits pits	itar Similar 1 intervess pits	far Simlar 1 pits	itar Similar 1 pits	liar Similar 1 pits	liar Similar 1 pits	ilar Similar t intervess ptts	liar Similar 1 intervess	ilar Similar 1 intervess ptts	liar Simple t semi- bordere	liar Simple t semi- bordene	d Similar 1 11 Intervess are pits	d Similar 1 11 intervess are pits
	Rays: cellu compositi	Heterooellu mixed	Heterooellu mixed	Heterocellu mixed	Heterocellu mixed	Heterocellu mixed	e	Heterocellu mixed	Heterocellu mixed	Heterocellu mixed	Heterocellu mixed	Heterocellu mixed	Heterocellu mixed	Heterocellu mixed	Heterocellu mixed	Heterocellu mixed	Heterocellu mixed	Heterocellu mixed	Heterocellu mixed	Heterocellu mixed	Heterocellu mixed	Heterocellu mixed	Homo and hetero with row of squs cells	Homo and hetero with row of sque
	Ray eer height	Hgh>1 mm	Hgh>1 mm	Hgh>1 mm	Hgh >1 mm	Hgh>1 mm	¢	High >1 mm	High >1 mm	High >1 mm	High >1 mm	High >1 mm	Hgh >1 mm	Hgh >1 mm	Hgh >1 mm	Hgh >1 mm	Short <1	Hgh>1 mm	Hgh>1 mm	Short <1 mm	Short <1 mm	۰.	Short <1 mm	Short <1 mm
Ray width	m In numt of cell	3 # 1	11 3±1	6 4±1	1 H CO	2±1	~	2±1	4±1	3 9±3	6±2	¢	5±1	8±2	9 2±1	5±3	4 # 1	3±1	4 #	4 ± 1	:3 1±0	4 ± 1	5 1±0	
	ture In µ	~	41±	707	e-	~	~	~	¢-	42 ±	~	~	~	~	20 Ŧ	~	c-	19 ±	¢.	e-	18±	e-	53 73	
	rma Stor s struc	ad adds	als d	oels Td	alls b	silis bi		ad the	al si	edis 1	sleo P	step p	dels.	step p	site Id	11 전	al b	al b	sile Personal	oells D	adis de la contra	alls b	48 72 48	d dels
	Parench strand	Four (3-4) per stra	Four (3-4) per stra	Four (3-4) per stra	Four (3-4) per stra	Four (3-4) per stra	~	Four (3-4) per stra	Four (3-4) per stra	Four (3-4) per stra	Four (3-4) per stra	Four (3-4) per stra	Four (3-4) per stra	Four (3-4) per stra	Eight (5-8) per stra	Four (3-4) per stra	Four (3-4) per stra	Four (3-4) per stra	Four (3-4) per stra	Four (3-4) per stra	Four (3-4) per stra	Four (3-4) per stra	Four (3-4) per stra	Four (3-4) per stra
	Diffuse parenchym:		•	•					•	•	•		•	•		·	·		•	•	•	•	•	•
Axial	parenchyma cell mean area (µm2)	r-	171±53	62 ± 22	e-	p	e	0-	e-	185±65	0-	0	¢.	0-	111 ± 44	r-	r	200 ± 66	155±35	ę.,	113 ± 37	ę.,	128±21	•
	Axial parenchyma frequency	~	% 4	\$ <u></u>	e-	e-	0-	0-	e-	6%	e-	e-	~	e-	3%	e-	e-	2%	1% %	e-	<u>%</u>	e-	4% %	
	Confluence	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Short	Absent	Absent	Absent	Absent
	latratracheal barenchyma	Scarfy	Scanty	Scanty	Scanty	Scarby	Scanty	Scanty	Scanty	Scanty	Scanty	Scanty	Scanty	Scanty to vasioentric	Scanty	Scanty	Scarby	Scarty	Scanty	Vasicentric	Scanty	Scarby	Scanty	Scantry
	Helical F hickening																÷						•	
	tarvessel t size (µm) 1	~	11.2 ± 3	6.4 ± 1	e-	r-	e-	¢	¢.	52 ±2	¢.	¢.	~	~	52 ±2	r-	r-	5.6 ± 3	72 ±1	e-	42±1	e-	5.3±2	
	erforation Ir plate pi	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple
	Tyloses P																							
diameter ean	Narrow vessels (µm)	r-	26 ± 10	12±4	e-	e-	e-	0-	e-	33±9	e-	e-	0	e-	19±8	e-	e-	28±8	27±8	e-	NA	19±6	16±9	
Vessel	y Wide () vessels (µm)	~	137 ± 28	70±15	e-	~	~	~	~	293 ± 60	~	~	~	~	106 ± 16	~	e-	137 ± 15	156 ± 29	e-	45±10	74 ± 22	111 ± 23	•
:	n frequenc	~	45±10	236±3;	~	~	~	~	¢.	36 ± 36	¢	c	~	c	122 ± 6	~	e-	131±2	48 ± 25	~	28±17	~	140 ± 4	,
	Vessel dimorphis	+	*	+	•				+	+	+	+	+	+	+	+	+	+	•	•	•	•	٠	+
	Vessels/group	~	1.52 ± 0.28	1.37 ± 0.47	¢.	c-	c.	~	~	4.73 ± 3.25	¢.	~	ć	1.55 ± 0.59	2,46 ± 1.06	2.31 ± 0.25	۴	3.55 ± 0.44	2.40 ± 0.87	1.90 ± 0.56	1.80±0.31	e-	2.13±0.52	1.32 ± 0.25
	Vessel grouping	Solitary to sultiples of 2-3	Solitary to uttiples of 2-3	Solitary to utliples of 2-3	Solitary to utliples of 2-3	Solitary to uttiples of 2-3	Solitary to uttiples of 2-3	Solitary to uttples of 2-3	Solitary to utiples of 2-3	Solitary (wide vessels)	Solitary to uttiples of 2-3	Solitary to uttiples of 2-3	Solitary (wide vessels)	Solitary to uttples of 2-3	Solitary to uttples of 2-3	Solitary to uttples of 2-3	Solitary to uttples of 2-3	Solitary to uttiples of 2-3	Solitary to uttiples of 2-3	Soltary (wide vessels)	Solitary to utliples of 2-3	Solitary to utliples of 2-3	Soltary (wide vessels)	Solitary (wide vessels)
	Vessel rrangement	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse
rowth ring	marker: fattened a fibers	÷	+	+	÷				+	+	+	+	NA	+	+	~	+	÷		·	+		÷	+
	owth ring ceriditated rays		+	+					+	+			NA					+					,	
	wth nng Gro larker: mari anchyma	÷	+	+					+	+	+	+	NA	+			+	+			+		+	+
	rosity Gro	mi-ring arous	iffuse	mi-ring orous	mi-ring orous	iffuse	iffuse	iñuse	mi-ring orous	mi-ring orous	mi-ring orous	mi-ring orous	wth ring bsent	ñuse	ifuse	ffuse	orous	ffuse	iffuse	iffuse	iffuse	iffuse	iffuse	iffuse
	abit Pc	8 -	eue	ene S c	g e	dunh	quu	hinb	я с щ	g d	s e	s -	iana Gro	ena D	ena D	ere D	ere P	eres D	eus	ensi D	qnų	ensi	ere D	Bina
	Ξ	estum Li	nsum L.	icatum L.	forum L	twictum S.	sum Si	prinum St	aneum Li	enum Li	Aum Lı	د	latum L.	د	2	2	د	E	E	L	ú	تـ	96 1	his Li
	Species	Adenocalymma bracl	Adenocalymma como	Adenocalymma divar	Adenocsiymma flevil	Adenocalymma neo®	Adenocalymma nodo	Adenocalymma perej	Adenocal)mma salm	Απρηίορηκη αυοίο	Amphilophium elonge	Amphilophium megnolitichium	Amphilophium panici	Amphilophium pulveralentum	Anemopaegma chamber/aynV	Bignonia campanulat	Bignonia capreolata	Bignonia magnifica	Bignonia prieurei	Cellchlamys letfolia	Cuspiderie pulchre	Cuspiderie corvalute	Dolichandra unguis-o	Dolichandra quadriva
	Tribe or clade												BIGNONIEAE											

	cumate of occurrence	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical		Tropical	Tropical	Tropical	Tropical
Type of	cambial	Four phloem wedges	Four phloem wedges	Four phloem wedges	Four phloem wedges	Four phloem wedges	Multiple of four philoem wedges	Multiple of four phloem wedges	Multiple of four philoem wedges	Four phloem wedges	Multiple of four philoam wedges	Multiple of four philoem wedges	Multiple of four phloem wedges	Four phloem wedges	Four phloem wedges	Four phloem wedges	Four phloem wedges	Four phloem arcs	Four phioem wedges	Four phloem wedges	Four phloem wedges	Multiple of four phioem weddes	Four phloem wedges	Four phloem wedges	Four phloem wedges	Four phloem wedges	Four phicem wedges	Four phloem wedges	Four phloem wedges
	Crystals		¢-										-		Present in rays	Present in rays	Present in rays												
	ray cells	+	+		٠	٠	+	+	+	+	+	+	+	+	+		+	+	·	+	÷	+	+	+		+	+	+	+
	ay septate fibers	+	+		+	+	+	*	+	+	+	+	+	+	+	*	+	+	*	*	+	+	+	+	0.18	*	+	+	+
	on pitting	similar 1 intervess ptts	Itar Similar 1 intervess cits	Idar Similar 1 intervess	semi- semi- bordere	similar 1 intervess pits	d Similar 1 11 intervess are pits	d Simlart 11 intervess are pits	d Simlar 1 are intervess	ilar Similar I intervess	similar 1 intervess pits	Idar Similar 1 pits	Idar Similar 1 intervess pits	idar Similar 1 pits pits	ilar Simlar 1 pits	Ilar Similar 1 intervess	dar Similar 1 intervess pits	ilar intervess pits	ilar Similar I intervess	ilar Similar I intervess	Ilar Similar I Intervess	ilar Similar 1 pits pits	similar 1 Similar 1 Dits	Idar Similar 1 intervess cits	illar I Similar 1 pits	ilar Simlar intervess plb	d Simlart are intervess	dar Simlart pds	idar Similar 1 pits
	compositi	Heterocellu mixed	Heterocellu mixed	Heterocellu mixed	Heterocellu mixed	Heterocellu mixed	Homo an hetero with row of squa cells	Homo an hetero with row of sque cells	Homo an hetero with now of squa cells	Heterocallu mixed	Heterocellu mixed	Heterocellu mixed	Heterocellu mixed	Helerocellu mixed	Heterocellu mixed	Heterocellu mixed	Heterocellu mixed	Heterocallu mixed	Heterocellu mixed	Heterocellu mixed	Heterocellu mixed	Heterocellu mixed	Heterocellu mixed	Heterocellu mixed	Heterocellu mixed	Heterocellu mixed	Homo an hetero with row of sque cells	Heterocellu mixed	Heterocellu mixed
å	ser height	Hgh >1 mm	Hgh >1 mm	Hgh >1 mm	Short <1 mm	Hgh >1 mm	Short <1 mm	Hgh >1 mm	Hgh >1 mm	Short <1 mm	Hgh >1 mm	Hgh >1 mm	Hgh >1 mm	Hgh >1 mm	Short <1 mm	Short <1	Hgh >1 mm	Hgh >1	Hgh 1	Hgh >1 mm	Hgh >1 mm	Hgh >1 mm	Short <1 mm	Hgh >1 mm	High >1 mm	Hgh >1	Short <1 mm	Hgh >1 mm	High >1 mm
Ray width	In num of cel	5 4±1	? 2±'	±1 3±	3±1	±5 3±1	±8 3±1	3 # 1	31	±5 2±1	±18 4±1	6	3±1	±8 3±7	•	±5 3±0	? 2±1	±8 3±1	±4 1±0	6	44	±5 4±1	±3 2±1	3±1	6	±18 3±1	±10 3±1	6	+20 5+1
	ructure									-	- 21			- 20		. 29	,	. 30	- 13			- 52	. 25			-	- 31		. 63
	strands st	Four (3-4) cells per strand	Four (3-4) cells per strand	Eight (5-8) cells per strand	Eight (5-8) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Eight (5-8) cells per strand	Eight (5-8) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand			
	umuse arenchyma																												
Axial	parencriyma cell mean area p (µm2)	~	~	171 ± 72	~	89 ± 23	212 ± 140	¢	¢	167 ± 60	154±45	0	~	244 ± 78		127 ± 45	113±50	116 ± 52	100 ± 55	0	e-	165 ± 32	103 ± 28	~	~	185 ± 44	123 ± 55	~	276 ± 53
Axial	parenchyma frequency	~	0	1%	~	ř.	14%	e-	¢	1%	\$	~	e-	8		35	\$	4%	\$ <u>5</u>	e-	e-	1%	8	e	r-	89	ř.	~	ŝ
	Confluence	Absent	Absent	Absent	Short	Short	Short	Absent	Absent	Short	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Short	Short	Absent
	arracracreal	Scanty	Scanty	Scanty	Vasioentric	Vasioentric	Vasioentric	Scanty	Vasioentric	Vasicentric	Scanty	Scanty	Scanty	Scanty	Scanty	Scanty	Scanty	Scanty	Scanty	Scanty	Scanty to vasioentric	Scanty	Scanty	Scanty	Scanty	Vasicentric	Aiform	Aiform	Afform
	thickening p																,												
	pit size (µm)	ċ	~	6.1 ±3	6	9.0 ± 1	9.4 ± 1	~	0	12.4±2	6.0±1	~	~	7.0 ± 4		7.6±2	88±3	8.4 ± 1	83±2	¢.	ć	9.6±2	6.9±3	6	ć	10.3 ± 2	83±3	6	1.6 ± 1
	plate	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple
	r Tyloses	•	•		•		•		•	•	•	•	•		÷	•	•	•	•	•	•		•	•		•	•		
issel diameter mean	de Narrov sels vessel m) (um)	~	~	± 20 NA	2	±37 20±1	∓ <i>51</i> 20∓6	~	~	±43 23±6	±25 22±6	~	~	±32 35±1	•	±25 16±5	+28 24 ±7	±15 23±8	±25 15±5	6	~	±26 29±9	±30 14±3	~	6	±54 21±7	±37 17±6	6	±66 15±5
Vessel	er mm2) wes	~	0	14±5 72	~	18±36 133	01±30 232	c-	~	13±20 216	09±14 139	~	~	l7±19 192		00±7 109	15±12 118	00±17 112	8±27 167	e-	¢-	15±18 138	i2±19 190	6	~	i0±40 290	l7±25 208	~	15 265 265
	norphism (p	٠	÷		٠	+			+			+		+		•	+	+	•		·	+	+	·	٠	•	+	٠	+
	sselsigroup di	~	292 ± 1.01	1.31 ± 0.26	~	3.01 ± 1.03	8.69 ± 1.48	c-	~	2.12 ± 0.59	2.80 ± 0.33	0	~	8.76 ± 1.33	~	2.83 ± 0.65	2.41 ± 0.57	225 ± 0.62	3.31 ± 0.85	0	¢-	2.03 ± 0.37	229±0.82	~	163 ± 1.77	e-	8.00 ± 0.41	~	248 ± 0.69
	ssel grouping Ve	Solitary to ultiples of 2-3	Solitary to ultiples of 2-3	Solitary to ultiples of 2-3	olitary (wide vessels)	olitary (wide vessels)	olitary (wide vessels)	olitary (wide vessels)	olitary (wide vessels)	Solitary to utiples of 2-3	Solitary to ultiples of 2-3	Solitary to ultiples of 2-3	Solitary to ultiples of 2-3	idial multiples of 4 or more common	Soltary to utiples of 2-3	Soltary to utiples of 2-3	Softary to utipies of 2-3 and small ssets in radial	Soltary to Utiples of 2-3	Soltary to utiples of 2-3	Soltary to utiples of 2-3	Solitary to ultiples of 2-3	Solitary to ultiples of 2-3	olitary (wide vessels)	Solitary to ubples of 2-3	Solitary to "	Soltary to utiples of 2-3	olitary (wide vessels)	Soltary to ultiples of 2-3	Solitary to ultiples of 2-3
	ressel sngement Ve	esniji d	Diffuse	Diffuse	Diffuse	osnjijo	iffuse to 5	iffuse to 5	Diffuse	esnulo	Biffuse	Diffuse	u esnjijo	R mattern R	esnyu	esnuid	m method fail	esnijio	esnuid	esnuid	Billuse	Diffuse	Diffuse	Diffuse	asnijid	esnyu	Diffuse	Diffuse	Diffuse
wth ring	anxer: Ittened arr Ibers		+	+			+	+	+	÷	+	+	+	+	+		+			÷	÷	+		+	+		+	+	
th ring Gro	ays							~															÷						
owth ring Grow	marker: marke renchyma ri	*	+		+	,				÷	,		,	*						•	÷	٠	+	+	•		+	+	
Gr	orosity i	ami-ring orous	smi-ring orous	osniji	emi-ring orous	asnyj	Diffuse	ami-ring ocrous	emi-ring orous	ami-ring orous	office	ositijo	office	ashiji	offuse	offuse	Offuse	emi-ring orous	esniji	ami-ring orous	ami-ring orous	tmi-ring crous	osnjij	osniji	asuffuse	offuse	ami-ring orous	jiffuse	smi-ring orous
	Habit P.	Liana Se p	Liana Se	Shrub D	Liana Se	Liana D	Liana D	Liana Se	Liana Se P	Liana Se	Liana D	Liana D	Liana D	Liana D	Liana D	Liana D	Liana D	Liana Se	Liana D	Liana Se	Liana Se	Liana Se	Liana D	Liana D	Liana D	Liana D	Liana Se	Liana D	Liana Se P
	Species	bia chica	bia conjugata	nia platyphylla	na samydoides	bia speciosa	· damazi	glazioviana	eđuoj,	sella cordifalla	e difficilis	e anahuelooides	e standley	sfla obovata	tertia mirabilis	terdia sp. nov.	stera karere	fhomega vellozor	tloms metoides	toms stichadente	itoma tetraqueta	egie venusta	muhada muhet	nuic bisbistum	num ducker	nim pramidatum	sutergeo suff	ragma mynianthum	astrations prationse
	Tribe or clade	Frideni	Frideni	Frideni	Frideni	Frideni	Tundia	Lundia	Frindle	oenah	Manso	Manso	Manso	Martin	BIGNONIEAE Neojoo	Neglor	Pachy	Perian	Pleana	Pleano	Pleano	Pyrost	Stizopt	Tanaec	ranaec	Tärraet	Tymant	Angel X	Xyidah

Table 1 continued

🖄 Springer

Table 1 continued

Climate of occurrence		Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical
Type of cambial variant		NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	W	NA	NA	NA	W	NA	NA	NA	NA	W
Crystals	December	Present in ays and axial parenchyma		Present in ays and axial parenchyma						Present in rays						Present in rays						Present in rays						
Perforated ray cells							.			,										,								
ay Septate fibers		9 78	9 78	9 8	9 %	+ 9 78		9 %	9 8	- 	- - 78	- - 18	9 18	9 78	9 18	9 8	9 8	9 8	9 38	- 	9 18	9 F	e 78	e 78	9 %	9 R	- 9 98	- - 3
ilar Vessel-r on pitting	Contrary.	lar interves pits	Similar Intervesi pits	Similar Iar intervesi pits	Similar Iar intervesi pits	Similar Infervesi pits	Similar lar intervesi pits	Bir intervesi pits	Similar Intervest pits	d Similar 11 intervesi are pits	Similar lar intervesi pits	Similar lar interves cits	Similar Iar intervesi pits	Iar Intervesi pits	Similar Bar intervesi ptts	lar intervesi pits	lar intervest pits	d Similar 11 Intervesi are pits	Similar Intervesi ptts	Similar Ian Intervesi pits	Similar Iar intervesi pits	Similar Iar intervesi pits	Similar lar intervesi ptts	Similar Iar intervesi pits	Similar Iar intervesi pits	Similar Iar intervesi pits	d Similar 11 intervesi are pits	d Similar 11 intervesi are pits
Rays: cellu compositi		Homocellu	Homoeilu	Homosellu	Homoellu	Homoellu	Homoellu	Homoellu	Homoellu	Homo an hetero wit row of squ	Homoellu	Homocellu	Homoellu	Homocellu	Homoellu	Homooellu	Homocellu	Homo an hetero with row of sque cells	Homoellu	Homosellu	Homoellu	Homocellu	Homosellu	Homoellu	Homoeilu	Homoellu	Homo an hetero wit row of squa cells	Homo an hetero wit row of squa cells
Ray height		Short <1	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm	Short <1 mm
Ray width In numt	of cell	±4 1±0	E6 1±0	±6 1±0	£7 1±0	E4 2±0	±4 2±0	Ł5 3±1	2±1	£5 3±1	3±0	3±0	£7 2±1	E6 3±0	2±0	2±1	Ł4 3±1	£7 2±0	63 240	2±0	e7 2±1	±3 1±0	2±1	2±0	2±0	Ŧ	E8 3±1	2±1
oried acture	Î	+ 17:	+	+	+	8	+ 21:	8	+	- 22 +	+	+	+ 21:	-28 +	*	+	+	- -		+	+ 24:	+ 12:	+	-3 (E)	*	+	9 +	+
ichyma Si ands str		alls per and	oolts per and	3-4) cells strand	3-4) cells strand	3-4) cells strand	3-4) cells strand	3-4) cells strand	sells per & Four (3- per strand	3-4) cells strand	alls per and	sells per and	olds per and	3-4) cells strand	sells per and	sells per & Four (3- per strand	3-4) cells strand	3-4) cells strand	5-4) cells strand	3-4) cells strand	3-4) cells strand	3-4) cells strand	8-4) cells strand	3-4) cells strand	alls per and	3-4) cells strand	3-4) cells strand	3-4) cells strand
se Parer yma str		o owT sb	Two c str	Four (; per	Four (Four (Four (Four (Two c strand { 4) cells	Four (Two c	o owT sb	Two c	Four (Two o str	Two c strand { 4) cells	Four (Four (; per	Four (Four ()	Four (Four (Four (Four (Two c	Four ()	Four ()	Four (
ma Diffu area parench						*		4					10		·					•								
Axial parenchy cell mean : (um2)		501 ± 13	811±44	187 ± 4	539 ± 14	165 ± 4	321±10	277 ± 11	0	504 ± 11	r-	c	492 ± 11	257 ± 9	e-	~	206±2	279±6	86 ± 42	e-	505 ± 26	366 ± 11	~	r-	e-	e-	291 ± 12	0
Axial parenchym frequency		29%	% <u>9</u>	25	45%	12%	19%	4%	~	18%	e-	e-	34%	5%	0	¢	3%	13%	4%	ć	26%	27%	~	~	¢	~	14%	ć
Confluence		forming bands	Long, forming bands	Short & Long, forming bands	Long, forming bands	Short & Long, forming bands	Long, forming bands	Short	Absent	Short	Short	Short	Long. forming bands	Short	Short	Absent	Short	Short	Short	Short	Long, forming bands	Short & Long, forming bands	Short & Long. forming bands	Short & Long. forming bands	Short & Long, forming heade	At short sectors	Long. forming bands	Long, forming bands
Patratracheal parenchyma		Alform	Alform	Alform	Alform	Aliform	Alform	Vasioentric	Scanty	Vasioentric	Miform	Alform	Alform	Alform	Aliform	Vasioentric	Vasioshtric	Vasioentric	Alform	Alform	Alform	Alform	Alform	Alform	Alform	Alform	Vasioentric	Vasioentric
Helical thickening		•	·	•	•			•		•			·	•	·			•		•					•			,
Intervessel pit size (µm)		¢	4.3 ± 3	5.4 ±2	¢-	4.3±2	3.1 ± 0.8	6.5±3	~	5.3±2	11.2 ± 4	12.4±2	19.1±3	12.2±2	11.3±2	~	5.1 ± 1	2.5±1	6.3 ± 1	5.2±2	4.3±1	8.3±2	~	~	e-	¢.	6.7±2	6.3±1
Perforation		Simple	Simple	Reticulate or foraminate plate present	Simple	Reticutate or foraminate plate present	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Reticulate or foraminate plate present	Reticulate or foraminate plate present	Simple	Simple	Simple	Simple	Simple	Simple	Reticulate or foraminate plate present	Simple
Tyloses		·	•	•	•		•	•	•	,	•		·	•	·		+	,		•	•	+						,
mean mean le Narrov	(mil) (tim)	25 NA	8 NA	11 NA	-9 NA	6 NA	6 NA	- 29 NA	NA	8: MA	MA	NA	11 NA	±2 NA	MA	NA	25 NA	18 NA	¥ ⊨	MA	15 NA	12 NA	MA	NA	MA	NA	13 NA	W
resel Ver mm2) Wi	(ht	±7 69±	I±6 63:	1±7 55±	5±4 59:	±10	3±4 45:	3±6 107:	~	±16 42:	r-	~	F 16 6 Ŧ 9	2±5 125	~	6	5±5 97±	±18 83±	±19 50±		±10 66±	F #5 _ L F J	~	r-	6	e.	±16 59±	6
ssel V ophism free (pe					-	4		÷					. 2				÷	in ,			-							
A mile		325	030	131	132	137	356	131		120		124	52	030	22	133	0.19	0.45	131		336	040					040	332
Vessels/g		3 1.55±(3 1.24±(3 1.34±(3 1.38±(3 1.58±(3 2.08±(3 1.51±0	2	3 2.22±(3 7	3 1.20±(3 1.40±(3 1.49±0	3 1.43±0	3 1.84±(3 1.20±0	3 1.83±(1.74±0	3	3 1.47±(3 1.74±(۰ د	~	3	¢.	3 1.85±(3 1.37±0
Vessel grouping		Soltary to multiples of 2-	Solitary to multiples of 2-	Soltary to multiples of 2-	Solitary to multiples of 2-	Solitary to multiples of 2-	Solitary to multiples of 2-	Solitary to multiples of 2-	Solitary to multiples of 2-	Softary to multiples of 2-	Soltary to multiples of 2-	Soltary to multiples of 2-	Solitary to multiples of 2-	Solitary to multiples of 2-	Solitary to multiples of 2-	Solitary to multiples of 2-	Solitary to multiples of 2-	Solitary to multiples of 2-	Soltary to multiples of 2-	Solitary to multiples of 2-	Solitary to multiples of 2-	Solitary to multiples of 2-	Solitary to multiples of 2-	Soltary to multiples of 2-	Solitary to multiples of 2-	Solitary to multiples of 2-	Solitary to multiples of 2-	Soltary to multiples of 2-
Vessel arrangement		Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Tangential bands	Diffuse	Diffuse	Tangential bands	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse
Growth ring marker: flattened flbers		•	·	•	•			•		•	•	+	+	٠	٠	+	+	+		•		+	+	+		+		,
rowth ring inker:dilated rays														÷	٠	+		+										
owth ring G marker: mu renchyma		+	÷	+	÷	+	÷	+	+	+		+	+			+	+	÷		+	÷	+	+	+		+	+	+
par Gr		Xffuse	Offluse	Affuse	Offluse	Offluse	Office	ami-ring torous	Affuse	smi-ring torous	Miluse	Xfluse	Bittinge	Offluse	Muse	Affuse	se&Semi- ring	Affuse	Offluse	Offuse	Office	Affuse	Xifuse	Xilluse	Offuse	Office	smiring	asuffic
Habit		Tros	Tree	Small tree	Small tree	Tree	Tree	Tree S	Lee	Tree	Tree	Tree	Tree	Tree	Tree	Tree	Tree DIM	Tree	Tree	e.	Tee	Tree	Tree	Tree	Tree	Tree	ee S	-Tree
Species		Amphileona latifolia	Amphilecna regalis	Crescentie stata	Crescentia cujere	Parmerdiera macrophylla	Cybistax antisyphilitica	Ekmaniantihe actinophylia	Ekmanienthe kongittora	Godmanie sescultole	Handroanthus albus	Handroanthus barbatus	Handroanthus chrysotrichus	Handroanthus impetightosus	Handroanthus serratifotus	Paratecoma peroba	Roseodenation downell- smithii	Sparattosperma leucanthum	Spircfecome spirats	Tabebula surea	Tabebula cassinoides	Tababuis fluviallis	Tabebuie hefenophylle	Tabebuis obtusifolia	Tabebule rigide	Tabebula roseoalba	Zeythenia montana	Zeyheria fuberculosa
Tribe or clade				TABEBUIA ALLIANCE (CRESCENTIEAE)															TABEBUIA ALLIANCE									

973

M. R. Pace et al.

	Type of Climate of Climate of cambial occurrence variant	NA Subtropical (and)	Present in NA Tropical rays	Present in NA Tropical rays	- Tropical	- NA Tropical	NA Tropical	Present in NA Tropical rays	? NA Tropical	Present in NA Tropical rays	- NA Tropical	Present in NA Subtropical rays	Present in NA Subtropical rays	. NA Tropical	Present in NA Tropical rays	- NA Tropical	- NA Tropical	- NA Tropical	- NA Tropical	Present in NA Tropical rdys	. NA Tropical	NA Tropical	. NA Tropical	Present in NA Tropical rays	Present in NA Tropical rays		- NA Tropical
	allular Vessel-ray Septate Perforated	and Similar to quare intervessel cuare pits	Similar to allular Intervessel pits	Similar to slutar intervessel cits	Similar to Bluiar intervessel pits	end Similar to with 1 intervessel quare pits	and Similar to vith 1 intervesed quare pits	and and Similar to quare pits	and and Simple to quare bordered +	and Simple to with 1 Semi- + quare bordered	s Simlar to silutar intervessel	and Similar to with 1 intervessel - quare pits	s	and Similar to with 1 intervessel quarte pits	Similar to slutar intervessel nits	and Simple to with 1 Simple to quare bondered (+)	s Similar to silutar intervessel - nits	and Similar to with 1 intervessel (+) - quare pits	and Similar to with 1 intervessel (+) quare pits	end Similar to with 1 Intervessel (+) s	with 1 Similar to with 1 intervessel (+) outer pits	and Similar to with 1 intervessel (+) quarte pits	s . Similar to silular intervessel -	pros Simitar to siturar intervessel pits	Similar to alular intervessel - cits		and Similar to with 1 intervessel quare
	Ray Rays:c sight compo	Home ort <1 helero mm row of s	ott <1 Homoo	ort <1 Homoo	ort <1 Homoc	ont <1 heam mm row of a	Hom: ort <1 helero mm row of s	ort <1 hellero mm row of s	ont<1 hellero mm row of s	Ham: ort <1 helero mm row of §	ort <1 Homoc	Hom: ort <1 hetero mm row of §	ot <1 hellero ort <1 hellero mm row of s	Hom. ort<1 helero mm row of s	ort <1 Homoo	cert <1 hetero mm row of 5	ort <1 Homoo	Homi cort <1 hetero mm row of s	cert <1 helsero mm row of 5	ort <1 hellero mm row of s	Hom: ort<1 helero mm row of s	on Home ont<1 hellero Tim row of s	ort <1 Homoo	ott <1 Homoo	ort <1 Homoo	1 terres	humu ort <1 hetero mm row of
	ried Ray width F cture In number ho of cells	- ? 2±1 SK	- ? 1±0 Sh	- 7 1±0 Sh	. 15±4 1±0 Sh	? 1±1 Sh	- 41±7 3±1 Sh	7 2±0 Sh	- 40±7 3±1 Sh	- ? 2±1 Sh	. 31±9 2±0 Sh	. 18±5 2±1 Sh	- 7 2±1 Sh	- 41±8 2±0 Sh	- 21±5 1±0 Sh	3±0 Sh	- 12±2 1±0 Sh	- 7 3±1 Sh	3±0 Sh	. 35±5 3±0 Sh	- 7 3±1 Sh	. ? 3±0 Sh	? 1±0 Sh	- ? 1±0 Sh	- 14±2 1±0 Sh		- 39±12 3±1 ^{Sh}
	Parenchyma St strands stn	Two cells per strand & Four (3- 4) cells per strand	Two cells per strand	Two cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand	Four (3-4) cells per strand		Two cells per strand
	Diffuse parenchyma		+	+											•								+	٠	+		
	Axial parenchyma cell mean area (µm2)	¢	~	¢	310 ± 109	¢-	300 ± 95	~	494 ± 141	e-	499 ± 144	213 ± 91	~	1198 ± 529	356 ± 97	~	126 ± 65	ć	~	278 ± 80	¢-	¢-	~	e-	259 ± 124		371 ± 126
	Axial parenchyma frequency	~	~	c-	952	e-	23%	e	13%	e-	27%	% 6	e-	38%	16%	~	5%	~	~	10%	e-	e-	~	e-	14%		18%
	Confluence	Short	Short	Short	Short & Long, forming bands	Short & Long, forming bands	Absent	Absent	Short	Absent	Long. forming bands	Short	Short	Long, forming bands	Short	Short	Short	Long. forming bands	Short	Short	Short	Short	Short	Short	Short	Long,	forming
	Patracheal parenchyma	Aliform	Vasioentric	Aliform	Alform	Alform	Aliform	Scanty	Alform	Scanty	Aliform	Aliform	Aliform	Alform	Alform	Aliform	Aliform	Alform	Aliform	Alform	Vasioentric	Vasioentric	Aliform	Alform	Vasioentric		Aliform
	el Helical n) thickening								•									•					•		+		•
	on Intervessi pit size (µr	0	e-	e-	or 16 6.1±1 ent		5.2 ± 1	0-	8.3±3	e-	7.2±2	5.2 ± 3	te or	:or le 4.7±2 ent	22±1	0	7.5±2	0	0	ior 16 4.3±2 ent	¢-	¢-	~	¢-	22±1		7.8±2
	ses Perforati plate	Simple	Simple	Simple	Reticulatic foramina plate pres	Reticulation foramina plate pres	Simple	Simple	Simple	Simple	Simple	Simple	Reticulatic foramina plate pres	Reticulati foramina plate pres	Simple) Simple	Simple	Simple	Simple	Reticulatik foramina plate pres	Simple	Simple	Simple	Simple	Simple		Simple
	seter arrow Tylos ssels	, NA	NA.	NA	W	W	NA	NA	NA	NA	NA	NA	W	W	NA	(+) VV	W	NA	NA	NA.	- NA	- NA	NA	NA	NA.		+ NA
	Vessel diar mean Wide N vessels w	~	~	~	72±22	e-	92 ± 19	P~	112 ± 26	е.	137 ± 26	96 ± 34	r-	133 ± 19	68±14	~	51 ± 13	¢	~	74±9	e-	e.	ć	e-	77 ± 14		136±34
	Vessel frequency (per mm2)	0	e-	e-	10±9	e-	73±21	e-	14±6	e-	6±4	49 ± 29	~	11±5	21 ± 12	0-	39 ± 14	e-	0-	24±9	e-	e-	¢-	e-	34±8		8±5
	Vessel dimorphis		•	·			•		,	·		•			·	•		•	•			•	•	•			•
	Vessels/group	0	1.97 ± 0.24	~	2.29 ± 1.02	¢-	2.58 ± 1.64	1.50 ± 0.23	1.29 ± 0.17	1.28 ± 0.20	1.12 ± 0.12	1.15 ± 0.19	e-	1.60 ± 0.36	1.68 ± 0.33	1.25 ± 0.47	1.61 ± 0.17	~	~	1.29 ± 0.18	¢-	¢-	~	e-	1.81 ± 0.36		1.30 ± 0.28
	sel grouping	Solitary to tiples of 2-3	Solitary to tiples of 2-3 and some	custers Soltary to tiples of 2-3	Solitary to tiples of 2-3	Solitary to tiples of 2-3	Soltary to tiples of 2-3	Soltary to tiples of 2-3	Solitary to tiples of 2-3	Solitary to tiples of 2-3	Solitary to tiplies of 2-3	Soltary to tiples of 2-3	Soltary to tiples of 2-3	Soltary to tiples of 2-3	Solitary to tiples of 2-3	Solitary to tiplies of 2-3	Soltary to tiples of 2-3	Solitary to tiplies of 2-3	Solitary to tiplies of 2-3	Solitary to tiples of 2-3	Soltary to tiples of 2-3	Soltary to tiples of 2-3	Solitary to tiples of 2-3	Solitary to tiples of 2-3 and some	cusers Solitary to tiples of 2-3	Solitary to	tiples of 2-3
	Vessel Ves	Diffuse m.	illi esnyild	ui esnijio	Diffuse m.	Diffuse	Diffuse	Diffuse	ie espyc	iế esnylici	Diffuse	illi esnijio	Diffuse m.	um esuño	ili esnyo	Diffuse m.	ili esnijio	Diffuse m.	Diffuse m.	Diffuse m.	ill esnylo	ш екрис	Diffuse m.	in asund	Diffuse m.		Ē
	wth ring harker: attened arra libers	+	+	+		+	+	+			+		+		•	+	+	+	+	+	+		+		+		
	wth ring Gr ar-dilated fi						+		,			÷															
	th ring Gro river: marks chyma	+																	+								
	Grow sity mai	esn	8	850	85	89	85	Hring Dus	8	esn	esn	Pring ous	Build Build	8	esn	650	85	esn	esn	89	-	esn	850	en	850		-
	abit Porc	hrub Diff	Belet Diff	eelet Diff	Diff	ee,	Diff	Sem por	Diff.	jiee Dill	Diff.	ree Poor	al tree Sem	e Dil	Lee Dill	Lee Diff	free Diff	Diff Diff	Line Diff	Jill Dill	Liee Diff	ue Diff	eelet Diff	eelet Diff	UH DH	10	B
ontinued	Species	phractes alexandrii S	a gentry/	a rosuprinata	frandrone atroviews	thandrone spathacea	andoa adenophylla	andoa magnifica	rophragma Niocolare	1 muenths emberdo	la athcana	f	hamia sipulata Sm	bouidite ise vis	ocales floribunds	neka kongifolia	arthron bojeranum	amachera ignea	rmachera gigarrioa	rmachere glandulosa	amschera pionsta	vmachera skrica	tocolea multifiora	tocalea nycteriphille Tr	Socolea felfarii		notes campanters
uble 1 cc	Tribe or clade	Cator	Coles	Cates	Dalier	Dake	Ferra	Ferra	Heter	Heter	Kigek	MaM	Aland	PALEOTROPICAL Newb CLADE	Optic	Pajan	Phylit	Rade	Rada	Rade	Rade	Rada	Rhod	Rhod	Rhod	Conth	unda

974



Fig. 2 General wood anatomical features of Bignoniaceae. a *Tabebuia rigida*, transverse section (TS), diffuse porous wood with aliform parenchyma with short confluences and growth rings delimited by a line of marginal parenchyma (*arrows*) associated with very narrow vessels (*arrowheads*). b *Chilopsis linearis*, TS, semi-ring porous wood, growth rings marked by a band of marginal parenchyma and radially flattened fibers, tyloses common. c *Mansoa difficilis*, TS, scanty paratracheal parenchyma, growth rings marked by radially flattened fibers (*arrows*) and dilated rays (*asterisks*). d *Roseodendron*

Jacarandeae

We sampled six of the 51 species representing both genera, *Digomphia* (one of three species) and *Jacaranda* (five of 49

donnell-smithii, longitudinal tangential section (LT), straight grain, multiseriate non-storied rays. **e** *Dolichandrone atrovirens*, LT, wavy grain, multiseriate non-storied rays. **f** *Tabebuia aurea*, TS, scanning electron microscopy of simple perforation plate. **g** *Handroanthus barbatus*, LT, intervessel pits alternate. **h** *Campsis radicans*, longitudinal radial section (LR), perforated ray cell **i** *Radermachera glandulosa*, LR, prismatic (*arrow*) and navicular (*arrowhead*) crystals in rays. *Scale bars* **a**, **c**, **d**, **e** 200 µm, **b** 400 µm, **f** 20 µm, **g**, **i** 50 µm, **h** 100 µm

species), currently included in the tribe (Lohmann and Ulloa 2006 onwards). Representatives of both *Jacaranda* sections *Monolobos (J. copaia, J. brasiliana* and *J. obtusifolia)* and *Dilobos (J. puberula* and *J. ulei)* were sampled.

Tribe or clade	Habit	Porosity	Growth ring marker: parenchyma	Growth ring marker:dilated rays	Growth ring marker: flattened fibers	Vessel arrangement	Vessel grouping	Vessel T dimorphism T	yloses P	Perforation plate t	Helical F hickening	² atratracheal parenchyma	Confluence	Diffuse parenchyma	Parenchyma strands	Storied structure	Ray height	Rays: cellular composition	Vessel-ray pitting	Septate fibers	Perforated ray cells	Crystals
JACARANDEAE	Trees, and a few subshrubs in arid zones	Diffuse	÷	+1	÷	Diffuse	Solitary to multiples of 2-3			Simple		Aliform	Short to long		Four (3-4) cells per strand		Short <1 mm	Homocellular in Jacaranda Monolobos and heterocellular in Jacaranda Dilobos	Similar to intervessel pits			Present in the rays of some species
TECOMEAE	Mostly lianas, with few trees and shrubs	Diffuse to ring- porous	+1		+	Diffuse	Solitary to multiples of 2-3	+ in lianas		Simple +	- in species ing-porous	Scanty to vasicentric	Absent from present	•	Mostly four (3- 4) cells per strand		Short <1 mm and hight > 1mm in lianas	Heterocellular	Similar to intervessel pits	+	+ in lianas	Present in the rays of some species
DELOSTOMA	Trees	Diffuse	+			Radial pattern	Solitary to multiples of 2-3 & Radial multiples			Simple		Scanty	Absent		Four (3-4) cells per strand		Short <1 mm	Homo and hetero with 1 row of square cells	Similar to intervessel pits	+		Present in rays
OROXYLEAE	Trees, a few lianas	Diffuse	+	+1	+	Diffuse	Solitary to multiples of 2-3	,	- tor	Reticulate, aminate and simple		Vasicentric to aliform	Short	•	Four (3-4) cells per strand		Short <1 mm	Homocellular	Similar to intervessel pits	+1	i	
CATALPEAE	Trees	Semi-ring porous	+		+	Diffuse	Solitary to multiples of 2-3		+	+ Simple	 in species semi-ring porous 	Scanty to aliform	Absent to short		Four (3-4) cells per strand		Short <1 mm	Homo and hetero with 1 row of square cells	Simple to semi- bordered	+1		Present in the rays of some species
BIGNONIEAE	Liana, a few shrubs	Diffuse to semi- ring porous	+	+	+	Diffuse	Solitary to multiples of 2-3	+		Simple		Scanty to aliform	Absent	•	Four (3-4) cells per strand	, present in but a few species	Generally high >1 mm	Heterocellular mixed	Predominantly similar to intervessel pits	+	+	Present in the rays of some species
TABEBUIA ALLIANCE	Trees	Diffuse	+	•	•	Diffuse	Solitary to multiples of 2-3	•	- W	ostly Simple		Aliform	Generally long, forming bands	•	2-4 cells per strand	+	Short <1 mm	Homocellular	Similar to intervessel pits		•	When present, in both rays and axial
PALEOTROPICAL CLADE	Trees and shrubs	Diffuse	+	+1	+1	Diffuse	Solitary to multiples of 2-3		- W	ostly Simple		Aliform	Short to long	+ in Coleeae	Four (3-4) cells per strand		Short <1 mm	Homo and hetero with 1 row of square cells	Similar to intervessel pits			parencnyma Present in the rays of some species
Key: + prese	ent, – at	sent, 2 i	unsample	pe																		

🖄 Springer

 Table 2
 Synopsis of the wood features and habits by tribe/clade

Diagnostic features

Jacarandeae have a unique combination of winged-aliform axial parenchyma, with short to long confluences, non-storied structure, and non-septate fibers.

Detailed description

Growth rings are distinct to indistinct, delimited by thickwalled and radially flattened fibers associated with narrow vessels (Fig. 3a), sometimes with dilated rays (e.g., Jacaranda puberula, J. ulei) and a line of marginal parenchyma (Fig. 3d). Porosity diffuse. Vessels solitary (Fig. 3a) or in multiples, predominantly of 2-3 (Fig. 3b-d), 1.68 ± 0.40 vessels/group, narrow, $70 \pm 8 \,\mu m$ in diameter (Jacaranda *copaia*, very wide 300 μ m), and 17 \pm 10/mm² in frequency (J. copaia 3 ± 5). Perforation plates are simple. Intervessel pits are medium (7-10 µm in diameter). Vessel-ray pits are similar in size and shape to the intervessel pits. Fibers are nonseptate, thin (Fig. 3a) to thick-walled (Fig. 3b), with simple to minutely bordered pits. Parenchyma is winged-aliform (Fig. 3a), lozenge to winged-aliform in *Digomphia* (Fig. 3b), with short (Fig. 3a-b) to long confluences (Fig. 3c-d) sometimes forming lines that vary from 1 to 4 cells; and marginal parenchyma forming lines of 1-2 cells (Fig. 3d). Parenchyma strands are mostly of 4 cells, except from J. copaia, which has 5-8 cells per strand. Rays are non-storied, with a contrasting composition between sections Monolobos and Dilobos. In Jacaranda section Monolobos rays are uniseriate and homocellular (J. brasiliana and J. obtusifolia; Fig. 3e, f), except from J. copaia (species atypical within section Monolobos), with 2-4-seriate homocellular to slightly heterocellular rays (with one row of marginal square cells). In Jacaranda section Dilobos rays are biseriate and heterocellular, with 2-4 marginal upright to square cells (J. puberula and J. ulei; Fig. 3g, h). In Digomphia, rays are biseriate, homo and heterocellular with one row of marginal square cells.

Tecomeae

We sampled nine of the 52 species currently included in Tecomeae s.s. (Lohmann and Ulloa 2006 onwards). Our sampling included members of eight of the 11 genera currently recognized in the tribe; only *Campsidium*, a monotypic genus from Chile and Argentina, *Incarvillea*, an herbaceous genus from the Himalayas, and *Lamiodendron*, a monotypic genus from Papua New Guinea, were not sampled. We sampled: *Campsis radicans* (1 of 2 species), *Deplanchea bancana* (1 of 5 species), *Pandorea jasminoides* (1 of 6 species), *Podranea ricasoliana* (monotypic), *Tecoma cochabambensis*, *T. fulva* and *T. stans* (3 of 12 species), *Tecomanthe dendrophila* (1 of 5 species), and *Tecomaria capensis* (1 of 2 species).

Wood anatomy of the Bignoniaceae



Fig. 3 Wood anatomy of Jacarandeae. a Jacaranda copaia, TS, winged-aliform parenchyma, with short confluences, and very wide vessels with about 300 µm. Growth rings delimited by radially flattened fibers (arrows). b Digomphia densicoma, TS, lozenge to winged-aliform parenchyma with short confluences, growth rings delimited by thicker-walled and radially flattened fibers (arrows). c Jacaranda puberula (section Dilobos), TS, winged-aliform parenchyma, with long confluences, growth rings delimited by thicker-

Diagnostic features

The wood anatomy of members of Tecomeae is fairly homogeneous (except for *Deplanchea bancana*), with most differences being associated with the habit. The wood of self-supporting Tecomeae is characterized by the combination of narrow vessels (generally in high frequencies; except in *Deplanchea bancana*), scanty paratracheal axial parenchyma (except *Deplanchea bancana*, with wingedaliform parenchyma with long confluences) and septate fibers. These characters are also encountered in the lianas, except for the vessel width, which reaches wider diameters in the lianas. The lianas also have vessel dimorphism. The rays are non-storied and heterocellular.

Detailed description

Growth rings are distinct, delimited by more abundant and wider vessels in the limits of the earlywood (Fig. 4a),

walled fibers associated with narrow vessels (*arrows*). **d**-**f** Jacaranda brasiliana (section Monolobos). **d** TS, Winged-aliform parenchyma, forming long confluences, growth rings delimited by a line of marginal parenchyma (*arrows*). **e** LT, uniseriate rays. **f** LR, homocellular rays. **g**, **h** Jacaranda puberula (section Dilobos). **g** LT, multiseriate and heterocellular rays. **h** LR, heterocellular rays with four rows of upright to square cells. Scale bars 200 µm

thick-walled and radially flattened fibers (Fig. 4b), and a line of marginal parenchyma (Fig. 4c). Very narrow vessels are sometimes associated with the marginal parenchyma (Fig. 4c). Porosity diffuse in the tropical species (Fig. 4b-d) and ring-porous to semi-ring porous (Fig. 4a) in the temperate and montane species (Table 1). Vessels are solitary to multiples of 2–3 (Fig. 4a, c, d), 2.54 ± 1.28 vessels/group. In Tecomaria capensis vessels are solitary to multiples of 2-4 or more, radially disposed (Fig. 4b). Vessels are narrow $(55 \pm 12 \ \mu m)$, with higher values in the lianas, and the highest values in the earlywood of Campsis radicans (average 300 µm). Perforation plates are simple, sometimes foraminate in Deplanchea bancana. Intervascular pits are small (5–7 µm). Vessel-ray pits are similar in size and shape to the intervessel pits. Fibers are septate (Fig. 4e), thin- to thick-walled, with simple pits. Parenchyma is normally scanty paratracheal to vasicentric, winged-aliform in Deplanchea bancana, forming long confluences (Fig. 4d); a line of marginal parenchyma often 978



Fig. 4 Wood anatomy of Tecomeae s.s. a *Tecoma stans*, TS, semiring porous wood, narrow vessels solitary to multiple of 2–3, scanty paratracheal parenchyma. b *Tecomaria capensis*, TS, diffuse porous wood, narrow vessels, solitary to multiples of 2–4 or more common, radially disposed, growth rings delimited by thicker-walled and radially flattened fibers (*arrows*). c *Podranea ricasoliana*, TS, diffuse porous wood, growth rings delimited by a line of marginal

delimits the growth rings (Fig. 4c). Parenchyma strands have 3–4 cells in the trees and shrubs, and 5–8 cells per strand in the lianas. *Rays* are non-storied (to irregularly storied in some samples of *Tecoma stans*), 2–3-seriate, heterocellular with 2–4 marginal upright to square cells (Fig. 4e); in the lianas heterocellular with procumbent, square and upright cells mixed (except in *Campsis radicans*, which has heterocellular rays with 2–3 marginal upright to square cells). In *Deplanchea bancana* rays homo and heterocellular with one row of square cells co-occur.

Delostoma

We sampled *Delostoma integrifolium*, one of the four species recognized in this genus (Lohmann and Ulloa 2006 onwards).

parenchyma (*arrows*), vessel dimorphism present, scanty paratracheal parenchyma. **d** *Deplanchea bancana*, TS, diffuse porous wood, vessels solitary to multiples of 2–3, winged-aliform parenchyma with long confluences. **e** *Tecomaria capensis*, LT, biseriate heterogeneous rays, non-storied. **f** *Tecoma cochabambensis*, LR, heterocellular ray with body cells procumbent and three to four marginal upright to square cells. *Scale bars* **a–d** 500 µm, **e**, **f** 200 µm

Diagnostic features

In this species vessels are narrow, the parenchyma is scanty paratracheal, rays are non-storied, heterocellular with one row of square marginal cells co-occurring with homocellular rays, and fibers are septate (Fig. 5a–d).

Detailed description

Growth rings are distinct, delimited by a line of marginal parenchyma (Fig. 5a, b). Very narrow vessels are sometimes associated with the marginal parenchyma (Fig. 5b). *Porosity* diffuse (Fig. 5a, b). *Vessels* are solitary to multiples of 3–5, (Fig. 5a, b), 2.93 ± 1.21 vessels/group, narrow (40 ± 20 µm), with 46 ± 20/mm² of frequency.

Wood anatomy of the Bignoniaceae



Fig. 5 Wood anatomy of *Delostoma integrifolium*. **a** TS, narrow vessels solitary to multiples of two to four, scanty paratracheal parenchyma to vasicentric, growth ring delimited by a line of marginal parenchyma. **b** TS, narrow vessels in radial arrangement,

scanty paratracheal parenchyma, growth ring delimited by a line of parenchyma and radially flattened fibers (*arrows*). **c** LT, rays two to three-seriate, non-storied. **d** LR, homocellular rays, septate fibers (*arrows*). *Scale bars* **a**, **c**, **d** 200 μ m, **b** 250 μ m

Perforation plates are simple. *Intervascular pits* are minute $(3-4 \mu m)$. *Vessel-ray pits* are similar in size and shape to the intervascular pits. *Fibers* are septate (Fig. 5d), thin- to thick-walled, with simple pits. *Parenchyma* is scanty paratracheal (Fig. 5a, b) to vasicentric, with a line of marginal parenchyma delimiting the growth rings (Fig. 5a, b). Parenchyma strands have 3-4 cells. *Rays* are non-storied, and predominantly 3-seriate (Fig. 5c, d), heterocellular with 1-2 rows of square marginal cells co-occurring with homocellular rays (Fig. 5c, d).

Crescentiina

Crescentiina are divided in two subclades, the *Tabebuia* alliance and the Paleotropical clade, each of which is described in detail below. Crescentiina are characterized by abundant, aliform confluent parenchyma, either with short or long confluences, short rays, generally homocellular or homocellular and heterocellular simultaneously, with the heterocellular rays having only one row of square marginal cells.

Tabebuia alliance (including Crescentieae)

We sampled 27 out of the 146 species currently included in the *Tabebuia* alliance, representing 13 out of the 14 genera currently included in this clade (Lohmann and Ulloa 2006 onwards); only *Romeroa*, a monotypic genus from Colombia, was not sampled. Sampling included *Amphitecna* (2 of 6 species), *Crescentia* (2 of 18 species), *Cybistax antisyphilitica* (monotypic), *Ekmanianthe* (both species), *Godmania* (1 of 2 species), *Handroanthus* (5 of 30 species), *Paratecoma peroba* (monotypic), *Parmentiera* (1 of 9 species), Roseodendron (1 of 2 species), Sparattosperma (1 of 2 species), Spirotecoma (1 of 4 species), Tabebuia (7 of 67 species), Zeyheria (both species). Of these, Amphitecna, Crescentia, and Parmentiera belong to tribe Crescentieae, a monophyletic group nested within the Tabebuia alliance.

Diagnostic features

The wood of representatives of the *Tabebuia* alliance is characterized by the small to medium vessels, associated with abundant vasicentric to aliform axial parenchyma with short to long confluences. All genera have storied or irregularly storied axial and radial elements. Fibers are non-septate. Lapachol (yellow compound) was encountered in the heartwood of a few genera, such as *Ekmanianthe*, *Godmania*, *Handroanthus* and *Zeyheria*.

Detailed description

Growth rings are distinct, delimited by a line (Fig. 6a, c, d) or band (Fig. 6b) of marginal parenchyma, sometimes associated with very narrow vessels (Fig. 6c), thick-walled and radially flattened fibers (very common in *Handroan*-thus and *Tabebuia*), and in some species dilated rays (e.g., *Handroanthus impetiginosus*, *H. serratifolius*, *Paratecoma peroba*, *Sparattosperma leucanthum*). *Porosity* diffuse (Fig. 6a, b, d) to semi-ring porous (Fig. 6c). Vessels are solitary to multiples of 2–3, 1.62 ± 0.30 vessels/group, arranged tangentially in *Cybistax antisyphilitica*, narrow $(60 \pm 26 \ \mu\text{m})$ in most genera, medium in *Handroanthus* and *Sparattosperma* (134 ± 45 \ \mum), numerous (20 ± 12/