

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
© 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 morpho-anatomical 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 sub-clades, the *Tabebuia* alliance and the Paleotropical clade, which share abundant aliform parenchyma, short and

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. Bignoniaceae 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 · Bignoniaceae · 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

R. G. Olmstead
Department of Biology, University of Washington,
Seattle, WA 98195, USA

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 Jacarandaeae. 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 slender-stemmed 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

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 Safranin (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 early-wood 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 measured 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

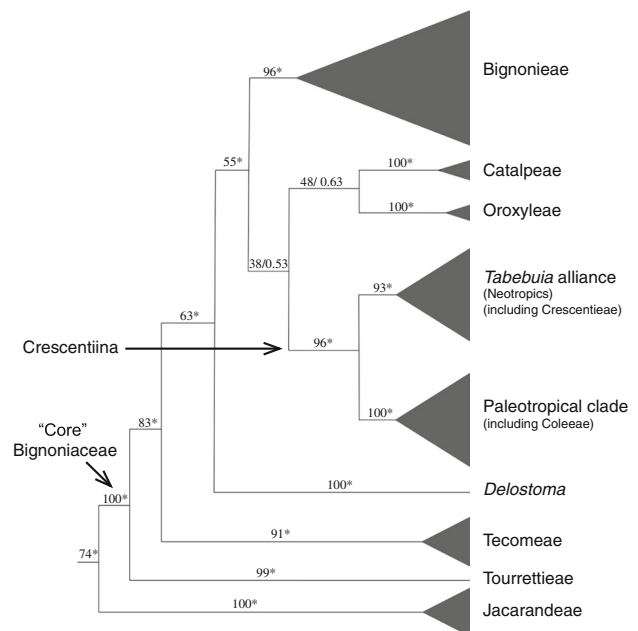


Fig. 1 Phylogenetic relationship of the nine major clades of Bignoniaceae as proposed by Olmstead et al. (2009). Number above branches represent bootstrap support, followed by posterior probabilities (recovered from Olmstead et al. 2009); Asterisk indicates 100 % posterior probabilities

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), thick-walled 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).

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

Title or code	Species	Habit	Porosity	Growth ring marker: macrotracheids	Growth ring marker: microfibrils	Vessel grouping	Vessel arrangement	Vessel diameter (µm)	Vessel frequency (per mm ²)	Vessel wall thickness (µm)	Vessel lumen diameter (µm)	Tracheids	Perforation plate	Helical thickening	Panniculate	Confusion	Axial parenchyma	Diffuse parenchyma	Panniculate strands	Striated structure	Ray width		Perforated rays	Crystals	Type of cambial variant	Climate of occurrence	
																					µm	µm					µm
	<i>Dysoxylum devocionis</i>	Tree	Diffuse	+	+	Solitary to multiples of 2-3	2.11 ± 1.22	?	?	?	?	NA	Single	?	Altium	Short	?	?	Four (3-4) cells per strand	?	2.1 ± 1	Short <1 mm	?	?	NA	Tropical	
	<i>Jacaranda brasiliensis</i>	Tree	Diffuse	+	+	Solitary to multiples of 2-3	1.64 ± 0.29	10 ± 6	68 ± 7	NA	?	Long, forming bands	Single	7.2 ± 2	Altium	Long	10%	313 ± 152	Four (3-4) cells per strand	?	26 ± 5	1.1 ± 1	Short <1 mm	Present in rays	NA	Tropical	
	<i>Jacaranda copata</i>	Tree	Diffuse	+	+	Solitary to multiples of 2-3	1.23 ± 0.23	3 ± 5	300 ± 40	NA	?	Long, forming bands	Single	8.4 ± 4	Altium	Long	9%	665 ± 130	Eight (5-8) cells per strand	?	32 ± 4	3.1 ± 1	Short <1 mm	Present in rays	NA	Tropical	
	<i>Jacaranda maculata</i>	Tree	Diffuse	+	+	Solitary to multiples of 2-3	1.37 ± 0.30	?	?	?	NA	?	Single	10.9 ± 2	Altium	Long	?	?	Four (3-4) cells per strand	?	?	1.0 ± 0	Short <1 mm	?	NA	Tropical	
	<i>Jacaranda zabala</i>	Tree	Diffuse	+	+	Solitary to multiples of 2-3	2.08 ± 0.20	21 ± 10	75 ± 8	NA	?	Short	Single	10.3 ± 2	Altium	Short	5%	279 ± 77	Four (3-4) cells per strand	?	24 ± 4	3.1 ± 1	Short <1 mm	?	NA	Tropical	
	<i>Jacaranda wii</i>	Tree	Diffuse	+	+	Solitary to multiples of 2-3	?	?	?	?	NA	?	Single	10.2 ± 3	Altium	Short	?	?	Four (3-4) cells per strand	?	?	3.0 ± 0	Short <1 mm	?	NA	Tropical	
	<i>Campnos radicans</i>	Liana	Porous	+	+	Solitary to multiples of 2-3	5.32 ± 0.51	370 ± 91	138 ± 36	26 ± 6	?	Scarcely	Single	8.2 ± 1	Scarcely	Absent	2%	192 ± 87	Four (3-4) cells per strand	?	28 ± 6	3.1 ± 1	Short <1 mm	?	?	Prevalent in plant	Temperate
	<i>Dysoxylum ibirovna</i>	Tree	Diffuse	+	+	Solitary to multiples of 2-3	1.34 ± 0.35	6 ± 5	125 ± 42	NA	?	Reconcile or plate present	Reconcile or plate present	8.4 ± 3	Altium	Long, forming bands	4%	351 ± 113	Four (3-4) cells per strand	?	27 ± 6	2.1 ± 1	Short <1 mm	+	NA	Tropical	
	<i>Pendana jamaicensis</i>	Liana	Scarcely porous	+	+	Solitary to multiples of 2-3	2.22 ± 0.58	165 ± 17	63 ± 14	14 ± 5	?	Scarcely	Single	?	Scarcely	Absent	3%	80 ± 32	Eight (5-8) cells per strand	?	32 ± 9	3.1 ± 1	High >1 mm	?	NA	Tropical	
	<i>Podocarpus rosulata</i>	Liana	Diffuse	+	+	Solitary to multiples of 2-3	2.64 ± 0.35	126 ± 20	68 ± 18	19 ± 7	?	Scarcely	Single	6.2 ± 3	Scarcely	Absent	4%	103 ± 38	Eight (5-8) cells per strand	?	19 ± 4	2.0 ± 0	Short <1 mm	+	NA	Tropical	
	<i>Rourea cordobensis</i>	Tree	Diffuse	+	+	Solitary to multiples of 2-3	?	?	?	?	NA	?	Single	?	Scarcely	Absent	?	?	Four (3-4) cells per strand	?	?	2.0 ± 0	Short <1 mm	?	NA	Subtropical (Moravia)	
	<i>Rourea kula</i>	Tree	Diffuse	+	+	Solitary to multiples of 2-3	?	?	?	?	NA	?	Single	?	Scarcely	Absent	?	?	Four (3-4) cells per strand	?	?	2.1 ± 1	Short <1 mm	?	NA	Subtropical (Moravia)	
	<i>Rourea stans</i>	Tree	Diffuse	+	+	Solitary to multiples of 2-3	2.08 ± 0.53	28 ± 11	70 ± 13	NA	?	Altium scores	Single	4.3 ± 1	Vascomitic	Absent	7%	338 ± 132	Four (3-4) cells per strand	?	21 ± 7	2.0 ± 0	Short <1 mm	+	Present in rays	NA	Temperate (Moravia)
	<i>Rourea vancouveria</i>	Liana	Diffuse	?	?	Solitary to multiples of 2-3	?	?	?	?	NA	?	Single	?	Scarcely	Absent	?	?	Four (3-4) cells per strand	?	?	?	High >1 mm	?	NA	Tropical	
	<i>Rourea expansa</i>	Shrubland or tree	Diffuse	+	+	Solitary to multiples of 2-4	1.59 ± 0.40	142 ± 38	30 ± 4	NA	?	Scarcely	Single	5.6 ± 4	Scarcely	Absent	0.5%	106 ± 40	Four (3-4) cells per strand	?	21 ± 3	2.0 ± 0	Short <1 mm	+	NA	Subtropical	
	<i>Rourea vuculata</i>	Tree	Scarcely porous	+	+	Solitary to multiples of 2-3	2.26 ± 0.65	26 ± 11	70 ± 23	NA	?	Long, forming bands	Single	9.0 ± 2	Vascomitic	Absent	7%	374 ± 114	Four (3-4) cells per strand	?	33 ± 7	3.0 ± 0	Short <1 mm	?	NA	Tropical	
	<i>Delostoma integrivola</i>	Tree	Diffuse	+	+	Solitary to multiples of 2-3	2.58 ± 1.21	46 ± 20	70 ± 12	NA	?	Scarcely	Single	4.0 ± 1	Scarcely	Absent	1%	268 ± 62	Four (3-4) cells per strand	?	33 ± 8	3.1 ± 1	Short <1 mm	+	Present in rays	NA	Subtropical
	<i>Melipone horvathi</i>	Tree	Diffuse	+	+	Solitary to multiples of 2-3	1.94 ± 0.30	27 ± 9	80 ± 26	NA	?	Reconcile or plate present	Reconcile or plate present	3.1 ± 3	Vascomitic	Short	8%	221 ± 105	Four (3-4) cells per strand	?	24 ± 6	3.0 ± 0	Short <1 mm	+	NA	Tropical	
	<i>Oryzias indicus</i>	Tree	Diffuse	+	+	Solitary to multiples of 2-3	1.24 ± 0.31	4 ± 4	179 ± 19	NA	?	Reconcile or plate present	Reconcile or plate present	5.3 ± 2	Altium	Short	10%	359 ± 44	Four (3-4) cells per strand	?	39 ± 6	3.0 ± 0	Short <1 mm	+	NA	Tropical	
	<i>Caesalpinia lignovites</i>	Tree	Scarcely porous	+	+	Solitary to multiples of 2-3	EW 45 ± 0.20 UV 13.90 ± 3.18	10 ± 3	204 ± 17	32 ± 8	?	Scarcely	Single	11.1 ± 3	Scarcely	Absent	2%	246 ± 65	Four (3-4) cells per strand	?	28 ± 3	3.1 ± 1	Short <1 mm	+	NA	Temperate	
	<i>Caesalpinia togasana</i>	Tree	Diffuse	+	+	Solitary to multiples of 2-3	1.56 ± 0.36	6 ± 4	151 ± 10	NA	?	Altium	Single	6.3 ± 4	Altium	Short	7%	268 ± 231	Four (3-4) cells per strand	?	32 ± 6	3.1 ± 1	Short <1 mm	+	Present in rays	NA	Subtropical
	<i>Caesalpinia speciosa</i>	Tree	Scarcely porous	+	+	Solitary to multiples of 2-3	EW 133 ± 0.18 UV 24.63 ± 9.88	14 ± 11	200 ± 36	26 ± 7	?	Vascomitic	Single	7.3 ± 2	Vascomitic	Absent	7%	557 ± 311	Four (3-4) cells per strand	?	25 ± 5	3.1 ± 1	Short <1 mm	+	NA	Temperate	
	<i>Chilopsis lewisii</i>	Small tree	Scarcely porous	+	+	Solitary to multiples of 2-3	EW 2.00 ± 0.75 UV 4.69 ± 2.40	34 ± 10	142 ± 18	31 ± 7	?	Scarcely	Single	4.1 ± 1	Scarcely	Absent	14%	354 ± 161	Four (3-4) cells per strand	?	35 ± 5	3.0 ± 1	Short <1 mm	+	NA	Subtropical (and)	

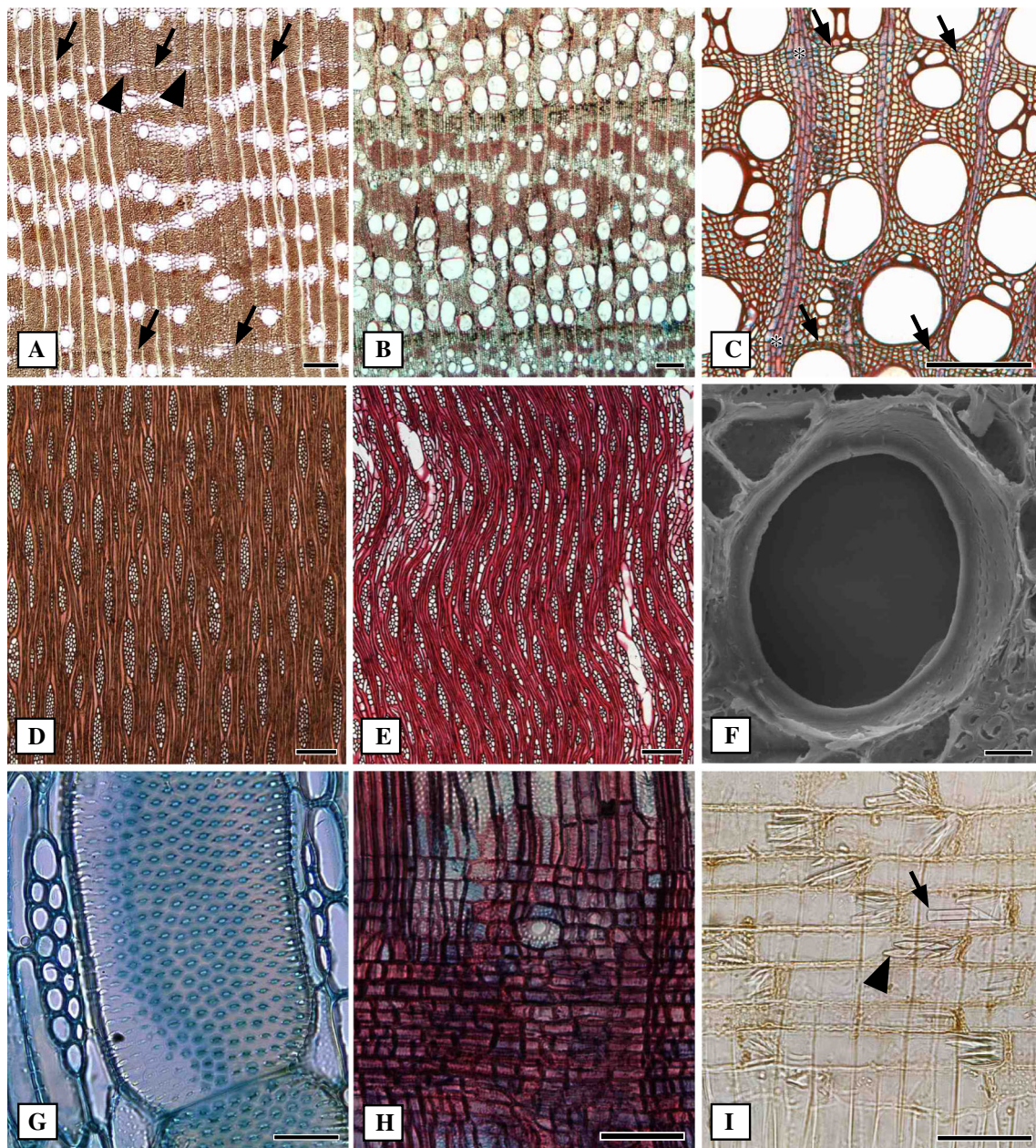


Fig. 2 General wood anatomical features of Bignoniaceae. **a** *Tabebuia rigida*, transverse section (TS), diffuse porous wood with aliform parenchyma with short confluences and growth rings delimited by a line of marginal parenchyma (arrows) associated with very narrow vessels (arrowheads). **b** *Chilopsis 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*

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

Jacarandaeae

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

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.

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

Tribe or clade	Habit	Porosity	Growth ring marker: parenchyma	Growth ring marker: flattened fibers	Vessel arrangement	Vessel grouping	Vessel dimorphism	Vessel tyloses	Perforation plate	Helical thickening	Paratracheal parenchyma	Confluence	Diffuse parenchyma	Parenchyma strands	Stored structure	Ray height	Rays: cellular composition	Vessel-ray pitting	Septate fibers	Perforated ray cells	Crystals
JACARANDEAE	Trees, and a few shrubs in and zones	Diffuse	+	+	Diffuse	Solitary to multiples of 2-3	.	.	Simple	.	Alliform	Short to long	.	Four (3-4) cells per strand	.	Short <1 mm	Homocellular in Jacaranda, Monolobos and heterocellular in Jacaranda Dibobos	.	.	Present in the rays of some species	
TECONIAE	Mostly lianas, with few trees and shrubs	Diffuse to ring-porous	±	+	Diffuse	Solitary to multiples of 2-3	+ in lianas	.	Simple	+ in species ring-porous	Scanty to vascentric	Absent from present	.	Mostly four (3-4) cells per strand	.	Short <1 mm and height > 1 mm in lianas	Heterocellular	+	+	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	+	.	Present in rays	
OROXYLEAE	Trees, a few lianas	Diffuse	+	+	Diffuse	Solitary to multiples of 2-3	.	.	Reticulate, foraminiate and simple	.	Vascentric to alliform	Short	.	Four (3-4) cells per strand	.	Short <1 mm	Homocellular	±	.	.	
CATALPEAE	Trees	Semi-ring porous	+	+	Diffuse	Solitary to multiples of 2-3	.	+	Simple	+ in species semi-ring porous	Scanty to alliform	Absent to short	.	Four (3-4) cells per strand	.	Short <1 mm	Homo and hetero with 1 row of square cells	±	.	Present in the rays of some species	
BIGNONIAE	Liana, a few shrubs	Diffuse to semi-ring porous	+	+	Diffuse	Solitary to multiples of 2-3	+	.	Simple	.	Scanty to alliform	Absent	.	Four (3-4) cells per strand	.	Generally high but a few >1 mm	Heterocellular mixed to intervessel pits	+	+	Present in the rays of some species	
TABERBUA ALLIANCE	Trees	Diffuse	+	.	Diffuse	Solitary to multiples of 2-3	.	.	Mostly Simple	.	Alliform	Generally long, forming bands	.	2-4 cells per strand	+	Short <1 mm	Homocellular	.	.	When present, in both rays and axial parenchyma	
PALEOTROPICAL CLADE	Trees and shrubs	Diffuse	+	±	Diffuse	Solitary to multiples of 2-3	.	.	Mostly Simple	.	Alliform	Short to long	+ in Coleae	Four (3-4) cells per strand	.	Short <1 mm	Homo and hetero with 1 row of square cells	.	.	Present in the rays of some species	

Key: + present, - absent, ? unsampled

Diagnostic features

Jacarandae 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 thick-walled 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, $70 \pm 8 \mu\text{m}$ in diameter (*Jacaranda copaia*, very wide $300 \mu\text{m}$), and $17 \pm 10/\text{mm}^2$ in frequency (*J. copaia* 3 ± 5). *Perforation plates* are simple. *Intervessel pits* are medium ($7\text{--}10 \mu\text{m}$ in diameter). *Vessel-ray pits* are similar in size and shape to the intervessel pits. *Fibers* are non-septate, 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. brasiliensis* 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), *Tecomantha dendrophila* (1 of 5 species), and *Tecomaria capensis* (1 of 2 species).

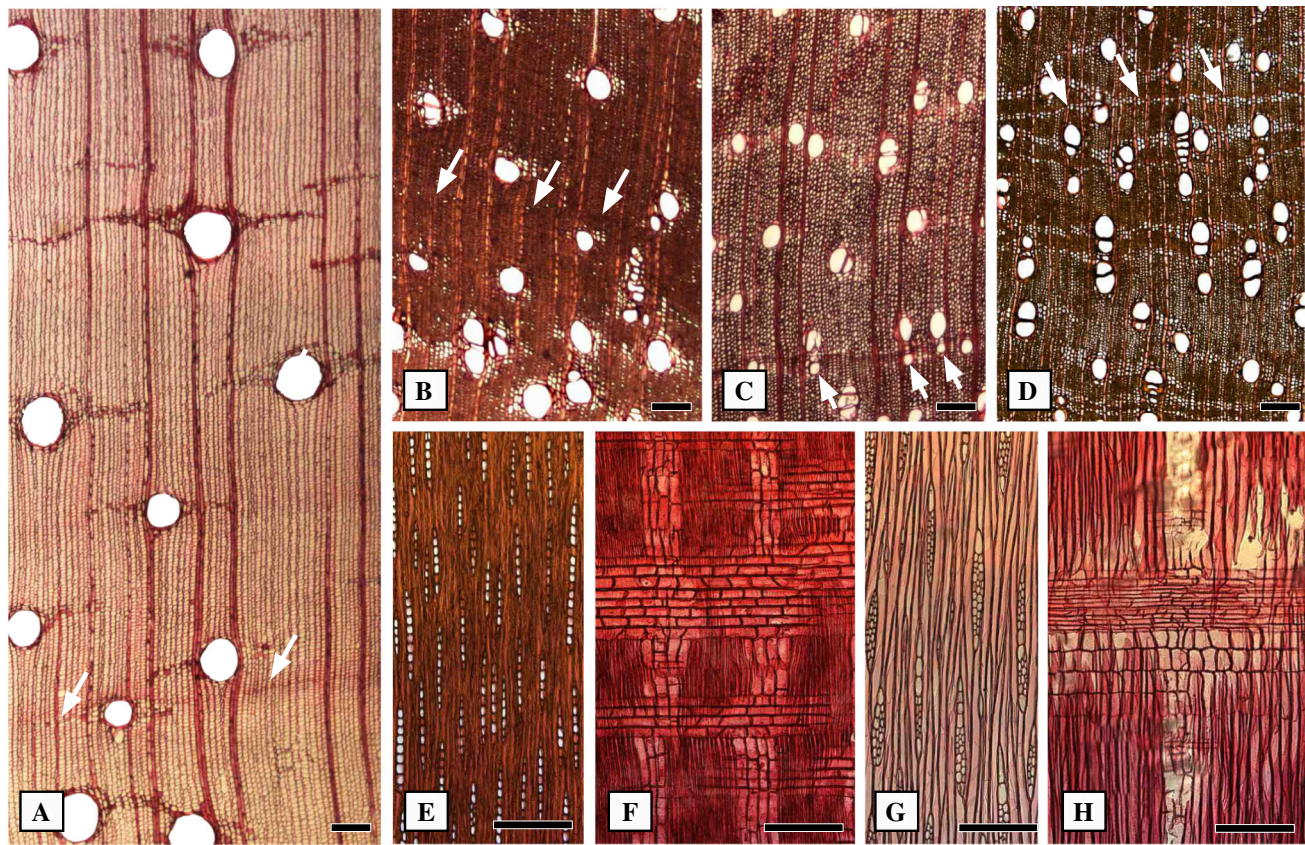


Fig. 3 Wood anatomy of Jacarandaeae. **a** *Jacaranda copaia*, TS, winged-aliform parenchyma, with short confluentes, and very wide vessels with about 300 μm . Growth rings delimited by radially flattened fibers (arrows). **b** *Digomphia densicoma*, TS, lozenge to winged-aliform parenchyma with short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

walled fibers associated with narrow vessels (arrows). **d-f** *Jacaranda brasiliana* (section *Monolobos*). **d** TS, Winged-aliform parenchyma, forming long confluentes, 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

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 winged-aliform parenchyma with long confluentes) 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),

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 ($55 \pm 12 \mu\text{m}$), with higher values in the lianas, and the highest values in the earlywood of *Campsis radicans* (average 300 μm). **Perforation plates** are simple, sometimes foraminata 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 confluentes (Fig. 4d); a line of marginal parenchyma often

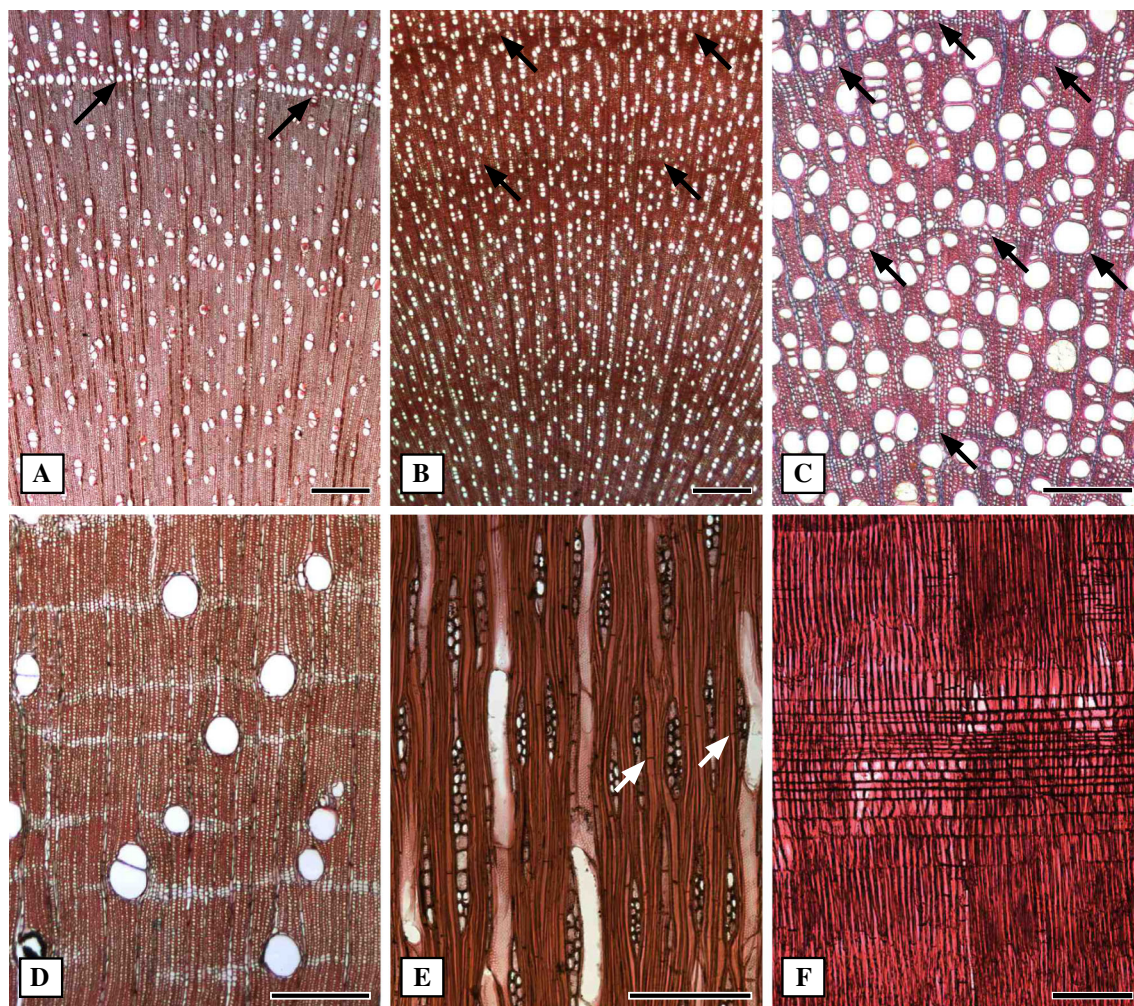


Fig. 4 Wood anatomy of Tecomeae s.s. **a** *Tecoma stans*, TS, semi-ring porous wood, narrow vessels solitary to multiple of 2–3, scanty paratracheal parenchyma. **b** *Tecomaria capensis*, TS, diffuse porous wood, narrow vessels, solitary to multiples of 2–4 or more common, radially disposed, growth 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

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

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).

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 ($40 \pm 20 \mu\text{m}$), with $46 \pm 20/\text{mm}^2$ of frequency.

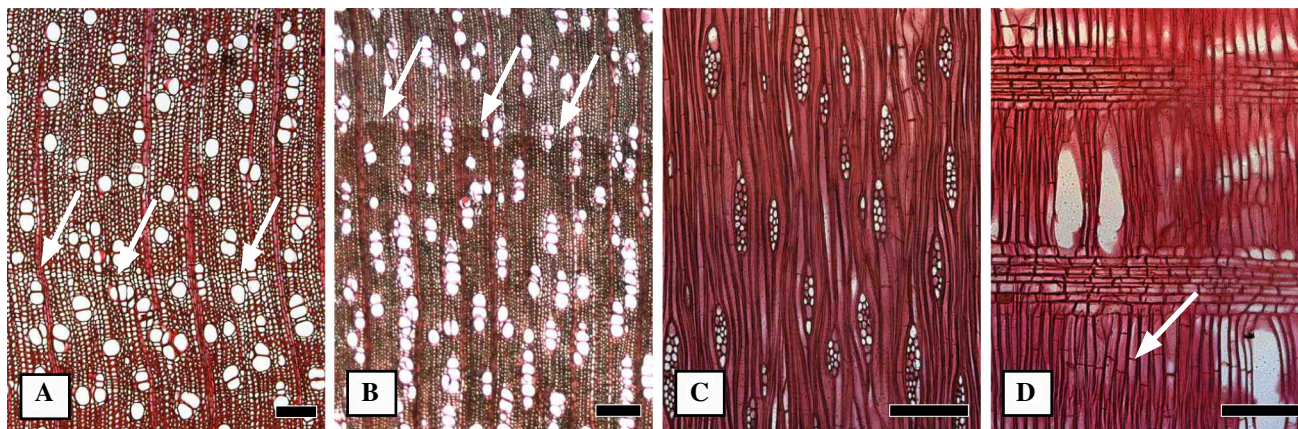


Fig. 5 Wood anatomy of *Delostoma integrifolium*. **a** TS, narrow vessels solitary to multiples of two to four, scanty paratracheal parenchyma to vasentric, growth ring delimited by a line of marginal parenchyma. **b** TS, narrow vessels in radial arrangement,

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 μ 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 vasentric, 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 confluent, 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 antisiphilitica* (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 vasentric to aliform axial parenchyma with short to long confluent. 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 *Handroanthus* 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 antisiphilitica*, narrow (60 ± 26 μ m) in most genera, medium in *Handroanthus* and *Sparattosperma* (134 ± 45 μ m), numerous ($20 \pm 12/$

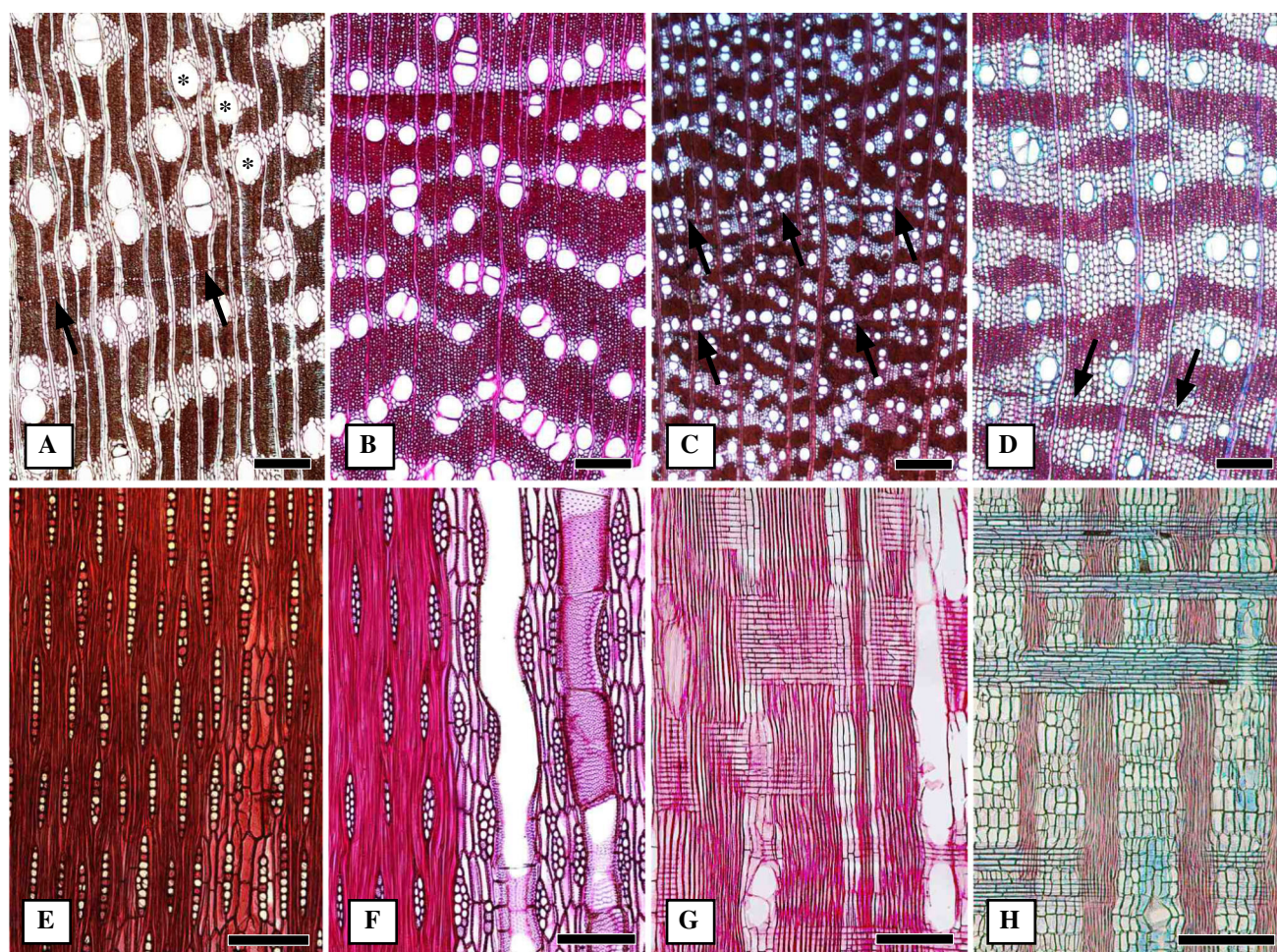


Fig. 6 Wood anatomy of the *Tabebuia* alliance (including *Crescentieae*). **a** *Handroanthus barbatus*, TS, diffuse porous wood, paratracheal aliform parenchyma, predominantly unilateral around certain vessels (*asterisks*), with short confluentes, thick-walled fibers, growth rings delimited by a line of marginal parenchyma (*arrows*). **b** *Tabebuia roseoalba*, TS, diffuse-porous wood, aliform parenchyma, sometimes unilateral, with short confluentes, growth rings delimited by a band of marginal parenchyma. **c** *Zeyheria montana*, TS, diffuse porous wood, aliform parenchyma with short to long confluentes, thick walled fibers, growth rings delimited by a line of marginal

parenchyma (*arrows*). **d** *Crescentia cujete*, TS, diffuse porous wood, abundant aliform parenchyma with long confluentes forming bands, growth rings delimited by a line of marginal parenchyma. **e** *Crescentia alata*, LT, axial and radial elements storied, uniseriate rays, sometimes biseriata, two cells per parenchyma strand. **f** *Handroanthus chrysotrichus*, LT, all axial and radial elements storied, biseriata rays, parenchyma paratracheal with two cells per strand, large intervessel pits. **g** *Tabebuia fluviatilis*, LR, homocellular rays. **h** *Crescentia cujete*, LR, abundant axial parenchyma, homocellular rays. *Scale bars a, b, d, g, h* 100 μm , *c* 500 μm , *e, f* 200 μm

mm^2), $43 \pm 4/\text{mm}^2$ in *Cydistax antisiphilitica*. Deposits of lapachol are common in *Handroanthus* and *Zeyheria*. Perforation plates are simple, sometimes foraminata in *Tabebuia*, *Spirotecoma*, *Crescentia* and *Parmentiera*. Intervessel pits vary from small ($\sim 5 \mu\text{m}$ in *Roseodendron donnel-smithii*) to large ($\sim 18 \mu\text{m}$ in *Handroanthus chrysotrichus*). Vessel-ray pits are similar in size and shape to the intervessel pits. Fibers are non-septate, thin- to thick-walled and frequently very thick walled (e.g., *Handroanthus*, *Paratecoma peroba*, *Zeyheria*; Fig. 6a, c). Parenchyma ranges from vasicentric to aliform, forming short (Fig. 6a, b) to long confluentes (Fig. 6c, d), usually forming bands (Fig. 6d). Unilateral aliform parenchyma

(Fig. 6a, b) is common in some species (e.g., *Handroanthus albus*, *H. impetiginosus*, *Tabebuia roseoalba*). A gradual change from aliform, to aliform-confluent with short to long confluentes and finally a marginal band within each growth ring is found in some members of this clade (*Crescentia alata*, *Handroanthus* and *Tabebuia*). All sampled species of *Amphitecna*, *Cydistax antisiphilitica*, *Crescentia alata* and some species of *Handroanthus* (e.g., *Handroanthus barbatus*, *H. chrysotrichus*, *H. impetiginosus*; Fig. 6e, f) have 2 cells per parenchyma strand, while others have 2–4 cells (e.g., *H. serratifolium*). Rays are usually storied (Fig. 6e, f) or irregularly storied, uniseriate (Fig. 6e) to 2–3-seriate (Fig. 6f), generally homocellular

(Fig. 6g, h), although homocellular and heterocellular rays with one marginal row of square cells are present in *Godmania aesculifolia*, *Sparattosperma leucanthum*, and in both species of *Zeyheria* sampled.

Paleotropical clade (including Coleeae)

We sampled 22 of the 139 species currently recognized in the Paleotropical clade, representing 15 out of the 19 genera currently included in this group (Lohmann and Ulloa 2006 onwards); only *Phylloctenium* (ditypic genus from Madagascar), *Dinklageodoxa* (monotypic genus from Liberia), and *Rhigozum* (seven species from Tropical Africa and Madagascar) were not sampled. More specifically, we sampled *Catophractes alexandri* (monotypic), *Colea* (2 of 21 spp), *Dolichandrone* (2 of 10 species), *Fernandoa* (2 of 14 species), *Heterophragma* (both species), *Kigelia africana* (monotypic), *Markhamia* (2 of 10 species), *Newbouldia laevis* (monotypic), *Ophiocolea floribunda* (1 of 5 species), *Pajanelia longifolia* (monotypic), *Phyllarthron bojeranum* (1 of 15 species), *Radermachera* (5 of 18 species), *Rhodocolea* (3 of 7 species), *Spathodea campanulata* (monotypic), *Stereospermum chelonoides* (1 of 20 species), and *Tecomella undulata* (monotypic). Of these, *Colea*, *Ophiocolea*, *Phyllarthron*, and *Rhodocolea* belong to tribe Coleeae, a monophyletic group nested within the Paleotropical clade.

Diagnostic features

The wood anatomy of most species from the Paleotropical clade is distinctive in having abundant paratracheal aliform confluent parenchyma, with short to long confluent, medium vessels, non-storied, 2–3-seriate, co-occurring homo and heterocellular rays, and thick walled, non-septate fibers. However, Coleeae differ from the rest of the clade by its apotracheal diffuse axial parenchyma that co-occurs with paratracheal vasicentric to aliform parenchyma, thin- to very thick-walled fibers, narrow vessels and homocellular uniseriate rays.

Detailed description

Growth rings are distinct, delimited by a line of marginal parenchyma associated with very narrow vessels (Fig. 7a, b), vessels of larger diameter (Fig. 7b), thicker-walled and radially flattened fibers (Fig. 7b), and sometimes dilated rays (e.g., *Fernandoa adenophylla*, *Markhamia lutea*, *Tecomella undulata*). *Porosity* is diffuse (Fig. 7a, e, f) or semi-ring porous (Fig. 7b), especially in species growing in more arid areas (e.g. *Catophractes alexandri*). *Vessels* are solitary or in multiples of 2–3 (Fig. 7a, b, e, f), 1.51 ± 0.44

vessels/group, medium ($110 \pm 20 \mu\text{m}$), except in Coleeae, where they are narrow ($60 \pm 10 \mu\text{m}$; Fig. 7f); frequencies are variable, ranging from 8 to 10/mm² in *Kigelia africana* and *Spathodea campanulata* to 24–40/mm² in *Tecomella undulata*, *Radermachera glandulosa*, and species of tribe Coleeae. *Intervessel pits* are small (4–5 μm) to minute in tribe Coleeae (<3 μm). *Vessel-ray pits* are similar in size and shape to intervessel pits. *Fibers* are thin- (Fig. 7b) to very thick-walled (Fig. 7a, e), with simple pits and occasionally septate. Within tribe Coleeae fibers are thin-walled in *Colea* and *Ophiocolea* and very thick-walled in *Rhodocolea* and *Phyllarthron*. Fibers are always septate in the sampled species of *Heterophragma*, *Radermachera*, and *Pajanelia longifolia*. *Parenchyma* is paratracheal vasicentric to aliform, with short (Fig. 7e) to long confluent (Fig. 7a, b). Apotracheal diffuse parenchyma is present in all genera from tribe Coleeae (Fig. 7e, f), less abundantly in *Phyllarthron bojeranum* and *Rhodocolea*, always co-occurring with paratracheal vasicentric to aliform parenchyma, with short to long confluent in *Rhodocolea multiflora* and *R. nycteriphilla*. Usually 3–4 cells per parenchyma strand (2 cells in *Spathodea campanulata*). *Rays* are non-storied, 3–4-seriate (Fig. 7c), homocellular (Fig. 7d) and heterocellular with one row of marginal square cells common (Fig. 7c). In representatives of tribe Coleeae rays are exclusively unicellular and homocellular (Fig. 7g, h), similarly to *Dolichandrone atrovirens*, *Kigelia africana*, *Stereospermum leucanthum*, and *Tecomella undulata* (which fall outside Coleeae).

Oroxyleae

We sampled *Millingtonia hortensis* (monotypic) and *Oroxylum indicum* (monotypic), two of the four genera and six species currently recognized in the tribe (Lohmann and Ulloa 2006 onwards). Only *Nyctocalos* (three species) and *Hieris curtisii* (monotypic), both lianas from Malesia, were not sampled.

Diagnostic features

The wood of Oroxyleae can be recognized by a unique combination of vessels with foraminate perforation plates, co-occurring with vessels of simple perforation plates, paratracheal vasicentric to aliform parenchyma, homocellular and non-storied rays, fibers generally non-septate.

Detailed description

Growth rings are distinct, delimited by a line of marginal parenchyma (Fig. 8a), thicker-walled and radially flattened

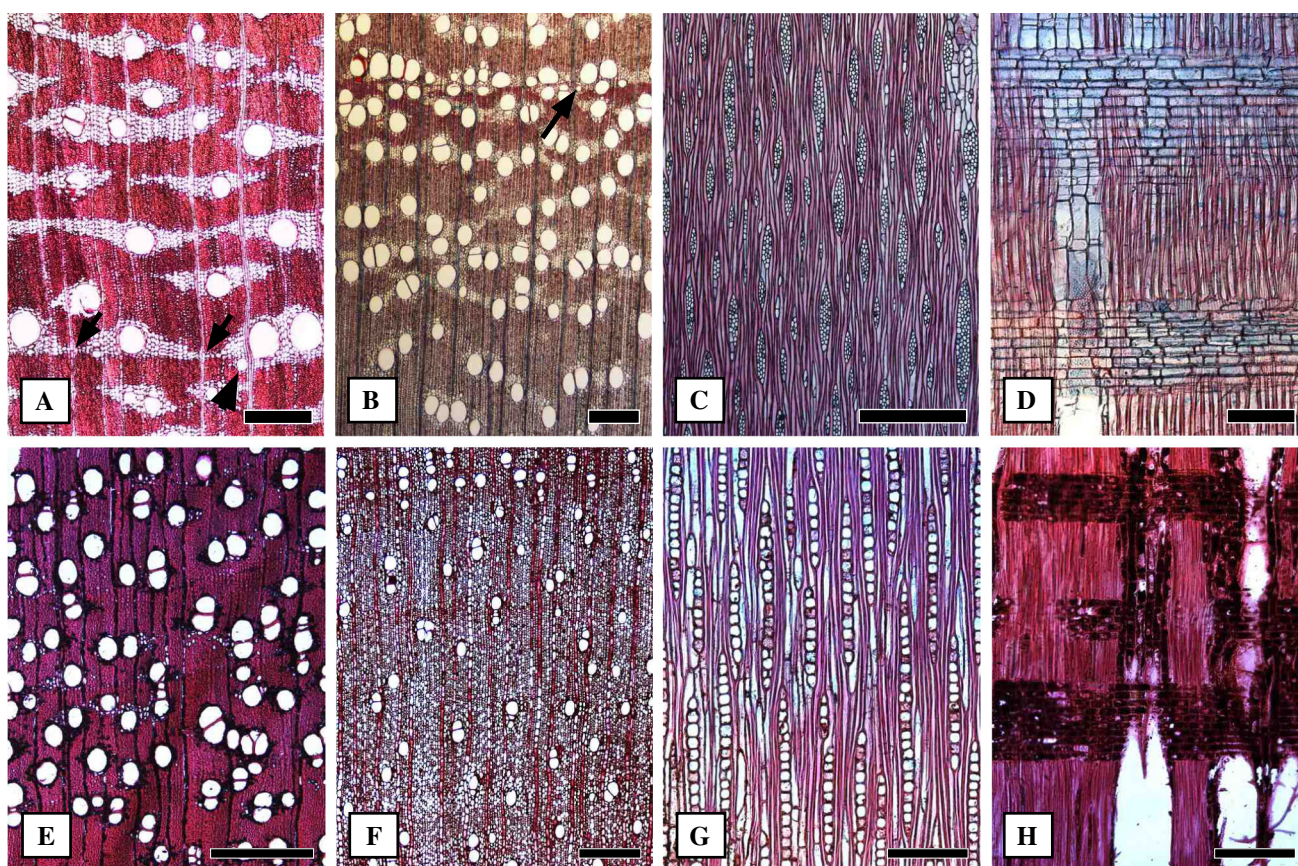


Fig. 7 Wood anatomy of the Paletropical clade (including Coleae). **a** *Stereospermum chelonoides*, TS, diffuse porous wood, vessels solitary to multiples of 2–3, growth rings delimited by a line of marginal parenchyma (arrows) associated with narrow vessels (arrowhead), paratracheal aliform parenchyma with short confluences. **b** *Markhamia lutea*, TS, semi-ring porous wood, vessels solitary to multiples 2–3, growth rings delimited by wide vessels (arrow), aliform parenchyma with short to long confluences. **c** *Spathodea campanulata*, LT, rays 2–3-seriate, non-storied.

d *Heterophragma roxburghii*, LR, homocellular rays. **e–h** Tribe Coleae. **e** *Rhodocolea telfairae*, TS, diffuse porous, vessels solitary to multiples of 2–3, paratracheal aliform parenchyma with short confluences, and scanty diffuse apotracheal parenchyma, fibers very thick-walled. **f** *Ophiocolea floribunda*, TS, vessels solitary to multiples of 2–3, abundant apotracheal diffuse parenchyma combined with vascentric paratracheal parenchyma, fibers thin-walled. **g** *Ophiocolea floribunda*, LT, uniseriate rays, non-storied. **h** *Rhodocolea telfairiae*, LR, homocellular rays. Scale bars **a**, **c**, **e**, **f** 500 μm , **b** 1 mm, **d**, **g**, **h** 200 μm

fibers, and dilated rays. *Porosity* diffuse (Fig. 8a, e). *Vessels* are solitary or in multiples of 2–3 (Fig. 8a, e), 1.59 ± 0.49 vessels/groups, narrow in *Millingtonia hortensis* ($80 \pm 26 \mu\text{m}$; Fig. 8a) and medium in *Oroxylum indicum* ($179 \pm 16 \mu\text{m}$; Fig. 8e); $25 \pm 8/\text{mm}^2$ of frequency in *Millingtonia hortensis* (Fig. 8a) and fewer, $4 \pm 4/\text{mm}^2$, in *Oroxylum indicum* (Fig. 8e). Vessels with foraminated perforation plates are common (Fig. 8d, h) co-occurring with vessels with simple perforation plates (more frequent). In *Millingtonia hortensis*, a combination of foraminated and reticulate perforation plates is frequently found at the same plate (Fig. 8d). *Intervessel pits* are small (4–5 μm). *Vessel-ray pits* are similar to the intervessel pits in size and shape. *Fibers* are thin- to thick-walled (Fig. 8a, e), with simple pits, non-septate to occasionally septate in some individuals of *Oroxylum indicum*. *Parenchyma* is vascentric (Fig. 8a) to aliform (Fig. 8e), both with short confluences; 3–4 cells per

parenchyma strand. *Rays* are homocellular (Fig. 8c, g), 3-seriate and non-storied (Fig. 8b, f).

Catalpeae

We sampled *Chilopsis linearis* (monotypic), and *Catalpa* (3 out of the 11), representing the two genera currently included in this clade (Lohmann and Ulloa 2006 onwards). In *Catalpa*, we sampled species from section *Macrocatalpa* (*Catalpa longissima*), and section *Catalpa* (*Catalpa bignonioides* and *Catalpa speciosa*).

Diagnostic features

Catalpeae are distinctive for the semi-ring porous to ring-porous wood found in *Chilopsis linearis* and *Catalpa*

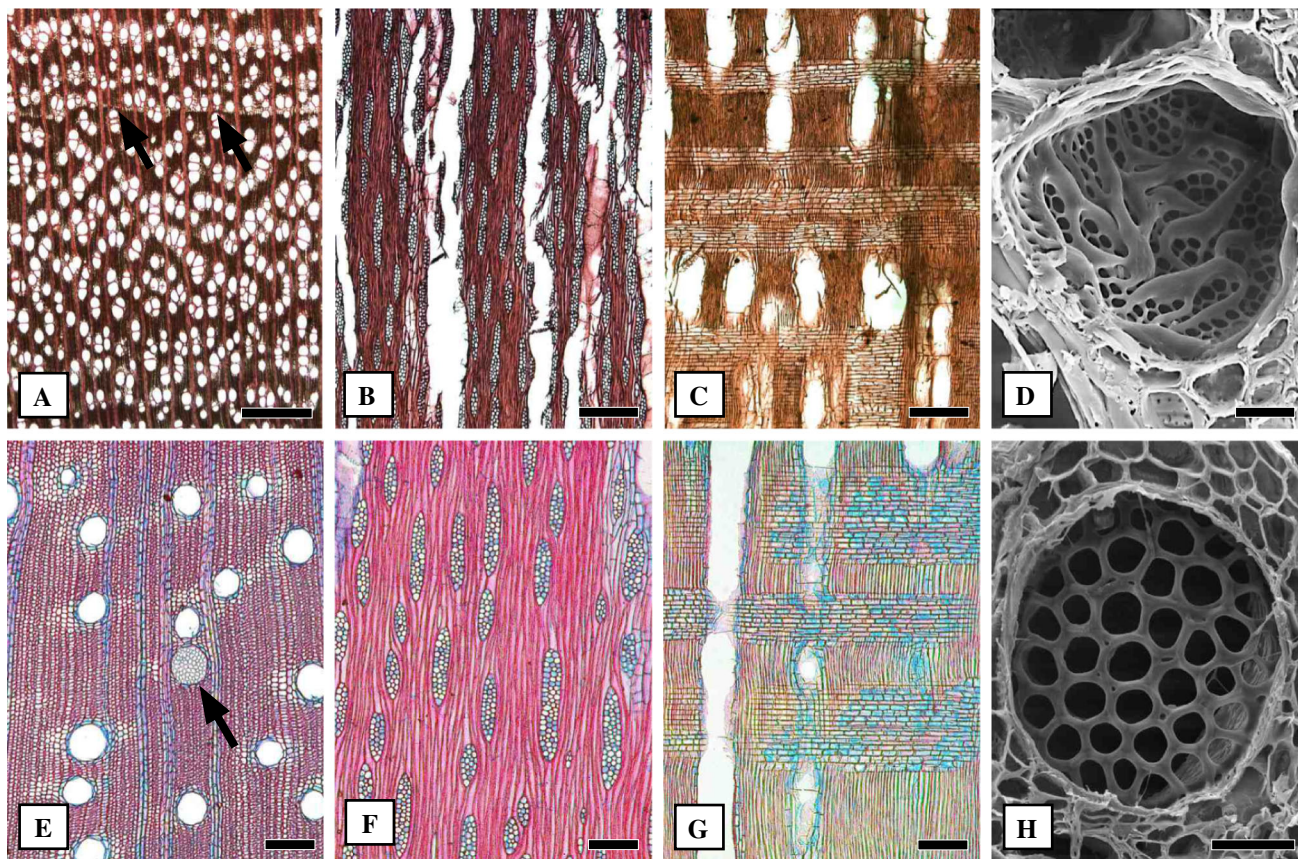


Fig. 8 Wood anatomy of Oroxyloae. **a–d** *Millingtonia hortensis*. **a** TS, vessels solitary to multiples of two to four, growth ring delimited by a line of marginal parenchyma (arrows) and thicker-walled and radially flattened fibers, vascentric parenchyma, with short conflues. **b** LT, rays 3-seriate, non-storied. **c** LR, rays homocellular. **d** Scanning electron microscopy (SEM) of a vessel with a combination of foraminiate and reticulate perforation plate together,

typical of this species. **e, f** *Oroxylum indicum*. **e** TS, solitary vessels common, paratracheal aliform parenchyma with short conflues, foraminiate perforation plate (arrow). **f** LT, rays 3-seriate, non-storied. **g** LR, rays homocellular. **h** SEM of a vessel with foraminiate perforation plate. Scale bars **a** 500 μm , **b, c, e–g** 200 μm , **d** 20 μm , **h** 50 μm

(section *Catalpa*), as well as the presence of scanty paratracheal to vascentric confluent parenchyma. In *Catalpa* (section *Macrocatapa*) the parenchyma is aliform confluent. Tyloses are abundant in both sections, as are the septate fibers in the tropical and subtropical species (*Chilopsis linearis* and *C. longissima*) and the unique presence of simple to semi bordered vessel-ray pits.

Detailed description

Growth rings are distinct, delimited by a band of marginal parenchyma, vessels of two different diameters in *Chilopsis linearis* (Fig. 9c), *Catalpa speciosa* and *C. bignonioides* (section *Catalpa*; Fig. 9a), thicker-walled and radially flattened fibers. **Porosity** diffuse in *Catalpa longissima* (section *Macrocatapa*; Fig. 9b), and semi-ring porous to ring-porous in *Catalpa speciosa*, *C. bignonioides* (section *Catalpa*; Fig. 9a), and *Chilopsis linearis* (Fig. 9c). **Vessels** are solitary or in multiples of 2–3, 1.43 ± 0.12

vessels/group in earlywood and tropical specimens, 19.27 ± 7.59 vessels/group in latewood, wide vessels with $200 \pm 18 \mu\text{m}$ in the semi-ring to ring-porous woods (i.e., *Catalpa* section *Catalpa* + *Chilopsis*), and medium vessels with $131 \pm 10 \mu\text{m}$ in *Catalpa longissima* (section *Macrocatapa*); narrow vessels of latewood of $30 \pm 6 \mu\text{m}$; and frequency of $12 \pm 5/\text{mm}^2$ in *Catalpa speciosa* and $34 \pm 10/\text{mm}^2$ in *Chilopsis linearis*. Helical thickening is present in all vessels of *Catalpa speciosa* (section *Catalpa*) and *Chilopsis linearis*. **Perforation plates** are simple (Fig. 9f). **Intervessel pits** are small (5–7 μm). **Vessel-ray pitting** is simple to semi-bordered. **Fibers** are septate in the tropical and subtropical species (Fig. 9d, e) and non septate in the temperate species (Table 1), thin- to thick-walled, with simple pits. **Parenchyma** is scanty paratracheal to vascentric in *Catalpa speciosa* and *Catalpa bignonioides* (section *Catalpa*) and *Chilopsis*, vascentric forming bands when associated with the narrow vessels in the latewood of *Chilopsis linearis*. Bands of marginal parenchyma are

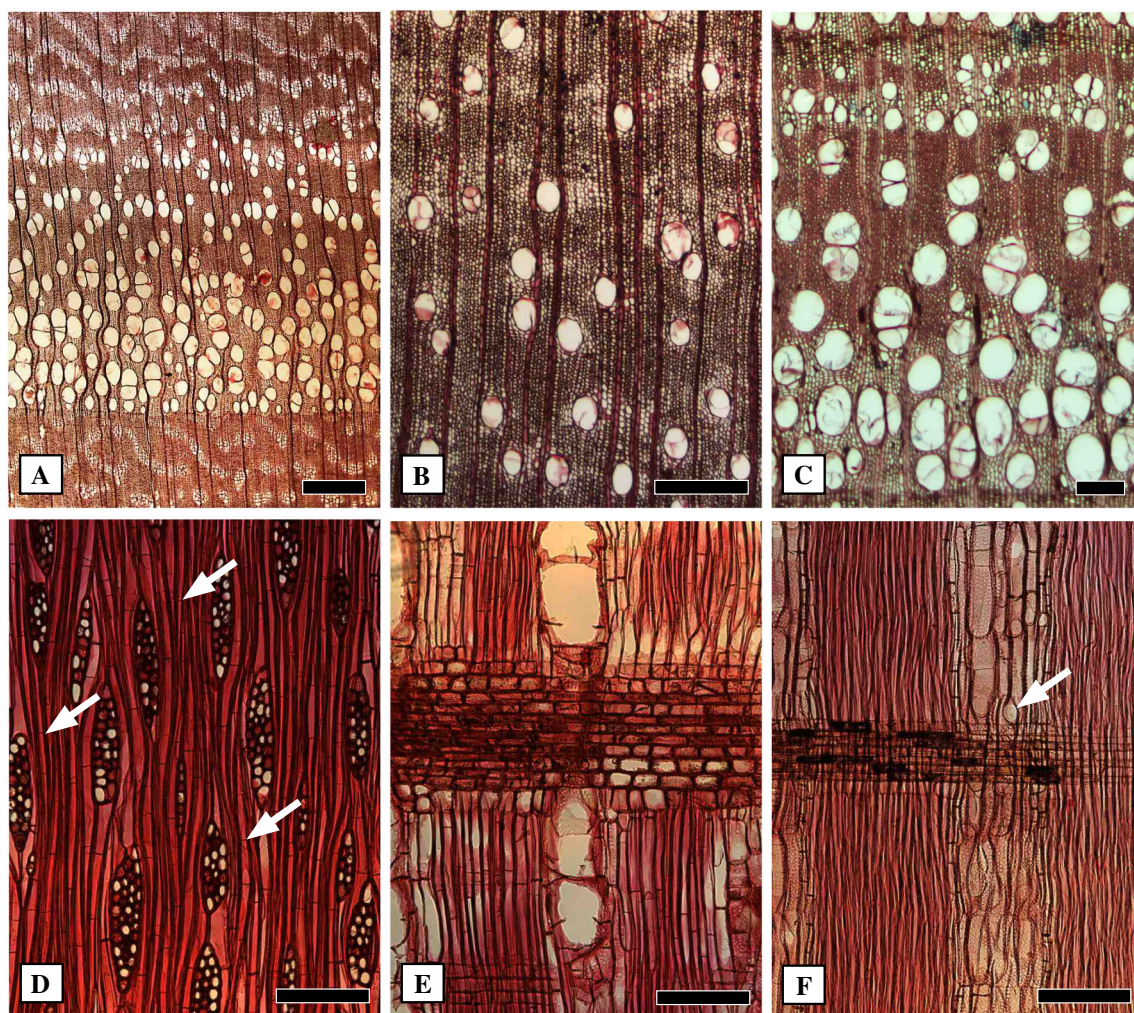


Fig. 9 Wood anatomy of Catalpeae. **a** *Catalpa speciosa* (section *Catalpa*), TS, semi-ring porous wood, earlywood vessels solitary to multiples of 2–3, associated with a band of marginal parenchyma, latewood vessels in clusters, scanty paratracheal parenchyma, tyloses common. **b** *Catalpa longissima* (section *Macrocalpa*), TS, wood diffuse porous, vessels solitary to multiples of 2–3, parenchyma aliform, with short confluences, tyloses common. **c** *Chilopsis linearis*, TS, semi-ring porous wood, earlywood vessels solitary to multiples of

2–3, associated with a band of marginal parenchyma, latewood vessels generally in multiples, with paratracheal vasicentric parenchyma forming bands, tyloses common. **d** *Catalpa longissima*, LR, 2–3-seriate rays, non-storied, septate fibers common (arrows). **e** *Chilopsis linearis*, LR, heterocellular rays with one row of square marginal cells. **f** *Catalpa speciosa*, LR, heterocellular ray, narrow vessels in clusters, showing simple perforation plates. Scale bars **a** 500 μm , **b–f** 200 μm

present. In *Catalpa longissima* (section *Macrocalpa*), the parenchyma is aliform with short confluences (Fig. 9b). Parenchyma strands have 3–4 cells, as seen in tangential section. Rays are 3-seriate, non-storied (Fig. 9d), and heterocellular with one row of marginal square cells (Fig. 9e, f) co-occurring with homocellular rays.

Bignoniaceae

We sampled all 21 genera and 49 out of the 393 species currently included in Bignoniaceae (sensu Lohmann and Taylor 2014). Sampling included *Adenocalymma* (8 of 82), *Amphilophium* (5 of 47), *Anemopaegma* (1 of 45), *Bignonia* (4 of 28), *Callichlamys latifolia* (monotypic),

Cuspidaria (2 of 19), *Dolichandra* (2 of 8), *Fridericia* (5 of 67), *Lundia* (3 of 13), *Manaosella cordifolia* (monotypic), *Mansoa* (3 of 12), *Martinella* (1 of 2), *Neojoberbia* (both species), *Pachyptera* (1 of 4 species), *Perianthomega vellozoi* (monotypic), *Pleonotoma* (3 of 17 species), *Pyrostegia* (1 of 2 species), *Stizophyllum* (1 of 3 species), *Tanaecium* (3 of 17 species), *Tynanthus* (1 of 15 species), and *Xylophragma* (2 of 7 species).

Diagnostic features

Bignoniaceae are characterized by the presence of a cambial variant, denominated furrowed xylem, with four or multiples of four phloem wedges that interrupt the xylem

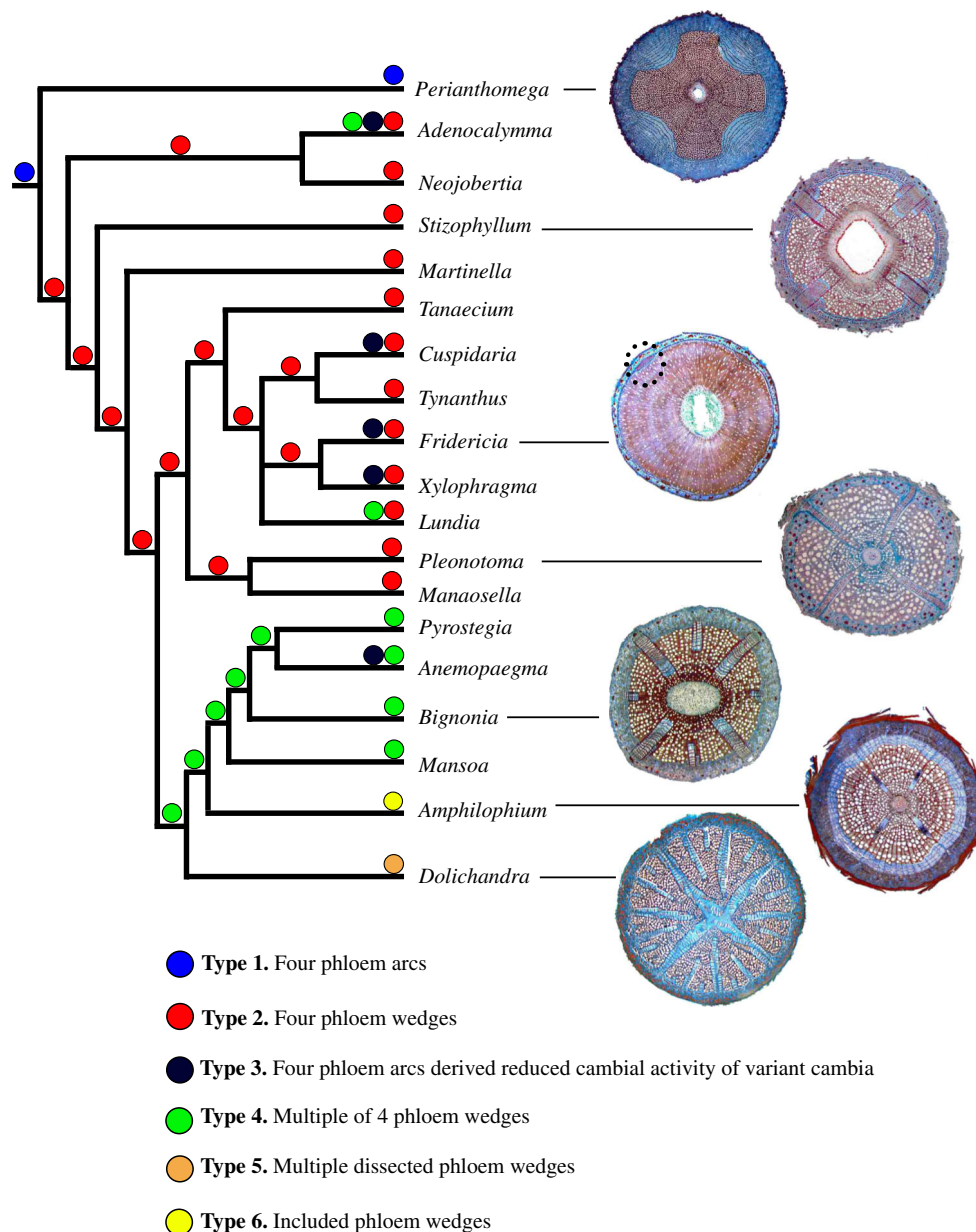


Fig. 10 Phylogenetic mapping of the six types of cambial variants found in Bignoniaceae; entire stem, as seen in transverse sections. *Type 1* *Perianthomega vellozoi*, four broad phloem arcs. *Type 2* *Stizophyllum riparium* and *Pleonotoma tetraquetra*, four phloem wedges. *Type 3* *Fridericia platyphylla*, four narrow phloem arcs derived from a

reduced activity of the variant cambia, typical of shrub species. *Type 4* *Bignonia binata*, multiple of four phloem wedges. *Type 5* *Dolichandra unguis-cati*, multiple dissected phloem wedges. *Type 6* *Amphilophium crucigerum*, included phloem wedges

(Fig. 10). The wood anatomy of members of Bignoniaceae is characterized by scanty paratracheal to vasicentric axial parenchyma, generally tall (>1 mm) and heterocellular rays, and septate fibers (Fig. 11)

Cambial variants in Bignoniaceae have the conspicuous form of a cross in transverse section (Fig. 10). The stems of Bignoniaceae can be sorted in six types, according to the form and distribution of the phloem arcs/wedges. *Type 1* corresponds to four broad equidistant phloem arcs (Fig. 10) and is exclusive of *Perianthomega*, a monotypic genus that

is sister to all other Bignoniaceae. In this type, the cambium lines the entire stem circumference, without disjunctions. *Type 2* corresponds to four equidistant phloem wedges, formed by the presence of a cambial disjunction and inclusion within the phloem wedges (Fig. 10). *Type 2* is most common in Bignoniaceae, and is present in 12 of the 21 genera of the tribe (Fig. 10). *Type 3* corresponds to four narrow phloem arcs (Fig. 10) derived from delayed development of the phloem wedges and is typical of the shrubby species. This type was recorded in *Adenocalymma*

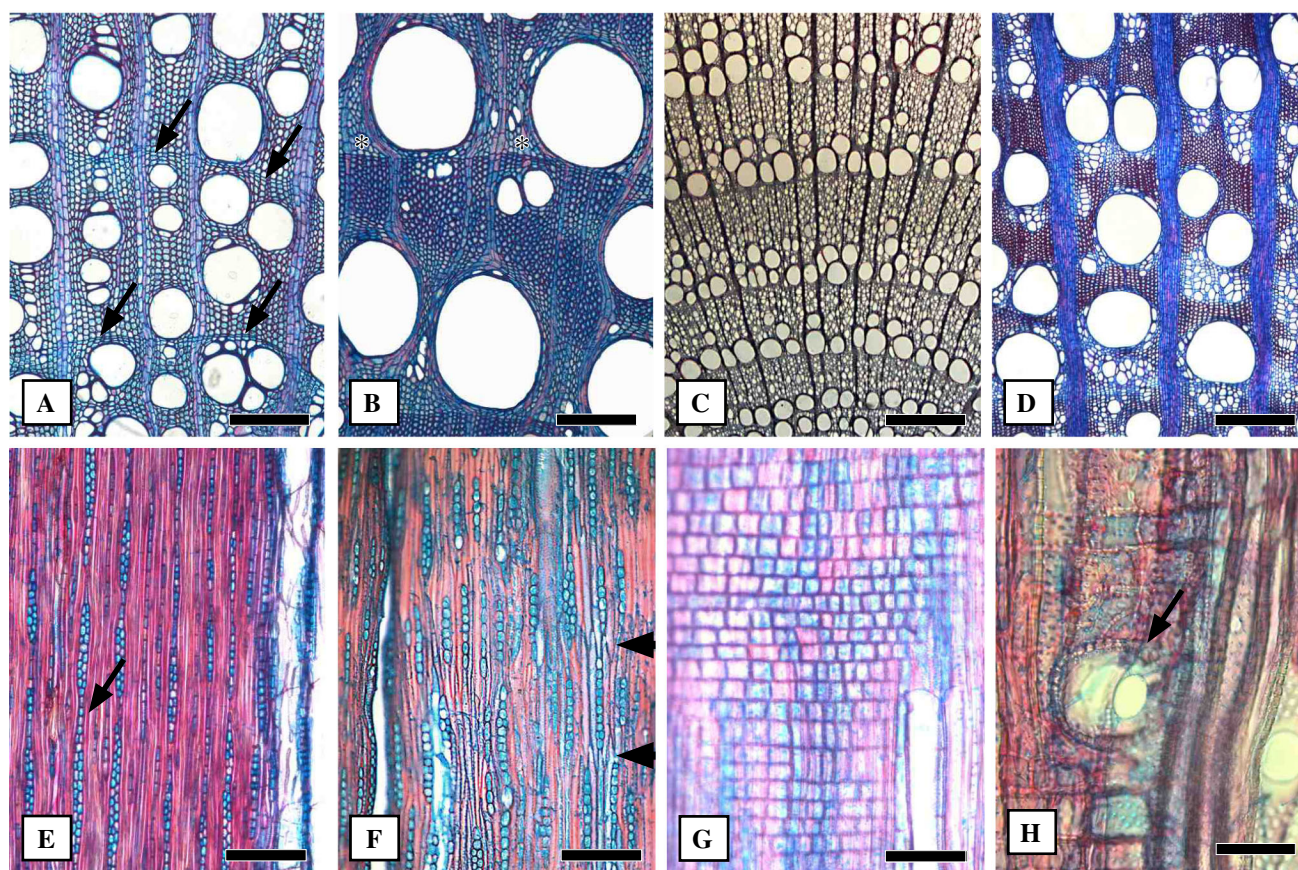


Fig. 11 Wood anatomy of Bignoniaceae. **a** *Mansoa difficilis*, TS, diffuse porous wood, growth rings delimited by thick-walled and radially flattened fibers (arrows), vessel dimorphism present. **b** *Tynanthus cognatus*, TS, semi-ring porous wood, delimited by radially flattened fibers and a marginal band of parenchyma, vessel dimorphism present. Wide vessels generally solitary. **c** *Bignonia capreolata*, TS, ring porous wood. **d** *Amphilophium crucigerum*, TS, diffuse porous wood, wide vessels generally solitary, combined with clusters

of narrow vessels, wide rays. **e** *Stizophyllum riparium*, LT, biseriate rays, fusion of rays common (arrow). **f** *Dolichandra unguis-cati*, LT, uniseriate and short rays storied. Fibers also storied (arrows). **g** *Fridericia speciosa*, LR, heterocellular mixed rays. **h** *Neojobertia mirabilis*, LR, perforated ray cell (arrow) with simple perforation plate. Scale bars **a, b, e, f** 200 μm , **c** 800 μm , **d** 300 μm , **g** 150 μm , **h** 40 μm

nodosum, *A. peregrinum*, *Cuspidaria pulchra*, and *Fridericia platyphylla*, all shrubs growing in the *Cerrado* (Brazilian savannah). The wedges may be very reduced making it impossible to detect without magnification (circled in Fig. 10). *Type 4* corresponds to multiple of four phloem wedges. These species start their development with four phloem wedges, but form additional wedges between the previous ones, always in multiples of four. This type is encountered in the all species from the clade formed by *Amphilophium*, *Anemopaegma*, *Bignonia*, *Dolichandra*, *Mansoa*, and *Pyrostegia*, in most species of *Lundia* and a few *Adenocalymma* (Fig. 10). *Amphilophium* and *Dolichandra*, however, go further in their development generating the next two types to be described. *Type 5* corresponds to the ‘multiple dissected type,’ in which multiple of four phloem wedges are also formed, and in which the proliferation of unligified axial and ray parenchyma dissects the secondary xylem in pieces. The presence of unligified axial and ray

parenchyma in the xylem, which produces this type, is exclusive to *Dolichandra* (Fig. 10). *Type 6* corresponds to the ‘included phloem wedges type,’ in which multiple of four phloem wedges are formed, but are gradually occluded by the regular cambium at the top of the phloem wedges, eventually including the secondary phloem within the secondary xylem. This type is exclusive to *Amphilophium* (Fig. 10).

Detailed description

Growth rings are distinct and are delimited by a line or band of marginal parenchyma (Fig. 11a, b), very narrow vessels, thicker-walled and radially flattened fibers (Fig. 11a, b) and dilated rays (Fig. 11b). Discontinuous and merging growth rings are common. *Porosity* usually semi-ring porous (Fig. 11b) to diffuse porous (Fig. 11a). The sole species growing in temperate latitudes, *Bignonia*

capreolata, has ring-porous wood (Fig. 11c). *Vessels* exhibit dimorphism, with wide and narrow vessels combined (Fig. 11a-b, d); wide vessels with $240 \pm 60 \mu\text{m}$, predominantly solitary in some species (e.g., *Amphilophium crucigerum*, *Stizophyllum riparium*, *Lundia damazii*) to solitary and multiples of 2–3 (Fig. 11a–d), 2.57 ± 0.91 vessels/group. Narrow vessels ($20 \pm 6 \mu\text{m}$) usually have a conspicuous arrangement, such as radial rows, around the wide vessels or in clusters (Fig. 11d). Frequency $>50/\text{mm}^2$. *Perforation plates* are simple. *Intervessel pits* are medium ($8\text{--}10 \mu\text{m}$ in diameter). *Vessel-ray pits* are similar to intervessel pits in size and shape. *Fibers* are septate in most species, thin- to thick-walled (Fig. 11a, b, d), and with simple pits. *Parenchyma* is scanty paratracheal in most species (Fig. 11a), except for the clade formed by *Cuspidaria*, *Fridericia*, *Lundia*, *Tanaecium*, *Tynanthus*, and *Xylophragma* (Fig. 11b; the *Arrabidaea* and allies clade in Lohmann 2006) and *Callichlamys latifolia* (not assigned to any clade; Lohmann 2006) in which vasicentric to aliform parenchyma with short confluent and a marginal band of parenchyma are present (Fig. 11b). *Rays* are heterocellular mixed (Fig. 11g), higher than 1 mm in most species, with variable width, ranging from uniseriate and short (e.g., *Dolichandra unguis-cati*; Fig. 11f), 2–4 cells wide (e.g., *Stizophyllum riparium*; Fig. 11e) and others are wider (Fig. 11d), 5–10 cells wide (e.g., *Amphilophium crucigerum*). The wood under the phloem wedges (variant secondary xylem) has narrower vessels, and rays unicellular and short. An increase in ray width was observed in some species from the stem center towards the bark (e.g. *Amphilophium crucigerum*). Fusion of rays is common in all species (Fig. 11e). *Storied structure* is absent in most species, but present in the axial, ray parenchyma and fibers of *Dolichandra* (Fig. 11f), and in the fibers of *Perianthomega vellozoi* and all sampled species of *Amphilophium*, and *Mansoa*. Perforated ray cells vary from very abundant (e.g., *Dolichandra unguis-cati*; *Stizophyllum riparium*; Fig. 11h) to rare (e.g., *Perianthomega vellozoi*). *Silica* is present in the ray cells of *Pachyptera kerere*.

Discussion

Molecular phylogenetic studies of Bignoniaceae have indicated that several tribes and genera were not monophyletic as traditionally recognized (Spangler and Olmstead 1999; Zjhra et al. 2004; Lohmann 2006; Grose and Olmstead 2007a, b; Li 2008; Olmstead et al. 2009), leading to many changes in the circumscription of taxa within the family. While most of the genus-level clades recognized are well supported by molecular and morphological characters (Grose and Olmstead 2007b; Lohmann and Taylor 2014), several of the higher-level clades (i.e., comparable

to tribal level), however, still lack morphological synapomorphies (Olmstead et al. 2009). In this study, we investigate the wood anatomy of representatives of all major lineages of the Bignoniaceae (except Tourretieae), highlighting the most conspicuous features of each clade (Table 2; Fig. 12), providing a thorough description of their wood anatomy, and suggesting potential synapomorphies (Table 3). The new systematic arrangement of the Bignoniaceae led to more homogeneous and predictable wood anatomical groups (Table 2; Fig. 12). Key features of each clade are summarized and discussed below.

Jacarandae were originally described as a tribe by Bentham and Hooker (1876) and later treated as part of Tecomeae s.l. (Gentry 1980; Fischer et al. 2004), but has been resurrected as a tribe and is now known to be sister to all other Bignoniaceae (Olmstead et al. 2009). The two genera of Jacarandae, *Digomphia* and *Jacaranda*, share wood anatomical traits that are common to other Bignoniaceae, such as the marginal parenchyma delimiting the growth rings, and paratracheal aliform parenchyma. However, *Digomphia* and *Jacaranda* share the presence of narrow vessels, winged-aliform parenchyma (more conspicuous in *Jacaranda*), and non-storied rays, which supports the circumscription of this tribe. Wood anatomical traits also support the traditional division of *Jacaranda* into sections *Monolobos* and *Dilobos* (Dos Santos and Miller 1997), which were delimited on the basis of number of anther thecae, one or two, respectively. *Jacaranda* section *Monolobos* is characterized by homocellular and uniseriate rays, while *Jacaranda* section *Dilobos* is characterized by heterocellular and multiseriate rays (Dos Santos and Miller 1997). The only exception to this rule is in *Jacaranda copaia*, which is currently assigned to section *Monolobos*, but has anatomical traits that are intermediate between both sections, having multiseriate rays of homocellular composition, and has a unique wood anatomy within the tribe, having the widest vessels in Bignoniaceae trees ($\sim 300 \mu\text{m}$). Additional sampling of *Jacaranda* in molecular phylogenetic studies is still needed in order to test the monophyly of the *Jacaranda* sections as traditionally circumscribed. *Jacaranda* is an ideal genus for further comparative anatomical studies since it presents a great deal of diversity of habits, from underground xylopodial shrubs and subshrubs in the *Cerrado*, treelets, medium-sized to very tall fast-growing trees in forests (e.g. *Jacaranda copaia*), and twigs were shown to represent consistently the wood anatomy of the main trunk wood in the genus (Dos Santos and Miller 1997).

Tecomeae sensu Olmstead et al. (2009) are much more narrowly circumscribed than the tribe Tecomeae previously recognized (Gentry 1992; Fischer et al. 2004). Even though morphological features are still lacking to diagnose this widely distributed tribe (occurring in America, Africa,

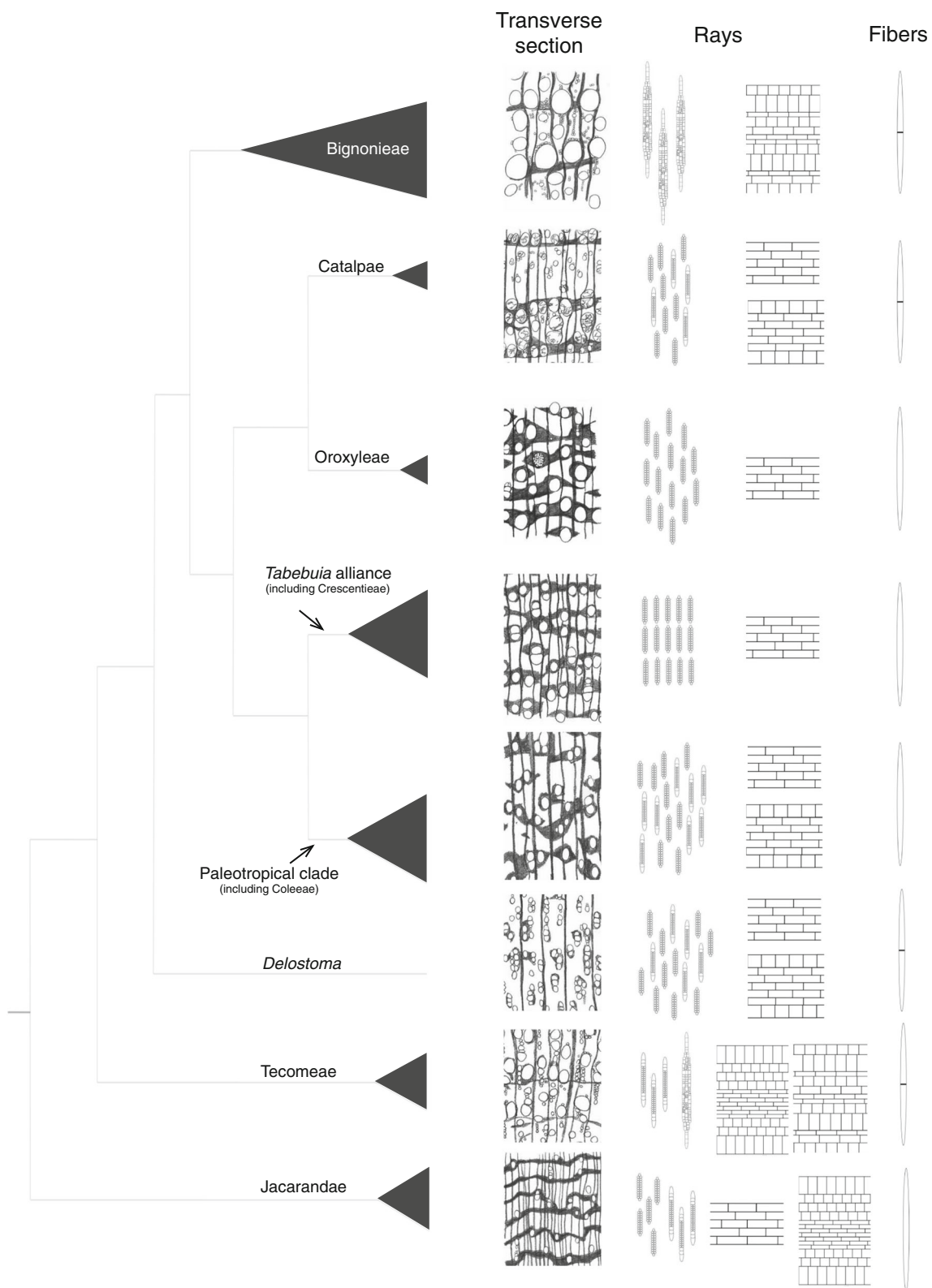


Fig. 12 Drawing summarizing of the most conspicuous wood anatomical features of major Bignoniaceae clades

Table 3 Potential wood anatomical synapomorphies

Taxa	Anatomical synapomorphy
Jacarandaeae	Axial parenchyma winged-aliform
Catalpeae	Vessel-ray pits simple to semi-bordered
Oroxyleae	Foraminate perforation plates common
Bignoniaceae	Cambial variant: xylem furrowed by four to multiple of four phloem arcs/wedges
<i>Tabebuia</i> alliance	Storied structure
Coleeae	Diffuse axial parenchyma
<i>Amphilophium</i>	Included phloem wedges
<i>Dolichandra</i>	Multiple dissected phloem wedges derived of unligified parenchyma proliferation
<i>Perianthomega</i>	Four broad phloem arcs

Asia and Oceania; see Olmstead et al. 2009), Tecomeae s.s. are quite homogeneous in wood anatomy (except from *Deplanchea*, whose wood anatomy looks very much like Jacarandaeae), combining features that set aside members of Tecomeae from most other Bignoniaceae. In particular, heterocellular rays with body procumbent and several marginal upright to square cells to heterocellular mixed in some lianas (e.g., *Pandorea jasminoides*), septate fibers, scanty paratracheal parenchyma, and rather narrow vessels (except in the lianas) characterize all members of this clade.

Delostoma is a clade of four species of Neotropical treelets and shrubs. Traditionally, *Delostoma* was included within Tecomeae s.l. (Gentry 1980; Fischer et al. 2004), however, *Delostoma*, which bears simple leaves and double calyx, has been difficult to relate to either Paleotropical or Neotropical Bignoniaceae both morphologically (Gentry 1980) and wood anatomically (Dos Santos and Miller 1992). In the most recent phylogeny of Olmstead et al. (2009), *Delostoma* emerged in its own clade, not closely related to any other representatives of Bignoniaceae. Wood anatomically this genus is most similar to Tecomeae s.s., exhibiting heterocellular rays, septate fibers and small vessels usually in radial disposition. It differs from other Tecomeae mainly by the longer tracheary elements (Dos Santos and Miller 1992).

The *Tabebuia* alliance (Olmstead et al. 2009) are composed primarily of Neotropical trees and shrubs with palmately compound leaves; only a few members have simple leaves (e.g., *Crescentia*, *Tabebuia nodosa*). Members of several genera within this clade have invaluable timbers for interior and civil construction (e.g., *Handroanthus*, *Roseodendron*, *Cybistax*, *Paratecoma*). *Tabebuia* s.l., the largest genus within this clade, was shown to be polyphyletic (Grose and Olmstead 2007a) and subdivided in three smaller genera (Grose and Olmstead 2007b):

Tabebuia (67 species), *Handroanthus* (30 species), and *Roseodendron* (two species).

Wood anatomical traits strongly support the new generic circumscription. More specifically, the *Tabebuia* Group I proposed by Dos Santos and Miller (1992), which coincides with the Lapacho group of Record and Hess (1943), is characterized by very dense wood and high specific gravity (higher than 0.74), olive brown to blackish heartwood, abundant lapachol in the heartwood vessels, coinciding perfectly with *Handroanthus*. Additional anatomical features of this clade are the large intervessel pits (usually >10 µm), very thick-walled fibers, storied structure and 2–3-seriate rays. The Bignoniaceae species with greatest economical value due to the high quality timber (Record and Hess 1943; Gentry 1992) are now included in this genus. In addition, *Tabebuia* Groups II and III proposed by Dos Santos and Miller (1992) correspond to the newly circumscribed *Tabebuia* s.s. (Grose and Olmstead 2007b). This clade is characterized by the medium basic specific gravity (0.40–0.74), light colored heartwood, not very distinct heartwood and sapwood, and lack of lapachol (Dos Santos and Miller 1992), as well as by small intervessel pits (5–8 µm), 1–2 seriate rays, that are irregularly storied, and thin to thick-walled fibers. Finally, *Tabebuia chrysea* and *Tabebuia donnell-smithii*, two of four species that did not belong to Groups I, II, or III proposed by Dos Santos and Miller (1992), are now treated under *Roseodendron*. The other two species, *Tabebuia nodosa* and *Tabebuia fluviatilis* are also considered quite anomalous anatomically (Dos Santos and Miller 1992) and further phylogenetic data is still needed to confirm their placement among the three segregated genera.

Lapachol (naphthoquinone) was first described in *Tabebuia avellanadae* (= *Handroanthus impetiginosus*) in the XIX century and has antimicrobial properties and numerous applications in pharmacology (Hussain et al. 2007). Inclusion of lapachol in the vessels was evident in dense woods of the *Tabebuia* alliance by Dos Santos and Miller (1992) and us, such as in the genera *Ekmanianthe*, *Godmania*, *Handroanthus* and *Zeyheria*. Studies involving chemical extractions found lapachol in a number of other Bignoniaceae (Hussain et al. 2007), such as *Fernandoa*, *Heterophragma*, *Kigelia*, *Newboldia*, *Phyllarthron*, *Radermachera*, *Stereospermum*, *Tecomella* (Paleotropical clade), *Cybistax*, *Paratecoma peroba* (*Tabebuia* alliance), *Catalpa* (Catalpeae), *Dolichandra unguis-cati* and *Dolichandra quadrivalvis* (Bignoniaceae). Broad chemical extractions of members of the entire family are needed to investigate further the exact distribution of this feature within the Bignoniaceae and its possible taxonomic value.

Tribe Crescentieae, a monophyletic group nested within the *Tabebuia* alliance (Grose and Olmstead 2007a; Olmstead et al. 2009), is also distinct anatomically, especially

due to the abundant aliform confluent parenchyma that forms large bands accounting for almost half of the cells in the wood.

The other seven genera scattered within the *Tabebuia* alliance clade (Olmstead et al. 2009) are much smaller [i.e., *Cybistax* (monotypic), *Ekmanianthe* (ditypic), *Godmania* (ditypic), *Paratecoma* (monotypic), *Sparattosperma* (monotypic), *Spirotecoma* (four species), and *Zeyheria* (ditypic)] and share with the rest of the *Tabebuia* alliance narrow to medium vessels, aliform paratracheal parenchyma, forming short to long confluences, storied or irregularly storied structure (likely an anatomical synapomorphy of the *Tabebuia* alliance; Pace and Angyalossy 2013), exclusively or mostly with homocellular rays and thin to thick-walled non-septate fibers. *Ekmanianthe* was described as having diffuse-in-aggregate axial parenchyma by Gasson and Dobbins (1991); however, neither our specimens nor the ones studied by Dos Santos and Miller (1992) had this feature.

The Paleotropical clade is composed of trees and a few shrubs of pinnately compound leaves (Olmstead et al. 2009), except for members of Coleeae, a tribe endemic to Madagascar, which includes shrubs with simple leaves (Zjhra et al. 2004; Olmstead et al. 2009). Members of this clade are anatomically similar to the *Tabebuia* alliance, except for the absence of storied structure and medium sized vessels.

Members of Coleeae, a monophyletic group nested within the Paleotropical clade are characterized by cauliflory, indehiscent fruits, and pinnately compound leaves (genus *Phylloctenium* with simple leaves and spines; Zjhra et al. 2004). Wood anatomy of Coleeae is unique, with apotracheal diffuse parenchyma and uniseriate rays. Within the tribe, two groups can be recognized by wood anatomy; the first formed by *Colea* and *Ophiocolea*, with thin-walled fibers and abundant apotracheal parenchyma, and the other by *Rhodocolea* and *Phyllarthron*, with very thick-walled fibers and scanty apotracheal parenchyma. The wood anatomical similarities of *Colea* and *Ophiocolea* support the sister group relationship suggested for both genera in the most recent phylogenies of the family (Zjhra et al. 2004; Olmstead et al. 2009).

Oroxyleae were treated initially within Bignoniaceae due to similarities in fruit dehiscence. Oroxyleae were subsequently set apart as a tribe due to the Asian distribution of its members (vs. Neotropical in Bignoniaceae), absence of tendrillate vines, and a stem without cambial variants (Gentry 1980). Oroxyleae have been shown to be a monophyletic group distinct from Bignoniaceae (Spangler and Olmstead 1999; Olmstead et al. 2009), supporting Gentry's proposal. Representatives of Oroxyleae have wood anatomical traits that set them apart, such as the

presence of foraminate perforation plates, homocellular non-storied rays, and lack of cambial variants.

Catalpeae include two genera, *Catalpa* and *Chilopsis*, with *Catalpa* being divided into two sections, *Catalpa* section *Catalpa* and *Catalpa* section *Macrocatalpa*. Species of *Catalpa* are disjunctly distributed, with some species occurring in North America (along with *Chilopsis*) and others in east Asia (Li 2008). Catalpeae are rather homogeneous anatomically, except for the absence of semi-ring to ring porous wood and its paratracheal aliform parenchyma with short confluences in the tropical species (e.g., *Catalpa longissima* in section *Macrocatalpa*). All species have vessels of medium diameter (130–200 µm), common presence of tyloses, 3-seriate rays, heterocellular, septate fibers in tropical and subtropical species, and the presence of simple to semi-bordered vessel-ray pittings, a novel character typical of this clade (and potential synapomorphy) that has been previously overlooked.

Bignoniaceae are the most species-rich clade of Bignoniaceae, accounting for almost half of the species in the family (Lohmann 2006; Olmstead et al. 2009). Bignoniaceae are clearly monophyletic (Spangler and Olmstead 1999; Lohmann 2006; Olmstead et al. 2009) and unite all Neotropical lianas of the family and a few shrubs (Lohmann 2006). This clade shares a series of unique morpho-anatomical features, such as terminal leaflets modified into tendrils and the presence of a cambial variant (Schenck 1893; Dobbins 1971; Gentry 1980; Dos Santos 1995; Lohmann 2006; Pace et al. 2009; Lohmann and Taylor 2014). The wood of representatives of Bignoniaceae is similar to that of other lianas (Carlquist 1985, 2001) exhibiting vessel dimorphism, heterocellular rays, and cambial variants (Angyalossy et al., in press). The wood of Bignoniaceae differs from lianas of other families by the presence of a generally scanty paratracheal parenchyma, septate fibers, and no vasicentric-tracheids. Parenchyma is only more abundant in the *Arrabidea* and allies clade (sensu Lohmann 2006), comprising *Cuspidaria*, *Fridericia*, *Lundia*, *Tanaecium*, *Tynanthus* and *Xylophragma*. The only genus not assign to any clade in Lohmann (2006), *Calliclamys latifolia* (monotypic), shares this unusual abundance of parenchyma with members of the *Arrabidea* and allies clade and might be better placed within this clade, although additional phylogenetic studies are still needed in order to confirm its placement. Storied structure is present in some species, sometimes only in fibers, and sometimes in the axial and ray parenchyma. Silica was found exclusively in one species of Bignoniaceae, *Pachyptera kerere*, and is absent elsewhere in the family. Sampling of the other four species of the genus is needed to determine whether this is a feature exclusive of this species or a potential synapomorphy of the entire genus within the Bignoniaceae.

The shape and distribution of the cambial variants represent synapomorphies of major clades in the tribe (Lohmann 2006) and are of great importance for the wood development of its species in this clade (Lima et al. 2010). Most Bignoniaceae (12 out of 21 genera) have four phloem wedges. Other clades, however, have a different anatomical architecture. *Perianthomega*, for instance, is the only genus with four broad phloem arcs. Three other clades are different by developing multiples of four phloem wedges, namely: *Lundia*, some *Adenocalymma* and a speciose clade that reunites *Amphilophium*, *Anemopaegma*, *Bignonia*, *Dolichandra*, *Mansoa*, and *Pyrostegia*. All these genera develop multiple of four phloem wedges that progress in a predictive manner from four, eight, 16, 32, 64 and so on. *Amphilophium* and *Dolichandra* go through additional developmental changes that are further described below.

Amphilophium is characterized by phloem wedges that get included within the secondary xylem (Dos Santos 1995; Pace et al. 2009), an anatomical feature that is derived from the outgrowth of the cambium at the sides of the phloem wedges including these wedges within the xylem (Pace et al. 2009), similarly to what happens in *Strychnos millepunctata* (Loganiaceae; Veenendaal and Den Outer 1993; Angyalossy et al., in press). *Amphilophium* is a newly circumscribed genus (Lohmann and Taylor 2014) that unites all species from six previously recognized genera (Fischer et al. 2004): *Amphilophium*, *Distictella*, *Distictis*, *Glaziovia*, *Haplolophium*, and *Pithecoctenium*; most of these were included in the subtribe Pithecocteniinae of Melchior (1927). Mapping the included phloem wedges onto the phylogeny of Bignoniaceae reconstructs this type of cambial variant as ancestral in this tribe (Pace et al. 2009), suggesting it as a potential synapomorphy of the clade and providing further support for the circumscription of this genus.

Dolichandra is one of the genera with multiple of four phloem wedges which develop a novel type of cambial variant called “multiple-dissected” phloem wedges (Dos Santos 1995; Pace et al. 2009). In this genus, non-lignified axial and ray parenchyma is present and proliferates during development dissecting the secondary xylem (Pace et al. 2009). *Dolichandra* (sensu Lohmann and Taylor 2014) reunites four genera previously treated as separate: *Dolichandra*, *Macfadyena*, *Melloa* and *Parabignonia* (Fischer et al. 2004). Members of these genera share this unique type of cambial variant (Dos Santos 1995; Lohmann 2006; Pace et al. 2009), supporting the new circumscription of these genera adopted by Lohmann and Taylor (2014). The evolution of cambial variants in Bignoniaceae seems to have involved terminal additions towards complexity enhancement and heterochrony (Pace et al. 2009).

The present study illustrates the diversity of wood anatomy encountered in Bignoniaceae and identifies key

diagnostic character that provide further support to the new circumscription of newly established genera (Grose and Olmstead 2007b; Lohmann and Taylor 2014), tribes and higher-level clades in the family (Olmstead et al. 2009; Table 3). The wood anatomical synapomorphies identified in this study are: (a) Jacarandaeae have a unique winged-aliform parenchyma, (b) Catalpeae are the only tribe where all members have simple to semi-bordered vessel-ray pits, (c) Oroxyleae have foraminated perforation plates common, (d) the *Tabebuia* alliance has storied structure, (e) Coleeae have apotracheal diffuse parenchyma, (f) Bignoniaceae have a cambial variant called furrowed xylem whose types also support genera within the tribe, such as (g) *Amphilophium*, which has included phloem wedges, (h) *Dolichandra*, with multiple-dissected phloem wedges, (i) *Perianthomega* with four broad phloem arcs. These results represent a first step towards a better characterization of Bignoniaceae clades with anatomical characters. These findings highlight the importance of wood anatomical studies as important sources of morphological characters to diagnose major plant clades as a whole.

Acknowledgments The authors are indebted to Alex C. Wiendhoeft, Mike Wiemann and Regis Miller from the Forest Products Laboratory for warmly hosting us and allowing the study of the entire MADw collection (Madison, Wisconsin); Maria José Miranda and Raphael Pigozzo from the Institute of Technological Research (IPT, BCTw, São Paulo) for slides of *Sparattosperma*, *Handroanthus* and *Tabebuia*; Alexandre Zuntini, Anselmo Nogueira, Diana Sampaio, Mariane Souza-Baena, Milton Groppo from the Universidade de São Paulo (Brazil), Márdel Lopes from the Universidade Federal de Viçosa (Brazil), and Luzmilla Arroyo and Daniel Villaboel of the Museo Noel Kempff Mercado (Bolivia) for collecting samples or for assistance in field collections, Harri Lorenzi for allowing us to collect samples at the Instituto Plantarum/Jardim Botânico Plantarium; Antonio Carlos Franco Barbosa sectioning *Stereospermum*; Julio C. Majcher for sectioning samples of Oroxyleae used in Scanning Electron Microscopy; Pieter Baas, Michelle Zjhra, Guillermo Angeles, and Giuliano Locosselli for invaluable suggestions in early versions of the manuscript; Gabriella Pace, Lizana Rezende and Carolina L. Bastos for valuable support, the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, grants 481034/2007-2; 486971/2012-0), and the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, grant 2012/01099-8; 2013/10679-0) for financial support. RGO is supported by US National Science Foundation (DEB-0309065, DEB-1353761). LGL and VA by CNPq productivity 307781/2013-5 and 308441/2012-5, respectively.

Appendix

Taxa sampled, followed by collector vouchers, wood collections and/or herbaria accession (following index Xylariorum and index Herbariorum) and collection location. The MAD herbarium was incorporated into the WIS herbarium in 2002 but is kept there as a separate collection.

Adenocalymma bracteatum DC., *Castanho 153*, *Lohmann 861* (SPFw, SPF), Rio Negro, Amazonas, Brazil.

- Adenocalymma comosum* (Cham.) DC., Pace 53 (SPFw, SPF), Living collection Plantarum Institute, Nova Odessa, São Paulo, Brazil. *Adenocalymma divaricatum* Miers, Udulutsch 2808 (SPFw, HRCB), Lençóis, Bahia, Brazil. *Adenocalymma flaviflorum* (Miq.) L.G. Lohmann, Sousa-Baena 2 (SPFw, SPF), Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil. *Adenocalymma neoflavidum* L.G. Lohmann, Zuntini 23 (SPFw, SPF), Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil. *Adenocalymma nodosum* (Silva Manso) L.G. Lohmann, Pace 20 (SPFw, SPF), Uberlândia, Minas Gerais, Brazil. *Adenocalymma peregrinum* (Miers) L.G. Lohmann, Pace 26 (SPFw, SPF), Living collection Plantarum Institute, Nova Odessa, São Paulo, Brazil. *Adenocalymma salmoneum* J.C. Gomes, Lohmann 658 (SPFw, SPF), Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil. *Amphilophium crucigerum* (L.) L.G. Lohmann, Pace 1, Pace 2, Pace 3, Pace 34 (SPFw, SPF), São Paulo, São Paulo, Brazil. *Amphilophium elongatum* (Vahl) L.G. Lohmann, Pace 45 (SPFw, SPF), Living collection Plantarum Institute, Nova Odessa, São Paulo, Brazil. *Amphilophium magnoliifolium* (Kunth) L.G. Lohmann, Lohmann 851 (SPFw, SPF), Rio Negro, Amazonas, Brazil; Dos Santos 272 (MADw, MAD, MO, MG), Porto de Moz, Pará, Brazil. *Amphilophium paniculatum* (L.) Kunth, Pace 46 (SPFw, SPF), Living collection Plantarum Institute, Nova Odessa, São Paulo, Brazil. *Amphilophium pulverulentum* (Sandwith) L.G. Lohmann, Dos Santos 279 (MADw, MAD, MO, MG), Senador Jose Porfirio (Sozel), Pará, Brazil. *Amphitecna latifolia* (Mill.) A.H. Gentry, Fairchild Tropical Garden x-3-369, Florida, USA. *Amphitecna regalis* (Linden) A.H. Gentry, Nee & Taylor 29900, Las Choapas, 5 km Nw of El Doce, Uxpanapa Region, Veracruz, Mexico. *Anemopaegma chamberlaynii* (Sims) Bureau & K. Schum., Zuntini 15 (SPF), Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil. *Bignonia campanulata* Cham., Pace 39 (SPFw, SPF), Living collection Plantarum Institute, Nova Odessa, São Paulo, Brazil. *Bignonia capreolata* L., Nogle s.n. (MADw), Norfolk County, Dismal swamp, Virginia, USA; Wilson 19 (MADw, F), Cow Creek, Texas, USA. *Bignonia magnifica* W. Bull, Pace 51 (SPFw, SPF), Living collection Plantarum Institute, Nova Odessa, São Paulo, Brazil. *Bignonia priurei* DC., Zuntini 13 (SPFw, SPF), Linhares, Espírito Santo, Brazil; Dos Santos 87 (MADw, MAD, MO, MG), Marabá, Pará, Brazil. *Callichlamys latifolia* (Rich.) K. Schum, Zuntini 175 (SPF), Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil.; Pace 42 (SPFw), Living collection Plantarum Institute, Nova Odessa, São Paulo, Brazil; Pace 63 (SPFw, SPF), Ducke Forest Reserve, Manaus, Amazonas, Brazil; *Campsis radicans* (L.) Seem., Hicoek 841 (SJRw, Y), Connecticut, USA; Pond 448 (MADw, MAD), Camden County, Dismal Swamp, North Carolina, USA. *Catalpa bignonioides* Walter, Erdman & DeVall s.n. (MADw, MAD, NY), Gainesville, Florida, USA. *Catalpa longissima* (Jacq.) Dum.Cours., Pimentel & Garcia 965 (SJRw, NCI), San Cristóbal, El Tablazo, Nigua riverside, Cordillera central, Dominican Republic; Collector unknown s.n. (USw2942, US), Hispaniola Island. *Catalpa speciosa* (Warder ex Barney) Warder ex Engelm., Collector unknown s.n. (SJRw, RBHw3217), location unknown; Collector unknown s.n. (SJRw, Uw17977), location unknown. *Catophractes alexandri* D. Don, Dechamps 1219 (MADw, Tw, MAD), Mocamedes, Angola. *Chilopsis linearis* (Cav.) Sweet, Pidgeon s.n. (SJRw, WIS), Otero County, New Mexico, USA; Johnson s.n. (MADw, BWCw), Campaign Wash, Arizona, USA; Collector unknown s.n. (Kw), location unknown. *Colea gentryi* M. L. Zhjra, Zhjra 714 (MADw, WIS), Masoala Peninsula, Madagascar, Africa. *Colea resupinata* M. L. Zhjra, Zhjra 785 (MADw, GAS holotype, TAN isotype, WIS), Vokoanina watershed, Masoala Peninsula, Antsiranana, Madagascar. *Crescentia alata* Kunth, Wiemann & Lemckert 23 (MADw, CR, LSU), Cañas, Guanacate, Costa Rica; Collector unknown s.n. (SJRw), Cuastecomate, Mexico; Ortega 12 (USw), Sinaloa, Mexico. *Crescentia kujete* L., Pace 80, São Paulo, São Paulo, Brazil; Dugand 149 (MADw, SJRW, MAD), Totuma, Colombia. *Cuspidaria pulchra* (Cham.) L.G. Lohmann, Pace 24 (SPFw, SPF), Uberlândia, Minas Gerais, Brazil. *Cybistax antisiphilitica* (Mart.) Mart., Reitz & Klein 7354 (MADw, HBRw, HBR), Salto do Pilão, Lontras, Santa Catarina, Brazil; Collector unknown s.n. (BWCw, SJRW42602), São Paulo, Brazil. *Delostoma integrifolium* D. Don, Acosta-Solis 6694 (MADw, SJRW, MAD, F), Limón, Bolívar, Ecuador; Acosta-Solis 11648-A (MADw, F), Ecuador. *Deplanchea bancana* (Scheff.) Steenis, Lai et al. 68559 (Kw, K), Sarawak, Malaysia; Forest Department of Java 2751 (SJRw, L), Menjabling, Dutch East Indies. *Digomphia densicoma* (Mart. ex DC.) Pilg., Nee 31168 (MADw, VEN, NY), Cerro de la neblina, Amazonas, Venezuela; Maguire 28311 (BWCw, USw), Mérida, Venezuela. *Dolichandra unguiculata* (Vell.) L.G. Lohmann, Zuntini 176 (SPFw, SPF), Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil. *Dolichandra unguis-cati* (L.) L.G. Lohmann, Ceccantini 2687 (SPFw, SPF), Matozinhos, Minas Gerais, Brazil; Groppo 322 (SPF), São Paulo, São Paulo, Brazil. *Dolichandra quadrivalvis* (Jacq.) L.G. Lohmann, Gentry 58691 (MADw, MO), São Paulo, São Paulo, Brazil. *Dolichandrone atrovirens* (Roth) K. Schum., Brown s.n. (DDw, DD), Dehradun, India; Collector unknown s.n. (SJRw), Myanmar.; Kanehira 132 (SJRw), Palau, Micronesia. *Ekmanianthe actinophylla* (Griseb.) Urb., Fors 11 (MADw, SJRW, MAD), Havana, Cuba; Leon 14358 (SJRw, NY), Cuba. *Fernandoa adenophylla* (Wall. ex G. Don) Steenis, collector unknown s.n. (Kw 108, 427, 433, 435), location unknown. *Fernandoa*

- magnifica* Seem., *Schlieben* 459 (SJRw, MAD), Tanganyika, Tanzania. *Fridericia chica* (Bonpl.) L.G. Lohmann, *Pace* 50 (SPFw), Living collection Plantarum Institute, Nova Odessa, São Paulo, Brazil. *Fridericia conjugata* (Vell.) L.G. Lohmann, *Pace* 44 (SPFw), Living collection Plantarum Institute, Nova Odessa, São Paulo, Brazil. *Fridericia platyphylla* (Cham.) L.G. Lohmann, *Pace* 22, *Pace* 23 (SPFw, SPF), Uberlândia, Minas Gerais, Brazil. *Fridericia samydoides* (Cham.) L.G. Lohmann, *Pace* 49 (SPFw, SPF), Living collection Plantarum Institute, Nova Odessa, São Paulo, Brazil. *Fridericia speciosa* Mart., *Pace* 40 (SPFw, SPF), Living collection Plantarum Institute, Nova Odessa, São Paulo, Brazil. *Godmania aesculifolia* (Kunth) Standl., *Breedlove* 9563 (MADw, DS), Chiapas, Mexico; *Williams* 10233 (MADw, F), Aragua, Venezuela; *Smith* 3368 (SJRw, MAD), British Guiana. *Handroanthus barbatus* (E.Mey.) Mattos, Loureiro s.n. (BCTw11727, INPA); *Maguire* 41572 (SJRw, NY), Rio Pacimoni-Yatua, Venezuela. *Handroanthus chrysotrichus* (Mart. ex DC.) Mattos, *Pinho* 6 (BCTw, SP), São Simão, São Paulo, Brazil; *Pace* 188, 190 (SPFw, SPF), São Paulo, São Paulo, Brazil. *Handroanthus impetiginosus* (Mart. ex DC.) Mattos, *Ducke* 363 (SJRw, MAD), Brazil; *Pinho* 2 (BCTw, SP), São Simão, São Paulo, Brazil. *Handroanthus serratifolius* (Vahl) S.O.Grose, *Lima* s.n. (BCTw), Pará, Brazil; *Silva* 3281 (BCTw, INPA), Jari, Pará, Brazil. *Heterophragma quadriculare* (Roxb.) K.Schum., *Brown* s.n. (SJRw, DDw1106), India; *Dehra Dun* s.n. (SJRw, DDw 241), India; *Pearson* s.n. (MADw), India. *Heterophragma sulfureum* Kurz, *Conservator of Forests* 1238 (SJRw), Burma. *Jacaranda brasiliana* Lam., *Collector unknown* s.n. (FPBw1755), Brazil; *Collector unknown* s.n. (SJRw, MAD), Brazil. *Jacaranda copaia* (Aubl.) D.Don, *Cabrera* 41, 42 (MADw, MAD), Puerto Carare, Santander, Colombia. *Jacaranda obtusifolia* Bonpl., *Conservator of Forests* 2049 (SJRw), British Guiana; *Smith* 3125 (SJRw, MAD), British Guiana. *Jacaranda puberula* Cham., *Hoehne* 28168 (SJRw, MAD), Brazil; *Reitz* 14198 (BWCw, MAD), Santa Catarina, Brazil. *Jacaranda ulei* Bureau & K.Schum., *Dos Santos* 167, 168 (MADw, MAD, MO, MG), Parauapebas, Pará, Brazil. *Kigelia africana* (Lam.) Benth., *Schlieben* 368 (SJRw, MAD), Tanganyika, Democratic Republic of Congo. *Lundia damazii* C. DC., *Pace* 55, *Pace* 56 (SPFw, SPF), São Paulo, São Paulo, Brazil. *Lundia glazioviana* Kraenzl., *Zuntini* 126 (SPFw, SPF), Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil. *Lundia longa* (Vell.) DC., *Zuntini* 1 (SPF), Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil; *Pace* 227 (SPFw, SPF), Biological Reserve of Poço das Antas, Rio de Janeiro, Brazil. *Manaosella cordifolia* (DC.) A.H. Gentry, *Pace* 41 (SPFw, SPF), Brazil, Living collection Plantarum Institute, Nova Odessa, São Paulo, Brazil; *Dos Santos* 88 (MADw, MAD, MO, MG), Marabá, Rio Doce S.A. Forest reserve, 48 km from Marabá, Pará, Brazil; *Dos Santos* 308 (MADw, MAD, MO, MG), Senador José Porfírio, Xingu riverside. *Mansoa difficilis* (Cham.) Bureau & K. Schum., *Pace* 35 (SPFw), São Paulo, São Paulo, Brazil; *Zuntini* 4 (SPF), Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil. *Mansoa onohualcoides* A.H. Gentry, *Zuntini* 276 (SPF), Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil. *Mansoa standleyi* (Steyererm.) A.H. Gentry, *Pace* 43 (SPFw), Living collection Plantarum Institute, Nova Odessa, São Paulo, Brazil. *Markhamia lutea* (Benth.) K.Schum., *collector unknown* s.n. (Kw525), Equatorial Guinea. *Markhamia stipulata* (Wall.) Seem., *collector unknown* s.n. (Kw440), Thailand. *Martinella obovata* (Kunth) Bureau & K. Schum., *Zuntini* 7 (SPF), Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil; *Dos Santos* 237 (MADw, MAD, MO, MG), Porto de Moz, Xingu riverside, Pará, Brazil; *Dos Santos* 317 (MADw, MAD, MO, MG), Gurupa, Moju riverside, tributary of the Amazon river, Pará, Brazil. *Millingtonia hortensis* L.f., *van Beusekom* 3426 (TWTw, L), Saeat Kanchanaburi, Thailand; *Brown* 3160 (SJRw, DDw), India; *collector unknown* s.n. (Kw), Thailand. *Neojobertia mirabilis* (Sandwith) L.G. Lohmann, *Dos Santos* 48 (MADw, MAD, MO, MG), Buriticupu Forest Reserve, Maranhão, Brazil. *Neojobertia* sp. nov., *Zuntini* 18, Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil. *Newbouldia laevis* (P.Beauv.) Seem., *Vigne* 1722 (SJRw, MAD), Gold Coast, Nsuta, Ghana. *Ophiocolea floribunda* (Bojer ex Lindl.) H.Perrier *Zhira* s.n. (MADw, MAD), Masoala Peninsula, Madagascar. *Oroxylum indicum* (L.) Kurtz, *China Academy of Forestry* s.n. (TWTw7424, CAFw13841), China; *Jacobs* 8493 (TWTw, L), Lampung, Sumatra; *Kanehira* s.n. (TWTw, FUw B.401), Java, Indonesia; *Brown* 1179 (SJRw, DDw), India. *Pachyptera kerere* (Aubl.) Sandwith, *Castanho* 143, *Lohmann* 834 (SPF), Negro riverside, Amazonas, Brazil; *Santos* 226 (MADw, MAD, MO, MG), Melgaco, Marajó Island; Mapiari riverside, Pará, Brazil; *Dos Santos* 274 (MADw, MAD, MO, MG), Porto de Moz; Xingu riverside near the Açai river, Pará, Brazil; *Dos Santos* 291 (MADw, MAD, MO, MG), Senador José Porfírio, Xingu river near foz do Igarapé Guará; *Dos Santos* 292 (MADw, MAD, MO, MG), Marabá, Rio Doce S.A. Forest reserve, Sororó riverside. *Pajanelia longifolia* (Willd.) K.Schum., *Conservator of Forests* 8188 (SJRw), Rangoon, Burma; *collector unknown* s.n. (Kw528), Malaya, Malaysia. *Pandorea jasminoides* (Lindl.) K.Schum., *Pace* 18, 19 (SPFw, SPF), Cultivated in Campinas, São Paulo, Brazil. *Paratecoma peroba* (Record) Kuhlmann, *Castro* 284, 578 (BCTw), Rio Doce, Espírito Santo, Brazil. *Parmentiera cereifera* Seem., *Curtis* s.n. Fairchild Bot. Gard. X4- 183 (MADw), Florida, USA. *Parmentiera macrophylla* Standl., *Cooper* 402 (MADw, SJRW, MAD), Panama; *Stork* 1894 (SJRw,

MAD), Costa Rica. *Perianthomega vellozoi* Bureau, Pace 10, Pace 15 (SPFw, SPF), Mata do Paraíso, Viçosa, Minas Gerais, Brazil; Pace 28, Pace 29 (SPFw, SPF), Santa Cruz de la Sierra, Santa Cruz, Bolivia. *Phyllarthron bojeranum* DC., G 31 (SJRw, CTFw), Region Cotier Est, Madagascar. *Pleonotoma melioides* (S. Moore) A.H. Gentry, Dos Santos 174 (MADw, MAD, MO, MG), Parauapebas, Serra dos Carajás Biological Reserve; Dos Santos 298 (MADw, MAD, MO, MG), Senador José Pontifício, Pará, Brazil. *Pleonotoma stichadenia* K. Schum., Zuntini 7 (SPF), Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil; Dos Santos 187 (MADw, MAD, MO, MG), Parauapebas, Pará, Brazil. *Pleonotoma tetraquetra* (Cham.) Bureau, Ozório-Filho 11, São Paulo, São Paulo, Brazil. *Podranea ricasoliana* (Tanfani) Sprague, Pace 11 (SPF), São Paulo, São Paulo, Brazil. *Pyrostegia venusta* (Ker Gawl.) Miers, Pace 17 (SPFw, SPF), Campinas, São Paulo, Brazil; Pace 36 (SPFw, SPF), São Paulo, São Paulo, Brazil. *Radermachera ignea* (Kurz) Steenis, Conservation of Forests 2444 (SJRw), Burma. *Radermachera gigantea* (Blume) Miq., Van de Koppel 4780 (SJRw, L), Java, Indonesia. *Radermachera glandulosa* (Blume) Miq., Janssonius 1214 g (SJRw), Java, Indonesia; collector unknown s.n. (Kw), Burma. *Radermachera pinnata* (Blanco) Seem., Philippine Bureau of Forestry 342 (SJRw), Philippines. *Radermachera sinica* (Hance) Hemsl., NTU 408, Taiwan. *Rhodocolea multiflora* Zhjra, Zhjra 836, Vokonina, Masoala Peninsula, Madagascar. *Rhodocolea nycteriphilla* Zhjra, Zhjra 810, Vokonina, Masoala Peninsula, Madagascar. *Rhodocolea telfairae* (Bojer ex Hook.) H. Perrier, collector unknown s.n. (SJRw10766), Madagascar. *Roseodendron donnell-smithii* (Rose) Miranda, Williams 8734 (MADw, F), Fortuno, Coatzacoalcos River, Veracruz, Mexico; Williams 9382 (MADw, F), Ubero, Oaxaca, Mexico; William 9458 (MADw, F), Mexico; collector unknown s.n. (Kw920), Venezuela. *Sparattosperma leucanthum* (Vell.) K. Schum., collector unknown s.n. (BCTw 2486), Brasília, Distrito Federal, Brazil. *Spathodea campanulata* P. Beauv., Chevalier 140 (SJRw, K), Gabon; collector unknown s.n. (Kw529), Uganda. *Spirotecoma spiralis* (C. Wright ex Griseb.) Pichon, Bucher 90 (SJRw, MAD), Cuba. *Stereospermum chelonoides* (L.f.) DC., Istituto Botanico dell'Università di Firenze 706 (BCTw), India. *Stizophyllum riparium* (Kunth) Sandwith, Pace 16, Pace 33 (SPFw, SPF), São Paulo, São Paulo, Brazil; Zuntini 9 (SPF), Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil. *Tabebuia aurea* (Silva Manso) Benth. & Hook.f. ex S. Moore, Gerolamo 3 (SPFw), São Paulo, São Paulo, Brazil. *Tabebuia cassinoides* (Lam.) DC., Williams 13809 (MADw, F), Puerto Ayacucho, Amazonas, Venezuela. *Tabebuia fluviatilis* (Aubl.) DC., Lobato 447 (MADw, MGw, MG), Barcarena, Pará, Brazil; Conservation of Forests 4071 (SJRw), British Guiana; collector

unknown (SJRw12019), location unknown). *Tabebuia heterophylla* (DC.) Britton, Dungand 33754 (BCTw), Colombia. *Tabebuia obtusifolia* (Cham.) Bureau, Kuhlmann (BCTw, RB), Espírito Santo, Brazil. *Tabebuia rigida* Urb., Instituto de Tecnologia do Rio Grande do Sul s.n. (BCTw), Rio Grande do Sul, Brazil. *Tabebuia roseoalba* (Ridl.) Sandwith, CVRD Morais Jesus s.n. (BCTw), Linhares, Espírito Santo, Brazil. *Tanaecium bilabiatum* (Sprague) L.G. Lohmann, Lohmann 850 (SPF), Rio Negro Amazonas, Brazil. *Tanaecium duckei* (A. Samp.) A.H. Gentry, Dos Santos 179, 186, Serra do Carajás Biological Reserve, Companhia Vale do Rio Doce, Parauapebas, Pará, Brazil. *Tanaecium pyramidatum* (Rich.) L.G. Lohmann, Pace 14, Pace 35 (SPFw, SPF), São Paulo, São Paulo, Brazil; Dos Santos 101 (MADw, MAD, MO, MG), Marabá, Rio Doce S.A. forest reserve, Sororó riverside, Pará, Brazil. *Tecoma cochabambensis* (Herzog) Sandwith, Salomon 6684 (MADw, MO) Murillo, La Paz, Bolivia. *Tecoma fulva* (Cav.) G. Don, collector unknown s.n. (SJRw32082), location unknown. *Tecoma stans* (L.) Juss. ex Kunth, Jack 5693 (SJRw, MAD), Santa Clara, Belmonte, Cuba; Dugant 216 (SJRw, MAD), Colombia; Williams 12254 (MADw, F), Federal District, Venezuela. Pace 422, 423 (SPFw, SPF, MO), Magdalena Ocotlán, Oaxaca, Mexico. *Tecomaria capensis* (Thunb.) Spach, Rimbach 832 (SJRw, MAD), Ecuador. *Tecomella undulata* (Sm.) Seem., collector unknown s.n. (Kw550), location unknown. *Tynanthus cognatus* (Cham.) Miers, Pace 9a, Pace 9b (SPFw, SPF), São Paulo, São Paulo, Brazil. *Xylophragma myrianthum* (Cham. ex Steud.) Sprague, Zuntini 263 (SPF), Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil. *Xylophragma pratense* (Bureau & K. Schum.) Sprague, Dos Santos 140 (MADw, MAD, MO, MG), Marabá, Rio Doce S.A. forest reserve, Pará, Brazil. *Zeyheria montana* Mart., Pacheco 2762 (SJRw), Minas Gerais, Brazil; Heringen 4130 (BCTw, MADw), Rio de Janeiro, Brazil. *Zeyheria tuberculosa* (Vell.) Bureau ex Verl., Schmidt 143 (SJRw, M), Bolivia.

References

- Angyalossy V, Angeles G, Pace MR, Lima AC, Dias-Leme CL, Lohmann LG, Madero-Vega C (2012) An overview on the anatomy, development and evolution of the vascular system of lianas. *Pl Ecol Divers* 5:167–182
- Angyalossy V, Pace MR, Lima AC (in press) Liana anatomy: a broad perspective on structural evolution of the vascular system. In: Schnitzer SA, Bongers F, Burnham R, Putz FE (eds) *Ecology of lianas*. Wiley-Blackwell, Oxford
- APG (Angiosperm Phylogenetic Group) II (2003) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants. *Bot J Linn Soc* 141:399–436
- APG (Angiosperm Phylogenetic Group) III (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants. *Bot J Linn Soc* 161:105–121

- Barbosa ACF, Pace MR, Witovsk L, Angyalossy V (2010) A new method to obtain good anatomical slides of heterogeneous plant parts. *IAWA J* 31:373–383
- Bentham G, Hooker JD (1876) *Genera plantarum* 2, London, pp 1026–1053
- Berlyn GP, Miksche JP (1976) *Botanical microtechnique and cytochemistry*. Iowa State University Press, Ames
- Bukatsch F (1972) Bemerkungen zur Doppelfärbung Astrablau-Safranin. *Mikroskopos* 61:255
- Carlquist S (1985) Observations on functional wood histology of vines and lianas: vessel dimorphism, tracheids, vasicentric tracheids, narrow vessels, and parenchyma. *Aliso* 11:139–157
- Carlquist S (2001) *Comparative wood anatomy*, 2nd edn. Springer, Berlin
- Chudnoff M (1984) *Tropical timbers of the world*. Forest Service Agriculture handbook number 607. United States Department of Agriculture, USA
- Dobbins DR (1971) Studies on the anomalous cambial activity in *Doxantha unguis-cati* (Bignoniaceae). II. A case of differential production of secondary tissues. *Amer J Bot* 58:697–705
- Dos Santos GMA (1995) Wood anatomy, chloroplast DNA, and flavonoids of the tribe Bignoniaceae (Bignoniaceae). PhD dissertation, University of Reading
- Dos Santos G, Miller RB (1992) Wood anatomy of Tecomeae. In: Gentry AH (ed) *Bignoniaceae, Part II (Tribe Tecomeae)*, *Flora Neotropica Monograph* 25(II)The New York Botanical Garden Press, New York, pp 336–358
- Dos Santos G, Miller RB (1997) Wood anatomy of *Jacaranda* (Bignoniaceae): systematic relationships in sections Monolobos and Dilobos as suggested by twig and stem wood rays. *IAWA J* 18:369–383
- Fischer E, Theisen I, Lohmann LG (2004) Bignoniaceae. In: Kubitzki K, Kadereit JW (eds) *The Families and genera of vascular plants. VII. Flowering plants. Dicotyledons. Lamiales (except Acanthaceae including Avicenniaceae)*. Springer, Berlin, pp 9–38
- Gasson P, Dobbins DR (1991) Wood anatomy of the Bignoniaceae, with a comparison of trees and lianas. *IAWA J* 12:389–417
- Gentry AH (1980) Bignoniaceae: Part I (Crescentia and Tourrettieae). *Flora Neot Mon*, vol 25(I). NYBG Press, New York
- Gentry AH (1992) Bignoniaceae part II (tribe Tecomeae). *Fl Neotrop Monogr*, vol 25(II). NYBG Press, New York
- Grose SO, Olmstead RG (2007a) Evolution of a charismatic neotropical clade: molecular phylogeny of *Tabebuia* s.l., Crescentieae, and allied genera (Bignoniaceae). *Syst Bot* 32:650–659
- Grose SO, Olmstead RG (2007b) Taxonomic revisions in the polyphyletic genus *Tabebuia* s.l. (Bignoniaceae). *Syst Bot* 32:660–670
- Hussain H, Krohn K, Ahmad VU, Miana GA, Green IR (2007) Lapachol: an overview. *Arkivoc* II:145–171
- IAWA Committee (1989) IAWA list of microscopic features for hardwood identification. *IAWA Bull* 10:219–332
- Li J (2008) Phylogeny of *Catalpa* (Bignoniaceae) inferred from sequences of chloroplast *ndhF* and nuclear ribosomal DNA. *J Syst Evol* 46:341–348
- Lima AC, Pace MR, Angyalossy V (2010) Seasonality and growth rings in lianas of Bignoniaceae. *Trees* 24:1045–1060
- Lohmann LG (2004) Bignoniaceae. In: Smith N, Mori S, Henderson A, Stevenson D, Held S (eds) *Flowering Plants of the Neotropics*. Princeton University Press, NYBG, New York
- Lohmann LG (2006) Untangling the phylogeny of neotropical lianas (Bignoniaceae, Bignoniaceae). *Amer J Bot* 93:304–318
- Lohmann LG, Taylor CM (2014) A new generic classification of Bignoniaceae (Bignoniaceae) based on molecular phylogenetic data and morphological synapomorphies. *Ann Missouri Bot Gard* 99:348–489
- Lohmann LG, Ulloa CU (2006) Bignoniaceae. In: *iPlants prototype checklist*. <http://www.iplants.org>. Accessed 29 July 2012
- Melchior H (1927) Der natürliche Formenkreis der *Pithecocteniinae* innerhalb der Familie der Bignoniaceae. *Repert Spec Nov Regni Veg Beih* 46:71–82
- Olmstead RG (2013) Phylogeny and biogeography in Solanaceae, Verbenaceae and Bignoniaceae: a comparison of continental and intercontinental diversification patterns. *Bot J Linn Soc* 171:80–102
- Olmstead RG, Zjhra ML, Lohmann LG, Grose SO, Eckert AJ (2009) A molecular phylogeny and classification of Bignoniaceae. *Amer J Bot* 96:1731–1743
- Pace MR, Angyalossy V (2013) Wood anatomy and evolution: a case study in the Bignoniaceae. *Int J Pl Sci* 147:1014–1048
- Pace MR, Lohmann LG, Angyalossy V (2009) The rise and evolution of the cambial variant in Bignoniaceae (Bignoniaceae). *Evol Develop* 11:465–479
- Rasband WS (2012) ImageJ. US National Institutes of Health, Bethesda, MD. <http://imagej.nih.gov/ij>
- Record SJ, Hess RW (1943) *Timbers of the new world*. Yale University Press, New Haven
- Refulio-Rodriguez NF, Olmstead RG (2014) Phylogeny of Lamiidae. *Amer J Bot* 101:287–299
- Schenck H (1893) Beiträge zur Biologie und Anatomie der Lianen im Besonderen der in Brasilien einheimischen Arten. In: Schimper AFW (ed) *Beiträge zur Anatomie der Lianen*. Botanische Mitteilungen aus den Tropen. Gustav Fisher, Jena
- Spangler RE, Olmstead RE (1999) Phylogenetic analysis of Bignoniaceae based on the cpDNA gene sequences *rbcL* and *ndhF*. *Ann Missouri Bot Gard* 86:33–46
- Veenendaal WLH, Den Outer RW (1993) Development of included phloem and organization of the phloem network in the stem of *Strychnos millepunctata* (Loganiaceae). *IAWA J* 14:253–265
- Zjhra ML, Sytsma KJ, Olmstead RG (2004) Delimitation of Malagasy tribe Coleae and implications for fruit evolution in Bignoniaceae inferred from a chloroplast DNA phylogeny. *Pl Syst Evol* 245:55–67