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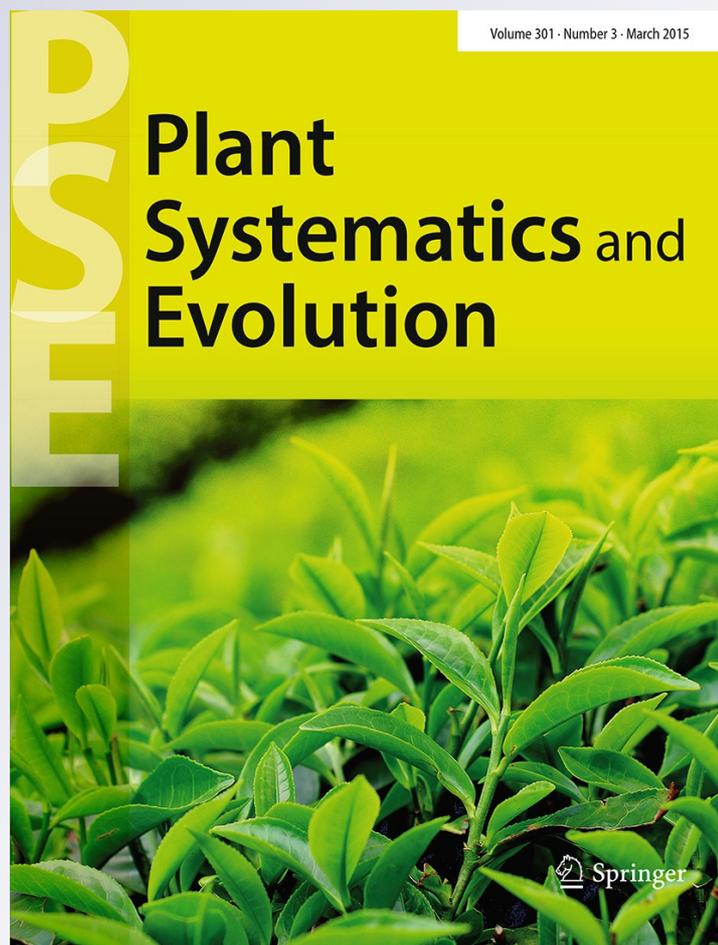
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Wood anatomy of major Bignoniaceae clades

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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 subclades, 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

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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 Schlegeliaceae (Gentry 1980, 1992; Fischer et al. 2004). However, Schlegeliaceae 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 Jacarandae. 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 earlywood and latewood measured separately, since vessels in latewood usually had a different grouping arrangement. In woods with vessels of two width classes (lianas and plants with ring-porous or semi-ring porous woods), both the wide and the narrow vessels were 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

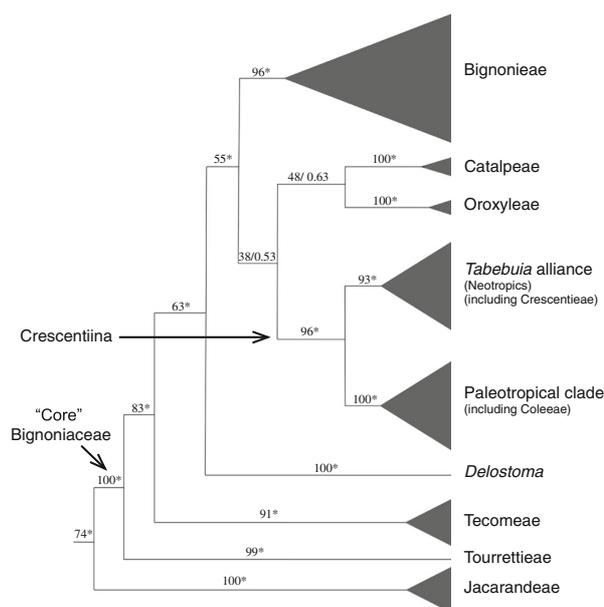


Fig. 1 Phylogenetic relationship of the nine major clades of Bignoniaceae as proposed by Olmstead et al. (2009). Number above branches represent bootstrap support, followed by posterior probabilities (recovered from Olmstead et al. 2009); Asterisk indicates 100 % posterior probabilities

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 continued

Tree or clade	Species	Habit	Poosity	Quartz (in mastic) marker: parenchyma	Growth ring meter: macrofibrils	Vessel arrangement	Vessel grouping	Vessel diameter (µm)	Vessel frequency (per mm ²)	Vessel wall thickness (µm)	Perforation plate	Interseptal plate	Hilical thickening	Petrified parenchyma	Confidence	Acid parenchyma frequency	Acid parenchyma cell area (µm ²)	Diffuse parenchyma	Parenchyma strands	Striated striate	Ray width in number of cells	Ray height in number of cells	Ray cubical comparison	Waxy resin pitting	Seriate fibers	Perforated ray cells	Crystals	Type of variant	Climate of occurrence	
	<i>Fraxinus sylvatica</i>	Liana	Semi-ring porous	-	-	Diffuse	Salitary to multiples of 2-3	?	?	?	?	?	?	?	Scanty	?	?	?	Four (3-4) cells per strand	?	4.4 ± 1	High >1 mm	Hexacubical mased	Similar to mased pits	+	+	+	Four prism wedges	Tropical	
	<i>Fraxinus spongata</i>	Liana	Semi-ring porous	-	-	Diffuse	Salitary to multiples of 2-3	2.92 ± 1.01	?	?	?	?	?	?	Scanty	?	?	?	Four (3-4) cells per strand	?	2.4 ± 1	High >1 mm	Hexacubical mased	Similar to mased pits	+	+	+	Four prism wedges	Tropical	
	<i>Fraxinus platyphloia</i>	Shrub	Diffuse	-	-	Diffuse	Salitary to multiples of 2-3	1.31 ± 0.26	14.4 ± 5	72 ± 20	NA	Simple	6.1 ± 3	-	Scanty	1%	171 ± 72	-	Edge (5-8) cells per strand	?	13 ± 5	1.1 ± 1	Hexacubical mased	Similar to mased pits	-	-	-	Four prism wedges	Tropical	
	<i>Fraxinus amygdalis</i>	Liana	Semi-ring porous	-	-	Diffuse	Salitary (wide vessels)	?	?	?	?	?	?	?	Vascentric	Short	?	?	Edge (5-8) cells per strand	?	3.1 ± 1	Short <1 mm	Hexacubical mased	Simple to banded	+	+	-	Four prism wedges	Tropical	
	<i>Fraxinus speciosa</i>	Liana	Diffuse	-	-	Diffuse	Salitary (wide vessels)	3.01 ± 1.03	118 ± 36	133 ± 37	20 ± 11	Simple	5.0 ± 1	-	Vascentric	Short	7%	88 ± 23	-	Four (3-4) cells per strand	?	3.4 ± 5	High >1 mm	Hexacubical mased	Similar to mased pits	+	+	-	Four prism wedges	Tropical
	<i>Liriodendron tulipifera</i>	Liana	Diffuse	-	-	Diffuse to tangential	Salitary (wide vessels)	3.69 ± 1.48	101 ± 30	232 ± 57	20 ± 9	Simple	8.4 ± 1	-	Vascentric	Short	14%	212 ± 140	-	Four (3-4) cells per strand	?	3.1 ± 8	Short <1 mm	Hexacubical mased	Similar to mased pits	+	+	-	Multiple of four prism wedges	Tropical
	<i>Liriodendron glaucovire</i>	Liana	Semi-ring porous	-	-	Diffuse to tangential	Salitary (wide vessels)	?	?	?	?	?	?	?	Scanty	?	?	?	Four (3-4) cells per strand	?	3.1 ± 1	High >1 mm	Hexacubical mased	Similar to mased pits	+	+	-	Multiple of four prism wedges	Tropical	
	<i>Liriodendron togae</i>	Liana	Semi-ring porous	-	-	Diffuse	Salitary (wide vessels)	?	?	?	?	?	?	?	Vascentric	?	?	?	Four (3-4) cells per strand	?	3.1 ± 1	High >1 mm	Hexacubical mased	Similar to mased pits	+	+	-	Multiple of four prism wedges	Tropical	
	<i>Miconia acutiloba</i>	Liana	Semi-ring porous	-	-	Diffuse	Salitary to multiples of 2-3	2.12 ± 0.59	33 ± 20	216 ± 43	22 ± 6	Simple	12.4 ± 2	-	Vascentric	Short	1%	187 ± 60	-	Four (3-4) cells per strand	?	15 ± 5	2.1 ± 1	Hexacubical mased	Similar to mased pits	+	+	-	Four prism wedges	Tropical
	<i>Miconia affinis</i>	Liana	Diffuse	-	-	Diffuse	Salitary to multiples of 2-3	2.89 ± 0.33	109 ± 14	139 ± 25	22 ± 9	Simple	6.0 ± 1	-	Scanty	1%	154 ± 45	-	Four (3-4) cells per strand	?	5.7 ± 18	4.1 ± 1	Hexacubical mased	Similar to mased pits	+	+	-	Multiple of four prism wedges	Tropical	
	<i>Miconia andoubaensis</i>	Liana	Diffuse	-	-	Diffuse	Salitary to multiples of 2-3	?	?	?	?	?	?	?	Scanty	?	?	?	Four (3-4) cells per strand	?	?	?	Hexacubical mased	Similar to mased pits	+	+	-	Multiple of four prism wedges	Tropical	
	<i>Miconia atrovirens</i>	Liana	Diffuse	-	-	Diffuse	Salitary to multiples of 2-3	?	?	?	?	?	?	?	Scanty	?	?	?	Four (3-4) cells per strand	?	?	?	Hexacubical mased	Similar to mased pits	+	+	-	Multiple of four prism wedges	Tropical	
	<i>Miconia obtusa</i>	Liana	Diffuse	-	-	Radial pattern	Salitary to multiples of 2-3	3.76 ± 1.33	87 ± 19	182 ± 32	35 ± 11	Simple	7.0 ± 4	-	Scanty	2%	244 ± 78	-	Four (3-4) cells per strand	?	5.0 ± 8	3.1 ± 1	Hexacubical mased	Similar to mased pits	+	+	-	Four prism wedges	Tropical	
	<i>Neopeltandra malabala</i>	Liana	Diffuse	-	-	Diffuse	Salitary to multiples of 2-3	?	?	?	?	?	?	?	Scanty	-	-	-	Four (3-4) cells per strand	?	?	?	Hexacubical mased	Similar to mased pits	+	+	-	Four prism wedges	Tropical	
	<i>Neopeltandra sp. nov.</i>	Liana	Diffuse	-	-	Diffuse	Salitary to multiples of 2-3	2.63 ± 0.65	100 ± 27	109 ± 25	16 ± 5	Simple	7.6 ± 2	-	Scanty	3%	127 ± 45	-	Four (3-4) cells per strand	?	2.8 ± 5	Short <1 mm	Hexacubical mased	Similar to mased pits	+	+	-	Four prism wedges	Tropical	
	<i>Pachypodium leucum</i>	Liana	Diffuse	-	-	Radial pattern	Salitary to multiples of 2-3 and radial common	2.41 ± 0.57	85 ± 12	118 ± 28	24 ± 7	Simple	8.8 ± 3	-	Scanty	1%	110 ± 50	-	Edge (5-8) cells per strand	?	?	2.1 ± 1	High >1 mm	Hexacubical mased	Similar to mased pits	+	+	-	Four prism wedges	Tropical
	<i>Pavanevanga villosa</i>	Liana	Semi-ring porous	-	-	Diffuse	Salitary to multiples of 2-3	2.29 ± 0.62	100 ± 17	112 ± 15	23 ± 8	Simple	8.4 ± 1	-	Scanty	4%	118 ± 52	-	Edge (5-8) cells per strand	?	3.0 ± 8	3.1 ± 1	Hexacubical mased	Similar to mased pits	+	+	-	Four prism wedges	Tropical	
	<i>Pisonotoma melioides</i>	Liana	Diffuse	-	-	Diffuse	Salitary to multiples of 2-3	3.31 ± 0.85	88 ± 27	187 ± 25	15 ± 5	Simple	8.3 ± 2	-	Scanty	1%	106 ± 35	-	Four (3-4) cells per strand	?	13 ± 4	1.0 ± 1	Hexacubical mased	Similar to mased pits	+	+	-	Four prism wedges	Tropical	
	<i>Pisonotoma actinostoma</i>	Liana	Semi-ring porous	-	-	Diffuse	Salitary to multiples of 2-3	?	?	?	?	?	?	?	Scanty	?	?	?	Four (3-4) cells per strand	?	?	?	Hexacubical mased	Similar to mased pits	+	+	-	Four prism wedges	Tropical	
	<i>Pisonotoma tenuipora</i>	Liana	Semi-ring porous	-	-	Diffuse	Salitary to multiples of 2-3	?	?	?	?	?	?	?	Scanty to vascentric	?	?	?	Four (3-4) cells per strand	?	4.1 ± 1	High >1 mm	Hexacubical mased	Similar to mased pits	+	+	-	Four prism wedges	Tropical	
	<i>Pyrostegia venusta</i>	Liana	Semi-ring porous	-	-	Diffuse	Salitary to multiples of 2-3	2.03 ± 0.37	75 ± 18	138 ± 26	29 ± 9	Simple	9.6 ± 2	-	Scanty	1%	166 ± 32	-	Four (3-4) cells per strand	?	5.2 ± 5	4.1 ± 1	Hexacubical mased	Similar to mased pits	+	+	-	Multiple of four prism wedges	Tropical	
	<i>Styphylidium sp. nov.</i>	Liana	Diffuse	-	-	Diffuse	Salitary (wide vessels)	2.29 ± 0.82	62 ± 19	180 ± 30	14 ± 3	Simple	6.9 ± 3	-	Scanty	2%	103 ± 28	-	Four (3-4) cells per strand	?	2.1 ± 3	Short <1 mm	Hexacubical mased	Similar to mased pits	+	+	-	Four prism wedges	Tropical	
	<i>Tournefortia hirsutum</i>	Liana	Diffuse	-	-	Diffuse	Salitary to multiples of 2-3	?	?	?	?	?	?	?	Scanty	?	?	?	Four (3-4) cells per strand	?	?	?	Hexacubical mased	Similar to mased pits	+	+	-	Four prism wedges	Tropical	
	<i>Tournefortia drakei</i>	Liana	Diffuse	-	-	Diffuse	Salitary to multiples of 2-3	4.63 ± 1.77	?	?	?	?	?	?	Scanty	?	?	?	Four (3-4) cells per strand	?	?	?	Hexacubical mased	Similar to mased pits	+	+	-	Four prism wedges	Tropical	
	<i>Tournefortia pyramidalis</i>	Liana	Diffuse	-	-	Diffuse	Salitary to multiples of 2-3	?	6.9 ± 4.0	260 ± 54	21 ± 7	Simple	10.3 ± 2	-	Vascentric	Absent	5%	185 ± 44	-	Four (3-4) cells per strand	?	5.3 ± 18	High >1 mm	Hexacubical mased	Similar to mased pits	+	+	-	Four prism wedges	Tropical
	<i>Trinnesia reginae</i>	Liana	Semi-ring porous	-	-	Diffuse	Salitary (wide vessels)	3.09 ± 0.41	4 ± 25	208 ± 37	17 ± 6	Simple	8.3 ± 3	-	Aliform	Short	7%	129 ± 55	-	Four (3-4) cells per strand	?	3.1 ± 10	Short <1 mm	Hexacubical mased	Similar to mased pits	+	+	-	Four prism wedges	Tropical
	<i>Xylocarpus myrsinifolium</i>	Liana	Diffuse	-	-	Diffuse	Salitary to multiples of 2-3	?	?	?	?	?	?	?	Aliform	Short	?	?	Four (3-4) cells per strand	?	?	?	Hexacubical mased	Similar to mased pits	+	+	-	Four prism wedges	Tropical	
	<i>Xylocarpus parsonsii</i>	Liana	Semi-ring porous	-	-	Diffuse	Salitary to multiples of 2-3	2.48 ± 0.69	20 ± 15	265 ± 65	15 ± 5	Simple	1.6 ± 1	-	Aliform	Absent	9%	278 ± 93	-	Four (3-4) cells per strand	?	6.3 ± 20	High >1 mm	Hexacubical mased	Similar to mased pits	+	+	-	Four prism wedges	Tropical

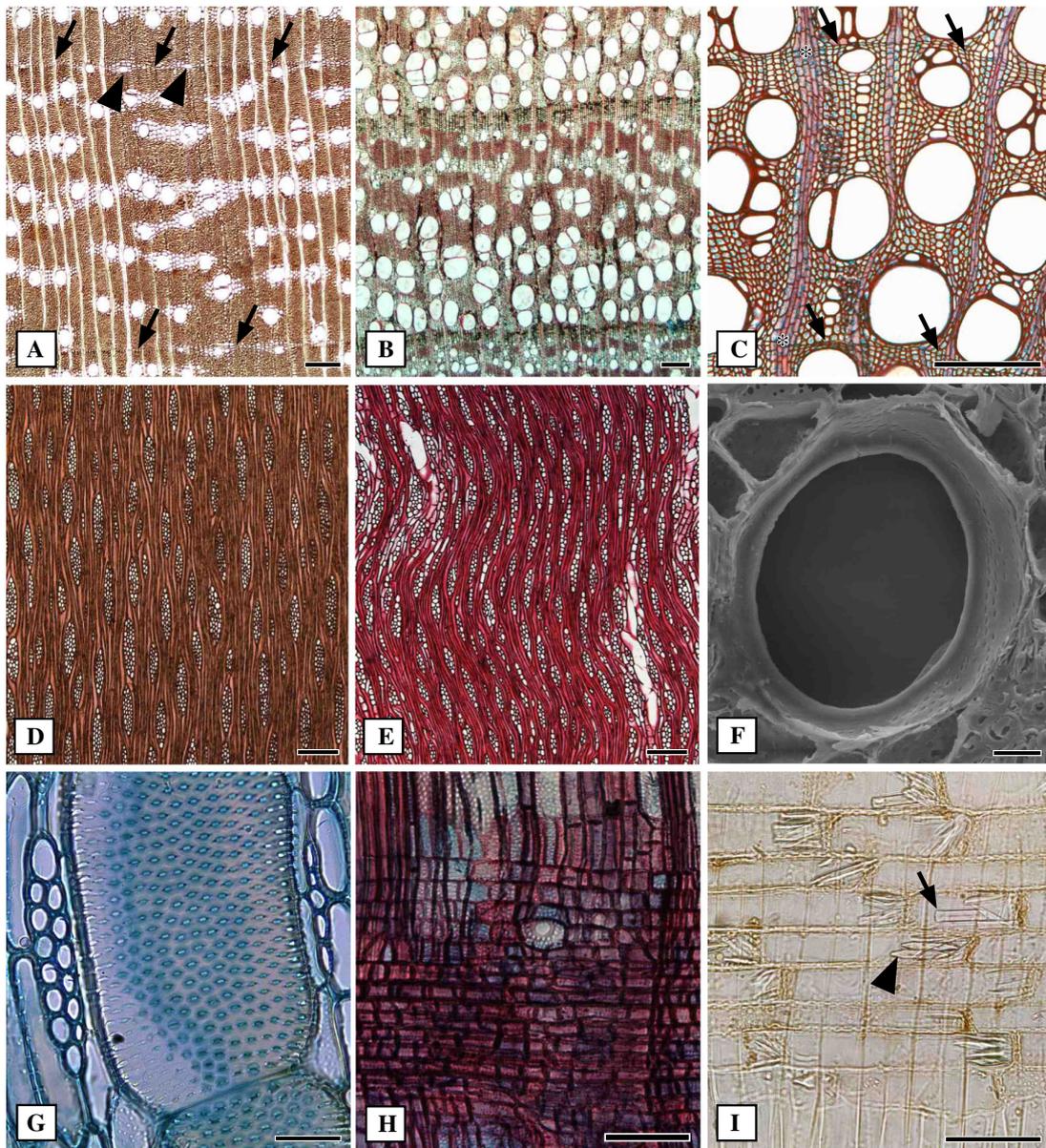


Fig. 2 General wood anatomical features of Bignoniaceae. **a** *Tabebuia rigida*, transverse section (TS), diffuse porous wood with aliform parenchyma with short confluences and growth rings delimited by a line of marginal parenchyma (arrows) associated with very narrow vessels (arrowheads). **b** *Chilopsis 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: dilated rays	Growth ring marker: flattened fibers	Vessel arrangement	Vessel grouping	Vessel dimorphism	Tyloses	Perforation plate	Helical thickening	Paratracheal parenchyma	Confluence	Diffuse parenchyma	Parenchyma strands	Storied structure	Ray height	Rays: cellular composition	Vessel-ray pitting	Septate fibers	Perforated ray cells	Crystals
JACARANDEAE	Trees, and a few subshrubs in arid zones	Diffuse	+	±	+	Diffuse	Solitary to multiples of 2-3	•	•	Simple	•	Alliform	Short to long	•	Four (3-4) cells per strand	•	Short <1 mm	Homocellular in <i>Jacaranda</i> , <i>Monolobos</i> and heterocellular in <i>Jacaranda</i> , <i>Dilobos</i>	Similar to intervessel pits	•	•	Present in the rays of some species
TECOMEA	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 > 1mm in lianas	Heterocellular	Similar to intervessel pits	+	+	Present in the rays of some species
DELOSTOMA	Trees	Diffuse	+	•	•	Radial pattern	Solitary to multiples of 2-3 & Radial multiples	•	•	Simple	•	Scanty	Absent	•	Four (3-4) cells per strand	•	Short <1 mm	Homo and hetero with 1 row of square cells	Similar to intervessel pits	+	•	Present in rays
OROXYLEAE	Trees, a few lianas	Diffuse	+	±	+	Diffuse	Solitary to multiples of 2-3	•	•	Reticulate, fenestrate and simple	•	Vascentric to alliform	Short	•	Four (3-4) cells per strand	•	Short <1 mm	Homocellular	Similar to intervessel pits	±	•	•
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	Simple to semi-bordered	±	•	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. When present, in both rays and axial parenchyma
TABEBUIA 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	Similar to intervessel pits	•	•	Present in the rays of some species
PALEOTROPICAL CLADE	Trees and shrubs	Diffuse	+	±	±	Diffuse	Solitary to multiples of 2-3	•	•	Mostly Simple	•	Alliform	Short to long	+ in Coleaseae	Four (3-4) cells per strand	•	Short <1 mm with 1 row of square cells	Homo and hetero with 1 row of square cells	Similar to intervessel pits	•	•	Present in the rays of some species

Key: + present, - absent, ? unsampled

Diagnostic features

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

Detailed description

Growth rings are distinct to indistinct, delimited by 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 (7–10 μm 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), *Tecomathe dendrophila* (1 of 5 species), and *Tecomaria capensis* (1 of 2 species).

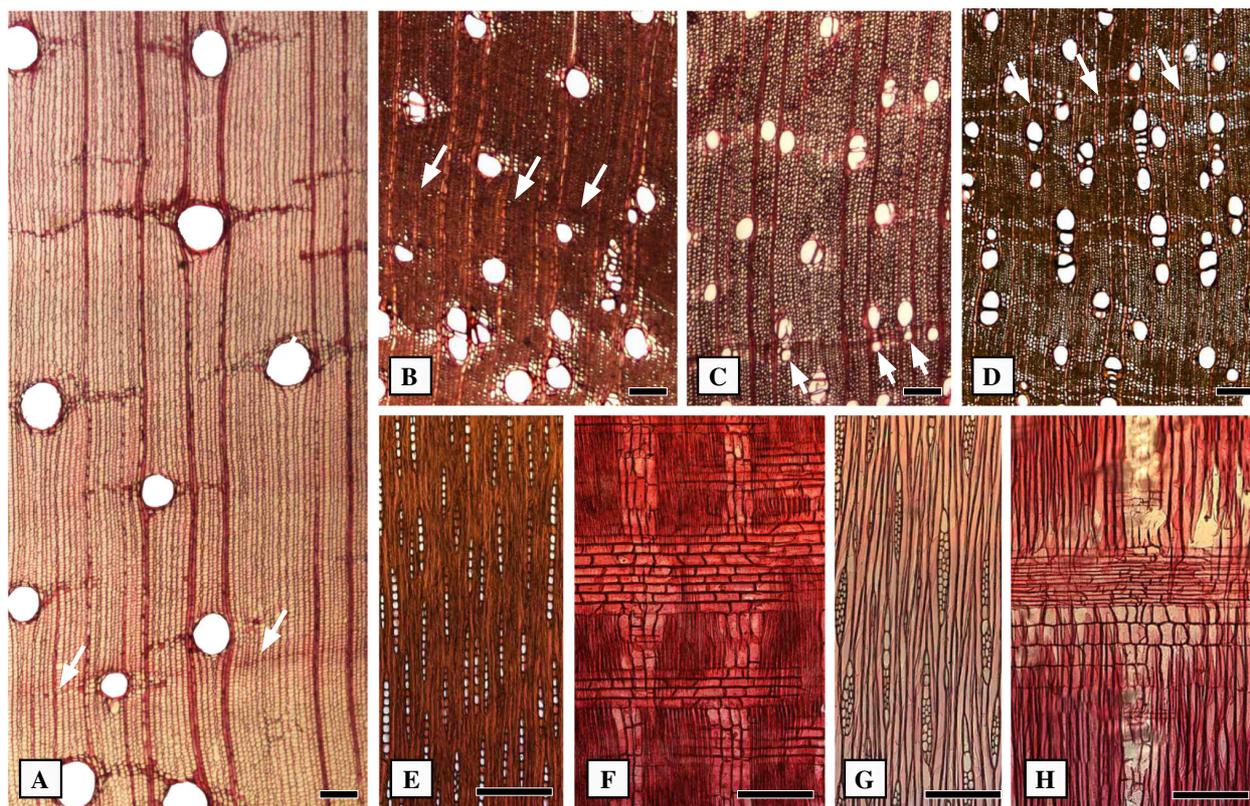


Fig. 3 Wood anatomy of Jacarandae. **a** *Jacaranda copaia*, TS, winged-aliform parenchyma, with short confluentes, and very wide vessels with about 300 μm . Growth rings delimited by radially flattened fibers (arrows). **b** *Digomphia densicoma*, TS, lozenge to winged-aliform parenchyma with short 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 brasiliiana* (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, multiserial 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

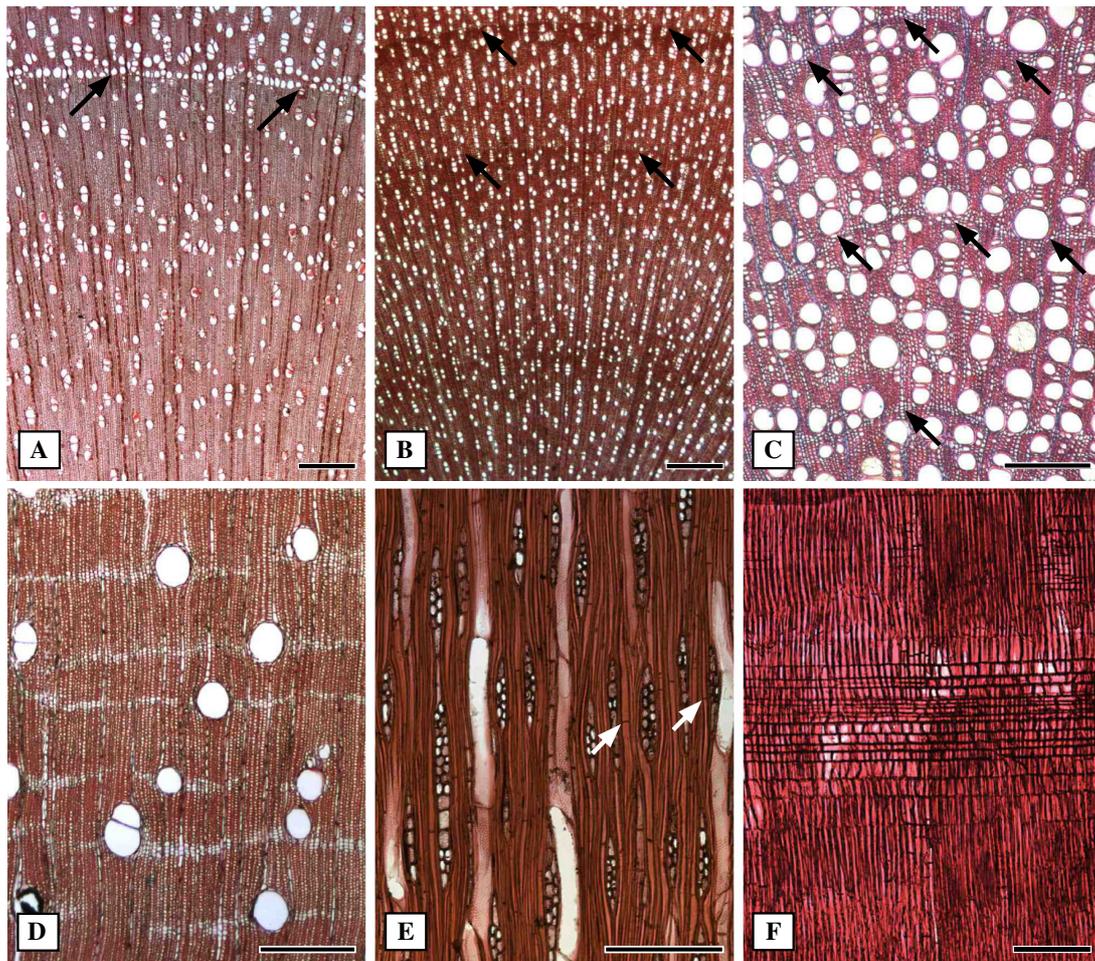


Fig. 4 Wood anatomy of Tecomeae s.s. **a** *Tecoma stans*, TS, semi-ring porous wood, narrow vessels solitary to multiple of 2–3, scanty paratracheal parenchyma. **b** *Tecomaria capensis*, TS, diffuse porous wood, narrow vessels, solitary to multiples of 2–4 or more common, radially disposed, growth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

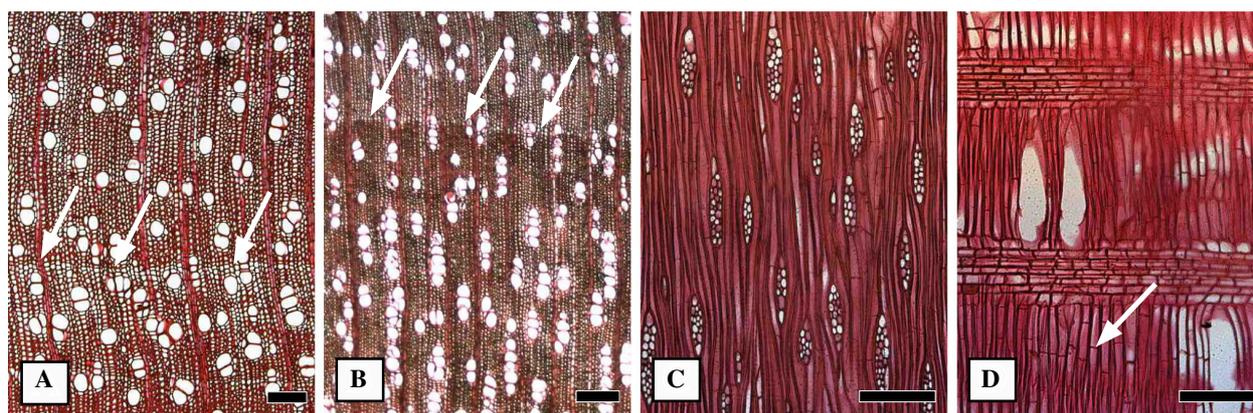


Fig. 5 Wood anatomy of *Delostoma integrifolium*. **a** TS, narrow vessels solitary to multiples of two to four, scanty paratracheal parenchyma to vascentric, growth ring delimited by a line of marginal parenchyma. **b** TS, narrow vessels in radial arrangement,

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 μm , **b** 250 μm

Perforation plates are simple. Intervascular pits are minute (3–4 μm). 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 vascentric, 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 vascentric 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 ($60 \pm 26 \mu\text{m}$) in most genera, medium in *Handroanthus* and *Sparattosperma* ($134 \pm 45 \mu\text{m}$), numerous ($20 \pm 12/$