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WOOD ANATOMY OF TECOMEAE[1]

by

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INTRODUCTION

The wood anatomy of Bignoniaceae has been studied but little, and that mostly over 50 years ago (Record & Mell, 1924; Record & Hess, 1940, 1943). Still today there have been no comprehensive systematic studies undertaken of the anatomy of the secondary xylem in Bignoniaceae. In this chapter the systematic wood anatomy of *Tabebuia* and its close relatives in the tribe Tecomeae, and the potential application of the data obtained to classification of the group are discussed. Intra and inter generic relationships are assessed based on the wood anatomy data. An attempt is made to delimit groups of related taxa within *Tabebuia.*

MATERIALS AND METHODS

Eleven of the 14 arborescent genera of Tecomeae exclusively native to the Neotropics (*Cybistax, Delostoma, Digomphia, Ekmanianthe, Godmania, Jacaranda, Paratecoma, Romeroa, Tabebuia, Tecoma* (sensu stricto), and *Zeyheria*) including 139 specimens of 56 species, were examined in the course of this study. No wood specimens were available for *Astianthus, Sparattosperma, Spirotecoma* and the mostly north temperate genera *Catalpa* and *Chilopsis* were also excluded from this study. Most specimens were accompanied by herbarium vouchers which were identified by A. H. Gentry. Available exsiccatae for each species examined are listed in Table I.

The terminology, procedures, and methodology used in this investigation follow those adopted by the International Association of Wood Anatomists (IAWA Committee, 1964; IAWA Committee, 1989). The anatomical descriptions follow Pernia and Miller's (1991) adaptation of the IAWA list of features for hardwood identification to the DELTA system (Dallwitz & Paine, 1986).

Wood anatomical techniques used are those described by Kukachka (1977) and Carlquist (1 982). Vessel element length, vessel diameter, libriform fiber (throughout the text called fiber) length, and ray height were measured with sonic digitizer equipment (Quirk, 198 1). Twenty-five randomly selected cells were measured for each character on each specimen. Average, minimum, and maximum values were obtained. Vessel element length and fiber length were measured from slides of macerated material while vessel diameters were measured from transverse sections and ray height from tangential sections.

Vessels per mm^2 (tranverse section), rays per linear mm (tangential section) and the number of storied ray tiers per mm (tangential section) were measured with the light microscope. Data were taken from five different fields of the slide for each character of each specimen.

Following Miller (1981) and IAWA (1989), tests for the presence or absence of natural saponins (froth test) and aluminum (chrome azurol-S test) were applied. Burning splinter test, fluorescence of heartwood as well as water and ethanol extracts: fluorescence and color have also been used as an aid for identification. The basic specific gravity was calculated for each sample following Heinriches and Lassen's (1970) method.

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Table 1
Wood specimens examined

Species[a]	Collector[b]	Collection locality	Herbarium[c]	Xylarium[d]
Tabebuia				
alba (Chamisso) Sandwith	Reitz and Klein 3974	Brazil – Santa Catarina	MAD[e]	SJRw[f] 5199
angustata Britton	J. J. Caw Tree J18	Jamaica	Nons	MADw 33921
aurea (Manso) Bentham & Hooker	?[h]	Brazil – Para	?	SJRw 38240
aurea	?	?	None	MADw 27569
barbata (E. Meyer) Sandwith	Krukoff 1469	Brazil	NY	MADw 27417
barbata	A. Ducke 153	Brazil	MAD	SJRw 22613
barbata	Maguire Wurdack & Keith 41572	Venezuela	NY	SJRw 52310
berteroi (A. de Candolle) Britton	E. C. Leonard 1726	Haiti	us	SJRw 4841
berteroi	A. Dugand G. 260 B.S.	Colombia	MAD	SJRw 22549
berteroi	A. Dugand G. 479	Colombia	MAD	SJRw 23906
berteroi	A. Dugand G. 505	Colombia	MAD	SJRw 27078
berteroi	A. Gentry; H. Cuadros 68259 5	Colombia	JBGP	MADw 46324
billbergii (Bureau & Schumann) Standley	A. Rimbach 62	Ecuador	MAD	SJRw 20755
capitata (Bureau & K. Schumann) Sandwith	Stahel 114	Surinam	MAD	SJRw 41180
capitata	Record 580B ?	Surinam	MAD	SJRw 5801
capitata	Krukoff 5049	Brazil	NY	MADw 18606
capitata	R. Fróes 1975	Brazil	NY	MADw 18506
chrysantha (Jacquin) Nicholson	A. Dugand G. 1011	Colombia	MAD	SJRw 33757
chrysantha	E. L. Little Jr. 6211	Ecuador	MAD	SJRw 40895
chrysantha	E. L. Little Jr. 6631	Ecuador	MAD	SJRw 40985
chrysantha	Stern & Chamber 130	Panama	MAD	SJRw 51624
chrysea Blake	A. Dugand G. 711	Colombia	MAD	SJRw 28534
chrysea	H. M. Curran SN	Venezuela	F	MADw 7733
chrysea	A. Dugand G. 74	Colombia	MAD	SJRw 22526
coralibe Standley	A. Dugand G. 693	Colombia	MAD	SJRw 28518
coralibe	A. Dugand G. 460	Colombia	MAD	SJRw 23912
coralibe	R. Espina & J. Giacometto A201	Colombia	MAD	SJRw 20976
donnell-smithii Rose	Ll. Williams 9007	Mexico	F	MADw 7856
donnell-smithii	Ll. Williams 9382	Mexico	MAD	JSRw 34830
donnell-smithii	Ll. Williams 8734	Mexico	F	MADw 27518
donnell-smithii	Ll. Williams 9458	Mexico	F	MADw 27520
donnell-smithii	Ll. Williams 9522	Mexico	F	MADw 7792

Table 1
Continued

Species[a]	Collector[b]	Collection locality	Herbarium[c]	Xylarium[d]
dubia (C. Wright ex Sauvalle) Britton ex Seibert	D. Matthews & Wm. Crosby 44	Cuba	MAD	SJRw 9198
fluviatilis (Aublet) A. de Candolle	Luis Carlos B. Lobato 447	Brazil, Para	MG	MADw 46325
haemantha (Bertero ex Sprengel)	Miller 1646 & USW 6073	Puerto Rico	US	SJRw 53921
heptaphylla (Vellozo) Toledo	Stearns 869	Argentina	MAD	MADw 11675
heptaphylla	Whitford 63	Brazil, Espírito Santo	MAD	SJRw 3260
heptaphylla	H. M. Curran 710	Argentina	MAD	SJRw 1717
heptaphylla	M. Noverraz 13	Argentina	MAD	SJRw 14970
heterophylla	J. S. Beard 246	Dominica	GH	SJRw 49519
heterophylla	Stem 2437, USW 35485	Dominica	MAD	MADw 24146
heterophylla	W. L. Stern, D. Wasshausen 2477 USW 35519	Dominica	MAD	MADw 24178
heterophylla	W. P. Dramer 1	Puerto Rico	?	SJRw 1384
heterophylla (A. de Candolle) Britton	Longwood 10	Puerto Rico	RPPR	MADw 17449
heterophylla	Goytia 165	Puerto Rico	Inst. Trop. Forestry Rio Piedras	MADw 23169
impetiginosa (Martius ex A. de Candolle) Standley	Krukoff 5637	Brazil	NY	MADw 19122
impetiginosa	H. N. Whittford & J. Pinzon 6	Colombia	MAD	SJRw 409
impetiginosa	A. Dugand G. 710	Colombia	MAD	SJRw 28533
insignis (Miquel) Sandwith	A. Ducke 363	Brazil	MAD	SJRw 40094
insignis	Aitken 990	British Guiana	MAD	SJRw 21128
insignis	Aitken 991	British Guiana	MAD	SJRw 21130
insignis	T. H. Gill 7	British Guiana	MAD	SJRw 12333
insignis	Louisiana State University 48	Guyana	?	MADw 7 I4
lepidophylla (A. Richard) Greenman	Fors 952	Cuba	?	MADw 13966
lepidota (Humboldt Bonpland & Kunth) Britton	Bro. Leon 13306	Cuba	MAD	SJRw 16289
leptoneura Urban	Fors 26	Cuba	MAD	SJRw 13363
maxonii Urban	Abbott 1280	Dominican Republic	GH	MADw 19502
myrtifolia (Grisebach) Britton	G. C. Bucher 2	Cuba	MAD	SJRw 15997
nodosa (Grisebach) Grisebach	H. M. Curran 34	Argentina	MAD	SJRw 14990
nodosa	?	Argentina	?	SJRw 1051
obtusifolia (Chamisso) Bureau	Serv. Florestal São Paulo 16	Brazil	?	MADw 11669

Table 1
Continued

Species[a]	Collector[b]	Collection locality	Herbarium[c]	Xylarium[d]
ochracea (Chamisso) Standley	A. Dugand G. 548	Colombia	MAD	SJRw 27086
ochracea	H. M. Curran 2	Brazil	MAD	SJRw 4672
ochracea	H. Pittier 12357	Venezuela	MAD	SJRw 10344
orinocensis (Sandwith) A. Gentry	Ll. Williams 13809	Venezuela	F	MADw 27491
pulcherrima Sandwith	Reitz, Klein 7263	Brazil	HBR	MADw 18163
revoluta (Urban) Britton	?	Dominican Republic	?	SJRw 8700
rosea (Bertoloni) A. de Candolle	Tatto 3	Guatemala	MAD	SJRw 3670
rosea	H. Kuylen G.57	Guatemala	MAD	SJRw 8888
rosea	?	Cuba	NY	SJRw 9030
rosea	Ll. Williams 11115	Venezuela	F	MADw 27527
rosea	Ll. Williams 9470	Mexico	F	MADw 16051
rosea	Steyermark 45923	Guatemala	F	MADw 16030
roseo-alba (Ridley) Sandwith	Curran 18	Brazil, Bahia	MAD	SJRw 4688
sauvallei Britton	Fors 1270	Cuba	?	MADw 14455
serratifolia (Vahl) Nicholson	H. M. Curran 16	Brazil	MAD	SJRw 4686
serratifolia	?	Brazil	F	SJRw 21239
serratifolia	Stahel 101	Surinam	MAD	SJRw 41168
serratifolia	J. M. Pires	Brazil	MAD	SJRw 45745
serratifolia	Navy Project 498	Surinam (Navy Project)	MAD	SJRw 45758
stenocalyx Sprague & Stapf	?	British Guiana	?	SJRw 43857
stenocalyx	Bernardi 7106	Venezuela	MER	MADw 24289
stenocalyx	L. Marcano Berti 148	Venezuela	MER	MADw 23205
stenocalyx	A. C. Mith 3497	British Guiana	MAD	SJRw 35960
stenocalyx	R. S. Cowan 39379	British Guiana	MO	SJRw 50111
trachycarpa (Grisebach) K. Schumann	?	Cuba	?	SJRw 26543
uleana (Kranzlin) A. Gentry	A. C. Smith 3100	British Guiana	MAD	SJRw 35799
Jacaranda				
arborea Urban	Crosby & Mattheus 61	Cuba	MAD	SJRw 9215
caucana Pittier	Stern et al. 743	Panama	MO	SJRw 54717
caucana	J. Cuatrecasas 17661	Colombia	VALLE	SJRw 43254
caucana	A. Dugand 1018	Colombia	MAD	SJRw 33762
caucana	H. M. Curran 162	Colombia	MAD	SJRw 1606
coerula (Linnaeus) Jussieu	J. G. Jack 7315	Cuba	MAD	SJRw 16766
copaia (Aublet) D. Don	Cabrera 41	Colombia	MAD	MADw 37924
copaia	Cabrera 40	Colombia	MAD	MADw 37923
copaia	Cabrera 42	Colombia	MAD	MADw 37925

Table 1
Continued

Species	Collector[b]	Collection locality	Herbarium[c]	Xylarium[d]
copaia	A. C. Smith 3474	British Guiana	MAD	SJRw 35952
copaia	J. Cuatrecasas 15264	Colombia	MAD	SJRw 42849
obtusifolia Humboldt & Bonpland	?	British Guiana	?	SJRw 46393
obtusifolia	A. C. Smith 3125	British Guiana	MAD	SJRw 35817
obtusifolia	A. C. Smith 2119	British Guiana	MAD	SJRw 35464
obtusifolia	Wurdack & Addley 42694	Venezuela	NY	SJRw 54136
puberula Chamisso	Reitz & Klein 3682	Brazil, Santa Catarina	MAD	SJRw 51988
puberula	O. Handro 28168	Brazil	MAD	SJRw 23445
puberula	?	Brazil, São Paulo	?	SJRw 3140
puberula	H. M. Curran 720	Argentina	MAD	SJRw 1724
Tecoma				
capensis (Thunberg) Lindley	A. Rimbach 832	Ecuador	MAD	SJRw 34 I83
castanifolia (D. Don) Melchior	?	? Argentina	?	SJRw 27574
garrocha Hieronymus	?		?	SJRw 32082
stans (Linnaeus) Jussieu ex Humboldt	A. Dugand G. 53	Colombia	MAD	SJRw 22505
stans	Ll. Williams 12254	Venezuela	F	MADw 27571
stans	?	Guatemala	MAD	SJRw 10061
stans	Stem & Brizieky 475	? Ecuador	MAD	SJRw 51258
stans	A. Rimbach 22		MAD	SJRw 19488
Ekmanianthe				
actinophylla (Grisebach) Urban	Bro. Leon 14358	Cuba	NY	MADw 39399
actinophylla	A. J. Fors 11	Haiti	MAD	SJRw 13572
longiflora (Grisebach) Urban	?		?	SJRw 19543
Zeyheria				
Montana Martius	Coronel Pacheco 2162	Brazil, Minas Gerais	?	SJRw 426 I3
tuberculosa (Vellozo) Bureau	Eberhard Schmidt, 143	Bolivia	M	SJRw 50220
Cybistax				
antisyphilitica (Martius) Martius	Reitz, Klein 7354	Brazil	HBR	MADw 21906
antisyphilitica	Schunke 4450	Peru	F, NY, US	MADw 38445
antisyphilitica	?	Brazil, São Paulo	?	SJRw 42602

Table 1
Continued

Species[a]	Collector[b]	Collection locality	Herbarium[c]	Xylarium[d]
Delostoma				
integrifolium D. Don	A. Rimbach 120	Ecuador	MAD	SJRw 22822
integrifolium	M. Acosta-Solis 6694	Ecuador	?	MADw 16619
integrifolium	M. Acosta-Solis 11648-A	Ecuador	F	MADw 21432
Digomphia				
densicoma (Martius ex A. de Candolle) Pilger	Nee 31168	Venezuela	NY	MADw 44266
Godmania				
aesculfolia (Humboldt, Bonpland & Kunth) Standley	Breedlove 9563	Mexico	DS	MADw 23824
aesculifolia	Record & Kuylen 129	Guatemala	MAD	MADw 21438
aesculifolia	Ll. Williams 10233	Venezuela	F	MADw 21439
aesculifolia	Williams 13256	Venezuela	F	MADw 21440
aesculifolia	Record & Kaylen 129	Guatemala	?	SJRw 10080
aesculifolia	A. C. Smith 3368	British Guiana	MAD	SJRw 35913
aesculifolia	Ll. Williams 10233	Venezuela	?	SJRw 36262
aesculifolia	?	Mexico	?	SJRw 48062
Paratecoma				
peroba (Record & Mell) Kuhlmann	World Colombian Exposition 1893	Brazil	?	MADw 21412
peroba	Whitford & Silveira 59	Brazil	MAD	SJRw 3251
peroba	Sterns 1265	Brazil	MAD	MADw 11672
Romeroa				
verticillata Dugand	Romero Castañeda & Jaramillo	Colombia	F	SJRw 49522
verticillata	3390			

[a] Species followed by the author's name.
[b] Refers to the collector and his number.
[c] Abbreviations follow those recommended by Holmgren et al. (1981) in Index Herbariorum.
[d] Abbreviations follow those recommended by Stem (1988).
[e] Refers to the herbarium maintained at the U.S. Forest Products Laboratory, Madison, Wisconsin, which combines the preexistent U.S. Forest Products Laboratory Herbarium with the herbarium formerly at Yale University School of Forestry (Y).
[f] Refers to the Samuel J. Record Memorial Wood Collection formerly cited as Yw and formerly at Yale University School of Forestry, now maintained at the U.S. Forest Products Laboratory, Madison, Wisconsin.
[g] Refers to specimens collected without accompanying herbarium material.
[h] No information is available.

RESULTS

Detailed generic descriptions including macroscopic and microscopic features follow. Genera are arranged in decreasing order by the number of species studied. Table I lists the more important features for fibers and vessel elements and Table II lists the more important macroscopic and ray features. A key to general groups of *Tabebuia* is given. Before the generic descriptions, a summary of features common to all the genera is provided.

It is noteworthy to mention that some members of Bignoniaceae are known to have storied structure (Record & Mell, 1924; Record & Hess, 1943; Carlquist, 1988). In this study various degrees of storying have also been reported in several genera of Tecomeae as mentioned in the generic description below. It is known that this variation can be an ontogenetic by product, which in this study can not be assured since most xylarium wood samples do not contain information on the location along the pith-to-bark radius.

Generic Descriptions

Common features for all the genera

Macroscopic features. Heartwood not fluorescent; chrome azurol-S test negative; froth test negative; and odor indistinct.

Microscopic features. Perforation plates typically simple with occasional occurrence of foraminate type. Intervessel pits alternate, circular, and nonvestured; vessel-ray pitting with a distinct border, similar to intervessel pits in size and shape. Helical thickenings absent in fibers and vessel elements. Fiber pitting simple; vascular or vasicentric tracheids absent. Rays not of two distinct sizes. Aggregate rays, sheath cells, tile cells, and perforated ray cells absent: disjunctive ray parenchyma cell walls indistinct. Prismatic crystals, druses, and silica absent. Oil or mucilage cells, intercellular canals, and tubes absent. Included phloem absent.

Key to Genera and to Groups of Tabebuia

1. Rays heterocellular. . . . 2
1. Rays homocellular. . . . 5
2 Fibers septate. . . . 3
2 Fibers not septate. . . . 4
3. Rays 2–5cells wide, 5–9per mm; fibers 945–1145 µm in length vessel elements 408–531 µm in length. . . . *Delostoma.*
3. Rays 2–3cells wide; 8–15 per mm; fibers 625–742µm in length vessel elements 209–286µm in length. . . . *Tecoma.*
4. Vessels angular in transverse section; rays very high, up to 686 µm; small intervessel pits, 3–4 µm in diameter. . . . *Romeroa.*
4. Vessels circular in transverse section; rays relatively short, up to 400 µm; large intervessel pits, 8–14 µm in diameter. . . . *Jacaranda puberula.*
5. Lapachol present. . . . 6
5. Lapachol absent. . . . 10
6. Lapachol abundant; parenchyma abundant forming large, sometimes concentric bands. . . . 7
6. Lapachol very little, parenchyma vasicentric. . . . 8
7. Basic specific gravity high (greater than 0.74); intervessel pits 8–14µm in diameter. . . *Tabebuia* Group I.
7. Basic specific gravity low (less than 0.40) to medium (0.40–0.74); intervessel pits 4–8 µm in diameter. . . . *Godmania.*
8. Wood semi-ring porous; dark colored heartwood. . . . *Ekmanianthe.*
8. Wood not semi-ring porous; light colored heartwood. . . . 9
9. Rays irregularly storied to non-storied; vessels without a particular arrangement; tyloses and crystals present. . . . *Tabebuia chrysea.*
9. Rays storied; vessels in very wavy arrangement; tyloses and crystals absent. . . . *Zeyheria.*
10. Axial parenchyma vasicentric and aliform confluent, mostly of winged type. . . . 11
10. Axial parenchyma aliform confluent, mostly of lozenge type, abundant, forming wide discontinuous bands. . . . 14
11. Rays non-storied parenchyma aliform-confluent, mostly of winged type. . . . *Jacaranda* spp. *Digomphia.*
11. Rays storied to non-storied parenchyma vasicentric not aliform or confluent. . . . 12
12. Rays and axial elements distinctly storied. . . . *Tabebuia nodosa.*
12. Rays and axial elements irregularly storied to non-storied. . . . 13

13. Rays 2–3 cells wide; axial parenchymaa 2–4 cells per strand; 53–96 vessels per mm²; dark colored heartwood. . . . . *Paratecoma peroba.*
13. Rays 3–5 cells wide, sometimes up to 8 cells wide; axial parenchyma 4–6 cells per strand 11–27 vessels per mm²; light colored heartwood. . . . . Tabebuia donnell-smithii.
14. Paratracheal parenchyma in very wide (up to 20 or more cells wide), mostly concentric bands enveloping the vessels, alternating with fibrous bands. . . . . *Cybistax.*
14. Paratracheal parenchyma normally in discontinuous bands, not more than 15 cells wide. 15
15. Rays of two very different sizes, from 181 to 766 µm in height. . . . . *Tabebuia fluviatilis.*
15. Rays not of two distinct sizes. 16
16. High variability within a species ray height (1–26 cells), width (uniseriate to 4 cells wide), and storied structure (storied, irregularly storied, and non-storied). . . . . Tabebuia Group III.
16. Rays relatively uniform in height, width, and storied structure (irregularly storied to non-storied). ... 17
17. Rays exclusively or mostly uniseriate, occasionally with a small portion biseriate. . . . . *Tabebuia* Group II, Subgroup B.
17. Rays mostly biseriate, occasionally uniseriate. . . . . *Tabebuia* Group II, Subgroup A.

Tabebuia

Description based on 87 specimens of 36 species.

Macroscopic features. Heartwood color varying from whitish to dark greenish brown or blackish. Sapwood color light brown to cream or tan and either similar to, or distinct from heartwood. Water extract mostly not fluorescent (except in *T. angustata* and *T. billbergii*); extract mostly colorless to shade of brown (red in *T. heterophylla* and *T. impetiginosa*). Ethanol extract fluorescent to not fluorescent; extract mostly colorless or shade of brown to yellow. Burning splinter test full ash, white to gray. Basic specific gravity varying from low (less than 0.40) in *T. obtusifolia* to high (greater than 0.74) in several species (e.g., *T. serratifolia, T. barbata, T. chrysantha*).

Microscopic features. Growth rings distinct to indistinct, diffuse-porous. Vessels mostly in short radial multiples, occasionally in diagnoal and/or radial pattern; 11 vessels per mm² in *T. stenocalyx* and *T. donnell-smithii* to 168 per mm² in *T. nodosa*; 53 µm in diameter in *T. billbergii* to 180 µm in *T. insignis*; 173 µm in length in *T. billbergii* to 455 µm in *T. insignis.* Perforation plates simple, sporadically foraminate. Intervessel pits 3–14 µm in diameter forming several distinct groups: 3–4 µm (e.g., *T. roseo-alba*); 5–6 µm (e.g., *T. dubia*); 6–8 µm (e.g., *T. nodosa*); 8–10 µm (e.g., *T. alba*); 10–12 µm (*T. ochracea*); 10–14 µm (*T. billbergii*). Tyloses common only in *T. chrysea, T. donnell-smithii* and *T. fluviatilis.* Fibers nonseptate, thin to very thick-walled; 618 µm in length in *T. aurea* to 1556 µm in *T. serratifolia.* Rays homocellular, 3 per mm in *T. donnell-smithii* to 20 per mm in *T. aurea*; uniseriate (e.g., *T. insignis*) to 5 cells wide (occasionally 8) in *T. donnell-smithii*; 105 µm in height in *T. billbergii* to 401 µm in *T. insignis.* Rays typically not of two distinct sizes. Rays and/or axial parenchyma stoned to non-storied or sometimes irregularly stoned 3–7 tiers per mm. Paratracheal parenchyma scanty or vasicentric (*T. donnell-smithii, T. nodosa, T. chrysea*) to abundantly aliform-confluent. Aliform parenchyma mostly lozenge type (Fig. 1A). Banded parenchyma more than three cells wide, in narrow lines up to three cells wide, and marginal. Axial parenchyma mostly one to four cells per strand. Calcium oxalate crystals (acicular, styloid, elongate, and of different shapes) occasionally present in some species (e.g., *T. chrysea, T. insignis, T. rosea*). More than one crystal of about the same size per ray cell.

Jacaranda

Description based on 19 specimens of 6 species.

Macroscopic features. Heartwood whitish to gray. Sapwood color not distinct from heartwood (in *J. caucana,* the only species available with heartwood). Water and ethanol extract not fluorescent; extracts colorless to shade of brown. Burning splinter test full ash, white to gray. Basic specific gravity low (less than 0.40) to medium (0.40–0.74).

Microscopic features. Growth rings distinct except for *J. pubemla*; diffuse-porous. Vessels generally without specific pattern; 8 vessels per mm² in *J. caucana* to 50 per mm² in *J. coerula* and *J. puberula*; 64 µm in diameter in *J. obtusifolia* to 261 µm in *J. copaia*; 236 µm in length in *J. obtusifolia* to 703 µm in *J. copaia.* Inter-

APPENDIX – Table I
Vessel elements and fiber features for Bignoniaceae

Species	# Specimens	Vessel Elements				Fibers	
		Frequency[a] (per mm²)	Diameter (µm)	Length- (µm)	Pit size (µm)	Length. (µm)	Septate
Tabebuia Group1							
alba	1	43	63	186	8–10	684	–[c]
barbata	3	14–33	94–114	226–241	8-10	912-1071	–
billbergii	5	46–122	53–72	173–218	10–14	628–907	–
capitata	4	24–37	91–98	253–286	8-10	1045–1130	–
coralibe	3	49–73	70-101	177–207	7–8	719-866	–
chrysantha	4	20-134	56-126	207–277	8	764–1307	–
heptaphylla	4	68–136	72–117	228–307	12–14	976–1445	–
impetiginosa	3	19–77	72–120	228–299	12	1132–1540	–
ochracea	3	79–94	68-89	203-245	10-12	886–1363	–
pulcherrima	1	48	59	178	10-12	885	–
serratifolia	5	21-49	86–133	245–381	10-12	915–1556	–
uleana	1	34	102	297	12	1249	–
Tabebuia Group II Subgroup A							
angustata	1	43	72	279	4-6	911	–
berteroi	1	53	58	214	3-4	665	–
haemantha	1	43	63	214	3–5	695	–
leptoneura	1	53	77	246	5-6	843	–
maxonii	1	102	55	280	4	661	–
orinocensis	1	22	95	277	4-5	776	–
Tabebuia Group II Subgroup B							
aurea	2	12–17	105	268–307	4-6	618-806	–
dubia	1	33	126	305	5-6	947	–
insignis	5	14–21	110–180	386-455	5-6	1137–1291	–
lepidophylla	1	76	81	242	4-5	754	–
lepidota	1	76	81	242	4–5	754	–
myrtifolia	1	48	71	236	4	897	–
obtusifolia	1	19	120	391	4	886	–
revoluta	1	76	73	312	4	720	–
trachycarpa	1	116	67	283	4	863	–
Tabebuia Group III							
heterophylla	6	26-69	88–101	262–350	4-5	737–1034	–
rosea	6	10–38	116–162	313–386	5–7	893–1189	–
roseo-alba	1	72	85	332	3-4	1167	–
sauvallei	1	95	90	232	4–5	781	–
stenocalyx	5	11–51	66–91	333–343	3-4	804–1382	–
Tabebuia chosea	3	96-145	59–84	192–321	6–7	786-895	–
Tabebuia donnell-smithii	5	11–27	84–158	269–345	5-8	890–1048	–
Tabebuia fluviatilis	1	42	102	281	3-4	885	–
Tabebuia nodosa	2	149–168	59-65	191–216	6-8	853–911	–

APPENDIX—Table I
Continued

Species	# Specimens	Vessel Elements				Fibers	
		Frequency[a] (per mm²)	Diameter (µm)	Length[a] (µm)	Pit size[b] (µm)	Length. (µm)	Septate
Jacaranda							
arborea	1	35	106	426	8	1160	–
caucana	3	8-32	77–132	278-434	8-10	802–1121	–
coerula	1	50	108	313	8	740	–
copaia	5	9–20	168–261	424–703	8-10	816–1308	–
obtusifolia	4	15–19	64-100	236-434	8-10	724-1082	–
puberula	4	31–50	70-101	350-507	8-14	783–1193	–
Tecoma							
capensis	1	195	48	286	4	742	+[e]
castanifolia	1	44	78	233	4	677	+
garrocha	1	86	74	270	3-4	665	+
stans	5	44–113	45–113	209–262	3-4	625-679	+
Ekmanianthe							
actinophylla	2	*[d]	118-223	240-283	7-8	763–963	–
longiflora	1	*	163	292	7-8	1004	–
Zeyheria							
montana	1	30	90	287	6	1219	–
tuberculosa	1	82	69	252	6–7	1154	–
Cybistax							
antisyphilitica	3	39-66	52	221–251	4-6	826–1112	–
Delostoma							
integrifolium	3	64-92	66–80	408-531	4–5	945–1145	+
Digomphia							
densicoma	1	9	136	614	10	1329	–
Godmania							
aesculifolia	8	24-64	83–102	266–296	4-8	710-1032	–
Paratecoma							
peroba	3	53–96	86–93	279–290	8	1044–1384	–
Romeroa							
verticillata	1	67	59	634	3-4	1030	–

[a] Average of mean values. Single numbers represent values from only one specimen.
[b] Minimum and maximum values.
[c] Character absent.
[d] Wood semi-ring porous (following IAWA list of microscopic features for hardwood identification, 1989).
[e] Character present.

vessel pits mostly 8-10 µm in diameter, *J. puberula* (8–14µm). Tyloses observed in *J. caucana.* Fibers nonseptate, thin to thick-walled; 724 µm in length in *J. obtusifolia* to 1308 µm in *J. copaia.* Rays homocellular, except for *T. puberula* which has rays heterocellular with mostly 1–2 rows of upright or square cells; 4 per mm in *J. copaia* to 19 in *J. coerula*; 1–3 cells in width; 219 µm in height in *J. obtusifolia* to 733 µm in *J. copaia.* Storied structure absent. Paratracheal parenchyma aliform to aliform confluent; when aliform mostly of winged type, occasionally lozenge type. Banded parenchyma, in narrow lines up to three cells wide and marginal. Axial parenchyma mostly four cells per strand except for *J. copaia.* which has six to twelve cells per strand. Calcium oxalate crystals (acicular, styloid, elongate, and of different shapes) present in *J. arborea* and *J.*

APPENDIX – Table II
Rays and macroscopic features for Bignoniaceae

Species	# Specimens	Rays: Frequency[a] (per mm)	Rays: Height[a] (µm)	Rays: Width (in cell)	Rays: Storied	Rays: Heterocellular	Macroscopic features: Basic spec. grav.	Macroscopic features: Lapachol	Macroscopic features: Tyloses	Macroscopic features: Crystal
Tabebuia										
Group I										
alba	1	8–13	148	2–3	±[b]	–[c]	*[d]	#[e]	–	–
barbata	3	7–10	139–153	2	+	–	H[f]	+[g]	–	–
billbergii	5	8–14	105–135	2	+	–	H	+	–	–
capitata	4	7–11	163–175	2–3	+	–	H	+	–	–
coralibe	3	10–19	112–127	1–2	+	–	H	#	–	+
chrysantha	4	9–18	158–177	1–2	+	–	H	+	–	+
heptaphylla	4	5–10	148–199	3	+	–	H	+	–	–
impetiginosa	3	7–11	141–196	2–3	+	–	H	+	–	–
ochracea	3	8–11	148–161	2–3	+	–	H	+	–	–
pulcherrima	1	12–14	138	2–3	+	–	H	#	–	–
serratifolia	5	6–11	159–253	2–3	+	–	H	+	–	–
uleana	1	5–9	212	2–3	+	–	H	#	–	–
Tabebuia										
Group II										
Subgroup A										
angustata	1	7–11	166	1–2	±	–	M[h]	–	–	–
berteroi	1	14–16	124	1–2	±	–	*	–	–	–
haemantha	1	8–10	165	1–2	–	–	*	–	–	–
leptoneura	1	11–16	142	1–2	±	–	M	–	–	+
maxonii	1	8–11	142	1–2	–	–	M	–	–	–
orinocensis	1	9–11	172	1–2	–	–	*	–	–	–
Tabebuia										
Group II										
Subgroup B										
aurea	2	10–20	159–176	1	±	–	M	–	–	–
dubia	1	9–12	184	1	±	–	M	–	–	–
insignis	5	5–10	237–401	1	–	–	M	–	–	+
lepidophylla	1	11–13	136	1	–	–	M	–	–	–
lepidota	1	12–16	136	1–2	±	–	M	–	–	–
myrtifolia	1	7–12	129	1	–	–	*	–	–	+
obtusifolia	1	12–15	236	1	±	–	L[i]	–	–	–
revoluta	1	6–8	140	1	–	–	*	–	–	+
trachycarpa	1	11–16	144	1	–	–	*	–	–	+
Tabebuia										
Group III										
heterophylla	6	7–16	145–235	1–3	+±–[j]	–	M	–	–	+
rosea	6	5–11	232–301	1–4	+±–	–	M	–	–	+
roseo-alba	1	9–15	274	1–3	±	–	M	–	–	+
sauvallei	1	6–10	162	2–3	±	–	M	–	–	+
stenocalyx	5	5–12	218–349	1–3	–	–	M	–	–	+
Tabebuia										
chrysea	3	8–11	198–211	2–3	±–	–	M	+	+	+
Tabebuia										
donnell-smithii	5	3–5	234–284	3–5	±–	–	M	–	+	–
Tabebuia										
fluviatilis	1	8–11	181	2–3	±	–	M	–	+	–

APPENDIX—Table II
Continued

Species	# Specimens	Rays: Frequency[a] (per mm)	Rays: Height[a] (μm)	Rays: Width (in cell)	Rays: Stoned	Rays: Heterocellular	Macroscopic features: Basic spec. grav.	Macroscopic features: Lapachol	Macroscopic features: Tyloses	Macroscopic features: Crystal
Tabebuia										
nodosa	2	11–16	137–149	2–3	+	–	M	–	–	+
Jacaranda										
arborea	1	10–12	368	1	–	–	*	–	–	+
caucana	3	12–15	329–350	1–2	–	–	L-M	–	+	+
coerula	1	15–19	302	1	–	–	M	–	–	–
copaia	5	4–8	315–733	2–3	–	–	L-M	–	–	–
obtusifolia	4	12–18	219–314	1	–	–	M	–	–	–
puberula	4	8–15	238–400	2–3	–	+	M	–	–	–
Tecoma										
capensis	1	10–14	170	2–3	–	+	*	–	–	–
castanifolia	1	12–15	196	2	–	+	M	–	–	+
garrocha	1	8–12	235	2–3	–	+	–	–	+	–
stans	5	8–12	190–244	2–3	–	+	M	–	+	+
Ekmanianthe										
actinophylla	2	6–8	187–274	2–3	±–	–	H	–	+	–
longiflora	1	6–8	224	2–3	±–	–	H	+	+	–
Zeyheria										
montana	1	8–10	195	2–3	+	–	M-H	+	–	–
tuberculosa	1	9–11	177	2–3	+	–	H	+	–	–
Cybistax										
antisyphilitica	3	9–11	204–227	2–3	±–	–	M	–	–	+
Delostoma										
integrifolium	3	5–9	191–274	2–5	–	+	M	–	–	–
Digomphia										
densicoma	1	6–10	219	2	–	–	M	–	–	–
Godmania										
aesculifolia	8	5–10	151–215	2–3	+±	–	L-M	+	–	+
Paratecoma										
peroba	3	4–9	241–402	2–3	±–	–	M	–	+	+
Romeroa										
verticillata	1	4–8	686	3–4	–	+	M	–	–	+

[a] Average of mean values. Single numbers represent values from only one specimen.
[b] Rays and axial elements irregularly storied.
[c] Character absent.
[d] *Sample too small to determine the basic specific gravity.
[e] #Heartwood not available.
[f] High basic specific gravity.
[g] Character present.
[h] Medium basic specific gravity.
[i] Low basic specific gravity.
[j] Storied structure present; rays and axial elements irregularly storied; storied structure not present.

caucana. More than one crystal of about the same size per ray cell.

Tecoma

Description based on 8 specimens of 4 species.

Macroscopic features. Heartwood whitish or gray to shade of yellow. Sapwood color not distinct from heartwood. Water extract not fluorescent. Ethanol extract fluorescent (blue); extracts colorless or shade of brown. Burning splinter test full ash, white to gray. Basic specific gravity medium (0.40-0.74).

Microscopic features. Growth rings distinct to indistinct; diffuse-porous. Vessels without arrangement or with a slight tendency toward diagonal and/or radial pattern; 44-195 per mm^2; 45–113 in diameter; 209–286 in length. Intervessel pits 34 µm in diameter. Tyloses common. Fiber septate; mostly thin to thick-walled 625–742 µm in length. Rays heterocellular, one or 2-4 rows of upright or square cells; 8–15 per mm; 2–3 cells in width; 170–244 µm in height; rays and axial parenchyma non-storied. Paratracheal parenchyma scanty to vasicentric. Banded parenchyma marginal. Axial parenchyma two to four cells per strand. Clacium oxalate crystals (acicular, styloid, elongate, and of different shapes) present in *T. castanifolia* and *T. stans.* More than one crystal of about the same size per ray cell.

Ekmanianthe

Description based on **3** specimens of **2** species.

Macroscopic features. Heartwood brown. Sapwood color distinct from heartwood. Water extract fluorescent (blue in *E. actinophylla* and green in *E. longiflora*). Ethanol extract fluorescent (bright green in *E. actinophylla* and light green in *E. longiflora*). Burning splinter test full ash, white to gray. Basic specific gravity high (greater than 0.74).

Microscopic features. Growth rings distinct; semi-ring porous. Vessels 118-223 µm in diameter, 240-292 µm in length. Intervessel pits 7–8 µm in diameter. Tyloses present. Fibers not septate. Thin to thick to very thick-walled; 763–1004 µm in length. Rays typically homocellular, 6–8 per mm; 2-3 cells in width, 187-274 µm in height. Rays and axial parenchyma irregularly storied or storied structure absent. Paratracheal parenchyma scanty to vasicentric. Banded parenchyma marginal. Axial parenchyma two to four cells per strand. Crystals absent.

Zeyheria

Description based on **2** specimens of 2 species.

Macroscopic features. Heartwood brown. Sapwood color distinct from heartwood. Water extract not fluorescent; extract strong red. Ethanol extract fluorescent (greenish); extract yellow. Burning splinter test full ash, bright white to yellow brown. Basic specific gravity medium (0.40-0.74) to high (greater than 0.74).

Microscopic features. Growth rings distinct: diffuse-porous. Vessels in tangential bands (very wavy); 30-82 per mm^2, 69–90 µm in diameter, 252–287 µm in length. Intervessel pits 6–7 µm in diameter. Tyloses absent. Fibers not septate; very thick-walled; 1154-1219 µm in length. Rays homocellular; 8–11 per mm; 2-3 cells in width 177–195 µm in height. All rays storied. Paratracheal parenchyma vasicentric. Banded parenchyma marginal. Axial parenchyma two to four cells per strand. Crystals absent.

Cybistax

Cybistax antisyphilitica (Martius) Martius.

Description based on **3** specimens.

Macroscopic features. Heartwood shade of yellow; sapwood mostly similar to heartwood. Water and ethanol extract not fluorescent; extracts colorless to shade of brown. Basic specific gravity medium (0.40-0.74).

Microscopic features. Growth rings distinct to indistinct. Vessels in tangential bands (a distinct pattern with very wide concentric bands of vessels and parenchyma alternating with bands of fibers); 39-66 per mm^2; 52 µm in diameter, 221-251 µm in length. Intervessel pits 4-6 µm in diameter. Tyloses absent. Fibers very thick-walled, 826-1112 µm in length. Rays homocellular (the marginal rows composed of enlarged procumbent cells); 9-11 per mm; 2-3 cells wide (occasionally uniseriate); 204-227 µm in height. Rays and/or axial elements irregularly storied or non-storied; 5 tiers per mm. Paratracheal parenchyma aliform and aliform-confluent. Aliform parenchyma lozenge type. Banded parenchyma more than three cells wide. Axial parenchyma two to four cells per strand. Calcium oxalate crystals (acicular, styloid, elongate, and of different

shapes) present. More than one crystal of about the same size per ray cell.

Delostoma

Delostoma integrifolium D. Don.

Description based on **3** specimens.

Macroscopic features. Heartwood brown; sapwood distinct from heartwood (not sufficient for chemical tests). Basic specific gravity medium (0.40-0.74).

Microscopic features. Growth rings distinct to indistinct; diffuse-porous. Vessels without specific pattern (occasionally with tendency towards radial arrangement); 64-92 per mm²; 66-80 µm in diameter; 408–531 µm in length. Intervessel pits 4–5 µm in diameter. Tyloses absent. Fibers septate; thin to thick-walled; 945–1145 µm in length. Rays heterocellular, one row of upright or square cells; 5–9 per mm; 2–5 cells wide (mostly 3 cells wide); 191–274 µm in height. Storied structure absent. Paratracheal parenchyma scanty. Banded parenchyma marginal. Axial parenchyma four cells per strand. Crystals absent.

Digomphia

Digomphia densicoma (Martius ex A. de Candolle) Pilger.

Description based on 1 specimen.

Macroscopic features. Heartwood not available, therefore color, fluorescence and chemical tests could not be done. Basic specific gravity medium (0.40-0.74).

Microscopic features. Growth rings indistinct; diffuse-porous. Vessels 9 per mm²; 136 µm in diameter, 614 µm in length. Intervessel pits 10 µm in diameter. Tyloses absent. Fibers thin to thick-walled; 1329 µm in length. Rays homocellular; 6–10 per mm; 2 cells wide; 219 µm in height. Stoned structure absent. Paratracheal parenchyma vasicentric and aliform-confluent. Aliform parenchyma winged. Axial parenchyma four cells per strand. Crystals absent.

Godmania

Godmania aesculfolia (Humboldt, Bonpland & Kunth) Standley.

Description based on **8** specimens.

Macroscopic features. Heartwood brown to shade of red: sapwood distinct from heartwood. Water extract not fluorescent; extract red. Ethanol extract fluorescent (greenish yellow); extract brownish to yellow. Basic specific gravity low (less than 0.40) to medium (0.40-0.74).

Microscopic features. Growth rings distinct; diffuse-porous (sometimes with a slight tendency towards semi-ring porous). Vessels in very wavy tangential bands (enveloped by wide parenchyma bands); 24-64 per mm²; 83–102 µm in diameter, 266–296 µm in length. Intervessel pits mostly 5–7 µm in diameter (MADw 27439 4 µm in diameter and MADw 23824 7–8 µm in diameter). Lapachol deposits present (observed in SJRw 35913 and SJRw 48062, the only specimens available with heartwood). Tyloses absent. Fibers thin to thick-walled; 710–1032 µm in length. Rays homocellular (the marginal rows with enlarged procumbent cells); 5–10 per mm; 2–3 cells wide. Rays and axial elements storied to irregularly stoned (MADw 27438, MADw 27440, SJRw 35913, and SJRw 10080 are well storied); 4–5 tiers per mm. Paratracheal parenchyma abundant aliform-confluent. Aliform parenchyma lozenge type (sometimes not well defined because of the wide bands). Banded parenchyma more than three cells wide and marginal. Axial parenchyma mostly two to four cells per strand (fusiform cells occasionally present in MADw 27438, SJRw 48062, and SJRw 10080; more than 4 cells occasionally present in MADw 23824). Calcium oxalate crystals (acicular, styloid, elongate, and of different shapes) present. More than one crystal of about the same size per ray cell.

Paratecoma

Paratecoma peroba (Record & Mell) Kuhlmann.

Description based on 3 specimens.

Macroscopic features. Heartwood brown (sometimes with a reddish hue); sapwood distinct from heartwood. Water extract not fluorescent; extract colorless to shade of brown (in SJRw 27472 the water extract is slightly reddish-brown). Ethanol extract fluorescent (bright green); extract yellow. Basic specific gravity medium (0.40-0.74).

Microscopic features. Growth rings distinct to indistinct: diffuse-porous. Vessels only slightly in diagonal and/or radial pattern; mostly in short radial multiples; 53–96 per mm²; 86–93 µm in diameter, 279–290 µm in length. Intervessel pits 8 µm in diameter. Tyloses common. Fibers very

thick-walled; 1044–1384 µm in length. Rays homocellular; 4–9 per mm; 2–3 cells wide (occasionally 4 cells wide); 241-402 µm in height. Rays and/or axial elements irregularly storied or storied structure absent; 4 tiers per mm. Paratracheal parenchyma vasicentric. Banded parenchyma marginal. Axial parenchyma two to four cells per strand. Calcium oxalate crystals (acicular, styloid, elongate, and of different shapes) present. More than one crystal of about the same size per ray cell.

Romeroa

Romeroa verticillata Dugand.

Description based on 1 specimen.

Macroscopic features. Heartwood not available, therefore color, fluorescence and chemical tests could not be done. Basic specific gravity medium (0.40-0.74).

Microscopic features. Growth rings distinct; diffuse-porous. Vessels in short radial multiples; 67 per mm^2; 59 µm in diameter, 634 µm in length. Intervessel pits 3-4 µm in diameter. Tyloses absent. Fibers thin to thick-walled (mostly thin-walled); 1030 µm in length. Rays heterocellular, one row of upright or square cells and heterocellular. 2-4 rows of upright or square cells; 4-8 per mm; 3-4 cells wide; 686 µm in height. Storied structure absent. Paratracheal parenchyma scanty to vasicentric. Axial parenchyma four cells per strand (cells very elongated). Calcium oxalate crystals of various shapes (mostly small) present. More than one crystal of about the same size per ray cell.

DISCUSSION AND CONCLUSIONS

Relationships Within Tribe Tecomeae

This study suggests that most of the 11 genera treated are fairly distinct anatomically. The following is a detailed discussion of the relationships among the genera. For complete anatomical data, see Appendix Tables I and II and the description under results.

Tabebuia

Tabebuia is morphologically the most variable genus of Bignoniaceae (Gentry, pers. comm.); likewise its wood has a wide range of character states. It was possible to subdivide the 36 species studied into three major groups (I, II, III). Only four species (*T. donnell-smithii. T. chrysea. T. fluviatilis,* and *T. nodosa*) did not fit this classification and are left out of the suggested groups.

Group I is composed mostly of large trees (up to 40 m tall) and is confined to continental tropical America, with the exception of *T. billbergii,* which also occurs on a few West Indian islands, and a few species like *T. alba,* which grow mostly in subtropical forests. With the exception of *T. heptaphylla, T. impetiginosa,* and *T. barbata,* which have a magenta corolla with a yellow throat, all the other species are yellow flowered. Eleven of the species placed in this group occur in dry habitats; the exception is *T. barbata,* which occurs mostly in blackwater inundated forests.

Macroscopically *Tabebuia* Group I has a very distinctive wood by the combination of three features: (1) the wood is very dense and has high basic specific gravity (greater than 0.74), (2) the olive brown to blackish heartwood is sharply distinct from the whitish, pinkish or yellowish sapwood, and (3) there is an abundance of yellow powder deposits (lapachol) in the heartwood vessels (for more detail on lapachol see Paterno, 1882; Hooker, 1896; and Fieser, 1927). Microscopically, this group is also very distinct and easy to recognize by the combination of four features: large intervessel pits, storied structure, fiber wall thickness, and ray width. Species of this group have the largest intervessel pits (8–14 µm in diameter) (Fig. 2A) of all *Tabebuia.* All species of this group have very thick-walled fibers. Except for *T. alba* which has irregularly storied elements, all species have a well defined storied structure (Fig. 2B).

Group II comprises the majority of *Tabebuia* species studied. The species of this group are shrubs or small trees mostly from the West Indies. Most of these species have white or pinkish corollas, but some have red flowers. The placement of *T. aurea* in this group is interesting. This is the only yellow flowered species in Group II and one of very few yellow flowered species that does not occur in Group I; it is also allied to the pink flowered species by various morphological characters (Gentry, 1992). This group was subdivided in subgroups A and B based on ray width. The species of subgroup A are characterized by having rays 1–2 cells wide, but with predominantly biseriate rays. On the other hand, sub-

group B comprises species with predominantly uniseriate rays and only occasionally has biseriate rays (Fig. 3A). *Tabebuia lepidota,* although having more biseriate rays than the other species of subgroup B, seems to be better placed in this subgroup than in subgroup A mostly because of the similarity (with Group II) in ray shape and arrangement.

Macroscopically, species of both subgroups have medium basic specific gravity (0.40-0.74) and light brown to reddish brown heartwood, which is not very distinct from the sapwood. Lapachol is not present in the heartwood vessels.

Microscopically, species of this group are easy to recognize. They have very small to relatively medium-sized intervessel pits (3-6 µm in diameter) (Fig. 2C), the rays and axial elements are irregularly storied and sometimes non-storied; and fibers are mostly thin to thick-walled. Exceptions with respect to the thicknes of fiber walls are *T. lepidophylla, T. myrtifolia,* and *T. orinocensis,* which have thick to very thick-walled fibers, and *T. maxonii* and *T. revoluta,* which have very thick-walled fibers. *Tabebuia obtusifolia* is the only species of *Tabebuia* studied that has very thin-walled fibers.

Group III is the most widespread in geographic distribution and most variable in morphological and anatomical features. This group contains the polymorphic *T. heterophylla,* the most variable morphologically of all species of *Tabebuia* (Gentry, 1992). Species of this group range from Central America and the West Indies to tropical South America and, have white or pinkish to lavender or occasionally wine-red corollas. These species occur in a variety of habitats, including limestone and serpentine substrates, cerrado, and swampy areas.

Macroscopically, there is not much variability among the woods of the species of Group III. They all have a medium specific gravity (0.40–0.74). The heartwood color vanes from pale yellow to brown, or whitish, and the sapwood is not very distinct from the heartwood. There is no lapachol in the heartwood vessels.

The species of this group are the most variable microscopically. It was decided to place these species together not only because all of them are highly variable within a species, but also because they show the same pattern of variability. The major anatomical inconsistency within a species is found in ray width and height, abundance of parenchyma, and storied structure. Within a species there is not much variation in intervessel pit size, although in the group it varies from 3 to 7 µm in diameter. With regard to stoned structure, *Tabebuia heterophylla* and *T. rosea* are the most variable species (Fig. 3B). Some specimens of these two species show a well defined storied structure, some are irregularly storied, and some are nonstoried. In ray width, there is also high variability, from one to four cells. *Tabebuia rosea* is the most variable species of *Tabebuia* in ray width. Also noteworthy is *T. stenocalyx,* which vanes from rays exclusively uniseriate to 2-3 cells in width. Species of this group also show an incredible variability in ray height. For example, both *Tabebuia rosea* and *T. stenocalyx* have rays one to a few, and more than 26 cells in height. Finally, there is also a high degree of variability in parenchyma abundance within a species. For example, in *T. rosea* the bands of paratracheal parenchyma vary from very narrow lines to very wide bands.

There are three yellow flowered species of *Tabebuia* (*T. chrysea, T. donnell-smithii,* and *T. no-*

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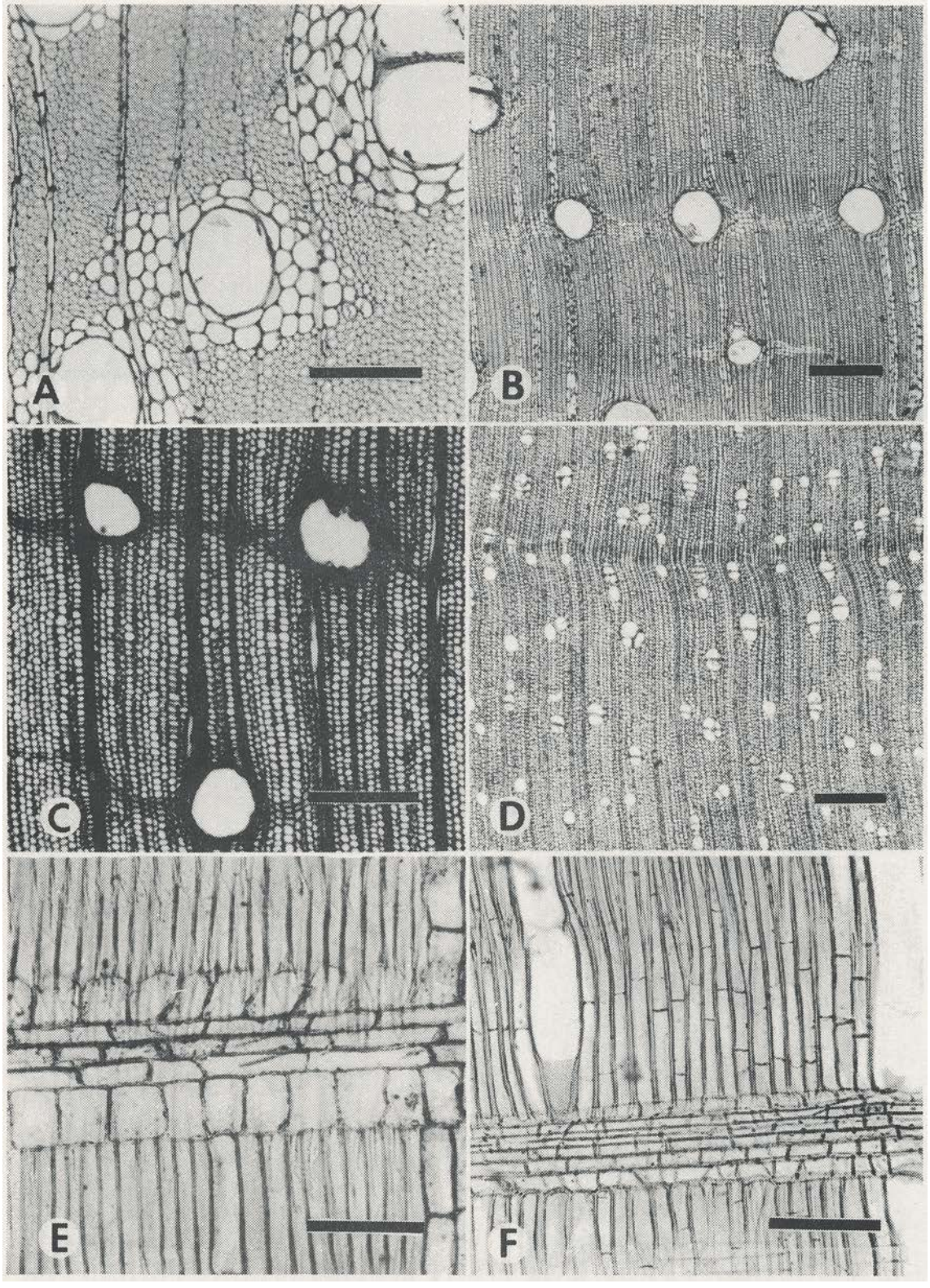
FIG. 1. Paratracheal axial parenchyma, heterocellular rays; and septate fibers. **A,** *Tabebuia barbata* (*Tabebuia* Group I). Paratracheal parenchyma typically aliform lozenge type. **B,** *Jacaranda copaia.* Paratracheal parenchyma aliform-confluent. mostly winged type with a slight tendency towards lozenge type. **C,** *Jacaranda copaia.* Parenchyma aliform-confluent typically winged type. **D,** *Romeroa verticillata.* Scanty paratracheal parenchyma. Figure A–D transverse section. **E,** *Jacaranda puberula.* Ray heterocellular. **F,** *Delostoma integrifolium.* Septate fibers. Figure E–F radial section.—Scalebar = 400 µm in A; 1 mm in B, D, 300 µm in C, F 200 µm in E.

FIG. 2. Intervessel pits and taxon specific variation in ray characteristics as seen in tangential sections. **A,** *Tabebuia billbergii* (*Tabebuia* Group I). Large (10–14 µm in diameter), alternate intervessel pits. **B,** *Tabebuia barbata* (*Tabebuia* Group I). Rays and axial elements stoned, rays exclusively two cells wide. **C,** *Tabebuia angustata* (*Tabebuia* Group II). Small (4–6 µm in diameter). alternate intervessel pits. **D,** *Tabebuia donnell-smithii.* Rays very wide, non-storied. **E,** *Tabebuia fluviatilis.* Rays of two distinct size classes. **F,** *Romeroa verticillata.* Ray mostly very tall.—Scalebar = 30 µm in **A, C;** 300 µm in **B;** 300 µm in D-F.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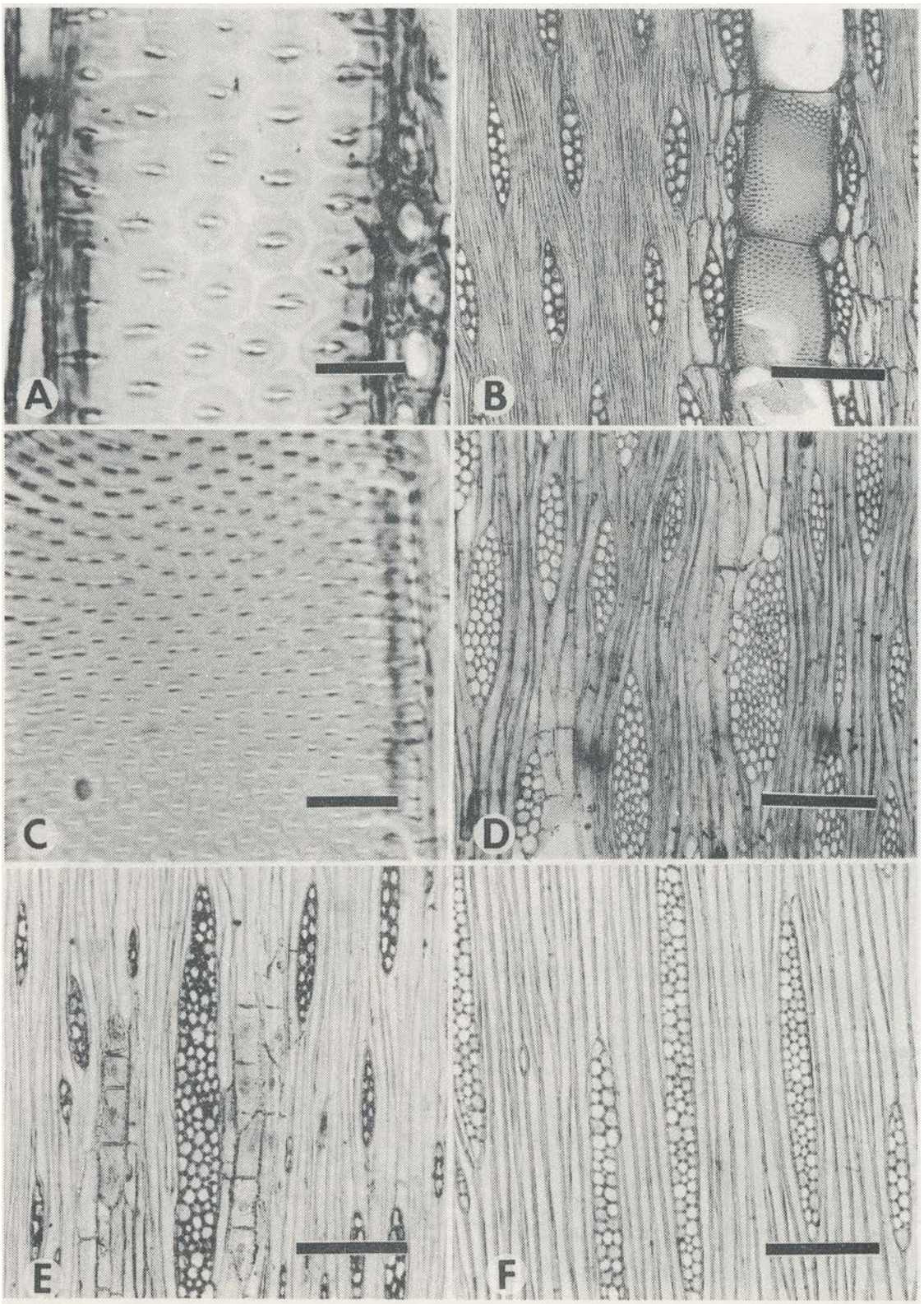
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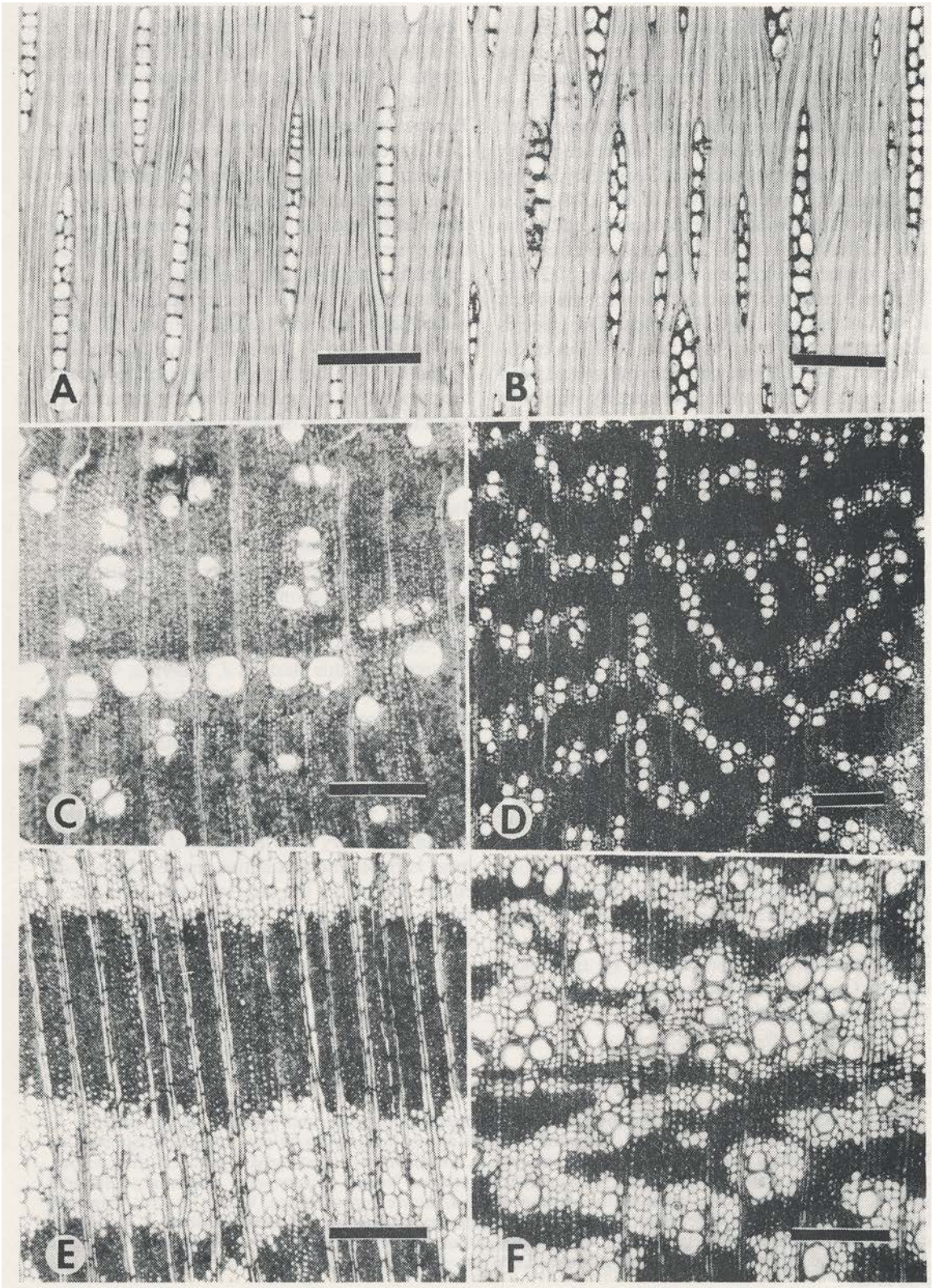
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dosa) and one white flowered species (*T. fluviatilis*) that anatomically do not fit into any of the groups suggested above. *Tabebuia chrysea* is the only yellow flowered species not placed in Group I that has at least some lapachol in the heartwood vessels and rays 2–3cells wide. Macroscopically, it differs from those species in Group I by having medium basic specific gravity (0.40–0.74), and a yellowish heartwood. Microscopically, one of the main differences is that *T. chrysea* has vasicentric paratracheal parenchyma, while species of Group I have abundant paratracheal parenchyma which is sometimes in very wide bands. This species also has smaller intervessel pits (6–7 μm in diameter), 2-6 cells per parenchyma strand, and rays and axial parenchyma irregularly storied to non-storied.

Tabebuia donnell–smithii is another yellow flowered species with vasicentric parenchyma. Macroscopically, it is similar to the species of Groups II and III. What makes this species unique is the unusual pattern of rays. This species has the widest rays (3-5, occasionally 8 cells wide) in *Tabebuia* (Fig. 2D). This is also the species of *Tabebuia* with the most cells (4-6) per parenchyma strand.

Taxonomically isolated *Tabebuia nodosa,* although a yellow flowered species with storied structure, rays 2-3 cells wide and very thick-walled fibers, does not fit in Group I, mainly because it has vasicentric paratracheal parenchyma and smaller intervessel pits (6-8 μm in diameter). It also has a medium basic specific gravity (0.40-0.74) and light colored wood. Gentry (1990) allies it with *T. aurea,* the anomalous yellow flowered species of Group II, but anatomically it does not fit well in that group. The main reason for not including *T. nodosa* in Group II is that the latter is characterized by the abundance of paratracheal parenchyma and an indistinctly storied structure.

Macroscopically, *Tabebuia fluviatilis,* like *T. donnell-smithii,* is not much different from the species of Groups II and III. However, microscopically it differs markedly from any other *Tabebuia* species by the presence of very tall rays (518 μm) contrasting with the much shorter ones (181 μm) (Fig. 2E), a pattern not found in any other Tecomeae. Although consistently present, these taller rays are very few in relation to the shorter ones so that in Appendix II we have included the ray height for the latter only.

Among the *Tabebuia* species studied, only the anatomically isolated taxa (*T. chrysea, T. donnell-smithii,* and *T. fluviatilis*) have tyloses. For *T. nodosa,* the other anatomically isolated taxon, the presence of tyloses could not be determined because of the lack of heartwood.

Jacaranda

In general, *Jacaranda* is anatomically fairly homogeneous. Taxonomically. the genus is divided into two sections, *Monolobos* and *Dilobos,* based on 1- and 2-thecate anthers, respectively. The only representative species of section *Dilobos* treated in this study is *J. puberula,* which is quite distinct from the other species, supporting the intrageneric taxonomy. This is the only species of *Jacaranda* with heterocellular rays. It has much larger intervessel pits (8-14 μm in diameter) than the other species and the rays are 2-3 cells wide. Within section *Monolobos,* the widespread secondary growth species *J. copaia* is the most variable and distinctive species. *Jacaranda copaia* has by far the largest vessel diameter in the genus. The other *Monolobos* species have mostly exclusively uniseriate rays, whereas *J. copaia* has rays mostly 2-3 cells wide. Another distinctive feature, not only for the genus but also for the whole tribe Tecomeae, is that this species

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FIG. 3. Ray size variation within species: vessel arrangement, porosity; and paratracheal parenchyma. **A,** *Tabebuia insignis* (*Tabebuia* Group II, Subgroup B). Rays mostly uniseriate with only small biseriate portion. **B,** *T. rosea* (Tabebuia Group III). Ray height variable. **C,** *Ekmanianthe actinophylla.* Wood semi-ring porous, axial parenchyma scanty to vasicentric. **D,** *Zeyheria tuberculosa.* Vessels in very wavy tangential to diagonal pattern, wood diffuse-porous, parenchyma vasicentric. **E,** *Cybistax antisyphilitica.* Vessels in wide tangential bands enveloped by very wide concentric bands of parenchyma. alternating with bands of fibers. **F,** *Godmania aesculiflolia.* Vessels in tangential pattern. wood diffuse-porous, parenchyma in wide discontinuous bands. Figure **A, B** tangential section; **C–F** transverse section.—Scalebar = 300 μm in **A;** 200 μm in **B;** 700 μm in **C, E, F;** 1 mm in **D.**

has the most cells (6–12)per strand of axial parenchyma.

Macroscopically, *Jacaranda* is not much different from the species of *Tabebuia* Groups II and III. Microscopically, it resembles the species of *Tabebuia* Group I in relation to the large intervessel pits (8-14 µm in diameter). *Jacaranda* completely lacks any stoned structure and its paratracheal parenchyma, when aliform-confluent, is characteristically of the winged type (Fig. 1B,C)

Tecoma

In the treatment of this genus we have included the African *T. capensis,* usually generically segregated as *Tecomaria,* which proved to be very much like the New World species, supporting Gentry's (1992) suggestion that the African and Neotropical species of this alliance are congeneric.

Tecoma and *Delostoma* are the only two genera of Tecomeae with septate fibers and heterocellular rays. It is interesting to note that nearly d the species of these two genera with heterocellular rays are montane, as are many populations of *Jacaranda puberula,* the only other species of Tecomeae with heterocellular rays (but differing in lacking separate fibers).

Tecoma is so homogeneous that it was difficult to separate the species based solely on wood anatomical characteristics. The species of this genus are also difficult to separate morphologically. Gentry (1982) considers this genus "incredibly difficult taxonomically."

Ekmanianthe

This genus shares several macroscopic and microscopic features with species of *Tabebuia* Group I. These are: very dark heartwood, sharply distinct from the light colored sapwood, lapachol present in the heartwood vessels (though mostly sporadic in nature), high basic specific gravity (greater than 0.74), relatively large intervessel pits (7-8 µm in diameter), and rays 2-3 cells wide. The main difference between *Ekmanianthe* and *Tabebuia* Group I is the pattern of paratracheal parenchyma, storied structure, and vessel arrangement. *Ekmanianthe* has very little paratracheal parenchyma (scanty to vasicentric), nearly lacks storied structure, and is semi-ring porous (Fig. 3C).

Although their flowers are very different, the two species of *Ekmanianthe* are so homogeneous anatomically that to separate them it was necessary to use mostly macroscopic features based on chemical tests.

Zeyheria

This genus, like *Ekmanianthe,* shares several features with species of *Tabebuia* Group I. These features are: dark colored heartwood which is very distinct from the light colored sapwood, high basic specific gravity (greater than 0.74), presence of lapachol (although sporadic), stoned structure, rays 2-3 cells wide, and fibers very thick-walled.

Zeyheria is the only yellow flowered genus with vasicentric parenchyma, well defined stoned structure, and relatively small intervessel pits (6-7 µm in diameter), but these features are shared with the anomalous simple leaved *Tabebuia, T. nodosa.*

This genus is differentiated from all species of *Tabebuia* especially by the tangential arrangement of vessels, which occur in a very wavy pattern (Fig. 3D). The two species of *Zeyheria* are very homogeneous, differing mostly in the frequency of vessels per mm^2 and chemically in the burning splinter test.

Cybistax

Cybistax shares several features with species of *Tabebuia* Group II. These features are: light colored heartwood, medium basic specific gravity (0.40-0.74), rays 2–3 cells wide with occasional uniseriate rays, and relatively small intervessel pits (4-6 µm in diameter). It is distinct from any other species of Tecomeae in the unusual vessels, parenchyma and fiber arrangement. The wide concentric bands of parenchyma envelope the vessels and alternate with large concentric bands of fibers, an arrangement found in no other Tecomeae (Fig. 3E).

Delostoma

As previously noted, ***Delostoma*** differs from the other genera (except *Tecoma*) in having the combination of heterocellular rays and septate fibers. *Delostoma* differs from *Tecoma* mainly in ray width, which vanes from 2–5 cells in *Delostoma,* and by the complete lack of stoned struc-

ture. It also has much longer tracheary elements than *Tecoma.*

Digomphia

Anatomically there are neither macroscopic nor microscopic differences between *Digomphia* and *Jacaranda.* Of the species of *Jacaranda* analyzed the wood of *Digomphia* is most like those of section *Monolobos* with homocellular rays. Within section *Monolobos, Digomphia* is closest to *J. copaia* on account of its relatively wide rays.

Godmania

Godmania, much more than any other genus, is very similar to the species of *Tabebuia* Group I. At first glance the wood of this genus could easily be confused with species of *Tabebuia* Group I, based on the abundance of lapachol in the dark colored heartwood. Microscopically, *Godmania* is also very similar to *Tabebuia* Group I by the abundance of paratracheal parenchyma (Fig. 3F), rays 2-3 cells wide and presence of storied structure, although the latter is not well defined in some specimens. *Godmania* differs from *Tabebuia* Group I, by having low (less than 0.40) to medium (0.40-0.74) basic specific gravity, much smaller intervessel pits (4-8 μm in diameter), and thinner-walled fibers (thin to thick-walled).

Paratecoma

Paratecoma also shares some features with species of *Tabebuia* Group I. These features are: dark colored heartwood distinct from the light colored sapwood, relatively large intervessel pits (8 μm in diameter), and rays mostly 2–3 cells wide. The main difference, however, from the species in *Tabebuia* Group I, is the lack of lapachol and the presence of vasicentric paratracheal parenchyma.

Romeroa

Romeroa is a completely distinct genus, with the longest tracheary elements in the tribe Tecomeae. *Romeroa* is also sharply differentiated from any other genus of Tecomeae by the very high rays (Fig. 2F) 3-4 cells wide, very long vessel elements, and by the very elongate axial parenchyma cells. It is also distinctive in having very small intervessel pits (3–4 μm in diameter) and very little paratracheal parenchyma (Fig. 1D).

Diagnostic Value of the Characters Used

For the tribe Tecomeae only a few wood anatomical characters seem to be of diagnostic value at the generic level. With the exception of the long tracheary elements of *Romeroa,* most quantitative values are quite variable, which make them of little use for diagnostic purposes. Qualitative features such as growth rings, vessel arrangement, tyloses, crystals, and chemical tests such as ethanol and water fluorescence are very unreliable. However, for each genus or group of *Tabebuia* there are some macro and/or microscopic diagnostic features.

Tabebuia Group I is characterized by the extremely abundant lapachol in the blackish, dense heartwood, large intervessel pits (8-14 μm in diameter), and well defined storied elements. Group II and Group III can be recognized by the combination of light colored heartwood, hardly distinct from the sapwood; abundance of paratracheal parenchyma; very small to relatively medium sized intervessel pits (3-6 μm in diameter); rays and axial parenchyma irregularly storied to non-storied. For *Tabebuia* Group II subgroups A and B the diagnostic features relate mostly to ray width. In subgroup A the rays are mostly 1-2 cells wide, while in subgroup B the rays are exclusively uniseriate or with only a small portion biseriate. For Group III the only diagnostic feature is the high degree of variability, even in a single section of a slide, in ray width, height, and storied structure.

Jacaranda and *Digomphia* are easy to identify mainly by the winged paratracheal parenchyma combined with large intervessel pits (8-14 μm in diameter) and non-storied structure. *Jacaranda puberula* is distinct from the other *Jacaranda* species in having heterocellular rays (Fig. 1E).

Tecoma and *Delostoma* stand out from the other genera by the presence of heterocellular rays and septate fibers (Fig. 1F). Quantitative values such as vessel element and fiber length as well as ray width are the most important characters to separate these two genera. *Delostoma* has much longer tracheary elements and wider rays than *Tecoma* (see Tables I and II).

For *Ekmanianthe* the outstanding feature is the presence of semi-ring porous vessel arrangement coupled with little lapachol in the dark, heavy heartwood. and the presence of vasicentric

parenchyma. *Zeyheria* is easily distinguished by the peculiar very wavy vessel arrangement. vasicentric parenchyma and well defined storied structure.

Godmania can easily be identified by the abundance of lapachol in the relatively light weight heartwood and very small to medium-sized intervessel pits (4-8 µm in diameter).

Romeroa is distinct in Tecomeae because of the extremely long tracheary elements, very tall rays, vessels somewhat angular in transverse section, scanty paratracheal parenchyma and very small intervessel pits (3-4 µm in diameter).

For *Cybistax* the most diagnostic feature is the very wide concentric bands of parenchyma enveloping the vessels, which alternate with fiber bands. *Paratecoma* can be distinguished by the dark colored heartwood with complete lack of lapachol, parenchyma vasicentric and medium-sized intervessel pits (8 µm in diameter).

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† A second part of this research on "The evolutionary trends within Tecomeae based on wood anatomy" is in preparation.

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