JOURNAL

OF THE

ARNOLD ARBORETUM

VOLUME 62

JANUARY 1981

NUMBER 1

WOOD ANATOMY OF THE NEW WORLD *Pithecellobium* (SENSU LATO)¹

DANIEL L. CASSENS AND REGIS B. MILLER

THE NEW WORLD *Pithecellobium* Martius s.l. consists of over 150 species of shrub- to tree-size plants. These species are mostly plants of tropical areas, ranging throughout Central and South America and the West Indies. In addition, *Ebenopsis* Britton & Rose and some species of *Havardia* Small occur in Texas and Mexico, and the range of a few species of *Pithecellobium* sensu stricto extends into southern Florida. The habitat of *Pithecellobium* s.l. is generally dry to mesic, but some species of *Zygia* P. Browne grow in or near water. Few specific uses of the wood are reported. However, some species of *Abarema* Pittier, *Arthrosamanea* Britton & Killip, *Cojoba* Britton & Rose, *Marmaroxylon* Killip, and *Samanea* Merr. reach tree size and are used locally. Occasionally these woods appear in foreign markets, where they may have commercial potential.

Pithecellobium s.l. is a mimosoid legume in the tribe Ingeae, which is characterized by Mohlenbrock (1963a) as follows: Calyx and corolla generally 5-lobed, cupular or tubular. Stamens numerous, indefinite, connate for a portion of their length. Ovary generally unicarpellate, but carpels varying from 1 to 15 per flower. Leaves usually bipinnate, once-pinnate in a few species; glands frequently present along winged or unwinged rachis; stipular spines sometimes present. Fruit or legume flat, terete, or moniliform; coriaceous, ligneous, fleshy, or papery; dehiscent, elastically dehiscent, or indehiscent and breaking irregularly and transversely between the seeds.

In 1874 Benthham recognized that the legume of *Pithecellobium* s.l. was diverse and described it as compressed; coriaceous, hard, or subfleshy; arcuate, circinnate, or rarely suberect; and indehiscent or dehiscent. The valves after

¹The research for this paper was conducted at the U. S. Forest Products Laboratory, Madison, Wisconsin, in partial fulfillment of Cassens's requirements for the Ph.D. degree at the University of Wisconsin-Madison. It is submitted as Journal Paper No. 7752, Purdue University Agricultural Experiment Station, West Lafayette, Indiana.

dehiscence are often twisted, but not elastic. Bentham relied heavily on this diversity of the legume to characterize his sections and series. Later taxonomists used the manner of legume dehiscence, the presence or absence of spines and arils, and leaf characters to distinguish segregate genera of *Pithecellobium* s.l.

The splitting of the New World *Pithecellobium* s.l. began with the formation of *Havardia* and *Siderocarpos* by Small (1901). Merrill (1916) described *Samanea*, Fawcett and Rendle (1920) revived *Zygia*, and Pittier (1927) described *Abarema*. Britton and Rose (1928) described *Chloroleucon*, *Cojoba*, *Ebenopsis* (= *Siderocarpos*), *Jupunba*, *Painteria*, and *Punjuba* as new genera and also recognized *Havardia*, *Samanea*, and *Zygia*. *Pseudosamanea* was described by Harms (1930), and later Britton and Killip (1936) described *Klugiodendron* and *Arthrosamanea*. In the same publication Britton and Rose founded *Macrosamanea*. Finally, Killip described *Marmaroxylon* (Record, 1940).

More recent taxonomic publications (Burkart, 1949; Dugand, 1948, 1966; Hutchinson, 1964; Kleinhoonte, 1940; Mohlenbrock, 1963a, 1963b) continue to recognize at least some segregates of *Pithecellobium*. Other publications (Irwin, 1966; Macbride, 1943; Cowan, 1961; Standley & Record, 1936; Standley & Steyermark, 1946; Woodson & Schery, 1950), however, indicate that *Pithecellobium* should not be divided into segregate genera.

Kostermans (1954) completed a monograph of the Asiatic, Malaysian, Australian, and Pacific species of Mimosaceae formerly included in *Pithecellobium*. Newly described genera include *Morolobium* Kosterm. (one species), *Parasamanea* Kosterm. (one species), *Serialbizzia* Kosterm. (two species), *Parenterolobium* Kosterm. (one species), *Cylindrokelupka* Kosterm. (three species), and *Paralbizzia* Kosterm. (three species). Kostermans reinstated *Cathormion* Hassk. (one species) and recognized *Zygia* (four species), *Painteria* (one species), and *Abarema* (44 species).

Maintaining *Pithecellobium* as one large genus or reducing it to several smaller ones continues to be the basis for considerable disagreement among taxonomists. Therefore, it was concluded that an investigation of the secondary xylem might provide additional information for developing a more acceptable classification system. Classical diagnostic features of the secondary xylem were examined to determine whether certain species form distinct groups. Observations of the secondary xylem can help determine the validity of a genus, and in complicated situations it can provide evidence for supporting or negating morphological findings. Thus, each of the groups recognized was compared with the proposed generic segregates. It was reasoned that if the groups and the generic segregates correspond, the secondary xylem provided evidence for the formation of distinct taxa within the *Pithecellobium* complex. However, if the secondary xylem is homogeneous, or the groups and the generic segregates do not correspond, the evidence would suggest maintaining *Pithecellobium* in a broad sense.

In addition, the relationships and specialization levels of different tissues are described and discussed. A practical benefit derived from an investigation of the secondary xylem is based on the macroscopic and microscopic characters that are key aids in the identification of unknown wood specimens.

MATERIALS AND METHODS

TABLE 1 lists the 266 wood specimens of 83 species examined from the *Pithecellobium* complex. All of the wood specimens included here have herbarium vouchers. Additional specimens and species without vouchers are included by Cassens (1973).

In all cases this investigation is based on the secondary xylem; hence, the use of such terms as "*Abarema* wood-type." The name *Abarema* may also be used in another sense; that is, as a particular genus segregated from *Pithecellobium*. The placement of a species with a different generic name into a particular wood type does not imply a taxonomic transfer of the epithet into that segregate genus. However, it does indicate the anatomical similarities of all species included in that wood type.

Standard methods were used in the preparation and examination of all microscope slides. However, some measurements need further explanation. For example, length measurements were taken for 25 vessel elements and 25 fibers. An average pore diameter was obtained by measuring 25 of the larger pores and then averaging the 10 largest. A numerical distribution of pores was determined from counts in 10 fields that covered a total of 8.48 sq. mm.

Ray width and height were calculated by cell count and micrometer measurements. Widths in micrometers were obtained from the measurement of 10 rays at their widest point. If the rays were less than 20 cells high, the height in micrometers and number of cells was calculated by measuring 25 of the higher rays and then averaging the 10 highest. Rays higher than 20 cells were only measured in micrometers.

For the wood descriptions, an average of all the specimens was calculated. For example, if the grand average was 900 and the lowest and highest specimen averages were 800 and 1000, respectively, then the figures are reported in the anatomical descriptions in the form "800(-900)-1000." The standard size classes for pore diameter and distribution, vessel element and fiber length, and intervacular pits are reported according to the definitions of the Committee on the Standardization of Terms of Cell Size (1937, 1939), Chattaway (1932), and Record and Chattaway (1939).

For each specimen the occurrence of amorphous inclusions, crystals, and natural saponins is reported. The crystal type, shape, and arrangement within the particular cell type was observed. When crystals were surrounded by a sheath that did not disintegrate when treated with Jeffrey's maceration solution or hydrofluoric acid, they are termed "integumented."

To test for the presence or absence of natural saponins, small chips of heartwood were placed in a vial and covered with distilled water. The vial was shaken by hand for several seconds. If very little or no froth appeared, the test was considered negative. If froth appeared and then disappeared in a few seconds, the test was "short positive." If abundant froth appeared and remained, the test was positive.

The fluorescence of dry heartwood is a character used for identification purposes. A freshly exposed wood surface was placed under a long-wave

TABLE 1. Wood specimens examined for each wood type.

Scientific name*	Collector and number	Geographic origin	Herbarium voucher	Xylarium and catalog number

<u>ABAREMA</u> WOOD-TYPE				
<u>Jupunba abbottii</u> (Rose & Leonard) Britton & Rose Anonymous s.n.		Dominican Republic	US	MADw 19522
<u>Pithecellobium arenarium</u> Ducke Maguire 42959		Guyana	NY	MADw 25501
<u>Pithecellobium auriculatum</u> Benth Krukoff 7938		Brazil	US	MADw 25412
<u>Samanea corymbosa</u> (Rich.) Pittier Krukoff 6743		Brazil	US	SJRw 36856
Stahel 360		Surinam	MAD	SJRw 42664
FDBG 2498		Guyana	K	SJRw 43630
Ducke 396		Brazil	MAD	SJRw 44314
Anonymous (WIBw 1047)		Surinam	U?	SJRw 49773
<u>Pithecellobium elegans</u> Ducke Navy Project 136, Fl2		Brazil	MAD	SJRw 45543
FDBG 4805		Guyana	K	SJRw 46466
<u>Pithecellobium fanshawei</u> Sandwith FDBG 4181 (type)		Guyana	NY	SJRw 46467

Pithecellobium gonggrijpii Kleinhoonte

Lanjouw & Lindeman 518
Stahel 88
FDBG 3313
Maguire 24273

Surinam
Surinam
Guyana
Surinam

U
MAD
K
NY

MADw 25489
SJRw 41157
SJRw 43744
SJRw 44106

Abarema jupunba (Willd.) Britton & Killip

Maguire 51953
Ll. Williams 12047
Persaud 64
Capucho 593
McArthur s.n.
Stahel 20
FDBG 3255
Beard 8
Maguire 40552
Inst. Nat. Sci. 17670

Brazil
Venezuela
Guyana
Brazil
Surinam
Surinam
Guyana
Grenada
Guyana
Colombia

NY
F
F
F
MAD
US
K
A
NY
COL

MADw 21611
MADw 25413
SJRw 9472
SJRw 23887
SJRw 32241
SJRw 42432
SJRw 43730
SJRw 49510
SJRw 50123
SJRw 52872

Pithecellobium langsdorfii Benth

Whitford 351
Hoehne 29842
Reitz & Klein 3912

Brazil
Brazil
Brazil

MAD
MAD
MAD

SJRw 3174
SJRw 23833
SJRw 52072

Samanea leucocalyx Britton & Rose

McClay & Clara 41
Brown II

Guatemala
Belize

MAD
MAD

MADw 23152
SJRw 13021

Pithecellobium leucophyllum Spruce ex Benth

Wurdack & Adderley 43317

Venezuela

NY

SJRw 54393

1981]

CASSENS & MILLER, PITHECELLOBIUM

5

TABLE 1. Wood specimens examined for each wood type (continued).

Scientific name *	Collector and number	Geographic origin	Herbarium voucher	Xylarium and catalog number

<u>ABAREMA</u> WOOD-TYPE, continued				
<u>Samanea</u> <u>macradenia</u> (Pittier) Britton & Rose	Christopherson 196 (type)	Panama	US	MADw 5718
	USNH 716482	Panama	US	SJRw 53764
<u>Samanea</u> <u>marginata</u> (Spruce ex Benth) Pittier	Krukoff 6715	Brazil	US	SJRw 36841
	Ll. Williams 14869	Venezuela	F	SJRw 41806
<u>Pithecellobium</u> <u>mataybifolium</u> Sandwith	Cowan 39332	Guyana	NY	SJRw 50101
<u>Jupunba</u> <u>obovalis</u> (A. Rich.) Britton & Rose	Alberto J. Fors 106	Cuba	SV?	MADw 14418
<u>Pithecellobium</u> <u>panurense</u> Spruce ex Benth	Wurdack & Adderley 54364	Venezuela	NY	SJRw 54364
<u>Samanea</u> <u>pedicellaris</u> (DC.) Killip	Maguire et al. 51777	Brazil	NY	MADw 21470
	Gutierrez R.85, R.111	Peru	MAD	MADw 22364
	FDBG s.n.	Guyana	K?	SJRw 32845
	Krukoff 10886	Bolivia	MAD	SJRw 39720

Ducke 354	Brazil	MAD	SJRw 40085
Stahel 125	Surinam	MAD	SJRw 41190
Stahel 237	Surinam	MAD	SJRw 42466
FDBG 3201	Guyana	K	SJRw 43611
Anonymous (WIBw 1059)	Surinam	U?	SJRw 49778
<u>Jupunba</u> <u>pinetorum</u> (Britton) Britton & Rose			
Bucher 11	Cuba	MAD	SJRw 14728
<u>Jupunba</u> <u>pseudo-tamarindus</u> Britton			
Cooper 461 (type)	Panama	MAD	SJRw 12079
<u>Pithecellobium</u> <u>villiferum</u> Ducke			
Maguire 24629	Surinam	NY	SJRw 44177
Wurdack & Adderley 43351	Venezuela	NY	SJRw 54373
<u>ALBIZIA</u> WOOD-TYPE			
<u>Albizia</u> <u>adinocephala</u> (Donn. Smith) Britton & Rose			
Dayton 3097	Costa Rica	MAD	MADw 10300
Record & Kuylen H.20	Honduras	MAD	SJRw 9966
<u>Albizia</u> <u>caribaea</u> (Urban) Britton & Rose			
Holdridge 6281	Panama	MO	MADw 24821
Ll. Williams 9720	Mexico	F	SJRw 34966
Curran & Turner V129	Venezuela	MAD	SJRw 45652
Turner V136	Venezuela	MAD	SJRw 45680
Curran & Turner V148	Venezuela	MAD	SJRw 45706
<u>Albizia</u> <u>colombiana</u> Britton			
Record & Kuylen 75 (type)	Colombia	MAD	SJRw 16474
Dugand 45	Colombia	MAD	SJRw 22478
Dugand 487	Colombia	MAD	SJRw 23920

TABLE 1. Wood specimens examined for each wood type (continued).

Scientific name*	Collector and number	Geographic origin	Herbarium voucher	Xylarium and catalog number
<hr/>				
<u>ALBIZIA</u> WOOD-TYPE, continued				
<u>Pithecellobium glabripetalum</u>	H. S. Irwin FDBG 5397 (type) (distributed as <u>Pithecellobium niopoides</u> Bentham)	Guyana	K	SJRw 46468
<u>Albizia hassleri</u> (Chodat)	Burkart Woolston T10	Paraguay	MAD	SJRw 48286
<u>Albizia tomentosa</u> (M. Micheli)	Standley Record B.H.27 (type)	Belize	MAD	SJRw 8795
	Brown 5	Belize	MAD	SJRw 13024
	Ll. Williams 8771	Mexico	F	SJRw 34689
	Ll. Williams 9863	Mexico	MAD	SJRw 34820
<u>ARTHROSAMANEAE</u> WOOD-TYPE				
<u>Arthrosamanea multiflora</u> (H.B.K.)	Kleinhoonte Novenaz 37	Argentina	MAD	SJRw 14993
	Capucho 451	Brazil	F	SJRw 22742
	Krukoff 6750	Brazil	US	SJRw 36861
<u>Arthrosamanea pistaciaefolia</u> (Willd.)	Britton & Rose Ll. Williams 12823	Venezuela	F	MADw 25493

Curran 43	Colombia	MAD	SJRw 1551
Curran 44	Colombia	MAD	SJRw 1552
Curran 300	Colombia	MAD	SJRw 1528
Dugand 138, 483	Colombia	MAD	SJRw 23915
Dugand 296	Colombia	F	SJRw 28504

CHLOROLEUCON WOOD-TYPE

<u>Pithecellobium acacioides</u> Ducke			
Capucho 356	Brazil	F	SJRw 21659
<u>Chloroleucon guantanamoense</u> (Britton) Britton & Rose			
Bucher 81	Cuba	MAD	SJRw 16252
<u>Chloroleucon leucospermum</u> (Brandeggee) Britton & Rose			
Winzerling II-2	Belize	MAD	SJRw 9851
Record & Kuylen H.59	Honduras	MAD	SJRw 10005
<u>Chloroleucon mangense</u> (Jacq.) Britton & Rose			
Dugand 220, 57	Colombia	MAD	SJRw 22509
Dugand 315, 150	Colombia	MAD	SJRw 23927A
Navy Project 433	Panama	MAD	SJRw 45673
Navy Project 452	Panama	MAD	SJRw 45677
Navy Project 453	Panama	MAD	SJRw 45678
Navy Project 454	Panama	MAD	SJRw 45679
Stern & Chambers 158	Panama	MAD	SJRw 51650
<u>Pithecellobium mathewsii</u> Benth			
Ll. Williams 5532	Peru	F	MADw 15936
Ll. Williams 5967	Peru	F	MADw 15937
Ll. Williams 6463	Peru	F	MADw 15938

1981]

CASSENS & MILLER, PITHECELLOBIUM

9

TABLE 1. Wood specimens examined for each wood type (*continued*).

Scientific name*	Collector and number	Geographic origin	Herbarium voucher	Xylarium and catalog number
<u>CHLOROLEUCON</u> WOOD-TYPE, continued				
<u>Chloroleucon</u> <u>tortum</u> (Martius) Pittier				
	Alberto J. Fors 27	Cuba	SV?	MADw 15860
	Ll. Williams 12879	Venezuela	F	MADw 25494
	Curran 331	Brazil	MAD	SJRw 1943
	Pittier 12363	Venezuela	MAD	SJRw 10345
<u>Chloroleucon</u> <u>vinhatico</u> (Record) Record				
	Curran 59 (type)	Brazil	MAD	SJRw 1806
	Curran 28	Brazil	F	SJRw 4698
<u>Chloroleucon</u> sp.				
	Curran & Haman 562	Venezuela	GH	SJRw 2832
	Curran 737	Venezuela	GH?	SJRw 16181
<u>COJOBA</u> WOOD-TYPE				
<u>Cojoba</u> <u>arborea</u> (L.) Britton & Rose				
	Alberto J. Fors 953	Cuba	SV?	MADw 13967
	Ll. Williams 9465	Mexico	F	MADw 15935
	Anonymous s.n.	Jamaica	US	MADw 20724
	Britton & Kramer XV	Puerto Rico	MAD	SJRw 3088
	Whitford & Stadtmiller 9A	Honduras	MAD	SJRw 3676

Hope II	Belize	MAD	SJRw 4797
Record 19	Belize	MAD	SJRw 8787
Gill & Whitford 50	Cuba	MAD	SJRw 9061
Gill & Whitford 124	Cuba	MAD	SJRw 9135
Mathews & Crosby 67	Cuba	MAD	SJRw 9220
Stevenson & Burns II	Belize	F	SJRw 9564
Brown III	Belize	MAD	SJRw 13022
Yuncker et al. 6157	Honduras	MAD	SJRw 33748
Ll. Williams 8805	Mexico	MAD	SJRw 34700
Stevenson 230	Belize	MAD	SJRw 37258
Shank 92	Nicaragua	MAD	SJRw 46882
<u>Cojoba costaricensis</u> Britton & Rose			
Austin Smith s.n.	Costa Rica	MAD	SJRw 38353
<u>Cojoba donnell-smithii</u> Britton & Rose			
Record G.138	Guatemala	MAD	SJRw 10089
Stevenson III	Belize	MAD	SJRw 14893
<u>Pithecellobium membranaceum</u> (Bentham) Schery			
Stern et al. 1131	Panama	US	SJRw 55040
<u>Cojoba rufescens</u> (Bentham) Britton & Rose			
Roadmaster Panama RR 40	Panama	MAD	SJRw 7239
Dugand 604	Colombia	MAD	SJRw 27126
Stern et al. 45	Panama	US	SJRw 54590
<u>Cojoba sophorocarpa</u> (Bentham) Britton & Rose			
Stevenson 6	Belize	MAD	SJRw 10688
Galusser 20	Guatemala	MAD	SJRw 10740

TABLE 1. Wood specimens examined for each wood type (continued).

Scientific * name	Collector and number	Geographic origin	Herbarium voucher	Xylarium and catalog number
<hr/>				
<u>COJOBA</u> WOOD-TYPE, continued				
<u>Cojoba tenella</u> Britton & Rose Hottle 54		Honduras	F	SJRw 15631
<u>EBENOPSIS</u> WOOD-TYPE				
<u>Ebenopsis flexicaulis</u> (Bentham) Britton & Rose				
Nogle 99		Texas	TAES	MADw 13215
Wilson M-1		Mexico	MAD	MADw 18344
MEXFw X-324		Mexico	ICF	MADw 25290
<u>HAVARDIA</u> WOOD-TYPE				
<u>Havardia leiocalyx</u> (Standley) Britton & Rose Page 9615		Mexico	DS	MADw 23863
<u>Havardia pallens</u> (Bentham) Britton & Rose				
Wilson M-7		Mexico	MAD	MADw 18342
Scott s.n.		Miami, Florida [†]	?	SJRw 44776
Cavazos 62A		Mexico	US	USw 19246
<u>Havardia platyloba</u> (Sprengel) Britton & Rose Curran & Haman 400		Curaçao	GH	SJRw 2775

Record & Don Jaca 51	Colombia	MAD	SJRw 16450
Dugand 1158	Colombia	MAD	SJRw 35287
<u>KLUGIODENDRON</u> WOOD-TYPE			
<u>Klugiodendron laetum</u> (Poeppig & Endl.) Britton & Killip			
Il. Williams 4190	Peru	F	MADw 15942
Krukoff 6457	Brazil	US	SJRw 36693
King 6170	Colombia	US	USw 37504
<u>MACROSAMANEIA</u> WOOD-TYPE			
<u>Macrosamanea aquatica</u> Pittier			
Wurdack & Adderley 42732	Venezuela	NY	SJRw 54144
<u>Pithecellobium consanguineum</u> Cowan			
Maguire et al. 41878 (type)	Guyana	NY	MADw 25503
<u>Macrosamanea discolor</u> (Humb. & Bonpl.) Britton & Rose			
NYBG 28422	Guyana	NY	MADw 25502
<u>Macrosamanea kegelii</u> (Meissner) Kleinhoonte			
Gonggrijp 4150	Surinam	NY	MADw 25682
<u>Macrosamanea simabifolia</u> (Spruce ex Bentham) Pittier			
Wurdack & Adderley 43023	Venezuela	NY	SJRw 54466
Wurdack & Adderley 42937	Venezuela	NY	SJRw 54521
<u>MARMAROXYLON</u> WOOD-TYPE			
<u>Pithecellobium basijugum</u> Ducke			
Lanjouw & Lindeman 2270	Surinam	U	MADw 25486
Wurdack & Maguire 41958	Guyana	NY	MADw 25504

1981]

CASSENS & MILLER, PITHECELLOBIUM

13

TABLE 1. Wood specimens examined for each wood type (*continued*).

Scientific * name	Collector and number	Geographic origin	Herbarium voucher	Xylarium and catalog number

<u>MARMAROXYLON</u> WOOD-TYPE, continued				
<u>Pithecellobium collinum</u> Sandwith				
FDBG 3976 (type)	Guyana	K	SJRw 46465	
<u>Pithecellobium dinizii</u> Ducke				
Krukoff 1302	Brazil	US	MADw 25118	
Cuatrecasas 17374	Colombia	F	SJRw 43205	
<u>Marmaroxylon racemosum</u> (Ducke) Killip				
BAFOG 81M	French Guiana	U	MADw 25487	
Van Hall 63	Surinam	U	MADw 25488	
Dahlgren s.n.	Brazil	F	SJRw 16780	
Ducke 39†	Brazil	MAD	SJRw 20720	
Capucho 274	Brazil	F	SJRw 21260	
Capucho 377	Brazil	F	SJRw 22055	
Smith 2721	Guyana	MAD	SJRw 35676 [§]	
Stahel 72	Surinam	MAD	SJRw 41145	
FDBG 3114	Guyana	K	SJRw 46469	
<u>Pithecellobium umbriflorum</u> Ducke				
Krukoff 6872	Brazil	F	SJRw 36937	

PITHECELLOBIUM (SENSU STRICTO) WOOD-TYPE

Pithecellobium dulce (Roxb.) Benth

Mell s.n.	Florida	US?	MADw 5122
Acosta-Solís 11930	Ecuador	F	MADw 11155
Alberto J. Fors 242	Cuba	SV	MADw 13887
Curran & Haman 502	Venezuela	GH	SJRw 2816
Pittier 11760	Venezuela	MAD	SJRw 7746
Record & Kuylen G.107	Guatemala	MAD	SJRw 10058
Record 32	Colombia	MAD	SJRw 16431
Record 43	Colombia	MAD	SJRw 16442
Record 59	Colombia	MAD	SJRw 16458
Espina & Giacometto B8A	Colombia	MAD	SJRw 20990
Dugand 223, 60	Colombia	MAD	SJRw 22512
Dugand 574	Colombia	MAD	SJRw 27104
Ll. Williams 9760	Mexico	F	SJRw 34984
Caldwell 8755	Florida	MAD	SJRw 49282

Pithecellobium guadalupense (Pers.) Chapman

Stern 131	Florida Keys	MAD	SJRw 49457
Stern & Brizicky 193	Florida Keys	MAD	SJRw 51043
Stern & Brizicky 205	Florida Keys	MAD	SJRw 51054
Stern & Brizicky 358	Florida Keys	MAD	SJRw 51174
Stern & Brizicky 362	Florida Keys	MAD	SJRw 51178
Stern & Chambers 252	Florida Keys	MAD	SJRw 51464

Pithecellobium lanceolatum (Humb. & Bonpl.) Benth

Ll. Williams 12888	Venezuela	F	MADw 25152
Mell 19	Mexico	MAD	SJRw 6997
Record & Kuylen 39	Colombia	MAD	SJRw 16438

Pithecellobium microchlamys Pittier

Dugand 345, 777	Colombia	MAD	SJRw 29622
-----------------	----------	-----	------------

[1981]

CASSENS & MILLER, PITHECELLOBIUM

15

TABLE 1. Wood specimens examined for each wood type (continued).

Scientific * name	Collector and number	Geographic origin	Herbarium voucher	Xylarium and catalog number
<hr/>				
<u>PITHECELLOBIUM</u> (SENSU STRICTO) WOOD-TYPE, continued				
<u>Pithecellobium oblongum</u> Benth				
	Record & Kuylen G.120	Guatemala	MAD	SJRw 10071
	Stern & Chambers 27	Panama	MAD	SJRw 51544
<u>Pithecellobium oblongum</u> Pittier				
	Dugand 847	Colombia	MAD	SJRw 29678
<u>Pithecellobium unguis-cati</u> (L.) Benth				
	Wilson F-5	Florida	MAD	MADw 15950
	Curran & Haman s.n.	Curaçao	IGH	MADw 19474
	Anonymous s.n.	Florida	US	MADw 20978
	MacDonald 24	Florida	MAD	SJRw 32536
	MacDonald 49	Florida	MAD	SJRw 32561
	Caldwell	Florida	MAD	SJRw 49290
	Stern & Brizicky 257	Florida	MAD	SJRw 51096
	Stern et al. 448	Florida	MAD	SJRw 51232
<u>Pithecellobium</u> sp.				
	Curran 425	Curaçao	GH	SJRw 2798
	Curran 616	Curaçao	GH	SJRw 2854

PSEUDOSAMANEA WOOD-TYPE

<u>Albizia cubana</u> Britton & Wilson			
Brother H. Leon 13720	Cuba	F	SJRw 16321
<u>Pseudosamanea guachapele</u> (H.B.K.) Harms			
Humberto Tasayco Tasayco 3	Peru	MAD	MADw 22546
Acosta-Solís 13003	Ecuador	F	MADw 25414
Acosta-Solís 11964	Ecuador	F	MADw 25415
Pittier 12184	Venezuela	MAD	SJRw 9520
Record & Kuylen G.126	Guatemala	MAD	SJRw 10077
Dugand 540	Colombia	MAD	SJRw 27084
Dugand 560	Colombia	MAD	SJRw 27093
Acosta-Solís 11716	Ecuador	F	SJRw 45429
Navy Project 79	Honduras	MAD	SJRw 45518
Dunlap s.n.	Honduras	MAD	SJRw 45796
Forgeson 77B	Panama	MAD	SJRw 50973

PUNJUBA WOOD-TYPE

<u>Punjuba racemiflora</u> (Donn. Smith) Britton & Rose			
Barbour 1014	Costa Rica	MAD	MADw 10284

SAMANEA WOOD-TYPE

<u>Samanea saman</u> (Jacq.) Merrill			
Whitford & Stadtmiller s.n.	Guatemala-Honduras Boundary	US	MADw 10851
Sarlin G50	Haiti	P	MADw 16946
RPPRw Tree 54	Puerto Rico	RPPR	MADw 17491
Anonymous s.n.	Venezuela	MER	MADw 23994
Curran 302	Colombia	MAD	SJRw 1529

TABLE 1. Wood specimens examined for each wood type (continued).

Scientific name*	Collector and number	Geographic origin	Herbarium voucher	Xylarium and catalog number
<u>SAMANEA</u> WOOD-TYPE, continued				
	Gill & Whitford 90	Cuba	MAD	SJRw 9101
	Cooper 442	Panama	MAD	SJRw 12060
	Ll. Williams 5495	Peru	F	SJRw 18758
	Espina & Giacometto A202	Colombia	MAD	SJRw 20977
	Capucho 479	Brazil	F	SJRw 22770
	Scarff 12G	Dominican Republic	MAD	SJRw 35404
	Smith 3316	Guyana	MAD	SJRw 35900
	Turner 111	Venezuela	MAD	SJRw 45751
	Turner 120	Venezuela	MAD	SJRw 45752
	Schmidt 99	Bolivia	HBG	SJRw 50188
<u>Samanea saman</u> (Jacq.) Merrill var. <u>acutifolium</u> Benth	Woytkowski 35145	Colombia	MAD	SJRw 44592
<u>ZYGIA</u> WOOD-TYPE				
<u>Zygia ampla</u> (Spruce ex Benth) Pittier	Ll. Williams 14747	Venezuela	F	SJRw 41738
<u>Zygia cauliflora</u> (Willd.) Killip	Maguire 55773	Surinam	NY	MADw 22954
	Ll. Williams 11424	Venezuela	F	MADw 25120
	BAFOG 172M	French Guiana	U	MADw 25485

Persaud 99	Guyana	F	SJRw 9493
Persaud 106	Guyana	F	SJRw 9496
Smith 2588	Guyana	MAD	SJRw 35617
Stahel 284	Surinam	MAD	SJRw 42513
<u>Zygia cognata</u> (Schlecht) Britton & Rose			
Ll. Williams 9208	Mexico	MAD	SJRw 34792
<u>Zygia conzattii</u> (Standley) Britton & Rose			
Ll. Williams 9438	Mexico	F	SJRw 34857
<u>Zygia divaricata</u> (Brongniart) Pittier			
Ll. Williams 15027	Venezuela	F	SJRw 41895
Wurdack & Adderley 43419	Venezuela	NY	SJRw 54536
<u>Zygia englesingii</u> (Standley) Record			
Englesing 205 (type)	Nicaragua	MAD	SJRw 13297
<u>Zygia glomerata</u> (Vell.) Pittier			
Ll. Williams 14238	Venezuela	F	SJRw 41472
Wurdack & Adderley 43314	Venezuela	NY	SJRw 54516
<u>Zygia inaequalis</u> (Poiret) Pittier			
Espina & Giacometto A72	Colombia	MAD	SJRw 20847
Ducke 384	Brazil	MAD	SJRw 40412
Ll. Williams 15172	Venezuela	F	SJRw 41995
Ll. Williams 15460	Venezuela	F	SJRw 42128
Wurdack & Adderley 42674	Venezuela	NY	SJRw 54490
<u>Pithecellobium juruanum</u> Harms			
Krukoff 4746	Brazil	F	MADw 18544

TABLE 1. Wood specimens examined for each wood type (continued).

Scientific name*	Collector and number	Geographic origin	Herbarium voucher	Xylarium and catalog number
<hr/>				
<u>ZYGIA</u> WOOD-TYPE, continued				
<u>Zygia</u> <u>latifolia</u> (L.) Fawcett & Rendle				
	Krukoff 5798	Brazil	F	MADw 25119
	Persaud 63	Guyana	F	SJRw 9471
	Krukoff 6212	Brazil	F	SJRw 36517
	Cuatrecasas 14251	Colombia	US	SJRw 42739
	FDBG 3618	Guyana	K	SJRw 46562
<u>Zygia</u> <u>longifolia</u> (Humb. & Bonpl.) Britton & Rose				
	Gutierrez R.74, R.93	Peru	MAD	MADw 22402
	Stern et al. 1897	Panama	US	MADw 24320
	Kluge 23	Panama	MAD	SJRw 7136
	Cooper & Slater 54	Panama	MAD	SJRw 10152
	Record & Kuylen 14	Colombia	MAD	SJRw 16413
	Danforth 45	Costa Rica	MAD	SJRw 32968
<u>Zygia</u> <u>peckii</u> (Robinson) Britton & Rose				
	Winzerling s.n.	Belize	F	SJRw 10172

<u>Zygia</u> <u>recordii</u> Britton & Rose				
Whitford & Stadtmiller 64	Guatemala-Honduras	MAD	SJRw	3724
	Boundary			
Record & Kuylen G.5 (type)	Guatemala	MAD	SJRw	8836
Winzerling I-20	Belize	MAD	SJRw	9869
<u>Zygia</u> <u>stevensonii</u> (Standley) Record				
Stevenson II (type)	Belize	MAD	SJRw	3338
Kinlock 17	Belize	MAD	SJRw	17141
<u>Zygia</u> cf. <u>unifoliolata</u> (Bentham) Pittier				
Krukoff 6710	Brazil	US	SJRw	36838
Krukoff 6716	Brazil	US	SJRw	36842
<u>Zygia</u> sp.				
Stevenson 90	Belize	F	SJRw	35021
Krukoff 10798	Bolivia	F	SJRw	39662

* Arranged alphabetically by specific epithet.

† From U. S. Plant Introduction Garden.

‡ Published incorrectly as A. Ducke 30 in Trop. Woods 63: 2. 1940.

§ Published incorrectly as SJRw 35671 in ibid.

ultraviolet light to reveal the presence or absence of yellowish fluorescence.

The specific gravity of several representative specimens was determined by the water-displacement technique. Oven-dry weight and volume at 5 percent moisture content were used in all calculations. The specific gravity for each wood type is given along with its class as defined by Panshin and de Zeeuw (1970).

KEY TO WOOD TYPES

- A. Parenchyma confluent, sometimes aliform.
 - B. Septate fibers present.
 - C. Rays bi- to quadriseriate. *Arthrosamanea*.
 - C. Rays uniseriate (available specimens small). . . . *Macrosamanea*.
 - B. Septate fibers absent.
 - D. Heartwood light brown with dark bands or totally dark brown. *Marmaroxylon*.
 - D. Heartwood light yellow without dark bands. *Zygia*.
- A. Parenchyma vasicentric, sometimes aliform.
 - E. Septate fibers present.
 - F. Rays bi- to quadriseriate; heartwood light yellow, rarely light brown. *Albizia* or *Arthrosamanea*.
 - F. Rays uniseriate; heartwood dark brown or red-brown.
 - G. Heartwood dark brown. *Havardia* (except *H. pallens*).
 - G. Heartwood red-brown.
 - H. Specific gravity 0.46–0.56. *Havardia pallens*.
 - H. Specific gravity 0.63–1.00. . . *Pithecellobium* (sensu stricto).
 - E. Septate fibers absent.
 - I. Intervascular pit diameter 3–4 μm *Cojoba*.
 - I. Intervessel pit diameter 5–10 μm .
 - J. Rays bi- or triseriate.
 - K. Intervascular pit diameter 7–10 μm ; heartwood dark brown. *Samanea*.
 - K. Intervascular pit diameter 6 μm ; heartwood yellow-brown. *Chloroleucon vinhatico*.
 - J. Rays uniseriate or only partially biseriate (any one specimen may have a few biseriate rays).
 - L. Diameter of largest pores averaging ca. 225 μm ; 3 or 4 pores or pore multiples/sq. mm.
 - M. Intervascular pit diameter 6–8 μm ; fluorescence bright yellow. *Pseudosamanea*.
 - M. Intervascular pit diameter 5–6 μm ; fluorescence negative to yellow. *Abarema*.
 - L. Diameter of largest vessels averaging ca. 130 μm ; 10 to 15 pores or pore multiples/sq. mm.
 - N. Heartwood vessels completely occluded with dark, amorphous substance; heartwood dark brown; wood with oily feel. *Ebenopsis*.
 - N. Heartwood vessels not completely occluded with dark, amorphous substance; heartwood yellow- or red-brown; wood without oily feel.

- O. Heartwood yellow-brown. *Chloroleucon*.
 O. Heartwood red-brown.
 Pithecellobium (sensu stricto).

ANATOMICAL DESCRIPTIONS

TABLE 2 summarizes the important anatomical characters for each wood type, and FIGURES 1-8 illustrate typical anatomical characteristics of the *Pithecellobium* complex. Complete descriptions of the individual wood types are given below. TABLE 3 lists the physical characters that are often of value in wood identification. The different heartwood colors referred to in the descriptions are illustrated by a color photo in Cassens (1973).

Pithecellobium s.l., including *Albizia*, is characterized by several features that do not vary significantly among the different wood types. These characters are not repeated in the wood descriptions. A general description of *Pithecellobium* s.l. is as follows: Heartwood light yellow, yellow-brown, red-brown, and dark brown to light brown with dark stripes. Specific gravity 0.52-1.09; fluorescence yellow, very pale yellow, or negative; froth test positive, short positive, or negative; growth increments more or less demarcated by fine bands of marginal parenchyma or by flattened cells. Wood diffuse porous; pores few to moderately numerous (3 to 17/sq. mm.), generally distinct without aid of a hand lens except in *Chloroleucon*, *Ebenopsis*, *Klugiodendron*, and *Zygia*; diameter moderately small to moderately large (78-273 μm). Vessel elements very short to medium sized (217-437 μm); perforation plates simple with mostly transverse to oblique end walls; intervacular pitting alternate, vestured, and minute, very small, or medium sized (3-10 μm). Rays homocellular, extremely fine to fine (1 to 5 cells wide, or 12-38 μm), generally uniseriate, many specimens occasionally biseriate in part, in some wood types consistently 3 to 5 cells wide; height extremely low (11 to over 20 cells, or 177-405 μm). Paratracheal parenchyma vasicentric to confluent; apotracheal parenchyma sometimes diffuse or in marginal bands; integumented, chambered, rhomboidal crystals often in long chains. Yellow to brown, nonbirefringent compound occasionally to frequently present in portions of the vessels and ray cells of all wood types except *Albizia*, *Klugiodendron*, and *Macrosamanea*; vessels and rays of the *Ebenopsis* wood-type completely occluded with this compound. Fibers moderately short to medium sized (728-1355 μm), septate or nonseptate; pits simple and inconspicuous.

Abarema wood-type (51 specimens, 20 species). Sapwood yellowish white, distinct; heartwood red-brown. Specific gravity 0.64; fluorescence yellow, very pale yellow, or negative; froth test positive except for *Pithecellobium villiferum* (SJRw 44177) and *P. mataybifolium* (SJRw 50101). Pores 71 percent solitary, mostly few to sometimes moderately few, 2 (to 4) to 7/sq. mm.; diameter medium sized to very large, mostly moderately large, 154(-222)-316 μm . Vessel elements moderately short to medium sized, 281(-437)-667 μm ; intervacular pitting small, 5-6 μm , apertures sometimes coalescent. Rays mostly uniseriate to sometimes biseriate, 10(-14)-17 μm wide; average height 12 to over 20 cells, 204(-310)-458 μm . Paratracheal parenchyma mostly

FIGURES 1-4. Anatomical characteristics typical in *Pithecellobium* complex: 1, *Abarema jupunba* (SJRw 49510), transverse section, vasicentric to aliform paratracheal parenchyma, medium-sized to moderately large pores, $\times 21$; 2, *Havardia pallens* (MADw 18342), transverse section, medium-sized pores, growth increments poorly defined by flattened, thick-walled fibers, $\times 21$; 3, *A. jupunba* (SJRw 49510), tangential section, uniseriate rays, longitudinal parenchyma surrounding vessel, nonseptate fibers, $\times 53$; 4, *H. pallens* (MADw 18342), tangential section, septate fibers (right arrow), crystalliferous strands (left arrow), $\times 53$.

TABLE 2. Anatomical characters of wood types.

Para- tracheal * parenchyma	Vessel elements				Inter- vascular pit diam- eter (μm.)	Fibers			Rays			
	Length (μm.)	Pores				Length (μm.)	F/V†	Sep- tate	Width (μm.)	Width (in cells)	Height (μm.)	Height (in cells)
		Diam- eter (μm.)	No./ sq. mm.	Soli- tary (%)								

					<u>ABAREMA</u> (51)‡							
Vas.- ali.; rarely conf.	437	222	4	71	5-6	1,193	2.7	-	14	1(2)§	310	12-20+
					<u>ALBIZIA</u> (16)							
Vas.- ali.	376	210	5	71	6-8 (8-10)	1,031	2.7	+	37	2-4 (1-5)	405	20+
					<u>ARTHROSAMANEA</u> (9)							
Vas.- ali.; some conf.	323	165	5	65	6-8	1,113	3.5	+	38	2-4 (1-5)	371	20+
					<u>CHLOROLEUCON</u> (22)							
Vas.- ali.; rarely conf.	218	131	10	74	6-7	728	3.3	-	12	1 or b // (2-3)	248	14-20+
					<u>COJOBA</u> (26)							
Vas.- ali; some conf.	324	171	7	60	3-5	1,072	3.3	-	15	1 or b (2)	298	12-20+

TABLE 2. Anatomical characters of wood types (*continued*).

Para- tracheal * parenchyma	Vessel elements				Inter- vascular pit diam- eter (μm.)	Fibers		Sep- tate	Rays			
	Length (μm.)	Pores		Length (μm.)		F/V †	Width (μm.)		Width (in cells)	Height (μm.)	Height (in cells)	
		Diam- eter (μm.)	No./ sq. mm.									Soli- tary (%)

<u>EBENOPSIS (3)</u>												
Vas.- ali; some conf.	228	129	17	50	6-7	855	3.7	-	12	1 or b (2)	297	20+
<u>HAVARDIA (7)</u>												
Vas.-; rare conf. bands	293	144	12	75	6-8	874	3.0	+	13	1 (b)	347	20+
<u>KLUGIODENDRON (2)</u>												
Vas.- conf.	354	78	12	72	5-6	1,006	2.8	-	12	1 (b)	177	11
<u>MACROSAMANE (6)</u>												
Ali.- conf.	350	138	8	58	5-6	926	2.7	+	14	1	246	13-20+
<u>MARMAROXYLON (15)</u>												
Vas.- mostly ali., conf.	423	189	3 (6)	69	5-7	1,355	3.2	-	13	1 or b (2)	360	20+

PITHECELLOBIUM (SENSU STRICTO) (37)

Vas.- ali.; some conf.	265	129	14	73	6-8	745	2.8	+¶	13	1 or b	243	10-20+
---------------------------	-----	-----	----	----	-----	-----	-----	----	----	--------	-----	--------

PSEUDOSAMANEA (12)

Vas.- ali.	319	237	3	58	6-8 (9)	958	3.0	-	15	1 or b (2)	251	17
------------	-----	-----	---	----	------------	-----	-----	---	----	---------------	-----	----

PUNJUBA (1)

Vas.- rarely ali. or conf.	382	273	4	78	6-7	1,108	2.9	-	15	1 (b)	300	14
----------------------------------	-----	-----	---	----	-----	-------	-----	---	----	----------	-----	----

SAMANEA (16)

Vas.- ali.	319	245	3	68	7-10	984	3.1	-	29	1-2 (3)	292	15-20+
------------	-----	-----	---	----	------	-----	-----	---	----	------------	-----	--------

ZYGIA (42)

Vas.- mostly ali., conf.	356	138	7	69	5-7	1,126	3.2	-	12	1 or b (2)	300	15-20+
-----------------------------	-----	-----	---	----	-----	-------	-----	---	----	---------------	-----	--------

* Vas. = vasicentric; ali. = aliform; conf. = confluent.

† Fiber length/vessel element length.

‡ Number in parentheses is the number of specimens examined.

§ Number in parentheses indicates that the size occurs sporadically.

¶ "b" indicates the presence of rays biseriate in part only.

¶¶ The presence of abundant gelatinous fibers severely reduces the number of septa present.

TABLE 3. Physical characters of wood types.

Wood type	Specific gravity [*]	Heartwood color	Froth [†]	Fluorescence [‡]
<u>Abarema</u>	0.64	Red-brown	+, rarely -	Negative to yel. to v.p. yel.
<u>Albizia</u>	0.68	Light yellow	- or short +	Negative
<u>Arthrosamanea</u>	0.67	Light brown	- or short +	Yel. to v.p. yel.
<u>Chloroleucon</u>	0.65	Yellow-brown	-	V.p. yel.
<u>Cojoba</u>	0.68	Red-brown	+ or short +	V.p. yel.
<u>Ebenopsis</u>	1.09	Dark brown	-	Bright yel.
<u>Havardia pallens</u>	0.52	Red-brown	- or short +	Negative to v.p. yel.
<u>Havardia</u> sp. (except <u>H. pallens</u>)	0.87	Dark brown	- or short +	Bright yel.

<u>Klugiodendron</u> [§]	0.77	--	--	--
<u>Macrosamanea</u> [§]	0.80	--	--	--
<u>Marmaroxylon</u>	1.00	Light brown with dark stripes	- or short +	Negative
<u>Pithecellobium</u> (sensu stricto)	0.89	Red-brown	-	Negative to v.p. yel.
<u>Pseudosamanea</u>	0.58	Red-brown	+	Bright yel.
<u>Punjuba</u>	0.56	Light yellow	+	Negative
<u>Samanea</u>	0.52	Dark brown	- or short +	Yel. to v.p. yel.
<u>Zygia</u>	0.82	Light yellow	- or short +	Negative

* Oven-dry weight and volume at 5% moisture content.

† + = positive; - = negative.

‡ Yel. = yellow; v.p. yel. = very pale yellow.

§ Specimens small and without apparent heartwood. Also, limited number of specimens.

FIGURES 5-8. 5, *Marmaroxylon racemosum* (SJRw 20720), transverse section, aliform to mostly confluent parenchyma and very thick-walled fibers, $\times 21$; 6, *Ebenopsis flexicaulis* (MADw 25290), transverse section, pores and parenchyma occluded with amorphous compound, $\times 21$; 7, *Albizia colombiana* (SJRw 22478), tangential section, rays 2 or 3 cells wide, septate fibers, alternate intervascular pitting, $\times 53$; 8, *Havardia pallens* (MADw 18342), radial section, showing homogeneous procumbent rays, crystalliferous chains, and septate fibers, $\times 53$.

vasicentric to aliform, rarely confluent; apotracheal parenchyma diffuse or sometimes forming marginal bands. Fibers mostly medium sized to moderately long, 948(–1193)–1680 $\mu\text{m.}$, nonseptate.

Albizia wood-type (16 specimens, 6 species). Sapwood light yellow; heartwood sometimes slightly darker, not sharply demarcated. Specific gravity 0.68; fluorescence negative; froth test negative, occasionally short positive. Pores 71 percent solitary, few to moderately few, 3 (to 5) to 8/sq. mm.; diameter medium sized to moderately large, 152(–210)–261 $\mu\text{m.}$ Vessel elements moderately short to mostly medium sized, 315(–376)–512 $\mu\text{m.}$; intervascular pitting mostly small, 6–8 $\mu\text{m.}$, rarely medium sized (8–10 $\mu\text{m.}$ in *A. tomentosa*), apertures sometimes coalescent. Rays 1 to 5 cells wide, mostly 2 to 4, rarely 1 or 2, 12(–37)–65 $\mu\text{m.}$; 20 or more cells high, 219(–405)–776 $\mu\text{m.}$ Marginal ray cells in *A. adinocephala* often containing crystals. Paratracheal parenchyma vasicentric to aliform; apotracheal diffuse parenchyma occasional or absent, fine marginal bands occasionally present. Fibers moderately short to mostly medium sized, 765(–1031)–1296 $\mu\text{m.}$, septate, septa sometimes scarce and difficult to observe.

Arthrosamanea wood-type (9 specimens, 2 species). Sapwood white; heartwood light brown, not sharply demarcated. Specific gravity 0.67; fluorescence yellow to very pale yellow; froth test negative or short positive. Pores 65 percent solitary, few to moderately few, 3 (to 5) to 7/sq. mm.; diameter mostly medium sized, few moderately large, 111(–165)–250 $\mu\text{m.}$ Vessel elements mostly moderately short to medium sized, 252(–323)–436 $\mu\text{m.}$; intervascular pitting mostly small, 6–8 $\mu\text{m.}$, apertures sometimes coalescent. Rays 1 to 5 cells wide, mostly 2 or more, 29(–38)–63 $\mu\text{m.}$; 20 or more cells high, 237(–371)–446 $\mu\text{m.}$ Marginal ray cells rarely containing crystals. Paratracheal parenchyma mostly vasicentric to aliform, sometimes confluent; apotracheal parenchyma rarely diffuse, sometimes with interrupted fine marginal bands. Fibers mostly medium sized, rarely moderately long, 990(–1113)–1323 $\mu\text{m.}$, septate, areas without septate fibers common, presence of gelatinous fibers seemingly precluding development of septate fibers.

Chloroleucon wood-type (22 specimens, 7 species). Sapwood yellowish white, distinct; heartwood yellow-brown turning darker upon exposure. Specific gravity 0.65; fluorescence very pale yellow; froth test mostly negative. Pores 74 percent solitary, moderately few to moderately numerous, 5 (to 10) to 15/sq. mm.; diameter moderately small to mostly medium sized, 96(–131)–187 $\mu\text{m.}$ Vessel elements extremely to moderately short, mostly very short, 164(–218)–266 $\mu\text{m.}$; intervascular pitting small, 6–7 $\mu\text{m.}$, apertures sometimes coalescent. Rays mostly uniseriate, occasionally biseriate, 8(–12)–15 $\mu\text{m.}$ wide (except *C. vinhatico*, where they are commonly 2 or 3 cells wide, or 27 $\mu\text{m.}$); average height 14 to over 20 cells, 148(–248)–359 $\mu\text{m.}$ Paratracheal parenchyma mostly vasicentric, sometimes short aliform, rarely confluent toward end of growth increment; apotracheal diffuse parenchyma common, marginal bands usually present. Fibers mostly very to moderately short, rarely medium sized, 574(–728)–924 $\mu\text{m.}$, nonseptate.

Cojoba wood-type (26 specimens, 7 species). Sapwood white or often with a brownish cast, giving the appearance of gradual transition between heartwood and sapwood; heartwood red-brown occasionally with isolated sapwood zones. Specific gravity 0.68; fluorescence generally very pale yellow in certain areas, brighter within vessels; froth test varying, usually positive or short positive, sometimes negative. Pores 60 percent solitary, few to moderately numerous, often moderately few, 3 (to 7) to 13/sq. mm.; diameter mostly medium sized to moderately large, 99(-171)-238 μm . Vessel elements moderately short to medium sized, 255(-324)-497 μm .; intervascular pitting very small to minute, 3-5 μm ., mostly 4 μm ., apertures sometimes coalescent. Rays mostly uniseriate, commonly biseriate in some specimens, 12(-15)-30 μm . wide; average height 12 to over 20 cells, 201(-298)-424 μm .; storied in localized areas. Paratracheal parenchyma always vasicentric to aliform, sometimes forming narrow, confluent bands; apotracheal diffuse parenchyma common, often with conspicuously large cells, marginal bands sometimes present. Fibers moderately short to mostly medium sized, 810(-1072)-1451 μm ., nonseptate.

Ebenopsis wood-type (3 specimens, 1 species). Sapwood yellowish white, distinct; heartwood dark brown, oily to touch. Specific gravity 1.09; fluorescence yellow; froth test negative. Pores 50 percent solitary, moderately numerous to numerous, 14 (to 17) to 21/sq. mm.; diameter medium sized, 114(-129)-141 μm . Vessel elements very short, 208(-228)-239 μm .; intervascular pitting small, 6-7 μm ., apertures occasionally coalescent. Rays mostly uniseriate, occasionally biseriate in some specimens, 10(-12)-13 μm . wide; usually 20 or more cells high, 258(-297)-361 μm . Paratracheal parenchyma mostly vasicentric to aliform, sometimes short confluent; apotracheal parenchyma diffuse, marginal bands usually present. Fibers moderately short, 799(-855)-889 μm ., nonseptate.

Havardia wood-type (7 specimens, 3 species). Sapwood yellowish, distinct; heartwood red-brown in *H. pallens*, dark brown in *H. platyloba*. Specific gravity of *H. pallens* 0.52, all other species 0.87; fluorescence in *H. pallens* negative or with pale yellow streaks, in *H. platyloba* bright yellow; froth test negative or short positive. Pores 75 percent solitary, moderately few to moderately numerous, 10 (to 12) to 16/sq. mm.; diameter medium sized, 118(-144)-169 μm . Vessel elements very short to medium sized, 246(-293)-354 μm .; intervascular pitting small to medium sized, 6-8 μm ., apertures sometimes coalescent. Rays mostly uniseriate or biseriate in part, 10(-13)-15 μm . wide; 20 or more cells high, 307(-347)-412 μm . Paratracheal parenchyma mostly vasicentric, rarely forming short, confluent bands; apotracheal parenchyma sometimes diffuse, marginal bands present. Fibers moderately short to medium sized, 766(-874)-1068 μm ., septate.

Klugiodendron wood-type (2 specimens, 1 species). Wood yellow to white, heartwood and sapwood not distinguishable on available material. Specific gravity 0.77; fluorescence negative; froth test positive. Pores 72 percent solitary, moderately numerous, 12/sq. mm.; diameter moderately small, 78 μm . Vessel elements barely medium sized, 354 μm .; intervascular pitting

small, 5–6 μm . Rays uniseriate, rarely biseriate in part, 12 μm . wide; average height 11 cells, 177 μm . Paratracheal parenchyma vasicentric to confluent; apotracheal parenchyma diffuse. Fibers medium sized, 1006 μm ., nonseptate. A third specimen (*Ll. Williams* 4190, MADw 15942) had septate fibers, in contrast to the others, and appeared to be from a tree buttress. It is, therefore, not included in the anatomical description but is listed in the specimens examined.

Macrosamanea wood-type (6 specimens, 5 species). All specimens branchlike, less than 3 cm. in diameter, without apparent heartwood; all wood yellow to white except that of *M. simabifolia*, which is light brown. Specific gravity 0.80; fluorescence negative; froth test negative or short positive. Pores 58 percent solitary, moderately few, 7 (to 8) to 10/sq. mm.; diameter medium sized, 117(–138)–153 μm . Vessel elements moderately short to medium sized, 279(–350)–420 μm .; intervacular pitting small, 5–6 μm . Rays uniseriate, 12(–14)–15 μm . wide; 13 to over 20 cells high, 222(–246)–280 μm . Paratracheal parenchyma mostly aliform or confluent; apotracheal diffuse parenchyma scarce or absent, marginal bands present. Fibers moderately short to medium sized, 797(–926)–1021 μm ., septate. Specimens examined contained gelatinous fibers, making observation of nongelatinous septate fibers difficult.

Marmaroxylon wood-type (15 specimens, 5 species). Sapwood not demarcated; heartwood distinctive due to dark stripes 5–25 mm. wide (heartwood in *Pithecellobium basijugum* solid dark brown). Specific gravity 1.00; fluorescence negative; froth test negative or short positive. Pores 69 percent solitary, few, 3/sq. mm. in *M. racemosum*, to moderately few, 6/sq. mm. in other species; diameter mostly medium sized to moderately large, 107(–189)–242 μm . Vessel elements moderately short to mostly medium sized, 268(–423)–548 μm .; intervacular pitting small, 5–7 μm ., apertures occasionally coalescent. Rays uniseriate or biseriate, uniseriates 10(–13)–22 μm . wide, biseriates 24 μm .; 20 or more cells high, 207(–360)–500 μm . Paratracheal parenchyma vasicentric to mostly aliform or short confluent; apotracheal diffuse parenchyma scarce, fine marginal bands present. Fibers mostly medium sized to moderately long, 1066(–1355)–1666 μm ., nonseptate.

Pithecellobium (*sensu stricto*) wood-type (37 specimens, 7 species). Sapwood yellowish white; heartwood red-brown; transition sometimes gradual. Specific gravity 0.89; fluorescence negative or very pale yellow, but conspicuous in the vessel lumens; froth test negative. Pores 73 percent solitary, moderately few to numerous, mostly moderately numerous, 6 (to 14) to 33/sq. mm.; diameter moderately small to moderately large, mostly medium sized, 98(–129)–218 μm . Vessel elements very short to medium sized, mostly moderately short, 209(–265)–338 μm .; intervacular pitting small to medium sized, 6–8 μm ., apertures sometimes coalescent. Rays mostly uniseriate, in some specimens rarely biseriate or triseriate, uniseriates 10(–13)–15 μm . wide, biseriates and triseriates 25 μm .; average height 10 to slightly over 20 cells, 160(–243)–428 μm . Paratracheal parenchyma vasicentric to slightly aliform, sometimes forming confluent bands; apotracheal parenchyma diffuse, marginal

bands common. Fibers very short to medium sized, mostly moderately short, 572(–745)–922 μm . Some specimens conspicuously septate while others not obviously so, apparently due to gelatinous fibers. Four wood specimens of *P. dulce* (SJRw 49282, SJRW 10058, MADw 13887, and MADw 5122) are coarser textured, with wider, higher rays, and lower specific gravity. These differences are probably the result of faster growth and are considered species variation.

Pseudosamanea wood-type (12 specimens, 2 species). Sapwood light gray, distinct; heartwood red-brown. Specific gravity 0.58; fluorescence bright yellow; froth test positive. Pores 58 percent solitary, mostly few, 2 (to 3) to 5/sq. mm.; diameter medium sized to very large, mostly moderately large, 182(–237)–299 μm . Vessel elements mostly moderately short to medium sized, 283(–319)–369 μm .; intervacular pitting small to medium sized, 6–8 μm ., apertures sometimes coalescent. Rays mostly uniseriate, occasionally biseriate, uniseriates 12(–15)–16 μm . wide, biseriates 30 μm .; average height 17 cells, 216(–251)–343 μm ., storied rays occasional in localized areas. Paratracheal parenchyma mostly vasicentric, sometimes short aliform; apotracheal diffuse parenchyma scarce, marginal bands rare. Fibers mostly medium sized, sometimes moderately short, 846(–958)–1105 μm ., nonseptate.

Punjuba wood-type (1 specimen). Wood light yellow; heartwood and sapwood not distinguishable; sample probably all heartwood. Specific gravity 0.56; fluorescence negative; froth test positive. Pores 78 percent solitary, few, 4/sq. mm.; diameter moderately large, 273 μm . Vessel elements medium sized, 382 μm .; intervacular pitting small, 6–7 μm . Rays uniseriate, 15 μm . wide; average height 14 cells, 300 μm . Paratracheal parenchyma mostly vasicentric to rarely short aliform or confluent; apotracheal parenchyma sometimes diffuse. Fibers medium sized, 1108 μm ., nonseptate.

Samanea wood-type (16 specimens, 1 species, 1 variety). Sapwood white to light gray, distinct; heartwood dark brown. Specific gravity 0.52; fluorescence yellow to very pale yellow; froth test generally negative, sometimes short positive. Pores 68 percent solitary, few, 2 (or 3) to 5/sq. mm.; diameter medium sized to very large, mostly moderately large, 152(–245)–312 μm . Vessel elements very short to medium sized, mostly moderately short, 227(–319)–366 μm .; intervacular pitting medium sized, 7–10 μm ., apertures sometimes coalescent. Rays uniseriate to triseriate, mostly biseriate, biseriates 25(–29)–35 μm . wide; average height 15 to over 20 cells, 207(–292)–473 μm . Marginal ray cells occasionally containing crystals. Paratracheal parenchyma mostly vasicentric, sometimes short aliform; apotracheal parenchyma diffuse, occasionally forming very narrow bands. Fibers moderately short to mostly medium sized, 721(–984)–1288 μm ., nonseptate.

Zygia wood-type (42 specimens, 15 species). Wood light yellow, heartwood not demarcated; pith flecks common, resulting in small, brown markings; brownish-colored wood sometimes around pith and knots. Specific gravity 0.82; fluorescence negative; froth occasionally short positive, otherwise negative. Pores 69 percent solitary, few to moderately numerous, mostly

moderately few, 3 (to 7) to 15/sq. mm.; diameter moderately small to moderately large, mostly medium sized, 86(–138)–207 μm . Vessel elements very short to medium sized, 224(–356)–492 μm .; intervascular pitting small, 5–7 μm ., mostly 6 μm ., apertures occasionally coalescent. Rays mostly uniseriate, rarely biseriate, 10(–12)–16 μm . wide; 15 to over 20 cells high, 197(–300)–469 μm . Paratracheal parenchyma vasicentric to mostly aliform and confluent; apotracheal diffuse parenchyma occasional or absent, fine marginal bands present. Fibers moderately short to mostly medium sized, 837(–1126)–1387 μm ., nonseptate.

COMPARATIVE ANATOMY OF SECONDARY XYLEM WITHIN PITHECELLOBIUM S.L.

Pithecellobium s.l. is a small part of the relatively large, anatomically specialized subfamily Mimosoideae of the Leguminosae. In a family or subfamily where the secondary xylem is specialized, large variations—particularly in those characters of phylogenetic significance—are generally not found. In the secondary xylem of the *Pithecellobium* complex, notable variations in tracheary element length, perforation plate type, vessel pitting, and ray structure were not observed (TABLE 2). However, based on anatomical characters that do not clearly suggest phylogenetic trends, the woods of *Pithecellobium* can still be divided into four groups, each group containing from one to six different wood types.

The four groups are based on the presence or absence of septate fibers and confluent parenchyma. Group 1 lacks both septate fibers and confluent parenchyma and is composed of the *Chloroleucon*, *Ebenopsis*, *Samanea*, *Pseudosamanea*, *Cojoba*, and *Abarema* wood-types. Group 2 has septate fibers but lacks confluent parenchyma; it is composed of *Pithecellobium* sensu stricto, *Havardia*, *Arthrosamanea*, and *Albizia* wood-types. Group 3, which lacks septate fibers but has confluent parenchyma, comprises *Zygia* and *Marmaroxylon* wood-types. Group 4 has both septate fibers and confluent parenchyma and contains only the *Macrosamanea* wood-type.

Although each of the four groups is anatomically distinct, relationships among the different groups are difficult to ascertain. Groups 3 and 4, however, appear to be more closely related than any other combination of groups. Both groups are characterized by confluent parenchyma, uniseriate rays, medium-sized vessel elements, and intervascular pits 5–7 μm . in diameter. Similarities and differences are about the same among the other groups; therefore, relationships cannot be determined. However, the groups provide a convenient context for discussing the characteristics found in each wood type.

GROUP 1 (both septate fibers and confluent parenchyma absent)

The *Cojoba* wood-type has moderately short vessel elements, medium-sized pores, red-brown heartwood, and very small to minute (3–5 μm .) intervascular pits. The minute vessel pitting in this wood type is unique in the *Pithecellobium* complex.

The *Samanea* wood-type has moderately short vessel elements, moderately large pores, biseriate rays, medium-sized (7–10 μm .) intervacular pits, and dark brown heartwood. The intervacular pitting and biseriate rays distinguish this wood type from all others in Group 1.

The *Abarema* wood-type has moderately short to medium-sized vessel elements, moderately large pores, small (5–6 μm .) intervacular pits, mostly uniseriate rays, and red-brown heartwood. This wood type is distinguished from others in Group 1 by the size of the pores and intervacular pits, and by the mostly uniseriate rays.

The *Pseudosamanea* wood-type has moderately short vessel elements, moderately large pores, uniseriate rays, small to medium-sized (6–8 μm .) intervacular pits, and red-brown heartwood. The presence of mostly uniseriate rays and the size of the intervacular pits and pores differentiates this wood type in Group 1.

The *Chloroleucon* wood-type has very short vessel elements, medium-sized pores, small (6–7 μm .) intervacular pits, uniseriate rays, yellow-brown heartwood, and a specific gravity of 0.65. The size of the pores, the color of the heartwood, and the specific gravity separate this wood type in Group 1.

The *Ebenopsis* wood-type has very short vessel elements, medium-sized pores, small (6–7 μm .) intervacular pits, uniseriate rays, dark brown heartwood, vessels filled with an amorphous substance, and a specific gravity of 1.09. This wood type is distinguished by the color of the heartwood and the high specific gravity.

The various wood types in Group 1 are identifiable by relative differences in cell dimensions and macroscopic characteristics. Phylogenetic relationships among the wood types are not clear, but interesting observations are noted.

The vessel element lengths of the *Chloroleucon* and *Ebenopsis* wood-types are nearly the same, but both are shorter than that of any other wood type in the *Pithecellobium* complex. The short vessel element length indicates that the two woods are probably at a higher level of specialization than any others in the *Pithecellobium* complex. Other microscopic features of these woods are nearly identical, and only the macroscopic features vary. Thus, the *Chloroleucon* and *Ebenopsis* woods appear more closely related to each other than to any others in Group 1.

The wood of *Chloroleucon vinhatico* (Record) Record deserves special mention. It has rays two or three cells wide, while those of other species of *Chloroleucon* are uniseriate. Thus, *C. vinhatico* is distinct, but it is maintained in the *Chloroleucon* wood-type because other anatomical characters are similar.

The vessel elements of the *Samanea*, *Pseudosamanea*, and *Cojoba* wood-types are similar in length, although they are longer than those of *Ebenopsis* and *Chloroleucon* types. The *Cojoba* wood-type has smaller intervacular pits and pores than do the *Samanea* and *Pseudosamanea* types. *Pseudosamanea* and *Cojoba* wood-types have uniseriate rays, whereas the *Samanea* wood-type is biseriate. *Samanea* and *Pseudosamanea* wood-types differ slightly in ray width and intervacular pit diameter. Therefore, the *Samanea* and *Pseudosa-*

manea wood-types appear closely related. The *Cojoba* type does not appear close to any other wood types in Group 1.

The *Abarema* wood-type has the longest vessel elements in Group 1 and is probably at the lowest level of specialization. Differences in vessel element length, intervacular pit diameter, pore diameter, wood color, and specific gravity suggest that the *Abarema* type does not appear closely related to *Ebenopsis*, *Chloroleucon*, or *Cojoba* wood-types. However, because of similarities of pore diameter and specific gravity, the *Abarema*, *Samanea*, and *Pseudosamanea* wood-types are somewhat similar.

GROUP 2 (septate fibers present, confluent parenchyma absent)

The wood types of *Albizia* and *Arthrosamanea* are characterized by rays two to four cells wide, vasicentric to aliform parenchyma, medium-sized to moderately large pores, small to medium-sized intervacular pits, moderately short to medium-sized vessel elements, and light yellow to light brown heartwood. These two wood types are discernible from all others in the group by ray width and heartwood color. The woods of *Albizia* and *Arthrosamanea* cannot be separated. They are maintained as two separate wood types on the basis of taxonomic findings.

The *Havardia* and *Pithecellobium* s.s. wood-types have medium-sized pores, small to medium-sized intervacular pits, very short to medium-sized vessel elements, and mostly uniseriate rays. These two wood types appear more closely related to each other than to any others in Group 2. Septate fibers, abundant in *Havardia* and scarce in *Pithecellobium* s.s., separate these two types. Heartwood color and specific gravity also vary among some species, suggesting that *Havardia* and *Pithecellobium* s.s. wood-types are distinct from each other.

Due to differences in ray width, pore diameter, vessel element length, and certain physical characters, the *Albizia* and *Arthrosamanea* wood-types do not appear closely related to the *Havardia* and *Pithecellobium* wood-types. The *Pithecellobium* s.s. and *Havardia* wood-types have shorter vessel elements and narrower rays than the *Albizia* and *Arthrosamanea* wood-types. Thus, the *Pithecellobium* s.s. and *Havardia* wood-types suggest a higher level of specialization within Group 2.

GROUP 3 (septate fibers absent, confluent parenchyma present)

The *Marmaroxylon* and *Zygia* wood-types have medium-sized vessel elements and pore diameters, nonseptate fibers, aliform to mostly confluent parenchyma, small intervacular pits, and mostly uniseriate rays. The heartwood of the *Marmaroxylon* wood-type is light brown with dark stripes, while that of the *Zygia* type is light yellow. The microscopic features of *Marmaroxylon* and *Zygia* wood-types are similar. These two wood types thus appear more closely related to each other than to any other types.

GROUP 4 (both septate fibers and confluent parenchyma present)

The *Macrosamanea* wood-type has moderately short to medium-sized vessel elements, medium-sized pores, small intervacular pits, uniseriate rays, septate

fibers, and aliform to mostly confluent parenchyma. The secondary xylem of the *Macrosamanea* wood-type appears distinct from all others in the *Pithecellobium* complex.

COMPARISON OF WOOD TYPES WITH TAXONOMIC CLASSIFICATION SYSTEMS

The secondary xylem of *Pithecellobium* s.l. may be an aid in developing a taxonomic classification system that more nearly reflects the relationships of this complex genus. Based on variation in the macro- and microscopic wood anatomy, 15 wood types are apparent. For the most part, these 15 types compare favorably with the existing classification systems that have been proposed for *Pithecellobium*.

In 1875 Benthams monographed the New World *Pithecellobium* complex. He did not split *Pithecellobium* into a number of new genera but arranged the species by sections and series (TABLE 4). Many of these sections and series are treated as genera by current taxonomists. Several of the species studied by Benthams are obscure today: their names do not appear in recent literature, and wood specimens are unavailable. Therefore, some recently proposed species names could be synonyms for those in Benthams monograph.

In TABLE 4 the various wood types are aligned with the corresponding sections and series proposed by Benthams (1875). Eight species in the *Abarema* wood-type, one in *Arthrosamanea*, three in *Chloroleucon*, two in *Havardia*, three in *Macrosamanea*, five in *Pithecellobium* s.s., and nine in *Zygia* were known to Benthams and correspond directly with the section and series as indicated. However, the only species in the *Samanea* wood-type (*Samanea saman* (Jacq.) Merr.) and one of seven species in the *Cojoba* wood-type (*Pithecellobium* (*Cojoba*) *sophorocarpum* (Benthams) Britton & Rose) also appear in series 2, Carnosae. *Klugiodendron laetum* (Poeppig & Endl.) Britton & Killip appears in section *Abaremotemo*, but observations of the secondary xylem suggest that *K. laetum* belongs in its own wood type, *Klugiodendron*. *Clypearia* is from the Old World and is thus not considered in this investigation. With few exceptions, the secondary xylem can be used as a basis to form the same groups that Benthams proposed as sections and series.

The *Pseudosamanea*, *Arthrosamanea*, *Cojoba*, and *Ebenopsis* wood-types also contain some species known to Benthams. He placed these species in such widely different genera as *Lysiloma*, *Mimosa*, *Acacia*, and *Inga*. Current practice dictates their placement in *Pithecellobium* s.l. or its segregates.

In 1928 Britton and Rose investigated the North and Central American species of *Pithecellobium*. In TABLE 4 their segregate genera are aligned with the various wood types. The *Cojoba*, *Chloroleucon*, *Ebenopsis*, *Havardia*, and *Pithecellobium* wood-types contain seven, four, one, three, and five species, respectively, from Central America, and Britton and Rose listed these same species in the respective genera. The eight Central American species in the *Abarema* wood-type correspond to six species of *Jupunba* and two species of *Samanea*. The *Samanea* wood-type contains one Central American species that Britton and Rose list in *Samanea*. Three of the five

TABLE 4. Comparison of wood types with two taxonomic classification systems.

Britton & Rose, 1928	Wood types	Bentham, 1875
	<u>Klugiodendron</u> [*]	Section 3 <u>Abaremotemo</u>
<u>Jupunba</u> —————	<u>Abarema</u> —————	Section 4 <u>Samanea</u>
<u>Samanea</u> —————	<u>Samanea</u> —————	Series 1 <u>Subarticulatae</u>
<u>Cojoba</u> —————	<u>Cojoba</u> —————	Series 2 <u>Carnosae</u>
<u>Albizia</u> —————	<u>Albizia</u> [†]	
	<u>Pseudosamanea</u>	
	<u>Arthrosamanea</u> [*]	Series 4 <u>Parviflorae</u>
<u>Chloroleucon</u> —————	<u>Chloroleucon</u> —————	Section 7 <u>Chloroleucon</u>
<u>Ebenopsis</u> —————	<u>Ebenopsis</u>	
<u>Havardia</u> —————	<u>Havardia</u> —————	Section 5 <u>Ortholobium</u>
	<u>Macrosamanea</u> [*]	Section 4 <u>Samanea</u>
		Series 3 <u>Coriaceae</u>
<u>Pithecellobium</u> —————	<u>Pithecellobium</u> —————	Section 1 <u>Unguis-cati</u>
<u>Zygia</u> —————	<u>Zygia</u> —————	Section 6 <u>Caulanthon</u>
	<u>Marmaroxylon</u> ^{*†}	
	<u>Punjuba</u> ^{*†}	

* Klugiodendron, Arthrosamanea, Macrosamanea, Marmaroxylon, and Punjuba are South American genera and are thus not reviewed by Britton and Rose (1928).

† Species included in the Punjuba, Marmaroxylon, and Albizia wood-types were not known to Bentham (1875).

species reported in Albizia by Britton and Rose correspond to the Albizia wood-type, and the remaining two to the Pseudosamanea wood-type. The Albizia wood-type is characterized by rays two to four cells wide, septate fibers, and a light yellow heartwood, whereas the Pseudosamanea wood-type has predominantly uniseriate rays, nonseptate fibers, and a red-brown heartwood; thus, these wood types do not appear closely related. The Zygia wood-type contains eight species from Central America: six are listed in Zygia by Britton and Rose; the other two were not named at the time of their 1928 publication.

With regard to Central American species, there are marked similarities among the wood types and the genera as proposed by Britton and Rose.

There are two exceptions—certain species of *Albizia* are included in the *Pseudosamanea* wood-type, and certain species of *Samanea* are included in the *Abarema* wood-type. A comparison of all species in the *Pithecellobium* complex studied by Benthams (1875) and by Britton and Rose (1928) with those species comprising the various wood types is included in Cassens (1973).

A study of the Mimosaceae and Caesalpiniaceae of Colombia was initiated by Britton and Rose and completed and published by Britton and Killip (1936). They recognized *Abarema*, *Albizia*, *Arthrosamanea*, *Chloroleucon*, *Cojoba*, *Havardia*, *Klugiodendron*, *Macrosamanea*, *Pithecellobium*, *Pseudosamanea*, *Punjuba*, *Samanea*, and *Zygia* as distinct genera. Although a limited number of Colombian species were examined in this study, observations of the secondary xylem support Britton and Killip's genera with few exceptions. Too few wood specimens were available to allow an understanding of the *Klugiodendron* and *Punjuba* wood-types. In addition, the *Albizia* and *Arthrosamanea* wood-types appear closely related and cannot be separated.

Mohlenbrock (1963a, 1963b) has reviewed the *Pithecellobium* complex and its segregate genera. His key to the natural genera includes *Albizia*, *Arthrosamanea*, *Chloroleucon*, *Ebenopsis*, *Havardia*, *Samanea*, and *Zygia*. *Pithecellobium* sensu Mohlenbrock contains the New World segregates *Abarema* and *Cojoba*. *Pseudosamanea* and *Macrosamanea* are listed as synonyms of *Albizia*. On the basis of the secondary xylem, *Albizia* and *Arthrosamanea* wood-types cannot be separated. However, the *Abarema* and *Cojoba* wood-types can be separated from *Pithecellobium*, and the woods of both *Pseudosamanea* and *Macrosamanea* can be separated from *Albizia*. With the exceptions noted, the genera accepted by Mohlenbrock and the proposed wood types correspond.

Hutchinson (1964) notes the taxonomic problems of *Pithecellobium* s.l. and suggests that a monograph be undertaken on a worldwide basis. However, he does cite *Samanea*, *Albizia*, *Pseudosamanea*, and *Zygia* as acceptable genera, which agrees with observations concerning the secondary xylem.

In summary, Benthams's monograph recognized six sections and four series in the New World *Pithecellobium* complex. Later taxonomists raised these sections and series to generic status and added other genera. If the secondary xylem is used as a basis, the *Abarema*, *Chloroleucon*, *Cojoba*, *Ebenopsis*, *Havardia*, *Macrosamanea*, *Marmaroxylon*, *Pithecellobium*, *Pseudosamanea*, *Punjuba*, *Samanea*, and *Zygia* wood-types can be defined. The woods of *Albizia* and *Arthrosamanea* are inseparable. With the exceptions noted, these wood types correspond closely with the various sections and series proposed by Benthams, and the segregate genera proposed by more recent taxonomists.

If the segregates of the *Pithecellobium* complex are to receive common acceptance, taxonomic study and possible transfer of a number of the species examined in this investigation will be required. Several transfers in the *Abarema* wood-type are necessary due to changes in nomenclatural procedure. Britton and Rose (1928) created the genus *Jupunba* and cited *Jupunba jupunba* (Willd.) Britton & Rose as the type species. This name is a tautonym and is thus incorrect according to the *International Code of Botanical Nomenclature*, Article 24.4. Therefore, Britton and Killip (1936) proposed *Abarema* and cited *A. jupunba* (Willd.) Britton & Killip as the type species. All species

with the generic name *Jupunba* should be transferred to *Abarema*. It is our opinion (based on our observations of the xylem anatomy) that the genus *Abarema* should include the following taxa: *Pithecellobium arenarium* Ducke, *P. auriculatum* Benthams, *P. elegans* Ducke, *P. fanshawei* Sandwith, *P. gonggrijpii* Kleinhoonte, *P. langsdorfii* Benthams, *P. leucophyllum* Spruce ex Benthams, *P. mataybifolium* Sandwith, *P. panurense* Spruce ex Benthams, *P. villiferum* Ducke, *Samanea corymbosa* (Rich.) Pittier, *S. leucocalyx* Britton & Rose, *S. macradenia* (Pittier) Britton & Rose, *S. marginata* (Spruce ex Benthams) Pittier, and *S. pedicellaris* (DC.) Killip. Additional species of *Pithecellobium* that appear to belong to other genera (again based on anatomical observation of the xylem) include the following: *P. glabripetalum* H. S. Irwin to *Albizia*; *P. acacioides* Ducke and *P. mathewsii* Benthams to *Chloroleucon*; *P. membranaceum* (Benthams) Schery to *Cojoba*; *P. consanguineum* Cowan to *Macrosamanea*; *P. collinum* Sandwith, *P. dinizii* Ducke, and *P. umbriflorum* Ducke to *Marmaroxylon*; and *P. juruanum* Harms to *Zygia*. Another transfer that might be made based solely on the wood structure is *Albizia cubana* Britton & Wilson to *Pseudosamanea*. Since in most cases the species in question was named by a taxonomist who did not support the segregation of small genera from *Pithecellobium*, the transfers have never been made to the appropriate segregate genera.

SPECIALIZATION OF PITHECELLOBIUM S.L.

Various authors have reported on the significance of the secondary xylem in the determination of phylogenetic relationships. The secondary xylem can be used to determine whether the wood of *Pithecellobium* s.l. is primitive or advanced (specialized) with respect to other species. Advanced (specialized) is a relative term that suggests that a particular wood is at a higher phylogenetic rank than a primitive one.

Pithecellobium s.l. is characterized by very short to moderately long libriform fibers with minute, slitlike simple pits. The vessel elements are very short to medium sized with simple perforation plates, transverse to oblique end walls, and alternate intervacular pitting. The fiber : vessel ratio of the different wood types ranges from 2.7 to 3.9. The pore diameters are moderately small to moderately large and appear circular to oval in cross section. The rays are extremely low in height, extremely fine to fine in width, and homogeneous. Most of the rays are uniseriate or in part biseriate and are without uniseriate wings. A few rays are two to five cells wide. Most woods in the *Pithecellobium* complex are characterized by abundant vasicentric to aliform paratracheal parenchyma. Confluent paratracheal bands are sometimes present. Distinct storied structure does not occur in the complex, but occasional isolated areas exist. These anatomical features indicate that the woods of *Pithecellobium* s.l. are relatively specialized. Features of a primitive xylem do not exist.

Although the woods of *Pithecellobium* s.l. contain only specialized tracheary elements and tissue types, there are statistically significant differences in vessel element and fiber lengths. Differences also exist in both ray width

and parenchyma type. Based on vessel element length, *Abarema* and *Marmaroxylon* wood-types with longer vessel elements suggest a lower level of specialization in the *Pithecellobium* complex, whereas the shorter vessel elements of *Chloroleucon* and *Ebenopsis* suggest a higher level. Based on fiber length, *Chloroleucon* is again the most specialized wood type, whereas *Marmaroxylon* is the least. When all wood types are considered, there is an overlapping of the confidence intervals for vessel element and fiber lengths, indicating a continuum throughout the generic complex.

Most woods in the *Pithecellobium* complex have rays that are uniseriate or partially biseriate. However, the rays in *Samanea*, *Albizia*, and *Arthrosamanea* are commonly two to four cells wide. Therefore, the ray tissue in these three wood types is less specialized than others in the *Pithecellobium* complex.

SUMMARY AND CONCLUSIONS

The secondary xylem of 83 species of the *Pithecellobium* complex indicates that on the basis of the presence or absence of septate fibers and confluent parenchyma, four distinct wood groups can be defined. Other anatomical characteristics indicate that these four groups can be further divided into 15 wood types: *Abarema*, *Albizia*, *Arthrosamanea*, *Chloroleucon*, *Cojoba*, *Ebenopsis*, *Havardia*, *Klugiodendron*, *Macrosamanea*, *Marmaroxylon*, *Pithecellobium* s.s., *Pseudosamanea*, *Punjuba*, *Samanea*, and *Zygia*. Although the woods of *Arthrosamanea* and *Albizia* are indistinguishable, they are maintained as two separate wood types because of published morphological findings. The woods of *Klugiodendron* and *Punjuba* constitute two additional types; due to insufficient and immature xylarium specimens, they have not been included in the key or discussed in detail.

When the various wood types are compared to the taxonomic classification systems proposed by Bentham (1875) and by Britton and Rose (1928), marked similarities become obvious. Based on the secondary xylem, the various species of the *Pithecellobium* complex fall into groups similar to those proposed by the various taxonomists who prefer the segregation of several small genera from *Pithecellobium*.

Observations of the secondary xylem indicate that 26 species could appropriately be transferred to segregate genera. In addition, name changes from *Jupunba* to *Abarema* are needed due to incorrect nomenclature.

Most anatomical features expressing specialization trends do not vary appreciably within the *Pithecellobium* complex. Therefore, the evolutionary relationships between different wood groups and types are unclear. However, differences in vessel element and fiber lengths and (to a lesser extent) ray width indicate some specialization levels among wood types. Based on vessel element length, the *Abarema* and *Marmaroxylon* wood-types appear at the lowest level of specialization in *Pithecellobium* s.l., whereas the *Chloroleucon* and *Ebenopsis* wood-types appear at the highest. The *Samanea*, *Albizia*, and *Arthrosamanea* wood-types have wider rays than others in the *Pithecellobium* complex, thereby indicating a lower level of specialization.

ACKNOWLEDGMENTS

The authors wish to express their appreciation to Dr. B. Francis Kukachka, who initially proposed the study and guided the research, and to Dr. Hans Kubler, University of Wisconsin-Madison, for serving as the major professor to the senior author. The authors are also grateful for the facilities, research support services, and wood specimens provided by the U. S. Forest Products Laboratory in Madison, Wisconsin, which houses both the Samuel James Record Memorial Wood Collection (SJRw) and the U. S. Forest Products Laboratory Wood Collection (MADw).

BIBLIOGRAPHY

- BENTHAM, G. 1875. Revision of the suborder Mimoseae. Trans. Linn. Soc. London **30**: 335-668.
- BRITTON, N. L., & E. P. KILLIP. 1936. Mimosaceae and Caesalpiniaceae of Colombia. Ann. N. Y. Acad. Sci. **35**: 101-208.
- & J. N. ROSE. 1928. Mimosaceae. N. Am. Fl. **23**: 1-76.
- BURKART, A. 1949. Leguminosae nuevas o criticas, III. Darwiniana **9**: 63-70.
- CASSENS, D. L. 1973. Systematic wood anatomy of the New World *Pithecellobium* (Leguminosae - Mimosoideae) complex. 211 pp. Unpubl. Ph.D. Thesis, University of Wisconsin, Madison, Wisconsin.
- CHATTAWAY, M. M. 1932. Proposed standards for numerical values used in describing woods. Trop. Woods. **29**: 20-28.
- COMMITTEE ON STANDARDIZATION OF TERMS OF CELL SIZE, International Association of Wood Anatomists. 1937. Standard terms of length of vessel members and wood fibers. Trop. Woods **51**: 21.
- . 1939. Standard terms of size for vessel diameter and ray width. *Ibid.* **59**: 51, 52.
- COWAN, R. S. 1961. Leguminosae - Mimosoideae. In B. MAGUIRE & J. J. WURDACK, The botany of the Guyana highland, IV. Mem. N. Y. Bot. Gard. **10**(4): 65-69.
- DUGAND, A. 1948. Algunas leguminosae de la Amazonia y Orinoco Colombianas. Caldasia **5**: 65-76.
- . 1966. Notes on the flora of Colombia and neighboring countries. Phytologia **13**: 389-392.
- FAWCETT, W., & A. B. RENDLE. 1920. Leguminosae. Pp. 124-154 in: Flora of Jamaica. Vol. 4. British Museum of Natural History, London.
- HARMS, H. 1930. Zur Kenntnis von *Lysiloma guachapele* (H.B.K.) Benth. Notizbl. Bot. Gart. Berlin **11**: 52-56.
- HUTCHINSON, J. 1964. The genera of flowering plants. Vol. 1. vii + 516 pp. Clarendon Press, Oxford.
- IRWIN, H. S. 1966. Leguminosae - Mimosoideae. In B. MAGUIRE, Contributions to the botany of Guiana, I-IV. Mem. N. Y. Bot. Gard. **15**: 96-111.
- KLEINHOONTE, A. 1940. Mimosaceae. In A. PULLE, ed., Flora of Suriname. Vol. 2, part 2, fasc. 2. (Meded. 30. Kolon. Inst. Amsterdam, Afd. Handelsmus no. 11).
- KOSTERMANS, A. J. G. H. 1954. A monograph of the Asiatic, Malaysian, Australian, and Pacific species of Mimosaceae, formerly included in *Pithecellobium* Mart. Bull. Organ. Sci. Res. Indonesia **20**(11): 1-122.

Cassens, Daniel L. and Miller, R B. 1981. "Wood Anatomy of the New World Pithecellobium (sensu lato)." *Journal of the Arnold Arboretum* 62(1), 1-44.
<https://doi.org/10.5962/bhl.part.11244>.

View This Item Online: <https://www.biodiversitylibrary.org/item/33625>

DOI: <https://doi.org/10.5962/bhl.part.11244>

Permalink: <https://www.biodiversitylibrary.org/partpdf/11244>

Holding Institution

Missouri Botanical Garden, Peter H. Raven Library

Sponsored by

Missouri Botanical Garden

Copyright & Reuse

Copyright Status: In copyright. Digitized with the permission of the rights holder.

Rights Holder: Arnold Arboretum of Harvard University

License: <http://creativecommons.org/licenses/by-nc-sa/3.0/>

Rights: <https://biodiversitylibrary.org/permissions>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.