JOURNAL
OF THE
ARNOLD ARBORETUM

VOLUME 62 JANUARY 1981 NUMBER 1

# WOOD ANATOMY OF THE NEW WORLD PITHECELLOBIUM (SENSU LATO)[1]

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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 Bentham 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

[1]The 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 intervascular 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 |
|---|---|---|---|---|
| | ABAREMA WOOD-TYPE | | | |
| Jupunba abbottii (Rose & Leonard) Britton & Rose | | | | |
| | Anonymous s.n. | Dominican Republic | US | MADw 19522 |
| Pithecellobium arenarium Ducke | | | | |
| | Maguire 42959 | Guyana | NY | MADw 25501 |
| Pithecellobium auriculatum Bentham | | | | |
| | Krukoff 7938 | Brazil | US | MADw 25412 |
| Samanea corymbosa (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 |
| Pithecellobium elegans Ducke | | | | |
| | Navy Project 136, F12 | Brazil | MAD | SJRw 45543 |
| | FDBG 4805 | Guyana | K | SJRw 46466 |
| Pithecellobium fanshawei Sandwith | | | | |
| | FDBG 4181 (type) | Guyana | NY | SJRw 46467 |

| | | | |
|---|---|---|---|
| *Pithecellobium gonggrijpii* Kleinhoonte | | | |
| Lanjouw & Lindeman 518 | Surinam | U | MADw 25489 |
| Stahel 88 | Surinam | MAD | SJRw 41157 |
| FDBG 3313 | Guyana | K | SJRw 43744 |
| Maguire 24273 | Surinam | NY | SJRw 44106 |
| *Abarema jupunba* (Willd.) Britton & Killip | | | |
| Maguire 51953 | Brazil | NY | MADw 21611 |
| Ll. Williams 12047 | Venezuela | F | MADw 25413 |
| Persaud 64 | Guyana | F | SJRw 9472 |
| Capucho 593 | Brazil | F | SJRw 23887 |
| McArthur s.n. | Surinam | MAD | SJRw 32241 |
| Stahel 20 | Surinam | US | SJRw 42432 |
| FDBG 3255 | Guyana | K | SJRw 43730 |
| Beard 8 | Grenada | A | SJRw 49510 |
| Maguire 40552 | Guyana | NY | SJRw 50123 |
| Inst. Nat. Sci. 17670 | Colombia | COL | SJRw 52872 |
| *Pithecellobium langsdorfii* Bentham | | | |
| Whitford 351 | Brazil | MAD | SJRw 3174 |
| Hoehne 29842 | Brazil | MAD | SJRw 23833 |
| Reitz & Klein 3912 | Brazil | MAD | SJRw 52072 |
| *Samanea leucocalyx* Britton & Rose | | | |
| McClay & Clara 41 | Guatemala | MAD | MADw 23152 |
| Brown II | Belize | MAD | SJRw 13021 |
| *Pithecellobium leucophyllum* Spruce ex Bentham | | | |
| Wurdack & Adderley 43317 | Venezuela | NY | SJRw 54393 |

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

| Scientific name* | Collector and number | Geographic origin | Herbarium voucher | Xylarium and catalog number |
|---|---|---|---|---|
| | ABAREMA WOOD-TYPE, continued | | | |
| Samanea macradenia (Pittier) Britton & Rose | | | | |
| | Christopherson 196 (type) | Panama | US | MADw 5718 |
| | USNH 716482 | Panama | US | SJRw 53764 |
| Samanea marginata (Spruce ex Bentham) Pittier | | | | |
| | Krukoff 6715 | Brazil | US | SJRw 36841 |
| | Ll. Williams 14869 | Venezuela | F | SJRw 41806 |
| Pithecellobium mataybifolium Sandwith | | | | |
| | Cowan 39332 | Guyana | NY | SJRw 50101 |
| Jupunba obovalis (A. Rich.) Britton & Rose | | | | |
| | Alberto J. Fors 106 | Cuba | SV? | MADw 14418 |
| Pithecellobium panurense Spruce ex Bentham | | | | |
| | Wurdack & Adderley 54364 | Venezuela | NY | SJRw 54364 |
| Samanea pedicellaris (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 |
| *Jupunba pinetorum* (Britton) Britton & Rose | | | |
| Bucher 11 | Cuba | MAD | SJRw 14728 |
| *Jupunba pseudo-tamarindus* Britton | | | |
| Cooper 461 (type) | Panama | MAD | SJRw 12079 |
| *Pithecellobium villiferum* Ducke | | | |
| Maguire 24629 | Surinam | NY | SJRw 44177 |
| Wurdack & Adderley 43351 | Venezuela | NY | SJRw 54373 |

*ALBIZIA* WOOD-TYPE

| | | | |
|---|---|---|---|
| *Albizia adinocephala* (Donn. Smith) Britton & Rose | | | |
| Dayton 3097 | Costa Rica | MAD | MADw 10300 |
| Record & Kuylen H.20 | Honduras | MAD | SJRw 9966 |
| *Albizia caribaea* (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 |
| *Albizia colombiana* 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 |
|---|---|---|---|---|
| | ALBIZIA WOOD-TYPE, continued | | | |
| Pithecellobium glabripetalum H. S. Irwin | FDBG 5397 (type) (distributed as Pithecellobium niopoides Bentham) | Guyana | K | SJRw 46468 |
| Albizia hassleri (Chodat) Burkart | Woolston T10 | Paraguay | MAD | SJRw 48286 |
| Albizia tomentosa (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 |
| | ARTHROSAMANEA WOOD-TYPE | | | |
| Arthrosamanea multiflora (H.B.K.) Kleinhoonte | Novenaz 37 | Argentina | MAD | SJRw 14993 |
| | Capucho 451 | Brazil | F | SJRw 22742 |
| | Krukoff 6750 | Brazil | US | SJRw 36861 |
| Arthrosamanea pistaciaefolia (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

| | | | |
|---|---|---|---|
| *Pithecellobium acacioides* Ducke | | | |
| Capucho 356 | Brazil | F | SJRw 21659 |
| *Chloroleucon guantanamense* (Britton) Britton & Rose | | | |
| Bucher 81 | Cuba | MAD | SJRw 16252 |
| *Chloroleucon leucospermum* (Brandegee) Britton & Rose | | | |
| Winzerling II-2 | Belize | MAD | SJRw 9851 |
| Record & Kuylen H.59 | Honduras | MAD | SJRw 10005 |
| *Chloroleucon mangense* (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 |
| *Pithecellobium mathewsii* Bentham | | | |
| Ll. Williams 5532 | Peru | F | MADw 15936 |
| Ll. Williams 5967 | Peru | F | MADw 15937 |
| Ll. Williams 6463 | Peru | F | MADw 15938 |

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

| Scientific name* | Collector and number | Geographic origin | Herbarium voucher | Xylarium and catalog number |
|---|---|---|---|---|
| | | CHLOROLEUCON WOOD-TYPE, continued | | |
| Chloroleucon tortum (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 |
| Chloroleucon vinhatico (Record) Record | | | | |
| | Curran 59 (type) | Brazil | MAD | SJRw 1806 |
| | Curran 28 | Brazil | F | SJRw 4698 |
| Chloroleucon sp. | | | | |
| | Curran & Haman 562 | Venezuela | GH | SJRw 2832 |
| | Curran 737 | Venezuela | GH? | SJRw 16181 |
| | | COJOBA WOOD-TYPE | | |
| Cojoba arborea (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 |
| *Cojoba costaricensis* Britton & Rose | | | |
| Austin Smith s.n. | Costa Rica | MAD | SJRw 38353 |
| *Cojoba donnell-smithii* Britton & Rose | | | |
| Record G.138 | Guatemala | MAD | SJRw 10089 |
| Stevenson III | Belize | MAD | SJRw 14893 |
| *Pithecellobium membranaceum* (Bentham) Schery | | | |
| Stern et al. 1131 | Panama | US | SJRw 55040 |
| *Cojoba rufescens* (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 |
| *Cojoba sophorocarpa* (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 |
|---|---|---|---|---|
| | COJOBA WOOD-TYPE, continued | | | |
| Cojoba tenella Britton & Rose | Hottle 54 | Honduras | F | SJRw 15631 |
| | EBENOPSIS WOOD-TYPE | | | |
| Ebenopsis flexicaulis (Bentham) Britton & Rose | Nogle 99 | Texas | TAES | MADw 13215 |
| | Wilson M-1 | Mexico | MAD | MADw 18344 |
| | MEXFw X-324 | Mexico | ICF | MADw 25290 |
| | HAVARDIA WOOD-TYPE | | | |
| Havardia leiocalyx (Standley) Britton & Rose | Page 9615 | Mexico | DS | MADw 23863 |
| Havardia pallens (Bentham) Britton & Rose | Wilson M-7 | Mexico | MAD | MADw 18342 |
| | Scott s.n. | Miami, Florida† | ? | SJRw 44776 |
| | Cavazos 62A | Mexico | US | USw 19246 |
| Havardia platyloba (Sprengel) Britton & Rose | Curran & Haman 400 | Curaçao | GH | SJRw 2775 |

| | | | |
|---|---|---|---|
| Record & Don Jaca 51 | Colombia | MAD | SJRw 16450 |
| Dugand 1158 | Colombia | MAD | SJRw 35287 |

KLUGIODENDRON WOOD-TYPE

*Klugiodendron laetum* (Poeppig & Endl.) Britton & Killip

| | | | |
|---|---|---|---|
| Ll. Williams 4190 | Peru | F | MADw 15942 |
| Krukoff 6457 | Brazil | US | SJRw 36693 |
| King 6170 | Colombia | US | USw 37504 |

MACROSAMANEA WOOD-TYPE

*Macrosamanea aquatica* Pittier

| | | | |
|---|---|---|---|
| Wurdack & Adderley 42732 | Venezuela | NY | SJRw 54144 |

*Pithecellobium consanguineum* Cowan

| | | | |
|---|---|---|---|
| Maguire et al. 41878 (type) | Guyana | NY | MADw 25503 |

*Macrosamanea discolor* (Humb. & Bonpl.) Britton & Rose

| | | | |
|---|---|---|---|
| NYBG 28422 | Guyana | NY | MADw 25502 |

*Macrosamanea kegelii* (Meissner) Kleinhoonte

| | | | |
|---|---|---|---|
| Gonggrijp 4150 | Surinam | NY | MADw 25682 |

*Macrosamanea simabifolia* (Spruce ex Bentham) Pittier

| | | | |
|---|---|---|---|
| Wurdack & Adderley 43023 | Venezuela | NY | SJRw 54466 |
| Wurdack & Adderley 42937 | Venezuela | NY | SJRw 54521 |

MARMAROXYLON WOOD-TYPE

*Pithecellobium basijugum* Ducke

| | | | |
|---|---|---|---|
| Lanjouw & Lindeman 2270 | Surinam | U | MADw 25486 |
| Wurdack & Maguire 41958 | Guyana | NY | MADw 25504 |

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

| Scientific name* | Collector and number | Geographic origin | Herbarium voucher | Xylarium and catalog number |
|---|---|---|---|---|
| | MARMAROXYLON WOOD-TYPE, continued | | | |
| Pithecellobium collinum Sandwith | | | | |
| | FDBG 3976 (type) | Guyana | K | SJRw 46465 |
| Pithecellobium dinizii Ducke | | | | |
| | Krukoff 1302 | Brazil | US | MADw 25118 |
| | Cuatrecasas 17374 | Colombia | F | SJRw 43205 |
| Marmaroxylon racemosum (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 |
| Pithecellobium umbriflorum Ducke | | | | |
| | Krukoff 6872 | Brazil | F | SJRw 36937 |

PITHECELLOBIUM (SENSU STRICTO) WOOD-TYPE

| | | | |
|---|---|---|---|
| *Pithecellobium dulce* (Roxb.) Bentham | | | |
| 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.) Bentham | | | |
| 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 |

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

| Scientific name* | Collector and number | Geographic origin | Herbarium voucher | Xylarium and catalog number |
|---|---|---|---|---|
| | PITHECELLOBIUM (SENSU STRICTO) WOOD-TYPE, continued | | | |
| Pithecellobium oblongum Bentham | | | | |
| | Record & Kuylen G.120 | Guatemala | MAD | SJRw 10071 |
| | Stern & Chambers 27 | Panama | MAD | SJRw 51544 |
| Pithecellobium oblongum Pittier | | | | |
| | Dugand 847 | Colombia | MAD | SJRw 29678 |
| Pithecellobium unguis-cati (L.) Bentham | | | | |
| | 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 |
| Pithecellobium sp. | | | | |
| | Curran 425 | Curaçao | GH | SJRw 2798 |
| | Curran 616 | Curaçao | GH | SJRw 2854 |

PSEUDOSAMANEA WOOD-TYPE

| | | | |
|---|---|---|---|
| *Albizia cubana* Britton & Wilson | | | |
| Brother H. Leon 13720 | Cuba | F | SJRw 16321 |
| *Pseudosamanea guachapele* (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

| | | | |
|---|---|---|---|
| *Punjuba racemiflora* (Donn. Smith) Britton & Rose | | | |
| Barbour 1014 | Costa Rica | MAD | MADw 10284 |

SAMANEA WOOD-TYPE

| | | | |
|---|---|---|---|
| *Samanea saman* (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 |
|---|---|---|---|---|
| | SAMANEA 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 |
| Samanea saman (Jacq.) Merrill var. acutifolium Bentham | | | | |
| | Woytkowski 35145 | Colombia | MAD | SJRw 44592 |
| | ZYGIA WOOD-TYPE | | | |
| Zygia ampla (Spruce ex Bentham) Pittier | | | | |
| | Ll. Williams 14747 | Venezuela | F | SJRw 41738 |
| Zygia cauliflora (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 |
| Zygia cognata (Schlecht) Britton & Rose | | | |
| Ll. Williams 9208 | Mexico | MAD | SJRw 34792 |
| Zygia conzattii (Standley) Britton & Rose | | | |
| Ll. Williams 9438 | Mexico | F | SJRw 34857 |
| Zygia divaricata (Brongniart) Pittier | | | |
| Ll. Williams 15027 | Venezuela | F | SJRw 41895 |
| Wurdack & Adderley 43419 | Venezuela | NY | SJRw 54536 |
| Zygia englesingii (Standley) Record | | | |
| Englesing 205 (type) | Nicaragua | MAD | SJRw 13297 |
| Zygia glomerata (Vell.) Pittier | | | |
| Ll. Williams 14238 | Venezuela | F | SJRw 41472 |
| Wurdack & Adderley 43314 | Venezuela | NY | SJRw 54516 |
| Zygia inaequalis (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 |
| Pithecellobium juruanum 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 |
|---|---|---|---|---|
| | ZYGIA WOOD-TYPE, continued | | | |
| Zygia latifolia (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 |
| Zygia longifolia (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 |
| Zygia peckii (Robinson) Britton & Rose | | | | |
| | Winzerling s.n. | Belize | F | SJRw 10172 |

| | | | |
|---|---|---|---|
| *Zygia recordii* Britton & Rose | | | |
| Whitford & Stadtmiller 64 | Guatemala-Honduras Boundary | MAD | SJRw 3724 |
| Record & Kuylen G.5 (type) | Guatemala | MAD | SJRw 8836 |
| Winzerling I-20 | Belize | MAD | SJRw 9869 |
| *Zygia stevensonii* (Standley) Record | | | |
| Stevenson II (type) | Belize | MAD | SJRw 3338 |
| Kinlock 17 | Belize | MAD | SJRw 17141 |
| *Zygia* cf. *unifoliolata* (Bentham) Pittier | | | |
| Krukoff 6710 | Brazil | US | SJRw 36838 |
| Krukoff 6716 | Brazil | US | SJRw 36842 |
| *Zygia* 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.

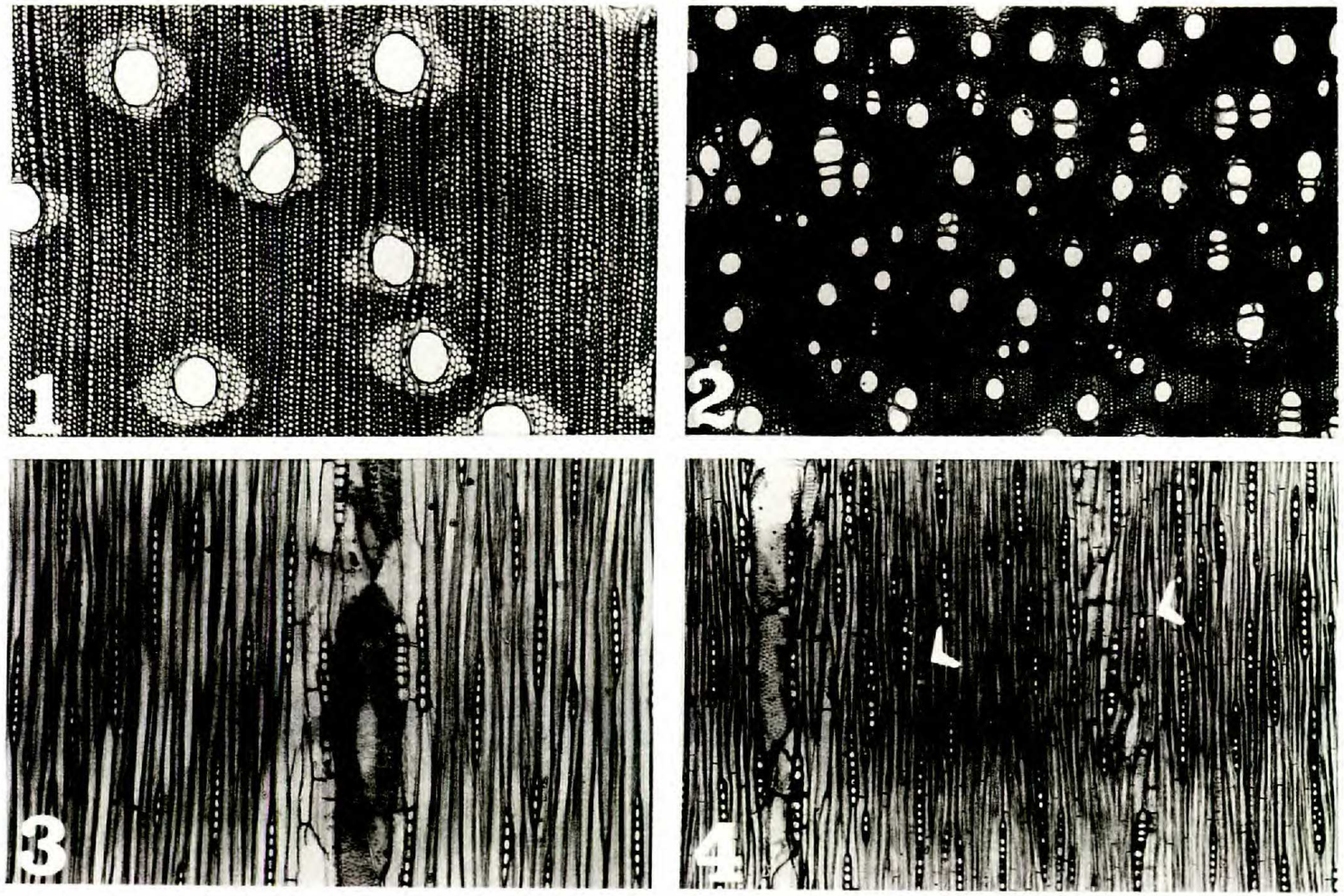
O. Heartwood yellow-brown. . . . . *Chloroleucon.*
O. Heartwood red-brown. . . . . .
. . . . . *Pithecellobium* (sensu stricto).

## 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; intervascular 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.; intervascular 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, × 21; 2, *Havardia pallens* (MADw 18342), transverse section, medium-sized pores, growth increments poorly defined by flattened, thick-walled fibers, × 21; 3, *A. jupunba* (SJRw 49510), tangential section, uniseriate rays, longitudinal parenchyma surrounding vessel, nonseptate fibers, × 53; 4, *H. pallens* (MADw 18342), tangential section, septate fibers (right arrow), crystalliferous strands (left arrow), × 53.

TABLE 2. **Anatomical characters of wood types.**

| Paratracheal parenchyma* | Vessel elements: Length (μm.) | Vessel elements: Pores: Diameter (μm.) | Vessel elements: Pores: No./sq. mm. | Vessel elements: Pores: Solitary (%) | Intervascular pit diameter (μm.) | Fibers: Length (μm.) | Fibers: F/V† | Fibers: Septate | Rays: Width (μm.) | Rays: Width (in cells) | Rays: Height (μm.) | Rays: Height (in cells) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | ABAREMA (51)‡ | | | | | | | |
| Vas.- ali.; rarely conf. | 437 | 222 | 4 | 71 | 5-6 | 1,193 | 2.7 | - | 14 | 1(2)§ | 310 | 12-20+ |
| | | | | | ALBIZIA (16) | | | | | | | |
| Vas.- ali. | 376 | 210 (8-10) | 5 | 71 | 6-8 | 1,031 | 2.7 | + | 37 | 2-4 (1-5) | 405 | 20+ |
| | | | | | ARTHROSAMANEA (9) | | | | | | | |
| Vas.- ali.; some conf. | 323 | 165 | 5 | 65 | 6-8 | 1,113 | 3.5 | + | 38 | 2-4 (1-5) | 371 | 20+ |
| | | | | | CHLOROLEUCON (22) | | | | | | | |
| Vas.- ali.; rarely conf. | 218 | 131 | 10 | 74 | 6-7 | 728 | 3.3 | - | 12 | 1 or b‖ (2-3) | 248 | 14-20+ |
| | | | | | COJOBA (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*).

| Paratracheal parenchyma* | Vessel elements: Length (μm.) | Vessel elements: Pores: Diameter (μm.) | Vessel elements: Pores: No./sq. mm. | Vessel elements: Pores: Solitary (%) | Vessel elements: Intervascular pit diameter (μm.) | Fibers: Length (μm.) | Fibers: F/V† | Fibers: Septate | Rays: Width (μm.) | Rays: Width (in cells) | Rays: Height (μm.) | Rays: Height (in cells) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | EBENOPSIS (3) | | | | | | | |
| Vas.- ali; some conf. | 228 | 129 | 17 | 50 | 6-7 | 855 | 3.7 | - | 12 | 1 or b (2) | 297 | 20+ |
| | | | | | HAVARDIA (7) | | | | | | | |
| Vas.-; rare conf. bands | 293 | 144 | 12 | 75 | 6-8 | 874 | 3.0 | + | 13 | 1 (b) | 347 | 20+ |
| | | | | | KLUGIODENDRON (2) | | | | | | | |
| Vas.- conf. | 354 | 78 | 12 | 72 | 5-6 | 1,006 | 2.8 | - | 12 | 1 (b) | 177 | 11 |
| | | | | | MACROSAMANEA (6) | | | | | | | |
| Ali.- conf. | 350 | 138 | 8 | 58 | 5-6 | 926 | 2.7 | + | 14 | 1 | 246 | 13-20+ |
| | | | | | MARMAROXYLON (15) | | | | | | | |
| 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+ |

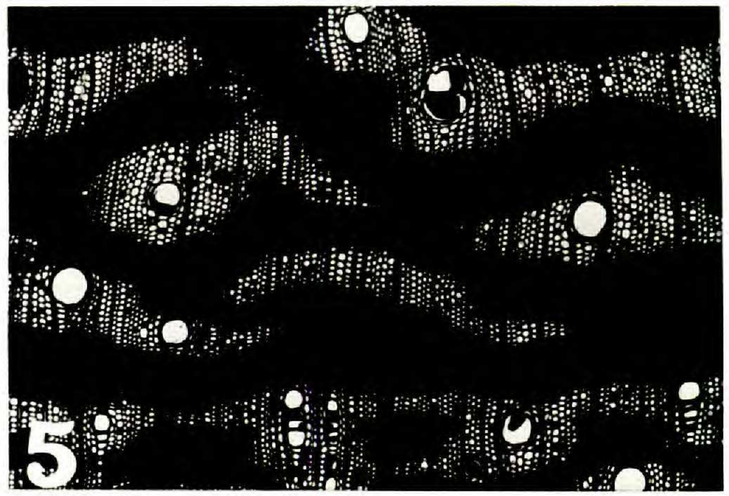
* Vas. = vasicentric; ali. = aliform; conf. = confluent.
† Fiber length/vessel element length.
‡
‡ Number in parentheses is the number of specimens examined.
§ Number in parentheses indicates that the size occurs sporadically.
// "b" indicates the presence of rays biseriate in part only.
¶ The presence of abundant gelatinous fibers severely reduces the number of septa present.

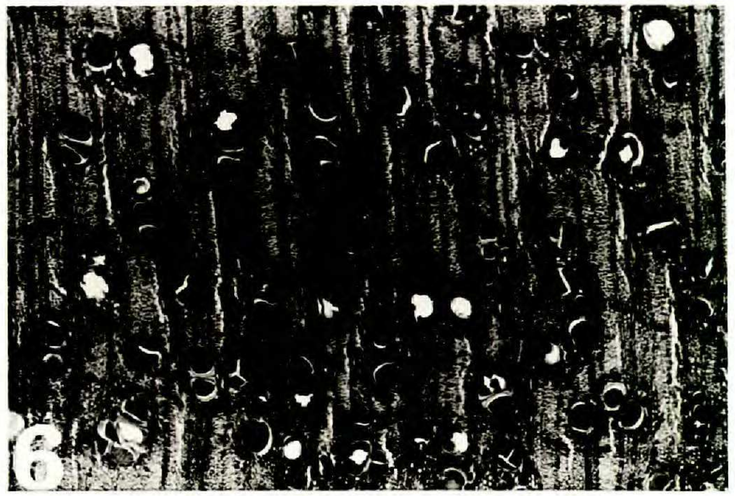
TABLE 3. **Physical characters of wood types.**

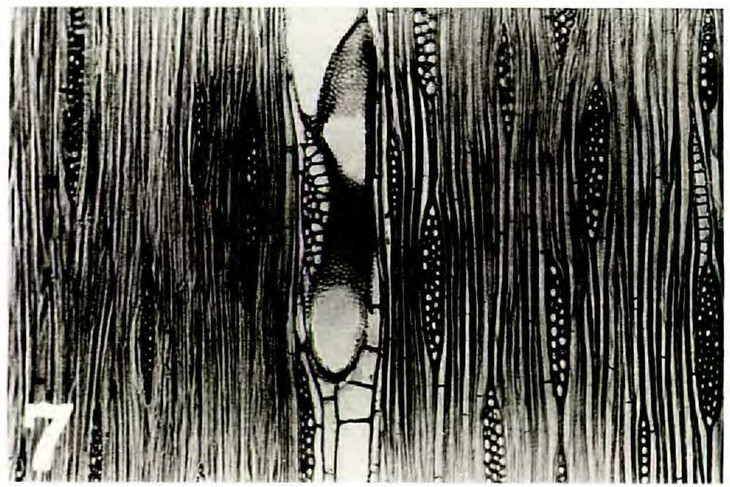
| Wood type | Specific gravity* | Heartwood color | Froth† | Fluorescence‡ |
|---|---|---|---|---|
| Abarema | 0.64 | Red-brown | +, rarely - | Negative to yel. to v.p. yel. |
| Albizia | 0.68 | Light yellow | - or short + | Negative |
| Arthrosamanea | 0.67 | Light brown | - or short + | Yel. to v.p.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

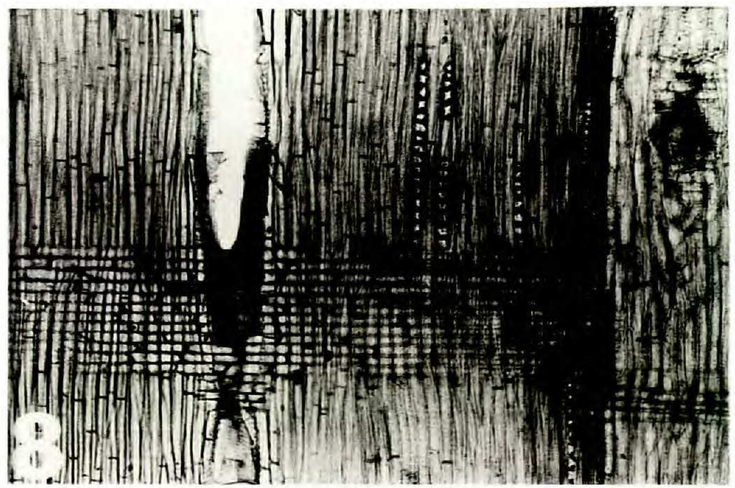
| | | | | |
|---|---|---|---|---|
| Klugiodendron[§] | 0.77 | -- | -- | -- |
| Macrosamanea[§] | 0.80 | -- | -- | -- |
| Marmaroxylon | 1.00 | Light brown with dark stripes | - or short + | Negative |
| Pithecellobium (sensu stricto) | 0.89 | Red-brown | - | Negative to v.p. yel. |
| Pseudosamanea | 0.58 | Red-brown | + | Bright yel. |
| Punjuba | 0.56 | Light yellow | + | Negative |
| Samanea | 0.52 | Dark brown | - or short + | Yel. to v.p. yel. |
| Zygia | 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, × 21; 6, *Ebenopsis flexicaulis* (MADw 25290), transverse section, pores and parenchyma occluded with amorphous compound, × 21; 7, *Albizia colombiana* (SJRw 22478), tangential section, rays 2 or 3 cells wide, septate fibers, alternate intervascular pitting, × 53; 8, *Havardia pallens* (MADw 18342), radial section, showing homogeneous procumbent rays, crystalliferous chains, and septate fibers, × 53.

vasicentric to aliform, rarely confluent; apotracheal parenchyma diffuse or sometimes forming marginal bands. Fibers mostly medium sized to moderately long, 948(–1193)–1680 μm., 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 μm. Vessel elements moderately short to mostly medium sized, 315(–376)–512 μm.; intervascular pitting mostly small, 6–8 μm., rarely medium sized (8–10 μm. in *A. tomentosa*), apertures sometimes coalescent. Rays 1 to 5 cells wide, mostly 2 to 4, rarely 1 or 2, 12(–37)–65 μm.; 20 or more cells high, 219(–405)–776 μm. 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 μm., 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 μm. Vessel elements mostly moderately short to medium sized, 252(–323)–436 μm.; intervascular pitting mostly small, 6–8 μm., apertures sometimes coalescent. Rays 1 to 5 cells wide, mostly 2 or more, 29(–38)–63 μm.; 20 or more cells high, 237(–371)–446 μm. 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 μm., 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 μm. Vessel elements extremely to moderately short, mostly very short, 164(–218)–266 μm.; intervascular pitting small, 6–7 μm., apertures sometimes coalescent. Rays mostly uniseriate, occasionally biseriate, 8(–12)–15 μm. wide (except *C. vinhatico*, where they are commonly 2 or 3 cells wide, or 27 μm.); average height 14 to over 20 cells, 148(–248)–359 μm. 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 μm., 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.; intervascular 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.; intervascular 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.; intervascular 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.; intervascular 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.; intervascular 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.; intervascular 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.) intervascular pits, and dark brown heartwood. The intervascular 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.) intervascular 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 intervascular 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.) intervascular pits, and red-brown heartwood. The presence of mostly uniseriate rays and the size of the intervascular 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.) intervascular 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.) intervascular 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 intervascular 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 intervascular 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, intervascular 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 intervascular 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 intervascular 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 intervascular 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 intervascular 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 Bentham 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 Bentham 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 Bentham's monograph.

In TABLE 4 the various wood types are aligned with the corresponding sections and series proposed by Bentham (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 Bentham 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* (Bentham) 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 Bentham proposed as sections and series.

The *Pseudosamanea, Arthrosamanea, Cojoba,* and *Ebenopsis* wood-types also contain some species known to Bentham. 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 |
|---|---|---|
| | Klugiodendron* | Section 3 Abaremotemo |
| Jupunba | Abarema | Section 4 Samanea |
| Samanea | Samanea | Series 1 Subarticulatae |
| Cojoba | Cojoba | Series 2 Carnosae |
| Albizia | Albizia† | |
| | Pseudosamanea | |
| | Arthrosamanea* | Series 4 Parviflorae |
| Chloroleucon | Chloroleucon | Section 7 Chloroleucon |
| Ebenopsis | Ebenopsis | |
| Havardia | Havardia | Section 5 Ortholobium |
| | Macrosamanea* | Section 4 Samanea |
| | | Series 3 Coriaceae |
| Pithecellobium | Pithecellobium | Section 1 Unguis-cati |
| Zygia | Zygia | Section 6 Caulanthon |
| | Marmaroxylon*† | |
| | Punjuba*† | |

* 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 Bentham (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, Bentham'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 Bentham, 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* Bentham, *P. elegans* Ducke, *P. fanshawei* Sandwith, *P. gonggrijpii* Kleinhoonte, *P. langsdorfii* Bentham, *P. leucophyllum* Spruce ex Bentham, *P. mataybifolium* Sandwith, *P. panurense* Spruce ex Bentham, *P. villiferum* Ducke, *Samanea corymbosa* (Rich.) Pittier, *S. leucocalyx* Britton & Rose, *S. macradenia* (Pittier) Britton & Rose, *S. marginata* (Spruce ex Bentham) 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* Bentham to *Chloroleucon*; *P. membranaceum* (Bentham) 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 intervascular 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).

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