Wood anatomy of tribe Detarieae and comparison with tribe Caesalpinieae (Leguminosae, Caesalpinioideae) in Venezuela

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Abstract: We studied the wood anatomy of 29 species belonging to 10 genera of the tribe Detarieae, subfamily Caesalpinioideae and compare them with tribe Caesalpinieae. Detarieae is the largest of four tribes of Caesalpinioideae, with 84 genera, only eleven occur in Venezuela with species of timber importance. The specimens were collected in Venezuela and include wood samples from the collection of the Laboratorio de Anatomía de Maderas de la Facultad de Ciencias Forestales y Ambientales de la Universidad de Los Andes, Venezuela, and of the Forest Products Laboratory of the USDA Forest Service in Madison, Wisconsin, USA. The terminology and methodology used followed the IAWA List of Microscopic Features for Hardwood Identification of the IAWA Committee, 1989. Measurements from each specimen were averaged (vessel diameters, vessel element lengths, intervessels pit size, fibre lengths and ray height). The species of Detarieae can be separated using a combination of diagnostic features. Wood characters that provide the most important diagnosis and may be used in systematics of Detarieae include: intercellular axial canals, rays heterocellular, rays exclusively or predominantly uniseriate, prismatic crystals common in ray cells, irregular storied structure and fibre wall thickness. For comparative anatomy between Detarieae and Caesalpinieae: intercellular axial canals, heterocellular rays, rays exclusively or predominantly uniseriate, prismatic crystals common in ray cells (in Detarieae) and regular storied structure, fibres septate, fibre wall thick or very thick, rays homocellular, multiseriate rays and silica bodies (in Caesalpinieae). Axial parenchyma is typically a good diagnostic feature for Leguminosae, but not for Detarieae and Caesalpinieae comparisons. Rev. Biol. Trop. 57 (1-2): 303-319. Epub 2009 June 30.

Key words: Leguminosae, Caesalpinioideae, Detarieae, Caesalpinieae, wood anatomy, identification.

The legume tribe Detarieae is the largest of four tribes of subfamily Caesalpinioideae, comprises 84 genera including approximately half of the genera of subfamily Caesalpinioideae. Most of these genera occur in tropical Africa, with a less diverse representation in tropical America and Asia (Barneby *et al.* 1998, Bruneau *et al.* 2000, Herendeen 2000, Gasson *et al.* 2003, Herendeen *et al.* 2003,). Only eleven genera of the Detarieae tribe are distributed in Venezuela (Barneby *et al.* 1998, Aristeguieta 2003). Wood anatomy study of the tribes, genera or species in the subfamily Caesalpinioideae that have attempted to identify important wood characters for taxonomic, systematic and properties of commercial timbers purposes include Reinders-Gouwentak (1955), Baretta-Kuipers (1981), Ranjani and Krishnamurthy (1988), Détienne and Welle (1989), Wheeler and Baas (1992), Nardi and Edlmann (1992), Gasson (1994), (1996), (1999), Höhn (1999), Herendeen (2000), Miller and Détienne (2001), Chauhan and Rao (2003), Gasson *et al.* (2003), Espinoza de Pernía and Melandri (2006a,b).

Some genera of the tribe Detarieae yield commercial timbers, particularly *Copaifera, Eperua, Hymenaea,* and *Peltogyne,* this last is known as "Purpleheart" high-quality wood

that is widely appreciated for its unusual color and resistance to insects (JUNAC 1981, INIA 1996, Barneby *et al.* 1998, Aristeguieta 2003). Others genera such as *Brownea* and *Dicymbe* are important ornamental trees, in gardens, city avenues and parks (Barneby *et al.* 1998, Aristeguieta 2003). Medicinal plants such as *Copaifera* are of high industrial value for their gum or balsam of Copaiba for medical treatments, manufacturing of varnishes and shellacs, and as a fixative of fragrances in soaps and perfumes. The *Elizabetha* genus yields a hallucinogenic drug, while *Hymenaea* genus is used for food and forage, medical treatments, canoe building and manufacturing of varnishes (Mabberley 1997, Barneby *et al.* 1998, Aristeguieta 2003). Some *Dicymbe*, *Eperua, Heterostemom* and *Macrolobium* species are endemic to the Venezuelan Guayana (Barneby *et al.* 1998).

This paper provides information about wood anatomy of native genera of the tribe Detarieae, that has not been adequately studied, and to compare them with the tribe Caesalpinieae (Espinoza de Pernía and Melandri 2006b). The microscopic wood anatomy of both tribes was studied because of its great importance in the timber industry and the complexity of its anatomy. The anatomical descriptions provide tools for the identification of the genera and groups within the tribe.

MATERIALS AND METHODS

Microscope slides from 70 wood samples representing 28 species from 10 genera the tribe Detarieae were examined (only 11 genera of the tribe are distributed in Venezuela: *Brownea, Copaifera, Crudia, Cynometra, Dicymbe, Elizabetha, Eperua, Heterostemon, Hymenaea, Macrolobium, Peltogyne*). The majority of the specimens were collected in Venezuela and includes specimens from the wood collection at the Laboratorio de Anatomía de Maderas de la Facultad de Ciencias Forestales y Ambientales de la Universidad de Los Andes, Mérida, Venezuela (MERw) and at the USDA Forest Service, Forest Products Laboratory, Madison, Wisconsin, USA (MADw and SJRw).

We followed the List of Microscopic Features for Hardwood Identification (IAWA Committee 1989) for terminology and methodology. The following characters were recorded for each specimen studied: presence/absence of growth rings, porosity, vessels distribution, intervessels pit size, vestured pits, fibre wall thickness, septate fibres, axial parenchyma patterns, number of the cells per axial parenchyma strand, ray size in height and width in cells, composition ray cell, storeyed structure, prismatic crystals, silica bodies, and axial canal, among others characters. Generic descriptions follow in alphabetical order and features not listed in the generic descriptions are either absent or do not apply. For vessel diameters, vessel element lengths, fibre lengths and ray height 25 measurements were taken from each specimen and averaged. The measurements are accurate only to the 10 um level, and are reported accordingly. The values reported [*e.g.* 30 (50–110) 150 μm], are minimum value, range of averages, and maximum value. For other quantitative values the most frequent range is reported. Photomicrographs were taken using a film camera with a light microscope.

RESULTS

Generic descriptions

Brownea Jacq. – Fig. 1 & 2

Growth rings distinct, marked by marginal parenchyma bands and/or thick-walled fibres. **Diffuse** porous. Vessels solitary and in radial multiples of 2-4, 3-17 per mm^2, 40(70-128)160 μm in diameter, 130(209-372)550 μm in element length. Simple perforation plates. Alternate intervessel pits circular or oval and polygonal, minute to small, 3-6 μm in diameter. Vessel-ray pits with distinct borders, similar to intervessel pits in size and shape, pits vestured. Brown gum-like deposits in vessels. **Fibres** non-septate, medium- to thick-walled, 700(908-1436)1680 μm in length. **Axial parenchyma** vasicentric (in *B coccinea*), aliform to

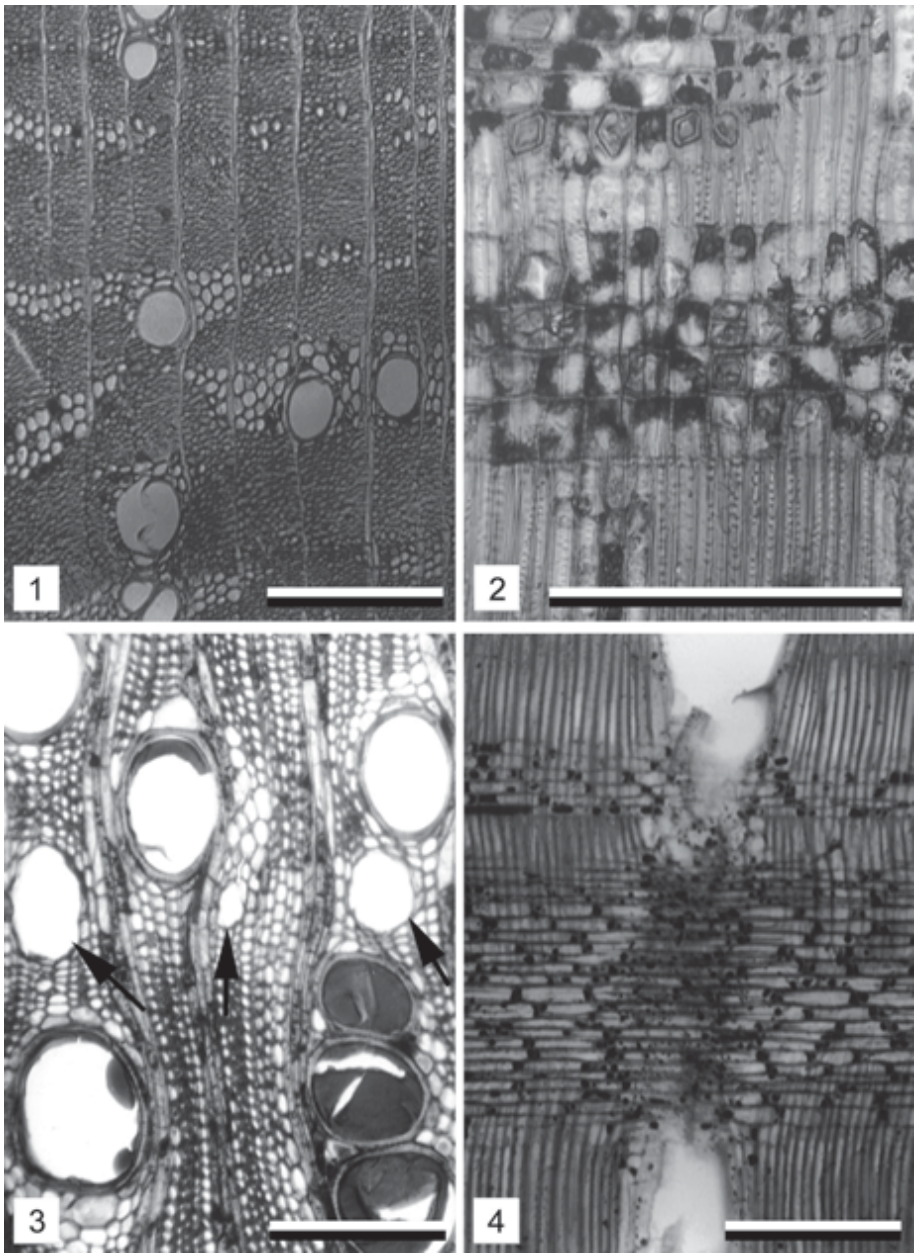

Fig. 1-4. (1 & 2): *Brownea* species.- 1: *B. coccinea,* aliform, confluent parenchyma.- 2: *B. grandiceps,* rays heterocellular and prismatic crystals in chambered ray cells.- 3 & 4: *Copaifera* species.- 3: *C. officinalis,* intercellular axial canals (arrow) in long tangential lines, brown gum-like deposits in vessels.- 4: *C. pubiflora*, homocellular rays composed of typically procumbent cells. Scale bars = 250 μm.

confluent in all species, aliform parenchyma of the lozenge type. Banded parenchyma of more than three cells wide in *B. grandiceps* and *B. macrophylla*. Marginal parenchyma bands present. Axial parenchyma 3-6 cells per parenchyma strand. *Rays* heterocellular with 1 to 2 rows of upright and/or square marginal cells, 9-20 per mm, exclusively (in *B. coccinea*) or mostly uniseriate (in *B. grandiceps, B. macrophylla*), 120(252-340)600 μm in height. **Prismatic crystals** common in ray cells (both upright and/or square and procumbent cells) and occasionally in short chains in axial parenchyma cells, one crystal per cell or chamber.

Material studied: 7 specimens, *B. coccinea* Jacq., MADw 32265, *B. grandiceps* Jacq., MADw 4835, MADw 4836, MADw 11163, MADw 14229, MADw 32266, *B. macrophylla* Hort. ex Mast., MERw 1277.

Copaifera L. – Fig. 3 & 4

Growth rings distinct, marked by marginal parenchyma bands. **Diffuse** porous. Vessels solitary and in radial multiples of 2-4, 3-8 per mm^2, 90(100-190)210 μm in diameter, 100(253-348)480 μm in element length. Simple perforation plates. Alternate intervessel pits small to medium, 6-10 μm in diameter. Vessel-ray pits with distinct borders, similar to intervessel pits in size and shape, pits vestured. Brown gum-like deposits in vessels. **Fibres** non-septate, medium-walled, 800(908-1264)1570 μm in length. **Axial parenchyma** vasicentric, aliform to confluent, aliform parenchyma of the lozenge type. Marginal parenchyma bands present. Axial parenchyma 2-4 cells per parenchyma strand. *Rays* mostly homocellular with typically procumbent cells to heterocellular, with 1 row of upright and/or square marginal cells, 6-8 per mm, 1 to 3 occasionally up to 4 cells wide, commonly less than 1 mm, to slightly more than 1 mm: 220(250-691)1050 μm in height. **Prismatic crystals** common in chains in axial parenchyma cells, one crystal per cell or chamber. **Intercellular canals axial** in long tangential lines and connecting or immersed in bands of marginal parenchyma, 60-170 μm in diameter.

Material studied: 13 specimens, *C. officinalis* (Jacq.) L., MERw 1533, MERw 1780, MERw 3297, MERw 5584, MERw 5585, MERw 5586, MERw 5587, MERw 5588, *C. pubiflora* Benth., MERw 4541, MERw 4542, MERw 4543, MERw 4544, MERw 4545.

Note: Metcalfe and Chalk (1950), Corothie (1967), Detienne *et al.* (1982), Richter and Dallwitz (2000) characterize the rays of *Copaifera* as homocellular (homogeneous), but Baretta-Kuipers (1981) described them as heterocellular. Additionally, JUNAC (1981) described homocellular rays *C. officinalis* and heterocellular rays in *C. pubiflora.* Mainieri and Chimelo (1989) report for *C.* cf. *langsdorffii* homocellular rays with tendency to heterocellular, and for *C.* cf. *reticulate,* heterocellular rays. Concerning fibres character JUNAC (1981), reports fibres partially septate, however, this feature was not observed in our specimens.

Cynometra L. – Fig. 5 & 6

Growth rings indistinct marked by marginal parenchyma bands. **Diffuse** porous. Vessels solitary and in radial multiples of 2-4; occasionally clusters; 9-16 per mm^2; 35(98-104)145 μm in diameter, 150(264-331)450 μm in element length. Simple perforation plates. Alternate intervessel pits minute to small, 3-7 μm in diameter. Vessel-ray pits with distinct borders, similar to intervessel pits in size and shape; pits vestured. Brown gum-like deposits in vessels. **Fibres** non-septate, thick-walled, 1050(1375-1605)1950 μm in length. **Axial parenchyma** aliform to confluent, aliform parenchyma of the lozenge type, occasionally unilateral. Banded parenchyma mostly in bands more than three cells wide. Marginal parenchyma bands occasionally present. Axial parenchyma 2-4 cells per parenchyma strand. **Rays** heterocellular with 1 to 2 rows of upright and/or square marginal cells, rarely up to 3 marginal rows, 8-16 per mm, 1 to 4 cells wide, 220(381-600)850 μm in height. **Prismatic crystals** common in upright and/or square ray cells and occasionally in short chains in

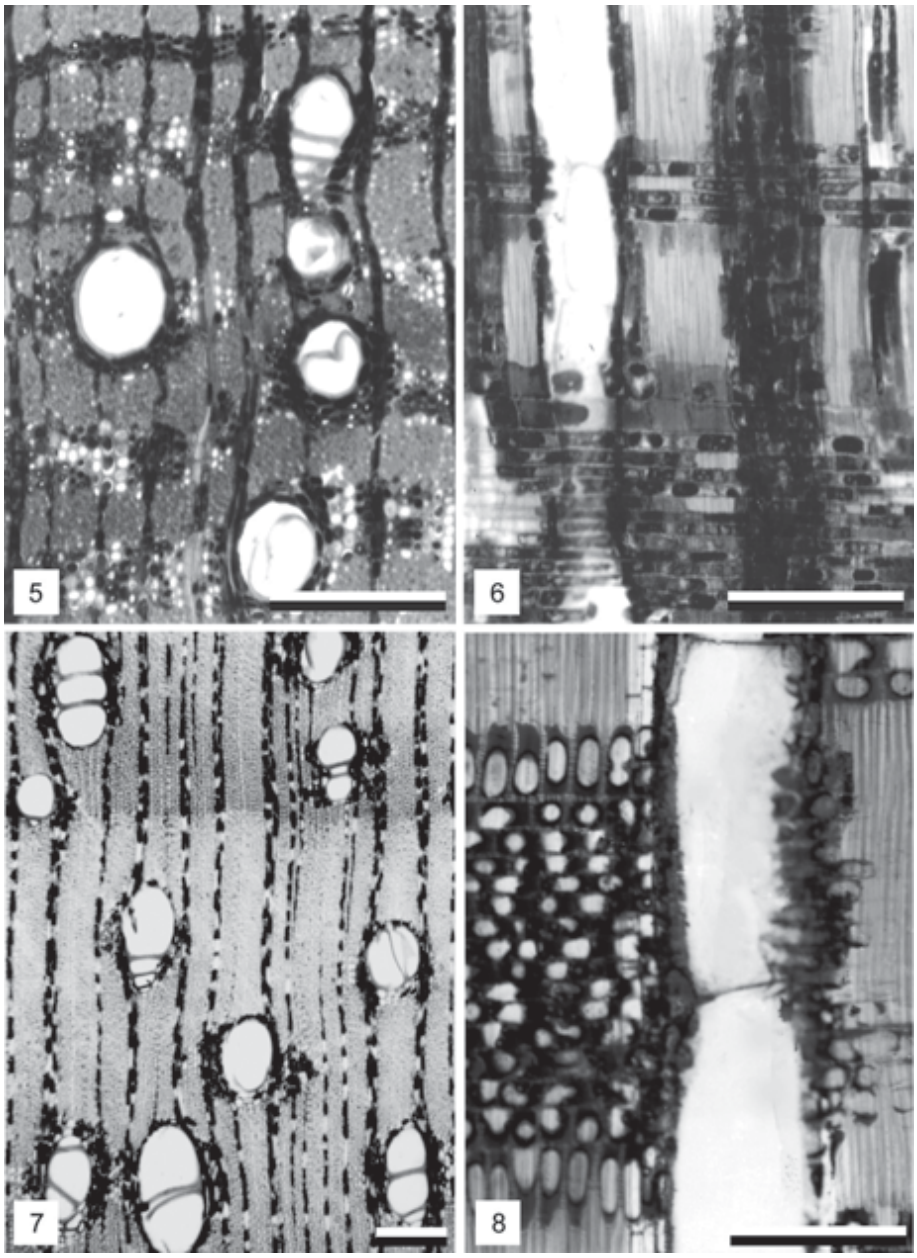

Fig. 5-8.- 5 & 6: *Cynometra spruceana* .- 5: bands of parenchyma more than three cells wide.- 6: rays heterocellular, 1-2 rows of upright and/or square cells.- 7 & 8: *Dicymbe bernardii*.- 7: growth rings distinct, aliform parenchyma.- 8: rays heterocellular, 1-2 rows of upright and/or square cells. Scale bars = 250 μm.

axial parenchyma cells, one crystal per cell or chamber.

Material studied: 3 specimens, *C. spruceana* Benth., MADw 32048; *C.* sp. L. MERw 2152, MERw 2233.

Note: Metcalfe & Chalk (1950) for *Cynometra* (except *C. ramiflora*) and Kribs (1968) for *C. alexandri* described the rays as homogeneous, but Baretta-Kuipers (1981); Richter & Dallwitz (2000) for *Cynometra* and Detienne et al. (1982) for *C. hostmanniana* and *C. parvifolia* described the rays as heterocellular.

Dicymbe Spruce ex Benth. – Fig. 7 & 8

Growth rings distinct, marked by marginal parenchyma bands and/or thick-walled fibres. **Diffuse** porous. Vessels solitary and in radial multiples of 2-5; sometimes up to 9; occasionally some clusters, 4-6 per mm^2; 80(121-150)210 μm in diameter, 200(307-327)520 μm in element length. Simple perforation plates. Alternate intervessel pits small, 4-6 μm in diameter. Vessel-ray pits with distinct borders, similar to intervessel pits in size and shape; pits vestured. Brown gum-like deposits in vessels. **Fibres** non-septate, thick- to very thick-walled, 800(918-1600)2000 μm in length. **Axial parenchyma** mostly aliform, aliform parenchyma of the lozenge type, vasicentric, confluent. Marginal parenchyma bands absent in MERw 239 and present in MADw 31798. Axial parenchyma 3-4 cells per parenchyma strand. **Rays** mostly homocellular with typically procumbent cells to heterocellular, with 1-4 rows of upright and/or square marginal cells, 8-14 per mm, mostly 1 to 2 cells wide (occasionally 3 cells wide), 100(275-706)930 μm in height. **Prismatic crystals** occasionally present in upright and/or square ray cells and in short chains in axial parenchyma cells, one crystal per cell or chamber.

Material studied: 2 specimens, *D. bernardii* R.S Cowan, MERw 239; *D.* sp. MADw 31798.

Note: Metcalfe & Chalk (1950) characterizes the rays of *Dicymbe* as homogeneous, but Baretta-Kuipers (1981) described the rays as heterocellular.

Elizabetha Schomburgk ex Benth. – Fig. 9 & 10

Growth rings distinct, marked by marginal parenchyma bands and/or thick-walled fibres. **Diffuse** porous. Vessels solitary and in radial multiples of 2-3, sometimes up to 5, occasionally some clusters, 5-10 per mm^2, 70(110-130)150 μm in diameter, 200(320-355)490 μm in element length. Simple perforation plates. Alternate intervessel pits small, 4-5 μm in diameter. Vessel-ray pits with distinct borders, similar to intervessel pits in size and shape, pits vestured. Brown gum-like deposits in vessels. **Fibres** non-septate, medium- to thick-walled, 950(1240-1365)1580 μm in length. **Axial parenchyma** aliform to confluent, aliform parenchyma of the lozenge type, occasionally vasicentric. Banded parenchyma mostly in bands 3-5 cells wide. Marginal parenchyma bands present. Axial parenchyma 3-4 cells per parenchyma strand. *Rays* heterocellular with 1 to 2 rows of upright and/or square marginal cells, 7-10 per mm, exclusively or mostly uniseriate, 110(220-230)420 μm in height. **Prismatic crystals** common in procumbent ray cells (occasionally in upright and/or square) and occasionally in short chains in axial parenchyma cells, one crystal per cell or chamber.

Material studied: 2 specimens, *E. princeps* Schomburgk ex Benth., MADw 31823, *E. macrostachya* Benth., MERw 5275.

Eperua Aublet. – Fig. 11 & 12

Growth rings distinct marked by marginal parenchyma bands. **Diffuse** porous. Vessels solitary and in radial multiples of 2-3, sometimes up to 8, occasionally some clusters, 3-13 per mm^2, 70(155-235) 300 μm in diameter, 200(364-436) 600 μm in element length. Simple perforation plates. Alternate intervessel pits circular or oval and poligonal, small to medium, 4-8 μm in diameter. Vessel-ray pits with distinct borders, similar to intervessel pits in size and shape, pits vestured. Brown

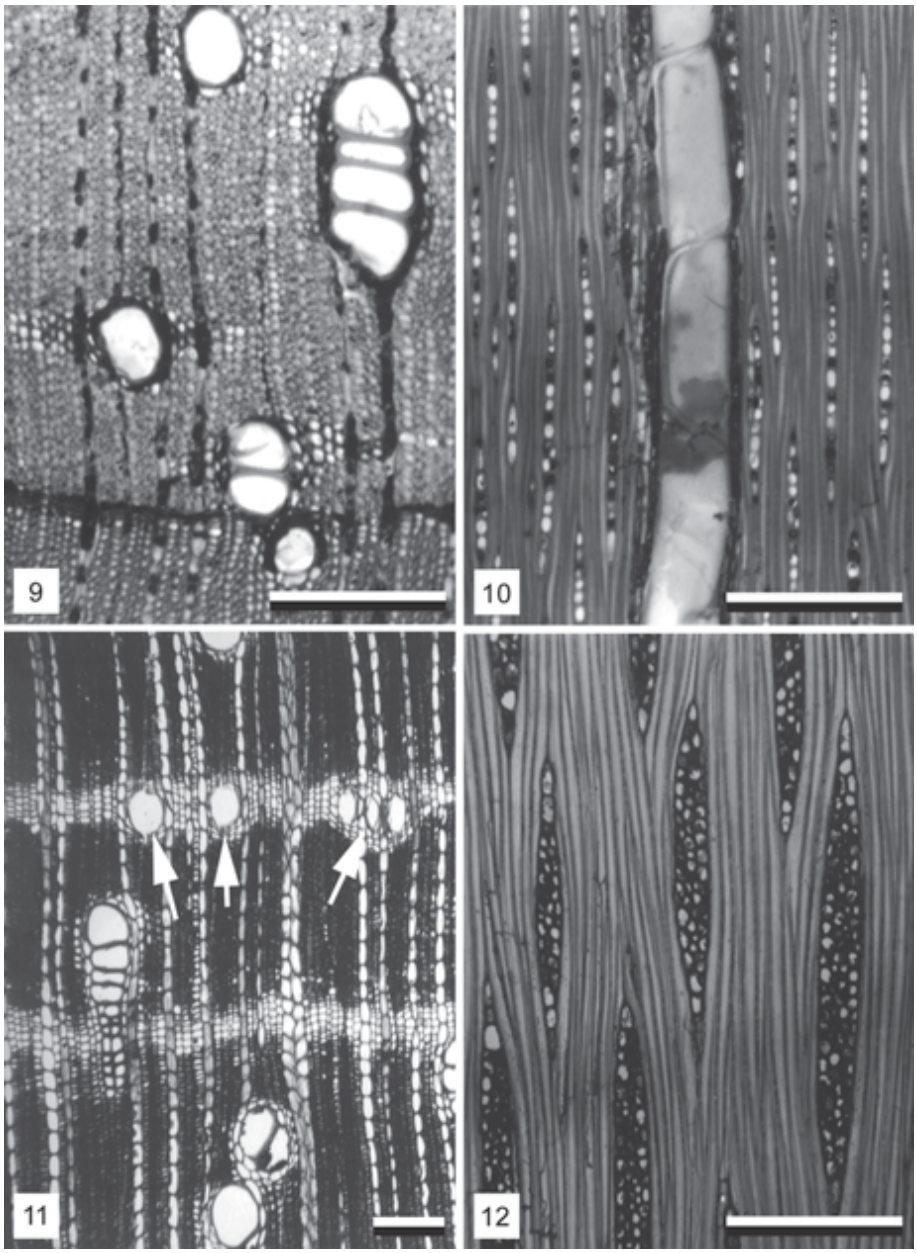

Fig. 9-12.- 9 & 10: *Elizabetha princeps*.-- 9: growth rings distinct, marked by thick-walled fibres and aliform parenchyma.- 10: rays exclusively uniseriate.-- 11 & 12: *Eperua* species.- 11: *E. leucantha,* intercellular axial canals (arrow), in long tangential lines and connecting or immersed in bands of marginal parenchyma.- 12: *E. purpurea,* rays mostly 3-4 wide cells. Scale bars = 250 μm.

gum-like deposits in vessels. **Fibres** non-septate, medium-walled, 970(1104-1459)1600 μm in length. **Axial parenchyma** scanty, vasicentric thin, sometimes diffuse-in-aggregates. Marginal parenchyma bands present. Axial parenchyma 3-4 cells per parenchyma strand. *Rays* heterocellular with 1 to 4 rows of upright and/or square marginal cells, 5-8 per mm, 1 to 4 cells wide, 180(200-510)750 μm in height. **Prismatic crystals** common in long chains in axial parenchyma cells, one crystal per cell or chamber. **Intercellular axial canals** in long tangential lines and connecting or immersed in bands of marginal parenchyma, occasionally diffuse (*E. purpurea*), 50-150 μm in diameter.

Material studied: 4 specimens, *E. grandiflora* (Aubl.) Benth., MERw 200, *E. leucantha* Benth., MERw 194, *E. purpurea* Benth., MERw 5273, MERw 5276.

Heterostemon Desf. – Fig. 13 & 14

Growth rings distinct, marked by marginal parenchyma bands and thick-walled fibres. **Diffuse** porous. Vessels solitary and radial multiples of 2-3, sometimes up to 5, occasionally some clusters, 7-15 per mm^2, 50(73-98)140 μm in diameter, 160(264-322)430 μm in element length. Simple perforation plates. Alternate intervessel pits circular or oval of them shape polygonal, minute to small, 3-6 μm in diameter. Vessel-ray pits with distinct borders, similar to intervessel pits in size and shape, pits vestured. Brown gum-like deposits in vessels. **Fibres** non-septate, medium- to thick-walled, 700(740-949)1240 μm in length. **Axial parenchyma** vasicentric, aliform to confluent, aliform parenchyma of the lozenge type. Banded parenchyma occasionally more than three cells wide in *H. conjugatus*. Marginal parenchyma bands present. Axial parenchyma 2-4 cells per parenchyma strand. *Rays* heterocellular with 1 to 4 rows of upright and/or square marginal cells, occasionally 5 in *H. conjugatus*, 7-17 per mm, exclusively or mostly uniseriate, 170(250-517)640 μm in height. **Prismatic crystals** not common, mostly present in procumbent ray cells, one crystal per cell or chamber.

Material studied: 6 specimens, *H. cauliflorus* Pittier, MADw 31929, MADw 31931, *H. conjugatus* Spruce ex Benth., MERw 5283, MADw 31932, MADw 31933, *H. mimosoides* Desf., MADW 31934.

Hymenaea L. – Fig. 15 & 16

Growth rings distinct, marked by marginal parenchyma bands and beside very thick-walled fibres in *H. oblongifolia.* **Diffuse** porous. Vessels solitary and radial multiples of 2-4, occasionally some clusters, 2-3 per mm^2, 90(132-202)300 μm in diameter, 160(238-354)520 μm in element length. Simple perforation plates. Alternate intervessel pits circular or oval, of them shape polygonal, small, 4-7 μm in diameter. Vessel-ray pits with distinct borders, similar to intervessel pits in size and shape, pits vestured. Reddish brown gum-like deposits in vessels. **Fibres** non-septate, thick- to very thick-walled, 1000(1340-1525)1890 μm in length. **Axial parenchyma** mostly aliform to confluent, aliform parenchyma of the lozenge type. Banded parenchyma of more than three cells wide in *H. courbaril* and *H. oblongifolia*. Marginal parenchyma bands present. Axial parenchyma 2-4 cells per parenchyma strand. *Rays* homocellular with typically procumbent cells (marginal cells sometimes slightly enlarged), 3-8 per mm, 1 to 6 cells wide, 110(192-450)650 μm in height. **Prismatic crystals** common in long chains in chambered axial parenchyma cells, one crystal per cell or chamber.

Material studied: 11 specimens, *H. courbaril* L., MERw 1507, MERw 3394, MERw 4564, MERw 4565, MERw 4566, MERw 4567, MERw 2489, *H. oblongifolia* Huber, MERw 2087, MERw 2533, MERw 2648, *H. parvifolia* Huber, MERw 2053.

Macrolobium Schreber. – Fig. 17 & 18

Growth rings distinct, marked by marginal parenchyma bands and/or thick-walled fibres. **Diffuse** porous. Vessels solitary and radial multiples of 2-3, sometimes up to 8, occasionally some clusters, 2-13 per mm^2, 60 (85-177)

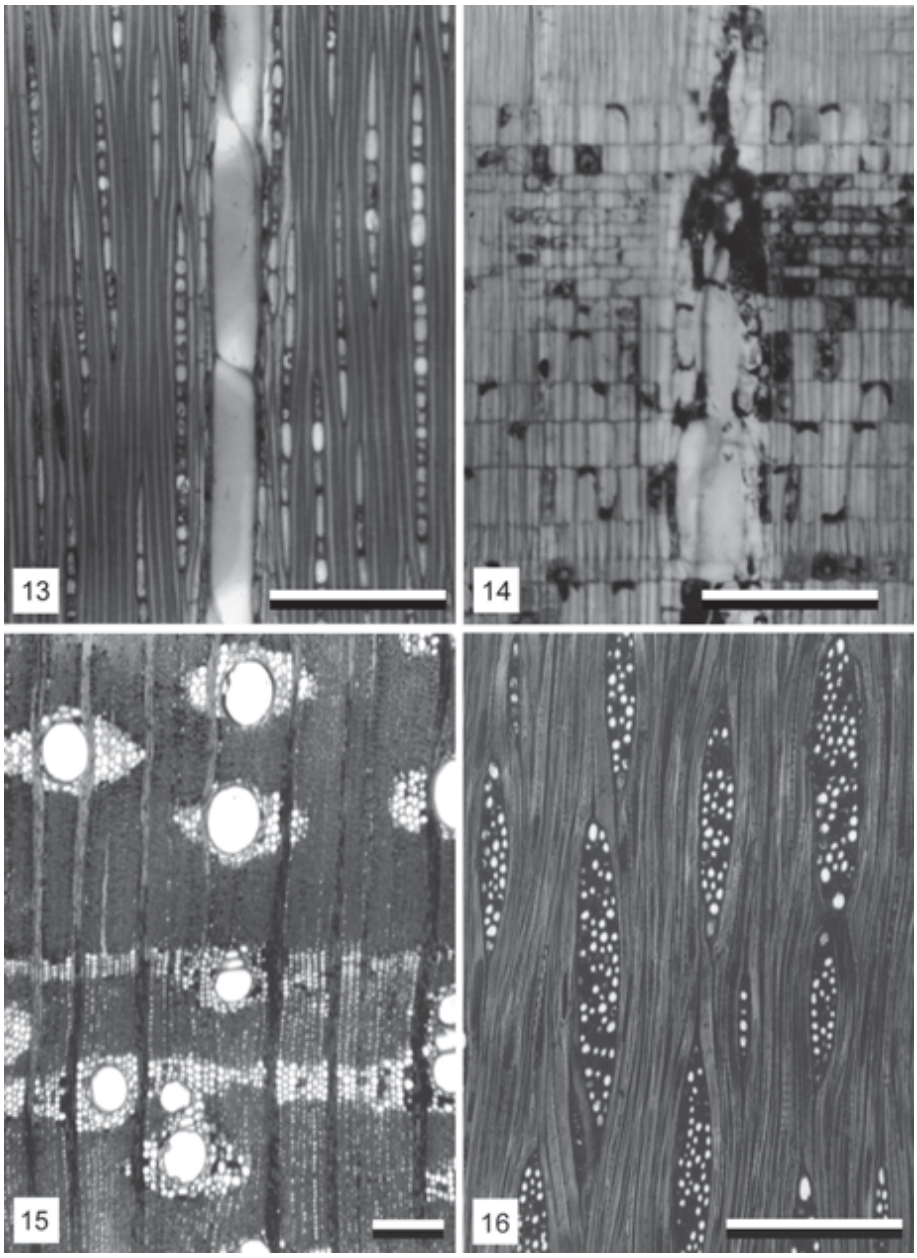

Fig. 13-16.- 13 & 14: *Heterostemon* species.- 13: *H. cauliflorus*, rays exclusively uniseriate.- 14: *H. conjugatus,* rays heterocellular, 2-4 rows of upright and/or square cells.- 15 & 16: *Hymenaea courbaril*- 15: aliform, confluent parenchyma and marginal banded.- 16: rays mostly 1-6 wide cells. Scale bars = 250 μm.

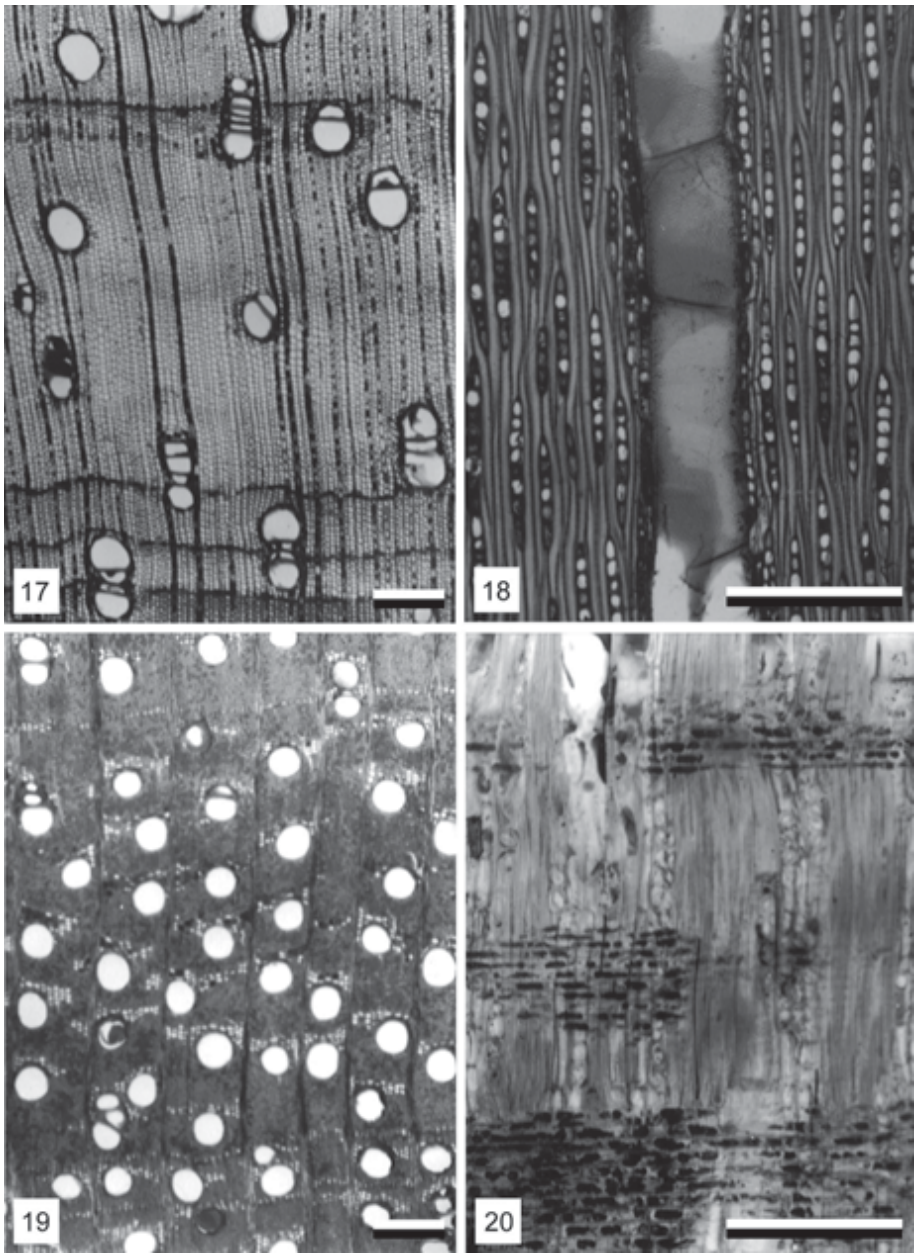

Fig. 17-20.- 17 & 18: *Macrolobium* species.- 17: *M. angustifolium,* growth rings distinct, marked by thick-walled fibres, vasicentric and aliform parenchyma.- 18: *M. molle,* rays mostly uniseriate.- 19 & 20: *Peltogyne* species.- 19: *P. paniculata,* aliform to confluent, unilateral parenchyma and banded parenchyma in narrow bands or lines, up to three cells wide.- 20: *P. porphyrocardia*, rays homocellular, composed of typically procumbent cells. Scale bars = 250 μm.

230 μm in diameter, 133 (236-439) 590 μm in element length. Simple perforation plates. Alternate intervessel pits circular or oval and polygonal, small, 5-8 μm in diameter. Vessel-ray pits with distinct borders, similar to intervessel pits in size and shape, pits vestured. Brown gum-like deposits in vessels. **Fibres** non-septate, thin-walled to thick-walled, 670(817-1765)2350 μm in length. **Axial parenchyma** vasicentric, aliform to confluent, aliform parenchyma of the lozenge type. Banded parenchyma of 2-4 cells wide. Marginal parenchyma bands present. Axial parenchyma 2-5 cells per parenchyma strand. *Rays* heterocellular with 1 to 2 rows of upright and/or square marginal cells (sometimes to 3), 9-20 per mm, exclusively or mostly uniseriate in *M. gracile, M. limbatum, M. molle* and *M. rubrum*, uniseriate and biseriate in *M. acaciifolium, M. angustifolium, M. multijugum* and *M. punctatum,* 100(220-390)650 μm in height. Storied structure not observed, only rays irregularly storied (rays in echelon) in *M. molle*. **Prismatic crystals** common in ray cells (both upright and/or square ray cells and procumbent cells) and occasionally in short chains in axial parenchyma cells in *M. angustifolium, M. gracile, M. limbatum, M. molle, M. multijugum* and *M. punctatum*. Prismatic crystals common in axial parenchyma cells and sporadic in ray cells in *M. acaciifolium* and *M. rubrum,* one to occasionally two crystals per cell or chamber.

Material studied: 15 specimens, *M. acaciifolium* (Benth.) Benth., MERw 2084, MERw 3374, MADw 14917, *M. angustifolium* (Benth.) Cowan, MADw 31604, MADw 31617, MADw 31620, *M. gracile* Spruce ex Benth., MADw 31611, *M. limbatum* Spruce ex Benth., MERw 2050, *M. molle* (Benth.) Cowan, MADw 14912, MADw 31613, MADw 31614, *M. multijugum* (DC.) Benth., MADw 31605, MADw 31612, *M. punctatum* Spruce ex Benth., MERw 2021, *M. rubrum* R.S Cowan, MADw 22398.

Peltogyne Vogel. – Fig. 19 & 20

Growth rings distinct, marked by marginal parenchyma bands in *P. paniculata* but absent in *P. floribunda.* **Diffuse** porous. Vessels solitary and in radial multiples of 2-3, sometimes up to 5, occasionally some clusters, 20-46 per mm^2, 50(60-120) 140 μm in diameter, 200 (260-390) 420 μm in element length. Simple perforation plates. Alternate intervessel pits circular or oval, of them shape polygonal, small to medium, 5-8 μm in diameter. Vessel-ray pits with distinct borders, similar to intervessel pits in size and shape, pits vestured. Reddish brown gum-like deposits in vessels. **Fibres** non-septate, very thick-walled, 860(1208-1700)1820 μm in length. **Axial parenchyma** mostly aliform to confluent, aliform parenchyma of the winged type, unilateral. Banded parenchyma in narrow bands or lines, up to three cells wide. Marginal parenchyma bands present in *P. paniculata*. Axial parenchyma 3-5 cells per parenchyma strand. *Rays* homocellular with typically procumbent cells, 5-10 per mm, 2 to 4 cells wide, 140(160-480)830 μm in height. Storied structure in axial parenchyma in *P. paniculata* and irregularly storied in axial parenchyma in *P. floribunda*. **Prismatic crystals** common in chains in chambered axial parenchyma cells, one crystal per cell or chamber. *Intercellular canals* of traumatic origin present in *P. floribunda*.

Material studied: 7 specimens, *P. paniculata* Benth., MERw 1760, MERw 2463, *P. floribunda* (Kunth) Pittier, MERw 1524, MERw 1771, MERw 4568, MERw 4569, MERw 4570.

Note: Metcalfe and Chalk (1950) mention tendencies to *s*toried axial parenchyma in some species of *Peltogyne.* This feature was also found in *P. floribunda* (= *P. porphyrocardia*) by JUNAC (1981), but is not mentioned by Corothie (1967) for the same specie and by

Detienne *et al.* (1982) and Nardi and Edlmann (1992) for *P. paniculata*. However, other species of the genus were described by Kribs (1968) for *P. densiflora*, Detienne *et al.* (1982) and Miller and Détienne (2001) for *P. venosa,* all with storied structure not observed.

DISCUSSION

All wood characters have been recorded, but only the most systematically and diagnostically important ones are displays in Table 1 and the following discussion. These characters emphasized the anatomical information to help in the identification of the species and genera of the Venezuelan Detarieae. Diagnostic features for reliable identification and potentially phylogenetically valuable information within the tribe Detarieae include: fibre wall thickness, ray composition, ray width, intercellular axial canals and storied structure, parenchyma type and prismatic crystals in ray cells. Quantitative features also vary (see Table 1), but most vary too much to be useful in identifications or comparisons. The exceptions are vessels per mm^2 (*e.g.* species of *Peltogyne*) ray width (*e.g.* species of *Hymenaea*) and intervessel pit size. Vessels per mm^2 and ray width are a good diagnostic quantitative character in these groups.

Comparison of Detarieae with Caesalpinieae

All legume woods have simple perforation plates, alternate intervessel pitting, vessel-ray pits similar to intervessel pits in size and shape, fibres with simple pits, vestured pits (with some exceptions) and in general axial parenchyma with mostly 2-4 cells per strand. In general, the species of the subfamily Caesalpinioideae have medium to thick fibre walls, aliform, confluent and marginal parenchyma, homocellular rays or with a row of square or upright marginals cells, biseriate rays non-storeyed and prismatic crystals in chambered axial parenchyma cells (Baretta-Kuipers 1981, Höhn 1999, Herendeen 2000, Gasson *et al.* 2003, Espinoza de Pernía and Melandri 2006a,b). While, the following wood characters provide the most systematically important characters between Detarieae and Caesalpinieae:

Fibres: septate only in *Schizolobium* (Caesalpinieae) and are absent in Detarieae genera. Usually thin to thick walled in Detarieae and thick and very thick in the most of Caesalpinieae.

Rays: there is considerable variation in ray cell composition and ray width between taxa. Homocellular rays are most common in Caesalpinieae, while in Detarieae, most common rays are heterocellular. Concerning width ray, in agreement with Metcalfe and Chalk (1950), Baretta and Kuipers (1981), Détienne and Welle (1989), Mainieri and Peres (1989), Miller and Détienne (2001) and Gasson *et al.* (2003), we observed in both tribes two groups: 1) Uniseriate (exclusively or predominantly) to biseriate rays in *Brownea, Elizabetha, Heterostemom, Macrolobium*, *Sclerolobium subbullatum* and *Tachigali.* 2) Multiseriate rays in *Caesalpinia, Campsiandra, Copaifera, Cynometra, Delonix regia, Dimorphandra, Dicymbe*, *Eperua, Hymenaea, Mora, Peltogyne* and *Schizolobium.*

Intercellular axial canals: the presence and distribution of axial canals is a good diagnostic and systematic character in Detarieae. They are found in long tangential lines and immersed in bands of marginal parenchyma in *Copaifera* and *Eperua* (Detarieae tribe), also reported and discussed by Barettta-Kuipers (1981), Détienne *et al.* (1982), Détienne and Welle (1989), Miller and Détienne (2001) and Gasson *et al.* (2003), occasionally diffuse in *Eperua purpurea*, absent in all Caesalpinieae genera.

Axial parenchyma in narrow bands uncommon in both tribes, however, common in C*aesalpinia coriaria, C. ebano* of Caesalpinieae tribe and *Macrolobium gracile, M. limbatum, M. molle, Peltogyne floribunda, P. paniculata* and occasionally in *Hymenaea oblongifolia* and *Macrolobium acaciifolium* of Detarieae tribe. Bands more than three cells wide in *Caesalpinia granadillo, C. sclerocarpa, Campsiandra, Dimorphardra cuprea*

TABLE 1
Synoptic table of anatomical features

Species studied	Growth rings	Vessels per mm^2	Intervessel pits size	Septate fibres	Fibres usually thin to thick walled	Fibres usually thick to very thick walled	Scanty parenchyma	Vasicentric parenchyma	Aliform parenchyma	Confluent parenchyma	Unilateral parenchyma	Parenchyma in narrow bands up to 3 cells wide	Parenchyma in bands more than 3 cells wide	Marginal parenchyma	N° cells per strand of parenchyma axial	Rays homocellular	Rays homocellular with slightly enlarged procumbent marginal cells	Rays heterocellular	Ray width	Storied structure, regular (R), Irregular (I)	Prismatic crystals: (A) in axial parenchyma cells, (B) in ray cells	Silica bodies	Intercellular axial canals
Brownea coccinea	•	7-17	3-5		•			•	•	•				•	3-6			•	1		+B, (A)		
B. grandiceps	•	4-12	3-5		•				•	•			•	•	3-4			•	1 (2)		+B, (A)		
B. macrophylla	•	3-5	3-6		•				•	•			•	•	3-4			•	1 (2)		+B, (A)		
Copaifera officinalis	•	3-8	8-10		•			•	•	•				•	2-4	•		(•)	1-3 (4)		A		•
C. pubiflora	•	6-7	6-8		•			•	•	•				•	3-4	•		(•)	1-3 (4)		A		•
Cynometra spruceana	(•)	9-11	3-5			•							•	(•)	2-4			•	1-4		+B, (A)		
Dicymbe bernardii	•	6-8	4-6		•			•	•	•					3-4			•	1-2 (3)		A, (B)		
Elizabetha macrostachya	•	7-10	4-5		•			•	•	•			•	•	3-4			•	1		+B, (A)		
E. princeps	•	5-8	4-5		•			•	•	•			•	•	3-4			•	1		+B, (A)		
Eperua grandiflora	•	4-13	4-7		•		•	•						•	3-4			•	1-3 (4)		A		•
E. leucantha	•	5-12	5-8		•			•						•	3-4			•	1-3 (4)		A		•
E. purpurea	•	3-10	6-8		•			•						•	3-4			•	1-4		A		•
Heterostemon cauliflorus	•	13-15	4-6		•			•	•		(•)			•	2-4			•	1		B		
H. conjugatus	•	7-13	3-6		•			(•)	•	•			(•)	•	2-4			•	1		B		
H. mimosoides	•	8-12	3-6		•			(•)	•	•				•	2-4			•	1		B		
Hymenaea courbaril	•	2-3	4-7			•			•	•			•	•	2-4	•	(•)		1-6		A		
H. oblongifolia	•	2-4	4-7			•			•	•		(•)	•	•	3-4	•	(•)		1-5		A		

TABLE 1
Synoptic table of anatomical features

Species studied	Growth rings	Vessels per mm^2	Intervessel pits size	Septate fibres	Fibres usually thin to thick walled	Fibres usually thick to very thick walled	Scanty parenchyma	Vasicentric parenchyma	Aliform parenchyma	Confluent parenchyma	Unilateral parenchyma	Parenchyma in narrow bands up to 3 cells wide	Parenchyma in bands more than 3 cells wide	Marginal parenchyma	N° cells per strand of parenchyma axial	Rays homocellular	Rays homocellular with slightly enlarged procumbent marginal cells	Rays heterocellular	Ray width	Storied structure, regular (R), Irregular (I)	Prismatic crystals: (A) in axial parenchyma cells, (B) in ray cells	Silica bodies	Intercellular axial canals
H. parvifolia	•	2-4	5-7			•			•	•				•	2-4	•	(•)		1-6		A		
Macrolobium acaciifolium	•	2-11	5-7		•			•	•	•		(•)	(•)	•	2-4			•	1-2		A, (B)		
M. angustifolium	•	4-13	4-7		•			•	•	•			•	•	4-5			•	1-2		A, B		
M. gracile	•	9-10	4-7		•				•	•		•	•	•	2-5			•	1		(A), (B)		
M. limbatum	•	3-5	5-7		•			•	•	•		•	(•)	•	2-4			•	1 (2)		A, B		
M. molle	•	5-11	5-6		•			•	•			•	•	•	2-5			•	1 (2)	I	B, (A)		
M. multijugum	•	4-12	5-7		•				•	•			•	•	3-4			•	1-2		A, B		
M. punctatum	•	2-4	5-7		•			•	•				•	•	2-4			•	1-2		B, (A)		
M. rubrum	•	6-10	5-7		•			•	•	•				•	2-4			•	1		A		
Peltogyne floribunda		36-46	5-8			•			•	•	•	•			3-5	•			2-4 +3	I	**A**		
P. paniculada	•	20-25	5-8			•			•	•	•	+•		•	3-4	•			2-4	R	A		

• = distinct feature; ( ) = occasionally distinct; + = predominantly distinct.

subsp. *ferruginea, D. davisii, Mora gonggrijpii,* of Caesalpinieae tribe and *Brownea grandiceps, B. macrophylla, Cynometra spruceana, Elizabetha, Hymenaea courbaril, H.oblongifolia, Magrolobium angustifolia, M. gracile, M. molle, M. multijugum, M. punctatum* of Detarieae tribe. Storeying in axial parenchyma in *P. paniculata* storied and *P. floribunda* irregularly storied, but rays never storied in Detarieae tribe. Storied structure in all the cell types only occurs in C*aesalpinia.*

Prismatic crystals are common in subfamily Caesalpinioideae, particularly frequent in axial parenchyma cells, however a of number important genera of the Detarieae tribe also have prismatic crystals common in ray cells, usually one crystal per cell or chamber: *Brownea, Cynometra, Dicymbe, Elizabetha, Heterostemon* and *Macrolobium* (except *M. rubrum*). This observation coincides with recorded by Détienne *et al.* (1982), Détienne and Welle (1989), Miller and Détienne (2001). *Silica* bodies only present in the tribe Caesalpinieae (*Tachigali* and *Sclerolobium* species), absent in all Detarieae studied, also discussed by Koeppen (1980), Barettta-Kuipers (1981) and Gasson *et al.* (2003).

Vessels per mm^2 of 2 to 10 in most species of Caesalpinieae and Detarieae tribes, however *Peltogyne* is very different, presents from 20 to 46 per mm^2. *Intervessel pit* size in most Caesalpinieae and Detarieae is commonly medium to large, while in *Brownea, Cynometra, Dimorphandra, Heterostemon* and *Mora,* there is a tendency towards minute to small.

Finally, in summary the diagnostic features important for identification of the tribe Detarieae and for comparison with Caesalpinieae are: intercellular axial canals, rays heterocellular, rays exclusively or predominantly uniseriate, prismatic crystals common in ray cells, storied structure, fibre wall thickness and absent of silica bodies. The interpretation of homocellular versus heterocellular rays in *Copaifera, Cynometra* and *Dicymbe* is not consistent in the literature with similar inconsistencies for the tribe Caesalpinieae (Espinoza de Pernía and Melandri 2006b). Therefore, this character may need to be re-examined in the wood of other legumes and possibly re-defined for use in keys and descriptions. In addition, the distribution of these diagnostic features in particular groups, often in agreement with phylogenies and also certain characters may have some relationship to ecological conditions (*e.g.* vessels per mm^2, intervessel pit size, axial parenchyma abundance and fibre wall thickness).

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RESUMEN

Se estudió la anatomía de la madera de 29 especies de 10 géneros de la tribu Detarieae, subfamilia Caesalpinioideae, enfocado hacia la identificación de la estructura de la madera y su comparación con la tribu Caesalpinieae. Los especímenes fueron recolectados en Venezuela y pertenecen a la colecciones de maderas del Laboratorio de Anatomía de Maderas de la Facultad de Ciencias Forestales y Ambientales de la Universidad de Los Andes, Mérida, Venezuela y del USDA Forest Service, Forest Products Laboratory, Madison, Wisconsin, USA. Las características anatómicas evaluadas siguen lo propuesto por IAWA List of Microscopic Features for Hardwood Identification (IAWA Committee 1989). Las especies de la tribu Detarieae pueden ser identificadas usando un número de características de diagnóstico combinadas: canales intercelulares longitudinales, radios heterocelulares exclusiva o predominantemente uniseriados, patrones del parénquima axial, cristales prismáticos en las células radiales, estructura estratificada y grosor de las paredes de las fibras. Estos caracteres también proporcionan una valiosa información para estudios sistemáticos y filogenéticos. Se presenta la descripción anatómica a nivel de género, una tabla sinóptica con los caracteres de diagnóstico principales y fotomicrografías de las características más importantes.

Palabras claves: Leguminosae, Caesalpinioideae, Detarieae, Caesalpinieae, anatomía de la madera, identificación.

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