Melandri, José Luis; Espinoza de Pernía, Narcisana
Wood anatomy of tribe Detarieae and comparison with tribe Caesalpinieae (Leguminosae, Caesalpinioideae) in Venezuela
Revista de Biología Tropical, vol. 57, núm. 1-2, marzo-junio, 2009, pp. 303-319
Universidad de Costa Rica
San Pedro de Montes de Oca, Costa Rica

Available in: http://www.redalyc.org/articulo.oa?id=44918836027
Wood anatomy of tribe Detarieae and comparison with tribe Caesalpinieae (Leguminosae, Caesalpinioideae) in Venezuela

José Luis Melandri1, 2 & Narcisana Espinoza de Pernía1
1. Laboratorio de Anatomía de Maderas, Facultad de Ciencias Forestales y Ambientales. Universidad de Los Andes, Mérida, Venezuela, melandri@ula.ve, nepernia@ula.ve
2. Author for correspondence: melandri@ula.ve


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.


Some genera of the tribe Detarieae yield commercial timbers, particularly Copaifera, Eperua, Hymenaea, and Pelogyne, 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, Heterostemon 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 Caesalpiniae (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, intervessel pit size, vested 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 μm 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 mm², 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 ve- stured. Brown gum-like deposits in vessels. Fibres non-septate, medium- to thick-walled, 700(908-1436)1680 μm in length. Axial parenchy- ma 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: *Copaefera* 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., MADw 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 mm², 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 vented. 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), Cotothie (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. langsдорffii* 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 mm²; 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 vented. 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 mm²; 80(121-150)210 μm in diameter, 200(307-327)520 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, thick- to very thick-walled, 800(918-1365)1600 μm in length. **Axial parenchyma** aliform to confluent, 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** 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, *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 mm², 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 mm², 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.


**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 2-4, occasionally some clusters, 2-3 per mm², 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 mm², 60 (85-177)
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: *Pelogyne* 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.


**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 mm², 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 storied 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 Pernia 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 subhullatum* 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 Baretta-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 *Caesalpinia 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, Dimorphandra cuprea*
<table>
<thead>
<tr>
<th>Species studied</th>
<th>Growth rings</th>
<th>Vessels per mm²</th>
<th>Intervessel pit size</th>
<th>Fibres usually thick to very thick walled</th>
<th>Fibres usually thin to thick walled</th>
<th>Intervessel pits size</th>
<th>Septate fibres</th>
<th>Unilaterial parenchyma</th>
<th>Marginal parenchyma</th>
<th>N’ cells per strand of parenchyma axial</th>
<th>Rays homocellular</th>
<th>Ray width</th>
<th>Storied structure, regular (R), Irregular (I)</th>
<th>Rays heterocellular</th>
<th>Prismatic crystals: (A) in axial parenchyma cells, (B) in ray cells</th>
<th>Silica bodies</th>
<th>Intercellular axial canals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brownea coccinea</td>
<td>? 7-17</td>
<td>3-5</td>
<td></td>
<td></td>
<td></td>
<td>3-6</td>
<td>1</td>
<td></td>
<td></td>
<td>!B, (A)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B. grandiceps</td>
<td>4-12</td>
<td>3-5</td>
<td></td>
<td></td>
<td></td>
<td>3-4</td>
<td>1 (2)</td>
<td></td>
<td></td>
<td>!B, (A)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B. macrophylla</td>
<td>4-5</td>
<td>3-5</td>
<td></td>
<td></td>
<td></td>
<td>3-4</td>
<td>1 (2)</td>
<td></td>
<td></td>
<td>!B, (A)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Copaifera officinalis</td>
<td>6-7</td>
<td>8-10</td>
<td></td>
<td></td>
<td></td>
<td>2-4</td>
<td>*</td>
<td>13 (4)</td>
<td>A</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. pulchiflora</td>
<td>6-7</td>
<td>6-8</td>
<td></td>
<td></td>
<td></td>
<td>3-4</td>
<td>*</td>
<td>13 (4)</td>
<td>A</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cynometra sprucea</td>
<td>9-11</td>
<td>3-5</td>
<td></td>
<td></td>
<td></td>
<td>(9)</td>
<td>1</td>
<td>4</td>
<td>!B, (A)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dicymbe bernardii</td>
<td>6-8</td>
<td>4-6</td>
<td></td>
<td></td>
<td></td>
<td>3-4</td>
<td>1 (2)</td>
<td>A</td>
<td>(B)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elizabetha macrostachya</td>
<td>7-10</td>
<td>4-5</td>
<td></td>
<td></td>
<td></td>
<td>3-4</td>
<td>1</td>
<td>!B, (A)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>E. princeps</td>
<td>5-8</td>
<td>4-5</td>
<td></td>
<td></td>
<td></td>
<td>3-4</td>
<td>1</td>
<td>!B, (A)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eperua grandiflora</td>
<td>4-13</td>
<td>4-7</td>
<td></td>
<td></td>
<td></td>
<td>3-4</td>
<td>1 (3)</td>
<td>A</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>E. leucantha</td>
<td>5-12</td>
<td>5-8</td>
<td></td>
<td></td>
<td></td>
<td>3-4</td>
<td>1 (3)</td>
<td>A</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>E. purpurea</td>
<td>3-10</td>
<td>6-8</td>
<td></td>
<td></td>
<td></td>
<td>3-4</td>
<td>1</td>
<td>!A</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Heterostemon caudiflorus</td>
<td>13-15</td>
<td>4-6</td>
<td></td>
<td></td>
<td></td>
<td>(9)</td>
<td>1</td>
<td>!B</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H. conjugatus</td>
<td>7-13</td>
<td>3-6</td>
<td></td>
<td></td>
<td></td>
<td>(9)</td>
<td>2</td>
<td>!B</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H. mimosoides</td>
<td>8-12</td>
<td>3-6</td>
<td></td>
<td></td>
<td></td>
<td>(9)</td>
<td>2</td>
<td>!B</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hymenaea courbaril</td>
<td>2-3</td>
<td>4-7</td>
<td></td>
<td></td>
<td></td>
<td>2-4</td>
<td>*</td>
<td>1</td>
<td>6</td>
<td>A</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H. oblongifolia</td>
<td>2-4</td>
<td>4-7</td>
<td></td>
<td></td>
<td></td>
<td>(9)</td>
<td>3-4</td>
<td>*</td>
<td>1</td>
<td>A</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species studied</td>
<td>Growth rings</td>
<td>Vessels per mm²</td>
<td>Intervessel pits</td>
<td>Septate fibres</td>
<td>Fibres usually thin to thick walled</td>
<td>Fibres usually thick to very thick walled</td>
<td>Unilateral parenchyma</td>
<td>Confluent parenchyma</td>
<td>parenchyma in narrow bands up to 3 cells wide</td>
<td>Parenchyma in bands more than 3 cells wide</td>
<td>Marginal parenchyma</td>
<td>N' cells per strand of parenchyma axial</td>
<td>Rays homogeneous, with slightly elongated procumbent marginal cells</td>
<td>Rays homogeneous</td>
<td>Rays scattered</td>
<td>Storied structure, regular (R), irregular (I)</td>
<td>Prismatic crystals (A) in axial parenchyma cells, (B) in ray cells</td>
</tr>
<tr>
<td>--------------------------------------</td>
<td>-------------</td>
<td>----------------</td>
<td>-----------------</td>
<td>---------------</td>
<td>-------------------------------------</td>
<td>-------------------------------------------</td>
<td>------------------------</td>
<td>---------------------</td>
<td>------------------------------------------------</td>
<td>------------------------------------------------</td>
<td>------------------</td>
<td>------------------------------------------</td>
<td>--------------------------------------------------------------------</td>
<td>--------------</td>
<td>----------------</td>
<td>------------------------------------------</td>
<td>--------------------------------------------------------------</td>
</tr>
<tr>
<td><strong>H. parvifolia</strong></td>
<td>* 2-4</td>
<td>5-7</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.4</td>
<td>(*)</td>
<td>1-2</td>
<td>* 1-6</td>
<td>* A</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Macrolobium acaciifolium</strong></td>
<td>* 2-11</td>
<td>5-7</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>( *)</td>
<td>(*)</td>
<td>2-4</td>
<td>* 1-2</td>
<td>A, (B)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>M. angustifolium</strong></td>
<td>* 4-13</td>
<td>4-7</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>4.5</td>
<td>( )</td>
<td>2-4</td>
<td>* 1-2</td>
<td>A, B</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>M. gracile</strong></td>
<td>* 9-10</td>
<td>4-7</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.5</td>
<td>( )</td>
<td>1</td>
<td>( A, (B)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>M. limbatum</strong></td>
<td>* 3-5</td>
<td>5-7</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>( *)</td>
<td>2-4</td>
<td>1 (2)</td>
<td>A, B</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>M. mollis</strong></td>
<td>* 5-11</td>
<td>5-6</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.5</td>
<td>( )</td>
<td>3-4</td>
<td>* 1-2</td>
<td>A, B</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>M. multiflorum</strong></td>
<td>* 4-12</td>
<td>5-7</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>3.4</td>
<td>( )</td>
<td>1-2</td>
<td>( A, B)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>M. paniculata</strong></td>
<td>* 2-4</td>
<td>5-7</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.4</td>
<td>( )</td>
<td>1-2</td>
<td>B, (A)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>M. rubrum</strong></td>
<td>* 6-10</td>
<td>5-7</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.4</td>
<td>( )</td>
<td>1</td>
<td>A</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Pelogyne floribunda</strong></td>
<td>36-46</td>
<td>5-8</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>3.5</td>
<td>( )</td>
<td>2-4</td>
<td>1 A</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>P. paniculata</strong></td>
<td>* 20-25</td>
<td>5-8</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>3.4</td>
<td>( )</td>
<td>2-4</td>
<td>R A</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* = distinct feature; ( ) = occasionally distinct; + = predominantly distinct.
subsp. ferruginea, D. davisi, Mora gong-grijpii, of Caesalpinieae tribe and Brownea grandiceps, B. macrophylla, Cynometra spruceana, Elizabetha, Hymenea 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 Caesalpinia.

**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, Dicymbie, 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 Caesalpinia (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 Dicyme 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).

**ACKNOWLEDGMENTS**

We thank Regis B. Miller, USDA Forest Service, Forest Products Laboratory, Madison, Wisconsin for helpful suggestions and also for providing the sectioning blocks of some materials studied. For the financial help we wish to thank C.D.C.H.T of the Universidad de Los Andes (Project: FO-392-96-01-B), Mérida, Venezuela.

**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 comunes: 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 filogénéticos. 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.
REFERENCES


