

## A SEARCH FOR PHYLOGENETICALLY INFORMATIVE WOOD CHARACTERS WITHIN LECYTHIDACEAE S.L.<sup>1</sup>

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The wood structure of 71 species representing 24 genera of the pantropical Lecythidaceae s.l., including the edible Brazil nuts (*Bertholletia excelsa*) and the spectacular cannon-ball tree (*Couroupita guianensis*), was investigated using light and scanning electron microscopy. This study focused on finding phylogenetically informative characters to help elucidate any obscure evolutionary patterns within the family. The earliest diverging subfamily Napoleonaeoideae has mixed simple/scalariform vessel perforations, scalariform vessel-ray pitting, and high multiseriate rays, all features that are also present in Scytopetaloidae. The wood structure of *Napoleonaea* is distinct, but its supposed close relative *Crateranthus* strongly resembles Scytopetaloidae. The isolated position of *Foetidia* (Foetidoidae) can be supported by a unique type of vessel-ray pitting that is similar in shape and size to intervessel pitting (distinctly bordered, <5 µm). The more derived Planchonioideae and Lecythidoideae share exclusively simple perforations and two types of vessel-ray pitting, but they can easily be distinguished from each other by the size of intervessel pitting, shape of body ray cells in multiseriate rays, and the type of crystalliferous axial parenchyma cells. The anatomical diversity observed is clearly correlated with differences in plant size (shrubs vs. tall trees): the percentage of scalariform perforations, as well as vessel density, and the length of vessel elements, fibers, and multiseriate rays are negatively correlated with increasing plant size, while the reverse is true for vessel diameter.

**Key words:** Ericales; Lecythidaceae s.l.; Lecythidaceae s.s.; Napoleonaeaceae; Scytopetalaceae; systematic wood anatomy.

Lecythidaceae s.l., including Napoleonaeaceae and Scytopetalaceae, comprise about 25 genera and 315 species. The family is represented by tall to small trees and shrubs largely distributed in the moist lowland neotropics, while other genera are restricted to tropical West and East Africa, Madagascar, Mauritius, and tropical Asia to North Australia (Appel, 2004; Prance, 2004; Prance and Mori, 2004). A main center of diversity is lowland Amazonia, in which the two most famous Lecythidaceae species grow: the Brazil nut (*Bertholletia excelsa* Humb. & Bonpl.), known for its edible seeds, and the spectacular cannon-ball tree (*Couroupita guianensis* Aubl.), which is commonly used as an ornamental plant in (sub)tropical gardens.

Although the family includes some well-known representatives, much more work is needed to clarify the controversial inter- and intrafamily relationships. With respect to its higher level classification, Lecythidaceae were previously placed close to Myrtaceae based on the shared occurrence of separate petals, numerous stamens, and a syncarpous inferior ovary with axile placentation (e.g., Miers, 1874). However, Lecythidaceae can be clearly distinguished from typical

Myrtales taxa based on their alternate leaves, bitegmic and tenuinucellar ovules, lack of intraxylary phloem and vested pits in wood, and a series of embryological features (see Prance and Mori, 1979 for a detailed taxonomic history; Jansen et al., 1998). These marked differences led Cronquist (1981) to the conclusion that Lecythidaceae must be removed from Myrtales (Rosidae) and included in an order of its own close to Theales and Malvales (both Dilleniidae). More recent morphological results (Tsou, 1994) and molecular sequence data (Morton et al., 1997; Anderberg et al., 2002; Schönenberger et al., 2005) support the Theales link and place the family in the enlarged Ericales sensu APG (APG II, 2003). Nevertheless, the search for the most closely related families of Lecythidaceae remains ongoing. Some recent molecular analyses hypothesize a sister relationship with Sapotaceae (Morton et al., 1997; Anderberg et al., 2002) or Ebenaceae (Bremer et al., 2002), but the most elaborate parsimony analysis based on 11 molecular markers places Lecythidaceae in a large polytomy together with the rest of the Ericales except for balsaminoids (Schönenberger et al., 2005). A Bayesian analysis of the same comprehensive data set results in a large tritomy including Lecythidaceae, Fouquieriaceae-Polemoniaceae, and the rest of the Ericales without balsaminoids (Schönenberger et al., 2005).

Following the family concept of Prance and Mori (1979), Lecythidaceae include 20 genera and four subfamilies, i.e., Lecythidoideae (neotropics), Foetidoidae (East Africa, Madagascar and Mauritius), Napoleonaeoideae (*Napoleonaea* and *Crateranthus* in tropical West Africa, *Asteranthos* in the neotropics) and Planchonioideae (Old World tropics). According to the embryological study of Tsou (1994), Lecythidoideae and Planchonioideae form the core group of Lecythidaceae, while Foetidoidae and Napoleonaeoideae should be segregated from it and recognized as separate families. Cladistic analyses based on morphological and molecular data further

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reveal that Scytopetalaceae (including *Asteranthos*) must be treated as a fifth subfamily in order to maintain the monophyly of the Lecythidaceae (Morton et al., 1997, 1998; APG II, 2003). The earliest diverging lineage is formed by Napoleonaeoideae followed by Scytopetaloidae (including *Asteranthos*), which is sister to a clade including Planchonioideae-Foetidioideae and Lecythidoideae (Morton et al., 1998). The inclusion of Scytopetalaceae into the enlarged Lecythidaceae agrees with general morphological resemblances, but both families can be easily distinguished from each other based on the presence/absence of stipules and endosperm, type of stomata, hypogynous vs. epigynous flowers, and the type of aestivation (Letouzey, 1961; Appel, 1996, 2004). According to Appel (1996, 2004), these distinctive characters provide sufficient arguments to split the diverse Lecythidaceae s.l. into three morphologically well-established families, i.e., Napoleonaeaceae (*Napoleonaea* and *Crateranthus*), Lecythidaceae s.s. (including subfamilies Foetidioideae, Planchonioideae, and Lecythidoideae), and the former Scytopetalaceae. The close relationships of these three evolutionary lines, however, have never been doubted (Prance, 2004; Prance and Mori, 2004).

The wood structure of Lecythidaceae has been the subject of several studies, although none of them intended to give an overview of all major lineages in the family. Most wood anatomical papers deal with neotropical representatives, i.e., Lecythidoideae plus *Asteranthos* (Diehl, 1935; Richter, 1982; D tienne and Jacquet, 1983; de Zeeuw and Mori, 1987; de Zeeuw, 1990). Carl de Zeeuw also started a detailed study of the Old World Foetidioideae, Napoleonaeoideae, and Planchonioideae, but unfortunately he passed away before completion of his work (de Zeeuw, [no date]a–f). In order to present a thorough overview of the entire family, we have chosen to evaluate de Zeeuw’s Old World descriptions and additional literature data (Moll and Janssonius, 1914; Pearson and Brown, 1932; Metcalfe and Chalk, 1950; Normand, 1960; Normand and Pacquis, 1976; Carlquist, 1988) in combination with original observations from all major lineages (Table 1, Appendix 1). In addition to the general descriptive wood studies, there are some papers on Lecythidaceae that focus on crystalliferous cells in the secondary xylem (Chattaway, 1956; ter Welle, 1976; Parameswaran and Richter, 1984).

The present work aims to present a detailed anatomical overview of the wood of the whole family in its widest sense. The species-diverse neotropical group may appear somewhat under-collected in our study, but this is amply compensated by detailed wood anatomical descriptions in the literature. The characters observed will be compared with the five subfamilies sensu Morton et al. (1998) in order to evaluate the evolutionary wood patterns and its taxonomic usefulness. We have chosen to focus our phylogenetic results on the subfamily level, because at this moment the current molecular framework has only strong support values at this taxonomic rank. Additional molecular data from *trnL-trnF* and *ndhF* regions support the basic Morton topology (Mori et al., 2007). A final objective is to correlate differences in wood structure with the huge variation in life forms (small shrubs vs. giant trees).

## MATERIALS AND METHODS

In total, 88 wood specimens of Lecythidaceae s.l. representing 71 species and 24 genera were investigated using LM and SEM (Appendix 1). Most samples were represented by mature sapwood, except for the juvenile twigs of

*Barringtonia macrostachya* Kurz (USw 1205) and *Grias peruviana* Miers (MADw 43463). The present paper presents the first detailed wood anatomical descriptions for the genera *Brazzeia*, *Oubanguia*, and *Pierrina* (Scytopetaloidae). No wood material could be obtained from *Abdulmajidia*, a small palaeotropical genus for which we have found no information in the literature.

The methodology of wood sectioning and the subsequent steps are described in Lens et al. (2005). The wood anatomical terminology follows the “IAWA list of microscopic features for hardwood identification” (IAWA Committee, 1989). This also applies for the terminology of crystalliferous axial parenchyma strands, except for the unusual wall thickenings that are not included in the IAWA list; these strands can be unilaterally thickened (only at one side that touches a neighboring fiber) or uniformly thickened (at all sides). Readers who are interested in a more specialized terminology of these strands may refer to Parameswaran and Richter (1984). When distinctly bordered vessel-ray pits are mentioned, we mean that the pit pairs are half-bordered, because the pit on the vessel side is bordered, but predominantly simple on the parenchyma cell side. Additional illustrations of microscopic wood pictures of Lecythidaceae can be found on the InsideWood website (<http://insidewood.lib.ncsu.edu/search>, micrographs taken by F. Lens).

To compare the observed wood diversity with habit, species are subdivided into three groups, i.e., shrubs to small trees growing in the understory (<25 m tall), canopy trees (25–35 m high), and giant emergent trees (up to 60 m) (cf. Mitchell and Mori, 1987; Mori and Lepsch-Cunha, 1995). Various floras and revisions were consulted to assign the species to one of the three groups (Perrier de la B thie, 1954; Letouzey, 1961; Payens, 1968; Liben, 1971; Mori and collaborators, 1987; Bosser, 1988; Mori and Prance, 1990), and all wood samples were taken into account, except for the two species with juvenile twigs. The statistical significance of differences in mean values of a given continuous wood character between the three habit categories was calculated using the software package Statistics Calculator version 8.0 (StatPac Inc., Bloomington, Indiana, USA).

## RESULTS

The material studied is described according to the subfamily classification of Morton et al. (1998). For each genus examined, the numerator represents the number of species studied and the denominator includes the total number of species. Numbers without parentheses are ranges of means, while numbers between parentheses represent minimum or maximum values. A summary of the results is shown in Table 1.

**Lecythidaceae-Napoleonaeoideae (*Crateranthus* 2/3, *Napoleonaea* 3/8; Figs. 1–10)**—Growth ring boundaries indistinct to absent (Figs. 1, 2). Diffuse-porous. Vessels (7–) 10–35 (–40)/mm<sup>2</sup>, mostly solitary and in radial multiples of 2–4 (–6) (Fig. 2), in *Napoleonaea* additional vessel clusters of 3–7 present (ranging from 5–40% of the total number of vessels) plus a few tangential multiples of 2–3 (Fig. 1); vessel outline rounded to elliptical; perforation plates in *Napoleonaea* usually simple but sometimes scalariform with 5–20 bars, exceptionally reticulate, in *Crateranthus* perforations plates equally mixed simple/scalariform with 1–12 (–21) bars (Fig. 5; Table 1). Intervessel pits alternate to opposite, pits 5–8  $\mu$ m (*Napoleonaea*) or 4–6  $\mu$ m (*Crateranthus*) in horizontal diameter, nonvestured. Vessel-ray pits in *Napoleonaea* typically scalariform (to opposite) with indistinct borders to even simple, pit borders 5–35  $\mu$ m in horizontal diameter, in co-occurrence with few smaller distinctly bordered pits often occurring in different ray cells (Fig. 6), pit borders 5–10  $\mu$ m in horizontal diameter; in *Crateranthus* scalariform vessel-ray pitting with strongly reduced borders (Fig. 7), pit cavities 15–55  $\mu$ m in horizontal diameter (up to 110  $\mu$ m in *Crateranthus talbotii*). Wall sculpturing absent. Tyloses occasionally present in both genera. Tangential diameter of vessels (30–) 50–100 (–130)  $\mu$ m, vessel elements (300–) 550 (–900)  $\mu$ m long in

*Napoleonaea*, and (300–) 1000 (–1600) in *Crateranthus*. Some vascentric tracheids present near vessel clusters in *Napoleonaea* (Fig. 8), (450–) 550–850 (–1200)  $\mu\text{m}$  long, occasionally co-occurring with tracheid-like elements with one small perforation. Nonseptate fibers (very few septa found in *C. talbotii*), with simple to minutely bordered pits concentrated in radial walls, thick- to very thick-walled in *Napoleonaea* but thin- to thick-walled in *Crateranthus*, (1700–) 2150 (–3000)  $\mu\text{m}$  long in *Napoleonaea* and (2000–) 2700 (–3200)  $\mu\text{m}$  in *Crateranthus*, pit borders 2–4  $\mu\text{m}$  in diameter. Axial parenchyma in *Napoleonaea* uniseriately banded (Fig. 1), diffuse-in-aggregates to uniseriately banded in *Crateranthus* (Fig. 2), in 3–10 celled strands. Uniseriate rays in *Napoleonaea* scarce to absent, 0–1 rays/mm, length (75–) 250 (–600)  $\mu\text{m}$ , consisting of square to upright cells; in *Crateranthus* uniseriate rays common, 4–6 rays/mm, length (200–) 750 (–2300)  $\mu\text{m}$ , consisting of square to upright cells. Multiseriate rays in *Napoleonaea* generally 5–10-seriate (Fig. 3), sometimes up to 17-seriate, (650–) 2100 (–5000)  $\mu\text{m}$  high, 1–5 rays/mm, consisting of procumbent and square body ray cells and 1–2 rows of upright to square marginal ray cells; in *Crateranthus* multiseriate rays 3–7-seriate (Fig. 4), (1200–) 2500 (>5000)  $\mu\text{m}$  high, consisting of generally procumbent body ray cells and more than four (up to 20) rows of upright to square marginal ray cells; sheath cells sometimes present in *Crateranthus*. Dark amorphous contents absent. Few solitary prismatic crystals in (sometimes chambered) marginal ray cells of *Crateranthus* and in body ray cells of *Napoleonaea* (Fig. 10), together with few small styloids in body ray cells of both genera; in *Crateranthus* integumented crystals abundantly present in chambered axial parenchyma cells with uniform wall thickenings (Fig. 9), in *Napoleonaea* prismatic crystals sometimes in nonchambered axial parenchyma cells without wall thickenings; silica bodies absent in both genera.

**Lecythidaceae-Scytopetaloidae** (*Asteranthos* 1/1, *Brazzeia* 2/3, *Oubanguia* 1/3, *Pierrina* 1/1, *Rhaptopetalum* 1/10, *Scytopetalum* 3/3; Figs. 11–28)—Growth ring boundaries often indistinct to absent, distinct in *Brazzeia* and *Pierrina* (Figs. 11, 12). Diffuse-porous. Vessels (2–) 5–60 (–70)/mm<sup>2</sup>, solitary or in radial multiples of 2–3 (Figs. 11–14), radial multiples up to six or even more in *Asteranthos* and *Pierrina*; vessel outline mostly rounded, sometimes slightly angular; perforation plates predominantly simple with few scalariform perforations in *Asteranthos* (3–12 bars), *Oubanguia* (3–7 bars; Fig. 18) and *Scytopetalum* (5–16 bars), and predominantly scalariform in *Brazzeia* (1–8 bars; Fig. 19), *Rhaptopetalum* (2–35 bars; Fig. 20), and *Pierrina* (2–12 bars) (Table 1). Intervessel pits generally alternate in *Oubanguia*, *Pierrina* and *Scytopetalum*, alternate to opposite in *Asteranthos*, *Brazzeia*, and *Rhaptopetalum* (Fig. 24), pits 6–10  $\mu\text{m}$  in horizontal diameter but 8–12  $\mu\text{m}$  in *Brazzeia*, nonvestured. Vessel-ray pits typically scalariform (to opposite) with distinctly bordered to (nearly) simple pits (Figs. 21, 22), pit cavities 10–20 (–50)  $\mu\text{m}$  in horizontal diameter, scalariform pits co-occur with infrequent smaller distinctly bordered pits usually in different ray cells (Fig. 23), pit borders 5–10  $\mu\text{m}$  in horizontal diameter; in *Asteranthos* scalariform to opposite pitting with strongly reduced borders. Wall sculpturing absent. Tyloses sometimes present in *Asteranthos* and *Scytopetalum*. Tangential diameter of vessels (20–) 30–160 (–210)  $\mu\text{m}$ , vessel elements (400–) 600–1050 (–1400)  $\mu\text{m}$  long. Tracheids absent.

Fibers generally nonseptate, but few septate fibers found in *Oubanguia*, fibers very thick-walled in *Asteranthos*, *Oubanguia*, and *Scytopetalum*, thin- to thick-walled in *Brazzeia*, *Pierrina*, and *Rhaptopetalum*; pits simple to minutely bordered and concentrated in radial walls, pit borders 2–3  $\mu\text{m}$  in diameter, but distinctly bordered pits in *Rhaptopetalum* (3–5  $\mu\text{m}$ ), and *Pierrina* (3  $\mu\text{m}$ ); fiber length (1400–) 1700–2800 (–3300)  $\mu\text{m}$ . Axial parenchyma diffuse-in-aggregates to narrowly banded (1 cell wide) in *Asteranthos*, *Brazzeia* (Fig. 12), *Pierrina* (Fig. 11), and *Rhaptopetalum* (Fig. 13), narrowly banded in *Oubanguia* and *Scytopetalum* (Fig. 14), additional vascentric parenchyma sometimes present in *Scytopetalum* (Fig. 14), banded marginal parenchyma of 2–6 cells wide in *Pierrina* and *Brazzeia* (Fig. 12); 5–14 cells per parenchyma strand. Uniseriate rays usually common (Figs. 15, 16), 3–10 rays/mm, but scarce in *Scytopetalum* (Fig. 17), (100–) 200–900 (–1900)  $\mu\text{m}$  long, consisting of square to upright cells. Multiseriate rays 2–4-seriate in *Asteranthos* (Fig. 15), 3–5-seriate in *Brazzeia*, *Oubanguia*, and *Scytopetalum* (Fig. 17), 5–7-seriate in *Pierrina* (Fig. 16), and 3–9 in *Rhaptopetalum*, (200–) 850–2500 (–4300)  $\mu\text{m}$  high, 2–10 rays/mm, consisting of almost exclusively procumbent body ray cells (Fig. 26) and more than four rows of square to upright marginal ray cells in *Asteranthos* (Fig. 15), *Oubanguia*, and *Rhaptopetalum*, 1–4 rows of upright marginal ray cells in *Scytopetalum*, and a variable number of rows in *Brazzeia* and *Pierrina* (Fig. 16); multiseriate rays sometimes fused; sheath cells absent. Dark amorphous contents in ray cells. Few prismatic crystals present in upright marginal ray cells (often chambered) of *Asteranthos*, *Brazzeia*, *Oubanguia*, and *Pierrina*, few small styloids present in body ray cells of *Brazzeia*; prismatic crystals always observed in chambered axial parenchyma with uniform wall thickenings (Figs. 27, 28), mostly confined to one or two cells per strand, often integumented; silica bodies absent.

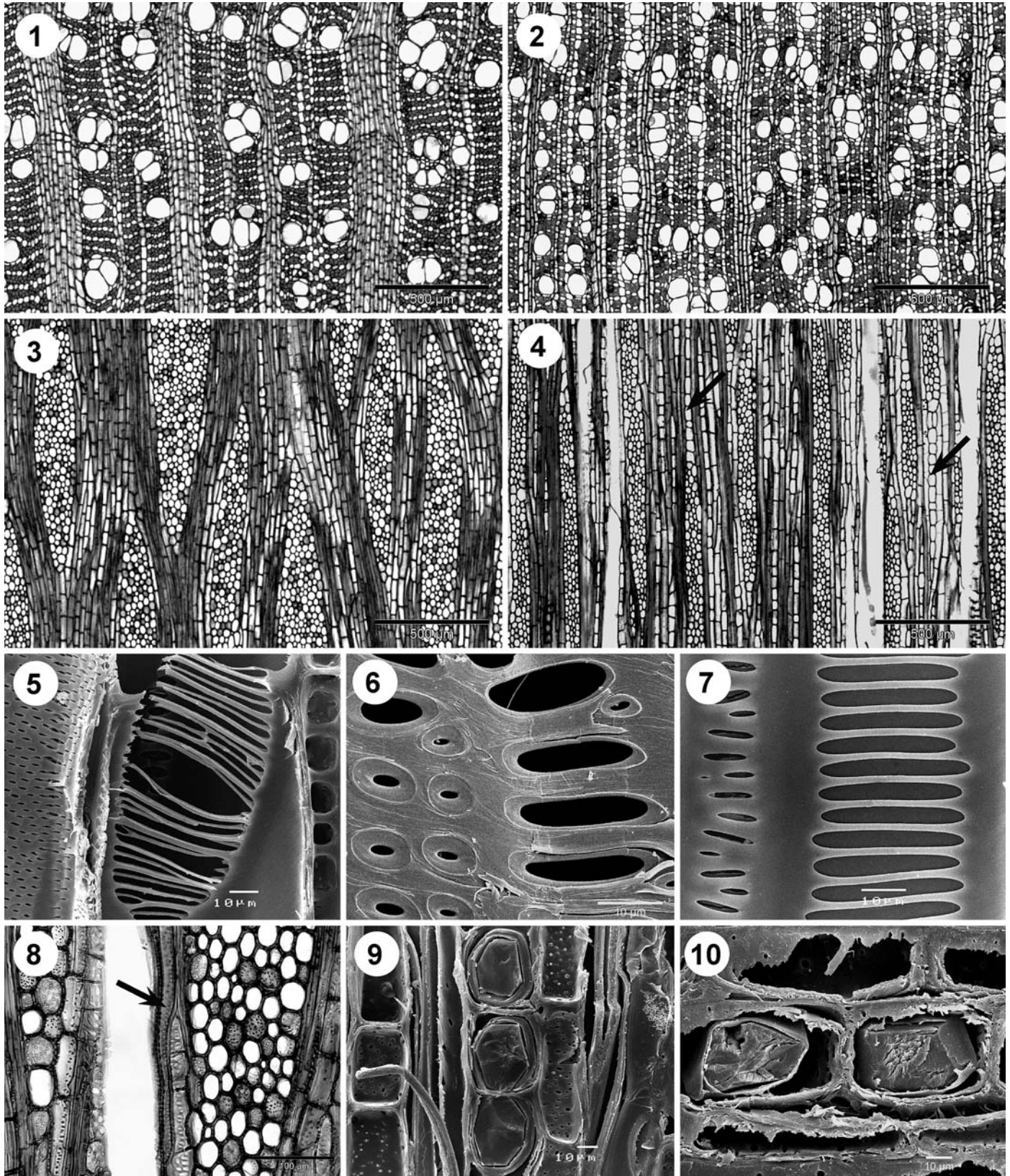
**Lecythidaceae-Foetidoidae** (*Foetidia* 1/17; Figs. 29–34)—Growth ring boundaries indistinct to distinct. Diffuse-porous, sometimes with a slight tendency to semi-ring-porosity. Vessels (15–) 20 (–30)/mm<sup>2</sup>, solitary or in radial multiples of 2–4 (Fig. 29); vessel outline rounded to elliptical; perforation plates simple. Intervessel pits alternate to sometimes opposite, pits 3–4  $\mu\text{m}$  in horizontal diameter, non-vestured. Vessel-ray pits similar to intervessel pits in shape and size (Fig. 31). Wall thickenings associated with pit apertures (coalescent or not; Fig. 33). Tyloses absent. Tangential diameter of vessels (30–) 70 (–100)  $\mu\text{m}$ , vessel elements (250–) 400 (–600)  $\mu\text{m}$  long. Tracheids absent. Fibers nonseptate with simple to minutely bordered pits concentrated in radial walls, thick- to very thick-walled, (700–) 1050–1350 (–1750)  $\mu\text{m}$  long, pit borders 2–3  $\mu\text{m}$  in diameter. Axial parenchyma narrowly banded, 1–2 cells wide (Fig. 29), sometimes also diffuse-in-aggregates, marginal parenchyma narrowly banded at beginning of growth ring; 2–7 cells per parenchyma strand. Uniseriate rays scarce (Fig. 30), 0–3 rays/mm, (50–) 100 (–250)  $\mu\text{m}$  high, consisting of square to procumbent ray cells. Multiseriate rays 2–4-seriate (Fig. 30), (100–) 250 (–400)  $\mu\text{m}$  high, 6–10 rays/mm, consisting of procumbent body ray cells 1–2 rows of square to upright marginal ray cells (Fig. 32); rays rarely fused; sheath cells absent. Dark amorphous contents in ray cells. Prismatic crystals absent in rays but present in uniformly thickened chambered axial parenchyma, often restricted to one cell per strand but sometimes filling the whole strand, crystals

TABLE 1. Overview of selected wood anatomical characters within Lecythidaceae s.l. Species are arranged alphabetically according to the subfamily classification of Morton et al. (1998). Numbers without parentheses are mean values, and numbers in parentheses represent exceptional values. For specimens of the same taxon, superscript numbers after the species name refer to the order of the specimens in the species list (see Appendix). HAB = habit (C = canopy, 25–35 m; U = understory, <25 m), SP = percentage of scalariform perforations, DIAM = tangential diameter of vessels ( $\mu\text{m}$ ), DENS = density of vessels ( $\text{mm}^2$ ), VEL = vessel element length ( $\mu\text{m}$ ), FL = fiber length ( $\mu\text{m}$ ), MRW = multiseriate ray width (no. of cells), HMR = height of multiseriate rays ( $\mu\text{m}$ ), DUR = density of uniseriate rays (mm), DMR = density of multiseriate rays (mm), PC = prismatic crystals, SIL = silica bodies; + = present, - = absent, ap = axial parenchyma cell, r = ray cell.

Species	HAB	SP	DIAM	DENS	VEL	FL	MRW	HMR	DUR	DMR	PC	SIL
<i>Crateranthus letestui</i> <sup>1</sup>	U	50	(40-) 70 (-90)	(20-) 26 (-32)	(500-) 945 (-1500)	(2000-) 2670 (-3100)	5-7	(1200-) 1790 (-2100)	4-5	2-5	ap, r	-
<i>C. letestui</i> <sup>2</sup>	U	60	(40-) 65 (-100)	(24-) 35 (-42)	(600-) 1130 (-1600)	(2250-) 2760 (-3200)	3-4 (-6)	(1500-) 2435 (-3700)	4-5	3-5	ap, r	-
<i>C. talbotii</i>	UC	40	(70-) 100 (-130)	(21-) 24 (-28)	(300-) 910 (-1400)	(2000-) 2610 (-3200)	5-7	1700->5000	4-6	2-4	ap, r	-
<i>Napoleonaea vogelii</i>	U	15	(30-) 65 (-90)	(7-) 12 (-17)	(300-) 500 (-750)	(1500-) 1940 (-2200)	5-9	(1400-) 2470 (-4800)	0-1	1-4	ap, r	-
<i>N. septentrionalis</i>	U	15	(30-) 50 (-80)	(14-) 18 (-22)	(400-) 680 (-900)	(2100-) 2465 (-3000)	(2) 5-10	(1100-) 2245 (-3150)	0-1	3-4	ap, r	-
<i>N. sp.</i> <sup>1</sup>	U	10	(30-) 80 (-120)	(8-) 13 (-25)	(300-) 455 (-650)	(1800-) 2340 (-2800)	5-15	(650-) 1520 (-2600)	0-1	2-4	-	-
<i>N. sp.</i> <sup>2</sup>	U	10	(40-) 75 (-100)	(10-) 13 (-16)	(350-) 595 (-800)	(1900-) 2340 (-2900)	(2) 5-10	(1000-) 2410 (-3900)	0-1	2-4	r	-
<i>N. vogelii</i> <sup>1</sup>	U	10	(60-) 80 (-110)	(7-) 12 (-17)	(350-) 545 (-700)	(1600-) 2010 (-2400)	6-17	(800-) 2020 (-5000)	0-1	3-5	r	-
<i>N. vogelii</i> <sup>2</sup>	U	10	(30-) 80 (-120)	(17-) 22 (-29)	(300-) 525 (-700)	(1700-) 1960 (-2300)	(2) 6-12	(1200-) 2020 (-2700)	0-1	2-4	r	-
<i>N. vogelii</i> <sup>3</sup>	U	20	(30-) 80 (-120)	(13-) 16 (-24)	(300-) 500 (-700)	(1700-) 2100 (-2600)	(2) 8-10	(600-) 1975 (-3700)	0-1	2-5	r	-
<i>Asteranthus brasiliensis</i> <sup>1</sup>	U	30	(60-) 80 (-90)	(31-) 34 (-40)	(550-) 860 (-1300)	(1500-) 1825 (-2200)	2-3	(900-) 1860 (-2800)	3-5	5-8	ap, r	-
<i>A. brasiliensis</i> <sup>2</sup>	U	20	(50-) 70 (-100)	(22-) 25 (-29)	(500-) 715 (-900)	(1400-) 1780 (-2100)	3-4	(900-) 1630 (-3000)	6-8	4-5	ap	-
<i>Brazzeia congoensis</i>	U	80	(50-) 75 (-100)	(15-) 19 (-24)	(550-) 820 (-1050)	(1700-) 2000 (-2300)	3-5 (-7)	(1300-) 1850 (-3300)	3-8	2-6	ap, r	-
<i>B. soyaxii</i>	U	95	(30-) 45 (-60)	(4-) 13 (-19)	(600-) 800 (-1100)	(1400-) 1810 (-2200)	(2) 3-4	(700-) 1150 (-1500)	5-6	6-10	ap	-
<i>Oubanguia africana</i>	UC	5	(60-) 95 (-120)	(11-) 15 (-19)	(500-) 950 (-1200)	(1900-) 2290 (-2800)	(2) 3-4 (-5)	(700-) 1125 (-2000)	1-3	6-8	ap	-
<i>O. sp.</i>	UC	10	(50-) 80 (-100)	(14-) 21 (-26)	(420-) 635 (-850)	(1650-) 1900 (-2250)	(2) 3-4 (-6)	(250-) 1880 (-4300)	2-4	5-7	ap, r	-
<i>Pierrina zenkeri</i>	U	95	(20-) 30 (-50)	(7-) 17 (-30)	(650-) 825 (-1100)	(1600-) 1730 (-1910)	(2) 5-7 (-9)	(400-) 1370 (-2500)	4-8	3-5	ap, r	-
<i>Rhaptopetalum begueti</i>	U	80	(40-) 70 (-90)	(48-) 57 (-70)	(500-) 860 (-1200)	(1500-) 1970 (-2200)	3-4	(800-) 1585 (-3500)	6-10	3-5	ap	-
<i>R. sp.</i>	U	85	(80-) 100 (-130)	(17-) 22 (-25)	(500-) 1050 (-1400)	(2300-) 2745 (-3200)	5-9	(1300-) 2435 (-3800)	3-7	2-3	ap	-
<i>Scytopetalum brevipes</i>	UC	10	(90-) 155 (-250)	(3-) 5 (-7)	(800-) 1030 (-1400)	(2100-) 2600 (-3200)	2-4 (-5)	(450-) 860 (-1350)	0-3	4-7	ap	-
<i>S. klaineanum</i>	UC	10	(120-) 160 (-180)	(4-) 6 (-7)	(450-) 610 (-750)	(2000-) 2830 (-3300)	(2) 3-4 (-5)	(950-) 1645 (-3200)	0-1	6-8	ap	-
<i>S. iteghemii</i> <sup>1</sup>	UC	20	(65-) 145 (-210)	(2-) 5 (-7)	(650-) 845 (-1150)	(2100-) 2450 (-2800)	(2) 3-4	(500-) 1070 (-2300)	0-1	7-9	ap	-
<i>S. iteghemii</i> <sup>2</sup>	UC	15	(70-) 110 (-140)	(7-) 9 (-10)	(600-) 920 (-1250)	(1700-) 2185 (-2600)	(2) 3-4	(200-) 1010 (-1800)	0-1	5-6	ap	-
<i>Foetidia mauritiana</i> <sup>1</sup>	U	0	(50-) 70 (-100)	(17-) 23 (-28)	(280-) 430 (-580)	(1000-) 1360 (-1750)	2-3	(150-) 260 (-350)	0-1	6-9	ap	r
<i>F. mauritiana</i> <sup>2</sup>	U	0	(30-) 65 (-90)	(14-) 19 (-25)	(250-) 380 (-600)	(700-) 1075 (-1400)	(2) 3 (-4)	(100-) 250 (-400)	0-3	6-10	ap	r
<i>Barringtonia acutangula</i>	U	0	(70-) 95 (-120)	(11-) 15 (-19)	(450-) 585 (-750)	(2100-) 2340 (-2700)	3-5	(700-) 1200 (-1700)	0-1	5-7	r	-
<i>B. asiatica</i>	U	0	(80-) 120 (-170)	(2-) 5 (-7)	(550-) 610 (-750)	(2550-) 2710 (-3100)	4-5	(400-) 715 (-900)	0-5	3-8	ap, r	-
<i>B. edulis</i>	U	0	(60-) 90 (-130)	(10-) 13 (-18)	(400-) 515 (-600)	(1500-) 1970 (-2300)	4-7	(700-) 1580 (-2500)	0-2	4-6	-	-
<i>B. lanceolata</i>	U	0	(60-) 120 (-180)	(8-) 11 (-14)	(600-) 700 (-1200)	(2200-) 2690 (-3100)	(2) 3-4	(600-) 1820 (-4000)	0-2	4-6	-	-
<i>B. longisepala</i>	U	0	(90-) 130 (-170)	(7-) 9 (-12)	(400-) 590 (-700)	(1900-) 2370 (-2800)	(2) 3-4 (-6)	(850-) 1520 (-2300)	1-3	4-7	r	-
<i>B. macrostachya</i> <sup>1</sup>	U	0	(70-) 150 (-240)	(3-) 6 (-9)	(500-) 690 (-950)	(3200-) 3625 (-4300)	(2) 4-6	(800-) 2090 (-3800)	0-2	5-8	r	-
<i>B. macrostachya</i> <sup>2</sup>	U	5	(30-) 70 (-100)	(28-) 40 (-70)	(350-) 530 (-800)	(1600-) 1920 (-2300)	3-4 (-5)	(800-) 1340 (-2200)	6-8	1-3	r	-
<i>B. pauciflora</i>	U	0	(80-) 120 (-160)	(5-) 7 (-12)	(400-) 610 (-800)	(1700-) 2110 (-2700)	4-6	(1000-) 1640 (-3300)	0-2	5-8	r	-
<i>B. procera</i>	U	0	(60-) 90 (-100)	(10-) 14 (-22)	(450-) 580 (-700)	(2000-) 2515 (-3100)	(2) 3-5 (-6)	(450-) 710 (-1000)	0-1	5-7	r	-
<i>B. samoensis</i>	U	0	(40-) 75 (-140)	(15-) 20 (-26)	(300-) 590 (-750)	(2000-) 2450 (-2800)	(2) 3-4 (-5)	(600-) 1390 (-4700)	1-3	6-9	r	-
<i>B. scortechinii</i>	U	0	(80-) 115 (-150)	(9-) 12 (-14)	(400-) 550 (-750)	(2000-) 2370 (-2800)	(2) 3-5	(1000-) 1640 (-3200)	0-3	6-9	r	-
<i>B. speciosa</i>	U	0	(50-) 85 (-120)	(1-) 5 (-9)	(350-) 440 (-550)	(1600-) 1995 (-2300)	(2) 4-6	(200-) 600 (-950)	0-3	5-6	r	-
<i>B. spicata</i>	U	0	(60-) 105 (-160)	(16-) 22 (-27)	(300-) 450 (-580)	(2000-) 2740 (-3300)	5-7	(250-) 1125 (-2900)	0-2	5-8	r	-
<i>Careya arborea</i>	C	0	(30-) 115 (-190)	(3-) 7 (-9)	(600-) 680 (-800)	(2000-) 2605 (-3200)	(2) 3-4	(350-) 790 (-1400)	0-2	9-10	ap, r	-
<i>Chydenanthus excelsum</i>	UC	0	(75-) 140 (-180)	(4-) 6 (-10)	(500-) 690 (-850)	(1900-) 2285 (-2700)	(2) 3-4	(350-) 1460 (-4000)	1-2	6-9	ap, r	-
<i>Peterianthus macrocarpus</i>	C	0	(70-) 140 (-190)	(8-) 11 (-15)	(700-) 1080 (-1350)	(1700-) 2545 (-3100)	(2) 3-4	(250-) 970 (-1400)	0-2	6-8	r	-
<i>P. quadrilobus</i>	C	0	(130-) 165 (-240)	(2-) 6 (-8)	(350-) 600 (-850)	(2100-) 2430 (-2900)	(2) 4-6	(450-) 800 (-1450)	0-2	4-7	-	ap, r
<i>Planckonia andamanica</i>	E	0	(110-) 150 (-200)	(8-) 10 (-14)	(600-) 780 (-1000)	(1600-) 2200 (-2500)	2-3	(250-) 625 (-1250)	1-3	7-10	ap, r	-
<i>P. papuana</i>	E	0	(60-) 125 (-160)	(5-) 7 (-10)	(400-) 550 (-850)	(1500-) 1900 (-2300)	2-4	(250-) 645 (-1100)	0-3	8-10	r	-
<i>P. spectabilis</i>	E	0	(80-) 115 (-180)	(4-) 7 (-9)	(350-) 570 (-850)	(1900-) 2290 (-3000)	(2) 3-4	(200-) 575 (-1250)	2-5	5-8	r	-
<i>P. timorensis</i>	E	0	(70-) 140 (-180)	(6-) 10 (-15)	(600-) 710 (-900)	(1650-) 2300 (-3000)	(2) 3-4	(550-) 910 (-1800)	0-3	7-10	ap, r	-
<i>P. valida</i>	E	0	(120-) 175 (-250)	(7-) 9 (-11)	(350-) 595 (-750)	(1700-) 2090 (-2400)	(2) 3 (-4)	(500-) 1085 (-1650)	0-3	7-9	ap, r	-
<i>Allantoma lineata</i> <sup>1</sup>	UC	0	(40-) 80 (-130)	(3-) 6 (-11)	(250-) 505 (-700)	(900-) 1220 (-1400)	2 (-3)	(200-) 305 (-500)	4-8	2-6	ap	r

TABLE 1. Continued.

Species	HAB	SP	DIAM	DENS	VEL	FL	MRW	HMR	DUR	DMR	PC	SIL
<i>A. lineata</i> <sup>2</sup>	UC	0	(30-) 70 (-100)	(2-) 6 (-10)	(350-) 510 (-750)	(1000-) 1260 (-1700)	2	(350-) 430 (-650)	4-8	3-4	ap	r
<i>Bertholletia excelsa</i>	E	0	(150-) 210 (-300)	(2-) 4 (-5)	(400-) 435 (-500)	(1300-) 1615 (-2050)	(2-) 3-4	(300-) 550 (-1200)	0-1	6-9	ap	-
<i>Cariniana decandra</i>	CE	0	(100-) 150 (-220)	(2-) 4 (-7)	(400-) 555 (-750)	(1500-) 1750 (-2100)	2 (-3)	(200-) 315 (-500)	1-3	7-10	ap	-
<i>C. micrantha</i>	E	0	(80-) 195 (-270)	(2-) 4 (-6)	(400-) 530 (-700)	(1100-) 1515 (-1900)	2-3	(250-) 420 (-600)	0-1	7-11	ap	r
<i>C. multiflora</i>	E	0	(40-) 90 (-140)	(0-) 4 (-6)	(450-) 580 (-800)	(1050-) 1520 (-1900)	2 (-3)	(150-) 340 (-500)	0-2	7-10	ap	r
<i>C. pyriformis</i>	E	0	(130-) 175 (-310)	(2-) 6 (-9)	(300-) 515 (-650)	(1300-) 1650 (-2200)	2-3	(200-) 390 (-500)	0-2	5-8	ap	r
<i>Corythophora alba</i>	C	0	(70-) 120 (-150)	(3-) 6 (-8)	(400-) 490 (-650)	(1050-) 1560 (-1900)	2	(150-) 325 (-500)	2-6	5-7	ap	-
<i>C. anapaensis</i>	C	0	(60-) 120 (-190)	(2-) 5 (-8)	(300-) 430 (-600)	(900-) 1180 (-1400)	2-3	(250-) 305 (-400)	0-1	7-10	ap	-
<i>C. rimosa</i>	C	0	(60-) 120 (-150)	(3-) 7 (-11)	(300-) 535 (-750)	(1200-) 1450 (-1900)	2 (-3)	(50-) 430 (-700)	1-4	7-9	ap	r
<i>Couratari guianensis</i>	E	0	(70-) 160 (-230)	(1-) 4 (-8)	(450-) 600 (-750)	(1150-) 1445 (-1650)	2-3	(250-) 550 (-1200)	0-1	5-8	ap	r
<i>C. guianensis</i>	E	0	(40-) 90 (-130)	(1-) 5 (-8)	(400-) 505 (-600)	(1200-) 1480 (-1700)	2-3 (-4)	(500-) 870 (-1300)	0-3	4-8	ap	r
<i>C. macrosperma</i>	E	0	(60-) 165 (-260)	(0-) 1 (-3)	(430-) 550 (-750)	(1100-) 1540 (-2000)	(2-) 3-4	(150-) 535 (-1050)	0-2	4-6	ap	r
<i>C. multiflora</i>	C	0	(110-) 175 (-270)	(2-) 4 (-6)	(250-) 490 (-750)	(1400-) 1620 (-2050)	(2-) 3-4 (-5)	(400-) 690 (-1300)	0-1	7-10	ap	r
<i>C. scottmori</i>	CE	0	(100-) 140 (-180)	(1-) 5 (-7)	(400-) 550 (-650)	(1300-) 1920 (-2250)	2-3	(400-) 600 (-1000)	0-1	6-8	ap	r
<i>Couroupita guianensis</i> <sup>1</sup>	C	0	(35-) 95 (-150)	(3-) 4 (-6)	(400-) 580 (-800)	(1500-) 1925 (-2200)	2-3	(250-) 510 (-900)	0-3	5-8	ap	-
<i>C. guianensis</i> <sup>2</sup>	C	0	(70-) 140 (-220)	(1-) 4 (-8)	(300-) 460 (-600)	(1400-) 1665 (-2200)	2-4 (-5)	(200-) 400 (-1000)	0-2	6-11	ap	-
<i>C. nicaraguensis</i>	E	0	(50-) 180 (-270)	(0-) 3 (-6)	(400-) 565 (-700)	(1500-) 1800 (-2200)	2-4	(250-) 720 (-1850)	0-2	6-10	ap	-
<i>C. subsessilis</i> <sup>1</sup>	E	0	(100-) 185 (-240)	(0-) 2 (-4)	(400-) 665 (-1100)	(1600-) 1900 (-2200)	2-3	(350-) 1120 (-2300)	0-1	8-11	ap	-
<i>C. subsessilis</i> <sup>2</sup>	E	0	(130-) 235 (-320)	(0-) 3 (-5)	(450-) 530 (-700)	(1600-) 2190 (-2600)	2-3 (-4)	(250-) 960 (-2400)	0-1	6-9	ap	-
<i>Eschweilera amazonica</i>	U	0	(50-) 85 (-130)	(3-) 9 (-16)	(350-) 540 (-700)	(1150-) 1590 (-2000)	2 (-3)	(200-) 630 (-1200)	0-3	8-10	-	r
<i>E. calyculata</i>	E	0	(60-) 90 (-120)	(3-) 6 (-9)	(300-) 580 (-750)	(1600-) 1820 (-2100)	2	(200-) 620 (-550)	1-3	8-10	ap	r
<i>E. gigantea</i>	E	0	(110-) 160 (-260)	(3-) 5 (-8)	(350-) 515 (-700)	(1700-) 2150 (-2800)	2-3	(400-) 670 (-1200)	0-1	7-9	ap	r
<i>E. sclerophylla</i>	UC	0	(50-) 85 (-120)	(3-) 6 (-9)	(450-) 540 (-650)	(1200-) 1580 (-2000)	2	(300-) 490 (-700)	6-10	1-4	ap	r
<i>Grias cauliflora</i> <sup>1</sup>	UC	0	(50-) 85 (-120)	(8-) 12 (-18)	(300-) 490 (-700)	(1900-) 2415 (-3000)	(2-) 3-5	(650-) 990 (-1700)	0-1	5-7	ap, r	-
<i>G. cauliflora</i> <sup>2</sup>	UC	0	(100-) 125 (-150)	(7-) 8 (-9)	(400-) 540 (-700)	(2000-) 2540 (-2950)	4-6	(500-) 1090 (-1950)	0-1	3-5	ap	-
<i>G. colombiana</i>	U	20	(40-) 100 (-190)	(8-) 18 (-28)	(500-) 600 (-750)	(1700-) 2160 (-2800)	(2-3-) 5-8	(500-) 1660 (-3600)	0-2	3-4	ap, r	-
<i>G. neuberthii</i>	U	5	(70-) 105 (-150)	(9-) 16 (-31)	(400-) 620 (-850)	(1400-) 2290 (-2800)	(6-) 8-12	(1200-) 1785 (-2500)	0-1	2-4	ap	-
<i>G. peruviana</i> <sup>1</sup>	UC	10	(20-) 75 (-110)	(22-) 32 (-49)	(350-) 525 (-600)	(2000-) 2495 (-2900)	(2-) 4-6	(450-) 2520 (-5100)	0-2	3-5	ap, r	-
<i>G. peruviana</i> <sup>2</sup>	UC	70	(25-) 75 (-120)	(20-) 29 (-35)	(500-) 750 (-1000)	(1900-) 2370 (-2700)	3-4	(700-) 2020 (-4000)	0-2	4-5	ap, r	-
<i>Gustavia augusta</i>	U	0	(30-) 60 (-90)	(20-) 29 (-35)	(480-) 550 (-700)	(1800-) 2160 (-2450)	(2-3-) 4-5	(350-) 890 (-1650)	0-2	3-6	r	-
<i>G. gigantea</i>	U	0	(50-) 90 (-120)	(9-) 12 (-16)	(400-) 715 (-1000)	(2400-) 2840 (-3100)	(2-) 5-8	(1800-) 2765 (-4100)	0-2	2-3	ap	-
<i>G. poeppigiana</i>	U	0	(30-) 50 (-70)	(26-) 43 (-54)	(500-) 590 (-800)	(1900-) 2265 (-2600)	(2-3-) 4-6	(700-) 1480 (-3000)	1-3	3-6	ap, r	-
<i>G. cf. pulchra</i>	U	0	(30-) 60 (-80)	(3-) 7 (-12)	(400-) 515 (-700)	(1400-) 1940 (-2400)	(2-) 3	(350-) 670 (-1150)	0-2	5-8	ap	-
<i>Lecythis ampla</i>	E	0	(50-) 150 (-240)	(3-) 7 (-12)	(350-) 465 (-600)	(1500-) 1725 (-2000)	2-3	(200-) 535 (-1250)	0-2	6-8	ap	r
<i>L. confertiflora</i>	C	0	(100-) 150 (-250)	(1-) 4 (-7)	(300-) 480 (-600)	(1100-) 1410 (-1800)	2 (-3)	(200-) 500 (-950)	0-2	8-10	ap	r
<i>L. corrugata</i>	C	0	(40-) 65 (-110)	(6-) 8 (-14)	(180-) 350 (-450)	(1150-) 1470 (-1950)	2-3	(150-) 260 (-450)	2-4	6-9	ap	r
<i>L. lurida</i>	E	0	(60-) 160 (-240)	(1-) 4 (-8)	(200-) 440 (-550)	(1550-) 1800 (-2300)	2-6	(550-) 1060 (-1900)	0-1	5-6	ap	-
<i>L. mesophylla</i>	E	0	(60-) 115 (-170)	(1-) 3 (-5)	(400-) 555 (-800)	(1700-) 2095 (-2400)	(2-) 3-4	(450-) 740 (-1150)	0-1	5-8	ap	r
<i>L. turyana</i>	E	0	(120-) 260 (-370)	(2-) 3 (-5)	(450-) 505 (-700)	(1600-) 2080 (-2500)	2-3 (-4)	(400-) 570 (-1150)	0-1	7-11	ap	r
<i>L. zabucajo</i>	E	0	(60-) 165 (-250)	(6-) 7 (-10)	(300-) 475 (-700)	(1300-) 1470 (-1750)	2-3	(250-) 390 (-750)	0-1	6-9	ap	r



Figs. 1–10. Wood anatomical sections (LM; Figs. 1–4, 8) and surfaces (SEM; Figs. 5–7, 9, 10) of Napoleonaeoideae. **1.** *Napoleonaea vogelii* MADw 41120: transverse section (TS), vessel grouping variable ranging from solitary to radial and tangential multiples or clusters, axial parenchyma uniseriately banded. **2.** *Crateranthus letestui* CTFw 8603: TS, vessels solitary or in radial multiples of 2–3, axial parenchyma diffuse-in-aggregates to short uniseriate

sometimes integumented (Fig. 32); silica bodies present throughout the ray and in axial parenchyma cells (Fig. 34).

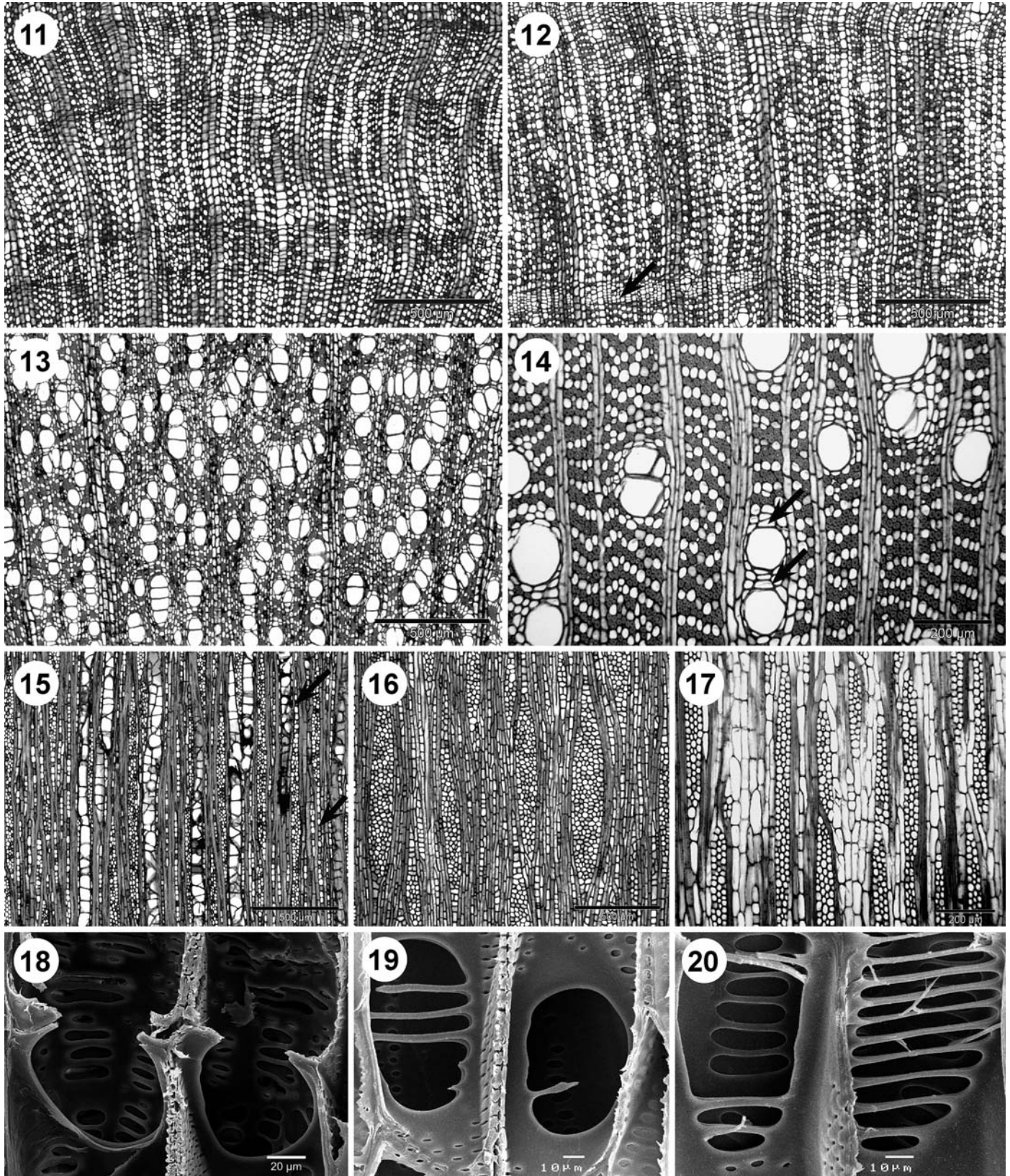
**Lecythidaceae-Planchonioideae** (*Barringtonia* 12/41, *Careya* 1/4, *Chydenanthus* 1/1, *Petersianthus* 2/2, *Planchonia* 5/8; Figs. 35–46)—Growth ring boundaries generally indistinct. Diffuse-porous. Vessels (2–) 5–20 (–30)/mm<sup>2</sup>, solitary or in radial multiples of 2–3 (Figs. 35–37), sometimes up to 6 in *B. edulis*, exceptionally in clusters of 3–5 in *B. asiatica* and *B. lanceolata*; vessel outline rounded to elliptical; perforation plates exclusively simple, but few scalariform perforations present in *B. macrostachya* (1–4 bars). Intervessel pits predominantly alternate (Fig. 41) to slightly opposite, pits 6–10 µm in horizontal diameter in *Planchonia*, 10–12 µm in *Careya*, 10–15 µm in *Chydenanthus*, 12–16 µm in *Petersianthus*, up to 20 µm in *Barringtonia*, nonvestured. Two types of vessel-ray pits present, often in different ray cells and more or less equally abundant: (1) round to oval pits with reduced borders to even simple (pits sometimes also elongated horizontally, diagonally, vertically, or irregularly), pit cavities usually 10–25 µm in diameter but sometimes up to 60 µm, (2) smaller distinctly bordered pits (comparable to intervessel pitting, but often somewhat smaller) (Figs. 42, 43). Wall sculpturing absent. Tyloses present in all genera, sometimes with large prismatic crystals in *Barringtonia*. Tangential diameter of vessels (30–) 70–170 (–250) µm, vessel elements (300–) 450–1100 (–1350) µm long. Tracheids absent. Septate fibers sometimes observed in *Planchonia andamanica*, *P. spectabilis*, and *P. valida*, fibers with simple to minutely bordered pits concentrated in radial walls, thick-walled fibers in *Careya*, wall thickness variable in the other genera, (1600–) 1900–3600 (–4300) µm long, pit borders 2–3 µm in diameter; sometimes gelatinous in *Barringtonia* and *Petersianthus*. Axial parenchyma in *Planchonia* (Fig. 35) and *Careya* diffuse-in-aggregates to narrowly banded (one cell wide), in *Chydenanthus* conspicuously banded (1–6-seriate) with a tendency to unilaterally paratracheal or vasicentric, in *Barringtonia* and *Petersianthus* parenchyma distribution extremely variable (Figs. 36, 37): apotracheal type most common and ranging from diffuse-in-aggregates to bands of various cells wide, 1–3 (–10)-seriate, additional scanty to vasicentric to even confluent paratracheal parenchyma in *Petersianthus*; 3–10 cells per parenchyma strand in *Barringtonia*, *Careya*, *Chydenanthus*, and *Planchonia*, 7–15 in *Petersianthus*. Uniseriate rays infrequent (Figs. 38–40), 0–3 rays/mm, but clearly present in *Planchonia spectabilis*, consisting of square to upright cells, length (100–) 330 (–1300) µm. Multiseriate rays 2–7-seriate (Figs. 38–40), (200–) 600–2100 (–4000) µm high, 3–10 rays/mm, generally consisting of mixed procumbent and square body ray cells in *Barringtonia*, *Careya*, and *Chydenanthus* (Fig. 44), predominantly procumbent in *Planchonia* and exclusively procumbent in *Petersianthus*, often with 1–2 rows

of upright to square marginal ray cells (Fig. 44), and sometimes up to 10 or 20 rows; a small percentage of rays fused; indistinct sheath cells sometimes present in species of *Barringtonia*, *Petersianthus*, and *Planchonia*. Dark amorphous contents in ray cells. Prismatic crystals often common in (not chambered) body and marginal ray cells of all genera (Fig. 45), sometimes also small styloids in *Barringtonia pauciflora* and *B. procera*, and in nonchambered axial parenchyma cells without wall thickenings in *Careya*, *Chydenanthus*, *Planchonia*, and in a few *Barringtonia* species; silica bodies only present in ray and axial parenchyma cells of *Petersianthus quadrialatus* (Fig. 46).

**Lecythidaceae-Lecythidoideae** (*Allantoma* 1/1, *Bertholletia* 1/1, *Cariniana* 4/15, *Corythophora* 3/4, *Couratari* 4/20, *Couroupita* 3/3, *Eschweilera* 4/ca. 85, *Grias* 4/6, *Gustavia* 4/40, *Lecythis* 7/26; Figs. 47–63)—Growth ring boundaries often indistinct (Fig. 48), sometimes distinct in *Allantoma*, *Cariniana* (Fig. 49), and *Couratari*. Diffuse-porous. Vessels (0) 1–30 (–50)/mm<sup>2</sup>, often 30–60/mm<sup>2</sup> in *Gustavia*; solitary or in short radial multiples of 2–3 (Figs. 47–50), exceptionally more (up to eight) in few species of most genera, clusters scarce in *Corythophora*, *Grias*, and *Lecythis* (Fig. 50); vessel outline rounded to elliptical; perforation plates predominantly simple (Fig. 55), sometimes scalariform (less than five bars) or reticulate (irregular in *Grias*; Fig. 56). Intervessel pits mostly alternate, alternate to slightly opposite in some species of *Allantoma*, *Bertholletia*, *Cariniana*, and *Couroupita*, tendency to opposite pitting is more pronounced in *Grias* and *Gustavia*, but the alternate type is dominant, pits usually 5–10 µm in horizontal diameter, 3–5 µm in *Gustavia* and 10–15 µm in *Couroupita*, nonvestured. Two types of vessel-ray pits present (Figs. 57, 58), often in the same ray cells: (1) few simple pits or with strongly reduced borders (pits round to oval or elongated horizontally or irregularly, or to a lesser extent elongated diagonally or vertically), pit cavities usually 10–25 µm in diameter but sometimes up to 50 µm, (2) many smaller and distinctly bordered pits (comparable to intervessel pits but usually somewhat smaller), in *Grias* distinction between two types of vessel-ray pits is less pronounced (Fig. 59). Wall sculpturing absent. Tyloses present in all genera. Tangential diameter of vessels (20–) 50–260 (–370) µm, vessel elements (180–) 350–700 (–1100) µm long. Few vasicentric tracheids present in *Grias peruviana* (USw 40764), 900–1200 µm long. Fibers nonseptate with minutely bordered pits concentrated in radial walls (tendency to distinctly bordered pits in *Allantoma*), thin-walled in *Allantoma*, *Bertholletia*, *Cariniana*, *Couratari*, and *Couroupita*, thick-walled in *Corythophora*, *Grias*, *Gustavia*, and *Lecythis*, and variable in *Eschweilera*, (850–) 1050–2850 (–3100) µm long, pit borders 2–4 µm in diameter; gelatinous fibers infrequent in most genera. Axial parenchyma predominantly banded apotracheal, narrow 1–2 (3)-seriate bands in *Allantoma*, *Cariniana*, *Corythophora*, *Couratari*,

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bands. **3.** *Napoleonaea* sp. MADw 32810: tangential longitudinal section (TLS), wide multiseriate rays with short uniseriate tails. **4.** *C. letestui* CTFw 8603: TLS, multiseriate rays with long uniseriate tails (arrows). **5.** *C. letestui* CTFw 8603: radial longitudinal section (RLS), scalariform perforation with many bars. **6.** *N. vogelii* MADw 36819: RLS, vessel-ray pitting scalariform with indistinct borders together with smaller distinctly bordered pits. **7.** *C. letestui* CTFw 8603: RLS, wide scalariform vessel-ray pits. **8.** *N. vogelii* MADw 41120: TLS, vasicentric tracheid next to vessel (arrow). **9.** *C. letestui* CTFw 8603: TLS, integumented prismatic crystals in chambered axial parenchyma cells with uniform wall thickenings. **10.** *N. vogelii* MADw 36819: RLS, integumented prismatic crystals in ray cells.



Figs. 11–20. Transverse (TS) and tangential longitudinal (TLS) sections (LM; Figs. 11–17) and radial longitudinal (RLS) surfaces (SEM; Figs. 18–20) of Scytopetaloidae. **11.** *Pierrina zenkeri*: TS, growth rings distinct, narrow vessel elements solitary or in short radial multiples, axial parenchyma diffuse-in-aggregates to short uniseriate bands. **12.** *Brazzeia soyauxii*: TS, growth rings distinct, vessel elements solitary or in short radial multiples, axial



*Couroupita*, *Eschweilera*, and *Grias* (Figs. 47–49); up to 4-seriate bands in *Bertholletia*, wider bands (up to more than 10-seriate) observed in *Lecythis* (Fig. 50); in *Gustavia* diffuse-in-aggregates to uniseriately banded; additional scanty paratracheal to vascentric parenchyma observed in all genera to a lesser extent, 3–11 cells per parenchyma strand. Uniseriate rays typically scarce, 0–3 rays/mm, although abundant in *Allantoma* and *Eschweilera sclerophylla*, (50–) 210 (–900)  $\mu\text{m}$  high, consisting of procumbent and square cells (also upright cells in *Grias* and *Gustavia*). Multiseriate rays generally 2–4-seriate (Figs. 51, 52), up to 8-seriate in *Gustavia* and up to 12-seriate in *Grias* (Figs. 53, 54), (500–) 300–2750 (–5100)  $\mu\text{m}$  high, 1–11 rays/mm, rays over 1000  $\mu\text{m}$  high common in *Grias* and *Gustavia*; multiseriate rays consisting of exclusively procumbent body ray cells and 1–2 rows of square to upright marginal ray cells (Fig. 60), also few square body ray cells in *Grias* and *Gustavia*, ray fusion infrequent to absent; sheath cells absent. Dark amorphous contents in ray cells. Few solitary prismatic crystals sometimes present in (sometimes chambered) body and marginal ray cells of *Grias* and *Gustavia* and more frequently in two types of axial parenchyma cells (Figs. 61, 62; crystals absent in *Eschweilera amazonia* and *Gustavia augusta*): (1) many integumented prismatic crystals in chambered axial parenchyma compartments with unilaterally thickened axial walls (*Allantoma*, *Bertholletia*, *Corythophora*, *Couratari*, *Cariniana*, *Eschweilera*, and *Lecythis*), crystalliferous chambers formed by thin-walled septa (Fig. 61), (2) prismatic crystals confined to few compartments per chambered strand showing more or less uniformly thickened axial walls in *Couroupita*, *Grias*, and *Gustavia* (Fig. 62), crystals sometimes integumented, crystalliferous compartments formed by parenchyma-like walls in *Grias* and *Gustavia* and by a combination of parenchyma-like walls and septa in *Couroupita*; silica bodies generally present in body and marginal ray cells of *Allantoma*, *Cariniana* (Fig. 63), *Corythophora*, *Couratari*, *Eschweilera*, and *Lecythis*.

## DISCUSSION

**Wood anatomical diversity within Lecythidaceae s.l.**—As defined by recent phylogenetic analyses, the broadly circumscribed Lecythidaceae show a high wood anatomical diversity (Figs. 1–63). Despite this conspicuous variation, some common wood features can be listed: solitary vessels that co-occur with distinct radial vessel multiples, simple vessel perforations, alternate intervessel pits, fibers with simple to minutely bordered pits, diffuse-in-aggregates to banded axial parenchyma of 1–3 cells wide, multiseriate heterocellular rays, and prismatic crystals in rays and/or axial parenchyma. More variation is observed in the average vessel diameter (30–260  $\mu\text{m}$ ) and vessel element length (350–1130  $\mu\text{m}$ ), size of intervessel pitting (3–20  $\mu\text{m}$  in horizontal diameter), arrange-

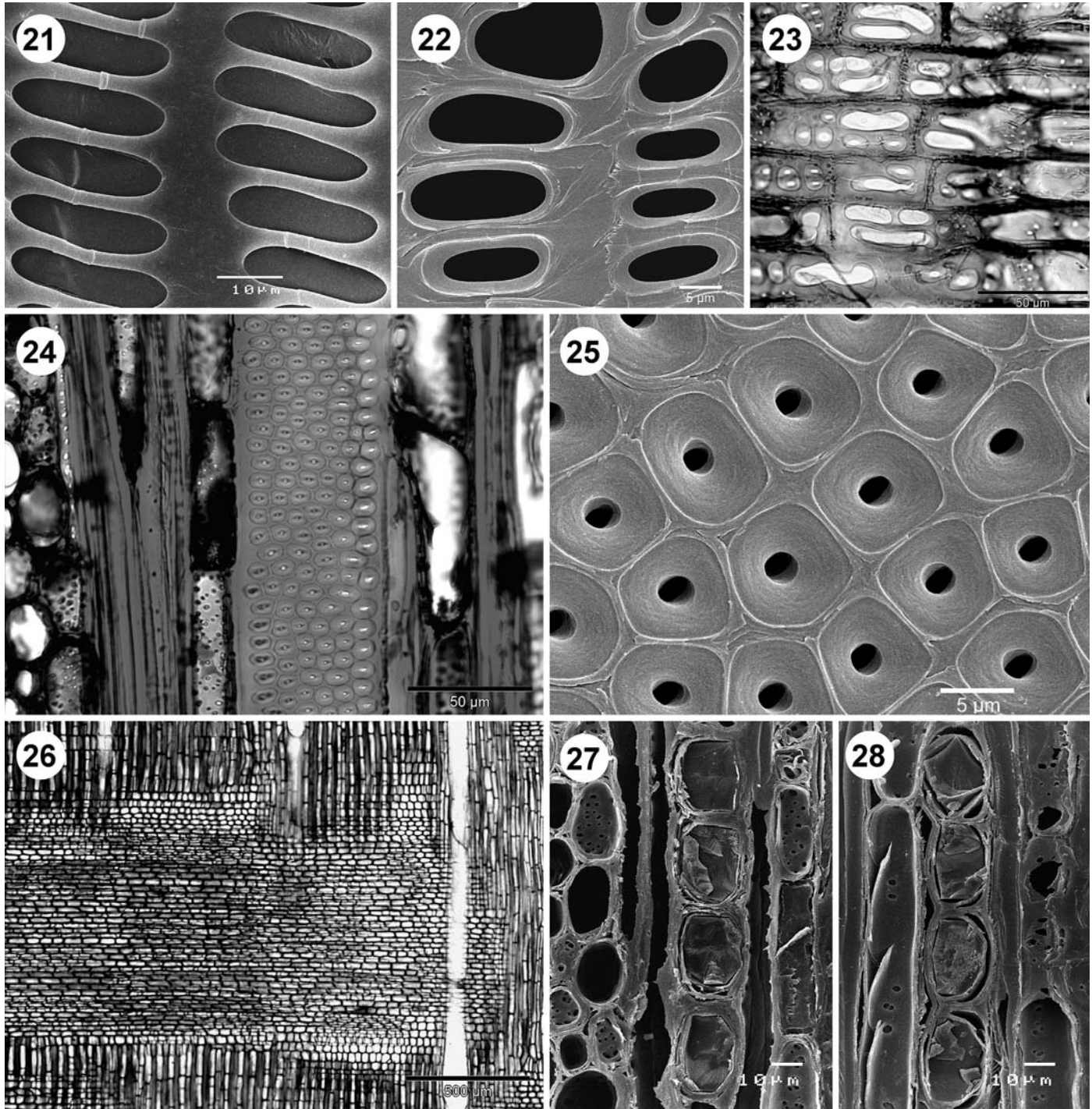
ment of vessel-ray pits (scalariform, opposite to scalariform, or alternate), fiber wall thickness (very thin- to very thick-walled), width of axial parenchyma bands (one to more than 10 cells wide), abundance of uniseriate rays, width and height of multiseriate rays (2–17-seriate and 260–2765  $\mu\text{m}$  high, respectively), and the number of rows of marginal ray cells in multiseriate rays (1–20). Compared to other ericacean families, a similarly large wood anatomical diversity within one family is only encountered in Ericaceae (Lens et al., 2003, 2004a, c).

Carl de Zeeuw's published and unpublished results can generally be confirmed, although the presence of septate fibers needs some comments: according to de Zeeuw (de Zeeuw, [no date]c, e, f), septate fibers occur in all seven species of *Planchonia* and sometimes in other Planchonioideae (few species of *Careya*, *Chydenanthus*, and *Barringtonia*). After a careful re-examination, we only found a very small proportion of septate fibers in few species of *Crateranthus*, *Oubanguia*, and *Planchonia*. The presence of dark amorphous material and wall fragments in fibers of these genera can easily be mistaken for septa. Therefore, we conclude that septate fibers are of very little significance in the family. Within *Foetidia*, variation in vessel diameter and vessel density is greater than described here: *F. asymerica* and *F. retusa* both have a mean vessel diameter of 50  $\mu\text{m}$  or less and a vessel density of more than 200/mm<sup>2</sup> (de Zeeuw [no date]a; P. D tienne, unpublished results, InsideWood website <http://insidewood.lib.ncsu.edu/search>). Additional minor differences that could not be corroborated in our study include few scalariform or reticulate perforations in *Barringtonia racemosa* and *B. scortechinii*, and silica bodies in *Planchonia andamanica* and *P. grandis* (de Zeeuw, [no date]e, f). Furthermore, we found two new wood features that were previously unknown in the family: (1) small styloids in *Brazzeia*, *Crateranthus*, *Napoleonaea*, and in a few *Barringtonia* species and (2) a small number of vascentric tracheids near vessel clusters in *Napoleonaea* and in *Grias peruviana* (USw 40764).

**Intrafamily relationships**—The genera *Napoleonaea* and *Crateranthus* of Napoleonaeoideae (NAP) can be identified by a combination of several characters, such as the occurrence of mixed simple and scalariform vessel perforations, predominantly scalariform vessel-ray pitting with distinct to strongly reduced borders, and broad (3–10-seriate) and high (2000–2500  $\mu\text{m}$ ) multiseriate rays (Figs. 3–7). Furthermore, silica bodies and parenchyma bands of over one cell wide are absent. The secondary xylem of NAP mostly resembles that of Scytopetaloidae (SCY), which is indicated by the mixed simple/scalariform perforations (also in *Barringtonia* and *Grias*), scalariform vessel-ray pitting, diffuse-in-aggregates to uniseriately banded axial parenchyma, and the abundance of uniseriate rays. Moreover, both subfamilies possess high multiseriate rays (on average more than 1 mm high; also present in *Barringtonia*, *Grias*, and *Gustavia*) with long

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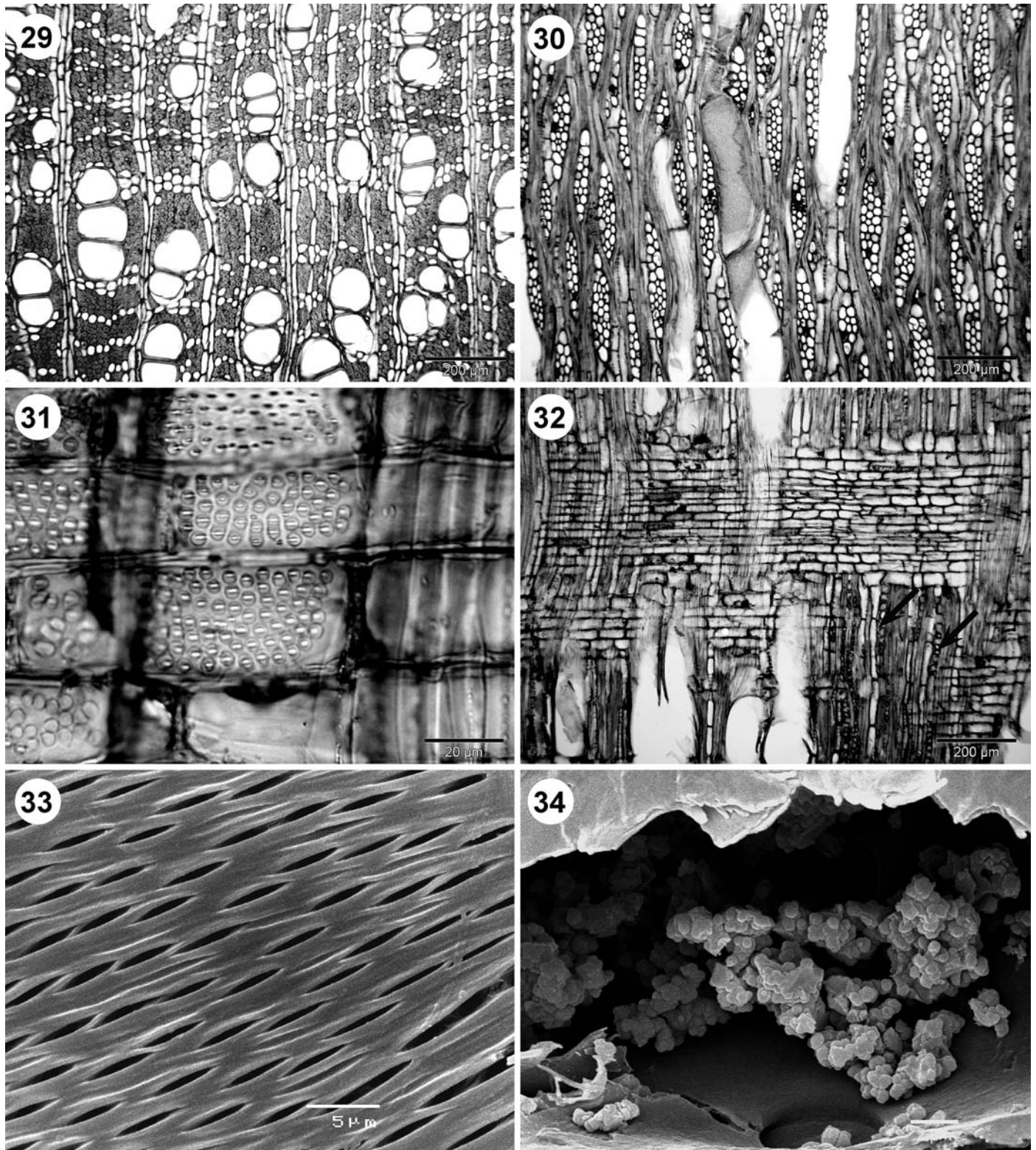
parenchyma diffuse-in-aggregates to short uniseriate bands, banded marginal parenchyma (arrow). **13.** *Rhaptopetalum beguei*: TS, vessel elements solitary or in radial multiples of 2–4, axial parenchyma diffuse-in-aggregates to short uniseriate bands. **14.** *Scytopetalum tieghemii* Tw 29979: TS, vessels wider, solitary or in short radial multiples, axial parenchyma uniseriately banded and vascentric (arrows). **15.** *Asteranthos brasiliensis* USw 8661: TLS, multiseriate rays with long uniseriate tails (arrows), uniseriate rays common. **16.** *P. zenkeri*: TLS, wide multiseriate rays with a variable amount of marginal rows. **17.** *S. tieghemii*: TLS, multiseriate rays with short uniseriate tails. **18.** *Oubanguia* sp.: RLS, simple vessel perforations. **19.** *B. congoensis*: RLS, scalariform perforations with few bars. **20.** *R. beguei*: RLS, scalariform perforations with few to many bars.



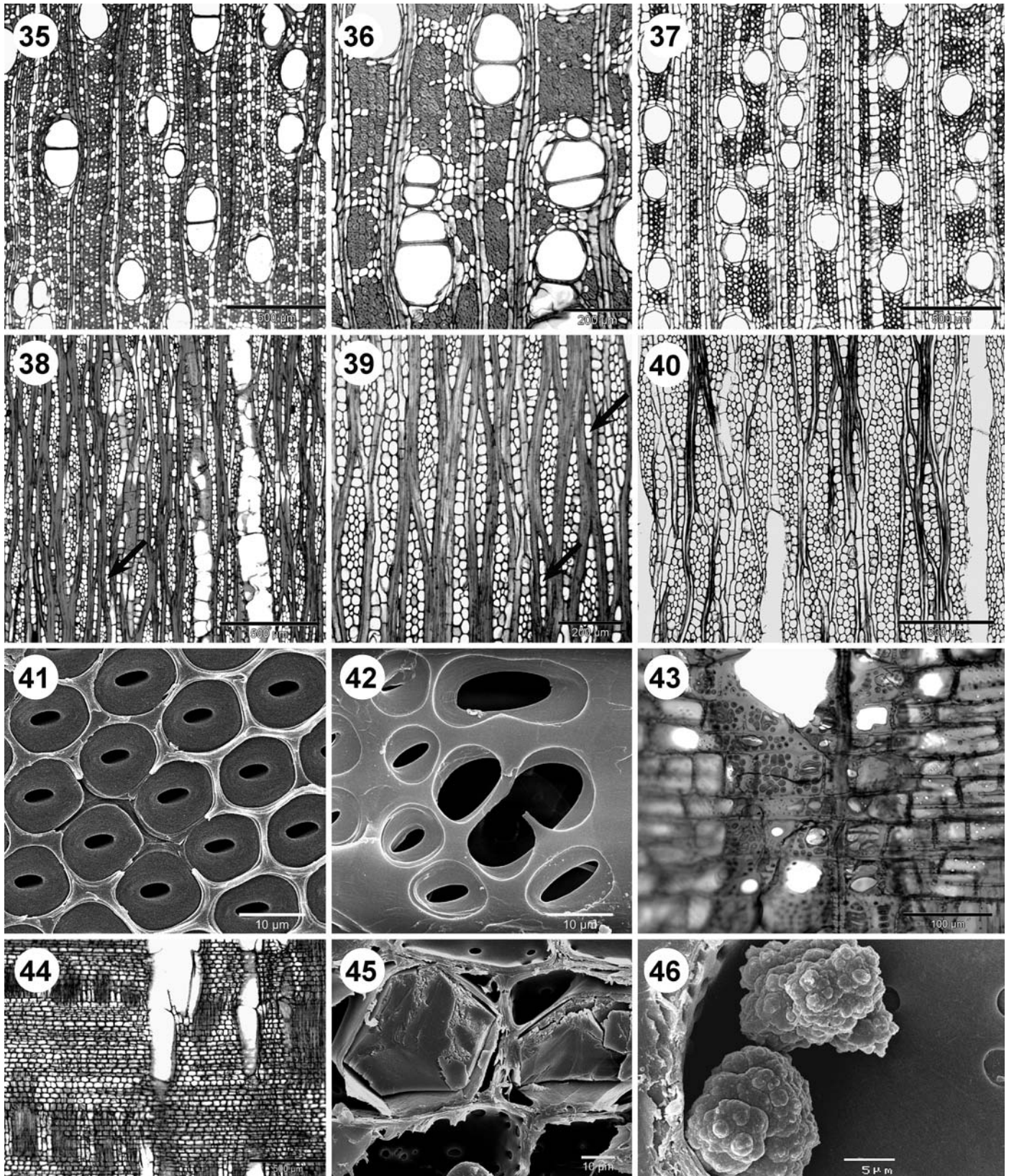
Figs. 21–28. Tangential (TLS) and radial longitudinal (RLS) sections (LM; Figs. 23, 24, 26) and surfaces (SEM; Figs. 21, 22, 25, 27, 28) of Scytopetaloidae. **21.** *Asteranthos brasiliensis* USw 8661: RLS, scalariform vessel-ray pits. **22.** *Oubanguia* sp.: RLS, scalariform vessel-ray pits with indistinct borders. **23.** *Scytopetalum tieghemii* Tw 29979: RLS, two types of vessel-ray pits. **24.** *Rhaptopetalum beguei*: TLS, opposite to alternate intervessel pitting. **25.** *S. tieghemii* Tw 29979: TLS, alternate intervessel pitting. **26.** *Brazzeia congoensis*: RLS, multiseriate rays with procumbent body ray cells. **27.** *Asteranthos brasiliensis* USw 8661: TLS, integumented prismatic crystals in chambered axial parenchyma cells with uniformly thickened walls. **28.** *B. congoensis*: TLS, integumented prismatic crystals in chambered axial parenchyma cells with uniformly thickened walls.

uniseriate tails (except in *Napoleonaea* and *Scytopetalum*), while silica bodies are always absent. No clear differences could be found to distinguish NAP from SCY because of the striking similarities of the SCY with *Crateranthus*. However, because

molecular sequence data of *Crateranthus* are still lacking at this moment, it is possible that this genus has more affinities to SCY than to *Napoleonaea*. If this should be the case, Napoleonaeidae comprises only the type genus, which can be supported by



Figs. 29–34. Wood anatomical sections (LM; Figs. 29–32) and surfaces (SEM; Figs. 33, 34) of *Foetidia mauritiana*. **29.** MADw 10231: transverse section (TS), vessels solitary or in short radial multiples of 2–3, axial parenchyma narrowly banded. **30.** MADw 10231: tangential longitudinal section (TLS), short and narrow multiseriate rays. **31.** MADw 10231: radial longitudinal section (RLS), small alternate to opposite vessel-ray pits with distinct borders. **32.** MADw 10231: RLS, multiseriate rays with procumbent body ray cells, prismatic crystals in chambered axial parenchyma cells (arrows). **33.** MADw 30811: TLS, wall thickenings accompanying pit apertures (coalescent or not) at the inside of vessel elements. **34.** MADw 30811: RLS, silica bodies in ray cell.



Figs. 35–46. Wood anatomical sections (LM; Figs. 35–40, 43, 44) and radial longitudinal surfaces (RLS) of Planchonioideae (SEM; Figs. 41, 42, 45, 46). **35.** *Planchonia papuana*: transverse section (TS), vessels solitary or in short radial multiples, axial parenchyma diffuse-in-aggregates. **36.** *Petersianthus macrocarpus*: TS, vessels in short radial multiples, axial parenchyma variable ranging from diffuse-in-aggregates to widely banded and

its distinctive wood structure (a limited number of vasicentric tracheids surrounding the vessel clusters, wide rays up to 17-seriate; Figs. 3, 8), but also by other distinguishing morphological features such as a chromosome number of  $x = 16$  and extrorse anther dehiscence (Morton et al., 1997).

Within SCY, two distinct groups can be made based on the vessel perforation plate morphology: (1) *Brazzeia*, *Pierrina*, and *Rhaptopetalum* have a high percentage of scalariform perforations (more than 80%), and (2) *Asteranthos*, *Oubanguia*, and *Scytopetalum* have predominantly simple perforations (Table 1; Figs. 18–20). This supports the recognition of subfamilies Rhaptopetaloideae and Scytopetaloideae sensu Appel (1996), a division that is based on differences in leaves, flowers, pollen, and seeds. Despite the systematic value of the vessel perforation type, this feature is clearly correlated with different life forms (shrubs and small trees vs. large trees; discussed later).

There are several morphological synapomorphies that indicate the isolated position of Foetidioideae (FOE), including amongst others the lack of petals (also observed in *Asteranthos*, *Crateranthus*, and *Napoleonaea*; Morton et al., 1997). The wood structure provides two additional characters that can be used to identify this monogeneric subfamily: small intervessel pits (3–4  $\mu\text{m}$ , also observed in *Gustavia*) that are similar in shape and size to the vessel-ray pits (Fig. 31) and weakly developed vessel wall thickenings that accompany pit apertures at the inside of vessel elements (Fig. 33). Furthermore, *Foetidia* has silica bodies in rays (Fig. 34) and in axial parenchyma, a combination that is only found elsewhere in *Cariniana*, *Eschweilera*, and *Petersianthus* (de Zeeuw, 1990).

Besides its unique syntriolpate pollen grains (Muller, 1972), Planchonioideae (PLA) have a distinctive wood structure due to the large intervessel pitting (more than 10  $\mu\text{m}$  in horizontal diameter, Fig. 41; also observed in *Couroupita*), multiseriate rays with mixed procumbent/square body ray cells (Fig. 44), and crystalliferous axial parenchyma cells without wall thickenings (also in *Napoleonaea*). Other common wood features within PLA include exclusively simple perforations and the presence of vessel-ray pitting consisting of small distinctly bordered pits that co-occur with larger simple pits in mostly different cells. This type of vessel-ray pitting is also sporadically found in *Napoleonaea* and in members of SCY, thereby forming a link with PLA (Figs. 6, 23, 42, 43). Also the occurrence of long uniseriate tails of multiseriate rays in *Crateranthus*, SCY, and PLA support this association (Figs. 4, 15, 16, 38, 39).

Most members of Lecythidoideae (LEC) can be identified by vessel-ray pitting consisting of many small distinctly bordered pits that co-occur with large simple pits in the same cells (Figs. 57, 58), scarce uniseriate rays, narrow (2–4-seriate) and low (<1000  $\mu\text{m}$ ) multiseriate rays (Figs. 51, 52), lack of prismatic crystals in rays, and chambered crystalliferous axial parenchyma strands showing many septa and unilaterally thickened walls (Fig. 61). Another common feature is the presence of

silica bodies in ray cells (Fig. 63). From a wood anatomical point of view, LEC resembles the sister clade including *Foetidia* (exclusively simple perforations, narrow and low multiseriate rays, and silica bodies) and PLA (predominantly simple perforations, two types of vessel-ray pits, and silica bodies) (de Zeeuw and Mori, 1987; de Zeeuw, 1990). In addition to the distinguishing wood anatomical characters, Lecythidoideae can be characterized by a specific basic chromosome number of  $x = 17$  (Morton et al., 1997).

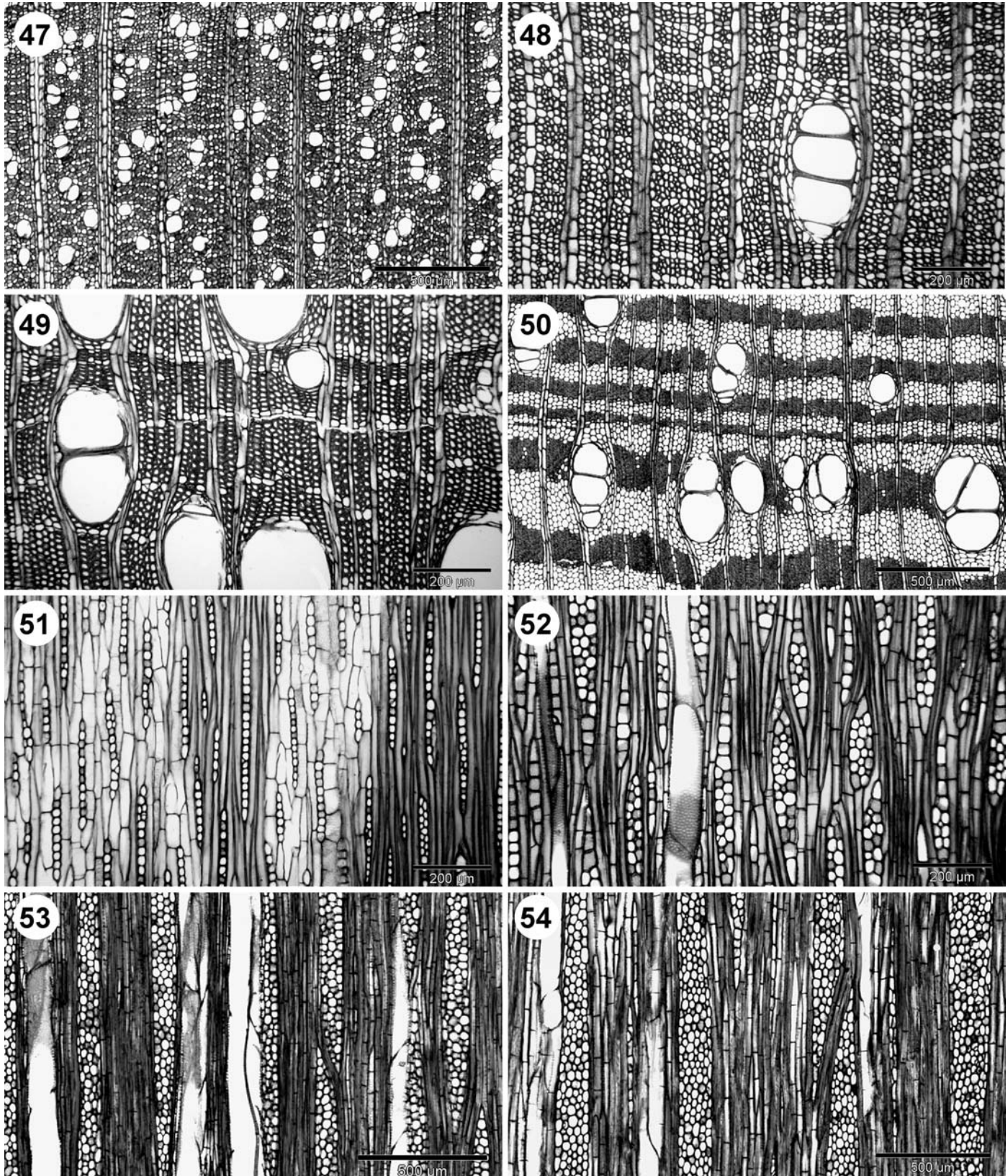
Within LEC, some wood characters agree with relationships hypothesized previously. For example, Mori et al. (2005) find that *Grias* and *Gustavia* are basal to the remaining LEC. This placement can be supported by their characteristically wide (more than 4-seriate) and high (on average more than 1 mm) multiseriate rays that have heterocellular body ray cells (Figs. 53, 54; also present in PLA), prismatic crystals in rays (also present in NAP, SCY, and PLA), and their nonseptate crystalliferous axial parenchyma cells with uniformly thickened walls (Fig. 62; also present in *Crateranthus* and SCY). Furthermore, the clade recognized by Morton et al. (1998), including *Allantoma*, *Cariniana*, *Corythophora*, *Couratari*, *Eschweilera*, and *Lecythis*, is the only LEC group in which silica bodies occur (Fig. 63). The sister genus of this group, *Bertholletia*, has several characters in common, such as the unique crystalliferous strands, and narrow and low multiseriate rays that lack prismatic crystals (Figs. 51, 52, 61). The wood structure of the latter clade is very homogeneous and does not permit commenting on the disputed generic boundaries of several genera (cf. Mori et al., 2005).

#### *Evolution of the wood structure within Lecythidaceae*

*s.l.*—As demonstrated in combined molecular/morphological analyses, NAP are the earliest diverging lineage followed by SCY, while FOE, LEC, and PLA have a more derived position (Morton et al., 1997, 1998). The wood structure provides arguments that seem to corroborate these relationships. Long vessel elements with scalariform perforations, common in NAP but also in SCY (mean length 770  $\mu\text{m}$ ), correspond to the primitive vessel type according to the Bailey trends (Bailey and Tupper, 1918), while derived vessels in the Bailey sense are much shorter (on average 530  $\mu\text{m}$  in LEC; 400  $\mu\text{m}$  in FOE) and have exclusively simple perforations. PLA have intermediate vessel element lengths. Despite the general phylogenetic value of vessel element length in woody angiosperms, the suggested character polarity must be treated with caution in Lecythidaceae *s.l.* because of its correlation with plant size (discussed later), but this does not always mean that taxonomically informative and habit-related characters are mutually exclusive (cf. ray width differences between lianous *Marcgravia* and other Marcgraviaceae; Lens et al., 2005). Another possible phylogenetically important character is the vessel-ray pitting that evolves from the so-called primitive scalariform type (NAP, SCY) to the more derived alternate type

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vasicentric. **37.** *Barringtonia pauciflora*: TS, axial parenchyma extremely variable ranging from diffuse-in-aggregates to banded and from vasicentric to unilaterally compound. **38.** *Planchonia papuana*: tangential longitudinal section (TLS), narrow multiseriate rays with sometimes long uniseriate tails (arrow). **39.** *Careya arborea*: TLS, scarce uniseriate rays (arrows). **40.** *B. pauciflora*: TLS, wide multiseriate rays. **41.** *Petersianthus macrocarpus*: RLS, alternate intervessel pitting. **42.** *B. longisepala*: RLS, two types of vessel-ray pitting. **43.** *Planchonia papuana*: RLS, two types of vessel-ray pitting. **44.** *Chydenanthus excelsus*: RLS, multiseriate ray with mixed procumbent/square body ray cells. **45.** *Careya arborea*: RLS, integumented prismatic crystals in ray cells. **46.** *Petersianthus quadrialatus*: RLS, silica bodies in ray cell.



Figs. 47–54. Transverse (TS) and tangential longitudinal (TLS) sections of Lecythidoideae (LM). **47.** *Gustavia poeppigiana*: TS, narrow vessels solitary or in short radial multiples, axial parenchyma diffuse-in-aggregates to narrowly banded. **48.** *Couroupita guianensis* Tw 34585: TS, indistinct growth ring, radial vessel multiple, uniseriately banded axial parenchyma. **49.** *Cariniana micrantha*: TS, distinct growth ring, vessels solitary or in short

on the one hand (FOE) and to the development of two distinct pit types on the other (LEC, PLA), although Frost (1931) also mentions a specialization from half-bordered to entirely simple vessel-parenchyma pits. There is also a general reduction in multiseriate ray height from more than 1500  $\mu\text{m}$  in NAP and most SCY toward less than 700  $\mu\text{m}$  in FOE and most LEC, while PLA have intermediate values. In addition, the proportion of uniseriate rays dramatically decreases from NAP and SCY toward the other subfamilies (on average 4–6 vs. 0–2 rays/mm, respectively). A final character that has taxonomic value is the morphology of the crystalliferous axial parenchyma cells: uniformly thickened cells in *Crateranthus*, FOE, and SCY evolve to nonthickened cells in PLA and to unilaterally thickened cells with many septa in most LEC. In other wood characters, more homoplasious variation is found, for instance in the distribution of axial parenchyma and the width of multiseriate rays.

**Interfamily relationships**—Considering the huge wood diversity of Lecythidaceae s.l. and its ambiguous taxonomic position within Ericales, it is difficult to assign its closest relatives. Based on the wood structure, several candidates can be suggested, such as Ebenaceae, Fouquieriaceae, Polemoniaceae, and Sapotaceae (Table 2). These families share the presence of radial vessel multiples with 2–4 cells that co-occur with solitary vessels, predominantly simple perforations, alternate intervessel pitting, diffuse-in-aggregates to banded axial parenchyma (more variation in Polemoniaceae), fibers with minutely bordered to simple pits (more variation in Polemoniaceae), and prismatic crystals in axial parenchyma cells (absent in Polemoniaceae) (Carlquist et al., 1984; Carlquist, 2001b; Lens, 2005; Table 2). A combined wood/molecular bootstrap analysis at the Ericales level shows that Lecythidaceae are sister to Fouquieriaceae-Polemoniaceae, although support value for this surprising relationship is low (Lens et al., in press).

Besides the wood anatomical similarities mentioned, Ebenaceae and Sapotaceae share some additional wood characters with Lecythidaceae, especially with Lecythidaceae s.s. (Table 2). Examples are the low (less than 1 mm) and narrow (2–4-seriate) multiseriate rays and the presence of silica bodies in rays (although infrequent in Ebenaceae). Ebenaceae mainly differ from Lecythidaceae s.s. based on the small opposite to alternate intervessel pits, numerous uniseriate rays, and the absence of two types of vessel-ray pitting, while Sapotaceae are characterized by crystal sand and a clear occurrence of vascentric tracheids (also present in *Napoleonaea*). On the other hand, Sapotaceae share two types of vessel-ray pits with Lecythidaceae, a unique feature in Ericales, which could support a possible sister relationship as suggested by Savolainen et al. (2000) and Anderberg et al. (2002). Indeed, the presence of two types of vessel-ray pits is restricted to a few woody angiosperm families, such as Erythroxylaceae (Malpighiales), Lecythidaceae and Sapotaceae (both Ericales), and

Olacaceae and Santalaceae (both Santalales) (IAWA Committee, 1989), and might therefore be considered as a phylogenetically informative character. However, a potential close relationship between Lecythidaceae and Sapotaceae is contradicted by striking differences in flowers and fruits (Appel, 2004; Pennington, 2004; Prance, 2004; Prance and Mori, 2004). It is more likely that Ebenaceae and Sapotaceae are more closely related to primuloids than to Lecythidaceae (Schönenberger et al., 2005; Lens et al., in press).

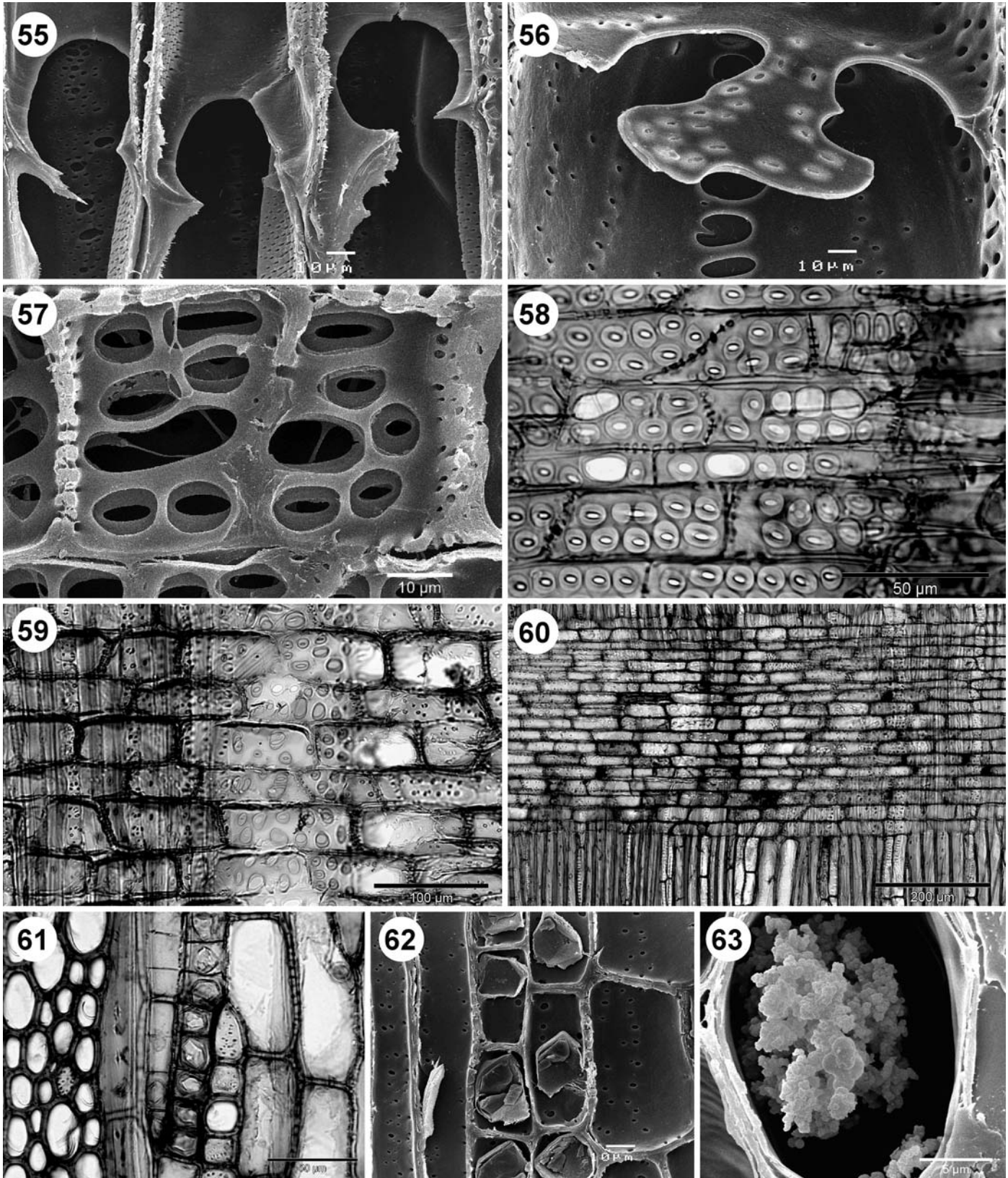
**Impact of environmental conditions and life form**—Lecythidaceae generally grow in moist tropical lowland forests, which may be periodically inundated, with only few species occurring at elevations above 1000 m a.s.l., while others are restricted to savannas (Lecomte, 1920; Letouzey, 1961; Payens, 1968; Liben, 1971; Prance and Mori, 1979; Mitchell and Mori, 1987; Bosser, 1988). We found no differences in wood structure between species that are typically growing in periodically flooded forests (e.g., species of *Allantoma*, *Brazzeia*, *Couroupita*, *Pierrina*, and *Rhaptopetalum*) or noninundated forests (the majority of the species studied). A minor exception is the presence of distinct growth rings, which is more pronounced in the inundated species (Figs. 11, 12) compared to the nonflooded ones (cf. Worbes, 1989), although indistinct growth rings are widespread among the nonflooded group. de Zeeuw's (1990) extensive sampling of *Eschweilera*, the only genus that occurs above 1000 m a.s.l., shows no altitudinal trends in the secondary xylem compared to the lowland genera.

de Zeeuw ([no date]a) and D tienne (P. D tienne, unpublished results, InsideWood website, <http://insidewood.lib.ncsu.edu/search>) found significant differences in the wood structure of *Foetidia*: *F. asymetrica* and *F. retusa* growing in the dry and hot regions of western Madagascar have significantly higher vessel densities and lower vessel diameters compared to the (sub)humid species in the central and eastern part of the country (on average 250 vs. 40 vessels/mm<sup>2</sup> and 45 vs. 70  $\mu\text{m}$  in tangential width, respectively) (Perrier de la B thie, 1954; Bosser, 1988). The single species in the present study, *F. mauritiana*, corresponds to the wet Malagassy group of species. It is the only sample with a slight development of wall sculpture accompanying the pit apertures (coalescent or not) on the inside of vessel elements (Fig. 33). In a more extensive shape, this character can develop into helical thickenings, a character that is most common in temperate and mediterranean zones (Baas and Schweingruber, 1987) or in areas that are drier or subject to freezing (Carlquist, 2001a). It is possible that other *Foetidia* species also show wall sculpture patterns in their vessels, although de Zeeuw's and D tienne's descriptions did not mention this character.

The great diversity of life forms in Lecythidaceae, ranging from small shrubs to giant emergent trees, provides the opportunity to relate the wood structure with different habits. Table 3 gives a summary of the most important results: the wood structure of canopy and emergent trees is almost identical

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radial multiples, uniseriately banded axial parenchyma. **50.** *Lecythis ampla*: TS, wide vessels usually in radial multiples, widely banded axial parenchyma. **51.** *Allantoma lineata* Tw 37426: TLS, many uniseriate rays that co-occur with a few narrow multiseriate ones. **52.** *Couroupita guianensis* Tw 34585: TLS, short and narrow multiseriate rays. **53.** *Grias peruviana* USw 40764: TLS, multiseriate rays wide and high, uniseriate rays nearly absent. **54.** *Gustavia gigantophylla*: TLS, multiseriate rays wide and high, uniseriate rays nearly absent.



Figs. 55–63. Longitudinal sections (LM; Figs. 58–61) and surfaces (SEM, Figs. 55–57, 62, 63) of Lecythidoideae. **55.** *Gustavia poeppigiana*: radial longitudinal section (RLS), simple vessel perforations. **56.** *Grias cauliflora* MADw 25993: RLS, irregular vessel perforation. **57.** *Couropita guianensis* Tw 34585: RLS, two types of vessel-ray pits in the same ray cells. **58.** *Bertholletia excelsa*: RLS, two types of vessel-ray pits in the same ray cells. **59.**



TABLE 2. Wood anatomical comparison between Napoleoneaeaceae (NAP), Scytropetalaceae (SCY), and Lecythydaceae s.s. (LEC), and selected members of Ericales: Sapotaceae (SAP), Ebenaceae (EBE), Fouquieriaceae (FOU), and Polemoniaceae (POL). + = always or predominantly present, ± = sometimes present, - = absent or very infrequent.

Wood character	NAP	SCY	LEC	SAP	EBE	FOU	POL
Alternate intervessel pitting	±	+	+	+	±	+	+
Two types of vessel-ray pitting	-	-	+	+	-	-	-
Vasicentric tracheids	±	-	-	+	±	+	-
Septate fibers	-	-	±	±	-	-	±
Banded axial parenchyma	+	+	+	+	+	-	±
Scanty to vasicentric axial parenchyma	-	-	±	-	±	-	+
Low multiserial rays (<1 mm)	-	±	+	+	+	±	±
Narrow multiserial rays (up to 4-seriate)	±	+	+	+	+	-	+
Uniseriate rays scarce to absent	±	±	+	+	-	±	±
Crystal sand	-	-	-	+	-	-	-
Crystals in axial parenchyma	+	+	+	+	+	+	-
Silica bodies	-	-	±	+	±	-	-

(except for a slightly larger vessel diameter in the emergent trees), but the two groups clearly differ from the understory woody plants in the presence of exclusively simple perforations, wider vessel diameters, lower vessel densities, and a shorter length of vessel elements, fibers, and multiserial rays. These habit trends generally agree with correlations found in previous studies, except for the length of vessel elements (and fibres) that are normally larger in tall trees compared to shrubs (Baas, 1976; Carlquist and Hoekman, 1985; Baas and Schweingruber, 1987; Carlquist, 2001a; Lens et al., 2004b). Furthermore, there is a tendency for wider rays in the understory species, although there is too much variation to generalize this. According to Carlquist (1988), the presence of fibers with conspicuously bordered pits in the genera *Rhaptopetalum* and to a lesser extent in *Pierrina* may be related to the understory habit, although this can be questioned because this fiber type is not encountered in other understory species. Within the understory group, we find similar correlations between the 15 larger trees (15–25 m high; UC in Table 1) and the 38 shrubs or low trees (below 15 m) for the percentage of species with scalariform perforations (8 vs. 19%), vessel diameter (110 vs. 85 µm), vessel density (11 vs. 19/mm<sup>2</sup>), and multiserial ray height (1200 vs. 1520 µm).

In conclusion, Lecythydaceae s.l. wood has a considerable amount of variation that has taxonomic value at the subfamily level. Inclusion of the former Scytropetalaceae is corroborated, and a basal position together with Napoleoneaeoideae is favored due to similar vessel perforations, vessel-ray pits, and rays. As a result of the striking similarities between *Crateranthus* (Napoleoneaeoideae) and Scytropetalaceae, both subfamilies cannot be separated from each other from a wood anatomical point of view. Furthermore, wood characters demonstrate that the genus *Foetidia* is taxonomically isolated within the family due to its unique type of vessel-ray pitting. The more derived

TABLE 3. Mean values and standard deviation of selected wood characters for understory shrubs and trees (<25 m; N = 53), canopy trees (25–35 m; N = 20) and emergent trees (>35 m; N = 14). Significant differences at the 0.5% level between mean values are indicated with superscript letters a and b.

	Understory	Canopy	Emergent
Percentage with scalariform perforations	15 ± 27 <sup>a</sup>	0 <sup>b</sup>	0 <sup>b</sup>
Vessel diameter (µm)	90 ± 29 <sup>a</sup>	135 ± 29 <sup>b</sup>	160 ± 43 <sup>b</sup>
Vessel density (/mm <sup>2</sup> )	17 ± 12 <sup>a</sup>	6 ± 2 <sup>b</sup>	5 ± 3 <sup>b</sup>
Vessel element length (µm)	640 ± 187 <sup>a</sup>	550 ± 172 <sup>b</sup>	560 ± 82 <sup>b</sup>
Fiber length (µm)	2200 ± 468 <sup>a</sup>	1800 ± 439 <sup>b</sup>	1850 ± 306 <sup>b</sup>
Height of multiserial rays (µm)	1430 ± 670 <sup>a</sup>	560 ± 225 <sup>b</sup>	660 ± 227 <sup>b</sup>

position of Planchonioideae and Lecythydoideae is supported by exclusively simple perforations and two types of vessel-ray pitting, while other features (size of intervessel pitting, shape of body ray cells in multiserial rays, and type of crystalliferous axial parenchyma cells) support their distinct status. Finally, some wood characters are clearly influenced by differences in life forms. When shrubs are compared with tall trees, shrubs clearly have a higher percentage of scalariform perforations and vessel densities in combination with longer vessel elements, fibers, and multiserial rays, while tall trees have a greater mean vessel diameter.

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*Griasp cauliflora* MADw 25993: RLS, no clear difference between types of vessel-ray pitting. **60.** *Cariniana multiflora*: RLS, multiserial ray showing procumbent body ray cells. **61.** *Lecythis lurida*: RLS, prismatic crystals in chambered axial parenchyma strand with many septa. **62.** *Gustavia poeppigiana*: RLS, prismatic crystals in axial parenchyma compartments formed by parenchyma-like walls. **63.** *Couratari guianensis* Tw 47829: tangential longitudinal section (TLS), silica grain in ray cell.

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APPENDIX. List of taxa investigated in this study with reference to their locality and vouchers. Institutional wood collections used in this study are abbreviated according to Index Xylarium (Stern, 1988).

#### Subfamily

Species—Locality; Voucher data.

#### Napoleonaeoideae

*Crateranthus letestui* H.Lec.—Gabon; *Normand* 196 (CTFw 5187). *C. letestui* H.Lec.—Gabon; *Forest Research Institute 1315* (CTFw 8603). *C. talbotii* Bak.f.—Cameroon; *Letouzey 10833* (CTFw 20321). *Napoleonaea leonensis* Hutch. & Dalziel—Liberia; *Cooper 86A* (MADw 30899). *N. septentrionalis* Liben—Democratic Republic of Congo; *Ntahobavuka s.n.* (Tw 57631). *N. sp.*—Ivory Coast; *Bamps 2377* (MADw 32810). *N. sp.*—Ivory Coast; *Bamps 2553* (MADw 32803). *N. vogelii* Hook. & Planch.—Ivory Coast; *Détienne 90* (MADw 36819). *N. vogelii* Hook. & Planch.—Democratic Republic of Congo; *Dechamps s.n.* (MADw 41143). *N. vogelii* Hook. & Planch.—Democratic Republic of Congo; *Dechamps s.n.* (MADw 41120).

#### Scytopetaloidae

*Asteranthos brasiliensis* Desf.—Venezuela (Amazonas); *Maguire et al. 41834* (Tw 36193). *A. brasiliensis* Desf.—Brazil; *Ducke 57* (USw 8661). *Brazzeia congoensis* Baill.—Democratic Republic of Congo; *Bertault 100* (CTFw 18363). *B. soyauxii* Tiegh.—Gabon; *Forest Research Institute 1088* (CTFw 8488). *Oubanguia africana* Baill.—Democratic Republic of Congo; *Louis 104* (Tw 32808). *O. sp.*—Democratic Republic of Congo; *Louis 1972* (Tw 33343). *Pierrina zenkeri* Engl.—Cameroon (near Kribi); *Bos 3856* (WAG). *Rhaptopetalum beguei* Mangenot—The Netherlands (Wageningen Botanic Gardens); *van Setten 478* (WAG). *R. sp.*—Cameroon; *Breteler 2754* (MADw 36223). *Scytopetalum brevipes* Tiegh.—Gabon; *Normand 194* (MADw 36939). *S. klaineinum* Pierre—Gabon; *Gavage s.n.* (Tw 25725). *S. tieghemii* Hutch. & Dalziel—Democratic Republic of Congo (Kasai); *Dechamps 292* (Tw 22970). *S. tieghemii* Hutch. & Dalziel—SE Ivory Coast; *Détienne 163* (Tw 29979).

#### Foetidoidae

*Foetidia mauritiana* Lam.—Mauritius; *Dentzman A1791* (MADw 10231). *F. mauritiana* Lam.—Mauritius; *Collector unknown* (MADw 30811).

#### Planchonioideae

*Barringtonia acutangula* Gaertn.—Burma; *Forest Botanist 1654* (MADw 30777). *B. asiatica* (L.) Kurz—Philippines; *Philippine Bureau of Forestry 28145* (MADw 6763). *B. edulis* Seem.—Fiji Islands; *Smith s. n.* (SJRw 27719). *B. lanceolata* (Ridl.) Payson—Brunei; *Ogata et al. s. n.* (MADw 48144). *B. pauciflora* Lauterb.—New Guinea (West Irian); *Collector unknown* (USw 34332). *B. longisepala* Payson—Malaysia; *Meijer 122304* (MADw 48591). *B. macrostachya* Kurz—Malaysia; *Forest Research Institute s.n.* (SJRw 28940). *B. macrostachya* Kurz—

Malaysia (Sumatra); *Boeeca 1205* (USw 1205). *B. procerca* (Miers) Knuth—Papua New Guinea (Gazelle Peninsula); *Waterhouse s.n.*

(SJRw 29763). *B. samoensis* A.Gray—Samoa (Tutuila); *Bryan Jr. s.n.* (SJRw 24496). *B. scortechinii* King—Malaysia; *Forest Research Institute s.n.* (SJRw 28939). *B. speciosa* J.R.Forst. & G.Forst.—Philippines; *Philippine Bureau of Forestry s.n.* (MADw 30779). *B. spicata* Blume—Java; *Janssonius 1655m* (SJRw 30916). *Careya arborea* Roxb.—India; *Stewart & Brandis 1479* (MADw 1439). *Chydenanthus excelsus* (Blume) Miers—origin unknown; *Collector unknown* (WIBw 5182, WAG). *Petersianthus macrocarpus* (Beauv.) Liben—Democratic Republic of Congo; *Martincic & Lju 85772* (MADw 39312). *P. quadrialatus* Merr.—Philippines; *Philippine Bureau of Forestry 12814* (MADw 36628). *Planchonia andamanica* King—India (Andaman Islands); *Lee s.n.* (USw 5075). *P. papuana* Knuth—New Guinea; *Collector unknown 20212* (USw 24046). *P. spectabilis* Merr.—Philippines; *Philippine Bureau of Forestry 1666* (MADw 30900). *P. timorensis* Blume—Papua New Guinea; *Department of Forests 39* (MADw 21794). *P. valida* Blume—Democratic Republic of Congo; *Collector unknown* (MADw 17791).

#### Lecythidoideae

*Allantoma lineata* Miers—Brazil (Amapa); *Collector unknown* (Tw 37426). *A. lineata* Miers—Brazil; *Maguire et al. 51738* (MADw 21433). *Bertholletia excelsa* Humb. & Bonpl.—Guiana; *Smith 2868* (Tw 27251). *Cariniana decandra* Ducke—Brazil; *Krukoff 7193* (MADw 12861). *C. micrantha* Ducke—Brazil (Matto-Grosso); *Krukoff 1439* (Tw 34677). *C. multiflora* Ducke—Brazil; *Krukoff 8624* (MADw 30790). *C. pyriformis* Miers—Colombia; *Curran 353* (MADw 30792). *Corythophora alta* Knuth—Brazil; *Pires & Cavalcante 52664* (MADw 22720). *C. amapaensis* S.A.Mori & Prance—Brazil (Amapa); *Collector unknown* (Tw 37160). *C. rimosa* W.A.Rodrigues—Brazil; *Ducke s.n.* (SJRw 21345). *Couratari guianensis* Aubl.—French Guyana; *Fouquet 1353* (Tw 47829). *C. guianensis* Aubl.—Brazil; *Maguire 51854* (MADw 21542). *C. macrosperma* A.C.Sm.—Brazil; *Krukoff 1653* (MADw 30796). *C. multiflora* Eyma—Brazil; *Krukoff 1901* (MADw 30794). *C. scottmorii* Prance—Costa Rica; *Wiemann 67* (MADw 42705). *Couroupita guianensis* Aubl.—Brazil (Para); *Krukoff 1236* (Tw 34585). *C. guianensis* Aubl.—Brazil; *Krukoff 1705* (MADw 30804). *C. nicaraguensis* DC.—Panama; *Cooper & Slater 302* (MADw 30808). *C. subsessilis* Pilg.—Brazil; *Krukoff 4741* (MADw 18541). *C.*

*subsessilis* Knuth—Brazil; *Krukoff* 8066 (MADw 30803). *Eschweilera amazonica* Knuth—Brazil; *Zarucchi et al.* 3190 (MADw 48836). *E. calyculata* Pittier—Panama; *Cooper* 475 (MADw 30853). *E. gigantea* Knuth—Brazil; *Krukoff* 8664 (MADw 30843). *E. sclerophylla* Cuatrec.—Colombia; *Cuatrecasas* 16517 (MADw 30882). *Grias cauliflora* L.—Costa Rica; *Nee & Mori* 3567 (MADw 25993). *G. cauliflora* L.—Costa Rica (Puntarenas); *Nee & Mori* 3574 (Tw 31515). *G. colombiana* Cuatrec.—Colombia; *Fuchs* 21914 (USw 38210). *G. neuberthii* J.F.Macbr.—Peru; *Williams* 2337 (MADw 15313). *G. peruviana* Miers—Ecuador; *Dorr et al.* 5822 (MADw 43463). *G. peruviana* Miers—Peru; *Schunke* 4463 (USw 40764). *Gustavia augusta* L.—Brazil (Matto-Grosso); *Krukoff* 1525 (Tw 33922). *G.*

*gigantophylla* Sandwith—Venezuela; *Nee & Mori* 4058 (MADw 25995). *G. poeppigiana* O.Berg—Brazil; *Krukoff* 8440 (MADw 30819). *G. cf. pulchra* Miers—Colombia; *Nee & Mori* 3801 (MADw 26001). *Lecythis ampla* Miers—Colombia; *Curran* 305 (MADw 7170). *L. confertiflora* (A.C.Sm.) S.A.Mori—Guyana; *British Guyana Forestry Department* 4806 (MADw 3783). *L. corrugata* Poit.—Guiana; *Smith* 2695 (Tw 27253). *L. lurida* (Miers) S.A.Mori—Brazil (Para); *Krukoff* 1213 (Tw 34583). *L. mesophylla* S. A.Mori—Colombia; *Nee & Mori* 3728 (MADw 26005). *L. turyana* Pittier—Panama; *Holdridge* 6286 (MADw 24829). *L. zabucajo* Aubl.—NW Guiana; *Maguire et al.* 40551 (Tw 37173).

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