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BARK AND WOOD ANATOMY OF THE TRIBE HAMELIEAE (RUBIACEAE)

Dorismilda Martínez-Cabrera[1], **Teresa Terrazas**[2], **Helga Ochoterena**[2], and **Lauro López-Mata**[1]

SUMMARY

We studied wood and bark anatomy of six (*Deppea, Hamelia, Hoffmannia, Omiltemia, Pinarophyllon*, and *Plocaniophyllon*) of the seven genera of the tribe Hamelieae *sensu* Robbrecht, and *Syringantha* with as main purposes to determine if there are characters that support the boundaries of the Hamelieae, to evaluate the status of *Syringantha* as a member of the Hamelieae, and to evaluate the taxonomic position of Hamelieae within the subfamilies Rubioideae or Cinchonoideae. In addition, we studied for comparative purposes representative species of *Psychotria* (Psychotrieae, Rubioideae), *Exostema*, and *Hintonia* (*Portlandia* group, Cinchonoideae), *Randia* (Gardenieae, Ixoroideae), and *Bouvardia* (*incertae sedis*). Bark of most genera studied had a single periderm, while a rhytidome was observed in *Exostema* and few species of *Psychotria*. The mineral inclusions allowed recognizing related genera, for example, raphides in Hamelieae and *Psychotria*, prisms in *Exostema*, and druses in *Randia*. Members of Hamelieae showed wood type II, distinctive by the occurrence of libriform septate fibres, vessels in radial multiples of 2–6 vessels (80–90%, vessel grouping index 1.79–2.74), and diffuse apotracheal parenchyma. *Syringantha* shares with members of Hamelieae the presence of an endodermis, raphides in the bark, and wood type II. The combination of other wood characters mainly lend quantitative support to the taxonomic delimitation of some genera within Hamelieae. Raphides and wood type II supported a close relationship between Hamelieae and Hillieae within Cinchonoideae; characters that distinguish them from the other members of Cinchonoideae. Our results suggest independent origins of wood type II within the Rubiaceae. In addition, vessel density and diameter are discussed as possible adaptations to the different forest types where members of Hamelieae occur.

Key words: Endodermis, Rubiaceae, Hamelieae, wood, bark, crystals, fibres, vessel grouping.

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1) Programa de Botánica, Colegio de Postgraduados, Montecillo, Estado de México 56230, Mexico.
2) Instituto de Biología, Universidad Nacional Autónoma de México, 70-367 México D.F. 04510, Mexico.

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INTRODUCTION

Wood anatomical studies in Rubiaceae cover a large number of genera, tribes, and subfamilies (Koek-Noorman 1969a, b, 1970; Koek-Noorman & Hogeweg 1974; Koek-Noorman & Puff 1983; ter Welle *et al*. 1983; Jansen *et al*. 1997, 2001, 2002; Lens *et al*. 2000, 2009) and have shown the great taxonomic importance of wood anatomical characters. Koek-Noorman (1977) recognized two types of wood for this family. Type I is distinctive for having fibre-tracheids, diffuse and in-aggregates apotracheal parenchyma or parenchyma bands, mainly solitary vessels, and narrow rays. Type II is characterized by its libriform fibres, lack of parenchyma or diffuse apotracheal parenchyma, relatively low number of solitary vessels, vessels in short radial rows (2–4 vessels) and wide rays (Jansen *et al*. 2002). However, little is known about wood of the Hamelieae tribe, whose members are mostly small trees, and the delimitation of which has been controversial (De Candolle 1830; Endlicher 1836; Verdcourt 1958, 1976; Bremekamp 1966; Elias 1976; Bremer 1987; Robbrecht 1988, 1993; McDowell 1996), as well as its assignment to a subfamily (Bremer *et al*. 1995; Andersson & Rova 1999; Robbrecht & Manen 2006). At the same time, few studies have been devoted to describe the bark of Rubiaceae species (Metcalfe & Chalk 1950; Roth 1981).

The genera classified in Hamelieae *sensu* Robbrecht (1993) are represented by neotropical small tree species with complete or divided interpetiolar stipules, raphides, imbricate or contorted right-hand aestivation, stamens adnate to the base of the corolla tube, small to large colporate pollen, supratectal elements present or absent, 2(–5)-locular ovaries with numerous ovules, fleshy or dry fruits, and seeds with granulate or tuberculate testa cells (Robbrecht 1988; Dessein *et al*. 2005).

The present study describes the wood and bark anatomy of six out of the seven genera included in Hamelieae *sensu* Robbrecht (1993), plus *Syringantha*. The ambiguous recognition of *Syringantha* as a member of Hamelieae will be evaluated based on stem anatomical characters. We compare wood and bark characters of Hamelieae species with representative species of other tribes and subfamilies (Cinchonoideae, Ixoroideae, and Rubioideae; *sensu* Robbrecht 1993) to evaluate their potential contribution to the tribal and generic classification and circumscription.

METHODS AND MATERIALS

Two to three samples of 15 species representing six of the seven Hamelieae genera, plus *Syringantha* were collected (Table 1). The monotypic genus *Eizia* could not be studied because we were unable to find it in the field, not even in its type locality. For comparison 15 representative species from other tribes were included, which were also collected or obtained from MEXUw (Table 1). Samples were cut with a saw; shrubs and small trees less than 1 m at 10 cm above ground, and taller trees at 1.20 m. All samples were fixed in formalin-acetic acid-ethanol (Ruzin 1999) and stored in a glycerin-water-alcohol (1 : 1 : 1) solution until sectioning. Transverse, radial, and serial tangential sections (20–35 μm) were obtained using a sliding microtome. For each sample, unbleached and bleached (50 % -v/v- aqueous solution of commercial Clorox) sections were stained with safranin-fast green (Ruzin 1999) and mounted in synthetic resin. Macerations were prepared using Jeffrey's solution (Berlyn & Miksche 1976) to gather data on vessel element and fibre lengths.

Table 1. List of the specimens studied. Arrangement follows the subfamily and tribal classification *sensu* Robbrecht (1993), vouchers deposited in MEXU and CHAPA (acronyms following Holmgren *et al.* 2004).

Rubioideae, tribe Hamelieae

Deppea cornifolia (Benth.) Benth., Guerrero, *D. Martínez 241, 242, 243* (CHAPA) — *D. grandiflora* Schltdl.,Veracruz, *H. Ochoterena y C. Gallardo 374* (MEXU) — *D. guerrerensis* Dwyer & Lorence, Guerrero, *D. Martínez 192, 193, 194* (CHAPA) — *D. purpusii* Standl., Zacualtipán, Hidalgo, *D. Martínez 252, 253, 254* (CHAPA).

Hamelia longipes Standl., Veracruz, *J. Barajas M. 197, 203* (MEXU) — *H. patens* Jacq., Hidalgo, *D. Martínez 261, 268, 271* (CHAPA) — *H. versicolor* A.Gray, Jalisco, *D. Martínez 302, 303, 304* (CHAPA) — *H. xorullensis* Kunth, México, *D. Martínez 298, 299, 300* (CHAPA).

Hoffmannia conzattii B.L.Rob., Hidalgo, *D. Martínez 177, 178, 179* (CHAPA) — *H. culminicola* Standl. & L.O.Williams, Hidalgo, *D. Martínez 184, 186, 187* (CHAPA).

Omiltemia filisepala (Standl.) C.V.Morton, Chiapas, *D. Martínez 175, 177, 178* (CHAPA) — *O. longipes* Standl., Guerrero, *D. Martínez 236, 237, 238* (CHAPA).

Pinarophyllon flavum Brandegee, Chiapas, *D. Martínez et al. 316, 317, 318* (CHAPA).

Plocaniophyllon flavum Brandegee, Chiapas, *D. Martínez et al. 311, 312, 313, 314* (CHAPA).

Rubioideae, tribe Psychotrieae

Psychotria chiapensis Standl., Veracruz, *I. Manríquez G. 1341, 1507* (MEXU) — *P. flava* Oerst. ex Standl., Veracruz, *I. Manríquez G. 1616* (MEXU) — *P. horizontalis* Sw., Jalisco, *D. Martínez & E. Domínguez L. 198, 199, 200* (CHAPA) — *P. microdon* (DC.) Urb., Jalisco, *D. Martínez & E. Domínguez L. 205, 206 207* (CHAPA) — *P. papantlensis* Hemsl., Veracruz, *I. Manríquez G. 1600* (MEXU) — *P. simiarum* Standl., Veracruz, *I. Manríquez G. 1479, 1258* (MEXU) — *P. veracruzensis* Lorence & Dwyer, Veracruz, *I. Manríquez G. 2508* (MEXU).

Cinchonoideae, tribe Cinchoneae

Bouvardia longiflora Kunth, Veracruz, *J. Barajas M., P. Solis & A. Salinas 449* (MEXU) — *B. ternifolia* (Cav.) Schltdl., Hidalgo, *D. Martínez 283, 284, 285* (CHAPA).

Cinchonoideae, *Portlandia* group

Exostema caribaeum (Jacq.) Roem. & Schult., Jalisco, *J. Barajas M. & A. Magallanes 136* (MEXU), *L. Gómez C.* 63 (MEXU), Campeche, *E. Martínez 30587* (MEXU), Jalisco, *D. Martínez & E. Domínguez L. 212, 213, 217* (CHAPA) — *E. mexicanum* A.Gray, Tabasco, *J.I. Calzada 2331* (MEXU), Campeche, *E. Martínez 30557* (MEXU), Jalisco, *D. Martínez & E. Domínguez L. 195, 197* (CHAPA).

Ixoroideae, tribe Gardenineae

Randia aculeata L., Campeche, *E. Martínez 30557* (MEXU) — *R. capitata* DC., Puebla, *L. Abundiz B. 824* (MEXU) — *R. pterocarpa* Lorence & Dwyer, Veracruz, *I. Manríquez 1329, 2389* (MEXU) — *R. tetracantha* (Cav.) DC., Jalisco, *J. Barajas M. 239* (MEXU), *L. Gómez C. 92* (MEXU) — *R. thurberi* S.Watson, Jalisco, *J. Barajas M. 229* (MEXU).

Incertae sedis

Hintonia latiflora (Sessé & Moc. ex DC.) Bullock, Jalisco, *J. Barajas M. 111* (MEXU), *L. Gómez C. 21* (MEXU), Sinaloa, *H. Ochoterena & D. Bailey 225* (MEXU), Jalisco, *D. Martínez & E. Domínguez L. 201, 202* (CHAPA).

Syringantha coulteri (Hook. f.) T. McDowell, Hidalgo, *D. Martínez 189, 190, 191* (CHAPA).

To characterize the intervascular pitting, tangential sections of 60 μm were cut, dehydrated, and fixed to aluminium specimen holders with double-sided tape and coated with gold in a Hitachi-S-2460N sputter coater prior to observation under a JEOL-JSM-5310LV at the Instituto de Biología, UNAM. The bark was described using the Trockenbrodt (1990) terminology and the wood anatomical definitions follow the International Association of Wood Anatomists (IAWA Committee 1989).

The quantitative wood anatomical characters were analysed using an image-analysis programme (Image ProPlus version 3.1, Media Cybernetics 1997); 25 measurements were made for each character. The quantitative data were analysed with the SAS statistical package version 9.2 (SAS Institute 2008). Pearson and Spearman correlation analyses (r & rs) were used to identify statistically significant correlations among characters. A covariance analysis also allowed us to eliminate the effect of individual stem height and diameter and to evaluate if statistical significant differences (Tukey) exist for the ten quantitative characters between the genera within the tribe. An index of vessel grouping as recommended by Carlquist (2001) and the F/V ratio (fibre length/vessel element length) were calculated. We explored the predictability of the wood type using a multiple logistic regression with vessel density, vessel grouping index, vessel diameter, type of parenchyma as independent factors and type of imperforate tracheary cells as the dependent factor.

RESULTS

For comparative purposes, a description of the bark and wood anatomical characters of the tribe Hamelieae (including *Syringantha*) is presented below. Character and character states of the representatives of other tribes are provided at the generic level in Tables 2 and 3. Illustrations are shown in Figures 1–5.

The Hamelieae tribe is composed of shrubs and small trees of 1–4 m high with 1.5–10 cm dbh, and they are mostly evergreen and inhabit mountain cloud forests, *Pinus-Quercus* forests, tropical evergreen forests, tropical dry forests or xeric-scrubs.

Outer bark — The bark is smooth or finely wrinkled, grey or brown in colour, without a rhytidome. Round or oval-shaped lenticels smaller than 3 mm are present.

Periderm — The genera studied exhibit a single bidirectional periderm (Fig. 1A). The phellogen differentiates from the cortical cells underneath the epidermis. The phellem has most commonly 4–10 layers of rectangular, thin-walled cells with the exception of some *Hamelia* species as well as *Syringantha*, which exhibit more than 10–12 layers. The phelloderm exhibits 3–6 layers of rectangular to square cells with thin walls in most of the genera (Fig. 1C) with the exception of some *Deppea* and *Hamelia* species where there are 10–12 layers. Tannins were only observed in the phellem.

Cortex — The cortex has parenchyma (Fig. 1D) and lamellar collenchyma. An endodermis with distinctive rectangular cells and Casparian strips in the anticlinal walls is present (Fig. 1E). Regardless of the stem diameter, the cortex is well conserved between the periderm and the secondary phloem in all of the Hamelieae genera. Tannins and raphides occlude the lumen of some parenchyma cells.

Table 2. Bark and wood characters of Hamelieae and other Rubiaceae. Values represent the minimum–mean–maximum or the mean.

A = absent, D = diffuse, Dr = druses, P = present, Pc = prismatic crystals, Ra = raphides, Sc = sandy crystals, Sr = semi-ring porous, St = styloids, Ta = tannins.

	Bark		Vessels						
Genus	Endodermis	Inclusions	Porosity	Vessel grouping index	Vessels / mm^2	Length (µm)	Diameter (µm)	Wall thickness (µm)	Pit diameter (µm)
Deppea	P	Ra, Ta	D (Sr)	2.37	57–136–225	220–597–1328	33	2.1	3.3
Hamelia	P	Ra, Ta	D (Sr)	2.25	20–44–82	331–647–1328	58	2.5	4.0
Hoffmannia	P	Ra, Ta	D	1.79	44–66–88	307–775–1447	34	2.0	4.0
Omiltemia	P	Ra, Ta	D	2.74	48–81–123	394–985–1604	40	2.5	3.7
Pinarophyllon	P	Ra, Ta	D	1.86	143–181–239	276–442–744	18	2.3	3.7
Plocaniophyllon	P	Ra, Ta	D	1.96	127–194–239	283–511–809	20	2.5	3.0
Syringantha	P	Ra, Ta	D	2.72	44–71–98	324–523–768	37	2.5	3.3
Psychotria	P, A	Ra, St,Ta	D	2.23	37–115–255	272–671–1398	34	3.1	3.1
Bouvardia	A	St	D, (Sr)	1.19	119–201–271	254–445–793	17	2.6	3.0
Exostema	A	Pc, St	Sr	1.10	67–168–335	240–512–780	39	3.8	3.6
Hintonia	A	Sc	Sr	1.12	89–255–399	266–452–771	29	3.5	3.3
Randia	A	Dr	Sr	1.17	56–129–319	255–517–1126	27	3.5	2.5

Secondary phloem. Sieve tube elements (STE) and companion cells (CC) — STE are polygonal in shape (Fig. 1F), with the exception of *Plocaniophyllon* and *Pinarophyllon*, where they exhibit an irregular round shape, with thin walls and a CC at one end. The STEs in the noncollapsed phloem are distributed in groups of 2 to 3 (Fig. 1G), with the exception of some *Hamelia* species that have groups of 3–5. Collapsed phloem is always present.

Axial parenchyma — The parenchyma cells have a random distribution among STE and CC in the noncollapsed phloem, and are mostly circular in shape. In the collapsed phloem the parenchyma is more abundant and it is interrupted by groups of 2–5 fibres or sclereids (Fig. 1H).

Radial parenchyma — In a cross section, the rays are straight in the noncollapsed phloem, with dilation in the collapsed phloem. The rays are heterogeneous, uni- and multicellular (Fig. 2A) and dilate close to the cortical region (Fig. 2C).

Inclusions — Tannins and raphides occluding the lumina of axial and radial parenchyma cells occur in all members of Hamelieae (Fig. 2E).

Secondary xylem — Most of the Hamelieae genera have distinctive growth rings (Fig. 3A), that are marked by differences in the fibre wall thickness, except in *Hoffmannia* and *Omiltemia* (*O. filisepala*) where they are inconspicuous (Fig. 3B). Porosity is mainly diffuse, with a mean density of 44 vessels/mm^2 in *Hamelia* and 194 vessels/mm^2 in *Plocaniophyllon*. Only a few species of *Deppea* and *Hamelia* exhibit semi-ring porosity, marked by 1–3 rows of vessels in the earlywood; the transition of earlywood to

Table 3. Wood characters of Hamelieae and other Rubiaceae. Values represent the minimum–mean–maximum or the mean.

Abbreviations: Ft = fibre-tracheids, Gu = gum, L = libriform fibres, Ns = non-septate, Pr = prisms, Ra = raphides, Sb = silica bodies, Ta = tannins.

Fibres

Genus	Type	No. of septa	Inclusions	Fibre length (μm)	Lumen diam. (μm)	Wall thickness (μm)	F/V ratio
Deppea	L	3–5	Sb	341–844–1276	10.0	2.2	1.41
Hamelia	L	3–6	Sb	563–1071–1869	11.5	2.6	1.65
Hoffmannia	L	3–4	–	685–993–1388	11.0	2.0	1.28
Omiltemia	L	2–3	–	813–1345–1961	10.0	2.7	1.36
Pinarophyllon	L	3–4	Sb	486–668–846	7.0	2.3	1.51
Plocaniophyllon	L	4–5	Sb	516–803–1193	7.0	2.1	1.57
Syringantha	L	4–5	Sb	411–826–1568	9.0	2.0	1.57
Psychotria	L	2–5	–	499–943–1570	7.5	3.1	1.40
Bouvardia	L, Ft	2–4	–	403–673–997	4.3	2.6	1.51
Exostema	Ft	Ns	–	580–896–1373	4.3	4.0	1.75
Hintonia	Ft	Ns	–	527–903–1463	5.3	3.6	1.99
Randia	Ft	Ns	–	421–976–1719	3.5	4.0	1.88

Rays

Genus	Cell type	Height (μm)	Width (μm)	Inclusions
Deppea	procumbent, upright, square	399–772–1074	52	–
Hamelia	procumbent, upright, square	209–512–916	34	Ra
Hoffmannia	upright, square	490–934–1625	30	Ta
Omiltemia	procumbent, upright, square	460–785–1399	48	Ta
Pinarophyllon	upright, square	>1950	15	Ta
Plocaniophyllon	upright, square	332–822–2001	20	Ta
Syringantha	procumbent, upright, square	159–382–840	25	–
Psychotria	procumbent, upright, square	315–596–898	48	Gu, Ra
Bouvardia	upright, square	196–620–1195	15	–
Exostema	procumbent, square	76–185–858	22	Pr
Hintonia	procumbent, upright, square	139–246–431	23	–
Randia	procumbent, upright, square	143–365–1158	22	Pr, Gu, Ta

latewood is gradual. The vessels are solitary and in radial multiples of 2–6 (8) vessels (Fig. 3C) with a vessel grouping index of 1.79–2.74; they are mostly angular in outline and rounded ones are scarce (Fig. 3F). Tangential vessel diameter varies from 18 ± 2 μm in *Pinarophyllon*, up to 58 ± 13 μm in *Hamelia*, exhibiting a greater variation than in the other studied genera (Table 2). The vessel elements have a mean length of 442 ± 87 μm in *Pinarophyllon* up to 985 ± 247 μm in *Omiltemia*. The vessel wall thickness in Hamelieae is <3 μm (Table 2). Perforations are simple (Fig. 3I) with slightly inclined end walls, with the exception of *Hoffmannia* (Fig. 4A), which exhibits two perforation plates per end plate in about 75% of the vessel elements. Intervascular pitting is alternate. Pits are circular in outline and vestured. Vestures associated with the outer pit apertures can be grouped into two pit types. The ones that are almost completely

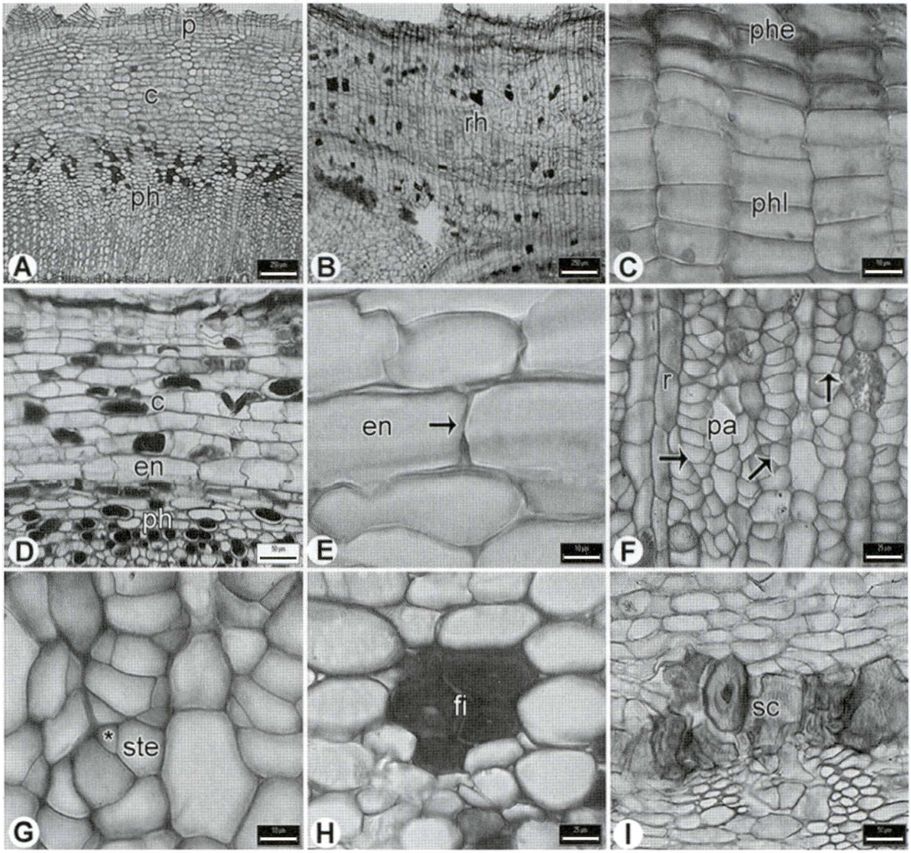

Figure 1. Bark anatomy of Hamelieae and other Rubiaceae, transverse sections. – A: Single periderm in *Omiltemia longipes*. – B: Rhytidome with 5 periderms in *Psychotria microdon*. – C: Phelloderm with rectangular cells thin-walled in *Deppea purpusii*. – D: Cortex in *Plocaniophyllon flavum*. – E: Endodermis with disctinctive Casparian strip (arrow) in *Pinarophyllon flavum*. – F: Sieve tube elements and companion cells in noncollapsed phloem in *Syringantha coulteri*. – G: Sieve tube elements with polygonal shape arranged in groups in *Hamelia patens*. – H: Fibres in collapsed phloem in *Hoffmannia culminicola*. – I: Sclereids in bands of collapsed phloem in *Exostema mexicanum*. — c = cortex; en = endodermis; fi = fibre; p = periderm; pa = parenchyma; ph = phloem; phe = phellem; phl = phelloderm; r = ray; rh = rhytidome; sc = sclereids; ste = sieve tube element, * = companion cell. — Scale bar 250 μm in A, B, D; 50 μm in I; 25 μm in F, H; 10 μm in C, E, G.

occluded by vestures (Fig. 4C, D), and those that are only poorly vestured, with the vestures restricted around the outer pit aperture as in *Deppea* and *Hoffmannia* (Fig. 4E), although vesturing can be variable within the same sample. The intervascular pit diameter varies between 3–4 μm. Vessel-ray pits are similar in size and pattern to the intervascular ones.

The libriform fibres are septate (Fig. 4G, H) with 2–6 septa per cell. Pitting is distinctive with minutely bordered pits (Fig. 4G, H). Mean fibre length varies from 668 ± 94

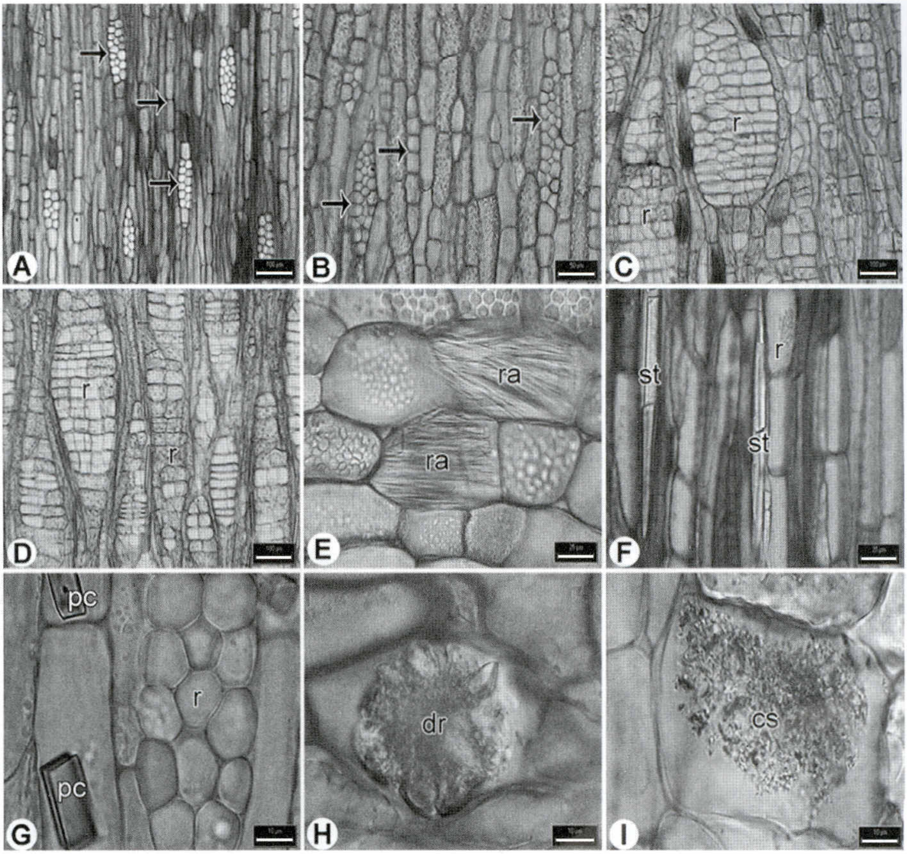

Figure 2. Bark anatomy of Hamelieae and other Rubiaceae, tangential sections. – A: Heterogeneous rays, uni- and biseriate in *Hamelia versicolor*. – B: Heterogeneous rays, uni- and multicellular in *Exostema mexicanum*. – C: Dilated rays in collapsed phloem in *Deppea guerrerensis*. – D: Dilated rays in collapsed phloem in *Exostema caribaeum*. – E: Raphides in cortical cells in *Syringantha coulteri*. – F: Styloids in axial parenchyma cells in *Psychotria horizontalis*. – G: Prismatic crystals in axial parenchyma cells in *Exostema mexicanum*. – H: Druses in axial parenchyma cells in *Randia tetracantha*. – I: Crystal sand in ray cells in *Hintonia latiflora*. — cs = crystal sand; dr = druse; pc = prismatic crystal; r = ray; ra = raphide, st = styloid. — Scale bar 100 µm in A, C, D; 50 µm in B; 25 µm in E, F; 10 µm in G, H, I.

µm in *Pinarophyllon* to 1345 ± 223 µm in *Omiltemia* (Table 3). Mean wall thickness is <3 µm and mean lumen diameter varies from 7 µm in *Plocaniophyllon* to 11.5 µm in *Hamelia*. F/V ratio fluctuates from 1.28 in *Hoffmannia* to 1.65 in *Hamelia* (Table 3).

The parenchyma is diffuse apotracheal (Fig. 5A), in strands of 2–6 cells. Rays are heterogeneous (Fig. 5D, E, G), with the exception of *Hoffmannia*, *Pinarophyllon*, and *Plocaniophyllon*, which have exclusively upright and square cells in their rays (Fig. 5E, H). Ray number varies from 2/mm in *Omiltemia* to 10/mm in *Syringantha*.

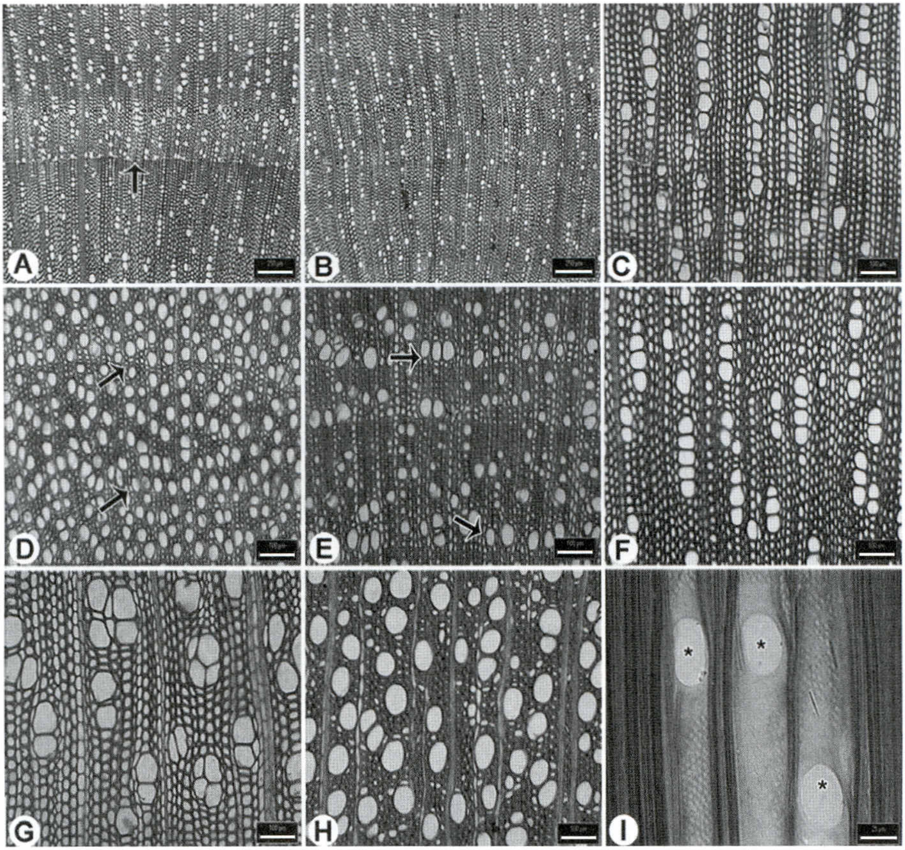

Figure 3. Wood anatomy of Hamelieae and other Rubiaceae, transverse sections. – A: Distinctive growth ring in *Hamelia xorullensis*. – B: Inconspicuous rings in *Omiltemia filisepala*. – C: Diffuse porosity in *Deppea purpusii*. – D: Diffuse to weakly semi-ring-porous wood in *Hintonia latiflora*. – E: Semi-ring porosity in *Bouvardia longiflora*. – F: Vessels in radial rows in *Deppea guerrerensis*. – G: Vessels in clusters in *Psychotria simiarum*. – H: Mostly solitary vessels in *Randia tetracantha*. – I: Simple perforation plate, radial section, in *Hamelia versicolor*. — * = simple perforation plates. — Scale bar 250 μm in A, B; 100 μm in C–H; 25 μm in I.

Ray height has a mean of 382 ± 108 μm in *Syringantha* to 934 ± 324 μm in *Hoffmannia* (Table 3). The multiseriate rays are 2–6 cells wide, mostly 3–4-seriate (22–52 μm). Multiseriate rays have a central portion of entirely procumbent cells and uniseriate marginal extensions of 2–6 upright cells (Fig. 5G) or have a central portion and uniseriate marginal extensions of upright and square cells.

The mineral inclusions in axial and radial parenchyma cells are raphides in *Hamelia* and *Omiltemia*, while they are silica bodies in libriform fibres in *Deppea*, *Hamelia*, *Plocaniophyllon*, *Pinarophyllon*, and *Syringantha*. *Hamelia* may have both mineral inclusions, while raphides always are present in axial or radial parenchyma cells, silica bodies occur exclusively in the libriform fibres of *H. patens* and *H. versicolor*.

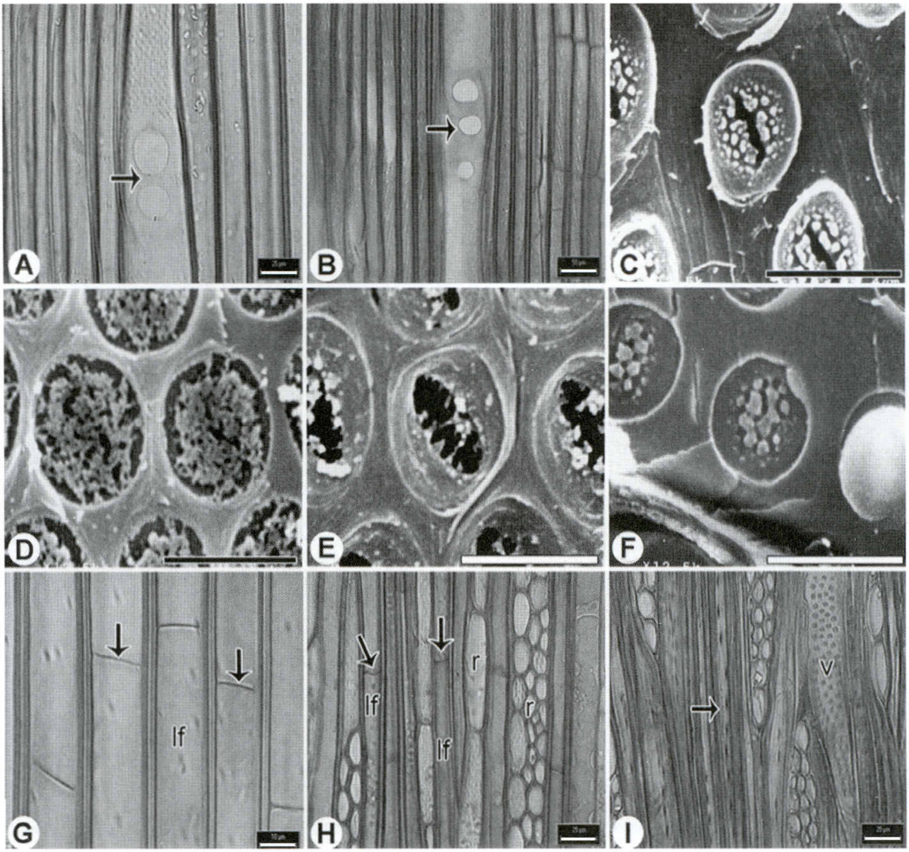

Figure 4. Wood anatomy of Hamelieae and other Rubiaceae, longitudinal sections. – A: Two perforation plates in *Hoffmannia conzattii*. – B: Three perforation plates in *Psychotria simiarum*. – C: Vestured pits with vestures near the outer pit aperture in *Hamelia versicolor*. – D: Vestured pits with vestures occluding the outer pit aperture in *Omiltemia filisepala*. – E: Vestured pits with vestures occluding the outer pit aperture in *Exostema caribaeum*. – G: Libriform septate fibres in *Plocaniophyllon flavum*. – H: Libriform septate fibres in *Syringantha coulteri*. – I: Fibre-tracheids in *Randia pterocarpa*. — lf = libriform fibre; r = ray; v = vessel element. — Scale bar 50 µm in B; 25 µm in A, H, I; 10 µm in G; 4 µm in C–F.

Statistical analyses

The correlation analysis showed a positive significant association between fibre length and vessel element length ($r = 0.81$, $P < 0.0001$, $N = 67$) and between vessel element length and ray height ($r = 0.63$, $P < 0.0001$, $N = 39$); and a negative association between ray number and ray height ($rs = -0.65$, $P < 0.0001$, $N = 40$) and between vessel number and vessel diameter ($rs = -0.75$, $P < 0.0001$, $N = 47$). The covariance analysis confirmed that there are differences among some genera for the following characters: vessel element length ($F = 12.6$, $P < 0.003$, d.f. = 11, $N = 51$); vessel density ($F = 100.8$, $P < 0.0001$, d.f. = 11, $N = 51$); vessel wall thickness ($F = 11.4$, $P < 0.005$, d.f. = 11,

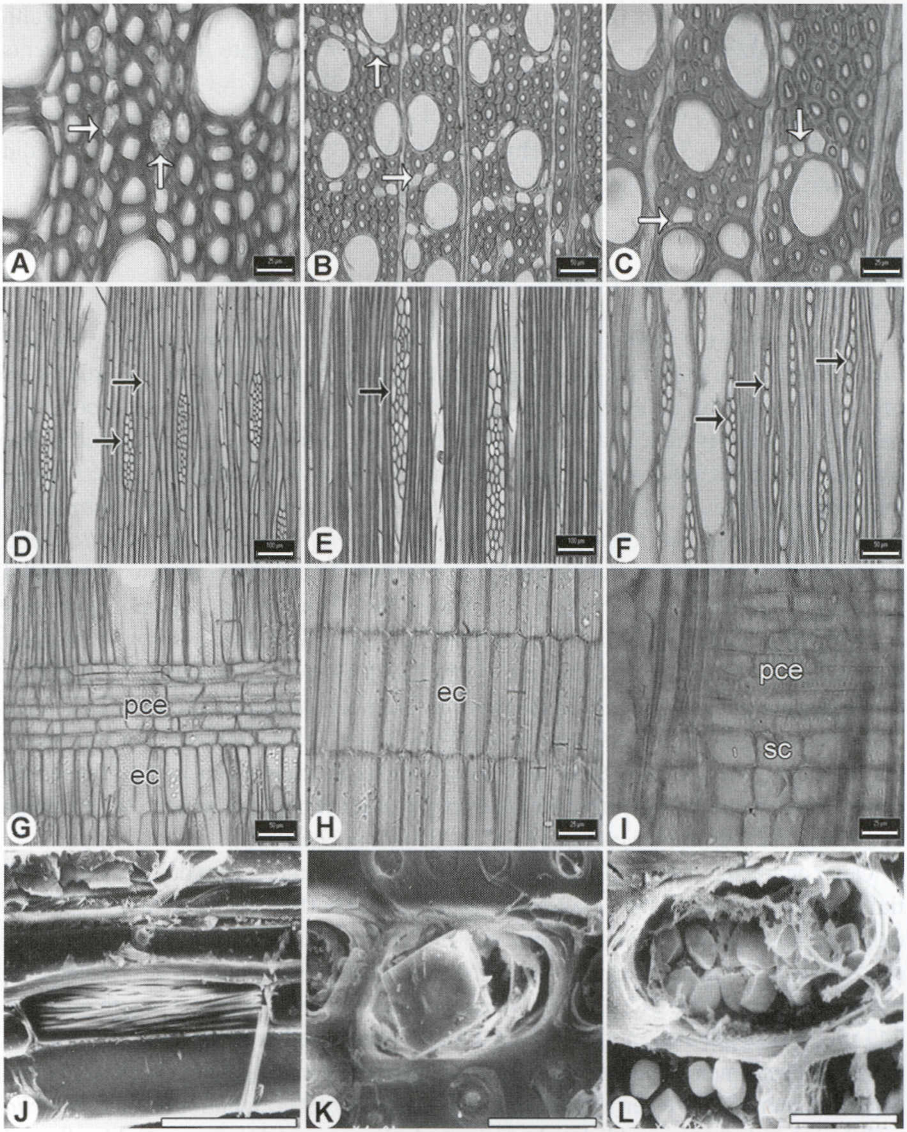

Figure 5. Wood anatomy of Hamelieae and other Rubiaceae, transverse and longitudinal sections. – A: Apotracheal diffuse parenchyma in *Hamelia versicolor*. – B: Diffuse-in-aggregates apotracheal parenchyma in *Randia tetracantha*. – C: Scanty paratracheal parenchyma in *Hintonia latiflora*. – D: Heterogeneous uni- and 2–3-seriate rays in *Deppea guerrensis*. – E: Heterocellular, 3-seriate rays in *Omiltemia filisepala*. – F: Uni- and biseriate rays in *Hintonia latiflora*. – G: Rays with upright and procumbent cells in *Hamelia xorullensis*. – H. Rays with upright cells in *Pinarophyllon flavum*. – I: Rays with square and procumbent cells in *Exostema mexicanum*. – J: Raphide in ray cells in *Hamelia patens*. – K: Prismatic crystal in ray in *Randia aculeata*. – L: Starch grains in ray in *Exostema caribaeum*. — ec = upright cells; fi = fibre; pce = procumbent cells; r = ray; sc = square cells, v = vessel. — Scale bar 100 μm in D, E; 50 μm in B, F, G; 25 μm in A, C, H, I; 4 μm in J–L.

N = 51); number of rays ($F = 661.3$, $P < 0.0001$, d.f. = 11, N = 51); and ray width ($F = 12$, $P < 0.004$, d.f. = 11, N = 51). The type of imperforate tracherary elements can be predicted by vessel grouping index (Wald $\chi^2 = 39.15$, d.f. = 1, $P < 0.0001$). However, vessel density (Wald $\chi^2 = 0.83$, d.f. = 1, $P > 0.36$), vessel diameter (Wald $\chi^2 = 0.84$, d.f. = 1, $P > 0.36$), and parenchyma type (Wald $\chi^2 = 0.48$, d.f. = 1, $P > 0.49$) did not contribute to predict the type of imperforate tracheary elements.

DISCUSSION

Tribe Hamelieae

The genera of the Hamelieae share bark with a single periderm, endodermis, and raphides, while in the wood they share septate libriform fibres, vessels in radial rows of 2–6 vessels with a vessel grouping index of 1.79–2.74, and diffuse apotracheal parenchyma. Other bark and wood characters are present only in a few genera. For example, *Hamelia* and *Syringantha* have more than 10 layers of phellem cells; *Deppea* and *Hamelia* have 10–12 layers of phelloderm cells; *Plocaniophyllon* and *Pinarophyllon* have STEs that are round in cross section; and *Hoffmannia*, *Pinarophyllon*, and *Plocaniophyllon* have wood with paedomorphic rays. These characters are of potential taxonomic and phylogenetic utility within the tribe. For example, paedomorphic rays supported the clade *Hoffmannia–Pinarophyllon–Plocaniophyllon* as a synapomorphy within Hamelieae (Fig. 6) (Martínez-Cabrera 2007). However, *Pinarophyllon* and *Plocaniophyllon*, unlike *Hoffmannia* and the other members of Hamelieae, have more than 135 vessels/mm^2, with a diameter of less than 20 µm. Also, *Hamelia* and *Omiltemia* are the only genera of this tribe that have raphides in axial parenchyma. These two genera also showed longer fibre length than the other Hamelieae genera, with a mean of 1071 ± 232 µm in *Hamelia* and 1345 ± 223 µm in *Omiltemia*.

Other characters may be useful as diagnostic for particular genera due to their potential generic autapomorphic or synapomorphic condition (Martínez-Cabrera 2007). For example, *Plocaniophyllon* has intervessel pits with a mean of 3 µm; *Hoffmannia* has more than one single perforation within the same perforation plate and vessel elements with a length of 775 ± 212 µm; *Omiltemia* possesses a vessel element length of 985 ± 247 µm, and *Deppea* had a pink coloured wood, interpreted as autapomorphic (Fig. 6). This rare phenomenon has been acquired independently in the genera *Cosmocalyx* and *Simira* (Lorence & Dwyer 1988). Although Delprete (1998) mentioned that *Hamelia* and *Syringantha* have a reddish coloured wood when exposed to air, our field collected samples indicate a pale yellow colour wood when exposed to air in both genera.

Inclusion of Syringantha in the Hamelieae tribe

Syringantha shares bark and wood characters with the other members of Hamelieae, among those are the presence of a single periderm, an endodermis, raphides, septate libriform fibres, and diffuse apotracheal parenchyma. These characters support the inclusion of the *Syringantha* as part of the tribe. Moreover a phylogenetic analysis based on morphological characters recovered *Syringantha* as a member of the tribe and sister to *Hamelia*. This sister taxa relationship was supported by various synapomorphies

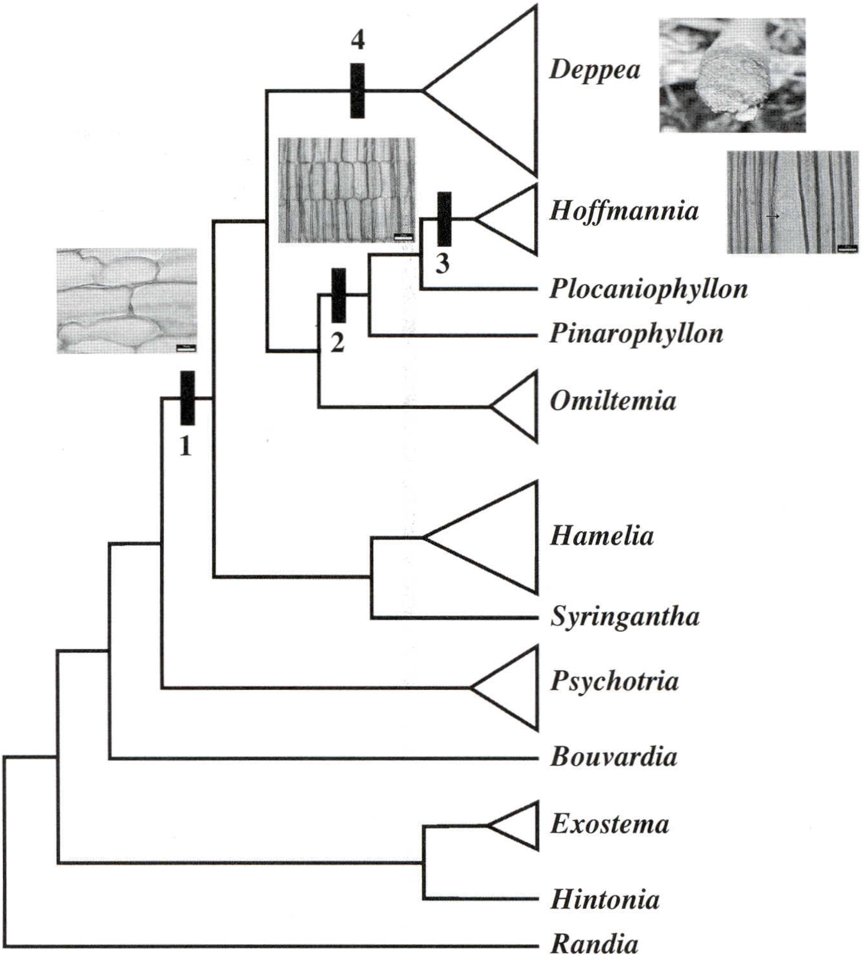

Figure 6. Stem characters in the strict consensus tree of Hamelieae (modified from Martínez-Cabrera 2007). Bars represent the following synapomorphies: 1) Endodermis, one of the novelties that support the monophyly of the Hamelieae tribe. 2) Paedomorphic rays, synapomorphy for the clade *Hoffmannia–Plocaniophyllon–Pinarophyllon*. 3) More than one simple perforation in a single plate, an autapomorphy for the genus *Hoffmannia*. 4) Pink-coloured wood, an autapomorphy for the genus *Deppea*.

such as the inflorescences in a modified dichasium with flowers on the same side of the branch, tubular flowers with five lobules, aestivation quincuncial, oblong filaments, and linear stigma (Martínez-Carbrera 2007).

The Hamelieae as members of the Rubioideae or Cinchonoideae

Jansen *et al*. (2002) studied the distribution of the two types of secondary xylem in the different clades of Rubiaceae, confirming that the wood type I predominates in the family. For example, type I is characteristic of most groups within Cinchonoideae, such as Cephalantheae, Chiococceae, Henriquezieae, Isertieae, Naucleeae, Rondeletieae, Corynanthe group, and *Portlandia* group. However, type II is found in three clades within Cinchonoideae: Hamelieae-Hillieae, Guettardeae, and Cinchoneae (Jansen *et al.* 2002). Our results confirm that type II wood is present in all genera of Hamelieae, as proposed in previous studies in which only one representative of the tribe was included (Koek-Noorman 1969b; Jansen *et al.* 2002). In contrast, the occurrence of raphides in the wood was not corroborated for each member of the Hamelieae; they were only observed in *Hamelia* and *Omiltemia*. It is worth mentioning, that this type of crystals is present in the bark of all the genera of Hamelieae. In general crystals are more consistently present in leaves and bark tissue than wood, so we suggest that crystals must be studied in both leaves and bark tissue to be able to confirm their taxonomic value as higher level markers.

Phylogenetic analyses based on molecular data recovered Hamelieae and Hillieae as having a most recent common ancestor within the Cinchonoideae (Robbrecht & Manen 2006). Therefore, the occurrence of wood type II provides evidence for a close relationship between these tribes (Jansen *et al.* 2002). On the other hand, *Exostema* and *Hintonia* of the *Portlandia* group (Cinchonoideae), which have been morphologically related to the Hamelieae tribe (Bremer 1996) have wood type I (non-septate fibre-tracheids, exclusively solitary vessels, and diffuse-in-aggregates apotracheal, and scanty paratracheal parenchyma); they also differ in ray number (greater than 15 rays/mm), ray height (less than 400 μm), and the type of ray crystals (prismatic in *Exostema*). Wood characters present in *Exostema* and *Hintonia* were similar to most of the known Cinchonoideae tribes (Cephalantheae, Henriquezieae, Isertieae, Naucleeae, Rondeletieae). Furthermore, these genera also exhibit bark features which differentiate them from Hamelieae. Within the subfamily, the occurrence of wood type II in Hamelieae and Hillieae distinguished them from other members of Cinchonoideae. Whether bark characters (presence of a periderm, endodermis, sclerenchyma, and raphides) are also shared with Hillieae remains in question until representative taxa from Hillieae are studied.

The six *Psychotria* species studied have characters of wood type II and raphides, which were previously registered for the genera within Psychotrieae and other groups within the Rubioideae like Argostemmateae, Coccosypseleae, Coussareeae, Paederieae, and the *Mitchella* group (Jansen *et al.* 1997, 2001, 2002). Raphides have been considered as a taxonomic marker in Rubiaceae, especially supporting the Rubioideae subfamily. The presence of this crystal type in bark, leaf, flower, and fruit in the Hamelieae members (Martínez-Cabrera 2007; Martínez-Cabrera *et al.* 2007, 2009) allows us to understand why the tribe was traditionally classified within this subfamily. *Randia* as a representative of the Ixoroideae subfamily also has wood type I, but of the five species of *Randia* studied only *R. aculeata* has prismatic crystals. Interestingly, *Bouvardia* (Cinchoneae/Hedyotideae) is the only genus that has both types of wood, which makes it interesting to study a greater number of species of this genus.

Molecular phylogenies are contributing new evidence towards our understanding of the Rubiaceae evolution. Consequently the analysis of character evolution suggests that raphides and wood type II did not evolve only once within the family, but that wood type II arose independently within the three subfamilies, Cinchonoideae, Ixoroideae, and Rubioideae, and that raphides show two independent origins in Rubioideae and in Cinchonoideae. Anatomical wood characters may, therefore, not support the classification of some taxa at the subfamily level, but they do have taxonomic value to delimit genera and tribes.

Miscelleaneous characters

Bark anatomical characters have been explored very little and have not been evaluated in Rubiaceae (Roth 1981). Previous studies reported an endodermis in young stems of *Cephaelis, Hoffmannia*, and *Mannetia* (Metcalfe & Chalk 1950). We confirmed the presence of the endodermis in all the genera of Hamelieae. The endodermis is probably present in the young stems of some dicotyledons and is lost in the adult stage (Carlquist 2001). However, in this study we confirmed that the endodermis is preserved in the adult stems of shrubs or small trees of Hamelieae and we interpret it as a derived condition that supports the monophyly of Hamelieae tribe (Fig. 6). Since this feature is present at least in some species of *Psychotria*, it is clear that within Rubiaceae the character persists in the adult stage independently. The retention of primary cortical tissues is explaining why even in very old plants of Hamelieae genera a single periderm is maintained. Probably other genera such as *Psychotria* attain wider stems and have longer life-spans, thus primary cortical tissues are replaced by deeper periderms as our data indicate.

The presence of fibres and sclereids in the phloem of the studied genera agrees with that described for *Alseis, Amaioua, Coutarea, Duroia*, and *Genipa* (Roth 1981). Roth points out that the crystals are diagnostic at the species level. Our result confirmed that the crystal type allowed distinguishing between species. For example, *Exostema caribaeum* has styloids, while *E. mexicanum* has prisms. Nevertheless, the crystal type can in other cases be constant at the generic level, as it is the case in the six studied species of *Randia*, which have druses.

Rays with exclusively upright and square cells are named paedomorphic rays by Carlquist (1962). Paedomorphic rays are common in the wood of the small trees or shrubs of some families (Carlquist 2001) and they have been described in several genera of Rubiaceae (Lens *et al.* 2009). Here we described them for the first time within Hamelieae in *Pinarophyllon* distinctive by its monocaul dwarf stems and in *Hoffmannia* and *Plocaniophyllon* represented by small trees reaching up to 2 m height. Paedomorphic rays were present in the few species of *Bouvardia* studied and they need to be confirmed in other members of this genus. Compared with other Cinchonoideae, all members of Hamelieae have relative small sizes (height < 5 m and diameter <15 cm). Within Hamelieae our cladistic analysis based on the structural characters showed that the smaller size, monocaul habit, is derived from an arboreal habit (Martínez-Cabrera 2007). The plesiomorphic woody condition suggests that small-size trees do not necessary maintain juvenile features. Moreover, the occurrence of paedomorphic rays is not a condition necessarily associated with secondary woodiness, as is here exemplified by the more derived members of Hamelieae, although it may be (Lens *et al.* 2009).

The correlations among Hamelieae wood characters agree with those previously documented for other dicotyledons (Giraud 1980; Whalen 1987; Zhang *et al*. 1992; Terrazas 1994; Rosell *et al*. 2007); specially the inverse relationship between vessel diameter and vessel density reported at different taxonomic levels (Baas 1973; Dickison *et al*. 1978; Terrazas 1994; Noshiro & Baas 1998; Rosell *et al*. 2007) and the positive association between vessel element length and fibre length (Chattaway 1936; Carlquist 2001). In Hamelieae woods, vessel element lengths longer than 647 µm are associated with long fibres. The low F/V ratios (<2) in Hamelieae genera suggest no specialization towards the presence of longer fibres, as it is the case of the specialized wood with an intrusive value greater than 2.6 of many species inhabiting drier environments (Carlquist 2001). However, the vessel grouping index is higher in Hamelieae compared with *Bouvardia, Exostema, Hintonia*, and *Randia* suggesting redundancy of vessels (Carlquist 2001). Moreover, vessel grouping index is the variable that can predict the type of imperforate tracheary element as has been previously suggested for other taxa (Carlquist 1984; Rosell *et al*. 2007). Thus wood type I or II in the Rubiaceae may be assigned evaluating only one of these two features.

Based in our phylogeny all members of Hamelieae share wood type II and inhabit pine-oak to evergreen humid forests as elements of the understorey generally with evergreen leaves. In the largest clade *Hoffmannia, Pinarophyllon* and *Plocaniophyllon*, inhabiting the most humid environments (montane cloud and tropical evergreen forests), share the lowest values for vessel grouping index with narrower vessels and higher vessel densities associated with smaller stems. The other two genera of this clade, *Omiltemia* and *Deppea*, share less mesomorphic woods inhabiting not only the mountain cloud forest but also the more drier oak forests. *Syringantha* and *Hamelia* have the highest vessel grouping index and both genera inhabit drier environments. While *Syringantha* is an evergreen inhabiting the xeric-scrub and shows the higher number of vessels, *Hamelia* species are mostly deciduous and inhabit the seasonal dry forest showing the lower vessel density and the wider vessels in the tribe.

We conclude that wood type II and the presence of an endodermis and raphides in the bark support the monophyly of Hamelieae including *Syringantha*. Quantitative attributes (vessel density, vessel diameter, intervascular pit diameter, and length of vessel elements and fibres) and type of rays lend some support to the taxonomic delimitation at the generic level within Hamelieae. While vessel grouping index predicts the type of wood, its range of variation together with vessel density and vessel diameter suggest functional-environmental adaptations of Hamelieae members to inhabit different types of forests.

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