
FOLIAR AND PETIOLE ANATOMY OF TRIBE HAMELIEAE AND OTHER RUBIACEAE¹

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ABSTRACT

In this study, foliar and petiole anatomy of several genera was compared to determine whether there are characteristics that can be used to reevaluate the circumscription and taxonomic position of Hamelieae (Rubiaceae). Our sample included a total of 36 species, which were sectioned using conventional embedding and staining methods. From these species, 23 represented six of the seven genera of Hamelieae sensu Robbrecht; *Syringantha* Standl. was included in order to reevaluate its putative inclusion within Hamelieae. For comparative purposes, the sample also included representative species of tribes Psychotriaceae (Rubiaceae), the *Portlandia* informal group (Cinchonoideae), and Gardenieae (Ixoroideae). Our results indicated that foliar and petiole anatomy contained taxonomic information that can be used in systematic studies. Members of Hamelieae shared the following characters: cuticle more than 3 µm, dorsiventral mesophyll, a single palisade parenchyma cell layer, loose spongy parenchyma, raphides, tannins, and vascular tissue of types I, II, or III in the midrib and petiole. *Plocaniophyllon* Brandegee is unique in having fibers associated with major and minor veins. The petiole vascular tissue has an open arc shape in all studied species except in *Randia* L., which has a closed cylinder. Hamelieae, *Syringantha*, and *Psychotria* L. have raphides, one layer of palisade parenchyma cells, and loose spongy parenchyma, while the other taxa have druses, two layers of palisade parenchyma cells, and compact spongy parenchyma. *Bowardia* Salisb. is unique, showing both raphides and druses. Our results show that comparative foliar and petiole anatomy may provide additional characters to be considered in taxonomic and phylogenetic studies within Rubiaceae. There was anatomical support for the inclusion of *Syringantha* within Hamelieae, while the presence of raphides and the mesophyll attributes suggest an understanding of why Hamelieae was morphologically treated as a member of Rubioideae.

Key words: *Bowardia*, druses, fibers, leaf trace, *Plocaniophyllon*, raphides, *Syringantha*.

The taxonomic usefulness of leaf and petiole anatomical features for recognizing genera or circumscribing generic, tribal, or family level is well known (Metcalf & Chalk, 1950; Smith & Stern, 1962; Baas & Kool, 1983; Wilkinson, 1983; Dickison, 1989; Engel, 1992; Mentink & Baas, 1992; Buijssen, 1995; Dickison & Weitzman, 1996; Sandoval-Zapotitla & Terrazas, 2001; Aoyama & Graças-Sajo, 2003; Fariña et al., 2003; Dos Reis et al., 2004; Souza et al., 2004; Andrés-Hernández & Terrazas, 2006). However, in Rubiaceae, which includes nearly 13,100 species classified into 611 genera (Govaerts et al., 2006), only a few studies have examined foliar and petiole anatomy (Metcalf & Chalk, 1950; Herman et al., 1986; Kocsis et al., 2004).

Robbrecht (1988, 1993) proposed a classification that divides the family into four subfamilies: Antirheoideae, Cinchonoideae, Ixoroideae, and Rubioideae. According to phylogenetic analyses based on molecular data, Antirheoideae is polyphyletic, while Rubioideae has been the most stable (e.g., Verdcourt, 1958; Bremekamp, 1966; Bremer, 1987; Robbrecht,

1988, 1993; Robbrecht & Manen, 2006). The tribe Hamelieae was traditionally placed into the subfamily Rubioideae, largely because of the presence of raphides. However, phylogenetic analyses based on molecular characters, which included a few representative species of this tribe, indicated that Hamelieae would be more appropriately classified in Cinchonoideae (Bremer et al., 1995; Andersson & Rova, 1999; Robbrecht & Manen, 2006).

The circumscription of the tribe Hamelieae itself has been controversial. Classifications have included between two (*Hamelia* Jacq. and *Hoffmannia* Sw. [Verdcourt, 1958, 1976; Bremekamp, 1966; Elias, 1976]) and 11 genera (*Alibertia* A. Rich. ex DC., *Axanthes* Blume, *Brignolia* DC., *Evosmia* Kunth, *Hamelia*, *Olostyla* DC., *Patima* Aubl., *Tepesia* C. F. Gaertn., *Urophyllum* Jack ex Wall., *Sabicea* Aubl., and *Schradera* Vahl [de Candolle, 1830; Endlicher, 1836]). More recently, Bremer (1987) redefined the tribe on the basis of morphological characteristics, the most important of which were inflorescences ebracteate or with very small scale-like bracts, alternate or

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right-rotated quincuncial imbricate corolla aestivation and tetramerous yellow flowers with a usually bicarpellate pistil. With this definition, the tribe includes *Deppea* Cham. & Schldtl., *Hamelia*, *Hoffmannia*, *Omitelia* Standl., and *Pinarophyllon* Brandegee. This delimitation was accepted by Robbrecht (1988). Subsequently, Robbrecht (1993) revised the classification of Rubiaceae and, based on comments by Lorence and Dwyer (1988), added to Hamelieae the genera *Eizia* Standl. and *Plocaniophyllon* Brandegee. A few years later, McDowell (1996) revived the monotypic genus *Syringantha* Standl. (considered by Robbrecht [1993] as a synonym of *Exostema* (Pers.) Bonpl.), asserting that it is closely related to *Hamelia*, with which it shares the presence of raphides and floral morphological characteristics, which suggests that *Syringantha* merits inclusion into the tribe Hamelieae. More recently, based on a supertree analysis, Robbrecht and Manen (2006) amended the tribe Hamelieae to include Hillieae (*Cosmibuena* Ruiz & Pav. and *Hillia* Jacq.), *Chione* DC. (formerly classified within Chiococceae = *Portlandia* group), and *Cosmocalyx* Standl. (formerly considered as incertae sedis). Nevertheless, in Robbrecht and Manen's (2006) proposal, only the genera with analyzed DNA sequences were mentioned, leaving out many taxa considered in previous classifications, among which are four genera included by Robbrecht (1993) as part of Hamelieae: *Eizia*, *Omitelia*, *Pinarophyllon*, and *Plocaniophyllon*, plus *Syringantha*. For this reason, the current most comprehensive proposal for the classification of the tribe is that of Robbrecht (1993) and this is the one followed in the present study.

In this study, the utility of leaf and petiole anatomy in the systematics of Hamelieae is evaluated. Six genera classified by Robbrecht (1993) within the tribe are studied (*Deppea*, *Hamelia*, *Hoffmannia*, *Omitelia*, *Pinarophyllon*, and *Plocaniophyllon*). In addition, *Syringantha* (tribe Cinchoneae, subfamily Cinchonoideae sensu Robbrecht [1988]) and a synonym of *Exostema* sensu Robbrecht (1993) was included in order to reevaluate McDowell's proposal (1996) to resurrect it and classify it within Hamelieae. For comparative purposes, other genera of different tribes and subfamilies were also considered in the study.

MATERIAL AND METHODS

To evaluate the utility of leaf and petiole anatomy for generic and tribal classification, complete leaves of 23 species representing six genera (Appendix 1) of Hamelieae sensu Robbrecht (1993) were described: *Deppea* (11/27 spp.), *Hamelia* (5/17 spp.), *Hoffmannia* (6/111 spp.), *Omitelia* (2/2 spp.), *Pinarophyllon* (1

spp.), and *Plocaniophyllon* (1 sp.). We sampled more than 25% of the recognized species for each genus in Hamelieae, except *Hoffmannia*, being careful to represent the described morphological diversity of each genus. For comparative purposes, 13 species of the following genera were also considered in the study (Appendix 1): *Exostema*, because of the previous consideration of *Syringantha* as a synonym of it; *Hintonia* Bullock, as potentially related to *Exostema* (both belonging to the informal *Portlandia* group, within Cinchonoideae); *Psychotria* L. (Psychotriaceae), as a comparative stable member of Rubioideae; *Randia* L. (Gardenieae), as a comparative stable member of Ixoroideae; and *Bowardia* Salisb., as another genus with unstable subfamilial affinities (Hedyotideae–Rubioideae or Cinchoneae–Cinchonoideae).

Leaves of those species were collected in the field and fixed in formalin-acetic acid-alcohol (FAA) (Ruzin, 1999). From Hamelieae sensu Robbrecht (1993), only *Eizia* is not included in this study because we have not been able to find it in the field, and this monotypic genus with a restricted distribution in the state of Chiapas, Mexico, is only known from the type collection. We attempted to include representative species of *Cosmibuena*, *Cosmocalyx*, and *Hillia*, which were considered as Hamelieae sensu Robbrecht and Manen (2006), but we have not been able to find them in the field and it was impossible to section leaves from herbarium material.

Voucher specimens of the newly collected material were deposited at MEXU and CHAPA herbaria (acronyms following Holmgren et al., 2004). In addition to the personal collections, leaves from herbarium specimens (Appendix 1) were used to complete the sampling and to increase the number of individuals sampled per species (two or more individuals were sampled per species). Leaves from the herbarium material were rehydrated in 5% NaOH at 60°C for 1 h. and fixed in FAA for 24 h. All samples were dehydrated in a Leica (Wetzlar, Germany) automatic TP1020 changer, embedded in paraffin, sectioned (transverse and paradermal) 14 µm thick with a rotary microtome, stained with safranin-fast green, and mounted in Euparal (Carolina Supplies, Burlington, North Carolina, U.S.A.) synthetic resin. Terminology follows Metcalfe (1979) and Mentink and Baas (1992) for leaf, Wilkinson (1979) for cuticle, and Howard (1979) for petiole anatomy. It should be noted that previous studies in which petiole vascular tissue was described have used the terms “main vascular bundle” and “lateral vascular bundle” or “median vascular strand and accessory bundles” to refer to the central trace and lateral bundles, respectively (Metcalfe & Chalk, 1950; Herman et

al., 1986; Kocsis et al., 2004). Because the position of the tissues is the same, we consider them homologous. In this paper, therefore, we use the terms “central trace” and “lateral bundles” proposed by Howard (1979).

RESULTS

INDUMENT

Simple unicellular and/or multicellular trichomes are present in most studied species; only *Plocaniophyllon* has glabrous leaves. Within Hamelieae, the simple multicellular trichomes are the most common, and unicellular trichomes are present only in *Hamelia* (Fig. 1A), where they are 27–48 μm long and thin walled ($< 2 \mu\text{m}$). Outside Hamelieae, *Syringantha* and *Bouvardia* also have simple unicellular trichomes, being exclusively of this type in the first genus. The simple multicellular trichomes have up to eight cells in most members of the tribe, but in *Pinarophyllon* they have 10 to 11 cells (Fig. 1B), a range also present only in *Hintonia*. Trichomes are commonly present on lamina, midrib, and margins (Table 1). They have mostly thin walls ($< 2 \mu\text{m}$), but within Hamelieae in *Deppea*, simple multicellular trichomes have thicker walls (3–5 μm), and *Syringantha* and *Bouvardia* have the thickest walls (5–6 μm) (Table 1).

CUTICLE

The cuticle may be smooth (Fig. 1C), but cuticular striations occur frequently, and both can be found in some genera of Hamelieae, as well as *Deppea* and *Hoffmannia*, and in *Psychotria* and *Randia* of other tribes (Table 1, Fig. 1D–F). Cuticle thickness is less than 3 μm in Hamelieae; genera of other tribes have thicker cuticles (Table 1).

EPIDERMAL CELLS

In surface views, unspecialized epidermal cells generally show the entire range from straight to undulating anticlinal walls (Fig. 1G, H), varying among the genera of Hamelieae and other tribes. Straight walls are common on the adaxial surface, while undulating walls dominate in the abaxial epidermis in some genera, namely *Hamelia* and *Pinarophyllon* of Hamelieae and *Exostema*, *Hintonia*, and *Randia* of the *Portlandia* group and *Gardenieae*. In transverse section, the epidermal cells are mostly square or rectangular on both surfaces, or exclusively ellipsoid shaped with a short dome in the outer periclinal cell walls in the cases of *Hamelia* and *Pinarophyllon* within Hamelieae (Fig. 1A, B), and in *Exostema*, *Hintonia*, and *Randia* outside Hamelieae

(Table 1), whereas *Bouvardia* has a nipple-shaped papillae in adaxial surface (Fig. 1F).

THE STOMATAL COMPLEX

Stomata occur on the lower epidermis and are superficial. Mostly paracytic stomata (Fig. 1I) with two to three subsidiary cells occur among the sampled species (Table 1), but paralelocytic stomata (Fig. 1J) are also present in *Hoffmannia*, *Omitemia*, and *Pinarophyllon* and are exclusive in *Plocaniophyllon*. Subsidiary cells show straight or undulating walls (Fig. 1I, J). However, in *Deppea*, only the larger subsidiary cells have undulating walls. Stomatal size mostly varies between 30 and 45 μm in length. Giant stomata are present in four genera of Hamelieae (*Hoffmannia*, *Omitemia*, *Pinarophyllon*, and *Plocaniophyllon*) and in *Psychotria* (Table 1).

MESOPHYLL

All the material studied showed dorsiventral mesophyll. The palisade tissue consists of one adaxial layer in Hamelieae (Fig. 2A) and *Syringantha*, one to two adaxial layers in *Bouvardia* and *Psychotria*, and two layers in the other genera (Table 1, Fig. 2B). The spongy zone varies from two to six cell layers. Cell arrangement is loose in all material studied from Hamelieae, *Syringantha*, and *Psychotria*, and compact in the remaining studied species (Table 1).

CELLULAR CONTENTS

Crystals are present exclusively as raphides in the mesophyll and midrib in genera of Hamelieae (Fig. 2C), *Syringantha*, and *Psychotria*. Druses occur in specialized cells, idioblasts, in the mesophyll of *Exostema* and *Randia* (Fig. 2D), while druses and raphides are present in *Bouvardia* (Fig. 2E). Dark-staining deposits are also common in the mesophyll (Fig. 2F) and are sometimes associated with the phloem of major and minor veins in Hamelieae (Table 1); they are present but scarce in *Syringantha* and *Psychotria*. The restriction of crystals and dark-staining deposits to particular tribes suggests the potential taxonomic value of these features. Only the leaves of *Hintonia* lack dark cell contents.

MIDRIB

In Hamelieae, the midrib is commonly raised on the abaxial surface and grooved or raised adaxially as seen in transverse sections (Fig. 3). The cuticle has similar characteristics to those of the lamina, but reaches higher (up to 6 μm) in *Deppea* and *Hoffmannia*; outside Hamelieae it is also thin in *Psychotria*

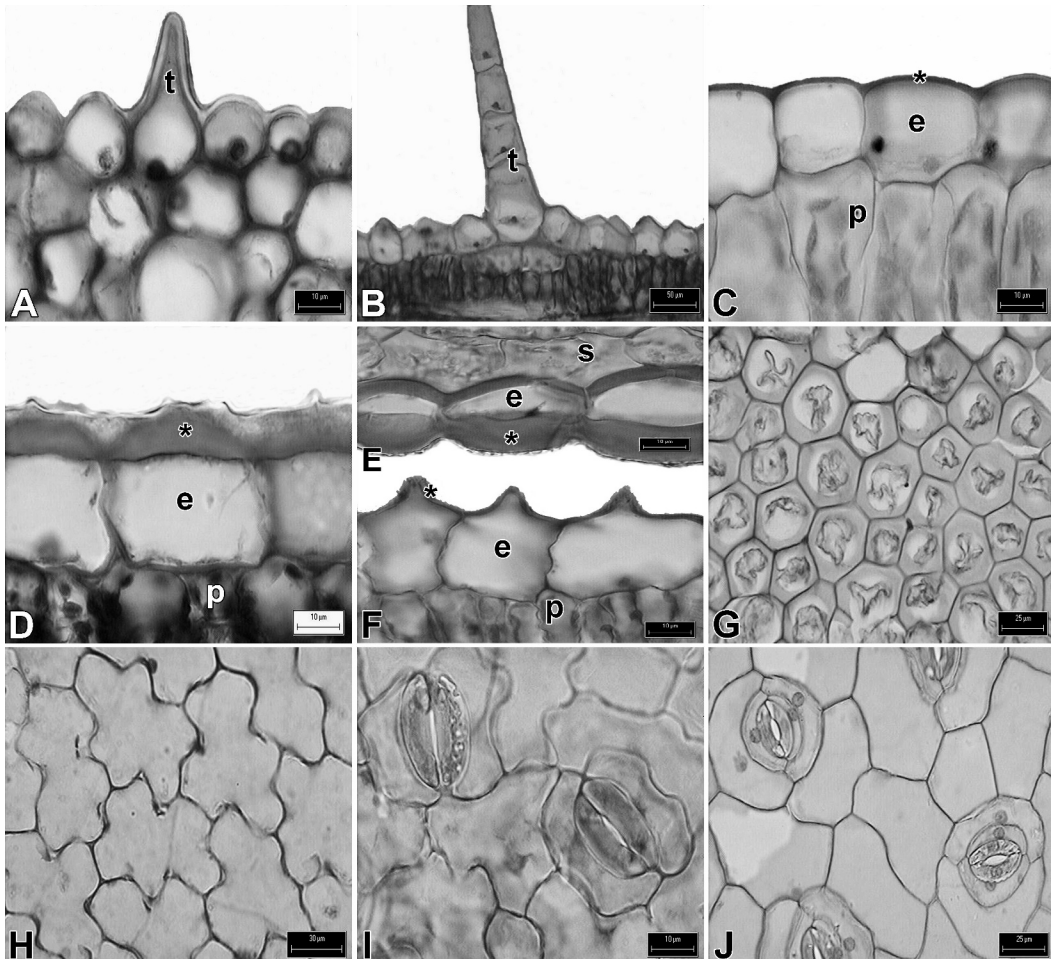


Figure 1. Foliar anatomy of the tribe Hamelieae and other Rubiaceae. —A. *Hamelia* (*H. Vibrans* 5885, MEXU), simple unicellular trichome. —B. *Pinarophyllon* (*D. Martínez et al.* 317, CHAPA), simple multicellular trichome. —C. *Deppea* (*H. Ochoterena* 335, MEXU), smooth cuticle in adaxial epidermis. —D. *Syringantha* (*D. Martínez* 190, CHAPA), cuticular striations in adaxial epidermis. —E. *Bouvardia* (*J. Rzedowski* 39784, MEXU), cuticular striations in abaxial epidermis. —F. *Bouvardia* (*J. Rzedowski* 39784, MEXU), cuticular striations in adaxial epidermis. —G. *Hamelia* (*D. M. Arias & D. Martínez* 2198, MEXU), adaxial epidermis with straight anticlinal cell wall. —H. *Hoffmannia* (*A. Log & M. A. Heath* 154, MEXU), adaxial epidermis with undulating anticlinal cell walls. —I. *Exostema* (*H. Ochoterena* 289, MEXU), paracytic stomata. —J. *Omiltemia* (*M. A. Heath & A. Long* 1173, MEXU), paracytic stomata. Scale bars: A = 50 µm; B–F, I = 10 µm; G, J = 25 µm; H = 30 µm. *, cuticle; e, epidermis; p, palisade parenchyma; s, spongy parenchyma; t, trichome.

and thicker and more variable in members of other tribes (Table 2). In transverse sections, the epidermal cells are ellipsoid shaped with a short dome in the outer periclinal cell walls in abaxial epidermis and periclinal elongated in adaxial epidermis in most genera, but exclusively ellipsoid shaped on both surfaces in *Hoffmannia* and *Pinarophyllon*, and in *Psychotria* and *Randia*. The angular or lacunar collenchyma consists of two to eight cell layers below the abaxial epidermis and two to 10 cell layers in the adaxial epidermis (Fig. 3, Table 2). The vascular bundles are collateral. The variation in the vascular tissue of the midrib was classified into five types

(Table 2). In *Deppea*, *Exostema*, *Hintonia*, and *Bouvardia*, it is a simple open arc (type I, Fig. 3A). In *Hamelia*, it is also a simple open arc, but with invaginated ends and a pair of lateral bundles (type II, Fig. 3B). In the remaining genera of Hamelieae as well as in *Syringantha*, it is a simple open arc with slightly curved ends and a pair of lateral bundles (type III, Fig. 3C). In *Psychotria*, the vascular pattern has a V-shaped open arc with invaginated ends and four to six lateral bundles below or between the invaginated ends (type IV, Fig. 3D, E). *Randia* is unique in having a closed ring (type V, Fig. 3F). The vascular tissue has xylem cells in radial rows separated by paren-

Table 1. Characters of foliar anatomy of the Hamelieae, *Syringantha*, and other representative genera.

Genera	Trichomes			Cuticle		Epidermal cell shape		Stomata		Mesophyll			Contents	
	Type	Cell number	Wall thickness (µm)	Distribution	Type	Thickness (µm)	Adaxial and abaxial	Type	Length (µm)	No. of palisade layers	Spongy parenchyma	Tannins	Crystals	Distribution
Hamelieae														
<i>Deppea</i>	m	3-6	3-5	l, mv, s, t, ma	st (sm)	< 3	el, sq	pc	38.9 (± 3.2)	1	lo	+	ra	me, ph, a
<i>Hamelia</i>	u, m	2-8	< 2	l, mv, s, ma	st	< 3	el	pc	34.0 (± 3.8)	1	lo	+	ra	me, ph
<i>Hoffmannia</i>	m	4	< 2	l, mv, ma	st (sm)	≤ 3	re, sq	pc (pl)	67.7 (± 4.9)	1	lo	+	ra	me, ph, a
<i>Omitelia</i>	m	6-8	< 2	l, mv, ma	sm	< 3	el, sq	pl (pc)	66.2 (± 7.2)	1	lo	+	ra	me, ph, a
<i>Pinarophyllon</i>	m	10-11	< 2	l, mv, ma	sm	≤ 2	el	pc (pl)	49.8 (± 3.5)	1	lo	+	ra	me, ph, a
<i>Plocaniophylon</i>	-	-	-	-	st	≤ 3	sq, re	pl	57.3 (± 6.8)	1	lo	+	ra	me, ph
Portlandia group														
<i>Syringantha</i> (= <i>Exostema</i>)	u	-	5-6	mv	st	> 7	re	pc	39.6 (± 3.7)	1	lo	+	ra	me
<i>Exostema</i>	m	2-7	< 2	mv, ma	st	4-5	el	pc	33.1 (± 5.0)	2	co	-	dr	me
<i>Hintonia</i>	m	10-11	< 2	mv	sm	3-4	el	pc	22.4 (± 2.7)	2	co	-	-	-
Psychotriaceae														
<i>Psychotria</i>	m	6-9	2-3	l, mv, s, ma	sm (st)	3-4	el, sq	pc	44.8 (± 7.0)	1 (2)	lo	+	ra	me
Gardenieae														
<i>Randia</i>	m	3-4	2-4	mv	st, sm	≤ 5	el	pc	30.5 (± 5.2)	2	co	-	dr	me, e
Cinchoneae														
Hedyotideae														
<i>Bouvardia</i>	u, m	3-5	5-6	l, mv, s	st	10-12	el, sq	pc	33.4 (± 3.2)	1 (2)	co	-	ra, dr	me

a, arc; co, compact; dr, druses; e, epidermis; el, ellipsoid between epidermis and lamina; l, lamina; lo, loosed; m, multicellular trichome; ma, margin; me, mesophyll; mv, midrib; pc, paracytic; ph, phloem; pl, parallelolytic; ra, raphides; re, rectangular; s, secondary veins; sm, smooth; sq, square; st, striate; t, tertiary veins; u, unicellular trichome; +, present; -, absent.

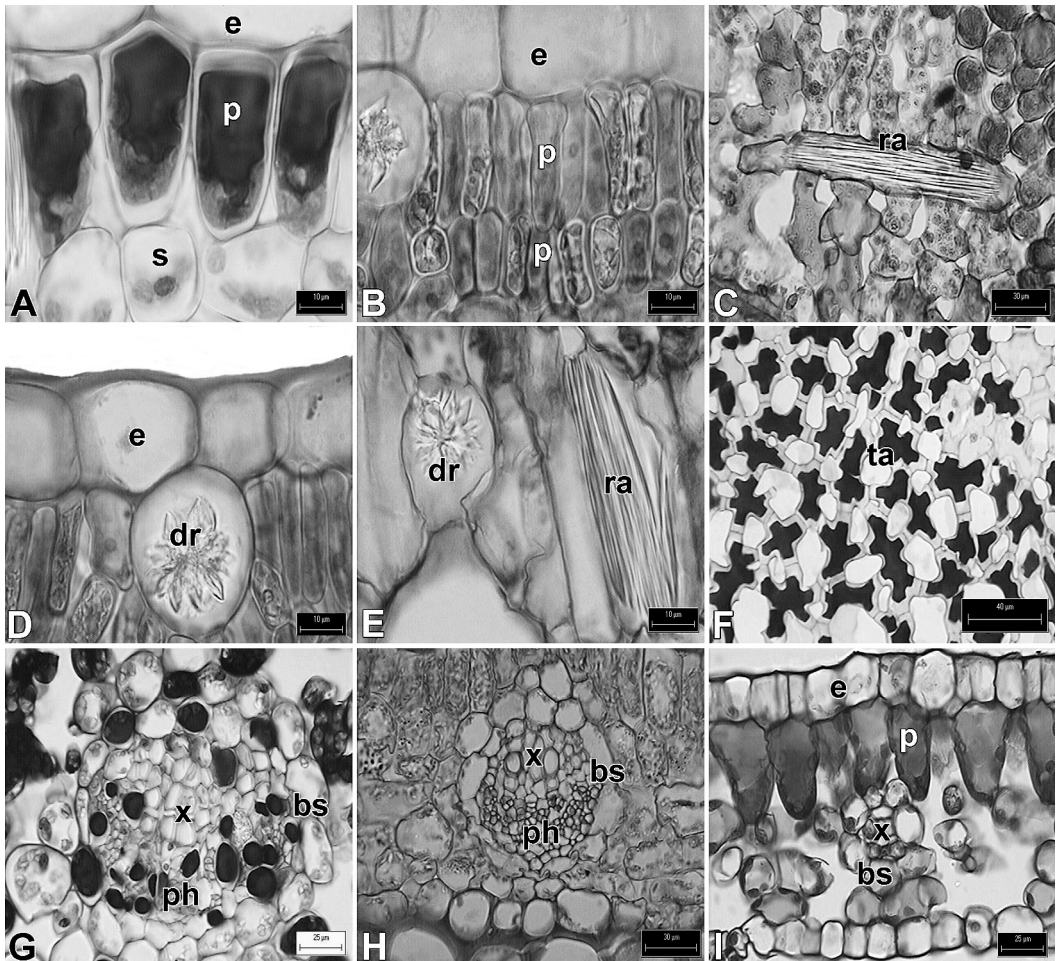


Figure 2. Foliar anatomy of the Hamelieae transverse sections. —A. *Plocaniophyllon* (D. Martínez et al. 312, CHAPA), single palisade parenchyma cell layer. —B. *Randia* (*H. Iltis* 29682, CHAPA), two palisade parenchyma cell layers. —C. *Syringantha* (A. Mora 5314, MEXU), raphides in mesophyll. —D. *Randia* (T. Wendt et al. 3131, MEXU), druses in mesophyll. —E. *Bouvardia* (P. Tenorio & C. Romero 1286, CHAPA), raphides and druses in mesophyll. —F. *Pinarophyllon* (D. Martínez et al. 316, CHAPA), tannins in spongy parenchyma. —G. *Omiletemia* (D. Martínez 236, CHAPA), secondary vein. —H. *Hintonia* (*H. Ochoterena* 224, MEXU), tertiary vein. —I. *Hoffmannia* (D. Martínez 187, CHAPA), quaternary vein. Scale bars: A, B, D, E = 10 μ m; C, H = 30 μ m; F = 40 μ m; G, I = 25 μ m. bs, bundle sheath; dr, druse; e, epidermis; p, palisade parenchyma; ph, phloem; ra, raphide; s, spongy parenchyma; ta, tannins; x, xylem.

chyma cells with dark-staining deposits. The vascular bundle is enclosed by an arc of parenchyma cells with distinctive dark-staining deposits in Hamelieae and *Syringantha*, except in the case of *Plocaniophyllon*, where the arc enclosing the vascular bundle is composed of fibers. In members of other tribes, the arc enclosing the vascular bundle is more variable, with collenchyma or sclerenchyma (Table 2).

MAJOR AND MINOR VEINS

Major veins are mostly similar to the midrib in their anatomy, with a bundle sheath of parenchyma cells (Fig. 2G, H). The minor veins are also collateral and

have one to two tracheary elements and a sheath of exclusively parenchyma cells in Hamelieae and *Hintonia*, *Psychotria*, and *Randia* (Fig. 2I) and fibers in *Plocaniophyllon*.

PETIOLE

In transverse sections, the petiole is mostly round at the base and winged toward the lamina, except in *Deppea* in which the petiole is reniform at the base, and in *Pinarophyllon* in which it is winged along its entire length. Indument, cuticle, and epidermal cells were observed to be mostly similar to the lamina in all material studied (Table 2, Fig. 4A–E). The number of

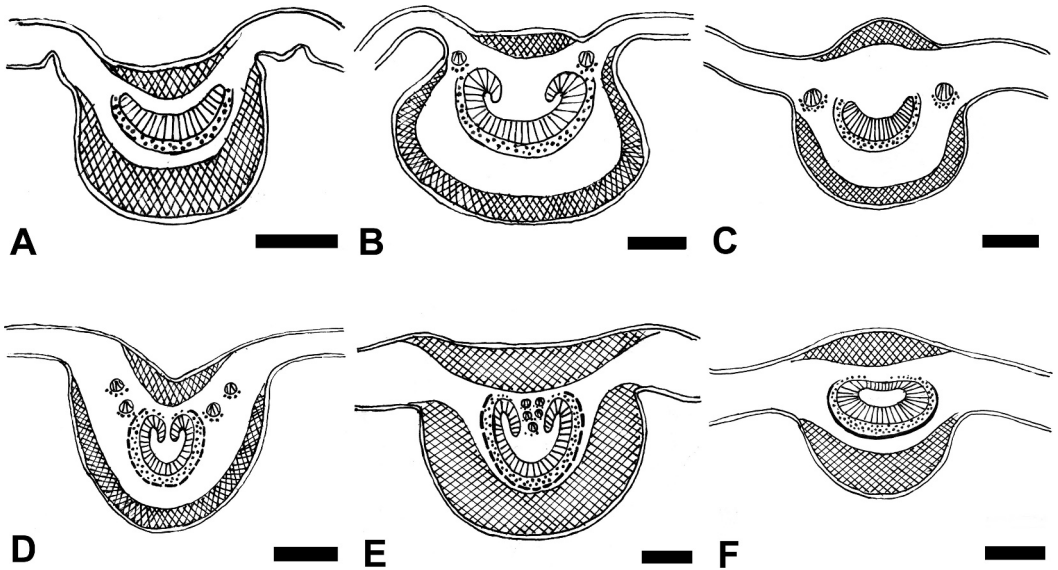


Figure 3. Blade midrib of the Hamelieae and other representatives: vascular tissue shape and distribution types. —A. *Exostema* (D. Lorence 3036, CHAPA), type I. —B. *Hamelia* (Maya 1868, CHAPA), type II. —C. *Omitelia* (A. Méndez 285, MEXU), type III. —D. *Psychotria* (Magallanes 3687, CHAPA), type IV. —E. *Psychotria* (S. Maya 1753, CHAPA), type IV. —F. *Randia* (E. Domínguez & H. Ochoterena 1775, MEXU), type V. Symbols: hatched line = collenchyma; continuous, thick black line above phloem = fibers; white = parenchyma; narrow black line above phloem = parenchyma with tannins; dotted line = phloem; discontinuous black line above phloem = sclerenchyma; vertical lines = xylem. Scale bars: A–E = 250 μ m; F = 100 μ m.

angular or lacular collenchyma cell layers is variable (Fig. 5A–C), with three to five layers being the most common, but up to 12 layers are present in *Deppea* and *Pinarophyllon*. In some species of *Hamelia* and in *Syringantha* and *Randia*, the vascular leaf trace was enclosed by collenchyma. The range of vascular leaf trace patterns in the petiole was classified into six types and is schematically illustrated in Figure 5. In *Deppea* and *Syringantha*, the vascular pattern has only an open arc and a pair of lateral bundles (type I, Fig. 5A) with a continuous parenchymatous sheath with dark-staining deposits occluding the cell lumina (Fig. 4F). In *Hamelia*, the open arc has invaginated ends and only one pair of lateral bundles (type II, Figs. 4G, 5B). Toward the lamina, the central trace is more curved toward the base of the petiole, with the lateral bundles in the same position. The most common leaf trace pattern in Hamelieae consists of an open arc with slightly curved ends, the central leaf trace, and two pairs of lateral bundles (type III, Fig. 5C). Toward the lamina, the central trace is more curved than toward the base of the petiole and it has a continuous parenchymatous sheath with dark-staining deposits occluding the cell lumina. The leaf trace pattern in members of other tribes consists of an open V-shaped arc with straight or invaginated ends and one to two pairs of lateral bundles (types IV, VI, Fig. 5D, E), and a closed ring in *Randia* (type V,

Figs. 4H, 5F). The central leaf trace has a sheath of sclereids in *Psychotria*, fibers in *Randia* (Fig. 4I), or the sheath is absent in members of other studied tribes (Table 2). Cellular contents are similar to those of the mesophyll and midrib (Tables 1, 2, Fig. 4J–L), except in *Hintonia*, which has druses in the collenchyma.

DISCUSSION

Leaf and petiole anatomical characters are quite homogeneous among genera of the tribe Hamelieae. There are, however, certain exceptions, e.g., the genus *Hamelia*, which is characterized by type II vascular tissue in the midrib and petiole, and unicellular and multicellular trichomes, and the genus *Plocaniophyllon*, characterized by the straight anticlinal walls in abaxial and adaxial epidermal cells, parallelocytic stomata with three to four straight-walled subsidiary cells arranged in a C shape, no trichomes, and fibers sheathing the midrib and other veins. Our multiple sampling for the species studied indicates that characters described within the species are constant; however, interspecific variation was found for the number of spongy parenchyma layers, as well as parenchyma and collenchyma layers in the midrib and the petiole. These features are not diagnostic at the genus level. Moreover, trichome type and distribution sometimes varied among species of *Deppea* and

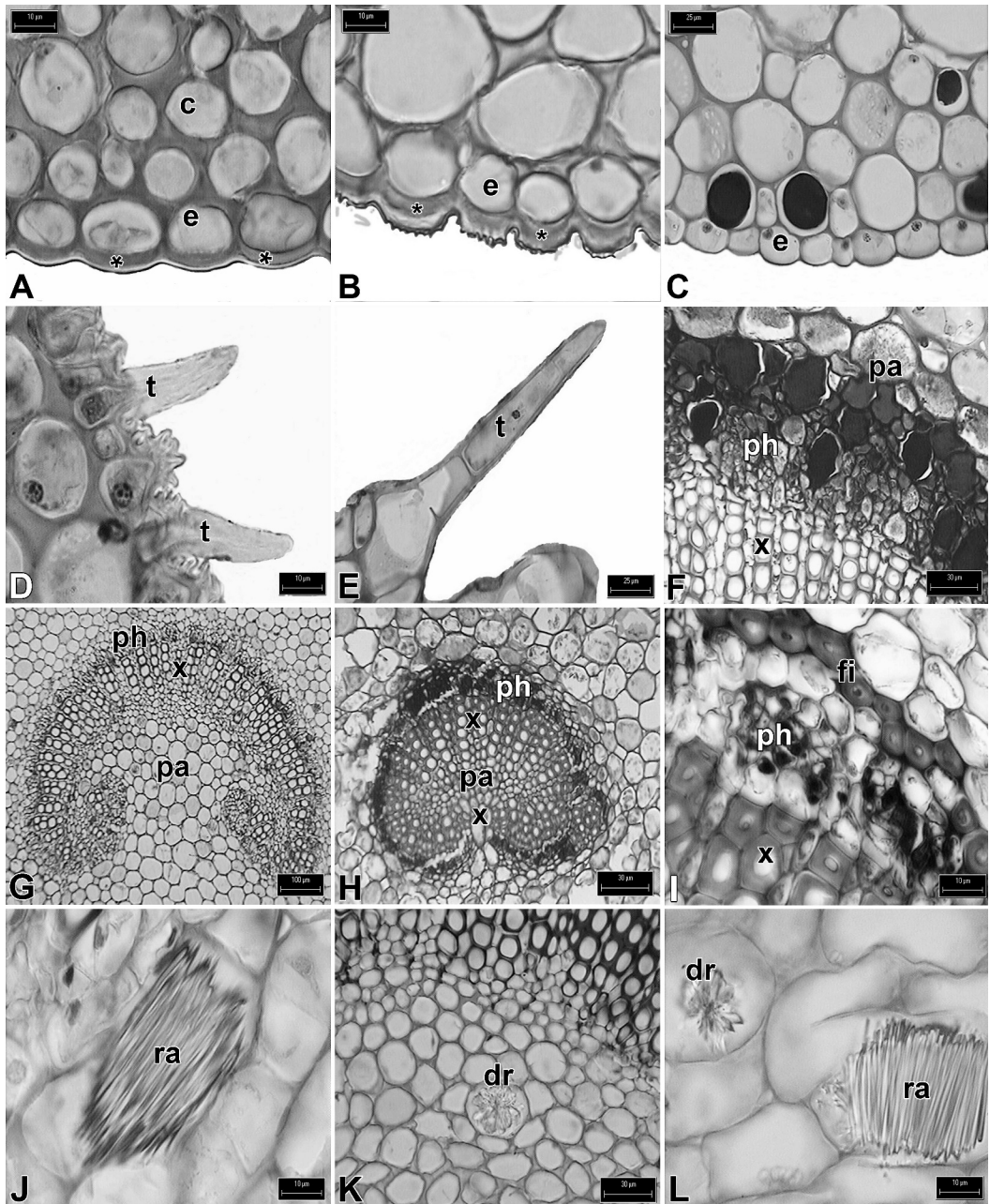


Figure 4. Petiole anatomy within the Hamelieae and other representatives. —A. *Hintonia* (D. Martínez & E. Domínguez 201, CHAPA), abaxial epidermis with smooth cuticle and angular collenchyma. —B. *Exostema* (E. Carranza 3362, CHAPA), abaxial epidermis with striated cuticle and lacunar collenchyma. —C. *Omitelia* (D. Martínez 275, CHAPA), abaxial epidermis with smooth cuticle and lacunar collenchyma. —D. *Syringantha* (F. González Medrano et al. 4659, MEXU), simple unicellular trichomes. —E. *Psychotria* (E. Martínez et al. 27882, MEXU), simple multicellular trichomes. —F. *Deppea* (D. Martínez 254, CHAPA), parenchyma with tannins above phloem. —G. *Hamelia* (D. Martínez 167, CHAPA), central trace forming an open arc. —H. *Randia* (E. Domínguez & H. Ochoterena 1775, MEXU), central trace forming a closed ring. —I. *Randia* (E. Domínguez & H. Ochoterena 1775, MEXU), fibers sheathing the vascular tissue. —J. *Plocantiophyllum* (D. Martínez et al. 311, CHAPA), raphides in parenchyma. —K. *Exostema* (E. Martínez et al. 29719, MEXU), druses in collenchyma. —L. *Bowardia* (J. Rzedowski 38901, CHAPA), raphides and druses in parenchyma. Scale bars: A, B, D, I, J, L = 10 μ m; C, E = 25 μ m; F = 100 μ m; G, H, K = 30 μ m. *, cuticle; c, collenchyma; dr, druse; e, epidermis; fi, fibers; pa, parenchyma; ph, phloem; ra, raphide; t, trichome; x, xylem.

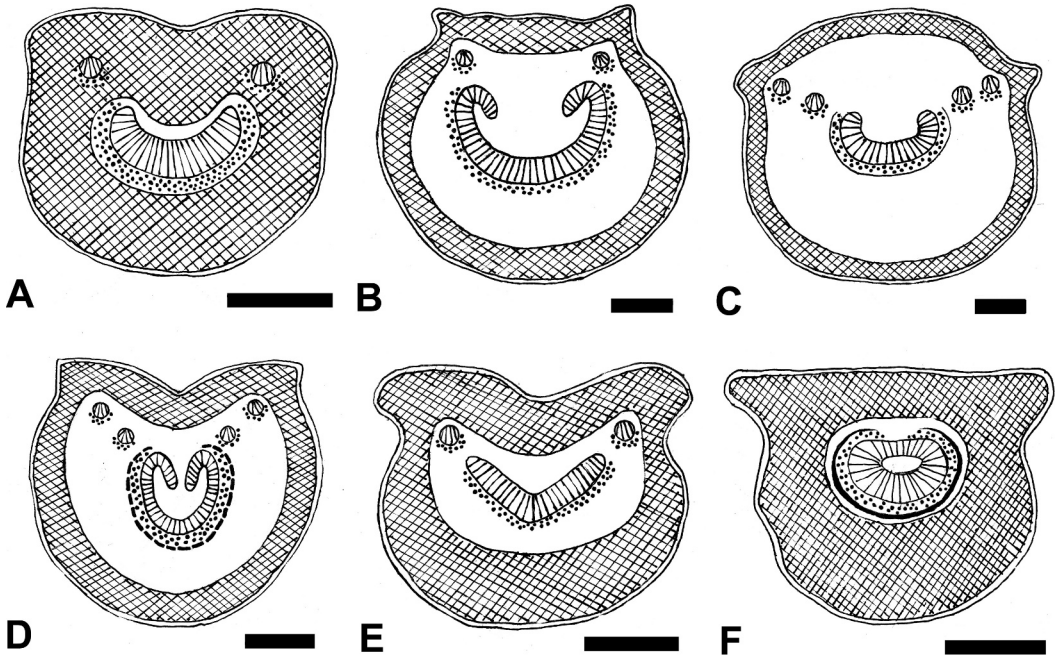


Figure 5. Petiole: vascular tissue types. —A. *Deppea* (J. I. Calzada 5470, MEXU), type I. —B. *Hamelia* (D. Martínez 167, CHAPA), type II. —C. *Hoffmannia* (Cuevas & Guzmán 4185, CHAPA), type III. —D. *Psychotria* (D. Martínez & E. Domínguez 200, CHAPA), type IV. —E. *Bouvardia* (H. Vibrans 4932, CHAPA), type VI. —F. *Randia* (E. Domínguez & H. Ochoterena 1775, MEXU), type V. Symbols: hatched line = collenchyma; continuous thick black line above phloem = fibers; white = parenchyma; narrow black line above phloem = parenchyma with tannins; dotted line = phloem; discontinuous black line above phloem = sclerenchyma; vertical lines = xylem. Scale bars: A–F = 250 μ m.

Hoffmannia, thus a larger sampling in those large genera such as *Deppea* and *Hoffmannia* needs to be studied.

Several types of vascular tissue distribution in the midrib and petiole were recognized, and they appear to be useful diagnostic characters at the generic level. Types I, II, and III were observed in different genera of Hamelieae. *Deppea* has type I, in which the petiole is formed by a multiple trace, with the central trace forming an open arc and a pair of lateral bundles. In the midrib, the lateral bundles are fused to the central trace. *Hamelia* has type II, which is characterized by a multiple trace and with the central trace forming an open arc, with invaginated ends and a pair of lateral bundles. The vascular tissue has the same distribution in the petiole and the midrib. The most common vascular tissue distribution type found in the tribe was type III, observed in the genera *Hoffmannia*, *Omiltemia*, *Pinarophyllon*, and *Plocaniophyllon*. In the petiole, the tissue is formed by a multiple trace with the central trace forming an arc, and two pairs of lateral circular bundles. Unlike the petiole, the midrib has only one pair of lateral bundles. In *Deppea*, *Hamelia*, *Hoffmannia*, *Omiltemia*, and *Pinarophyllon*, the vascular tissue contains an arc formed by parenchyma cells with tannins above the phloem.

This, together with morphological characters such as the dry, capsular fruit, axial placentation, and numerous small seeds with foveolated-reticulated testa, supports a relationship between *Deppea*, *Omiltemia*, *Pinarophyllon*, and *Plocaniophyllon* (Lorence & Dwyer, 1988).

Syringantha shares many lamina and petiole features with Hamelieae, including the single palisade parenchyma layer, loose spongy parenchyma, raphides, and vascular tissue type I in the petiole (as in *Deppea*); and it shares common features of the midrib with *Hoffmannia*, *Omiltemia*, *Pinarophyllon*, and *Plocaniophyllon*. These characters support the proposal from McDowell (1996) to include *Syringantha* in the tribe. In addition, *Syringantha* shares with some species of *Hamelia*, as mentioned by McDowell (op. cit.), deciduous stipules, secundiflorous inflorescences, yellow flowers, stamens with flattened filaments, introrse dehiscence, subconical nectariferous disc shape, and smooth to reticulate exine of the pollen grain. *Syringantha* is the only member of the tribe to inhabit drier environments, and its narrowly elliptical leaves and thick cuticle are doubtlessly adaptations to these environments.

Members of Hamelieae share some lamina and petiole characters with the studied representatives of

Table 2. Characters for foliar and petiole anatomy of Hamelieae tribe, *Syringantha*, and other representative genera.

Genera	Midrib				Petiole							
	Cuticle (μm)	Collenchyma (abaxial and adaxial)	Vascular pattern	Vascular type ¹	Arc	Trichome	Cuticle (μm)	Leaf trace type ¹	Central strand sheath	Tannin	Crystals	Distribution
Hamelieae												
<i>Deppea</i>	3-6	3-6, 5-7	o	I	pa	m (u)	< 2	I	pa	+	ra	pa, co ph, vs
<i>Hamelia</i>	< 3	3-5, 5-6	o	II	pa	u, m	\approx 3	II	-	+	ra	pa, co, ph
<i>Hoffmannia</i>	3-6	3, 3	o	III	pa	m	\approx 2	III	pa	+	ra	pa, co, ph, vs
<i>Omitelia</i>	\approx 3	2-6, 2-6	o	III	pa	m	\approx 2	III	pa	+	ra	pa, co, ph, vs
<i>Pinarophyllon</i>	\approx 2	3-4, 10	o	III	pa	m	\approx 3	III	pa	+	ra	pa, co, ph, vs
<i>Plocaniophyllon</i>	\approx 3	5, 5	o	III	fi	-	\approx 3	III	pa	+	ra	pa, co, ph, vs
Cinchoneae												
<i>Syringantha</i>	6-7	8, 10	o	III	pa	u	4-6	I	-	+	ra	pa, co, ph
<i>Exostema</i>	5-6	4-7, 10	o	I	co	u	5-12	VI	-	-	dr	pa, co
<i>Hintonia</i>	4-5	4-5, 4-6	o	I	co	-	4-6	VI	-	-	dr	co
Psychotriaceae												
<i>Psychotria</i>	\approx 3	3-6, 3-6	o	IV	scl	m (u)	\approx 3	IV	scl	-	ra	pa, ph
Gardeniaceae												
<i>Randia</i>	4-5	4-5, 6	c	V	fi	m	4-5	V	fi	-	dr	co
Cinchoneae/Hedyotideae												
<i>Bouardia</i>	10-12	4-5, 8	o	I	co	-	5-10	VI	-	-	ra, dr	pa, co

c, closed cylinder; co, collenchyma; dr, druses; fi, fibers; m, multicellular trichome; o, open arc; pa, parenchyma; ph, phloem; ra, raphides; scl, sclerenchyma; u, unicellular trichome; vs, vascular sheath; +, present; -, absent.

¹ For type definition, see text.

Rubioideae, Cinchonoideae, and Ixoroideae, namely a simple epidermis, stomata restricted to the abaxial surface, and dorsiventral mesophyll. In addition, they share with *Psychotria* (Rubioideae) multicellular trichomes, a single layer of palisade parenchyma cells, loose spongy parenchyma, and occurrence of raphides and tannins. *Psychotria* differs from members of Hamelieae, however, by its lignified elements sheathing the phloem and the presence of vascular tissue type IV in the midrib and petiole. To date, type IV is unique to *Psychotria*, as it has not been recorded in any other member of the family. It is important to study additional species of the genus and other members of tribe Psychotrieae to confirm the diagnostic potential of this characteristic.

The genera *Exostema* and *Hintonia* of the *Portlandia* group (Cinchonoideae) share the presence of midrib vascular tissue type I with *Deppea*, but are distinguished from the tribe Hamelieae by having two layers of palisade parenchyma cells and compact spongy parenchyma with druses, and by the absence of a sheath in the petiole vascular tissue. *Bowardia* shows vascular tissue type I in the midrib and type VI in the petiole as in *Exostema* and *Hintonia*, but, unlike these genera, *Bowardia* had raphides and druses in both the lamina and petiole. *Bowardia* had previously been classified in the tribe Hedyotideae (Rubioideae) because of reports of raphides. Its winged seeds, however, motivated Robbrecht (1988, 1993) to consider it a member of the tribe Cinchoneae (Cinchonoideae). This has not been supported by molecular data (e.g., Robbrecht & Manen, 2006). The presence of raphides and druses in the leaves of this taxon adds support to the idea of an independent origin of raphides and to the exclusion of *Bowardia* from Rubioideae.

The genus *Randia* of the subfamily Ixoroideae was the only one to have a closed vascular trace in the midrib and petiole (type V). Moreover, the vascular tissue was sheathed by a discontinuous layer of fibrous elements. These characteristics and the presence of druses are a unique combination of characters that distinguish this genus from the other taxa studied. Further sampling should test the taxonomic value of this character and the rank at which it may be useful.

Attributes observed in the studied genera, such as simple epidermis, hypostomatic leaves, and dorsiventral mesophyll, have also been recorded for other taxa of Rubiaceae (Metcalfe & Chalk, 1950). Most of the leaf trace types recognized here are described for the first time for the family; thus, vascular tissue diversity in the petiole is higher than that reported by Metcalfe and Chalk (1950). Except in *Randia*, the petiole was characterized by an open vascular trace in the genera

observed in the present study. Comparisons of photographs of petiole vascular tissues of *Rondeletia* L. (Cinchonoideae, Kocsis et al., 2004) and *Pavetta* L. (Ixoroideae, Herman et al., 1986) enabled us to confirm that type I, described for *Deppea* of Hamelieae, has a broader distribution. The differences among vascular tissue types recognized in this study are related to the particular shape of the central trace and to whether its endings are curved or straight, and to the number of lateral bundles. Moreover, the number of lateral bundles decreases from the base of the petiole to the midrib in types I, III, and VI. Howard (1979) reported that reduction in the number of traces is a common modification in petiole vascular tissue. Notably, no modification of the foliar trace was observed in types II, IV, and V.

Raphides have been considered a taxonomic marker within Rubiaceae, in particular in delimiting the subfamily Rubioideae (Bremekamp, 1966). It is understandable that Hamelieae has traditionally been classified in this subfamily, as all genera of Hamelieae have raphides. Phylogenetic analyses of molecular data, however, suggest that the tribe should be assigned to the subfamily Cinchonoideae (Bremer et al., 1995; Andersson & Rova, 1999; Robbrecht & Manen, 2006). The presence of raphides in both Rubioideae and Cinchonoideae indicates that these crystals appeared independently in both subfamilies. We consider that it is therefore important to study their ontogeny and chemical composition to evaluate potential homologies within these subfamilies.

The single palisade parenchyma layer, the distribution of vascular tissue in the midrib and petiole (type I, II, or III), and the presence of raphides and tannins are a unique combination of characters that circumscribe the tribe Hamelieae including *Syringantha*. Some of these characters also enable taxonomic delimitation at the genus level within the tribe. This and other studies show that anatomical leaf and petiole characters have taxonomic potential (Herman et al., 1986; Dessein et al., 2001; Piesschaert et al., 2001; Kocsis et al., 2004).

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APPENDIX 1. List of specimen vouchers used to produce permanent slides. Species are arranged alphabetically.

Bowardia cordifolia DC. MEXICO. México: *H. Vibrans* 4932 (CHAPA). Michoacán: *J. Rzedowski* 39784 (MEXU). Oaxaca: *A. Campos & L. Cortés* 2203 (MEXU). *B. chrysantha* Mart. MEXICO. Guerrero: *P. Tenorio et al.* 1286 (CHAPA), *R. Torres* 9951 (MEXU). México: *J. A. López & S. E. Hernández* 1277 (CHAPA). *B. ternifolia* (Cav.) Schltld. MEXICO. Hidalgo: *M. Martínez* 58 (CHAPA), *D. Martínez* 284 (CHAPA). Michoacán: *J. Rzedowski* 38901 (CHAPA).

Deppea cornifolia (Benth.) Benth. MEXICO. Guerrero: *D. Martínez* 241 (CHAPA), *J. Rzedowski* 16049 (MEXU). Hidalgo: *R. Hernández et al.* 6119 (MEXU). Oaxaca: *J. Reyes* 419 (MEXU). *D. grandiflora* Schltld. MEXICO. Chiapas: *M. González et al.* 1015 (CHAPA, MEXU), *S. Maya* 4346 (MEXU), *F. Ventura* 19572 (MEXU). Veracruz: *H. Ochoterena & C. Gallardo* 374 (MEXU). *D. guerrenensis* Dwyer & Lorence. MEXICO. Guerrero: *D. Martínez* 193 (CHAPA), *D. Martínez* 195 (CHAPA), *H. Ochoterena & D. Bailey* 335 (MEXU). *D. hintonii* Bullock. MEXICO. Chiapas: *T. B. Croat* 47234 (CHAPA). Oaxaca: *A. Campos* 1840

- (MEXU), *R. E. Gereau et al.* 1075 (MEXU), *T. B. Croat* 46153 (MEXU), *D. miahuatlantica* Lorence. MEXICO. Oaxaca: *A. Campos & L. Cortés* 2260 (MEXU), *H. Ochoterena & D. Bailey* 331 (MEXU), *R. Torres & A. Campos* 10847 (MEXU), *D. microphylla* Greenm. MEXICO. Hidalgo: *D. Lorence* 4895 (MEXU), *J. Rzedowski* 23429 (MEXU). Puebla: *D. Gold* 223 (MEXU), *D. obtusiflora* (Benth.) Benth. MEXICO. Oaxaca: *D. Lorence* 4200 (MEXU), *D. Lorence* 4338 (MEXU), *J. Rivera* 0965 (MEXU), *D. pubescens* Hemsl. MEXICO. Oaxaca: *A. Campos & J. Reyes* 1333 (CHAPA), *H. Ochoterena & D. Bailey* 333 (MEXU), *R. Torres* 1403 (MEXU), *D. purpusii* Standl. MEXICO. Hidalgo: *R. Hernández* 5767 (MEXU), *D. Martínez* 254 (MEXU). Veracruz: *J. I. Calzada* 5470 (MEXU), *D. tenuiflora* Benth. MEXICO. Veracruz: *I. A. Vargas* 189 (MEXU), *I. A. Vargas* 243 (MEXU), *D. umbellata* Hemsl. MEXICO. Oaxaca: *R. Torres* 6546 (MEXU). Veracruz: *J. Fay & J. I. Calzada* 734 (MEXU), *H. Ochoterena et al.* 370 (MEXU), *M. G. Zola* 0390 (MEXU).
- Exostema caribaeum* (Jacq.) Roem. & Schult. MEXICO. Campeche: *C. Chan* 7698 (CHAPA). Oaxaca: *D. Lorence* 3036 (CHAPA). Querétaro: *E. Carranza* 3362 (CHAPA), *E. mexicanum* A. Gray. MEXICO. Campeche: *E. Martínez* 29166 (CHAPA), *E. Martínez* 29719 (MEXU). Chiapas: *A. Chamé et al.* 159 (CHAPA). Oaxaca: *H. Ochoterena et al.* 289 (MEXU).
- Hamelia axillaris* Sw. MEXICO. Chiapas: *E. Martínez* 14707 (MEXU). Tabasco: *R. H. Magaña & C. Cowan* 3136 (CHAPA, MEXU). Veracruz: *T. Wendt et al.* 4231 (CHAPA, MEXU), *O. Zambrano* 1026 (CHAPA), *H. patens* Jacq. MEXICO. Chiapas: *F. Ventura* 90 (CHAPA). Hidalgo: *D. Martínez* 167 (CHAPA). Oaxaca: *S. Maya* 1868 (CHAPA), *H. rovirosae* Wernham. MEXICO. Chiapas: *M. González et al.* 796 (CHAPA), *M. González et al.* 797 (CHAPA). Oaxaca: *H. Hernández* 1508 (CHAPA), *H. versicolor* A. Gray. MEXICO. Guerrero: *C. Catalán* 3 (CHAPA). Jalisco: *H. Ochoterena & D. Bailey* 217 (MEXU). Morelos: *D. M. Arias & D. Martínez* 2198 (MEXU), *H. xorullensis* Kunth. MEXICO. Jalisco: *H. Ochoterena & D. Bailey* 220 (MEXU). México: *D. Martínez* 298 (CHAPA), *H. Vibrans* 5885 (MEXU).
- Hintonia latiflora* (Sessé & Moc. ex DC.) Bullock. MEXICO. Jalisco: *A. Flores* 3655 (CHAPA), *D. Martínez & E. Domínguez* 201 (CHAPA). Sinaloa: *H. Ochoterena & D. Bailey* 224 (MEXU). Sonora: *A. Flores & O. Gutiérrez* 511 (CHAPA), *H. octomera* (Hemsl.) Bullock. MEXICO. Yucatán: *H. Ochoterena & H. Flores* 168 (MEXU).
- Hoffmannia angustifolia* Standl. MEXICO. Chiapas: *D. E. Breedlove* 24801 (MEXU), *D. E. Breedlove* 35293 (CHAPA), *A. Log & M. Heath* 154 (MEXU), *H. conzattii* B. L. Rob. MEXICO. Chiapas: *U. Bachem & R. Rojas* 891 (CHAPA). Guerrero: *E. Martínez et al.* 5070 (MEXU). Hidalgo: *J. Rzedowski* 12341 (CHAPA). Oaxaca: *T. Wendt & M. Ishiki* 4956 (CHAPA), *H. culminicola* Standl. & L. O. Williams. MEXICO. Hidalgo: *D. Martínez* 171 (CHAPA). Oaxaca: *S. Maya* 1173 (CHAPA), *P. Tenorio & R. Torres* 11059 (MEXU), *H. cuneatissima* B. L. Rob. MEXICO. Guerrero: *E. Martínez* 5471 & *F. Barrie* (CHAPA). Jalisco: *R. Cuevas & L. Guzmán* 4185 (CHAPA, MEXU). México: *D. Lorence & D. Tejero* 4887 (MEXU), *H. excelsa* (Kunth) K. Schum. MEXICO. Oaxaca: *S. Maya* 3305 (CHAPA). Veracruz: *D. Lorence* 3890 (MEXU), *G. Castillo* 12149 (MEXU), *H. nicotanaefolia* (M. Martens & Galeotti) L. O. Williams. MEXICO. Chiapas: *M. González et al.* 1718 (CHAPA), *E. Martínez* 18864 (MEXU). Oaxaca: *T. Wendt et al.* 4661 (CHAPA).
- Omitelia filisepala* (Standl.) C. V. Morton. MEXICO. Chiapas: *M. Heath & A. Long* 771 (MEXU), *M. Heath & A. Long* 1173 (MEXU), *D. Martínez* 275 (CHAPA). Veracruz: Standl. MEXICO. Guerrero: *F. Lorea* 2048 (MEXU), *D. Martínez* 236 (CHAPA), *A. Méndez* 285 (MEXU).
- Pinarophyllon flavum* Brandegee. MEXICO. Chiapas: *D. E. Breedlove* 30795 (MEXU), *D. Martínez* 318 (CHAPA), *E. Ventura & E. López* 2053 (MEXU).
- Plocaniophyllon flavum* Brandegee. MEXICO. Chiapas: *M. Heath & A. Long* 899 (MEXU), *D. Martínez* 312 (CHAPA), *E. Matuda* 17763 (MEXU).
- Psychotria erythrocarpa* Schltdl. MEXICO. Guerrero: *C. Catalán & F. Terán* 709 (CHAPA). Oaxaca: *S. Maya* 1691 (CHAPA), *S. Maya* 1753 (CHAPA), *P. faxlucens* Lorence & Dwyer. MEXICO. Veracruz: *R. Cedillo* 3587 (CHAPA), *S. Sinaca* 579 (CHAPA), *P. horizontalis* Sw. MEXICO. Chiapas: *E. Martínez* 9030 (MEXU). Jalisco: *D. Martínez* 200 (CHAPA), *J. A. S. Magallanes* 3687 (CHAPA), *P. microdon* (DC.) Urb. MEXICO. Campeche: *E. Martínez* 27882 (MEXU). Chiapas: *E. Palacios* 1995 (CHAPA, MEXU). Jalisco: *D. Martínez* 205 (CHAPA).
- Randia aculeata* L. MEXICO. Jalisco: *E. Domínguez & H. Ochoterena* 1775 (MEXU). Nayarit: *O. Téllez* 12663 (CHAPA). Veracruz: *T. Wendt et al.* 3131 (CHAPA), *R. tetraantha* (Cav.) DC. MEXICO. Jalisco: *D. Martínez* 309 (CHAPA), *H. Illis et al.* 29682 (CHAPA).
- Syringantha coulteri* (Hook. f.) T. McDowell. MEXICO. Hidalgo: *D. Martínez* 190 (CHAPA), *F. G. Medrano et al.* 9631 (MEXU). Guanajuato: *E. Ventura & E. López* 7989 (MEXU). Tamaulipas: *Mora* 5314 (MEXU).