Seed morphology of Hamelieae with emphasis on the Deppea complex (Cinchonoideae, Rubiaceae)

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Background and aims – The neotropical tribe Hamelieae currently includes 16 genera mainly characterized by raphides, ebracteolate inflorescences, and 4-merous flowers with contorted corolla aestivation. Within this tribe, the circumscription of Deppea has been particularly controversial, as depending on the authors, several morphologically closely related genera are either treated as synonyms or accepted as such. This generic group, hereafter referred to as the Deppea complex, consists of up to 10 genera. Within Rubiaceae, seed morphology has proved to have taxonomic value for generic circumscriptions, however, it remained unexplored for Hamelieae and the Deppea complex.

Material and methods – We present a detailed study of the seed morphology of 37 species representing 15 out of the 16 genera recognized within Hamelieae, including all putative genera of the Deppea complex. Using scanning electron and light microscopy, we investigate 16 quantitative and qualitative seed characters that could have taxonomic value.

Key results – Our results show that the combination of some seed characters, such as shape and colour, dorsiventral compression, hilum position, and the periclinal microrelief, helps to distinguish some genera and most species, supporting or refuting the current taxonomic circumscription.

Conclusion – We conclude that the seed morphology within Hamelieae has taxonomic value but should be combined with other characters to achieve unequivocal delineation of the genera.

Keywords – Generic circumscription; LM; morphology; seed; SEM; systematics; testa.

INTRODUCTION

Hamelieae is a Neotropical tribe comprising 16 genera and approximately 225 species, notably diverse in Mexico where it has 14 genera and ca 100 species (Lorence & Dwyer 1988; Borhidi 2006, 2012). It is characterized by shrubs or treelets, presence of raphides, typically ebracteolate inflorescences, often yellow or yellowish 4-merous flowers, contorted corolla aestivation, and berries or capsular fruits (Bremer 1987; Borhidi et al. 2004a, 2004b; Manns & Bremer 2010; Stranczinger et al. 2014).

The tribe Hamelieae was traditionally classified in subfamily Rubioideae due to the presence of raphides (Bremerkamp 1966). Nevertheless, molecular phylogenetic analyses including relatively few species of Hamelieae have indicated that this tribe is more appropriately classified within Cinchonoideae (Bremer et al. 1995; Andersson & Rova 1999; Robbrecht & Manen 2006), even when using phylogenomic data, although this analysis only represented the tribe with one species (Antonelli et al. 2021).

Within the tribe, the generic circumscription has been controversial; the first classification systems for Rubiaceae (De Candolle 1830; Endlicher 1836) recognized eleven genera within Hamelieae: Alibertia A.Rich., Aphanes Blum, Brignolia DC., Eosmina Humb. & Bonpl., Hamelia Jacq., Olostyla DC., Patima Aubl., Tepesia Gartn., Urophyllum Jack ex Wall., Sabicea Aubl., and Schradera Vahl. Hooker (1873) considered only six genera based on the contorted
and imbricate corolla aestivation plus fleshy fruits: Bertiera Aubl., Bothriospora Hook.f., Gouldia A.Gray, Hamelia, Heinsia DC., and Hoffmannia Sw. According to Schumann (1897), Hamelieae was considered a subtribe within Gardenieae, including five genera: Bothriospora, Catesbaea L., Hamelia, Hoffmannia, and Phyllacantha Hook.f. Later on, Verdcourt (1958) recognized in Hamelieae only Bertiera, Hamelia, and Heinsia, while Bremerkamp (1966) restricted it even more, including only two genera, Hamelia and Hoffmannia, based on raphide presence plus fleshy fruits. Bremer (1987) recognized five genera within Hamelieae based on raphide presence and imbricate corolla aestivation: Deppea Schltdl. & Cham., Hamelia, Hoffmannia, Omiltemia Standl., and Pinarophyllon Brandegee. Lorence & Dwyer (1988) considered the genus Schenckia K.Schum. to be a synonym of Deppea. The genus Edithea Standl. was included within Hamelieae by Robbrecht (1988), but treated as Omiltemia by Kirkbride (1984), as Deppea by Lorence & Dwyer (1988), and resurrected by Borhidi et al. (2004a). Robbrecht & Bridson (1993) added Eizia Standl. and Plocaniophyllon Brandegee to the tribe, while McDowell (1996) included the monotypic genus Syringantha Standl. Finally, Borhidi et al. (2004b) segregated Bellizincia Borhidi and Csapodya Borhidi from Deppea, both genera included in Hamelieae by the same authors.

Based on molecular evidence, Manns & Bremer (2010) recognized seven genera within Hamelieae: Cosmocalyx Standl., Deppea, Hamelia, Hoffmannia, Omiltemia, Pinarophyllon, and Plocaniophyllon, plus two tentatively included (Eizia and Patima), while the genera Bellizincia, Csapodya, Edithea, and Schenckia were suggested as synonyms of Deppea.

In total, nine genera are morphologically closely related to Deppea, even treated as synonyms by some authors (Lorence & Dwyer 1988; Manns & Bremer 2010; Lorence 2012). These genera will be hereafter referred to as the Deppea complex: Bellizincia, Csapodya, Deppea, Deppeopsis, Edithea, Omiltemia, Pinarophyllon, Plocaniophyllon, Pseudomiltemia Borhidi, and Schenckia (fig. 1). Hence, the Deppea complex constitutes the majority of the Hamelieae tribe, including 10 out of the 16 genera and ca 50 species.

Molecular phylogenetic analyses retrieved a monophyletic and highly supported Hamelieae but did not solve the Deppea taxonomic problem: Manns & Bremer (2010) used a set of six markers (nrITS, atpB-rbcL, ndhF, rbcL, rps16, and trnL-F), but only studied six genera of the Deppea complex with a few species each, leaving many questions related to their generic circumscription open. Stranczinger et al. (2014), on the other hand, included representatives of all genera in the Deppea complex, but they only used two markers (ITS and trnL-F) resulting in a consensus tree with many polytomies that made the taxonomic decisions untenable. Their phylogenetic analysis showed that none of the genera in the Deppea complex were supported as monophyletic and that the genus Renistipula Borhidi should be included as a member of Hamelieae despite its lack of the diagnostic raphides. A phylogenetic analysis by Torres-Montúfar (2018) however placed Renistipula within Guettardeae and treated it as a synonym of Arachnothryx Planch. All morphological evidence indicates that Renistipula belongs in Guettardeae and so we favour the results by Torres-Montúfar (2018), suggesting that the results by Stranczinger et al. (2014) are most likely an artifact of a methodological error.

In the literature, some morphological characters have been used to differentiate among the genera within Hamelieae and more precisely within the Deppea complex, such as the position of the stamen insertion on the corolla, calyx lobe form, and corolla length and shape, as well as fruit form and dehiscence (Borhidi et al. 2004a, 2004b; Borhidi 2006, 2012; Borhidi & Stranczinger 2012). Nevertheless, these characters display a complex overlapping mosaic and none of them is useful to clearly distinguish genera when not used in combination with other characters.

Therefore, the morphological and molecular data gathered so far does not provide convincing evidence for the adequate generic circumscription within Hamelieae, particularly among genera in the Deppea complex. Consequently, the number of genera that should be recognized within Hamelieae remains unclear and new sources of evidence should be incorporated to solve this problem.

Even though seed morphology has not been commonly used in Rubiaceae systematics, some studies indicate its taxonomical potential (e.g. Hayden & Dwyer 1969; Terrell et al. 1986; Robbrecht 1988; Khalik et al. 2008). Several seed characters have thus potential to be good taxonomic markers, such as seed shape (Breedlove & Lorence 1987), testa ornamentation (Hayden & Dwyer 1969), general form and hilum position (Terrell et al. 1986), seed size and antical and perical cell wall boundary (Khalik et al. 2008). This information has helped the delimitation of some taxa at species level (e.g. Khalik et al. 2008) or at generic level (e.g. Hayden & Dwyer 1969). For the tribe Hamelieae, Robbrecht (1988) mentioned that the exotestal outer cells walls are granulate or tuberculare, while Martinez-Cabrera et al. (2014) observed unigemmic orthotropous ovules, horizontally oriented in the ovary locule. Other than that, information on the taxonomic value of the seed morphology within Hamelieae and among genera in the Deppea complex is scattered. It is important to mention that the seeds of species within the Deppea complex are in general very small, resembling dust, and this might be a reason why they have not been thoroughly studied. However, the seeds of Plocaniophyllon were described by Martinez-Cabrera et al. (2008) in a study of the genus including morphology and anatomy. In addition, studies by Borhidi et al. (2004a, 2004b) indicated the existence of seed differences in shape, hilum position, perpendicular wall thickness, and horizontal wall type and ornamentation among Bellizincia, Csapodya, Deppea, Edithea, Omiltemia, and Pseudomiltemia. Regardless of the evidence that seed morphology can provide taxonomically useful information within Hamelieae and the Deppea complex, there is no study using uniform terminology devoted to systematically comparing seed morphology among genera within the tribe.

Therefore, our aims in this work are to provide a thorough seed description for all genera of Hamelieae and to examine the potential utility of seed morphology for the generic circumscription in the tribe, mainly focusing on the genera within the Deppea complex.
Figure 1 – Different species representing the genera within Hamelieae. A–L. Flowers. A. Bellizinca scoti (Ochoterena et al. 1119). B. Csapodya splendens (Ochoterena et al. 1147). C. Deppea cornifolia (Ochoterena et al. 1120). D. Deppea purpurascens (Ochoterena et al. 1175). E. Deppeopsis anisophylla (Ochoterena et al. 1102). F. Eizia mexicana (Ochoterena et al. 1126). G. Edithea miahuatlanica (Ochoterena et al. 1095). H. Edithea schiblii (Ochoterena et al. 1112). I. Hamelia patens (Ochoterena et al. 1074). J. Hoffmannia sp. (Ochoterena et al. 1166). K. Omiltemia parvifolia (Ochoterena et al. 1105). L. Schenckia blumenaviensis. M–P. Fruits. M. Hoffmannia sp. (Ochoterena et al. 1164) N. Deppea grandiflora (Ochoterena et al. 1142). O. Pinarophyllum flavum (Ochoterena et al. 1133). P. Pseudomiltemia davidsonii (Ochoterena et al. 1162). All photographs by Helga Ochoterena, except G by Alejandro Torres.
MATERIAL AND METHODS

Our study includes all 16 genera within Hamelieae except for the South American *Patina* (with two species) for which we could not obtain seeds. This study includes all 10 genera within the *Deppea* complex. Seeds of at least one species of all the genera of the *Deppea* complex and five other genera in Hamelieae were examined. The voucher specimens of the 37 species are listed in supplementary file 1. Seeds were obtained from herbarium specimens at the Herbario Nacional de México (MEXU) and the Copenhagen herbarium (C). All seeds were chosen from mature fruits, with several seeds randomly selected, and the seeds were not treated or cleaned before microscopy due to their small size. For each sample, two groups of seeds were formed to be subsequently processed with different microscope techniques at the Laboratorio de Microscopía y Fotografía de la Biodiversidad at Instituto de Biología, UNAM. For scanning electron microscopy (SEM), the sampled seeds were sputter-coated with gold-palladium for 2–3 minutes with a HUMMER V Sputter Coater and they were observed and photographed using a Hitachi S-4000. For light microscopy (LM), the seeds did not receive any pre-treatment and stereoscopic photographs were taken using a Leica microscope equipped with a Leica Z16 APO A camera.

Seed colours were defined by placing the eyedropper tool of Photoshop (we used Photoshop CS3) on top of the central portion of the seed on the captured image and once the RGB colour palette was displayed, the colours were assigned to the standardized nearest colour: black, around brown as brownish, around red as reddish, or around yellow as yellowish.

Measurements were taken using the software Leica Application Suite v.2.8.1; at least five seeds per specimens were measured for size, length, and width. All measurements are presented in mm. Boxplots were created in Microsoft Excel and boxes represent the interquartile range, the horizontal line inside the box represents the median, the “X” represents the mean, and the circles are outliers.

The terminology proposed by Koch et al. (2009) and Barthlott & Hunt (2000) was adopted to describe the seed coat micromorphology observed using SEM, the other characters were defined here by the authors or follow Harris & Harris (2001). The micropyle position was defined assuming the orthotropous ovule nature described for the tribe by Martínez-Cabrera et al. (2014) or the anatropous position described for most Rubiaceae (Robbrecht 1988). A character matrix was constructed using Winclada (Nixon 1999) to show parallel descriptions of the 15 characters in the studied species. An illustrated overview of the 15 characters and character states is presented in supplementary file 2. Full seed descriptions for the 37 studied species in 15 genera are presented in the supplementary file 3, including the seed size that is not considered in the supplementary file 2 because it is a continuous character.

The seed morphology of the 15 studied genera is graphically summarized in fig. 2; we also compared the 28 species within the *Deppea* complex (fig. 3). The boxplots comparing seed length and width of the 15 studied genera are shown in fig. 4. The SEM micrographs are shown in figs 5–10 and the LM micrographs are shown in figs 11–13.

RESULTS

In total, seeds from 15 genera and 37 species within Hamelieae were studied, among which 10 genera and 28 species belonging in the *Deppea* complex. Our results show high morphological overlap among the studied genera (fig. 2). Seed length and width (fig. 4) only allow for the recognition of *Cosmocalyx*, which has the largest seeds (7.9–10.7 × 4.8–5.8 mm) of linear form (fig. 11C) and has the straight anticlinal wall boundaries (fig. 5F–H). The only other genus among Hamelieae that can be easily recognized by its seeds is *Syringantha*, because of the winged margins (figs 10A, 13Q, R).

The other 13 genera show a diversity in general shape, dorsiventral shape (figs 5–10), colour, anticlinal wall boundary, periclinial microlrelief, and micropyte position (figs 11–13). Only a combination of these characters allows for taxonomic grouping, which is not necessarily similar to the current generic circumscription.

Outside the *Deppea* complex, the genus *Eizia* can be distinguished by the combination of black seeds (fig. 12S, T) with evidently depressed dorsiventral shape of cells (fig. 8I), and a sub-central micropyte position. These character states are each present in at least one species within the *Deppea* complex, but never in this combination. The studied *Hamelia* species share a rhomboidal seed shape, straight anticlinal wall boundaries, and papillose periclinial microlrelief (figs 8M–X, 12U–Z). The rhomboidal seed shape is also present in *Deppea erythrorhiza* (figs 5Y, 11M) and *Omitlemia longipes* (figs 9I, 13E), from which *Hamelia* is easily distinguished by the straight anticlinal wall boundaries and the evident hilum, in contrast to the U-undulate anticlinal wall boundaries and the inconspicuous hilum in the former two species (figs 5Z–AA, 9J–K, 11M, 13E). The genus *Hoffmannia* shows variation among the studied species and therefore is hard to characterize at generic level by its seeds (fig. 2). Among the evaluated species in this genus, *H. ghiesbrechtii* and *H. oaxacensis* are similar by the exotesta cells with verrucose periclinial microlrelief (fig. 9D, H), a character state shared with *Bellizincia* (fig. 5C–D) and *Deppea grandiflora*. This is in contrast to the concave outlines with sunken profile of the periclinial microlrelief in *H. gesnerioides* (fig. 8AB), which is a character state shared with many other species within the studied genera.

Within the *Deppea* complex, dorsiventrally flattened seeds is one of the main character states useful for taxon grouping. The genera *Csapodya, Deppeopsis, Omitlema, and Pseudomiletma* have flattened seeds, in contrast to the polygonal seeds in *Bellizincia, Deppea, Edithea, Pinarophyllon, Plocanophyllon*, and *Schencokia* (fig. 2). Among the taxa with flattened seeds, *Csapodya* and *Pseudomiletma* have concave outlines with a sunken profile periclinial microlrelief (fig. 5L, P), while it is papillose in *Deppeopsis* (fig. 7L, P, T), *Omitlemia* (fig. 9L, P), *Pinarophyllon*, and *Plocanophyllon*. Most of the character states of *Pseudomiletma* seeds overlap with those of at least one of the *Csapodya* species (fig. 2), however, both genera
Figure 2 – Graphical representation of the variation within 15 seed characters and their character states for 15 Hamelieae genera.

Figure 3 – Graphical representation of the variation within the 15 seed characters and their character states of representative species within the Deppea complex.
can be distinguished by the shape of the cells next to the micropyle that differ from the shape of the lateral cells, in combination with the elongated lateral cells, and the straight anticalinal wall boundary in *Pseudomiltemia*. The seeds differ between *Deppeopsis* and *Omiltemia* in that the latter has elongated lateral cells, and the micropyle in central/sub-central position (fig. 9I–P), isodiametric lateral cells, and lateral micropyle position of *Deppeopsis* (fig. 7I–T).

Among the genera which have polygonal seeds, differences in the periclinal microrelief are useful for grouping them. The genus *Bellizinca* is easily recognizable by the verrucose microrelief (fig. 5D), which is only shared with *Deppea grandiflora* (fig. 6D), but *Bellizinca* is distinguishable by the V-undulate anticalinal wall boundary and the elongated cells surrounding the micropyle (fig. 5A–C), in contrast to the U-undulate and isodiametric cells surrounding the micropyle in *D. grandiflora* (fig. 6A–C).

The genera *Pinarophyllon* and *Plocaniophyllon* share a papillose microrelief (fig. 9T, X), also found in several *Deppea* species (fig. 3). The genera can be distinguished by the elongated cells surrounding the micropyle in *Plocaniophyllon* (fig. 9U–V), in contrast to the isodiametric cells surrounding the micropyle in *Pinarophyllon* (fig. 9Q–R). The combination of seed colour, anticalinal wall boundary, and micropyle position is useful to differentiate both genera from *Deppea*, even though they share a papillose microlrelief (fig. 3). The genus *Schenckia* shares the concave outline with a sunken profile microrelief (fig. 10E–H) with species of *Edithea* and *Deppea* (fig. 3), however, *Schenckia* is characterized by the V-undulate anticalinal wall boundary (fig. 10G), while the *Deppea* and *Edithea* species have straight anticalinal wall boundaries (figs 5Q–AB, 8A–H).

The genus *Deppea* is morphologically heterogeneous and shows overlap among the character states with all other genera: its seed shape, colour, and periclinal microlrelief are variable. At species level, the rhomboidal seeds allow for the recognition of *Deppea erythrorhiza* (figs 5Y, 11M) among the other studied species in the genus, since the other species have circular or ellipsoidal seeds. Among the species with ellipsoidal seeds, *D. grandiflora* can be distinguished by the verrucose periclinal microrelief (fig. 6D) instead of the papillose or concave outlines with a sunken profile in the other species. The rest of the species with ellipsoidal seeds can be distinguished by the colour: *D. amaranthina* has brown seeds (fig. 11I–J), *D. hamelioides* yellowish (fig. 11Q–R), *D. purpurascens* black (fig. 11AA–AB), and *D. purpusii* and *D. umbellata* have reddish seeds (fig. 12A–D). The latter two differ from each other by their testa cells: well-defined in *D. purpusii* (fig. 7B) but not well-defined in *D. umbellata* (fig. 7F). It is worth mentioning that for *D. umbellata*, the cells surrounding the micropyle could not be observed and therefore these character states were coded in the matrix with a question mark “?”; this is the only taxon that has this state.

Among the *Deppea* species with circular seeds (fig. 3), *D. obtusiflora* is distinguishable by the U-undulate anticalinal wall boundaries (fig. 6R–S), while the rest of the species in the genus have straight boundaries; among these, the seeds of *D. hintonii* have isodiametric lateral cells (figs 6I, 11S–T), while *D. cornifolia* and *D. microphylla* have elongated lateral cells (figs 5U, 6M, 11K, U). The differences between *D. cornifolia* and *D. microphylla* are the prominent anticlinal wall boundaries in the former in contrast to the only slightly prominent anticalinal wall boundaries in the latter (figs 5V–W, 6N–O).

For the genera sampled with more than one species, the examined *Csapodya* species are very different (figs 5I–P, 11E–H) from each other: brown seeds in *C. sousae* and reddish in *C. splendens*; elongated lateral cells in *C. sousae* and isodiametric in *C. splendens*; V-undulate anticalinal wall boundaries in *C. sousae* and straight in *C. splendens*; sub-central micropyle position in *C. sousae* and lateral in *C.
Figure 5 – SEM photographs showing, left to right, a general view of a seed, lateral cells, a detail of the anticlinal wall boundaries, and a detail of the periclinal microrelief. A–D. *Bellizinca scoti*. E–H. *Cosmocalyx spectabilis*. I–L. *Csapodya sousae*. M–P. *Csapodya splendens*. Q–T. *Deppea amaranthina*. U–X. *Deppea cornifolia*. Y–AB. *Deppea erythorhiza*. 
Figure 6 – SEM photographs showing, left to right, a general view of a seed, lateral cells, a detail of the anticlinal wall boundaries, and a detail of the periclinal microrelief. **A–D.** Deppea grandiflora. **E–H.** Deppea hameloides. **I–L.** Deppea hintonii. **M–P.** Deppea microphilla. **Q–T.** Deppea obtusiflora. **U–X.** Deppea pubescens. **Y–AB.** Deppea purpurascens.
Figure 7 – SEM photographs showing, left to right, a general view of a seed, lateral cells, a detail of the anticlinal wall boundaries, and a detail of the periclinal micrelief. A–D. Deppea purpusii. E–H. Deppea umbellata. I–L. Deppeopsis anisophylla. M–P. Deppeopsis hernandezii. Q–T. Deppeopsis tenuiflora. U–X. Edithea floribunda. Y–AB. Edithea guerrerensis.
Figure 8 – SEM photographs showing, left to right, a general view of a seed, lateral cells, a detail of the anticlinal wall boundaries, and a detail of the periclinal microlief. **A–D.** *Edithea miahuatlanica.* **E–H.** *Edithea schiblii.* **I–L.** *Eizia mexicana.* **M–P.** *Hamelia axillaris.* **Q–T.** *Hamelia patens.* **U–X.** *Hamelia xorullensis.* **Y–AB.** *Hoffmannia gesnerioides.*
Figure 9 – SEM photographs showing, left to right, a general view of a seed, lateral cells, a detail of the anticlinal wall boundaries, and a detail of the periclinal microrelief. A–D. Hoffmannia ghiesbreghtii. E–H. Hoffmannia oaxacensis. I–L. Omiltemia longipes. M–P. Omiltemia parvifolia. Q–T. Pinarophyllon flavum. U–X. Plocaniophyllon flavum. Y–AB. Pseudomiltemia filisepala.
splendens; inconspicuous hilum in C. sousae and evident in C. splendens.

Within Deppeopsis (figs 7I–T, 12G–J), D. hernandezii can be distinguished from the other species in the genus by the isodiametric cells surrounding the micropyle (figs 7M–O), in contrast to the elongated cells surrounding the micropyle of the other two species (figs 7I–L, Q–T), for which no seed characters were found to differentiate between them.

The Omiltemia species can be distinguished by the general seed shape and hilum visibility: O. longipes has rhomboidal seeds and an inconspicuous hilum (figs 9I, 13E–F), while O. parvifolia has ellipsoidal seeds and an evident hilum (figs 9M, 13G–H).

The Edithea species are variable (figs 7U–AB, 8A–H): E. mihuantlanica can be distinguished from other species by the not well-defined testa cells, elongated lateral cells, and the lateral micropyle position (figs 8A–B, 12O–P). The species E. guerrerensis and E. schiblii share the cells surrounding the micropyle different from the lateral ones, the elongated cells surrounding the micropyle plus the concave outline with a sunken profile microrelief (figs 7Y–AA, 8E–G); they differ by the evidently flattened seeds and the slightly anticlinal wall boundary in relief of E. schiblii (fig. 8F–G). The species E. floribunda and E. guerrerensis differ mainly by the smooth periclinal microrelief of the former (fig. 7W–X) in contrast to the concave outline with a sunken profile of the latter (fig. 7AA–AB).

**DISCUSSION**

This study includes species from all genera in Hamelieae, except for the South American genus Patima, and it demonstrates the usefulness of seed morphology for the circumscription of genera and species, at least in most cases, but almost always using combinations of seed character states. Our sampling even included the monotypic genus Eizia, which was presumed extinct until it was rediscovered a few years ago (Martínez-Camilo et al. 2015).

**Seed morphology in Hamelieae**

Some Hamelieae genera are easily recognizable by unique character states such as the winged seeds in the monotypic Syringantha or the seed size and anticlinal wall boundaries in Cosmocalyx. Other genera have a unique combination of character states: e.g. Hamelia (with ca 16 spp) has rhomboidal seeds, straight anticlinal wall boundaries, and papillose microrelief. The genus Hoffmannia, the largest in the tribe (ca 100 spp.), requires more sampling to firmly make conclusions about the homogeneity or variability of its seed characters, given that only three species were included in our study. Nevertheless, there are several constant characters in the randomly sampled species (see supplementary file 3) and they might be constant at genus level as well. Hamelia and Hoffmannia have fleshy fruits, an uncommon character state in the tribe since all other genera have capsular fruits, although more species of Hoffmannia should be investigated to confirm if these are constant characters related to fruit texture.

For the genus Patima (not studied here), Delprete (1998) described the seeds as minute (ca 0.3–0.5 mm), globose, deeply reticulate, with regular shaped cells, with (4)5 or 6 sides per cell. Based on this description, we consider that the seeds of Patima are different from those of any other genus in Hamelieae.

Winged seeds are associated with some lineages in Rubiaceae, and this character state is generally constant at tribal or generic level. For example, Cinchoneae is identified by this character state (Andersson 1995), as well as Bouvardia Salisb. and Manettia Mutis ex L. (Terrell & Robinson 2004). The wings can be highly diverse: they can be equal and present all around the margin of the seed (e.g. Bouvardia), or unequal with edges at both poles of the seeds (e.g. Cinchona), or unilateral with only one pole developed (e.g. Simira) (Bremer & Eriksson 1992). Within Hamelieae, a winged margin is not a constant character state and, although it is only well-defined in one genus (i.e. Syringantha), in some species it is possible to see a more translucent or thinly

**Figure 10** – SEM photographs showing, left to right, a general view of a seed, lateral cells, a detail of the anticlinal wall boundaries, and a detail of the periclinal microrelief. A–D. Syringantha coulteri. E–H. Schenckia blumenaviensis.
Figure 11 – LM photographs showing a dorsal (left) and a ventral (right) seed view. A–B. Bellizinca scoti. C–D. Cosmocalyx spectabilis. E–F. Csapodya sousae. G–H. Csapodya splendens. I–J. Deppea amaranthina. K–L. Deppea cornifolia. M–N. Deppea erythrorhiza. O–P. Deppea grandiflora. Q–R. Deppea hamelioidea. S–T. Deppea hintonii. U–V. Deppea microphylla. W–X. Deppea obtusiflora. Y–Z. Deppea pubescens. AA–AB. Deppea purpurascens.
Figure 12 – LM photographs showing a dorsal (left) and a ventral (right) seed view. A–B. Deppea purpusii. C–D. Deppea umbellata. E–F. Deppeopsis anisophylla. G–H. Deppeopsis hernandezii. I–J. Deppeopsis tenuiflora. K–L. Edithea floribunda. M–N. Edithea guerrerensis. O–P. Edithea miahuatlanica. Q–R. Edithea schiblii. S–T. Eizia mexicana. U–V. Hamelia axillaris. W–X. Hamelia patens. Y–Z. Hamelia xorullensis. AA–AB. Hoffmannia gesnerioides.
slimmed edge (e.g. *Deppeopsis*; fig. 12I–J), but because it is very narrow we did not consider it as a true wing.

Seed shape could be related to the number of seeds per fruit or per locule, as discussed by Robbrecht (1988), who mentioned that seed shape can be dependent on available space, and small seeds with a convex abaxial side and angular radial sides are common in many-seeded fruits. However, this hypothesis is not corroborated by our observations, since the capsular fruits of the genera in the *Deppea* complex are many-seeded, and among them there are taxa with flattened seeds (e.g. *Deppeopsis*) and with polygonal seeds (e.g. *Deppea*), independent of fruit and seed size. Among Hamelieae, there are two types of mature fruit according to texture: fleshy berries in *Hamelia*, *Hoffmannia*, and *Patima* (Delprete et al. 2005; Lorence 2012) and dry capsular fruits in the rest of the genera (Borhidi 2012; Lorence 2012). Nevertheless, there is no correlation between seed size or shape with fruit type as, for example, capsular fruits have seeds with different sizes and shapes. Typically, fleshy fruits are associated with zoochory (Bremer & Eriksson 1992) and in these cases, the seeds are sometimes covered by sclerified testa walls that protect the embryo from the digestive tract acids of the animals (e.g. Schaumann & Heinken 2002). We did not observe major differences between the testa walls

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**Figure 13** – LM photographs showing a dorsal (left) and a ventral (right) seed view. A–B. *Hoffmannia ghiesbreghtii*. C–D. *Hoffmannia oaxacensis*. E–F. *Omitemia longipes*. G–H. *Omitemia parvifolia*. I–J. *Pinarophyllon flavum*. K–L. *Plocaniophyllon flavum*. M–N. *Pseudomiltemia filisepala*. O–P. *Schenckia blumenaviensis*. Q–R. *Syringantha coulteri*. 
from seeds in fleshy fruits (e.g. in *Hamelia*) as compared to those of seeds in dry fruits (e.g. in *Deppea*).

**Systematics of the *Deppea* complex**

The great generic diversity of Hamelieae is directly related to the *Deppea* complex, for which a phylogenetic framework is not yet conclusive. In the most complete phylogeny for the Hamelieae tribe, Stranzcinger et al. (2014) included 13 genera and 33 species; their results showed that among the non-monotypic genera only *Hamelia* was retrieved as monophyletic, while all the genera in the *Deppea* complex were placed inside an unsolved clade or retrieved as paraphyletic. These results could reflect an artificial classification of the tribe, but they could also be an artifact of the few characters used to reconstruct the phylogenetic hypothesis (two molecular markers only). The seed morphological mosaic among the sampled taxa in this study does not solve the conflictive circumscription of *Deppea*, which depending on the author is synonymized with *Bellizinca*, *Csapodya*, *Deppeopsis*, *Edithea*, and *Schenckia* (Lorence & Dwyer 1988; Manns & Bremer 2010; Lorence 2012) or accepted as separate generic entities (Borhidi et al. 2004a, 2004b; Borhidi 2006, 2012). Either these genera are not monophyletic or the seed characters used here are in many cases highly homoplastic; only a robust phylogeny constructed with a diverse set of data will reveal which of these two explanations, if any, is more supported.

The phylogenetic hypothesis presented by Stranzcinger et al. (2014) retrieved a clade without resolution in which *Bellizinca*, *Csapodya*, *Edithea*, and *Schenckia* are paraphyletic with respect to *Deppea*. This could support the recognition of a single large genus *Deppea*. Nevertheless, the flower morphology is very different in *Deppea* with respect to the other genera (fig. 1), not only regarding the colour of the petals, but also the corolla tube size. Morphologically, *Bellizinca*, *Csapodya*, and *Edithea* are different from *Deppea* by the corolla tube length being larger than 1 cm (Borhidi et al. 2004a). In addition, there are other differences in flower morphology among the genera: *Bellizinca* is recognized by the tubular corolla of 1.4 to 2.6 cm long, the foliaceous calyx lobes up to 1.8 cm long and the stamens attached at the base of the corolla tube (Borhidi et al. 2004a); *Csapodya* is characterized by the 5 to 5.5 cm tubular or salverform corolla, the foliaceous calyx lobes, 8 to 25 mm long, and the stamens attached at the middle portion of the corolla tube (Borhidi et al. 2004a; Borhidi & Reyes-Garcia 2007), while *Edithea* is well characterized by the salverform corolla with the stamens attached near the corolla throat (Borhidi et al. 2004a). The corolla length and colour differences are interpreted as shifts in the pollination mechanism, with a bee pollination syndrome in *Deppea* and a hummingbird pollination syndrome in the other genera (Lorence & Dwyer 1988; Lorence 2012).

**Taxonomic implications of seed morphology in the *Deppea* complex**

Seed morphology for the *Deppea* complex was briefly studied by Borhidi et al. (2004a), who compared seed differences among *Bellizinca*, *Csapodya*, *Edithea*, and *Deppea* mentioning shape, hilum position, and testa ornamentation differences. Our results partially agree with those of Borhidi et al. (2004a) in that the seed shape among these genera is different. However, we found discrepancies in certain characters, particularly regarding the hilum position: we treat as the micropyle what Borhidi and collaborators considered to be the hilum, based on our SEM microphotographs and on the orthotropous nature of the ovule in most of the studied genera (Martínez-Cabrera et al. 2014). Orthotropic ovules were described using anatomical methods for many Hamelieae members by Martínez-Cabrera et al. (2014) including *Deppea*, *Hamelia*, *Hoffmannia*, *Omitlemia*, *Pinarophyllum*, *Plocanophyllum*, and *Syringantha*. Nevertheless, for *Csapodya splendens*, the hilum and micropyle positions indicate a more likely anatropous ovule nature, a condition common in most Rubiaceae genera (Robbrecht 1988; Martínez-Cabrera et al. 2014). Further anatomical studies are however needed to corroborate the ovule nature in *Csapodya*.

**Csapodya and Bellizinca** – The seeds of *Csapodya* are easily recognized from those of *Deppea* by being flattened, a character state shared with *Deppeopsis*, *Omitlemia*, and *Pseudomiltemia*. *Csapodya* differs by the combination of the concave profile with a sunken profile micrelief plus V-undulate anticalinal wall boundaries and the evident hilum. It should be noted that in the phylogenetic framework presented by Stranzcinger et al. (2014), *Csapodya* is placed in a different lineage with respect to *Deppeopsis*, *Omitlemia*, and *Pseudomiltemia*, which share a recent common ancestor. The seeds in the genus *Bellizinca* can be distinguished by the V-undulate anticalinal wall boundary in contrast to the U-undulate or straight anticalinal wall boundary in *Deppea*. This character state, in addition to the corolla characters, could support the recognition of *Bellizinca* and *Csapodya* as separate generic entities. The genus *Csapodya* was segregated from *Deppea* based on *D. splendens* (Borhidi et al. 2004a) and currently could include two or three species (Borhidi & Reyes-Garcia 2007). However, in the Rubiaceae treatment of the Mesoamerican Flora (Lorence 2012), *Csapodya* is treated as a synonym of *Deppea*, and only one species potentially belonging in *Csapodya* (i.e. *D. splendens*) is recognized, arguing that the other species were described based on immature inflorescences. Despite several attempts to collect *C. challengeri*, we failed as there appear to be errors in the type locality (the provided coordinates do not coincide with the vegetation or elevation description), however, our results support that *C. sousae* and *S. splendens* are different species, since they have several contrasting characters, including the colour, exotesta cell shape, anticalinal wall boundaries, micropyle position, and hilum visibility.

**Edithea** – The seed morphology of the genus *Edithea* is variable and overlaps with most of the other genera; some species are easily recognizable by the smooth periclinal micrelief (*E. floribunda* and *E. Miahuatlanica*), a unique character state among all the Hamelieae taxa studied. However, the other species in the genus have concave outlines with a sunken profile (*E. guerrerensis* and *E. schiblii*), a common character state among the species in the *Deppea* complex. In contrast to *Csapodya* and *Bellizinca*, which in the Stranzcinger et al. (2014) phylogeny formed
a clade within Deppea in an unsolved position, the Edithea species are placed inside a clade with other Deppea species, highlighting the possibility of a polyphyletic Deppea. Seed morphology may support the previously suggested synonymy of Edithea and Deppea by using other morphological characters and molecular evidence (Lorence & Dwyer 1988; Manns & Bremer 2010; Lorence 2012). However, further studies with other sources of evidence and broader taxon sampling are needed to reliably take decisions upon the synonymy of the names or the acceptance of these taxa.

Deppeopsis – Another genus sometimes synonymized with Deppea is Deppeopsis, which was primarily segregated by its cylindrical fruit shape (Borhidi & Stranzcinger 2012). Currently, it includes five species from Mexico and Guatemala (Borhidi 2012; Borhidi & Stranyczinger 2012). In the Mesoamerican Rubiaceae treatment (Lorence 2012), only two species of this genus are included, and they are treated under Deppea. Using seed morphology, Deppeopsis is easily distinguishable from Deppea by the flattened seeds, but other character states, such as the yellowish testa colour (only shared with Deppea hamelioioides), U-undulate anticlinal wall boundaries, papillose periclinal microrelief, and the lateral position of the micropyyle are shared with at least one species of Deppea. Based on our seed character observations, we support the separation of Deppeopsis from Deppea, as it was also suggested by the Stranyczinger et al. (2014) phylogenetic hypothesis, in which Deppeopsis is clearly a separate lineage from Deppea, more closely related to other taxa with flattened seeds such as Omiltemia and Pseudomiltemia.

Pseudomiltemia and Omiltemia – The Mexican genus Pseudomiltemia was segregated from Omiltemia (Borhidi et al. 2004b) and has two species characterized by the stamen insertion near the corolla throat (vs near the base in Omiltemia) and the funneliform corolla (vs campanulate in Omiltemia) (Martinez-Camilo et al. 2011; Borhidi 2012). The Mexican genus Omiltemia was described by Standley (1918) based on the red and solitary flowers and has three species (Borhidi & Velasco-Gutiérrez 2010; Borhidi 2012; Lozada-Pérez & Rojas-Gutiérrez 2016). Both share flattened seeds, while the main difference is the periclinal microrelief, papillose in Omiltemia and concave outlines with a sunken profile in Pseudomiltemia. Borhidi et al. (2004b) also used seed morphology in conjunction with other evidence to justify the transfer of Omiltemia filisepala to Pseudomiltemia using differences in the hilum position (lateral in Omiltemia and central P. filisepala); perpendicular walls surface (slightly undulate in Omiltemia and slightly tuberculcated in P. filisepala), and horizontal wall microrelief (smooth in Omiltemia and densely tuberculcated in P. filisepala). Our study differs in the description of the micropyle position, presumably treated as hilum in Borhidi et al. (2004b), considered to be for both species as sub-central, as well as in the microrelief that was considered to be smooth in Omiltemia, while our results evidently show a papillose microrelief. Based on the seed morphology, both genera, Pseudomiltemia and Omiltemia, should be recognized.

Pinarophyllon and Plocaniophyllon – The other genera of the Deppea complex are Pinarophyllon and Plocaniophyllon. The genus Pinarophyllon was recognized by the herbaceous habit and the turbinate fruits (Brandegee 1914; Lorence 2012) and has two species in Mexico and Guatemala. The monotypic Mexican genus Plocaniophyllon was described based on the lineolate leaf venation (Brandegee 1914; Lorence 2012). In both genera, the seeds are polygonal and ellipsoid with straight anticlinal wall boundaries. These are the same character states as in Hoffmannia, but they differ in that Pinarophyllon and Plocaniophyllon have smooth or papillose periclinal wall microrelief, while Hoffmannia has verrucose or concave outlines with a sunken profile. The seeds of Plocaniophyllon were described by Martinez-Cabrera et al. (2008) as ovoid, “irregular”, 0.4–0.6 mm long, with large polygonal shaped cells and foveolate multicellular sculpture, anticlinal walls boundaries slightly undulated, and outer periclinal walls concave with tuberculcated micro-ornamentation. Our description agreed in the seed shape, size, and cell shape; however, Martinez-Cabrera et al. (2008) defined the cells boundaries as slightly undulated while we consider them to be straight, as well as the microrelief to be papillose instead of tuberculcated. The seed character state to distinguish Pinarophyllon and Plocaniophyllon is the shape of the cells surrounding the micropyyle: isodiametric in Pinarophyllon and elongated in Plocaniophyllon.

Schenckia – In the literature, there is consensus to treat Schenckia as a synonym of Deppea (Lorence & Dwyer 1988; Lorence 2012). Its inclusion gives the distribution of Deppea to a disjunct pattern since Schenckia is only known from Blumenau in Brazil and from the north of Argentina (Lorence & Dwyer 1988), whereas Deppea is practically restricted to the Mesoamerican region. The seed morphology, as the molecular evidence (Manns & Bremer 2010), supports its synonymy as there is no unique combination of characters to distinguish Schenckia from Deppea.

CONCLUSION

Our study reveals why the Deppea complex is so problematic from a taxonomic point of view and reflects the fact that a comprehensive approach with different lines of evidence, such as morphological, molecular, and phylogenetic characters, is needed to evaluate the generic circumscriptions within the Deppea complex in the Hamelieae tribe. Despite this, we addressed the importance of seed morphology as a source of characters in Hamelieae systematics and taxonomy and we highlight the broad diversity of seed morphological character states in this tribe.

Although the characters evaluated here show high overlap across the genera, there is some evidence that seed morphology can contribute to taking taxonomic decisions within the Deppea complex. Based on our study, we consider that there is support for the recognition of Bellizina, Csapodya, and Deppeopsis, currently considered to be synonyms of Deppea by some authors. Also, seed morphology supports the synonymy of Edithea and Schenckia with Deppea, and provided additional morphological evidence for the recognition of Omiltemia, Pinarophyllon, Plocaniophyllon, and Pseudomiltemia. However, for these taxonomic decisions to be definitive, an integrative approach using a robust phylogenetic context is still necessary. In particular to establish the generic limits within the Deppea complex inside the Hamelieae tribe, a full
perspective that includes micro- and macromorphology plus molecular evidence is desirable to unravel this conflictive group.

SUPPLEMENTARY FILES

Supplementary file 1 – Voucher information of the studied specimens, which are all deposited at MEXU except for Schenckia blumenavensis, which is deposited at C.
https://doi.org/10.5091/plecevo.84486.supp1

Supplementary file 2 – Illustrated overview of the seed characters and character states.
https://doi.org/10.5091/plecevo.84486.supp2

Supplementary file 3 – Full seed descriptions of the 37 studied species in 15 genera of the Hamelieae.
https://doi.org/10.5091/plecevo.84486.supp3

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REFERENCES

Andersson L. 1995. Tribes and genera of the Cinchonae complex (Rubiaceae). Annals of the Missouri Botanical Garden 82: 409–427. https://doi.org/10.2307/2399891

Andersson L. & Rova H.E. 1999. The rps16 intron and the phylogeny of the Rubioideae (Rubiaceae). Plant Systematics & Evolution 214: 161–186. https://doi.org/10.1007/ BF00985737

Antonelli A., Clarkson J.J., Kainulainen K., et al. 2021. Settling a family feud: a high-level phylogenomic framework for the Gentianales based on 353 nuclear genes and partial plastomes. American Journal of Botany 108: 1143–1165. https://doi.org/10.1002/ajb2.1697

Barthlott W. & Hunt D. 2000. Seed-diversity in the Cactaceae subfamily Cactoideae. Succulent Plant Research vol. 5. David Hunt, Milborne Port.

Borhidi A. 2006. Rubiáceas de México. Akadémiai Kiadó, Budapest.

Borhidi A. 2012. Rubiáceas de México. Second edition. Akadémiai Kiadó, Budapest.

Borhidi A. & Stranczinger S. 2012. Deppeopsis, a género nuevo (Hamelieae, Rubiaceae) de México y Guatemala. Acta Botanica Hungarica 54: 86–89. https://doi.org/10.1556/abot.54.2012.1-2.10

Borhidi A., Darók J., Kocsis M., Stranczinger S. & Kaposvári F. 2004a. Critical revision of the Deppea complex (Rubiaceae, Hamelieae). Acta Botanica Hungarica 46: 77–89. https://doi.org/10.1556/abot.46.2004.1-2.7

Borhidi A., Darók J., Kocsis M., Stranczinger S. & Kaposvári F. 2004b. Critical revision of the Omiltemia complex (Rubiaceae, Hamelieae). Acta Botanica Hungarica 46: 69–76. https://doi.org/10.1556/abot.46.2004.1-2.6

Borhidi A. & Reyes-García A. 2007. Estudios sobre Rubiáceas Mexicanas XI Revisión del género Cosapodya Borhidi (Rondeletieae), endémico de Chiapas con tres especies. Acta Botanica Hungarica 49: 13–25. https://doi.org/10.1556/abot.49.2007.1-2.2

Borhidi A. & Velasco-Gutiérrez K. 2010. Estudios sobre Rubiáceas Mexicanas XXV. Una especie nueva en el género Omiltemia Standl. (Hamelieae). Acta Botanica Hungarica 52: 35–39. https://doi.org/10.1556/abot.52.2010.1-2.4

Breedlove D.E. & Lorence D.H. 1987. New species of Deppea (Rubiaceae) from Chiapas, México. Phytologia 63: 43–47.

Bremekamp C.E.B. 1966. Remarks on the position, the delimitation and the subdivision of the Rubiaceae. Acta Botanica Neerlandica 15: 1–33. https://doi.org/10.1111/j.1438-8677.1966.tb00207.x

Bremer B. 1987. The sister group of the paleotropical tribe Argostemmateae: a redefined neotropical tribe Hamelieae (Rubiaceae). Cladistics 3: 35–51. https://doi.org/10.1111/j.1096-0031.1987.tb00495.x

Bremer B., Andreasen K. & Olsson D. 1995. Subfamilial and tribal relationships in the Rubiaceae based on rbcL sequence data. Annals of the Missouri Botanical Garden 82: 383–397. https://doi.org/10.2307/2399889

Bremer B. & Eriksson O. 1992. Evolution of fruit characters and dispersal modes in the tropical family Rubiaceae. Biological Journal of the Linnean Society 47: 79–95. https://doi.org/10.1111/j.1096-3842.1992.tb00657.x

Brandegge T.S. 1914. Plantae Mexicanae Purpusianae VI. University of California Publications in Botany 6: 71.

De Candolle A.P. 1830. Prodromus systematis naturalis regni vegetabilis. Treuttel & Würtz, Paris.

Delprete P.G. 1998. Notes on calycophyllous Rubiaceae. Part III. Systematic position of the monotypic Mexican genus Cosmocalyx and notes on the calycophyll development. Brittonia 50: 309–317. https://doi.org/10.2307/2807774

Delprete P.G., Nee M. & Koek-Noorman J. 2005. Resurrection and dispersal modes in the tropical family Rubiaceae. Biological Journal of the Linnean Society 84: 79–95. https://doi.org/10.1001/j.1096-0013.1992.tb00657.x

Endlicher S. 1836. Genera Plantarum secundum ordinem naturales disposita. Apud Fr. Beck Universitatis Bibliopolam, Vincloboanae. https://doi.org/10.5962/bhl.title.728

Harris J.G. & Harris M.W. 2001. Plant identification terminology. An illustrated glossary. Second edition. Spring Lake Publishing, Spring Lake.

Hauenstein M.V. & Dwyer J.D. 1969. Seed morphology in the tribe Morinaceae (Rubiaceae). Bulletin of the Torrey Botanical Club 96: 704–710. https://doi.org/10.2307/2483550

Hooker J.D. 1873. Rubiaceae. In: Bentham G. & Hooker J.D. (eds) Genera Plantarum vol. 2(1): 7–151. Reeve & Co., London.

Hrubá A. 2009. Critical revision of the tribe Argostemmateae (Rubiaceae). Cladistics 25: 89–134. https://doi.org/10.1111/j.1095-8677.2008.00427.x

Hrubá A. & Stranczinger S. 2012. Deppeopsis, a género novo (Hamelieae, Rubiaceae) de México y Guatemala. Acta Botanica Hungarica 54: 86–89. https://doi.org/10.1556/abot.54.2012.1-2.10

Hrubá A., Darók J., Kocsis M., Stranczinger S. & Kaposvári F. 2004a. Critical revision of the Deppea complex (Rubiaceae, Hamelieae). Acta Botanica Hungarica 46: 77–89. https://doi.org/10.1556/abot.46.2004.1-2.7

Hrubá A., Darók J., Kocsis M., Stranczinger S. & Kaposvári F. 2004b. Critical revision of the Omiltemia complex (Rubiaceae, Hamelieae). Acta Botanica Hungarica 46: 69–76. https://doi.org/10.1556/abot.46.2004.1-2.6

Hrubá A. & Stranczinger S. 2012. Deppeopsis, a género nuevo (Hamelieae, Rubiaceae) de México y Guatemala. Acta Botanica Hungarica 54: 86–89. https://doi.org/10.1556/abot.54.2012.1-2.10

Mead T. & McDonald P.I. 2002. Seed diversity in the Cactaceae. Cladistics 18: 673–702. https://doi.org/10.1111/j.1095-8677.2002.tb00078.x

Mead T. & McDonald P.I. 2002. Seed diversity in the Cactaceae. Cladistics 18: 673–702. https://doi.org/10.1111/j.1095-8677.2002.tb00078.x

Mead T. & McDonald P.I. 2002. Seed diversity in the Cactaceae. Cladistics 18: 673–702. https://doi.org/10.1111/j.1095-8677.2002.tb00078.x

Schenckia blumenaviensis
Khalik K.A., El-Ghani M.A. & El Kordy A. 2008. Fruit and seed morphology in Galium L. (Rubiaceae) and its importance for taxonomic identification. *Acta Botanica Croatica* 67: 1–20.

Kirkbride H.J. 1984. Manipulus Rubiacearum III. Deppeae, a new tribe of Rubioideae (Rubiaceae). *Brittonia* 36: 317–320. https://doi.org/10.2307/2806533

Koch K., Bhushan B. & Barthlott W. 2009. Multifunctional surface structures of plants: An inspiration for biomimetics. *Progress in Materials Science* 54: 137–178. https://doi.org/10.1016/j.pmatsci.2008.07.003

Lorence D.H. & Dwyer J.D. 1988. A revision of *Deppea* (Rubiaceae). *Allertonia* 4: 389–436.

Lorence D.H. 2012. *Deppea*. In: Davidse G., Sousa M., Knapp S. & Chinat F. (eds) Flora Mesoamericana vol. 4(2): 75–78. Missouri Botanical Garden Press, St. Louis.

Lozada-Pérez L. & Rojas-Gutiérrez J. 2016. Una nueva especie, *Omiltemia guerrerensis* de Guerrero, México. *Novon* 24: 365–368. https://doi.org/10.3417/2012041

Manns U. & Bremer B. 2010. Towards a better understanding of intertribal relationships and stable tribal delimitations within Cinchonioideae s.s. (Rubiaceae). *Molecular Phylogenetics and Evolution* 56: 21–39. https://doi.org/10.1016/j.ympev.2010.04.002

Martínez-Cabrera D., Terrazas T., Flores H. & Ochoterena H. 2008. Morphology, anatomy, and taxonomic position of *Plocaniophyllon* Brandegee (Rubiaceae): a monotypic genus endemic to Mesoamerica. *Taxon* 57: 33–42. https://doi.org/10.2307/25065946

Martínez-Cabrera D., Terrazas T. & Ochoterena H. 2014. *Morfología y anatomía floral de la tribu Hamelieae (Rubiaceae)*. *Brittonia* 66: 89–106. https://doi.org/10.1636/s12228-013-9301-5

Martínez-Camilo R., Martínez-Meléndez N., Martínez-Meléndez M., Pérez-Farrera M.A. & Lorence D.H. 2011. Una nueva especie de *Pseudomiltemia* (Rubiaceae) de Chiapas, Mexico. *Brittonia* 63: 197–202. https://doi.org/10.1636/s12228-010-9150-4

Martínez-Camilo R., Martínez-Meléndez N., Martínez-Meléndez M., Pérez-Farrera M.A. & Lorence D.H. 2015. Redescubrimiento de *Eizia mexicana*, una especie endémica de la familia Rubiaceae presumiblemente extinta. *Botanical Sciences* 93: 679–682. https://doi.org/10.17129/botsci.242

McDowell T. 1996. *Syringantha coulteri* (Hooker f.) McDowell, and new combination and remarks on the relationships of the monotypic Mexican genus *Syringantha* Standley (Rubiaceae). *Novon* 6: 273–279. https://doi.org/10.2307/3392093

Nixon K.C. 1999. WinClada ver. 1.0000. Published by the author, Ithaca, NY, USA.

Robbrecht E. 1988. Tropical woody Rubiaceae. *Opera Botanica Belgica* vol. 1. National Botanic Garden of Belgium, Meise.

Robbrecht E. & Bridson K.A. 1993. Nomenclatural notes on three Rubiaceae genera. *Opera Botanica Belgica* vol. 6: 199–200. National Botanic Garden of Belgium, Meise.

Robbrecht E. & Manen J.F. 2006. The major evolutionary lineages of the coffee family (Rubiaceae, angiosperms). Combined analysis (nDNA and cpDNA) to infer the position of *Coptosapelta* and *Luculia*, and supertree construction based on rbcL, rps16, trnL-trnF and atpB-rbcL data. A new classification in two subfamilies, Cinchonoideae and Rubioidae. *Systematics and Geography of Plants* 76: 85–146. https://doi.org/10.2307/20649700

Schaumann F. & Heikken T. 2002. Endozoocorous seed dispersal by martens (*Martes foina, M. martes*) in two woodland habitats. *Flora - Morphology, Distribution, Functional Ecology of Plants* 197: 370–378. https://doi.org/10.1078/0367-2530-00053

Schumann K. 1897. Rubiaceae. In: *Engler A. & Prantl K. (eds) Die natürliche Pflanzenfamilien* 19(4): 1–156. Engelmann, Leipzig.

Standley P.C. 1918. *Omitlemia*, a new genus of Rubiaceae from Mexico. *Journal of the Washington Academy of Sciences* 8: 426–427. https://www.jstor.org/stable/24521406

Stranzinger S., Galambos A., Szenas D. & Szalontai B. 2014. Phylogenetic relationships in the Neotropical tribe Hamelieae (Rubiaceae, Cinchonoideae) and comments on its generic limits. *Journal of Systematics and Evolution* 52: 643–650. https://doi.org/10.1111/jse.12103

Terrell E.E., Lewis W.H., Robinson H. & Nowicke J.W. 1986. Phylogenetic implications of diverse seed types, chromosome numbers, and pollen morphology in *Hastozoa* (Rubiaceae). *American Journal of Botany* 73: 103–115. https://doi.org/10.1002/j.1537-2197.1986.tb09686.x

Terrell E.E. & Robinson H. 2004. Seed and capsule characters in *Arcytophyllum*, *Bouvardia*, and *Manetia* (Rubiaceae), with notes on *A. serpyllaceum*. *SIDA, Contributions to Botany* 21: 911–927.

Torres-Montúfar A. 2018. Sistemática del complejo *Rondeletia* (Rubiaceae). PhD thesis, Universidad Nacional Autónoma de México, México. Available from https://repositorio.unam.mx/contenidos/64735 [accessed 8 Sep. 2021].

Verd court B. 1958. Remarks on the classification of the Rubiaceae. *Bulletin du Jardin botanique de l’État à Bruxelles* 28: 209–281. https://doi.org/10.2307/3667090

Robbrecht E., Bridson K.A. & Ochoterena H. 2015. Seed macro- and micromorphology of Hamelieae. *Acta Botanica Croatica* vol. 69.

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