Three new combinations in Villaria (Octotropideae, Rubiaceae), an endemic genus from the Philippines

A.H. Arriola¹, G.J.D. Alejandro²

Key words

Hypobathrum Ixoroideae Octotropideae Philippine endemics Rubiaceae Villaria

Abstract Three new species combinations are made under Villaria for the Philippine endemics Hypobathrum coriaceum, H. multibracteatum and H. purpureum. Morphological features of these three Hypobathrum species revealed a closer resemblance with Villaria than with Hypobathrum, as the three Philippine endemics possess a unilocular ovary with parietal placentation; a character that is not found in any genera of Octotropideae except in Villaria. Lectotypes and a neotype are selected.

Published on 26 June 2020

INTRODUCTION

Botanical inventories and exploration, gearing towards the development of a much-updated knowledge of Philippine Rubiaceae, lead to the discovery of various taxa that required taxonomic solutions due to an outdated classification. This is evident in various taxonomic amendments in Philippine Rubiaceae such as in tribes Coffeeae (Ali & Robbrecht 1991), Vanguerieae (Alejandro et al. 2013, 2014, Arriola et al. 2016a, b), Mussaendeae (Alejandro et al. 2016), Ixoreae (Banag et al. 2017), and Morindeae (Razafimandimbison & Bremer 2011). Tribe Octotropideae is also in need of revision. This palaeotropical tribe was first separated from Gardenieae s.lat. based on morphology, and initially placed under the name 'Hypobathreae' (Robbrecht 1980, Robbrecht & Puff 1986), but later on a little known Indian genus Octotropis Bedd., also belonging to this tribe, necessitated the re-instatement of the tribal name Octotropideae (Robbrecht et al. 1993, Robbrecht & Manen 2006). Octotropideae is characterized by the following morphological characters: fruits drupe-like berries, seeds pendulous, imbricate, embryo radicle directed upwards and a fibrous seed coat consisting of linear cells (Robbrecht 1980). In the Philippines, Octotropideae is represented by two genera, Villaria Rolfe and Hypobathrum Blume.

Villaria is a small genus endemic to the Philippines thriving in lowland to coastal forests. The genus is easily distinguished by the following morphological features: young stems flattened, stipules pilose at the inner side, corolla pentamerous, stigma hairy, ovules numerous and horizontally arranged, fruit > 1 cm diam with a leathery mesocarp and membranous endocarp, and seeds with exotestal cells having radial and tangential thickenings (Alejandro et al. 2011). Robbrecht & Puff (1986) state, that among the genera of Octotropideae, only Villaria possesses a unilocular ovary with a parietal placentation. A revision of Villaria (Alejandro et al. 2011) recognized six species, namely V. acutifolia (Elmer) Merr., V. fasciculiflora Quisumb & Merr.,

V. glomerata (Bartl. ex DC.) Mulyan. & Ridsdale, V. leyetensis Alejandro & Meve and V. odorata (Blanco) Merr. Recently, V. uniflora Arriola & Alejandro (2013) was recognized as the seventh species, the only one with uniflorous inflorescences. Alejandro & Meve (2016) transferred Randia lanceolata Merr. to Villaria since Randia L. belongs to the tribe Gardenieae and it has been regarded as a misused name for palaeotropical taxa for a long time (Keay 1958). Recently, Arriola et al. (2018) described the 9th species of the genus named as V. marinduquensis Arriola & Alejandro, whereby the etymology of the name was based on the type locality.

Hypobathrum is a genus created to describe a plant from the Burangrang Mountain (Java) and it is characterized by having features of a typical Rubiaceae; it has a habit that resembles Coffea L. due to its densely packed flowers in axillary fascicles (Blume 1826). Hypobathrum was placed under group III of the 'Hypobathreae' by Robbrecht & Puff (1986) based on fruit size, number of ovules and type of exotestal cells. Its distribution is strictly limited to Malesia after its Madagascan and Mauritian representatives were accommodated in tribe Coffeeae (Davis et al. 2006, Ranarivelo-Randriamboavonjy et al. 2007). In 2002, Mulyaningsih & Ridsdale revised Hypobathrum, in which they recognized 26 species; however, this work focused only on Bornean species. In the Philippines, Hypobathrum is represented only by three species, namely, H. coriaceum Merr., H. multibracteatum Elmer and H. purpureum (Elmer) Merr. Examination of their type specimens and recent collections revealed interesting results.

Based on our morphological examination, the three Philippine Hypobathrum species deviate from Blume's (1826) earlier treatment of the genus. Furthermore, several features of the genus Hypobathrum, as enumerated by Robbrecht & Puff (1986), such as tetramerous corolla, bilocular ovary with axillary placentation, pendulous ovules, fruit < 1 cm diam with fleshy mesocarp and chartaceous endocarp, and wrinkled exotesta with elongated cells are evidently absent in our material. Instead, our samples show the features typical for Villaria as mentioned above (Robbrecht & Puff 1986, Alejandro et al. 2011). Furthermore, other characters of Villaria as enumerated by Alejandro et al. (2011) are likewise present in the three Philippine Hypobathrum species: the unilocular ovary with a parietal placentation, as

Non-commercial:

¹ Department of Biological Sciences, College of Arts and Sciences, University of the East, 2219 C.M. Recto Ave, Manila, Philippines;

corresponding author e-mail: axel.arriola@ue.edu.ph. ² College of Science, The Graduate School and Research Center for the

Natural & Applied Sciences, University of Santo Tomas, España, Manila, 1015 Philippines.

^{© 2020} Naturalis Biodiversity Center

You are free to share - to copy, distribute and transmit the work, under the following conditions:

Attribution You must attribute the work in the manner specified by the author or licensor (but not in any way that suggests that they endorse you or your use of the work). You may not use this work for commercial purposes.

No derivative works: You may not alter, transform, or build upon this work

For any reuse or distribution, you must make clear to others the license terms of this work, which can be found at http://creativecommons.org/licenses/by-nc-nd/3.0/legalcode. Any of the above conditions can be waived if you get permission from the copyright holder. Nothing in this license impairs or restricts the author's moral rights.



Fig. 1 Serial cross sections of the fruits (left to right: apical side; upper median, lower median, basal side). a–d. *Villaria purpurea* (Elmer) Arriola & Alejandro; e–h. *Villaria multibracteata* (Elmer) Arriola & Alejandro; i–l. *Villaria coriacea* (Merr.) Arriola & Alejandro (a–d. *Arriola & Alejandro 11-048*; e–h. *Arriola T023*; i–l. *Arriola & Cruz T027*; all USTH). — Scale bars: a–d = 1 cm; e–h. = 0.5 cm; i–l. = 0.7 cm. — Photos taken by A.H. Arriola.

revealed by our serial cross sections of the fruits, is particularly relevant to our assessment on their generic affiliation (Fig. 1). As mentioned above the unilocular ovary with a parietal placentation is very rare in *Octotropideae* and exists only in *Villaria*. Apparently, this attribute is valuable taxonomically and considered to be a synapomorphy for a likely monophyletic *Villaria*. In fact, this was the major reason that prompted the transfer of *H. glomeratum* (Bartl. ex DC.) K.Schum. to *Villaria* (Mulyaningsih & Ridsdale 2004). Table 1 summarizes the features that differentiate *Hypobathrum* and *Villaria*.

Based on our morphological survey it is now clear that *H. co*riaceum, *H. multibracteatum* and *H. purpureum* have many salient features of *Villaria* that contradicts its current generic

 Table 1
 A comparison between Hypobathrum (Robbrecht & Puff 1986) and

 Villaria (Alejandro et al. 2011).

	Hypobathrum	Villaria
Ovary	Bilocular	Unilocular
Placentation	Axillary	Parietal
Fruit size (diam)	< 1 cm	> 1 cm
Mesocarp	Fleshy	Leathery
Endocarp	Chartaceous	Membranous

affiliation as previously proposed by Merrill (1923, 1926) and Elmer (1934). We therefore formally present here three new combinations.

TAXONOMIC TREATMENT

1. Villaria coriacea (Merr.) Arriola & Alejandro, comb. nov.

Hypobathrum coriaceum Merr. (1926) 490. — Lectotype (designated here): BS (Ramos) 42615, (lecto US [photo! (US00138112)]; isolecto K! (K0003039)), Philippines, Province of Bohol, Bilar.

Shrubs to small trees, 3-6 m high; branches glabrous. *Stipules* ovate to narrowly ovate, 7-8.2 by 4-5 mm, keel prominent from the lower 1/3 up to the tip, outer surface glabrous; inner surface densely pilose at the base, margin glabrous; colleters numerous, basally inside, 0.2-0.4 mm long. *Leaves*: petioles 2-3 by 1-1.5 mm, glabrous; blades oblong to oblanceolate, 3-16 by 2.5-4.5 cm, base acute, apex acuminate, coriaceous, glabrous on both sides except midrib sparsely pubescent beneath; secondary veins 10-11 on each side. *Inflorescences* supraaxillary, subsessile, 2-3 mm above the node; many-flowered glomerules; peduncle very short, < 5 mm long; bracts ovate, 0.9-1.2 by c. 0.5 mm, apex acuminate, pubescent outside, densely pilose inside, colleters few at the base inside. *Flowers* subsessile, pedicel suppressed. *Calyx*: tube infundibuliform,

2.5–3 by c. 2.5 mm, pubescent throughout; lobes ovate, c. 1 by 1.5 mm, pubescent outside, densely pilose inside, margins densely ciliate. *Corolla*: tube infundibuliform, 1.5–2.5 by c. 1.5 mm, glabrous outside, densely pilose inside; lobes ovate, 2.5–3 by c. 2.5 mm, glabrous outside, densely pilose at the base inside, margins sparsely ciliate. *Anthers* 2–2.5 by 0.3–0.5 mm, with upper 1/3 partially exserted. *Style* 0.5–0.9 mm long; stigmatic branches elliptic, 2–2.3 by 0.9–1.3 mm, papillate, projected beyond the mouth of the corolla tube. *Fruits* green, 0.6–1 by 0.7–1.2 cm; stalk 0.5–1.5 cm long, glabrous. *Seeds* ovate to oblong, 1–2 mm long, yellow.

Distribution — Philippines (Aurora, Bataan, Bohol, Bulacan, Camarines Sur, Laguna, Quezon, Sorsogon, Tarlac, Zambales Prov.).

Habitat & Ecology — In primary forest at 300–450 m, also in coastal areas. Flowering: April to June; fruiting: May to September.

Additional specimens studied. THE PHILIPPINES, Bataan, Arriola & Banag TA025 (USTH); Bilar, Arriola T028 (USTH); Camarines Sur, PPI (Reynoso, Sagcal & Fuentes) 14909 (K); Cavite, Arriola & Cruz T027 (USTH); Rizal, Arriola T031 (USTH); Tarlac, Vidal y Soler 387 (K); Zambales, BS (Edaño) 38339 (K).

Note — This species resembles *V. glomerata* because of its oblong to oblanceolate leaf blades (leaf blades broadly lanceolate in *V. glomereta*) and many-flowered glomerules. *Villaria coriacea* is distinct by its abaxially sparsely pilose stipules, apically acuminate bracts, larger corolla tube, and shorter fruit stalk.

2. Villaria multibracteata (Elmer) Arriola & Alejandro, comb. nov.

Hypobathrum multibracteatum Elmer (1934) 3250. — Lectotype (designated here): *Elmer* 15674 (lecto NY131934), Philippines, Province of Sorsogon, Irosin.

Shrubs to small trees, 2-2.5 m tall; branches glabrous. Stipules triangular, 5.5-6 by 1.5-2 mm, keel prominent from the lower 1/3 to the tip, outer surface glabrous, inner surface densely pilose at the base, margin sparsely ciliate, colleters few, 0.3–0.5 mm long. Leaves: petioles 2-4 by c. 2 mm, glabrous; blades lanceolate to ovate, 2.5-5.5 by 2.5-4 cm, recurved towards the tip, base obtuse, apex acuminate, submembranous, glabrous on both sides except for the sparsely pubescent midrib underneath; secondary veins 8-11 on each side. Inflorescences supra-axillary, 2-2.5 mm above the node, few-flowered dichasial cymes; peduncles 1-3.5 cm long, glabrous; pedicels 4-8 mm long, glabrous; bracts triangular, 0.6-1.5 by c. 0.4 mm, apex acute, glabrous outside, densely pilose inside, margin sparsely ciliate; colleters few at the base inside. Calyx: tube infundibuliform, 2-3 by 1.5-2 mm, glabrous throughout; lobes triangular, 0.3-0.5 by c. 0.2 mm, glabrous on both sides, margins sparsely ciliate. Corolla: tube infundibuliform, 2.5-3 by 0.8-1.5 mm, glabrous inside and outside; lobes ovate, c. 1.5 by 0.5-1 mm, glabrous outside, sparsely pilose at the base inside, margins glabrous. Anthers 0.9-1.2 by c. 0.5 mm, with upper 1/3 partially exserted. Style 1-1.5 mm long; stigmatic branches narrowly elliptic to elliptic, c. 2.5 mm long, papillate inside, projected beyond the mouth of the corolla tube. Fruits green, 1–2.3 by 1–1.5 cm; stalk 1–2.5 cm long, glabrous. Seeds ovate to oblong, 3-5 mm long, brown.

Distribution — Philippines (Aurora, Bataan, Bulacan, Laguna, Quezon, Samar, Sorsogon, Zambales Prov.).

Habitat & Ecology — Along forest trails and deep ravines in primary forest. Flowering: January to March; fruiting: March to May.

Additional specimens studied. THE PHILIPPINES, Bataan, Arriola T023 (USTH), Arriola & Banag TA023 (USTH), Vidal y Soler 3076 (K), Whitford 1061 (K), Williams 1061 (K); Irosin, Elmer 15925 (P); Mariveles, Loher 1477 (K); Quezon, BS (Ramos & Edaño) 28586 (K); Samar, BS (Ramos) 17503 (K, P); Sorsogon, Arriola & Buera T012 (USTH), Elmer 15511 (P).

Note — *Villaria multibracteata* resembles *V. purpurea* in its lanceolate leaf blades and cymose inflorescences. However, *V. multibracteata* differs by its narrower leaf blades with fewer nerves and the presence of multiple triangular bracts. This feature of the bracts distinguishes the species from all other *Villaria* species.

3. Villaria purpurea (Elmer) Arriola & Alejandro, comb. nov.

Tricalysia purpurea Elmer (1906) 70. — Hypobathrum purpureum (Elmer) Merr. (1923) 534. — Type: Elmer 7659 (lost in PNH, no duplicates found), Philippines, Province of Tayabas, Mount Banahaw. Neotype (designated here): FB (Borden) 2928 (neo Kl; isoneo Kl, L), Philippines, Province of Bataan, Mount Mariveles. See note 2.

Shrubs to small trees, up to 3 m tall; branches glabrous. Stipules triangular, 5-7 by 3-4 mm, keel prominent from the base to the tip, outer surface glabrous, inner surface pilose at the base, margin sparsely ciliate, colleters numerous, 0.8–1 mm long. Leaves: petioles 7–8 by 1.5–2 mm, glabrous; blades lanceolate to narrowly ovate, 7-12 by 2.5-4 cm, base acute, apex acuminate, subcoriaceous, glabrous on both sides; secondary veins 8–12 on each side. Inflorescences supra-axillary, 3.5–5 mm above the node, few- to many-flowered dichasial cymes; peduncle 3-4.5 by c. 0.9 mm, glabrous; pedicels 1-1.3 cm long, glabrous; bracts triangular, 0.3–0.8 by c. 0.3 mm, apex acuminate and sharply pointed, glabrous outside, densely pilose inside, margins sparsely ciliate; colleters numerous at the base inside. Calyx: tube infundibuliform, 2.5-5 by c. 3 mm, glabrous throughout; lobes ovate, 0.9–1.3 by 0.5–1 mm, glabrous on both sides, margin sparsely ciliate. Corolla: tube infundibuliform, 1.5-2 mm long, glabrous on both sides; lobes ovate, 3-3.5 by 2-2.5 mm, glabrous outside, sparsely pilose on the base inside, margin sparsely ciliate. Anthers 2.5-3 by c. 1 mm, base truncate, apex obtuse. Style 1-2.3 mm long; stigmatic branches elliptic, 4–4.5 by c. 1 mm, papillate inside. Fruits green, purple when mature, 2.4-4 by c. 2 cm; stalk 3.5-4.6 cm long, glabrous. Seeds angular-ovoid, 6-8 mm long, greenish to yellow.

Distribution — Philippines (Bataan, Quezon, Aurora, Sorsogon, Surigao, Visayas, Zambales Prov.).

Habitat & Ecology — In primary forest to deep wooded ravines, also near coastal areas. Flowering: April to June; fruiting: May to September.

Additional specimens studied. THE PHILIPPINES, Alabat, Quezon, BS (Ramos & Edaño) 48148 (P); Alas-asin, Bataan, Arriola & Banag TA002 (USTH); Angat, Bulacan, BS (Ramos & Edaño) 34067 (P); Baler, Aurora, Alejandro et al. 10-110 (USTH); Bataan, FB (Pascual) 28779 (P); Bulusan, Elmer 15925 (L); Ilocos, BS (Ramos) 33007 (K); Irosin, Elmer 16598 (K); Lamao, Bataan, Borden 2928 (P), Borden 21726 (K); Maria Aurora, Arriola & Alejandro 11-048 (USTH); Montalban, Rizal, Loher 6428 (K); Quezon, Merrill 34067 (P); Rizal, BS (Ramos) 41871 (P); Surigao, Banag & Tandang SU024 (PNH); Visayas, Langenberger 2074 (L).

Notes — 1. The lanceolate to narrowly ovate leaf shape of *V. purpurea* resembles that of *V. acutifolia* and *V. glomerata*. However, *V. purpurea* differs from all other known *Villaria* species by having the longest fruit stalks of all.

2. Elmer (1906) indicated *Elmer* 7959 to be the type. No duplicate with this number was found. In the Biodiversity Heritage Library, the number in the scan of Elmer (1906) has been changed by hand to 7616 (a number, among others, also mentioned by Merrill 1923), of which a duplicate is present in E. However, it is not clear that Elmer made a typing error. Therefore, we select a neotype here.

KEY TO THE SPECIES OF VILLARIA

1. 1.	Inflorescences strictly to rarely uniflorous2Inflorescences few-flowered cymes to many-floweredglomerules4
2.	Pedicel glabrous. Calyx tube < 1 mm long
2.	Pedicel puberulous. Calyx tube > 1 mm long 3
3.	Corolla tube cylindrical; lobes elliptic to ovate, glabrous on both sides. Fruits < 2 cm diam
3.	Corolla tube infundibuliform; lobes orbicular, glabrous outside, densely pillose inside at the base. Fruits > 2 cm diam
4. 4.	Peduncle very inconspicuous to short, < 5 mm long 5 Peduncle longer to very prominent, > 6 mm long 7
5. 5.	Stipules glabrous outsideV. coriaceaStipules pilose outside near the keel6
6.	Leaf blades elliptic to ovate. Calyx tube glabrous outside
6.	Leaf blades lanceolate to narrowly elliptic. Calyx tube puberulous outside
7. 7.	Leaf blades elliptic, oblong to obovate
8.	Petioles 3–5 mm long. Corolla tube 3–4 by 2.5–3 mm; lobes 4–4.5 by c. 4 mm. Stigma adaxially papillate. Fruits 9–11 by 8–9 mm
8.	Petioles 5–10 mm long. Corolla tube 5–6 by c. 5 mm; lobes 5–7 by 5–6 mm. Stigma adaxially glabrous. Fruits 14–16 by 10–14 mm
9.	Corolla tube puberulent outside, densely pillose inside.
9.	Corolla tube glabrous throughout
10.	Petioles \leq 4 mm long; leaf blades $<$ 6 cm long, base obtuse, submembranous V multibracteata
10.	Petioles > 4 mm long; leaf blades > 6 cm long, base acute, subcoriaceous

Acknowledgements The authors wish to thank the following herbaria for providing access to collections: L, P, PNH, and USTH. We thank the Research Center for the Natural and Applied Sciences, University Santo Tomas, for the utilization of facilities. This project was funded by Commission on Higher Education (CHED) Thesis grant and CHED-PHERNet.

REFERENCES

- Alejandro GJD, Arenas EH, Cremen CM, et al. 2013. A new record of Pyrostria (Vanguerieae – Rubiaceae) from the Philippines inferred from molecular and morphological data. Philippine Journal of Systematic Biology 7: 1–12.
- Alejandro GJD, Magdaleno CMM, Pacia JAT, et al. 2014. Generic affiliation of Canthium species placed under Pyrostria group B sensu Bridson (Vanguerieae – Rubiaceae) inferred from morphology and molecular data. Botanical Studies 55: 1–8.
- Alejandro GJD, Meve U. 2016. Recollection of former Randia species, recognition of a rheophytic species of the Philippine endemic Villaria (Octotropideae – Rubiaceae). Phytotaxa 253 (2): 171–175.
- Alejandro GJD, Meve U, Liede-Schumann S. 2016. A taxonomic revision of Philippine Mussaenda (Rubiaceae, Mussaendeae). Annals of the Missouri Botanical Garden 101 (3): 457–524.
- Alejandro GJD, Meve U, Mouly A, et al. 2011. Molecular phylogeny and taxonomic revision of the Philippine endemic Villaria Rolfe (Rubiaceae). Plant Systematics and Evolution 296: 1–20.
- Ali SJ, Robbrecht E. 1991. Remarks on the tropical Asian and Australian taxa included in Diplospora or Tricalysia (Rubiaceae-Ixoroideae-Gardenieae). Blumea 35: 279–305.
- Arriola AH, Alejandro GJD. 2013. A new species of Villaria (Octotropideae, Rubiaceae) from Luzon, Philippines, including its conservation status. Phytotaxa 111: 57–60.
- Arriola AH, Dalit B, Alejandro GJD. 2018. Villaria marinduquensis (Octotropideae, Rubiaceae) a new species from Marinduque, Philippines. Annales Botanici Fennici 55: 325–328.
- Arriola AH, Meve U, Alejandro GJD. 2016a. Canthium elmeri Merr. lectotypified and transferred to Pyrostria (Rubiaceae). Annales Botanici Fennici 53: 216–218.
- Arriola AH, Paraguison L, Alejandro GJD. 2016b. Kanapia (Vanguerieae): a new endemic genus of Philippine Rubiaceae. Plant Systematics and Evolution 302: 911–920.
- Banag CI, Mouly A, Alejandro GJD, et al. 2017. Ixora (Rubiaceae) in the Philippines crossroads or cradle. BMC Evolutionary Biology 17: 131.
- Blume CL. 1826. Bijdragen tot de Flora van Nederlandsch Indië: 1007. Ter Lands Drukkerij, Batavia.
- Davis AP, Govaerts R, Bridson DM, et al. 2006. An annotated taxonomic conspectus of the genus Coffea (Rubiaceae). Botanical Journal of Linnean Society 152: 465–512.
- Elmer ADE. 1906. Philippine Rubiaceae. Leaflets of Philippine Botany 1: 70.
- Elmer ADE. 1934. New Urticaceae and Rubiaceae. Leaflets of Philippine Botany 9: 3250.
- Keay RWJ. 1958. Randia and Gardenia in West Africa. Bulletin du Jardin Botanique de l'État à Bruxelles 28: 15.
- Merrill ED. 1923. An enumeration of Philippine flowering plants 2. Bureau of Printing, Manila.
- Merrill ED. 1926. The genus Hypobathrum Blume. Philippine Journal of Science 29: 490.
- Mulyaningsih T, Ridsdale CE. 2002. The Bornean genus Hypobathrum (Rubiaceae) an investigation of its characters and taxonomic status. Reinwardtia 12: 95–116.
- Mulyaningsih T, Ridsdale CE. 2004. An additional species of Villaria Rolfe (Rubiaceae) from the Philippines. Reinwardtia 12: 195–197.
- Ranarivelo-Randriamboavonjy T, Robbrecht E, Rabakonandrianina E, et al. 2007. Revision of the Malagasy species of the genus Tricalysia (Rubiaceae). Botanical Journal of Linnaean Society 155: 97.
- Razafimandimbison SG, Bremer B. 2011. Nomenclatural changes and taxonomic notes in the tribe Morindeae (Rubiaceae). Adansonia 33: 283–309.
- Robbrecht E. 1980. The Hypobathreae (Rubiaceae Ixoroideae). 1. Delimitation and division of a new tribe. Bulletin du Jardin Botanique National de Belgique 50: 69–77.
- Robbrecht E, Bridson DM, Deb DB. 1993. The South Indian genus Octotropis (Rubiaceae). An investigation of its characters and reinstatement of the tribal name Octotropideae. Opera Botanica Belgica 6: 81–91.
- Robbrecht E, Manen J. 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 Rubioideae. Systematics and Geography of Plants 76: 85–146.
- Robbrecht E, Puff C. 1986. A survey of the Gardenieae and related tribes (Rubiaceae). Botanische Jahrbücher für Systematik 108: 63–137.