Harvard Papers in Botany

Volume 29, Number 1 June 2024

A Publication of the Harvard University Herbaria Including

The Journal of the Arnold Arboretum

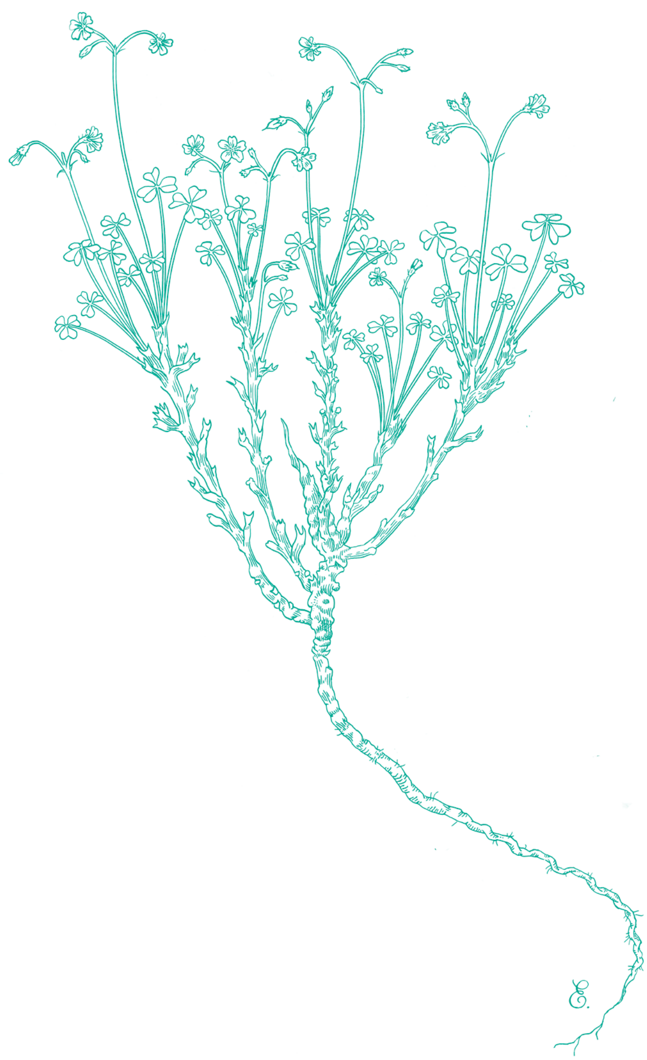
Arnold Arboretum

Botanical Museum

Farlow Herbarium

Gray Herbarium

Oakes Ames Orchid Herbarium



ISSN: 1938-2944

Harvard Papers in Botany

Initiated in 1989

Harvard Papers in Botany is a refereed journal that welcomes longer monographic and floristic accounts of plants and fungi, as well as papers concerning economic botany, systematic botany, molecular phylogenetics, the history of botany, relevant and significant bibliographies, and book reviews. Harvard Papers in Botany is open to all who wish to contribute.

Instructions for Authors

http://huh.harvard.edu/pages/manuscript-preparation

Manuscript Submission

Manuscripts, including tables and figures, should be submitted via email to papers@oeb.harvard.edu. The text should be in a major word-processing program for either Microsoft Windows or the Apple macOS, or in a compatible format. Authors should include a submission checklist available at http://huh.harvard.edu/files/herbaria/files/submission-checklist.pdf

Availability of Current and Back Issues

Harvard Papers in Botany publishes two numbers per year, in June and December. The two numbers of volume 18, 2013, made up the last issue distributed in printed form. Starting with volume 19, 2014, Harvard Papers in Botany became an electronic serial. It is available by subscription from volume 10, 2005, to the present via BioOne (http://www.bioone.org/). The content of the current issue is freely available at the Harvard University Herbaria & Libraries website (http://huh.harvard.edu/pdf-downloads). The content of back issues is also available from JSTOR (http://www.jstor.org/) volume 1, 1989 through volume 12, 2007, with a five-year moving wall.

Publication Exchange Agreements

Please send inquiries to botserials@oeb.harvard.edu or to the Serials Acquisition Manager at Serials Acquisitions & Exchanges, Harvard Botany Libraries, 22 Divinity Avenue, Cambridge, MA 02138, U.S.A.

To meet our publication exchange agreements, we are currently developing a mechanism to supply an electronic copy of each issue to the institutions with which we maintain an exchange program.

For all other questions and/or to order back issues, please email papers@oeb.harvard.edu.

***Harvard Papers in Botany* Volume 28, Number 2, was published online December 31, 2023.**

Oxalis paramoensis Canelón, Dorr & S.M. Niño (page 51, Figure 3A).
Drawn by E. M. Ellis.

Harvard Papers in Botany

Volume 29, Number 1 June 2024

A Publication of the Harvard University Herbaria Including

The Journal of the Arnold Arboretum

(Continued on page ii)

(Continued from page i)

CATASETUM ×*STEYERMARKII* (CATASETINAE: ORCHIDACEAE) A NEW PUTATIVE NATURAL HYBRID OF *CATASETUM* (CATASETINAE, ORCHIDACEAE) FROM THE VENEZUELAN GUAYANA

Gustavo A. Romero-González[1,2,3] and Germán Carnevali[1,3]

Abstract. Based on evidence found in a specimen collected by J. A. Steyermark in the vicinity of Mount Roraima in 1944, such as the described colors of the flowers and shape of the labellum, and the shape and size of the antennae, the pollinarium, and the pollinia, a new natural hybrid between *Catasetum discolor* and *C. planiceps* is described and illustrated as *C.* ×*steyermarkii*. Both putative parents have been collected in the same area. An annotated list of all the species of *Catasetum* hitherto reported in the vicinity of Mount Roraima is presented in Appendix I, and new nothospecies (*pro sp.*) and a nomenclatural notes in Appendix II.

Keywords: *Catasetum*, Guayana, Mount Roraima, nothospecies, Orchidaceae

Some years ago, while the two authors and a group of colleagues prepared a treatment of Orchidaceae for the project "Flora of the Venezuelan Guayana," one peculiar specimen of *Catasetum* at AMES could not be identified and was set aside. It still remained a puzzle by the time the flora was published (Carnevali et al., 2003). Many years later, the authors have re-examined its identification now that we have many more resources available.

Catasetum Rich. ex Kunth (Catasetinae, Orchidaceae) is a Neotropical genus ranging from northwest Mexico to southern Brazil and northern Argentina. It consists of approximately 200 accepted species (Govaerts et al., 2024) and 30 natural hybrids (Krahl et al., 2023). The Amazon river Basin is considered the center of diversity of the genus, where more than half of the species occur (Petini-Benelli, 2024). For the most recent overview of the genus see Romero-González et al. (2009).

While we were aware of natural hybridization in *Catasetum* in the past (Dodson, 1962; Pabst, 1975; Dodson, 1978; Romero and Carnevali, 1989a, 1989b, 1990, 1991a, 1991b, 1992; Romero and Jenny, 1992), there is growing evidence of its relevance as an evolutionary force within the genus as shown by an ever increasing number of recently proposed nothospecies (e.g., Lacerda and Castro, 2005; Ferreira, 2013; Petini-Benelli, 2016; Krahl et al. 2020, Ferreira, 2016, 2019; Ferreira and Filho, 2019; Ferreira and Malaspina, 2019; Cantuária et al., 2021). Furthermore, as pointed out by Krahl et al. (2023), many recently described so called "species" of *Catasetum* have turned out to be natural infrageneric hybrids. Some of these nothospecies could be attributed to the novel habitats created by the advancement of the agricultural and animal husbandry frontiers as well as the removal of natural habitat barriers that have brought together species that otherwise would have never come in contact without the effects of these anthropogenic activities. Natural hybrids have been detected between all subgeneric ranks of *Catasetum* (Table 1).

The degree of natural hybridization within this group supports the hypothesis that the evolution of *Catasetum* has been highly reticulate, where natural hybridization appears to have taken place both ancestrally and currently, rendering phylogenetic reconstructions with previously used methods difficult, i.e., "hampered by incongruent gene trees, especially closely related species complexes with high degrees of hybridization and polyploidy" (Krak et al., 2013; see also Wang et al., 2021; Moran et al., 2021; for evidence of polyploidy in *Catasetum*, see Oliveira et al., 2013 and references therein). We thus argue that the results and interpretations of recently published phylogenies (e.g., Mauad et al., 2022) are contentious.

The subject of this publication, a *Catasetum* sample collected by Julian A. Steyermark in 1944 (*Steyermark 58568*; see type below), had already puzzled C. Schweinfurth, who knew the genus reasonably well (he had described three species from Perú). Schweinfurth first identified it as *C. planiceps* Lindl. (1957: 868) and later as *Catasetum macroglossum* Rchb.f. (1967: 167), a species mainly from the Pacific drainage of Ecuador; Foldats (1970: 98), who also knew the genus fairly well, identified it as *C. planiceps*.

One of us (GAR-G) first examined a sheet of this collection at AMES in the late 1990s. The sheet included a copy of Steyermark's original field sketch and a packet with what appear to be one flower, in pieces, including a single pollinarium (Fig. 1). At the time it seemed that, geographically, *Catasetum planiceps* (subgenus *Catasetum*, section *Isoceras*) was a better fit than *C. macroglossum* (subgenus *Catasetum*, section *Catasetum*), the former known to occur in the same area where Steyermark's specimen was collected, while the latter was and is currently known to occur only in Ecuador. Furthermore, the shape of the

The authors thank M. L. Kawasaki (F) for her assistance with the specimens from F cited in the text, J. D. Edquén and G. A. Salazar (MEXU) for supplying images of *Catasetum discolor* from Perú, and G. Gerlach, P. Ormerod, and an anonymous reviewer for their comments on an early version of the text.

[1] Orchid Herbarium of Oakes Ames, Harvard University Herbaria, 22 Divinity Avenue, Cambridge, Massachusetts 02138, U.S.A.
[2] Corresponding author: romero@oeb.harvard.edu
[3] Herbarium CICY, Centro de Investigación Científica de Yucatán, A.C.. Calle 43 No. 130 x 32 y 34, Chuburná de Hidalgo. CP 97205, Mérida, Yucatán, México; carneval@cicy.mx

Harvard Papers in Botany, Vol. 29, No. 1, 2024, pp. 1–13.

ISSN: 1938-2944, DOI: 10.3100/hpib.v29iss1.2024.n1, Published online: 30 June 2024

Table 1. Natural hybrids between infrageneric ranks of *Catasetum* with examples from Venezuela.[1]

Subgeneric and sectional ranks	Subg. *Catasetum* sect. *Catasetum*	Subg. *Catasetum* sect. *Isoceras*	Subg. *Pseudocatasetum*
Subg. *Catasetum* sect. *Catasetum*	×[2]	×[3]	×[4]
Subg. *Catasetum* sect. *Isoceras*	×[3]	×[5]	×[6]
Subg. *Pseudocatasetum*	×[4]	×[6]	×[7]

[1] "×" indicates published natural hybrids;

[2] *C. pileatum* Rchb.f. × *C. macrocarpum* Rich. ex Kunth = *C.* ×*tapiriceps* Rchb.f.;

[3] *C. pileatum* × X. *C. planiceps* Lindl. = *C.* ×*wendlingeri* Foldats;

[4] *C. pileatum* × *C. discolor* (Lindl.) Lindl. = *C.* ×*dunstervillei* G.A. Romero & Carnevali;

[5] *C. barbatum (Lindl.) Lindl.* × *C. bicolor Kl.* = *C.* ×*merchae* G.A. Romero (see Appendix II);

[6] *C. discolor* × *C. planiceps* = *Catasetum* ×*steyermarkii* G.A. Romero & Carnevali;

[7] *C. discolor* × *C. longifolium* Lindl. = *C.* ×*roseo-album* (Hook.) Lindl.

Figure 1. Contents of the packet on *Steyermark 58568* at AMES. **A**, pollinarium; **B**, crushed remains of one flower.

pollinia in the specimen at AMES fit perfectly the size ratio of species in subgenus *Catasetum* section *Isoceras* (a ratio of width:length of more than 2.5; see Romero, 1986: 74, Table 3–2 therein). Yet, the shape of the stipe, narrowing considerably towards the base, and with a unique folding pattern at the base (see Romero, 1990: 165, Fig. 2D–E therein) placed it in subgenus *Pseudocatasetum*. Yet again, both male and female flowers of *Catasetum planiceps* have a fairly green, pale greenish bronze to yellowish-green uniform coloration, and the description given by the collector (see protologue below) was incongruent. It was impossible to identify the specimen at that time.

More recently, we had access to images of Steyermark's collection housed at F (see type), consisting of two sheets (labelled, in pencil, "1st" and "2nd" on the specimen labels; Fig. 2–3). The first one has an inflorescence with eight male flowers (based on the presence of well-developed anthers and antennae and a copy of Steyermark's

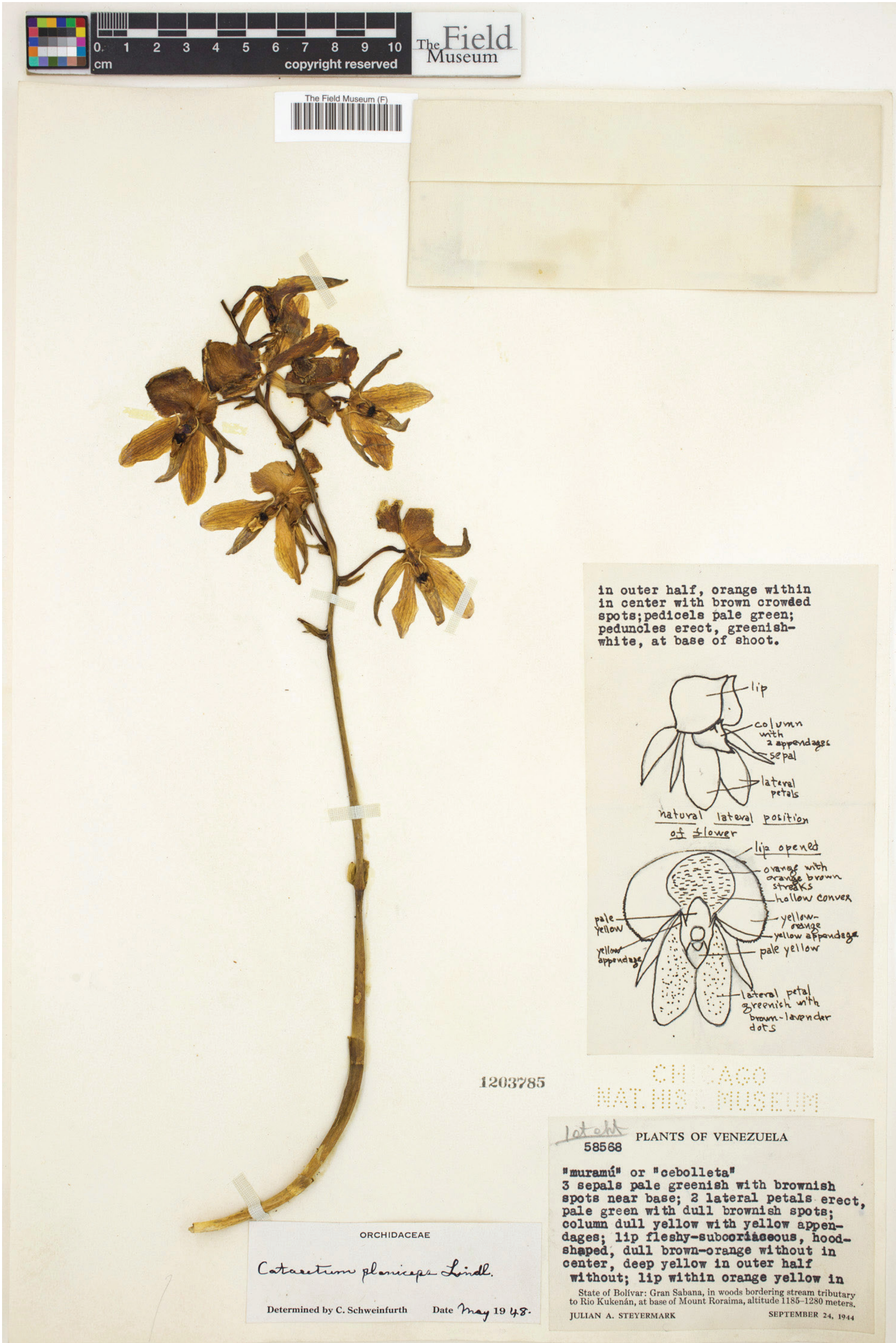


FIGURE 2. *Catasetum ×steyermarkii* G.A. Romero & Carnevali. First sheet of the holotype (F). Courtesy of the Field Museum (https://collections-botany.fieldmuseum.org/).

FIGURE 3. *Catasetum* ×*steyermarkii* G.A. Romero & Carnevali. second sheet of the holotype (F). Courtesy of the Field Museum (https://collections-botany.fieldmuseum.org/).

field sketch); the antennae are similar to those in species of subgenus *Catasetum*, section I*soceras*, subsection *Divaricata* (*sensu* Ortíz and Arango, 1994: 33), like the antennae of *C. planiceps*, although shorter (Fig. 2). The second sheet only has a pseudobulb with leaves that could be assigned practically to any species of *Catasetum* (Fig. 3). We also examined a flower preserved in glycerine recently found at AMES.

After examining the evidence, the authors hypothesize that Steyermark's specimen represents a natural hybrid between *Catasetum planiceps* Lindl. and *Catasetum discolor* (Lindl.) Lindl. (Fig. 4), which is herein described and illustrated using documentation left by the collector and additional data gathered by the authors.

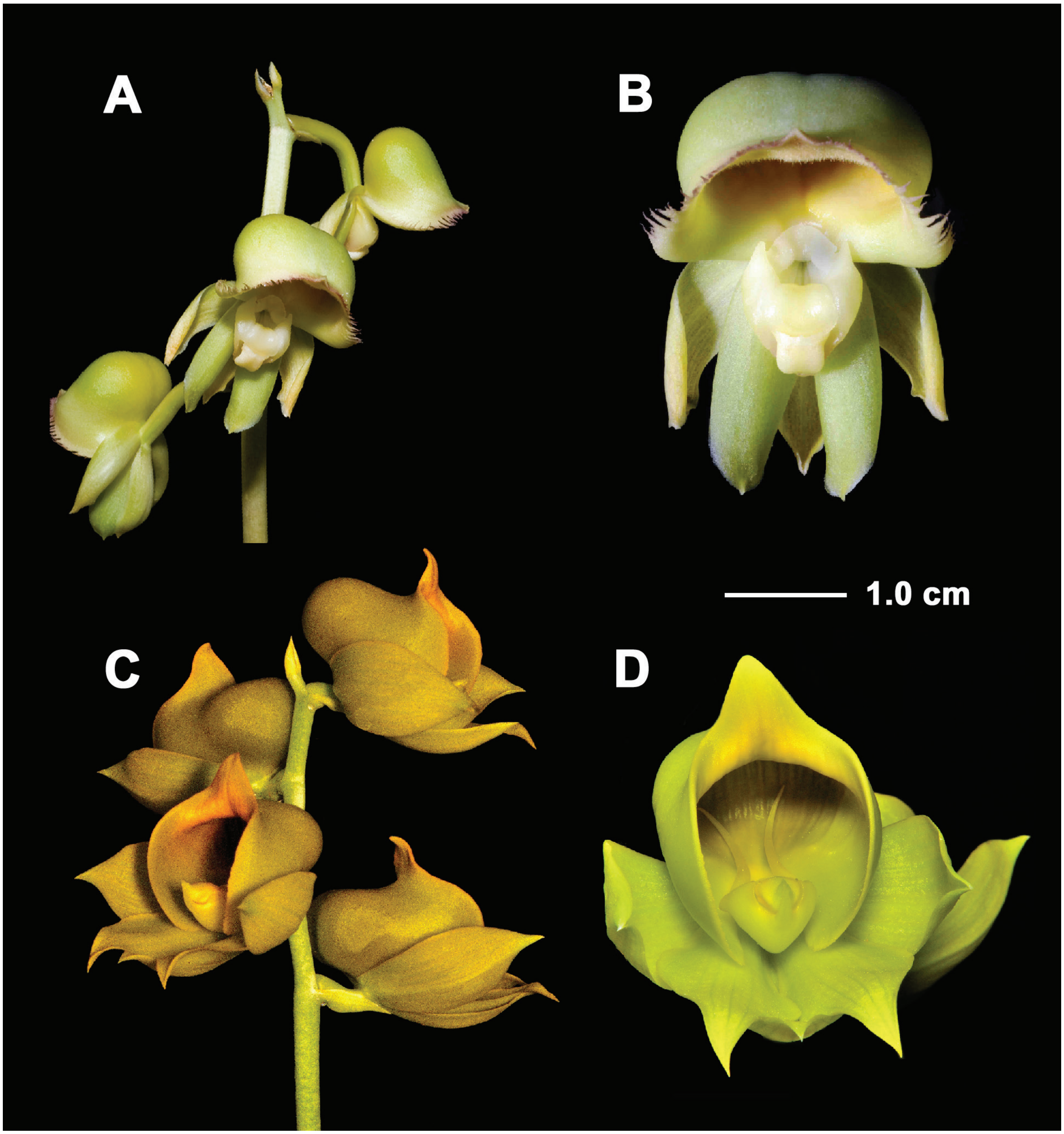


FIGURE 4. Putative parents of *Catasetum ×steyermarkii* G.A. Romero & Carnevali. **A–B**, *C. discolor* (Lindl.) Lindl.; **C–D**, *C. planiceps* Lindl. A–B, Gran Sabana, Bolívar, Venezuela, photographed by G. A. Romero-G. (no voucher prepared); C–D, El Castaño, Maracay, Aragua, Venezuela, cultivated and photographed by G. Carnevali (*Carnevali 8511*, CICY, spirit collection).

Catasetum ×*steyermarkii* G.A. Romero & Carnevali, *nothosp. nov.*

TYPE: VENEZUELA. Bolívar: Municipio Gran Sabana, in woods bordering stream tributary to Río Kukenán, at base of Mount Roraima, 1185–1280 m, 24 September 1944, *J. A. Steyermark 58568* (Holotype: F [Sheet 1 of 2, accession 1203785, barcode V0435581F; sheet 2 of 2: accession 1203782, barcode V0435820]; Isotypes: AMES [accession 64864, barcode 02288977]) flower on glycerine slide (AMES [00085806]). Fig. 1–3.

Usage synonyms: *Catasetum planiceps* Auct., *non* Lindl. (Schweinfurth, 1957: 868; Foldats, 1970: 98).

Catasetum macroglossum Auct., *non* Rchb.f., (Schweinfurth, 1967: 167).

A putative natural hybrid between *Catasetum discolor* (Lindl.) Lindl. (subgenus *Pseudocatasetum*) and *C. planiceps* Lindl. (subgenus *Catasetum*, section *Isoceras*) combining features of both parents but distinguishable from the former by the presence of well-developed antennae and from the latter by the color of the sepals (greenish with lateral brown-lavender dots versus solid light green to yellowish green), a shallow, wide opening of the labellum, the relatively short antennae (not reaching the base of the labellum versus reaching the bottom of the labellum), and by the morphology of the pollinarium, the stipe of which considerably narrows toward the base, and with a folding pattern at the base, as in species of subgenus *Pseudocatasetum*, which renders it rigid (versus hinged in *C. planiceps*).

Pseudobulbs and *leaves* indistinguishable from those of most species in the genus. *Peduncle* erect, greenish-white, arising from the base of the fully developed pseudobulb. *Pedicel* pale green. *Flowers* non-resupinate, with spreading sepals and petals. *Dorsal sepal* 2.4–2.6 cm × 0.65–0.72 cm, 11-nerved, oblong obovate, obtuse to rounded, lateral sepals 2.70–2.75 × 0.77 × 0.8 cm, 13-nerved, oblong obovate, broadly acute, petals 2.97–3.1 × 0.9–1.1 cm, 11-nerved, elliptic, obtuse, pale green with dull brownish spots; *labellum* fleshy-subcoriaceous, hood-shaped, margin finely serrate, outside dull brown-orange in center, deep yellow in outer half, inside orange-yellow in center half, inside orange in center with brown crowded spots. *Column* pale yellow, antennae yellow, relatively short, barely reaching the base of the labellum, divaricate. Pollinarium as in *Catasetum discolor*.

Distribution and phenology: Known only from the type, which was found flowering in September.

Vernacular name: "Muramú"(Pemón) or "cebolleta" (Spanish).

Eponymy: Dedicated to Julian Alfred Steyermark (1909–1988), a renowned botanist and plant collector expert on the flora of Guatemala and Venezuela, particularly on the flora of the Guayana highlands, and sponsor of the project "Flora of the Venezuelan Guayana."

Catasetum ×*steyermarkii* is the first reported natural hybrid between a species of *Catasetum,* subgenus *Catasetum*, section *Isoceras* and a species in subgenus *Pseudocatasetum*. It is a rarity because these two groups rarely share pollinators: most species of section *Isoceras* are pollinated by species of *Euglossa* Latreille, whereas all known species of subgenus *Pseudocatasetum* are pollinated by species of *Eulaema* Lepeletier.[4] *Catasetum planiceps* is the only species of section *Isoceras* that is pollinated by a species of *Eulaema*, *E. cingulata* (Fabricius), which it happens to share with *Catasetum discolor* (Fig. 5).

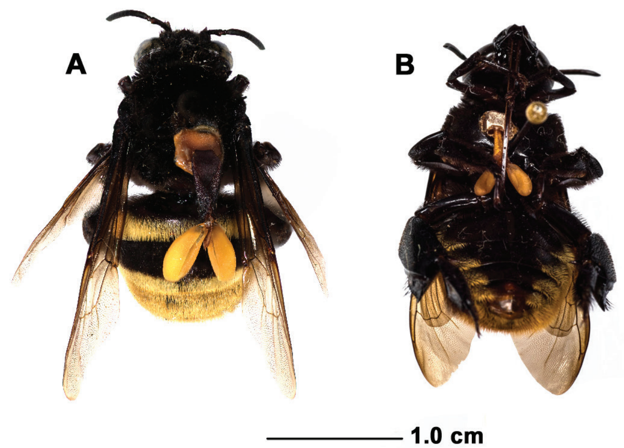


FIGURE 5. *Eulaema cingulata* (Fabricius). **A**, carrying a pollinarium of *Catasetum planiceps* Lindl.; **B**, carrying a pollinarium of *C. discolor* (Lindl.) Lindl. Photographs by G. A. Romero-González. Supporting material available upon request.

Nonetheless, the pollination dynamics of these two *Catasetum* groups make a natural hybrid between them nearly impossible. The hinged pollinarium of species of section *Isoceras* is always placed on the dorsum of the bee's thorax, whereas the rigid one from species in subgenus *Pseudocatasetum* is always placed on the ventrum of the thorax (Hills et al., 1972; Dodson, 1978; Romero, 1990; Fig. 5 herein). Furthermore, pollination within species of section *Isoceras* occurs when the bee enters the female flower upside down, hanging from the apex of the labellum, above the column; the hinged pollinarium hangs down and, as the bee moves in and out of the female flower, eventually a pollinium is caught in the stigmatic cleft. In species of subgenus *Pseudocatasetum*, bees enter the female flower right-side up, with their ventrum facing the column: again, as the bee moves in and out of the flower, eventually a pollinium is caught in the stigmatic cleft.[5]

[4] Pinheiro and Gerlach (2017: 25–26, Table 1) listed *Euglossa ignita* as a "Visitor/Pollinator" of *Catasetum discolor* (see also Roubik and Hanson, 2004: 250), most likely based on the next two references. Williams and Dodson (1972: 85, Table 1) listed *Euglossa chlorosoma* Cockerell as visitors of flowers of *C. discolor* (*E. chlorosoma* is considered a synonym of *E. ignita* F. Smith; Kimsey and Dressler, 1986: 232). Later, Dodson (1978: 167, Table 1), again cited bees of the same *Euglossa* species visiting *C. discolor* but, in a footnote, he clearly labelled them as "not effective as pollinators." Dodson, in the same publication, listed *Eulaema cingulata* visiting flowers of *Catasetum thompsonii* Dodson (section *Isoceras*) but also labelled the bees as "not effective as pollinators."

[5] Pollination of female flowers of *Catasetum longifolium* Lindl. (subgenus *Pseudocatasetum*) is a special case: the pollinator enters the flower upside down, but its ventrum still faces the column (see photograph in Hills et al., 1972: 70, Fig. 1).

Although it is possible that a bee carrying a pollinarium of *Catasetum planiceps* on the dorsum (Fig. 5) could pollinate a female flower of *C. discolor*, entering it upside down, it is highly unlikely. Bees, at first, apparently find much easier to enter female flowers right-side up, with their ventral side facing the column,[6] and if the pollinarium is on the dorsum it never contacts the column; it is much more likely that a bee, carrying a pollinarium of *C. discolor* on its ventrum, pollinates the female flower of *C. planiceps* while entering the flower right-side up. Moreover, the size of the pollinium (Fig. 6) may also hinder two-way genetic flow between *C. discolor* and *C. planiceps*: the pollinium of the latter is too thick to be inserted in the stigmatic cleft of the column of *C. discolor*, whereas the opposite is quite feasible (see discussion in Romero-González et al., 2017: 151).

The authors, based on the pollinarium found in the sheet at AMES, conclude that this natural hybrid is an evolutionary end, that is, it cannot reproduce with itself or any of the putative parents. If the pollinarium is rigid, as suggested by the one shown in Fig. 1A, and it is placed on the dorsum of the pollinarium (as suggested by the morphology of the labellum and column of the nothospecies, Fig. 2), a bee carrying such a pollinarium could not pollinate female flowers of the nothospecies or either of the putative parents.

We present an annotated list of all the species of *Catasetum* hitherto reported in the vicinity of Mount Roraima in Appendix I, and propose new nothospecies (*pro sp.*) in Appendix II.

Figure 6. *Catasetum* pollinaria adaxial and abaxial views. **A–B**, *Catasetum discolor* (Lindl.) Lindl.; **C–D**, *C. planiceps* Lindl. A, C within minutes of discharge; B, within hours of discharge; D, after several years of storage. Photographs by G. A. Romero-González. Supporting material available upon request.

Literature Cited

Bateman, J. 1834. Arrival, from Demerara, of the botanical collector, Mr. Thomas Colley. The Gardener's Magazine 10, No. 56: 571–572.

Cantuária, P. de Castro, D. R. P. Krahl, A. H. Krahl, G. Chiron, and J. B. Fernandes da Silva. 2021. *Catasetum ×sheyllae* (Orchidaceae: Catasetinae), a new natural hybrid from Brazilian Amazon. Phytotaxa 527, No. 4: 257–265.

Carnevali, G., I. M. Ramírez-Morillo, G. A. Romero-González, C. A. Vargas, and E. Foldats. 2003. Pages 200–619 in P. E. Berry, K. Yatskievych, and B. K. Holst, volume editors, Flora of the Venezuelan Guayana 7. Missouri Botanical Garden Press, St. Louis, Missouri.

Cogniaux, A. 1902. *Catasetum* L.-C. Rich. Pages 387–446 in C. F. P. von Martius and A. G. Eichler, eds., Flora Brasiliensis 3, part 5. R. Oldenbourg, Munich and Lipsig.

Dodson, C. H. 1962. Pollination and variation in the subtribe Catasetinae (Orchidaceae). Annals of the Missouri Botanical Garden 49, No. 1–2: 35–56.

———. 1978. The catasetums of Tapakuma, Guyana. Selbyana 2, No. 2–3: 159–168.

Edquén, J. D., E Yrigoín, G. A. Salazar, E. Hágsater, E. Santiago, L. I. Cabrera, R. Jiménez-Machorro, D. Trujillo, K. Edquén, J. P. Arista, J. Duarte, and M. Oliva. **In press**. Los Géneros de Orquídeas del Bosque de Protección Alto Mayo—Una Guía Ilustrada. Conservación Internacional, and Servicio Nacional de Áreas Naturales Protegidas por el Estado, Lima, Perú.

Ferreira, U. L. C. 2013. *Catasetum ×valdisonianum* U.L.C. Ferreira, um novo híbrido natural. Orchidário (Rio de Janeiro) 27, No. 3: 93–97.

———. 2016. *Catasetum ×mesquitae* U.L.C. Ferreira, novo híbrido natural. Orquidário (Rio de Janeiro) 30: 37–43.

———. 2019. Two new natural hybrids in *Catasetum* (Orchidaceae) from centre-west Brazil. 2019. Richardiana N.S. 3: 80–91.

———. and R. M. C. Filho. 2019. Two new natural hybrids in *Catasetum* (Orchidaceae) from Brazil. Richardiana 3: 39–49.

[6] Observing euglossine bees collecting fragrances from female flowers of species of *Catasetum* subgenus *Catasetum*, or non-resupinate male flowers thereof, one can easily distinguish "naïve" bees from "trained" ones: the former, at first, do not appear to know how to enter the flower, to reach the most active fragrance-producing osmophores located in the upper portion of the inside of the flowers; it takes a "naïve" bee many landings on the flower before they learn to enter it "correctly" (as far as the flower is concerned), that is, upside down, hanging from the apex of the labellum and having their dorsum facing the column. "Trained" bees, on the other hand, enter the flowers "correctly" after one or two landings on the flower. In contrast, pollinators that approach female and male flowers of subgenus *Pseudocatasetum* rapidly learn what is the "correct" approach in this case, that is, entering the flower right-side up, with their ventrum facing the column (see previous footnote, regarding *C. longifolium*, the pollination of which has not been observed by the authors).

———. and T. K. Malaspina. 2019. *Catasetum ×aikoae*. U.L.C. Ferreira & T.K. Malaspina *hyb. nat. nov*. Coletânea de Orquídeas Brasileiras 15: 594–597.

Foldats, E. 1970. *Catasetum* L. C. Rich. Pages 48–109 in T. Lasser, ed., Flora de Venezuela XV (Orchidaceae part 4). Instituto Botánico, Caracas.

Govaerts, R., J. Dransfield, S. Zona, D. R. Hodel, and A. Henderson. 2024. World Checklist of Orchidaceae. Facilitated by the Royal Botanic Gardens, Kew. Available from: http://apps.kew.org/wcsp/ (accessed April 29, 2024).

Hills, H. G., N. H. Williams, and C. H. Dodson. 1972. Floral fragrances and isolating mechanisms in the genus *Catasetum* (Orchidaceae). Biotropica 4, No. 2: 61–76.

Krahl, D. R. P., A. H. Krahl, and G. R. Chiron. 2020. *Catasetum ×luisiae* (Orchidaceae: Catasetinae), a new natural hybrid for the Brazilian Amazon. Richardiana N.S. 4: 214–223.

Krahl, D. R. P., P. Schmal, G. Chiron, J. B. Fernandes Da Silva, A. H. Krahl, and P. De Castro Cantuária. 2023. *Catasetum ×grasineideae* (Orchidaceae: Catasetinae), a new nothospecies from Brazilian Amazon and taxonomic notes for the genus. Phytotaxa 594, No. 2: 89–104.

Krak, K., P. Caklova, J. Chrtek, and J. Gehrer. 2013. Reconstruction of phylogenetic relationships in a highly reticulate group with deep coalescence and recent speciation (Hieracium, Asteraceae). Heredity 110, No. 2: 138–151.

Lacerda Jr., K. G. de and Castro Neto. 2005. New natural hybrids in *Catasetum*. Orchid Review 113, No. 1266: 308–311.

Linden, J., L. Linden, and E. Rodigas. 1895. Lindenia—Iconographie des Orchidées 11. Eug. Vander Haeghen, Gand, Belgium.

Lindley, J. 1840. *Catasetum longifolium*. Sertum Orchidaceum t. 31. James Ridgway and Sons, London.

———. 1843. *Catasetum planiceps*. Edwards's Botanical Register 29: t. 9.

Link, H. F., F. Klotzsch, and F. Otto. 1844. *Catachaetum recurvatum*. Icones Plantarum Rariorum Horti Regii Botanici Berolinensis 2, No. 3: tab. 42.

Mauad, A. V. S. R., A. Petini-Benelli, T. J. Izzo, and E. C. Smidt. 2022. Phylogenetic and molecular dating analyses of *Catasetum* (Orchidaceae) indicate a recent origin and artificial subgeneric groups. Brazilian Journal of Botany 45, No. 4: 1235–1247.

McConnell, F. V. and J. J. Quelch. 1901. Report on two botanical collections made by Mssrs. F. V. McConnell and J. J. Welch at Mount Roraima in British Guiana. The Transactions of the Linnean Society of London, 2nd Series Botany, 6, No. 1: 1–107, plates 1–14.

Milet-Pinheiro, P. and G. Gerlach. 2017. Biology of the Neotropical Orchid genus Catasetum: a historical review on floral scent chemistry and pollinators. Perspectives in Plant Ecology, Evolution and Systematics 27: 23–34.

Moran, B. M., C. Payne, Q. Langdon, D. L. Powell, Y. Brandvain, and M. Schumer. 2021. The genomic consequences of hybridization. ELife 10:e69016. DOI: https://doi.org/10.7554/eLife.69016

Oliveira, L. V. R., F. de Barros, and E. R. Forni-Martins. 2013. Chromosome numbers and karyotypes of *Catasetum* species (Orchidaceae). Plant Biosystematics 148, No. 3: 499–507.

Ortíz V., P. and G. Arango. 1994. Una nueva especie de *Catasetum* de Colombia. Orquideología (Medellín) 19, No. 2: 29–33 [text in English on pages 34–36].

Pabst, G. F. J. 1975. New or critical orchids from Brazil—VII. Orchid Review 86, No. 990: 405–406.

Petini-Benelli, A. 2016. Un nouvel hybride naturel de *Catasetum* (Cymbidieae, Epidendroideae, Orchidaceae) du Mato Grosso (Brésil). Richardiana 16: 327–342.

———. 2024 [continuously updated]. *Catasetum*. Flora e Funga do Brasil. Jardim Botânico do Rio de Janeiro. http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB11312 (accessed April 30, 2024).

Ridley, H. N. 1886. Orchidaceae. Pages 202–206 in E. F. im Thurn, ed., Notes on the Plants of Roraima. Timehri 5: 145–223.

Rolfe, R. A. 1890. On the sexual forms of *Catasetum*, with special reference to the researches of Darwin and others. The Journal of the Linnean Society, Botany 27, No. 183–184: 206–225, plate VIII.

———. 1913. *Catasetum darwinianum*. Bulletin of Miscellaneous Information 1913, No. 3: 99–102.

Romero, G. A. 1986. Evolutionary dynamics in a *Catasetum* community in southern Venezuela. Ph.D. dissertation, Indiana University, Bloomington, Indiana.

———. Phylogenetic relationships in subtribe Catasetinae (Orchidaceae, Cymbidieae). Lindleyana 5, No. 3: 160–181.

———. and G. Carnevali. 1989a. Novelties in the orchid flora of southern Venezuela. Annals of the Missouri Botanical Garden 76, No. 2: 454–461.

———. and ———. 1989b. A new combination for the orchid flora of southern Venezuela: *Catasetum ×tapiriceps* Rchb.f. (*pro sp*.). Lindleyana 4: 127–134.

———. and ———. 1990. *Catasetum* natural hybrids from southern Venezuela—1. *Catasetum ×tapiriceps*. American Orchid Society Bulletin 59, No. 12: 1214–1220.

———. and ———. 1991a. *Catasetum* natural hybrids from southern Venezuela—2. *Catasetum ×dunstervillei*. American Orchid Society Bulletin 60, No. 2: 115–120.

———. and ———. 1991b. *Catasetum* Natural Hybrids From Southern Venezuela—3. *Catasetum ×roseo-album* and *C. ×wendlingeri*. American Orchid Society Bulletin 60, No. 8: 770–774.

———. and ———. 1992. *Catasetum* Natural Hybrids From Southern Venezuela—4. Biology and nomenclature. American Orchid Society Bulletin 61, No. 4: 355–360.

Romero, G. A. and R. Jenny. 1992. New natural hybrids and nomen-clatural novelties in *Catasetum* (Orchidaceae) from the Guianas, Ecuador, and Peru. Novon 2, No. 3: 241–248.

———. and ———. Contributions toward a monograph of *Catasetum* (Catasetinae, Orchidaceae) I: A checklist of species, varieties, and natural hybrids. Harvard Papers in Botany 1, No. 4: 59–84.

Romero-González, G. A. 2003. History of orchid botanical exploration in the Venezuelan Guayana. Pages 200–203 in in P. E. Berry, K. Yatskievych, and B. K. Holst, volume editors, Flora of the Venezuelan Guayana 7. Missouri Botanical Garden Press, St. Louis, Missouri.

———., G. Carnevali, and A. M. Pridgeon. 2009. *Catasetum*. Pages 13–18 in A. M. Pridgeon, P. J. Cribb, M. W. Chase, and F. N. Rasmussen, eds., Genera Orchidacearum 5. Oxford University Press, Oxford.

———., G. Carnevali, R. E. López, and S. C. Pérez. 2017. *Catasetum ×dunstervillei* (Orchidaceae: Catasetinae), a natural hybrid confirmed by artificial hybridization. Harvard Papers in Botany 22, No. 2: 145–155.

Roubik, D. W. and P. E. Hanson. 2004. Orchid Bees of Tropical America. Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica.

Schweinfurth, C. 1957. Orchidaceae. Pages 845–881 in J. A. Steyermark, ed., Contributions to the Flora of Venezuela. Botanical Exploration in Venezuela—IV. Fieldiana: Botany 28, No. 4: 679–1225.

———. 1960. *Catasetum* L. C. Rich. Pages 583–592 in C. Schweinfurth, Orchids of Peru. Fieldiana: Botany 30, No. 3: i–vi, 533–786.

———. 1967. Orchidaceae of the Guayana Highland. Memoirs of the New York Botanical Garden 14, No. 3: 69–214.

Steyermark, J. A. 1957. Contributions to the Flora of Venezuela. Botanical Exploration in Venezuela—IV. Fieldiana: Botany 28, No. 4: 679–1225.

———. 1981. Erroneous citations of Venezuelan localities. Taxon 30, No. 4: 816–817.

Thurn, E. F. im. 1886. Notes on the Plants observed during the Roraima expedition of 1884. Timehri 5: 145–223.

———. 1887. The botany of the Roraima Expedition of 1884. The Transactions of the Linnean Society of London, 2nd Series Botany, 2, No. 13: 249–300, plates I–LVI.

Wang, Y., Z. Cao, H. A. Ogilvie, and L. Nakhlen. 2021. Phylogenomic assessment of the role of hybridization and introgression in trait evolution. PLoS Genetics 17, No. 8: e1009701. https://doi.org/10.1371/journal.pgen.1009701

Williams, N. H. and C. H. Dodson. 1972. Selective attraction of male Euglossine bees to orchid floral fragrances and its importance in long distance pollen flow. Evolution 26, No. 1: 84–95.

Appendix I

The following are the species of *Catasetum* that have been reported hitherto from the vicinity of Mount Roraima; localities are cited following Steyermark (1981).

Catasetum darwinianum Rolfe can be discarded as a possible putative parent because of the small size of the flowers (Rolfe, 1913), indicating that this species is pollinated by an equally small species of *Euglossa*.

Catasetum longifolium Lindl. also occurs in this area (seen by one of the authors, GC), growing on *Mauritia flexuosa* L.f. (Arecaceae), one of the palm hosts of *Catasetum longifolium*, plants of which grow on the leaf bases of these palms (e.g., R. H. Schomburgk in Lindley, 1840; Dodson, 1978). Nonetheless, the involvement of *C. longifolium* in intergeneric natural hybrids imparts several morphological signals (e.g., narrow leaves and/or pendent habit; Romero and Carnevali, 1991) not detected in the nothospecies described herein.

Catasetum darwinianum Rolfe, Gardeners' Chronicle Ser. 3, 5, No. 118: 394. 1889. TYPE: VENEZUELA. Bolívar: municipio Gran Sabana, vicinity of Mount Roraima, Sander, St. Albans, *ex Hort. Kewensis* (See Rolfe, 1913: 101 for the most precise type locality given by the author; see note on the collector below) (Holotype: K). Fig. 7.

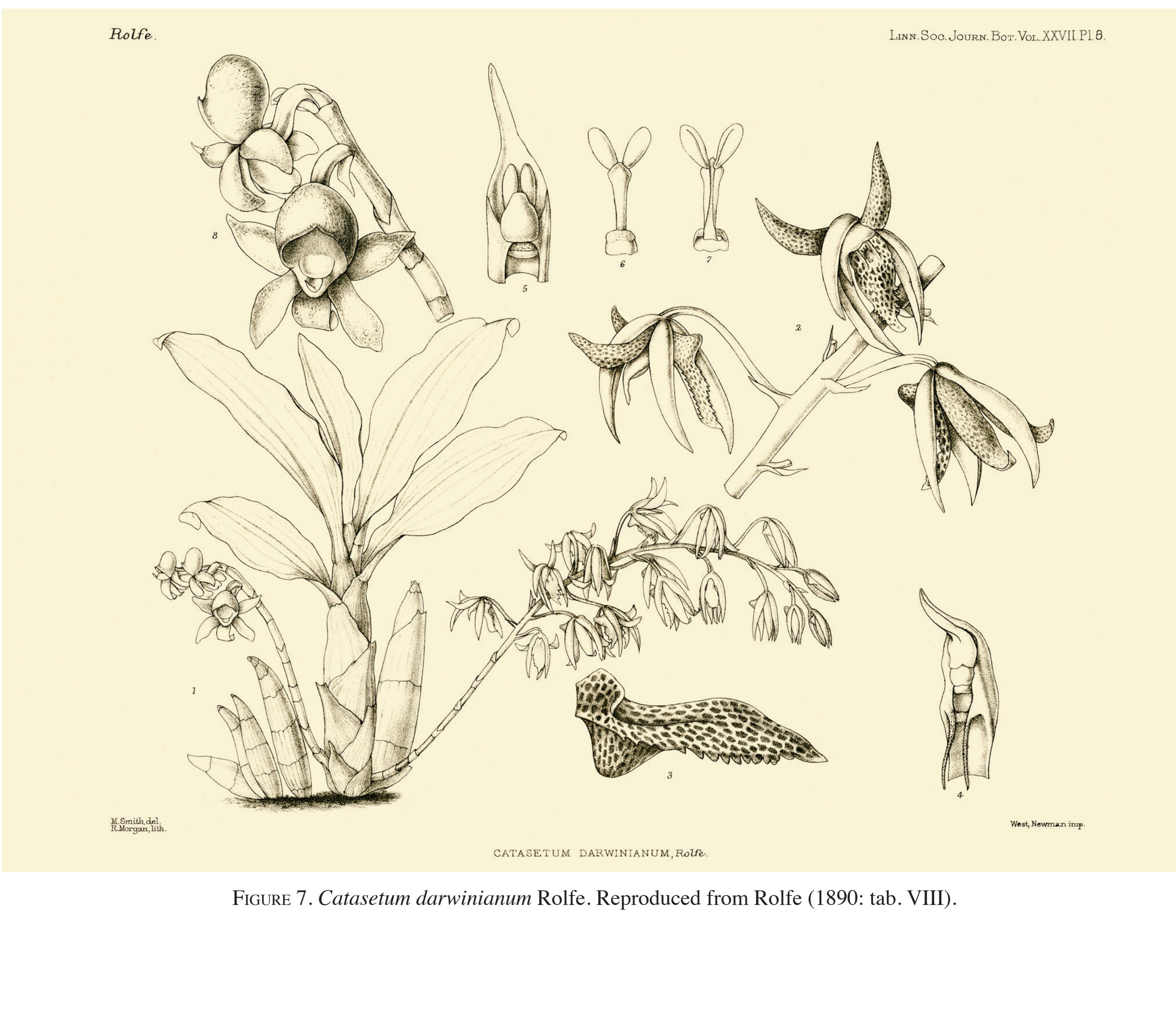


Figure 7. *Catasetum darwinianum* Rolfe. Reproduced from Rolfe (1890: tab. VIII).

Distribution: Known only from the type locality.

Habitat and Phenology: No information was provided for habitat, but most of the species in this group, in this case, apparently quite close to if not conspecific with *Catasetum callosum* Lindl., are epiphytes. The only existing phenological data for this species were provided by Rolfe (1890: 218): "This … plant… flowered in the Kew collection during the autumn of 1888" and Rolfe (1913: 99): "The plant flowered last autumn in the Kew collection."

The type specimen of this species was most likely collected by E. Seidel (sometimes spelled Seidle or Seidl) who visited the vicinity of Roraima twice in 1884 on behalf of the Sander establishment (Romero-González, 2003: 201).

Catasetum discolor (Lindl.) Lindl., Edwards's Botanical Register 27: sub t. 34. 1841.

Basionym: *Monachanthus discolor* Lindl., Edwards's Botanical Register 20: t. 1735. 1834. TYPE: GUYANA ["Demerara"]. Without precise locality (Holotype: K).

Distribution: Venezuela (Amazonas and Bolívar), Guyana, Surinam, French Guiana, Colombia, Brazil, and Perú.

Additional specimen examined: VENEZUELA. Bolívar: municipio Gran Sabana, Mount Roraima, upper slopes, *F. V. McConnell & J. J. Quelch 6* (K, not seen); Cited by McConnell and Welch, 1901: 63 and Cogniaux, 1902: 446); Roraima, stony slopes with sandy soil, Philipp Camp, 5200–6000 ft. [1580–1820 m], 7 November 1927, *G. H. H. Tate 312* (NY ♀ [00547435]) .

Habitat and Phenology: Found growing in sand or on sandstone outcrops, from sea level to 2500 m. Based on herbarium records from the northern hemisphere, flowering all year round.

The type of *Catasetum discolor* was collected by Thomas Colley in the Demerara region (name derived from the Dutch *Demerary*, a colony of Holland from 1745 to 1803). Bateman (1834) cited, as sites where Colley collected orchids in 1834, "… large portion of the Essequibo, Massarony, and Corgonni rivers; and the whole of the adjacent colony of Berbice… for a space of four months."

Catasetum discolor displays a wide range of variation in color, from light yellowish green (Fig. 4A–B) to almost solid dull red (Edquén et al., in press: 97, Fig. 49), and morphology (the degree of revoluteness and dentition found along the edges of the labellum and the shape and ornamentation of the labellum apex), varying apparently without any pattern within the geographical distribution of the species. This variation is perhaps due to genetic exchange with with *C. longifolium* and backcrossing with the natural hybrid between these two species, *C.* ×*roseo-album* (Hook.) Lindl. In the literature and herbarium collections, *Catasetum discolor* is often confused with *C.* ×*roseo-album*, from which, in most cases, it can be distinguished by the dentate edges of the labellum in the former, versus fimbriate in the latter. Furthermore, only *C.* ×*roseo-album* is found growing on a variety of palms (including *M. flexuosa*).

Catasetum planiceps Lindl., Edwards's Botanical Register 29, t. 9. 1843. Type: "Spanish main," June 1841, *ex Hort*. "Messrs. Loddiges" (Holotype: K). Fig. 8–10.

Heterotypic synonyms: *Catachaetum recurvatum* Link, Klotzsch & Otto, Icones Plantarum Rariorum Horti Regii Botanici Berolinensis 2: 105, t. 42. 1844. TYPE: VENEZUELA. Bolívar: municipio Piar, near Upata, *C. F. E. Otto s.n.* (Holotype: B, destroyed).

Catasetum chloranthum Cogn., Journal des Orchidées 5: 251. 1894. TYPE: PERU. Without locality, *ex Hort*. Linden establishment (Holotype: BR).

Catasetum hymenophorum Cogn., Journal des Orchidées 6: 215. 1895. TYPE: VENEZUELA. Without precise locality, *ex Hort*. Linden establishment (Lectotype [designated by Romero and Jenny, 1993:]: BR; Isolectotype: BR).

Distribution: Venezuela, Guyana, Surinam, French Guiana, Colombia, and Brazil. The locality of the type of *Catasetum chloranthum* ("Peru"; see also Schweinfurth, 1960: 586) is doubtful, but not impossible, as many orchid species from the Guayana highlands also occur in mountainous sandstone outcrops in eastern Perú. Notice that Linden et al. (1895: 14, 24), soon after the name *C. chloranthum* was published, describe this species as "… originaire de l'Amerique du Sud," perhaps doubting the precise country of origin that Cogniaux provided.

Habitat and Phenology: Found growing among rocks and on granite or sandstone outcrops from 160 to 1400 m. This species tends to flower from the developing pseudobulb. Based on herbarium records, flowering from October to May.

Additional specimen examined: VENEZUELA. Bolívar: Mount Roraima, *E. F. im Thurn 148* (presumably at BM or possibly at K, not seen); cited by im Thurn 1886: 154, 1887: 254 as "*Catasetum cristatum*?," cited by Ridley (1886: 205) as "*Catasetum cristatum*? *Monachanthus* form;" by Cogniaux (1902: 400), as *Catasetum fuliginosum* Lindl.; and by Schweinfurth, 1967: 168, as *C. planiceps*).

The country of origin of the type locality of this species was most likely Venezuela. *Catasetum planiceps* also displays a wide range of variation in color, from greenish bronze (Fig. 4A) to light green throughout, with yellow tinge in the sepals and petals and inside and at the apex of the labellum (Fig. 4B, Fig. 8), and the sepals, petals, and interior of labellum of uniform color (figures herein) or rarely spotted with reddish brown (as in *B. Maguire 26211*, NY [04013851]; photographs AMES).

It also varies morphologically, particularly in the proportions and openness of the labellum, the size, shape, and revoluteness of the apex of the labellum (Fig. 4A–B and Fig. 9 versus Fig. 10), and the degree of dentition along the lower edges of the labellum (Fig. 4C–D, 8–10). The authors, based on pollination data, estimate that introgression between this species and *C. pileatum* Rchb. f., in areas where the latter is found, is currently taking place (for which *C.* ×*wendlingeri* Foldats was proposed; see Romero and Carnevali, 1989a: 460), and likewise entirely possible between *C. planiceps* and *C. macrocarpum* Rich. ex Kunth in the Guayana region.

FIGURE 8. *Catasetum planiceps* Lindl. From Lindley (1843).

FIGURE 9. *Catasetum planiceps* Lindl. From Link et al. (1844), as *Catachaetum recurvatum* Link, Kltzsch & Otto.

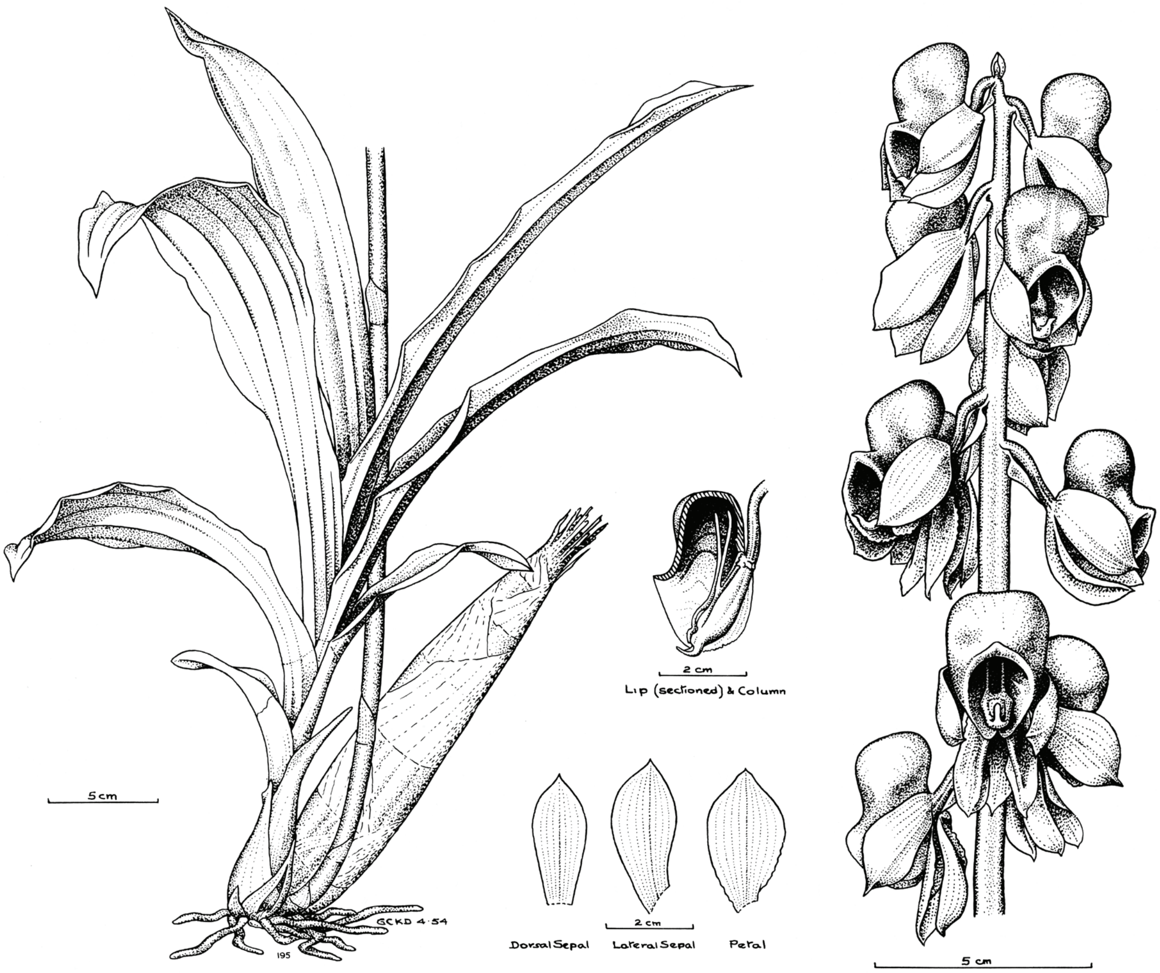


FIGURE 10. *Catasetum planiceps* Lindl. Drawn by G. C. K. Dunsterville based on *Dunsterville 195* (Village of Miranda, west of Valencia, Carabobo, Venezuela; AMES). From a photostat at AMES.

APPENDIX II

New nothospecies (*pro sp*.) and nomenclatural notes.

Catasetum ×gomezii G.A. Romero and Carnevali (*pro sp*.), *hybr. nat. nov. inter Catasetum bergoldianum* Foldats *et C. barbatum* (Lindl.) Lindl. Annals of the Missouri Botanical Garden 76, No, 2: 455. 1989.
TYPE: VENEZUELA. Municipio Atures, Río Cataniapo, cerca de la desembocadura del Río Gavilán, 30 June 1987, *G. A. Romero & C. Gómez 1333* (Holotype: VEN; Isotypes: K, TFAV).

Although first proposed as a species, later it was suspected to be a nothospecies (Romero and Carnevali, 1992: 355, 359; *C. ochraceum* Lindl. mistakenly cited as one of the putative parents). However, the nothospecies had not been proposed before.

Catasetum ×merchae G.A. Romero (*pro sp*.), *hybr. nat. nov. inter Catasetum bicolor* Klotzsch *et C. barbatum* (Lindl.) Lindl. Selbyana 10, No. 1: 73. 1988.
TYPE: VENEZUELA. Amazonas: Río Cataniapo, cerca de Gavilán, epífita, poco frecuente, 23 April 1986, *G. A. Romero 1275* (Holotype: VEN; Isotype: TFAV).

Although first proposed as a species, later it was suspected to be a nothospecies (Romero and Carnevali, 1992: 358–359; *C. ochraceum* Lindl. again mistakenly cited as one of the putative parents on page 358). However, the nothospecies had not been proposed before.

Catasetum ×wendlingeri Foldats, Acta Botanica Venezuelica 2: 167. 1958. TYPE: VENEZUELA. Amazonas: Municipio Atabapo, "planta comprada en San Fernando de Atabapo," *Ex Hort*. K. Wendlinger *sub E. Foldats 2890* (Lectotype, designated here: VEN [sheet bearing an inflorescence with six flowers]; Isolectotype: VEN [sheet bearing an inflorescence with two flowers]). Proposed as a nothospecies in Romero and Carnevali (1989: 460).

There are two sheets of *Catasetum wendlingeri* at VEN, both labelled "Holotypus" and both bearing the same herbarium accession number, "41847," which in this herbarium is also the barcode number, making necessary the designation of a lectotype. In addition, there is a flower in the glycerine slide collection at AMES, but it is not known whether it came from the lectotype or the isolectotype designated here.

Page 14 intentionally left blank.

SARCOGLOTTIS WOODSONII (ORCHIDACEAE: SPIRANTHINAE)—REDISCOVERED IN COSTA RICA AFTER 80 YEARS, WITH A PRELIMINARY SURVEY ON AQUATIC AND OTHER WETLAND ORCHIDS

Rafael Acuña-Castillo,[1,2,7] Mario A. Blanco,[1,2,4] Miguel Artavia,[1]
José Esteban Jiménez,[3,4] and Diego Bogarín[1,4,5,6]

Abstract: Orchidaceae, a highly diverse family of angiosperms, exhibits remarkable ecological and morphological adaptations, with most of its species being epiphytic or terrestrial. Nonetheless, their occurrence in aquatic and wetland habitats in the tropics is relatively uncommon, with only a few species adapted to these environments. Consequently, our current understanding of orchids inhabiting wetland ecosystems is limited. This research focuses on *Sarcoglottis woodsonii*, an aquatic orchid species exclusively found in palustrine wetlands of southern Central America. Previously considered endemic to western Panama, our recent collections (the first since 1940) extend its known distribution to include southern Costa Rica. We provide an updated description, a modern illustration, a conservation assessment based on IUCN criteria, and novel ecological data that shed light on its aquatic habit. With this recent discovery, the number of known *Sarcoglottis* species in Costa Rica stands at six. We provide a preliminary survey of reported wetland and aquatic orchid species from the Neotropics and give novel definitions for both wetland and aquatic plants. We also present an inventory of the vascular plant species found in the Cañas Gordas/Valle Azul wetland in Costa Rica, where *S. woodsonii* occurs. This study enhances our understanding of orchid diversity in wetland ecosystems and emphasizes the importance of conserving these unique habitats, often inadequately protected and surrounded by heavily altered ecosystems.

Keywords: aquatic orchids, Flora of Costa Rica, Flora of Panama, new records, wetland habitats

Orchidaceae are among the most species-rich families of seed plants in the Americas (Ulloa-Ulloa et al., 2017). This is particularly evident in Mesoamerica (Dressler, 2023) and the tropical Andean countries (Ulloa-Ulloa et al., 2017; Pérez-Escobar et al., 2022). The remarkable diversity of orchids is reflected in their extensive ecological and morphological adaptations (Dressler, 1981; Stevens, 2001 onwards). Although most orchid species are epiphytic, approximately 20% are terrestrial, and an estimated 5% can grow facultatively as terrestrials or epiphytes (Dressler, 1981). Surprisingly, despite their vast diversity, the Orchidaceae have not extensively colonized aquatic and wetland habitats in the tropics. Only a limited number of species within the family have successfully adapted to thrive in these environments (e.g., Arber, 1920, and Cook et al., 1974, do not even mention Orchidaceae in their classic treatises on aquatic plants; Sculthorpe, 1967, does not include it in his table of families of aquatic vascular plants).

In this context, it is important to define what we mean by wetlands and to distinguish between aquatic and wetland plants. We adhere in general to the wetland definition agreed in the Ramsar Convention (1971): "wetlands are areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salty, including areas of marine water the depth of which at low tide does not exceed six meters;" however, we also include areas with waterlogged substrates, even if standing water is not visible to the human eye. Or, as Ervin (2023) defines them, wetlands are "areas where shallow surface waters or saturated soils are present during a biologically significant portion of the year."

Some authors (most notably den Hartog and Segal, 1964, and Ervin, 2023) have explored the complexities associated with defining aquatic and wetland plants. Our study defines *aquatic plants* as those that regularly complete their life cycle while growing in or on standing or flowing water, whether fully or partially submerged, and for most of their active growing period. It is worth noting that some authors (e.g., den Hartog and Segal 1964) exclude plants with emergent vegetative organs from this definition, even if their basal parts grow constantly in water. Additionally, we define *wetland plants* as those that regularly occur in wetland habitats,

We thank Ingrid P. Lin and Sue Lutz from the U.S. National Herbarium (US) for providing a digital image of *Cornman 2050*, and the curators of the CR, HLDG, PMA, and UCH herbaria for allowing us to examine specimens of *Sarcoglottis*. Gerardo Salazar (MEXU) kindly shared information on Mexican wetland orchids. We acknowledge the Organization for Tropical Studies (OTS) and the Rexford Daubenmire fund for granting us the funding to conduct field studies. Both Ministerio de Ambiente y Energía (MINAE) and Sistema Nacional de Áreas de Conservación (SINAC) of Costa Rica are acknowledged for granting us scientific permits (R-SINAC-SE-DT-PI-006-2021 and R-SINAC-SE-DT-PI-006-2023). This contribution is a result of two research projects: C0255, "Guía de las plantas de los humedales de Costa Rica" and C1059, "Flora Costaricensis: taxonomía y filogenia de la subtribu Spiranthinae (Orchidaceae) en Costa Rica," supported by Vicerrectoría de Investigación, Universidad de Costa Rica.

[1] Escuela de Biología, Universidad de Costa Rica, San Pedro de Montes de Oca, 11501-2060 San José, Costa Rica
[2] Herbario Luis A. Fournier Origgi (USJ), Centro de Investigación en Biodiversidad y Ecología Tropical (CIBET), Universidad de Costa Rica, San Pedro de Montes de Oca, 11501-2060, San José, Costa Rica
[3] University of Florida Herbarium (FLAS), Florida Museum of Natural History, and Department of Biology, University of Florida, Gainesville, FL 32611, U.S.A.
[4] Centro de Investigación Jardín Botánico Lankester, Universidad de Costa Rica, 302-7050 Cartago, Costa Rica
[5] Herbario UCH, Universidad Autónoma de Chiriquí, 0427, David, Chiriquí, Panamá
[6] Naturalis Biodiversity Center, Evolutionary Ecology Group, 2333 CR Leiden, The Netherlands
[7] Corresponding author: rafael.acuna_cast@ucr.ac.cr

Harvard Papers in Botany, Vol. 29, No. 1, 2024, pp. 15–33.

ISSN: 1938-2944, DOI: 10.3100/hpib.v29iss1.2024.n2, Published online: 30 June 2024

regardless of whether they are in direct contact with standing or running water. This includes epiphytes and plants that grow around bodies of water but not directly growing in the water. According to these definitions, almost all aquatic plants are wetland plants (except for rare cases of plants that regularly grow in phytotelmata in non-wetland habitats, e.g., *Anthurium bromelicola* Mayo & L.P.Felix, *Anthurium sterilispadix* K.M.Pimenta & Mayo, both Araceae, and *Utricularia humboldtii* R.H.Schomb., Lentibulariaceae, when they grow in the water impounded in bromeliad tanks away from wetlands), but at the same time, many wetland plants are not aquatic. Also, according to our definitions, plants growing on waterlogged substrates without open bodies of water (either standing or running water), are classified as wetland plants, not as aquatic plants. However, exceptions to this latter definition might arise when the substrate remains consistently saturated. Numerous plants, such as members of Alismataceae or *Heteranthera* Ruiz & Pav. (Pontederiaceae), typically deemed aquatic by our criteria, occasionally thrive in moist soils without visible surface water.

According to our definitions given above, most wetland orchids are not aquatic; they are either epiphytes or, lithophytes, or terrestrials that can grow on water-saturated soils, but normally not with standing water. Truly aquatic orchid species are rare in the family, and the occurrence of this habit has been either overlooked or received little attention from orchidologists. For example, the Identification Manual for Wetland Plant Species of Florida (Dressler et al. 1991), whose authors include two prominent orchid experts, includes a single aquatic orchid species. However, McCartney (1998) mentions three additional ones that meet our definition, which also occur in the state. According to Ervin´s (2023) classification of growth forms of aquatic plants, all aquatic orchid species are emergent (i.e., rooted in or on the submerged substrate, with stems and leaves that extend above the water surface). We do not know of any orchid species whose normal growth habit fits Ervin´s other categories of aquatic plants: floating-leafed (i.e., rooted in or on the substrate, with leaf blades that float on the water surface; e.g., *Nymphaea* L., Nymphaeaceae), submersed (i.e., rooted in or on the substrate, with stems and leaves beneath the water surface; e.g., Podostemaceae), or free-floating (i.e., not rooted in or on the substrate, with stems and leaves that float freely on or beneath the water surface; e.g., Araceae subfamily Lemnoideae).

A related plant habit category is that of rheophytes, i.e., those that are adapted to endure fast-moving water currents, either all or most of the time when they grow on riverbeds (therefore also aquatic, e.g., Podostemaceae), or occasionally when river levels rise seasonally or for brief periods during rainstorms (therefore not necessarily aquatic). The only (facultatively) rheophytic orchids from the Neotropics that we know of are a few species of *Phragmipedium* Rolfe, which belong in the second sub-category (see below). Vermeulen and Tsukaya (2011) enumerate some allegedly rheophytic orchids from southeast Asia.

In the Neotropics, *Habenaria* Willd. is probably the most likely orchid genus to be encountered in wetland habitats (Rolfe, 1901; Horich, 1983), with at least four widely distributed species (*H. gourlieana* Gillies ex Lindl., *H. pringlei* B.L. Rob., *H. repens* Nutt., and *H. sartor* Lindl.) frequently growing as aquatics. In Mexico, *Spiranthes graminea* Lindl. ex Benth. grows alongside *H. repens* amid floating vegetation mats. *Bletia purpurea* (Lam.) DC. and *H. pringlei* can thrive in flooded grasslands, or swampy regions called "popales," where the water level remains low (Hágsater et al., 2005). Plants of *Phragmipedium klotzschianum* (R.H. Schomb. ex Rchb.f.) Rolfe and *P. longifolium* (Warsz. & Rchb. f.) Rolfe often grow associated with running water, usually on seepages where the water flow is slow on its roots; however, they can also facultatively grow as rheophytes on riverbanks and around waterfalls (Dunsterville and Dunsterville, 1982; Díaz-Morales et al., 2021). The ecologically versatile *Epidendrum radicans* Pav. ex Lindl. and *Spathoglottis plicata* Blume (the latter native to southeast Asia and the western Pacific but naturalized in parts of the Neotropics), which inhabit primarily non-wetland habitats, are occasionally seen growing in wetlands (Horich, 1983). Records from other terrestrial genera, such as *Aspidogyne* Garay (*Aspidogyne tuerckheimii* (Schltr.) Garay, "Bosque lluvioso, pantanoso-yolilloso de Suerre y Dos Bocas," *P. Shank and A. Molina 4144* AMES [66497]); *Microchilus* C. Presl (*Microchilus tessellatus* Ormerod, "Terrestrial in low, swampy areas…," *M. Grayum et al. 8925* MO [713953/A:3709414]); and *Palmorchis* Barb. Rodr. (*Palmorchis paludicola* Dressler, "*Raphia taedigera* palm swamp," *S. Mori and R. Anderson 129* BM [000061071], F [1648825/F0076614F]), could indicate that some species of other, mostly terrestrial clades, can occasionally grow in wetland environments, possibly as facultatively aquatic plants. In tropical South America, besides some of the previously cited species, Kahn et al. (1993), Velásquez (1994), Pott and Pott (2000, 2021), Chocce et al. (2004), Batista and Bianchetti (2010), Batista et al. (2014), Lasso et al. (2014), Mereles et al. (2015), Madriñán et al. (2017), and Pansarin et al. (2020) report *Aspidogyne debilis* (Lindl.) Meneguzzo, *Cleistes rosea* Lindl., *Cyrtopodium paludicola* Hoehne, *Duckeella pauciflora* Garay, *Epistephium parviflorum* Lindl., *Eulophia alta* (L.) Fawc. & Rendle, *Galeandra styllomisantha* (Vell.) Hoehne, *Habenaria amambayensis* Schltr., *H. aricaensis* Hoehne, *H. bicornis* Lindl., *H. glazoviana* Kraenzl., *H. leprieurii* Rchb. f., *H. nabucoi* Ruschi, *H. orchiocalcar* Hoehne, *H. polycarpa* Hoehne, *H. pratensis* (Salzm. *ex* Lindl.) Rchb.f., *H. sartor* Lindl., *H. spathulifera* Cogn., *Liparis inundata* (Barbosa Rodrigues) A.W. Hill, *Otostylis paludosa* (Cogn.) Schltr. and three epiphytic species, *Catasetum roseo-album* (Hook.) Lindl., *Epidendrum lacustre* Lindl., and *Rodriguezia venusta* (Lindl.) Rchb. f., from wetland habitats. Most likely, most of those species (with the likely exception of some of the *Habenaria* species, *L. inundata* and *O. paludosa*) are not truly aquatic plants. At the tops of some tepuis in Venezuela, *Guanchezia maguirei* (C. Schweinf.) G.A.Romero & Carnevali grows on boggy soil (even with its pseudobulbs immersed in the wet substrate). However, at other sites, it grows terrestrially or as an epiphyte (Dunsterville and Dunsterville, 1973, 1976, as

Bifrenaria maguirei C. Schweinf.). Lot et al. (2013) and Les (2020) also list the genera *Arethusa* L., *Bletia* Ruiz & Pav., *Calopogon* R. Br., *Cypripedium* L., *Epipactis* Zinn, *Galearis* Raf., *Malaxis* Sol. ex Sw., *Platanthera* Rich., *Pogonia* Juss., *Ponthieva* R. Br., *Schiedeella* Schltr., *Spiranthes* Rich., and *Warrea* Lindl. as having wetland inhabiting representatives, but those genera are either mostly north temperate or have been only rarely recorded in wetlands south of Mexico. In Florida and other regions of North America, in addition to *H. repens*, species such as *Platanthera nivea* (Nutt.) Luer, *Spiranthes odorata* (Nutt.) Lindl., and *S. laciniata* (Small) Ames facultatively grow in aquatic environments (McCartney, 1998). *Spiranthes odorata* is occasionally sold as an aquarium plant (Salazar, 2003b). In southern Florida (but not in Cuba), the epiphytic *Dendrophylax lindenii* (Lindl.) Benth. ex Rolfe grows exclusively on trunks and branches that overhang standing water in swamps, apparently because of the protective thermal insulation against occasional freezing winter temperatures provided by the high relative humidity (Mújica et al. 2018).

Coastal lagoons and brackish river deltas with flooded forests dominated by mangroves can also be classified as wetlands. Though orchids are not commonly found in such habitats, a few epiphytic species that can tolerate certain salinity levels have been reported to grow on mangroves even when in occasional contact with brackish water or saline spray. Examples include *Brassavola nodosa* (L.) Lindl., *Encyclia alata* (Bateman) Schltr., *Myrmecophila brysiana* (Lem.) G.C. Kenn., *M. christinae* Carnevali & Gómez-Juárez, *M. tibicins* (Bateman) Rolfe, and *Prosthechea cochleata* (L.) W.E. Higgins, mostly found along the Caribbean coast of Mexico and Central America (Hágsater et al., 2005). According to our definitions above, these species can be classified as occasional wetland plants, but none are truly aquatic. A synopsis of the Neotropical and other New World orchid species previously reported as associated with wetlands (including aquatic and non-aquatic species) is provided in Table 1. No attempt has been made here to list wetland orchids from other parts of the world.

Sarcoglottis C. Presl., a primarily terrestrial genus of orchids, includes approximately 45–50 species distributed from Mexico to northern Argentina (Salazar, 2003a; POWO, 2022). The genus belongs to the subtribe Spiranthinae, the most species-rich clade of mainly terrestrial orchids in the Neotropics (Salazar et al., 2018). *Sarcoglottis* appears monophyletic and sister to a clade that includes most of *Brachystele* Schltr., polyphyletic *Odontorrhynchus* M.N. Correa, polyphyletic *Pelexia* Poit. ex Lindl., and *Sauroglossum corymbosum* (Lindl.) Garay (Salazar et al., 2018). Morphological characteristics of *Sarcoglottis* include its usually very abbreviated vegetative stem, usually clustered, fleshy roots, pseudopetiolate, non-plicate leaves, usually arranged in a rosette, commonly deciduous in anthesis, and inflorescences arranged as erect racemes, with relatively large flowers for the subtribe (Dressler, 2003). One of the most distinctive traits of the genus is the fusion of the proximal parts of the lateral sepals, which extend beneath the ovary, forming a nectary (Salazar, 2003a; Salazar et al., 2019).

Sarcoglottis woodsonii (L.O. Williams) Garay is one of the most peculiar species in the genus due to its elongated rhizome and its relatively short leaves that are persistent during anthesis (traits reminiscent of species in the subtribe Goodyerinae). Unlike most *Sarcoglottis* species, *S. woodsonii* is confined to palustrine wetland environments, distinguishing it as one of the few Mesoamerican orchids restricted to these habitats (Williams, 1946, as *Spiranthes woodsonii* L.O. Williams). As detailed below, *S. woodsonii* is a true aquatic orchid.

Bogarín et al. (2014) listed this species as endemic to Panama, with known specimens collected near Boquete in Chiriquí. Aside from our gatherings, the only other collections, to our knowledge, date back to 1918, 1938, and 1940. This work aims to update the description of *S. woodsonii* by incorporating our recent collections (the first ones from Costa Rica) and providing basic observations on its natural history and the flora associated with its habitat. With this new record, six species of *Sarcoglottis* are now known in Costa Rica (Pupulin et al., 2023).

Materials and Methods

Fieldwork was conducted on 16 June 2022 and 10 June 2023 between Cañas Gordas and Valle Azul in the Agua Buena district, Coto Brus county in Puntarenas province, Costa Rica. The study site is a wetland in a palustrine depression at ca. 8°45'19.2"N, 82°55'23.1"W, at 1130 m elevation, with its main longitudinal axis running from east to west (Fig. 1). The depression is situated approximately 100 meters from the international border with Panama at its easternmost point. It is drained by a small stream at its westernmost end. The area falls within the premontane wet-to-pluvial transition forest life zone (Tosi, 1969). Although municipal laws protect the local wetlands, they have suffered extensive degradation due to human activities, including trampling and waste from domesticated animals.

The vegetation in the study area is primarily composed of various species of grasses (Poaceae) and sedges (Cyper–aceae) that emerge from the standing water and form a "floating mat," almost completely hiding the water surface from view. Woody plants are scarce in the wetland itself. Plant material was studied in situ, with specimens of *Anagallis pumila* Sw., *Bacopa salzmannii* (Benth.) Wettst. ex Edwall, *Sarcoglottis woodsonii*, and *Syngonanthus caulescens* (Poir.) Ruhland collected and transported to the greenhouses of the School of Biology or the Lankester Botanical Garden Research Center, both of which belong to the University of Costa Rica. Herbarium specimens were deposited in the JBL (spirit) and USJ herbaria. Specimens of the genus *Sarcoglottis* were physically examined in the CR, HLDG, JBL, PMA, UCH and USJ herbaria, and digital images were studied from AMES, MO, and US herbaria (acronyms according to Thiers, 2023).

Photographic documentation through a Lankester Composite Dissection Plate (LCDP) was conducted at the Lankester Botanic Garden's Photography Laboratory.

TABLE 1. Reported Neotropical and other New World orchid species associated with wetlands. Indication of habit as "aquatic" for some species follows our definition of aquatic plants given in the Introduction. References mentioned here are included in the Literature cited section. Suprageneric classification follows Chase et al. (2015).

SUBFAMILY TRIBE SUBTRIBE	SPECIES	HABIT	REFERENCE OR HERBARIUM VOUCHER
Vanilloideae Pogonieae	*Cleistes rosea* Lindl.	Terrestrial, facultatively on flooded terrain	Madriñán et al. (2017)
	Cleistes tenuis (Rchb.f.) Schltr.	Terrestrial, facultatively on seasonally flooded savannas	Chocce et al. (2004)
	Duckeella pauciflora Garay	Terrestrial, facultatively on flooded terrain	Madriñán et al. (2017)
Vanilleae	*Epistephium parviflorum* Lindl.	Terrestrial, facultatively on seasonally flooded savannas	Chocce et al. (2004), Madriñán et al. (2017)
	Vanilla bicolor Lindl.	Hemiepiphytic facultatively on wetlands dominated by the palm *Mauritia flexuosa* L.f.	Householder et al. (2010)
	Vanilla guianensis Splitg.	Hemiepiphytic facultatively on wetlands dominated by the palm *Mauritia flexuosa*	Householder et al. (2010)
	Vanilla karen-christianae Karremans & P. Lehm.	Hemiepiphytic facultatively on wetlands dominated by the palm *Mauritia flexuosa*	Householder et al. (2010, as *Vanilla ribeiroi* Hoehne)
	Vanilla marowynensis Pulle	Hemiepiphytic facultatively on wetlands dominated by the palm *Mauritia flexuosa*	Householder et al. (2010, as *Vanilla cristato-callosa* Hoehne)
	Vanilla palmarum (Salzm. ex Lindl.) Lindl.	Hemiepiphytic facultatively on wetlands dominated by the palm *Mauritia flexuosa*	Householder et al. (2010)
	Vanilla planifolia Andrews	Hemiepiphytic facultatively on wetlands	Own unpublished data
	Vanilla pompona Schiede	Hemiepiphytic facultatively on wetlands dominated by the palm *Mauritia flexuosa*	Householder et al. (2010)
Cypripedioideae	*Phragmipedium klotzschianum* (R.H. Schomb. ex Rchb. f.) Rolfe	Terrestrial or lithophyte, occasionally as a rheophyte	Dunsterville and Dunsterville (1982)
	Phragmipedium longifolium (Warsz. & Rchb. f.) Rolfe	Terrestrial or lithophyte, facultatively on flooded seepage terrain, occasionally as a rheophyte	Díaz-Morales et al. (2021)
	Phragmipedium vittatum (Vell.) Rolfe	Terrestrial or aquatic? on flooded terrain	Batista and Bianchetti (2010)
Orchidioideae Cranichideae Goodyerinae	*Aspidogyne debilis* (Lindl.) Meneguzzo	Terrestrial, facultatively on flooded terrain or floating vegetation	Pott and Pott (2000, as *Erythrodes* cf. *pumila*, 2021)
	Aspidogyne tuerckheimii (Schltr.) Garay	Apparently facultatively on flooded terrain	*P. Shank y A. Molina 4144* (AMES 66497)
	Microchilus tessellatus Ormerod	Apparently facultatively on flooded terrain	*M. Grayum et al. 8925* (MO-713953/A:3709414)

Table 1 cont. Reported Neotropical and other New World orchid species associated with wetlands. Indication of habit as "aquatic" for some species follows our definition of aquatic plants given in the Introduction. References mentioned here are included in the Literature cited section. Suprageneric classification follows Chase et al. (2015).

Subfamily Tribe Subtribe	Species	Habit	Reference or Herbarium Voucher
Spiranthinae	*Sarcoglottis simplex* (Griseb.) Schltr.	Terrestrial, facultatively on seasonally flooded savannas	Chocce et al. (2004)
	Sarcoglottis uliginosa (Barb.Rodr.) Barb.Rodr.	Aquatic? on flooded terrain	Batista and Bianchetti (2010)
	Sarcoglottis woodsonii (L.O. Williams) Garay	Aquatic, on floating vegetation	Woodson and Schery (1942), this study
	Schiedeella durangensis (Ames & C. Schweinf.) Burns-Bal.	Terrestrial?, on flooded terrain	Lot et al. (2013)
	Schiedeella tenella (L.O. Williams) Burns-Bal.	Terrestrial?, facultatively on flooded terrain	Lot et al. (2013)
	Spiranthes delitescens	Aquatic in marshy meadows	Hágsater et al. (2005), Gerardo Salazar, pers. comm.
	Spiranthes graminea Lindl. ex Benth.	Aquatic	Hágsater et al. (2005), Lot et al. (2013), McCartney 1998
	Spiranthes laciniata (Small) Ames	Terrestrial, facultatively on flooded terrain	McCartney (1998)
	Spiranthes nebulorum Catling & V.R. Catling	In *Sphagnum* sp. bogs	Hágsater et al. (2005)
	Spiranthes odorata (Nutt.) Lindl.	Terrestrial, facultatively on flooded terrain	McCartney (1998)
	Veyretia hassleri (Cogn.) Szlach.	Terrestrial, facultatively on flooded terrain	Pott and Pott (2000, as *Sarcoglottis hassleri* (Cogn.) Schltr.)
Orchidae Orchidinae	*Habenaria amambayensis* Schltr.	Terrestrial, facultatively on flooded terrain	Pott and Pott (2000, 2021)
	Habenaria anisitsii Kraenzl.	Terrestrial, facultatively on flooded terrain	Pott and Pott (2000)
	Habenaria aricaensis Hoehne	Aquatic	Pott and Pott (2000, 2021)
	Habenaria balansae Cogn.	Terrestrial on flooded terrain	Batista and Bianchetti (2010)
	Habenaria bicornis Lindl.	Terrestrial?, on permanently wet savannas	Batista et al. (2014)
	Habenaria bractescens Lindl.	Aquatic	Lot et al. (2013)
	Habenaria crucifera Rchb.f. & Warm. *var. brevidactyla* J.A.N. Bat. & Bianch.	Terrestrial on flooded terrain	Batista and Bianchetti (2010)
	Habenaria floribunda Lindl.	Aquatic or terrestrial	Lot et al. (2013)
	Habenaria edwallii Cogn.	Terrestrial on flooded terrain	Batista and Bianchetti (2010)
	Habenaria glazioviana Kraenzl. ex Cogn.	Terrestrial, facultatively on flooded terrain	Pott and Pott (2000, 2021)

TABLE 1 CONT. Reported Neotropical and other New World orchid species associated with wetlands. Indication of habit as “aquatic” for some species follows our definition of aquatic plants given in the Introduction. References mentioned here are included in the Literature cited section. Suprageneric classification follows Chase et al. (2015).

SUBFAMILY TRIBE SUBTRIBE	SPECIES	HABIT	REFERENCE OR HERBARIUM VOUCHER
Orchidae Orchidinae cont.	*Habenaria gourlieana* Gillies ex Lindl.	Aquatic	Batista and Bianchetti (2010), Madriñán et al. (2017), Mereles et al. (2015)
	Habenaria guaraensis J.A.N. Bat. & Bianch.	Aquatic on flooded terrain	Batista and Bianchetti (2010)
	Habenaria leprieurii Rchb. f.	Terrestrial, facultatively on seasonally flooded savannas	Chocce et a. (2004), Madriñán et al. (2017)
	Habenaria leucosantha Barb.Rodr.	Terrestrial on flooded terrain	Batista and Bianchetti (2010)
	Habenaria mesodactyla Griseb.	Terrestrial, facultatively on seasonally flooded savannas	Chocce et al. (2004)
	Habenaria montiswilhelminae Renz	Terrestrial, on seasonally or permanently humid grassy fields	Batista and Bianchetti (2010)
	Habenaria nabucoi Ruschi	Terrestrial, facultatively on flooded terrain or floating vegetation	Pott and Pott (2021)
	Habenaria nuda Lindl. var. *pygmaea* Hoehne	Terrestrial on flooded terrain	Batista and Bianchetti (2010)
	Habenaria orchiocalcar Hoehne	Terrestrial, facultatively on flooded terrain	Pott and Pott (2000, 2021)
	Habenaria polycarpa Hoehne	Terrestrial, facultatively on flooded terrain	Pott and Pott (2021)
	Habenaria pratensis (Salzm. ex Lindl.) Rchb. f.	Terrestrial, facultatively on flooded terrain	Pott and Pott (2000, 2021)
	Habenaria pringlei B.L Rob.	Aquatic or terrestrial, including floating vegetation	Aburto-Oropeza et al. (2021), Hágsater et al. (2005)
	Habenaria pubidactyla subsp. *brasiliensis* J.A.N. Bat. & Bianch.	Terrestrial on flooded terrain	Batista and Bianchetti (2010)
	Habenaria repens Nutt.	Aquatic or terrestrial, including floating vegetation	Aburto-Oropeza et al. (2021), Hágsater et al. (2005), Hawkes (1953), Horich (1979, 1983), Lasso et al. (2014), Lot et al. (2013), Madriñán et al. (2017), McCartney (1998), Mereles et al. (2015), Pott and Pott (2000, 2021), Velásquez (1994)
	Habenaria sartor Lindl.	Aquatic or terrestrial	Kahn et al. (1993), Madriñán et al. (2017), Velásquez (1994)
	Habenaria spathulifera Cogn.	Terrestial, facultatively on flooded terrain	Pott and Pott (2021)
	Platanthera brevifolia (Greene) Kraenzl.	Terrestrial, facultatively on flooded terrain	Hágsater et al. (2005), Gerardo Salazar, pers. comm

Table 1 cont. Reported Neotropical and other New World orchid species associated with wetlands. Indication of habit as "aquatic" for some species follows our definition of aquatic plants given in the Introduction. References mentioned here are included in the Literature cited section. Suprageneric classification follows Chase et al. (2015).

Subfamily Tribe Subtribe	Species	Habit	Reference or Herbarium Voucher
Orchidae Orchidinae cont.	*Platanthera calderoniae* López-Ferr. & Espejo	Aquatic	Gerardo Salazar, pers. comm.
	Platanthera limosa Lindl.	Aquatic	Lot et al. (2013)
	Platanthera nivea (Nutt.) Luer	Terrestrial, facultatively on flooded terrain	McCartney (1998)
Epidendroideae Neottieae	*Epipactis gigantea* Dougl. ex Hook.	Terrestrial, facultatively on flooded terrain	Lot et al. (2013)
	Palmorchis paludicola Dressler	Terrestrial?, apparently facultatively on flooded terrain	*S. Mori and R. Anderson 129* (BM 000061071, F 1648825/ F0076614F)
Malaxideae Malaxidinae	*Liparis inundata* (Barb.Rodr.) A.W. Hill	Aquatic	Pansarin et al. (2020)
	Malaxis aff. *abieticola*	Terrestrial, facultatively in flooded montane grasslands	Hágsater et al. (2005), Gerardo Salazar, pers. comm.
	Malaxis aff. *brachystachys*	Terrestrial, facultatively on flooded terrain	Hágsater et al. (2005), Gerardo Salazar, pers. comm.
	Malaxis aff. *mysurus*	Terrestrial, facultatively on flooded terrain	Hágsater et al. (2005), Gerardo Salazar, pers. comm.
	Malaxis zempoalensis López-Ferr. & Espejo	Aquatic	Hágsater et al. (2005, as *Malaxis palustris* Espejo & López-Ferrari) Lot et al. (2013)
Collabieae	*Calanthe calanthoides* (A. Rich. & Galeotti) Hamer & Garay	Terrestrial, facultatively on flooded terrain	Hágsater et al. (2005)
	Spathoglottis plicata Blume	Terrestrial, facultatively on flooded terrain	This study
Cymbidieae Catasetinae	*Catasetum bergoldianum* Foldats	Epilithic, facultatively on flooded rock cavities	Madriñán et al. (2017)
	Catasetum integerrimum Hook.	Epiphytic, on mangroves	Aburto-Oropeza et al. (2021)
	Catasetum kamatawara Damián, Mitidieri & Bonilla	Epiphytic, on "aguajales" dominated by the palm *Mauritia flexuosa*	Damián et al. (2021)
	Catasetum roseo-album (Hook.) Lindl.	Terrestrial or epilithic, facultatively on flooded terrain or epiphytic	Madriñán et al. (2017, as *Catasetum discolor* (Lindl.) Lindl.)
	Galeandra styllomisantha (Vell.) Hoehne	Terrestrial, facultatively on flooded terrain	Pott and Pott (2000, 2021)
Cyrtopodiinae	*Cyrtopodium paludicola* Hoehne	Terrestrial, facultatively aquatic? on flooded terrain	Batista and Bianchetti (2010), Pott and Pott (2021)
	Cyrtopodium parviflorum Lindl.	Terrestrial, facultatively on seasonally flooded savannas	Chocce et al. (2004)

Table 1 cont. Reported Neotropical and other New World orchid species associated with wetlands. Indication of habit as "aquatic" for some species follows our definition of aquatic plants given in the Introduction. References mentioned here are included in the Literature cited section. Suprageneric classification follows Chase et al. (2015).

Subfamily Tribe Subtribe	Species	Habit	Reference or Herbarium Voucher
Eulophiinae	*Eulophia alta* (L.) Fawc. & Rendle	Terrestrial, facultatively on flooded terrain, floating vegetation mats or epiphytic	Kahn et al. (1993), Lot et al. (2013), Madriñán et al. (2017), Mereles et al. (2015), Pott and Pott (2021)
Maxillariinae	*Guanchezia maguirei* (C. Schweinf.) G.A. Romero & Carnevali	Terrestrial or epiphytic, facultatively on boggy soil on tops of tepuis	Dunsterville and Dunsterville (1973, 1976), as *Bifrenaria maguirei* C. Schewinf.
	Maxillaria tenuifolia Lindl.	Epiphytic, on mangroves	Aburto-Oropeza et al. (2021)
Oncidiinae	*Gomesa hydrophila* (Barb.Rodr.) M.W. Chase & N.H. Williams	Terrestrial or aquatic? on flooded terrain	Batista and Bianchetti (2010, as *Oncidium hydrophilum* Barb.Rodr.)
	Macradenia brassavolae Rchb.f.	Epiphytic, in wetlands dominated by *Raphia taedigera*	Pupulin and Ossenbach (2016)
	Notylia orbicularis A.Rich. & Galeotti	Epiphytic, facultatively on wetland trees and mangroves	Aburto-Oropeza et al. (2021)
	Oncidium sphacelatum Lindl.	Epiphytic, facultatively on wetland trees and mangroves	Aburto-Oropeza et al. (2021)
	Rodriguezia venusta Rchb. f.	Epiphytic, facultatively on wetland savannas or trees	Madriñán et al. (2017)
	Trichocentrum lindenii (Brongn.) M.W. Chase & N.H. Williamsq	Epiphytic, facultatively on wetland trees and mangroves	Aburto-Oropeza et al. (2021)
Zygopetalinae	*Otostylis brachystalix* (Rchb. f.) Schltr.	Terrestrial, facultatively aquatic on seasonally flooded savannas	Chocce et al. (2004)
	Otostylis paludosa (Cogn.) Schltr.	Aquatic, on boggy "aguajales" dominated by the palm *Mauritia flexuosa*	Chocce et al. (2004)
	Warrea costaricensis Schltr.	Terrestrial, facultatively on flooded terrain	Lot et al. (2013)
Epidendreae Bletiinae	*Bletia catenulata* Ruiz & Pav.	Terrestrial or aquatic? on flooded terrain	Batista and Bianchetti (2010)
	Bletia purpurea (Lam.) D.C.	Terrestrial, facultatively on flooded terrain	Hágsater et al. (2005), Lot et al. (2013)
	Bletia tenuifolia Ames & C. Schweinf.	Terrestrial, facultatively on flooded terrain	Lot et al. (2013)
Laeliinae	*Brassavola nodosa* (L.) Lindl.	Epiphytic, on mangroves	Hágsater et al. (2005)
	Encyclia alata (Bateman) Schltr.	Epiphytic, on mangroves	Aburto-Oropeza et al. (2021), Hágsater et al. (2005)
	Epidendrum lacustre Lindl.	Epiphytic or epilithic, facultatively on partially submersed trunks?	Velásquez (1994)
	Epidendrum nocturnum Jacq.	Epiphytic, on mangroves	Aburto-Oropeza et al. (2021)
	Epidendrum radicans Pav. ex Lindl.	Terrestrial, facultatively on flooded terrain or adjacent floating vegetation	Horich (1983), this study
	Myrmecophila brysiana (Lem.) G.C. Kenn.	Epiphytic, on mangroves	Hágsater et al. (2005)

Table 1 cont. Reported Neotropical and other New World orchid species associated with wetlands. Indication of habit as "aquatic" for some species follows our definition of aquatic plants given in the Introduction. References mentioned here are included in the Literature cited section. Suprageneric classification follows Chase et al. (2015).

Subfamily Tribe Subtribe	Species	Habit	Reference or Herbarium Voucher
Laeliinae cont.	*Myrmecophila christinae* Carnevali & Gómez-Juárez	Epiphytic, on mangroves	Hágsater et al. (2005)
	Myrmecophila tibicinis (Bateman) Rolfe	Epiphytic, on mangroves	Aburto-Oropeza et al. (2021), Hágsater et al. (2005)
	Prosthechea cochleata (L.) W.E. Higgins	Epiphytic, on mangroves	Aburto-Oropeza et al. (2021), Hágsater et al. (2005)
Sobralieae	*Sobralia abel-arayae* Dressler, Mel. Fernández & Pupulin	Terrestrial, facultatively on flooded terrain	Dressler et al. (2014)
Vandeae Agraecinae	*Dendrophylax lindenii* (Lindl.) Benth. ex Rolfe	Epiphytic in swamps	Mújica et al. (2018)
Polystachyinae	*Polystachya caracasana* Rchb. f.	Epiphytic, on mangroves	Aburto-Oropeza et al. (2021)

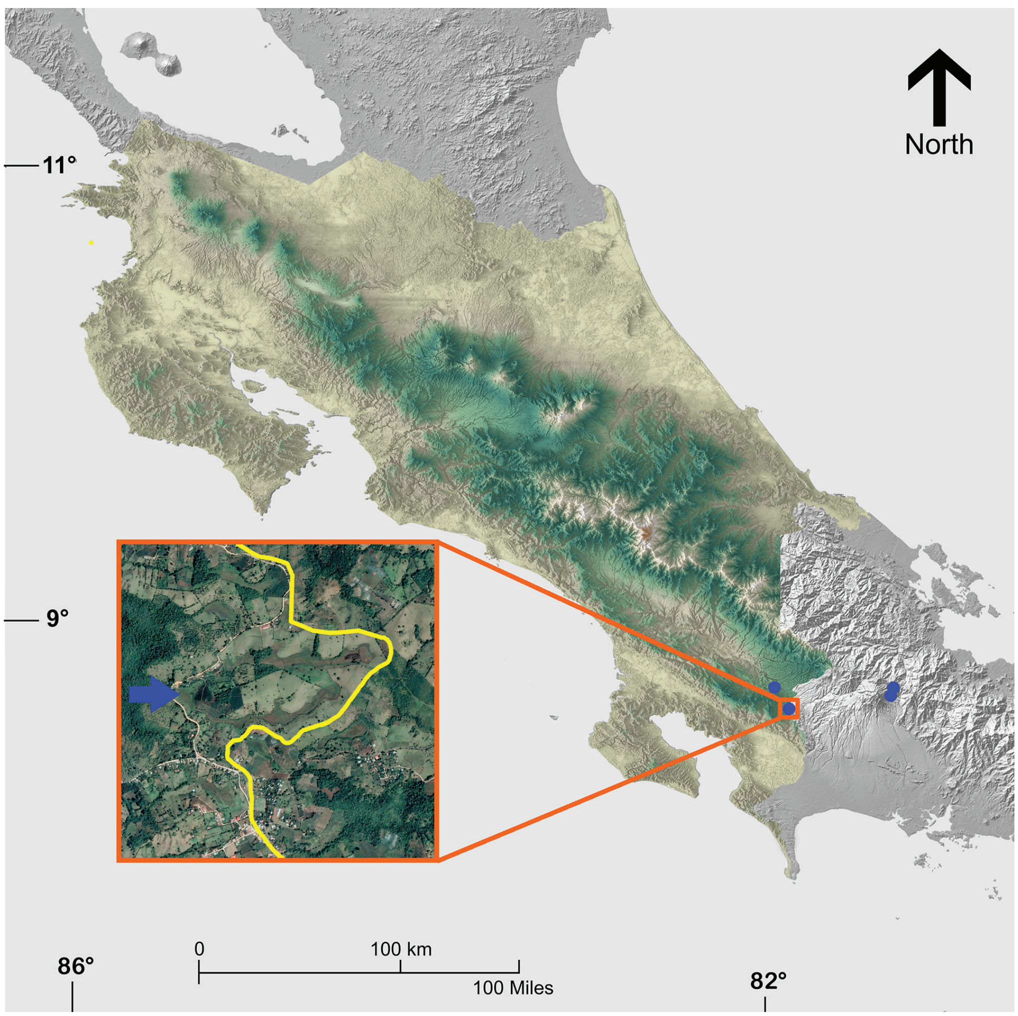


Figure 1. Study site and distribution map of S*arcoglottis woodsonii* in Costa Rica and Panama. Inset: satellite image showing the study site with the wetland surrounded by highly altered habitat. The yellow line and blue arrow denote the Costa Rica-Panama border and sample collection site, respectively. Blue dots represent the localities of examined herbarium specimens and one iNaturalist report. The map was adapted from Guzmán Q., J. Antonio (2021). Costa Rica exaggerated relief map. https://doi.org/10.6084/m9.figshare.16613515.v1 by J. Antonio Guzmán Q. and GoogleEarth Pro 7.3 2022.

A Nikon D850 camera was employed with a Nikon AF-S DX NIKKOR 18–105mm f/3.5-5.6 G ED macro lens. For achieving optimal focus and depth of field, photo stacking was performed using a Nikon PB-6 bellows equipped with a Zeiss 40 mm 1:4.5 Luminar macro lens, along with the Cognysis StackShot automated macro rail for focus stacking and Broncolor Siros 800 S flashes. The resulting stack of individual images was aligned and blended using the Zerene Stacker software. The LCDP was diagrammed with Adobe Photoshop 2023.

A preliminary assessment of the conservation status of the species was made using the International Union for Conservation of Nature criteria (IUCN, 2017). The area of occupancy (AOO) and the extent of occurrence (EOO) were calculated using GeoCat (Bachman et al., 2011).

Results

Sarcoglottis woodsonii (L.O. Williams) Garay, Bot. Mus. Leafl. 28(4): 355. 1980 [1982].

Basionym: *Spiranthes woodsonii* L.O. Williams, Ann. Missouri Bot. Gard. 29(4): 337. 1942. TYPE: PANAMA. Chiriquí: Vicinity of Boquete, elev. 1200–1500 m, 24–26 July 1940, *R. E. Woodson Jr. and R. W. Schery 753* (holotype: AMES [59595]; isotypes: AMES [85462], MO [not seen]). (Fig. 2).

Palustrine *herb* of up to 180 cm in length. *Roots* up to 30 cm long, uniformly 3–5 mm in diameter, pubescent, arising from the rhizome nodes. *Stems* unbranched, or with few (2–3) branches arising from a horizontal rhizome, to 5 mm in diameter in the aerial portions, decumbent, the proximal part forming a long, creeping rhizome up to 80 cm long or longer, covered with scarious remnants of leaf sheaths, the distal, erect portion to 55 cm long (excluding the inflorescence). *Leaves* elliptic to oblong, 3.0–10.5 × 1.1–3.3 cm, acute to obtuse, pseudopetiolate, conduplicate, slightly concave, adaxially dark green, slightly glaucous, glossy, with the central vein paler and grooved, with a tubular, sheathing base of 2.2–4.0 cm long; up to 17 leaf blades present at flowering, spirally arranged, on the lower half of the erect portion of the stem, with progressively smaller blades distally, the most terminal leaves amplexicaul, bract-like, and adpressed to the stem; pseudopetiole 0.8 × 1.0 cm. *Inflorescence* an apical, erect, pedunculate raceme, pubescent with densely glandular hairs, stout, to 60 cm long, 6 mm in diameter, peduncle 30–45 cm long, with 5–6 tightly appressed tubular, ensiform, amplexicaul, acute to acuminate bracts to 8.0–9.0 × 0.8–1.0 cm, rachis 5–10 cm long, with 5–14 helically arranged (with up to 7 simultaneously open flowers), closely spaced flowers opening in succession, with widely ovate, acute to acuminate, not amplexicaul, bracts, basally glandular-pubescent, shorter or sometimes as long as the ovary, 3.6–6.5 × 1.2–1.6 cm. *Flowers* mildly fragrant, up to 5.2 cm long, densely white-pubescent on the ovary and outer part of the floral segments, resupinate, basally tubular, arcuate toward the apex; flower buds rostrate; ovary glandular-pubescent, cylindrical, with parietal placentation, to 2.5–3.5 × 0.6–0.8 cm; sepals dark green and covered with white hairs abaxially, white with faintly green longitudinal veins adaxially; petals white on both surfaces, with 2–3 conspicuous green lines adaxially; labellum greenish white on both surfaces, with ca. 7 conspicuous green lines adaxially. *Dorsal sepal* ovate to elliptic-lanceolate, acute or subacute, deeply concave over the lip and column, with the apex slightly pointing upwards, adherent but not adnate with the petals, 1.5–1.9 × 0.3–0.4 cm. *Lateral sepals* narrowly oblong, basally connate, and decurrent on the ovary for about 1.5 cm, forming a saccate mentum (nectary), subacute, the free portion falcate, reflexed, spreading (the tips sometimes crossing), and somewhat involute-navicular apically, 3.5–3.7 × 0.3–0.5 cm. *Petals* linear-ligulate, subfalcate, acute, pubescent along the lower margin, slightly reflexed apically and connivent with the dorsal sepal forming a hood (galea) over the column and labellum, 1.5–1.8 × 0.2–0.3 cm. *Labellum* clawed, strongly arcuate apically, adnate to the lateral sepals, with two basal, digitate, filiform, acute projections up to 7 mm long, canaliculate; blade linear-oblong, constricted basally and below the apex, the hypochile oblong-obovate or subpandurate, widened apically, the epichile reniform, emarginate, strongly reflexed, with 2 convergent oblique keels, each one running from each side of the apical constriction of the *hypochile* to the middle of the *epichile*, pubescent at the base of the projections, the *mesochile* and along keels of the *epichile*, 2.8–3.5 × 0.6–0.7 cm. *Nectary* to 1.6 cm long. *Column* subulate, abaxially pubescent, to 1.4 × 0.3 cm. *Pollinia* 2, narrowly ovoid to oblong, sulcate, puberulent with a short, rhombic greyish viscidium. *Stigma* ventral, bilobed, wet, shiny. *Anther cap* cucullate, oblong-elliptic, rostrate, with two cells (thecae). *Fruit* a fusiform capsule, erect, pubescent, longitudinally dehiscent, to 4 cm long.

Etymology: This species is named after Robert Everard Woodson Jr. (1904–1963), a prominent botanist from the Missouri Botanical Garden. He co-discovered the species and was a key contributor to the pioneering Flora of Panama Project.

Additional Specimens Examined: COSTA RICA. Puntarenas: Coto Brus, Distrito Agua Buena, palustrine depression between Cañas Gordas and Valle Azul, at 08°45'19.2"N, 82°55'23.1"W, 1130 m, 16 June 2022, *R. Acuña, M. Blanco, and M. Artavia 3282* (JBL spirit); same locality, 9 June 2023, *R. Acuña et al. s.n.* (USJ, JBL). PANAMA. Chiriquí: Finca Lérida to Boquete, elevation ca. 1300–1700 m, in swampy meadows; flowers pale yellowish-green, 8–10 July 1938, *R. E. Woodson Jr., P. H. Allen, and R. W. Siebert 1148* (AMES [55697, 58836, 58837, 58838]; MO [780400/accession 1172202]); Vicinity of El Boquete, woods near O'Donnell Hacienda, altitude 1000–1500 m, 14 February 1918, *L. R. Cornman 2050* (US [00017906]).

iNaturalist observation: COSTA RICA. Puntarenas: Coto Brus, Distrito San Vito at 8.795242 N, 82.961644 W, 31 October 2023, Marcel Esquivel (https://www.inaturalist.org/observations/189567668).

Distribution: This species has been documented from only three locations: the vicinity of Boquete in Chiriquí province, Panama (its type locality), between Valle Azul and Cañas Gordas (a few hundred meters from the border with Panama), and near Las Cruces Biological Station, both in Puntarenas province, Costa Rica (Fig. 1).

FIGURE 2. *Sarcoglottis woodsonii* (L.O.Williams) Garay. **A**, Plant (rhizome extended; in its natural orientation, the rhizome lays horizontally on top of other aquatic plants, at or just above the water level); **B**, Flower side, front, and oblique views; **C**, Perianth, dissected and flattened; **D**, Ovary, column and lip, side view; **E**, Ovary and column, abaxial, adaxial, and side views; **F**, Pollinarium and anther cap. LCDP from *R. Acuña et al. s.n.* (coll. date: 9 June 2023, USJ, JBL).

Habitat and Ecology: *Sarcoglottis woodsonii* appears restricted to freshwater wetlands at middle elevations (1000–1700 m) in southeastern Costa Rica and western Panama on the Pacific slopes of the Cordillera de Talamanca and Fila Costeña. In Costa Rica, we discovered a small population near the western edge of the wetland, where the specimens studied for this research were collected (Fig. 3). This wetland is a marsh that has water throughout the year. Long sections of the vegetative stems (up to 80 cm) of *Sarcoglottis woodsonii* were observed growing horizontally on semi-submerged vegetation, more or less at surface level. Evidently, the erect, leafy portions of the decumbent stems gradually become horizontal (turning into a "rhizome") as the stem apex continues elongating and producing new leaves; only the portion immediately below the apex stays erect. The bases of the plants were rooted on small emergent lumps of wet soil, the horizontal rhizomes produced roots into the water, and the distal part of the stems were erect (up to 1 m, including the inflorescence). Louis O. Williams (in Woodson and Schery, 1942) indicated that this species has a "creeping underground rhizome or stem," but this was likely a misinterpretation, based on his examination of the morphology of the dried herbarium specimens only, whose labels have a meager description of the plants and their habitat. The vascular plant wetland community growing alongside *S. woodsonii* comprises at least 71 species (Table 2). It is dominated by sedges and grasses (Figs. 4–5), a common pattern in many wetlands in Costa Rica (R. Acuña-Castillo et al., unpubl. data). Our observations and herbarium data indicate that Cyperaceae, with 18 recorded species, has the highest species richness in this locality, followed by Poaceae, with ten species, and

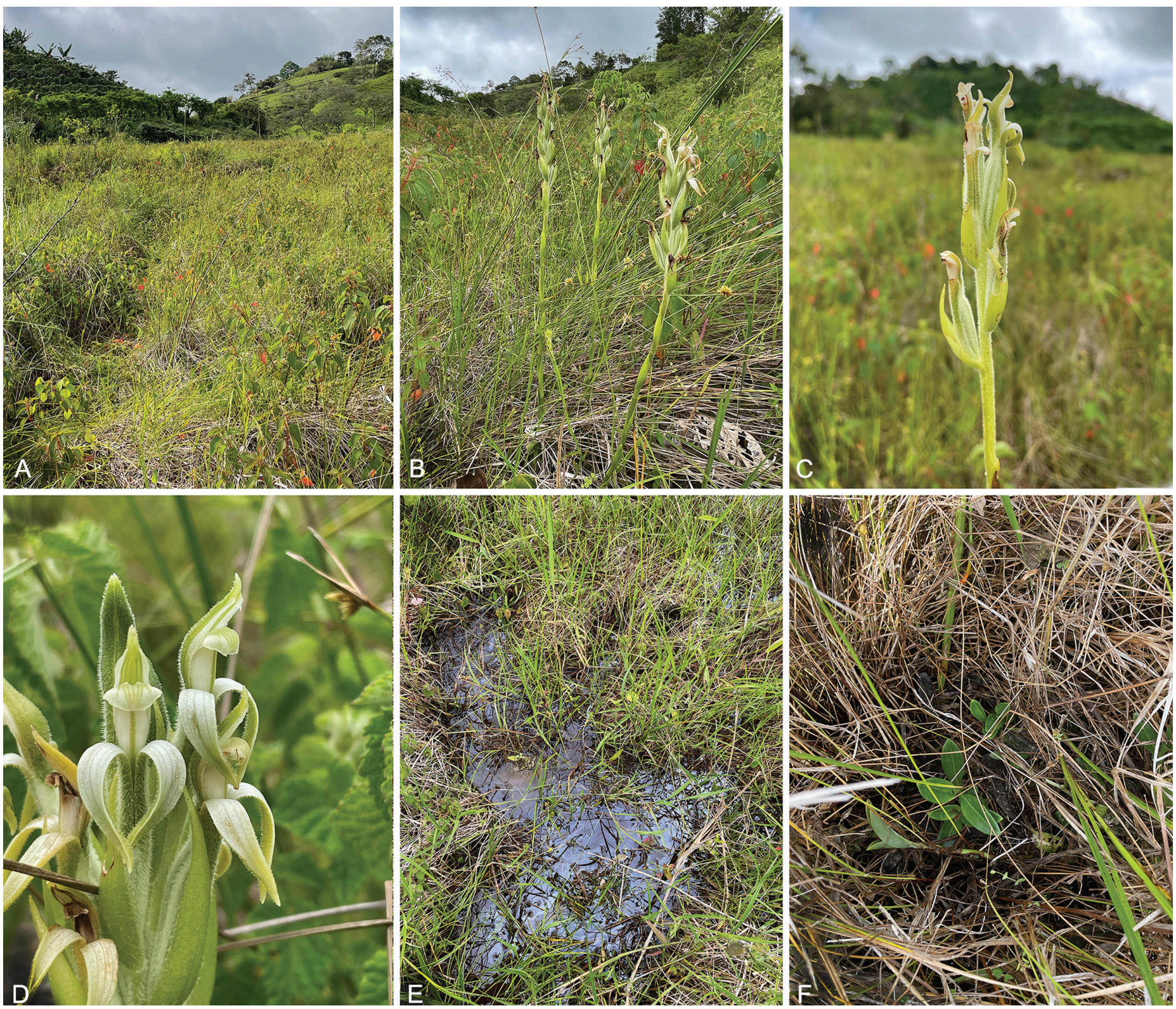


FIGURE 3. Natural habitat of *Sarcoglottis woodsonii* in Agua Buena, Costa Rica. **A**, View of the palustrine depression where *S. woodsonii* plants grow; **B**, Plants with flowers and fruits; **C**, Inflorescences with herbivore damage; **D**, Inflorescence with undamaged flowers of various ages, and a bud; **E–F**, Juveniles and seedlings growing in the water and among grasses and sedges.

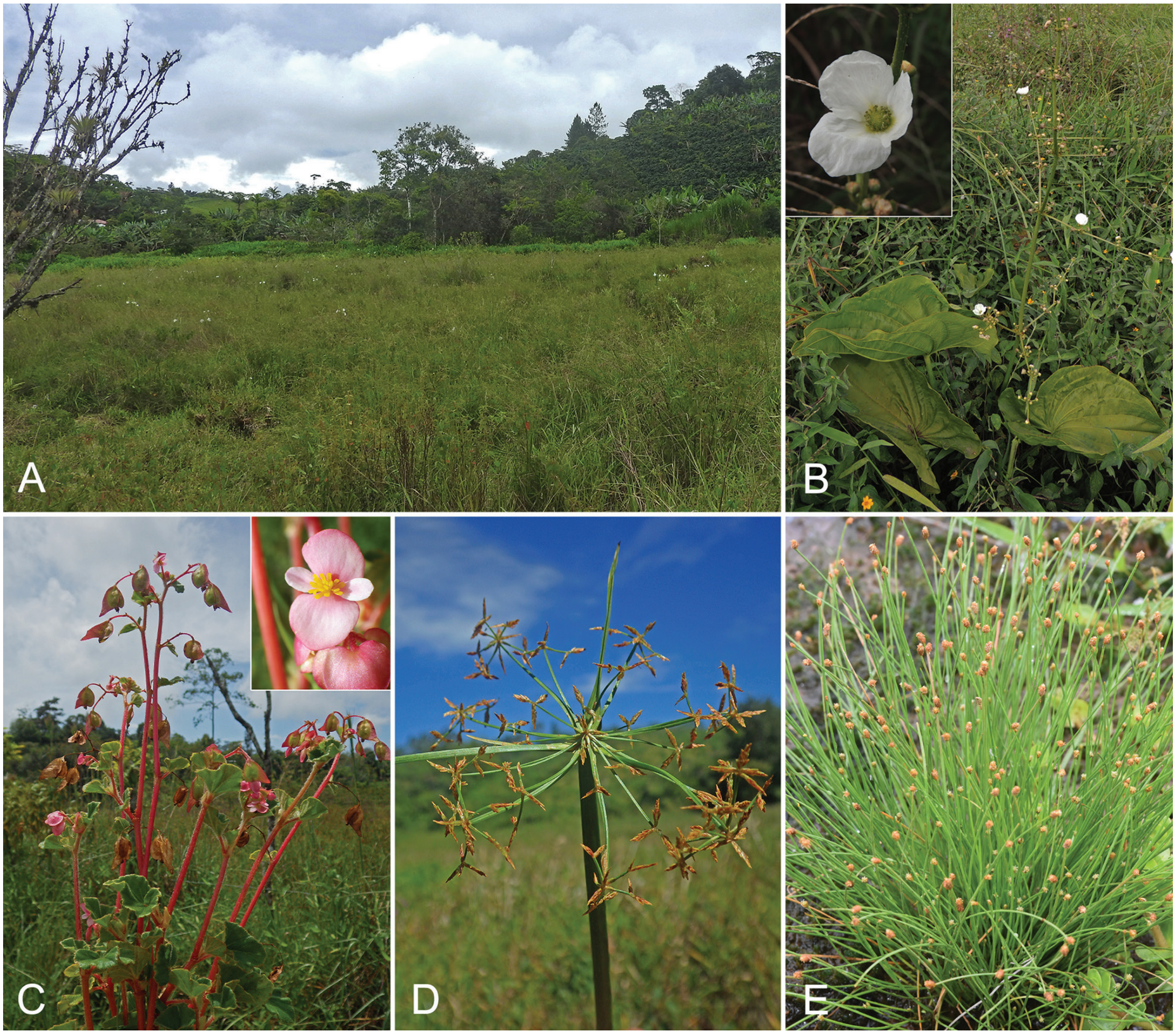


FIGURE 4. Palustrine depression in Agua Buena between Cañas Gordas and Valle Azul, Costa Rica, where **A**, *Sarcoglottis woodsonii* was found, as well as **B–E**, some representative species growing in sympatry; **B**, *Echinodorus floribundus* (Alismataceae); **C**, *Begonia fischeri* (Begoniaceae); **D**, *Cyperus haspan* (Cyperaceae); **E**, *Eleocharis filiculmis* (Cyperaceae).

Fabaceae, with four. Regarding genera, the most species-rich is *Eleocharis* R. Br., with seven species, followed by *Cyperus* L., *Hyptis* Jacq., *Ludwigia* L., *Persicaria* (L.) Mill., and *Rhynchospora* Vahl, with three species each. Some remarkable species growing in the same wetland but that are either rare or have not been collected in other localities in Costa Rica, include *Ageratum riparium* B.L. Rob., *Coelorachis aurita* (Steud.) A. Camus, *Echinodorus floribundus* (Seub.) Seub. (Fig. 4), *Eriochrysis cayanensis* P. Beauv. (Fig. 5), *Escobedia grandiflora* (L. f.) Kuntze (Fig. 5), *Fuirena incompleta* Nees (Fig. 5), *Rhynchospora velutina* (Kunth) Boeckeler (Fig. 5), and *Syngonanthus caulescens* (Poir.) Ruhland (Fig. 5), underlining that *S. woodsonii* is part of a very interesting wetland plant flora (Table 2).

Phenology: We found plants of *Sarcoglottis woodsonii* during June in anthetic and fruiting reproductive stages, with some capsules already open and dispersing seeds. Similarly, two collections from Panama (*Woodson and Schery 753*, *Woodson et al. 1148*) were collected in July and were fertile. The plants we have cultivated *ex-situ* since June 2022 are developing inflorescences for the first time as of June 2024. However, a specimen (*Cornman 2050*) was collected in flower in February (but see Discussion), and a recent record of a flowering plant (iNaturalist, see information above) was made in October.

Provisional Conservation Status: Based on a generous cell width of 3 km, the GeoCAT assessment tentatively considers *Sarcoglottis woodsonii* as Endangered (EN), under the IUCN categories and criteria B2ab(iii); D. The

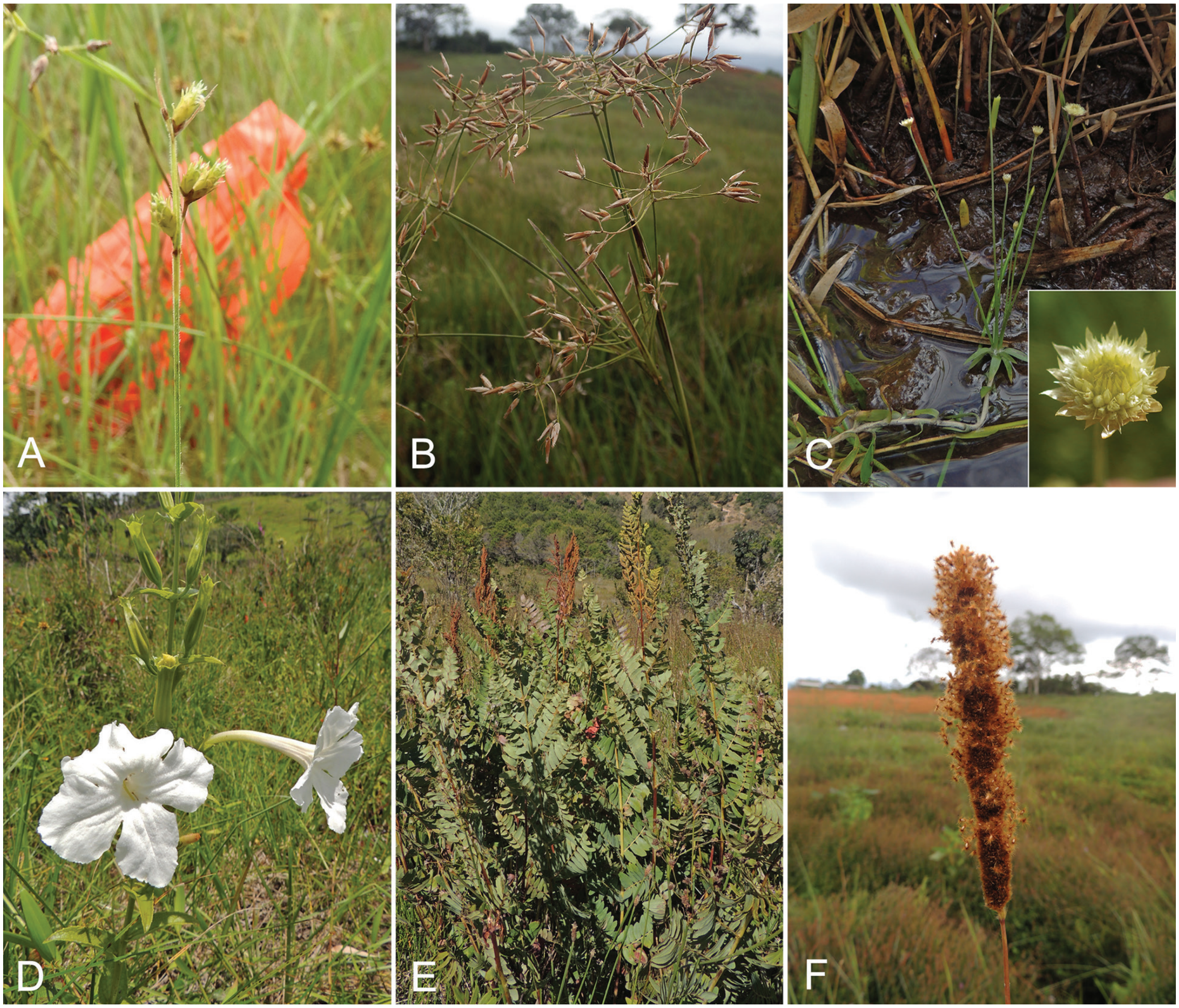


FIGURE 5. More representative species growing in the palustrine depression in Agua Buena, between Cañas Gordas and Valle Azul, Costa Rica; **A**, *Fuirena incompleta* (Cyperaceae); **B**, *Rhynchospora velutina* (Cyperaceae); **C**, *Syngonanthus caulescens* (Eriocaulaceae); **D**, *Escobedia grandiflora* (Orobanchaceae); **E**, *Osmunda regalis* (Osmundaceae); **F**, *Eriochrysis cayanensis* (Poaceae).

criterion B2 was selected because its Area of Occupancy is between 10 and 500 km^2 (36 km^2, the Extent of Occurrence of ca. 220 km^2 would also fall in the EN category range). The criterion "a" was selected because the species shows a fragmented distribution known only from three localities in a botanically well-inventoried area. The "b(iii)" criterion was chosen because there is a projected decline in the area, extent, and quality of the species' habitat, resulting from land use changes, overgrazing, siltation, and wetland drainage for agricultural, livestock grazing, or infrastructure development purposes. Wetlands are frequently perceived as "useless land" by farmers and developers in Panama and Costa Rica, and many wetlands near the area of study have been either highly altered or completely drained in the last two decades (J. Flores-Rojas, pers. comm.). The Cañas Gordas and Valle Azul wetlands are classified by the Costa Rican Wetlands Vulnerability Index as highly vulnerable (Jiménez, 2016; Veas-Ayala et al., 2022). In June 2023, three of the authors noticed that a large amount of lateritic soil from a nearby small landslide was moved very close to the margins of the wetland where *S. woodsonii* was studied in Costa Rica. This could pose an immediate and serious threat to this population of the species, as torrential rainfalls may cause material movement toward the wetland, which may cover some of the vegetation and cause siltation. Likewise, the Panamanian government has been pursuing an agenda to settle natural savannas and wetlands from middle elevations in Chiriquí province, which are viewed as suitable for human infrastructure development, with the mistaken belief that there would not be significant ecological

Table 2. Vascular plant species known from the wetland sampled in this study.

Family	Species	Voucher Specimen
Acanthaceae	*Lepidagathis alopecuroidea* (Vahl) R. Br. ex Griseb.	*J.E. Jiménez et al. 4206* (USJ)
Alismataceae	*Echinodorus floribundus* (Seub.) Seub.	*J.E. Jiménez et al. 4211* (USJ)
Alismataceae	*Limnocharis laforestii* Griseb.	*J.E. Jiménez et al. 4209* (USJ)
Araceae	*Spathiphyllum atrovirens* Schott	*R. Acuña et al. s.n.* 16.Ago.2019 (USJ)
Araliaceae	*Hydrocotyle umbellata* L.	*R. Acuña et al. s.n.* 16.Ago.2019 (USJ)
Asteraceae	*Ageratum riparium* B. L. Rob.	*J. Gómez-Laurito & R. Ortiz 13348* (USJ)
Asteraceae	*Wedelia filipes* Hemsl.	*J.E. Jiménez et al. 4201* (USJ)
Begoniaceae	*Begonia fischeri* Schrank	*R. Acuña 724* (USJ)
Caryophyllaceae	*Drymaria villosa* Schltdl. & Cham.	*J.E. Jiménez et al. 4210* (USJ)
Commelinaceae	*Floscopa glabrata* (Kunth) Hassk.	*J.E. Jiménez et al. 4198* (USJ)
Commelinaceae	*Tripogandra serrulata* (Vahl) Handlos	*J. Gómez-Laurito et al. 14942* (USJ)
Cyperaceae	*Cyperus haspan* L.	*J. Gómez-Laurito & R. Ortiz 13341* (USJ)
Cyperaceae	*Cyperus lanceolatus* Poir.	*R. Acuña 721* (USJ)
Cyperaceae	*Cyperus unioloides* R. Br.	*R. Acuña 739* (USJ)
Cyperaceae	*Eleocharis acutangula* (Roxb.) Schult.	*J. Gómez-Laurito et al. 14922* (USJ)
Cyperaceae	*Eleocharis elegans* (Kunth) Roem. & Schult.	*J.E. Jiménez et al. 4207* (USJ)
Cyperaceae	*Eleocharis filiculmis* Kunth	*R. Acuña 726* (USJ)
Cyperaceae	*Eleocharis montana* (Kunth) Roem. & Schult.	*R. Acuña et al. 2009* (USJ)
Cyperaceae	*Eleocharis pachystyla* (C. Wright) C.B. Clarke	*J. Gómez-Laurito 10722* (USJ)
Cyperaceae	*Eleocharis retroflexa* (Poir.) Urb.	*J.E. Jiménez et al. 4197* (USJ)
Cyperaceae	*Eleocharis sellowiana* Kunth	*J. Gómez-Laurito et al. 14966* (USJ)
Cyperaceae	*Fimbristylis dichotoma* (L.) Vahl	*R. Acuña et al. 2010* (USJ)
Cyperaceae	*Fuirena incompleta* Nees	*J. Gómez-Laurito et al. 14947* (USJ)
Cyperaceae	*Fuirena umbellata* Rottb.	*J.E. Jiménez et al. 4205* (USJ)
Cyperaceae	*Kyllinga pumila* Michx.	*R. Acuña 741* (USJ)
Cyperaceae	*Rhynchospora marisculus* Lindl. ex Nees	*J. Gómez-Laurito et al. 14968* (USJ)
Cyperaceae	*Rhynchospora radicans* (Schltdl. & Cham.) H. Pfeiff.	*J. Gómez-Laurito & R. Ortiz 13348* (USJ)
Cyperaceae	*Rhynchospora velutina* (Kunth) Boeckeler	*R. Acuña 723* (USJ)
Cyperaceae	*Scleria distans* Poir.	*J. Gómez-Laurito 10703* (USJ)
Equisetaceae	*Equisetum giganteum* L.	*J. Gómez-Laurito et al. 13744* (USJ)
Eriocaulaceae	*Syngonanthus caulescens* (Poir.) Ruhland	*J.E. Jiménez et al. 4199* (USJ)
Fabaceae	*Desmodium adscendens* (Sw.) DC.	*J. Gómez-Laurito et al. 14913* (USJ)
Fabaceae	*Mimosa debilis* Humb & Bonpl. ex Willd.	*R. Acuña et al. 2019* (USJ)
Fabaceae	*Senna cobanensis* (Britton) H.S. Irwin & Barneby	*J. Gómez-Laurito 10700* (USJ)
Fabaceae	*Vigna luteola* (Jacq.) Benth.	*R. Acuña et al. 2030* (USJ)
Lamiaceae	*Hyptis lantanifolia* Poit.	*J.E. Jiménez et al. 4204* (USJ)

Table 2 cont. Vascular plant species known from the wetland sampled in this study.

Family	Species	Voucher Specimen
Lamiaceae	*Hyptis recurvata* Poit.	*J. Gómez-Laurito et al. 13769* (USJ)
Lamiaceae	*Hyptis sinuata* Pohl ex Benth.	*J. Gómez-Laurito 10747* (USJ)
Lythraceae	*Cuphea carthagenensis* (Jacq.) J.F. Macbr.	*R. Acuña 719* (USJ)
Malvaceae	*Peltaea trinervis* (C. Presl) Krapov & Cristóbal	*R. Acuña et al. s.n.* 16.Ago.2019 (USJ)
Melastomataceae	*Graffenrieda galeottii* (Naudin) L.O. Williams	*J. Gómez-Laurito 10689* (USJ)
Melastomataceae	*Rhynchanthera paludicola* (Donn. Sm.) Gleason	*R. Acuña 733* (USJ)
Ochnaceae	*Sauvagesia erecta* L.	*J. Gómez-Laurito et al. 14914* (USJ)
Onagraceae	*Ludwigia leptocarpa* (Nutt.) H. Hara	*R. Acuña 743* (USJ)
Onagraceae	*Ludwigia peruviana* (L.) H. Hara	*R. Acuña et al. 2025* (USJ)
Onagraceae	*Ludwigia rigida* (Miq.) Sandwith	*J. Gómez-Laurito 10741* (USJ)
Orchidaceae	*Epidendrum radicans* Pav. ex Lindl.	*J. Gómez-Laurito 10714* (USJ)
Orchidaceae	*Sarcoglottis woodsonii* (L.O. Williams) Garay	*R. Acuña et al. 3282* (JBL)
Orobanchaceae	*Escobedia grandiflora* (L. f.) Kuntze	*J.E. Jiménez et al. 1325* (CR)
Osmundaceae	*Osmunda regalis* L.	*R. Acuña 737* (USJ)
Phyllanthaceae	*Phyllanthus stipulatus* (Raf.) G. L. Webster	*J.E. Jiménez et al. 4196* (USJ)
Plantaginaceae	*Bacopa salzmannii* (Benth.) Wettst. Ex Edwall	*R. Acuña 727* (USJ)
Poaceae	*Andropogon bicornis* L.	*R. Acuña et al. 2024*(USJ)
Poaceae	*Coelorachis aurita* (Steud.) A. Camus	*R. Acuña 722* (USJ)
Poaceae	*Echinochloa polystachya* (Kunth) Hitchc.	*J. Gómez-Laurito 10755* (USJ)
Poaceae	*Eriochrysis cayanensis* P. Beauv.	*J. Gómez-Laurito et al. 13778* (USJ)
Poaceae	*Homolepis glutinosa* (Sw.) Zuloaga & Soderstr.	*J. Gómez-Laurito 10733* (USJ)
Poaceae	*Isachne polygonoides* (Lam.) Döll	*J. Gómez-Laurito 10761* (USJ)
Poaceae	*Leersia hexandra* Sw.	*R. Acuña 742* (USJ)
Poaceae	*Paspalum boscianum* Flüggé	*R. Acuña et al. 2038* (USJ)
Poaceae	*Rugoloa polygonata* (Schrad.) Zuloaga	*R. Acuña 735* (USJ)
Poaceae	*Trichanthecium parvifolium* (Lam.) Zuloaga & Morrone	*R. Acuña 720* (USJ)
Polygalaceae	*Monnina sylvicola* Chodat	*J. Gómez-Laurito 10691* (USJ)
Polygalaceae	*Persicaria acuminata* (Kunth) M. Gómez	*J.E. Jiménez & J. Porras 4178* (USJ)
Polygalaceae	*Persicaria meisneriana* (Cham. & Schltdl.) M. Gómez	*R. Acuña et al. 2042* (USJ)
Polygonaceae	*Persicaria punctata* (Elliott) Small	*J.E. Jiménez & J. Porras 4180* (USJ)
Pontederiaceae	*Heteranthera reniformis* Ruiz & Pav.	*R. Acuña et al. 1999* (USJ)
Primulaceae	*Anagallis pumila* Sw.	*R. Acuña 731* (USJ)
Rubiaceae	*Galium hypocarpium* (L.) Endl. ex Griseb.	*J. Gómez-Laurito et al. 14955* (USJ)
Rubiaceae	*Palicourea padifolia* (Humb. & Bonpl. ex Roem. & Schult.) C.M. Taylor & Lorence	*J. Gómez-Laurito 10731* (USJ)
Rubiaceae	*Spermacoce prostrata* Aubl.	*J. Gómez-Laurito 10721* (USJ)
Xyridaceae	*Xyris laxifolia* Mart.	*R. Acuña 728* (USJ)

trade-offs derived from changes in land use (as opposed to the impact caused by forest clearing). This view ignores that these savannas and wetlands are habitats for many endemic or rare species (R. Flores pers. comm.). Furthermore, to our knowledge, the species has not been collected near its type locality in Panama for several decades.

The wetlands around Valle Azul and Cañas Gordas constitute a complex of small wetlands and lagoons. They have been listed in previous Costa Rican National Wetland Censuses: as Codes 826 and 827 in Windevoxhel et al. (1998) and as part of the Alta Talamanca Unit in Proyecto Humedales del SINAC-PNUD-GEF (2018b). However, only very condensed geographical location information is provided by those authors, offering no elaboration on other basic biotic and abiotic characteristics. In contrast, other wetlands in the same general area (Laguna Zoncho, Humedal Paraguas, Laguna El Campo, Laguna San Joaquín), albeit less biodiverse or in a more degraded condition, are described in greater detail by both Windevoxhel et al. (1998) and Proyecto Humedales del SINAC-PNUD-GEF (2018b), and for some of these, even very basic biotic inventories are provided by these authors. The relative lack of knowledge about the Valle Azul and Cañas Gordas wetlands could pose an additional risk factor for conserving *S. woodsonii* and other rare species. Despite documentation of some of the common taxa in these areas (Proyecto Humedales del SINAC-PNUD-GEF 2018a), a detailed list of their wetland flora was still lacking. It is important to note that this wetland is on the buffer zone of the UNESCO-declared Biosphere Reserve of La Amistad, recognized as part of a major global Center of Plant Diversity: the Costa Rica-Chocó Center, specifically in the Central Cordillera of Costa Rica and Panama Sub-center (Barthlott et al., 2005; Kappelle and Horn, 2016).

Discussion

Sarcoglottis woodsonii is easily distinguished from other species in the genus by its unique decumbent, elongated stems, which can reach lengths of up to 1.8 meters (including both rhizomes and aerial stems). In contrast, other *Sarcoglottis* species have stems and rhizomes with highly abbreviated internodes (the plants appear rosulate). Additionally, *S. woodsonii* produces uniformly long and slender roots (less than 5 mm in diameter) developed from the elongated internodes of the rhizome. The other species of this genus show thicker, succulent, fasciculate roots. Furthermore, the aerial stems of *S. woodsonii* exhibit leaves separated by very obvious, elongated internodes. This is unlike the very short internodes found in the stems of other species of *Sarcoglottis* (Salazar, 2003a).

The specimen *Cornman 2050* (determined as *Spiranthes woodsonii* by L. O. Williams in 1942 and cited as such by Allen, 1949) could not be determined with certainty by us because it consists of two incomplete plant fragments. One fragment includes the stem apex with two leaves and an inflorescence, while the other consists of only a single inflorescence. Since the specimen lacks stems and roots, we consider its affinities to *Sarcoglottis woodsonii* uncertain. While some characteristics, such as oblong leaves with elongated internodes, match *S. woodsonii*, disparities in the flowering date (February) and collection environment (in woods) exist when compared to our observations and protologue data. Conclusive identification would require a physical examination of the flowers, which was not possible at the time since we could only access a digital image of the specimen. Therefore, we have provisionally identified it as *S. woodsonii* based on L. O. Williams' identification (Allen, 1949).

Despite being described as a palustrine species in the protologue (Williams, 1946), this information has been overlooked due to the limited availability of data on *Sarcoglottis woodsonii*. This species is a truly aquatic orchid because of its shallowly submerged rhizomes and roots, and its microhabitat is restricted to grassy swamps with standing water. There is another known aquatic representative of the genus (*Sarcoglottis uliginosa* (Barb.Rodr.) Barb. Rodr.), which, according to Batista and Bianchetti (2010), can grow on water-saturated soils with water over the surface.

Our study contributes to a better understanding of orchid diversity in wetland ecosystems in the Neotropics and emphasizes the urgent need to inventory and conserve these unique habitats. Unfortunately, these areas are often unprotected, suffer from high human pressure, and are surrounded by fragmented landscapes.

Literature cited

Aburto-Oropeza, O., C. Manuel, E. Ezcurra, P. Ezcurra, C. L. Henriquez, S. E. Vanderplank, and F. Zapata. 2021. Relict inland mangrove ecosystem reveals Last Interglacial sea levels. Proc. Natl. Acad. Sci. U.S.A, 118(41): e2024518118. https://doi.org/10.1073/pnas.2024518118

Allen, P. H. 1949. Orchidaceae. Pages. 133–245 in R. E. Woodson, Jr. and R. W. Schery, editors, Flora of Panama. Part III, Fascicle 5. Ann. Missouri Bot. Gard. 36. http://dx.doi.org/10.2307/2394574

Arber, A. 1920. Water plants—A study of aquatic angiosperms. Cambridge University Press, Cambridge (U.K.).

Bachman, S., J. Moat, A. W. Hill, J. de la Torre, and B. Scott. 2011. Supporting Red List threat assessments with GeoCAT: geospatial conservation assessment tool. ZooKeys 150: 117–126. https://doi.org/10.3897/zookeys.150.2109

Barthlott, W., J. Mutke, D. Rafiqpoor, G. Kier, and H. Kreft. 2005. Global centers of vascular plant diversity. Nova Acta Leop. 92(342): 61–83.

Batista, J.A.N., and L. B. Bianchetti. 2010. Taxonomy, distribution and new taxa from the *Habenaria crucifera* (section *Nudae*, Orchidaceae) aggregate from Brazil and the Guianas. Brittonia 62: 57–79. http://www.jstor.org/stable/40793379

Batista, J., K. Proite, B. M. Carvalho, A. A. Vale, and L. P. Felix. 2014. From Cuba to most of the neotropic: *Habenaria bicornis* (Orchidaceae) is widespread from Mexico to southeastern Brazil. Lankesteriana 13(3): 165–184. https://doi.org/10.15517/lank.v13i3.14351

Bogarín, D., Z. Serracín, Z. Samudio, R. Rincón, and F. Pupulin. 2014. An updated checklist of the orchids of Panama. Lankesteriana 14(1): 135–364. https://doi.org/10.15517/lank.v14i3.17958

Chase, M. W., K. M. Cameron, J. V. Freudenstein, A. M. Pridgeon, G. Salazar, C. van den Berg, and A. Schuiteman. 2015 An updated classification of Orchidaceae, Bot. J. Linn. Soc. 177(2): 151–174.

Chocce, M., J. P. Janovec and E. A. Christenson. 2004. A synopsis of the genus *Otostylis* (Orchidaceae: Maxillarieae subtribe Zygopetalinae) with a new record from southern Peru. Sida 21(2): 841–852.

Cook, C. D. K., B. J. Gut, E. M. Rix, J. Schneller, and M. Seitz. 1974. *Water Plants of the World*. Dr. J. W. Junk b.v. Publishers, The Hague.

Damián, A., N. Mitidieri, M. Bonilla, and J. Tapara Huayllani. 2021. A new species, lectotypification and new records in *Catasetum* (Orchidaceae: Catasetinae) from Peruvian Amazon. Bot. Lett. 168(2): 191–199. https://doi.org/10.1080/23818107.2020.1871404

den Hartog, C., and S. Segal. 1964. A new classification of the water plant communities. Acta Bot. Neerl. 13: 367–393. https://doi.org/10.1111/j.1438-8677.1964.tb00163.x

Díaz-Morales, M., F. Pupulin, and S. Strigari. 2021. The new Refugium Botanicum: *Phragmipedium longifolium*. Orchids (West Palm Beach) 90(8): 586–589.

Dressler, R. L. 1981. *The orchids: natural history and classification*. Harvard University Press. Cambridge, Massachusetts.

———. 2003. Orchidaceae. In B. E. Hammel, M. H. Grayum, C. Herrera, and N. Zamora, editors, Manual de Plantas de Costa Rica Vol III Monocotiledóneas (Orchidaceae—Zingiberaceae). Monogr. Syst. Bot. Missouri Bot. Gard. 93: 1–595.

———. 2023. Orchidaceae. In C. Ulloa-Ulloa, H. M. Hernández, G. Davidse, F. Barrie, and S. Knapp, editors, *Flora Mesoamericana 7(2) Orchidaceae*. Universidad Nacional Autónoma de México, México D. F.

Dressler, R. L., M. Fernández, and F. Pupulin. 2014. *Sobralia abel-arayae*, a new and scarce species from Costa Rica. Orchid Digest 78(3): 146–148.

Dressler, R. L., D. W. Hall, K. D. Perkins, and N. H. Williams. 1991. *Identification Manual for Wetland Plant Species of Florida*. University of Florida, Gainesville.

Dunsterville, G. C. K., and E. Dunsterville. 1973. Orchids of Cerro Autana, Venezuela. Amer. Orch. Soc. Bull. 42(5): 388–401.

Dunsterville, G. C. K., and E. Dunsterville. 1976. *Bifrenaria maguirei*, *Zygosepalum tatei*, and *Otoglossum arminii*—Three fine orchids safe in Venezuela´s hinterland. Amer. Orch. Soc. Bull. 45(9): 783–787.

Dunsterville, G. C. K., and E. Dunsterville. 1982. Hunting *Phragmipedium klotzscheanum*—An agony of eight fits. Amer. Orch. Soc. Bull. 51(7): 709–712.

Ervin, G. N. 2023. *The biology of aquatic and wetland plants*. CRC Press, Taylor & Francis Group, Boca Raton, London, New York.

Hágsater, E., M. A. Soto Arenas, G. A. Salazar, R. Jiménez-Machorro, M. A. López Rosas, and R. L. Dressler. 2005. *Las orquídeas de México*. Instituto Chinoín México. México D. F.

Hawkes, D. D. 1953. An aquatic orchid. Orchid Journal 2(5): 203.

Horich, C .K. 1979. *Habenaria repens* Nutt.: eine authentische Wasserpflanze. Die Orchidee 30(4): 157–160.

Horich, C. K. 1983. Orquídeas acuáticas... un encuentro insólito!, Orquídeas (Asociación Costarricense de Orquideología) 2: 9–12.

Householder, E., J. Janovec, A. Balarezo, H. Maceda, J. Wells, and R. Valega. 2010. Diversity, natural history, and conservation of *Vanilla* (Orchidaceae) in amazonian wetlands of Madre de Dios, Peru. J. Bot. Res. Inst. Texas 4: 227–243. http://www.jstor.org/stable/41971995

IUCN. 2017. *Guidelines for using the IUCN red list categories and criteria, version 13*. Prepared by the Standards and Petitions Subcommittee of the IUCN Species Survival Commission. http://www.iucnredlist.org/documents/RedListGuidelines.pdf (accessed November 1, 2022, 18:30 GMT).

Jiménez, J. A. 2016. Bogs, marshes, and swamps of Costa Rica. Pages 683–709 in M. Kapelle, ed., *Costa Rican Ecosystems*. University of Chicago Press, Chicago and London.

Kahn, F., B. León, and K. R. Young. 1993. *Las plantas vasculares en las aguas continentales del Perú*. IFEA, Lima.

Kappelle, M., and S. P. Horn. 2016. The Paramo ecosystem of Costa Rica's highlands. Pages 492–523 in M. Kapelle, ed., *Costa Rican Ecosystems*. University of Chicago Press, Chicago and London.

Lasso, C. A., A. Rial, G. Colonnello, A. Machado-Allison, and F. Trujillo. 2014. *Humedales de la Orinoquia (Colombia-Venezuela). Serie Editorial Recursos Hidrobiológicos y Pesqueros Continentales de Colombia 11*. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH), Bogotá D. C.

Les, D. H. 2020. *Aquatic monocotyledons of North America. Ecology, life history and systematics*. CRC Press, Taylor & Francis Group, Boca Raton, London and New York.

Lot, A., R. Medina, and F. Chiang Cabrera. 2013. *Plantas acuáticas Mexicanas. Vol. 1. Monocotiledóneas*. Universidad Nacional Autónoma de México, México D. F.

Madriñán, S., A. Rial, A. M. Bedoya, and M. Fernández, M. 2017. *Plantas acuáticas de la Orinoquia colombiana*. Universidad de los Andes, Bogotá D. C.

McCartney, C. 1998. Florida's aquatic orchids. Palmetto 18(2): 20–23.

Mereles, F., J. E. Elsam, G. Céspedes, M. C. Peña-Chocarro, and R. D. Arrúa. 2015. Bryophyta, Pteridophyta, Angiospermae Monocotyledonae. Plantas Acuáticas y Palustres del Paraguay 1. Rojasiana Serie Especial 2(1): 1–236.

Mújica, E. B., J. J. Mably, S. M. Skarha, L. L. Corey, L. W. Richardson, M. W. Danaher, E. H. González and L. W. Zettler. 2018. A comparison of ghost orchid (*Dendrophylax lindenii*) habitats in Florida and Cuba, with particular reference to seedling recruitment and mycorrhizal fungi. Bot. J. Linn. Soc. 186: 572–586.

Pansarin, E. R., S. G. Augusto, and W. C. Ferreira. 2020. Resurrection of *Liparis inundata* (Orchidaceae). Phytotaxa 441 (3): 294–300.

Pérez-Escobar, O. A., A. Zizka, M. A. Bermúdez, A. S. Meseguer, F. L. Condamine, C. Hoorn, H. Hooghiemstra, Y. Pu, D. Bogarín, L. M. Boschman, R. T. Pennington, A. Antonelli, and G. Chomicki. 2022. The Andes through time: evolution and distribution of Andean floras. Trends Pl. Sci. 27 (4): 364–378. https://doi.org/10.1016/j.tplants.2021.09.010

Pott, V. J., and A. Pott. 2000. *Plantas Aquáticas do Pantanal*. EMBRAPA Centro de Pesquisa Agropecuária do Pantanal, Corumbá.

———. 2021. Chapter 4 Aquatic Plants. Pages 229–288 in G. A. Damasceno-Junior and A. Pott, editors, *Flora and Vegetation of the Pantanal Wetland*. Springer, Cham (Switzerland).

POWO. 2022. *Plants of the World Online*. Facilitated by the Royal Botanic Gardens, Kew. http://www.plantsoftheworldonline.org/ (accessed March 25, 2023, 19:00 GMT).

Proyecto Humedales del SINAC-PNUD-GEF. 2018a. *Guía de plantas comunes de los humedales del Área de Conservación La Amistad Pacífico—ACLAP, Costa Rica*. SINAC/PNUD/GEF, San José.

———. 2018b. *Inventario Nacional de Humedales*. SINAC/PNUD/GEF, San José.

Pupulin, F., D. Bogarín, and A.P. Karremans. 2023. The Lankester Catalogue of Costa Rican Orchidaceae. Lankesteriana: International Journal on Orchidology, 23(Supplement): 1–254. https://doi.org/10.15517/lank.v23iSupplement.58145

Pupulin, F., and C. Ossenbach. 2016. *Macradenia* (Orchidaceae): a confirmed genus for Costa Rican Flora. Lankesteriana 3: 15–17. https://doi.org/10.15517/lank.v2i1.23138

Ramsar Convention. 1971. *Convention on Wetlands of International Importance especially as Waterfowl Habitat*. Ramsar, Iran.

Rolfe, R. A. 1901. *Habenaria repens* Nutt. Icon. Pl. 27(4): pl. 2686.

Salazar, G. A. 2003a. *Sarcoglottis*. Pages 246–250 in A. M. Pridgeon, P. J. Cribb, M. W. Chase, and F. N. Rasmussen, eds., *Genera Orchidacearum 3: Orchidoideae (Part Two), Vanilloideae*. Oxford University Press, Oxford and New York.

Salazar, G. A. 2003b. *Spiranthes*. Pages 258–266 in A. M. Pridgeon, P. J. Cribb, M. W. Chase, and F. N. Rasmussen, editors, *Genera Orchidacearum 3: Orchidoideae (Part Two), Vanilloideae*. Oxford University Press, Oxford and New York.

Salazar, G. A., J. A. N. Batista, L. I. Cabrera, C. van Den Berg, W. M. Whitten, E. C. Smidt, C. R. Buzatto, R. B. Singer, G. Gerlach, R. Jiménez-Machorro, J. A. Radins, I. S. Insaurralde, L. R. S. Guimarães, F. de Barros, F. Tobar, J. L. Linares, E. Mújica, R. L. Dressler, M. A. Blanco, E. Hágsater, and M. W. Chase. 2018. Phylogenetic systematics of subtribe Spiranthinae (Orchidaceae: Orchidoideae: Cranichideae) based on nuclear and plastid DNA sequences of a nearly complete generic sample. Bot. J. Linn. Soc. 186: 273–303. https://doi.org/10.1093/botlinnean/box096.

Salazar, G. A., F. Tobar, R. Jiménez-Machorro, E. Freire, and M. Peñafiel-Cevallos. 2019. *Sarcoglottis neillii* (Orchidaceae: Spiranthinae), a new species from the Andean Tepui Region of Ecuador and Peru. Phytotaxa 427: 1–8. https://doi.org/10.11646/phytotaxa.427.1.1

Sculthorpe, C. D. 1967. *The biology of aquatic vascular plants*. Edward Arnold, London.

Stevens, P. (2001 onward). *Angiosperm Phylogeny Website*. Version 14, July 2017 [continuously updated since]. https://www.mobot.org/MOBOT/research/APweb/ (accessed October 20, 2023, 20:00 GMT).

Thiers, B. 2023. *Index Herbariorum, A global directory of public herbaria and associated staff*. New York Botanical Garden., New York. http://sweetgum.nybg.org/science/ih/ (accessed March 25, 2023, 19:00 GMT).

Tosi, J. A. 1969. *Mapa ecológico, República de Costa Rica: según la clasificación de zonas de vida del mundo de L. R. Holdridge*. Instituto Geográfico Nacional, San José.

Ulloa-Ulloa, C., P. Acevedo-Rodríguez, S. Beck, M. J. Belgrano, R. Bernal, P. E. Berry, L. Brako, M. Celis, G. Davidse, R. C. Forzza, S. R. Gradstein, O. Hokche, B. León, S. León-Yánez, R. E. Magill, D. A. Neill, M. Nee, P. H. Raven, H. Stimmel, M. T. Strong, J. L. Villaseñor, J. L. Zarucchi, F. O. Zuloaga, and P. M. Jørgensen. 2017. An integrated assessment of the vascular plant species of the Americas. Science 358: 1614–1617. https://doi.org/10.1126/science.aao0398

Veas-Ayala, N., M. Alfaro-Córdoba, and A. Quesada-Román. 2022. Costa Rican wetlands vulnerability index. Progress in Physical Geography: Earth and Environment 47(4): 521–540. https://doi.org/10.1177/03091333221134189

Velásquez, J. 1994. *Plantas acuáticas vasculares de Venezuela*. Universidad Central de Venezuela, Caracas.

Vermeulen, J. J. and H. Tsukaya. 2011. An assumed rheophytic orchid: *Bulbophyllum rheophyton* n.sp., from Borneo. Plant. Syst. Evol. 293: 71–73.

Williams, L. O. 1946. Orchidaceae [pro parte]. Pages 1–140 in R. E. Woodson, Jr. and R. W. Schery, eds., Flora of Panama. Part III, Fascicle 2. Ann. Missouri Bot. Gard. 33(1). https://doi.org/10.2307/2394519

Windevoxhel, N. J., R. Córdoba Muñoz, and J. C. Romero Araya. 1998. *Inventario de los humedales de Costa Rica*. SINAC/MINAE/Embajada de los Países Bajos/UICN, San José.

Woodson, R. E., Jr., and R. W. Schery. 1942. Contributions toward a Flora of Panama. VI. Collections Chiefly by Von Wendel in Bocas Del Toro. Ann. Missouri Bot. Gard. 29(4): 317–379. https://doi.org/10.2307/2394325

Page 34 intentionally left blank.

MENONVILLEA LINEARIFOLIA (BRASICACEAE), A NEW COMBINATION FOR A CHILEAN ENDEMIC

Ihsan A. Al-Shehbaz[1,2] and Diego L. Salariato[3]

Abstract. The long-overlooked, Chilean-endemic *Cremolobus linearifolius* turned out to be a species of *Menonvillea* synonymous with the much-later published *M. minima*. The new combination *M. linearifolia* is proposed, and a lectotype is designated for it.

Keywords: Brassicaceae, Chile, *Cremolobus*, Cruciferae, *Menonvillea*

During work with Dr. Dmitry A. German (ALTB) to determine the most accurate number of accepted species and infraspecific taxa in the Brassicaceae, the status of one species, *Cremolobus linearifolius* Hook. & Arn., came into question. The name was not recognized by all botanists who dealt with the South American members of the family, including Rollins (1955) and Khanna and Rollins (1965), who revised the genera *Menonvillea* DC. and *Cremolobus* DC., respectively. Khanna and Rollins excluded the species from *Cremolobus* based on their observation of a photo of one type collection sheet (*Cuming 905* at GL and now permanently housed at E) and indicated that the fruiting specimens lacked the fruit valves and suggested that the plants belong to *Menonvillea* rather than *Cremolobus*. However, their fruit observation was made on *Bridges 1283* mounted on the same sheet of the above type. They indicated that *C. linearifolius* is affiliated with *M. gayi* Phil. or *M. chilensis* (Turcz.) Jackson. In fact, Hooker and Arnott (1833: 138) provided an adequate description of the fruit by stating "…siliculae lobis subglobosis rugosis immarginatis, stylo thecaphorum aequante." and that "It differs from *Cremolobus* by the turgid lobes of the silicle, which are quite destitute of margin, and it may perhaps form the type of a new genus." Furthermore, Al-Shehbaz (2008) did not deal with the species in his account of the Brassicaceae catalogue of the Southern Cone (Argentina and Chile), though late in the following year (28 September 2009) he annotated both sheets of *Cuming 905* as *M. minima* Rollins. More recently, Salariato et al. (2014) recognized *M. minima*, but nothing was said on *C. linearifolius* due to oversight by one of us (IAS).

In order to use the acceptable name in two manuscripts submitted by the authors for publication, the status of *Cremolobus linearifolius* vs. *Menonvillea minima*, two binomials published 132 years apart, has to be resolved, and there are two alternatives The first is to submit a proposal to reject the first name *C. linearifolius*. In order to do so, a rejection proposal has to be published in Taxon, then accepted by the Committee on Spermatophytes, which is highly unlikely because *M. minima* is dealt with taxonomically only in Rollins (1955) and Khanna and Rollins (1965). Should the rejection proposal pass, it is almost certain that it will miss being included in the program of the Nomenclature Section and approved by it and the XX International Botanical Congress in Madrid in July 2024. Otherwise, it has to wait until the XXI Botanical Congress in ca. 2030. The second alternative is to transfer *C. linearifolius* to *Menonvillea* and reduce the later-published *M. minima* to synonymy, as in the following new combination. This will facilitate the use of *M. linearifolia* immediately, an alternative which we strongly prefer.

Menonvillea linearifolia (Hook. & Arn.) Al-Shehbaz & Salariato, *comb. nov.*

Basionym: *Cremolobus linearifolius* Hook. & Arn., Bot. Misc. 3: 138. 1833.

TYPE: CHILE. [Región de Coquimbo [Región IV]: Coquimbo, *H. Cuming 905*. Lectotype, here designated: E [00298966]; Isolectotype: E [00298967].

Heterotypic synonym: *Menonvillea minima* Rollins, Contr. Gray Herb. 177: 52. 1955, *syn. nov.* TYPE: CHILE. Región de Atacama [Región III]:, Prov. Huasco, Huasco, September 1885, *F. Philippi 1848,* Lectotype, designated by Salariato et al. (2014: 281): SGO [77941]; Isolectotypes: G, SGO [77940].

Literature Cited

Al-Shehbaz, I. A. 2008. Brassicaceae. Pages 1663–1709 in F. O. Zuloaga, O. Morrone, and M. J. Belgrano, eds., Catálogo de las Plantas Vasculares del Cono Sur. Vol. 2. Missouri Botanical Garden Press.

Hooker, W. J., and G. A. W. Arnott. 1833. Contributions towards a flora of South America and the islands of the Pacific. Bot. Misc.3: 129–211.

Khanna, K. R., and R. C. Rollins. 1965. A taxonomic revision of *Cremolobus* (Cruciferae). Contrib. Gray Herb. 195: 135–157.

Rollins, R. C. 1955. A revisionary study of the genus *Menonvillea* (Cruciferae). Contr. Gray Herb. 177: 3–57.

Salariato, D. L., F. O. Zuloaga, and I. A. Al-Shehbaz. 2014. A revision of the genus *Menonvillea* (Brassicaceae). Phytotaxa 162(5): 241–298.

We are grateful to the herbarium curatorial staff of the Royal Botanic Garden Edinburgh for sending images of the type collection of *Cremolobus linearifolius*.

[1] Missouri Botanical Garden, 4344 Shaw Boulevard, St. Louis, Missouri 63110, U.S.A.

[2] Corresponding author: Ihsan.Al-Shehbaz@mobot.org

[3] Instituto de Botánica Darwinion (CONICET-ANCEFN), Labardén 200, Casilla de Correo 22, B1642HYD San Isidro, Buenos Aires, Argentina

Harvard Papers in Botany, Vol. 29, No. 1, 2024, p. 35.

ISSN: 1938-2944, DOI: 10.3100/hpib.v29iss1.2024.n3, Published online: 30 June 2024

Page 36 intentionally left blank.

A NEW SPECIES OF *DOLIOCARPUS* (DILLENIACEAE, DOLIOCARPOIDEAE) FROM THE AMAZON FORESTS AND AN UPDATED KEY FOR THE COLOMBIAN SPECIES

Gerardo A. Aymard-Corredor[1,2] and João Victor Longhi Monzoli[3]

Abstract. *Doliocarpus daironii,* an endemic species to the Colombian Amazon forests, is described and increases to 25 the number of species of the genus recorded from this country. This new species shows certain similarities with *D. amazonicus, D. duckeanus*, and *D. guianensis*. Nonetheless, *D. daironii* is more related to *D. guianensis,* but differs from the latter in its branches, branchlets, leaves, inflorescence rachis, bracteole and sepal pubescence, leaf shape, and petiole and inflorescence size. A detailed description, comparisons with similar species, an illustration, and comments on its etymology, distribution, habitat, conservation status, and morphology are provided. Additionally, an updated key to the species of *Doliocarpus* of Colombia is also presented, and a previously described subspecies from Brazil is elevated to the rank of species (i.e., *Doliocarpus amazonicus* subsp. *duckeanus* to *D. duckeanus*).

Keywords: Flora of Colombia, Amazon forests, Vaupés, Taraira, Dilleniaceae, *Doliocarpus*, Colombia

Resumen. Se describe *Doliocarpus daironii*, una especie endémica de los bosques de la Amazonía colombiana, incrementando en 25 el número de especies para esta país. Está nueva especie posee cierta similitud con *D. amazonicus*, *D. duckeanus*, y *D. guianensis*. No obstante, *D. daironii* está más relacionada con *D. guianensis*, sin embargo difiere en la pubescencia de las ramas, ramitas, hojas, ráquis de las inflorescencias, bractéolas, sépalos, forma de las hojas y en el tamaño de los pecíolos e inflorescencias. Se incluye una descripcion detallada, información acerca de la morfología, comparaciones con las especies similares, una ilustración, comentarios acerca de la etimología, distribución, hábitat e informacion del estado actual de conservación. Se presenta una clave actualizada de las especies del género *Doliocarpus* para Colombia y se eleva una subespecie descrita de Brasil al rango de especie (i.e., *Doliocarpus amazonicus* subsp. *duckeanus* a *D. duckeanus*).

Palabras clave: Flora de Colombia, Bosques amazónicos, Vaupés, Taraira, Dilleniaceae, *Doliocarpus*, Colombia

The pantropical family Dilleniaceae, with 11 genera and ca. 500 species, is notably diverse in the Neotropics, where more than one fifth of these taxa are found (Fraga and Stehmann, 2010; Aymard and Kelloff, 2016; Aymard, 2020; Aymard and Todzia, 2024), with representatives extending into the tropical Old World and temperate Australia (Horn, 2006, 2009). The infra classification of the family has changed over the last decade from the results of several phylogenetic analyses (Horn, 2009; Fraga, 2012) and morphological data. As a consequence, four subfamilies have been recognized (*Delimoideae* Burnett, *Dillenioideae* Burnett, *Doliocarpoideae* J.W. Horn, and *Hibbertioideae* J.W. Horn, see Horn, 2006, 2009), and the genus *Neodillenia* Aymard was phylogenetically recognized by Fraga (2012). These works also confirm that *Doliocarpus* Rol. is a monophyletic genus (Horn, 2009; Fraga, 2012).

Doliocarpoideae includes six genera endemic to the Neotropical region (Horn, 2006, 2009; Fraga, 2012): *Curatella* Loefl., *Davilla* Vand., *Neodillenia* Aymard, *Pinzona* Mart & Zucc., and *Doliocarpus* Rol., which is the most diverse. The latter genus includes about 50 species distributed throughout southern Mexico, Central America, the Antilles, the Guianas, Venezuela, Colombia, Ecuador, Peru, Bolivia, Brazil, and Paraguay (Fraga and Paula-Souza, 2015; Aymard and Kelloff, 2016; Aymard, 2020; Monzoli et al., 2022).

Within the family, this genus is defined by its lianas (rarely erect or scandent shrubs), its racemose, fasciculate, or glomerate ramiflorous inflorescences, a unicarpellate, 1-celled ovary, its fruit, a berry that sometimes opens irregularly, and seeds that are completely covered by a white aril (Kubitzki, 1971). *Doliocarpus* comprises two well-delimited sections, based on the monograph by Kubitzki (1971). Most of the species belong to *Doliocarpus* sect. *Calinea* (Aubl.) Eichler and are characterized by having leaves with subparallel (rarely reticulate) tertiary nerves, erect, flexuose filaments with introrse anthers at anthesis, and a glabrous or pilose ovary. In contrast, the species of *Doliocarpus* sect. *Doliocarpus* Kubitzki have

The first author is grateful to the staff of "Instituto Amazónico de Investigaciones Científicas" (SINCHI), in particular, the late D. Cárdenas-López for his support and help for more than a decade in Herbario Amazónico Colombiano (COAH). The second author is grateful to CNPq for the scholarship 200335/2023-5 that made it possible to consult type specimens in Europe, due to the partnership between the REFLORA Program and the Natural History Museum of Vienna. The second author would also like to thank the International Association for Plant Taxonomy (IAPT) for a Research Grant in 2023. The authors thank N. Castaño Arboleda, W. Rodríguez, J. M. Vélez, and P. Gallego for their assistance at COAH, and G. A. Romero for his assistance at GH. The authors are also grateful to M. Sánchez for preparing the illustration. This work would not be possible without the International Plant Names Index (https://www.ipni.org/), JSTOR Global Plants (https://plants.jstor.org/), and Tropicos (http://legacy.tropicos.org/Home.aspx).

[1] UNELLEZ-Guanare, Programa de Ciencias del Agro y el Mar, Herbario Universitario (PORT), Mesa de Cavacas, estado Portuguesa 3350, Venezuela; Compensation International Progress S.A. – Ciprogress Greenlife, Bogotá, D.C., Colombia; Jardín Botánico de Bogotá José Celestino Mutis, Calle 63 #68–95, Bogotá, D.C., Colombia
[2] Corresponding author: cuyuni24@hotmail.com
[3] Universidade Estadual Paulista "Júlio de Mesquita Filho," Instituto de Biociências, Letras e Ciências Exatas, Rua Cristovão Colombo 2265, Jardim Nazareth, 15054-000, São José do Rio Preto, SP, Brazil

Harvard Papers in Botany, Vol. 29, No. 1, 2024, pp. 37–44.

ISSN: 1938-2944, DOI: 10.3100/hpib.v29iss1.2024.n4, Published online: 30 June 2024

leaves with reticulate tertiary nerves, reflexed filaments with extrorse anthers at anthesis, and a pilose (rarely glabrous) ovary. Although the stamen character (filaments at anthesis) represents a reliable morphological feature when assigning specimens of *Doliocarpus* to these two sections, most specimens do not have flowers at anthesis, or have flowers lacking petals, many having instead young fruit with persistent sepals and stamens. Leaf venation, therefore, is perhaps the most valuable character to define the two sections of this genus (Aymard, 2017, 2020).

This contribution increases the number of species of Doliocarpus known from Colombia to twenty-five, six of which are endemic (*D. chocoensis* Aymard, *D. daironii* Aymard, *D. lopez-palacii* Aymard, *D. putumayensis* Aymard, *D. schultesianus* Aymard, and *D. triananus* Aymard). An updated key for all species of Doliocarpus from Colombia is provided. The new species was identified by Dairon Cárdenas-López† based on a misidentified collection stored in COAH.

Materials and methods

We consulted the original protologues of other species of the genus included in the latest monograph of *Doliocarpus* (Kubitzki, 1971) and those of several new species described from Colombia after the latter monograph (Aymard, 1991, 1993, 1997, 2007, 2017). The available Dilleniaceae treatments were also reviewed: “Sinopsis y adiciones a las Dilleniaceae del Perú” (Aymard and Miller, 1994), Flora of Venezuela Guayana (Aymard, 1998), Flora of the Guianas (Aymard and Kelloff, 2016), and Flora of Ecuador (Aymard, 2020). Dilleniaceae checklists were also reviewed: “Nuevo Catálogo de la Flora de Venezuela” (Aymard, 2008),“Lista de Especies da Flora do Brasil” (Fraga and Paula-Souza, 2015), and “Catálogo de Plantas y Líquenes de Colombia” (Aymard, 2016).

We analyzed specimens either from online botanical collections or in person: B, COAH, COL, F, G, GH, K, M, NY, P, PORT, US, and W (herbarium acronyms after Thiers, 2023). Additionally, the type specimens of species of *Doliocarpus* were examined in person or using online images from JSTOR Global Plants (https:// plants.jstor. org/). The latter is a useful tool because it focuses on type collections and allowed us to be confident that the new species had contrasting features from the known species of *Doliocarpus*.

A 1:1 solution of glycerin and physiological solution was used over three days to hydrate and soften the dried flowers.

The specific terminology for vegetative characters, vestiture description, inflorescences, and flower and fruit morphology used in the description and taxonomic key follows Kubitzki (1971), Font-Quer (2001), and Harris and Harris (2006).

Conservation status [extent of occurrence (EOO) and area of occupancy (AOO)] proposed in IUCN categories and criteria (IUCN 2022) were not calculated because this new species is known only from the type specimen (see discussion in conservation status).

Taxonomy

Doliocarpus daironii Aymard & Monzoli, *sp. nov.*
TYPE: COLOMBIA. Vaupés: Município de Taraira, Estación Biológica Caparú (Mosiro-Itajura), 3 km North of Lago Taraira, bosque sobre terraza, 1˚00'S; 69˚49'W, 200 m, 23 March 1990, *Sara Defler 1150* (Holotype: COAH [017039]). Fig. 1.

Doliocarpus daironii has certain similarities to *D. amazonicus* Sleumer, *D. duckeanus* (Kubitzki) Aymard & Monzoli, and *D. guianensis* (Aubl.) Gilg. This new species is most similar to the latter, but differs in its branches and branchlets with adpressed yellow pubescence; oblong or oblong-elliptic leaves with a rounded base, a rounded to emarginate apex, blades that are shiny and lead-colored on the adaxial surface, dull brown on the abaxial surface, glabrous, except along the midrib and the secondary nerves, where they are covered with erect and adpressed golden-yellow trichomes, and a slightly crenate margin mostly in the upper half; petiole 1–2 cm long with adpressed yellow pubescence; inflorescence 0.5–0.6 cm long, 1- to 3-flowered, rachis with dense, white adpressed pubescence, ovate bracteoles, sepals with sparse, adpressed pubescence abaxially, sericeous adaxially, more densely on the midrib.

Liana, branches and branchlets sulcate, adpressed yellow pubescent, glabrescent when mature, bark flaking off when mature. *Leaves* coriaceous, oblong or oblong-elliptic, 9–14 × 5–8 cm, base rounded, apex rounded to emarginate, blade glabrous, lead-colored and shiny on the adaxial surface, dull and brown on the abaxial surface, glabrous on the abaxial surface, except along the sulcate midrib and the secondary nerves, that are covered with erect and adpressed golden-yellow trichomes, margin slightly revolute, entire on the lower half, crenate mostly on the upper half, lateral nerves 7–11, linking ca. 1 mm close to the margin, elevated on the abaxial surface, tertiary venation subparallel, evident on both surfaces; petiole stout at the base, 1–2 cm long, 1–2 mm wide, subwinged on the upper half, canaliculate, adpressed yellow pubescent. *Inflorescence* ramiflorous, racemose, 5–6 mm long, 1- to 3-flowered, rachis with dense, white adpressed pubescence, bracteoles 1, ovate, 1–2 × 1.0–1.5 mm, situated at the base of the pedicel, pubescence like the inflorescence rachis on both surfaces. *Flowers* pedicelate, pedicel ca. 1 mm long, pubescence like the inflorescence rachis; sepals 5, subequal, wide-ovate, external 2, ca. 2.5 × ca. 2.0 mm, internal 3, ca. 3.5 × ca. 3.0 mm, sparse, adpressed pubescence externally, sericeous internally, more dense on the midrib; petals not seen; stamens 55–60, filaments cylindrical 3.0–3.3 mm long, glabrous, anthers oblong, ca. 0.5 mm long, glabrous; ovary globose, sulcate, ca. 1.5 × 1.5 mm, glabrous, pistil ca. 1 mm long, glabrous, stigma flattened to rotate, ca. 1 mm diam., glabrous. *Fruit* not seen.

Phenology: Known only from mature flower in March.

Eponymy: This species is named in honor of Dairon Cárdenas-López (1957–2022), a prominent Colombian botanist from Instituto Amazónico de Investigaciones

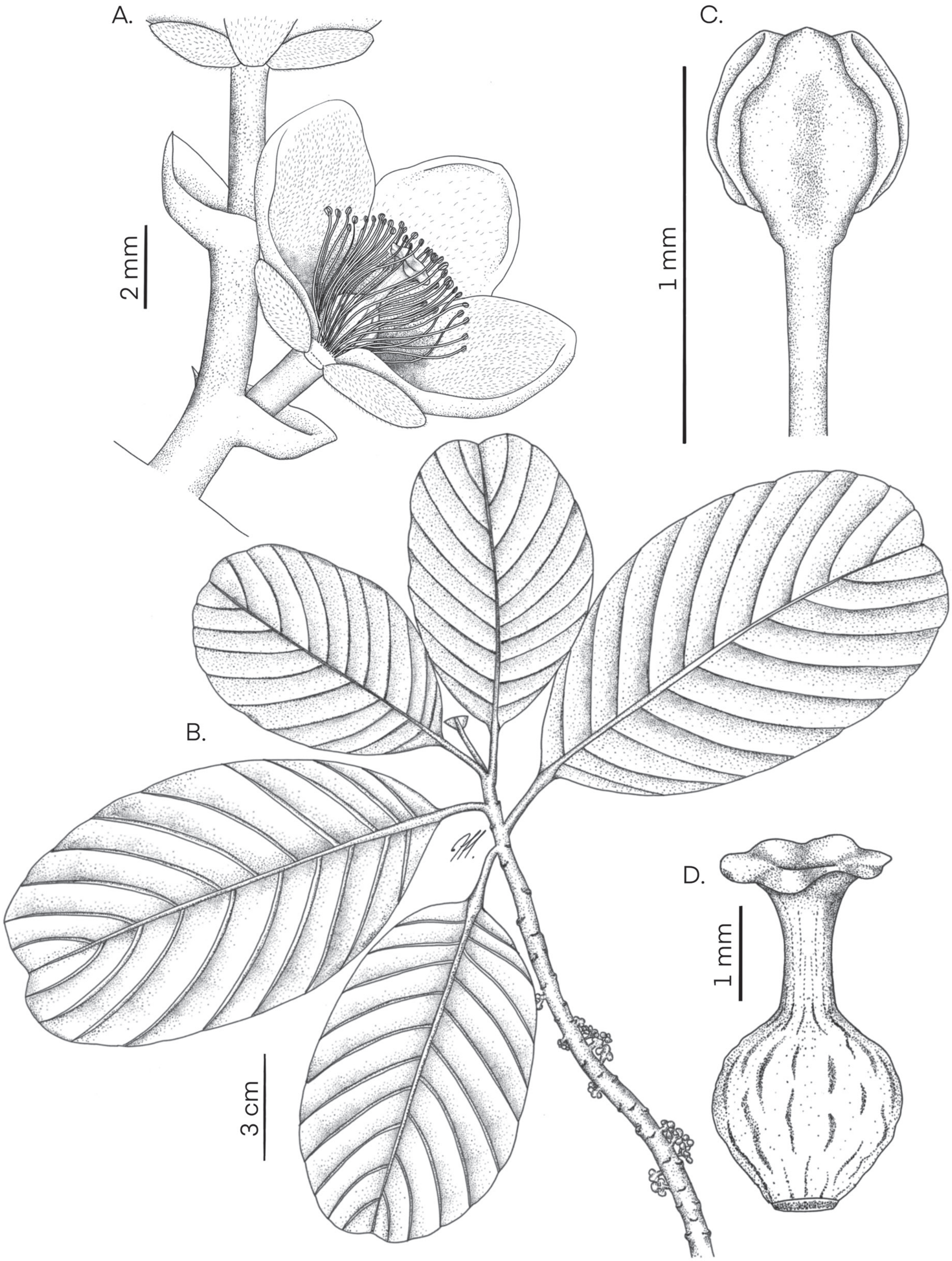


FIGURE 1. FIGURE 1. *Doliocarpus daironii* Aymard & Monzoli. **A**, Lateral view of a portion of inflorescence showing the flower and bracteole; **B**, Habit showing the branch and leaves; **C**, Frontal view of the anther showing the broadened connective; **D**, Carpel. Drawn by M. Sánchez based on the holotype.

Científicas (SINCHI). He was an expert in the Amazonian flora and worked tirelessly for more than three decades in the herbarium COAH in order to better understand the flora and vegetation of the Amazon basin. His great spirit of collaboration and his work ethic inspired generations of young Colombian botanists and numerous national and foreign colleagues to continue researching in the fascinating world of tropical vegetation. He holds the distinction of having collected more specimens (> 54,000) than any other Colombian plant collector, to date.

Distribution and ecology: This species is known only from the type locality near Lake Taraira, a region on terraces that originated in the Pleistocene. The area is an ancient meander of the lower Apaporis River basin, located in the southeast of Vaupés department (Defler, 1999), harbors a diverse flora (Clavijo, 2006; Clavijo et al., 2009; Cárdenas-López et al., 2010), with several endemic taxa of the Amazonian Colombia such as *Duguetia vaupesana* Westra & Maas (Annonaceae) and *Costus fissicalyx* N.P. Salinas, Clavijo & Betancur (Costaceae). The Caparú Biological Station, also known as Mosiro-Itajura, is located in this area, and is where important research on monkey behavior and diets has been done (Defler and Defler, 1996; Clavijo, 2006; Defler, 2010; González et al., 2016).

Doliocarpus daironii was collected in "bosques de terraza," which is a type of non-flooded wet forest found in the north/northwestern portion of the Amazonia region (i.e., Rio Negro basin; for a review see Arellano-Peña et al., 2023). In general, these communities have trees 30–40 m tall, a dense understory, and are dominated by *Oenocarpus bataua* Mart. (Arecaceae) and *Micrandra spruceana* (Baill.) R.E. Schult. (Euphorbiaceae) (Mantilla-Meluk & Barrios-Rodríguez, 1999; Clavijo et al., 2009). However, this new species probably has a wider distribution in the moist forests located in this portion of the northwestern Amazon region, an area not sufficiently explored botanically.

Conservation status: This new species is so far only known from the type locality, and, under IUCN (2022) guidelines, a taxon with one or two localities would indicate that its conservation status should be categorized as deficient data (DD). Additional information and research may eventually reveal that this species should be placed under the threatened classification (IUCN, 2022). Nevertheless, it should be regarded as Endangered due the gold mining exploitation in the last four decades in the ecosystems located in the lower Apaporis and Tairara river basins (for a review see Rubiano Galvis, 2014). The good news is that the type locality is part of Parque N. N. Yaigojé Apaporis, a region that is protected by the Colombian National Park Service (Parques Nacionales Naturales de Colombia).

Because its leaves have subparallel tertiary venation without verrucosities, *Doliocarpus daironii* belongs in section *Calinea* (Kubitzki, 1971). By its racemose inflorescence and glabrous carpel, this new species is morphologically related to three other taxa in section *Calinea: D. amazonicus* Sleumer, *D. duckeanus* (Kubitzki) Aymard & Monzoli, and *D. guianensis*. Nonetheless, *D. daironii* differs from these three species in the characters presented in Table 1 and in the *Doliocarpus* key of Colombian species below.

Doliocarpus duckeanus (Kubitzki) Aymard & Monzoli, comb. et stat. nov. Fig. 2.

Basionym: *Doliocarpus amazonicus* Sleumer subsp. *duckeanus* Kubitzki, Mitt. Bot. Staatssamml. München 9: 38–39. 1971. TYPE: BRAZIL. Amazonas: Manaus, loco estrada do Aleixo, 25 May 1937, *W. A. Ducke 501* (holotype: F [902226], isotypes: A [53239], K [220358], MG [195579], MO [279575], NY [428736], R [75375], RB [542269; 538306], US [110013], S [08-21383]), SP [598].

Taxonomic history: *Doliocarpus amazonicus* subsp. *duckeanus* was described as a new subspecies in a revision of *Doliocarpus* (Kubitzki 1971). However, the examination of the original protologues, the type specimens, and numerous additional material in person and of several online botany collections (i.e., Specieslink.net/search [https://specieslink.net/search/index]; JSTOR Global Plants [https:// plants.jstor.org/]; GBIF [https://www.gbif.org/species/search]) indicates that it should be treated as a separate species that can be distinguished from *D. amazonicus* by the characters discussed in Table 1 and in the following key to the species of *Doliocarpus*.

Additional specimens examined: BRAZIL. **Amapá:** Macapá. Margem do rio Dois Irmãos, a 12 km de Cupixi, proximo a rodovia Perimetrel Norte, *W. A. Ducke 327* (NY). **Amazonas:** Presidente Figueiredo, Estrada do Canteiro de obras da Usina Hidrelétrica de Balbina, *C. A. Cid F. 7611* (INPA, NY); km 115 de la Rondovia Manaus-Caracaraí, 01°58'S, 60°02'W, 200 m, *O. Huber & L. O. Adão T. 10694* (NY); Km 130 Manaus-Caracaraí road, *G. T. Prance et al. 20355* (INPA, NY); Vicinity of Manaus, Cachoeira Baixa Tarumã, *G. T. Prance et al. 11615*, *11616* (INPA, M, NY, US); Vicinity of Manaus, Cachoeira Alta Tarumã, *W. A. Rodrigues & J. Chagas 8803* (INPA, M); Vicinity of Manaus, Parque 10 de Nov., *J. Chagas 3832* (INPA, M); 3 km ao Sul da parte central da Serra Aracá; 08 km à Leste do rio Jauari, *W. A. Rodrigues IL4-1* (INPA, NY); Manaus-Caracaraí Highway, forest at km 130, *W. C. Steward et al. 20355* (NY); Km 45, Manaus, -2.73644 S, -59.817968 W, *W. A. Rodrigues 2358* (INPA); Manaus, Comunidade do Novo Amanhecer, Campina, -2.856294 S, -60.232914 W, *J. V. L. Monzoli & J. A. Vieira 553, 555, 557* (SJRP); Manaus-Itacoatiara, km 26, Reserva Florestal Adolfo Ducke, -2.88333333 S, -59.96666667 W, *C. A. Sothers 901* (INPA, US); Rio Cuieiras, -2.48 S, -60.28 W, *W. A. Rodrigues 1635* (INPA); Manaus, margem do igarapé da Cachoeira do Tarumã, -3.10193991661072 S, 60.0250015258789 W, *F. N. Chagas 21805* (IAN); Rio Uaupés São Gabriel da Cachoeira, 0.09672 N, -67.33163 W, *F. A. Carvalho 1497* (INPA); Uatumã, São Sebastião do Uatumã, -2.19194444 S, -59.21833333 W, *L. O. Demarchi1260* (INPA); Presidente Figueiredo, Igarapé das Lajes, -1.98889 N, -60.0275 W, *M. H. Terra-Araujo 482* (INPA); Presidente Figueiredo, BR 174, km 120, Fazenda Agroindustrial Chibata, -1.939596 S, -60.03 W, *C. A. C. Ferreira 11013* (INPA); Along Manaus-Caracaraí Road (BR-174), km 115, campina adjacent to Igarapé Lajes, *J. L. Zarucchi et al. 2573* (US). **Pará:** Santana do Araguaia, 100 km S of Redenção on road to Barreiras dos Campos, between Rio Inajazinho and Rio Inajá, 08°45'S; 50°25'W, 210 m, *T. Plowman et al. 8868* (GH, US).

TABLE 1. Comparison of diagnostic morphological characters of *Doliocarpus daironii* Aymard & Monzoli and closely related species.

CHARACTER	*D. AMAZONICUS*	*D. DAIRONII*	*D. DUCKEANUS*	*D. GUIANENSIS*
Branches and branchlets	adpressed white pilose, glabrescent when mature	adpressed yellow pubescent	densely ferrugineuos-tomentose	laxly white pilose to glabrescent when mature
Leaves	obovate-oblong, base acute, apex wide rotundate, or acute (short acuminate), blades shiny and glabrous (pilosule along the midrib and secondary veins) on the upper surface, adpressed pilose at the lower surface, margins serrate to crenate, mostly in the upper half	oblong or oblong-elliptic, base rounded, apex rounded to emarginate, blades shiny on the upper surface, glabrous on both sides, except along the midrib and the secondary nerves on the lower surface, where they are covered by erect and adpressed golden-yellow trichomes, margins slightly crenate mostly in the upper half	oblanceolate-elliptic, base, acute, apex acute to rounded, blades dull and glabrous (shorty ferrugineous-tomentose along the midrib and secondary veins) on the upper surface, densely shorty ferrugineous-tomentose on the lower surface, more evident along the midrib and secondary nerves, margins crenate-dentate mostly in the upper half	obovate-oblong, base cuneate, apex rounded, obtuse-apiculate, the blades dull on the upper surface, completely glabrous on both sides, margins slightly sinuate mostly in the upper half
Petiole	ca. 0.8–9 cm long, shortly white pubescent to glabrescent when mature	1–2 cm long, adpressed yellow pubescent	1–1.5 cm long, shorty ferrugineous-tomentose	0.5–1 cm long, laxe white pilose
Inflorescence	0.5–1cm long, 4-8-flowered, rachis yellow pubescent	0.5–0.6 cm long, 1-3-flowered, rachis white adpressed pubescent	0–0.4 cm long; 10-25-flowered, rachis ferrugineous-tomentose	1.5–4.5 cm long, 2–4-flowered, rachis laxe pilose
Sepals	obovate or elliptic, 2–4 mm long, puberulous externally, glabrous internally	wide-ovate, ca. 2.5 mm long, sparsely adpressed pubescent externally, sericeous internally	wide-ovate or obovate, ca. 2 mm long, shorty ferrugineous-tomentose externally, glabrous internally	obovate-oblong, 3–5 mm long, pilosule externally, glabrous internally
Stamens	ca. 35	55–60	ca. 35	ca. 60

AMENDED KEY TO THE SPECIES OF *DOLIOCARPUS* OF COLOMBIA

Modified from Aymard (2017); species indicated with an asterisk (*) are endemic to Colombia

1a. Leaves with reticulate tertiary venation with verrucosities on the abaxial surface 2
1b. Leaves with subparallel tertiary venation without verrucosities on the abaxial surface 4
2a. Lateral nerves terminating at the margin; sepals glabrous externally; fruit covered by trichomes 3–5 mm long . . . . . *D. olivaceus* (Antioquia, Chocó; San Andrés y Providencia)
2b. Lateral nerves arched and joined close to the margin; sepals adpressed pilose externally; fruit covered with trichomes 0.5–1.0 mm long 3
3a. Branches terete; leaves shiny on the adaxial surface, glabrous on the abaxial surface; margins entire to subsinuate . . . . . *D. nitidus* (Antioquia, Chocó, Cundinamarca, Huila, Tolima, Santander)
3b. Branches angulate; leaves dull on the adaxial surface, adpressed pubescent on the abaxial surface; margins sinuate to dentate mostly in the upper half. . . . . *D. major* (Amazonas, Antioquia, Caquetá, Chocó, Guaviare)
4a. Erect or scandent shrubs 5
4b. Woody lianas or vines 8
5a. Petioles glabrous; sepals appressed pubescent or lax pilose on the abaxial surface 6
5b. Petioles tomentose or appressed pilose; sepals glabrous to sparsely pilose or sericeous on the abaxial surface 7
6a. Leaves coriaceous, not conduplicate (in herbarium specimens), base attenuate, apex obtuse, rotundate or short acuminate, petiole stout, 3–5 mm wide; inflorescence not longer than 4 mm, pedicels 0–1 mm long. . . . . *D. leiophyllus* (Guianía, Vichada)
6b. Leaves rigid-coriaceous, always conduplicate, base acute, apex acuminate; petiole slender, ca. 1.5 mm wide; inflorescence 5–10 mm long, pedicels 2–4 mm long . . . . . *D. spraguei* (Vichada)
7a. Petioles not winged, 5–8 mm long; blades obovate-elliptic, 5–7 cm long, shiny and strongly reticulate on the adaxial surface; lateral nerves 5–7, pilose on the adaxial surface; sepals sericeous on the abaxial surface; fruit glabrous . . . . . *D. paucinervis* (Guianía)
7b. Petioles subwinged, 10–20 mm long; blades obovate, lanceolate-obovate, 7–20 cm long; dull and venation evident or inconspicuous on the adaxial surface; lateral nerves 9–14(16), glabrous on the adaxial surface; sepals glabrous to sparsely pilose on the abaxial surface, fruit sparsely pilose . . . . . *D. savannarum* (Caquetá, Guianía)

AMENDED KEY TO THE SPECIES OF *DOLIOCARPUS* OF COLOMBIA CONT.

Modified from Aymard (2017); species indicated with an asterisk (*) are endemic to Colombia

8a. Inflorescence sessile or 1–10 mm long 9
8b. Inflorescence longer than 12 mm 23
9a. Inflorescence racemose (peduncle with 2 to 6 flowers) 10
9b. Inflorescence (sub)sessile, fasciculate, or glomerulate, not racemose (peduncle with a single flower) 15
10a. Leaves conduplicate, rigid-coriaceous; margins in the upper half of the leaf blade entire . . . . . *D. spraguei* (Vichada)
10b. Leaves not conduplicate, subcoriaceous or coriaceous; margins dentate or sinuate mostly in the upper half 11
11a. Leaves obovate-oblong, oblong, oblong-elliptic or oblanceolate-elliptic 12
11b. Leaves obovate, lanceolate to elliptic 14
12a. Leaves 9–14 cm long; inflorescence 1- to 3-flowered; sepals with sparse, adpressed pubescence abaxially, sericeous adaxially; stamens 55–60 . . . . . *D. daironii** (Vaupés)
12b. Leaves 16–24 cm long; inflorescence 4- to 25-flowered; sepals puberulent to glabrescent or short ferrugineous tomentose abaxially, glabrous adaxially; stamens ca. 35 13
13a. Branches and branchlets adpressed white pilose, glabrescent when mature; leaves obovate-oblong, blades shiny and glabrous (pilosule along the midrib and secondary veins) on the adaxial surface, adpressed pilose on the abaxial surface; inflorescence 0.5–1.0 cm long, 4- to 8-flowered, rachis yellow pubescent . . . . . *D. amazonicus* (Amazonas)
13b. Branches and branchlets dense ferrugineuos tomentose; leaves oblanceolate-elliptic, blades dull and glabrous (short ferrugineous tomentose along the midrib and secondary veins) on the adaxial surface, dense, short ferrugineous tomentose on the abaxial surface, more evident along the midrib and secondary nerves; inflorescence 0.0–0.4 cm long; 10- to 25-flowered, rachis ferrugineous tomentose . . . . . *D. duckeanus* (probably, Amazonas, Caquetá, Guianía, Vaupés)
14a. Leaves lanceolate to elliptic, 6–15 cm long, 6–9 secondary nerves, base attenuate; pedicels sparsely pilose, sepals ovate-elliptic, fruit 5–6 mm in diameter, glabrous . . . . . *D. brevipedicellatus* (Antioquia, Bolívar, Chocó, Córdoba, Guainía, Guaviare, Meta, Vaupés, Vichada)
14b. Leaves obovate or lanceolate, 15–29 cm long, 13–14 secondary nerves, base cuneate; pedicels pubescent, sepals wide-ovate, fruit ca. 12 mm in diameter, dense, adpressed pubescent . . . . . *D. putumayensis** (Amazonas)
15a. Leaves 2–4 cm wide, petioles 4–7 mm long; sepals oblong; fruit 4–6 mm in diameter . . . . . *D. chocoensis** (Chocó)
15b. Leaves 4–15 cm wide, petioles 0.7–5.0 cm long; sepals obovate, ovate, elliptic or obovate-elliptic; fruit 5–20 mm in diameter 16
16a. Leaf blades with tertiary venation prominently areolate on the abaxial surface . . . . . *D. areolatus* (Guianía)
16b. Leaf blades with tertiary venation without areoles 17
17a. Leaves 14–35 cm long 18
17b. Leaves 5–12 cm long 20
18a. Branches, branchlets, petioles and blades covered with yellow trichomes; leaves opposite, petioles 5–6 mm long, peduncles 0.5–1.0 mm long . . . . . *D. pruskii* (Antioquia, Guaviare)
18b. Branches, branchlets, petioles and blades glabrescent, or if pubescent, not covered with yellow trichomes; leaves alternate, petioles 1.5–5.0 cm long, peduncles 0.5–7.0 mm long 19
19a. Leaves black punctate on the abaxial surface; petioles 3–5 cm long; peduncles 4–7 mm long . . . . . *D. lopez-palacii** (Antioquia)
19b. Leaves without black dots on the abaxial surface; petioles 1.5–3.0 cm long; peduncles 0.5–1.0 mm long . . . . . *D. foreroi* (Chocó, Valle)
20a. Leaves pilose, tomentulose or pubescent on adaxial surface 21
20b. Leaves glabrous on adaxial surface 22
21a. Leaves elliptic, dense pubescent on the abaxial surface; peduncles ca. 2 mm long, sepals ciliate at the margins, fruit completely pubescent (covered with yellow, stinging trichomes) . . . . . *D. schultesianus** (Vaupés)
21b. Leaves obovate or obovate-elliptic, tomentulose on the abaxial surface, peduncles 2–7 mm long, sepals not ciliate at the margins, fruit sparsely adpressed pilose (white, non-stinging trichomes) . . . . . *D. macrocarpus* (Amazonas, Santander, Vaupés)
22a. Leaves lanceolate or lanceolate-elliptic, coriaceous, margins subrevolute; petioles 0.5–2.0 mm wide; sepals elliptic, 2.0–4.5 mm long, glabrous or sparsely pilose on the abaxial surface . . . . . *D. savannarum* (Guainía)
22b. Leaves elliptic or elliptic-oblong, rigid-coriaceous, margins strongly revolute; petioles 3–4 mm wide; sepals ovate-elliptic, 5.5–6.0 mm long, appressed pilose on the abaxial surface . . . . . *D. liesneri* (Guainía)
23a. Inflorescence racemose (peduncle with 2 to 10 flowers) 24
23b. Inflorescence fasciculate not racemose (peduncle with a single flower) 25
24a. Leaves coriaceous, oblanceolate-obovate or lanceolate, margins entire or subsinuate; sepals elliptic . . . . . *D. novogranatensis* (Amazonas, Chocó, Meta)
24b. Leaves subcoriaceous, obovate-lanceolate, margins dentate; sepals obovate or obovate-oblong . . . . . *D. multiflorus* (Amazonas, Antioquia, Caquetá, Chocó, Valle)
25a. Sepals lax pubescent to glabrescent on the abaxial surface; fruit glabrous 26
25b. Sepals on the abaxial surface; fruit densely pubescent 31
26a. Leaves 14–30 × 10–20 cm 27
26b. Leaves 6–12 × 5–8 cm 28
27a. Stems, petioles, and leaf blades glabrous or with sparse, non-ferrugineous pubescence . . . . . *D. dentatus* subsp. *latifolius* (Guianía, Vaupés)
27b. Stems, petioles, and leaf blades with spreading, ferrugineous pubescence . . . . . *D. dentatus* subsp. *ferrugineus* (Chocó)
28a. Leaves chartaceous or subcoriaceous, serrate mostly in the upper half of blades 29
28b. Leaves coriaceous to rigid-coriaceous, crenate or sinuate mostly in the upper half of blades 30
29a. Leaves glabrous or with sparse, non-ferrugineous pubescence . . . . . *D. dentatus* subsp. *dentatus* (Amazonas, Arauca, Bolívar, Boyacá, Caquetá, Chocó, Cesár, Magdalena, Meta, Vaupés)
29b. Leaves densely ferrugineous pubescent . . . . . *D. dentatus* subsp. *esmeraldae* (Caquetá)

AMENDED KEY TO THE SPECIES OF *DOLIOCARPUS* OF COLOMBIA CONT.
Modified from Aymard (2017); species indicated with an asterisk (*) are endemic to Colombia

30a. Leaves crenate, ovate-elliptic, apex rounded or short acuminate . . . . *D. dentatus* subsp. *undulatus* (Caquetá, Guianía, Vaupés)
30b. Leaves sinuate, obovate, or elliptic, apex strongly cuspidate . . . . *D. dentatus* subsp. *obovatus* (Amazonas)
31a. Leaf margin entire or subsinuate; petioles 3.0–4.5 cm long; sepals pubescent on the adaxial surface . . . . *D. robustus* (Valle)
31b. Leaf margin dentate or sinuate-crenate; petioles 1.0–2.5 cm long; sepals glabrous on the adaxial surface 32
32a. Leaves obovate, obovate-elliptic, or rhombic-ovate; margins sinuate-crenate; peduncles adpressed pubescent; fruit covered with short and long trichomes . . . . *D. hispidobaccatus* (Amazonas, Caquetá)
32b. Leaves elliptic or elliptic-obovate; margins dentate; peduncles hispid; fruit covered with a single trichomes size 33
33a. Leaves wide elliptic or elliptic-obovate, 10–21 × 4–10 cm, base cuneate, margins in the upper half of the leaf blade dentate, petiole ca. 15 mm long; peduncles with 2 coriaceous bracteoles; sepals broad ovate to suborbicular, dense, yellow hispid pubescent abaxially; fruit 9–10 mm diam., covered with yellow trichomes . . . . *D. hispidus* (Caquetá, Valle)
33b. Leaves elliptic, 5–13 × 3–6 cm, base attenuate, margins dentate along the blade, petiole 5–10 mm long; peduncles with 3 papyraceous bracteoles; sepals ovate, adpressed sericeous pubescent abaxially; fruit ca. 12 mm diam., covered with white trichomes . . . . *D. trianamus** (Antioquia)

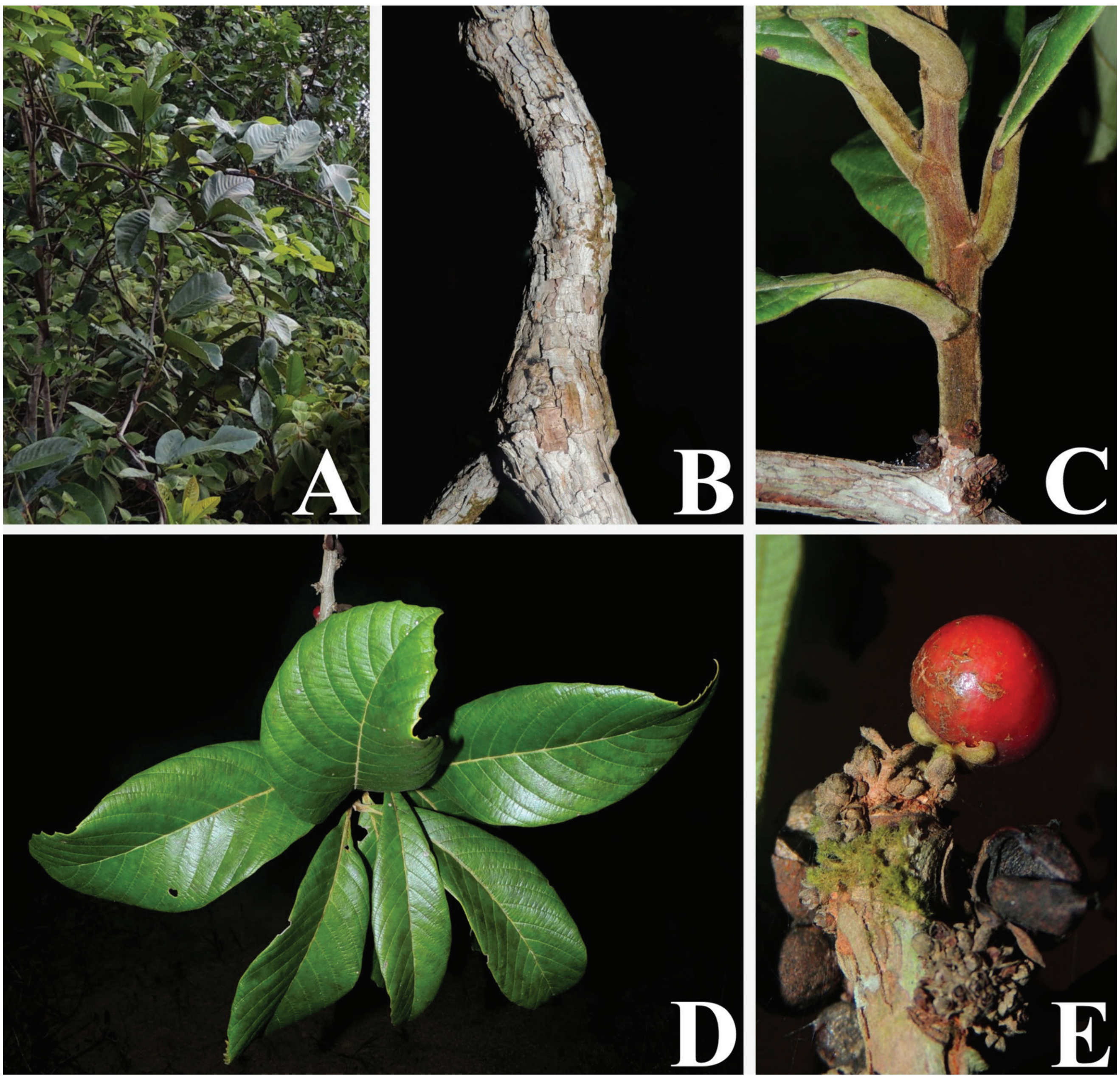


FIGURE 2. *Doliocarpus duckeanus* (Kubitzki) Aymard & Monzoli. **A**, Overall view of the species in nature, municipality of Manaus, state of Amazonas, Brazil. **B**, Mature stem. **C**, Young branch showing the ferrugineous tomentose indument. **D**, Mature leaves, adaxial view. **E**, Fruit. Photographs by João Monzoli based on *Monzoli & Vieira 553*.

Literature Cited

Arellano-Peña, H., D. Cárdenas-López, J. Stropp, N. Castaño, G. Romero-González, F. Castro-Lima, A. Lozano, M. C. Montilla, H. ter Steege, and G. A. Aymard-Corredor. 2023. The forests of the upper Rio Negro (north-western Amazon) and adjacent south-western Orinoco basins: a phytosociological classification. Pages 55–109 in J. A. Zinck, O. Huber, P. García, and E. Medina, eds., Psammic Peinobiomes: Nutrient-Limited Ecosystems of the Upper Orinoco and Rio Negro Basins. Springer-Verlag. Berlin, Germany.

Aymard, G. 1991. Dilleniaceae Novae Neotropicae. I. Dos nuevas especies y una nueva subespecie de *Doliocarpus* de la Guayana Venezolana. Anales del Jardín Botánico de Madrid 49(2): 195–200.

———. 1993. Dilleniaceae Novae Neotropicae II. Tres nuevas especies y dos nuevas subespecies del género *Doliocarpus*. Novon 3(4): 317–320.

———. 1997. Dilleniaceae Novae Neotropicae V. El género *Doliocarpus* en Colombia. Anales del Jardín Botánico de Madrid. 55: 17–30.

———. 1998. Dilleniaceae. Pages 676–685 in J. A. Steyermark, P. E. Berry, and B. Holst, eds., Flora of Venezuelan Guayana 4 (Caesalpiniaceae-Ericaceae). Missouri Botanical Garden Press. St. Louis.

———. 2007. Two new species of *Doliocarpus* (Dilleniaceae) from Colombia. Novon 17: 288–293.

———. 2008. Dilleniaceae. Pages 353–355 in O. Hokche, P. E. Berry, and O. Huber, eds., Nuevo Catálogo de la Flora Vascular de Venezuela. Fundación Instituto Botánico de Venezuela "Dr. T. Lasser." Caracas.

———. 2016. Dilleniaceae (continuously updated). Pages 1172–1175 in R. Bernal, S. R. Gradstein, and M. Celis, eds., Catálogo de plantas y líquenes de Colombia I. Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, (accessed 3 February 2024). Available at: www.catalogoplantasdecolombia.unal.edu.co

———. 2017. Novelties in Neotropical Dilleniaceae. Journal of the Botanical Research Institute of Texas 11(1): 45–51.

———. 2020. Dilleniaceae. Pages 1–36 in C. Persoon, R. Eriksson, K. Romoleroux, and B. Ståhl, eds., Flora of Ecuador No. 97. Department of Biological and Environmental Sciences, University of Gothenburg, Sweden.

———., and J. Miller. 1994. Dilleniaceae Novae Neotropicarum III. Sinopsis y adiciones a las Dilleniaceae del Perú. Candollea 49(1):169–182.

———., and C. Kelloff. 2016. Dilleniaceae. Pages 1–41 in S. Mota de Oliveira and M. J. Jansen Jacobs, eds., Flora of the Guianas. Ser. A, Phanerogams. Fascicle 31. Royal Botanic Gardens, Kew.

———., and C. A. Todzia. 2024. Dilleniaceae. Pages (**in press**) in C. Ulloa Ulloa, H. M. Hernández, F. R. Barrie, and S. Knapp, eds., Flora Mesoamericana 2(1). (Cycadaceae a Cactaceae). Missouri Botanical Garden Press, St. Louis.

Cárdenas-López, D., J. Betancur, N. R. Salinas, A. Zuluaga, and L. Clavijo. 2010. De Jirijirimo a Caparú: Una expresión de la diversidad vegetal en el río Apaporis. Colombia Amazónica 1: 5–56.

Clavijo, L. 2006. Estación Biológica *Mosiro Itajura* (Caparú), Río Apaporis,Vaupés Colombia. Frutos consumidos por primates. Rapid Color Guide # 200 versión 1. Environmental & Conservation Programs, The Field Museum, Chicago, Illinois.

Clavijo, L., J. Betancur, y D. Cárdenas-López. 2009. Las plantas con flores de la estación biológica Mosiro-Itajura-Caparú, Vaupés, Amazonia Colombiana. Pages 55–98 in G. Alarcón-Nieto and E. Palacios, eds., Estación Biológica Mosiro Itajura-Caparú, biodiversidad en el territorio del Yaigojé-Apaporis. Conservación Internacional, Bogotá.

Defler, T. R. 1999. Estación Biológica Caparú, Colombian Amazon. Neotropical Primates 7: 24–26.

———. 2010. Historia de los Primates Colombianos, Ed. 2. Universidad Nacional de Colombia, Facultad de Ciencias, Conservacion Internacional, Bogotá.

Defler, T. R., and S. Defler. 1996. Diet of a group of *Lagothrix lagotrhicha lagothricha* in southeastern Colombia. International Journal of Primatology 17: 161–190.

Font-Quer, P. 2001. Diccionario de Botánica. Ediciones Península, Barcelona.

Fraga, N. C. 2012. Filogenia e revisão taxonômica de *Davilla* Vand. (Dilleniaceae). Ph.D. Thesis. Universidade Federal de Minas Gerais, Instituto de Ciências Biológicas, Departamento de Botânica. Belo Horizonte, Brasil.

Fraga, N. C., and J. R. Stehmann. 2010. Novidades taxonómicas para Dilleniaceae Salisb. Brasileiras. Rodriguésia 61(Suppl.): 1–6.

Fraga, N. C., and J. Paula-Souza. 2015. Dilleniaceae in Lista de Especies da Flora do Brasil. Jardim Botânico do Rio de Janeiro. http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB7356 (accessed January 23, 2024).

González, M., L. Clavijo, J. Betancur, and P. R. Stevenson. 2016. Fruits eaten by woolly monkeys (*Lagothrix lagothricha*) at local and regional scales. Primates 57: 241–251.

Harris, J. G., and M. W. Harris. 2006. Plant Identification Terminology: an illustrated Glossary. Spring Lake Publishing, Spring Lake, Utah.

Horn, J. W. 2006. Dilleniaceae. Pages.132–154 in K. Kubitzki, ed., The families and genera of vascular plants 9. Springer, Berlin.

———. 2009. Phylogenetics of Dilleniaceae using sequence data from four plastid loci (rbcL, infA, rps4, rpl16 Intron). International Journal of Plant Science 170(6): 794–813.

IUCN (Standards and Petitions Committee) 2022. Guidelines for using the IUCN Red List Categories and Criteria. Version 15.1. Prepared by the Standards and Petitions Committee. Gland, Switzerland, and Cambridge, England. https://www.iucnredlist.org/documents/RedListGuidelines.pdf.

Kubitzki, K. 1971. *Doliocarpus*, *Davilla*, und verwandte Gattungen (Dilleniaceae). Mitteilungen der Botanischen Staatssammlung München 9: 1–105

Mantilla-Meluk, H., and L. F. Barrios-Rodríguez. 1999. Ecología básica de *Cebus apella* en la región del bajo Apaporis, Amazonia Colombiana. Tesis de Pregrado, Departamento de Biología, Facultad de Ciencias, Universidad Nacional de Colombia, Bogotá.

Monzoli, J. V. L., M. D. F.Araújo, C. N. de Fraga, and D. S. Sampaio. 2022. Two new species of *Doliocarpus* (Dilleniaceae) from Eastern Brazil, with an emended key for species of Brazilian Atlantic Forest. Systematic Botany 47(4): 952–961.

Rubiano Galvis, S. 2014. En busca del oro en la selva: Colonización minera y disputas por el ordenamiento territorial enTaraira y el bajo río Apaporis, 1984–2014. M.Sc. Tesis. Universidad de los Andes, Facultad de Ciencias Sociales, Departamento de Historia, Bogotá. Colombia.

Thiers, B. 2023. [continuously updated]. Index Herbariorum. A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. New York Botanical Garden. http://sweetgum.nybg.org/science/ih (accessed January 22, 2024).

DOS NUEVAS ESPECIES DE *OXALIS* (OXALIDACEAE) DE LOS ANDES DE VENEZUELA

Daniela S. Canelón,[1,2] Laurence J. Dorr[3] y Santos M. Niño[1]

Abstract. Two new species of *Oxalis* (Oxalidaceae) are described from the Andes of Venezuela and Colombia: *O. amicorum* from the páramo forest of sector El Pumar in the Ramal de Guaramacal, Trujillo, Venezuela, and *O. paramoensis* from the subpáramo and páramo of Venezuela and Colombia. Ecological and taxonomic aspects are compared to closely related species: *O. debilis, O. fendleri*, *O. medicaginea*, and *O. spiralis*. Illustrations of the new species and a map of their distribution also are provided.

Keywords: Flora of Venezuela, Guaramacal, *Oxalis*, páramo

Resumen. Se describen dos nuevas especies de *Oxalis* (Oxalidaceae) para los Andes de Venezuela y Colombia: *O. amicorum* de los bosques parámeros del sector el Pumar en el Ramal de Guaramacal, Trujillo, Venezuela y *O. paramoensis* de los subpáramos y páramos de Venezuela y Colombia. Se discuten aspectos ecológicos y taxonómicos con las especies cercanas: *O. debilis, O. fendleri*, *O. medicaginea*, y *O. spiralis*. También se proporcionan ilustraciones de las especies nuevas y un mapa de su distribución.

Palabras claves: Flora de Venezuela, Guaramacal, *Oxalis*, páramo

Oxalidaceae actualmente comprenden cinco géneros con 500–900(–950) especies extendidas en zonas tropicales y templadas de todo el mundo (Lourteig, 1980; Cocucci, 2004; POWO, 2023; Stevens, 2024). La mayor cantidad de especies se concentra en el género *Oxalis* L. con unas 500–800 especies (POWO, 1994; Cocucci, 2004; POWO, 2024; Stevens, 2024), género particularmente diverso en las partes más secas de Suramérica (Heibl y Renner, 2012). La complejidad de *Oxalis* es interpretada por Lourteig (1994), quien intentó hacer un ordenamiento, pero igual señala que dentro de algunos subgéneros posiblemente existan especies puentes, es decir, que se familiarizan con dos secciones en la cual participan sus caracteres, esto es debido a la gran variabilidad morfológica de los subgéneros; también indica que es "difícil identificar especies cercanas por caracteres tan finos" que generalmente son utilizados en sus descripciones. En vista de la complejidad del género, se espera que, en un futuro cercano se pueda resolver o clarificar a través de filogenias moleculares. Por ahora la clasificación subgénerica de *Oxalis* es la de Knuth (1930) comprendida por cuatro subgéneros, *Oxalis, Monoxalis* (Small) Lourteig, *Thamnoxys* (Endl.) Reiche, y *Trifidus* Lourteig, y 34 secciones (Lourteig, 1994, 2000; Cocucci, 2004). En *Oxalis* las secciones existentes se basan en los caracteres del hábito y de las hojas.

En Venezuela se han reportado 17 especies de *Oxalis*, distribuidas desde 40–3000 m (Emshwiller, 2008), de las cuales 16 se encuentran en los Andes. Revisamos estas especies en previsión de preparar un tratamiento del género para la Flora de Guaramacal (Dorr et al., 2000; Dorr, 2014), que trata las plantas vasculares que se encuentran en el Parque Nacional Guaramacal, ubicado al noreste de los Andes venezolanos en los estados Portuguesa y Trujillo. Con el material recopilado hasta ahora se han reconocido dos especies de *Oxalis* (*O. medicaginea* Kunth y *O debilis* Kunth) para el parque. Mientras que con el material indeterminado de colecciones recientes se proponen dos nuevas especies para la ciencia de *Oxalis* sección *Lotoideae* Lourteig, donde actualmente se reconocen unas 33 especies, siendo que ambas poseen los caracteres típicos del grupo como son el tallo suculento con entrenudos evidentes y semillas verrugosas oblongas (Lourteig, 2000).

Oxalis amicorum Canelón, Dorr & S.M. Niño, *sp. nov.* TIPO: VENEZUELA. Trujillo: Municipio Boconó, Parque Nacional Guaramacal, sector El Pumar, Coord. UTM. 369330–1019798, 3040 m, 6 octubre 2019, *S. Niño, D. Canelón, R. Caracas y M. Hidalgo 6194* (Holotipo: PORT; Isotipo: US [04170405]). Fig. 1, 2, 4A.

Oxalis amicorum differs from *O. fendleri* Lourteig by its stem length (10–25 cm versus 1 m long) and glabrous (glabrous versus pubescent); roots (axonomorphic with small tubercles versus fibrous adventitious without tubercles); leaflet apices (mucron-less versus mucron present in the fold of the blade); and inflorescences (solitary or cymose with 1–4 flowers versus bifid with numerous flowers).

Hierba suculenta de 10–25 cm de altura, erecta. *Raíz* axonomorfa, 7–10 cm de largo, con pequeños tubérculos falciformes, 5–9 × 1–2 mm, estrigoso. *Tallos* rojizos de 3–5 mm de ancho (en seco), glabros; internodios 1–2,5 cm de largo. *Hojas* trifoliadas, verdes por el haz y rojizos por el envés (planta viva); en el haz pubescencia esparcida, por el envés pubescencia moderada adpresa y muy abundante en el raquis; bordes lisos e irregulares, poco tomentoso; *pecíolo* delgado, 4–8 × 0,1–0,15 cm, suculento; estípulas 5–7 mm de largo, adheridas a la base del pecíolo articulado, libres

Los autores agradecen a A. R. Tangerini (US) y a E. M. Ellis (California State University, Monterey Bay) por preparar los dibujos, a R. A. Gulledge (US) por preparar la lámina fotográfica, a J. Méndez por la elaboración de los mapas y R. Caracas por su apoyo en campo. Esta investigación se realizó como parte del proyecto Flora de Guaramacal que se desarrolla entre el Museo Nacional de Historia Natural, Instituto Smithsoniano, Washington, DC, U.S.A. y la Universidad de los Llanos Occidentales "Ezequiel Zamora" (UNELLEZ), Guanare, Venezuela.

[1] INBIO-UNELLEZ, Herbario PORT, Mesa de Cavacas, Guanare, estado Portuguesa, Venezuela; santosmiguelnino@gmail.com; Instituto Venezolano de Investigaciones Científicas (IVIC), Caracas, Venezuela

[2] Autor de correspondencia: canelonbarraezdaniela@gmail.com

[3] Department of Botany, MRC-166, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, Washington DC 22013-7012, U.S.A.; dorrl@si.edu

Harvard Papers in Botany, Vol. 29, No. 1, 2024, pp. 45–52.

ISSN: 1938-2944, DOI: 10.3100/hpib.v29iss1.2024.n5, Published online: 30 June 2024

FIGURA 1. *Oxalis amicorum* Canelón, Dorr & S.M. Niño. **A**, Hábito, mostrando una planta completa con detalles de la raíz; **B**, Hoja vista por el haz con evidente pubescencia esparcida, incluyendo el pecíolo; **C**, Vista ampliada de un tubérculo; **D**, Vista ampliada de una estipula, en la base del pecíolo; **E**, Inflorescencia en prefloración; **F**, Vista frontal de una flor; **G**, Detalles de los estambres al secar con restos del cáliz; **H**, Vista de los estigmas al secar, con apariencia de estar fusionados con restos del cáliz; **I**, Semilla. Dibujo de A. R. Tangerini basado en *Niño et al. 6194*.

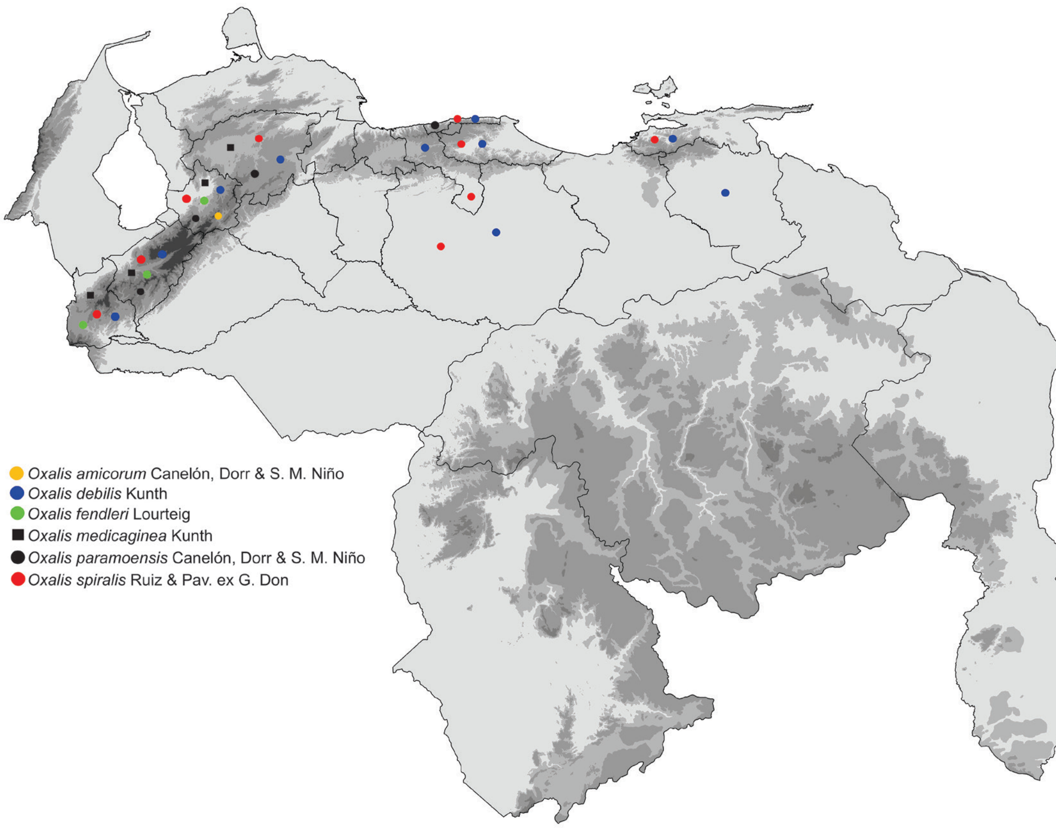


FIGURA 2. Distribución en Venezuela de las especies de *Oxalis* discutidas en este artículo, incluyendo las nuevas especies *O. amicorum* y *O. paramoensis*.

y bífidas en el ápice, glabras o con ocasionales tricomas unicelulares, adpresos o erguidos en los bordes, caducas; *lámina central* (folíolo) 0,9–2 × 0,8–1,3 cm, base cuneada, ápice obcordado, cortamente peciolulado, peciólulo ca. 1 mm de largo; láminas laterales (folíolos) 0,5–1.9 × 0,5–1,2 cm, asimétricos, bases cuneadas, ápices emarginados, sésiles. *Inflorescencias* axilares y/o terminales, solitarias o cimosas con 1–4 flores ± péndulas; inflorescencias axilares de 10–15 cm de largo y terminales 1–3 cm de largo; pedúnculo 9–14 cm de largo, con indumento lanoso blancuzco-amarillento, muy abundante; brácteas lineares 3–5 mm de largo; *pedicelos* 0,5–1 cm de largo. *Sépalos* 5–8 × 2–3 mm, ápices acuminados, verdes, pubescentes; pétalos 8–10 × 4–6 mm, amarillos con venas rojizas. *Ovario* glanduloso y pubescente, 5 estigmas con apariencia de estar fusionados al secar, 3–4 mm de largo. *Fruto* capsular, oblongo, 5–8 mm de largo. *Semillas* inmaduras, 1 × 0,5 mm, lisas con surcos transversales.

Fenología: Se cuenta con sólo una colección, con periodo de floración en octubre.

Distribución y hábitat: Es una hierba poco frecuente, por ahora sólo conocida en el Parque Nacional Guaramacal, específicamente en el sector El Pumar a unos 3040 m, a orillas de un bosque paramero (aislado) conocido como bosque alto andino de la asociación *Gaultheria anastomosans* (L.f.) Kunth–*Hesperomeles obtusifolia* (Pers.) Lindl. (Cuello y Cleef, 2011). La planta se ubica en las orillas de taludes, justo por encima de las aguas de una laguna glaciar, ya colmatada, lo que hace suponer que no soporta suelos con aguas permanentes o aguachinados.

Etimología: Hace referencia a los queridos amigos Carol Blythe y Rick Goodman, quienes de manera consecuente nos apoyan en nuestras aventuras con las plantas de Venezuela.

Oxalis amicorum poseé similtud a simple vista con *O. fendleri* que se encuentra en la región andina de Venezuela entre 2000–3000 m (Emshwiller, 2008) y Colombia entre 3600–3650 m. Mientras que *O. amicorum* ha sido colectada únicamente en Trujillo a unos 3040 m en el sector el Pumar.

Por su parte, *Oxalis fendleri* es una hierba decumbente que puede llegar a medir hasta 1 m de longitud, con pubescencia ferrugínea en toda la planta, sus raíces son adventicias fibrosas (sin tubérculos); tallos muy pubescentes, con tricomas ferrugíneos, sus internodios de 1–5 cm, estípulas con forma rectangular de 3–4 mm, el ápice de la lámina central es obovado-oblonga, con un mucrón en el repliegue, folíolos sésiles. Cabe destacar que *O. fendleri* tiene variabilidad en el material examinado, sin embargo, la mayoría de sus caracteres definitorios de especies se mantienen constantes. Con respecto a las inflorescencias, se apreció en *O. fendleri* brácteas lineares de 7–10 mm y bractéolas 2–3 mm, con cimas bífidas y numerosas flores, inflorescencias 10–25 cm de largo. Las semillas son verrucosas. A diferencia de *O. amicorum* que es una hierba erecta de 10–25 cm de altura, con raíces axonomorfas y pequeños tubérculos de 5–9 × 1–2 mm con forma falciforme y estrigados. Esto concuerda con Oberlander et al. (2009), quienes indican que las especies del Nuevo Mundo que son bulbosas tienen bulbos escamosos (tunicados), o escamas carnosas nacen a lo largo de un rizoma; estas escamas pueden ser equivalentes a estípulas o hojas enteras, así como se aprecia en la Figura 1.

Los tallos son totalmente glabros con internodios 1–2,5 cm de largo con estípulas bífidas de 5–7 mm de largo. El ápice de la lámina central es obcordado, cortamente peciolulado, el peciólulo ca. 1 mm de largo (sin mucrón en el repliegue), folíolo laterales son asimétricos (sésiles). En cuanto a las inflorescencias, contiene solo brácteas lineares 3–5 mm de largo (bractéolas no vistas), solitarias o cimosas (no bífidas), inflorescencias axilares son más largas (10–15 cm de largo) que las terminales (1–3 cm de largo), estas pueden contener 1–4 flores. Las semillas son lisas con surcos longitudinales (immadura)

En Tabla 1 se compara a *Oxalis amicorum* con las especies cercanas morfológica y geográficamente. Como se aprecia *O. medicaginea* Kunth es una hierba rastrera que puede llegar a medir más de 1,5 m de longitud, sus estípulas con forma oblonga, ensanchada hacia el ápice la distingue de las demás. *Oxalis debilis* Kunth, también presenta muchos caracteres que pueden ayudar a separarla rápidamente del resto de especies cercanas. Prácticamente es inconfundible, ya que es una hierba erecta de 20–30 cm de largo, acaule, con tubérculos cónicos (estrigoso–escarioso), sus pecíolos son largos de 9–15 cm con flores rosadas, por ahora es la única hierba de la familia con estos caracteres en Guaramacal.

Oxalis paramoensis Canelón, Dorr & S.M. Niño, *sp. nov.* TIPO: VENEZUELA. Trujillo: Municipio Boconó, Parque Nacional Guaramacal, sector Las Antenas, Coord. UTM. 369707–1020651, 3129 m, 6 octubre 2019, *S. Niño, D. Canelón, R. Caracas y M. Hidalgo 6218* (Holotipo: PORT; Isotipo: US [04170399]). Fig. 2, 3, 4B.

Oxalis paramoensis differs from *O. spiralis* Ruiz & Pav. ex G. Don in habit and size (± erect herbs 6–17 cm tall versus decumbent herbs with stems 70+ cm long); stem pubescence (occasional or scattered hairs versus dense ferruginous pubescence); and leaflet dimensions and apices (central leaflet blades 0,4–1 × 0,3–1 cm, petiolules ca. 0,1 long, and without a mucron versus central leaflet blades 0,4–4 × 0,3–4,5 cm, sessile, and with a small mucron). In addition, the lateral leaflet blades of *O. paramoensis* are smaller (0,2–0,9 × 0,1–0,9 cm) than those of *O. spiralis* (0,7–3,5 × 0,9–3,5 cm) and shortly petiolulate (versus sessile).

Hierba suculenta de 6–17 cm de altura, erecta. *Raíz* axonomorfa de 3–11 cm de largo, sin tubérculos. *Tallos* suculentos rojizos de 1–6 mm de ancho (en seco) con tricomas ocasionales o esparcidos; internodios muy angostos desde 2–6 mm de largo. *Hojas* trifoliadas, glandulosos, granuloso, con notables y abundantes tricomas, más por el envés, verdes por el haz y verde-rojizo por el envés (planta viva); *estípulas* bífidas 1–8 mm de largo, soldadas al pecíolo, glabras o con tricomas unicelulares y septados en los bordes, ± piloso; lámina central (folíolo) 0,4–1 × 0,3–1 cm, base cuneada, ápice obcordado, cortamente peciolulado, peciólulo ca. 1 mm de largo; láminas laterales (folíolos) asimétricos, 0,2–0,9 × 0,1–0,9 cm, bases cuneadas, cortamente peciolulado, peciólulos ca. 1 mm de largo. *Inflorescencias* en cimas bífidas con 2–5 flores, terminales o axilares, de 3–11 cm de largo, con abundantes tricomas pilosos, amarillos, unicelular, multicelular hasta glandulosos; *pedúnculos* de 3–11 cm de largo, rojizos; *pedicelos* 0,5–2 cm de largo, rojizos; *brácteas* lineares más anchas en la base, 1–1,5 mm de largo, caducas; *bractéolas* 0,5–1 mm de largo, caducas. *Flores* péndulas, 4–10 mm de largo; sépalos 3–7 mm de largo, rojizos hasta purpúreos; pétalos amarillos con venas rojizas a purpureas; ovario ± pubescente; estilo ± pubescente; estigma bifido, subcapitado, lobulado. *Fruto* una cápsula oblonga 2–6 mm de largo, agudo en el ápice, con 1–10 semillas. *Semilla* marrón, verrucosa de 1 × 0,5 mm.

Fenología: Mantiene flores y frutos durante todo el año.

Distribución y hábitat: Hierba frecuente en los subpáramos y páramos de Venezuela y Colombia entre 2400 y 3600 msnm. En Venezuela en la Cordillera de la Costa (Distrito Capital) y en los estados Lara, Mérida y Trujillo. En áreas abiertas, rocosas o en orillas de riachuelos.

Etimología: Hace referencia a los ecosistemas donde se encuentra la especie, entre subpáramo y páramo.

Nombre común: Vinagrera (tomado de *Ginés 1663*).

Oxalis paramoensis ha sido confundida con *O. spiralis*. Ahora es posible separar a *O. paramoensis* dado a que existe suficiente material para su estudio. Vareschi (1970) indicó la necesidad de una revisión del género *Oxalis* en Venezuela, la cual no se ha logrado todavía. Esto es importante, pues por ejemplo muchas especies determinadas como *O. spiralis* no se corresponden con el lectotipo designado por Lourteig (2000) y regularmente en los herbarios nacionales son confundidas con otras especies cercanas de la sección *Lotoideae*.

Oxalis paramoensis es bastante distinta a *O. spiralis*, aunque pueden compartir altitudes similares según el Nuevo Catálogo de la Flora Vascular de Venezuela (Emshwiller, 2008). Sin embargo, existen diferencias morfológicas muy notorias en el material colectado de Venezuela y Colombia. De acuerdo con el material examinado *O. paramoensis* es consistente en sus caracteres morfológicos desde los 2400–3600 msnm. Además, es una hierba de pequeño porte hasta 17 cm de largo, siempre erecta, con tricomas ocasionales o esparcidos pilosos-glandulosos en el tallo y más abundante en el pecíolo, hojas e inflorescencias y frutos. En cuanto a los folíolos son bastantes pequeños: los pecíolos cortos hasta 4 cm de largo, la lámina central puede variar de 0,4–1 × 0,3–1 cm (cortamente peciolulado con el peciólulo ca. 1mm de largo), sin mucrón, las láminas laterales 0,2–0,1 × 0,3–0,9 cm (cortamente peciolulados con los peciólulos ca. 1 mm de largo). En cuanto a las inflorescencias son cimas bífidas con pequeñas brácteas (1–1,5 mm de largo) y bractéolas (0,5–1 mm de largo) ambas lineares y caducas. Las inflorescencias pueden llegar a medir hasta 11 cm de largo, con muy pocas (2–5) flores.

Por su parte, *Oxalis spiralis* es una especie de amplia distribución desde Centro América hasta Sur América y que mantienen sus caracteres definitorios de especie. La misma es una hierba que puede llegar a medir hasta (+70 cm) de largo, erecta o decumbente, con pubescencia densa, ferrugínea desde el tallo, pecíolo, hojas, inflorescencias y fruto. Folíolos grandes en relación con *O. paramoensis* que son bastantes pequeños, los pecíolos pueden llegar hasta 15 cm de largo, la lámina (folíolo) central pueden variar de 0,4–4 × 0,3–4,5 cm (sésil con un pequeño mucrón por el envés), las láminas (folíolos) laterales 0,7–3,5 × 0,9–3,5 cm (sésiles). Con respecto a las inflorescencias pueden ser umbeliformes o cimas bífidas con brácteas grandes (4–6 mm de largo) y bractéolas (1–5 mm de largo) ambas lineares y caducas. Con relación a las inflorescencias, estas pueden llegar a medir hasta (+27 cm) de largo, generalmente con muchas flores (multiflora) 5–(+14).

TABLA 1. Comparación de *Oxalis amicorum* y *O. paramoensis* con las especies más cercanas en los Andes venezolana.

CARACTERES	*O. AMICORUM*	*O. DEBILIS*	*O. FENDLERI*	*O. MEDICAGINEA*	*O. PARAMOENSIS*	*O. SPIRALIS*
Altitud (msnm)	3040	1500–(ca. 2000)	2000–3000	1600–3600	2400–3600	1100–4200
Planta (tamaño)	10–25 cm	20–30 cm	20–100 cm	50–(+100) cm	6–17 cm	11–(+70) cm
Hábito	Erecta	Erecta	Decumbente	Rastrera	Erecta	Erecta o decumbente
Raíces	Axonomorfa con tubérculos	Napiforme, ramificaciones fibrosas	Adventicias fibrosas	Fibrosa ramificada	Axonomorfa	Fibrosa ramificada
Tubérculo (forma)	Falciforme, estrigoso	Cónico, estrigoso–escarioso	No posee	No posee	No posee	No posee
Tubérculos (tamaño)	5–9 × 1–2 mm	2–4 × 1–3 mm	No posee	No posee	No posee	No posee
Tallos (indumento)	Glabro	Acaule	Pubescencia ferrugínea	Glabro	Con tricomas ocasionales o esparcidos	Pubescencia ferrugínea
Internodios (tallo)	1–2,5 cm	No posee	1–5 cm	1–11 cm	2–6 mm	1–10 cm
Estípulas (tamaño)	5–7 mm	3–8 mm	3–4 mm	1–5 mm	1–8 mm	0,5–1,5 cm
Estípulas (forma)	Bífida	Escariosa–lineares	Rectangular	Oblonga, ensanchada hacia el ápice	Bífida	Rectas con lóbulos libres
Pecíolos	2,5–8 cm	9–15 cm	1–15 cm	2–5 cm	0,5–4 cm	1–15 cm
Peciólulos (lámina central)	ca. 1 mm	Sésil	Sésil	Sésil	ca. 1 mm	Sésil
Ápices (lámina central)	Obcordado	Obcordado	Obovado-oblonga	Obcordado-retuso	Obcordado	Obcordado
Tamaño (lámina central)	0,9–2 × 0,8–1,3 cm	0,8–4 × 0,9–4 cm	0,7–3 × 0,3–2,5 cm	0,8–3 × 0,8–2 cm	0,4–1 × 0,3–1 cm	0,4–4 × 0,3–4,5 cm
Peciólulos (láminas laterales)	Sésil	Sésil	Sésil	Sésil	ca. 1 mm	Sésil
Ápices (láminas laterales)	Asimétrico	Obcordado	Asimétrico	Obcordado-retuso	Obcordado, asimétrico	Asimétrico

TABLA 1 CONT. Comparación de *Oxalis amicorum* y *O. paramoensis* con las especies más cercanas en los Andes venezolana.

CARACTERES	*O. AMICORUM*	*O. DEBILIS*	*O. FENDLERI*	*O. MEDICAGINEA*	*O. PARAMOENSIS*	*O. SPIRALIS*
Tamaño (láminas laterales)	0,5–1,9 × 0,5–1,2 cm	0,6–3,5 × 0,6–3,8 cm	0,7–3 × 0,4–2 cm	0,8–2 × 0,6–2 cm	0,2–0,9 × 0,1–0,9 cm	0,7–3,5 × 0,9–3,5 cm
Mucrón	No posee	No posee	Presente en el repliegue de la lámina	No posee	No posee	Presente en el repliegue de la lámina
Inflorescencias	Solitarias o cimosas	Cimas bífidas o subumbeliforme	Cimas bífidas	Cimas 2–4 fidas	Cimas bífidas	Cimas bífidas o subumbeliformes
Brácteas	3–5 mm	0,8–1 mm	7–10 mm	3–5 mm	1–1,5 mm	4–6 mm
Bractéolas	No posee	0,2–0,3 mm	2–3 mm	1–2 mm	0,5–1 mm	1–5 mm
Pedúnclos	9–14 cm	15–20 cm	7–15 cm	8–12 cm	3–10 cm	8–(+20) cm
Inflorescencias (tamaño)	Axilares de 10–15 cm de largo; terminales 1–3 cm de largo	12–20 cm	15–25 cm	5–15 cm	3–11 cm	8–(+27) cm
N° de flores	1–4	3–15	Numerosas	3–7	2–5	5–(+14)
Color de flores	Amarillas	Rosadas	Amarillas	Amarillas	Amarillas	Amarillas—anaranjadas
Pedúnculos (tipo de indumento)	Lanoso	Glabro	Pubescente	Glabro	Lanoso y glanduloso	Pubescente
Semillas	Lisa con surcos longitudinales (inmadura)	No visto	Verrucosa	Verrucosa	Verrucosa	Verrucosa

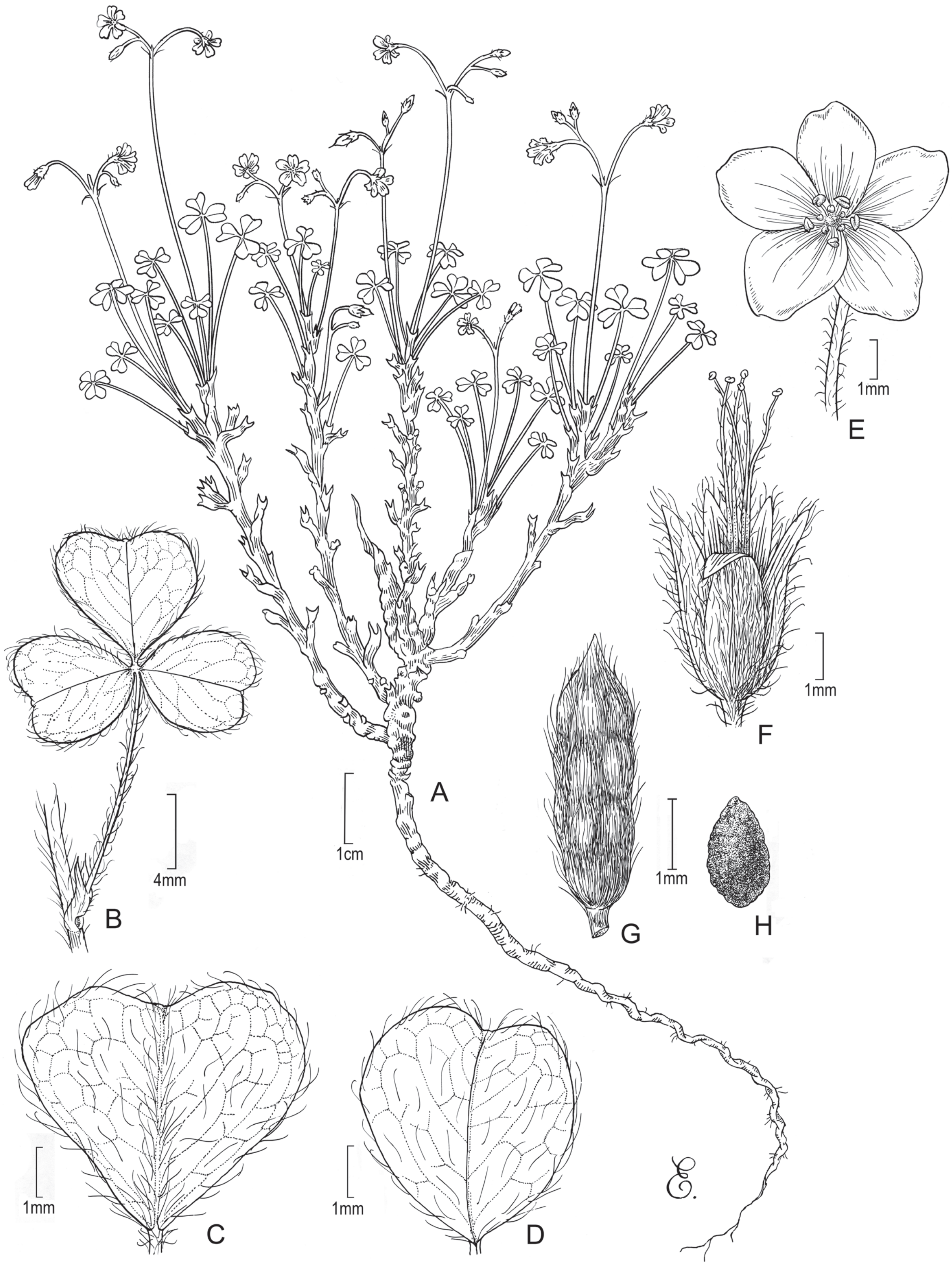


FIGURA 3. *Oxalis paramoensis* Canelón, Dorr & S.M. Niño. **A,** Hábito, mostrando una planta completa con detalles de la raíz; **B,** Hoja con pecíolo y tallo con abundantes tricomas; **C,** Folíolo central, vista por el envés; **D,** Folíolo lateral, vista por el haz; **E,** Vista frontal de una flor; **F,** Vista de los estilos pubescentes; **G,** Fruto; **H,** Semilla. Dibujo de E. M. Ellis basado en *Niño et al. 6218*.

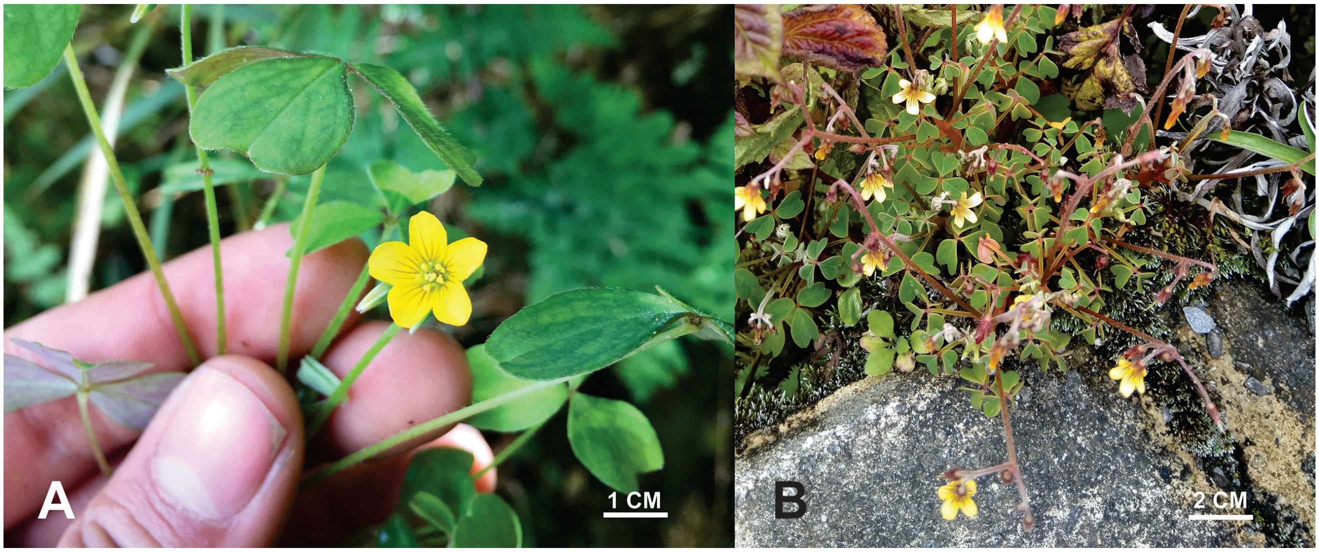


Figura 4. **A**, *Oxalis amicorum* Canelón, Dorr & S.M. Niño; **B**, *O. paramoensis* Canelón, Dorr & S.M. Niño (B). Fotografías de Daniela Canelón basadas en *Niño et al. 6194* y *6218*, respectivamente.

Además de estas diferencias que existen entre ambas especies, las colecciones existentes de *Oxalis paramoensis* indican que la especie se encuentra en altitudes superiores a los 2400 m. En cuanto a los usos o propiedades químicas de la planta, algunos autores (Steyermark y Huber, 1978; Lourteig, 2000) coinciden en la tradición de uso de las especies de genero *Oxalis*, como fuente de vitamina C, ya que posee alto contenido de ácido oxálico, indicando que la mayor concentración ácido se encuentra en los frutos y hojas.

Material adicional examinado: COLOMBIA. Cundinamarca: Carretera a Fusagasuga, entre San Miguel y la Quebrada de Niño Dios, ± 2800 msnm, 20 enero 1975, *A. Lourteig y J. M. Idrobo 3039* (P [05551861], US [03296310]). Norte de Santander: Quebrada Quemada, Cordillera de Hoya Grande, 35 km E [and] S of Pamplona, 07˚05'N, 072˚33–35'W, 3385 msnm, 19 November 1942, *F. R. Fosberg 19164* (US [03296262]). VENEZUELA. Distrito Capital: Parque Nacional El Ávila, Cordillera de la Costa, Pico Occidental, 10˚32'30"N, 066˚51'O, 2400–2400 msnm, 8 febrero 2004, *W. Meier 10002* (US [03296290]). Lara: Parque Nacional Dinira, Páramo de Jabón, 09˚34'N, 070˚06'W, 2900 msnm, 29 diciembre 1999, *R. Riina et al. 996* (US [03296268]). Mérida: Laguna de Mucubají, Páramo Sto. Domingo, 3600 msnm, octubre 1950, *Brother Ginés 1663* (US [00401851]). Trujillo: Parque Nacional Dinira, Páramo de Jabón, fila ca. de la cumbre del Pico Jabón, 09˚34'24"N, 070˚07'03"W, ca. 3100 msnm, 14 agosto 1999, *R. Riina et al. 624* (US [03296266]); Mun. Carache, arriba de Mesa Arriba, P.N. Dinira, Páramo de Jabón, 09˚32'52"N, 070˚04'51"W, ca. 3020 msnm, 7 marzo 1993, *R. Riina & R. Duno de Stefano 473* (US [03296267]).

Literatura Citada

Cocucci, A. A. 2004. Oxalidaceae. Páginas 285–290 en K. Kubitzki, ed., *The Families and Genera of Vascular Plants*. Vol. 6. Springer, Berlin.

Cuello A., N. L. y A. M. Cleef. 2011. Bosques de los Andes de Venezuela: Caso el Ramal de Guaramacal. BioLlania, Edición Especial 10: 74–105.

Dorr, L. J. 2014. Flora of Guaramacal (Venezuela): Monocotyledons. Smithsonian Contr. Bot. 100: i–xiv, 1–289.

———., B. Stergios, A. R. Smith, y N. L. Cuello A. 2000 [2001]. Catalogue of the vascular plants of Guaramacal National Park, Portuguesa and Trujillo states, Venezuela. Contr. U.S. Natl. Herb. 40: 1–155.

Emshwiller, E. 2008. Oxalidaceae. Páginas 538–540 en O. Hokche, P. Berry, y O. Huber, eds., *Nuevo Catálogo de la Flora Vascular de Venezuela*. Fundación Instituto Botánico de Venezuela Dr. Tobias Lasser, Caracas, Venezuela.

Heibl, C. y S. S. Renner. 2012. Distribution models and a dated phylogeny for Chilean *Oxalis* species reveal occupation of new habitats by different lineages, not rapid adaptive radiation. Syst. Biol. 61(5): 823–834.

Knuth, R. 1930. Oxalidaceae. Páginas 1–481 en A. Engler, ed., *Das Pflanzenreich*. [Heft 95] IV, 130. Wilhelm Engelmann, Leipzig.

Lourteig, A. 1980. Flora of Panama, Part IV. 84. Oxalidaceae. Ann. Missouri Bot. Gard. 67(4): 823–850.

———. 1994. *Oxalis* L. subgénero *Thamnoxys* (Endl.) Reiche emend. Lourt. Bradea 7(1): 1–199.

———. 2000. *Oxalis* L. subgéneros *Monoxalis* (Small.) Lourt., *Oxalis* y *Trifidus* Lourt. Bradea 7(2): 201–629.

Oberlander, K. C., E. Emshwiller, D. U. Bellstedt, y L. L. Dreyer. 2009. A model of bulb evolution in the eudicot genus *Oxalis* (Oxalidaceae). Molec. Phylogen. Evol. 51: 54–63.

POWO. 2024. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. http://www.plantsoftheworldonline.org/ (accessed 05 febrero 2024).

Stevens, P. F. 2024. *Angiosperm Phylogeny Website*. Version 14 July 2017 (continuously updated). http://www.mobot.org/MOBOT/research/APweb/ (accessed 05 febrero 2024).

Steyermark, J. A. y O. Huber. 1978. *Flora del Ávila*. Publicación Especial de la Sociedad Venezolana de Ciencias Naturales, Caracas, Venezuela.

Vareschi, V. 1970. *Flora de los Páramos de Venezuela*. Universidad de los Andes, Ediciones del Rectorado, Mérida, Venezuela.

INCACLEOME: A NEW ANDEAN GENUS OF CLEOMACEAE

Xavier Cornejo,[1,2]

Abstract. Based on morphology, previous molecular studies, and a distinctive geographic pattern of distribution that is restricted to the Central Andes in South America, *Incacleome gen. nov.*, a Neotropical new genus segregated from *Andinocleome* (Cleomaceae), is here formally proposed. The respective three new combinations (*I. chilensis*, *I. limoneolens*, and *I. mathewsii*) and a key to the species are also provided.

Keywords: *Andinocleome*, central Andes, Chile, Cleome, Peru

Resumen. Con base en la morfología, estudios moleculares previos, y un distintivo patrón geográfico de distribución, esto es, restringido a los Andes Centrales en América del Sur, aquí se propone formalmente *Incacleome gen. nov.*, un nuevo género neotropical segregado de *Andinocleome* (Cleomaceae). Además, se proveen las respectivas tres nuevas combinaciones (*I. chilensis*, *I. limoneolens,* y *I. mathewsii*) y una clave de las especies.

Palabras claves: Andes centrales, *Andinocleome*, Chile, Cleome, Peru

Cleomaceae are a family that include ca. 32 genera and 270 species, principally from tropical and subtropical regions of both the Eastern and Western Hemispheres, but with a few genera from temperate regions (Iltis et al., 2011; Cardinal-McTeague et al., 2016; Bayat et al., 2018). It is characterized by the predominantly herbaceous to subshrubby habit, sometimes treelets, flowers with free stamens whose filaments at the base are inserted in floral nectaries, at the base of the gynophores, otherwise on androphores, a 1-locular ovary, usually exserted on an elongate gynophore, 2 to numerous ovules attached on 2 parietal placentas, fruit capsules, dehiscent or mostly dehiscent by 2 valves, with a lateral replum, an absent mesocarp, small seeds, 1–3 mm in diameter, usually with elaiosomes (see previous references). Phylogenetic studies have shown that the genus *Cleome* L. s.l., as traditionally circumscribed, is not monophyletic (Hall et al., 2002; Sánchez-Acebo, 2005; Hall, 2008; Inda et al., 2008; Barret et al., 2017; Roalson & Hall, 2017). The division of *Cleome* into segregate genera was first proposed in the nineteenth century (Candolle, 1824; Rafinesque,1838), and expanded in the Flora of North America and Flora Mesoamericana during the past two decades (Iltis and Cochrane, 2007, 2014; Tucker and Vanderpool, 2010). Among those, *Andinocleome* was established as a new genus, in which combinations for three species (*A. lechleri* (Eichler) Iltis & Cochrane, *A. magnifica* (Briq.) Iltis & Cochrane, and *A. pilosa* (Benth.) Iltis & Cochrane) were initially provided (Iltis and Cochrane, 2014). The remaining genera and species in the Cleomaceae, and the respective delimitation, have been formally recognized (Patchell et al., 2014; Soares Neto et al. 2017, 2018, 2020, 2022; McGinty and Roalson, 2020).

In the generic reorganization and nomenclatural synopsis of the Andean clade of Cleomaceae (McGinty and Roalson, 2020), *Andinocleome* comprises two clades, informally named as the Lechleri (*Adinocleome s.s.*) and the Chilensis clades, both regarded as morphologically similar (McGinty and Roalson, 2020). However, a detailed morphological examination of all species of both clades in herbarium and fresh material during the preparation for the study of Cleomaceae for the Flora of Ecuador (Cornejo and Cochrane, manuscript submitted) revealed a set of consistent characters (see Table 1) that make clear two well-defined genera. Therefore, the Chilensis clade is here formally recognized as a new South American genus of Andean origin, as previously discussed (McGinty and Roalson, 2020), and the proper combinations are presented here.

Taxonomy

Incacleome Cornejo, *gen. nov.*
TYPE: *Cleome chilensis* Candolle, Prodr. 1:238 (1824). Fig. 1–2.

Annual, often ephemeral herbs, 8 cm to 1 m tall; leaves 3–5(–7)–foliolate, tertiary veins inconspicuous; flowers always with 3–foliolate bracts at least at the base of the rachis of the inflorescence; petals white or purplish; floral nectary disciform, slightly broader than the receptacle, centrally depressed adaxially, margins not wavy; anthers with 2 pollinic sacs.

Annual, often ephemeral herbs, unarmed; puberulent to pilose or glabrous. *Leaves* 3–5(–7)–foliolate, petiolate, exstipulate; folioles eucamptodromous, tertiaries inconspicuous on both sides. *Racemes* terminal and axillary, loose to dense, bracteate; bracts leafy, 3–foliolate, at least at the base of the rachis. *Flowers* bisexual. *Sepals* free, narrowly lanceolate to linear lanceolate, straight at apex. *Corolla* with open aestivation at anthesis. *Petals* erect, narrowly clawed, adaxially fan-like arranged in a single row, white. Floral nectary symmetric, disciform, slightly

The author is grateful to the staff of F, MO, NY, US, and WIS for allowing access to their respective collections and digital images for this study. The image of the holotype of *Cleome chilensis*, has been kindly granted by Muséum national d'Histoire naturelle (MNHN)–Paris Herbarium (P).

[1] Herbario GUAY, Departamento de Botánica, Facultad de Ciencias Naturales, Universidad de Guayaquil, Av. Raúl Gómez Lince s.n. y Av. Juan Tanca Marengo (campus Mapasingue), Guayaquil, Ecuador; xcornejoguay@gmail.com
[2] https://orcid.org/0000-0002-4081-4047

Harvard Papers in Botany, Vol. 29, No. 1, 2024, pp. 53–58.

ISSN: 1938-2944, DOI: 10.3100/hpib.v29iss1.2024.n6, Published online: 30 June 2024

FIGURE 1. Distribution map of *Incacleome* Cornejo based on herbarium collections.

TABLE 1. Morphological differences between *Incacleome* and *Andinocleome*.

FEATURE	*INCACLEOME*	*ANDINOCLEOME*
habit	Annual herbaceous, often as dwarf to short herbs, 8 to 10 cm tall up to 1 m tall	Biannual to perennial subhrubs to treelets, 0.8 to 4.0 m tall
leaf venation	folioles eucamptodromous and tertiary veins inconspicuous on both sides	folioles brochydrodomous and tertiary veins sulcate above and conspicuously prominent beneath
floral bracts	always trifoliolate at least at base of inflorescence	usually simple, sometimes trifoliolate
shape of nectaries	disciform, 2–3 mm wide	massive bowl shape, subhexagonal, 5–10 mm wide, with 6 shallow infrastaminal depressions often separated by 6 radial interstaminal elevations or crests, fleshy, margins wavy or dentate
petal color	white or purplish-white	light green to yellowish or purple
number of polinic anther sacs	2	4
fruit valves	thin, foliaceous to thinly chartaceous	thick, coriaceous to subwoody
fruit style	acicular	usually short and thick or absent

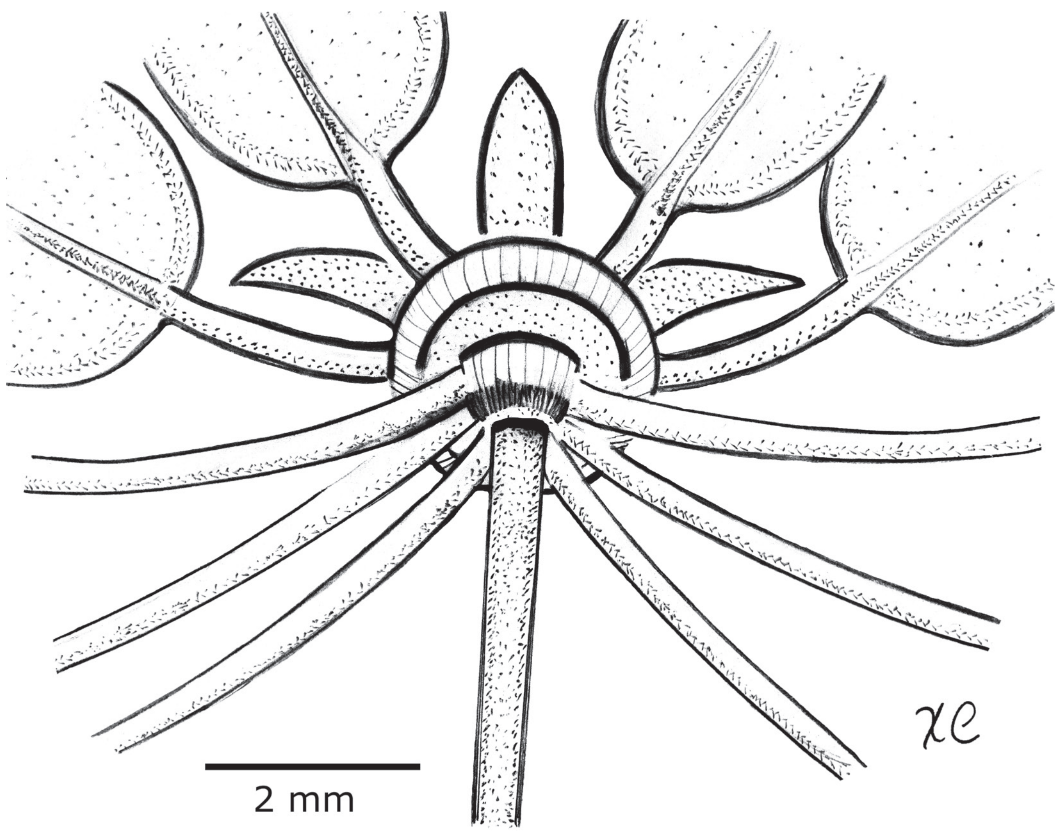


FIGURE 2. *Incacleome* Cornejo. Close-up of disciform floral nectary, the six staminal filaments and central gynophore inserted at the base of the gynophore, four upright petals in adaxial arrangement, and three reflexed sepals (the fourth sepal not visible).

broader than the receptacle, centrally depressed adaxially. Androphore absent. *Stamens* 6, exserted, radially inserted in 1 whorl in the central summit of the floral nectary around gynophore at the base; anthers green to purple, connective narrowly oblong, pollen sacs 2. *Gynophore* sometimes ± off centered. *Ovary* laterally ± compressed, linear to narrowly oblong, acute at the apex; style present, acicular, stigma undeveloped. *Capsules* slender, cylindric, deflexed or pendulous, at maturity splitting bilaterally, valves foliaceous to thinly chartaceous, deciduous. Seeds suborbicular, with open cleft and cleft chamber filling elaiosome.

In the generic reorganization and nomenclatural synopsis of the Andean Clade (Cleomaceae; McGinty and Roalson, 2020), four genera were formally recognized based on molecular analysis: *Andinocleome*, *Cochranella*, *Podandrogyne*, and *Pterocleome*. *Andinocleome* comprises two clades: Lecheri (*Adinocleome s.s.*) and Chilensis. The former clade includes *Cleome lecheri* Eichler, the nomenclatural type. The Chilensis clade (also reported as the "Chilensis group" in McGinty and Roalson, 2020), whose name was taken from *Cleome chilensis*, was recognized as a separate genus, but the apparent lack of morphological evidence during that study did not warrant such recognition (McGinty and Roalson, 2020). Furthermore, it has been stated that *Andinocleome* s.l. has not been fully sampled and that with additional "molecular phylogenetic studies there is the possibility that the rest of *Andinocleome* will not be monophyletic with the removal of the chilensis group" (McGinty and Roalson, 2020). However, two of a total of three species of the Chilensis clade (including *C. chilensis*, the nomenclatural type of *Incacleome*) and all species known at the time (with only the exception of *A. magnifica*) from the Lecheri clade have been molecularly sampled (Soares Neto et al., 2020). The later molecular results reinforced the diphyletic status of *Adinocleome*, which is fully consistent with the distinctive generic morphological characters and geographic pattern of distribution discussed herein (i.e., that it is restricted to the Central Andean block in South America). During herbarium and, mainly, field study of *Andinocleome* for the taxonomic treatment of Cleomaceae in the Flora of Ecuador, a set of consistent morphological differences were found, that do not warrant maintaining the members of both clades under the same generic name. Those clear-cut differences led the author to recognize and propose *Incacleome* as a new genus. The morphological differences between *Incacleome* and *Andinocleome* are presented in Table 1.

Etymology: The generic name *Incacleome* means the Inca's *Cleome* and refers, in an ethnohistorical sense, to the geographic extent of Tawantinsuyu during the Inca Empire (Stehberg and Sotomayor, 2012), which is very similar to that of the new genus.

Habitat and distribution: From Pacific coastal "lomas" (fog deserts) to ca. 3200 m in the high Andes of Chile to N Peru (Dept. Amazonas) in the central Andean block, South America.

Incacleome comprises three small herbs of Pacific to Andean xerophytic communities. The combinations are proposed here:

1. Incacleome chilensis (Candolle) Cornejo, *comb. nov.* Fig. 3.

Basionym: *Cleome chilensis* Candolle, Prodr. 1. 238 (1824). TYPE: CHILE. without locality or date, *J. Dombey 622* (Lectotype, designated by McGinty and Roalson, 2020: P [00076125], image seen).

Homotypic synonym: *Andinocleome chilensis* (Candolle) McGinty & Roalson, Phytotaxa 456: 262. 2020, *syn. nov.*

Habitat and distribution: From Pacific coastal "lomas" (fog deserts) to ca. 3200 m in high Andes, N Peru to Chile, on rocky and loose soils.

2. Incacleome limoneolens (J.F. Macbr.) Cornejo, *comb. nov.*

Basionym: *Cleome limoneolens* J.F. Macbr., Field Museum Publ. Bot. 4: 169 (1929). TYPE: PERU. Junin: San Rafael, 4 April 1923, *J. F. Macbride 3145* (holotype: F [0042683], image seen; isotypes: B [100242714], image seen; G [00226274], image seen; G [00226275], image seen; K [000220479], image seen; S [7315], image seen; US [00100483], image seen).

Homotypic synonym: *Andinocleome limoneolens* (J.F. Macbr.) McGinty & Roalson, Phytotaxa 456: 264. 2020, *syn. nov.*

Habitat and distribution: Andes of Peru, 1600–3000 m, on rocky and loose soils.

3. Incacleome mathewsii (Briquet) Cornejo, *comb. nov.*

Basionym: *Cleome mathewsii* Briquet, Ann. Conserv. & Jard. Genève 17: 374 (1914).

TYPE: PERU. Amazonas: Chachapoyas, ca. 2300 m, 1840, *A. Mathews 3044* (Lectotype, designated by McGinty and Roalson, 2020: G [00226272], image seen; Isolectotypes: BM [000629067], image seen; F [fragment from G, F0042684F], image seen; G [00226273], image seen; GH [00042335], image seen; K [000220481], image seen; K [000220482], image seen; K [000220483], image seen; MO [1813093], image seen; P [P00741917], image seen; WIS [v0259057], image seen).

Homotypic synonym: *Andinocleome mathewsii* (Briquet) McGinty & Roalson, Phytotaxa 456: 264. 2020, *syn. nov*.

Habitat and distribution: Eastern Andes of northern Peru, ca. 2300 m. Known only from the type.

KEY TO THE SPECIES OF *INCACLEOME*

1a. Gynophore 4–6 mm . . . . *I. mathewsii*
1b. Gynophore 12–30(–45) mm 2
2a. Petals 7–10 mm . . . . *I. chilensis*
2b. Petals 3–6 mm . . . . *I. limoneolens*

FIGURE 3. Holotype of *Cleome chilensis*, the nomenclatural type, courtesy of Muséum national d'Histoire naturelle (MNHN)–Paris Herbarium (P).

Literature cited

Barrett, R. L., E. H. Roalson, K. Ottewell, M. Byrne, S. P. Govindwar, S. R. Yadav, A. S. Tamboli, and A. R. Gholave. 2017. Resolving generic boundaries in Indian-Australasian Cleomaceae: circumscription of *Areocleome*, *Arivela*, and *Corynandra* as distinct genera. Systematic Botany 42: 694–708.

Bayat, S., M. E. Schranz, E. H. Roalson, and J. C. Hall. 2018. Lessons from Cleomaceae, the sister of crucifers. Trends in Plant Science 23(9): 808–821.

Candolle, A. P. de. 1824. Cleomeae in Candolle, A. P. de, editor, Prodr. (DC.) 1: 237–242.

Cardinal-McTeague, W. M., K. J. Systma, and J. C. Hall. 2016. Biogeography and diversification of Brassicales: A 103 million year tale. Molecular Phylogenetics and Evolution 99: 204–224.

Hall, J. C. 2008. Systematics of Capparaceae and Cleomaceae: an evaluation of the generic delimitations of *Capparis* and *Cleome* using plastid DNA sequence data. Botany 86: 682–696.

Hall, J. C., K. J. Sytsma, and H. H. Iltis. 2002. Phylogeny of Capparaceae and Brassicaceae based on chloroplast sequence data. American Journal of Botany 89: 1826–1842.

Iltis, H. H., and T. S. Cochrane. 2007. Studies in the Cleomaceae V: A new genus and ten new combinations for the Flora of North America. Novon 17: 447–451.

———. 2014. Studies in the Cleomaceae VI: a new genus and sixteen new combinations for the Flora Mesoamericana. Novon 23: 51–58.

Iltis, H. H., J. C. Hall, T. S. Cochrane, and K. J. Sytsma. 2011. Studies in the Cleomaceae I. On the separate recognition of Capparaceae, Cleomaceae, and Brassicaceae. Annals of the Missouri Botanical Garden 98: 28–36.

Inda, L. A., P. Torrecilla, P. Catalán, and T. Ruiz-Zapata. 2008. Phylogeny of *Cleome* L. and its close relatives *Podandrogyne* Ducke and *Polanisia* Raf. (Cleomoideae, Cleomaceae) based on analysis of nuclear ITS sequences and morphology. Plant Systematics and Evolution 274: 111–126.

McGinty, E. M., and E. H. Roalson. 2020. Generic reorganization and nomenclatural synopsis of the Andean Clade (Cleomaceae). Phytotaxa 456: 256–268.

Patchell, M. J., E. H. Roalson, and J. C. Hall. 2014. Resolved phylogeny of Cleomaceae based on all three genomes. Taxon 63: 315–328.

Rafinesque, C. S. 1838. Sylva Telluriana, Mantissa Synoptica. *New Genera and Species of Trees and Shrubs of North America*. Printed for the author and publisher, Philadelphia.

Roalson, E. H., and J. C. Hall. 2017. New generic concepts for African Cleomaceae. Systematic Botany 42: 925–942.

Sánchez-Acebo, L. 2005. A phylogenetic study of the New World *Cleome* (Brassicaceae, Cleomoideae). Annals of the Missouri Botanical Garden 92: 179–201.

Soares Neto, R. L., M. R. Vasconcellos Barbosa, and E. H. Roalson. 2017. *Cleoserrata* (Cleomaceae): taxonomic considerations and a new species. Phytotaxa 324(2): 179–186.

Soares Neto, R. L., W. W. Thomas, M. R. Vasconcellos Barbosa, and E. H. Roalson. 2018. New combinations and taxonomic notes for *Tarenaya* (Cleomaceae). Acta Botanica Brasilica 32: 540–545.

———. 2020. Diversification of New World Cleomaceae with emphasis on *Tarenaya* and the description of *Iltisiella*, a new genus. Taxon 69: 321–336.

Soares Neto, R. L., W. W. Thomas, E. H. Roalson, and M. R. Vasconcellos Barbosa. 2022. Taxonomic revision of *Tarenaya* (Cleomaceae). Annals of the Missouri Botanical Garden 107: 250–313.

Stehberg, R., and G. Sotomayor. 2012. Mapocho Incaico. Boletín del Museo Nacional de Historia Natural, Chile 61: 85–149.

Tucker, G. C., and S. S. Vanderpool. 2010. Cleomaceae in Flora of North America. Editorial Committee, eds., Flora of North America North of Mexico 7: 199–223.

VASCONCELLEA JOSSEI (CARICACEAE): A NEW SPECIES OF HIGHLAND PAPAYA WITH EDIBLE FRUITS FROM THE ANDES OF ECUADOR

Xavier Cornejo[1,2] and José Flores Cedeño[1]

Abstract. Based on previous molecular work, *Vasconcellea jossei*, a new species from the Andes of central western Ecuador, is formally described and illustrated, and its relationship to morphologically closely related species is discussed.

Keywords: Chimborazo, food resources, Neotropics

Resumen. Con base a un estudio molecular previo, *Vasconcellea jossei*, una nueva especie de los Andes al centro occidente de Ecuador, es formalmente descrita, se discute sus relaciones con las especies morfológicamente cercanas.

Palabras claves: Chimborazo, recursos alimenticios, neotrópicos

Vasconcellea A. St.-Hil. is a Neotropical genus in the Caricaceae, that comprises 23 to 26 species (including the new one presented here) and a [natural?] hybrid, *V.* × *heilbornii* (V.M. Badillo) V.M. Badillo, of shrubby to arborescent herbs commonly known as wild papayas. The genus is distributed from Mexico to Argentina and centered in Ecuador and Peru (Badillo, 2000; Peña et al., 2017; Tineo Flores et al., 2020). In the treatment of the Caricaceae for the Flora of Ecuador (Badillo, 1983), 10 species of *Vasconcellea* were recorded for the country. Subsequent field exploration led to the discovery of *Vasconcellea palandensis* (V.M. Badillo, Van den Eynden, & Van Damme) V.M. Badillo, an endemic to southeastern Ecuador (Van den Eynden, 2000; Badillo, 2000), and new records for the country for the mostly Colombian species, *V. goudotiana* Triana & Planch. (Peña et al., 2017) and *V. sphaerocarpa* (García Barr. & Hern. Cam.) V.M. Badillo. The latter was found in Cosanga, Napo, in northeastern Ecuador (*Jim McClarin s.n.*, GUAY). Molecular studies on *Vasconcellea* from northern Peru amazingly yielded five new species (Tineo Flores et al., 2020). In this paper, a new species of *Vasconcellea* from the central and southern Andes of Ecuador is formally presented, based on previous molecular work (Peña et al., 2017).

Vasconcellea jossei Cornejo, *sp. nov.*
TYPE: ECUADOR. Chimborazo: Reserva El Corazón, 2°03'S, 78°54'W, 2300 m, 23 March 2024 (fl, fr), *X. Cornejo, J. Josse, A. M. Josse, S. Noroña, & J. P. Noroña 10181* (Holotype: GUAY; Isotype: QCA). Fig. 1–2.

The new species of *Vasconcellea* is similar to *V. cundinamarcensis* V.M. Badillo, but differs by having leaf blades apparently glabrous with the naked eye, with abundant short, hyaline, glandular trichomes, ovoid to napiform fruit, and a verruculose epicarp, that is purple or burgundy to dark brown at maturity (versus leaf blades that are tomentose to tomentulose abaxially, elliptic-obovoid to obovoid fruit, and a smooth epicarp, that is yellow at maturity).

Arborescent *herb*, monocaule or few-branched, to 8 m tall, dioecious; bark light brown, covered with prominent petiolar scars; stipules present at the distal end of the stem, leaf-like, subpersistent, with hyaline, glandular trichomes. *Latex* milky white. *Leaves* chartaceous, spirally spreading, crowded at the top of the stem, simple-palmate, 5- to 7-lobes, deeply cut; petioles up to 100 cm long, somewhat compressed adaxially, hollow in upper leaves, light green; blades broadly ovate in outline, 30–40 × 35–50 cm, dark green, hemibullate, glossy and glabrous throughout, petiolar insertion with a glandular field and several narrow, short, conical-muricate projections, 1–2 mm tall, radial main veins at center of blade often pinkish, impressed to prominent throughout, and scattered, erect, multiseriate glandular trichomes along all veins adaxially; pale green, opaque, appears glabrous to the naked eye, but with abundant short, hyaline, glandular trichomes on epidermal leafy tissue; primary, secondary and tertiary veins prominent, veins of fourth and fifth order impressed, all veins apparently glabrous abaxially; radially arranged basal and lateral lobes 20–32 × 4–7 cm, each with 2 triangular to lanceolate secondary lobes on upper side, central lobe oblong-lanceolate, 28–43 × 4–7 cm, apex acuminate, with 2 pairs of opposite to subopposite lateral lobes, that are lanceolate to triangular, decreasing in size toward the apex; apex acute to acuminate. *Pistillate inflorescences* axillary, racemose, few-flowered, to 9 cm long; peduncle 10–35 × 3–4 mm, adaxially compressed; pedicels ca. 5 mm long, with a few small bracts ca. 1 mm long. *Pistillate flowers* 5-merous; sepals greenish, triangular, 3–4 × 2–3 mm; petals light green, purplish at base, mostly free, ligulate, ca. 20 × 3–4 mm, apex obtuse, reflexed, base laterally connate ca. 3 mm. *Ovary* superior, 5-carpelar, 5-locular, 5-angular, ca. 15–18 × 7–8 mm, attenuate toward the apex; numerous anatropous ovules, parietal placentation; style 2–3 mm long; stigmas 5, linear-digitate, 5–7 mm long, inconspicuously forked apically. *Male inflorescences* and staminate flowers unknown. *Fruit* a berry, ovoid to napiform, 80–95 × 50–70 mm,

Thanks to Mr. Luis Ojeda for allowing the senior author to do botanical explorations on his property, the Reserva El Corazón, and to Marcos Sinoluisa for sharing his field experiences with *Vaconcellea jossei*.

[1] Herbario GUAY, Departamento de Botánica, Facultad de Ciencias Naturales, Universidad de Guayaquil, Av. Raúl Gómez Lince s.n. y Av. Juan Tanca Marengo (campus Mapasingue), Guayaquil, Ecuador
[2] Corresponding author: xcornejoguay@gmail.com

Harvard Papers in Botany, Vol. 29, No. 1, 2024, pp. 59–62.

ISSN: 1938-2944, DOI: 10.3100/hpib.v29iss1.2024.n7, Published online: 30 June 2024

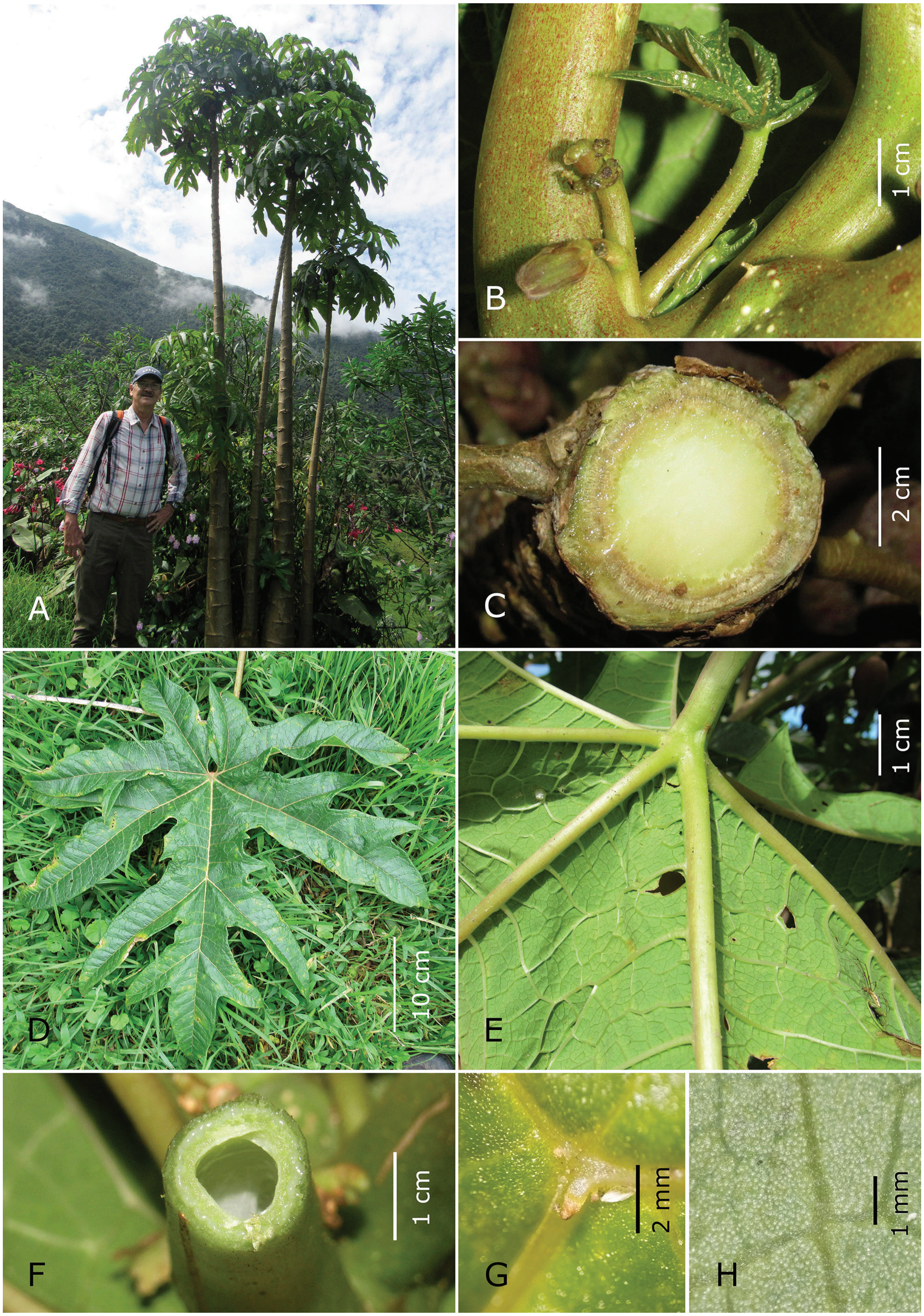


FIGURE 1. *Vasconcellea jossei* Cornejo. **A**, arborescent habit and co-collector, Jorge Josse; **B**, leafy stipule, young pistillate inflorescence, and petiole, lateral view; **C**, stem, cross section; **D**, mature leaf blade, adaxial view; **E**, close up of mature leaf blade with radial main veins, reticulate tertiaries, and distal part of petiole, abaxial view; **F**, hollow petiole; **G**, multiseriate, erect, glandular trichome on leaf blade surface, adaxial view; **H**, close up of leaf blade with abundant short, hyaline, glandular trichomes, abaxial view. A–E, are based on the holotype. F–H, are based on *Cornejo et al. 10180*. Photographs by X. Cornejo.

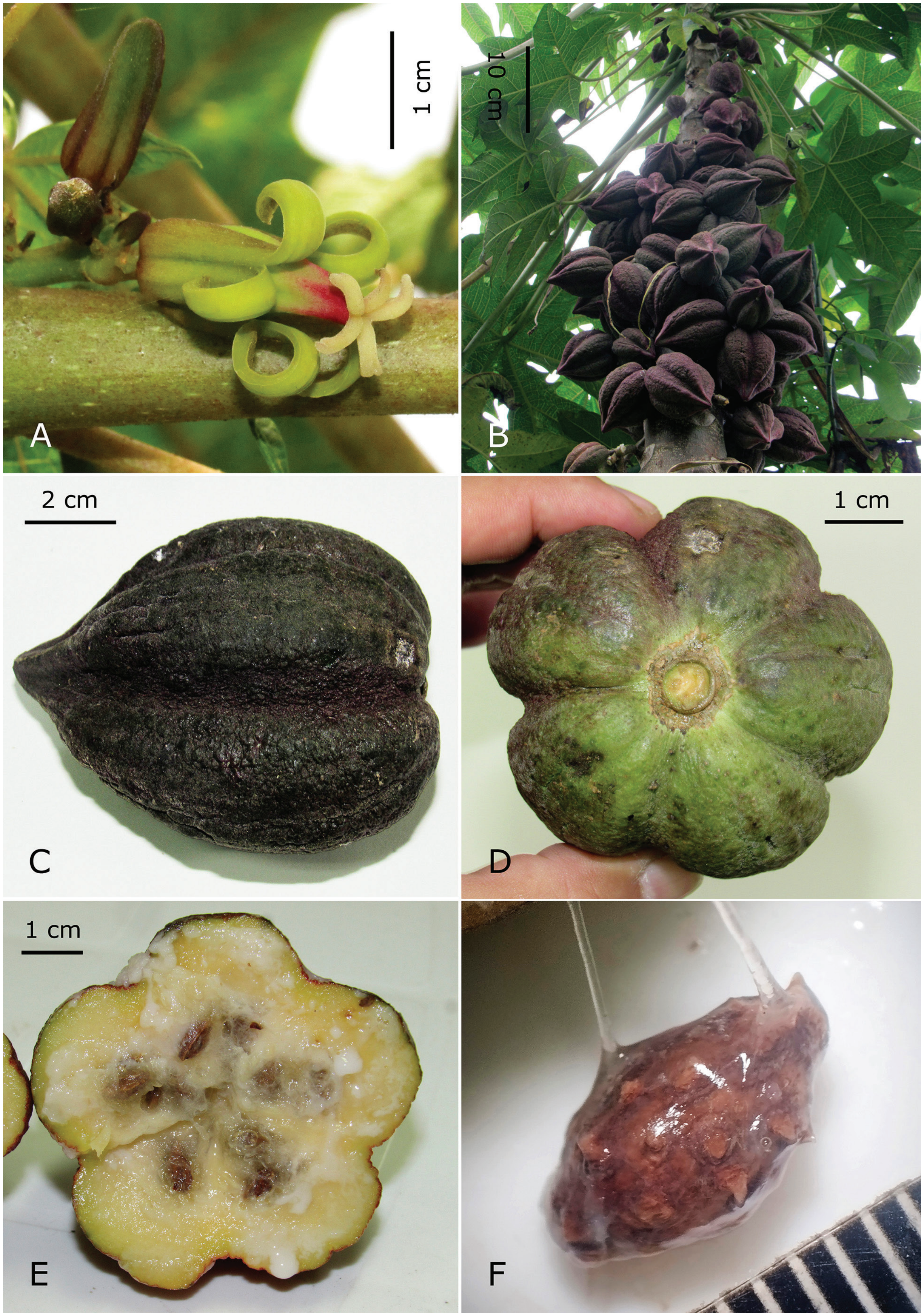


FIGURE 2. *Vasconcellea jossei* Cornejo. **A**, pistillate inflorescence and flower at anthesis; **B**, pistillate monocaule individual bearing fruit, lateral abaxial view; **C**, fruit near maturity, lateral view; **D**, 5-sulcate fruit near maturity and central circular pedicel scar, basal view; **E**, fruit at maturity, cross section; **F**, removed fresh seed embedded in a mucilaginous, hyaline sarcotesta, note the conical tuberculate protuberances. A, E, F, are based on the type (*Cornejo et al. 10181*). B–D, are based on *Cornejo et al. 10180*. Photographs A–H by X. Cornejo.

longitudinally 5-sulcate, purple-red or burgundy to dark brown at maturity, base broadly obtuse to emarginate, apex acuminate; exocarp verruculose, glabrous; mesocarp 5–10 mm, yellowish at maturity; pedicel of fruit 10–16 × 6–9 mm. Seeds light brown, 6–8 × 3–4 mm, narrowly ovoid to ellipsoidal-ovoid, sclerotesta with 1 to 2 lateral longitudinal ridge(s) and conical to short-truncate protuberances, each seed surrounded by a mucilaginous, hyaline sarcotesta, seeds arranged in 5 groups. Central cavity absent. The sugar content (tested twice on fruit from two collections, type and paratype) is 10˚ Brix.

Additional specimens examined: ECUADOR. Chimborazo: Jalubi, 2˚03'S, 78˚55'W, 2250 m, 23 March 2024 (fl, fr), *X. Cornejo, J. Josse, A. M. Josse, S. Noroña, & J. P. Noroña 10180* (GUAY, QCA).

Vasconcellea jossei resembles *V. cundinamarcensis*, another Andean highland papaya with edible fruits that is distributed from Panama to Peru, but the former species differs from the latter by the characters provided in the diagnosis. In a previous molecular study (Peña et al., 2017), the subgroup B4 represented by a species of *Vasconcellea* that is "clearly defined" and "could not be placed in any of the known species" (see also field images of fruit and leaf blade in Peña et al., 2017: 101, "Anexo" 3b, d, respectively), forms a sister clade to that of subgroup B5, which is *V. cundinamarcensis*. The *Vasconcellea* sp. of subgroup B4 (sensu Peña et al., 2017), that is molecularly related to *V. cundinamarcensis,* is formally presented and named here *V. jossei*.

Etymology: The epithet honors Jorge Josse, a nature lover and agronomic engineer with vast experience in papaya cultivation and other crops in Ecuador. Josse provided logistic support and was a field companion and co-collector on six trips between 2020 and 2024 to the type locality and areas nearby, that led to the discovery of this new *Vasconcellea* and several other taxonomic novelties.

Common names: Jigacho is the indigenous name (Marcos Sinoluisa, pers. comm.).

Uses: The mature and sweet raw mesocarp is edible; the epicarp is boiled in water and mixed with cinnamon and other ingredients for preparing tasty desserts.

Habitat and distribution: This species is restricted to the central and southern Andes of Ecuador, between 2000 and 2500 m, in the provinces of Chimborazo, Azuay, and Cañar (Peña et al., 2017).

Field observations: *Vasconcellea jossei* is often monocaule; however, it is said that the species can produce one to few lateral branches if the stem is cut off. A monocaule pistillate individual can produce 20 to 50 fruits. *Vasconcellea jossei* can be vegetatively propagated by cuttings (Marcos Sinoluisa, pers. comm. to XC), and it is sometimes planted along trails. Solitary individuals can be floristic elements in living fences. If the milky white latex comes in contact with skin, it may produce a burning sensation and irritation.

Phenology: During six field trips to the type locality and environs between 2020 and 2024, flowers were observed from January to July, and fruits from March to August.

Conservation status: At present, due to the scarce information, the new species is designated as DD (data deficient; IUCN 2022).

Literature cited

Badillo, V. M. 1983. Caricaceae. Pages 27–48 in G. Harling and B. Sparre, editors, Fl. Ecuador 20. University of Gothenburg, Goteborg, Sweden.

———. 2000. *Carica* L. vs. *Vasconcellea* St.-Hill. (Caricaceae) con la rehabilitación de este último. *Ernstia* ser. 2, 10(2): 74–79.

IUCN Standards and Petitions Committee. 2022. Guidelines for Using the IUCN Red List Categories and Criteria. Version 15. Prepared by the Standards and Petitions Committee. Downloadable from http://www.iucnredlist.org/documents/RedListGuidelines.pdf (accessed July 1, 2022).

Peña, D. F., P. G. Villena, A. J. Aguirre, and C. Jiménez Merino. 2017. Diversidad genética de accesiones de la familia Caricaceae en el sur de Ecuador. *Maskana* 8(1): 85–102.

Tineo Flores, D., D. E. Bustamante, M. S. Calderón, and J. E. Mendoza. 2020. An integrative approach reveals five new species of highland papayas (Caricaceae, *Vasconcellea*) from northern Peru. *PlosOne* 15(12): e0242469. https://doi.org/10.1371/journal.pone.0242469

Van den Eynden, V. 2000. *Carica palandensis* (Caricaceae), a new species from Ecuador. *Novon* 10: 4–6

A CONSPECTUS OF ANGIOSPERM SUPERTRIBES

Zacky Ezedin[1]

Abstract. The inconspicuous rank of supertribe is rarely used in botanical classification, being only reserved for large families with high tribal-level diversity. The purpose of the supertribe is to provide further hierarchical resolution within a tribally rich subfamily by allowing clades containing multiple tribal-level taxa to be recognized at rank level. Thus far, this rank has been proposed for six angiosperm families: Asteraceae, Brassicaceae, Poaceae, Rosaceae, Rubiaceae, and Sapindaceae. Here, the rank of supertribe is further extended to the families Araceae, Cactaceae, and Fabaceae, along with new additions in Rubiaceae and Sapindaceae. In the subfamily Aroideae s.l., four well-supported clades are newly recognized as supertribes Arodae, Philodendrodae, Schismatoglottidodae, and Zamioculcadodae. In Cactoideae, the two largest and commonly recognized core clades I and II are validated as supertribes Echinocereodae and Cereodae, respectively. In Papilionoideae, supertribes Dalbergiodae, Galegodae, Genistodae, Myroxylodae, and Phaseolodae are newly validated, corresponding to five commonly recovered supra-tribal clades. In Rubiaceae, five tribal alliances are newly equated to the supertribes Coffeodae, Dialypetalanthodae, Lasianthodae, Mussaendodae, and Urophyllodae. The publication of the two Maloideae supertribes Kerriodae and Pyrodae, originally published improperly, are herein validated. In Sapindoideae, Cupaniodae is newly described while the limits of Paulliniodae are expanded, and its effective publication corrected through typification. Additionally, the tribal name Chesneyeae is newly validated and corrected. This account brings the total number of currently accepted supertribes across the angiosperms to 36. A brief synopsis of all published and accepted supertribal names is provided.

Keywords: infrafamilial classification, suprageneric classification, tribal alliance, Fabaceae, Araceae

Very few plant families are large enough to require an infrafamilial rank of the fourth order. In some rare instances, however, the use of such a rank may be justified when increased phylogenetic resolution is favored within a given subfamily (Robinson, 2004). The supertribe (names ending in "-*odae*") is available as an additional rank in the traditional Linnean hierarchy positioned below the subfamily and above tribe (Reveal, 2012). A rather obscure rank in botanical taxonomy, its use is only recommended for large subfamilies with a high enough tribal count to justify additional hierarchical stratification above the tribal level, particularly when the rank of subtribe has already been filled.

Groups of tribes within subfamilies have long been recognized informally by taxonomists in some of the largest families. Morphologically heterogeneous, yet strongly supported clades made up of multiple tribal-level taxa which are consistently recovered and well-supported by molecular analyses are regularly given informal clade names. These groups are sometimes referred to as "tribal alliances," such as those in Araceae (e.g., Schismatoglottid alliance), Asteraceae (e.g., Heliantheae alliance), and Rubiaceae (e.g., Coffeeae alliance). While many authors continue to use informal non-Linnean names, some authors have alternatively begun recognizing these multi-tribal clades more formally at rank level as supertribes. The earliest record of validly published supertribal names were for the Poaceae subfamily Pooideae (Liu, 1980).

Given how underutilized this rank is by plant taxonomists, as compared to their zoological counterparts, it is understandable as to why it has not yet been recognized as an official rank through Art. 4.2 of the *Code* (Turland et al., 2018). Yet even the continued maintenance of its unofficial status as a rank in the *Code* has not stopped plant taxonomists working on large families from continuously invoking it (Liu, 1980; Macfarlane and Watson, 1982; Watson et al., 1985; Avetisyan, 1990; Robinson, 2004, 2005; Robbrecht and Manen, 2006; Potter et al., 2007; Acevedo-Rodríguez et al., 2017; Soreng et al., 2017; German et al., 2023). Although, in fairness, its usage offers but a slight convenience in the classification of only a few large families and its official recognition in the *Code* would have little bearing on the classification system as a whole. With ever-increasing phylogenetic resolution of generic and tribal relations across the angiosperms, however, there may come a need for further taxonomic stratification of certain groups. Thus, eventual codification of the supertribe under Art. 4 may become increasingly inevitable.

In contrast to most tribes and subtribes, the rank of supertribe does not usually adhere to traditional rules of morphological recognizability—and this is for the better. Groups of multiple tribes, regardless of how strongly supported their monophyly is, may not easily be defined by uniformly shared morphology, nor should they be expected to. In order to give the rank increased flexibility in recognition, supertribes are not generally expected to exhibit any guaranteed (syn)apomorphic traits or otherwise be diagnoseable in the traditional sense. Thus, strong molecular support uniting a clade of multiple tribal-level taxa may be all that is necessary to allow for supertribal designation. Any morphological similarities found among the contained tribes may serve to further the case for their recognition at this rank; however, this is not deemed a prerequisite. Unlike most other ranks, the adoption of the supertribe within a given subfamily may be sought for purely hierarchical grouping purposes, essentially taking the excessive tribal "load" off the subfamily rank by transferring it to the supertribe.

I thank G. Weiblen for comments on an earlier version of the manuscript, and I. Al-Shehbaz and two anonymous reviewers for their comments and suggestions.

[1] Harvard University Herbaria, 22 Divinity Avenue, Cambridge, Massachusetts 02138, U.S.A.; zezedin@fas.harvard.edu

Harvard Papers in Botany, Vol. 29, No. 1, 2024, pp. 63–78.

ISSN: 1938-2944, DOI: 10.3100/hpib.v29iss1.2024.n8, Published online: 30 June 2024

When recognizing supertribes, the broadest, most inclusive clade is usually chosen in preference over smaller less inclusive nodes to be named at rank level. This allows for an increased number of tribes to be accommodated, leading to more useful higher-order taxonomic groupings. Choosing deeper nodes within a subfamily's backbone allows for tribes to be placed within a more informative hierarchy. Furthermore, supertribes that do not convey any additional taxonomic information are not recognized in this account. This includes those that are monotypic (delimited with a single tribe) or those that encompass all but one or a few tribes in a given subfamily. These all help to minimize the rank's excessive and unnecessary proliferation.

Thus far in the literature, there have been a total of 32 supertribal-level names published for six families (Appendix I). Of those previously published, 28 were validly published, three invalidly so, and one published without typification. In this account, 17 of the previously published names are accepted and an additional 19 are newly proposed for five families, while the publication of two others are corrected and the tribal limits of some updated. A total of 36 supertribes are recognized as accepted for nine families (Appendix II).

Araceae

Of the now seven accepted subfamilies, Aroideae is both the largest and most morphologically complex (Zhao et al., 2022; Haigh et al., 2023). This complexity is reflected in the 26 tribes that have been recognized thus far. Here, four commonly recovered and informally recognized supratribal clades are formalized at supertribal level. These clades correspond to major groupings of tribes that were all once recognized as separate subfamilies until eventually being subsumed under the now expanded Aroideae s.l. concept that is currently accepted. Under the proposed classification here, only four tribes remain unplaced to supertribal level, all of which are monotypic. While the tribes and supertribes themselves are well-supported as monophyletic in molecular analyses, their arrangement along the phylogenetic backbone of the subfamily is still unresolved as placement of the isolated monotypic tribes remains disputed (Cusimano et al., 2011; Nauheimer et al., 2012; Zhao et al., 2022).

1. Arodae Ezedin, *supertrib. nov.*, based on Aroideae Arn., Botany: 136. 1832. [subfam. Aroideae]
TYPE: *Arum* L., Sp. Pl. 966. 1753.

Included tribes: Alocasieae A.Hay; Areae R. Br. ex Duby; Arisaemateae Nakai; Arisareae Dumort.; Arophyteae A. Lemee ex Bogner; Caladieae Schott; Colocasieae Brongn.; Peltandreae Engl.; Pistieae Lecoq & Juill.; Protareae Engl.; Thomsonieae Blume; and Typhonodoreae Engl.

This clade generally corresponds to the old core Aroideae sensu Keating (2004). Informally known as the *Dracunculus* clade in Cusimano et al. (2011: clade 37) and likewise corresponding to clade 47 in Fig. 3 of Nauheimer et al. (2012). A brief morphological characterization of this clade is given by Cusimano et al. (2011). The supertribe can be divided into three further subunits that have been informally named the *Amorphophallus*, *Colletogyne*, and *Pistia* clades by Cusimano et al. (2011), which respectively correspond to the clades numbered 48, 62, and 68 in Fig. 3 of Nauheimer et al. (2012). These nodes are not chosen to be named at rank level due to not being the most inclusive nodal grouping of tribes available, as well as not containing any morphologically significant features when compared to the broader *Dracunculus* clade (Nauheimer et al., 2012).

The genus *Typhonodorum* Schott occupies an isolated position in relation to *Peltandra* Raf. and is thus here recognized in its own tribe, for which a name is already available. The tribe Alocasieae was recently recognized to incorporate the four closely related genera *Alocasia* (Schott) G. Don, *Englerarum* Nauheimer & P.C.Boyce, *Leucocasia* Schott, and the recently described *Vietnamocasia* N.S. Lý, S.Y. Wong, & P.C. Boyce which form a decently- to well-supported clade (Lý et al., 2017; Baker et al., 2022).

2. Philodendrodae Ezedin, *supertrib. nov.*, based on Philodendroideae Engl., Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 39: 146. 1876. [subfam. Aroideae]
TYPE: *Philodendron* Schott, Wiener Z. Kunst 3: 780. 1829.

Included tribes: Aglaonemateae Engl.; Culcasieae Engl.; Nephthytideae Engl.; Philodendreae Schott; Spathicarpeae Schott; and Zantedeschieae Engl.

This clade roughly corresponds with the now defunct subfamily Philodendroideae sensu Keating (2004) upon the exclusion of four tribes: Anubiadeae, Montrichardieae, Stylochaetoneae, Zamioculcadeae. In molecular phylogenies, it is informally known as the *Zantedeschia* clade in Cusimano et al. (2011: clade 32) and likewise corresponds to clade 109 in Fig. 3 of Nauheimer et al. (2012). Support for this clade appears to range from good to strong, but interestingly appears to be non-monophyletic in the RAxML-ASTRAL trees in Figs. 1 and 2 of Zhao et al. (2022), with Spathicarpeae appearing to disassociate from the rest; although, the group appears monophyletic again in their IQTREE tree results in Appendix S6. The genera *Anubias* Schott and *Montrichardia* Cureg., both placed in their own monotypic tribes, while initially included by Keating (2004) in his concept of Philodendreae, appear to resolve in isolated positions outside it with strong support.

3. Schismatoglottidodae Ezedin, *supertrib. nov.*, based on Schismatoglottidoideae R.C. Keating, Ann. Missouri Bot. Gard. 91: 494. 2004. [subfam. Aroideae]
TYPE: *Schismatoglottis* Zoll. & Moritzi in A. Moritzi, Syst. Verz. Java: 83. 1846.

Included tribes: Cryptocoryneae Blume; Philonotieae S.Y. Wong & P.C. Boyce; and Schismatoglottideae Nakai

Informally known as the rheophytes clade or the

Schismatoglottid alliance and corresponds to the former subfamily Schismatoglottidoideae sensu Keating (2004). It is well-supported in molecular analyses in Cusimano et al. (2011: clade 28), in Fig. 3 of Nauheimer et al. (2012: clade 96), and in Baker et al. (2022). The clade is best known for exhibiting high levels of rheophytism, as its members are often found growing on rocks in slow to fast flowing streams and rivers, either in partial or total submergence. Other than the Neotropical *Philonotion* Schott, the entire supertribe is restricted to S and SE Asia, where many species are narrow endemics limited to specific rivers or drainage basins (Yeng, 2013).

4. Zamioculcadodae Ezedin, *supertrib. nov.*, based on Zamioculcadoideae, Bogner & Hesse, Aroideana 28: 13. 2005. [subfam. Aroideae]
TYPE: *Zamioculcas* Schott, Syn. Aroid.: 71. 1856.

Included tribes: Stylochaetoneae Schott and Zamioculcadeae Schott ex Engl.

This supertribe encompasses the expanded concept of the now defunct subfamily Zamioculcadoideae, with the two tribes recently having been subsumed under a further expanded Aroideae s.l. by Haigh et al. (2023). In phylogenetic studies, this clade is alternatively referred to as the *Stylochaeton* clade, corresponding to clade 25 of Cusimano et al. (2011) and clade 39 of Nauheimer et al. (2012). The clade is well-supported as sister to the remainder of the Aroideae, the latter now more clearly defined by unisexual flowers (Zhao et al., 2022). Morphologically, this supertribe may be diagnosed primarily via pollen, which differs from the remainder of Aroideae s.l. (Hesse et al., 2001).

Asteraceae

The rank of supertribe was first introduced into Asteraceae for the subfamily Asteroideae by Robinson (2004). Three were recognized in his account: Asterodae, Senecionodae, and Helianthodae. The first two are closely related and may even be reciprocal sisters, although there are prominent topological conflicts surrounding that clade requiring further investigation (Watson et al., 2020). Morphologically, Asterodae and Senecionodae are differentiated by the presence of raphides in the achene walls (Robinson, 2004). Due to currently containing only a single tribe (Senecioneae), however, the monotypic supertribe Senecionodae is not recognized here, as it offers no additional taxonomic information. Although, it could still be recognized if either the delimitation of Asterodae changes or if the tribe Senecioneae itself were to be reclassified as a supertribe and its current subtribes raised to tribal level.

5. Asterodae H. Rob., Phytologia 87(2): 73. 2005. [subfam. Asteroideae]
TYPE: *Aster* L., Sp. Pl. 872. 1753.

Includes tribes: Calenduleae Cass.; Anthemideae Cass.; Astereae Cass.; and Gnaphalieae Lecoq & Juill.

Informally known as the Astereae alliance. The delimitation of Asterodae remains unchanged from Robinson (2004) as it was originally defined with the four tribes. Phylogenetically, there appears to be a significant conflict in the topology between these four tribes, primarily with respect to the placement of Anthemideae, most likely due to reticulate evolution following ancient hybridization (Watson et al., 2020). The supertribe was initially designated in Robinson (2004), but was not validly published until a year later in Robinson (2005).

6. Helianthodae H. Rob., Phytologia 86: 118. 2004. [subfam. Asteroideae]
TYPE: *Helianthus* L., Sp. Pl. 904. 1753.

Included tribes: Athroismeae Panero; Bahieae B.G. Baldwin; Chaenactideae B.G. Baldwin; Coreopsideae Lindl.; Eupatorieae Cass.; Feddeeae Pruski, Herrera, Anderb., & Franc.-Ort.; Helenieae Lindl.; Heliantheae Cass.; Inuleae Cass.; Madieae Jeps.; Millerieae Lindl.; Neurolaeneae Rydb.; Perityleae B.G. Baldwin; Polymnieae Panero; and Tageteae Cass.

Informally known as the Heliantheae alliance. Helianthodae was originally delimited by Robinson (2004) to include seven tribes: Athroismeae, Coreopsideae, Eupatorieae, Helenieae, Heliantheae, Inuleae, and Tageteae. Here the supertribe is expanded to encompass the entire Heliantheae alliance, comprising 15 tribes which form a well-supported clade (Mandel et al., 2019). The linear sequence of Susanna et al. (2020) shows the tribes Athroismeae and Inuleae excluded from the Heliantheae alliance.

Brassicaceae

This family was the second after Poaceae to receive supertribes, with three supertribal names being published by Avetisyan (1990). However, due to the family's complex taxonomic history and unresolved phylogenetic relations, a supra-tribal classification was not capable of being properly implemented by taxonomists. Until very recently, this family had been without a stable internal classification with tribal boundaries experiencing regular disruption. Due to this, a reliable suprageneric classification system for the family had been unavailable until the recent advances made towards increased resolution of the family's internal relations (Guo et al., 2017; Nikolov et al., 2019; Hendriks et al., 2023). Despite lingering uncertainties, supra-tribal groups had nonetheless started being hypothesized since early molecular work in the family (Beilstein et al., 2008).

This recent taxonomic effort has now culminated in the recognition of two subfamilies, Aethionemoideae and Brassicoideae: the former with only *Aethionema* R. Br. and the latter containing the remainder of the family, classified into 58 tribes. Following the results of a recent family-wide phylogenomic study, a revised supertribal classification was proposed for the latter by German et al. (2023), with the authors proposing five such taxa. Their classification is mirrored here. In the currently proposed scheme, all but six tribes in the Brassicoideae are assigned to a supertribe. It should be noted that a subtribal classification has yet to be implemented in the subfamily, despite some tribes appearing large enough to potentially accommodate them.

7. Arabodae D.A. German et al., PhytoKeys 220: 129. 2023. [subfam. Brassicodae]
TYPE: *Arabis* L., Sp. Pl. 664. 1753.

Included tribes: Arabideae DC.; Alysseae DC.; Asperuginoideae Al-Shehbaz et al.; and Stevenieae Al-Shehbaz, D.A. German & M. Koch

In recent phylogenies known as Lineage IV. German et al. (2023) note that the limits of the supertribe are not yet stable due to discordance in the positions of all tribes except Arabideae.

8. Brassicodae V.E. Avet., Biol. Zhurn. Armenii 43: 602. 1990. (*Brassicidinae*) [subfam. Brassicoideae]
TYPE: *Brassica* L., Sp. Pl. 666. 1753.

Included tribes: Aphragmeae D.A. German & Al-Shehbaz; Bivonaeeae M. Koch & Warwick; Brassiceae DC.; Calepineae Horan.; Coluteocarpeae V.I. Dorf; Conringieae D.A. German & Al-Shehbaz; Eutremeae Al-Shehbaz, Beilstein, & E.A. Kellogg; Fouraeeae Al-Shehbaz, M. Koch, R. Karl, & D.A. German; Isatideae DC.; Kernereae Al-Shehbaz, Warwick, Mumm., & M. Koch; Plagiolobeae Khosravi & Eslami-Farouji; Schrenkielleae Al-Shehbaz et al.; Sisymbrieae DC.; Thelypodieae Prantl; and Thlaspieae DC.

In recent phylogenies known as Lineage II. The tribe Cochlearieae remains unplaced to supertribe due to discordant relations seen in nuclear versus plastid data (Hendriks et al., 2023).

9. Camelinodae D.A. German et al., PhytoKeys 220: 130. 2023. [subfam. Brassicoideae]
TYPE: *Camelina* Crantz, Stirp. Austr. Fasc. 1: 18. 1762.

Included tribes: Alyssopsideae Al-Shehbaz, Warwick, Mumm., & M. Koch; Arabidopsideae Al-Shehbaz et al.; Boechereae Al-Shehbaz, Beilstein, & E.A. Kellogg; Camelineae DC.; Cardamineae Dumort.; Crucihimalayeae D.A. German & Al-Shehbaz; Descurainieae Al-Shehbaz, Beilstein, & E.A. Kellogg; Erysimeae Dumort.; Halimolobeae Al-Shehbaz, Beilstein, & E.A. Kellogg; Hemilophieae Al-Shehbaz et al.; Lepidieae DC.; Malcolmieae Al-Shehbaz & Warwick; Microlepidieae Al-Shehbaz, Warwick, Mumm., & M. Koch; Oreophytoneae Al-Shehbaz, Warwick, Mumm., & M. Koch; Physarieae B.L. Rob.; Smelowskieae Al-Shehbaz, Beilstein, & E.A. Kellogg; Turritideae Buchenau; and Yinshanieae Al-Shehbaz, Warwick, Mumm., & M. Koch

In recent phylogenies known as Lineage I. Two genera remain unplaced to tribal level here (German et al., 2023).

10. Heliophilodae D.A. German et al., PhytoKeys 220: 131. 2023. [subfam. Brassicoideae]
TYPE: *Heliophila* Burm.f. ex L., Sp. Pl. ed. 2.: 926. 1763.

Included tribes: Anastaticeae DC.; Asteae Al-Shehbaz, Warwick, Mumm., & M. Koch; Biscutelleae Dumort.; Chamireae Sond.; Cremolobeae R. Br.; Eudemeae Al-Shehbaz, Warwick, Mumm., & M. Koch; Heliophileae DC.; Hillielleae H.L. Chen, T. Deng, J.P. Yue, Al-Shehbaz, & H. Sun; Iberideae Webb & Berthel.; Notothlaspideae Al-Shehbaz, Warwick, Mumm., & M. Koch; Schizopetaleae R. Br. ex Barnéoud; and Subularieae DC.

In recent phylogenies known as Lineage V. The tribe Scoliaxoneae is now synonymized under Asteae. The limits of this supertribe are not yet stable with the placement of five tribes still disputed (German et al., 2023).

11. Hesperodae D.A. German et al., PhytoKeys 220: 132. 2023. [subfam. Brassicoideae]
TYPE: *Hesperis* L., Sp. Pl. 663. 1753.

Included tribes: Anchonieae DC.; Buniadeae DC.; Chorisporeae Ledeb., C.A. Mey., & Bunge; Dontostemoneae Al-Shehbaz & Warwick; Euclidieae DC.; Hesperideae Prantl; and Shehbazieae D.A. German

In recent phylogenies known as Lineage III.

Cactaceae

The cactus family has no prior history of supertribal classification. The largest subfamily, Cactoideae, is commonly divided into three major groups: the tribe Cacteae and the informally named Cactoideae I and II clades (Guerrero et al., 2019). The latter two clades are further subdivided into two(–three) and three(–six) tribal-level clades, respectively. In addition to these three major clades, the tribes Copiapoeae, Fraileeae, Lymanbensonieae, and sometimes Rhipsalideae have variously been recovered forming part of the grade leading up to the core and thus remain unplaced to supertribe (Guerrero et al., 2019; Romeiro-Brito et al., 2022). Both supertribes recognized here have decent support, despite tribal limits within them remaining partially unresolved. Additionally, the family's overall phylogenetic backbone at the subfamily and tribal level is only still moderately resolved.

12. Cereodae Ezedin, *supertrib. nov.*, based on Cereoideae Drude in C. F. P. von Martius, Fl. Bras. 4(2): 193. 1890. [subfam. Cactoideae]
TYPE: *Cereus* Mill., Gard. Dict. Abr. ed. 4: s.p. 1754.

Included tribes: Cereeae Salm-Dyck and Notocacteae Buxb.

Informally known as the Cactoideae II or the RNBCT clade. Traditionally, the tribe Rhipsalideae has been included in this group, as several phylogenies have recovered the clade [Rhipsalideae [Notocacteae + Cereeae]] (Korotkova et al., 2010; Hernández-Hernández et al., 2014; Guerrero et al., 2019; Romeiro-Brito et al., 2022). However, whereas the [Notocacteae + Cereeae] clade is often recovered in molecular studies with good support, the support often weakens upon inclusion of the Rhipsalideae (Hernández-Hernández et al., 2011; Baker et al., 2022). In their

512-targeted loci phylogeny of the family, Romeiro-Brito et al. (2022) again recovered Rhipsalideae disassociating from the rest of the Cactoideae II clade. Due to the problematic molecular placement of Rhipsalideae, it is here excluded from the supertribe as a precautionary measure.

It should be noted that the expanded concept of Cereeae is recognized here, inclusive of Trichocereeae, which is now reduced to subtribal level, essentially covering the entire "BCT" clade. Currently, three dubiously supported subtribes are included within it: Cereinae, Trichocereinae, and Rebutiinae (Romeiro-Brito et al., 2022).

13. Echinocereodae Ezedin, *supertrib. nov.* [subfam. Cactoideae]
TYPE: *Echinocereus* Engelm. in F. A. Wislizenus, Mem. Tour N. Mexico: 91. 1848.

Low-growing, scandent, creeping, shrubby, epiphytic, epilithic, or tree-like and columnar. Stems erect, ascending, pendulous, or procumbent, cylindric or angular, sometimes flattened when epiphytic, ribs (2–)6–10(–30). Spines present (rarely absent), straight to sometimes hooked, hair-like or bristly to stout and harsh, short to very long. Flowers usually subapical or 1 to 2 per areole, (tubular-)campanulate, urceolate, funnelform, salverform, or rarely rotate (when epiphytic), diurnal or nocturnal, tubes short, scales small to prominent and sometimes numerous, stamens few to numerous, sometimes in 1 or 2 series. Fruits (sub)globose to oblong, sometimes berry-like, usually spiny, hairy, and/or scaly, fleshy (rarely dry), with floral remnants persistent or not.

Included tribes: Hylocereeae Buxb.; Leptocereeae Buxb.; and Pachycereeae Buxb.

Informally known as the Cactoideae I or the ACHLP clade. This clade is reported to be well-supported by several studies (Hernández-Hernández et al., 2011; Hernández-Hernández et al., 2014; Baker et al., 2022). The supertribe contains six major tribal-level clades: *Corryocactus*, *Pfeiffera*, [*Austrocactus* + *Eulychnia*], Leptocereeae, Hylocereeae, and Pachycereeae. The first two phylogenetically isolated genera, *Corryocactus* Britton & Rose and *Pfeiffera* Salm-Dyck, are commonly recovered in isolated positions along the basal grade successively sister to the rest of Cactoideae I, leading up to the "PHB" clade (Korotkova et al., 2010; Hernández-Hernández et al., 2011; Hernández-Hernández et al., 2014; Guerrero et al., 2019). However, they were found to be well-supported in a sister clade relationship including *Eulychnia* Phil. in Baker et al. (2022). Further work is needed to assess the tribal placement of these two genera, along with *Austrocactus* Britton & Rose and *Eulychnia*. For now, all four genera remain unplaced to tribal level.

Fabaceae

As one of the largest and morphologically diverse angiosperm subfamilies, it may at first seem rather surprising that the Leguminosae subfamily Papilionoideae has gone on so long without being assigned a supertribal classification. However, this is likely, in part, due to our poor understanding of supra-tribal groupings and the relations among subfamilies until only recently (Cardoso et al., 2013; LPWG, 2017; Zhao et al., 2021; Choi et al., 2022). Here, five supertribes are newly validated for five commonly referenced and molecularly well-supported groups in the Papilionoideae. Due to issues surrounding the tribal limits within the mirbelioids clade, comprising the paraphyletic sister tribal pair Bossiaeeae and Mirbelieae, along with the possibility of a future merger between the two (Barrett et al., 2021), the clade is left without supertribal designation. Recognition of these supra-tribal taxa allows for greater consolidation in the internal hierarchy of the Papilionoideae, where cladistic relations can now be summarized in the following short-hand manner: [Myroxylodae [Swartzieae [Cladrastieae [Exostyleae ["vataireoid" clade [[Dalbergiodae + Genistodae] [*Andira* clade [Baphieae [Hypocalypteae [[Bossiaeeae + Mirbelieae] [Galegodae + Phaseolodae]]]]]]]]]] (Zhao et al., 2021; Choi et al., 2022).

The mimosoid clade, formerly circumscribed as the subfamily Mimosoideae and now known to be deeply embedded within Caesalpinioideae s.l. (LPWG, 2017), is better suited to being entirely limited at tribal level (as Mimoseae) and is therefore not treated at supertribal level here. Although diverse, the deep ladder-like topology of the group's phylogenetic backbone (Koenen et al., 2020) hinders any meaningful multi-tribal classification. As such, it may be preferrable to split the mimosoids into subtribal-level clades, if any at all. Similarly, if the Australian mirbelioids are to be merged into a single tribe, a subtribal classification may be preferable as a means to preserve any internal divisions.

14. Dalbergiodae Ezedin, *supertrib. nov.*, based on Dalbergioideae Burnett, Outlines Bot.: 661. 1835. [subfam. Papilionoideae]
TYPE: *Dalbergia* L. f., Suppl. Pl.: 52. 1782.

Included tribes: Amorpheae Boriss. and Dalbergieae DC.

Informally known as the dalbergioids. The supertribe includes two tribes that are resolved in a sister relationship with good support (Wojciechowski et al., 2004; Zhao et al., 2021). Previously, the two tribes were united under the suggested name "Dalbergioids s.l." by Wojciechowski et al. (2004: Fig. 3) and Choi et al. (2022: Fig. 5). Here, the limits of Dalbergieae follow that indicated by Zhao et al. (2021: Fig. 3), which is essentially the sensu lato concept. Although not known by any reliable synapomorphies, according to Lavin et al. (2001), the dalbergioids (including Dipterygeae, now placed in the ADA clade) can be broadly defined by a base chromosome count of $x = 10$, wood with uniseriate stored rays, vegetative growth with glandular punctae, flowers with fused keel petals or staminal filaments, and seeds that do not accumulate nonprotein amino acids.

15. Galegodae Ezedin, *supertrib. nov.*, based on Galegoideae Schimp. in E. A. Strasburger, Lehrb. Bot.: 480. 1894. [subfam. Papilionoideae]
TYPE: *Galega* Tourn. ex L., Sp. Pl. 714. 1753.

Included tribes: Astragaleae Dumort.; Caraganeae Boriss.; Chesneyeae Ezedin; Cicereae Alef.; Galegeae Bronn; Glycyrrhizeae Rydb.; Hedysareae DC.; Loteae DC.;

Robinieae Hutch.; Sesbanieae Hutch.; Trifolieae Endl.; Vicieae DC.; and Wisterieae X.Y. Zhu

Informally known as the Hologalegina clade, comprising tribes that are largely temperate in distribution and herbaceous in habit (Wojciechowski et al., 2000). This supertribe is strongly supported as monophyletic and incorporates four informally named subclades which are not recognized at rank level: the IR-lacking clade, robinioids, vicioids, and hedysaroids (Zhao et al., 2021). The Hologalegina clade is chosen to be represented at supertribal level in preference over the latter four lower nodes, as it incorporates a greater extent of tribes, allowing for a more inclusive classification and deeper stratification of the subfamily.

A correction is made here to the publication of the tribe "Chesneyeae L. Duan, Zhao Y. Chang, & J. Wen," which is problematic as it was originally published in a Chinese language thesis dissertation by Duan (2015: 76). A copy of the whole Chinese dissertation was then attached as Suppl. Data File 1 in the journal article by Duan et al. (2021), where the authors made a brief reference to the tribal name in the main text of the journal article (on page 6). Yet due to being originally published in a non-serial dissertation work, along with the original Chinese diagnosis provided, the tribal name Chesneyeae is not considered validly published under ICN Art. 30.9 and Art. 39.2, respectively. Fortunately, the subtribal name Chesneyinae was already validly published a year earlier by Ranjbar et al. (2014: 82) with a full English diagnosis. Here, the subtribal name is formally raised to tribal rank with a full and direct reference to the original description in order to correct the publication of Chesneyeae.

Chesneyeae Ezedin, *trib. nov.*, based on Chesneyinae Ranjbar, F. Hajmoradi, & Waycott in Feddes Repert. 125(3–4): 82. TYPE: *Chesneya* Lindl. ex Endl., Gen. Pl.: 1275. 1840.

16. Genistodae Ezedin, *supertrib. nov.*, based on Genistoideae F. Schwarz, Forstl. Bot.: 347. Oct 1891. [subfam. Papilionoideae]
TYPE: *Genista* L., Sp. Pl. 709. 1753.

Included tribes: Brongniartieae Hutch.; Camoensieae Yakovlev; Crotalarieae Hutch.; Diplotropideae Yakovlev; Genisteae Bronn; Ormosieae Yakovlev; Podalyrieae Benth.; and Sophoreae Spreng. ex DC.

Informally known as the genistoids clade. Here, the expanded concept of the group is adopted, which includes Ormosieae (Wojciechowski et al., 2004). The monophyly of the clade as a whole is strongly supported in molecular studies (LPWG, 2017; Zhao et al., 2021). Although not known by any morphological synapomorphies, the genistoids are perhaps best known for their accumulation of quinolizidine alkaloids (Cardoso et al., 2013). The group also has been described as representing an evolutionarily transitory clade based on its topological position in relation to the rest of the Papilionoideae along with evidence from their flavonoid and alkaloid chemistry (Feitoza and Lima, 2021).

There are at least five genera that remain unplaced to tribal level within the supertribe: *Cabari* Gregório & D.B.O.S. Cardoso, *Neoharmsia* R. Vig., *Orphanodendron* Barneby & J.W. Grimes, *Pericopsis* Thwaites, and *Sakoanala* R. Vig. Despite sharing similar alkaloid chemistry with the genistoids, the exact placement of *Dermatophyllum* Scheele continuous to remain uncertain even after recent phylogenomic efforts (Choi et al., 2022). The tribe Diplotropideae is often referred to as "Leptolobieae" in recent literature; however, neither authorship nor original publication source for this name could be found.

17. Myroxylodae Ezedin, *supertrib. nov.* [subfam. Papilionoideae]
TYPE: *Myroxylon* L. f., Suppl. Pl.: 34. 1782.

Small understory to large and buttressed canopy trees. Leaves alternate, compound imparipinnate, (3–)6–19(–43)-foliolate, the leaflets often with translucent dots and streaks. Inflorescences paniculate or racemose, terminal, axillary, or ramiflorous to cauliflorous. Flowers dioecious or rarely androdioecious, variously papilionoid, sub-papilionoid, caesalpinioid, irregular, or mimosoid in general appearance, pedicellate, the pedicels often bracteolate; calyx persistent, often large, cup-shaped or tubular, truncate or lobed, sometimes splitting into (2–)3(–5) reflexed lobes at anthesis; petals present or reduced (rarely absent), 5-merous, the vexillum often large and prominent, the wing and keel petals similar, often reduced (rarely absent); stamens 10(–many), free to weakly connate at the base; ovary stipitate, ellipsoid to elongate-linear. Fruits leguminous or globose to ellipsoid drupe-like pods or rarely two-winged samaras.

Included tribes: Amburaneae Nakai; Angylocalyceae Yakovlev; and Dipterygeae Polhill

Informally known as the ADA clade. This small group of tribes is well-supported as sister to the remainder of the Papilionoideae (Cardoso et al., 2013; Zhao et al., 2021). Although monophyletic, this clade is not known to have any clear morphological synapomorphies, as both floral and fruit characters for the group are highly heterogeneous. This supertribe is almost entirely Neotropical, with the exception of the African genera *Angylocalyx* Taub., *Cordyla* Lour., *Mildbraediodendron* Harms, the Malagasy *Dupuya* J.H. Kirkbr., the Afro-Malagasy *Xanthocercis* Baill., and the Australian *Castanospermum* A. Cunn. ex Mudie. The members of this group are largely confined to tropical wet forests but are also found to a lesser extent in seasonally dry forests and woodlands. Several species often become large emergent canopy trees of commercial value.

Myroxylon (of Amburaneae) is chosen as the type genus. It is one of the oldest genus names published in the group and is among the most economically important, namely for its timber and aromatic balsam resin.

18. Phaseolodae Ezedin, *supertrib. nov.*, based on Phaseoloideae Burnett in Outlines Bot.: 661. 1835. [subfam. Papilionoideae]
TYPE: *Phaseolus* L., Sp. Pl. 723. 1753.

Included tribes: Abreae Baill.; Diocleeae Hutch.; Indigofereae Benth.; Millettieae Miq.; and Phaseoleae DC.

Informally known as the millettioids or phaseoloids clade. The tribal makeup of this clade still needs further clarification, while the limits of the current tribes need revision. Here, four tribes are listed, corresponding to the four largest cladistic divisions of the supertribe. There remain at least six genera that are as of yet unplaced to tribal level: *Aganope* Miq., *Austrosteenisia* R. Geesink, *Craibia* Harms & Dunn, *Dalbergiella* Baker f., *Dewevrea* Micheli, and *Ostryocarpus* Hook. f. (Zhao et al., 2021; Choi et al., 2022). The large and speciose tribe Phaseoleae s.l., which here encompasses Psoraleeae, is likely worthy of being given a subtribal classification. The supertribe is here cladistically defined as the most inclusive clade incorporating *Indigofera* L. and *Psoralea* L. but excluding Galegodae, which is the immediate sister to this clade (Zhao et al., 2021).

Despite being traditionally excluded from the phaseoloids clade, Indigofereae is here included in the supertribe, as it has a well-supported sister relationship to the rest of the supertribe (Choi et al., 2022). The monotypic Malagasy *Disynstemon* R. Vig. is currently considered unplaced within this supertribe (Vatanparast et al., 2018). The genus was previously recovered as sister to Indigofereae by Schrire et al. (2009), but the authors stopped short of including it within the tribe.

Poaceae

Supertribes have been recognized in the grass family since 1980, when the first names were published at this rank (Liu, 1980). In the latest revision of the internal classification of Poaceae, the rank of supertribe is recognized for the subfamilies Panicoideae and Pooideae, each currently containing 14 and 15 accepted tribes, respectively (Soreng et al., 2017). A total of eight supertribes have thus far been named to allow for further resolution of the family's internal hierarchy. Here, only five of them are accepted. Two of them, supertribes Panicodae and Poodae, are ignored, as they each currently contain a single tribe, Paniceae and Poeae, respectively. Thus, they are deemed unnecessary lest any new tribally ranked taxa be described or the current tribes themselves be split apart. Additionally, the formerly recognized supertribe Bambusodae is no longer accepted, as it merely encompasses two of the three tribes making up the subfamily Bambusoideae (Bambuseae and Olyreae), thus rendering it taxonomically ineffective as per Soreng et al. (2017).

19. Andropogonodae L. Liu, Acta Phytotax. Sin. 18: 325. 1980. (*Andropogodae*) [subfam. Panicoideae]
TYPE: *Andropogon* L., Sp. Pl. 1045. 1753.

Included tribes: Andropogoneae Dumort.; Arundinelleae Stapf; Jansenelleae Voronts.; and Paspaleae J. Presl

According to Soreng et al. (2017), members of the supertribe tend to exhibit a base chromosome number of x = 10 along with the occurrence of paired spikelets, which are commonly sessile and pedicelled.

20. Melicodae Soreng, J. Syst. Evol. 55(4): 263. 2017. [subfam. Pooideae]
TYPE: *Melica* L., Sp. Pl. 66. 1753.

Included tribes: Brylkinieae Tateoka and Meliceae Link ex Endl.

Some common traits of the supertribe include fused leaf sheaths, multi-flowered spikelets, two lodicules, two subapical styles with persistent bases, and caryopses that are hard without lipid and compound starch grains and with a long linear hilum (Soreng et al., 2017).

21. Nardodae Soreng, J. Syst. Evol. 55(4): 263. 2017. [subfam. Pooideae]
TYPE: *Nardus* L., Sp. Pl. 53. 1753.

Included tribes: Lygeeae Willk. and Nardeae W.D.J. Koch

This clade represents the second earliest diverging node in Pooideae. Each tribe contains a single genus, both of which apparently share little in common. In the linear sequence of Soreng et al. (2017), the tribes Duthieeae Röser & Jul. Schneid. and Phaenospermateae Renvoize & Clayton appear to be erroneously listed under this supertribe but are not immediately sister to the [Lygeeae + Nardeae] clade; instead, both tribes themselves form a sister clade that is successively sister to the rest of the subfamily. Thus, the clade [Duthieeae + Phaenospermateae] could possibly be recognized as a separate supertribe.

22. Stipodae L. Liu, Acta Phytotax. Sin. 18: 324. 1980. [subfam. Pooideae]
TYPE: *Stipa* L., Sp. Pl. 78. 1753.

Included tribes: Ampelodesmeae Tutin and Stipeae Martinov

Soreng et al. (2017) note that this supertribe could possibly be expanded to incorporate the early diverging tribes Duthieeae and Phaenospermateae on some morphological grounds, but then the supertribe would appear to be rendered paraphyletic. In the linear sequence of Soreng et al. (2017), the tribes Brachypodieae and Diarrheneae appear to be listed under this supertribe but are not sister to the [Ampelodesmeae + Stipeae] clade; instead, both tribes appear phylogenetically isolated, forming a grade leading up to the Triticodae.

23. Triticodae T.D. Macfarl. & L. Watson, Taxon 31(2): 192. 1982. (*Triticanae*) [subfam. Pooideae]
TYPE: *Triticum* L., Sp. Pl. 85. 1753.

Included tribes: Bromeae Martinov; Littledaleeae Soreng & J.I. Davis; and Triticeae Dumort.

Originally described by Macfarlane and Watson (1982). Sister to the Poodae (not recognized here), this supertribe is often compared to the latter and can be distinguished from it along some morphological lines. The presence of branched fructans appears to be a key chemical factor that distinguishes members of Triticodae from Poeae (Bonnett et al., 1997).

Rosaceae

Although not as large as the other families here in terms of genera and tribes, the Rosaceae were nonetheless assigned a supertribal classification by Potter et al. (2007). Three supertribes were recognized by those authors: two in subfamily Maloideae (sometimes as Amygdaloideae), currently with nine tribes, and one in subfamily Rosoideae, with six tribes. The two supertribes in Maloideae were used to group two pairs of tribes and are accepted here. However, the three supertribal names in this family were all originally published without a morphological description, the authors instead providing a purely cladistic definition based on molecular sequences. This does not meet the requirements for proper validation under the *Code* which requires morphological descriptions be used in validating names (Turland et al., 2018). Subsequent publications on Rosaceae have continued to refer to the supertribes, despite all three names remaining invalid (Zhang et al., 2017; Sun et al., 2018). Although the cladistic definitions given by Potter et al. (2007) remain unchanged, in order to validate their publication, brief diagnostic descriptions are provided here.

The single supertribe named for Rosoideae, the Rosodae, is neither recognized nor validated here, as it was originally defined to encompass the entire subfamily except *Filipendula* Mill., the sole member of tribe Ulmarieae. This does not convey additional taxonomic information, as the proposed supertribe essentially covers the entire subfamily minus the basalmost tribe. Additionally, in the Maloideae, despite the use of genomic-level data (Xiang et al., 2016; Sun et al., 2024), much confusion remains regarding the phylogenetic placements of the tribes Lyonothamneae, Sorbarieae, and Spiraeeae, likely due to ancient hybridization along their stems.

24. Kerriodae Ezedin, *supertrib. nov.* [subfam. Maloideae]
TYPE: *Kerria* DC., Trans. Linn. Soc. London 12: 156. 1818.

Shrubs to small trees; unarmed or rarely armed. Monoecious, rarely dioecious. Leaves simple, stipulate, margins once to doubly serrate (rarely entire). Inflorescences terminal, solitary on short shoots or racemose. Flowers (4-) or 5-merous, bisexual or unisexual, stamens many, pistils (2–)5(–8). Fruits drupaceous achenes or coccetums.

Included tribes: Kerrieae Focke and Exochordeae Schulze-Mentz ex Reveal

Originally circumscribed with two tribes, both of which have been consistently recovered as sisters. The placement of Sorbarieae in relation to the supertribe appears to fluctuate. It appears sister to the [Kerrieae + Exochordeae] clade with strong support in the phylogeny by Xiang et al. (2016: ML BS = 97) and more recently in the large tree by Baker et al. (2022). Yet another recent study demonstrated a notable conflict in the tribal topologies recovered from nuclear and plastid genomes (Hodel et al., 2022). In the prior study by Potter et al. (2007), Sorbarieae was recovered, with weak support, in an isolated position as sister to an even more weakly-defined [Spiraeeae + Pyrodae] clade. It is plausible the supertribe could be expanded to incorporate Sorbarieae; however, this may be unwarranted given the outstanding topological conflicts outside this clade.

25. Pyrodae Ezedin, *supertrib. nov.* [subfam. Maloideae]
TYPE: *Pyrus* L., Sp. Pl. 479. 1753.

Trees, shrubs, or perennial rhizomatous herbs. Leaves simple or 3-foliolate, stipulate, margins serrate. Inflorescences terminal, corymbose or compound racemes. Flowers 5-merous, bisexual, stamens 10–20, pistils 5. Fruits indehiscent fleshy pomes, achenes, or dry dehiscent follicles.

Included tribes: Gillenieae Maxim. and Maleae Small
The origins of this economically important supertribe, while still not entirely clear, appears to be the result of ancient hybridization between distantly related tribes—likely involving the ancestors of the modern-day Spiraeeae, Sorbarieae, and [Kerrieae + Exochordeae] clades (Hodel et al., 2022). Due to this, the sister clade to this supertribe is unresolved with the placement of either Spiraeeae or Sorbarieae appearing with near equal likelihood. Potter et al. (2007) make a preliminary note that members of this clade appear to exhibit an association with rust fungi from the genus *Gymnosporangium* (Pucciniaceae) and *Phragmidium* (Phragmidiaceae). The tribe Maleae is sometimes referred to as Pyreae in older publications.

The genus *Gillenia* Moench, traditionally placed in its own tribe, Gillenieae, was suggested for reclassification as a subtribe in an expanded Maleae s.l. by Sun et al. (2024), with the authors arguing against upholding a monotypic tribe for the genus. If this is preferred, the supertribe would become defunct. However, the tribe is retained here as there are some notable differences, mainly the diploid chromosome count of $x = 9$ (vs. tetraploid $x = 15$ or 17), herbaceous habit (vs. woody trees or shrubs), flowers with bilateral symmetry (vs. radial), and compound leaves (vs. simple or lobed).

Rubiaceae

Rubiaceae are among the most tribally diverse families. Formerly circumscribed with three subfamilies, recent phylogenomic studies have revealed conflicts between the traditional Cinchonoideae s.s. and Ixoroideae subfamilies, eventually leading to the proposal of merging the two into a single subfamily as Cinchonoideae s.l. (Rydin et al., 2017; Antonelli et al., 2021), more recently renamed to Dialypetalanthoideae (Razafimandimbison and Rydin, 2024). Now with merely two subfamilies together housing an overwhelming 68 tribes, the need for additional resolution between the rank of subfamily and tribe becomes even more justified. Recognizing this need early on, Robbrecht and Manen (2006) introduced the rank of supertribe for four well-known and well-supported supra-tribal clades in the Rubiaceae. The original published names contained the incorrect suffix ending "-*idinae*" which is corrected here. Five additional supertribes are newly validated here, giving a total of nine for the family, corresponding to the nine tribal alliances outlined in Razafimandimbison and Rydin (2024).

All tribes in Rubioideae except Coussareeae are assigned to a supertribe, whereas four tribes in Dialypetalanthoideae remain without supertribal placement. It should be noted that none of the 38 tribes of Dialypetalanthoideae s.l. currently have any accepted subtribal classifications. However, there are a few tribes large enough to potentially accommodate a future subtribal classification.

26. Cinchonodae Robbr. & Manen, Syst. & Geogr. Pl. 76: 134. 2006. (*Cinchonidinae*) [subfam. Dialypetalanthoideae]
TYPE: *Cinchona* L., Sp. Pl. 172. 1753.

Included tribes: Chiococceae Benth. & Hook. f.; Chioneae Razafim. & Rydin; Cinchoneae DC.; Guettardeae DC.; Hamelieae A. Rich. ex DC.; Hillieae Bremek. ex S.P. Darwin; Hymenodictyoneae Razafim. & B. Bremer; Isertieae A. Rich. ex DC.; Naucleeae Burnett; Rondeletieae Burnett; and Strumpfieae Delprete & Motley

This supertribe encompasses the subfamily Cinchonoideae *sensu stricto*, before its recent merger with Ixoroideae (see justifications by Antonelli et al., 2021; Razafimandimbison and Rydin, 2024). Long recognized as a distinct subfamily from Ixoroideae, this clade is here designated at supertribal level as a means of preserving its taxonomic recognition at rank level post-merger.

27. Coffeodae Ezedin, *supertrib. nov.* [subfam. Dialypetalanthoideae]
TYPE: *Coffea* L., Sp. Pl. 172. 1753.

Monocaul to pachycaul trees, shrubs, lianas, (hemi-) epiphytes or herbs. Monoecious or dioecious. Raphides absent. Stipules intrapetiolar, entire or apiculate (rarely fimbriate), rarely sheathing. Inflorescences (pseudo-)terminal or axillary, sessile or pedunculate, solitary to multiflorous, paniculate, cymose, rarely thyrsoid or corymbose. Flowers hermaphroditic (rarely gynomonoecious), 4–5(–12)-merous, calyx often persistent (rarely expanded and petaloid), corolla aestivation contorted left (rarely right), anthers exserted (rarely included), ovaries usually 2-locular. Fruits indehiscent fleshy berries or drupes (rarely dehiscent dry schizocarps). Pollen usually in monads, (2–)3–4(–7)-aperturate, usually colporate.

Included tribes: Alberteae Sond.; Augusteae Kainul. & B. Bremer; Bertiereae Bridson; Coffeeae DC.; Cordiereae A. Rich. ex DC.; Gardenieae A. Rich. ex DC.; Octotropideae Bedd.; Pavetteae Dumort.; and Sherbournieae Mouly & B. Bremer

Informally known as the Coffeeae alliance but alternatively referred to as the Gardenieae alliance by some older publications. Since Robbrecht and Manen (2006) had treated this clade as part of a broader Vanguerieae alliance, they never adopted a supertribal name for the group. This clade has long been known in the literature, as it represents a critical node in the family's phylogeny. A highly derived and well-diversified clade, it is nested deeply within the Cinchonoideae and is molecularly well established (Wikström et al., 2020; Antonelli et al., 2021). Of the included tribes, Alberteae is among the most morphologically deviant, whereas Octotropideae is the most poorly known and characterized. The tribe Airospermeae, formerly included here, was excluded by Razafimandimbison and Rydin (2024) due to lingering uncertainty in its placement with respect to this clade.

28. Dialypetalanthodae Ezedin, *supertrib. nov.* [subfam. Dialypetalanthoideae]
TYPE: *Dialypetalanthus* Kuhlm., Arch. Jard. Bot. Rio de Janeiro 4: 363. 1925.

Small to medium-sized trees or shrubs, rarely large trees or perennial herbs. Raphides absent, rod-like crystals and crystal sand sometimes present. Stipules interpetiolar or rarely intrapetiolar. Leaves simple, elliptic to ovate, decussate, or rarely whorled, petiolate, with or without domatia. Inflorescences terminal or axillary, thyrsoid or cymose (rarely solitary or fasciculate), bracteate, the bracts often persistent. Flowers bisexual, often pedicellate, (4-) or 5-merous, sometimes distylous, calyx campanulate to spreading, hypanthium present, narrowly obovoid, subcylindric, or globose, often lobed, corolla infundibular to salverform (hypocrateriform), often externally glabrous and pubescent inside, ovary 2-locular. Fruits capsules, globose to ellipsoid or flattened, rarely drupaceous, often with leathery to woody mesocarps, indehiscent or loculicidally (or septicidally) dehiscent. Seeds usually many, flattened, elliptic or circular, marginally winged or not.

Included tribes: Dialypetalantheae Reveal; Henriquezieae Benth. & Hook. f.; Posoquerieae Delprete; and Sipaneeae Bremek.

Informally referred to as the Dialypetalantheae (former Condamineeae) alliance, comprising four tribes which in recent analyses have been found to form a clade, although there appears to be some conflict in their placements. The topology [Dialypetalantheae [Sipaneeae [Henriquezieae + Posoquerieae]]] was recovered in the plastid phylogeny by Kainulainen et al. (2013: Fig. 2) with rather weak support (BS = 72, PP = 79). The same clade, albeit with the placement of the first two tribes switched, was recovered in the coalescent nuclear trees recovered by Antonelli et al. (2021) and Baker et al. (2022), both with strong support. Contrasting both plastid and nuclear results, the mitochondrial-based phylogeny of Rydin et al. (2017), with only Sipaneeae and Posoquerieae sampled, showed the two as non-monophyletic in all analyses of their dataset except for the non-clock analysis of protein coding sequences (Appendix S3), where the tribes resolved as sisters. Additional support comes from the analyses of Thureborn et al. (2022), with only Dialypetalantheae and Posoquerieae sampled and nonetheless both resolving as sisters with strong support (BS, LPP = 100). Despite the strong support values seen in the recent studies, however, the ASTRAL trees appear to consistently show high incongruence in tree topologies, with alternate topologies being at equal to near equal frequencies to the species tree (Antonelli et al., 2021; Thureborn et al., 2022).

This supertribe is morphologically ambiguous and made up of taxa almost entirely restricted to the Neotropics. The biogeographic exceptions to this are the Asian genera *Dolicholobium* A. Gray, *Emmenopterys* Oliv., *Mastixiodendron* Melch., and *Mussaendopsis* Baill., along with the Nearctic genus *Pinckneya* Michx. from the southeast United States. Most genera are small, with less than 20 species. The largest genus, *Simira* Aubl., with ca. 40 species, is also the most widespread, covering an extensive range which essentially overlaps with the entirety of the Neotropics realm (from Michoacán, México to Misiones, Argentina).

Dialypetalanthus (of Dialypetalantheae) automatically becomes the type of this supertribe by default due to its status as the type genus of a conserved family name, Dialypetalanthaceae (see Razafimandimbison and Rydin, 2024).

29. Ixorodae Robbr. & Manen, Syst. & Geogr. Pl. 76: 132. 2006. (*Ixoridinae*) [subfam. Dialypetalanthoideae]
TYPE: *Ixora* L., Sp. Pl. 110. 1753.

Included tribes: Aleisanthieae Mouly, J. Florence, & B. Bremer; Crossopterygeae F. White ex Bridson; Greeneeae Mouly, J. Florence, & B. Bremer; Ixoreae Benth. & Hook. f.; Scyphiphoreae Kainul. & B. Bremer; Trailliaedoxeae Kainul. & B. Bremer; and Vanguerieae Dumort.

Informally known as the Vanguerieae alliance. This alliance has consistently been recovered as monophyletic using both plastid (Kainulainen et al., 2013; Wikström et al., 2020) and mitochondrial (Rydin et al., 2017) data. This consensus was somewhat challenged when a recent phylogenomic study based on nuclear genes recovered the alliance as a non-monophyletic grade leading up to the Coffeeae alliance, albeit with poor support (Antonelli et al., 2021). This is in contrast to previous molecular results, which had recovered the Vanguerieae alliance as monophyletic with consistently good support. For now, the supertribe is accepted here with a cautionary note on possible cytonuclear discord resulting in conflicting topologies. Due to uncertainty in its placement, tribe Jackieae is currently considered unplaced to supertribe (Razafimandimbison and Rydin, 2024).

30. Lasianthodae Ezedin, *supertrib. nov.* [subfam. Rubioideae]
TYPE: *Lasianthus* Jack, Trans. Linn. Soc. London 14: 125. 1823.

Herbs or (sub)woody (sub)shrubs. Raphides present. Stipules interpetiolar, often persistent. Leaves opposite, subsessile to petiolate, rarely reduced or absent. Flowers axillary or rarely terminal, solitary, paired, cymose, or fasciculate, sessile or pedunculate, (4-) or 5-merous, corolla salverform or funnelform, aestivation valvate or imbricate, often villous inside, anthers included or exserted. Fruits indehiscent drupes or dehiscent dry capsules, usually with persistent calyx.

Included tribes: Lasiantheae B. Bremer & Manen and Perameae Bremek. ex S.P. Darwin

Informally known as the Perameeae alliance. The two tribes are in a well-supported sister relationship according to multiple phylogenetic studies (Antonelli et al., 2021; Baker et al., 2022; Thureborn et al., 2022). Members of this group are distributed pantropically and are generally characterized by their shrubby habit. While the two tribes appear to share little in common morphologically, the genus *Perama* Aubl. is noted to be an aluminum hyperaccumulator similar to that of *Lasianthus* and *Trichostachys* Hook. f. (Robbrecht and Manen, 2006). The inferred ancestral area of this supertribe is the Neotropics, with either long-distance dispersal or boreotropical expansion into the Paleotropics occurring in Lasiantheae within the last ca. 50 Ma (Smedmark et al., 2014).

31. Mussaendodae Ezedin, *supertrib. nov.*, based on Mussaendoideae Luerss., Handb. Syst. Bot. 2: 1083. [subfam. Dialypetalanthoideae]
TYPE: *Mussaenda* Burm. ex L., Sp. Pl. 177. 1753.

Included tribes: Mussaendeae Benth. & Hook. f. and Sabiceeae A. Stahl

Informally known as the Mussaendeae alliance. This clade is well-supported and occupies a position along a grade within the former subfamily Ixoroideae, sister to a large clade that includes both the Vanguerieae and Coffeeae alliances (Razafimandimbison and Rydin, 2024). The sister relationship of these two tribes is supported by several studies (Kainulainen et al., 2013; Rydin et al., 2017; Wikström et al., 2020).

32. Psychotriodae Robbr. & Manen, Syst. & Geogr. Pl. 76: 136. 2006. (*Psychotriidinae*) [subfam. Rubioideae]
TYPE: *Psychotria* L., Syst. Nat. ed. 10, 2: 929. 1759.

Included tribes: Craterispermeae Verdc.; Gaertnereae Endl.; Mitchelleae Razafim. & B. Bremer; Morindeae Burnett; Palicoureeae Robbr. & Manen; Prismatomerideae Y.Z. Ruan; Psychotrieae Cham. & Schltdl.; Schizocoleeae Rydin & B. Bremer; and Schradereae Bremek.

Informally known as the Psychotrieae alliance. Sister to the Spermacoceae alliance, from which it differs by its primarily woody habit. Biogeographical analyses show the tribal alliance had originated in Africa during the late Cretaceous, with numerous subsequent long-distance dispersals across oceans, continents, and island systems to result in its current pantropical distribution (Razafimandimbison et al., 2017).

33. Rubiodae Robbr. & Manen, Syst. & Geogr. Pl. 76: 137. 2006. (*Rubiidinae*) [subfam. Rubioideae]
TYPE: *Rubia* L., Sp. Pl. 109. 1753.

Included tribes: Anthospermeae Cham. & Schltdl.; Argostemmateae Bremek. ex Verdc.; Cyanoneuroneae Razafim. & B. Bremer; Danaideae B. Bremer & Manen; Dunnieae Rydin & B. Bremer; Foonchewieae R.J. Wang; Knoxieae Benth. & Hook. f.; Paederieae DC.; Putorieae Lange; Rubieae Baill.; Spermacoceae Cham. & Schltdl. ex DC.; and Theligoneae Baill.

Informally known as the Spermacoceae alliance. Sister to the Psychotrieae alliance, from which it differs by its primarily herbaceous habit. Despite woodiness being considered an ancestral trait to the group, with the basalmost tribe Danaideae being woody, secondary woodiness has evolved in some of the more derived tribes such as Knoxieae and Spermacoceae (Lens et al., 2009). Members of the supertribe are found in a wide variety of climates, both tropical and temperate.

34. Urophyllodae Ezedin, *supertrib. nov.*, based on Urophylloideae Bremek. ex S.P. Darwin in Taxon 25: 607. 1976. [subfam. Rubioideae]
TYPE: *Urophyllum* Wall. in Roxb., Fl. Ind. 2: 184. 1824.

Included tribes: Colletoecemateae Rydin & B. Bremer; Ophiorrhizeae Bremek. ex Verdc.; Seychelleeae Razafim., Kainul., & Rydin; Temnopterygeae Razafim. & Rydin; and Urophylleae Bremek. ex Verdc.

Informally referred to as the SCOUT clade by Thureborn et al. (2022) and the Urophylleae alliance by Razafimandimbison and Rydin (2024). This clade has been recovered as well-supported by several plastid and nuclear analyses (Kainulainen et al., 2013; Antonelli et al., 2021; Baker et al., 2022; Thureborn et al., 2022). However, in the mitochondrial analyses of Rydin et al. (2017), Ophiorrhizeae appears to disassociate from the [Colletoecemateae + Urophylleae] clade.

Sapindaceae

Until recently, this family had no history of supertribal classification. However, advances in the understanding of the phylogeny of Sapindaceae have allowed for the recognition of supra-tribal clades at rank level in the largest and most diverse subfamily, Sapindoideae. The supertribe Paulliniodae was recently proposed by Acevedo-Rodríguez et al. (2017) to encompass four tribes. The publication of the supertribal name, which was not properly published by the authors, is corrected here and its limits expanded to cover a far greater extent of tribes. Additionally, a second supertribe is newly designated here to contain the remaining sister clade. Within Sapindoideae, all but four tribes are now placed into a supertribe, with internal relations summarized as follows: [Ungnadieae [Koelreuterieae [Schleichereae [Nephelieae [Cupaniodae + Paulliniodae]]]]] (Buerki et al., 2021). It should be noted that there are no tribes in Sapindoideae which currently have an assigned subtribal classification, although there are tribes within the subfamily which appear large enough to possibly allow future subtribal classifications (i.e., Cupanieae, Nephelieae, Sapindeae).

35. Cupaniodae Ezedin, *supertrib. nov.* [subfam. Sapindoideae]
TYPE: *Cupania* L., Sp. Pl. 200. 1753.

Trees or shrubs. Domatia often present. Leaves compound (rarely simple), alternate, 1- or 2-pinnate, pari- or imparipinnate, (2–)4–8(–22)-jugate, margins serrate or entire. Inflorescences (pseudo-)terminal, axillary, ramiflorous, or cauliflorous thyrsoid panicles or rarely racemose, with bracts and bracteoles often present. Flowers actinomorphic, functionally unisexual (rarely bisexual), sepals (4–)5(–6) or rarely absent, petals (4–)5(–7) or rarely absent, often clawed and/or with appendages, stamens (4–)5–8(–14), disk (semi)annular to 5–8-lobed, ovary (2–)3(–4)-carpellate, 1 ovule per carpel, stigma with 2–3 lobes or branches. Fruits dry dehiscent 1–3-locular capsules (rarely fleshy or indehiscent), sometimes hairy inside and out. Seeds usually arillate. Pollen syncolporate to parasyncolporate (rarely colporate).

Included tribes: Cupanieae Blume and Stadmanieae Buerki & Callm.

Recovered as monophyletic and sister to Paulliniodae s.l. with strong support by Buerki et al. (2021) as the clades numbered 20 and 21. Likewise, the sister relation of the two tribes is well-supported in the analyses by Baker et al. (2022). Cupanieae, the largest tribe in the family, is pantropical, while Stadmanieae is restricted to the West Indian Ocean Islands region and tropical Africa.

36. Paulliniodae Avec.-Rodr. et al., Syst. Bot. 42: 108. 2017. [subfam. Sapindoideae]
TYPE: *Paullinia* L., Sp. Pl. 365. 1753.

Trees, shrubs, or lianas. Leaves compound (rarely simple and lobed), alternate, 1(–3)-pinnate, (1–)3(–5)-foliolate, or 1- or 2-ternate, pari- or imparipinnate, (1–)4–6(–8)-jugate, margins usually serrate. Inflorescences (pseudo-)terminal, axillary thyrses or cymes, or solitary (rarely in racemes or spikes). Flowers zygomorphic (rarely actinomorphic), bisexual or functionally unisexual, sepals 4–5(–7), petals (2–)4–5(–8) or rarely absent, often with appendages, sometimes clawed, stamens 5–8(–30), disk (semi)annular to (2–)4–8(–10)-lobed, ovary (1–)2–3(–5)-carpellate, 1 ovule per carpel, stigma (sub)capitate or with 3 lobes or branches. Fruits dry or (sub)fleshy, dehiscent or sometimes indehiscent, 1–3(–5)-locular capsules or schizocarps splitting into (1–)3 samaroid mericarps, the mericarps usually 1-winged. Seeds usually exarillate. Pollen usually colporate (rarely brevicolporate).

Included tribes: Athyaneae Acev.-Rodr.; Blomieae Buerki & Callm.; Bridgesieae Acev.-Rodr.; Guindilieae Buerki, Callm., & Acev.-Rodr.; Haplocoeleae Buerki & Callm.; Melicocceae Blume.; Thouiniaeae Blume; Tristiropsideae Buerki & Callm.; Paullinieae DC.; and Sapindeae DC.

Although the supertribe was originally published with an English description, there are two issues surrounding its validation. First, the name was published without direct ascription or association of author(s) alongside the description, in a paper authored by ten people. In this case, according to Note 5 of Art. 46 and Art. 46.6 of the *Code* (Turland et al., 2018), the correct author(s) of the supertribe Paulliniodae are all ten authors of the paper (Acevedo-Rodríguez et al., 2017). Secondly, the supertribe was published without indication of the type. In this case, the type genus for Paulliniodae would be *Paullinia* L., but this was never cited by Acevedo-Rodríguez et al. (2017: 108). This goes against Art. 7.1 of the *Code*, which states names of taxa at the rank of family and below must include indication of the nomenclatural type to be validly published (Turland et al., 2018). The publication of the supertribe is corrected here.

Another separate issue involves the proposed limits of the supertribe. Originally, the supertribe was delimited to encompass only four tribes representing the well-supported yet deeply-nested clade [Athyaneae [Bridgesieae [Thouiniaeae + Paullinieae]]] (Buerki et al., 2021). This clade was once formerly recognized as the subfamily Paullinioideae Burnett and then subsequently at tribal level as Paullinieae s.l. (Acevedo-Rodríguez et al., 2011). However, this does not represent the broadest available well-supported clade. Thus, the delimitation of the supertribe becomes phylogenetically uninformative toward Sapindoideae's major internal divisions. Here, Paulliniodae is expanded to encompass six additional tribes which form the broadest, most inclusive, well-supported node possible, corresponding to the clades numbered 10–19 in Buerki et al. (2021: Fig. 1, S2, S3).

The new Paulliniodae s.l. can be cladistically defined as the most inclusive clade incorporating *Tristira* Radlk. and *Paullinia* but excluding the broadest clade containing *Tina* Schult. and *Beguea* Capuron. Due to the considerable changes to its circumscription proposed here, an emended general description inclusive of all 10 tribes is provided. Morphologically, Paulliniodae s.l. may now be characterized by its predominantly zygomorphic flowers (sometimes weakly so) and seeds mostly lacking arils, as opposed to the entirely actinomorphic Cupaniodae with seeds that are mostly arillate.

If recognition of the former Paulliniodae s.s. is desired at rank level, the four innermost tribes may again be reduced to subtribes, as they previously were under the broadened Paullinieae s.l. tribal concept (Acevedo-Rodríguez et al., 2011). This solution may also prove beneficial given the rank of subtribe has yet to be filled in the subfamily. However, Acevedo-Rodríguez et al. (2017) state that it would not be preferrable to recognize the *sensu lato* concept of tribe Paullinieae, instead arguing to keep it limited to its *sensu stricto* delimitation to allow for ease of morphological recognition at tribal level. Their suggestion is followed here, and the tribal limits retained as is.

Literature Cited

Acevedo-Rodríguez, P., P. C. van Welzen, F. Adema and R. W. J. M. van der Ham. 2011. Sapindaceae. Pages 357–407 in K. Kubitzki ed., Flowering Plants. Eudicots: Sapindales, Cucurbitales, Myrtaceae, Springer Berlin Heidelberg, Berlin, Heidelberg.

Acevedo-Rodríguez, P., K. J. Wurdack, M. S. Ferrucci, G. Johnson, P. Dias, R. G. Coelho, et al. 2017. Generic Relationships and Classification of Tribe Paullinieae (Sapindaceae) with a New Concept of Supertribe Paulliniodae. Systematic Botany 42, No. 1: 96–114.

Antonelli, A., J. J. Clarkson, K. Kainulainen, O. Maurin, G. E. Brewer, A. P. Davis, 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, No. 7: 1143–1165.

Avetisyan, V. E. 1990. New suprageneric taxa of the family Brassicaceae. Biologicheskii Zhurnal Armenii 43, No. 7: 601–602.

Baker, W. J., P. Bailey, V. Barber, A. Barker, S. Bellot, D. Bishop, et al. 2022. A Comprehensive Phylogenomic Platform for Exploring the Angiosperm Tree of Life. Systematic Biology 71, No. 2: 301–319.

Barrett, R. L., J. A. R. Clugston, L. G. Cook, M. D. Crisp, P. C. Jobson, B. J. Lepschi, et al. 2021. Understanding Diversity and Systematics in Australian Fabaceae Tribe Mirbelieae. Diversity 13, No. 8: 391.

Beilstein, M. A., I. A. Al-Shehbaz, S. Mathews and E. A. Kellogg. 2008. Brassicaceae phylogeny inferred from phytochrome A and ndhF sequence data: tribes and trichomes revisited. American Journal of Botany 95, No. 10: 1307–1327.

Bonnett, G. D., I. M. Sims, R. J. Simpson and A. J. Cairns. 1997. Structural diversity of fructan in relation to the taxonomy of the Poaceae. New Phytologist 136, No. 1: 11–17.

Buerki, S., M. W. Callmander, P. Acevedo-Rodriguez, P. P. Lowry II, J. Munzinger, P. Bailey, et al. 2021. An updated infra-familial classification of Sapindaceae based on targeted enrichment data. American Journal of Botany 108, No. 7: 1234–1251.

Cardoso, D., R. T. Pennington, L. P. de Queiroz, J. S. Boatwright, B. E. Van Wyk, M. F. Wojciechowski, et al. 2013. Reconstructing the deep-branching relationships of the papilionoid legumes. South African Journal of Botany 89: 58–75.

Choi, I.-S., D. Cardoso, L. P. de Queiroz, H. C. de Lima, C. Lee, T. A. Ruhlman, et al. 2022. Highly Resolved Papilionoid Legume Phylogeny Based on Plastid Phylogenomics. Frontiers in Plant Science 13, No. 823190: 1–22.

Cusimano, N., J. Bogner, S. J. Mayo, P. C. Boyce, S. Y. Wong, M. Hesse, et al. 2011. Relationships within the Araceae: Comparison of morphological patterns with molecular phylogenies. American Journal of Botany 98, No. 4: 654–668.

Duan, L., S.-J. Li, C. Su, Y. Sirichamorn, L.-N. Han, W. Ye, et al. 2021. Phylogenomic framework of the IRLC legumes (Leguminosae subfamily Papilionoideae) and intercontinental biogeography of tribe Wisterieae. Molecular Phylogenetics and Evolution 163: 107235.

Feitoza, R. B. B. and H. R. P. Lima. 2021. Chemosystematic and evolutionary trends of the genistoid clade sensu stricto (Papilionoideae, Fabaceae). Phytochemistry 183: 112616.

German, D. A., K. P. Hendriks, M. A. Koch, F. Lens, M. A. Lysak, C. D. Bailey, et al. 2023. An updated classification of the Brassicaceae (Cruciferae). PhytoKeys 220: 127–144.

Guerrero, P. C., L. C. Majure, A. Cornejo-Romero and T. Hernández-Hernández. 2019. Phylogenetic Relationships and Evolutionary Trends in the Cactus Family. Journal of Heredity 110, No. 1: 4–21.

Guo, X., J. Liu, G. Hao, L. Zhang, K. Mao, X. Wang, et al. 2017. Plastome phylogeny and early diversification of Brassicaceae. BMC Genomics 18, No. 176: 1–9.

Haigh, A. L., M. Gibernau, O. Maurin, P. Bailey, M. M. Carlsen, A. Hay, et al. 2023. Target sequence data shed new light on the infrafamilial classification of Araceae. American Journal of Botany 110, No. 2: e16117.

Hendriks, K. P., C. Kiefer, I. A. Al-Shehbaz, C. D. Bailey, A. Hooft van Huysduynen, L. A. Nikolov, et al. 2023. Global Brassicaceae phylogeny based on filtering of 1,000-gene dataset. Current Biology 33, No. 19: 4052-4068.e6.

Hernández-Hernández, T., H. M. Hernández, J. A. De-Nova, R. Puente, L. E. Eguiarte and S. Magallón. 2011. Phylogenetic relationships and evolution of growth form in Cactaceae (Caryophyllales, Eudicotyledoneae). American Journal of Botany 98, No. 1: 44–61.

Hernández-Hernández, T., J. W. Brown, B. O. Schlumpberger, L. E. Eguiarte and S. Magallón. 2014. Beyond aridification: multiple explanations for the elevated diversification of cacti in the New World Succulent Biome. New Phytologist 202, No. 4: 1382–1397.

Hesse, M., J. Bogner, H. Halbritter and M. Weber. 2001. Palynology of the perigoniate Aroideae: Zamioculcas, Gonatopus and Stylochaeton (Araceae). Grana 40, No. 1-2: 26–34.

Hodel, R. G. J., E. A. Zimmer, B.-B. Liu and J. Wen. 2022. Synthesis of Nuclear and Chloroplast Data Combined With Network Analyses Supports the Polyploid Origin of the Apple Tribe and the Hybrid Origin of the Maleae—Gillenieae Clade. Frontiers in Plant Science 12, No. 820997: 1–15.

Kainulainen, K., S. G. Razafimandimbison and B. Bremer. 2013. Phylogenetic relationships and new tribal delimitations in subfamily Ixoroideae (Rubiaceae). Botanical Journal of the Linnean Society 173, No. 3: 387–406.

Keating, R. C. 2004. Vegetative Anatomical Data and Its Relationship to a Revised Classification of the Genera of Araceae. Annals of the Missouri Botanical Garden 91, No. 3: 485–494.

Koenen, E. J. M., C. Kidner, É. R. de Souza, M. F. Simon, J. R. Iganci, J. A. Nicholls, et al. 2020. Hybrid capture of 964 nuclear genes resolves evolutionary relationships in the mimosoid legumes and reveals the polytomous origins of a large pantropical radiation. American Journal of Botany 107, No. 12: 1710–1735.

Korotkova, N., L. Zabel, D. Quandt and W. Barthlott. 2010. A phylogenetic analysis of Pfeiffera and the reinstatement of Lymanbensonia as an independently evolved lineage of epiphytic Cactaceae within a new tribe Lymanbensonieae. Willdenowia 40, No. 2: 151–172.

Lavin, M., R. T. Pennington, B. B. Klitgaard, J. I. Sprent, H. C. de Lima and P. E. Gasson. 2001. The dalbergioid legumes (Fabaceae): delimitation of a pantropical monophyletic clade. American Journal of Botany 88, No. 3: 503–533.

Lens, F., I. Groeninckx, E. Smets and S. Dessein. 2009. Woodiness within the Spermacoceae–Knoxieae alliance (Rubiaceae): retention of the basal woody condition in Rubiaceae or recent innovation? Annals of Botany 103, No. 7: 1049–1064.

Liu, L. 1980. The characteristics and geographical sudivision of the Gramineae flora in Xizang (Tibet). Acta Phytotaxonomica Sinica 18, No. 3: 316–327.

LPWG. 2017. A new subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny: The Legume Phylogeny Working Group (LPWG). Taxon 66, No. 1: 44–77.

Lý, N.-S., W. S. Yeng, T. Haevermans, N. V. Dư and P. C. Boyce. 2017. Vietnamocasia, a new genus from Central Vietnam belonging to the Alocasia-Colocasia clade (Araceae). Phytotaxa 303, No. 3: 253–263.

Macfarlane, T. D. and L. Watson. 1982. The Classification of Poaceae Subfamily Pooideae. Taxon 31, No. 2: 178–203.

Mandel, J. R., R. B. Dikow, C. M. Siniscalchi, R. Thapa, L. E. Watson and V. A. Funk. 2019. A fully resolved backbone phylogeny reveals numerous dispersals and explosive diversifications throughout the history of Asteraceae. Proceedings of the National Academy of Sciences 116, No. 28: 14083–14088.

Nauheimer, L., D. Metzler and S. S. Renner. 2012. Global history of the ancient monocot family Araceae inferred with models accounting for past continental positions and previous ranges based on fossils. New Phytologist 195, No. 4: 938–950.

Nikolov, L. A., P. Shushkov, B. Nevado, X. Gan, I. A. Al-Shehbaz, D. Filatov, et al. 2019. Resolving the backbone of the Brassicaceae phylogeny for investigating trait diversity. New Phytologist 222, No. 3: 1638–1651.

Potter, D., T. Eriksson, R. C. Evans, S. Oh, J. E. E. Smedmark, D. R. Morgan, et al. 2007. Phylogeny and classification of Rosaceae. Plant Systematics and Evolution 266, No. 1: 5–43.

Ranjbar, M., F. Hajmoradi, M. Waycott and K.-J. Van Dijk. 2014. A phylogeny of the tribe Caraganeae (Fabaceae) based on DNA sequence data from ITS. Feddes Repertorium 125, No. 3-4: 78–84.

Razafimandimbison, S. G., K. Kainulainen, N. Wikström and B. Bremer. 2017. Historical biogeography and phylogeny of the pantropical Psychotrieae alliance (Rubiaceae), with particular emphasis on the Western Indian Ocean Region. American Journal of Botany 104, No. 9: 1407–1423.

Razafimandimbison, S. G. and C. Rydin. 2024. Phylogeny and classification of the coffee family (Rubiaceae, Gentianales): Overview and outlook. Taxon: 1–45.

Reveal, J. L. 2012. Newly required infrafamilial names mandated by changes in the Code of Nomenclature For Algae, Fungi, and Plants. Phytoneuron 2012-33: 1–32.

Robbrecht, E. and J.-F. Manen. 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, No. 1: 85–145.

Robinson, H. 2004. New supertribes, Helianthodae and Senecionodae, for the subfamily Asteroideae (Asteraceae). Phytologia 86, No. 3: 116–120.

———. 2005. Validation of the supertribe Asterodae. Phytologia 87, No. 2: 73–74.

Romeiro-Brito, M., M. C. Telhe, D. T. Amaral, F. F. Franco and E. M. Moraes. 2022. A target Capture Probe Set Useful for Deep- and Shallow-Level Phylogenetic Studies in Cactaceae. Genes 13, No. 4: 707.

Rydin, C., N. Wikström and B. Bremer. 2017. Conflicting results from mitochondrial genomic data challenge current views of Rubiaceae phylogeny. American Journal of Botany 104, No. 10: 1522–1532.

Schrire, B. D., M. Lavin, N. P. Barker and F. Forest. 2009. Phylogeny of the tribe Indigofereae (Leguminosae–Papilionoideae): Geographically structured more in succulent-rich and temperate settings than in grass-rich environments. American Journal of Botany 96, No. 4: 816–852.

Smedmark, J. E. E., S. G. Razafimandimbison, N. Wikström and B. Bremer. 2014. Inferring geographic range evolution of a pantropical tribe in the coffee family (Lasiantheae, Rubiaceae) in the face of topological uncertainty. Molecular Phylogenetics and Evolution 70: 182–194.

Soreng, R. J., P. M. Peterson, K. Romaschenko, G. Davidse, J. K. Teisher, L. G. Clark, et al. 2017. A worldwide phylogenetic classification of the Poaceae (Gramineae) II: An update and a comparison of two 2015 classifications. Journal of Systematics and Evolution 55, No. 4: 259–290.

Sun, J., S. Shi, J. Li, J. Yu, L. Wang, X. Yang, et al. 2018. Phylogeny of Maleae (Rosaceae) Based on Multiple Chloroplast Regions: Implications to Genera Circumscription. BioMed Research International 2018: 7627191.

———., D. Zhao, P. Qiao, Y. Wang, P. Wu, K. Wang, et al. 2024. Phylogeny of genera in Maleae (Rosaceae) based on chloroplast genome analysis. Frontiers in Plant Science 15, No. 1367645: 1–10.

Susanna, A., B. G. Baldwin, R. J. Bayer, J. M. Bonifacino, N. Garcia-Jacas, S. C. Keeley, et al. 2020. The classification of the Compositae: A tribute to Vicki Ann Funk (1947–2019). Taxon 69, No. 4: 807–814.

Thureborn, O., S. G. Razafimandimbison, N. Wikström and C. Rydin. 2022. Target capture data resolve recalcitrant relationships in the coffee family (Rubioideae, Rubiaceae). Frontiers in Plant Science 13, No. 967456: 1–19.

Turland, N., J. Wiersema, F. Barrie, W. Greuter, D. Hawksworth, P. Herendeen, et al. 2018. International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile. Koeltz Botanical Books.

Vatanparast, M., A. Powell, J. J. Doyle and A. N. Egan. 2018. Targeting legume loci: A comparison of three methods for target enrichment bait design in Leguminosae phylogenomics. Applications in Plant Sciences 6, No. 3: e1036.

Watson, L., H. Clifford and M. Dallwitz. 1985. The Classification of Poaceae: Subfamilies and Supertribes. Australian Journal of Botany 33, No. 4: 433–484.

Watson, L. E., C. M. Siniscalchi and J. Mandel. 2020. Phylogenomics of the hyperdiverse daisy tribes: Anthemideae, Astereae, Calenduleae, Gnaphalieae, and Senecioneae. Journal of Systematics and Evolution 58, No. 6: 841–852.

Wikström, N., B. Bremer and C. Rydin. 2020. Conflicting phylogenetic signals in genomic data of the coffee family (Rubiaceae). Journal of Systematics and Evolution 58, No. 4: 440–460.

Wojciechowski, M. F., M. J. Sanderson, K. P. Steele and A. Liston. 2000. Molecular phylogeny of the "temperate herbaceous tribes" of papilionoid legumes: a supertree approach. Advances in Legume Systematics 9: 277–298.

———., M. Lavin and M. J. Sanderson. 2004. A phylogeny of legumes (Leguminosae) based on analysis of the plastid matK gene resolves many well-supported subclades within the family. American Journal of Botany 91, No. 11: 1846–1862.

Xiang, Y., C.-H. Huang, Y. Hu, J. Wen, S. Li, T. Yi, et al. 2016. Evolution of Rosaceae Fruit Types Based on Nuclear Phylogeny in the Context of Geological Times and Genome Duplication. Molecular Biology and Evolution 34, No. 2: 262–281.

Yeng, W. S. 2013. Rheophytism in Bornean Schismatoglottideae (Araceae). Systematic Botany 38, No. 1: 32–45.

Zhang, S.-D., J.-J. Jin, S.-Y. Chen, M. W. Chase, D. E. Soltis, H.-T. Li, et al. 2017. Diversification of Rosaceae since the Late Cretaceous based on plastid phylogenomics. New Phytologist 214, No. 3: 1355–1367.

Zhao, L., Y.-Y. Yang, X.-J. Qu, H. Ma, Y. Hu, H.-T. Li, et al. 2022. Phylotranscriptomic analyses reveal multiple whole-genome duplication events, the history of diversification and adaptations in the Araceae. Annals of Botany 131, No. 1: 199–214.

Zhao, Y., R. Zhang, K.-W. Jiang, J. Qi, Y. Hu, J. Guo, et al. 2021. Nuclear phylotranscriptomics and phylogenomics support numerous polyploidization events and hypotheses for the evolution of rhizobial nitrogen-fixing symbiosis in Fabaceae. Molecular Plant 14, No. 5: 748–773.

Appendix I

List of all known published supertribal names and their full citations, excluding new names proposed in this account. Accepted names appear in bold, synonymized or invalid names in italics.

Andropogonodae L. Liu in Acta Phytotax. Sin. 18: 325. 1980. (*Andropogodae*) [Poaceae]

Arabodae D.A. German et al., PhytoKeys 220: 129. 2023. [Brassicaceae]

Arundinarodae L. Liu in Acta Phytotax. Sin. 18: 324. 1980. [Poaceae]

Arundinodae L. Liu in Acta Phytotax. Sin. 18: 324. 1980. (*Arundodae*) [Poaceae]

Asterodae H. Rob. in Phytologia 87: 73. 2005. [Asteraceae]

Bambusodae L. Liu in Acta Phytotax. Sin. 18: 323. 1980. [Poaceae]

Brassicodae V.E. Avet. in Biol. Zhurn. Armenii 43: 602. 1990. (*Brassicidinae*) [Brassicaceae]

Camelinodae D.A. German et al., PhytoKeys 220: 130. 2023. [Brassicaceae]

Cinchonodae Robbr. & Manen in Syst. & Geogr. Pl. 76: 134. 2006. (*Cinchonidinae*) [Rubiaceae]

Eragrostodae L. Liu in Acta Phytotax. Sin. 18: 324. 1980. [Poaceae]

Helianthodae H. Rob. in Phytologia 86: 118. 2004. [Asteraceae]

Heliophilodae D.A. German et al., PhytoKeys 220: 131. 2023. [Brassicaceae]

Hesperodae D.A. German et al., PhytoKeys 220: 132. 2023. [Brassicaceae]

Ixorodae Robbr. & Manen in Syst. & Geogr. Pl. 76: 132. 2006. [Rubiaceae]

Kerriodae D. Potter, S.H. Oh, & K.R. Robertson in D. Potter et al., Pl. Syst. Evol. 266: 38. 2007. *nom inval*. [Rosaceae]

Melicodae Soreng, J. Syst. Evol. 55(4): 263. 2017. [Poaceae]

Nardodae Soreng, J. Syst. Evol. 55(4): 263. 2017. [Poaceae]

Olyrodae Soderstr. & R.P. Ellis in T. R. Soderstrom et al. (eds.), Grass Syst. Evol.: 238. 1988. [Poaceae]

Oryzodae L. Watson, Clifford, & Dallwitz in Austral. J. Bot. 33: 458. 1985. (*Oryzanae*) [Poaceae]

Panicodae L. Liu in Acta Phytotax. Sin. 18: 324. 1980. [Poaceae]

Paulliniodae Avec.-Rodr. et al., Syst. Bot. 42: 108. 2017. [Sapindaceae]

Pharodae L. Liu in Acta Phytotax. Sin. 18: 324. 1980. [Poaceae]

Poodae L. Liu in Acta Phytotax. Sin. 18: 324. 1980. [Poaceae]

Psychotriodae Robbr. & Manen in Syst. & Geogr. Pl. 76: 136. 2006. (*Psychotriidinae*) [Rubiaceae]

Pyrodae C.S. Campbell, R.C. Evans, D.R. Morgan, & T.A. Dickinson in D. Potter et al., Pl. Syst. Evol. 266: 39. 2007. *nom inval*. [Rosaceae]

Rosodae T. Eriksson, Smedmark, & M.S. Kerr in D. Potter et al., Pl. Syst. Evol. 266: 36. 2007. *nom. inval*. [Rosaceae]

Rubiodae Robbr. & Manen in Syst. & Geogr. Pl. 76: 137. 2006. (*Rubiidinae*) [Rubiaceae]

Senecionodae H. Rob. in Phytologia 86: 119. 2004. [Asteraceae]

Sisymbriodae V.E. Avet. in Biol. Zhurn. Armenii 43: 602. 1990. (*Sisymbriidinae*) [Brassicaceae]

Stipodae L. Liu in Acta Phytotax. Sin. 18: 324. 1980. [Poaceae]

Thelypodiodae V.E. Avet. in Biol. Zhurn. Armenii 43: 602. 1990. (*Thelypodiinae*) [Brassicaceae]

Triticodae T.D. Macfarl. & L. Watson, Taxon 31(2): 192. 1982. (*Triticanae*) [Poaceae]

APPENDIX II

List of accepted supertribal taxa recognized in the angiosperms and their respective subordinate taxa. Genera and species count data mostly taken from the World Checklist of Vascular Plants database (WCVP, https://wcvp.science.kew.org/, initially accessed January–February 2022), with emendations taken from recent literature.

FAMILY	SUBFAMILY	SUPERTRIBE	NO. TRIBES	NO. GENERA	NO. SPECIES
Araceae	Aroideae	Arodae	12	41	1069
Araceae	Aroideae	Philodendrodae	6	27	984
Araceae	Aroideae	Schismatoglottidodae	3	4(–33)[a]	300
Araceae	Aroideae	Zamioculcadodae	2	3	26
Asteraceae	Asteroideae	Asterodae	4	532	7518
Asteraceae	Asteroideae	Helianthodae	15	558	6938
Brassicaceae	Brassicoideae	Arabodae	4	46	844
Brassicaceae	Brassicoideae	Brassicodae	15	123	916
Brassicaceae	Brassicoideae	Camelinodae	18	86	1478
Brassicaceae	Brassicoideae	Heliophilodae	8	27	198
Brassicaceae	Brassicoideae	Hesperodae	7	47	354
Cactaceae	Cactoideae	Cereodae	2	58	688
Cactaceae	Cactoideae	Echinocereodae	3	38	286
Fabaceae	Papilionoideae	Dalbergiodae	2	55	1574
Fabaceae	Papilionoideae	Galegodae	12	70	5931
Fabaceae	Papilionoideae	Genistodae	8	95	2854
Fabaceae	Papilionoideae	Myroxylodae	3	18	79
Fabaceae	Papilionoideae	Phaseolodae	4	203	3638
Poaceae	Panicoideae	Andropogonodae	4	135	1917
Poaceae	Pooideae	Melicodae	2	8	147
Poaceae	Pooideae	Nardodae	2	2	2
Poaceae	Pooideae	Stipodae	2	34	547
Poaceae	Pooideae	Triticodae	3	25	568
Rosaceae	Maloideae	Kerriodae	2	7	11
Rosaceae	Maloideae	Pyrodae	2	45	1158
Rubiaceae	Dialypetalanthoideae	Cinchonodae	11	117	1728
Rubiaceae	Dialypetalanthoideae	Coffeodae	9	142	2048
Rubiaceae	Dialypetalanthoideae	Ixorodae	8	39	1246
Rubiaceae	Dialypetalanthoideae	Mussaendodae	2	11	385
Rubiaceae	Dialypetalanthoideae	Dialypetalanthodae	4	48	396
Rubiaceae	Rubioideae	Lasianthodae	2	6	348
Rubiaceae	Rubioideae	Psychotriodae	9	45	3486
Rubiaceae	Rubioideae	Rubiodae	13	146	3312
Rubiaceae	Rubioideae	Urophyllodae	5	24	699
Sapindaceae	Sapindoideae	Cupaniodae	2	46	528
Sapindaceae	Sapindoideae	Paulliniodae	10	34	953[b]

[a] Generic concepts in Schismatoglottideae are contentious.
[b] Species count varies depending on the concept of the genus *Allophylus* L.

QUARARIBEA CENTINELAE (MALVACEAE), UNA NUEVA ESPECIE ENDÉMICA DE CENTINELA, OCCIDENTE DE ECUADOR

JOSE LUIS FERNÁNDEZ-ALONSO,[1,2] Y XAVIER CORNEJO[3]

Resumen. El género de árboles *Quararibea* (Malvaceae) agrupa a más de 60 especies de Mesoamérica y del norte de Sudamérica, propias principalemente de los bosques húmedos. Como avance al trabajo de revisión que se está llevando a cabo en el grupo morfológico "grandifolia" del género *Quararibea,* se describe en este trabajo una especie nueva considerada endémica de los bosques húmedos del Occidente de Ecuador y se propone su categorización de conservación de acuerdo con IUCN.

Palabras clave: Centinela, conservación, Flora de Ecuador; *Quararibea grandifolia,* Provincia de Santo Domingo de los Tsáchilas.

Abstract. The *Quararibea* genus of trees (Malvaceae) groups some 60 species restricted mainly to neotropical moist forests, in Mesoamerica and northern South America. As an advance of the review work that is being carried out in the morphological group "*grandifolia*" of the genus *Quararibea*, a new species is described in this work, considered endemic to the wet forests of Western Ecuador and its IUCN categorization is proposed.

Keywords: Centinela, conservation, Flora of Ecuador; *Quararibea grandifolia,* Provincia de Santo Domingo de los Tsáchilas

El género *Quararibea* Aubl. (Malvaceae) se distribuye ampliamente a lo largo del Neotrópico desde México hasta Argentina (Alverson 1989; Fernández-Alonso 1999) y agrupa a algo más de 60 especies, principalmente de los bosques húmedos, con alguna especie creciendo también en ambientes azonales del bosque seco (Fernández-Alonso, 2021, 2024). Forma parte de la pequeña tribu Matisieae Benth. (subfamilia Malvoideae), junto con *Matisia* Bonpl. y *Phragmotheca* Cuatrec., géneros ambos diversificados principalmente en el Norte de Sudamérica (Baum et al. 2004; Fernández-Alonso 1996, 2021, 2023). De Ecuador se conocen actualmente doce especies descritas de *Quararibea*, a las que hay que añadir la especie que aquí se propone (Fernández-Alonso, 2024). *Quararibea* se diferencia morfológicamente del género cercano *Matisia* básicamente por la columna estaminal distalmente dentada o lobada (raramente rasgado-digitada, con lóbulos de más de 4 mm de longitud) y radialmente simétrica, y por el ovario con solo 2–4 lóculos y fruto con 1–3(–4) semillas versus 5 carpelos y cinco semillas en el caso de *Matisia* (Alverson 1989; Fernández-Alonso 1996, 1999).

Como continuación del trabajo de revisión que actualmente se ultima en el grupo de 14 especies de *Quararibea* que presentan columna estaminal claramente digitada (Fernández-Alonso, en prep.), se propone aquí una nueva especie asignable al subgrupo que presenta hojas generalmente amplias y c*álices alados* (siete especies), que se encuentra diversificado principalmente en los bosques del Pacífico de Ecuador y de Colombia en menor medida. El análisis de nuevas recolecciones de campo del género *Quararibea*, efectuadas en los bosques húmedos de la vertiente del Pacífico de Ecuador y Colombia, permite ahora desentrañar el gran rango de variación en algunos caracteres florales y proponer nuevos taxones como el que ahora se describe.

Para este trabajo se estudiaron colecciones del género *Quararibea* depositadas principalmente en herbarios de Colombia y Ecuador: COL, GUAY, MA, MO, NY, PSO, QCA, QCNE y US (acrónimos de acuerdo con Thiers, 2023). En este estudio morfológico se siguió la metodología clásica ya indicada en contribuciones anteriores (Fernández-Alonso, 1996, 2001, 2024). Se contó también con abundantes registros fotográficos de campo obtenidos por uno de los autores (XC), en el desarrollo de sus proyectos.

Quararibea centinelae Fern. Alonso & Cornejo, *sp. nov.* TIPO: ECUADOR. Provincia de Santo Domingo de los Tsáchilas: Montañas de Ila, línea divisoria cerca de La Centinela, al N de Centinela, pequeña villa de San Pedro de Bimbe; 12 Km al Oeste en línea recta desde Patricia Pilar, ca. 6 km al SE desde Palmar de Bimbe; bosque secundario a lo largo de la carretera, 570 m, 0°33'S, 79°16'O, árbol 12 m, 8 cm diámetro, (fl), 13 noviembre 2021, *T.L.P. Couvreur, J.N. Zapata, A. Lozinguez, & W.J. Santillán Zurita 1507* (Holótipo: QCA 248280; Isotipo WAG). Fig. 1–3.

Quararibea centinelae within the genus, is assigned to the "grandifolia group" and can be easily separated from other related species such as *Q. grandifolia* (Little) Cuatrec. and *Q. calycoptera* Fern. Alonso & Cornejo because it has: leaves slightly fleshy, subcartaceous (dry), glabrous; floral pedicels (8–) 10–13 mm long, with 3–4 (–5) small bracteoles, 2–3(–4) mm long arranged sparsely on the distal half of the pedicel, and the floral calyx subcylindrical, urceolate, uniformly 10-sulcate with broad, obtuse ribs elevated 1–2 mm.

Se agradece a los curadores de los herbarios COL, MO, QCA, QCNE, WAG las facilidades para la consulta de las colecciones y el envío de algunos préstamos (MO, QCNE). Agradecemos a Carmen Ulloa (MO) en envío de una imagen solictada (colección *Dodson 7287*) y al colega mirmecólogo Fernándo Fernández (ICN UN), su ayuda con la identificacion de la hormiga asociada a la especie que se describe. Este estudio se llevó a cabo gracias al apoyo del Real Jardín Botánico del Consejo Superior de Investigaciones Científicas (CSIC) y al Ministerio de Ciencia e Innovación de España por facilitar los trabajos de revisión en plantas tropicales con cargo al proyecto CGL2010-19747.

[1] Real Jardín Botánico CSIC, Departamento de Biodiversidad y Conservación, Claudio Moyano 1, 28014 Madrid, España

[2] Autor de correspondencia: jlfernandeza@rjb.csic.es

[3] Departamento de Botánica, Facultad de Ciencias Naturales, Universidad de Guayaquil, Av. Raúl Gómez Lince s.n. y Av. Juan Tanca Marengo (campus Mapasingue), Guayaquil, Ecuador

Harvard Papers in Botany, Vol. 29, No. 1, 2024, pp. 79–85.

ISSN: 1938-2944, DOI: 10.3100/hpib.v29iss1.2024.n9, Published online: 30 June 2024

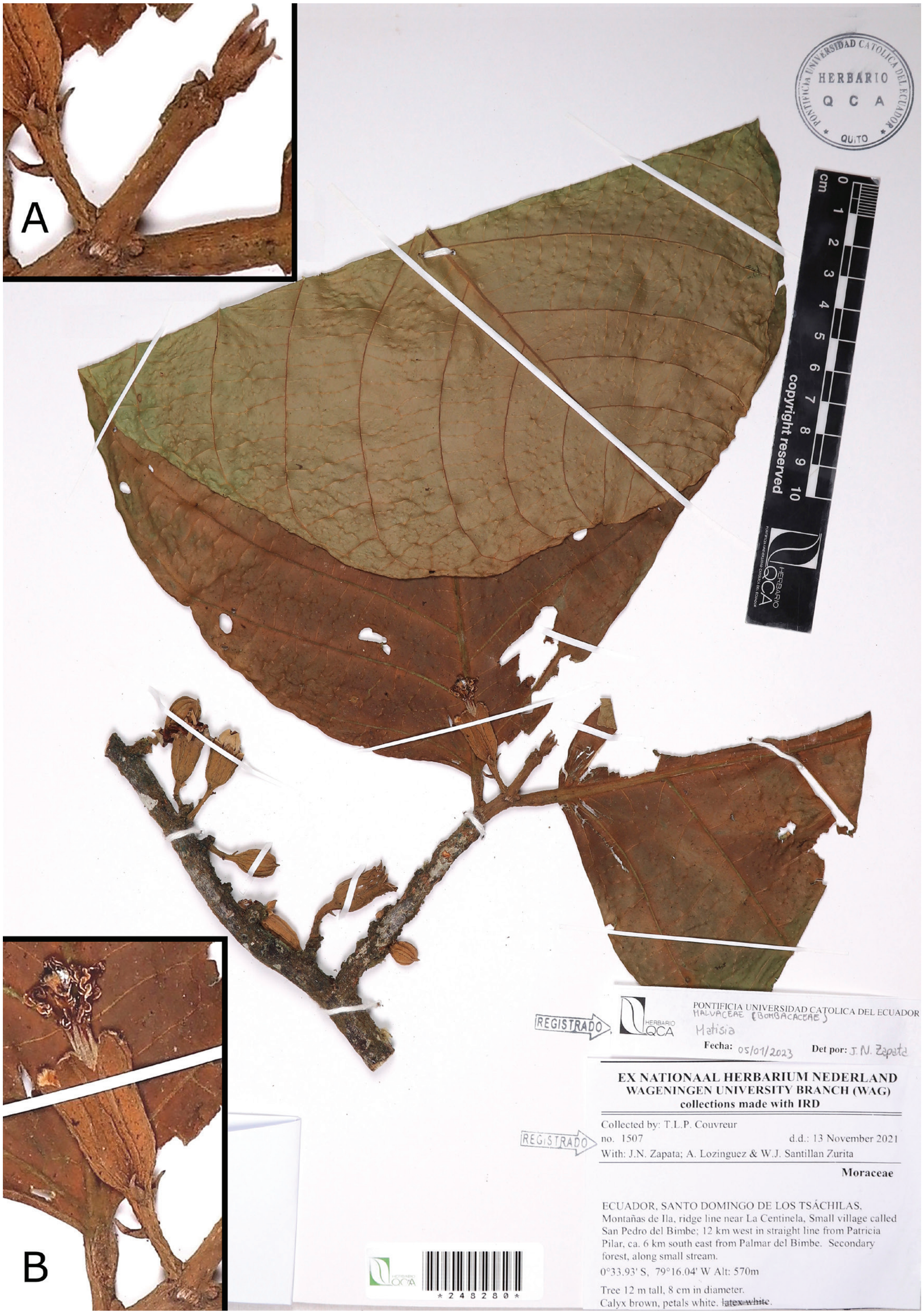


FIGURA 1. *Quararibea centinelae* Fern.Alonso & Cornejo. **A**, Detalle de la yema terminal con los primordios foliares (sup. der.), y de la disposición de la flor opuesta a la hoja (inf. izq.); **B**, Detalle de una flor (vista lateral) mostrando las bractéolas falcadas en el pedicelo, los lóbulos distales del cáliz, la columna estaminal y las ramas estaminales anchas. Fotografías del holotipo, Couvreur & al. 1507 (QCA).

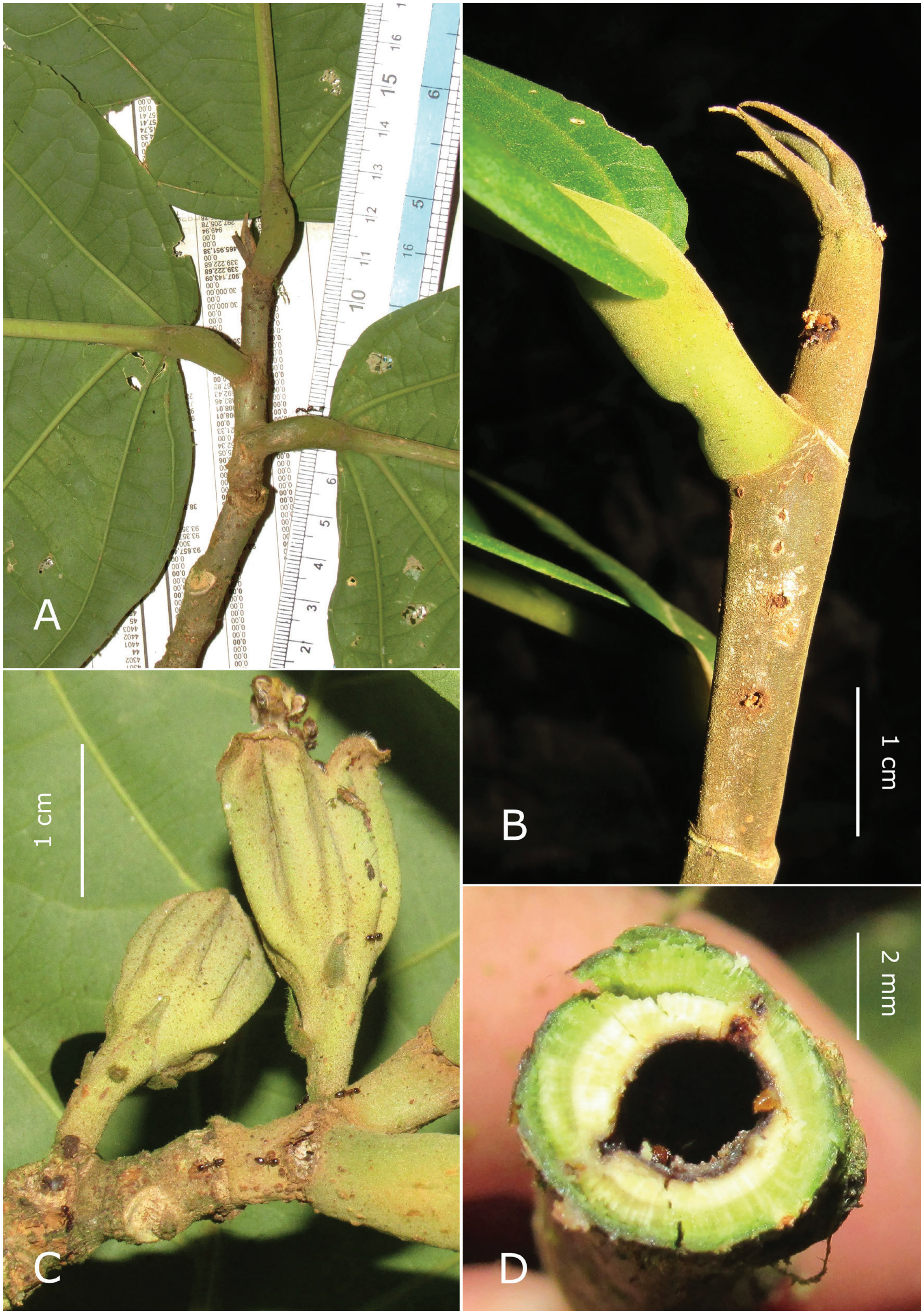


FIGURA 2. *Quararibea centinelae* Fern.Alonso & Cornejo. Algunos detalles de la morfología. **A**, Rama terminal mostrando la disposición de las hojas y los pecíolos con pulvínulos; **B**, Detalle del apice de una ramita con la yema terminal, las cicatrices estipulares en la base del pecíolo y algunas perforaciones en los entrenudos (domacios); **C**, Ramita con dos flores y con algunas hormigas (obreras) del género *Crematogaster,* responsables de los domacios de los entrenudos; **D**, Corte transversal de una ramita hueca con evidencia de actividad de las hormigas. Fotos de *X. Cornejo,* Noviembre de 2021, Centinela, Provincia de Santo Domingo de Tsáchilas.

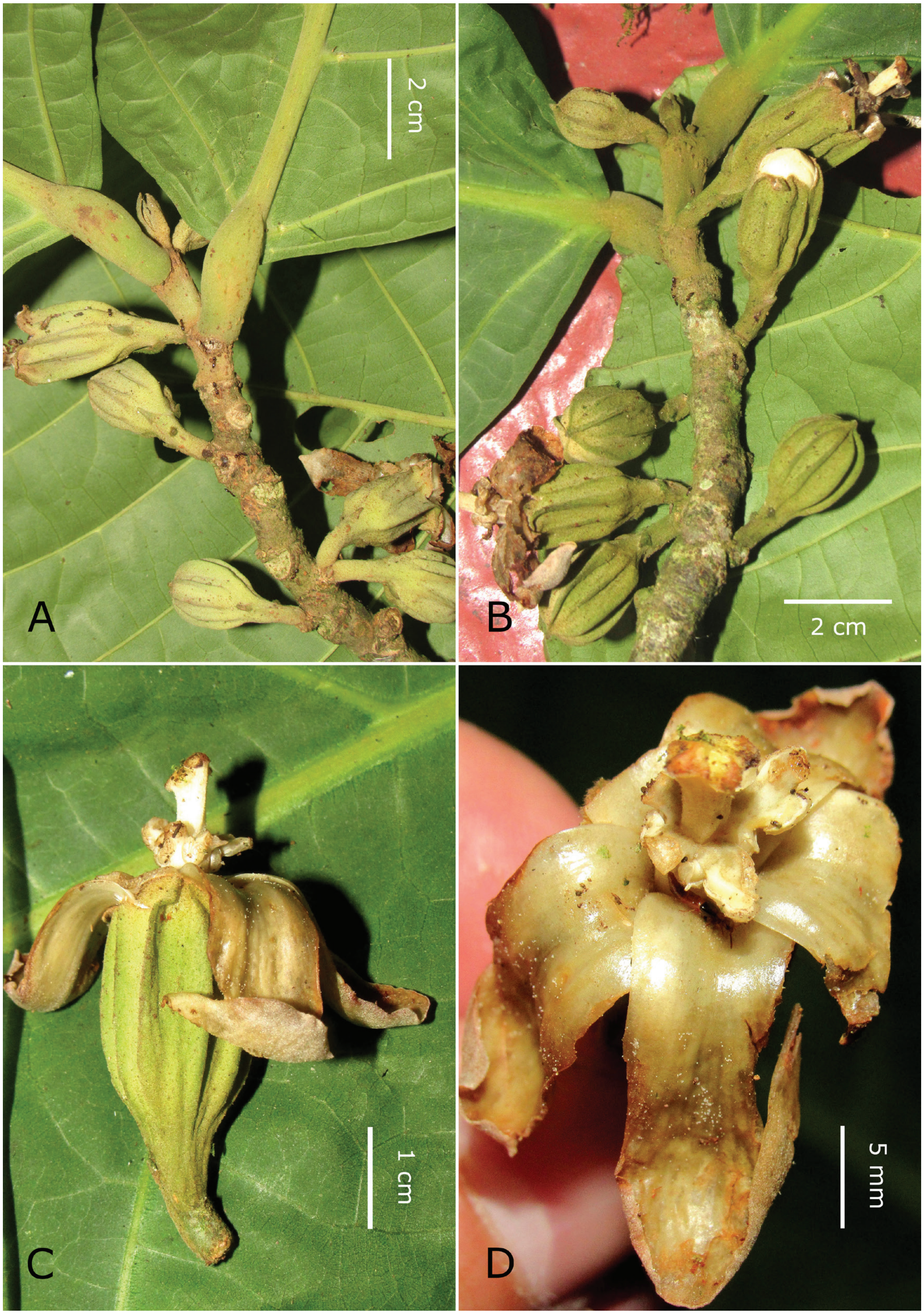


FIGURA 3. *Quararibea centinelae* Fern.Alonso & Cornejo. **A–B**, Parte distal de una ramita con las flores solitarias o pareadas junto a los rastros foliares del tallo y también opuestas a las hojas en el extremo de la rama; **C**, Flor en vista lateral, mostrando las costillas del cáliz, los petalos recurvados, el androceo con restos de las ramas estaminales y el estilo en posición central; **D**, Flor al final de la antesis, vista desde arriba, mostrando los pétalos y las lobulaciones de las ramas estaminales. Fotografías, de X. Cornejo, del árbol donde se recolectó el holotipo.

Árbol pequeño, ca. 10–12 m alto, tronco 6–9(–10) cm DAP; *ramas* de primer orden verticiladas; *ramitas* terminales, articuladas, aspecto ligeramente carnoso, cilíndricas, 6–9 mm de diámetro, con indumento marrón pálido, muy fino, fasciculado-lepidoto; *entrenudos* cortos, 5–15 mm de largo, huecos en su interior, a menudo con orificios circulares—*domacios* de hormigas—parcialmente obturados por restos vegetales; *corteza* grisácea o marrón-verdosa, lisa en los estrenudos distales y torulosa o cicatricosa en las zonas inferiores, con numerosos rastros foliares semicirculares y ligeramente prominentes; *yemas* apicales generalmente con un fascículo de 3–6 primordios foliares estipulares, linear-subulados, falcados, 8–10 × 1–2 mm, con denso indumento muy fino, marron pálido, equinado-lepidoto (Fig. 1A, 2B). *Hojas* alternas, dispuestas de modo dístico; *pecíolo* cilíndrico, ligeramente arqueado, 15–20 × 5–6 mm, con pulvínulo proximal inconspícuo o muy breve, pulvínulo distal cilíndrico 13–18 mm de largo (Fig. 2A, B), parcialmente soldado a la base del limbo decurrente en ca. 5 mm; *estípulas* estrechamente triangulares, subulado-falcadas, 5–9 × 2–3 mm en su base, muy prontamente caducas, dejando cicatrices lineares, perpendiculares y conspicuas en las ramitas (Fig. 2B); láminas oliváceas, concóloras en haz y envés, subcartáceas y ligeramente carnosas (en fresco), obovadas, elípticas o anchamente elípticas, 35–50 × 14–25 cm; limbo generalmente inequilátero, ligeramente más estrecho hacia la base, obtuso, redondeado y levemente auriculado, escasamente decurrente en la zona de unión al pecíolo; ápice más o menos obtuso; margen entero, ligeramente ondulado o sinuoso; venación por el haz impresa, amarillenta, levemente reticulado-bullada, con las venas terciarias y cuaternarias de aspecto poligonal y venación submarginal broquidódroma; envés con vena media muy resaltada; 2(–4) venas basales de muy corto recorrido en el limbo y 7–10 venas secundarias a cada lado; divergentes, dispuestas de modo erecto-patente con respecto a la vena media, en el envés muy resaltadas; venas de tercer y cuarto orden reticuladas y resaltadas; haz glabérrimo, envés subglabro, con indumento inconspícuo estrellado-pubérulo, solo en la base de la vena media. *Flores* dispuestas en los 2–3 nudos terminales de las ramas jóvenes, solitarias y opuestas a las hojas, o frecuentemente también dispuestas en las ramitas (braquiblastos), en la porción contigua inferior (Fig. 3A–B), desprovista de hojas, donde se ubican (ramifloras), 1 ó 2 flores, en las yemas axilares asociadas a los rastros foliares (Fig. 1, 3); *botón floral* elíptico-ovoide, umbonado apicalmente, uniformemente 10 costillado, irregularmente rasgado en la parte distal, al inicio de la antesis; externamente con indumento marron-verdoso, conspícuo, lepidoto, con pedicelos cortos de ca. 8 mm de largo, con las bractéolas más o menos agrupadas en la mitad distal del pedicelo; flor completa, -sin el pedicelo- ca. 40 x 40–43 mm; *pedicelo* verde oliváceo, (8–)10–13 × 2–3 mm, con indumento lepidoto; *bractéolas* 3–4(–5), persistentes (Fig. 1B,2C), dispuestas de modo disperso en la mitad superior del pedicelo; grisáceo-verdosas, adpresas o a veces erecto-patentes, triangular-subuladas, agudas, 2–3(–4) × 1–2 mm en su zona basal; con fino indumento lepidoto; *cáliz* verde oliváceo a marrón claro, cilíndrico-urceolado o ligeramente campanulado, 20–22 × 12–13 mm en la zona media y distal; tubo 17–20 mm de largo, 3–6 lobado-rasgado irregularmente en el 1/5 distal; lóbulos 2–3 mm de largo, recurvados; con 10 costillas longitudinales, uniformemente distribuidas, obtusas y gruesas, notorias, 1–2 mm de alto (Fig. 3C); externamente con denso indumento lepidoto, muy fino; en el interior con indumento color crema (en seco), seríceo, acostado, densamente dispuesto; *corola,* con pétalos blanco níveo, que se vuelve blanco crema o blanco grisáceo después de la antesis, patentes y arqueado-recurvados (Fig. 3C–D); estrechamente espatulados, unguiculados en la base y obtusos y recurvados distalmente, 40–47 mm de largo, 8–10 mm de ancho en la zona media y distal, ca. 3 mm de ancho en el tercio basal; glabros y lustrosos en su cara interna, con indumento muy fino estrellado-seríceo en la cara externa; *androceo* con columna estaminal blanca (en fresco), cilíndrica, ligeramente estriada longitudinalmente, 21–23 mm de largo, y 3–3,5 mm de grosor, de aspecto glabrescente, finamente pubescente en su zona apical; gradualmente ensanchada y rasgada en su zona apical, ca. 5 mm de diámetro; 5 ramas estaminales erecto-patentes o patentes al final de la antesis, irregularmente definidas (Fig. 1B,2D), con bifurcaciones cortas y margen sinuoso, de aspecto crenado, 4–5,5 × 2–2,5 mm, con 4–6 tecas en cada rama en posición marginal o submarginal; *ovario* ca. 4 mm de largo, con 2–4 carpelos desarrollados; *estilo* recto, 28–30 mm de largo, con indumento blanco, estrellado, muy fino, en la parte distal; *estigma* marrón-amarillento, 4–5 mm de diámetro, capitado-poligonal con 4–5 lobulaciones, lóbulos obtusos. *Fruto* no visto.

Etimología: El epíteto hace referencia a la región de procedencia de las estas plantas, zona de influencia del Cerro Centinela, en la provincia de Santo Domingo de los Tsáchilas, donde se han catalogado numerosas especies endémicas del noroccidente de Ecuador (Dodson & Gentry, 1991; Skog y Kvist, 2000 Cornejo, 2022).

Distribución y hábitat: Especie conocida hasta ahora solo de la región de Centinela, en la Provincia de Santo Domingo de Los Tsáchilas y más específicamente en Montañas de Ila, al N de La Centinela y cerca del caserío de San Pedro de Pambil. Fue recolectada en un fragmernto de bosque muy húmedo secundario, entre 500 y 600 m. Este emplazamiento coincide con una de las localidades recientes en las que se ha reencontrado la gesneriácea *Gasteranthus extinctus* L.E. Skog & L.P. Kvist, que es endémica de este sector y por casi 4 décadas considerada extinta (Skog y Kvist, 2000; Pitman et al., 2022). Otros árboles endémicos, recientemente descritos que caracterizan este hábitat son *Amyris centinelensis* Cornejo (Rutaceae) y *Eschweilera podoaquilae* Cornejo (Cornejo, 2022, 2023).

Fenología: La especie fue recolectada con flores en los meses de marzo y noviembre.

Evaluación del estado de conservación: (IUCN): *Quararibea centinelae* se conoce solo de 2 localidades próximas, ubicadas entre los 500 y los 700 m en la región de Centinela, al norte de las Montañas de Ila y en el Palmar de

Bimbe, en la Provincia de Santo Domingo de los Tsáchilas; a pocos kilómetros de los limites provinciales con Los Rios (Municipio de Patricia Pilar) y Manabí (Municipio de Chone). Esta región desde finales de los años 70s ha sufrido un agresivo proceso de alteración antrópica del bosque original (bosque húmedo nublado) exhibiendo un fuerte proceso de fragmentación y conversión del uso de suelo para dar paso a extensas áreas de pastos para ganado y amplios cultivos de cacao, balsa, *Gmelina arborea* Roxb., etc. (Dodson y Gentry, 1991; Pitman & al. 2022). *Quararibea centinelae* ocupa una superficie inferior a 5.000 km^2, en donde hasta el presente solamente tres poblaciones han sido observadas en campo. Debido a la presión antrópica por la tala permanente en la región (XC, obs. en campo), y de acuerdo con las categorías y criterios de la UICN (2022), aquí se asigna a esta nueva especie la categoría de (EN) En Peligro B2 ab(iii).

Dentro del "grupo grandifolia" ya mencionado, *Q. centinelae* se adscribe claramente al subgrupo de siete especies que presenta cálices florales con alas o costillas longitudinales, diversificado de forma llamativa en el occidente de Ecuador (Fernández-Alonso, 2024). Dentro de este subgrupo, tendría mayor afinidad general en caracteres vegetativos y florales con las especies *Q. grandifolia* y *Q. tafallae* Fern.Alonso, pero a diferencia de la que se describe, ambas presentan pedicelos florales con bractéoelas subverticiladas en el tercio distal.

Curiosamente, de esta misma región de Centinela, de la vía Santo Domingo a Quevedo existe una colección histórica de C. Dodson de la década de 1970 (*Dodson 7287*, MO1442659, QCA 940) que corresponde a *Quararibea tafallae*, estos son árboles generalmente de mayor porte con diferencias claras en las bractéolas, que en esta especie son verticiladas en posición distal y en las alas del cáliz, en este caso solo 5 alas no engrosadas (Fernández-Alonso, 2024).

Por otra parte *Q. centinelae* presenta dos caracteres inusuales, 3–5 bractéolas en el pedicelo (siempre tres en las otras especies) y costillas del cáliz engrosadas y obtusas, de 1–2 mm de altura (costillas agudas o subagudas de 0,5–1 mm de alto en las otras dos especies). Otras dos especies, *Q. calycoptera* y *Q. silverstonei*, aunque comparten con *Q.centinelae* la presencia de bractéolas dispersas en el pedicelo floral, se separan muy bien por la presencia de solo 3 bracteólas y de mayor tamaño (4–11 mm de longitud), ramas estaminales también más largas (6–10 mm de longitud) y otras diferencias en las alas del cáliz que se indican en la clave que se incluye en este trabajo.

En esta especie, al igual que en *Quararibea calycoptera* (Fernandez-Alonso y Cornejo, 2021), tambien se observa la asociación con hormigas en los ejes huecos de los extremos de las ramas jóvenes. La presencia de orificios más o menos circulares y parcialmente obturados, en los diferentes entrenudos huecos, asi como la presencia de un tipo de hormiga (obreras) en las ramas fotografiadas (Fig. 2), permitió efectuar una consulta a especialista (Fernando Fernández-C., UN-ICN), quien la identificó (Fig. 2C) como del género *Crematogaster* Lund. (Formicidae: Myrmicinae). Con base en el material estudiado de las diferentes especies del "grupo grandifolia" en proceso de revisión, se puede confirmar la constancia de este tipo de asociación en la mayoría de los taxones del occidente de Ecuador asignados a este grupo del género *Quararibea* (Fernandez-Alonso, en prep).

Especímenes adicionales examinados: ECUADOR. Provincia de Santo Domingo de los Tsáchilas: Al N de Centinela, Area privada de conservación Bosque y Cascadas Las Rocas, 600-700 m, 0°28'S, 79°11'O, remanente de bosque húmedo nublado a lo largo del rio Bolo, 4 marzo 2023 (fl.), *X. Cornejo et al. s.n.* (Fotografías, GUAY, MA).

Clave para la identificación de las especies de *Quararibea* "grupo grandifolia" con cálices alados

1a. Hojas membranáceas, cartáceas o subcoriáceas, glabras o glabrescentes, no acuminadas, cálices de más de 14 mm de longitud y androceo con ramas estaminales generalmente de más de 4 mm de longitud 2

1b. Hojas membranáceas, pubescentes y acuminadas, con cálices de hasta 12–14 mm de longitud y androceo con ramas estaminales de menos de 4 mm de longitud 6

2a Pedicelo floral 9–20 mm de longitud, bractéolas dispersas en la mitad superior del pedicelo 3

2b. Pedicelo floral 4–11(–13) mm de longitud, bractéolas agrupadas en el tercio o cuarto distal del pedicelo 5

3a. Pedicelo floral con 3–4(–5) bractéolas pequeñas 2–3(–4) mm de longitud, alas del caliz romas 1–2 mm de alto, androceo con ramas estaminales 4–5,5 mm de longitud, ensanchado-lobadas en la parte distal 2–2,5 mm de ancho . . . . . *Q. centinelae* Fern.Alonso & Cornejo

3b. Pedicelo floral con 3 bractéolas 4–11 mm de longitud, caliz con alas agudas 2–3 mm de alto o con aristas poco conspícuas 0,5 mm de alto, androceo con ramas estaminares de 6–10 mm de longitud uniformemente desarrolladas 4

4a. Hojas membranáceas, pecíolo hasta 10 mm de longitud, láminas estrechamente cuneadas en la base, cáliz floral anchamente campanulado, 27–31 x 10–12 mm, botón floral y cáliz con 5–10 alas muy conspicuas, 2–3 mm de alto . . . . . *Q. calycoptera* Fern.Alonso & Cornejo

4b. Hojas cartáceas o subcartáceas, pecíolo 10–20 mm de longitud, láminas generalmente redondeadas o subcordadas en la base, cáliz floral cónico-infundibuliforme, 19–20 x 5–6 mm, botón floral y cáliz con 10 alas o aristas poco desarrolladas, hasta 0,5 mm de alto . . . . . *Q. silverstonei* Fern.Alonso

5a. Hojas con pecíolo menor de 10 mm de longitud, láminas oblanceoladas, agudas en la base, pedicelo floral 4–7 mm de longitud, cáliz floral con 10 alas longitudinales bien marcadas ca.1 mm de alto . . . . . *Q. grandifolia* (Little) Cuatrec.

5b. Hojas con pecíolo (10–)12–20 mm de longitud, láminas oblongas, redondeadas o subcordadas en la base, pedicelo floral 8–11(–13) mm de longitud, cáliz floral anguloso con 5–10 aristas ó alas longitudinales poco marcadas, 0,5–0,7(–1,0) mm de alto . . . . . *Q. tafallae* Fern.Alonso

6a. Flores con pedicelos 8–10 mm de longitud, cáliz 12–14 mm de longitud con 10 alas longitudinales notorias, corola 25–30 mm longitud, columna estaminal 25–28 mm de longitud, ramas estaminales cortas hasta 2 mm de longitud . . . . . *Q. recondita* Fern.Alonso

6b. Flores con pedicelos 3–4 mm de longitud, cáliz 8–9 mm de longitud con 10 alas longitudinales poco conspicuas, corola ca. 15 mm longitud, columna estaminal 8–9 mm de longitud, ramas estaminales de 3 mm longitud . . . . . *Q. cornejoi* Fern.Alonso

Literatura Citada

Alverson, W. S. 1989. *Matisia* and *Quararibea* (Bombacaceae) should be retained as separate genera. Taxon 38(3): 377–388. DOI: https://doi.org/10.2307/1222268

Baum, D., S. Smith, A. Yen, W. S. Alverson, R. Nyffeler, B. Bhitlock y R. Oldham. 2004. Phylogenetic relationships of Malvatheca (Bombacoideae and Malvoideae; Malvaceae sensu lato) as inferred from plastid DNA sequences. Amer. J. Bot. 91: 1863–1871.

Cornejo, X. 2022. Estudios botánicos en la costa de Ecuador. Rev. Cient. Cien. Nat. Ambien. 16(2): 407–421. ISSN: 2773-7772.

———. 2023. *Eschweilera podoaquilae*: A new species of Lecythidaceae from northwestern Ecuador. Phytotaxa 579(2): 139–142. DOI: https://doi.org/10.11646/phytotaxa.579.2.8

Dodson, C. H. y A. H. Gentry. 1991. Biological extinction in western Ecuador. Ann. Missouri Bot. Gard. 78(2): 273–295. DOI: https://doi.org/10.2307/2399563

Fernández-Alonso, J. L. 1996. Contribuciones al conocimiento del género *Phragmotheca* Cuatrec. (BombacaceaeQuararibeae). Caldasia 18(3): 253–284.

———. 1999. Nueva especie y notas del género *Quararibea* (Bombacaceae). Revista Acad. Colomb. Ci. Exact. 23 (Suplemento especial): 49–52.

———. 2001. Bombacaceae neotropicae novae vel minus cognitae I. Novedades taxonómicas y corológicas en *Matisia*, *Quararibea* y *Spirotheca*. Revista Acad. Colomb. Ci. Exact. 25(95): 183–206.

———. 2021. Malvaceae Neotropicae novae vel minus cognitae X. Nuevas especies de *Quararibea* de Colombia y Ecuador. Anales Jard. Bot. Madrid, 78 (2): 1–16. e112. whttps://doi.org/10.3989/ajbm.2584

———. 2022. *Matisia, Phragmotheca* y *Quararibea*. En: Bernal, R., S. R. Gradstein y M. Celis (eds.). *Catálogo de plantas y líquenes de Colombia*. Instituto de Ciencias Naturales, Universidad Nacional de Colombia. http://catalogoplantasdecolombia. unal. edu.co

———. 2024. Malvaceae Neotropicae novae vel minus cognitae XII. Cuatro nuevas especies de *Quararibea* "grupo grandifolia" de Colombia y Ecuador. Revista Acad. Colomb. Ci. Exact. 48(186): 1–27. https://doi.org/10.18257/ raccefyn.2233

———. y X. Cornejo. 2021. *Quararibea calycoptera* (Malvaceae), una nueva especie de los bosques muy húmedos del Pacífico de Ecuador y Colombia. Acta Bot. Mex. 128: e1960, 1–10. https://doi.org/10.21829/abm128.2021.1960

———. y J. L, Campos-Pineda E. 2023. *Matisia gentryi* and *M. tinamastiana* (Malvaceae), two species newly recorded from Panama and an updated key to *Matisia* species in this country. Check List 19 (6): 1013–1020. https://doi.org/10.15560/19.6.1013

IUCN. 2022. *Guidelines for using the International Union for Conservation of Nature, Red List Categories and Criteria,* Version 14, prepared by the Standards and Petitions Committee. Gland, Suiza. http://www.iucnredlist.org/documents/RedList Guidelines.pdf (consultado en febrero de 2024).

Pitman, N. C. A., D. M. White, J. E. Guevara, T. O. P. Couvreur, R.P. Fortier, J. N. Zapata, X. Cornejo, J. L. Clark, K. J. Feeley, M. K., Johnston, A. Lozinguez y G. Rivas-Torres 2022. Rediscovery of *Gasteranthus extinctus* L.E. Skog y L.P. Kvist (Gesneriaceae) at multiple sites in western Ecuador. Phytokeys 194: 33–46. https://doi.org/10.3897/phytokeys.194.79638

Skog, L. E., y L. P. Kvist. 2000. Revision of *Gasteranthus* (Gesneriaceae). Syst. Bot. Monogr., 59: 1–118. https://doi. org/10.2307/25027883

Thiers, B. 2023. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. New York, U.S.A. http://sweetgum.nybg. org/science/ih/ (consultado Marzo de 2024).

Page 86 intentionally left blank.

REVISED CIRCUMSCRIPTIONS OF *SPHEDAMNOCARPUS* AND *PHILGAMIA* (MALPIGHIACEAE)

Jackson Kehoe,[1] Justin Williams,[1] Yujing Yan,[1]
Liming Cai,[2] Xiaoshan Duan,[3] and Charles Davis[1,4]

Abstract. Ongoing phylogenetic investigations of the large and diverse plant clade Malpighiaceae have clarified many novel phylogenetic relationships. Results from these insights in turn have necessitated reconciling the taxonomy of numerous genera in the family. Our recent findings indicate that the genera *Sphedamnocarpus* and *Philgamia*, which collectively represent a single paleotropical clade of Malpighiaceae whose species occur in Africa and Madagascar, are not monophyletic as currently circumscribed. Here, we resolve each of these genera as monophyletic. This involves reducing the composition of *Sphedamnocarpus* to include only the African members of this genus and expanding *Philgamia* to include the Malagasy members of this clade, including former species of *Sphedamnocarpus* which compose this island radiation. In addition to geography, morphology plays an important role in justifying these divisions, which we detail here as further justification for our reclassification of these genera.

Keywords: Island endemism, taxonomy, systematics, stigmaphylloid clade

Malpighiaceae are a monophyletic angiosperm family (Chase et al., 2002; Davis and Chase, 2004; Wurdack and Davis, 2005; Davis and Anderson, 2010), whose species exhibit a pantropical distribution and a rich evolutionary and biogeographic history (Anderson, 1979; Vogel, 1990; Davis, 2002; Davis, Bell, Fritsch, et al., 2002; Davis, Bell, Mathews, et al., 2002; Davis et al., 2004; Zhang, Kramer, and Davis, 2010, 2012, 2016; Zhang et al., 2013; Davis et al., 2014; Cai et al., 2016). The center of diversity for the ~1300 species in 77 genera in this clade are the Neotropics (Anderson, 2004), although ~19% of species in Malpighiaceae (~250 spp./ 17 genera) are found in the Paleotropics, the result of at least 7 independent dispersal events from the Neotropics (Davis, Bell, Mathews, et al., 2002; Davis and Anderson, 2010; Cai et al., 2016). The family consists of trees, shrubs, and vines characterized by their simple, often opposite leaves, modified unicellular hairs, and five-petaled flowers that possess distinctly clawed petals. Most neotropical Malpighiaceae bear conspicuous paired oil glands at the base of their sepals and are implicated in specialized pollinator mutualisms with oil bees (Vogel, 1974; Anderson, 2004; Davis et al., 2014). In contrast, most paleotropical lineages, like *Sphedamnocarpus* Planchon ex. Bentham & Hooker (1862: 256) and *Philgamia* Baillon (1894: 265), exhibit a suite of floral characters that depart from the canonical New World Malpighiaceae floral morphology (Davis, 2002; Davis et al., 2014), including eglandular sepals and reduced zygomorphy.

Over the last 20 years, phylogenetic investigations in Malpighiaceae have revealed traditional generic concepts based on fruit type utilized by Niedenzu (1928) to be misleading for representing evolutionary relationships (Cameron et al., 2001; Davis, Anderson, and Donoghue, 2001; Davis, 2002; Davis et al., 2004; Davis and Anderson, 2010). These insights have prompted extensive taxonomic changes to the family, especially among genera (Anderson and Davis, 2005, 2006, 2007; Anderson, 2011).

One such example, and the focus of our present study, involves members of the informally designated stigmaphylloid clade *sensu* Davis and Anderson (2010), which, among others, includes the two paleotropical genera *Sphedamnocarpus* and *Philgamia*, whose species are distributed in Africa and Madagascar (Arènes, 1943a,b). These genera were delimited by Arènes based on their fruit type: *Philgamia* possesses a wingless nut often with a remnant dorsal crest where the samara wing would be found, as opposed to the conspicuous winged samaras of *Sphedamnocarpus*. As currently circumscribed, *Philgamia* is restricted to Madagascar, while the distribution of *Sphedamnocarpus* includes species in both Africa and Madagascar (Fig. 1).

In 1894, Baillon illustrated a single fruitless specimen of the species *P. hibbertioides* Baill. (P: P00048061). The genus was later formally described in 1908 by Dubard & Dop., remaining monotypic until 1943 when Arènes added three species to the genus: *P. brachystemon* Arènes, *P. denticulata* Arènes, and *P. glabrifolia* Arènes (Arènes, 1943a). Arènes also was the first to describe the unique wingless fruits of this genus. Both he (1943a) and William Anderson (pers. comm.) remarked on the restricted distribution of species in this genus, which only inhabit quartzite outcrops in central Madagascar. Edaphic variation is known to influence plant diversity, and unique soil types are associated with high rates of endemism (Lichter-Marck et al., 2023).

We are thankful to Christiane Anderson for her advice, as well as for sharing the late Bill Anderson's notes with us. We are also grateful to the staff of the Harvard University Herbaria and Botany Libraries, without whom none of this work would have been possible, especially Kanchi N. Gandhi, who clarified some uncertainty around taxonomy. We would like to thank Pete Lowry, Marina Rabarimanarivo, and Peter Phillipson for sharing their insight into these genera and for guidance with the MADCAT portal.

[1] Department of Organismic and Evolutionary Biology, Harvard University Herbaria, Harvard University, Cambridge, Massachusetts, 02138, U.S.A.
[2] Department of Integrative Biology, The University of Texas at Austin, Austin, Texas, 78712 U.S.A.
[3] College of Forestry, Northwest Agriculture & Forestry University, Yangling 712100, Shaanxi, China
[4] Corresponding author: cdavis@oeb.harvard.edu

Harvard Papers in Botany, Vol. 29, No. 1, 2024, pp. 87–96.

ISSN: 1938-2944, DOI: 10.3100/hpib.v29iss1.2024.n10, Published online: 30 June 2024

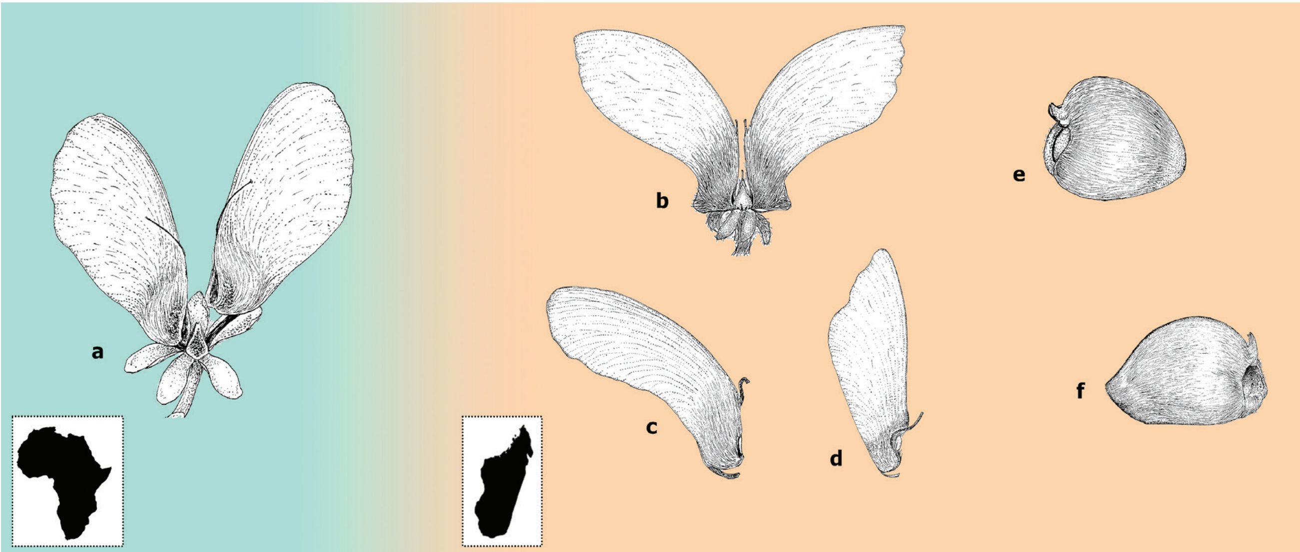


FIGURE 1. Fruit types in *Sphedamnocarpus* and *Philgamia*. **A**, *S. angolensis*; **B**, *S. poissonii*; **C**, *S. andersonii*; **D**, *S. dubardii*; **E**, *P. glabrifolia*; **F**, *P. hibbertioides*. Background colors indicate geographic distributions. Illustrations by Karin Douthit, adapted with permission from University of Michigan Malpighiaceae Nomenclature website (http://malpighiaceae.herb.lsa.umich.edu/nomhome.html).

The taxonomic history of *Sphedamnocarpus* is, in contrast, more dynamic. The genus was first published in 1862 by Bentham & Hooker and consisted of up to three species originally described as *Acridocarpus* by Adrien de Jussieu—likely *A. angolensis* A.Juss., *A. pruriens* A.Juss., and *A. argyrophyllus* A.Juss. Jussieu described these in particular as "three-styled" and indicated his uncertainty about their placement in the genus (Jussieu, 1843; Bentham & Hooker, 1862). The type species, *S. angolensis* (A. Juss.) Planch. ex. Oliv., was later published by Oliver in 1868, with a reference to Jussieu's *A. angolensis*. However, since Jussieu included no type specimen in his description, Oliver (1868) designated a lectotype for the species.

The first published Malagasy species in *Sphedamnocarpus* was *S. madagascariensis* Baker in 1884. This species was originally published by Jussieu as *Banisteria multiflora* Bojer mss., and Jussieu did highlight morphological similarities of his *Banisteria multiflora* to the "three-styled" and dubious species of *Acridocarpus* he published, expressing his doubts that the genera were distinguishable. Baker used the epithet *madagascariensis* rather than *multiflorus* for his publication because in 1924, almost 20 years before Jussieu's monograph of the Malpighiaceae, de Candolle published a different *Banisteria multiflora*, which was endemic to the neotropics (de Candolle, 1824).

Jussieu's four contentious paleotropical species were united together under *Sphedamnocarpus* when Niedenzu treated the genus in 1924. He recognized seven species, three of which were endemic to Madagascar: *S. argyrophyllus* Ndz., *S. multiflorus* (Juss.) Ndz., and *S. hibbertioides* (Baill.) Ndz. A notable expansion of *Sphedamnocarpus* was later published by Arènes as a part of his floristic treatment of the Malpighiaceae of Madagascar in 1943, in which he recognized 12 species on the island, many of them novel. He kept only one of Niedenzu's Malagasy designations (*S. multiflorus*) and transferred the others to different genera: *S. argyrophyllus* Ndz. became *Microsteira argyrophylla* (Juss.) Dub. et Dop, while *S. hibbertioides* (Baillon) Ndz. became *Philgamia hibbertioides* Baillon (Arènes, 1943b). Arènes recognized two more Malagasy species in this genus during the following several years (Arènes, 1946, 1947). He was the last researcher to publish a treatment of this genus. A most recent species from Madagascar was published in 2018, *Sphedamnocarpus andersonii* C.E. Anderson. For the species of *Sphedamnocarpus* found on continental Africa today, there is a history of taxonomic changes and shifting infraspecific arrangements, especially in *S. pruriens*, which may indicate the existence of a species complex that warrants further investigation of phenotypically and geographically variable populations with modern methods (de Villiers and Botha, 1986).

MATERIAL AND METHODS

DNA extraction, library prep, sequencing

We isolated total genomic DNA from 0.01–0.02 g of herbarium collections using the Maxwell® 16 DNA Purification Kit (Promega Corporation, Inc., Madison, Wisconsin, U.S.A.). DNA integrity and concentration were checked on a 4200 TapeStation System using D5000 ScreenTape (Agilent Technologies, Inc., Waldbronn, Germany). Genomic libraries were prepared using ca. 70 ng of genomic DNA where possible. For library preparation, we used the KAPA HyperPlus DNA library prep with IDT TrueSeq barcodes (Integrated DNA Technologies, Inc., IO, USA) and Nextflex-Ht barcodes (Bioo Scientific Corporation, Texas, U.S.A.). We fragmented DNA to an average of 350–400 base pairs (bp) and indexed for Illumina multiplex sequencing. We verified the DNA concentrations and fragment sizes of these libraries using the Qubit dsDNA HS Assay Kit on a Qubit 2.0 Fluorometer (Invitrogen, Carlsbad, California, U.S.A.) and the 4200 Agilent

Tapestation system (Agilent Technologies, Inc., Waldbronn, Germany). All total genomic DNA libraries were pooled in equimolar rations and sequenced with the Illumina Hi-Seq 5000 (Illumina, Inc., San Diego, California, U.S.A.) at the Bauer Core Genomics Sequencing Core Facility at Harvard University, Cambridge, Massachusetts, U.S.A., which resulted in 125 bp paired-end reads. The genome skimming pipeline we applied is described by Weitemier et al. (2014).

Reads curation, assembly, and annotation

Raw reads were filtered with FastQC V0.10.1 to remove reads with average Phred scores lower than 30 (Andrews, 2010). We further trimmed the adaptors and filtered homopolymer (threshold 95%) using ea-utils and PRINSEQ-lite v0.20.4, respectively (Aronesty, 2011; Schmieder and Edwards, 2011). All reads shorter than 33 bp after trimming were discarded for downstream analysis. Plastid genome and nuclear rDNA assembly was conducted in GetOrganelle v1.7.7 (Jin et al., 2020). We used the built-in database from GetOrganelle for both assemblies and applied a wide range of kmer sizes (k = 21, 35, 55, 85, 95) to accommodate for variations in sequence coverage.

Ortholog identification and phylogenetic reconstruction

Ortholog identification was conducted using the *PhyloHerb* bioinformatic pipeline (Cai et al., 2022). Output orthologous sequences were aligned using PASTA v1.8.5 to accommodate the high sequence variation of intergenic regions (Mirarab et al., 2015). A draft maximum likelihood (ML) phylogeny was subsequently inferred from the concatenated sequences in IQTREE v2.2.2 under the default settings to facilitate manual curation of alignments (Nguyen et al., 2015). We visualized the alignment in Geneious Prime R9 (https://www.geneious.com/) to remove erroneous sequences such as paralogs. These filtered sequences were aligned in PASTA again using the ML phylogeny as the guidance. The resulting alignments were reordered and manually examined in Geneious again to remove misaligned regions. The curation of the ribosomal DNA sequences (partial ETS–18S–ITS1–5.8S–ITS2–28S) followed a similar procedure.

To infer a phylogeny based on the plastid and nuclear genes, an optimum partition scheme was determined using the AICc information criterion and the 'rcluster' search algorithm in PartitionFinder v2 (Lanfear et al., 2016). Phylogenies for individual locus, concatenated plastid loci, and combined plastid-rDNA loci were then inferred using the optimum partition and the GTR+GAMMA model with 1000 ultrafast bootstrap replicates in IQTREE (Minh et al., 2013). The phylogeny inferred from the combined plastid-rDNA dataset was used for downstream analyses. Sequence data for the species examined in this study are available in GenBank, accessions PP792599–PP792610.

Species Range Evaluations

For each species in our tree, as well as all species published but not included in our sampling, we evaluated ranges based on data available from Kew Plants of the World Online (POWO) and the type localities. Each species was scored as either African or Malagasy if its range was limited to continental Africa or Madagascar and Mauritius, respectively. There were no species with a range that spanned both of these geographic areas.

Specimen Examination

To assess morphological variation in *Sphedamnocarpus* and *Philgamia*, we used a multi-pronged approach, including examination of herbarium specimens in person at HUH, high-definition photos of specimens from multiple herbarium databases online, and data from GBIF (https://www.gbif.org/) and iNaturalist (https://www.inaturalist.org/), including photos of plants in the field. Supplemental photos for the Malagasy species were shared by Marcelo Pace, David Boufford, and Wenheng Zhang. All specimens or field photos reviewed were scored by geography (island or mainland). See Appendix I for a complete list of specimens examined.

At first, available specimens were reviewed in person to identify morphological differences between the island and mainland clades. After putative morphological differences between the clades were identified (see Results and Discussion), more specimens and photographs from the field were examined virtually, including the type specimens for each species. When syntypes existed but not a holotype, a lectotype designation was made. It was observed from field photographs of living flowers that styles that project beyond the staminal ring in the horizontal plane are abundant in African species, but not present in the Malagasy species. This trait was not always immediately apparent in dried and pressed herbarium specimens. For the Malagasy species that generally lacked many photographs of living flowers, dried flowers were extracted from available specimens at HUH, boiled and observed under a microscope to determine style orientation. Although the structural integrity of the flowers is diminished after drying and pressing, these characters were still observed and recorded (Fig. 2).

Results and Discussion

Our recent and ongoing phylogenomic investigations in Malpighiaceae reveal that *Sphedamnocarpus* and *Philgamia* are not monophyletic as currently circumscribed (Fig. 3), necessitating a recircumscription of these genera. On the basis of our results, which include both geographic and morphological evidence to support our phylogenetic findings, we propose merging the Malagasy *Sphedamnocarpus* with the genus *Philgamia* and recognize a greatly reduced *Sphedamnocarpus*, whose species are restricted to Africa. This ensures the reciprocal monophyly of both genera and recognizes an endemic island lineage in Madagascar, which exhibits among the highest rates of species endemism in the world (Antonelli et al., 2022).

Geography, not fruit type, appears to be a much better arbiter of monophyletic species groups in this clade. Here, our analyses identify two subclades, one restricted to mainland Africa, including only species of *Sphedamnocarpus*, and a second confined to Madagascar, which includes members of both *Sphedamnocarpus* and *Philgamia* (Fig. 3).

Examinations of herbarium specimens revealed that

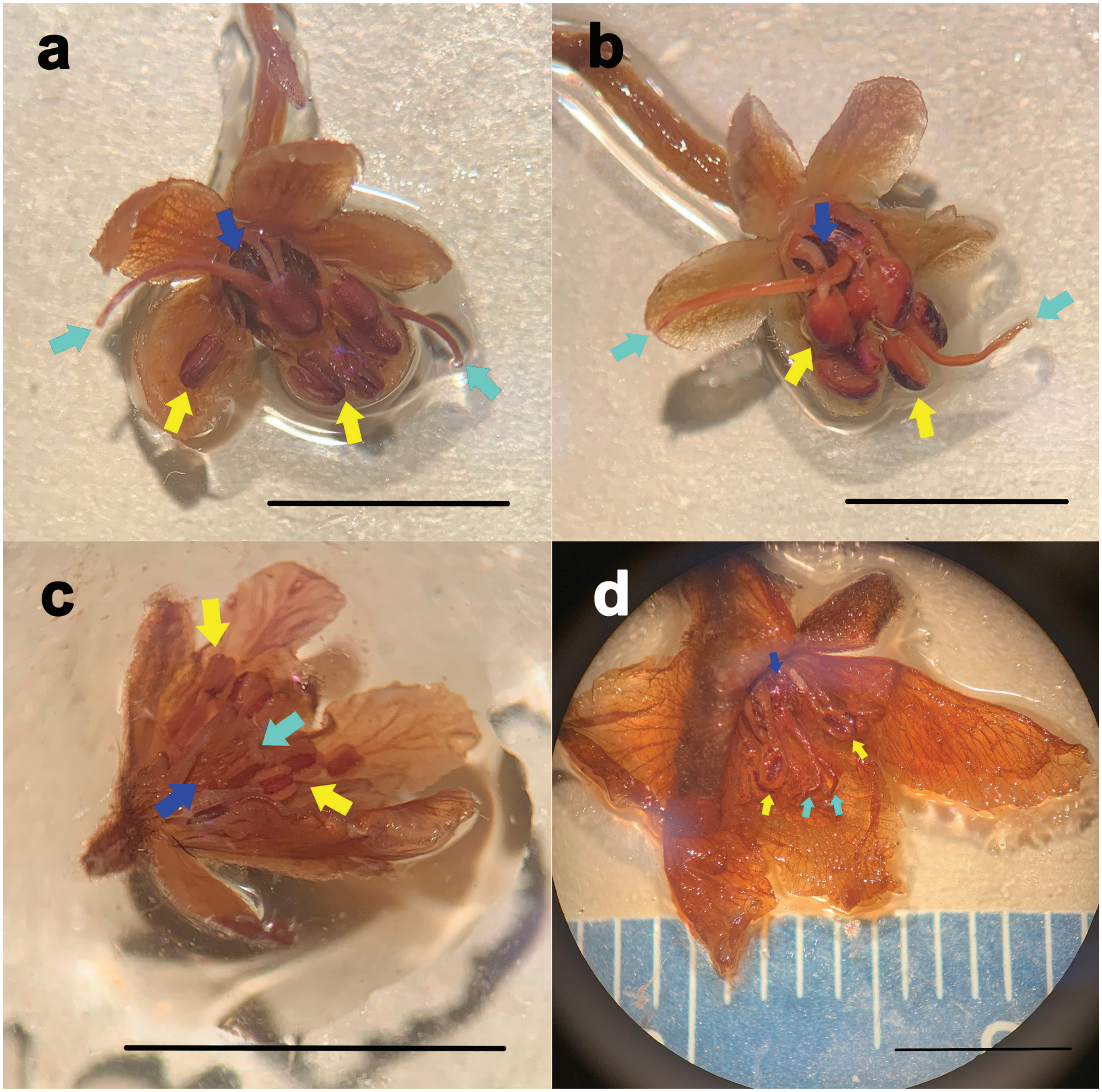


FIGURE 2. Flowers examined for investigation of morphological differences between mainland (**A, B**) and island (**C, D**) clades. Dark blue arrows indicate ovaries, light blue indicate styles, and yellow indicate anthers. **A**, *S. angolensis* (A.Juss.) Planch. ex. Oliv., based on *F. A. Rogers 13095*; **B**, *S. galphimiifolius* (A.Juss.) Szyszył., based on *Werdermann & Oberdieck 1938*; **C**, *P. glabrifolia* Arènes, based on *Zhang et. al. 129*; **D**, *S. humbertii* Arènes, based on *Phillipson et al*. 5840. Scale bars = 5.0 mm. All specimens cited in Appendix I.

continental and island lineages differ in their inflorescence and floral morphology. In both groups, flowers are umbellate and emanate in bunches, often in groups of three or four, from a node that is subtended by visible bracts. In the African *Sphedamnocarpus*, flowers are borne on a pedicel which is subtended by two bracteoles, a floriferous peduncle, and a bract (Fig. 4a–b). In contrast, the Malagasy specimens observed lack a floriferous peduncle, with bracteoles often hidden behind the bracts (Fig. 4e–f). The presence/absence of the floriferous peduncle is the most salient observable difference between these subclades and provides further support to the phylogeny for delimiting these two genera by geography.

Examinations of the flowers themselves revealed differences in style morphology across these two clades. Members of the African clade have flowers with longer, horizontally oriented styles that extend out beyond the staminal ring in the horizontal plane (Fig. 4c–d). The Malagasy clade's members exhibit shorter, vertically oriented styles that remain within the staminal ring in the horizontal plane (Fig. 4 h–j).

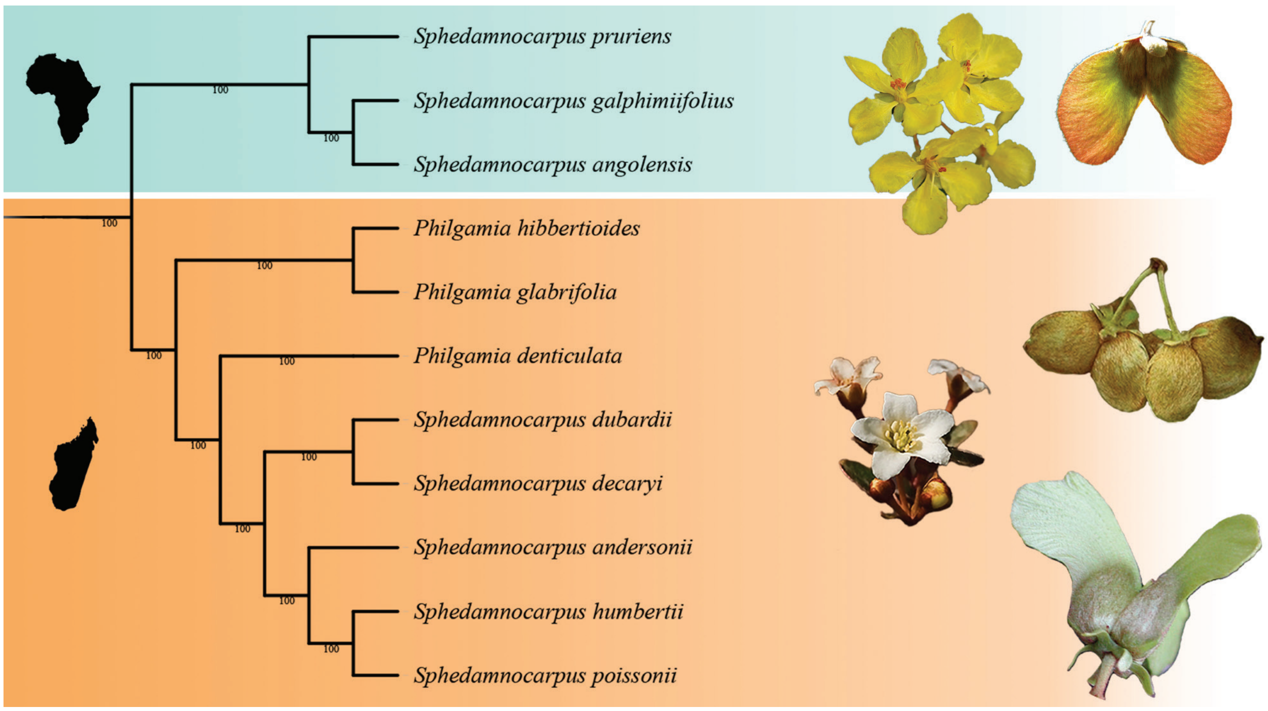


FIGURE 3. Maximum likelihood tree built with chloroplast genomes and nuclear DNA showing hypothesized evolutionary relationships between members of *Sphedamnocarpus* and *Philgamia* and revealing non-monophyly of both genera. Background colors indicate geographic distributions. Photographs from top to bottom, left to right: *S. pruriens* flower by Andre Harmse (https://www.inaturalist.org/observations/183058148); *S. pruriens* samara by JMK (https://en.wikipedia.org/wiki/Sphedamnocarpus#/media/File:Sphedamnocarpus_pruriens,_samara,_a,_Groenkloof_NR.jpg), *P. glabrifolia* fruits by G. E. Schatz (https://www.mobot.org/MOBOT/research/conspectus/malpigh.shtml), *P. hibbertioides* flowers by Fabien Rahaingoson (https://www.inaturalist.org/observations/10848867), *S. andersonii* fruits by Thomas Daniel (adapted from Anderson 2018 with permission).

In light of our results, we suggest that the Malagasy species of *Sphedamnocarpus* be transferred to *Philgamia* and list below the new combinations that we propose. To be as thorough as possible in our nomenclatural revisions, we used the names proposed by Arènes when he last treated the genus. Presently, the Missouri Botanical Gardens' Catalogue of the Plants of Madagascar (http://legacy.tropicos.org/Project/Madagascar) has combined many of the species concepts in *Sphedamnocarpus*, suggesting Arènes may have split them too finely. A fresh treatment of this group would help to resolve the issue of which species concepts best reflect biological reality.

To summarize, this study is part of a larger effort to refine the taxonomy of Malpighiaceae using new phylogenetic evidence. We propose a merging of the Malagasy members of the genus *Sphedamnocarpus* with the genus *Philgamia* and support this proposal with phylogenetic, geographic, and morphological evidence. In contrast to traditional generic delimitations founded on fruit morphology in the Malpighiaceae, our study groups together species with differing fruit morphologies. Future studies in this clade may explore the evolution of fruit type in the newly defined *Philgamia*. Additionally, notes of the late William Anderson point out that some of the Malagasy species may exhibit cryptic dioecy based on his observations of the size, shape and development of anthers and carpels across species (C. E. Anderson, pers. comm.). This is another avenue for potential future investigations of this island radiation to explore. Finally, our study did not address the taxonomy of the African *Sphedamnocarpus*, the sister genus to *Philgamia*. The existence of sympatric species, as well as sympatric subspecies with histories of taxonomic shifting, indicate this clade could benefit from more intensive studies that include phylogenetic data.

NEW COMBINATIONS PROPOSED

Philgamia ambovombensis (Arènes) Kehoe, C. Davis, & J.T. Williams, *comb. nov.*

Basionym: *Sphedamnocarpus ambovombensis* Arènes (1943b: 108).

TYPE: MADAGASCAR. Ambovombe District, Antanimora; 23 October 1924, *Decary 3278* (Holotype: P [P00048031], Isotype: P [P00048032]).

Philgamia andersonii (C.E. Anderson) Kehoe, C. Davis, & J.T. Williams, *comb. nov.*

Basionym: *Sphedamnocarpus andersonii* C.E. Anderson (2018: 248).

TYPE: MADAGASCAR. Ihorombe Region: Isalo National Park, vicinity of Mangily and Tombeaux Bara on trail to Piscine Naturelle, ca. 4 km SW of Ranohira, ca. 850 m, 22°33'72"S, 45°22'95"E, 9 March 2007, *T. F. Daniel 11025* (Holotype: MICH [1566012]; Isotype: CAS [692699]).

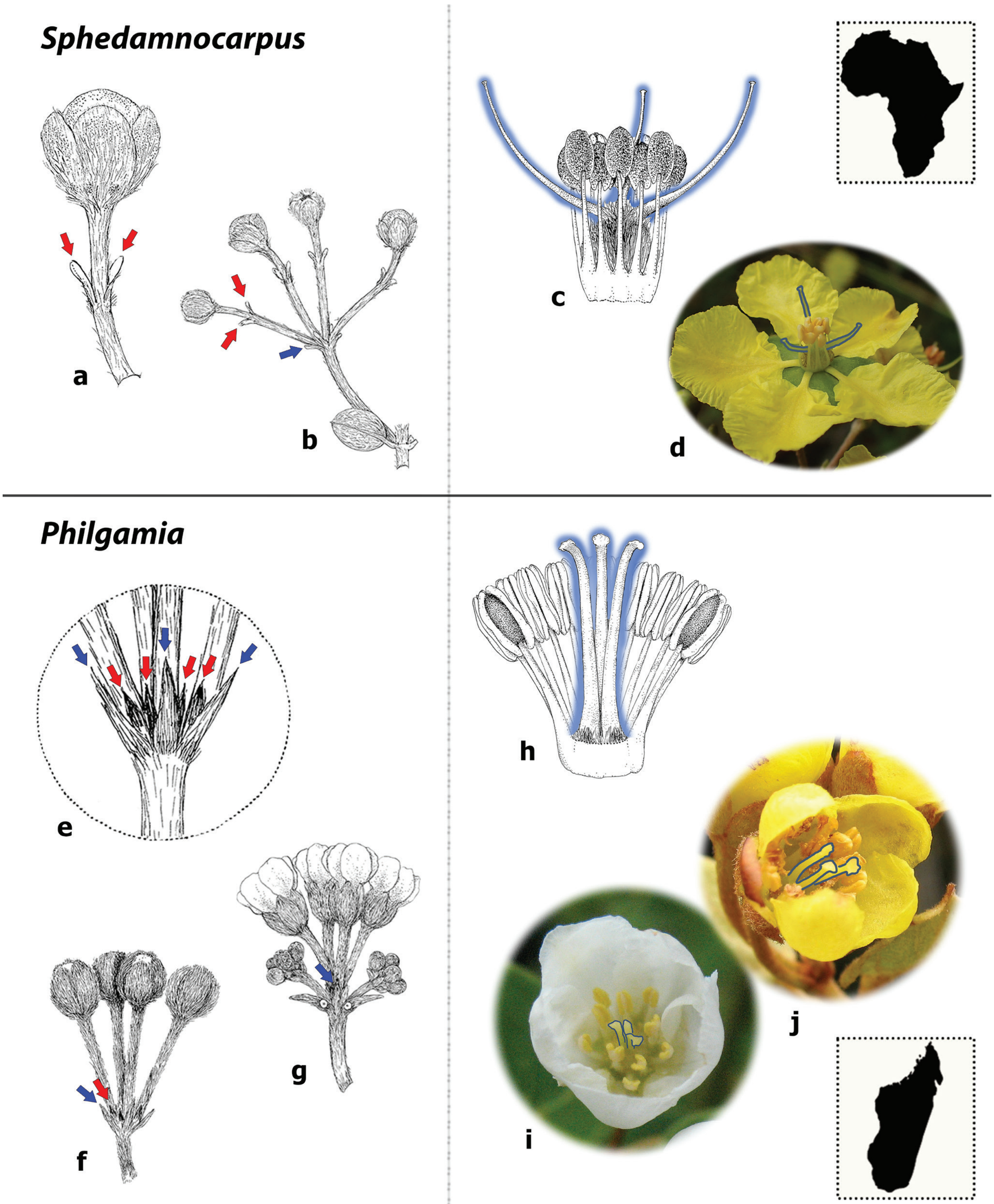


FIGURE 4. Morphological differences between the mainland (*Sphedamnocarpus*) and island (*Philgamia*) clades, highlighting inflorescence morphology on the left and floral morphology on the right. Red arrows indicate bracteoles and blue arrows indicate bracts. **A**, flower bud of *S. angolensis*; **B**, inflorescence of *S. angolensis*; **C**, reproductive parts of *S. angolensis*, with styles highlighted in blue; **D**, photograph of *S. pruriens* flower with gynoecium outlined in blue; **E**, close-up umbel base of *P. glabrifolia*; **F**, inflorescence of *P. glabrifolia*; **G**, inflorescence of *S. andersonii*; **H**, reproductive parts of *S. dubardii*, with styles highlighted in blue; **I**, photograph of *Philgamia sp.*; **J**, photograph of *S. dubardii* flower, with styles outlined in blue. Illustrations adapted from an unpublished drawing by Karin Douthit with permission from the University of Michigan Herbarium (http://malpighiaceae.herb.lsa.umich.edu/nomhome.html).

Philgamia coursii (Arènes) Kehoe, C. Davis, & J.T. Williams, *comb. nov.*
Basionym: *Sphedamnocarpus coursii* Arènes (1944: 185).
TYPE: MADAGASCAR. Alaotra-Mangoro region, Ambatondrazaka district, Alaotra station, 780 m, December 1937, *G. Cours 1413 (S-195)* (Holotype: P [P00048033]).

Philgamia cuspidifolia (Arenés) Kehoe, C. Davis, & J.T. Williams, *comb. nov.*
Basionym: *Sphedamnocarpus cuspidifolius* Arenés (1946: 184–185).
TYPE: MADAGASCAR. Boeny Region, Ankarafantsika (7th Reserve), Bevasaka, sandy plateau, 200 m, *Service Forstier* [Forest Service] *71* (Holotype: P [P00048034]; Isotype: P [P00048035]).

Philgamia decaryi (Arènes) Kehoe, C. Davis, & J.T. Williams, *comb. nov.*
Basionym: *Sphedamnocarpus decaryi* Arènes (1943b: 109).
TYPE: MADAGASCAR. Ranopiso, District of Fort Dauphin, in the Savoka, July 1932, *R. Decary 10193* (Lectotype [designated here]: P [P06170053]; Isolectotypes: P [P06170059], [P06170054]).

Philgamia dubardii (Viguier & Humbert ex Arènes) Kehoe, C. Davis, & J.T. Williams, *comb. nov.*
Basionym: *Tricomariopsis madagascariensis* Dubard (1907: 1191), *Sphedamnocarpus dubardi* Viguier & Humbert ex Arènes (1943b: 101).
TYPE: MADAGASCAR. Analamanga Region, Mandraka Forest, *d'Alleizette 476* (Holotype: P [P00048039]; Isotype: P [P00048040]).

Philgamia heterophylla (Arènes) Kehoe, C. Davis, & J.T. Williams, *comb. nov.*
Basionym: *Sphedamnocarpus heterophyllus* Arènes (1947: 108).
TYPE: MADAGASCAR. Androy Region, Ampandrandava, east ridge, 1000 m, *Seyrig 527* (Holotype: P [P00048044]).

Philgamia humbertii (Arènes) Kehoe, C. Davis, & J.T. Williams, *comb. nov.*
Basionym: *Sphedamnocarpus humbertii* Arènes (1943b: 113).
TYPE: MADAGASCAR. Anosy Region, reception basin of the Mananara, tributary of the Mandraré, western slopes of the mountains between Andohahela and Elakelaka, between Ampahiso et Mahamavo (gneiss), 400–700 m, January–February 1934, *Humbert 13707* (Lectotype [designated here]: P [P00413515]; Isolectotypes: P [P00413516], [P00413517]).

Philgamia madagascariensis (Arènes) Kehoe, C. Davis, & J.T. Williams, *comb. nov.*
Basionym: *Banisteria multiflora* Bojer ex A. Juss. (1840: 286), non *B. multiflora* DC. (1824), *Sphedamnocarpus madagascariensis* Baker (1884: 110), *Banisterioides madagascariensis* Dubard & Dop (1908: 356), *Triaspis chrysophylla* Nied. (1915: 21), *Sphedamnocarpus multiflorus* (Bojer ex A. Juss.) Nied. (1924: 16).
TYPE: MADAGASCAR. Near Mazangay. *Bojer s.n.* (Holotype: P [P00048045]).

Philgamia orbicularis (Arènes) Kehoe, C. Davis, & J.T. Williams, *comb. nov.*
Basionym: *Sphedamnocarpus orbicularis* Arènes (1943b: 112).
TYPE: MADAGASCAR. Amoron'i Mania Region, woods-quartzites, 600 m, March 1919, *Perrier de la Bâthie 12537* (Holotype: P [P00048046]; Isotype: P [P00048047]).

Philgamia perrieri (Arènes) Kehoe, C. Davis, & J.T. Williams, *comb. nov.*
Basionym: *Sphedamnocarpus perrieri* Arènes (1943b: 116).
TYPE: MADAGASCAR. Alaotra-Mangoro Region, between Andilamena et Mandritsara, forest, 900 m, November 1921, *Perrier de la Bâthie 14999* (Holotype: P [P00048048]; Isotypes: P [P00048049], [P00048050]).

Philgamia poissonii (Arènes) Kehoe, C. Davis, & J.T. Williams, *comb. nov.*
Basionym: *Sphedamnocarpus poissonii* Arènes (1943b: 114).
TYPE: MADAGASCAR. Former Toliara Province, route from Sakaména to Ejeda, 11 April 1922, *Poisson 442* (Holotype: P [P00048051]).

Philgamia vohitrotsyensis (Arènes) Kehoe, C. Davis, & J.T. Williams, *comb. nov.*
Basionym: *Sphedamnocarpus vohitrosyensis* Arènes (1943b: 107).
TYPE: MADAGASCAR. Anosy Region, middle valley of Mandrare, near Anadabolava, Mount Vohitrotsy, 800–850 m, December 1933, *H. Humbert 12725* (Holotype: P [P00048052]; Isotypes: P [P00048053], [P00048054]).

Author Contribution Statement

C. D., J.W., and J. K. developed the study. C. D., L. C., Y. Y., and X. D. collected and curated phylogenetic data with methods they developed. J. K., L. C., and C. D. analyzed and interpreted the phylogenetic data for species included in this study. J. K. and J.W. conducted taxonomic research. J. K. examined all herbarium specimens. J. K. and C. D. wrote the main text. J. K. produced all figures and nomenclatural changes with input from C. D. and J.W.

Literature Cited

Anderson, C. E. 2011. Revision of *Ryssopterys* and transfer to *Stigmaphyllon* (Malpighiaceae). Blumea 56: 73–104.
———. 2018. *Sphedamnocarpus andersonii* (Malpighiaceae), a new species from Madagascar. Brittonia 70(2): 248–251.
Anderson, W. R. 1979. Floral conservatism in neotropical Malpighiaceae. Biotropica 11: 219–223.
———. 2004. Malpighiaceae (Malpighia Family). Pages 229–232 in Smith, N., S. A. Mori, A. Henderson, D. W. Stevenson, and S. V. Heald, eds., Flowering plants of the Neotropics. Princeton: Princeton University Press, published in association with The New York Botanical Garden.

Anderson, W. R., and C. C. Davis. 2005. The *Mascagnia* Cordiifolia Group (Malpighiaceae). Contributions from the University of Michigan Herbarium 24: 33–44.
———. 2006. Expansion of *Diplopterys* at the expense of *Banisteriopsis* (Malpighiaceae). Harvard Papers in Botany 11(1): 1–16.
———. 2007. Generic adjustments in neotropical Malpighiaceae. Contributions from the University of Michigan Herbarium 25: 137–166.
Andrews, S. 2010. *FastQC: A Quality Control Tool for High Throughput Sequence Data,* Babraham Bioinformatics, Cambridge U.K. Available from: http://www.bioinformatics.babraham.ac.uk/projects/fastqc/ (accessed October 21, 2023).
Antonelli, A. et al. [83 co-authors]. 2022. Madagascar's extraordinary biodiversity: Threats and opportunities. Science (American Association for the Advancement of Science), *378* (6623), 963—eadf1466. https://doi.org/10.1126/science.adf1466
Arènes, J. 1943a. Le genre Philgamia Baillon, genre endémique Malgache de Malpighiaceés. Notulae Systematicae (Paris) 11: 85.
———. 1943b. Revision du genre Sphedamnocarpus Planchon (Malpighiacées). Notulae Systematicae (Paris) 11: 97.
———. 1944. Un *Sphedamnocarpus* Nouveau pour la Flore Malgache. Notulae Systematicae (Paris) 11: 185.
———. 1946. Nouvelle contribution à l'étude des Malpighiacées Malgaches. Notulae systematicae (Paris) 12: 184
———. 1947. Un nouveau *Sphedamnocarpus* Malgache. Notulae Systematicae (Paris) 13: 108.
Aronesty, E. 2011. ea-utils: Command-line tools for processing biological sequencing data; https://github.com/ExpressionAnalysis/ea-utils (accessed April 1, 2024, 11:00 am EDT).
Baillon, H. 1894. Histoire physique, naturelle et politique de Madagascar t. 265
Baker, J. G. 1884. Mr J. G. Baker on the Flora of Madagascar. Journal of the Linnaean Society Botany 20: 110.
Bentham, G., and J. D. Hooker. 1862. Genera plantarum: ad exemplaria imprimis in Herberiis Kewensibus servata definita 1(1): 256.
Cai, L., H. Zhang, and C. C. Davis. 2022. PhyloHerb: A high-throughput phylogenomic pipeline for processing genome skimming data. Applications in Plant Sciences 10.3: e11475.
Cai, L., Z. Xi, K. Peterson, C. Rushworth, J. Beaulieu, and C. C. Davis. 2016. Phylogeny of Elatinaceae and the tropical Gondwanan origin of the Centroplacaceae (Malpighiaceae, Elatinaceae) clade. PloS ONE 11 (9): e0161881.
Cameron, K. M., M. W. Chase, W. R. Anderson, and H. G. Hills. 2001. Molecular systematics of Malpighiaceae: evidence from plastid *rbcL* and *matK* sequences. American Journal of Botany 88(10): 1847–1862.
de Candolle, A. P. 1824. Prodromus systematis naturalis regni vegetabilis, sive, Enumeratio contracta ordinum generum specierumque plantarum huc usque cognitarium, juxta methodi naturalis, normas digesta 1: 589.
Chase, M. W., S. Zmarzty, M. D. Lledó, K. J. Wurdack, S. M. Swensen, and M. F. Fay. 2002. When in doubt, put it in Flacourtiaceae: a molecular phylogenetic analysis based on plastid rbcL DNA sequences. Kew Bulletin 57: 141–181.
Davis, C. C. 2002. *Madagasikaria* (Malpighiaceae): a new genus from Madagascar with implications for floral evolution in Malpighiaceae. American Journal of Botany 89 (4): 699–706.
———., W. R. Anderson, and M. J. Donoghue. 2001. Phylogeny of Malpighiaceae: evidence from chloroplast *ndhF* and *trnL-F* nucleotide sequences. American Journal of Botany 88 (10): 1830–1846.
———., C. D. Bell, P. W. Fritsch P, and S. Mathews. 2002. Phylogeny of *Acridocarpus-Brachylophon* (Malpighiaceae): implications for Tertiary tropical floras and Afroasian biogeography. Evolution 56 (12): 2395–2405.
———., C. D. Bell, S. Mathews, and M. J. Donoghue. 2002. Laurasian migration explains Gondwanan disjunctions: evidence from Malpighiaceae. Proceedings of the National Academy of Sciences of the United States of America 99 (10): 6833–6837. doi: 10.1073/pnas.102175899.
———., and M. W. Chase. 2004. Elatinaceae are sister to Malpighiaceae; Peridiscaceae belong to Saxifragales. American Journal of Botany 91 (2): 262–273.
———., P. W. Fritsch, C. D. Bell, and S. Mathews. 2004. High latitude Tertiary migrations of an exclusively tropical clade: evidence from Malpighiaceae. International Journal of Plant Sciences 165 (4): S107–S121.
———., and W. R. Anderson. 2010. A complete generic phylogeny of Malpighiaceae inferred from nucleotide sequence data and morphology. American Journal of Botany 97 (12): 2031–2048. doi: 10.3732/ajb.1000146.
———., H. Schaefer, Z. Xi, D. A. Baum, M. J. Donoghue, and L. J. Harmon. 2014. Long-term morphological stasis maintained by a plant—pollinator mutualism. Proceedings of the National Academy of Sciences of the United States of America 111 (16): 5914–5919. doi: 10.1073/pnas.1403157111.
Dubard, M. M. 1907. Remarques sur les affinités des Malpighiacées de Madagascar, à propos du genre nouveau *Tricomariopsis*. Comptes rendus hebdomadaires des séances de l'Académie des sciences 145: 1191.
Dubard, M. M., and P. L. A. Dop. 1908. Contribution à l'Étude des Malpighiacées de Madagascar. Revue Général de Botanique Paris 20: 356.
Jin, J., W. Yu, J. Yang, Y. Song, C. W. dePamphilis, T. Yi, and D. Li. 2020. GetOrganelle: a fast and versatile toolkit for accurate de novo assembly of organelle genomes. Genome Biology 21, 241 (2020). https://doi.org/10.1186/s13059-020-02154-5
Jussieu, A. D. 1840. Malpighiacearum synopsis. Annales des Sciences Naturelles; Botanique Série 2, 13: 286.
———. 1843. Monographie des Malpighiacées: ou, Exposition des caractères de cette famille de plantes, des genres et espèces qui la composent, accompagnée de 23 planches.
Lanfear, R., P. B. Frandsen, A. M. Wright, T. Senfeld, and B. Calcott, B. 2016. PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. Molecular biology and evolution. DOI: dx.doi.org/10.1093/molbev/msw260
Lichter-Marck, I. H., and B. Baldwin. 2023. Edaphic specialization onto bare, rocky outcrops as a factor in the evolution of desert angiosperms. Proceedings of the National Academy of Sciences 120(6) e2214729120
Minh, B. Q., M. A. T. Nguyen, and A. von Haeseler. 2013. Ultrafast approximation for phylogenetic bootstrap. Molecular Biology and Evolution 30: 1188–1195. (DOI: 10.1093/molbev/mst024)
Mirarab, S., N. Nguyen, S. Guo, L. Wang, J. Kim, and T. Warnow. 2015. PASTA: ultra-large multiple sequence alignment for nucleotide and amino-acid sequences. Journal of Computational Biology 22(5): 377–386.
Nguyen, L. T., H. A. Schmidt, A. von Haeseler, and B. Q. Minh. 2015. IQ-TREE: A fast and effective stochastic algorithm for estimating maximum likelihood phylogenies. Molecular Biology and Evolution 32: 268–274. (DOI: 10.1093/molbev/msu300)
Niedenzu, F. 1915. Malpighiaceae paleotropicae. Arbeiten aus dem Botanischen Institut der Staatliche Akademie in Braunsberg 21.

———. 1924. Malpighiaceae paleotropicae. Verzeichnis der Vorlesungen an der Akademie zu Braunsberg im Sommer *1924* 15–19.

———. 1928. Malpighiacecae. Das Pflanzenreich *IV* 141: 254.

Oliver, D., W. T. T. P. Dyer, D. Hill, and A. William. 1868. Malpighiaceae. Flora of Tropical Africa 1: 279.

Schmieder, R., and R. Edwards. 2011. Quality control and preprocessing of metagenomic datasets. Bioinformatics 27: 863–864. [PMID: 21278185]

de Villiers, P. D., and D. J. Botha. 1986. Sphedamnocarpus. Pages 66–69 in Codd, L. E., R. A. Dyer, H. B. Rycroft, and B. Winter, eds., *Flora of Southern Africa: the Republic of South Africa, Basutoland, Swaziland and South West Africa*. Dept. of Agricultural Technical Services, South Africa.

Vogel, S. 1974. Ölblumen und ölsammelnde Bienen. Tropische und Subtropische Pflanzenwelt 7: 283–547.

———. 1990. History of the Malpighiaceae in the light of pollination ecology. Memoirs of the New York Botanical Garden 55: 130–142.

Weitemier, K., S. C. K. Straub, R. C. Cronn, M. Fishbein, R. Schmickl, A. McDonnell, and A. Liston. 2014. Hyb-Seq: Combining Target Enrichment and Genome Skimming for Plant Phylogenomics. Applications in Plant Sciences 2(9): apps.1400042. https://doi.org/10.3732/apps.1400042

Wurdack, K. J., and C. C. Davis. 2005. New insights in the phylogeny and evolution of Malpighiales. International Botanical Congress, Vienna.

Zhang, W., E. M. Kramer, and C. C. Davis. 2010. Floral symmetry genes and the origin and maintenance of zygomorphy in a plant-pollinator mutualism. Proceedings of the National Academy of Sciences of the United States of America 107 (14): 6388-6393. doi: 10.1073/pnas.0910155107.

———. 2012. Similar genetic mechanisms underlie the parallel evolution of floral phenotypes. *PLoS ONE* 7 (4): e36033. doi: 10.1371/journal.pone.0036033.

———. 2016. Differential expression of *CYC2* genes and the elaboration of floral morphologies in *Hiptage*, an Old World genus of Malpighiaceae. International Journal of Plant Sciences 177: 551–558

Zhang, W., V. W. Steinmann, L. Nikolov, E. M. Kramer, and C. C. Davis. 2013. Divergent genetic mechanisms underlie reversals to radial floral symmetry from diverse zygomorphic flowered ancestors. Frontiers in Plant Science 4. doi: 10.3389/fpls.2013.00302.

Appendix I

Specimens Examined

Philgamia brachystemon Arènes
MADAGASCAR. Amoron'i Mania Region, Fianarantsoa. Ambositra. Ihadilaganana, Ambohipiandrianana-Ambohibary- Montage d'Ambatonanahary. Végétation sur substrat quartzitique. 20˚26'43"S 047˚03'42"E; 1303 m, 04 November 2014, *S. Andriambololonera, Tefy Andriamihajarivo & Fortunat 309* (GH).

Philgamia glabrifolia Arènes
MADAGASCAR. Fianarantsoa Province: Mt. Ibity. On ridge across valley from limestome quarry and cement plant. 20˚3'55"S, 47˚0'3"E; 1660-1680 m, 20 January 2008, *W. H. Zhang, J. Andrianatina & D. E. Boufford 129* (AA).

Sphedamnocarpus angolensis (A.Juss.) Planch. ex. Oliv.
ZIMBABWE. Salisbury [Harare]. December 1913. *F. A. Rogers 13095* (AA).

Sphedamnocarpus decaryi Arènes
MADAGASCAR. Anosy: Environs de Fort Dauphin [Tolagnaro]. 1–25 m, 20 September–6 October 1928. *H. Humbert 5714* (AA).

Sphedamnocarpus galphimiifolius (A.Juss.) Szyszył.
SOUTH AFRICA. Transvaal: Soutpansberg, Willies Port, Louis Trichardt; 900–1000 m, 21 January 1959, *E. Werdermann & H. D. Oberdieck 1938* (AA). Mariepskop, in undergrowth in forestry reserve on the road to Klaserie. 16 January 1959, *H. P. v. d. Schiff 4509* (AA).

Sphedamnocarpus humbertii Arènes
MADAGASCAR. Atsimo-Andrefana: N of Toliara, between Fiherenana and Manombo Rivers, Ranobe Forest. Ankilimalinike Commune. About 14 km inland from RN9 on norther seismic line. 22˚57'16"S, 43˚39'53"E; 115 m, 12 March 2006, *P. B. Phillipson, R. Ranaivojaona, N. M. Andrianjafy & R. A. Lubke 5840* (GH).

Sphedamnocarpus madagascariensis Baker
MADAGASCAR. Boeny: Environs de Majunga. Lieux sablonneux, dunes. 2–15 m, 28–30 July 1924. *H. Humbert 2038* (AA).

Sphedamnocarpus pruriens (A.Juss.) Szyszył.
NAMIBIA. Zwischen Grootfontein und Otavi. 1400 m, 2 March 1959. *E. Werdermann et H. D. Oberdieck 2405* (AA); Otavi. 7 February 1925. *K Dinter. 5550* (AA); SOUTH AFRICA. Guatang Province, Pretoria: E of the city of Pretoria at Plumbago Conservation area. 25˚46'17"S, 28˚17'46"E; 1425 m, 4 February 2008. *W. H. Zhang, R. H. Archer & D. E. Boufford 148* (AA); Makapan Valley, near Potgietersrus, Transvaal. Sourveld, very rocky steep grassland with scattered shrubs, ca. 1500 m, 7 April 1985, *M. Bourell 2755* (GH); Waterberge, zwischen Nylstroom und Warmbad, 1150–1250 m, 21 Jan 1959. *E. Werdermann et H. D. Oberdieck 2012* (AA); *Natal s.n.* (GH).

Sphedamnocarpus pruriens *var.* ***latifolius*** Engl.
BOTSWANA. 10 miles N of Molepolole, 11 June 1955. *R. Story 4874* (ECON); NAMIBIA. Cigarette, N. E. of Karakuwise, 11 Feb 1953. *B. Maguire 2477* (ECON); SOUTH AFRICA. Nelspruit [Mbombela], Transvaal, April 1920. *F. A. Rogers 23781* (AA).

Sphedamnocarpus rehmanii Szyszył.
SOUTH AFRICA. Zoutpansberg, 1936. *M C. Gillet 4747* (GH).

Sphedamnocarpus transvaalicus (Kuntze) Burtt Davy
SOUTH AFRICA. Gauteng Province, Pretoria: Slope on N side of Fort Klapperkop. 25˚46'32"S, 28˚12'30"E; 1490 m, 8 February 2008. *W. H. Zhang, R. H. Archer & D. E. Boufford 152* (AA); Gauteng Province, Pretoria: E of the city of Pretoria at Plumbago Conservation area. 25˚46'14"S, 28˚17'34"E; 1390 m, 4 February 2008. *W. H. Zhang, R. H. Archer & D. E. Boufford 149* (AA).

Sphedamnocarpus Indeterminate

Sphedamnocarpus sp., det. C. C. Davis. MADAGASCAR. Fiannarantsoa Province, Isalo National Park, NW side of road 600m southwest from park. 24°37'54"S, 45°21'22"E; 850 m, January 18, 2001. *Charles C. Davis 03-01* (AA).

Sphedamnocarpus sp. MADAGASCAR. Fianarantsoa Province: S of Isalo National PArk and NE of the town of Ilakaka on road to Toliara at Maison de l'Isalo geological park. 22°37'09"S, 45°21'41"E; 855 m, January 22, 2008. *W. H. Zhang, J. Andrianatina & D. E. Boufford 132* (AA).

Sphedamnocarpus sp. MADAGASCAR. Toamasina (Tamatave), Forêt de Mantady, N of graphite mines. Rain forest. 18°52'20"S, 48°29'60"E; 935 m, October 27, 1993. *F. I. van Nek 1989* (AA).

ACANTHACEAE, AN ADDITIONAL FAMILY OF ANGIOSPERMS WITH STAMINAL LEVERS

Ricardo Kriebel[1,2] and Thomas F. Daniel[1]

Abstract. We report for the first time the occurrence of a staminal lever mechanism in Acanthaceae. Pressing the staminal appendage in two species of *Justicia* causes the anther to descend in a manner similar to the genus *Salvia*. Anther movement via a lever may affect where pollen is deposited on the body of potential pollinators. Acanthaceae are one of only a few families where staminal levers have been reported, and most of those families are in the order Lamiales.

Keywords: anther appendage, convergent evolution, *Justicia*, Lamiaceae, Linderniaceae, Plantaginaceae, Zingiberaceae

Resumen. Reportamos por primera vez un mecanismo de palanca staminal en Acanthaceae. Presionar el apéndice staminal en dos especies de *Justicia* causó que la antera descendiera en una forma similar al género *Salvia*. Movimiento de las anteras con una palanca puede afectar donde el polen es depositado en el cuerpo de potenciales polinizadores. Acanthaceae es una de las pocas familias donde se han reportado palancas estaminales, y la mayoría de las familias están en el orden Lamiales.

Palabras claves: apéndice de la antera, convergencia evolutiva, *Justicia*, Lamiaceae, Linderniaceae, Plantaginaceae, Zingiberaceae

The stamen is the pollen producing and presenting structure in flowers. Consisting of a filament or stalk and the pollen-bearing anther, stamens show remarkable diversity in shape, size, color, and number per flower. When an anther consists of two pollen sacs (thecae), the portion of the filament between them is known as the connective. The connective can be enlarged and highly modified into structures that aid in their interactions with floral visitors, including pollinators. In the genus *Salvia* L. (Lamiaceae), for example, the connective is modified into a long structure, which, when pressed by a potential pollinator, acts as a lever mechanism to lower the anther for precise pollen placement (Fig 1A; Claßen-Bockhoff et al. 2003). It has been suggested that the evolution of the lever has been a key innovation in *Salvia* that led to species diversification (Claßen-Bockhoff et al. 2004).

Staminal levers are rare in plants and known mainly in the families Lamiaceae and Zingiberaceae (Zhang et al. 2010). The similarity between levers in species of these two distantly related families has long been recognized (Lynch, 1882). The lever in Zingiberaceae differs from that of *Salvia*, the primary genus of Lamiaceae with staminal levers, in that it is produced by a variously modifed thecal appendage instead of an expanded connective tissue (Zhang et al. 2010; Paudal and Li, 2020). Another family where staminal levers have been documented is the Linderniaceae. For example, in the genus *Torenia* L., the thecal wall has a lateral flange-like outgrowth that functions as a lever (Armstrong, 1992). The fourth family that has a lever mechanism is the Plantaginaceae, where the staminode in some species of *Penstemon* Schmidel helps lever the stamens and style (Walker-Larsen and Harder, 2001).

Thecal appendages of various shapes and sizes occur in another family, the Acanthaceae, including species in subfamilies Thunbergioideae (Borg et al., 2008) and the mega-diverse Acanthoideae (e.g., tribes Acantheae, Justicieae, and Ruellieae; Manzitto-Tripp et al., 2022). Among Justicieae, thecal appendages and variously elongated connectives are common in the genus *Justicia* L. (Graham, 1988), in which appendages were found to have evolved at least twice (Kiel et al., 2017, 2018). Thecal appendages have been widely used as taxonomic characters among Acanthaceae, but their function remains unknown.

We hypothesize that at least some thecal appendages in *Justicia* are part of a lever mechanism that most likely functions in the placement of pollen onto floral visitors. This hypothesis is supported by manipulations and observations on two Mexican species described below. As in species of *Salvia*, such as garden sage (*S. officinalis* L., Fig. 1A), the appendages/levers in these species of *Justicia* are positioned such that an insect visitor seeking nectar at the base of the corolla tube would contact them. Using plants of two species of *Justicia* from Michoacán, Mexico, *J. salviiflora* Kunth (*Daniel 11917cv* grown from seeds of *Daniel & Steinmann 11917*) and *J. wilburii* T.F. Daniel (*Daniel 11919cv* grown from seeds of *Daniel & Steinmann 11919*), with all voucher specimens at CAS, we experimented with their flowers by contacting the appendage with the blunt bottom end of a paper clip and forceps. Contact of the appendage on one or both anthers by either instrument causes the stamen to move downward, confirming the lever-like function (Fig. 1C–F). Pollen from dehisced thecae was deposited onto the instrument used. As in *Salvia*, once pressure is no longer applied to the appendage, the stamen with anthers returns to its original position. The anther displacement via the lever mechanism was possible multiple times.

Previous observations on *Justicia salviiflora* noted that "the androecium conforms to the back and sides of a visiting

We are grateful to Emily Magnaghi for help with imaging the lever mechanism. We also thank the editor and reviewers for their input and Bryan Drew and Carrie Kiel for their comments.

[1] Department of Botany, Institute of Biodiversity Science and Sustainability, California Academy of Sciences, 55 Music Concourse Drive, San Francisco, California, 94118-4599, U.S.A.

[2] Corresponding authors: rkriebel@calacademy.org; tdaniel@calacademy.org

Harvard Papers in Botany, Vol. 29, No. 1, 2024, pp. 97–99.

ISSN: 1938-2944, DOI: 10.3100/hpib.v29iss1.2024.n11, Published online: 30 June 2024

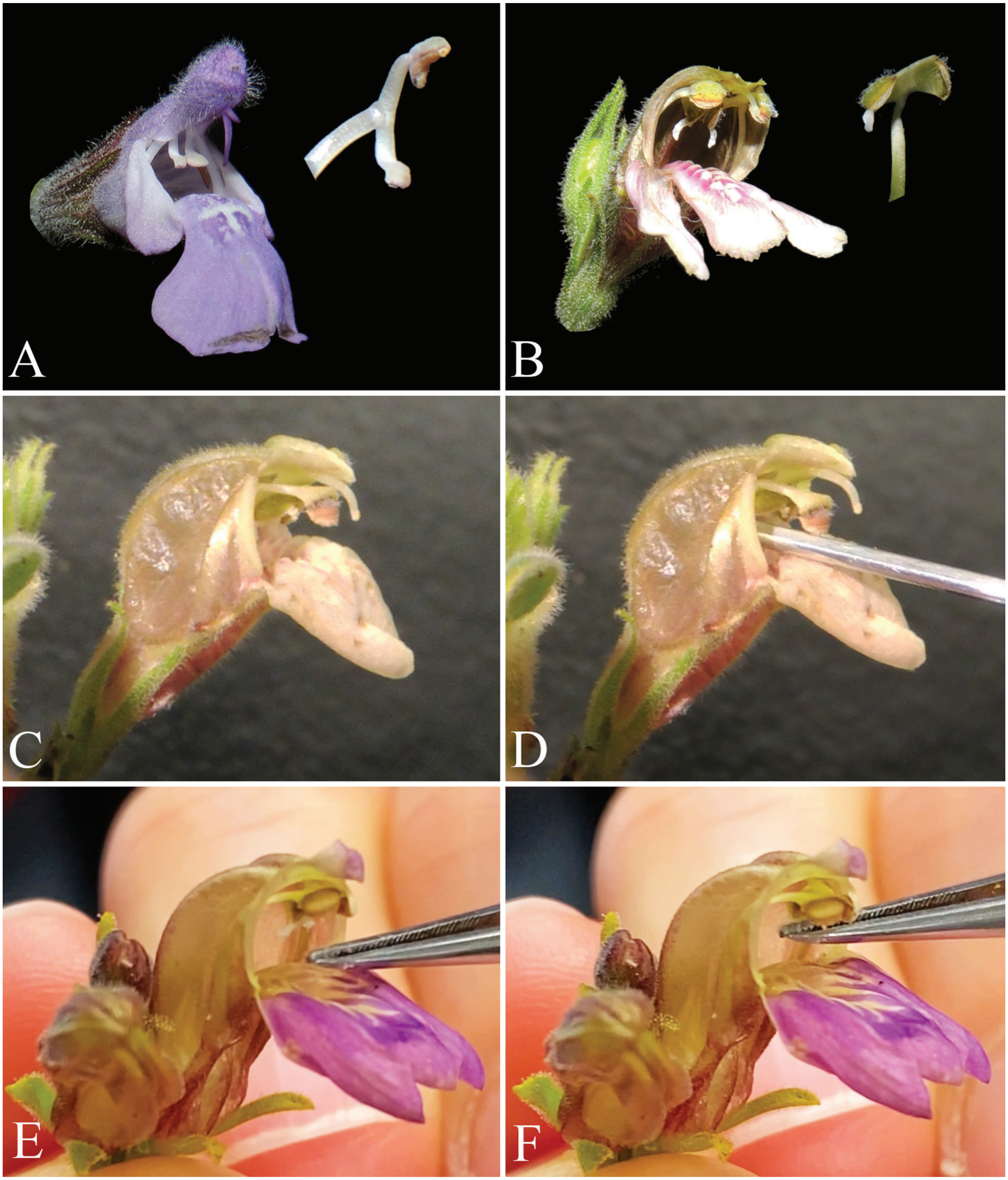


FIGURE 1. **A**, *Salvia officinalis* and close-up of one of its stamens. **B–D**, *Justicia salviiflora*. **B**, View of the corolla showing the stamens and their respective appendages and close-up of a stamen. **C**, Lateral view of the corolla, stamens and style. **D**, Lateral view of the corolla, stamens, and style with a pin inserted into the corolla and touching the anther appendages, causing the anther to lever down. **E–F**, *J. wilburii*. **E**, Lateral view of the corolla, stamens and style. **F**, Lateral view of the corolla, stamens, and style with a pin inserted into the corolla and touching the anther appendages, causing the anther to lever down.

bee as it enters the mouth and throat of the corolla, seeming to clamp onto the bee's body" (Kiel et al., 2023: 55). The authors hypothesized "that this mechanism deposits pollen on bees' bodies in locations where it cannot be reached by the grooming bee" and suggested that experiments would shed light on the function of this thecal shape variation. Our experiments indeed confirmed a function for the asymmetric thecae with an elongated connective and a basal appendage on the lower theca: a lever mechanism that assists in the deposition of pollen onto a floral visitor.

Among species of *Justicia* in the New World, basal appendages are rarely more than one millimeter long. Those of *J. salviiflora* and *J. wilburii* vary from 0.8 to 1.5 mm in length. Whereas there is only moderate elongation of the connective (e.g., to 0.5 mm) in these two species, other species of *Justicia* have stamens bearing more elongated anther connectives (e.g., Graham, 1988, Fig. 2; Kiel et al., 2017, Fig. 4, 2018, Fig. 2) that more closely resemble those in *Salvia*. These may also serve as levers in the absence of basal appendages or assist in levering of pollen placement when basal appendage functioning as levers are present. Hopefully, our observations will stimulate future investigations on the evolution and morphological diversification of thecal appendages and staminal levers among Acanthaceae and their impacts on evolution within the family.

Literature Cited

Armstrong, J. E. 1992. Lever action anthers and the forcible shedding of pollen in *Torenia* (Scrophulariaceae). Amer. J. Bot. 79: 34–40.

Borg, A. J., L. A. McDade, and J. Schönenberger. 2008. Molecular phylogenetics and morphological evolution of the Thunbergioideae (Acanthaceae). Taxon 57: 1–12. https://doi.org/10.1002/tax.573012

Classen-Bockhoff, R., P. Wester, and E. Tweraser. 2003. The staminal lever arm mechanism in *Salvia*—A review. Plant Biol. (Stuttgart). 5: 33–41. https://doi.org/10.1055/s-2003-37973

Classen-Bockhoff, R., T. Speck, E. Tweraser, P. Wester, S. Thimm, and M. Reith. 2004. The staminal lever mechanism in *Salvia* L. (Lamiaceae): A key innovation for adaptive radiation? Org. Divers. Evol. 4: 189–205. https://doi.org/10.1016/j.ode.2004.01.004

Graham, V. A. W. 1988. Delimitation and infra-generic classification of *Justicia* (Acanthaceae). Kew Bull. 43: 551–624.

Kiel, C. A., T. F. Daniel, I. Darbyshire, and L. A. McDade. 2017. Unraveling relationships in the morphologically diverse and taxonomically challenging 'justicioid' lineage (Acanthaceae, Justicieae). Taxon 66: 645–674. https://doi.org/10.12705/663.8

Kiel, C. A., T. F. Daniel, and L. A. McDade. 2018. Phylogenetics of New World 'justicioids' (Justicieae: Acanthaceae): Major lineages, morphological patterns, and widespread incongruence with classification. Syst. Bot. 43: 459–484. https://doi.org/10.1600/036364418X697201

Kiel, C. A., E. Manzitto-Tripp, A. E. Fisher, J. M. Porter, and L. A. McDade. 2023. Remarkable variation in androecial morphology is closely associated with corolla traits in Western Hemisphere Justiciinae (Acanthaceae: Justicieae). Ann. Bot. (Oxford) 132: 43–60.

Lynch, R. I. 1882. On a contrivance for cross-fertilization in *Roscoea purpurea*; with incidental reference to the structure of *Salvia grahami*. J. Linn. Soc., Bot. 19: 204–206.

Manzitto-Tripp, E. A., I. Darbyshire, T. F. Daniel, C. A. Kiel, and L. A. McDade. 2022. Revised classification of Acanthaceae and worldwide dichotomous keys. Taxon 71: 103–153. https://doi.org/10.1002/tax.12600

Paudel, B. R., and Q. J. Li. 2020. Functional implications of the specialized staminal appendages in alpine ginger (*Roscoea* spp.: Zingiberaceae). J. Evol. Biol. 33: 1265–1275. https://doi.org/10.1111/jeb.13670

Walker-Larsen, J., and L. D. Harder. 2001. Vestigial organs as opportunities for functional innovation: The example of the *Penstemon* staminode. Evolution 55: 477–487.

Zhang, B., S. Sun, Z. Q. Zhang, and Q. J. Li. 2010. A review of the evolutionary and ecological significance of lever-like stamens. Chin. J. Pl. Ecol. 34: 89–99.

Page 100 intentionally left blank.

DISPERSAL SYNDROMES IN A CONSERVATION AREA IN A BRAZILIAN SEMIARID REGION

Guilherme Araújo da Luz,[1] Dilma Maria de Brito Melo Trovão,[2] Bernardo de Farias Rocha,[1] Thávyla Ellen Duarte Correia,[3] and José Iranildo Miranda de Melo[2,4]

Abstract. The Brazilian semiarid region, the phytogeographic domain of the Caatinga, presents a wide floristic diversity and, paradoxically, human actions, such as deforestation for agriculture and livestock, that present constant threats to the reduction of its vegetation cover. In order to avoid the complete loss of plant and animal diversity, Conservation Units have been created, areas for which it is necessary to understand ecological processes, especially those that maintain biodiversity. In this context, the present study verified the dispersal strategies of angiosperms in the Ecological Reserve Olho d'Água das Onças (REODDO), a conservation area located in the municipality of Picuí, a semiarid region of Paraíba state, Northeast Brazil. Twelve field trips were made between August 2022 and July 2023. The specimens obtained are incorporated into the HACAM Herbarium collection (not indexed). Ninety-five species of angiosperms belonging to 28 families were recorded, and we verified that 74.5% of those species had dry fruits and disperse their seeds through abiotic mechanisms (autochory or anemochory). Only 25.5% of the total number of species disperse their seeds via zoochoric means. This is likely a result of the semiarid nature of this phytogeographical domain, where fruits with large pericarps that are normally attractive to larger animals are atypical. Our results are fundamental to understanding ecological processes in natural environments in the semiarid regions of Brazilian and demonstrate the predominance of abiotic syndromes even in an Ecological Reserve area, where faunal diversity is probably greater than in non-protected areas. These results also contribute essential information that can be incorporated into management and restoration plans in Caatinga areas.

Keywords: biodiversity, conservation, ecological processes, flora, semiarid

Resumo. No semiárido brasileiro, o domínio fitogeográfico da Caatinga apresenta uma ampla diversidade florística e paradoxalmente as ações antrópicas, como o desmatamento para a agricultura e pecuária, representam ameaças constantes à redução da sua cobertura vegetal. No intuito de evitar a perda completa da diversidade vegetal e animal vêm sendo criadas as Unidades de Conservação, áreas para as quais torna-se necessário compreender as interações ecológicas, em especial, àquelas mantenedoras da biodiversidade. Nesse contexto, o presente estudo verificou as estratégias de dispersão das angiospermas na Reserva Ecológica Olho d'Água das Onças (REODDO), área de conservação localizada no município de Picuí, semiárido paraibano, Nordeste brasileiro. Os trabalhos de campo foram feitos entre agosto/2022 e julho/2023, totalizando 12 incursões. Os espécimes obtidos incorporados ao acervo do Herbário HACAM (não indexado). Foram registradas 95 espécies de angiospermas pertencentes a 28 famílias e verificou-se a prevalência das plantas que se dispersam por meio de vetores abióticos, ou seja, por autocoria e anemocoria, Condição esperada dadas a presença conspícuas de frutos secos, totalizando 74,5% das espécies, enquanto as espécies zoocóricas totalizaram apenas 25,5% do total, resultado da deficiência hídrica característica desse domínio fitogeográfico que não permite a presença de frutos de pericarpo com biomassa elevada, normalmente atrativos de animais de maior porte e, portanto, atípicos na vegetação xérica. Nossos resultados são fundamentais para a compreensão do funcionamento em ambientes naturais no semiárido brasileiro, demonstrando a predominância de síndromes abióticas mesmo em uma área de Reserva Ecológica, onde provavelmente a diversidade faunística seria maior que em áreas não protegidas; contribuindo com informações indispensáveis para a incorporação em planos de manejo e restauração em áreas de Caatinga.

Palavras-chave: biodiversidade, conservação, flora, processos ecológicos, semiárido

The Caatinga phytogeographic domain typically has a low forest phytophysiognomy, due to low soil water availability, and has relatively high floristic diversity (Francisco et al., 2020; Prado and Trovão, 2023; Silva et al., 2010). Annual precipitation rates vary between 250–1200 mm (Braga, 2016), and the region boasts 6348 recorded species of angiosperms belonging to 177 families (Flora e Funga do Brasil, continuously updated). In the Caatinga domain, deforestation is due to several factors, such as agriculture, harvesting of firewood, and pasture formation (Alves et al., 2008). Other aggravating factors, such as the incorrect disposal of waste produced in urban centers (which sometimes do not have suitable places for their treatment) and the installation of wind farms, cause significant changes in the floristic composition (Araújo and Moura, 2017; Lima et al., 2020). In this scenario, diaspore dispersal (fruits and seeds) is an extremely important phase in the life cycle of all plants, constituting one of the ways in which they expand their populations and geographic range (Venzke et al., 2014). The study of dispersal modes is, therefore, an important

The authors thank CNPq (National Council for Scientific and Technological Development) for the scholarship awarded to the first author through the Scientific Initiation Program of the State University of Paraíba (PIBIC/UEPB) and for the Research Productivity Scholarship-PQ2 (Proc. no. 306658/2022-4) awarded to J. I. M. Melo; FAPESq (Foundation for Research Support of the State of Paraíba) for financing the research conducted in the Olho d'Água das Onças Ecological Reserve through Contract 510/2022 (Call: Appropriation Tax Amendment No. 484- LOA 2022); Rubens Germano Costa, the owner of the RE Olho d'Água das Onças (REOODO), for permission to carry out this study and for all of the facilities to which we were granted access; Marcio Gleisson Medeiros Gonçalves for obtaining images of species during fieldwork at RE Olho d'Água das Onças (REOODO); and the State University of Paraíba (UEPB) for facilitating transportation to carry out the fieldwork.

[1] Universidade Estadual da Paraíba, 58429-500 Campina Grande, Paraíba, Brasil

[2] Department of Biology and Postgraduate Program in Ecology and Conservation, Universidade Estadual da Paraíba, 58429-500 Campina Grande, Paraíba, Brasil

[3] Postgraduate Program in Science Teaching and Mathematics Education, Universidade Estadual da Paraíba, Centro de Ciências Biológicas e da Saúde, 58429-500 Campina Grande, Paraíba, Brasil

[4] Corresponding author: tournefort@gmail.com

Harvard Papers in Botany, Vol. 29, No. 1, 2024, pp. 101–118.

ISSN: 1938-2944, DOI: 10.3100/hpib.v29iss1.2024.n12, Published online: 30 June 2024

tool for planning actions that could promote the expansion of species populations, and is, likewise, fundamental to the recovery of degraded areas (Howe, 2016; Oliveira et al., 2022).

Dispersal syndromes are classified according to how a plant's seeds are dispersed and can be abiotic (principally autochory, in which the seeds fall from the fruit close to the mother plant, and anemochory, where the seeds are wind-dispersed) or biotic (zoochory, when the dispersal vectors or agents are animals) (Stefanello et al., 2009). There is still no full understanding of which factors define the strategies plants use to disperse their diaspores, making such detailed ecological studies informative (Valenta and Nevo, 2020). Concomitantly, conservation areas are necessary for the preservation of native vegetation fragments, that can provide diaspore sources for repopulating degraded areas, as well as sites for future studies of dispersal syndromes.

There are currently 234 conservation areas in the Caatinga phytogeographic domain that are recognized by the Brazilian National Register of Conservation Areas (CNUC); 12 of them are located in Paraíba State. The Olho d'Água das Onças Ecological Reserve, located in the Seridó-Curimataú Paraibano region, represents an important protected area with high biodiversity within the Caatinga domain.

The present study presents a survey of dispersal syndromes in the Olho d'Água das Onças Ecological Reserve in the municipality of Picuí, in the semiarid region of Paraíba State in northeastern Brazil and aims to contribute to the knowledge concerning the ecological processes that maintain Caatinga biodiversity.

Materials and Methods

Study area

The present study was carried out in the Olho d'Água das Onças Ecological Reserve (REODDO), a conservation area of dry forest located in the municipality of Picuí, Seridó-Curimataú transition zone, Paraíba State, in northeastern Brazil. Picuí (6˚28'–6˚69'S, 36˚21'–36˚46'W covers 668 km^2) Instituto Brasileiro de Geografia e Estatística (IBGE) 2021, and is located between the Borborema mesoregion and the Seridó Paraibano microregion (Francisco et al., 2012).

The Olho d'Água das Onças Ecological Reserve is located in a rural area approximately 11 km from the municipal seat (Fig. 1). The Reserve occupies an area of 20.73 ha, of which approximately 18.26 ha correspond to the conservation area. According to the Köppen system (1936), the municipality of Picuí has a BShw type climate, which is hot and semiarid, with temperatures ranging between 78.8˚F–89.6˚F. The expected annual average rainfall is approximately 339.1mm/year. However, the years 2022 and 2023 (the period during which this study was carried out) were atypical, since the average recorded rainfall exceeded expectations, reaching 453.1 mm/yr and 481.5 mm/yr, respectively, with rainfall peaks between the months of March and May (Accuweather, continuously updated; AESA, continuously updated; Francisco et al., 2012).

Sampling procedures

Botanical collections were made monthly between August 2022 and July 2023, covering both the dry and rainy seasons. Photographic records were made of the collected plants and their reproductive structures (especially their fruits), as well as of the surrounding environment; geographic coordinates were also noted. The specimens were dried (Rotta et al., 2008) in the Manuel de Arruda Câmara Herbarium (HACAM), Campus I, at the State University of Paraíba (UEPB), Campina Grande, Paraíba State, Brazil.

Laboratory procedures

Taxonomic identifications of species were based mainly on the scientific literature, principally Queiroz (2021) and Ferreira et al. (2009) for the identification of Fabaceae and Poaceae species, respectively, and the Flora e Funga do Brasil website (continuously updated) was consulted for the species of other angiosperm families. The collected material was also compared with specimens deposited in the following herbaria: the Manuel de Arruda Câmara Herbarium (HACAM), Campus I, State University of Paraíba; the Lauro Pires-Xavier Herbarium (JPB) and the Jayme Côelho de Moraes Herbarium (EAN), both located at the Federal University of Paraíba (UFPB) in the municipalities of João Pessoa (Campus I) and Areia (Campus II), respectively, and were accessed through the *SpeciesLink* platform.

Data analyses

Dispersal syndrome types were verified based on field observations and complemented by the specialized literature, mainly Spjut (1994) for the identification of fruit types, and Van der Pijl (1982) to verify diaspore distribution vectors.

Results and Discussion

Dispersal syndromes were identified for 95 species belonging to 28 families, including basal angiosperms (ANA grade = Amborellales, Nymphaeales and Austrobaileyales) and Mesangiosperms (Magnoliids, Chloranthales, monocots, Ceratophyllales and eudicots) (Table 1 and Fig. 2–4). Of these 95 species, Fabaceae was the most diverse (18 species), followed by Euphorbiaceae (11 species), Malvaceae (seven species), and Poaceae (six species, five of which are native and one naturalized [*Digitaria ciliaris* (Retz.) Koeler)]). Fabaceae and Euphorbiaceae are often identified as the most diverse families in Caatinga areas in the Brazilian semiarid region (Guedes et al., 2012; Flora e Funga do Brasil, continuously updated; Silva et al. 2013), corroborating the results of our study.

The types of habit identified in the study area were: herbaceous (35 spp.; 37.2%), for which autochory predominated, with 26 species showing this type of dispersal, followed by anemochory with four species, epizoochoric, with three species each, and saurochory and ornithochoric syndromes, represented by one species each (Fig. 5A). The shrubby habit is associated with 26 species (27.2%), of which 18 are autochoric, six ornithochoric, one mammaliochoric, and one anemochoric (Fig. 5B). The arboreal habit included 18 species (19.1%), of which seven were autochoric, four ornithochoric, three mammaliochoric, one epizoochoric, two anemochoric, and one saurochoric

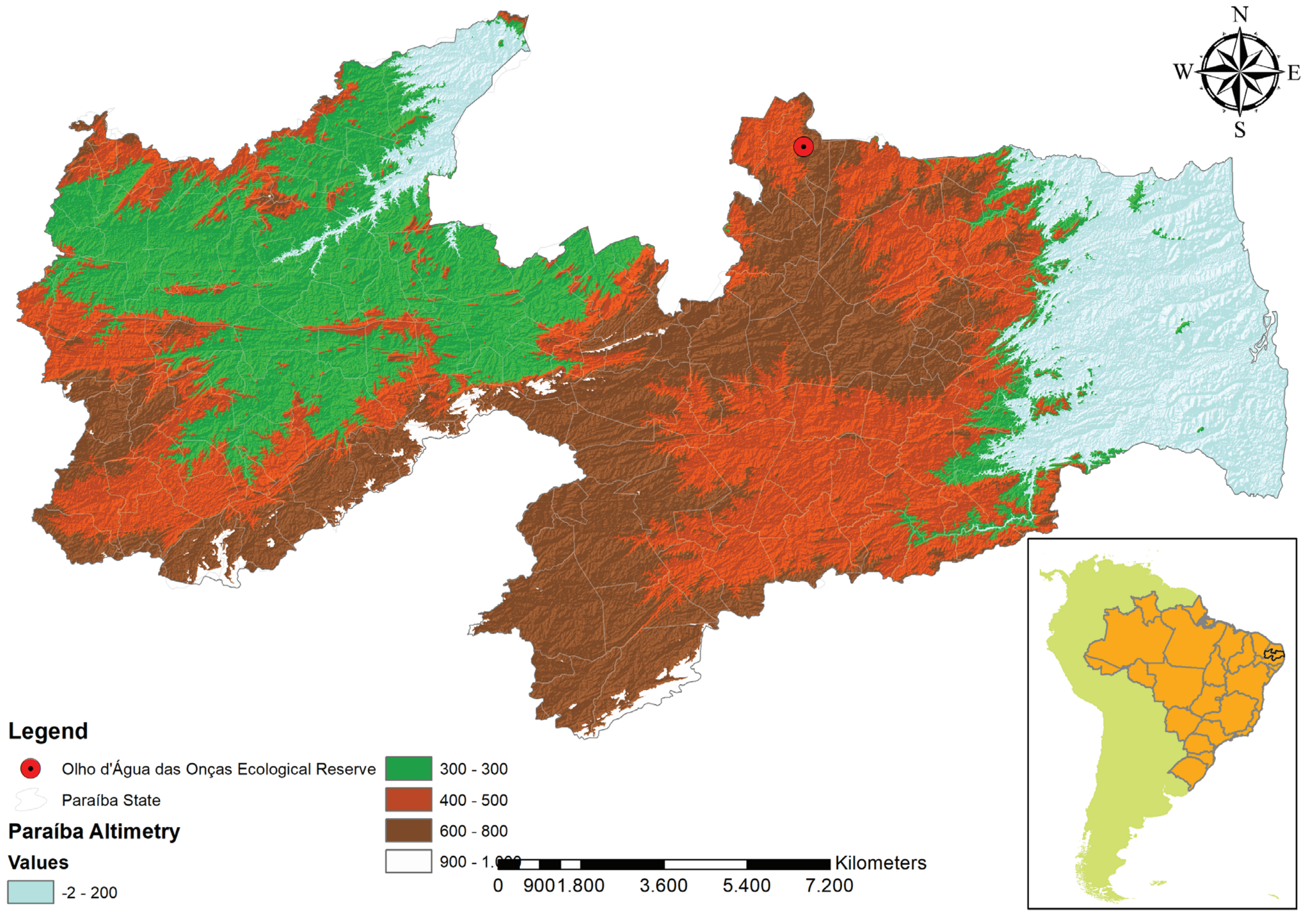


FIGURE 1. Map of the Paraíba State, Brazil, highlighting the study area, Olho d'Água das Onças Ecological Reserve, municipality of Picuí. By E. M. Rodrigues.

(Fig. 5C). The subshrub habit encompassed 15 spp. (16%), of which nine are autochoric, two ornithochoric, two epizoochoric, and two anemochoric (Fig. 5D).

The predominant dispersal syndrome was autochory, observed in 63.8% of the total sampled species (N = 60 spp.); of these, 45% were herbaceous (N = 27 spp.), 30% shrubs (N = 18 spp.), 15% subshrubs (N = 9 spp.), and 10% trees (N = 6 spp.) (Fig. 6A). The second most common dispersal syndrome was zoochory, observed in 27.7% of the species (25 spp.); of these, 36% were arboreal (N = 9 spp.), 28% shrubs (N = 7 spp.), 20% herbaceous (N = 5 spp.), and 16% subshrubs (N = 4 spp.) (Fig. 6B). Anemochory was the least prevalent dispersal syndrome, 8.5%, and was associated with eight species. With regard to anemochory, the predominant habit type was herbaceous (3 spp.; 37.5%), followed by arboreal and subshrub plants (2 spp. each; 25% each), and, finally, shrubs (1 spp.; 12.5%) (Fig. 6C).

The diaspores exhibiting autochoric and anemochoric syndromes were observed on fully fruiting species during the dry season, which is similar to reports from other Caatinga areas in northeastern Brazil (e.g., Córdula et al., 2014). According to Howe and Smallwood (1982) and Pereira et al. (2022), anemochory and autochory predominate in seasonal open-canopy environments (e.g., the Caatinga sensu stricto). This fact is related to the lack of physical barriers, such as understories and plants with a very large leaf area, which makes these types of syndromes more efficient, causing diaspores to reach areas farther away from the mother plant, thus avoiding the competition (Silva et al., 2012 Pereira et al., 2022). Furthermore, in the Caatinga there are constant episodes of drought, reducing the number of biotic dispersers due to the reduced supply of meatier fruits (Costa et al., 2004; Butler et al., 2007; Silva and Rodal, 2009; Silva et al., 2013; Santos et al., 2020). According to Vieira et al. (2008), this dispersal strategy can be advantageous for dispersing diaspores over wide territorial extensions.

Silva and Rodal (2009), studying the distribution of patterns of plant dispersion syndromes in the Caatinga vegetation, observed that vertical stratification had no influence on changing the type of dispersion, with autochory and anemochory prevailing, a fact also not observed in this work, where in all strata both dispersion syndrome types prevailed.

According to the type of vector and the type of fruit, zoochoric syndromes are divided into subcategories (Fig. 7). Zoochoric species predominated during the rainy season given that they have a greater dependence on water during the development of their fruits, and, in the dry season, seeds of species dispersed by abiotic vectors predominated, (Costa et al., 2004; Domingues et al. 2013; Paula et al., 2021; Silva and Rodal, 2009). In the study area, we observed that

TABLE 1. Families, species, and types of habit and dispersal syndromes in the study area, Olho d'Água das Onças Ecological Reserve, Picuí, Paraíba State, Brazil, followed by voucher. Legends: Habits (H); Herb (Her); Subshrub (Sub); Shrub (Shr); Tree (Tre); Dispersal syndromes (D.S.): Anemochory (Ane); Autochory (Aut); Zoochory (Zoo).

FAMILY/SPECIES	H	D.S.	VOUCHER
Amaranthaceae			
Quaternella ephedroides Pedersen	Her	Aut	*Rocha et al. 102*
Anacardiaceae			
Schinopsis brasiliensis Engl.	Tre	Ane	*Luz et al. 46*
Spondias tuberosa Arruda	Tre	Zoo	*Rocha 195*
Apocynaceae			
Aspidosperma pyrifolium Mart. & Zucc.	Tre	Ane	*Luz et al. 70*
Bromeliaceae			
Aechmea aquilega (Salisb.) Griseb.	Her	Aut	*Luz et al. 40*
Tillandsia recurvata (L.) L.	Her	Ane	*Luz et al. 36*
Tillandsia streptocarpa Baker	Her	Ane	*Luz et al. 39*
Cactaceae			
Cereus jamacaru DC.	Tre	Zoo	*Luz et al. 60*
Melocactus zehntneri (Britton & Rose) Luetzelb.	Her	Zoo	*Rocha et al. 188*
Pilosocereus pachycladus F. Ritter	Tre	Zoo	*Luz et al. 69*
Tacinga inamoena (K. Schum.) N.P. Taylor & Stuppy	Sub	Zoo	*Luz et al. 19*
Xiquexique gounellei (F.A.C. Weber) Lavor & Calvente	Shr	Zoo	*Luz et al. 68*
Capparaceae			
Cynophalla flexuosa (L.) J. Presl	Tre	Zoo	*Luz et al. 38*
Neocalyptrocalyx longifolium (Mart.) Cornejo & Iltis	Tre	Zoo	*Luz et al. 35*
Combretaceae			
Combretum leprosum Mart.	Tre	Ane	*Luz et al. 72*
Convolvulaceae			
Evolvulus filipes Mart.	Her	Aut	*Rocha et al. 384*
Evolvulus frankenioides Moric.	Her	Aut	*Rocha et al. 46*
Evolvulus glomeratus Nees & Mart.	Her	Aut	*Luz et al. 45*
Cordiaceae			
Varronia globosa Jacq.	Shr	Zoo	*Rocha et al. 171*
Varronia leucomalloides (Taroda) J.S. Mill.	Shr	Zoo	*Rocha et al. 231*
Varronia mariana E.C.O. Chagas & Costa-Lima	Shr	Zoo	*Luz et al. 73*

TABLE 1 CONT. Families, species, and types of habit and dispersal syndromes in the study area, Olho d'Água das Onças Ecological Reserve, Picuí, Paraíba State, Brazil, followed by voucher. Legends: Habits (H); Herb (Her); Subshrub (Sub); Shrub (Shr); Tree (Tre); Dispersal syndromes (D.S.): Anemochory (Ane); Autochory (Aut); Zoochory (Zoo).

FAMILY/SPECIES	H	D.S.	VOUCHER
Euphorbiaceae			
Acalypha multicaulis Müll. Arg.	Sub	Aut	*Rocha et al*. *203*
Argythamnia malpighiacea Ule	Shr	Aut	*Luz et al*. *26*
Cnidoscolus urens (L.) Arthur	Sub	Aut	*Rocha et al*. *104*
Croton adenocalyx Baill.	Shr	Aut	*Luz et al*. *83*
Croton blanchetianus Baill.	Shr	Aut	*Luz et al*. *53*
Croton glandulosus L.	Her	Aut	*Luz et al*. *85*
Croton grewioides Baill.	Shr	Aut	*Luz et al*. *25*
Croton heliotropiifolius Kunth	Shr	Aut	*Luz et al*. *23*
Jatropha mollissima (Pohl) Baill.	Tre	Aut	*Luz et al*. *64*
Jatropha ribifolia (Pohl) Baill.	Shr	Aut	*Luz et al*. *17*
Manihot carthagenensis (Jacq.) Müll. Arg.	Tre	Aut	*Luz et al*. *79*
Stillingia trapezoidea Ule	Shr	Aut	*Rocha et al*. *192*
Erythroxylaceae			
Erythroxylum caatingae Plowman	Shr	Zoo	*Luz et al*. *32*
Erythroxylum pyan Costa-Lima	Tre	Zoo	*Luz et al*. *44*
Fabaceae			
Bauhinia cheilantha (Bong.) Steud.	Tre	Aut	*Rocha et al*. *308*
Cenostigma nordestinum Gagnon & G.P. Lewis	Tre	Aut	*Luz et al*. *66*
Chamaecrista absus (L.) H.S. Irwin & Barneby	Sub	Aut	*Rocha et al*. *360*
Chamaecrista calycioides (DC. ex Collad.) Greene	Sub	Aut	*Luz et al*. *55*
Chamaecrista duckeana (P. Bezerra & Afr. Fern.) H.S. Irwin & Barneby	Sub	Aut	*Rocha et al*. *298*
Chamaecrista rotundifolia (Pers.) Greene	Sub	Aut	*Luz et al*. *59*
Chamaecrista zygophilloides (Taub.) H.S. Irwin & Barneby	Shr	Aut	*Luz et al*. *34*
Indigofera suffruticosa Mill.	Shr	Aut	*Luz et al*. *14*
Libidibia ferrea (Mart. ex Tul.) L.P. Queiroz	Tre	Aut	*Luz et al*. *48*
Mimosa candollei R. Grether	Sub	Aut	*Rocha et al*. *61*
Mimosa paraibana Barneby	Shr	Aut	*Luz et al*. *90*
Mimosa tenuiflora (Willd.) Poir.	Shr	Aut	*Luz et al*. *07*
Peltogyne pauciflora Benth.	Shr	Aut	*Luz et al*. *52*

TABLE 1 CONT. Families, species, and types of habit and dispersal syndromes in the study area, Olho d'Água das Onças Ecological Reserve, Picuí, Paraíba State, Brazil, followed by voucher. Legends: Habits (H); Herb (Her); Subshrub (Sub); Shrub (Shr); Tree (Tre); Dispersal syndromes (D.S.): Anemochory (Ane); Autochory (Aut); Zoochory (Zoo).

FAMILY/SPECIES	H	D.S.	VOUCHER
Fabaceae cont.			
Senna macranthera (DC. ex Collad.) H.S. Irwin & Barneby	Shr	Zoo	*Luz et al. 71*
Senna trachypus (Benth.) H.S. Irwin & Barneby	Shr	Aut	*Luz et al. 88*
Zornia brasilensis Vogel	Sub	Zoo	*Rocha et al. 179*
Zornia leptophylla (Benth.) Pittier	Sub	Zoo	*Rocha et al. 36*
Zornia reticulata Sm.	Sub	Zoo	*Rocha et al. 26*
Heliotropiaceae			
Euploca procumbens (Mill.) Diane & Hilger	Her	Aut	*Rocha et al. 32*
Heliotropium angiospermum Murray	Sub	Aut	*Luz et al. 58*
Loranthaceae			
Pusillanthus pubescens (Rizzini) Caires	Her	Zoo	*Luz et al. 10*
Lythraceae			
Cuphea impatientifolia A. St.-Hil.	Sub	Aut	*Rocha et al. 359*
Malvaceae			
Gaya domingensis Urb.	Sub	Aut	*Luz et al. 57*
Helicteres eichleri K. Schum.	Shr	Aut	*Luz et al. 42*
Herissantia tiubae (K. Schum.) Brizicky	Shr	Aut	*Luz et al. 18*
Melochia tomentosa L.	Sub	Aut	*Luz et al. 30*
Sida galheirensis Ulbr.	Sub	Aut	*Luz et al. 12*
Sida spinosa L.	Sub	Aut	*Luz et al. 54*
Sidastrum paniculatum (L.) Fryxell	Sub	Aut	*Luz et al. 49*
Nyctaginaceae			
Boerhavia coccinea Mill.	Her	Zoo	*Luz et al. 51*
Boerhavia erecta L.	Her	Zoo	*Luz et al. 74*
Plantaginaceae			
Scoparia dulcis L.	Sub	Aut	*Luz et al. 61*
Poaceae			
Cenchrus echinatus L.	Her	Aut	*Luz et al. 03*
Chloris barbata Sw.	Her	Aut	*Rocha et al. 216*
Chloris virgata Sw.	Her	Aut	*Rocha et al. 198*
Digitaria ciliaris (Retz.) Koeler	Her	Aut	*Rocha et al. 199*
Tragus berteronianus Schult.	Her	Aut	*Luz et al. 56*
Urochloa mollis (Sw.) Morrone & Zuloaga	Her	Aut	*Luz et al. 87*

TABLE 1 CONT. Families, species, and types of habit and dispersal syndromes in the study area, Olho d'Água das Onças Ecological Reserve, Picuí, Paraíba State, Brazil, followed by voucher. Legends: Habits (H); Herb (Her); Subshrub (Sub); Shrub (Shr); Tree (Tre); Dispersal syndromes (D.S.): Anemochory (Ane); Autochory (Aut); Zoochory (Zoo).

FAMILY/SPECIES	H	D.S.	VOUCHER
Polygalaceae			
Asemeia martiana (A.W. Benn.) J.F.B. Pastore & J.R. Abbott	Sub	Aut	*Rocha et al. 142*
Asemeia violacea (Aubl.) J.F.B. Pastore & J.R. Abbott	Her	Aut	*Rocha et al. 259*
Portulacaceae			
Portulaca elatior Mart. ex Rohrb.	Her	Aut	*Luz et al. 82*
Portulaca halimoides L.	Her	Aut	*Rocha et al. 35*
Portulaca mucronata Link	Her	Aut	*Rocha et al. 338*
Sapotaceae			
Sideroxylon obtusifolium (Roem. & Schult.) T.D. Penn.	Tre	Zoo	*Luz et al. 24*
Solanaceae			
Schwenckia americana Rooyen ex L.	Her	Aut	*Luz et al. 11*
Rhamnaceae			
Sarcomphalus joazeiro (Mart.) Hauenschild	Tre	Zoo	*Luz et al. 27*
Rubiaceae			
Cordiera rigida (K. Schum.) Kuntze	Tre	Zoo	*Luz et al. 16*
Hexasepalum teres (Walter) J.H. Kirkbr.	Her	Aut	*Luz et al. 75*
Mitracarpus baturitensis Sucre	Her	Aut	*Rocha et al. 31*
Talinaceae			
Talinum fruticosum (L.) Juss.	Her	Aut	*Rocha et al. 17*
Talinum paniculatum (Jacq.) Gaertn.	Her	Aut	*Luz et al. 28*
Turneraceae			
Piriqueta viscosa Griseb.	Her	Aut	*Rodrigues et al. 60*
Turnera blanchetiana Urb.	Shr	Aut	*Luz et al. 03*
Turnera pumilea L.	Her	Aut	*Rocha et al. 42*
Turnera subulata Sm.	Her	Aut	*Rocha et al. 215*
Verbenaceae			
Lantana radula Sw.	Shr	Zoo	*Luz et al. 65*
Lantana tiliaefolia Cham.	Shr	Zoo	*Luz et al. 06*
Stachytarpheta coccinea Schauer	Shr	Aut	*Luz et al. 05*
Violaceae			
Pombalia arenaria (Ule) Paula-Souza	Her	Aut	*Luz et al. 76*

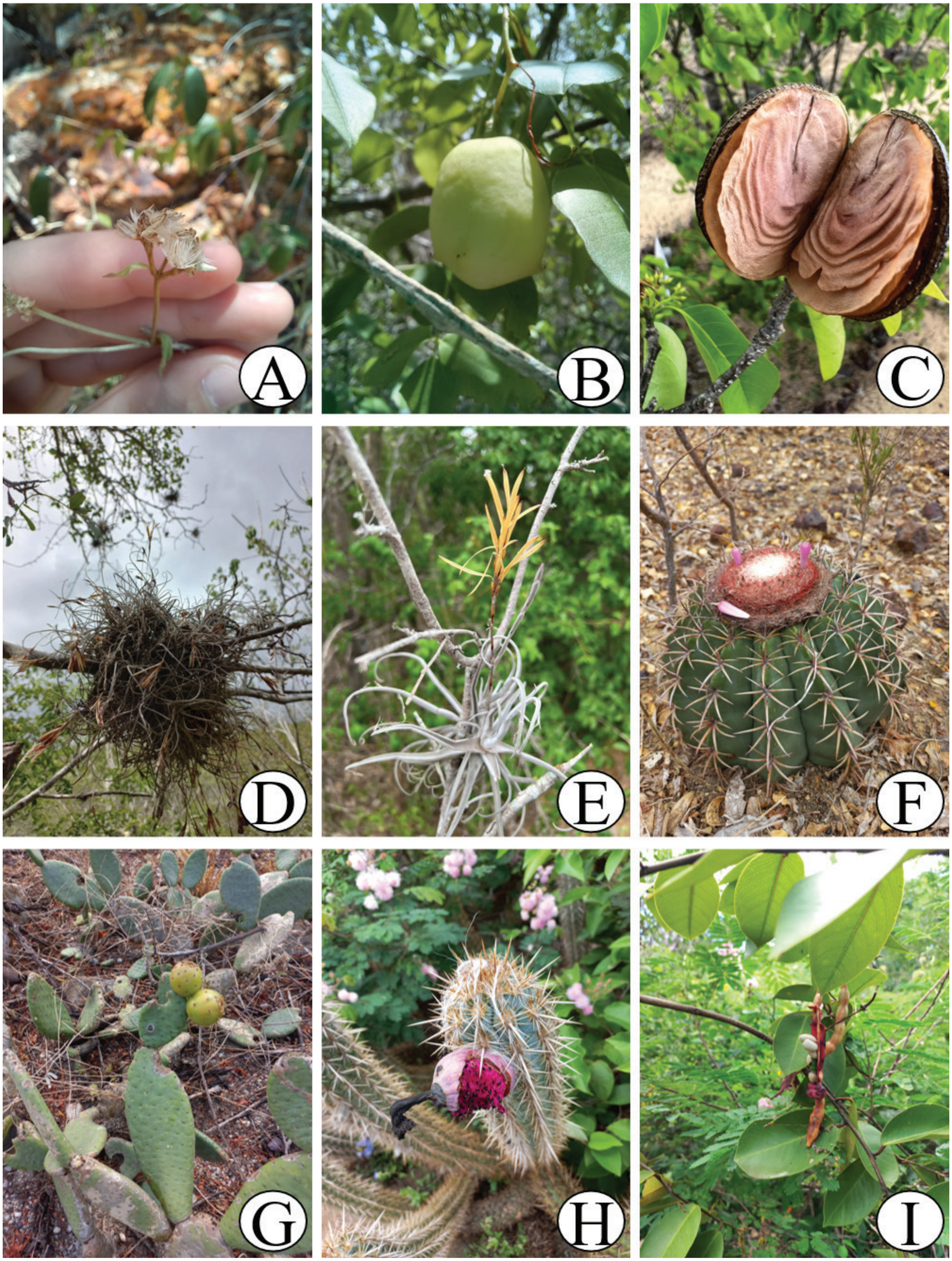


FIGURE 2. Species found in the study area, Olho d'Água das Onças Ecological Reserve, Picuí, Paraíba State, Brazil: **A**, Amaranthaceae, *Quaternella ephedroides*; **B**, Anacardiaceae, *Spondias tuberosa*; **C**, Apocynaceae, *Aspidosperma pyrifolium*; **D**, Bromeliaceae, *Tillandsia recurvata*; **E**, Bromeliaceae, *Tillandsia streptocarpa*; **F**, Cactaceae, *Melocactus zehntneri*; **G**, Cactaceae, *Tacinga inamoena*; **H**, Cactaceae, *Xiquexique gounellei*; **I**, Capparaceae, *Cynophalla flexuosa*. Photographs by B. F. Rocha (A–B, F, H–I), M. G. M. Gonçalves (C, E), and T. E. D. Correia (D, G).

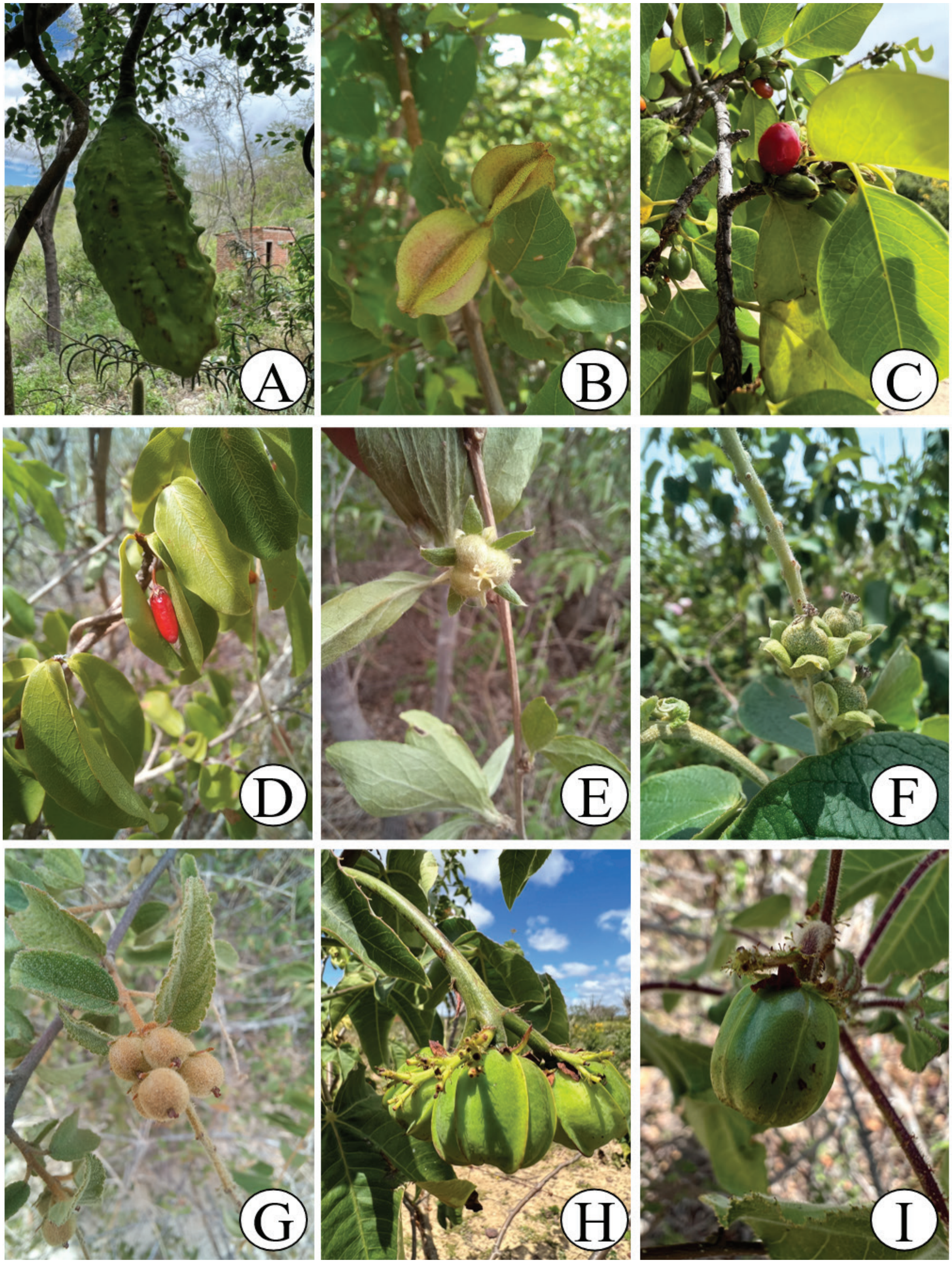


FIGURE 3. Species found in the study area, Olho d'Água das Onças Ecological Reserve, Picuí, Paraíba State, Brazil: **A**, Capparaceae, *Neocalyptrocalyx longifolium*; **B**, Combretaceae, *Combretum leprosum*; **C**, Erythroxylaceae, *Erythroxylum caatingae*; **D**, Erythroxylaceae, *Erythroxylum pyan*; **E**, Euphorbiaceae, *Argythamnia malphigiacea*; **F**, Euphorbiaceae, *Croton blanchetianus*; **G**, Euphorbiaceae, *C. grewioides*; **H**, Euphorbiaceae, *Jatropha mollissima*; **I**, Euphorbiaceae, *J. ribifolia*. Photographs by M. G. M. Gonçalves (A, G, H–I) and B. F. Rocha (B–F).

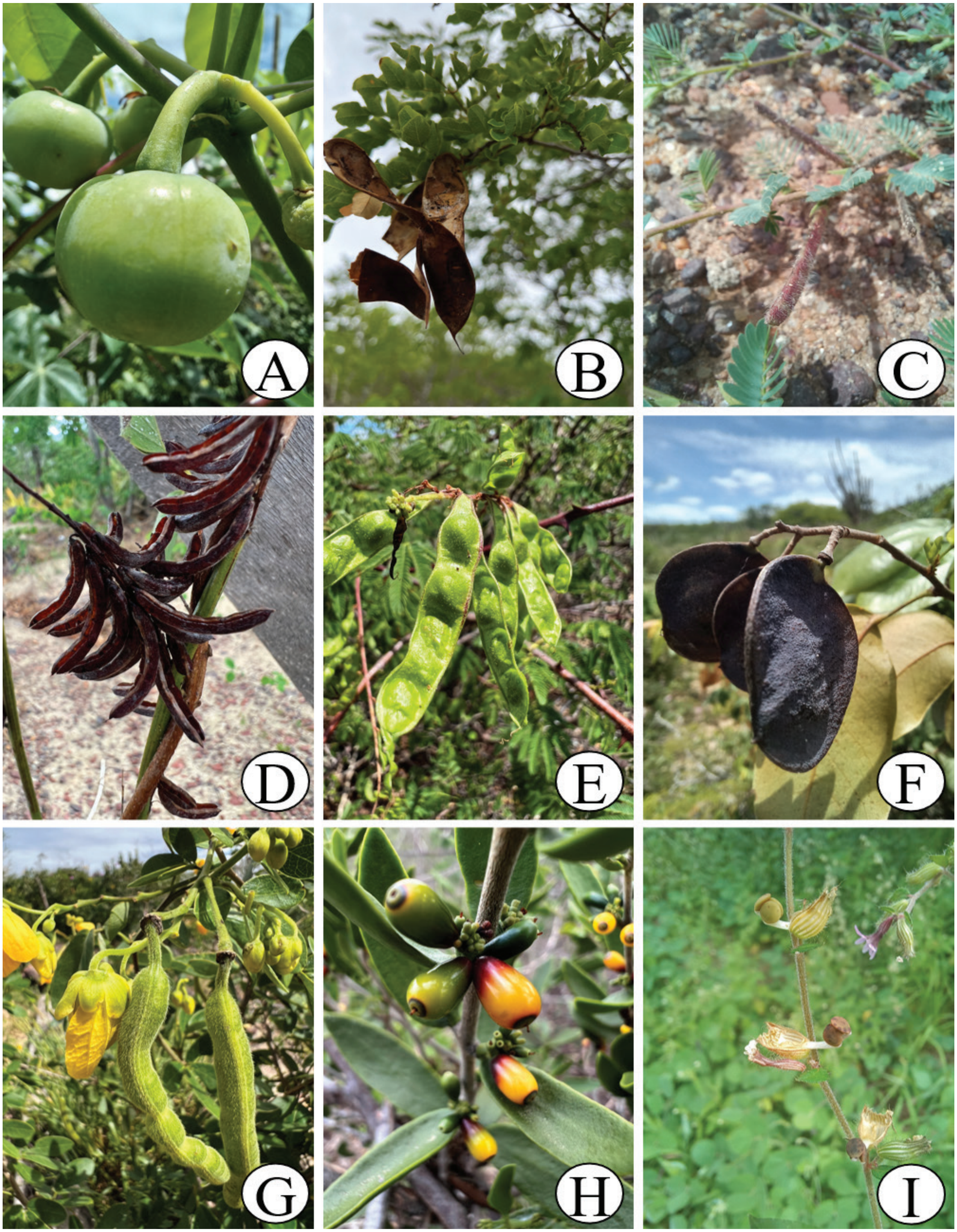


FIGURE 4. Species found in the study area, Olho d'Água das Onças Ecological Reserve, Picuí, Paraíba State, Brazil: **A**, Euphorbiaceae, *Manihot carthagenensis*; **B**, Fabaceae, *Cenostigma nordestinum*; **C**, Fabaceae, *Chamaecrista calycioides*; **D**, Fabaceae, *Indigofera suffruticosa*; **E**, Fabaceae, *Mimosa tenuiflora*; **F**, Fabaceae, *Peltogyne pauciflora*; **G**, Fabaceae, *Senna macranthera*; **H**, Loranthaceae, *Pusillanthus pubescens*; **I**, Lythraceae, *Cuphea impatientifolia*. Photographs by B. F. Rocha (9A, C, F, I) and M. G. M. Gonçalves (B, D–E, G–H).

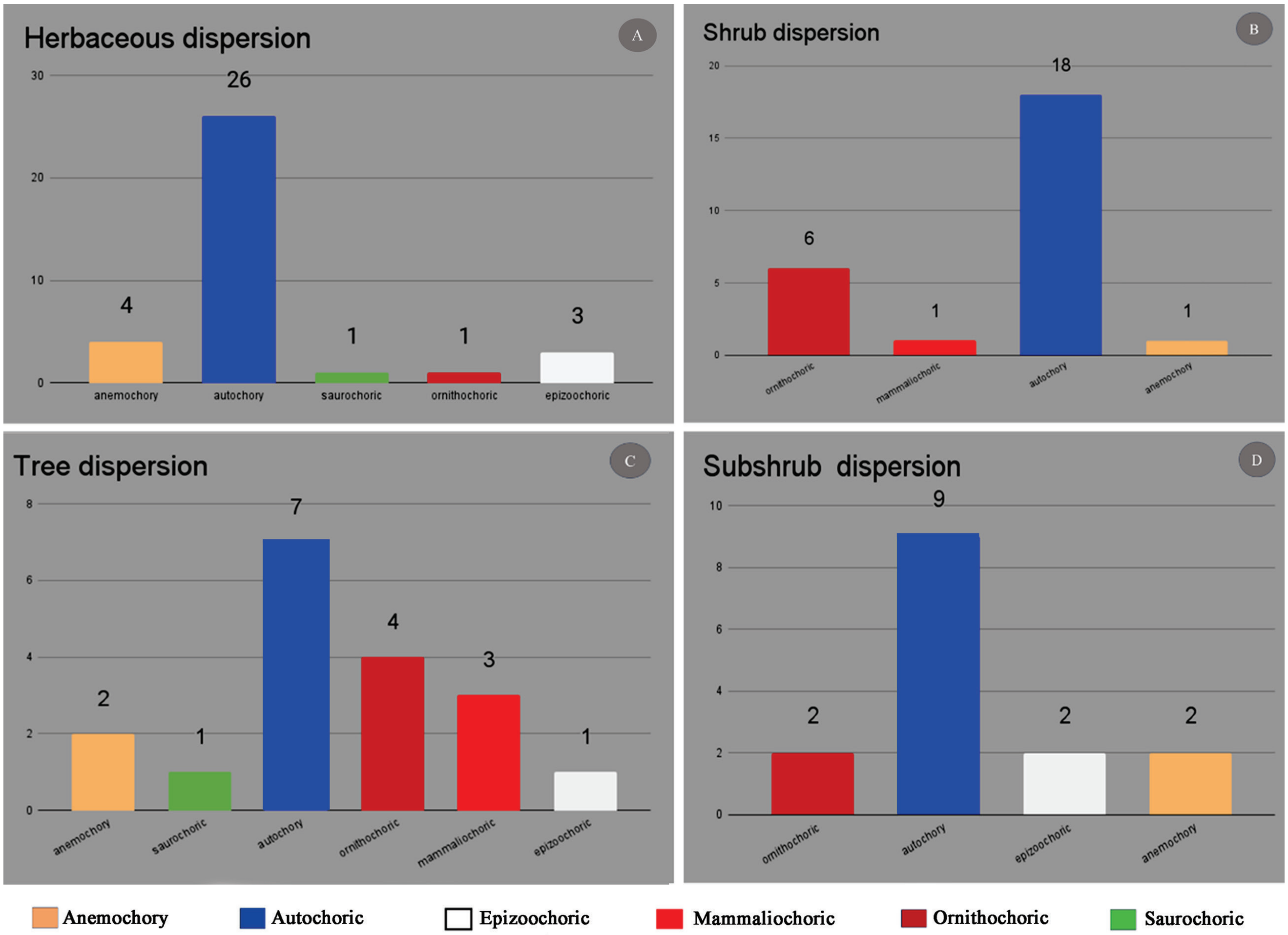


FIGURE 5. Dispersal types associated with the types of habitats recorded, Olho d'Água das Onças Ecological Reserve, Picuí, Paraíba State, Brazil; **A**, Herbaceous; **B**, Shrub; **C**, Arboreal; **D**, Subshrub. By: Luz, G.A.

fleshy fruits are available mainly close to the rainy season, while dry fruits are dispersed in the dry season, as they, for the most part, are epizoochoric (Table 2). On the other hand, autochoric and anemochoric species depend less on abundant water resources, especially because they do not need to develop mucilage.

The results obtained here corroborate other studies with similar ecological focuses undertaken within the Caatinga phytogeographic domain, where abiotic syndromes predominate over all others in all seasons. This is probably associated with soil types and rainfall instability and led to the predominance of dry as opposed to fleshy fruits (e.g., Griz and Machado, 2001; Costa et al., 2015; Lima and Melo, 2015). According to Gentry (1982), this predominance would be expected in dry forests. Although the species recorded in this study principally disperse their diaspores through primary syndromes, they can also exhibit secondary dispersal mechanisms, which are likewise of great importance to the maintenance of the ecosystem (Silva et al., 2013).

Additionally, two alien species were recorded at the study site: *Digitaria ciliaris* (Retz.) Koeler (Poaceae), a naturalized herbaceous plant that does not heavily compete with the native flora, and *Neltuma juliflora* (Sw.) Raf. (Fabaceae), an arboreal plant that presents a great invasive capability (allelopathic) and competitively occupies spaces previously populated by native species (Pegado et al., 2006; Andrade et al., 2010).

Based on the studied components of the flora of the REODDO, autochory is the predominant dispersal syndrome, and zoochory was second, followed by anemochory. These data reinforce the results found in other studies conducted in areas of the Caatinga vegetation and are probably related to low water availability and high temperatures in the semiarid Caatinga domain of northeastern Brazil. This ecological approach in a conservation area allowed a better understanding of the functioning of the Ecological Reserve ecosystem and its importance to other groups of organisms in the Brazilian semiarid region.

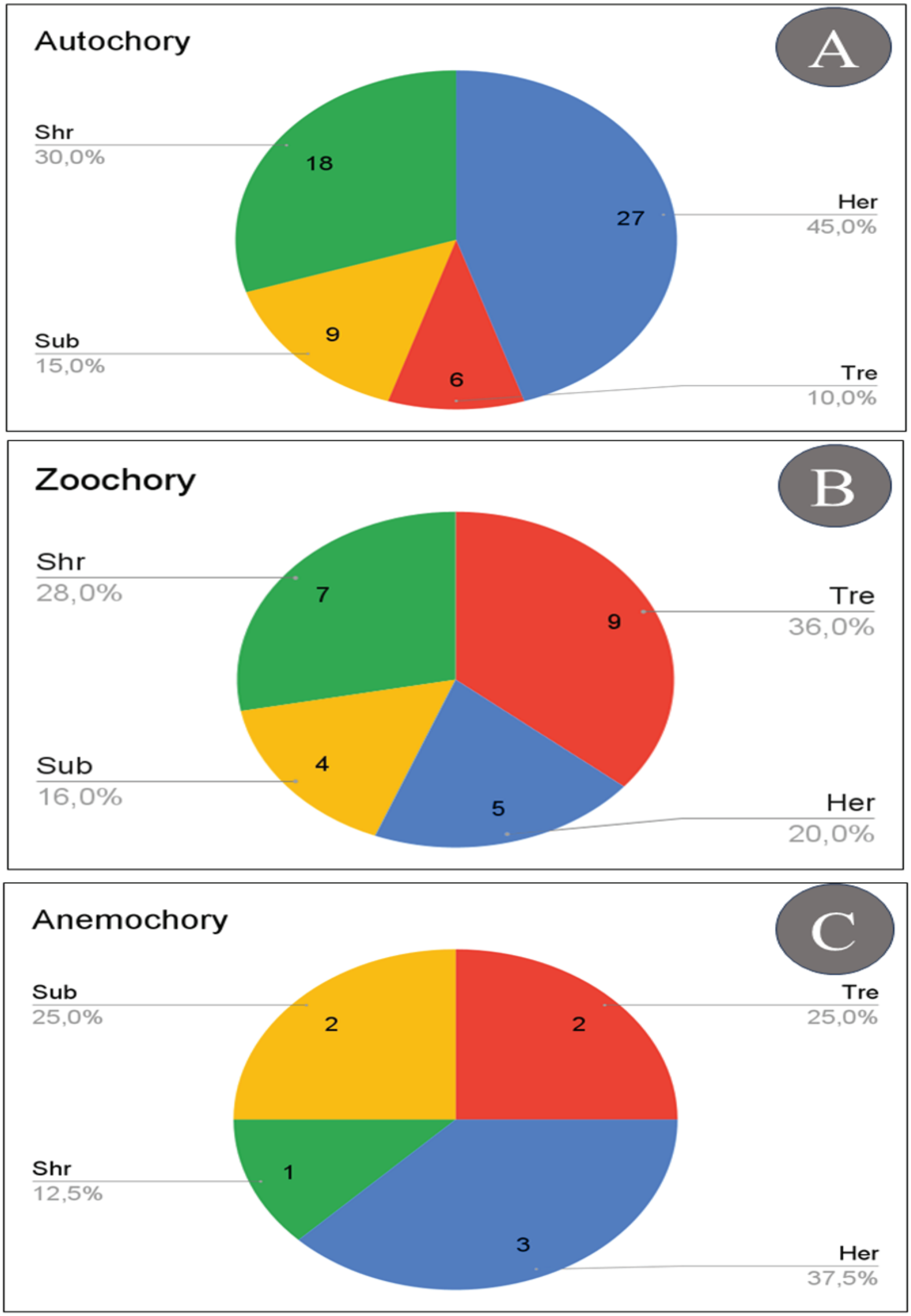


FIGURE 6. **A**, Percentage of the types of habits associated with autochoric syndromes, Olho d'Água das Onças Ecological Reserve, Picuí, Paraíba State, Brazil; **B**, Percentage of the types of habits associated with zoochoric syndromes; **C**, Percentage of the types of habits associated with anemochoric syndromes. Legends: Her= Herb; Sub=Subshrub; Shr=Shrub; Tre=Tree. By G. A. Luz.

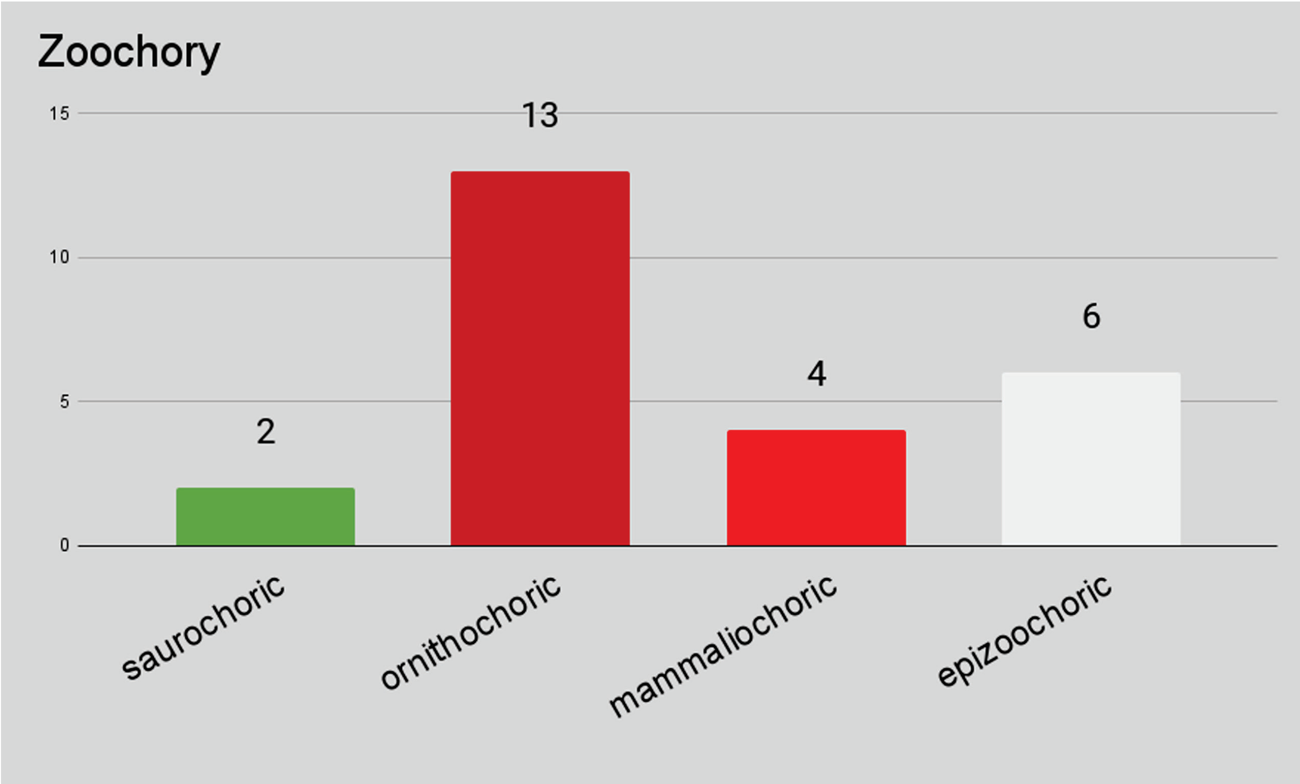


FIGURE 7. Zoochoric sub syndrome most recorded, Olho d'Água das Onças Ecological Reserve, Picuí, Paraíba State, Brazil. By G. A. Luz.

LITERATURE CITED

ACCUWEATHER. Meteorologia mensal em Picuí, Paraíba, Brasil (accessed December 12, 2023). https://www.accuweather.com/pt/br/picu%C3%AD/39936/september-weather/39936?year=2023

AGÊNCIA EXECUTIVA DE GESTÃO DAS ÁGUAS (AESA). Meteorologia—Chuvas https://www.aesa.pb.gov.br/aesa-website/meteorologia-chuvas/ (accessed December 11, 2023).

ALVES, J. J. A., M. A. ARAÚJO, AND S. S. NASCIMENTO. 2008. Degradação da Caatinga: Uma investigação ecogeográfica. Caminhos de Geografia 9(27): 143–155.

ANDRADE, L. A., J. R. FABRICANTE, AND F. X. OLIVEIRA. 2010. Impactos da invasão de *Prosopis juliflora* (Sw.) DC. (Fabaceae) sobre o estrato arbustivo-arbóreo em áreas de Caatinga no Estado da Paraíba, Brasil. Acta Scientiarum, Biological Sciences 32(3): 249–255.

ARAUJO, A. A., AND G. J. B. MOURA. 2017. A literatura científica sobre os impactos causados pela instalação de parques eólicos: análise cienciométrica. Revista Tecnologia e Sociedade 13(28): 207–223.

BRAGA, R. A. P. 2016. As águas invisíveis nos rios intermitentes. Águas de areia. Recife, Clã, pp. 11–37.

BUTLER, D. W., R. J. GREEN, D. LAMB, W. J. F. MCDONALD, AND P. I. FORSTER. 2007. Biogeography of seed dispersal syndromes, life forms and seed sizes among woody rain forest plants in Australia's subtropics. Journal of Biogeography 34(10): 1736–1750.

CÓRDULA, E., M. P. MORIM, AND M. ALVES. 2014. Morfologia de frutos e sementes de Fabaceae ocorrentes em uma área prioritária para a conservação da Caatinga em Pernambuco, Brasil. Rodriguésia 65(2): 505–516.

COSTA, E. C. S., S. F. LOPES, AND J. I. M. MELO. 2015. Floristic similarity and dispersal syndromes in a rocky outcrop in semi-arid Northeastern Brazil. Revista de Biología Tropical 63(3): 827–843.

DOMINGUES, C. Â. J., V. N. GOMES, AND Z. G. M. QUIRINO. 2013. Síndromes de dispersão na maior área de proteção da Mata Atlântica paraibana. Biotemas 26(3): 99–108.

FERREIRA, C. G. T., R. C. OLIVEIRA, J. F. M. VALLS, AND M. I. B. LOIOLA. 2009. Poaceae da Estação Ecológica do Seridó, Rio Grande do Norte, Brasil. Hoehnea 36(4): 679–707.

FLORA E FUNGA DO BRASIL. Continuously updated. Online; http://reflora.jbrj.gov.br/reflora/PrincipalUC/PrincipalUC.do (accessed August 31, 2023).

FRANCISCO, P. R. M., F. C. PEREIRA, R. M. MEDEIROS, AND T. F. F. SÁ. 2012. Zoneamento de Risco Climático e Aptidão de Cultivo para o Município de Picuí—PB. Revista Brasileira de Geografia Física 4(5): 1043–1055.

FRANCISCO, P. R. M., I. B. CHAVES, AND L. H. G. CHAVES. 2020. Bioma caatinga e degradação: modelo de mapeamento. EPGRAF, Campina Grande.

GENTRY, A. H. 1982. Patterns of Neotropical Plant Species Diversity. Pages 1–84 in M. K. HECHT, B. WALLACE, AND G. T. PRANCE, EDS., Evolutionary Biology. Springer, Boston, Massachusetts. https://doi.org/10.1007/978-1-4615-6968-8_1

GRIZ, L. M. S., AND I. C. S. MACHADO. 2001. Fruiting phenology and seed dispersal syndromes in caatinga, a tropical dry forest in the northeast of Brazil. Journal of Tropical Ecology 17(2): 303–321.

GUEDES, R. S., F. C. V. ZANELLA, J. E. V. COSTA-JÚNIOR, G. M. SANTANA, AND J. A. SILVA. 2012. Caracterização florístico-fitossociológica do componente lenhoso de um trecho de Caatinga no Semiárido Paraibano. Revista Caatinga 25(2): 99–108.

Howe, H. F. 2016. Making dispersal syndromes and networks useful in tropical conservation and restoration. Global Ecology and Conservation 6: 152–178.

Instituto Brasileiro de Geografia e Estatística—IBGE. 2021. https://cidades.ibge.gov.br/brasil/pb/picui/panorama (accessed August 31, 2023).

Köppen, W., and R. Geiger. 1936. Das geographische System der Klimate. Handbuch der Klimatologie 1: 1–44. Borntraeger, Berlin.

Lima, E. A., and J. I. M. Melo. 2015. Biological spectrum and dispersal syndromes in an area of the semi-arid region of north-eastern Brazil. Acta Scientiarum, Biological Sciences 37(1): 91–100.

Lima, V. G. S., M. M. P. Silva, R. F. Faustino, and G. F. Barbosa. 2020. Resíduos Sólidos e Impactos Adversos Sobre o Bioma Caatinga em Município Paraibano de Pequeno Porte. Revista Brasileira de Desenvolvimento 6(9): 70493–70614.

Ministério do Meio Ambiente e Mudanças do Clima, (MMA). Online. Cadastro Nacional de Unidades de Conservação (CNUC); https://cnuc.mma.gov.br/powerbi (accessed 3 August 2023).

Oliveira, P., C. R. Benevides, A. V. Greco, L. C. S. Leão, A. T. A. Rodarte, and H. A. Lima. 2022. Fruiting phenology and dispersal syndromes in a sandy coastal plain in southeastern Brazil. Rodriguésia 73: 1–15.

Paula, A., I. M. Barberena, A. O. Soares-filho, P. A. B. Barreto-Garcia, R. C. A. L. Paula, L. R. Prata, and W. P. Medeiros. 2021. Fitossociologia e síndrome de dispersão em floresta estacional semidecidual montana no Nordeste do Brasil. Holos 1: 1–15.

Pegado, C. M. A., L. A. Andrade, L. P. Félix, and I. M. Pereira. 2006. Efeitos da invasão biológica de algaroba: *Prosopis juliflora* (Sw.) DC. sobre a composição e a estrutura do estrato arbustivo-arbóreo da caatinga no Município de Monteiro, PB, Brasil. Acta Botanica Brasilica 20(4): 887–898.

Pereira, C. C., D. M. Arruda, F. F. S. Soares, and R. S. Fonseca. 2022. The importance of pollination and dispersal syndromes for the conservation of Cerrado Rupestre fragments on ironstone outcrops immersed in an agricultural landscape. Neotropical Biology and Conservation 17(1): 87–102. https://doi.org/10.3897/neotropical.17.e79247

Prado, C. H. B. A., and D. M. B. M. Trovão. 2023. The woody crown network model incorporates maximum height. Ecological Modelling, vol. 481. DOI: https://doi.org/10.1016/J.ECOLMODEL.2023.110345

Queiroz, R. T. 2021. Fabaceae do Cariri Paraibano. Pantanal Editora, Nova Xavantina.

Rotta, E., L. C. C. Beltrami, and M. Zonta. 2008. Manual de prática de coleta e herborização de material *botânico*. 1ª ed. Colombo: Embrapa Florestas.

Santos, W. B., L. C. Marangon, F. J. Freire, R. L. Braz, J. E. Lima-Torres, and C. S. Freire. 2020. Patterns of Seed Dispersal Syndromes at Different Altitudes In The Semiarid Region. Floresta 50(4): 1751–1760.

Silva, A. C. C., A. P. N. Prata, A. A. Mello, and A. C. A. S. Santos. 2013. Síndromes de dispersão de Angiospermas em uma Unidade de Conservação na Caatinga, SE, Brasil. Hoehnea 40(4): 601–609.

Silva, M. C. N. A., and M. J. N. Rodal. 2009. Padrões das síndromes de dispersão de plantas em áreas com diferentes graus de pluviosidade, PE, Brasil. Acta Botanica Brasilica 23(4): 1040–1047.

Silva, P. C. G., M. S. B. Moura, L. H. P. Kill, L. T. L. Brito, L. A. Pereira, I. B. Sá, R. C. Correia, A. H. C. Teixeira, T. J. F. Cunha, and C. Guimarães-Filho. 2010. Caracterização do Semiárido brasileiro: fatores naturais e humanos. Pages 18–48 in I. B. Sá and P. C. G. Silva, eds., *Semiárido brasileiro: pesquisa, desenvolvimento e inovação*, Petrolina: Embrapa Semiárido.

Spjut, R. W. 1994. A Systematic Treatment of Fruit Types. New York Botanical Garden 70(3): 1–181; http://www.worldbotanical.com/fruit_types.htm (accessed November 6, 2023).

Stefanello, D., C. Fernandes-Bulhão, and S. V. Martins. 2009. Síndromes de dispersão de sementes em três trechos de vegetação ciliar (nascente, meio e foz) ao longo do rio Pindaíba, MT. Revista Árvore 33(6): 1051–1061.

Valenta, K., and O. Nevo. 2020. The dispersal syndrome hypothesis: How animals shaped fruit traits, and how they did not. Functional Ecology 34(6): 1158–1169.

Van der Pijl, L. 1982. Dispersal Strategy and the Biocenosis. Pages 91–114 in L. van der Pijl, Principles of Dispersal in Higher Plants. Springer Berlin, Heidelberg.

Venzke, T. S., S. V. Martins, A. V. Neri, and S. H. Kunz. 2014. Síndromes de dispersão de sementes em estágios sucessionais de mata ciliar, no extremo sul da Mata Atlântica, Arroio do Padre, RS, Brasil. Revista Árvore 38(3): 403–413.

Vieira, D. L. M., V. V. Lima, A. C. Sevilha, and A. Scariot. 2008. Consequences of dry-season seed dispersal on seedling establishment of dry forest trees: Should we store seeds until the rains? Forest Ecology and Management 256(3): 471–4

TABLE 2. Species fruiting calendar of the species in the study area, Olho d'Água das Onças Ecological Reserve, Picuí, Paraíba State, Brazil. Legends: F = in fruit; – not in fruit.

SPECIES	JAN.	FEB.	MAR.	APR.	MAY	JUN.	JUL.	AUG.	SEP.	OCT.	NOV.	DEC.
Quaternella ephedroides Pedersen	–	–	–	–	–	–	–	–	F	–	–	—
Schinopsis brasiliensis Engl.	–	–	F	–	–	–	–	–	–	F	F	–
Spondias tuberosa Arruda	–	F	F	–	–	–	–	–	–	–	–	–
Aspidosperma pyrifolium Mart. & Zucc.	–	–	F	–	–	–	F	–	–	–	–	F
Aechmea aquilega (Salisb.) Griseb.	–	F	–	–	–	–	–	–	–	–	F	–
Tillandsia recurvata (L.) L.	F	F	–	–	–	–	–	–	F	–	–	–
Tillandsia streptocarpa Baker	–	F	–	–	–	–	–	–	F	–	–	F
Cereus jamacaru DC.	–	–	F	–	–	–	–	–	–	–	–	–
Melocactus zehntneri (Britton & Rose) Luetzelb.	–	F	–	–	–	–	–	–	–	–	–	–
Pilosocereus pachycladus F. Ritter	–	F	F	–	–	–	–	–	–	–	–	–
Tacinga inamoena (K. Schum.) N.P. Taylor & Stuppy	–	–	–	–	–	–	–	–	F	–	–	F
Xiquexique gounellei (F.A.C. Weber) Lavor & Calvente	–	F	F	–	–	–	–	–	–	–	–	–
Cynophalla flexuosa (L.) J. Presl	F	–	F	–	–	–	–	–	–	–	–	F
Neocalyptrocalyx longifolium (Mart.) Cornejo & Iltis	F	F	–	–	–	–	–	–	–	–	–	–
Combretum leprosum Mart.	–	–	F	–	–	–	–	–	–	–	–	–
Evolvulus filipes Mart.	–	–	–	F	–	F	F	–	–	–	–	–
Evolvulus frankenioides Moric.	–	–	–	–	–	–	F	F	–	–	–	–
Evolvulus glomeratus Nees & Mart.	–	–	–	–	–	–	–	F	–	–	–	F
Varronia globosa Jacq.	F	–	F	–	–	–	–	–	–	–	–	–
Varronia leucomalloides (Taroda) J.S. Mill.	–	–	F	–	–	–	–	–	–	–	–	–
Varronia mariana E.C.O. Chagas & Costa-Lima	–	–	F	F	–	–	–	–	–	–	–	–
Acalypha multicaulis Müll. Arg.	–	–	F	–	–	–	–	–	–	–	–	–
Argythamnia malpighiacea Ule	F	–	–	–	–	–	–	–	–	–	F	–
Cnidoscolus urens (L.) Arthur	–	F	–	–	–	–	–	–	F	–	–	–

TABLE 2 CONT. Species fruiting calendar of the species in the study area, Olho d'Água das Onças Ecological Reserve, Picuí, Paraíba State, Brazil. Legends: F = in fruit; – not in fruit.

SPECIES	JAN.	FEB.	MAR.	APR.	MAY	JUN.	JUL.	AUG.	SEP.	OCT.	NOV.	DEC.
Croton adenocalyx Baill.	–	–	F	F	–	–	–	–	–	–	–	–
Croton blanchetianus Baill.	–	–	F		–	–	–	–	–	–	–	F
Croton glandulosus L.	–	–	F	F	–	–	–	–	–	–	–	–
Croton grewioides Baill.	F	–	–	–	–	–	–	–	–	–	–	–
Croton heliotropiifolius Kunth	F	F	F	F	–	–	–	–	–	–	–	–
Jatropha mollissima (Pohl) Baill.	–	–	F	–	–	–	–	F	–	–	–	F
Jatropha ribifolia (Pohl) Baill.	F	F	–	–	–	–	–	–	–	–	–	F
Manihot carthagenensis (Jacq.) Müll. Arg.	–	F	F	–	–	–	–	–	–	–	–	–
Stillingia trapezoidea Ule	–	F	–	–	–	–	–	–	–	–	–	–
*Erythroxylum caatinga*e Plowman	F	F	–	–	–	–	–	–	–	–	–	–
Erythroxylum pyan Costa-Lima	F	–	–	–	–	–	–	–	–	–	–	F
Bauhinia cheilantha (Bong.) Steud.	–	–	–	F	–	–	–	–	–	–	–	–
Cenostigma nordestinum Gagnon & G.P. Lewis	–	F	–	–	–	–	F	–	–	–	–	F
Chamaecrista absus (L.) H.S. Irwin & Barneby	–	–	–	F	–	–	–	–	–	–	–	–
Chamaecrista calycioides (DC. ex Collad.) Greene	–	–	F	–	–	–	–	F	–	–	–	–
Chamaecrista duckeana (P. Bezerra & Afr. Fern.) H.S. Irwin & Barneby	–	–	F	–	–	–	F	–	–	–	–	–
Chamaecrista rotundifolia (Pers.) Greene	–	–	F	–	–	–	F	–	–	–	–	–
Chamaecrista zygophilloides (Taub.) H.S. Irwin & Barneby	F	–	F	–	–	–	–	–	–	–	–	F
Indigofera suffruticosa Mill.	–	–	F	F	–	–	–	–	–	–	–	F
Libidibia ferrea (Mart. ex Tul.) L.P. Queiroz	–	–	F	–	–	–	–	–	–	–	–	–
Mimosa candollei R. Grether	–	–	–	–	–	–	–	F	–	–	–	F
Mimosa paraibana Barneby	–	–	–	F	–	–	F	–	–	–	–	–
Mimosa tenuiflora (Willd.) Poir.	–	–	–	–	–	–	–	–	–	–	–	F

TABLE 2 CONT. Species fruiting calendar of the species in the study area, Olho d'Água das Onças Ecological Reserve, Picuí, Paraíba State, Brazil. Legends: F = in fruit; – not in fruit.

SPECIES	JAN.	FEB.	MAR.	APR.	MAY	JUN.	JUL.	AUG.	SEP.	OCT.	NOV.	DEC.
Peltogyne pauciflora Benth.	–	–	F	–	–	–	–	–	–	–	–	–
Senna macranthera (DC. ex Collad.) H.S. Irwin & Barneby	–	–	F	–	–	–	F	F	–	–	–	–
Senna trachypus (Benth.) H.S. Irwin & Barneby	–	–	F	–	–	–	–	–	–	–	–	–
Zornia brasilensis Vogel	F	–	–	–	–	–	–	–	–	–	–	–
Zornia leptophylla (Benth.) Pittier	–	–	–	F	–	–	–	F	–	–	–	–
Zornia reticulata Sm.	–	–	–	–	–	–	F	F	–	–	–	–
Euploca procumbens (Mill.) Diane & Hilger	–	–	–	–	–	–	–	F	–	–	–	–
Heliotropium angiospermum Murray	–	–	F	–	–	–	–	F	–	–	–	–
Pusillanthus pubescens (Rizzini) Caires	–	–	–	–	–	–	–	–	F	–	–	F
Cuphea impatientifolia A. St.-Hil.	–	–	–	F	F	F	–	–	–	–	–	–
Gaya domingensis Urb.	–	–	F	F	–	–	–	–	–	–	–	–
Helicteres eichleri K. Schum.	–	F	–	–	–	–	–	–	F	–	–	F
Herissantia tiubae (K. Schum.) Brizicky	F	–	–	–	–	–	–	F	F	–	–	F
Melochia tomentosa L.	F	–	–	–	–	–	–	–	–	–	–	–
Sida galheirensis Ulbr.	–	–	–	–	–	–	–	F	–	–	–	F
Sida spinosa L.	–	–	F	–	–	–	–	–	–	–	–	–
Sidastrum paniculatum (L.) Fryxell	–	–	F	–	–	–	–	–	–	–	–	–
Boerhavia coccinea Mill.	–	–	F	–	–	–	–	–	–	–	–	–
Boerhavia erecta L.	–	–	F	–	–	–	–	–	–	–	–	–
Scoparia dulcis L.	–	–	F	–	–	–	–	–	–	–	–	–
Cenchrus echinatus L.	–	–	–	–	–	–	–	F	–	–	–	–
Chloris barbata Sw.	–	–	F	–	–	–	–	–	–	–	–	–
Chloris virgata Sw.	–	F	–	–	–	–	–	–	–	–	–	–
Digitaria ciliaris (Retz.) Koeler	–	F	–	–	–	–	–	–	–	–	–	–
Tragus berteronianus Schult.	–	F	F	–	–	–	–	–	–	–	–	–

TABLE 2 CONT. Species fruiting calendar of the species in the study area, Olho d'Água das Onças Ecological Reserve, Picuí, Paraíba State, Brazil. Legends: F = in fruit; – not in fruit.

SPECIES	JAN.	FEB.	MAR.	APR.	MAY	JUN.	JUL.	AUG.	SEP.	OCT.	NOV.	DEC.
Urochloa mollis (Sw.) Morrone & Zuloaga	–	–	F	–	–	–	–	–	–	–	–	–
Asemeia martiana (A.W. Benn.) J.F.B. Pastore & J.R. Abbott	–	–	F	F	–	–	F	–	–	–	–	F
Asemeia violacea (Aubl.) J.F.B. Pastore & J.R. Abbott	–	–	F	F	–	–	–	–	–	–	–	–
Portulaca elatior Mart. ex Rohrb.	–	–	F	–	–	–	–	–	–	–	–	–
Portulaca halimoides L.	–	–	–	–	–	–	–	F	F	–	–	–
Portulaca mucronata Link	–	–	–	F	–	–	–	–	–	–	–	–
Sideroxylon obtusifolium (Roem. & Schult.) T.D. Penn.	F	–	–	–	–	–	–	–	–	–	–	–
Schwenckia americana Rooyen ex L.	–	–	–	–	–	–	–	–	–	–	–	F
Sarcomphalus joazeiro (Mart.) Hauenschild	F	F	–	F	–	–	–	–	–	–	–	F
Cordiera rigida (K. Schum.) Kuntze	–	–	–	–	–	–	–	–	–	F	–	F
Hexasepalum teres (Walter) J.H. Kirkbr.	–	–	F	–	–	–	–	F	–	–	–	–
Mitracarpus baturitensis Sucre	–	–	–	–	–	–	F	–	–	–	–	–
Talinum fruticosum (L.) Juss.	–	–	F	–	–	–	–	–	–	–	–	–
Talinum paniculatum (Jacq.) Gaertn.	F	–	–	–	–	–	–	F	–	–	–	–
Piriqueta viscosa Griseb.	–	–	F	–	–	–	–	–	–	–	–	–
Turnera blanchetiana Urb.	F	–	F	F	–	–	–	–	–	–	–	–
Turnera pumilea L.	–	–	–	–	–	–	–	F	–	–	–	–
Turnera subulata Sm.	–	F	F	F	–	–	–	–	–	–	–	–
Lantana radula Sw.	–	–	F	–	–	–	–	–	–	–	–	–
Lantana tiliaefolia Cham.	–	F	–	F	–	–	–	–	–	–	–	F
Stachytarpheta coccinea Schauer	–	–	–	–	–	–	–	–	–	–	F	F
Pombalia arenaria (Ule) Paula-Souza	–	–	F	–	–	–	F	–	–	–	–	–

CLUSIA AEQUATORIENSIS, A NEW COMBINATION BASED ON *TOVOMITA AEQUATORIENSIS* (CLUSIACEAE)

Lucas C. Marinho[1,3] and Angy V. Caro-Sánchez[2]

During the investigation of some taxa of Clusiaceae from the Andean region, as part of the taxonomic review of *Tovomita* Aubl. by the senior author and the review of *Chrysochlamys* Poepp. from Colombia by the junior author, we found that the type collection of *Tovomita aequatoriensis* Benoist (Fig. 1A–B), consisting of at least two isosyntypes (NY, P [with flowers, Fig. 1C]), does not exhibit a few critical characters of the genus; e.g., the outer sepals are slightly smaller than the internal ones and do not cover the floral buds (Fig. 1D–E, as stated in the protologue: "Flores dioici: feminei: sepala imbricata [...] duo interiora majora"); the pistillate flowers have a 5-carpellate ovary and lack visible staminodes (protologue: "androecaeum nullum"; Benoist, 1933). It is likely that the P specimen bears five small staminodia hidden at the base of the ovary (B. Hammel, pers. comm. to both authors). Although it is hard to determine the identity of the members of the sections of *Clusia* in the absence of staminate flowers, we assert that the leaf venation and coloration, the 5-carpellate ovary with thick and angular stigmas emerging from short styles, and the Andean distribution are indicative of the fact that the species *T. aequatoriensis* belongs to *Clusia* sect. *Anandrogyne* Planch. & Triana (Gustafsson et al., 2007). Therefore, we transfer *T. aequatoriensis* to the genus *Clusia*, and we herewith propose the new combination *Clusia aequatoriensis* (Benoist) L. Marinho & A. Caro.

We speculate that Benoist's (1933) description was based on the single specimen housed at P, since this specimen only has pistillate flowers. Moreover, Benoist did not designate a holotype and its herbarium. Consequently, we designate the specimen P05096162 as the lectotype in accordance with ICN Art. 9.3, Art. 9.6, Art. 9.14 and following the 9A recommendation (Turland et al., 2018).

Clusia aequatoriensis (Benoist) L. Marinho & A. Caro, *comb. nov.*

Basionym: *Tovomita aequatoriensis* Benoist, *Bull. Soc. Bot. France* 80: 333. 1933.

Type: ECUADOR. Santo Domingo de los Tsáchilas: Santo Domingo de Los Colorados, 10 September 1930, *R. Benoist 3056* (lectotype [designated here]: P [P05096162]; isolectotype: NY [NY00073944]). Fig. 1.

Literature Cited

Benoist, R. 1933. Guttifères *in* Descriptions d'espèces nouvelles de Phanérogames sudamêricaines. Bulletin de la Société Botanique de France 80: 333–334.

Gustafsson, M. H., K. Winter, and V. Bittrich. 2007. Diversity, phylogeny and classification of *Clusia*. Pages 95–116 in U. Lüttge, ed., *Clusia*: a woody neotropical genus of remarkable plasticity and diversity. Ecological Studies 194. Springer, Berlin. https://doi.org/10.1007/978-3-540-37243-1_7

Turland, N. J., J. H. Wiersema, F. R. Barrie, W. Greuter, D. L. Hawksworth, P. S. Herendeen, S. Knapp, W.-H. Kusber, D.-Z. Li, K. Marhold, T. W. May, J. McNeill, A. M. Monro, J. Prado, M. J. Price, and G. F. Smith, eds. 2018. International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159. Koeltz Botanical Books, Glashütten. https://doi.org/10.12705/Code.2018

The authors thank José Elvino Nascimento Jr. and Barry Hammel for help with the placement of *Clusia aequatoriensis* in section *Anandrogyne* and the staff of the herbaria cited in the text for their assistance. The visits to NY and P herbaria were carried out by LCM with the support of the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq-Brazil), Ph.D. fellowships (#141561/2015-7), and the Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, throughout the REFLORA Project. We are indebted to Kanchi Gandhi for reading and reviewing the text.

[1] Universidade Federal do Maranhão, Centro de Ciências Biológicas e da Saúde, Departamento de Biologia, Av. dos Portugueses 1966, Bacanga, 65080-805, São Luís, Maranhão, Brazil

[2] Universidad de Antioquia, Instituto de Biología, Facultad de Ciencias Exactas y Naturales, Calle 67 Nº 53-108, Medellín, Colombia; angy.caro@udea.edu.co

[3] Corresponding author: lc.marinho@ufma.br

Harvard Papers in Botany, Vol. 29, No. 1, 2024, pp. 119–120.

ISSN: 1938-2944, DOI: 10.3100/hpib.v29iss1.2024.n13, Published online: 30 June 2024

FIGURE 1. *Tovomita aequatoriensis* Benoist. **A**, lectotype of (≡ *Clusia aequatoriensis*) (P05096162); **B**, label affixed by L. C. Marinho in 2016 indicating the type; **C**, content (pistillate flowers) available in the packet; **D**–**E**, detail of the flowers; **F**, detail of the sheet label.

A COMMENTARY ON THE *CINNAMOMUM* AND *CAMPHORA* (LAURACEAE) TYPES OF ATHANASE DE LUKMANOFF

PAUL ORMEROD[1]

Abstract. Notes are supplied on the types of the species and varieties proposed in *Cinnamomum* and *Camphora* (Lauraceae) by Athanase de Lukmanoff. Four new combinations and one new name are proposed: viz. *Camphora blandfordii, C. camphorata, C. glaucescens, Cinnamomum cubittii,* and *Timonius pedunculatus*.

Keywords: *Cinnamomum, Camphora, Timonius,* types, lectotypes, Lukmanoff

In 1878, Athanase de Lukmanoff (1825–1890) published a small monograph of the genera *Cinnamomum* and *Camphora* using such characters as leaf shape and venation, fragrance of the dried material, and length of the inflorescence. These characters are helpful to some degree but must be supplemented with examination of the leaf surface and the type of pubescence present, floral structure, and fruit. Lukmanoff based his studies on dried material in the Paris herbarium, along with living specimens he encountered in various European gardens. He donated his personal herbarium to Paris on 4 April 1878.

Lukmanoff's monograph was overlooked until it was included in Supplement 6 of Index Kewensis, published in 1926. Here, two major errors occurred. First, Lukmanoff's monograph was credited to the year 1889. It would not be until Doweld (2017), who showed that February 1878 was the correct publication date. The second error occurred when all of Lukmanoff's varieties were treated as species, thus creating an unnecessary plethora of names.

Lukmanoff's taxa have, for the most part, been ignored in regional treatments (e.g., Borneo, Soh, 2011), or scarcely mentioned in regional synopses (e.g., India, Geethakumary et al., 2021; Sri Lanka, Kostermans, 1995). Part of the reason for this is that many of Lukmanoff's types have not been identified in the Paris herbarium, and, thus, authors have been reluctant to discuss obscure names.

This paper is an attempt to identify the types of Lukmanoff's taxa where possible. It is, however, evident that a number of these types are no longer present in Paris (Deroin, pers. comm.). Lukmanoff's ways of citing type data often also clouds the identity of the material he studied. For example, he often credits the distributing institution or person as the collector, rather than the actual collector. Sometimes it appears that he has just guessed the origin of a collection. Nevertheless, Lukmanoff did give measurements and illustrated the leaves of every taxon he described.

Cinnamomum Schaeff., Bot. Exped.: 74. 1760 *nom. cons.*
Type species: *Laurus cinnamomum* L. (= *Cinnamomum verum* J. Presl).

This genus is well-known as the source of the spice cinnamon. It consists of around 220 species (excluding *Camphora* and Neotropical taxa) distributed from India and Sri Lanka to Fiji, south to eastern Australia.

Cinnamomum africanum Lukman., Nomencl. Icon. Cannel.: 8. 1878.
TYPE: SAO TOME and PRINCIPE. Prince's Island [= Principe], 1861, *G. Mann 1132* (Lectotype, here designated: P [01752534], image seen; Isolectotype: K [002235073], image seen).

The original type citation only referred to Tropical Africa, ex Kew. The proposed lectotype has a West Tropical Africa label and was distributed from Kew. It has been identified as *C. zeylanicum* Blume (= *C. verum* J. Presl) in Paris.

Cinnamomum alatum Lukman., Nomencl. Icon. Cannel.: 16. 1878.
TYPE: JAPAN [as "China"]. Loo-Choo Islands [= Ryukyu Islands], U.S. North Pacific Exploring Expedition, 1853–1856, *C. Wright 253* (Lectotype, here designated: P [01978414], image seen; Isolectotypes: GH [02222270], US [61488], images seen).

The original type citation referred to China, Loo-Choo Islands, collected by Asa Gray. Gray did not travel to Japan, but in 1859 distributed specimens collected there by Wright. The winged leaf base depicted by Lukmanoff is, in my opinion, a misinterpretation and not a real character. In Paris, the specimen is found under the unpublished name *C. zollingeri* (Lukman.) Kosterm. (Basionym: *Camphora zollingeri* Lukman.). This is not to be confused with *Cinnamomum zollingeri* (Lukman.) A.W. Hill (Basionym: *Cinnamomum zeylanicum* Blume var. *zollingeri* Lukman.). In more recent literature (e.g., Li et al., 2007), the name *Cinnamomum japonicum* Siebold (*nom. illeg.* because it included the available name *Laurus pedunculata* Thunb., see Addendum under *Timonius*) has been used for *C. zollingeri* (Lukman.) Kosterm. On POWO, the next valid available name, *C. insularimontanum* Hayata, has been taken, but this is predated by *C. alatum* by 35 years. Thus, *Cinnamomum alatum* is the correct name in *Cinnamomum* for this taxon.

I wish to thank herbarium curators and staff at A, BM, BO, C, CAL, CGE, FI, GH, K, LY, M, MEL, P, PDA, and UPS for their help in searching for and arranging the scanning of specimens. Wise advice from Rubiaceae specialists Junhao Chen, Steve Darwin, Pui Khat Hoo, Charlotte Taylor, and Khoon Meng Wong was greatly appreciated.

[1] P.O. Box 8210, Cairns 4870, Queensland, Australia; wsandave1@bigpond.com

Harvard Papers in Botany, Vol. 29, No. 1, 2024, pp. 121–139.

ISSN: 1938-2944, DOI: 10.3100/hpib.v29iss1.2024.n14, Published online: 30 June 2024

Cinnamomum albiflorum Nees, in Wallich, Pl. Asiat. Rar. 2: 75. 1831 *nom. illeg.* (cites the available name *Laurus soncaurium* Buch.-Ham. in synonymy).

This name, as applied by earlier authors, is now considered a synonym of *C. tamala* (Buch.-Ham.) T. Nees & C.H. Eberm. As noted above, *C. albiflorum* included *Laurus soncaurium* in its synonymy, so in reality the name is rather a homotypic synonym of *Cinnamomum bejolghota* (Buch.-Ham.) Sweet. Three varieties were proposed under *C. albiflorum* by Lukmanoff, and all are considered to be synonyms of *C. tamala*. However, *C. albiflorum* var. *zwartzii* is considered here to be a synonym of *C. burmannii* (Nees & T. Nees) Blume, a taxon that can have superficially similar leaf venation to *C. tamala*.

Lukmanoff cited a specimen (India, Saharanpour, *Hooker*) as representing typical *C. albiflorum*. This collection is extant in Paris (P 01748415, sub *C. soncaurium*). The label shows it was cultivated in Saharunpore (= Saharanpur), India, and was collected by T. Thomson. The sheet was distributed by J. D. Hooker and T. Thomson from Kew. The specimen is representative of *C. tamala*.

var. ***lindleyi*** Lukman., Nomencl. Icon. Cannel.: 10. 1878.
TYPE: INDIA. Cult., *J. D. Hooker s.n.* (Holotype: not found).
Homotypic synonym: *Cinnamomum lindleyi* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

The type locality is ambiguous, but the plant is likely one cultivated in Calcutta Botanic Gardens.

var. ***veitchii*** Lukman., Nomencl. Icon. Cannel.: 10. 1878.
TYPE: INDIA. Kumaon, Kupkot, 3000 ft [915 m], 1843, *R. Strachey & J. E. Winterbottom 1* (Lectotype, here designated: P [01748416], image seen).
Homotypic synonym: *Cinnamomum veitchii* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

The specimen chosen as the lectotype was originally identified as *C. albiflorum,* and Lukmanoff likely saw it under this name. Lukmanoff cites the locality as Himalaya, Kumaon, Kupkot, *Strachey*. Kostermans identified the specimen as *C. soncaurium* (Buch.-Ham.) T. Nees & C.H. Eberm., now considered a synonym of *C. bejolghota* (Buch.-Ham.) Sweet. However, the material is clearly not the latter species and is probably best included in *C. tamala*. *Cinnamomum stracheyi* Lukman. was also based on a *Strachey & Winterbottom* collection from the same region.

var. ***zwartzii*** Lukman., Nomencl. Icon. Cannel.: 10. 1878.
TYPE: WITHOUT ORIGIN [see notes]. Cultivated, *J. D. Hooker s.n.* (Lectotype, here designated: P [01748521], image seen; Isolectotype: L [1791581], image seen).
Homotypic synonym: *Cinnamomum zwartzii* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926

Lukmanoff cited the type data as “Indes. Cultive a Batavia, *Hooker*.” From this one would assume the origin is Batavia (now Jakarta) on Java in Indonesia, a place Joseph Hooker never visited. Nor can any material be found that was cultivated in Batavia and distributed by Hooker or Kew. The Kew label of the lectotype has no country of origin, only “*Patria cult*.” (i.e., origin cultivated), with Hooker as the collector. The Paris label has “Indes Orientalis” (i.e., East Indies) on it. So it is possible to think the plant came from the East Indies (what is mostly now Indonesia). Added to this, the “*Patria*” on the Kew label does look a bit like Batavia. Kostermans added a note that the specimen likely came from a tree in the Calcutta Botanic Garden called *Laurus dulcis* Roxb. He identified the material as *Cinnamomum burmannii*. The duplicate in L is currently misidentified as *C. tamala*.

Cinnamomum alibertii Lukman., Nomencl. Icon. Cannel.: 19. 1878.
TYPE: BORNEO. *O. Beccari s.n.* (Holotype: not found). Neotype, here designated: Malaysia, Sarawak, Sumungian [=? Simanggang], October 1867, *O. Beccari 3935* (Holoneotype: FI [078195, right-hand plant], image seen).

Since the original material of this entity seems to be missing in Paris, a search for matching specimens was kindly undertaken by Anna Donatelli in FI. In FI, the only matching sheet appears to be composed of two seedlings (left-hand plants) and an older branchlet (right-hand specimen). This latter specimen agrees tolerably well with Lukmanoff’s protologue and is here selected as the neotype. Although the neotype is sterile, I would suggest it is representative of *C. iners* Reinw. ex Blume. The two left-hand plants are referred to under *C. beccarii* below.

Cinnamomum andersonii Lukman., Nomencl. Icon. Cannel.: 13. 1878.
TYPE: INDIA. *Cult. Hort. Bot. Calcuttensis*, *comm. T. Anderson 28* (Holotype: P [01752728], image seen).

The specimen appears to have a misplaced label by Lukmanoff that does not have the name, but “N 27 Espece.” Species 27 in Lukmanoff’s monograph is *C. brownei*, which is based on “Indes, *Hooker*.” I agree with Kostermans’ annotations on the sheet, that it is, rather the type of *C. andersonii,* and referrable to *C. iners* Reinw. ex Blume.

In Paris, several collections of different species of *Cinnamomum* sent by Thomas Anderson from the Calcutta Botanic Garden bear the number 28. This number appears to have been added later and is not a collection or field number.

Cinnamomum angustifolium Lukman., Nomencl. Icon. Cannel.: 17. 1878 *nom. illeg.* (*non* Raf. 1838).
TYPE: INDIA. Khasia, *T. Anderson 28* (Lectotype, here designated: P [01991861], image seen).

Additional specimens examined: INDIA. Khasia Hills, *Native Collector s.n.* (L [0035793], P [01991859], images seen); Khasia, *sine coll. s.n.* (P [01991862], image seen); Khasia, *T. Anderson s.n. (= Herb. Pierre 5162)* (P [01991860], image seen).

The specimen chosen as the lectotype is the only one that Lukmanoff is likely to have seen of this distinctive narrow-leaved, glabrous-flowered species. The other three sheets cited above are from the herbaria of Drake and Pierre and were not available to Lukmanoff at the time. The sheets cited from Khasia Hills (L, P) are isotypes of *C. bishnupadae* M. Gangop., which is the correct name for this taxon.

All of the Paris specimens cited here were previously identified as *C. glabriflorum* Kosterm., an unpublished name. The earlier name, *C. angustifolium* Raf., is listed on POWO as a synonym of the Caribbean *Licaria parvifolia* (Lam.) Kosterm. This seems to be an error, since Rafinesque gave Borneo and Mindanao as the origin for his taxon.

Cinnamomum aromaticum Nees, in Wallich, Pl. Asiat. Rar. 2: 74. 1831.

Lukmanoff (1878) does not cite Nees as the author, but it is unlikely that he was proposing a new species.

var. ***longifolium*** Lukman., Nomencl. Icon. Cannel.: 11. 1878.
TYPE: CHINA. Cultivated in the gardens of Europe, *A. de Lukmanoff s.n.* (Holotype: P [00757082], image seen).
Homotypic synonym: *Cinnamomum longifolium* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

The type is annotated by Lukmanoff and only mentions that the plant was cultivated in the gardens of Europe. In the protologue, the botanical garden of St. Petersburg is also mentioned. This variety is considered a synonym of *C. aromaticum*.

Cinnamomum asagrayi Lukman., Nomencl. Icon. Cannel.: 9. 1878.
TYPE: CHINA. Hong Kong, U.S. North Pacific Exploring Expedition, 1853–1856, *C. Wright 401* (Lectotype, here designated: P [01748526], image seen; Isolectotype: GH [00871563], image seen).

The original type citation referred to Hong Kong, *Wright*. The specimen can be found in Paris under the name *C. burmannii*. There are at NY two possible isolectotypes (NY [47123117, NY 512012], images seen) of *C. asagrayi*, but they lack the number 401.

Cinnamomum assamicum Lukman., Nomencl. Icon. Cannel.: 11. 1878.
TYPE: INDIA. Assam, *Colonel F. Jenkins s.n.* (Lectotype, here designated: P [01978760], image seen; Isolectotypes: BO [0122536], BO [0122545], BO [0122546], BR [0000029323821], G [00693677], K [002133383], L [1795314], L [1795315], NY [4723258], P [01978800], images seen; S [S14-55988], not seen).

The specimens cited as type material above are all filed under the name *C. bejolghota*. The duplicate seen by Lukmanoff seems to be no longer present at Paris.

Cinnamomum aubletii Lukman., Nomencl. Icon. Cannel.: 17. 1878.
TYPE: MAURITIUS. Cult. at Le Reduit, *J. B. C. F. Aublet s.n.* (Lectotype, here designated: P [01748525], image seen).

Kostermans suspected the above cited specimen (under *C. burmannii* in P) might be the type, even though the leaves have a more oblique base than the leaf depicted by Lukmanoff. The original locality was given as "Indes," but Aublet did not visit Asia. Aublet established a garden in 1764 at Le Reduit on Mauritius, which is where the specimen discussed was cultivated.

Cinnamomum bahianum Lukman., Nomencl. Icon. Cannel.: 6. 1878.
TYPE: BRAZIL. Bahia, *H. A. Weddell s.n.* (Holotype: not found); Neotype, here designated: Brazil, Bahia, *J. S. Blanchet s.n.* (Holoneotype: P [01978287], image seen).

No Weddell collection from Bahia can be located. There is one from Minas Gerais, but it is the type of *C. orbiculatum* Lukman. Therefore, another Bahia specimen collected by J. S. Blanchet has been chosen as the neotype. This has a leaf about the same size (15 × 6 cm) as indicated by Lukmanoff, but the shape does not agree (being more subacuminate in Lukmanoff's drawing), although some of the narrower leaves (ca. 5 cm wide) do agree well with the drawing.

Cinnamomum baillonii Lukman., Nomencl. Icon. Cannel.: 10. 1878.
TYPE: CHINA. Cultivated in the Faculty of Medicine, Paris, *A. de Lukmanoff s.n.* (Holotype: P [01752702], image seen).

The type bears a label from Lukmanoff with the name and the place where it was cultivated. The specimen was identified as *C. iners* Reinw. ex Blume by Kostermans.

Cinnamomum bamoense Lukman., Nomencl. Icon. Cannel.: 14. 1889.
TYPE: INDIA? 1843, *W. Griffith s.n.* (Lectotype, here designated: P [01978807], image seen); possible Isolectotypes: BR [0000029323838, Assam, 1843], L [1795312, Khasya Hills], L [1795321, Khasya Hills], images seen).

The specimen chosen as the lectotype agrees with the description (leaves erect, 15 × 5 cm) and illustration (showing the missing leaf apex) in the protologue. Lukmanoff gave the origin as "Birman, *Griffith*," with the specific epithet of *bamoensis*. From this one would assume that the plant is from Bhamo in Myanmar. The lectotype sheet only has "Inde" as the locality on it, but the Kew Distribution number 4244 was added later by Kostermans. Lukmanoff possibly guessed the origin was "Birman," because there is another Griffith specimen (Kew Distr. 4244) [P 01978812] of *C. bejolghota* labelled as from "Birma," that also has erect (but badly damaged) leaves. He likely gave the epithet after one of the places Griffith was known to have visited. No Griffith specimens of *Cinnamomum* are known to have come from Bhamo; all of his Myanmar *Cinnamomum* collections originate from the Mergui region. All of the cited material was identified as *C. bejolghota* (Buch.-Ham.) Sweet by Kostermans.

The entity, *C. bhamoense* M. Gangop., described in 2006 should, in my opinion, be treated as a homonym of *C. bamoense*, since both are named after the same place and are pronounced the same. The former is renamed *C. cubittii* in the addendum to this paper.

Cinnamomum barlowii Lukman., Nomencl. Icon. Cannel.: 16. 1878.
TYPE: CHINA. Cultivated in the Tsar's Imperial Garden, St. Petersburg, *A. de Lukmanoff s.n.* (Holotype: P [00732271], image seen).

The type bears a label from Lukmanoff with the name and place where it was cultivated. The specimen has been identified as *C. verum*. Due to an error during databasing, the origin of the specimen is given as Mexico.

Cinnamomum beccarii Lukman., Nomencl. Icon. Cannel.: 19. 1878.
TYPE: BORNEO. *O. Beccari s.n.* (Holotype: not found); Neotype, here designated: Malaysia, Sarawak, Sumungian [=? Simanggang], October 1867, *O. Beccari 3935* (Holoneotype: FI [086066], two left-hand plants, image seen).

Lukmanoff described and depicted the leaves of this entity as alternate, ovate-lanceolate, boldly cross-reticulated, and about 12 × 4 cm. In FI, the only tolerably matching material is two seedlings on the left-hand side of a Beccari collection that was kindly located by Anna Donatelli. Although the material is sterile, I place it with *C. iners* Reinw. ex Blume, a species that often has some subalternate leaves. Most other species of *Cinnamomum* have strictly opposite leaves.

Cinnamomum blumei Lukman., Nomencl. Icon. Cannel.: 7. 1878.
TYPE: INDIA. *Peninsula India Orientalis,* [Courtallam, August 1835], *Herbarium R. Wight 2238* (Lectotype, here designated: P [01978293], image seen; Isolectotypes: E [01073384], E [01073385], images seen).

The specimen designated as the type has been identified as *C. malabatrum* (Burm.f.) J. Presl. The size of the leaf (22.0 × 9.5 cm), its venation, and its broken off apex agree with the description and figure in the protologue of *C. blumei*. Lukmanoff gives "Indes, Malabar, *Wight*" as the type data, but it is possible he misremembered the name "*C. malabathrum*" that was on the sheet as the locality Malabar (which is not on the sheet). The two isolectotypes in E are filed under *C. iners* Reinw. ex Blume (a taxon with quite similar leaves), which is a historical misnaming of this collection. One [E 01073384] has additional details of its origin and collection date, with an alternative Wight number (no. 718). The former details have been added to the type citation.

Cinnamomum borneense Lukman., Nomencl. Icon. Cannel.: 9. 1878 *nom. illeg.* (*non* Meissn. May 1864, *nec* Miq. Oct 1864).
TYPE: MALAYSIA. Sarawak [as Borneo]. Without locality [Kuching], *O. Beccari 270* (Lectotype, here designated: P [01978448], image seen; Isolectotypes: A [02537093], A [02537100], BM [015153036], FI [076893, 2 sheets], G [00412209], M [0147234], images seen).

Lukmanoff was aware this name was a homonym when he proposed it ("non DC"; i.e., Meissn. in DC). Kostermans identified the Paris specimen as *C. verum* J. Presl and wrote on the sheet that it is not from Borneo. However, the species is cultivated on Borneo, especially in the neighbourhood of Kuching (Sarawak, Malaysia), which Beccari visited in 1865 and 1866. Indeed, the duplicate in FI [076893] does have the locality "Kutcin" [= Kuching].

Cinnamomum brogniartii Lukman., Nomencl. Icon. Cannel.: 8. 1878.
TYPE: INDONESIA. Java, comm. 1862, *ex Herbario Lugduno-Batavo, sine coll. s.n.* (Lectotype, here designated: P [01978118], image seen).

The specimen matches Lukmanoff's protologue in leaf shape, size (18.5 × 9.5 cm), and damage (one side mostly missing). The collection has been identified as *C. zeylanicum* Blume (= *C. verum* J. Presl).

Cinnamomum brownei Lukman., Nomencl. Icon. Cannel.: 10. 1878.
TYPE: INDIA. *J. D. Hooker s.n.* (Holotype: not found).

Cinnamomum bureaui Lukman., Nomencl. Icon. Cannel.: 14. 1878.
TYPE: BANGLADESH. Sylhet, *ex Herbarium A. L. Jussieu, N. Wallich 2574A* (Lectotype, here designated: P [01978750], image seen; Isolectotypes: BR [0000005115204], E [00393165], E [00393166], FI [086046], GZU [000254048], GZU [000254049], L [0308457], L [0035711], P [00757068], images seen).

The specimen chosen as the lectotype matches the description and figure in the protologue quite well. The collection *Wallich 2574A* is a widely distributed number, also treated as the type of *Laurus obtusifolia* Roxb. It is difficult to be certain that Roxburgh based his taxon on Wallich material, since in the protologue the localities of Silhet and Chittagong [both now in Bangladesh] are mentioned. No collector is given. This name is a synonym of *Cinnamomum bejolghota* (Buch.-Ham.) Sweet.

Cinnamomum calleryi Lukman., Nomencl. Icon. Cannel.: 16. 1878.
TYPE: CHINA. Without locality, 1844, *J. M. M. Callery 144* (Lectotype, here designated: P [01978710], image seen).

The specimen was determined as *C. burmannii* (Nees & T. Nees) Blume by Kostermans. Its leaves match the dimensions and features as described and illustrated by Lukmanoff. Another Chinese taxon, *C. maximoviczii* Lukman., also has a Callery collection designated as the type, but that has not been located.

Cinnamomum carrierei Lukman., Nomencl. Icon. Cannel.: 14. 1878.
TYPE: INDIA. Khasia, 3–4000 ft [915–1220 m], *J. D. Hooker & T. Thomson s.n.* (Lectotype, here designated; P [01978595], image seen; Isolectotypes: BM [002134635], CAL [0000021499], CGE [00085188], G [00693834], K [002133687], K [002133689], L [1791575, upper plant], L [1792708], NY [354993], images seen).

Lukmanoff gave the type details as "Khasia, 3–4000 ft, *Hooker*." In Paris, a sheet identified as *C. tamala* (Buch.-Ham.) T. Nees & C.H. Eberm. has these details but was actually collected by Hooker and Thomson. It agrees fairly well with the protologue, except the largest leaf is about 16 × 6 cm (vs. 16 × 5 cm) and is more elliptic in shape. The

Paris lectotype is a fruiting collection of the species. Some supposed duplicates, such as one in Kew [K002133689], are of sterile younger branchlets. This particular sheet also has specific field data [Churra, 15 June 1850, lower single leaf; and Churra, 17 June 1850, no. 874, main specimen].

Cinnamomum cassia T. Nees & C.H. Eberm. ex Blume, Bijdr. Fl. Ned. Ind. 11: 570. 1826 *nom. illeg.* (*non* [L.] J. Presl 1823–1824).

This name, as applied by Blume, is a synonym of *C. aromaticum*.

var. ***medium*** Lukman., Nomencl. Icon. Cannel.: 11. 1878.
TYPE: CHINA. Cultivated in the Botanical Garden, Paris, *A. de Lukmanoff s.n.* (Holotype: P [00757083], image seen).
Homotypic synonym: *Cinnamomum medium* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

The type has a label by Lukmanoff stating the plant was cultivated at the Museum (Botanical Garden Paris). In the protologue, it was only said to be cultivated in several European gardens. This entity is treated under *C. aromaticum* in Paris.

Cinnamomum decaisnei Lukman., Nomencl. Icon. Cannel.: 6. 1878.
TYPE: INDIA. Mountains bordering China, *W. Griffith s.n.* (Holotype: not found).

A collection matching the details provided by Lukmanoff has not been located. It is possible the type locality is in Bhutan, rather than India.

Cinnamomum decourtilzii Lukman., Nomencl. Icon. Cannel.: 19. 1878.
TYPE: INDONESIA. Java, *J. B. Leschenault s.n.* (Lectotype, here designated: P [01978022], image seen; possible Isolectotype: P [01978023], image seen).

The specimen chosen as the lectotype matches well with Lukmanoff's description and illustration. The sheet was determined as *C. burmannii* (Nees & T. Nees) Blume by Blume, and later by Kostermans.

Cinnamomum donii Lukman., Nomencl. Icon. Cannel.: 15. 1878.
TYPE: INDIA. *J. D. Hooker s.n.* (Holotype: not found).

The leaves of this taxon somewhat resemble those of *C. burmannii* (Nees & T. Nees) Blume, so this taxon may not be native to India and is perhaps a cultivated one.

Cinnamomum dulce Nees, in Wallich, Pl. Asiat. Rar. 2: 75. 1831 *nom. illeg.* (cites the available name *C. chinense* Blume in synonymy).

This name is treated as a synonym of *C. burmannii* (Nees & T. Nees) Blume.

var. ***ammannii*** Lukman., Nomencl. Icon. Cannel.: 7. 1878.
TYPE: JAPAN. *P. Commerson s.n.* (Holotype: not found).
Homotypic synonym: *Cinnamomum ammannii* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 45. 1926.

Commerson did not collect in Japan, so the type is likely a collection cultivated on Mauritius that originated from Japan.

var. ***sieboldii*** Lukman., Nomencl. Icon. Cannel.: 7. 1878.
TYPE: MAURITIUS. 1768, *P. Commerson s.n.* (Lectotype, here designated: P [02006675], image seen).
Homotypic synonym: *Cinnamomum sieboldii* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926 *nom. illeg.* (*non* Meissn. 1864).

The specimen chosen as the lectotype matches the leaf dimensions (10 × 4 cm) and drawing in the protologue. Kostermans identified it as *C. burmannii* (Nees & T. Nees) Blume.

var. ***thunbergii*** Lukman., Nomencl. Icon. Cannel.: 7. 1878.
TYPE: JAPAN. *Herbarium A. T. Brogniart s.n.* (Holotype: not found).
Homotypic synonym: *Cinnamomum thunbergii* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

Cinnamomum gaudichaudii Lukman., Nomencl. Icon. Cannel.: 18. 1878.
TYPE: VIETNAM [as Cochinchina]: *C. Gaudichaud s.n.* (Holotype: not found).

This was possibly collected in the Tourane (= Da Nang) area, near Hue in central Vietnam.

Cinnamomum goeringii Lukman., Nomencl. Icon. Cannel.: 16. 1878.
TYPE: CHINA [see note]. Java (Indonesia), [*leg. H. Buerger*], *P. F. W. Goering s.n.* (Holotype: not found).

Goering did not collect in China or Japan. Instead, he came into the possession of specimens Buerger had collected in the Nagasaki region of Japan, so sometimes Japanese collections are wrongly accredited to Goering. Some of the material Goering had was later incorporated into the herbarium of Zollinger. In my opinion, *C. goeringii* resembles a large-leaved form of *C. alatum* Lukman., such as observed on the isolectotype of *Camphora zollingeri* Lukman. (P [01978396, left-hand plant]). The latter was based on *Zollinger 219*, but the collection was surely made by Buerger in Japan. The Nagasaki region is likely the true origin of *C. goeringii*; thus, I consider it as a synonym of *C. alatum*.

Cinnamomum guyanense Lukman., Nomencl. Icon. Cannel.: 10. 1878.
TYPE: FRENCH GUIANA. Without locality, 1842, *E. M. Melinon 226* (Lectotype, here designated: P [01978684], image seen; Isolectotypes: P [01978682], P [01978683], images seen).

The specimen chosen as the lectotype has a label by Lukmanoff identifying it as *C. guyanense*. It is filed under the name *C. verum* J. Presl in Paris.

Cinnamomum helferi Lukman., Nomencl. Icon. Cannel.: 15. 1878.

TYPE: MYANMAR. Tenasserim and INDIA. Andamans. Without locality, *J. W. Helfer (Kew Distr.) 4242* (Lectotype, here designated: U [0002656], image seen; Isolectotypes: K, not found, L [0035807], M [0293171], images seen).

Kostermans (1998) accepted this taxon as a distinct species, and he identified Helfer (Kew Distr.) 4242 as the type collection but did not designate a lectotype. This collection is no longer extant in Paris, so the duplicate in U is chosen as the lectotype. Another Helfer collection (Kew Distr. 4245), with the same locality data, was treated by Lukmanoff (1878) under *C. iners* Reinw. ex Blume. Kostermans (1998) found this was a misidentification and determined that material as *C. lucens* Miquel.

Cinnamomum heudelotii Lukman., Nomencl. Icon. Cannel.: 7. 1878.
TYPE: SENEGAL. Without locality, cult. in garden of *Richard Toll,* 1831, *J. Heudelot s.n*. (Lectotype, here designated: P [01752533], image seen).

The lectotype agrees with Lukmanoff's protologue and has been identified as *C. zeylanicum* Blume (= *C. verum* J. Presl).

Cinnamomum hookeri Lukman., Nomencl. Icon. Cannel.: 10. 1878.
TYPE: INDIA. Sikkim, 6000 ft [1830 m], *J. D. Hooker s.n*. (Holotype: not found). Neotype, here designated: India, Sikkim, 4000–6000 ft [1220–1830 m], *J. D. Hooker s.n*. (Holoneotype: P [01748411, left-hand plant], image seen; Isoneotypes: BM [014605811], C [no barcode], CGE [00085190], CGE [00085197], CGE [00085198], L [1791575, lower plant], L [1791576], images seen).

The collection that Lukmanoff based this entity on seems to be no longer extant in Paris, so a neotype is chosen from a similar, but later acquired, specimen from Herbarium Cosson. This specimen agrees with Lukmanoff's protologue in having a narrowly oblong-lanceolate leaf that is 11 × 3 cm. However, other leaves are about 4 cm wide and more elliptic. Kostermans identified the plant as *C. soncaurium* (Buch.-Ham.) T. Nees & C.H. Eberm., now regarded as a synonym of *C. bejolghota*. The neotype comes from an area where Joseph Hooker collected material of *C. tamala* and what would be the type material of *C. impressinervium* Meissn. Thus, as here neotypified, *C. hookeri* could be determined as *C. tamala sensu lato*; however, there is a possibility it is a natural hybrid between *C. impressinervium* and *C. tamala*, due to the intermediate foliage features (some acuminate to subacuminate leaves with moderately impressed veins above).

Cinnamomum houlletii Lukman., Nomencl. Icon. Cannel.: 9. 1878.
TYPE: JAPAN. Cultivated in the Botanic Garden, Paris, *A. de Lukmanoff s.n*. (Holotype: P [00757073], image seen).

The specimen has a Lukmanoff label with the name of the species. Kostermans identified it on the sheet as *C. burmannii*.

Cinnamomum jacquemontii Lukman., Nomencl. Icon. Cannel.: 13. 1878.
TYPE: INDIA. Bodwellgad [as Boiwellgad] Valley, *V. Jacquemont 522* (Lectotype, here designated: L [1792714], image seen).

No Jacquemont *Cinnamomum* specimens remain in Paris. However, a specimen collected from the type locality by Jacquemont was found in L under the name *C. soncaurium*. This has slightly smaller leaves than the lost Paris duplicate described by Lukmanoff, but clearly represents the same species; i.e., *C. tamala* (*C. soncaurium sensu* Kostermans).

Cinnamomum ligneum Lukman., Nomencl. Icon. Cannel.: 12. 1878.
TYPE: SRI LANKA [as Ceylan] and INDONESIA. Java, *Herbarium S. Vaillant s.n*. (Holotype: not found).

This taxon is possibly based on an unimaged Herbarium Vaillant collection in Paris [00499729] from Sri Lanka. Unfortunately, this collection cannot be located (Deroin, pers. comm.)

Cinnamomum lindenii Lukman., Nomencl. Icon. Cannel.: 14. 1878.
TYPE: [INDIA]. Himalaya, cult. in Gand [Belgium] by *Messrs. Linden s.n*. (Holotype: not found).

Cinnamomum linnei Lukman., Nomencl. Icon. Cannel.: 15. 1878.
TYPE: CHINA. Cult. Bot. Gard. Paris, *A. de Lukmanoff s.n*. (Holotype: P [00757074], image seen).

The specimen was annotated by Lukmanoff as *C. linnei*. Kostermans identified it on the sheet as *C. burmannii*.

Cinnamomum litseifolium Thwaites, Enum. Pl. Zeyl.: 253. 1861 as *litseaefolium*.

This species occurs in Sri Lanka and southern India. Lukmanoff cited the specimen he saw as "Ceylan, 5000 ft, *Thwaites*." This collection (*G. H. K. Thwaites CP 392* [P 00757033], image seen) is regarded as an isotype of the species.

var. ***willdenowii*** Lukman., Nomencl. Icon. Cannel.: 15. 1889.
TYPE: SRI LANKA [as Ceylon]. 5000 ft [1525 m], *G. H. K. Thwaites CP 392* (Lectotype, here designated: FI [086053, left-hand plant], image seen).
Holotype: *Cinnamomum willdenowii* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

This taxon was based on a broad-leaved specimen of *Thwaites CP 392,* but the relevant duplicate is no longer extant in Paris. Therefore, a duplicate in FI closely matching Lukmanoff's description (leaves 8 × 5 cm, apex missing) is chosen as the lectotype. The FI duplicate has slightly smaller leaves (7 × 4 cm) and a missing apex.

Cinnamomum lowii Lukman., Nomencl. Icon. Cannel.: 15. 1878.
TYPE: CHINA. Cult. Bot. Gard. Paris (Holotype: not found).

Cinnamomum lubbersii Lukman., Nomencl. Icon. Cannel.: 18. 1878.
TYPE: [INDIA]. Himalaya, cult. Bot. Gard. Brussels (Holotype: not found).

Cinnamomum lucienii Lukman., Nomencl. Icon. Cannel.: 18. 1878.
TYPE: CHINA/JAPAN. Cult. in Gand [Belgium], *Messrs. Linden s.n.* (Holotype: not found).

Cinnamomum luddemannii Lukman., Nomencl. Icon. Cannel.: 12. 1878.
TYPE: INDIA. Bengal, *Herbarium S. Vaillant s.n.* (Holotype: not found).

Cinnamomum lunatum Lukman., Nomencl. Icon. Cannel.: 11. 1878.
TYPE: CHINA. Cult. Bot. Gard. Brussels (Holotype: not found).

Cinnamomum maheanum Lukman., Nomencl. Icon. Cannel.: 8. 1878.
TYPE: SEYCHELLES. Mahe, *L. H. Boivin s.n.* (Lectotype, here designated: P [02006544], image seen; Isolectotypes: P [02006543], P [02006545], images seen).

The specimen chosen as the lectotype matches the species as named and described by Lukmanoff. It has been identified as *C. zeylanicum* Blume (= *C. verum* J. Presl).

var. ***karrouwa*** Lukman., Nomencl. Icon. Cannel.: 8. 1878.
TYPE: SRI LANKA. Cultivated from plants brought from the mountains of Cottalam [India, Andra Pradesh], *J. B. Leschenault 192* (Lectotype, here designated: P [01978447], image seen; Isolectotypes: L [1791311], P [01978458], images seen).
Homotypic synonym: *Cinnamomum karrouwa* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

Lukmanoff gave the type locality as "Seychelles, *Leschenault*." However, Leschenault did not collect in the Seychelles. In Paris, there are two sheets of *Cinnamomum* collected by Leschenault in Sri Lanka, both of which have the number 192, note the introduction of the plant from the mountains of Cottalam, and record the indigenous name as *karrouwa*. The lectotype matches Lukmanoff's protologue and also explains the epithet *karrouwa* (the Tamil name for *C. verum*). The isolectotype at L has a mistaken annotation ascribing the Cottalam Mountains to the Philippines, presumably due to the similar Philippine locality name of Cotabato. Variety *karrouwa* is also a synonym of *C. verum*.

Cinnamomum malabatrum (Burm.f.) J. Presl, Prir. Rostlin 2: 46. 1823–1825.

Treated by Lukmanoff under the variant spelling of "*malabtricum*." Two of the varieties proposed by Lukmanoff belong to *C. iners* Reinw. ex Blume, which has very similar leaves to *C. malabatrum*.

var. ***rheedei*** Lukman., Nomencl. Icon. Cannel.: 8. 1878.
TYPE: MALAYSIA. Penang [Island], *N. Wallich s.n.* (Lectotype, here designated: P [01752701], image seen).
Homotypic synonym: *Cinnamomum rheedei* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

Lukmanoff gave the type data as "Indes, *Wallich*," thus one would assume the type is from India. The sheet chosen as the lectotype was distributed as "*Laurus malabathricus*" and has an oblong leaf (15 × 5cm) with a damaged, notched apex as described and depicted by Lukmanoff. The specimen was identified as *C. iners* Reinw. ex Blume by Kostermans, who added the Wallich Catalogue number, 2583A, to it.

var. ***smithii*** Lukman., Nomencl. Icon. Cannel.: 8. 1878.
TYPE: INDIA. Malabar, *Herbarium J. B. Leschenault s.n.* (Holotype: not found).
Homotypic synonym: *Cinnamomum smithii* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

var. ***wrightii*** Lukman., Nomencl. Icon. Cannel.: 8. 1878.
TYPE: INDONESIA. Java, (cult. near Batavia [= Jakarta], October 1845), *H. Zollinger 2990* (Lectotype, here designated: P [01978068], image seen; Isolectotypes: BM [014605815], FI [086064], G [00693882], NY [355016], P [01978074], images seen).
Homotypic synonym: *Cinnamomum wrightii* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

The lectotype matches Lukmanoff's protologue in leaf shape and size (16 × 6 cm). The type citation is supplemented by label details on the Paris isolectotype, which originated from herbarium Drake (acquired by Paris in 1904). Both specimens were identified as *C. iners* Reinw. ex Blume by Kostermans.

Cinnamomum manillarum Lukman., Nomencl. Icon. Cannel.: 9. 1878.
TYPE: PHILIPPINES. Luzon, Manila, *J. Barthe s.n.* (Holotype: P [00732254], image seen).

Kostermans identified the above cited specimen as the type of this species. He refers it to the earlier *C. iners* Reinw. ex Blume.

Cinnamomum martiniquense Lukman., Nomencl. Icon. Cannel.: 13. 1878.
TYPE: MARTINIQUE. Cult. Bot. Gard. Paris, *A. de Lukmanoff s.n.* (Holotype: P [00729467], image seen).

The specimen has a Lukmanoff label and was later determined as *C. verum* J. Presl.

Cinnamomum maximoviczii Lukman., Nomencl. Icon. Cannel.: 19. 1878.
TYPE: CHINA. *J. M. M. Callery s.n.* (Holotype: not found).

So far, only one Chinese collection by *Callery* has been located, but it is properly the type of *C. calleryi*.

Cinnamomum morrenii Lukman., Nomencl. Icon. Cannel.: 17. 1878.
TYPE: WITHOUT ORIGIN. Cult. Bot. Gard. Paris (Holotype: not found).

Cinnamomum mutabile Blume ex Lukman., Nomencl. Icon. Cannel.: 12. 1878.
TYPE: INDONESIA. Java, *ex Herbario Lugduno-Batavo, C. L. Blume s.n.* (Holotype: P [01978026], image seen; Isotype: L [0035729], image seen).

The lectotype bears the name *C. mutabile* in Blume's handwriting and was determined by Kostermans on the sheet as the holotype. It is identified as *C. burmannii* (Nees & T. Nees) Blume.

Cinnamomum neesii Lukman., Nomencl. Icon. Cannel.: 13. 1878.
TYPE: INDIA. Sikkim, 1–4000 ft [1220 m], *J. D. Hooker s.n.* (Lectotype, here designated: P [01978809], image seen; Isolectotypes: BM [015153035], C [no barcode], FI [086047], CGE [00085158], CGE [00085192], CGE [00085201], CGE [00085202], G [00693674], G [00693688], K [00213361], K [002133362], K [002133364], K [00213365], K [002133366], K [00213367], K [002133368], L [1795328], L [1795329], NY [4723263], P [01978817], P [01978751], P [01988541], U [1400127], images seen).

A precise match to the specimen seen by Lukmanoff cannot be made, possibly because it is no longer extant in Paris. Therefore, another duplicate has been chosen as the lectotype. All three Paris sheets were identified as *C. bejolghota* (Buch.-Ham.) Sweet by Kostermans.

var. ***khasianum*** Lukman., Nomencl. Icon. Cannel.: 13. 1878.
TYPE: INDIA. Khasia, 1–2000 ft [305–610 m], *J. D. Hooker & T. Thomson s.n.* (Lectotype, here designated: P [01978805], image seen; Isolectotypes: G [00693878], L [1795325, right-hand leaf], images seen).
Homotypic synonym: *Cinnamomum khasianum* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

The specimen chosen as the lectotype matches Lukmanoff's description and illustration in the protologue quite well. It was identified as *C. bejolghota* (Buch.-Ham.) Sweet by Kostermans.

Cinnamomum neumannii Lukman., Nomencl. Icon. Cannel.: 14. 1878.
TYPE: INDIA? *W. Griffith s.n.* (Holotype: not found).

A specimen collected by Griffith matching Lukmanoff's protologue in leaf shape (oblong-lanceolate) and size (9 × 3 cm) has not been located.

Cinnamomum nitidum W.J. Hook., Exot. Fl. 3, 26: t.176. 1827.

This name is regarded as a synonym of *C. burmannii* (Nees & T. Nees) Blume; however, it was misapplied to several taxa, including *C. iners* Reinw. ex Blume, *C. sulphuratum* Nees, and *C. verum* J. Presl.

var. ***curtisii*** Lukman., Nomencl. Icon. Cannel.: 19. 1878.
TYPE: INDIA. Malabar, *J. D. Hooker s.n.* (Holotype: not found).
Homotypic synonym: *Cinnamomum curtisii* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

Lukmanoff cited the type details as "Indes, Malabar, *Hooker*." The only Paris collection with similar details is a specimen assigned to *C. sulphuratum* Nees. It is from Malabar and is a J. E. Stocks and J. S. Law specimen distributed under a J. D. Hooker and T. Thomson label. However, parameters of the leaves described by Lukmanoff do not match this collection.

Cinnamomum obtusifolium Nees, in Wallich, Pl. Asiat. Rar. 2: 73. 1831 *nom. illeg.* (cites the available name *Laurus bejolghota* Buch.-Ham. in synonymy).

This name is a synonym of *C. bejolghota* (Buch.-Ham.) Sweet.

var. ***sikkimense*** Lukman., Nomencl. Icon. Cannel.: 12. 1878.
TYPE: INDIA. Sikkim, *J. D. Hooker s.n.* (Holotype: not found). Neotype, here designated: India, Sikkim, *J. D. Hooker & T. Thomson s.n.* (Holoneotype: P [01978810], image seen; possible Isoneotype: S [S14-55991], not seen).
Homotypic synonym: *Cinnamomum sikkimense* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

Lukmanoff cited a collection by Hooker from Sikkim as the type. He described it as having leaves 19 × 5 cm and depicted such a leaf showing the underside of it. A matching collection has not been found. The specimen chosen as the neotype is a similar specimen, but the most similar leaf is larger (to ca. 21.5 × 6.0 cm) with a slightly different shape and damaged apex. It is identified as *C. bejolghota* (Buch.-Ham.) Sweet.

var. ***vanhouttei*** Lukman., Nomencl. Icon. Cannel.: 12. 1878.
TYPE: INDES. *N. Wallich s.n.* (Holotype: not found).
Homotypic synonym: *Cinnamomum vanhouttei* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

Cinnamomum odoratum Lukman., Nomencl. Icon. Cannel.: 10. 1878.
TYPE: INDIA. East Himalaya, [BHUTAN. Above Panukha], *W. Griffith (Kew Distr.) 4243* (Lectotype, here designated: P [01748400], image seen; Isolectotypes: K [02133672], M [0147247], U [1400131], images seen).

Lukmanoff cited only "Himalaya, *Griffith*" in the protologue. The specimen chosen as the lectotype matches the foliar dimensions (11.0 × 4.5 cm) and shape as detailed by Lukmanoff. The specimen was originally identified as *C. albiflorum* Nees, then it was identified as *C. soncaurium* (Buch.-Ham.) T. Nees & C.H. Eberm. by Kostermans. It is probably best referred to *C. tamala*. The isolectotype in Kew has an original label recording the locality as above Panukka [= Panukha, the former capitol of Bhutan]; the Griffith number is 873. The former details are added to the type citation above.

Cinnamomum orbiculatum Lukman., Nomencl. Icon. Cannel.: 6. 1878 *nom. illeg.* (*non* Saporta 1861).
TYPE: BRAZIL. Minas Gerais, 1844, *H. A. Weddell 1363* (Lectotype, here designated: P [01978692], image seen).
Homotypic synonym: *Cinnamomum weddellii* Doweld, Phytotaxa 326, 3: 193. 2017.

The specimen chosen as the lectotype matches Lukmanoff's description and illustration in the protologue. It is annotated as *C. zeylanicum* Blume by Lukmanoff, but he obviously changed his mind and described it as *C. orbiculatum*. It is filed under the name *C. verum* J. Presl in Paris.

Cinnamomum pauciflorum Nees, in Wallich, Pl. Asiat. Rar. 2: 75. 1831.

This name is regarded as a synonym of *C. tazia* (Buch.-Ham.) Kosterm. ex M. Gangop. All four varieties proposed by Lukmanoff are also regarded as synonyms of the latter.

var. ***fischeri*** Lukman., Nomencl. Icon. Cannel.: 16. 1878.
TYPE: INDIA. Khasia, 4000 ft [1220 m], *J. D. Hooker & T. Thomson s.n.* (Lectotype, here designated: P [01978513, right-hand plant], image seen; Isolectotypes: CGE [00085193, left hand plant], K [000778622], L [1791500], NY [354988, upper plant], images seen).
Homotypic synonym: *Cinnamomum fischeri* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

The specimen chosen as the lectotype matches Lukmanoff's description (leaves 6 × 4 cm) and figure; it is on the right-hand side of the cited sheet.

var. ***jacquii*** Lukman., Nomencl. Icon. Cannel.: 16. 1878.
TYPE: BANGLADESH. Sylhet, *N. Wallich Catal. No. 2579* (Lectotype, here designated: P [01978515], image seen; Isolectotypes: G [00693696], L [1791503, upper plant], images seen).
Heterotypic synonym: *Cinnamomum jacquii* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

The specimen chosen as the lectotype matches Lukmanoff's description (leaves 6.5 × 2.5 cm) and figure. This specimen is treated in Paris as an isotype of *Laurus pauciflora* Wall. (*nom. nud.*), but it is actually an isotype of *Cinnamomum pauciflorum* Nees, a synonym of *C. tazia* (Buch.-Ham.) Kosterm. ex M. Gangop.

var. ***paxtonii*** Lukman., Nomencl. Icon. Cannel.: 16. 1878.
TYPE: INDIA. Khasia, 4000 ft [1220 m], *J. D. Hooker & T. Thomson s.n.* (Lectotype, here designated: P [01978513, left-hand plant], image seen; Isolectotypes: CGE [00085193, right hand plant], G [00693826], NY [354988, lower plants], images seen).
Homotypic synonym: *Cinnamomum paxtonii* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

The specimen on the left-hand side of the sheet, chosen as the lectotype, matches Lukmanoff's description and illustration. On the right-hand side is a form with suborbicular leaves that is the lectotype of var. *fischeri*.

var. ***verschaffeltii*** Lukman., Nomencl. Icon. Cannel.: 16. 1878.
TYPE: INDIA. East Bengal, *W. Griffith (Kew Distr.) 4239* (Lectotype, here designated: P [01978508], image seen; Isolectotypes: FI [086049], K [002133707], K [002133708], P [01978507], U [1400130], images seen).
Homotypic synonym: *Cinnamomum verschaffeltii* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1889.

The lectotype designated above matches Lukmanoff's description (leaves 7 × 3 cm) and figure.

Cinnamomum poissonii Lukman., Nomencl. Icon. Cannel.: 13. 1878.
TYPE: INDIA. *V. Jacquemont s.n.* (Holotype: not found); Neotype, here designated: India, without locality, *V. Jacquemont 647* (Holoneotype: L [1791577], image seen).

As noted above under *C. jacquemontii,* no Jacquemont *Cinnamomum* specimens remain in Paris. The neotype has leaves about the same size as described by Lukmanoff (14 × 5 cm), but these are more subacuminate. The specimen has been identified as *C. tamala,* an identification here agreed with and thus making *C. poissonii* a synonym of the latter.

Cinnamomum reichenbachii Lukman., Nomencl. Icon. Cannel.: 19. 1878.
TYPE: SRI LANKA [as Ceylon]. 1854, *G. H. K. Thwaites CP 263* (Lectotype, here designated: P [01752097 left-hand plant], image seen; Isolectotypes: BM [000950929], BM [014605823], BR [000005115532], CGE [00085225], FI [086051], G [00693887], G [00693888], K [000778610], K [000778612], MPU [1294082], P [01752098], P [01752101], P [10752103], images seen).

The specimen on the left-hand side of the lectotype sheet is the one that best matches Lukmanoff's description and illustration. All of the above material is filed as *C. ovalifolium* Wight.

Cinnamomum reinwardtii Lukman., Nomencl. Icon. Cannel.: 19. 1878 *nom. illeg.* (*non* Reinw. ex Nees 1836).
TYPE: CHINA. Cult. Bot. Gard. St. Petersburg, 1861, *sine coll. s.n.* (Lectotype, here designated: P [01978003], image seen; Isolectotype: FI [086048], image seen; possible Isolectotypes: L [1795720], P [01978001], P [01978002], images seen).

The above collection was donated to Paris by St. Petersburg in 1861. It was annotated with the name *C. reinwardtii* Nees by Meissner. It fits quite well with Lukmanoff's protologue, although there is no indication on the sheet that the plant came from China. Kostermans determined it as *C. burmannii*. The three sheets that are possible isolectotypes lack dates.

Cinnamomum riedelii Lukman., Nomencl. Icon. Cannel.: 6. 1878.
TYPE: BRAZIL. Without locality. *L. Riedel 489* (Lectotype, here designated: P [01978197], image seen; Isolectotype: MEL [0080263], image seen).

The sheet chosen as the lectotype matches Lukmanoff's protologue. It was donated by the Botanical Garden in St. Petersburg. No duplicate was found in LE (L. Averyanov, *pers. comm*.). Moraes (2012) reduced *C. riedelii* to *C. verum* J. Presl and listed a Riedel collection in NY ([459832], image seen) as an isotype of *C. riedelii*. Since the specimen lacks the number 489, it is not likely an isotype. Moraes (2012) said Riedel collected the number 489 in Rio de Janeiro. No locality was found on the specimens seen.

Cinnamomum rougieri Lukman., Nomencl. Icon. Cannel.: 7. 1878.
TYPE: CHINA ["Birman?"]. Cult. in the garden of *M. Rougier, A. de Lukmanoff s.n*. (Holotype: P [00729468], image seen).

The holotype is in Paris and was identified by Kostermans as *C. verum* J. Presl.

Cinnamomum rumphii Lukman., Nomencl. Icon. Cannel.: 12. 1878.
TYPE: INDONESIA. Java, *C. L. Blume s.n*. (Holotype: not found).

Lukmanoff quotes in brackets "*C. sintok* var. Blume" for an entity found in Java. A matching collection cannot be found in Paris or Leiden. While there is some similarity to *C. sintoc* Blume, there is also the possibility that an introduced plant cultivated on Java may also match with *C. rumphii*. For example, there exists in L [1795277] a Reinwardt collection of *C. burmannii* (Nees & T. Nees) Blume with the unpublished name, *C. sintok* var. *angustifolium*, on the label. This is not the same as *C. burmannii* var. *angustifolium* Meissn., a taxon with a different type.

Cinnamomum scabridum Blume ex Lukman., Nomencl. Icon. Cannel.: 14. 1878.
TYPE: SRI LANKA [as Ceylan]. Without locality, *J. B. Leschenault s.n*. (Lectotype, here designated: P [01748597], image seen; Isolectotype: L [0308880], image seen).

Lukmanoff cited "Ceylan, *Blume*" as the type. Blume did not collect on Sri Lanka but did have in his possession a number of Leschenault collections, some of which he sent to Paris. The lectotype in Paris was annotated by Blume as "*Cinnamomum nitidum* var. *scabridum*," and is a collection made by Leschenault. Kostermans determined it as *C. dubium* Nees.

Cinnamomum sericeum Lukman., Nomencl. Icon. Cannel.: 19. 1878 *nom. illeg*. (*non* [Blume] Siebold 1830).
TYPE: JAPAN. Cultivated at the Botanical Gardens, Paris, *A. de Lukmanoff s.n*. (Lectotype, here designated: P [01748603], image seen).

This taxon is regarded as a synonym of *C. daphnoides* Siebold & Zuccarini. The specimen chosen as the lectotype has a label by Lukmanoff identifying it as *C. sericeum* with reference to the species and figure number in his monograph (No. 91, f. 143). Although Lukmanoff said it was cultivated in several gardens in Europe, the lectotype merely says "Cult. au Muse." The earlier *C. sericeum* (Blume) Siebold (based on *Laurus sericea* Blume) is now known as *Neolitsea sericea* (Blume) Koidz.

Cinnamomum spurium Blume ex Lukman., Nomencl. Icon. Cannel.: 14. 1878.
TYPE: INDONESIA. Java, *C. L. Blume s.n*. (Lectotype, here designated: P [01752079, left-hand plant], image seen).

Lukmanoff attributed this name to Blume. Blume did have this epithet in brackets with the name *C. sintoc* Blume (described in 1826) in Rumphia (1: 30. 1836). It is difficult to ascertain Blume's intention, whether this is a *nom. alt*. or meant to indicate a synonym. The lectotype (left-hand plant) in Paris is on a sheet filed under the Indian taxon *C. perrottetii* Meissn. (right-hand plant), and it bears the name *C. spurium* in Blume's hand. Kostermans identified the lectotype as an isotype of *C. sintoc*. To add to the confusion, it should be noted that *C. nitidum* W.J. Hook. var. *spurium* Blume (Tijdschr. Natuurl. Gesch. Physiol. 1: 64. 1834) is a different taxon (*C. iners* Reinw. ex Blume).

Cinnamomum stracheyi Lukman., Nomencl. Icon. Cannel.: 8. 1878.
TYPE: INDIA. Kumaon, 3000–4500 ft [915–1370 m], *R. Strachey & J. E. Winterbottom 1* (Lectotype, here designated: BR [0000029323487], image seen; Isolectotypes: BR [0000029324071], L [1792709], images seen).

Additional specimen examined: INDIA. Kumaon, *R. Strachey & J. E. Winterbottom s.n*. (BR [0000029324088], image seen).

The Strachey and Winterbottom collection studied by Lukmanoff is not present in Paris, so a lectotype is chosen from one of their specimens in BR. The lectotype is an excellent specimen in good condition with numerous flowers; it is misidentified as *C. impressinervium* Meissn. in BR. The BR isolectotype is correctly identified as *C. tamala*, but it only has undeveloped inflorescences. Another Strachey and Winterbottom collection citing the specific locality, Kupkot, is the type of *C. albiflorum* Nees var. *veitchii* Lukman.

Cinnamomum suaveolens Lukman., Nomencl. Icon. Cannel.: 9. 1878.
TYPE: CHINA. Cult. in Bot. Gard. Paris, *A. de Lukmanoff s.n*. (Holotype: P [00757075], image seen).

The type was identified by Kostermans as representing *C. burmannii*.

Cinnamomum sulphuratum Nees, in Wallich, Pl. Asiat. Rar. 2: 74. 1831.

This is an accepted species, endemic to India. The collection Lukmanoff saw (P [01978596], image seen) is extant in Paris; it was collected from the Nilgiri Hills.

var. ***wagneri*** Lukman., Nomencl. Icon. Cannel.: 17. 1878.
TYPE: INDIA. *J. D. Hooker s.n.* (Holotype: not found). Neotype, here designated: India, Malabar, Concan and area, *J. E. Stocks & J. S. Law et al. s.n.* (Holoneotype: P [01978597], image seen).
Homotypic synonym: *Cinnamomum wagneri* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

This variety is distinguished from the typical species by its narrowly oblong (vs. elliptic to ovate-elliptic) leaves, 8.5 × 2.0 cm. However, such variation is typical for this species (Kostermans, 1983). A sheet matching the details supplied by Lukmanoff (1878) in the protologue cannot be found in Paris, so a specimen with slightly broader leaves is chosen as the neotype. This collection was distributed as "*Cinnamomum zeylanicum*?."

Cinnamomum thomsonii Lukman., Nomencl. Icon. Cannel.: 9. 1878.
TYPE: NEPAL or INDIA. Sikkim, *J. D. Hooker & T. Thomson s.n.* (Lectotype, here designated: P [01752466], image seen).

Lukmanoff gave "Himalaya, *Hooker & Thomson*" as the type details. His figure shows the leaves to be narrowly oblong, and the measurements are 7 × 3 cm. The collection chosen as the lectotype has similar leaves (but slightly narrower, ca. 2.5 cm wide). One leaf has the broken off, bilobed tip like that depicted by Lukmanoff. On the label, conflicting localities are recorded, Nepal and Sikkim (in brackets below the former). I suspect Lukmanoff gave "Himalaya" as a way of resolving the two different localities recorded. The lectotype has been identified as *C. impressinervium* Meissn.

Cinnamomum thwaitesii Lukman., Nomencl. Icon. Cannel.: 14. 1878.
TYPE: SRI LANKA [as Ceylon]. Without locality, *G. H. K. Thwaites CP 2282* (Lectotype, here designated: P [01748592, left-hand plant], image seen; Isolectotypes: BM [014605825], BM [014605826], FI [086054], G [00693884], G [00693896], K [002133443], MEL [0080257], MPU [1294107], PDA [00000274], images seen; LE, not seen).

The lectotype agrees with Lukmanoff's description and figure in the protologue. Kostermans questionably identified it as *C. dubium* Nees. The type number of *C. thwaitesii* is still frequently found under the name *C. zeylanicum,* and was distributed as that. Kostermans (1995) identified *Thwaites s.n.* (PDA) as the type of *C. thwaitesii,* but this cannot be accepted as an inadvertent typification, because Lukmanoff had stated that the type was in Paris, and a matching specimen is extant there, as noted above. *Thwaites s.n.* has not been found in PDA, but it could be the sheet from PDA listed here, which had the number CP 2282 added to it later. However, a packet covers the top right corner of this specimen, and this is usually where the original CP numbers were written on the sheet.

Cinnamomum tournefortii Lukman., Nomencl. Icon. Cannel.: 6. 1878.
TYPE: SRI LANKA [as Ceylan]: cultivated, *sine coll. s.n.* (Lectotype, here designated: L [1791337, lower plant], image seen; Isolectotype: G [00693699], image seen).

Lukmanoff cited the type as "Ceylan, *Hooker*." Joseph Hooker did not collect plants in Sri Lanka. The lectotype has an "Herb. Ind. Or." label, and is a collection cultivated in Sri Lanka. There is no collector indicated. It was distributed from Kew by J. D. Hooker and T. Thomson. The specimen is referrable to *C. verum* J. Presl. The upper half of the lectotype sheet in L bears an isotype of *C. zeylanicum* Blume var. *madrassicum* Lukman.

Cinnamomum verlotii Lukman., Nomencl. Icon. Cannel.: 19. 1878.
TYPE: JAPAN. Cult. Bot. Gard. Paris, *A. de Lukmanoff s.n.* (Holotype: P [00745542], image seen).

The holotype was annotated by Lukmanoff. This taxon was identified as a synonym of *Lindera aggregata* (Sims) Kosterm. by Kostermans on the type sheet.

Cinnamomum villosum Thwaites ex Lukman., Nomencl. Icon. Cannel.: 9. 1878 *nom. illeg.* (*non* Wight 1839).
TYPE: SRI LANKA [as Ceylon]. Without locality, *G. H. K. Thwaites CP 37* (Lectotype, here designated: P [01748594], image seen; Isolectotypes: BM [014605824], BR [0000029323425], CGE [00085221], FI [086052], G [00693894], G [00693885], K [002133441, left-hand plant], PDA [00000275], images seen).

The specimen chosen as the lectotype is annotated *C. villosum* in Thwaites's hand and is filed under the name *C. dubium* Nees. It matches Lukmanoff's description and figure in the protologue.

Cinnamomum wallichii Lukman., Nomencl. Icon. Cannel.: 11. 1878.
TYPE: INDIA. *V. Jacquemont s.n.* (Holotype: not found).

Cinnamomum walteri Lukman., Nomencl. Icon. Cannel.: 18. 1878.
TYPE: CHINA. Cult. Bot. Gard. Brussels (Holotype: not found).

Cinnamomum williamsii Lukman., Nomencl. Icon. Cannel.: 18. 1878.
TYPE: INDIA. *J. D. Hooker s.n.* (Holotype: not found).

Cinnamomum zeylanicum Garcin. ex Blume, Bijdr. Fl. Ned. Ind. 11: 568. 1826.

This taxon is a synonym of *C. verum* J. Presl. Sometimes Breyne is cited as the author of *C. zeylanicum,* but all of the pertinent references are pre-Linnaean and, therefore, do not affect the ascription of the authorship to Blume.

Lukmanoff (1878) ascribed three categories (probably the equivalent of subspecies) to this species, to which he gave Latin names: *C. zeylanicum commune* Nees (with 13 varieties), *C. zeylanicum asperifolium* (8 varieties), and *C. zeylanicum chartaceum* (10 varieties). In total, this makes 31 varieties. These infrataxa are arranged alphabetically here and not placed in their original groups.

var. ***antillarum*** Lukman., Nomencl. Icon. Cannel.: 5. 1878. TYPE: MARTINIQUE. *F. Sieber 107* (Lectotype, here designated: P [01978675], image seen).
Homotypic synonym: *Cinnamomum antillarum* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 45. 1926.

This and var. *decandollei* are based on Sieber collections from Martinique. Neither of the Sieber collections in Paris from Martinique match Lukmanoff's concepts of these taxa, so it is assumed that the specimens he saw are no longer extant. The lectotype of var. *antillarum* is a later acquired duplicate from Herbarium Drake that agrees reasonably well with Lukmanoff's protologue, except the leaves have a slightly different shape and are a little smaller (ca. 12.5 × 7.0 cm vs. 14 × 8 cm).

var. ***barthei*** Lukman., Nomencl. Icon. Cannel.: 5. 1878. TYPE: RÉUNION. *J. Barthe s.n.* (Lectotype, here designated: P [02006724], image seen).
Homotypic synonym: *Cinnamomum barthei* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 45. 1926.

Lukmanoff cited the type as "Mauritius, *Barthe*," but in Paris the matching collection by Barthe comes from Réunion. This collection agrees in having an apically bilobed (damaged?) leaf that is 13.0 × 7.5 cm. There are no known Barthe collections from Mauritius, even though some appear to be labelled "Ile M.." The "M" is actually an "R," as can be seen when the abbreviation is fully spelled out to Réunion, as is the case on a specimen of the fern *Elaphoglossum heterolepis* (Fee) T. Moore [P 00605374], image seen.

var. ***bengalense*** Lukman., Nomencl. Icon. Cannel.: 5. 1878. TYPE: INDIA. East Bengal, *W. Griffith (Kew Distr.) 4246/1* (Lectotype, here designated: P [01752730], image seen).
Homotypic synonym: *Cinnamomum bengalense* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 45. 1926.

The specimen seen matches with Lukmanoff's protologue. It was distributed as *C. zeylanicum*, but was identified as *C. iners* Blume by Kostermans. Kostermans (1998) later published *C. pachyphyllum* based on a Thai specimen, and recorded specimens from India, Myanmar, and Thailand. The possibility is strong that *C. bengalense* is an earlier name for *C. pachyphyllum* (if the latter is really different from *C. iners*). On POWO, *Camphora griffithii* Lukman. and its variety *lanceolata* Lukman. are listed among the synonyms of *Cinnamomum pachyphyllum*, but this is due to confusion with the similar type number of *Camphora griffithii* (*W. Griffith [Kew Distr.] 4246/2*). The latter is a synonym of the quite different *Camphora officinarum* Boerh. ex Fabr.

var. ***biafranum*** Lukman., Nomencl. Icon. Cannel.: 5. 1878. TYPE: EQUATORIAL GUINEA. Bioko [as Fernando-Po], cultivated, *C. Barter s.n.* (Lectotype, here designated: P [01752532], image seen; Isolectotype: K [002235072], image seen).
Homotypic synonym: *Cinnamomum biafranum* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

Lukmanoff gave the type data as "Ile Fernando-Po, Guinee. Herb. Kew."

var. ***bonplandii*** Lukman., Nomencl. Icon. Cannel.: 5. 1878. TYPE: INDONESIA. Java, *Herbarium A. T. Brogniart s.n.* (Holotype: not found).
Homotypic synonym: *Cinnamomum brogniartii* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

var. ***boutonii*** Lukman., Nomencl. Icon. Cannel.: 4. 1878. TYPE: MAURITIUS. 1830, *L. Bouton s.n.* (Lectotype, here designated: P [02006674], image seen).
Homotypic synonym: *Cinnamomum boutonii* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

The lectotype matches the details provided in Lukmanoff's protologue.

var. ***capense*** Lukman., Nomencl. Icon. Cannel.: 5. 1878. TYPE: SOUTH AFRICA. Cape of Good Hope, *P. Sonnerat s.n.* (Lectotype, here designated: P [01752515], image seen).
Homotypic synonym: *Cinnamomum capense* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

var. ***cayennense*** Lukman., Nomencl. Icon. Cannel.: 5. 1878. TYPE: FRENCH GUIANA. Cayenne, *J. Martin 40* (Lectotype, here designated: P [01978685], image seen).
Homotypic synonym: *Cinnamomum cayennense* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

The lectotype matches the protologue of Lukmanoff.

var. ***commersonii*** Lukman., Nomencl. Icon. Cannel.: 5. 1878.
TYPE: MAURITIUS. *P. Commerson s.n.* (Holotype: not found).
Homotypic synonym: *Cinnamomum commersonii* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

var. ***cordifolium*** Lukman., Nomencl. Icon. Cannel.: 4. 1878 *nom. illeg.* (*non* Hayne 1833).
TYPE: INDONESIA. Java, *P. Commerson s.n.* (Lectotype, here designated: P [01978123], image seen; Isolectotype: P [01978122], image seen).
Homotypic synonym: *Cinnamomum cordifolium* A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

Kostermans identified the specimen chosen as the lectotype as the type. This has a leaf (lower left, 9.0 × 6.5 cm) matching the one described and illustrated by Lukmanoff. The second sheet (isolectotype) has the name *C. zeylanicum* var. *cordifolium* written on it by Blume, but it has much broader (to ca. 10 cm) leaves.

var. ***decandollei*** Lukman., Nomencl. Icon. Cannel.: 5. 1878. TYPE: MARTINIQUE. *F. Sieber 107* (Lectotype, here designated: P [01978676], image seen; Isolectotypes: BM [014605813], L [1791382], L [1791383], M [0293169], MPU [1294102], images seen).

Homotypic synonym: *Cinnamomum decandollei* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

As above, under var. *antillarum*, the Sieber collections from Martinique that Lukmanoff saw seem to be no longer extant in Paris. The specimen chosen as the lectotype has smaller leaves (to 10 cm long vs. 13 cm), but some of the leaves are oblong like the one depicted by Lukmanoff.

var. ***delessertii*** Lukman., Nomencl. Icon. Cannel.: 5. 1878.
TYPE: TRINIDAD AND TOBAGO. Trinidad, [*leg. F. Wrbna*], *F. Sieber 122* (Lectotype, here designated: P [01978289], image seen; Isolectotypes: CGE [00085169], G [00693816], L [1791379], L [1791380], L [1791381, lower plant], MEL [0080108], MEL [0080243], P [01978201], P [01978657], images seen).
Homotypic synonym: *Cinnamomum delessertii* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

The lectotype comes from Herbarium Delessert and matches Lukmanoff's protologue.

var. ***ellipticum*** Lukman., Nomencl. Icon. Cannel.: 5. 1878.
TYPE: SRI LANKA [as Ceylan]. *G. H. K. Thwaites CP 2284* (Neotype, here designated: P [01978436], image seen; Isoneotypes: BM [014605827], FI [086063], G [00693810], PDA [00000271], images seen).
Homotypic synonym: *Cinnamomum ellipticum* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926 *nom. illeg.* (*non* Knowlt. 1894, fossil).

The specimen Lukmanoff saw seems to be no longer extant, so the above collection, which also has elliptic leaves, is chosen as the neotype. Kostermans (1995) credited Alexander Moon as the collector of CP 2284 in PDA, but there is no collector's name on that sheet. Nor were any collectors' names given on the other duplicates seen.

var. ***erectum*** Lukman., Nomencl. Icon. Cannel.: 5. 1878.
TYPE: SRI LANKA [as Ceylan]. Without locality, *C. P. Thunberg 54* (Holotype: P [01978434], image seen).
Homotypic synonym: *Cinnamomum erectum* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

The type was identified by Kostermans. The number 54 was added later and is not one used by Thunberg.

var. ***humboldtii*** Lukman., Nomencl. Icon. Cannel.: 6. 1878.
TYPE: SRI LANKA [as Ceylan]. Without locality, *A. Moon s.n.* (Holotype: P [01978449], image seen; Isotype: G [00693820], image seen).
Homotypic synonym: *Cinnamomum humboldtii* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

Lukmanoff gave the type details as "Ceylan, Mt. Trito, *Hooker*." The mysterious Mt. Trito is from the label which reads "Regio trop.;" the "trop." does, indeed, look like Trito. The sheet is one of those distributed from Kew by J. D. Hooker and T. Thomson. Kostermans identified it as the holotype.

var. ***leschenaultii*** Lukman., Nomencl. Icon. Cannel.: 6. 1878.
TYPE: SRI LANKA. *J. B. Leschenault s.n.* (Lectotype, here designated: P [01978456], image seen); Isolectotype: FI [086055], image seen).
Homotypic synonym: *Cinnamomum leschenaultii* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

Lukmanoff gave the type as "Java, *Blume*." The collection chosen as the lectotype has a leaf matching the dimensions (13 × 7 cm) given in the protologue. The specimen is annotated by Blume with the name *C. zeylanicum,* but it comes from Sri Lanka and was collected by Leschenault (perhaps the reason this variety was named after him). I have accepted that the collection in FI is an isolectotype, since its leaves appear to have the same facies as the lectotype and also have the remnants of soft brown scale insects (*Coccus hesperidum* L.) on them.

var. ***madrassicum*** Lukman., Nomencl. Icon. Cannel.: 5. 1878.
TYPE: INDIA. Madras, *sine coll. s.n.* (Holotype: P [01978443], image seen; Isotypes: G [00693639], L [1791337, upper plant], images seen).
Homotypic synonym: *Cinnamomum madrassicum* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

The holotype was identified by Kostermans. Lukmanoff cited Hooker as the collector, but there is no collector on the label. The specimen was distributed by J. D. Hooker and T. Thomson.

var. ***mauritianum*** Lukman., Nomencl. Icon. Cannel.: 4. 1878.
TYPE: MAURITIUS. *Flora Mauritiana exsicc. II, F. Sieber 343* (Lectotype, here designated: P [02006725], image seen; Isolectotypes: E [00653432], G [00693699], GZU [000253980], L [1791436], MEL [0080271], images seen).
Homotypic synonym: *Cinnamomum mauritianum* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

The specimen chosen as the lectotype seems to fit best with Lukmanoff's protologue in leaf shape and size (8 × 4 cm). Another very similar collection (*Sieber 127*) was chosen as the lectotype of var. *sieberi*.

var. ***meissneri*** Lukman., Nomencl. Icon. Cannel.: 5. 1878.
TYPE: INDONESIA. Java, *ex Herbario Lugduno-Batavo s.n.* (Holotype: not found). Neotype, here designated: Indonesia, Java, *ex Herbario Lugduno-Batavo, C. L. Blume s.n.* (Holoneotype: A [02537096], image seen).
Homotypic synonym: *Cinnamomum meissneri* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

A matching collection has not been located in Paris, so a similar collection, described and depicted by Lukmanoff (leaves 11 × 6 cm) found at Harvard, has been chosen as the neotype.

var. ***ovatum*** Lukman., Nomencl. Icon. Cannel.: 4. 1878.
TYPE: INDIA [as Indes Orientalis]. *R. Wight s.n.* (Holotype: not found).
Homotypic synonym: *Cinnamomum ovatum* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

The specimen identified by Kostermans as the holotype (*R. Wight 2240* [P 01978450]) doesn't agree with Lukmanoff's protologue, in that the leaves are badly damaged, and, thus, none match the one depicted by him. A duplicate [P 01978466] has more oblong-elliptic leaves but does not match either. Another Wight collection (no. 2511 [P 00732270]) is also not a match. Thus, it seems the type is no longer extant in Paris, and a neotype may need to be chosen.

var. ***pallasii*** Lukman., Nomencl. Icon. Cannel.: 6. 1878.
TYPE: SRI LANKA [as Ceylan]. *G. H. K. Thwaites CP 2285* (Lectotype, here designated: P [01749472], image seen; Isolectotypes: BM [014605828], CGE [00085212], FI [086056], G [00693636], MEL [0080262], P [01978495], PDA [00000270], images seen).
Homotypic synonym: *Cinnamomum pallasii* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

The original specimen seen by Lukmanoff seems not to be extant in Paris; therefore, an almost matching, later acquired duplicate is chosen as the lectotype.

var. ***pleei*** Lukman., Nomencl. Icon. Cannel.: 5. 1878.
TYPE: MARTINIQUE. *A. Plee s.n.* (Lectotype, here designated: P [01978671], image seen); possible Isolectotypes: L [1791375], L [1791384], P [01978670], images seen).
Homotypic synonym: *Cinnamomum pleei* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

The sheet chosen as the lectotype has a leaf matching the dimensions (11 × 5 cm) noted by Lukmanoff, but it perhaps differs slightly in shape. It is possible the duplicate Lukmanoff saw is no longer extant in Paris.

var. ***pourretii*** Lukman., Nomencl. Icon. Cannel.: 5. 1878.
TYPE: MARTINIQUE. *P. A. Pourret s.n.* (Holotype: not found).
Homotypic synonym: *Cinnamomum pourretii* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

var. ***regelii*** Lukman., Nomencl. Icon. Cannel.: 5. 1878.
TYPE: SRI LANKA [as Ceylan]. *Herbarium A. T. Brogniart s.n.* (Holotype: not found).
Homotypic synonym: *Cinnamomum regelii* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

var. ***roxburghii*** Lukman., Nomencl. Icon. Cannel.: 6. 1878.
TYPE: SRI LANKA [as Ceylan]. *Herbarium A. T. Brogniart s.n.* (Holotype: not found).
Homotypic synonym: *Cinnamomum roxburghii* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

var. ***sieberi*** Lukman., Nomencl. Icon. Cannel.: 4. 1878.
TYPE: MAURITIUS. *Flora Mauritiana exsicc. II, F. Sieber 127* (Lectotype, here designated: P [02006723], image seen; Isolectotypes: B [10 0159025], BM [014605817], G [00693656], G [00693697], G [00693815], GZU [000253981], K [002235152], L [1791433], L [1791434], L [1791435], MEL [0080245], MEL [0080273], P [02006671], images seen).
Homotypic synonym: *Cinnamomum sieberi* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

var. ***vaillantii*** Lukman., Nomencl. Icon. Cannel.: 4. 1878.
TYPE: WITHOUT LOCALITY. *Herbarium S. Vaillant s.n.* (Lectotype, here designated: P [00659170], image seen).
Homotypic synonym: *Cinnamomum vaillantii* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

The specimen chosen as the lectotype matches the description and illustration provided in the protologue. On one of the labels, an unknown hand (possibly Lukmanoff) has written "*vaillantii*." The collection is of unknown origin (Java was assumed by Lukmanoff), but either Sri Lanka or Java are possibilities. It was not collected by Sebastien Vaillant (1669–1722), a notable French botanist who did not leave Europe.

var. ***variabile*** Lukman., Nomencl. Icon. Cannel.: 4. 1878.
TYPE: INDONESIA. Java, *C. L. Blume s.n.* (Lectotype, here designated: P [01978268], image seen).
Homotypic synonym: *Cinnamomum variabile* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

The specimen chosen as the lectotype is from Java, was apparently collected by Blume, and has a pair of overlapping leaves of different sizes which gave rise to Lukmanoff's varietal epithet *variabile*. However, in Paris, a sheet has Lukmanoff's original label seemingly mistakenly attached to it. This sheet [P 00732270], image seen is a Robert Wight collection (no. 2511) from Peninsular India. It does not have the features described and depicted for var. *variabile* by Lukmanoff.

var. ***wolkensteinii*** Lukman., Nomencl. Icon. Cannel.: 6. 1878.
TYPE: INDONESIA. Java, [in the garden of Tjiringin, 19 May 1843], *H. Zollinger 1316* (Lectotype, here designated: P [01978269], image seen; Isolectotypes: FI [086058], G [00693698], P [01978124], U [1359921], images seen).
Homotypic synonym: *Cinnamomum wolkensteinii* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

The lectotype matches details supplied in the protologue. The duplicate Lukmanoff saw only had Zollinger's number on it; further details, such as locality and date, are taken from the Herbarium Drake specimen in Paris.

var. ***zollingeri*** Lukman., Nomencl. Icon. Cannel.: 4. 1878.
TYPE: INDONESIA. Java, cultivated, *H. Zollinger 580* (Lectotype, here designated: P [01978266], image seen; Isolectotypes: BR [0000029324552], FI [086057], G [00693638], G [00693640], K [000350931], L [1791414], MEL [0080248], P [01978126], P [01978274], images seen).
Homotypic synonym: *Cinnamomum zollingeri* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 46. 1926.

The lectotype matches Lukmanoff's protologue. On one duplicate [P 01978126], Zollinger noted that it flowers from June to July, and fruits from July to September. He recorded the indigenous name as Kaju manis.

Camphora Fabr., Enum.: 218. 1759.
Type species: *Laurus camphorifera* Kaempf. ex Fabr.

Lukmanoff (1878) accepted 27 species in this genus, of which 23 (plus 8 varieties) were newly proposed by him. The taxa are arranged here alphabetically, as above. Molecular studies [Yang et al., 2022, and references therein] show *Camphora* can now again be recognised as distinct from *Cinnamomum*. Currently, *Camphora* has about 16 species, most of which are in China.

Camphora baillonii Lukman., Nomencl. Icon. Cannel.: 24. 1878.
TYPE: JAPAN. *Cult. in the gardens of the Faculty of Medicine, Paris, A. de Lukmanoff s.n.* (Holotype: P [00757024], image seen).

The specimen has a label by Lukmanoff that identifies it as the type of *C. baillonii*. Kostermans identified the plant as *Cinnamomum porrectum* (= *Camphora parthenoxylon* [Jack] Meissn.).

Camphora blumei Lukman., Nomencl. Icon. Cannel.: 22. 1878.
TYPE: JAPAN. Cultivated in Java [Indonesia], *C. L. Blume s.n.* (Holotype: not found).

Camphora brogniartii Lukman., Nomencl. Icon. Cannel.: 23. 1878.
TYPE: CHINA/JAPAN. April 1872, *Cult. St. Cloud s.n.* (Lectotype, here designated: P [00757065], image seen).

The specimen chosen as the lectotype was questionably suspected to be the holotype of *C. brogniartii* by Kostermans. I believe his suspicions are correct, since there is a leaf the shape and size (14.0 × 5.5 cm) as indicated by Lukmanoff in the protologue. There is no locality on the specimen, and it is likely Lukmanoff just guessed China or Japan. Kostermans identified the plant as *Cinnamomum camphora* (i.e., *Camphora officinarum*).

Camphora camelliifolia Lukman., Nomencl. Icon. Cannel.: 22. 1878, as *camelliaefolia*.
TYPE: JAPAN. *Cult. in the gardens of the Faculty of Medicine, Paris, A. de Lukmanoff s.n.* (Holotype: P [00757064], image seen).

The specimen has a label identifying it as *Camphora camelliaefolia* by Lukmanoff. Kostermans identified the specimen as *Cinnamomum camphora* (= *Camphora officinarum*).

Camphora decaisnei Lukman., Nomencl. Icon. Cannel.: 23. 1878.
TYPE: INDIA. Cult. Bot. Gard. Calcutta, *J. D. Hooker s.n.* (Holotype: not found).

Camphora decandollei Lukman., Nomencl. Icon. Cannel.: 23. 1878.
TYPE: CHINA. Hong Kong, 1855, *Abbot L. Furet 26* (Holotype: P [00757016], image seen).

The specimen was identified as the type by Kostermans, and identified as *Cinnamomum porrectum* (= *Camphora parthenoxylon*). The collection number was added later; it is not one of Abbot Furet's.

Camphora griffithii Lukman., Nomencl. Icon. Cannel.: 22. 1878.
TYPE: INDIA. East Bengal, *W. Griffith (Kew Distr.) 4246/2* (Holotype: P [00757060], image seen).

The specimen was identified as the type by Kostermans and determined as *Cinnamomum camphora* (= *Camphora officinarum*) by him.

var. ***lanceolata*** Lukman., Nomencl. Icon. Cannel.: 22. 1878.
TYPE: RÉUNION. *J. Barthe s.n.* (Lectotype, here designated: P [02006550], image seen).
Homotypic synonym: *Camphora lanceolata* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 35. 1926.

Lukmanoff gave "Mauritius, *Barthe*" as the type data. The collection chosen as the lectotype comes from Réunion and seems to have slightly wider leaves (4.0 vs. 3.5 cm) with more veins branching off the midvein. As noted above under *Cinnamomum zeylanicum* var. *barthei*, there are no known Barthe collections from Mauritius.

Camphora himalayica Lukman., Nomencl. Icon. Cannel.: 23. 1878.
TYPE: INDIA. Himalaya, *W. Griffith s.n.* (Holotype: not found). Neotype, here designated: India, East Himalaya, *W. Griffith (Kew Distr.) 4247* (Holoneotype: CAL [0000033160], image seen; Isoneotypes: CAL [0000033159], S [S-G-1140, East Bengal], U [0002655], images seen).

A matching collection has not been located in Paris. The collection *Griffith (Kew Distr.) 4247* from East Himalaya matches Lukmanoff's protologue rather well in leaf shape and size (10 × 6 cm). The duplicate in Stockholm has "East Bengal" on the label, but has the correct Kew Distribution number of 4247. Kostermans' annotations on the latter indicate it is *Cinnamomum glaucescens* (Nees) Hand.-Mazz., a name here moved to *Camphora* as *Camphora glaucescens* (Nees) Ormerod (see Addendum).

Griffith (Kew Distr.) 4247 is sometimes misidentified as an isosyntype of *Cinnamomum glanduliferum* (Wall.) Meissn. var. *caniflorum* Meissn. However, it is *Griffith (Kew Distr.) 2476* from Bhutan that is an isosyntype of the latter.

Camphora hookeri Lukman., Nomencl. Icon. Cannel.: 23. 1878.
TYPE: INDIA. *J. D. Hooker s.n.* (Holotype: not found).

Camphora humboldtii Lukman., Nomencl. Icon. Cannel.: 24. 1878.
TYPE: JAPAN AND ARCHIPELAGO. Without locality, *R. Oldham 704* (Lectotype, here designated: P [00757059], image seen; Isolectotypes: GH [02620352], K [002133041, lower specimen], L [0308679], images seen).

Lukmanoff gave the type data as "Japan et Archipel., *Oldham*." These details agree with a label on a sheet identified as the holotype by Kostermans, who determined it as *Cinnamomum camphora* (= *Camphora officinarum*). The isolectotype in L [0308679] agrees with the lectotype in Paris in the handwritten label annotation and script style. This latter specimen was identified as an isosyntype of *Cinnamomum camphora* var. *parvifolium* Miq. Another collection, numbered *Oldham 704* from Nagasaki, Japan, is the type of *Camphora thunbergii* Lukman.

var. ***syringifolia*** Lukman., Nomencl. Icon. Cannel.: 24. 1878 as *syringaefolia*.
TYPE: WITHOUT ORIGIN. *Cult. Bot. Gard. Calcutta, comm. T. Anderson 28* (Lectotype, here designated: P [01748496], image seen).
Homotypic synonym: *Camphora syringifolia* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 35. 1926.

The specimen chosen as the lectotype is probably not the duplicate Lukmanoff saw, as it has slightly broader (4 vs. 3 cm) leaves of a more elliptic (vs. ovate) shape. The original duplicate is possibly no longer extant at Paris. I suspect it was not annotated "Japan," and that this was a guess on the origin by Lukmanoff. The specimen was identified as *Cinnamomum camphora* (= *Camphora officinarum*) by Kostermans. In Paris, Kostermans identified another sheet [P 00757014], image seen as the type of var. *syringifolia*, but this has much larger (10 × 5 cm), elliptic to elliptic-obovate (vs. 6 × 3 cm, ovate) leaves and belongs to *Camphora parthenoxylon*.

Camphora jussieui Lukman., Nomencl. Icon. Cannel.: 23. 1878.
TYPE: INDIA. East Bengal, *W. Griffith (Kew Distr.) 4248* (Lectotype, here designated: P [01748896], image seen; Isolectotype: K [002133473], image seen).

Kostermans identified the specimen chosen as the lectotype as the probable type. I agree that this is the type, because the specimen matches the dimensions (13.0 × 4.5 cm) of the leaf and its shape as depicted in the protologue. Kostermans identified it as *Cinnamomum porrectum* (= *Camphora parthenoxylon*).

Camphora mauritiana Lukman., Nomencl. Icon. Cannel.: 22. 1878.
TYPE: MAURITIUS. *P. Commerson s.n.* (Lectotype, here designated: P [02006549], image seen).

The specimen chosen as the lectotype matches the leaf dimensions (9 × 3 cm) and shape described by Lukamnoff in the protologue. Kostermans identified the specimen as *Cinnamomum camphora* (= *Camphora officinarum*).

Camphora neesii Lukman., Nomencl. Icon. Cannel.: 22. 1878.
TYPE: JAPAN. Without locality [Simoda], U.S. North Pacific Exploring Expedition, 1853–1856, *C. Wright s.n.* (Lectotype, here designated: P [00757062, right-hand plant], image seen: Isolectotypes: GH [00415037, right-hand plant], NY [391948], US [61455], images seen).

The specimen chosen as the lectotype agrees with Lukmanoff's description and drawing in the protologue. There is no specific locality on the lectotype sheet in Paris, but the isolectotypes have the locality of Simoda (= Shimoda, on the Izu Peninsula, Honshu Island). Another specimen (left-hand side) on the same sheet as the lectotype is the type of the variety *microphylla*. It has been identified as *Cinnamomum camphora* (= *Camphora officinarum*).

var. ***microphylla*** Lukman., Nomencl. Icon. Cannel.: 22. 1878.
TYPE: SOUTH KOREA. Tsu-sima Island, *C. Wilford s.n.* (Lectotype, here designated: P [00757061, left-hand plant], image seen; Isolectotypes: CGE [00085195], GH [00415036, left-hand plant], K [002133035], images seen).
Homotypic synonym: *Camphora microphylla* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 35. 1926.

Kostermans identified the specimen chosen as the lectotype as the holotype of this taxon. He identified it as *Cinnamomum camphora* (= *Camphora officinarum*).

var. ***pharbitifolia*** Lukman., Nomencl. Icon. Cannel.: 22. 1878.
TYPE: JAPAN. 1862, *ex Herbario Lugduno-Batavo s.n.* (Lectotype, here designated: P [00757058], image seen).
Homotypic synonym: *Camphora pharbitifolia* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 35. 1926.

The lectotype was identified as the probable holotype by Kostermans, a view here agreed with. Thus, the sheet in question is chosen as the lectotype, since it agrees with details supplied in the protologue by Lukmanoff.

Camphora officinarum Boerh. ex Fabr., Enum., ed. 2 [Fabr.]: 400. 1763 (Isonym: Nees, in Wallich, Pl. Asiat. Rar. 2: 72. 1831).

This is an accepted taxon also known as *Cinnamomum camphora* (L.) J. Presl. The specimen from the Botanical Garden in Paris that was used to describe and illustrate it for Lukmanoff's (1878) account is extant [P 01748566], image seen.

var. ***hahnemannii*** Lukman., Nomencl. Icon. Cannel.: 22. 1878.
TYPE: JAPAN. *Herbarium A. T. Brogniart s.n.* (Holotype: not found).
Homotypic synonym: *Camphora hahnemannii* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 35. 1926.

var. ***hippocratei*** Lukman., Nomencl. Icon. Cannel.: 22. 1878.
TYPE: JAPAN. *Herbarium A. T. Brogniart s.n.* (Holotype: not found).
Homotypic synonym: *Camphora hippocratei* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 35. 1926.

Camphora oldhamii Lukman., Nomencl. Icon. Cannel.: 23. 1878.
TYPE: TAIWAN [as Formosa]. Without locality, 1864, *R. Oldham 449* (Lectotype, here designated: P [00757057], image seen; Isolectotypes: GH [0260350], K [002133113], images seen).

Kostermans identified the specimen cited above as the probable holotype of *Camphora oldhamii*. I agree with his determination of the collection, since it matches

Lukmanoff's protologue in leaf size (8.0 × 3.5 cm) and shape. He determined it as *Cinnamomum camphora* (= *Camphora officinarum*). In Paris, the type number has been understandably misinterpreted as *Oldham 4425*, but it is 449. In L [0035737], image seen, an Oldham collection was identified as an isotype of *Camphora oldhamii*, but the specimen is from Nagasaki, Japan.

Camphora procera Lukman., Nomencl. Icon. Cannel.: 23. 1878.
TYPE: INDONESIA. Cultivated on Java, *ex Herbario Lugduno-Batavo s.n.* (Lectotype, here designated: P [01978111], image seen); Isolectotypes: G [00694109], L [0035742], L [0035743], U [0002648], images seen).

The specimen was annotated with the name *Camphora officinarum* var. *procera,* is from Java, and was distributed from Leiden. Its leaf measurements (10 × 6 cm) and shape (ovate) match those provided by Lukmanoff in the protologue, and, thus, it is chosen as the lectotype. The specimen is filed under the name *Cinnamomum camphora* (= *Camphora officinarum*) in Paris.

Camphora rougieri Lukman., Nomencl. Icon. Cannel.: 22. 1878.
TYPE: JAPAN. Without locality, cultivated in the garden of *M. Rougier, A. de Lukmanoff s.n.* (Holotype: P [00757063], image seen).

The holotype bears a label by Lukmanoff identifying it as *Camphora rougieri*. The locality "Japan" is not mentioned. Kostermans identified the specimen as *Cinnamomum camphora* (= *Camphora officinarum*).

var. ***glandulifera*** Lukman., Nomencl. Icon. Cannel.: 23. 1878.
TYPE: MAURITIUS. Cultivated, *P. Commerson 239* (Lectotype, here designated: P [02006561], image seen; Isolectotype: L [0423745], not seen). AUSTRALIA. New South Wales, Port Jackson, *sine coll. s.n.* (Syntype: P [00256011], image seen).
Homotypic synonym: *Camphora glandulifera* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 35. 1926 *nom. illeg.* (*non* [Wall.] Nees 1831).

The specimen chosen as the lectotype agrees with the protologue supplied by Lukmanoff. The other syntype from Australia is filed as a *Cinnamomum sp.,* but Lukmanoff was correct to treat it as the same as the Mauritian plant. Both are identified as *Camphora officinarum*.

Camphora sieboldii Lukman., Nomencl. Icon. Cannel.: 22. 1878.
TYPE: JAPAN. Without locality, *sine coll. s.n.* (Lectotype, here designated: P [01991854], image seen).

Kostermans identified the specimen chosen as the lectotype as the probable holotype of this entity; he determined it as *Cinnamomum camphora* (= *Camphora officinarum*). I agree with his determination of the material, since it matches Lukmanoff's protologue quite well (e.g., leaves 7 × 4 cm).

Camphora thomsonii Lukman., Nomencl. Icon. Cannel.: 24. 1878.
TYPE: INDIA. Cultivated in Saharunpur, *T. Thomson s.n.* (Lectotype, here designated: P [00757056], image seen; Isolectotype: K [002133412], image seen).

Kostermans identified the specimen chosen as the lectotype as the holotype of this taxon; he determined it as *Cinnamomum camphora* (= *Camphora officinarum*).

Camphora thouarsii Lukman., Nomencl. Icon. Cannel.: 24. 1878.
TYPE: JAPAN. *Herbarium A. A. Petit du Thouars s.n.* (Holotype: not found).

The type of this plant was possibly obtained on Mauritius, where Japanese material of *Camphora officinarum* was cultivated.

Camphora thunbergii Lukman., Nomencl. Icon. Cannel.: 22. 1878.
TYPE: JAPAN. Nagasaki, 1862, *R. Oldham 704* (Lectotype, here designated: K [002133041, upper plant], image seen; Isolectotypes: GH [02620351], L [1795679], LY [0746654], M [0293174], images seen).

A matching collection has not been found in Paris, so a sheet in Kew (the distributing institution) is chosen as the lectotype. *Camphora humboldtii* Lukman. in Paris has the same collector and number as the type, but with a handwritten label without the locality, Nagasaki, and year, 1862. Unnumbered Oldham collections in GH [02620349] and L [0035737, misidentified as an isotype of *Camphora oldhamii*] from Nagasaki, Japan, have both younger and smaller leaves than that described by Lukmanoff (8 × 4 cm) for *Camphora thunbergii*. All material seen has been identified as *Cinnamomum camphora* (L.) J. Presl (= *Camphora officinarum*).

Camphora thwaitesii Lukman., Nomencl. Icon. Cannel.: 23. 1878.
TYPE: JAPAN. Cultivated in Java [Indonesia], *H. Zollinger s.n.* (Holotype: not found).

More than likely this collection was originally made by H. Buerger in Japan, and that material was then incorporated into the herbarium of Zollinger. Zollinger did not collect in Japan.

Camphora wrightii Lukman., Nomencl. Icon. Cannel.: 24. 1878.
TYPE: CHINA. Hong Kong, U.S. North Pacific Exploring Expedition, 1853–1856, *C. Wright 402* (Lectotype, here designated: P [00757015], image seen; Isolectotypes: GH [00871568], K [002133245], NY [354966], US [614444], images seen).

The lectotype was identified as the probable holotype of this taxon by Kostermans; he determined it as *Cinnamomum porrectum* (= *Camphora parthenoxylon*). In L [0035735], image seen, a sheet has been wrongly identified as an isotype of *Camphora wrightii*. A later hand crossed out "Japan" and wrote "Hong Kong." It is more likely this specimen of *Camphora officinarum* is an isotype of *C. neesii*.

var. ***multinerva*** Lukman., Nomencl. Icon. Cannel.: 24. 1878.
TYPE: JAPAN/CHINA. *Herbarium A. T. Brogniart s.n.* (Holotype: not found).
Homotypic synonym: *Camphora multinerva* (Lukman.) A.W. Hill, Index Kew., Suppl. 6: 35. 1926.

Camphora zollingeri Lukman., Nomencl. Icon. Cannel.: 24. 1878.
TYPE: JAPAN. "Cultivated in Java," [*leg. H. Buerger*], *H. Zollinger 219* (Lectotype, here designated: P [01978395], image seen; Isolectotypes: BM [015153037], G [00693858], G [00693860], P [01978396], U [1603970], images seen).

The lectotype was identified as the holotype by Kostermans; the specimen matches Lukmanoff's protologue. Lukmanoff assumed the plant had been cultivated on Java (Indonesia), but more likely the specimen is one of those collected by H. Buerger in the Nagasaki region of Japan, and later incorporated into Zollinger's herbarium. The Paris isotype has a stem (left-hand plant) with much larger (ca. 12 × 5 cm) leaves. Also, on the Paris isotype, the Japanese vernacular name Kurotsusu is recorded, a name already recorded for this plant by Siebold (1830, as *Cinnamomum japonicum* Siebold). Kostermans annotated all the material in Paris of this species as *Cinnamomum zollingeri* (Lukman.) Kosterm., but that combination appears to be unpublished and is not available because of the earlier *C. zollingeri* (Lukman.) A.W. Hill (= *C. verum* J. Presl). As noted above, this taxon should be called *Cinnamomum alatum* Lukman.; it does not belong in *Camphora*.

Addendum

The following observations came about as a result of the above research.

Camphora blandfordii (M. Gangop.) Ormerod, *comb. nov.*
Basionym: *Cinnamomum blandfordii* M. Gangop., Bull. Bot. Surv. India 48(1–4): 110. 2006.
TYPE: MYANMAR. Katha District, 180 m, 8 March 1917, *H. R. Blandford 115* (Holotype: CAL [0000021481], image seen; Isotype: CAL [0000021482], image seen).

Distribution: India and Myanmar.

This species is related to *Camphora glandulifera* (Wall.) Nees and, therefore, requires transfer to *Camphora*.

Camphora camphorata (H. Lév.) Ormerod, *comb. nov.*
Basionym: *Machilus camphoratus* H. Lév., Repert. Spec. Nov. Regni Veg. 9: 460. 1911.
TYPE: CHINA. Guizhou [as Kouy-Tcheou]: Pingfa [as Pin-Fa], May 1903 and April 1908, *J. Cavalerie 1002* (Holotype: E [00386438], image seen; Isotypes: A [00415028], K [000778566, April 1908], K [000778567, May 1903], L [0035749], P [00757048], images seen).
Homotypic synonyms: *Alseodaphne camphorata* (H. Lév.) C.K. Allen, J. Arnold Arbor. 17: 326. 1936.

Alseodaphne caudata Lecomte, Nouv. Arch. Mus. Hist. Nat. ser. 5, 5: 97. 1913 *nom. illeg.*

Cinnamomum caudifer Kosterm., Reinwardtia 8: 35. 1970 as *caudiferum*.

Heterotypic synonyms: *Beilschmiedia foveolata* Merr., J. Arnold Arbor. 19: 30. 1938.
TYPE: VIETNAM [as Indo-China]. Tonkin, Sapa [as Chapa], 1700 m, August 1930, *P. A. Petelot 5380* (Syntypes: A [00041196], BO [1276866], BO [1278374], K [000350897, see note], NY [00354900], NY [00354901], P [00745506], US [00099403], images seen).

Litsea foveolata (Merr.) Kosterm., Reinwardtia 8: 98. 1970.

Cinnamomum foveolatum (Merr.) H.W. Li & J. Li, Fl. China 7: 170. 2008.

Camphora foveolata (Merr.) Y. Yang, Bing Liu & Zhi Yang, Ecol. Evol. 12(10): e9378: 8. 2022.

Distribution: China and Vietnam.

The earliest name for this taxon is *Machilus camphoratus,* the specific epithet of which is available in *Camphora*. Therefore, the required transfer is made here.

I have followed Yang et al. (2022) in treating *Machilus camphoratus* and *Alseodaphne caudata* as homotypic. Léveillé cited two specimens collected by Cavalerie in the protologue of *Machilus camphoratus*, but the original label on the holotype in E has both of the dates he cited. I assume from this that Cavalerie combined the material he collected at Pingfa in May 1903 and April 1908 into a single collection. Lecomte (in the protologue of *Alseodaphne caudata*) cited no collection date for the duplicate of *Cavalerie 1002* in Paris. It is my suspicion that a later hand (probably Kostermans) added the date of April 1908 to the specimen.

The Kew isotype of *Beilschmiedia foveolata* has the number *Petelot 3380* and collection date of 7 August 1939. These are transcription errors. The "7 August 1939" date is when Paris received the material from Petelot.

Camphora glaucescens (Nees) Ormerod, *comb. nov.*
Basionym: *Cecidodaphne glaucescens* Nees, in Wallich, Pl. Asiat. Rar. 2: 70. 1831.
TYPE: BANGLADESH. Sylhet, *F. de Silva in N. Wallich Catal. 2560A* (Syntypes: B [10-0277097], G [00694103, right-hand plant], GZU [000253894], K-W [001116446], K-W [001116447], NY [00354954], images seen; Sylhet, *F. Buchanan-Hamilton in N. Wallich Catal. 2560B* (Syntypes: GZU [000253895], K-W [001116448], images seen); Sylhet, *N. Wallich Catal. 2560* (Syntypes: BM [000880629], G [00694103, two left-hand plants], GZU [000253893A], GZU [00253893B], PH [00030194], images seen); Sylhet, February 1815, *F. Buchanan-Hamilton 987* (Syntype: E [00393162], image seen). INDIA. Without locality, *N. Wallich s.n.* (possible Syntype: BR [0000029323326], image seen).
Homotypic synonyms: *Cinnamomum cecidodaphne* Meissn., Prodr. [A. P. de Candolle] 15(1): 25. 1864 *nom. illeg.*

Cinnamomum glaucescens (Nees) Hand.-Mazz., Oesterr. Bot. Zeitschr. 85: 214. 1936.

Distribution: India, Bangladesh, Bhutan, Myanmar, Laos, Thailand, Vietnam, and China.

Yang et al. (2022) argued that the monospecific genus *Cecidodaphne* was a synonym of *Cinnamomum*, because its only species had tripliveined leaves. This is, however, evidently untrue, as all material seen has pinnately veined leaves, and, therefore, *Cecidodaphne* is a synonym of *Camphora*.

Besides *Cinnamomum glanduliferum* (Wall.) Meissn. var. *caniflorum* Meissn., all of the other possible synonyms identified by Kostermans are currently recognised as valid taxa on POWO. These entities are *Cinnamomum balansae* Lecomte, *Cinnamomum illicioides* A. Chev., *Cinnamomum longipetiolatum* H.W. Li, and *Cinnamomum siamense* Craib. As noted above, *Camphora himalayica* Lukman. is also treated here as *Camphora glaucescens*.

Cinnamomum cubittii Ormerod, *nom. nov.*

Basionym: *Cinnamomum bhamoense* M. Gangop., Bull. Bot. Surv. India 48(1–4): 104. 2006 (*non Cinnamomum bamoense* Lukman. 1878).

TYPE: MYANMAR. Bhamo, 1910, *G. E. S. Cubitt 531* (Holotype: CAL [0000025889], image seen).

Etymology: Named after G. E. S. Cubitt, who collected plants in Myanmar.

It is necessary to rename this taxon due to the earlier *Cinnamomum bamoense* Lukman. Both entities are named after Bhamo in Myanmar, and their epithets are pronounced the same. A small irony, as explained above, is that Lukmanoff's taxon likely came from India and not Bhamo in Myanmar.

Timonius pedunculatus (Thunb.) Ormerod, *comb. nov.*

Basionym: *Laurus pedunculata* Thunb., Syst. Veg., ed. 14 (J. A. Murray): 383. May–June 1784; Fl. Jap. (Thunberg): 174. August 1784.

TYPE: NOT CITED. JAPAN [as Japonia], without specific locality, *C. P. Thunberg s.n.* (Lectotype, here designated: UPS-Thunb 9384 [= V-084738], image seen).

Homotypic synonyms: *Cinnamomum pedunculatum* (Thunb.) J. Presl, Prir. Rostlin 2: 37. 1823–1824.

Cinnamomum japonicum Siebold, Verh. Batav. Genootsch. Kunst. 12: 23. 1830 *nom. Illeg.*

Hedyotis pedunculata (Thunb.) Nakai, Bot. Mag. (Tokyo) 41: 518. 1927.

Distribution: Uncertain (see notes).

This species was mistakenly assigned to the genus *Laurus* (Lauraceae) by Thunberg, and then later its name was misapplied to a Japanese species of *Cinnamomum*, due to Philipp von Siebold (1830) identifying his own Japanese collections with it. The Japanese collections of Siebold are here considered to belong to *Cinnamomum alatum* Lukman. (Synonyms include: *Camphora zollingeri* Lukman., *Cinnamomum goeringii* Lukman., and *C. insularimontanum* Hayata).

Japanese botanist Takenoshin Nakai discovered that *Laurus pedunculata* belonged in Rubiaceae, and thus he transferred it to *Hedyotis* L. However, Thunberg's woody plant does not fit in that genus of mostly herbaceous plants. It does, however, fit in *Timonius* Rumph ex DC (Taylor, *pers. comm.*), a genus that is not found in temperate Japan, where Thunberg supposedly collected it. Thunberg also collected in Java (Indonesia) and Sri Lanka. *Timonius* is curiously rare and almost absent from Java, so this leaves Sri Lanka as a probable place of collection.

A single species of *Timonius* has been accepted as occurring in Sri Lanka. Online databases (e.g., POWO) call it *T. flavescens* (Jack) Baker, but specialists (Junhao Chen and Pui Kiat Hoo, *pers. comm.*) in southeast Asian *Timonius* point out that the Sri Lankan plants of *Timonius* have chartaceous leaves and eight-lobed fruits (vs. coriaceous leaves and four-lobed fruits in *T. flavescens*). The type of *Laurus pedunculata* bears pistillate (male) flowers and, in my view, agrees rather well with some of these Sri Lankan plants, but it is clear that critical revision of material from there is needed.

Literature Cited

Doweld, A. B. 2017. New names in *Cinnamomoides*, *Cinnamomum* and *Neolitsea* (Lauraceae), and *Pterospermum* (Malvaceae), fossil and living. Phytotaxa 326(3): 189–201.

Kostermans, A. J. G. H. 1983. The South Indian species of *Cinnamomum* Schaeffer (Lauraceae). Bull. Bot. Surv. India 25(1–4): 90–133.

———. 1995. Lauraceae (pp. 105–172) in M. D. Dassanayake, F. R. Fosberg, and W. D. Clayton, editors, A Revised Handbook to the Flora of Ceylon IX. A. A. Balkema. Rotterdam/Brookfield.

———. 1998. The Burmese *Cinnamomum* (Lauraceae). Reinwardtia 11(3): 195–214.

Lukmanoff, A. de. 1878. Nomenclature et iconographie des Canneliers et Camphriers. Typographie F. Debois et Cie, Paris.

Moraes, P. L. R. de. 2012. The Lauraceae collected in Brazil by Ludwig Riedel—I. Harvard Papers Botany 17(1): 185–216.

Siebold, P. F. B. von. 1830. Synopsis Plantarum Oeconomicarum Universi Regni Japonici. Verh. Batav. Genootsch. Kunst. 12: 1–74.

Soh, W. K. 2011. Taxonomic revision of *Cinnamomum* (Lauraceae) in Borneo. Blumea 56(3): 241–264.

Yang, Z., B. Liu, Y. Yang, and D. K. Ferguson. 2022. Phylogeny and taxonomy of *Cinnamomum* (Lauraceae). Ecology and Evolution. 12(10): e9378.

Page 140 intentionally left blank.

NOTES ON SOME MALESIAN ORCHIDACEAE VII

Paul Ormerod[1,2] and Lina Juswara[3]

Abstract. Continuing herbarium and literature research on Malesian orchids has identified five new synonyms and two new combinations.

Keywords: Malesia, orchids, synonymy, *Anoectochilus, Crepidium, Galeola*

This paper continues our studies (e.g., Ormerod and Juswara, 2023) of Malesian orchids with the intent of updating floristic knowledge of the region. As per usual, most of the taxa dealt with occur in Indonesia.

Anoectochilus Blume, Bijdr. Fl. Ned. Ind. 8: 411. 1825; Tabellen: f.15. 1825 (as *Anecochilus*). *nom. cons.*
Type species: *Anoectochilus setaceus* Blume.

This is a genus of subtribe Goodyerinae with about 40 species distributed from Sri Lanka and India to Samoa. The plants often have a basal rosette of reddish-brown to blackish, cordate to suborbicular leaves intricately veined with nerves colored gold, pink, or silver. Thus, they are often referred to as jewel orchids. The species discussed here, unlike most of its congeners, is highly variable in leaf color and several floral characters. Thus, a number of taxa are here proposed as new synonyms of it.

Anoectochilus setaceus Blume, Bijdr. Fl. Ned. Ind. 8: 411. 1825; Tabellen: f. 15. 1825 as *Anecochilus*.
TYPE: INDONESIA. Java, Mt. Salak, Mt. Gede, and Tankuwan Prahu, *C. L. Blume 1957* (Lectotype [here designated]: L [0058589]; possible Isolectotype: P [00333662, image seen]). Fig. 1–2.
Homotypic synonym: *Anoectochilus setaceus* Blume var. *aureoreticulatus* W.J. Hook., Curtis's Bot. Mag. 86: sub t.5208. 1860 *nom. illeg.*
Heterotypic synonyms: *Anoectochilus reinwardtii* Blume, Fl. Javae Ins. Adj. n.s. 1: 40. 1858; Coll. Orch. Arch. Ind.: 48. 1858 *syn. nov.*
TYPE: INDONESIA. Java, Mt. Pantjar, *C. L. Blume s.n.* (Lectotype [here designated]: L [0058588]); Java, icon *C. Reinwardt s.n.* (Syntype: L?, not seen); Sumatra, collector not cited (Syntype: L?, not seen).
Anoectochilus croseus Rchb.f., Hamb. Gartenz. 16: 424. 1860 *syn. nov.*
TYPE: WITHOUT ORIGIN. *Cult. H. Kramer for Mrs. Jenisch s.n.* (Holotype: W-R [37797, image seen]).
Anoectochilus narasimhanii Sumathi, Jayanthi, Karthig. & Sreek., Blumea 48(2): 285. 2003 *syn. nov.*
TYPE: INDIA. North Andaman Islands, Saddle Peak National Park, 20 September 2001, *R. Sumathi, J. Jayanthi, & K. Karthigeyan 17368* (Holotype: CAL; Isotypes: D, PBL [none found, but see note]).

Anoectochilus falconis Ormerod, Taiwania 50(1): 3. 2005 *syn. nov.*
TYPE: MALAYSIA. Kedah, Kedah Peak, 29 November 1915, *H. C. Robinson 5977A* (Holotype: AMES [00217448]).

Distribution: India (Andamans), Thailand, Malaysia (Peninsula), and Indonesia (Sumatra to Flores).

Additional specimens examined: THAILAND. Peninsular region, Nakhorn Si Thammarat, Khao Luang area, 800 m, 18 May 1968, *C. F. van Beusekom & Phlengkai 848* (L). MALAYSIA. Peninsula. Kedah, Kedah Peak, 29 November 1915, *H. C. Robinson 5977* (AMES, BM, L). INDONESIA. Sumatra. Tapianoeli Residency, area of Loemban Loboe, Toba, near KM 142, road from Porsea to Parapat, 27–31 July 1946, *R. Si Boeea 9803* (L, MICH); N of Sibajak, 1700 m, 5 June 1920, *J. A. Lorzing 7313* (L); E of Sibajak, above Petanital, 1275 m, 5 February 1929, *J. A. Lorzing 15157* (L); Java. Without locality, *T. Horsfield s.n.* (BM); Gunung Manggisan, SE of Malang, S of Semeru, 850 m, 1 November 1981, *J. B. Comber 1260* (K); NW of Pujon, near Malang, 1300 m, 15 May 1980, *J. B. Comber 1176* (K); Puncak, 1550 m, 29 August 1986, *J. B. Comber 1686* (K); Pateungteung, 1500 m, *W. M. Docters van Leeuwen 2620* (L); Preanger Regency, Bukit Goenggael, 1800 m, 3 August 1924, *C. A. Wisse 1201* (L); Preanger Regency, near Gunung Toegoe, Tjampaka (Tjibeber), 1000 m, 19 June 1923, *J. J. Smith 870* (L); Preanger Regency, near Padalarang, 700 m, 11 June 1916, *J. Docters van Leeuwen-Reijnvaan 2375* (L, 2 sheets); Lombok, Rindjani volcano, lower half of Tengengeah, 1350 m, 3 May 1909, *J. Elbert 980* (L); Sumba, Yawila, 750 m, 18 July 1974, *J. A. J. Verheijen 4104* (L, sterile); Flores, Rana?, 900 m, 19 April 1966, *E. Schmutz 47* (L, no fls); Wae Mao, near Rane Messe,

The first author wishes to thank herbarium and library staff at A, BM, AMES, GH, and K. L and MICH kindly loaned material for study. The second author would like to thank colleagues at the Directorate of Scientific Collection Management, National Research and Innovation Agency, BO for their ongoing help and advice.

[1] P.O. Box 8210, Cairns 4870, Queensland, Australia
[2] Corresponding author: wsandave1@bigpond.com
[3] Herbarium Bogoriense, Research Center for Biosystematics and Evolution, National Research and Innovation Agency (BRIN), KST Soekarno, Jl. Raya Jakarta KM 46, Pakansari, Cibinong, Bogor Regency 16911, West Java, Indonesia; linajuswara@gmail.com

Harvard Papers in Botany, Vol. 29, No. 1, 2024, pp. 141–145.

ISSN: 1938-2944, DOI: 10.3100/hpib.v29iss1.2024.n15, Published online: 30 June 2024

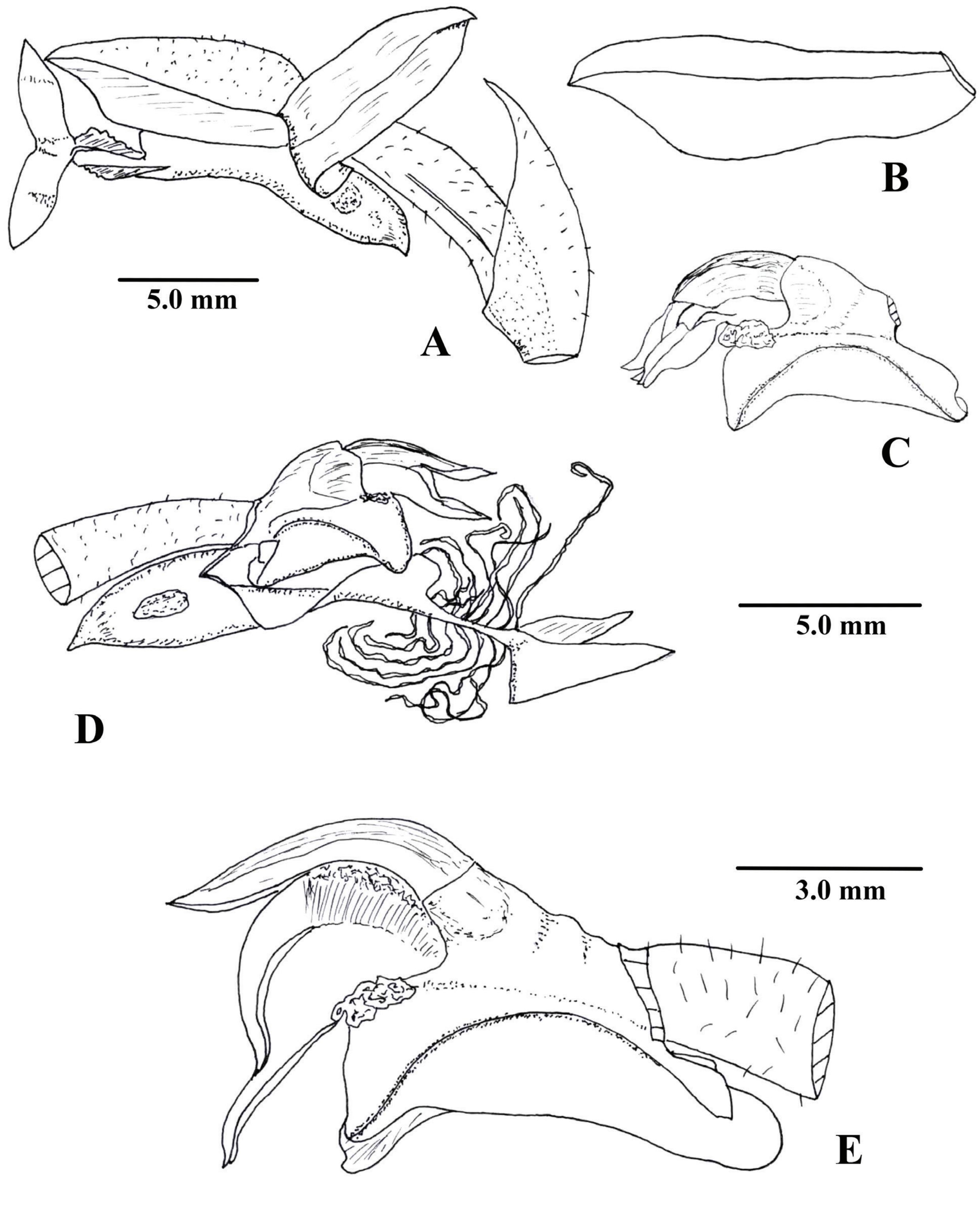


FIGURE 1. *Anoectochilus setaceus* Blume. **A**, flower; **B**, petal; **C**, column; **D**, flower; **E**, column. A–C drawn by P. Ormerod from *J. Comber 1260* (K), D from *A. Kostermans & Wirawan* 839 (L), and E from *J. J. Smith 870* (L).

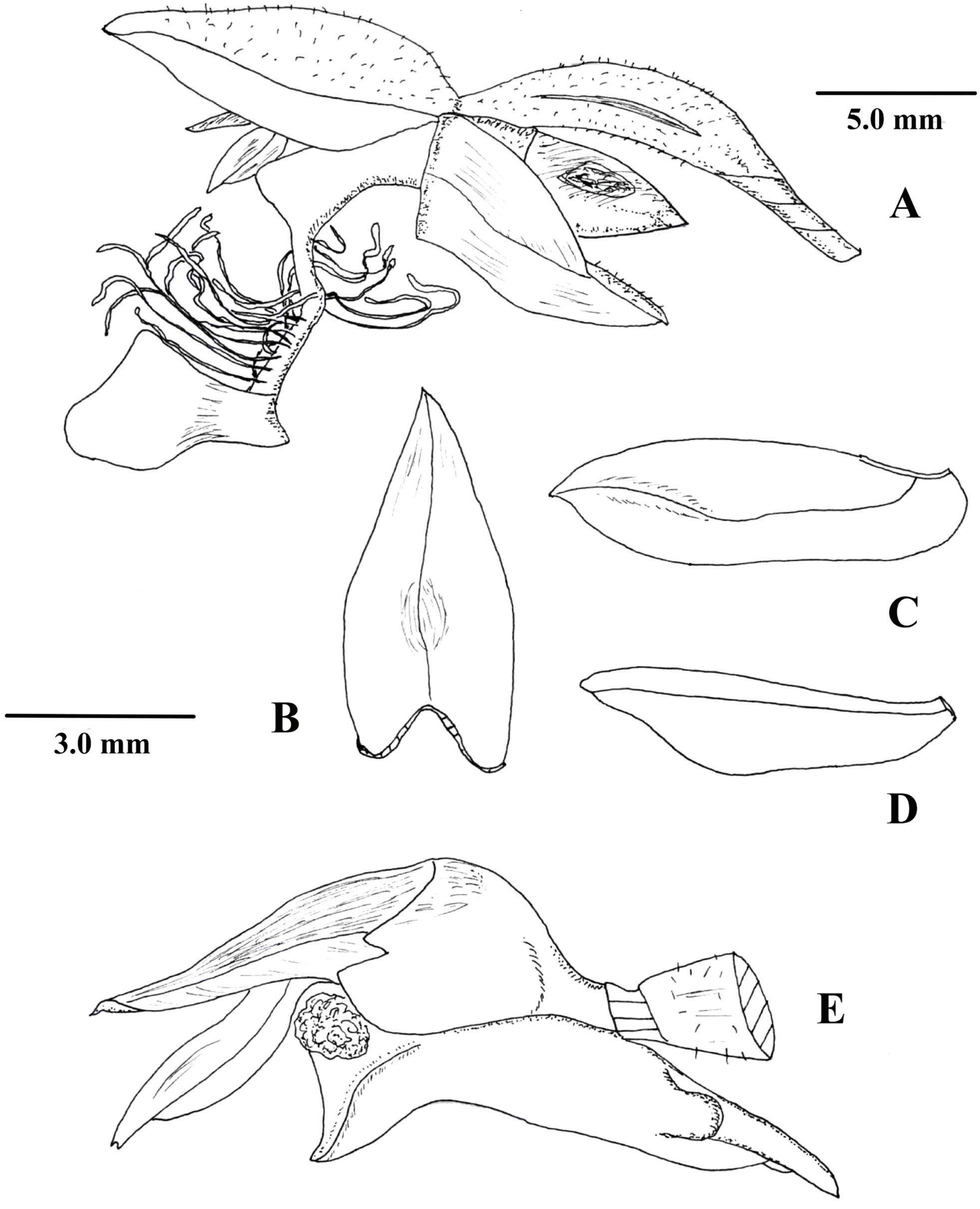


FIGURE 2. *Anoectochilus setaceus* Blume. **A**, flower; **B**, dorsal sepal; **C**, lateral sepal; **D**, petal; **E**, column. Drawn by P. Ormerod from *R. Si Boeea 9803* (MICH).

1000 m, 7 April 1965, *A. G. H. Kostermans & N. Wirawan* 839 (L); Gunung Putih, 3 June 1964, *J. A. J. Verheijen 1837* (L); Gunung Putih, 3 June 1964, *J. A. J. Verheijen 1838* (L); Numang, 1000 m, 1 May 1980, *E. Schmutz 4681* (L).

Vernacular names: belong-boelong babiat (*Si Boeea 9803*); nokhum (*van Beusekom & Phlengkai 848*).

Ethnobotany: Used as a medicine by local people (Thai Peninsula, *van Beusekom & Phlengkai 848*).

An examination of several collections of this species showed that it is highly variable in leaf coloration, the length of its floral spur (5–7 mm long on average, but can be to 8 mm long), the number and density of fringes on the labellum mesochile, the shape of epichile lobules (lanceolate, ligulate, to obliquely cuneate), and the shape and length of the retrorse portion of the column wings (oblong to lanceolate, 1.5–3.0 mm long).

Smith (1905) distinguished *A. reinwardtii* from *A. setaceus* by the former having reddish-black leaves with strong, copper-red nervation, and the lip with more or less 10 fringes on each side of the mesochile. While *A. setaceus* was supposed to have greenish black leaves finely veined silver white, and the lip with more or less 7 fringes on each side of the mesochile. Leaf coloration is highly variable and is hardly detectable on the types of *A. reinwardtii* and *A. setaceus*; it is the same for the number of fringes on each side of the lip mesochile. Comber (1990) used similar characters to distinguish the two entities but reported both had blackish-green leaves. He further noted some variation in the color of the venation and that *A. reinwardtii* had fewer fringes on the lip (contrary to Smith) that were shorter (5.0 vs. 8.5 mm) than those of *A. setaceus*. Comber's concept of *A. reinwardtii* doesn't agree with the type material, which has longer fringes on the lip. However, his material does fit into the broader variation of *A. setaceus* as interpreted here. In Kew, the collection *Comber 1260* has only laminate flanges (instead of distinct fringes) on the lip mesochile (see Fig. 2A–C), somewhat approaching the plant pictured by Comber (1990). In our opinion, it is just an extreme form of *A. setaceus* and does not have any other salient features to show that a new taxon is at hand.

No distinguishing features were found for *A. croseus* after examination of photographs of the type and the original sketches made by Reichenbach f. The first author is most grateful to the late Leslie Garay for sending copies of the aforesaid type photographs and drawings.

The first author was kindly sent some material of *A. narasimhanii* by P. V. Sreekumar, one of the co-authors of this taxon. Location of the type material cited in the protologue remains unknown (Bhattacharjee and Chowdhery, 2018). At the time it seemed to be distinct, but the advice to that effect was incorrect because the variability of *A. setaceus* was not understood at the time. We can find no characters to justify its maintenance.

Anoectochilus falconis was distinguished from *A. reinwardtii* based on features of its column wings. Those features appear to be an aberrant development, and other specimens of the type number have the usual column wings here attributed to *A. setaceus*.

We believe further study is needed of *A. elatus* Lindl., *A. monicae* J.J. Wood, and *A. nicobaricus* N.P. Balakr & Chakr. At the moment, they do not appear particularly different from *A. setaceus*. A similar problem exists with the Sumatran species, *A. dewildeorum* Ormerod. It is currently identified by its slightly longer column wings (4.0 vs. 1.5–3.0 mm), that perhaps have different dorsal membranes, and denser fringes on the lip mesochile.

Crepidium Blume, Bijdr. Fl. Ned. Ind. 8: 387. 1825.
Type species: *Crepidium flavescens* Blume.

A genus of Malaxidinae with about 270 species distributed from the Seychelles, Sri Lanka, and India to Tahiti, with most species found in Indonesia. The taxa transferred here to *Crepidium* belong in section *Oistochilus* (Schltr.) Ormerod *sensu lato* (including genera *Pseudoliparis* Finet and *Saurolophorkis* Marg. & Szlach.).

Crepidium malinowskianum (Marg.) Ormerod & Juswara, *comb. nov.*
Basionym: *Pseudoliparis malinowskiana* Marg., Phytotaxa 435(3): 243. 2020.
TYPE: PAPUA NEW GUINEA. Morobe Prov., Yoangen area, mountain trail, 1525 m, 18 June 1936, *J. Clemens & M. S. Clemens 3393* (Holotype: AMES [02175303, image seen]).

Distribution: Papua New Guinea.

Crepidium papuanum (Marg.) Ormerod & Juswara, *comb. nov.*
Basionym: *Saurolophorkis papuana* Marg., Wulfenia 24: 286. 2017.
TYPE: PAPUA NEW GUINEA. Western Highlands Prov., near Minj, Korubun Creek, 1800 m, *leg. E. F. de Vogel, W. Bandisch, A. Vogel, & B. Gravendeel,* cult. Leiden Botanical Garden, *Hort. Leiden 20032236* (Holotype: L [0661500, not seen]; Isotype: L [spirit, not seen]).

Distribution: Papua New Guinea.

Galeola Lour., Fl. Cochinch. 2: 520. 1790.
Type species: *Galeola nudifolia* Lour.

A genus of five holomycotrophic, leafless, viny orchids distributed from Madagascar and the Comoros into southeast Asia, through Malesia to western New Guinea.

Galeola nudifolia Lour., Fl. Cochinch. 2: 521. 1790.
TYPE: VIETNAM [as Cochinchinae]. In woods, *J. Loureiro s.n.* (Holotype: BM [000062885]).
Homotypic synonyms: *Epidendrum galeola* Raeusch., Nomencl. Bot. [Raeusch.] ed. 3: 265. 1797 *nom. illeg.* *Cranichis nudifolia* (Lour.) Pers., Syn. Pl. [Persoon] 2(2): 511. 1807.
Heterotypic synonym: *Cassytha corniculata* Burm.f., Fl. Ind. [N.L. Burman]: 93. 1768, *syn. nov.*
TYPE: INDONESIA. Java, *C. Kleynhoff s.n.* (Lectotype [here designated]: G [00802255, image seen]).

Distribution: India, Bhutan, Myanmar, China, Vietnam, Laos, Cambodia, Thailand, Malaysia, Singapore, Philippines, and Indonesia (Sumatra to Papua).

Merrill (1921) was the first to suggest that a plant described in the Lauraceae, *Cassytha corniculata*, was, in fact, a species of *Galeola*. Smith (in Merrill, 1921) suggested to him it could be either *G. altissima* (Blume) Rchb.f. or *G. pterosperma* Schltr. (a *nomen nudum* based on an earlier *nomen nudum*, *Vanilla pterosperma* Lindl.). The former is a glabrous plant now placed in the genus *Erythrorchis* Blume, while the latter is the pubescent species we know today as *Galeola nudifolia*. Examination of the flowerless type of *Cassytha corniculata* shows it to have pubescent inflorescences characteristic of *Galeola nudifolia*, and, therefore, we treat the two as conspecific. Burman also cited in the protologue the pre-Linnaean name *Cassytha cornea* Rumph in synonymy, but this was correctly excluded by Merrill (1921), since it is a quite different fungal taxon now known as *Marasmius crinisequi* F. Muell. The name *Galeola nudifolia* is now well entrenched in the literature and widely used. We expect that it will be necessary to conserve it against the earlier taxon of Burman.

Currently, *Cassytha corniculata* is listed as a synonym of *C. filiformis* L. (e.g., POWO), but the two bear no similarity since the latter is a slender, wiry, glabrous plant. Other synonyms of *Galeola nudifolia* can be found on POWO; for example, *Conchoglossum silvestre* Breda, *Erythrorchis kuhlii* Rchb.f., *Galeola torana* J.J. Sm., and *Vanilla rubiginosa* Griff.

Literature Cited

Bhattacharjee, A., and H. J. Chowdhery. 2018. Orchidaceae: Orchidoideae. Cranichideae: Subtribe Goodyerinae. Fascicles Flora of India 28: 1–284.

Comber, J. B. 1990. Orchids of Java. Bentham-Moxon Trust. Royal Botanic Gardens, Kew.

Merrill, E. D. 1921. A review of the new species of plants proposed by N. L. Burman in his Flora Indica. Philipp. J. Sci. 19: 329–388.

Ormerod, P., and L. Juswara. 2023. Notes on Some Malesian Orchidaceae VI. Harvard Pap. Bot. 28(2): 715–719.

Smith, J. J. 1905. Die Orchideen von Java. E. J. Brill, Leiden.

Page 146 intentionally left blank.

A NEW SPECIES OF *MALAXIS* (MALAXIDINAE: ORCHIDACEAE) WITH WHITE FLOWERS FROM COLOMBIA

Mario Alexei Sierra-Ariza,[1,6] Juan Sebastián Moreno,[1,2,3] and Isler F. Chinchilla[4,5]

Abstract. *Malaxis susanae* from the Colombian Andes is described and illustrated as a new species of orchid. It resembles *Malaxis carpinterae* (Schltr.) Ames, but differs by the flowers that have a white (vs. green) lip and the disc cavity with the margin inconspicuously raised (vs. conspicuously raised in a retuse margin) at the apex. Notes on its distribution, habitat, floral phenology, etymology, related taxa, and conservation assessment are provided.

Keywords: Andes orchids, *Malaxis caracasana*, *Malaxis carlos-parrae*, *Malaxis excavata*, *Malaxis lobulata*, *Malaxis pittieri*

Resumen. *Malaxis susanae* de los Andes colombianos es descrita e ilustrada como una nueva especie de orquídea. Se asemeja a *Malaxis carpinterae* (Schltr.) Ames, pero se diferencia por tener flores con el labio blanco (en comparación con verde) y la cavidad del disco con el margen discretamente elevado (en comparación conspicuamente elevado en un margen retuso) en el ápice. Se proporcionan notas sobre su distribución, hábitat, fenología floral, etimología, taxones relacionados y evaluación de conservación.

Palabras claves: orquídeas andinas, *Malaxis caracasana*, *Malaxis carlos-parrae*, *Malaxis excavata*, *Malaxis lobulata*, *Malaxis pittieri*

Malaxis Sol. ex Sw., (Swartz, 1788) is a genus of orchids belonging to the tribe *Malaxidinae* (Bentham and Hooker, 1883: 465). In its traditional circumscription, this genus is cosmopolitan and comprises approximately 300 species. It is widely distributed in pantropical zones, with some species growing in temperate regions of the Americas, Asia, and Europe (Pridgeon et al., 2005). Species growing in the tropics occupy a variety of habitats that range from dry and humid lowland forests to the paramos in mountain ranges, from sea level to 3650 m (González-Tamayo, 2002; Bogarín and Pupulin, 2021; Chinchilla et al., 2022).

In the Americas, 143 species of *Malaxis sensu lato* have been recognized, with Mexico having the highest diversity with 71 published species (Chinchilla et al., 2022). The genus includes terrestrial or epiphytic plants, frequently with rhizomatous stems that produce small pseudobulbs covered by membranous cataphylls. Each sympodial unit produces one or two leaves and has inflorescences in racemes or corymbs that emerge at the apex of the pseudobulbs. The flowers are generally small, green, and not resupinate, and the lip often has a concave disc at the base divided by a longitudinal costa; the column is short, erect, and dorsiventrally complanate (Pridgeon et al., 2005; Pérez-Escobar and Blanco, 2014; Chinchilla et al., 2022).

In Colombia, 13 species of *Malaxis* have been identified so far, eight of which are endemic (Ministerio de Ambiente y Desarrollo Sostenible and Universidad Nacional de Colombia, 2015; Bernal et al., 2016). Due to the taxonomic complexity of *Malaxis* and the few taxonomic studies on these plants in Colombia, the known diversity of the genus in the country, as well as its ecological and taxonomic particularities, is preliminary. It's quite possible that there could be more species of *Malaxis* in Colombia, but more exploration as well as taxonomic, systematic, and ecological studies are necessary for this genus. Here, we describe and illustrate a new species of *Malaxis* distributed in the three mountain ranges of Colombia, and compare it with its morphologically most similar species.

Materials and Methods

Field work to collect material from the new species of *Malaxis* was carried out in December 2018 during an expedition for the research project titled "*Síntesis de las orquídeas del río Azufrado, Tolima-Colombia*." From this project, seven new orchid species were discovered, identified, and published under the following names: *Acianthera villahermosae* Sierra-Ariza, Rinc.-González, & Karremans, *Oncidium tolimense* Sierra-Ariza & A. Albino-Bohórquez, *Pleurothallis petroana* Sierra-Ariza, *Pleurothallis villahermosae* Sierra-Ariza, Rinc.-González, & Villanueva, *Epidendrum villahermosaense* Sierra-Ariza & Hágsater, *Epidendrum rioazufrense* Sierra-Ariza, Hágsater, & E. Santiago, and *Kefersteinia universitatis-tolimae* Sierra-Ariza. Images of the specimens were captured using a Nikon D5300 camera equipped with a Micro NIKKOR AF 105 mm f/2.8 D lens. Subsequently, flowers of the specimens were kept in spirit. The collected material was incorporated into the collection of the TOLI Herbarium at the University of Tolima. Specimens of *Malaxis*—including types—were examined in the following herbaria: AMES,

Our most sincere thanks to A. Albino Bohórquez for her participation and company in the expedition in which orchids of the new species were discovered. Thanks to H. López Toscano, R. Garza, and C. Alzate for sharing with us photographs of the new species with their respective locality data, which served to determine the distribution of the species. We thank our friend and colleague, K. Gil Amaya, for helping us locate *Malaxis* specimens in the herbarium of Universidad Nacional de Colombia (COL) and the staff at COL for allowing access to their orchid collections.

[1] Grupo de Investigación Schultes, Fundación Ecotonos, 760001, Valle del Cauca, Cali, Colombia
[2] Departamento de Biología, Universidad del Valle, Calle 13 # 100-00, Cali, Colombia
[3] Jardín Botánico de Cali-FZC, Cra. 2 Oe. #21, Valle del Cauca, Cali, Colombia
[4] Centro de Investigación Jardín Botánico Lankester, Universidad de Costa Rica, P.O. Box 302-7050, Cartago, Costa Rica
[5] Escuela de Biología, Universidad de Costa Rica, Apartado11501-2060, San José, Costa Rica
[6] Corresponding author: mrsierraariza80@gmail.com

Harvard Papers in Botany, Vol. 29, No. 1, 2024, pp. 147–152.

ISSN: 1938-2944, DOI: 10.3100/hpib.v29iss1.2024.n16, Published online: 30 June 2024

CR, COL, F, HLDG, JBL, MO, SEL, TOLI, US and USJ (physically), and B, BM, BRIT, COLO, DAO, G, GH, GM, GOET, HPUJ, IBUG, JBB, K, L, M, NY, P, PMA, UCH, and W (through digital images).

A Lankester Composite Dissection Plate (LCDP) of the new species was created using Adobe Photoshop® CS6, and the geographical distribution map was made with QGIS 3.36.2 tools. The conservation status of the species was assessed according to the International Union for Conservation of Nature Red List categories and criteria (IUCN, 2022). The Extent of Occurrence (EOO) and Area of Occupancy (AOO) were estimated based on the studied specimens using geographical data with the Geospatial Conservation Assessment Tool (GeoCAT, Royal Botanic Gardens, Kew: http://geocat.kew.org).

Taxonomy

Malaxis susanae Sierra-Ariza, J.S. Moreno, & Chinchilla, *sp. nov*. Fig. 1–2.
TYPE: COLOMBIA. Tolima: Municipio de Villahermosa, Vereda la Lorena, 2216 m, 17 December 2018, *M. A. Sierra Ariza & A. Albino Bohórquez 99* (Holotype: TOLI [029458]).

The new species is similar to *Malaxis carpinterae* (Schltr.) Ames, but is distinguished from it by the flowers that have a white (vs. green) lip, and the disc cavity that has an inconspicuously raised margin (vs. conspicuously raised in a retuse margin) at the apex.

A terrestrial, erect, caespitose *herb* up to 29 cm tall, including the inflorescence. *Roots* flexuous, short, up to 15 cm long, 2 mm in diameter, pubescent. *Pseudobulbs* 4.5–5.3 × 1.4–2.2 cm, epigeous, heteroblastic, conical, greenish, separated by an ascending rhizome with two internodes, each with one cataphyll, 2–3 cm long, greenish when immature, covered with leaf sheaths that become scarious and papyraceous with age, and one ovate, obtuse, green cataphyll, 3.5–5.3 × 1.3–2.4 cm, the margins connate below the proximal half, shedding as the pseudobulb matures. *Leaves* two per sympodial unit, produced from the base of the pseudobulb, long-petiolate, conduplicate, soft-textured; sheaths light green, margins connate above 3/4 of their length, forming a pseudostem, 8.0–8.6 × 0.4–0.6 cm; blade ovate, round, acuminate, margins slightly wavy, nine-veined, 8.5–11.0 × 4.5–5.5 cm, slightly anisophyllous, horizontal to ascending, subopposite to alternate, adaxially dark green, lustrous, abaxially light green, dull. *Inflorescence* produced from the apex of the pseudobulb, erect, corymbose, 18.5 cm long; peduncle 15–17 × 0.2–0.3 cm, light green, covered up to the proximal half with leaf sheaths, seven-keeled; rachis 2 cm long. *Floral bracts* ovate, caudate to acute, concave, greenish, lustrous, 0.8–1.4 × 0.5–0.7 mm. *Pedicels* plus ovaries terete, inconspicuously keeled, with 180-degree twisting, 6–10 mm long, white on lower 3/4, apically greenish. *Flowers* nonresupinate, spreading, lustrous; sepals and petals white to greenish-white, lip white, slightly greenish at the apex, column greenish, with a yellowish operculum; flowers becoming ocher with age. *Dorsal sepal* ovate, acute, convex, adpressed to the ovary, three-veined, 2.4–3.2 × 1.4–1.7 mm. *Lateral sepals* elliptic, obtuse, convex, divergent, margins becoming recurved as anthesis progresses, three-veined 2.8–3.2 × 1.1–1.5 mm, connate at the base 0.6–0.8 mm. *Petals* linear, obliquely truncate, recurved, arcuate, sometimes surrounding the ovary, margins revolute, one-veined, 2.1–2.3 × 0.25–0.40 mm. *Lip* trilobed, sagittate, trifid, deeply concave, papillose, fleshy, margins entire, thick, 3.0–3.5 × 2.0–2.2 mm; lateral lobes triangular, acute, recurved, spreading, 8 × 7 mm; midlobe ovate, trifid, 2.6–3.0 × 2.0–2.2 mm, with the disc cavity ovate in outline, subcordate, obtuse, 1.1–1.5 × 1.0–1.5 mm × 0.9 mm deep, divided by a pandurate costa, similar in width at the base and apex, adaxially tapered, flattened above, with subcavities abaxially deeply convex, laterally cavate by ca. 0.2 mm, apically delimited by a semilunate, emergent thickening, with the margin inconspicuously raised; apical margin short, transversely elliptic, trifid, margins incurved, 0.8 mm long, lateral teeth obtuse, convergent, 0.4 mm, central tooth obtuse, incurved, 0.4 mm. *Column* 0.8–1.3 × 0.8–1.2 mm, subquadrate, dorsiventrally complanate, apex ventrally four-lobed; rostellum erect, truncate, abaxially incurved, appearing retuse, bearing two viscaria at the apex; stigma obcordate, concave, longitudinally bilobed. *Pollinia* four in two obovoid, ventrally concave hemipollinaria, 0.4 × 0.2 mm. Fruits not seen.

Distribution and habitat: Known only from Colombia. In the type locality, the plants grow in a fragment of very humid montane forest (BMH-MB) in the Azufrado River basin in the municipality of Villahermosa in the northern area of the Tolima department, between 2000 and 2300 m elevation, as a terrestrial, understory plant, on soils with abundant humus and humidity, and with limited exposure to sunlight.

Plants of this species inhabit the three mountain ranges of the Colombian Andes. In the Eastern Andes, it is found in the municipality of Floridablanca, Santander Department; in the Central Andes, in the municipalities of Medellín and Amalfi, Antioquia Department; and in the type locality, Tolima Department. Additionally, in the Western Andes, it has been found in the municipality of Roldanillo, Valle del Cauca Department (Fig. 3–4).

Phenology: Plants were documented in flower in January, April, September, and December.

Eponymy: Named in honor of María Susana Muhamad González, a distinguished Colombian political scientist and environmentalist, who currently serves as the Minister of Environment of Colombia. She is celebrated for her unwavering commitment to the care, restoration, and conservation of Colombia's environment. In 2023, she was recognized by Reuters Impact as one of the top 25 female leaders globally in the fight against climate change. Additionally, in 2024, the Women Economic Forum honored her as the Woman of the Decade in Colombia for her exceptional efforts. Her achievements include securing significant resources to combat deforestation in the Amazon and leading Colombia's successful bid to host COP16 on biodiversity in 2024.

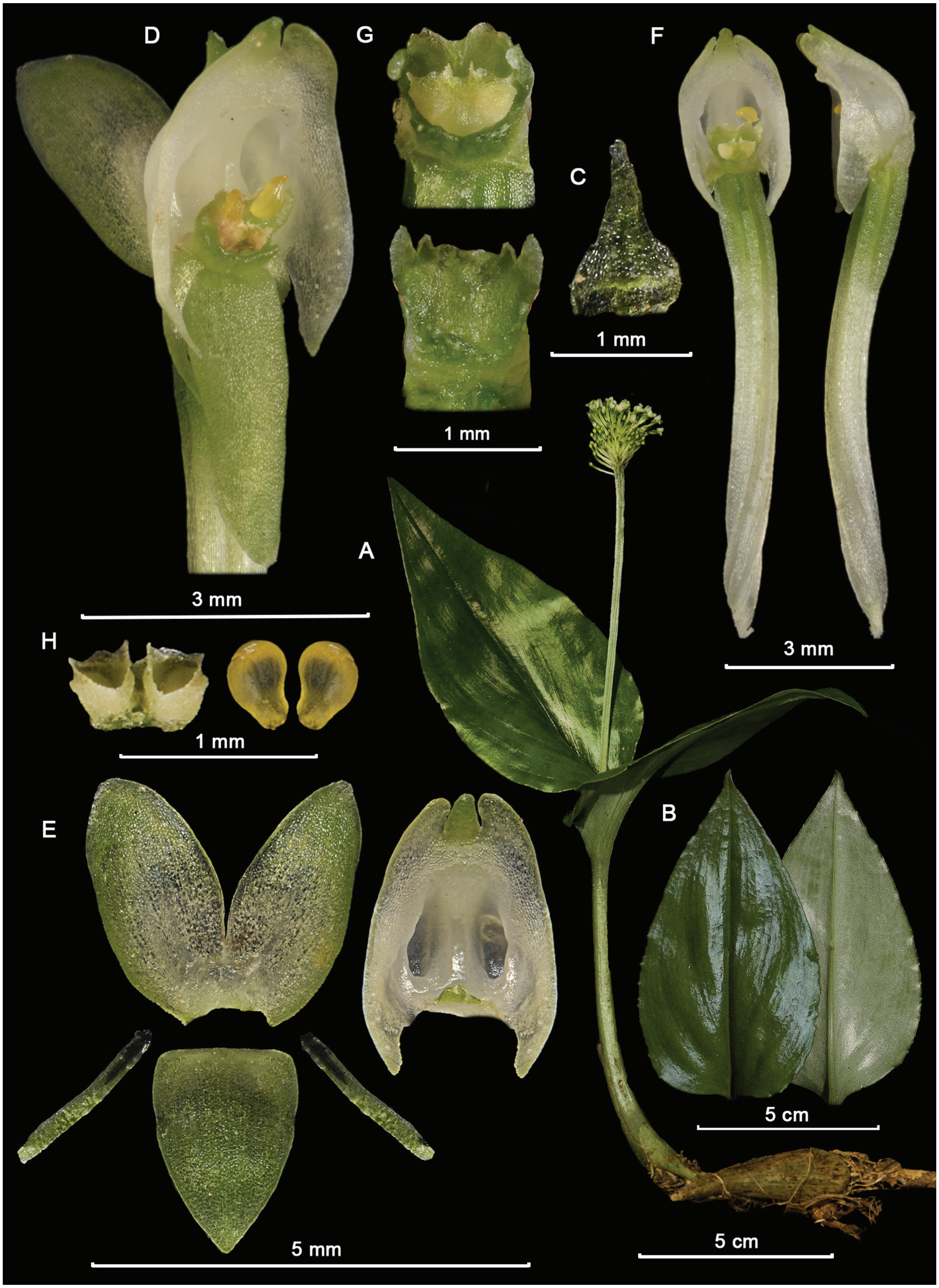


FIGURE 1. Lankester Composite Digital Plate of *Malaxis susanae* Sierra-Ariza, J.S. Moreno, & Chinchilla. **A**, Habit; **B**, Leaves; **C**, Floral bract; **D**, Flower, oblique view; **E**, Dissected perianth (lip to the right); **F**, Pedicel and ovary, lip and column, frontal (left) and lateral (right) views; **G**, Column, dorsal (top) and ventral (bottom) views.; **H**, Operculum (left) and pollinia (right). LCDP by M. A. Sierra-Ariza from the holotype (*Sierra Ariza & Albino Bohórquez 99*, TOLI).

FIGURE 2. Flowers of *Malaxis susanae* Sierra-Ariza, J.S. Moreno, & Chinchilla. From left to right: front, oblique, lateral and back views. By M. A. Sierra-Ariza from the holotype (*Sierra Ariza & Albino Bohórquez 99*, TOLI).

FIGURE 3. Comparison of flowers of *Malaxis susanae* Sierra-Ariza, J.S. Moreno, & Chinchilla from different locations in Colombia. **A**, Valle del Cauca Department, 2 May 2015 by C. Alzate; **B**, Tolima, 18 December 2018 by M. A. Sierra-Ariza; **C**, Santander, 24 September 2018 by H. López. Prepared by M. A. Sierra-Ariza.

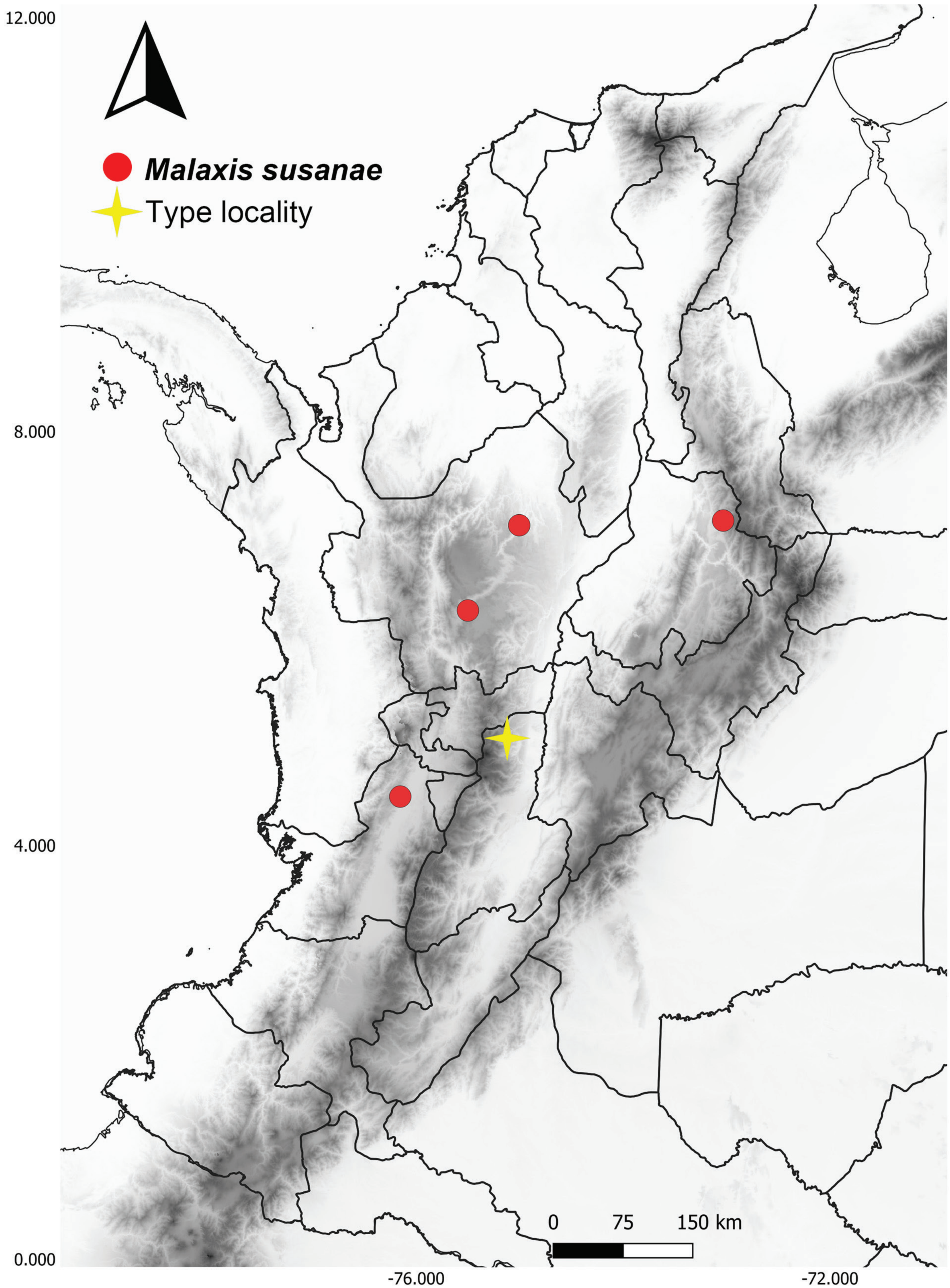


FIGURE 4. Distribution of *Malaxis susanae* Sierra-Ariza, J.S. Moreno, & Chinchilla in western Colombia based on field observations (no vouchers were made) and on the type locality. Prepared by J. S. Moreno.

Conservation status: *Malaxis susanae* is endemic to Colombia and known from five locations in the Andes Cordillera. Its extent of occurrence (EOO) was estimated to be 38,847 km^2 with an area of occupancy (AOO) of 20 km^2. In these known localities, plants of *Malaxis susanae* grow in forest relicts, which are not protected, or near protected wildlife areas. Fragmentation and loss of habitat caused by deforestation and expansion of the agricultural frontier are the main latent threats in the surrounding area. Studies on the population size and ecology of this species are needed to further assess its conservation status. Therefore, the species is listed as Vulnerable (VU), under criteria B1ab(i, ii)+2ab (i, ii).

Malaxis susanae can be easily recognized by its caespitose growth, with two leaves per sympodial unit, with ovate, rounded, acuminate blades. The corymbose inflorescence has flowers with white to greenish-white sepals and petals, and the lip is white, trilobate, sagittate, trifid, deeply concave, with two cavities. The whitish flowers of *Malaxis susanae* are similar to the flowers of *Malaxis pittieri* (Schltr.) Ames, a species native to Costa Rica and Panama, but the latter is morphologically very different: it is proportionally smaller, has one leaf per sympodial unit, with the cordate-amplexicaul blade at the base, has a lax, racemose inflorescence, and the lip has an entire midlobe at the apex (see Chinchilla et al., 2022).

The new species is also similar to *M. carpinterae*, a species endemic to Costa Rica; however, in addition to the characteristics included in the diagnosis, *M. susanae* is distinguished by its dark green (vs. light green) leaf blades, an inflorescence with whitish (vs. greenish) pedicels, flowers with whitish (vs. greenish) sepals and petals, and the lip, as it ages, with incurved (vs. erect) apical margins.

Among species of *Malaxis* that grow in Colombia, *Malaxis susanae* is morphologically similar to *Malaxis caracasana* (Klotzsch ex Ridl.) Kuntze, *Malaxis lobulata* L.O. Williams, and *Malaxis carlos-parrae* Szlach. & Kolan., because of its caespitose growth, ovate, acuminate leaf blades, corymbose inflorescence, flowers with the three-lobed, sagittate, concave lip, with triangular, recurved lateral lobes, and the ovate, trifid midlobe, with two subcavities. *Malaxis susanae* is distinguished from *M. caracasana* by its ovate (vs. lanceolate), larger leaf blades (8.5–11.0 × 4.5–5.5 cm vs. 3.8–4.8 × 1.2–1.6 cm), flowers with whitish (vs. greenish) sepals and petals, its ovate (vs. lanceolate) dorsal sepal, the elliptic (vs. lanceolate) lateral sepals, and the white lip (vs. green), with an ovate (vs. oblong-quadrate) midlobe. *M. lobulata* can be distinguished from *M. susanae* by its greenish sepals, petals, and lip, the midlobe of which is oblong, subpandurate (vs. ovate), with rounded (vs. obtuse) apical lobes forming shallow (vs. deep) sinuses, and the midlobe exceeds more than twice the length of the lateral lobes (vs. subequal teeth). *M. carlos-parrae* is differentiated from *M. susanae* by its lip that has a bipartite disc cavity with a broad (vs. narrow) costa, apically delimited by a crescentic emerging thickening, raised on an erose (vs. inconspicuously raised) margin at the apex; the apical margin has inconspicuous, rounded (vs. conspicuous, up to 0.4 mm, obtuse) lateral lobes, and the middle lobe exceeds twice the length of the lateral lobes (vs. subequal).

From the set of characters discussed above, *M. susanae* may somewhat resemble *Malaxis excavata* (Lindl.) Kuntze, a species from Mexico, but the latter has flowers with green (vs. white) sepals, petals and lips, the sepals approximately exceeding double the length of the lip (vs. subequal), and the midlobe of the lip has an elongated middle tooth, more than twice the length of the lateral teeth.

Literature Cited

Bentham, G., and J. D Hooker. 1883. Genera Plantarum 3, Pars II. L. Reeve, Londini.

Bernal, R., S. R. Gradstein, and M. Celis (editors). 2016. Catálogo de plantas y líquenes de Colombia. Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá: http://catalogoplantasdecolombia.unal.edu.co

Bogarín, D., and F. Pupulin. 2021. The orchid flora of Barra Honda National Park, Nicoya, Guanacaste, Costa Rica. Harvard Papers in Botany 26(1): 7–99.

Chinchilla, I. F., A. P. Karremans, and M. A. Blanco. 2022. New Species and a New Record of *Malaxis* (Malaxidinae) from Costa Rica. Lankesteriana 22(1): 37–51.

Chinchilla, I. F., A. P. Karremans, and M. A. Blanco. 2023. *Malaxis dressleriana*, a new orchid species honoring a botanist for all seasons, Robert Louis Dressler. Orchids, The Magazine of the American Orchid Society 92(8): 608–613.

González-Tamayo, R. 2002. *Malaxis* (Orchidaceae), breve discusión de los rasgos específicos y dos taxones nuevos. Ibugana 10(1–2): 67–75.

IUCN Standards And Petitions Committee. 2022. Guidelines for Using the IUCN Red List Categories and Criteria, version 15.1. Prepared by the Standards and Petitions Committee: https://nc.iucnredlist.org/redlist/content/attachment_files/RedListGuidelines.pdf

Ministerio De Ambiente Y Desarrollo Sostenible Y Universidad Nacional De Colombia. 2015. Plan para el estudio y la conservación de las orquídeas en Colombia. Texts by: Betancur, J., H. Sarmiento-L., L. Toro-González, y J. Valencia. Ministerio de Ambiente y Desarrollo Sostenible, Colombia. Universidad Nacional de Colombia, Bogotá D.C.

Pérez-Escobar, O. A., and M. A. Blanco M. 2014. Rediscovery of *Malaxis nana* (Orchidaceae: Malaxideae) in Costa Rica, with an updated description. Lankesteriana 14: 109–114.

Pridgeon A. M., P. J. Cribb., M. W. Chase, and F. Rasmussen. 2005. Genera Orchidacearum, Vol. 4: Epidendroideae (Part 1). Oxford University Press, Oxford.

Swartz, O. 1788. Orchidaceae. Pages 118–126 in M. Swederi, ed., Nova Genera et Species Plantarum seu Prodromus. Holmiæ, Upsala & Abo.

COGNIZING BOTANICAL ARCHITECTURAL MODELS IN THE CAATINGA VEGETATION OF NORTHEASTERN BRAZIL

Daniele Ancelmo Souza,[1] Bianca Volponi da Silva,[1] Fernanda Kelly Gomes da Silva,[2] José Iranildo Miranda de Melo,[2,3] and Dilma Maria de Brito Melo Trovão[2]

Abstract. Architectural models reflect the genetic designs of tree growth and development from their juvenile to adult phases and the balance between endogenous growth processes and exogenous environmental restrictions. We analyzed six species growing in xeric *Caatinga* vegetation in northeastern Brazil (*Jatropha mollissima* var. *mollissima*, *Mimosa paraibana*, *Sarcomphalus joazeiro*, *Aspidosperma pyrifolium*, *Croton blanchetianus*, and *Pityrocarpa moniliformis*) in terms of their architectural models and axis categories (growth modes, types of branching, branch geometry, and the presence or absence of reproductive structures). All of the species studied exhibited orthotropic orientation axes and rhythmic growth. As for the other axis categories, there were differences. Two architectural models were identified for the species: the Leeuwenberg model for *J. mollissima* and *A. pyrifolium*, and Rauh's model for *C. blanchetianus*, *M. paraibana*, *S. joazeiro*, and *P. moniliformis*. We identify the architectural models associated with the species analyzed, demonstrate their axis patterns, and provide a basis for future studies involving canopy architecture, especially with regard to the Brazilian semiarid region.

Keywords: axis categories, canopy architecture, semiarid

Architectural models represent inherent growth strategies that describe how plants develop their shapes and architectures throughout their life cycles, thus illustrating the balance between endogenous growth processes and exogenous restrictions exerted by the environment (Barthélemy and Caraglio, 2007; Taugourdeau et al., 2012). Architectural analysis represents a detailed, multi-level, comprehensive, and dynamic approach to evaluating plant development, bringing together concepts and analytical methods that provide powerful tools for studying the shapes and ontogenies of the various morphological expressions of plants, considering them as a whole, from germination to death (Barthélémy and Caraglio, 2007).

Plants show broad interspecific variability in terms of their shapes that reflect their genetic origins, ontogenetic variability (which encompasses differences between individuals, or juvenile and adult individuals), and phenotypic plasticity, through their variable responses to different environmental conditions (Aguiar, 2014). While there can be variations, each tree follows a specific development program after germination that is controlled by its genes (Hallé, 2010). The final shape of an adult tree, however, can be modified by ecological factors, even though developmental rules are persistent; analyzing these rules is the goal of plant architectural studies. The genetic program for the growth and development of a young tree is referred to as its architectural model (Hallé, 2010; Prado et al., 2020).

Twenty-three architectural models have been described, but the number of variants can be as large as the number of species (Vester, 2002). There are known cases of plants that follow 2–3 architectural models before reaching their adult phase (Aguiar, 2014), with those variations resulting from factors such as reiteration. Reiteration mechanisms were first described by the Dutch botanist, Roelof Oldeman, and generally refer to the development of a model within another model (Hallé, 2010), a process by which the architecture of a tree adjusts not only to damage suffered in its environment (such as the loss of branches, or stress), but also to environmental pressures, causing it to assume architectural characteristics different from its original model (Hallé et al., 1978; Tourn et al., 1999).

The identification of plant architectural models is possible through the observation and analysis of their architectural units; architectural units, in turn, can be defined as the basic functional and morphological units of a species (Edelin, 1984; Barthélémy et al., 1997), the set of different categories of axes that a species produces until the emergence of its reproductive structures (Barthélémy et al., 1997; Tourn et al., 1999; Barthélemy and Caraglio, 2007). The axis categories can be described by a series of morphological characteristics that include, first, the growth mode, which can be determinate (when meristematic activity is automatically interrupted after a genetically determined structure is completed) or indeterminate (when the apical meristem remains indefinitely operational). Continuous growth is observed when, in general, there are no interruptions during the entire developmental phase (Barthélemy and Caraglio, 2007), although detailed observations have shown that irregular interruptions can occur that are not always correlated with environmental variables (Hallé et al., 1978). Rhythmic growth occurs when vegetative growth is suspended or interrupted during a developmental season (Barthélemy and Caraglio, 2007).

D. A. S., D. M. B. M. T., J. I. M. M., and F. K. G. S. thank FAPESq-PB and PELD INTEGRADO RIO PARAÍBA (FAPESq/PELD Call N. 21/2020 Grant term N. 403/2021) for financial support in conducting the research. J. I. M. M. thanks CNPq (National Council for Scientific and Technological Development) for the Research Productivity Scholarship-PQ2 (Proc. no. 306658 /2022-4).

[1] Departamento de Biologia, Universidade Estadual da Paraíba, 58429-500 Campina Grande, Paraíba, Brazil

[2] Programa de Pós-Graduação em Ecologia e Conservação, Departamento de Biologia, Universidade Estadual da Paraíba, 58429-500 Campina Grande, Paraíba, Brazil

[3] Corresponding author: tournefort@gmail.com

Harvard Papers in Botany, Vol. 29, No. 1, 2024, pp. 153–158.

ISSN: 1938-2944, DOI: 10.3100/hpib.v29iss1.2024.n17, Published online: 30 June 2024

The second morphological characteristics is the type of branching, which can vary from monopodial (when the branches present an indefinite growth series) to sympodial (when the branches present a defined growth series). In other words, indeterminate growth is observed in plants with monopodial elongation, while determinate growth is observed in plants showing sympodial elongation (Aguiar, 2014). Third, the geometry of branching can be orthotropic (when they grow vertically) or plagiotropic (when they grow horizontally), and, fourth, the presence or absence of reproductive structures, and their positions, which can be terminal or axillary (Barthélemy and Caraglio, 2007; Costa and Longhi, 2018; Prado and Trovão, 2023).

Twenty-three architectural models were recognized among seed plants by Hallé and Oldeman (1970) (Tourn et al., 1999), whether herbaceous or woody. The greatest variability of these structural models is found in the tropics. Architectural models are genetically determined, and have descriptive utility in perceiving plant forms, although their ecological and evolutionary significance is unclear (Tomlinson, 1983). Each model is defined by a combination of the above-mentioned morphological characteristics, and they are named for the botanists who contributed to that knowledge or who carried out morphological research on plants exhibiting a particular model (Hallé et al., 1978). In light of the structural complexity of the Brazilian semiarid vegetation and the general lack of data and studies related to this topic, we sought to investigate the axis categories of Caatinga species and described the architectural models found in the Caatinga domain.

MATERIALS AND METHODS

Study area and the species studied

The present study was undertaken between November 2022 and October 2023, during which time we examined individual plants growing in the Vereda Grande Farm (07°31'31.5"S, 036°03'05.7"W) and the Trovão de Mello Farm (07°30'10.7"S, 035°57'40.8"W), both located in the municipality of Barra de Santana, Paraíba State, Brazil (Fig. 1). The species were chosen because of their common occurrence in the region (Silva et al., 2014): *Jatropha mollissima* (Pohl) Baill. var. *mollissima* (Euphorbiaceae), *Croton blanchetianus* Baill. (Euphorbiaceae), *Mimosa paraibana* Barneby (Fabaceae), *Aspidosperma pyrifolium* Mart. & Zucc. (Apocynaceae), *Pityrocarpa moniliformis* (Benth.) Luckow & R.W. Jobson (Fabaceae), and *Sarcomphalus joazeiro* (Mart.) Hauenschild (Rhamnaceae). A total of 30 individuals (five specimens per species) were selected that fulfilled the basic inclusion criteria described by Rodal et al. (2013), where, to be considered an adult, a woody Caatinga individual must have a diameter at ground level of ≥ 3 cm and a height of ≥ 1m.

Observations of axis categories and the identification of variables

Individuals of each species were observed and photographed in the field; photographic records were also made focusing on their crowns. Schematic drawings were made of each individual to facilitate comparisons with the 23 models currently available in the specialized literature (Hallé et al., 1978; Costa and Longhi, 2018). After initial observations of the species and the 23 models, those that appeared to be most similar were selected for detailed studies and comparisons. The analyses consisted of the examination of sets of three basic characteristics (keys) that could be used to determine the architectural models (Hallé, 2010). The first key evaluated the orientation of the principal axes, which could be orthotropic or plagiotropic; the second key evaluated the arrangement of the species' axes, which could be continuous or rhythmical; the third key evaluated the position of the reproductive structures (terminal or axillary). The definition of the latter variable could be used to confirm other axis categories, such as whether the growth mode is determinate or indeterminate, and whether the species has monopodial or sympodial axes. The union of these series of characteristics, and their combinations, allowed the search for compatible architectural models.

Data analysis

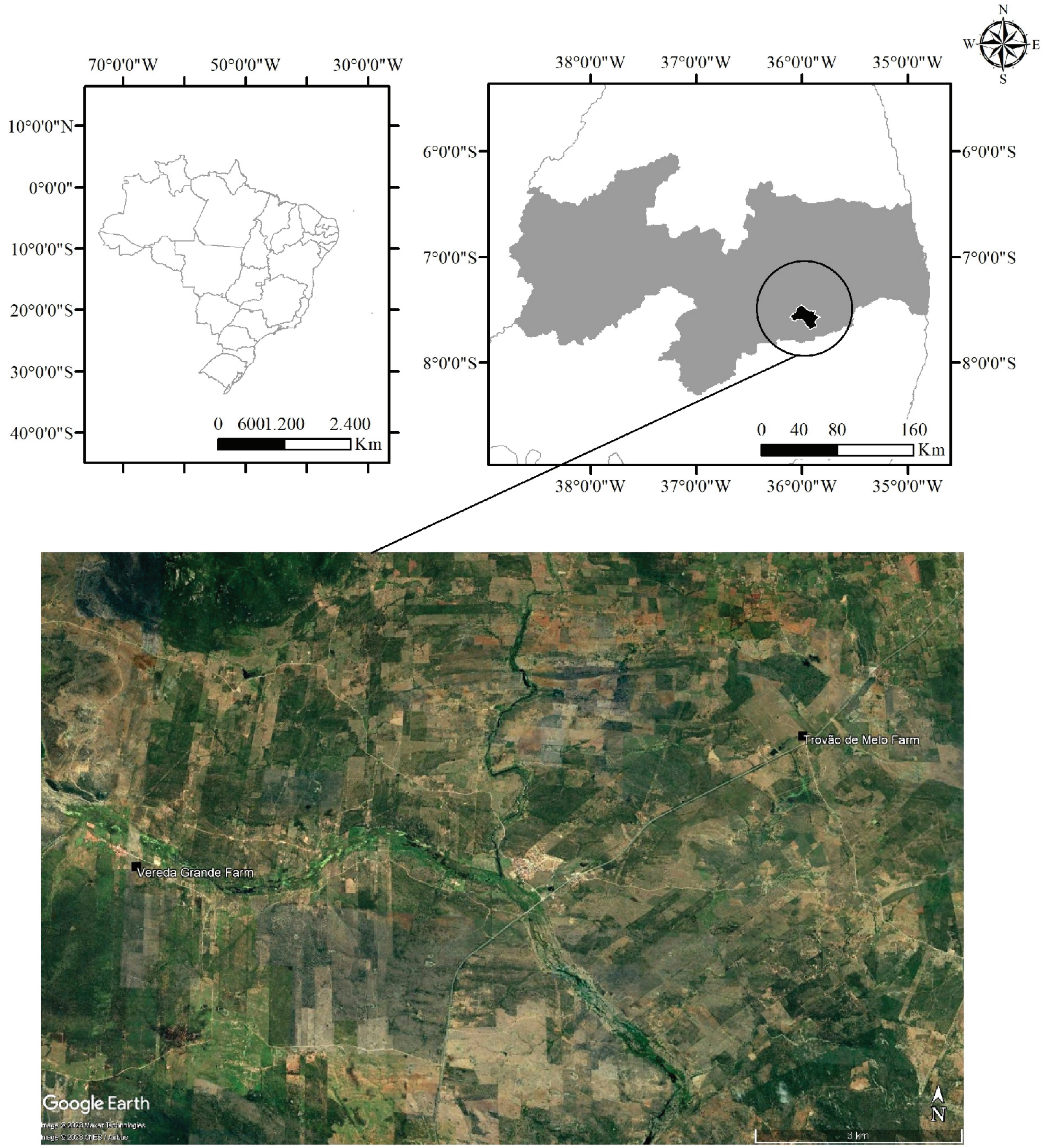
The data resulting from these observations and the identification of the architectural model corresponding to each plant were gathered in a descriptive table (Table 1) designed to identify possible patterns and similarities.

RESULTS AND DISCUSSION

Table 1 brings together the axis categories (according to Hallé, 2010) identified in the study species.

All of the species analyzed in this study showed rhythmic growth, which is characteristic of plants having intermittent growth. Another characteristic in common among all of the study species was the presence of orthotropic orientation axes, with vertical (or close to vertical) growth. Regarding the presence and positioning of the reproductive structures, there were variations among the species having terminal or lateral (or even both) reproductive structures, as was seen in *Croton blanchetianus* and *Sarcomphalus joazeiro*. Plants with axillary inflorescences had sympodial branches, as the apical meristem differentiates into other structures (reproductive structures, in this case) (Aguiar, 2014). The species that had lateral reproductive structures had monopodial branches, with the meristem remaining functional and elongation continuing through the juxtaposition of monopodial extension units (Aguiar, 2014). As such, the growth of plants with sympodial branching was determinate; the growth of plants with monopodial branching was indeterminate.

Two architectural models were recognized: the Leeuwenberg Model and the Rauh Model. The Leeuwenberg model (Fig. 2A-C) is characterized by a series of orthotropic modules, with three-dimensional sympodial branches that are determinate in their growth due to the production of a terminal inflorescence (Hallé et al., 1978). The species that met the characteristics of this model were *Jatropha*



Source: Google Earth Pro

Figure 1. Location of the study areas: Vereda Grande and the Trovão de Mello Farm, municipality of Barra de Santana, Paraíba State, Brazil.

TABLE 1. Axis categories found in Caatinga plant species. **A1,** growth mode; **A2,** type of branching; **A3,** geometry of the branches; and **A4,** reproductive structures and their positions.

SPECIES	A1	A2	A3	A4
Jatropha mollissima (Pohl) Baill. var. *mollissima*	determinate and rhythmic	sympodial	orthotropic	terminal
Croton blanchetianus Baill.	indeterminate and rhythmic	monopodial	orthotropic	lateral and terminal
Mimosa paraibana Barneby	indeterminate and rhythmic	monopodial	orthotropic	lateral
Sarcomphalus joazeiro (Mart.) Hauenschild	indeterminate and rhythmic	monopodial	orthotropic	lateral and terminal
Aspidosperma pyrifolium Mart. & Zucc.	determinate and rhythmic	sympodial	orthotropic	terminal
Pityrocarpa moniliformis (Benth.) Luckow & R.W. Jobson	indeterminate and rhythmic	monopodial	orthotropic	lateral

mollissima and *Aspidosperma pyrifolium*. The Rauh Model (Fig. 2D-F) is defined by a determinate architecture, with a monopodial trunk that grows rhythmically and, thus, develops layers of branches morphogenetically identical to the trunk; the flowers are lateral and do not affect the growth of the branches. The Caatinga species studied here that combine the characteristics of this model were *Croton blanchetianus*, *Mimosa paraibana*, *Sarcomphalus joazeiro*, and *Pityrocarpa moniliformis*. Caatinga vegetation is characterized by intermittent growth due to strong climatic seasonality that influences water availability and, therefore, the growth of perennial plants (Silva et al., 2017; Prado and Trovão, 2023). Fluctuations of water availability select for adaptations that reflect climate and soil conditions in this dynamic and seasonal vegetation (Souza et al., 2017; Silva and Cruz, 2018). The fact that the species growing in the Caatinga domain exhibit rhythmic growth is therefore not surprising, as woody species in areas having marked dry seasons evidence interrupted growth that can ensure their survival through inhospitable periods, with the resumption of growth at the beginning of the rainy season (Bathélémy and Caraglio, 2007; Aguiar, 2014).

Orthotropic orientation was another dominant characteristic in the species analyzed. That pattern was found by Costa and Longhi (2018) to be common in species growing in a subtropical deciduous forest. Woody plants with orthotropic axes have, in addition to a vertical (or close to vertical) orientation, radial symmetry, with spiral leaves and branches that extend in all directions (Bathélémy and Caraglio, 2007), aspects observed in the species studied here, which had branches arranged three-dimensionally. Costa and Longhi (2018) identified the Rauh model (Fig 2F) as one of the most common in temperate and tropical regions, reflecting, according to Hallé et al. (1978), its architectural flexibility and capacity for rapid regeneration (Vester and Saldarriaga, 1993; Vester and Cleef, 1998; Vester, 2002; Costa and Longhi, 2018).

The second model identified was the Leeuwenberg model (Fig 2C), which is characterized by having axis categories similar to those of the Rauh model, but differing primarily in the position of the inflorescences (which are terminal, and consequently influence the determinate growth of the sympodial axes). It is well-established that plant species have genetically determined growth patterns and architectural organization, although environmental factors will influence their development (Bathélémy and Caraglio, 2007; Hallé, 2010; Aguiar, 2014). The Leeuwenberg model is characteristic not only of secondary vegetation species, but also of species growing in areas subject to intense environmental disturbances, such as the Caatinga (Beltrán-Rodríguez et al., 2015; Moreno et al., 2017). Similarly, in a study undertaken in a Tropical Semideciduous Rainforest in Yucatan, Mexico, Vester (2002) identified 108 species distributed among 15 models. Another study undertaken in a Tropical Evergreen Rainforest in the Colombian Amazon reported 306 species distributed among 17 architectural models (Vester and Saldarriaga, 1993; Costa and Longhi, 2018), corroborating the idea that the numbers of models tend to decrease with increasing environmental stress arising from seasonality, as is commonly observed in seasonal forests and in accordance with the expectations of Hallé et al. (1978).

Therefore, both of the models identified in this study have characteristics compatible with the Caatinga domain, and it is not surprising that the Rauh and Leeuwenberg architectural models identified are characteristic of temperate and tropical climates with constant and regular disturbances.

Architectural complexity appears to be quite broad in the Caatinga domain, for in a sample of just six species, both Leeuwenberg and Rauh well-characterized axis architectural models were recognized. This work has both pioneering and exploratory characteristics, and should provide a framework for new studies on plant architecture in the semiarid region in Brazil.

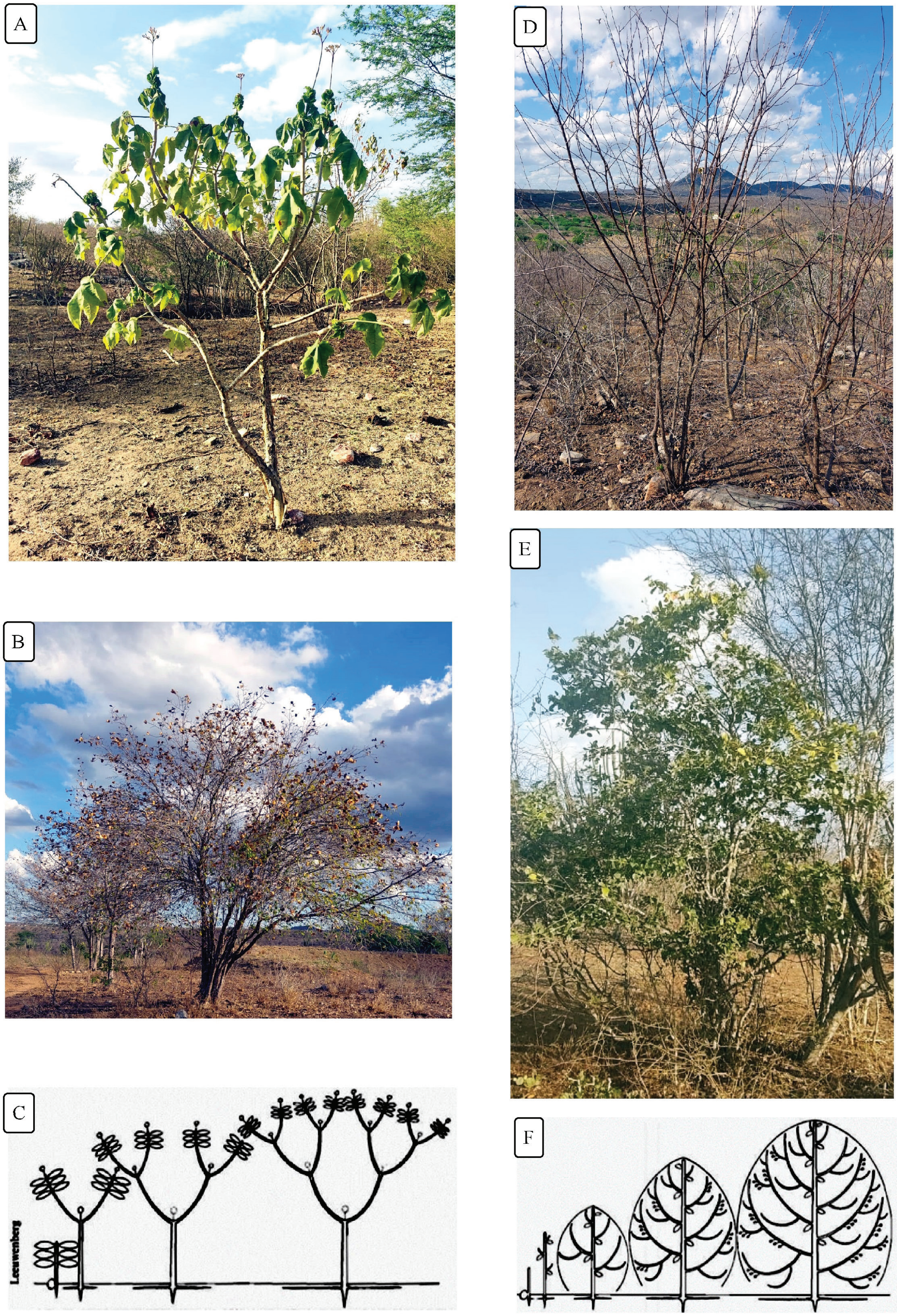


FIGURE 2. Canopy architecture. **A**, canopy of *Jatropha mollissima* var. *mollissima*; **B**, canopy of *Aspidosperma pyrifolium*. Photographs by D. A. Souza; **C**, botanical model of Leeuwenberg described by Hallé (2010); **D**, canopy of *Croton blanchetianus*; **E**, canopy of *Sarcomphalus joazeiro*. Photographs by D. A. Souza; **F**, botanical model of Rauh described by Hallé (2010).

Literature Cited

Aguiar, C. 2014. Arquitetura de Plantas. Instituto Politécnico de Bragança, Escola Superior Agrária, Bragança.

Barthélémy, D., Y. Caraglio, and E. Costes. 1997. Architecture, gradients morphogénétiques et age physiologique chez les végétaux. Pages 89–136 in J. Bouchon, P. de Reffye, and D. Barthèlèmy, eds., *Modelisation et simulation de l'architecture des végétaux*. Sciences Update, Editions INRA, Paris.

Barthélémy, D., and Y. Caraglio. 2007. Plant architecture: a dynamic, multilevel and comprehensive approach to plant form, structure and ontogeny. Ann. Bot. 99(3): 375–407.

Beltrán-Rodríguez, L., A. Romero-Manzanares, M. Luna-Cavazos, H. Vibrans, F. Manzo-Ramos, J. Cuevas-Sánchez, and E. García-Moya. 2015. Historia natural y cosecha de corteza de quina amarilla *Hintonia latiflora* (Rubiaceae). Bot. Sci. 93(2): 261–272.

Costa, M. P., and S. J. Longhi. 2018. Modelos arquitetônicos para as espécies arbóreas de uma floresta estacional subtropical no Rio Grande do Sul. Cienc. Florest. 28(4): 1418–1430.

Edelin, C. 1984. L'architecture monopodiale: L'exemple de quelques arbres d'Asie tropicale. Thèse de Doctorat d'État, Université Montpellier II, Montpellier.

Hallé, F., and R. A. A. Oldeman. 1970. *Essai sur l'architecture et la dynamique de croissance des arbres tropicaux*. Masson & CIE, Paris.

Hallé, F., R. A. A. Oldeman, and P. B. Tomlinson. 1978. *Tropical trees and forests: an architectural analysis*. Springer-Verlag, Berlin.

Hallé, F. 2010. Arquitectura de los árboles. Bol. Soc. Argent. Bot. 45(3–4): 405–418.

Moreno, E. C., S. L. Ortiz, C. O. Palacios, A. S. Islas, J. I. V. Hernández, and E. P. Herrera. 2017. Fenología y arquitectura arbórea de *Calyptranthes schiedeana* O. Berg, *Lysiloma acapulcense* (Kunth) Benth y *Tabebuia chrysantha* (Jacq.) G. Nicholson en agroecosistemas de Veracruz. Rev. Mex. Cienc. Forest. 8(40): 19–36.

Prado, C. H. B. A., D. M. B. M. Trovão, and J. P. Souza. 2020. A network model for determining decomposition, topology, and properties of the woody crown. J. Theor. Biol. 499: 110318.

Prado, C. H. B. A., and D. M. B. M. Trovão. 2023. The woody crown network model incorporates maximum height. Ecol. Modelling. 481: 110345.

Rodal, M. J. N., E. V. S. B. Sampaio, and M. A. Figueiredo. 2013. *Manual sobre métodos de estudo florístico e fitossociológico: ecossistema caatinga*. Sociedade Botânica do Brasil, Brasília.

Silva, F. K. G., S. F. Lopes, L. C. S Lopez, J. I. M. Melo, and D. M. B. M. Trovão. 2014. Patterns of species richness and conservation in the Caatinga along elevational gradients in a semiarid ecosystem. J. Arid Environ. 110:47–52.

Silva, J. M. C., I. R. Leal, and M. Tabarelli. 2017. Caatinga: The largest tropical dry forest region in South America. Switzerland, Springer.

Silva, D. V. S., and C. B. M. Cruz. 2018. Tipologias de Caatinga: uma revisão em apoio a mapeamentos através de sensoriamento remoto orbital e GEOBIA. Rev. Depart. Geog. 35: 113–120.

Souza, M. P., J. M. C. P. Coutinho, L. S. Silva, F. S. Amorim, and A. R. Alves. 2017. Composição e estrutura da vegetação de caatinga no sul do Piauí, Brasil. Rev. Verde Agroecol. Des. Sust. 12(2): 210–217.

Taugourdeau, O., F. Chaubert-Pereira, S. Sabatier, and Y. Guédon. 2012 Deciphering the Developmental Plasticity of Walnut Saplings in Relation to Climatic Factors and Light Environment. J. Experim. Bot. 62: 5283–5296.

Tomlinson, P. B. 1983. Tree Architecture. Amer. Sci. 71: 141–149.

Tourn, G. M., D. Barthélémy, and J. Grosfeld. 1999. Una aproximación a la arquitectura vegetal: conceptos, objetivos y metodología. Bol. Soc. Argent. Bot. 34(1–2): 85–99.

Vester, H. F. M., and A. M. Cleef. 1998. Tree architecture and secondary tropical rain forest development: a case study in Araracuara, Colombian Amazonia. Flora 193(1): 75–97.

Vester, H. F. M., and J. G. Saldarriaga. 1993. Algunas Características Estructurales, Arquitectónicas y Florísticas de la Sucesión Secundaria sobre Terrazas Bajas en la Región de Araracuara (Colombia). Rev. Fac. Nac. Agron. Medellín 64(1–2): 15–45.

Vester, H. F. M. 2002. Modelos arquitectónicos en la flora arbórea de la Península de Yucatán. Bot. Sci. 71: 45–57.

RECLASSIFICATION OF THE BERTHOLLETIA CLADE OF THE BRAZIL NUT FAMILY (LECYTHIDACEAE) BASED ON A PHYLOGENETIC ANALYSIS OF PLASTOME AND TARGET SEQUENCE CAPTURE DATA

Oscar M. Vargas,[1,11] Drew A. Larson,[2] Juvenal Batista,[3] Xavier Cornejo,[4] Bruno Garcia Luize,[5] Diana Medellín-Zabala,[8] Michel Ribeiro,[6] Nathan P. Smith,[7] Stephen A. Smith,[8] Alberto Vicentini,[9] Christopher W. Dick[8,10,11]

Abstract. The Neotropical clade of Lecythidaceae—Lecythidoideae—comprises 10 genera and more than 230 woody species that are usually rainforest trees. Lecythidoideae range from Mexico to southeast Brazil but are most diverse and abundant in the central Amazon and Guiana Shield regions. Previous studies found weak support for monophyly in the two species rich Amazon-centered genera, *Eschweilera* and *Lecythis*, and ambiguous relationships within the Bertholletia clade (*Eschweilera*, *Lecythis*, *Bertholletia* and *Corythophora*). We performed a phylogenomic analysis of Lecythidoideae with focus on the Bertholletia clade, using target capture sequencing of 343 nuclear loci and 10 informative plastome regions. Our sampling included 206 individuals from 130 described Neotropical species and ca. 10 undescribed taxa. Our limited sampling outside the Bertholletia clade confirmed the monophyly of *Grias*, *Gustavia*, *Couroupita*, *Allantoma*, *Cariniana*, and *Couratari*. Within the Bertholletia clade, however, our work shows that *Lecythis* and *Eschweilera*, as currently circumscribed, are polyphyletic. To align Lecythidaceae taxonomy with phylogeny, we propose six genus name changes within the former *Lecythis* and *Eschweilera*. Our new circumscription maintains the core *Lecythis* (Ollaria clade) and *Eschweilera* (Parvifolia clade). For the clade comprising the Poiteau and Chartacea sections of *Lecythis* we reinstate *Chytroma* Miers. For the former Pisonis section of *Lecythis* we reinstate *Pachylecythis* Ledoux. For the former Tetrapetala section of *Eschweilera* we propose *Imbiriba gen. nov*. For the Corrugata clade (formerly of *Lecythis*) we propose *Guaiania gen. nov*. We propose to elevate the Integrifolia clade of *Eschweilera* as a new genus, *Scottmoria gen. nov*. We determined that the Manaus-area endemic, *Eschweilera amazoniciformis*, is an isolated sister lineage to *Corythophora* and *Imbiriba*. We recognize this species as the monotypic genus *Waimiria gen. nov*. Our proposal for taxonomic changes highlights distinct evolutionary histories and eliminates paraphyletic and polyphyletic genera, resulting in 60 name changes for species or subspecies.

Keywords: Bertholletia clade, Ericales, *Eschweilera*, phylogenomics, *Lecythis*, Neotropics, tropical rainforest

Lecythidaceae is a pantropical family of woody plants belonging to the order Ericales. It is classified into either five (APG IV, 2016) or three (Huang et al., 2015, Mori et al., 2017) subfamilies. In the latter classification, used here, Napoleonaeoideae and Scytopetaloideae are considered families, leaving Lecythidaceae with three subfamilies: Foetidioideae (predominantly in Madagascar), Barringtonioideae (synonym: Planchonioideae; Asia and Africa), and Lecythidoideae (Neotropics). Lecythidoideae is the most species-rich subfamily containing ca. 230 species (Mori et al., 2017) out of the ca. 278 known species in the family (Mori et al., 2007; Huang et al., 2015; Mori et al., 2017) with several new species described each year.

Lecythidoideae are understory, canopy, and emergent trees with distinctive woody fruits and often highly specialized zygomorphic flowers (Prance and Mori, 1979;

This research was funded by several National Science Foundation awards, including Dimensions of Amazon Biodiversity (DEB 124086 C. Dick and Scott Mori), The Dynamics of Mountains, Landscapes and Climate in the Distribution and Generation of Biodiversity of the Amazon/Andean Forest (FESD Type I 1338694 to C. Dick and S. Smith) and, most recently, Temperate radiations and tropical dominance: the diversification and evolution of the plant clade Ericales (NSF DEB 1917146 to S. Smith and C. Dick). We thank the Institute for Amazon Study (INPA) and the Biological Dynamics of Forest Fragments Project (BDFFP) for facilitating access to field sites north of Manaus for field study and collections; The New York Botanical Garden (NYBG) provided silica dried leaf tissues; the Smithsonian Tropical Research Institute (STRI) facilitated permits and field research in Panama. The Ministerio de Ambiente (MIAMBIENTE) in Panama provided permits for field collections in Panama. B. Garcia Luiz acknowledges grants #2019/24823-2, #2020/03379-4 and #2021/11670-3, São Paulo Research Foundation (FAPESP) and the Center for Research on Biodiversity Dynamics and Climate Change FAPESP Grant #2021/10639-5. M. Ribeiro thanks the "Coordernação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES). We are all grateful for the enduring contributions of Scott Mori (1941–2020), who dedicated most of his professional career to understanding the Lecythidaceae and trained many students to carry on this research. We also want to acknowledge Paulo Apostolo (1956–2021), who was trained as a woodsman and field technician in the BDFFP Km 41 Lecythidaceae project and became a renowned Amazon Forest botanist in his own right. Paulo taught several of us to identify dozens of species in the field. We thank three anonymous reviewers for important criticisms and suggestions. Reviewer 2 suggested the name *Guaiania* and provided text on some ethnobotanical uses of Lecythidaceaae. This is publication number 872 in the BDFFP series.

[1] Department of Biological Sciences, California State Polytechnic University, Humboldt, Arcata, California, 95521, U.S.A.
[2] Department of Biology, Indiana University, Bloomington, Indiana, 47405, U.S.A.
[3] Herbario PMA, Departamento de Botánica, Universidad de Panamá, Estafeta Universitaria, Panamá City, Republic of Panama
[4] Herbario GUAY, Departamento de Botánica, Facultad de Ciencias Naturales, Universidad de Guayaquil, Guayaquil, Ecuador
[5] Laboratory of Evolutionary Ecology and Plant Genomics, Department of Plant Biology, Institute of Biology, University of Campinas, Campinas, Brazil
[6] Laboratório de Ecologia de Restinga e Mata Atlântica, Universidade Federal do Espírito Santo, São Mateus, Espírito Santo, Brazil
[7] Rio das Furnas Private Natural Heritage Reserve, Alfredo Wagner, Santa Catarina, Brazil
[8] Department of Ecology and Evolutionary Biology and Herbarium. University of Michigan, Ann Arbor, Michigan 48109, U.S.A.
[9] National Institute of Amazonian Research (INPA), Manaus, AM, Brazil
[10] Smithsonian Tropical Research Institute, Panama City, Republic of Panama
[11] Corresponding authors: ov20@humboldt.edu; cwdick@umich.edu

Harvard Papers in Botany, Vol. 29, No. 1, 2024, pp. 159–179.

ISSN: 1938-2944, DOI: 10.3100/hpib.v29iss1.2024.n18, Published online: 30 June 2024

Mori and Prance, 1990). Lecythidaceae are ranked as the third most abundant family of trees in Amazonian forests based on forest inventory data (ter Steege et al., 2013) with *Eschweilera* Mart. ex DC. and *Eschweilera coriacea* (DC.) S.A. Mori being the most common Amazon tree genus and species, respectively (ter Steege et al., 2013). In addition to their large role in carbon sequestration, Lecythidaceae host diverse interactions with animals: bees and bats pollinate their flowers, and the seeds are dispersed by rodents, birds, monkeys, bats, and fish (Prance and Mori, 1979; Mori and Prance, 1990). The family includes economically important timber trees (e.g., *Cariniana legalis* (Mart.) Kuntze), foods (e.g., Brazil nut, *Bertholletia excelsa* Bonpl.), ornamentals (e.g., cannonball tree, *Couroupita guianensis* Aubl.), and some of the longest-lived rain forest trees, with individual trees of *Cariniana micrantha* Ducke near Manaus, Brazil, estimated via carbon dating to be more than 1400 years old (Chambers et al., 1998). In the Amazon and Orinoco river basins, the inner bark of several species of Lecythidaceae, e.g., *Eschweilera subglandulosa* (Steud. ex O. Berg) Miers and *Lecythis alutacea* (A.C. Sm.) S.A. Mori (*J. A. Steyermark* 60767), are an ancestral source of cordage and head bands, and that of others, e.g., *Allantoma lineata* (Mart. ex O. Berg) Miers and *Couratari guianensis*, as a source of cigarette paper (Mori et al., 2010 and onwards), called *Tabarí* (Mori and Prance, 1999).

The classification of Lecythidoideae is relatively stable thanks to the comprehensive monographs published by Prance and Mori (1979) and Mori and Prance (1990). The incorporation of molecular phylogenetics using chloroplast markers and the internal transcribed spacer (ITS) confirmed Lecythidoideae as monophyletic and sister to the other two subfamilies (Mori et al., 2007). Molecular phylogenies also grouped several zygomorphic-flowered genera (*Eschweilera*, *Lecythis* Loefl., *Corythophora* R. Knuth, and *Bertholletia* Bonpl.) into the Bertholletia clade, which is nested within a grade of actinomorphic-flowered (*Grias* L., *Gustavia* L., and *Allantoma* Miers) and zygomorphic-flowered genera (*Cariniana* Casar., *Couroupita* Aubl., and *Couratari* Aubl.) (Mori et al., 2007; Huang et al. 2015; Mori et al., 2017; Vargas and Dick, 2020). All prior molecular phylogenies have inferred monophyly for *Allantoma* (8 spp.), *Cariniana* (9 spp.), *Corythophora* (4 spp.), *Couroupita* (3 spp.), *Grias* (14 spp.), and *Gustavia* (47 spp.), while the large Amazon-centered genera *Eschweilera* (ca. 97 spp.) and *Lecythis* (ca. 31 spp.) have been inferred as polyphyletic (Mori et al., 2007; Huang et al., 2015; Mori et al., 2017; Vargas and Dick, 2020). Huang et al. (2015) recognized the need for a generic circumscription within the Bertholletia clade (see Table 1 for clade names) but refrained from making nomenclatural changes because relationships among the internal clades were largely unresolved.

The goal of this study was to resolve these uncertain phylogenetic relationships within Lecythidoideae, especially within the zygomorphic-flowered and Amazon-centered Bertholletia clade. We performed phylogenomic analyses using nuclear genomic dataset based on family-specific probes developed by Vargas et al. (2019) and plastome regions shown to be informative for the subfamily (Thomson et al., 2018). Based on sampling of 130 species (~57% of Lecythidoideae), we resolved the internal clades within *Lecythis* and *Eschweilera* and propose a circumscription of genera within the Bertholletia clade that better reflects phylogenetic relationships.

Materials and Methods

Sampling

Although we sampled broadly from the Lecythidoideae, our greatest sampling efforts were focused on the Bertholletia clade from the central Amazon and Guiana Shield regions. We sampled a total of 206 individuals comprising 130 described Neotropical species and seven outgroup species (Table S1). NYBG provided about half of our samples from their silica-dried tissue collections, whose corresponding vouchers are at NYBG. Many of the NYBG collections came from an intensively studied forest in French Guiana (Mori, 1987). About a quarter of the samples come from recent collections within a forest inventory plot of Lecythidaceae trees known as the Lecythidaceae plot (Mori and Lepsch da Cunha, 1995) within Reserve 1501 (km 41) of the Biological Dynamics of Forest Fragments Project (BDFFP) 70 km north of Manaus, Brazil. We sampled multiple individuals for some species, especially within the *Eschweilera* Parvifolia clade, because of reports of hybridization (Caron et al., 2019; Larson et al., 2021). Within the Parvifolia clade, *E. coriacea* was of special interest because of its genetic and morphological variability and taxonomic uncertainty (Heuertz et al., 2020). Voucher specimens of new collections were deposited at the BDFFP reference collection and at INPA in Manaus. While most of the species sampled are represented by Latin binomials, we included undescribed species, indicated as "sp. nov" in the cladograms, and some samples with ambiguous identities are represented only by their sample code "sp." Most of these latter samples are recent collections by coauthors and have associated herbarium vouchers (Table S1).

DNA Sequencing

To infer robust nuclear- and plastome-based phylogenies for Lecythidoideae we sequenced 344 nuclear genes previously identified as phylogenetically informative (Vargas et al., 2019) and ten informative chloroplast regions through genome skimming (Thomson et al., 2018). We performed DNA extractions using the NucleoSpin Plant Mini Kit II (Macherey-Nagel, Düren, Germany) following the manufacturer's protocol but extending the digestion step to an hour and adding 5 uL of proteinase K (20 mg/mL, Qiagen). Library preparation and HiSeq4000 (Illumina Inc.) sequencing was performed by Rapid Genomics (Gainesville, Florida) for samples with 100–1000 ng of DNA. Sequencing of bait enriched libraries (for the nuclear data) and un-enriched ones (for the plastome data) were performed independently. Our sequencing output comprised paired end reads of 150 bp that were processed with SeqyClean (Zhbannikov et al., 2017), removing low-quality reads and adaptors, and trimming read sections with a Phred score < 20 using a window of 10 bp. Sequence data are available from NCBI Bioproject PRJNA641333 in GenBank.

TABLE 1. Clades within the Bertholletia clade that we propose to recognize as distinct genera (Col. 1) are from Huang et al. (2015) with the exception of *E. amazoniciformis*. In column 3 we provide our justification for the revised classification.

GENUS AND PRIOR CLADE OR SECTION NAME	PROPOSED CHANGE	JUSTIFICATION OF NAME CHANGE
Lecythis Pisonis clade	*Pachylecythis* Ledoux	The Pisonis clade is polyphyletic in relation to core *Lecythis*.
Lecythis Poiteauii clade Chartacea clade	*Chytroma* Miers	The sister clades are polyphyletic in relation to core *Lecythis*. There is insufficient morphological variation to justify separating the clades into two genera.
Eschweilera *E. amazoniciformis* S. A. Mori	*Waimiria* C.W. Dick & O.M. Vargas *gen. nov*.	The species *E. amazoniciformis* is morphologically distinctive and polyphyletic with respect to other subclades of *Eschweilera s.l.*
Lecythis Corrugata clade	*Guaiania* O.M. Vargas & C.W. Dick *gen. nov*.	The Corrugata clade is polyphyletic in relation to core *Lecythis*.
Eschweilera Tetrapetala clade	*Imbiriba* O.M. Vargas, M. Ribeiro, & C.W. Dick *gen. nov*.	The Tetrapetala clade is polyphyletic in relation to core *Eschweilera*.
Eschweilera Integrifolia clade	*Scottmoria* Cornejo *gen. nov*.	This clade could be combined with core *Eschweilera*, but its distinctive morphology combined with the mostly Pacific pattern of distribution justify its elevation to genus.

Nuclear DNA Phylogeny

We employed HybPiper v1.3.1 (Johnson et al., 2016) to assemble the 344 target genes, of which we dropped one gene because of unsuccessful assembly. The Hybpiper pipeline uses Exonerate (Slater and Birney, 2005), BLAST+ (Camacho et al., 2009), Biopython (Cock et al., 2009), BWA (Li and Durbin, 2009), SAMtools (Li et al., 2009), GNU Parallel (Tange, 2011), and SPAdes (Bankevich et al., 2012) as dependencies. For each gene we aligned exons and introns independently and employed an exhaustive algorithm (linsi, 1k iterations) in Mafft v7.407 (Katoh and Standley, 2013). For the 39 introns for which the exhaustive alignment failed, a less exhaustive algorithm (fftnsi,1k iterations) was implemented (Table S2). Subsequently, exon and intron matrices were concatenated by gene, and these alignments were filtered with trimAl v1.4.rev22 (Capella-Gutiérrez et al., 2009) for problematic regions using the "-automated1" command, and for outlier sequences using the "-resoverlap 0.33 -seqoverlap 75" command. We employed RAxML v8.2.12 (Stamatakis, 2014) to calculate our 343 gene trees; exons and introns were treated as independent partitions. In order to identify taxa bearing extreme long branches, we employed TREESHRINK "-q 0.05" (Mai and Mirabab, 2018) for every gene tree produced by the RAxML per-gene analysis. We concatenated the 343 genes into a single matrix after removing the outlier taxa per-gene identified by THREESHRINK. We used the concatenated alignment to infer a species tree (referred from now onwards as the concatenated tree). We used ASTRAL v.5.6.3 (Zhang et al., 2018) to calculate a maximum quartet support species tree (MQSST), using trees pruned from outlier taxa identified with THREESHRINK and with nodes collapsed when bootstrap support was < 60%. We calculated the number of genes supporting every node on the RAxML concatenated tree using phyparts (Smith et al., 2015). The results were illustrated with phypartspiecharts.py (https://github.com/mossmatters/MJPythonNotebooks).

Chloroplast phylogeny

We generated a plastome phylogeny using a supermatrix consisting of 10 chloroplast regions: *ccs*A-*ndh*D, *rpl*16-*rps*3, *psb*M-*trn*D, *trn*G-*psa*B, *pet*D-*rpo*A, *psb*Z-*trnf*M, *trn*E-*trn*T, *trn*T-*psb*D and two segments of *ycf*1. These regions were identified as phylogenetically informative in a previous analysis of 24 Lecythidaceae chloroplast genomes (Thomson et al., 2018). To generate the sequences, a draft plastome was assembled for each sample using raw reads and GetOrganelle (Jin et al., 2020) with the options "-R 15 -k 21,45,65,85,105" and "-F embplant_pt" (Camacho et al., 2009; Bankevich et al., 2012; Langmead and Salzberg, 2012). In cases where multiple possible structural configurations were recovered, the first configuration was used. All contigs per assembly were merged prior to analysis. Each of the target regions were identified in one draft assembly (L289; Table S1) by using the primers reported in Thomson et al. (2018). We then identified the target regions in each of the other draft assemblies by conducting a BLAST search (Altschul et al., 1990; Camacho et al., 2009) for each region using an e-value cutoff of $1x10^{-3}$ and extracted the top hit, including bases that matched to the primers, with a custom script. We aligned sequences for each region with MAFFT v7.490 and the options "-genafpair," "-maxiterate 1000," and "-adjustdirectionaccurately." Alignments were each visually inspected for evidence of misidentified homology or other issues and primers were removed from each alignment. We also masked 10 columns of the *ccs*A-*ndh*D alignment because of suspected assembly issues and removed the last 394 columns of the *psb*Z-*trnf*M alignment because we found that it exactly matched the beginning of the *trn*G-*psa*B region. Sites with less than 50% matrix occupancy were removed with pxclsq and the 10 regions were concatenated with the program pxcat in phyx (Brown et al., 2017). An ML tree and 200 standard, non-parametric bootstraps were estimated with RAxML v8.2.11, with a single GTRCAT model partition. Conflict with the nuclear tree was assessed using the pxbp program in phyx and visualized with Figtree (http://tree.bio.ed.ac.uk/software/figtree/).

Taxonomic Circumscription

We obtained taxonomic information (e.g., accepted names, type specimen information, diagnostic characters, and specialized morphological terms) from Mori and Prance (1990) and from the Lecythidaceae Pages (Mori et al., 2010 and onward), which is an online resource maintained by the New York Botanical Garden. For nomenclatural changes at the genus level, we prioritized available names within the clade of interest, following rules of the International Code of Nomenclature (Turland et al., 2018). If there were no available generic names within a clade, we assigned a new name and provided an etymological justification. We consulted the International Plant Names Index (IPNI, 2020) for standardized taxonomic author names. We only provide synonyms if widely used; a full list of synonyms for each species is available on the Lecythidaceae Pages. We did not sample DNA from all of the new combinations. The assignment of unsampled species to a clade was based on their subgeneric classification (e.g., sections) as recognized by Mori and Prance (1990) and Mori et al. (2010 and onward). Our proposed nomenclature follows suggestions outlined by Huang et al. (2015) except in cases in which our data supported different phylogenetic relationships.

Results

Nuclear dataset

We obtained sequence data for 343 of the 344 targeted gene regions. On average, we recovered 321 regions per sample, with a maximum of 338 and minimum of 130 (Table S1). A concatenated alignment of all 343 nuclear gene regions generated 1,702,870 columns with a cell occupancy of 93.3%, with 285,682 parsimony-informative characters. We inferred a concatenated- and a coalescent-consistent topology (Fig. 1, S1); both topologies are robust with the majority of their nodes having high bootstrap support and posterior probabilities, respectively. Both trees are virtually identical regarding the relationships of genera and the major clades within Lecythidoideae. *Grias, Gustavia, Couroupita, Allantoma, Cariniana,* and *Couratari* are monophyletic with full support in both phylogenies. *Eschweilera* and *Lecythis* are polyphyletic in both topologies, in agreement with previous studies (Huang et al. 2015). Both trees show the same relationships among the major clades (Pisonis, Ollaria, Poiteau, Chartacea, *Corythophora,* Tetrapetala, Corrugata, Integrifolia, Parvifolia) described by previous studies (Huang et al., 2015). We infer monophyly for the Bertholletia clade and for the first time recover high support for the polyphyly of *Eschweilera* and *Lecythis,* which confirms the results of Huang et al. (2015) and justifies recircumscribing both genera.

Corythophora's monophyly is the only exception to the congruence between the backbone topologies of the concatenated and the coalescent-consistent analyses. *Corythophora alta* R. Knuth (bearing a long branch) is sister to a clade composed of the remaining sampled *Corytophora* species and the *Eschweilera* Tetrapetala clade in the concatenated topology, rendering *Corythophora* paraphyletic; while *C. alta* is sister to the Bertholletia clade in the coalescent-consistent topology, making *Corythophora* polyphyletic.

Considering the high level of congruence between the two topologies and the finding that many gene-trees present too little phylogenetic signal to inform shallow relationships (Fig. S2), we selected the concatenated topology—with all the phylogenetic signal analyzed in a single matrix—as the best hypothesis representing the relationships among Neotropical Lecythidaceae. Therefore, from this point forward we will focus our results and discussion in the nuclear concatenated topology, which we refer to as the "nuclear tree."

Our nuclear tree suggests that *Eschweilera s.l.* contains two main clades (Tetrapetala and Integrifolia+Parvifolia), with *E. amazoniciformis* S.A. Mori outside of these two clades and sister to a clade composed of *Corythophora* and the Tetrapetala clade (Fig. 1). *Lecythis* s.l. comprises three main clades (Pisonis, Poiteaui+Chartacea, and Corrugata clades), with *L. minor* Jacq. outside of these three clades and sister to the clade composed of all members of the Bertholletia clade minus the Pisonis clade (Fig. 1).

The majority of the nuclear tree was fully supported by bootstrapping (Fig. 1). There was 100% bootstrap support along the backbone phylogeny with the exception of nodes inside the Parvifolia clade. Bootstrapping also fully supported the monophyly of the genera *Grias, Gustavia, Couroupita, Allantoma, Cariniana,* and *Couratari*, and the monophyly of the clades Pisonis, Poiteaui, Chartacea, Tetrapelata, Corrugata, Integrifolia, and Parvifolia. *Corythophora* was paraphyletic, and we only sampled one species in the Ollaria clade and therefore cannot evaluate its monophyly. Support by gene was high for *Grias, Gustavia, Couroupita, Allantoma, Cariniana,* and *Couratari,* for which monophyly was supported by 322, 213, 339, 331, 124, and 308 genes, respectively, out of the 343 sequenced (Fig. S2). The clade of *Corythophora* that excludes *Corythophora alta* was supported by 184 genes. High support per gene was also found for the main *Lecythis s.l.* and *Eschweilera s.l.* clades: Pisonis, Poiteaui, Chartacea, Tetrapelata, Corrugata, Integrifolia, and Parvifolia were supported by 331, 207, 247, 286, 279, 175, and 88 genes respectively (Fig. S2).

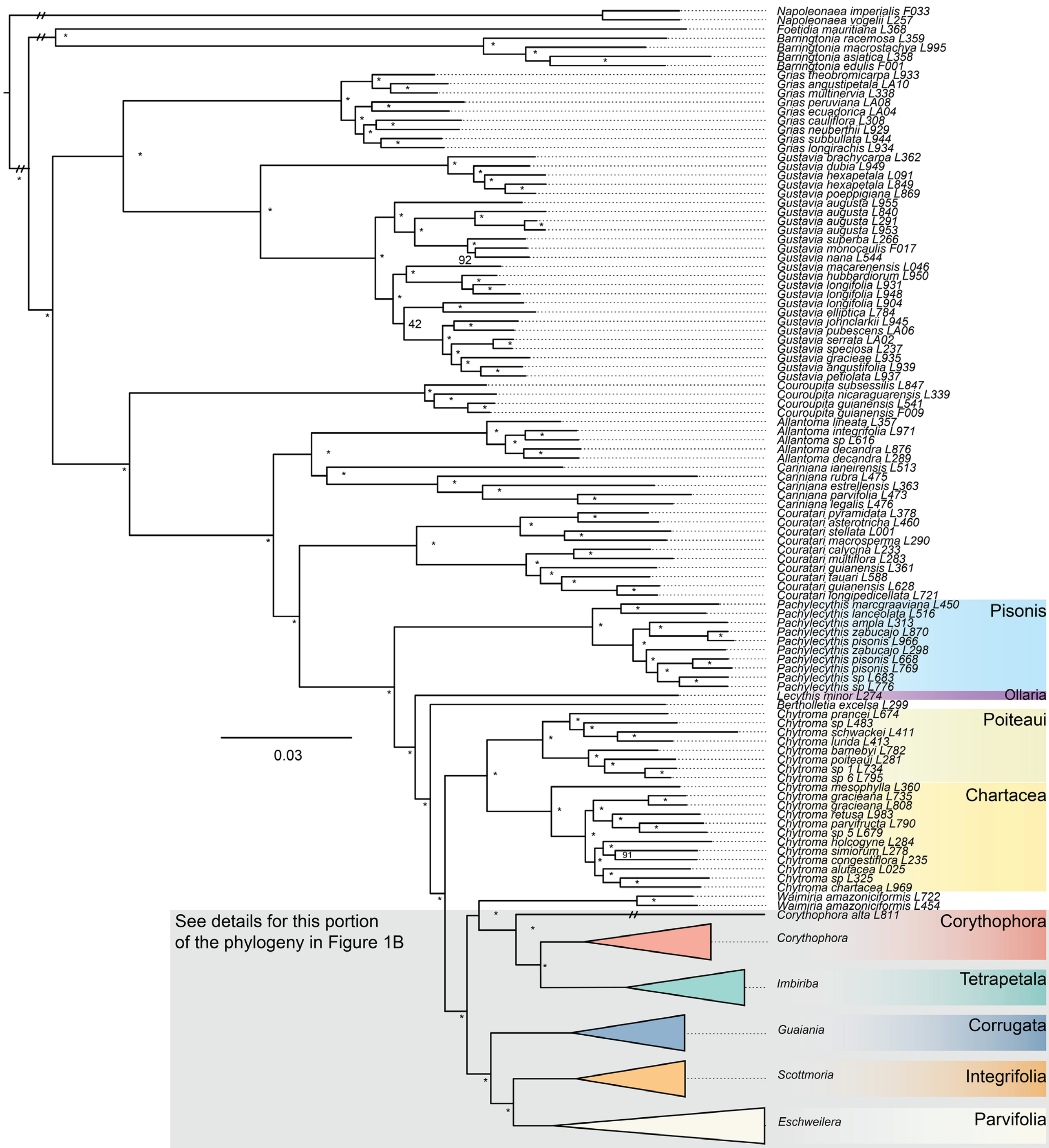


FIGURE 1A. Neotropical Lecythidaceae concatenated phylogeny of 343 nuclear genes. All shaded clades belong to the Bertholletia clade. Stars indicate full bootstrap support. Branch lengths are in units of substitutions per base pair.

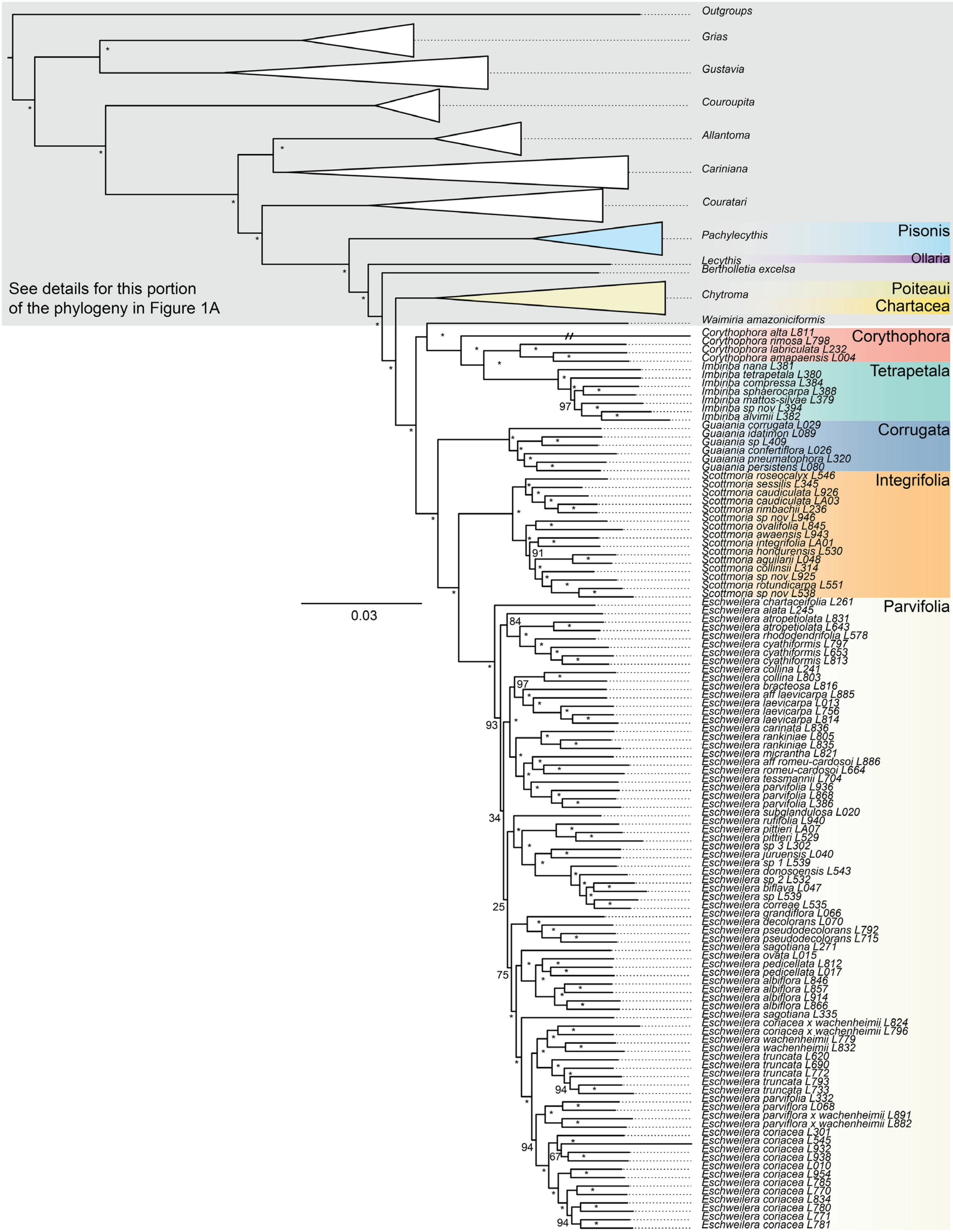


Figure 1B. Neotropical Lecythidaceae concatenated phylogeny of 343 nuclear genes. All shaded clades belong to the Bertholletia clade. Stars indicate full bootstrap support. Branch lengths are in units of substitutions per base pair.

Plastome Dataset

The final concatenated plastome alignment contained 10,047 sites (2624 parsimony-informative) and 5.4% gaps. There was generally support for the monophyly of the major clades of Lecythidaceae in the plastome tree, though relationships among clades, in many cases, differed from those of the nuclear tree (Fig. 2). However, the Parvifolia and Integrifolia clades were not recovered as monophyletic in the plastome tree because one sample (L302, *Eschweilera* sp.) was recovered as a member of the Integrifolia clade in the plastome tree, but was placed within the Parvifolia clade in the nuclear phylogeny. With the exception of sample L302, the Parvifolia clade was monophyletic with 100% support, as was the Integrifolia clade. *Corythophora*, including *Corythophora alta*, was monophyletic in the plastome tree with 100% support. The Corrugata clade was sister to the Parvifolia clade (100% support) and *Corythophora* was sister to those (95% support). *Eschweilera amazoniciformis* was sister to the Tetrapetala clade (99% support) with those being sister to a clade consisting of the Pisonis, *Corythophora*, Corrugata, and Parvifolia clades (51% support). *Lecythis mesophylla* S.A. Mori (Chartacea clade, sample L360) was recovered as sister to a clade consisting of the Integrifolia clade and the other members of the Chartacea clade (79% support), with *Bertholletia* sister to the Chartacea + Integrifolia clades. The Guianensis and Echinata clades of *Couratari* were sister clades (100% support), with *Cariniana* sister to those (96 % support). *Couroupita* was monophyletic and *Gustavia* and *Grias* formed a clade that was sister to the rest of the Lecythidoideae. Several terminal branches in the plastome tree were inferred to have near-zero branch lengths, including individuals of different species (Figure S3).

Because plastome phylogenies are expected to be biased when hybridization is present due to the uniparental nature of it its inheritance (Rieseberg and Soltis, 1991, Vargas et al., 2017), and there is evidence of hybridization in the Bertholletia clade (Larson et al., 2021), we selected the nuclear topology as the best hypothesis to base our classification for Lecythidoideae. We provide illustrations for only one of the genera with updated names because photos and illustrations for clades are available in Huang et al. (2015).

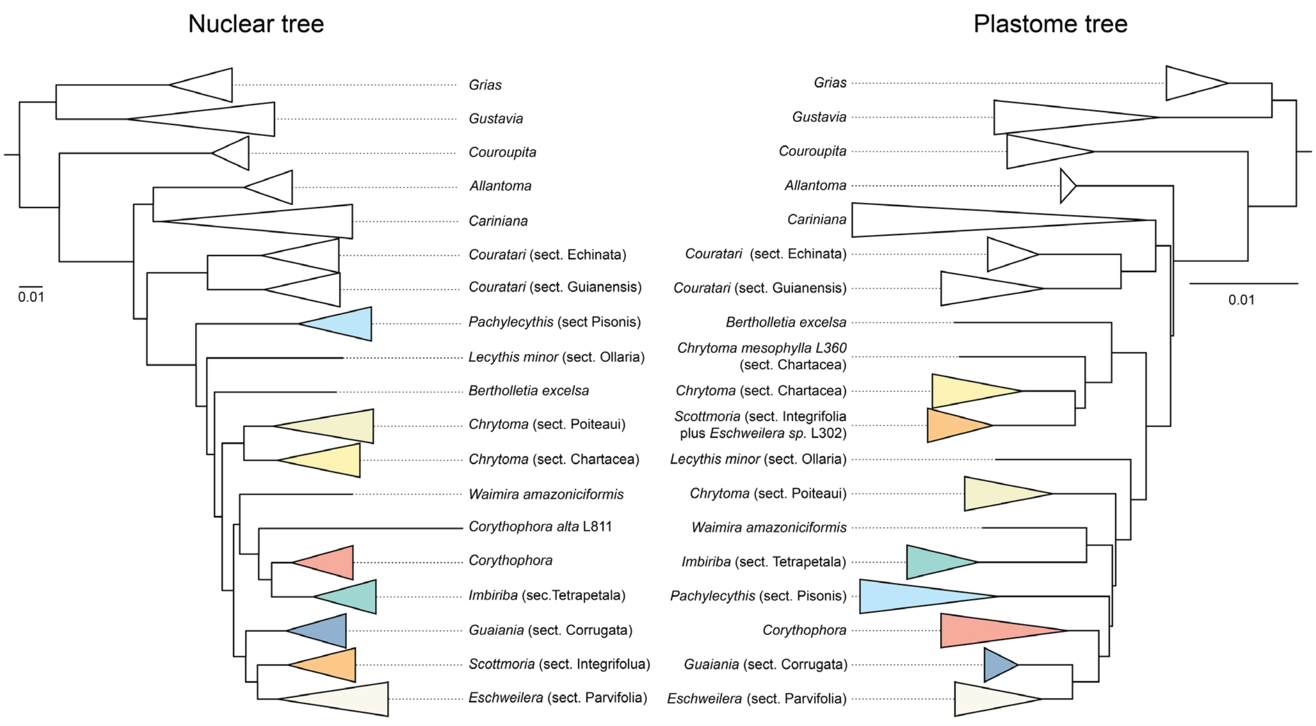


FIGURE 2. Nuclear and plastome trees with major clades collapsed. Colors correspond to those of the nuclear tree in Figure 1. Branch lengths are in units of substitutions per base pair and the scales for branch lengths differ between the two trees.

Taxonomy

Key to genera of the Bertholletia clade

See Prance and Mori (1990) and the NYBG Lecythidaceae Pages (Mori et al., 2010 and ongoing) for an explanation of the specialized fruit and floral terminology used in this key.

1a. Hypanthia and/or calyx-lobes often with mucilage ducts; petals usually pressed against the androecial hood/androecium; androecial hood often with posterior and anterior hood extensions; style linear, (2–)3–10 mm long 2

1b. Hypanthia and/or calyx-lobes without mucilage ducts; petals not pressed against the androecial hood/androecium; androecial hood without posterior and anterior hood extensions; style thickly oblongoid, up to 3 mm long 3

2a. Corolla buds enclosed by calyx; calyx with 2 lobes at anthesis; style ca. 8–10 mm long. Fruits perfectly globose, with inwardly falling operculum. Seeds with thick, bony testa, without aril, remaining inside fruit at maturity . . . . ***Bertholletia***

2b. Corolla buds not enclosed by calyx; calyx with 6 lobes at anthesis; style up to 7 mm long. Fruits usually subglobose (=depressed globose) or turbinate, and usually with freely falling operculum. Seeds without thick, bony testa, usually with an aril, usually falling out of fruit at or after maturity . . . . ***Chytroma*** (Poiteaui and Chartacea clades)

3a. Androecial hood with a single coil or no coil; ovary 2–5(–8)-locular 4

3b. Androecial hood with 2 to 4 coils; ovary 2-locular 8

4a. Pedicels and hypanthium densely rugose to muricate; androecial hood broadly open at anthesis, with a laterally expanded, concave ligule, exhibiting staminal ring. Fruits conical with horizontally oriented rugae (rugose) exterior (see exceptions for *G. corrugata*) . . . . ***Guaiania*** (sect. Corrugata)

4b. Pedicels and hypanthium smooth or nearly so; androecial hood inwardly closed or nearly closed at anthesis, usually with a narrower ligule, covering staminal ring. Fruits turbinate, globose or cupuliform (=cup-shaped), without horizontally oriented rugae/rugose exterior 5

5a. Androecial hood with a space between appendage-free ligule and coil; single coiled ligule with staminal appendages found only on the exterior part of the coil . . . . ***Lecythis*** (Ollaria clade)

5b. Androecial hood without coil, otherwise without a space between appendage-free ligule and coil 6

6a. Androecial hood with single coil, with staminal appendages arranged on both sides of coil. Seeds with basal or sub-basal aril poorly developed. Restricted to Brazilian Atlantic Forest and Cerrado . . . . ***Imbiriba*** (Tetrapetala clade)

6b. Androecial hood without coil; Seeds with long, basal aril, usually more than one-half length of seed. From Nicaragua to Ecuador, Venezuela, and throughout Guianas, Amazonia, and the Atlantic Forest 7

7a. Androecial hood ± flat, anterior staminal appendages projected forward; stylar collar present; flower tissue often oxidizing bluish-green when damaged. Fruits globose or broadly turbinate, usually ≥10–30 cm diam., with a convex operculum . . . . ***Pachylecythis*** (sect. Pisonis)

7b. Androecial hood dorsiventrally thickened and curved, anterior staminal appendages projected downwards; stylar collar absent. Fruits campanulate or cylindrical, ≤ 10 cm diam., with a flat operculum . . . . ***Corythophora***

8a. Flowers with 4 calyx lobes and 4 petals. Fruits narrowly turbinate; infracalycine zone narrow, conspicuously longer than wide. Seeds longitudinally ridged, with basal aril. Restricted to the Manaus area in Brazil . . . . ***Waimiria***

8b. Flowers with 6 calyx lobes and 6 petals. Fruits globose, globose-depressed or oblate; infracalycine zone undeveloped, otherwise broader than long. Seeds either (1) not ridged, with a lateral aril, sometimes with a soft, thin white sarcotesta, or (2) seeds surrounded by a mostly free, white rubbery coat (only in *S. awaensis*). From Mesoamerica to Amazonia 9

9a. Androecial hood with 3–4 inner coils, petals predominantly dark-purple or burgundy to rose, occasionally yellow to white. Seed covering of two types: (1) a soft, thin, white sarcotesta that is infiltrated with testa, arranged over the entire or most of the mature seed or at least present in young seeds and mostly dissolving at maturity, and with a thick, yellow to white lateral aril, often half I-beam shaped with rubber-like texture and overlapping ends on seed; or (2) seeds surrounded by a mostly free, white rubbery coat (only in *S. awaensis*). Predominantly on the Pacific side of NW South America (from Ecuador) to Mesoamerica . . . . ***Scottmoria***

9b. Androecial hood with 2 inner coils, petals usually white or yellow. Seeds with lateral, thick, white, rubbery aril with ends not overlapping; sarcotesta or rubbery coat absent. Predominantly in central and western Amazonia with a few species in Mesoamerica. . . . . . ***Eschweilera*** *s.s.*

Pachylecythis Ledoux, Lecointea 2: 2–4. 1964.
TYPE: *Pachylecythis pisonis* (Cambess.) O.M. Vargas & C.W. Dick.

Pachylecythis comprises a clade of five species informally recognized by Mori and Prance (1981) as the "sapucaia" group within *Lecythis*, and subsequently by Mori and Prance (1990) as *Lecythis* section *Pisonis*. Based on genetic and morphological evidence, Huang et al. (2015) named it the Pisonis clade (Huang et al., 2015). *Pachylecythis* species are canopy to emergent trees with deeply, vertically fissured bark and large woody fruit capsules known variously as monkey pot, *olla de mono* and *coco de mono* in Spanish (Sp.), and *sapucaia* in Portuguese (Port.). *Pachylecythis* species are found in lowland forests from Nicaragua to Brazil's Atlantic Forest. The edible seeds are consumed locally and sporadically marketed in Europe and the United States as paradise or cream nuts. The biology of the sapucaia group is discussed in Mori and Prance (1981) and Mori et al. (2017).

Diagnosis: Leaves, flowers, and fruits oxidize blue-green when bruised; flowers with short styles, flat androecium hood; fruits large and dehiscent; seeds with cord-like funicles surrounded by a large aril.

Etymology: *Pachylecythis egleri* Ledoux (1964) is the oldest Linnean synonym for *Lecythis pisonis*. *Jacapucaya brasiliensis* Marcgr. (1648) is pre-Linnaean and does not have priority following articles 32.1 and 13.1 of the International Code of Nomenclature.

Pachylecythis ampla (Miers) O.M. Vargas & C.W. Dick, *comb. nov*.
Basionym: *Lecythis ampla* Miers, Trans. Linn Soc. London 30(2): 204–205 pl. 43, Fig. 1. 1874.

TYPE: COLOMBIA. Antioquia: without locality, no date, (fr only), *W. R. Jervis s.n.* (Lectotype: designated by Mori and Prance, 1990, K).

Habitat and distribution: Canopy to canopy-emergent trees in lowland wet or moist forest from Nicaragua and Costa Rica to the Chocó bioregion of Panama, Colombia and Ecuador; middle and lower Magdalena river valley; and Central and Western Cordilleras of Colombia (Mori and Prance, 1990).

Pachylecythis lanceolata (Poir.) O.M. Vargas & C.W. Dick, *comb. nov.*

Basionym: *Lecythis lanceolata* Poir., Encycl. Méth. 6: 27. 1804.

TYPE: MAURITIUS. Cultivated on the Île de France (=Mauritius), no date (fl), *P. Commerson 518* (Lectotype: designated by Mori and Prance, 1990, P-Juss., photograph NY; Isolectotypes: F [accession No. 537888], K, LINN [accession No. 943.3], US [accession No. 1112080]).

Habitat and distribution: Large trees (to 30 m) found in coastal moist forests of eastern Brazil from Rio de Janeiro to Pernambuco (Smith et al., 2016b). Sometimes cultivated as a street tree in Sao Paulo and Rio de Janeiro (Mori et al., 2010 and onward).

Pachylecythis marcgraaviana (Miers) O.M. Vargas & C.W. Dick. *comb. nov.*

Basionym: *Lecythis marcgraaviana* Miers (1874: 210–211, t. 48, Fig. 1).

TYPE: BRAZIL. Espirito Santo, Linhares, Reserva Natural Vale, Estrada Aceiro Marco de Ferro, 19°9'02"S, 40°04'13"W, 7 January 2010 (fl), *D. A. Folli 6527* (Neotype: designated by Smith et al., 2016b; CVRD; Isoneotype: NY).

Habitat and distribution: Canopy tree or shrub found in coastal Atlantic Forest between the states of Espírito Santo and Rio Grande do Norte (Smith et al., 2016a). This taxon was until recently considered part of morphologically variable species *Lecythis pisonis*.

Pachylecythis pisonis (Cambess.) O.M. Vargas & C.W. Dick, *comb. nov.*

Basionym: *Lecythis pisonis* Cambess., St. Hil., Fl. Bras. merid. 2: 377. 1829.

TYPE: BRAZIL. Espírito Santo: Without locality, 1816–1862 (fl), *A. Saint-Hilaire 365* (Lectotype: designated by Mori and Prance, 1990, P); Isolectotypes: MPU, NY [photo neg. No. 8782]).

Habitat and distribution: Canopy-emergent tree to 50 m found in lowland moist forests in the Amazon basin (especially eastern Amazonia) and in Brazil's Atlantic Forest. Common names are sapucaia (Brazil) and monkey pot (English). The species is planted along city streets in Brazil and in tropical botanical gardens around the world. The seed "castanha de sapucaia" is highly edible (Mori et al., 2010 and onward).

Pachylecythis zabucaja (Aubl.) O.M. Vargas & C.W. Dick, *comb. nov.*

Basionym: *Lecythis zabucaja* Aubl., Hist. pl. Guiane 1: 718–721. 1775, pro parte quoad fructum tantum.

TYPE: Plate 283 in Aublet (1775) (Lectotype: designated by Mori and Prance, 1990).

Habitat and distribution: Emergent trees (to 55 m) of lowland rain forest in the Guianas and eastern Venezuela and less commonly in the central and eastern Amazon.

The species epithet was originally masculine, *L. zabucajo*; however, Mori et al. (2010 and onward) changed the epithet spelling to *L. zabucaja* to agree in gender with the genus name.

Chytroma Miers, Trans. Linn. Soc. London 30: 229. 1874.

Basionym: *Lecythis schomburgkiana* O. Berg, Linnaea 27456: 230–231.1856.

TYPE: *Chytroma schomburgkiana* (O. Berg) Miers

Diagnosis: Some members of the clade have an androecial hood with appendages swept inward, mucilage ducts in the ovary and/or the calyx lobes, and a long obliquely oriented or geniculate style. No single apomorphy is yet known that unites all the species in this clade. However, Huang et al. (2015) cites the aforementioned combination of diagnostic characters.

Chytroma includes two sister clades consisting of the Lecythis section Poiteaui (Mori and Prance, 1990; Poiteaui clade of Huang et al., 2015) and the Chartacea clade described by Huang et al. (2015). The morphology of the Poiteaui clade and Chartacea clade overlaps and these groups have no uniting synapomorphies, hence we have opted to combine the two clades into the single genus *Chytroma*. The Chartacea clade and some species in the Poiteaui clade possess an androecial hood with swept-in appendages, and some species in both clades contain secondarily indehiscent fruits. Many of the same fruit and flower characters are found in *Bertholletia excelsa,* although *B. excelsa* has a dehiscent fruit with an inwardly falling operculum (Huang et al., 2015). Taxonomic treatments combined with phylogenetic studies are necessary to better delimit their morphological differences.

Etymology: *Chytroma schomburgkii* (O. Berg) Miers and *Chytroma ibiriba* Miers, both published in Miers (1874), are the earliest valid available names for species in this clade. *Cercophora* Miers is a synonym for another species in this clade and was also published in Miers (1874). However, *Cercophora* was previously published by Fuckel (1870) as a genus of fungi. The word *Chytroma* derives from the greek *chytra*, which is an earthenware cooking pot, and *oma*, meaning tumor or swollen, in likely reference to the fruits.

Chytroma alutacea (A.C. Sm.) O.M. Vargas & C.W. Dick, *comb. nov.*

Basionym: *Eschweilera alutacea* A.C. Sm., American Journal of Botany 26(5): 409. 1939.

TYPE: GUYANA. Essequibo River, near the mouth of Orono Creek, ca. 1°35'N, 17 December 1937 (fl), *A. C. Smith 2690* (Lectotype: designated by Mori and Prance, 1990, NY; Isolectotypes: F, G, K, MO, P, S, U).

Homotypic synonym: *Lecythis alutacea* (A.C. Sm.) S.A. Mori, Brittonia 33: 362. 1981.

Habitat and distribution: Canopy tree of lowland forest found primarily along rivers in eastern Venezuela, Guyana, Surinam and northern Pará state in Brazil (Mori et al., 2010 and ongoing). Chartacea clade.

Chytroma barnebyi (S.A. Mori) O.M. Vargas & C.W. Dick, *comb. nov*.

Basionym: *Lecythis barnebyi* S.A. Mori 1981. Brittonia 33: 360.

TYPE. BRAZIL. Amazonas: Manaus-Caracarai Rd., km 130.5, 13 February 1974 (fl), *W. C. Steward et al. P.20242* (Holotype: INPA; Isotypes: COL, F, MO, NY, OXF, P, U, US, VEN).

Habitat and distribution: Understory tree restricted to *terra firme* forests in the Central Amazon region (Mori et al., 2010 and ongoing).

Clade: Poiteaui clade (based on Mori and Prance, 1990).

Chytroma brancoensis R. Knuth (Engler) Pflanzenr. IV, fam. 291a: 84. 1939.

Homotypic synonym: *Lecythis brancoensis* (R. Knuth) S.A. Mori 1981, Brittonia 33: 359. TYPE: BRAZIL. Roraima: Rio Branco, São Marcos, 1913 (fl), *J. G. Kuhlann 913* (RB [accession No. 3517]) (Neotype: RB, designated by Mori and Prance, 1990, NY).

Habitat and distribution: Small tree (to 5 m) of savanna and forest fragments in Roraima state in northern Brazil and adjacent Guyana.

Clade: Poiteaui clade (based on Mori and Prance, 1990).

Chytroma chartacea (O. Berg) Miers Trans. Linn. Soc. London 30: 229. 1874.

Basionym: *Lecythis chartacea* Berg, Linnaea 27: 450–451. 1856. TYPE: GUYANA. Pomeroon River, Sep (fl), *R. Schomburgk 1432* (Lectotype: K).

Habitat and distribution: Medium to large tree (to 35 m) of riparian and *terra firme* forests in the Guiana Shield and Amazon basin regions.

Clade: Chartacea clade.

Chytroma congestiflora (Benoist) R. Knuth (Engler) Pflanzenr. IV, fam. 291a. 1939.

Basionym: *Lecythis congestiflora* Benoist, Notul. Syst. (Paris) 3: 177. 1915. TYPE: FRENCH GUIANA. Charvein, 11 January 1914 (fl), *R. Benoist 578* (Lectotype: designated by Mori and Prance, 1990, P).

Habitat and distribution: Canopy trees (to 25 m) known from *terra firme* forest of northern Surinam, French Guiana, and Surinam (Mori and Prance, 1990).

Clade: Chartacea clade.

Chytroma gracieana (S.A. Mori) O.M. Vargas & C.W. Dick, *comb. nov*.

Basionym: *Lecythis gracieana* Mori, Mem. New York Bot. Gard. 75: 47–49. 1995.

TYPE: BRAZIL. Amazonas: Distrito Agropecuário, Reserve 1501 (Km 41) of the Biological Dynamics of Forest Fragments Project, 2°24'26"–2°25'31"S, 59°43'40"–59°45'50"W. ca. 50–125 m, *terra firme* forest, tree 1991, 9 January 1991 (fl), *M. A. de Freitas et al. 577* (Holotype: INPA; Isotypes: K, NY).

Habitat and distribution: Trees to 30 m in height in *terra firme* forest. Known only from the Manaus region (Mori and Lepsch da Cunha, 1995).

Clade: Chartacea clade.

Chytroma holcogyne (Sandwith) R. Knuth. (Engler) Pflanzenr. IV, fam. 291a. 1939.

Basionym: *Eschweilera holcogyne* Sandwith Kew Bulletin 1935: 126. 1935. TYPE: GUYANA. Kartabo Rd. nr. Confluence of Cuyuni and Mazaruni Rivers, 7 February 1931 (fl), *T. A. W. Davis D17* (=Forest Dept. British Guiana 1019) (Lectotype: designated by Mori and Prance, 1990, K; Isolectotypes: FDG, K).

Habitat and distribution: Canopy tree (to 35 m) found in *terra firme* forest of Guyana, French Guiana, and the northern part of Amapá state, Brazil.

Clade: Chartacea clade.

Chytroma ibiriba Miers 1874, Trans. Linn. Soc. London 30: 236–237. TYPE: BRAZIL. Alagoas, Maceió, February 1838 (imm. Fr), *G. Gardner 1312* (Lectotype: designated by Mori and Prance, 1990, K).

Homotypic synonym: *Lecythis ibiriba* (Miers) N.P. Sm., S.A. Mori, & Popovkin J. Torrey Bot. Soc. 139(4): 447. 2013.

Habitat and distribution: Small to medium trees known from the northeastern Brazilian states of Alagoas, Bahia, and Sergipe (Mori et al., 2010 and ongoing).

Clade: Poiteaui clade (Huang et al., 2015).

Chytroma lurida (Miers) O.M. Vargas & C.W. Dick, *comb. nov*.

Basionym: *Eschweilera lurida* Miers, Trans. Linn. Soc. London 30: 262. 1874.

TYPE: BRAZIL. Para: vicinity of Belem, 30 December 1929, *Burchell 10000* (Lectotype: designated by Mori and Prance, 1990, K; Isolectotypes: NY, OXF, P, US).

Homotypic synonym: *Lecythis lurida* (Miers) S.A. Mori, Brittonia 33: 362. 1981.

Habitat and distribution: Small to large trees of *terra firme* moist forests, secondary vegetation, and savanna, ranging from Rio de Janeiro to eastern Amazonia.

Clade: Poiteaui clade.

Chytroma mesophylla (S.A. Mori) O.M. Vargas & C.W. Dick, *comb. nov*.

Basionym: *Lecythis mesophylla* S.A. Mori, Ann. Missouri Bot. Gard. 57: 386. 1971.

TYPE: PANAMA. Darien: N slope of Cerro Pirre, 15 November 1967 (empty fr), *S. A. Mori 364* (Holotype: WIS; Isotypes: BM, F, GH, MO, NY, UC, US).

Habitat and distribution: Large trees (to 50 m) from lowland tropical forests in lower Central America (Osa Peninsula in Costa Rica and Darien in Panama) and the Magdalena Valley in Colombia.

Clade: Chartacea clade.

Chytroma parvifructa (S.A. Mori) O.M. Vargas & C.W. Dick, *comb. nov*.

Basionym: *Lecythis parvifructa* S.A. Mori, Fl. Neotrop. Monogr. 21(2): 312. 1990.

TYPE: Brazil. Manaus-Itacoatiara Rd., EPLAC, km 30, 29 March 1976 (fr), *J. F. Ramos* 380 (Holotype: INPA; Isotypes: K, NY, RB).

Habitat and distribution: Trees of up to 35 m in height found in *terra firme* forest. Known only from the Central Amazon near Manaus, Brazil.

Clade: Chartacea clade.

Chytroma poiteaui (O.Berg) O.M. Vargas & C.W. Dick, *comb. nov*.

Basionym: *Lecythis poiteaui* O. Berg Fl. Bras. (Martius) 14(1): 615. 1859.

TYPE: FRENCH GUIANA. Cayenne, no date (fl), *J. Martin s.n.* (Lectotype: designated by Mori and Prance, 1990, P, photograph NY; Isolectotypes: K, P, photograph of specimen at P, NY).

Habitat and distribution: Trees of up to 35 m in height found in *terra firme* forest in the eastern Amazon (east of Manaus), Surinam, and French Guiana (Mori et al., 2010 and ongoing).

Clade: Poiteaui clade.

Chytroma prancei (S.A. Mori) O.M. Vargas & C.W. Dick, *comb. nov*.

Basionym: *Lecythis prancei* S.A. Mori Fl. Neotrop. Monogr. 21(2): 304. 1990.

TYPE: BRAZIL. Amazonas: Acara Trail, Reserva Ducke, km 26 Manaus-Itacoatiara Rd., 24 October 1974 (fl), *G. Prance et al. 23062* (Holotype: INPA; Isotypes: AAU, COL, FHO, K, MEXU, MO, NY, P, RB, U, US, VEN).

Habitat and distribution: Tree up to 35 m in height known only from the central Amazon region near Manaus (Mori et al., 2010 and ongoing).

Clade: Poiteaui clade.

Chytroma retusa (Spruce ex O. Berg) Miers, Trans. Linn. Soc. London 30(2): 243–244. 1874.

Basionym: *Lecythis retusa* Spruce ex O.Berg, Fl. Bras. (Martius) 14(1): 487. 1858. TYPE: BRAZIL. Amazonas: Vicinity of Barra (Manaus), prov. Rio Negro, flowering December–March, 1850–1851 (fl) (Lectotype: designated by Mori and Prance, 1990, *R. Spruce 1166*, BM; Isolectotypes: K, LE, M, NY).

Habitat and distribution: Canopy tree (to 30 m) of *terra firme* forest known only from the central Amazon region near Manaus, Brazil

Clade: Chartacea clade.

Chytroma schomburgkii (O. Berg) Miers, Trans. Linn. Soc. London 30(2): 230–231, t. 58. 1874.

Basionym: *Lecythis schomburgkii* O. Berg, Linnaea 27: 456. 1856.

TYPE: GUYANA. Without locality, 1868 (fl), *R. Schomburgk 792* (Lectotype, designated by Mori and Prance, 1990: BM).

Habitat and distribution: Small trees of up to 12 m in height found in the savannas of Roraima, Brazil.

The original publication names this species as *C. schomburgkiiana*; however, this termination is contrary to the standard required by the International Code of Nomenclature (art. 60.8b; the suffix "ana" applies to places not people), so we have chosen to use the corrected spelling for the epithet here, also previously corrected in Mori and Prance (1990).

Clade: Chartacea clade (Mori et al., 2017)

Chytroma schwackei (R.Knuth) O.M. Vargas & C.W. Dick, *comb. nov.*

Basionym: *Sapucaya schwackei* R. Knuth, Repert. Spec. Nov. Regni Veg. 38: 113. 1935.

TYPE: BRAZIL. Minas Gerais: Virgem da Lapa, 9 April 1959 (fr), *M. Magalhães 15322* (Neotype: IAN, designated by Mori and Prance, 1990).

Habitat and distribution: Small trees known only from the states of Minas Gerais and Rio de Janeiro, Brazil (Mori et al., 2010 and ongoing).

Clade: Poiteaui clade.

Chytroma serrata (S.A. Mori) O.M. Vargas & C.W. Dick, *comb. nov.*

Basionym: *Lecythis serrata* S.A. Mori, Fl. Neotrop. Monogr. 21(2): 320. 1990.

TYPE: BRAZIL. Pará: Road to Munguba, 23 May 1969 (fl), *N. T. Silva 2035* (Holotype: IAN; Isotype: NY).

Habitat and distribution: Small to medium trees (4 to 20 m) of *terra firme* forest known from the central and eastern Amazon basin.

Clade: Likely Chartacea clade (Mori and Prance, 1990).

Chytroma simiorum (Benoist) R. Knuth, Pflanzenr. (Engler) IV, 219a: 81. 1939.

Basionym: *Lecythis simiorum* Benoist, Notul. Syst. (Paris) 3: 178. 1915.

TYPE: FRENCH GUIANA. Saint Jean du Maroni, 1 April 1914 (fr), *R. Benoist 1065* (Lectotype: designated by Mori and Prance, 1990, P; Isolectotype: K).

Habitat and distribution: Tree of up to 25 m in height found in *terra firme* forests in northern Guyana, Surinam, and French Guiana to Amapá, Brazil. Some collections from Amazonas, Brazil, suggest that the species may have a disjunct distribution.

Clade: Chartacea clade.

Waimiria C.W. Dick & O.M. Vargas, *gen. nov*.

TYPE: *Waimiria amazoniciformis* (S.A. Mori) C.W. Dick & O.M. Vargas, *comb. nov.*

Diagnosis: Flower with four petals; the androecial hood 3-coiled; fruits narrowly turbinate to turbinate; seeds with salient veins and basal aril.

Eschweilera amazoniciformis was so named because of the similarity of its fruit morphology with that of *E. amazonica* R. Knuth. *Waimiria amazoniciformis* is narrowly endemic to the vicinity of Manaus, Brazil, and is most frequently collected in the Ducke Reserve and the BDFFP reserves north of Manaus. The combination of four petals, tri-coiled hood, and narrowly turbinate fruit set this taxon apart morphologically from all other Lecythidaceae species. The narrowly endemic range and evolutionary distinctiveness of *W. amazoniciformis* should make it a conservation priority. We look forward to basic studies of its pollination, seed dispersal, and other aspects of its biology in the future.

Etymology: We name the genus for the Waimiri people whose ancestral lands overlap with the small geographic range of its eponymous genus. The Waimiri were forcibly displaced from their lands to make way for construction of the Balbina Dam (Davis, 1977). Their numbers were reduced by violence and disease, and they currently occupy a small portion of their former land.

Waimiria amazoniciformis (S.A. Mori) C.W. Dick & O.M. Vargas, *comb. nov.*

Basionym: *Eschweilera amazoniciformis* S.A. Mori, Fl. Neotrop. Monogr. 21(2): 227. 1990.

TYPE: BRAZIL. Amazonas: Manaus-Itacoatiara Rd., km 178, May 1972 (fr), *L. Coelho 161* (Holotype: INPA; Isotype: NY).

Habitat and distribution: Canopy to emergent tree (to 40 m) of *terra firme* forest known only from the central Amazon region near Manaus, Brazil.

Imbiriba O.M. Vargas, M. Ribeiro, & C.W. Dick, *gen. nov.*
TYPE: *Imbiriba tetrapetala* (S.A. Mori) O.M. Vargas, M. Ribeiro, & C.W. Dick, *comb. nov.*

Diagnosis: Inflorescence with horizontal scales on the rachis. Flowers with imbricated calyx lobes or fused at base and forming calycine rim; 4(–6) petals; androecium hood single coiled, with presence of staminal appendages on both sides of the single coil; ovary 2-locular, more than one row of ovules per locule. Seeds with impressed venation; basal aril poorly developed (Ribeiro et al., 2019).

Imbiriba subsumes the former *Eschweilera* sect. Tetrapetala proposed by Mori and Prance (1990) to include three species characterized by flowers with four petals and an androecium hood that does not form a complete coil. Huang et al. (2015) recognized the broader Tetrapetala clade which includes four additional species. Although the presence of four petals is unusual and one of the initial morphological characters defining section Tetrapetala (including in 3 unpublished new species, M. Ribeiro, in prep.), two species, *Imbiriba nana* and *Imbiriba mattos-silvae*, have six petals. Outside of this clade only *Waimiria amazoniciformis* and *Eschweilera perumbonata* Pittier have four petals (Mori and Prance, 1990). *Imbiriba* currently contains seven recognized taxa (three additional species are being described, M. Ribeiro, pers. comm.), all endemic to the Brazilian Atlantic Forest (Ribeiro et al., 2016a; Ribeiro et al., 2016b; Ribeiro, 2019; Smith et al., 2016b) with exception of *Imbiriba nana* which occurs in the Cerrado; six species of the genus are listed in the Brazilian endangered flora list (Lima da Venda et al., 2013; Brazil, Ministry of the Environment, 2022).

Etymology: The name *Imbiriba* is derived from the indigenous name used commonly for these species.

Although *Lecythopsis glabra* (Cambess.) O. Berg is a synonym of *Eschweilera compressa* (Vell.) Miers., *Lecythopsis* was not assigned a nomenclatural type and its description of fruit characters fit *Couratari* and do not apply to *E. compressa*. *Lecythopsis* was cited by Mori and Prance (1990) as a synonym of *Couratari*.

Imbiriba alvimii (S.A. Mori) O.M. Vargas, M. Ribeiro, & C.W. Dick, *comb. nov.*

Basionym: *Eschweilera alvimii* Mori, Brittonia 33: 469. 1981.

TYPE: BRAZIL. Bahia: Mun. Santa Cruz de Cabrália, vic. Pau-Brasil ecological reserve, 18 October 1978 (fl, fr), *S. A. Mori et al. 10819* (Holotype: CEPEC; Isotypes: K, RB, US).

Habitat and distribution: Small to medium trees of 4 to 30 m in height found in lowland forests in southeastern Bahia (Mori and Prance, 1990; Smith et al., 2016b).

Imbiriba complanata (S.A. Mori) O.M. Vargas, M. Ribeiro, & C.W. Dick, *comb. nov.*

Basionym: *Eschweilera complanata* S.A. Mori, Bol. Bot. Univ. São Paulo 14: 16. 1995.

TYPE: BRAZIL. Bahia: Mun. Porto Seguro, new road uniting BR 367 to Ajuda camp, 17 km from entrance, ca. 30 km W or Porto Seguro, 19 October 1978, *S. A. Mori et al. 10878* (Holotype: CEPEC; Isotypes: A, F, K, NY, P, RB, U, US).

Habitat and distribution: Medium sized trees (12 to 20 m) only known from the state of Bahia in Brazil's Atlantic forests (Smith et al., 2016b; Mori, 1995).

Imbiriba compressa (Vell.) O.M. Vargas, M. Ribeiro, & C.W. Dick, *comb. nov.*

Basionym: *Eschweilera compressa* (Vell.) Miers, Trans. Linn. Soc. London 30: 248. 1874.

TYPE: Plate 87 in Vellozo, Fl. Flum. Icon. V, t. 85. 1831 (1830) designated as Lectotype by Mori and Prance, 1990, in lieu of extant collection.

Habitat and distribution: Understory trees (3 to 10 m) of lowland moist forests endemic to Rio de Janeiro and Espírito Santo states (Mori and Prance, 1990; Ribeiro et al., 2016b).

Imbiriba mattos-silvae (S.A. Mori) O.M. Vargas, M. Ribeiro, & C.W. Dick, *comb. nov.*

Basionym: *Eschweilera mattos-silvae* S.A. Mori, Bol. Bot. Univ. São Paulo 14: 22. 1995.

TYPE: BRAZIL. Bahia, Mun. Uruçuca, 7.3 km N of Serra Grande, 14˚25'S, 39˚03'W, 6 May 1992 (fl., immature fr), *W. W. Thomas et at. 9165* (Holotype: CEPEC; Isotypes: K, MO, NY, U, US).

Habitat and distribution: Small to medium sized tree of 10 to 25 m in height found in Brazil's Atlantic forests and endemic to southeastern Bahia.

Imbiriba nana (O. Berg) O.M. Vargas, M. Ribeiro, & C.W. Dick, *comb. nov.*

Basionym: *Lecythis nana* O. Berg, Trans. Linn. Soc. London 30: 261. 1874.

TYPE: BRAZIL. Mato Grosso: in sandy savanna near Camapuan, October (fl), *L. Riedel s.n.* (Holotype: LE fide Berg; Isotypes: P, photograph of specimen at P, NY).

Habitat and distribution: A shrub or small tree of savanna (Cerrado Biome) widely found at 400–800 m in the Planalto and northeastern Brazil (Mori and Prance, 1990; Smith et al., 2016b).

Imbiriba sphaerocarpa (M. Ribeiro & S.A. Mori) O.M. Vargas, M. Ribeiro, & C.W. Dick. *comb. nov.*

Basionym: *Eschweilera sphaerocarpa* M. Ribeiro & S.A. Mori, Phytotaxa 255: 268. 2016.

TYPE: BRAZIL. Espírito Santo: Jaguaré, Jaguaré road toward Fátima, 18°54'50"S, 40°06'22"W, 28 December 2010, *D. A. Folli 6755* (Holotype: CVRD, Isotype: NY).

Habitat and distribution: Medium sized trees of 23 to 27 m in height, known only from one population of three trees in an Atlantic Forest fragment in the municipality of Jaguaré, Esprito Santos, Brazil and is classified as critically endangered by Ribeiro et al. (2016a).

Imbiriba tetrapetala (S.A. Mori) O.M. Vargas, M. Ribeiro, & C.W. Dick. *comb. nov.*

Basionym: *Eschweilera tetrapetala* Mori, Brittonia 33: 467. 1981.

TYPE: BRAZIL. Bahia: Mun. of Andaraí, 3 km NE of Andaraí, ca. 400 m alt., 5 March 1980 (fl), *S. A. Mori & L. S. Funch 13421* (Holotype: CEPEC; Isotypes: INPA, K, MG, MO, NY, P, RB, US).

Habitat and distribution: Medium sized tree of up to 15 m in height found in moist forest on plateaus in central Bahia, Brazil.

Guaiania O.M. Vargas & C.W. Dick, *gen. nov*.

TYPE *Lecythis idatimon* Aubl.

Diagnosis: Flowers with rugose or tuberculate pedicels and hypanthia that may persist in the fruits; androecial hood flat and thin with ligular flanges (except for *Guaiania corrugata*); seeds with basal and short aril.

Guaiania O.M. Vargas & C.W. Dick was first recognized as *Lecythis* section Corrugata by Mori and Prance (1990) and as a clade by Huang et al. (2015). All five species are located in the Guiana Shield/Central Amazon region.

Etymology: There were no published names with priority within this clade, so we propose a new name, *Guaiania*, derived from one of the Latin words for Guiana, which is the geographic center of the newly recognized genus and its ancestral area according to the biogeographic analysis of Vargas and Dick (2020). The word Guiana (Guayana, Guyana) is phonetically derived from an indigenous word meaning "land of many waters."

Guaiania confertiflora (A.C. Sm.) O.M. Vargas & C.W. Dick, *comb. nov.*

Basionym: *Lecythis confertiflora* (A.C. Sm.) Mori. Mem. New York Bot. Gard. 44: 31. 1987.

TYPE: GUYANA. Kumuparu Creek, Demerara River, 150 feet [ca. 50 m], 5 November 1937 (fl), *Forest Dept. British Guiana 2557* (Holotype: NY; Isotypes: K-2 sheets, MAD).

The aforementioned types are listed as lectotypes in Mori and Prance (2010). However, the basionym protologue indicates that the specimen *Forest Dept. British Guiana 2557* is a holotype.

Habitat and distribution: Typically canopy trees of up to 35 m in height but occasionally small trees (to 15m) found in *terra firme* forest throughout the Guianas and extending to Amapá, Brazil.

Guaiania corrugata (Poit.) O.M. Vargas & C.W. Dick, *comb. nov.*

Basionym: *Lecythis corrugata* Poit., Mém. Mus. Hist. Nat. 13: 146. 1825.

TYPE: FRENCH GUIANA. Without locality, July 1824 (fl), *P. A. Poiteau s.n.* (Lectotype: designated by Mori and Prance, 1990, K, photo K neg. 16376 at NY)

Habitat and distribution: Large trees of up to 35 m in height found in *terra firme* forest ranging from Venezuela through the Guianas and to eastern Brazil. Two subspecies are recognized.

Guaiania corrugata *subsp.* rosea (Spruce ex O. Berg) O.M. Vargas & C.W. Dick, *comb. nov.*

Basionym: *Lecythis rosea* Spruce *ex* Berg in Martius, Fl. bras. 14(1): 488–489. 1858. TYPE: BRAZIL. Amazonas: Rio Negro, Barcellos, November 1851 (fl), *R. Spruce 1920* (Holotype: M).

Homotypic synonym: *Lecythis corrugata* subsp. *rosea* (O.Berg) S.A. Mori, Brittonia 33: 363. 1981.

Habitat and distribution: Found in *terra firme* forest and along rivers and has been collected in Venezuela and Roraima Territory of Brazil (Mori et al., 2010 and ongoing).

Guaiania idatimon (Aubl.) O.M. Vargas & C.W. Dick. *comb. nov.*

Basionym: *Lecythis idatimon* Aubl., Hist. Pl. Guiane 2: 721. 1775.

TYPE: FRENCH GUIANA. Without locality, no date (fl), *J. B. C. F. Aublet s.n.* (Lectotype: designated by Mori and Prance, 1990, BM, photograph [F negative. 402], NY; Isolectotypes: BM-fragment, S).

Habitat and distribution: Typically an understory tree of 10 to 20 m in height and infrequently a canopy tree (to 35 m), locally common in *terra firme* forest from Suriname to Maranhão, Brazil.

Guaiania persistens (Sagot) O.M. Vargas & C.W. Dick, *comb. nov.*

Basionym: *Lecythis persistens* Sagot, Ann. Sci. Nat., Bot. VI, 20: 201. 1885.

TYPE: FRENCH GUIANA. Without locality, 1842 (fl), [initial(s)] *E. Melinon 59* (Lectotype: Designated by Mori and Prance, 1990, P, photograph, NY).

Habitat and distribution: Understory to canopy trees of up to 35 m in height frond in *terra firme* forest in the Guiana Shield region. Known only from Guyana, French Guiana, and Amapá, Brazil. This taxon has two subspecies. In Mori et al. (2007), *Lecythis persistens* subs. *persistens* was sister to *L. persistens* subs. *aurantiaca* + L. *pneumatophora*, suggesting that the subspecies may eventually be elevated to species.

Guaiania persistens *subsp.* aurantica (S.A. Mori) O.M. Vargas & C.W. Dick, *comb. nov.*

Basionym: *Lecythis aurantica* S.A. Mori, Memoirs of The New York Botanical Garden 44: 32. 1987.

TYPE: FRENCH GUIANA. Saul: Monts La Fume, 10 October 1982, *S. A. Mori et al 15075* (Holotype: NY; Isotypes: B, CAY, HAMAB, K, MG, MO, P, U, WIS).

Homotypic synonym: *Lecythis persistens* subsp. *aurantiaca* S.A. Mori, Mem. New York Bot. Gard. 44: 32. 1987.

Habitat and distribution: Canopy tree of unflooded forest known only from French Guiana.

Guaiania pneumatophora (S.A. Mori) O.M. Vargas & C.W. Dick, *comb. nov.*

Basionym: *Lecythis pneumatophora* S.A. Mori, Fl. Neotrop. Monogr. 21(2): 288. 1990.

TYPE: FRENCH GUIANA. Comté River, nr. bridge of Route de l'est, 45 km S of Cayenne, 26 January 1977 (fr), *S. A. Mori & Y. Veyret 8983* (Holotype: NY; Isotype: CAY).

Habitat and distribution: Medium sized trees (to 15 m) found in dense stands along rivers in French Guiana (Oldeman, 1971).

Scottmoria Cornejo, *gen. nov*.

TYPE: *Lecythis integrifolia* Ruiz & Pav. ex Miers, Trans. Linn. Soc. London 30(2): 225. 1874, designated here.

Diagnosis: *Scottmoria* is a clade of Neotropical trees characterized by an androecial hood with three to four inner coils, as seen in medial longitudinal section, and two kinds of seed covering: (1) a thin white sarcotesta over the entire or most of the mature seed that is infiltrated with testa or a thin white sarcotesta present over the entire or most of the seed in young seeds but mostly dissolving at maturity, and with a thick, yellow to white, half I-beam shaped aril, with rubber-like texture and overlapping ends on seed; or (2) seeds with a finely tuberculate testa, surrounded by a mostly free, white rubbery coat; funicle surrounded by the aril (Fig. 3).

Etymology: The genus honors Scott Alan Mori (1941–2020), an extraordinary and prolific American botanist, who achieved the greatest discoveries on Neotropical Lecythidaceae during the past half of century (Prance et al., 2020). His profound dedication to the research and training of students throughout decades has deeply impacted our understanding of this family. The new genus is befittingly named after him.

Twenty-three new combinations are presented based on species formerly in *Eschweilera s.l.*, corresponding to the *Eschweilera integrifolia* clade (Mori et al., 2017; Vargas and Dick, 2020) to *Scottmoria*. The eight species of this clade studied in the field by Cornejo are marked with an asterisk (*).

Scottmoria aguilarii (S.A. Mori) Cornejo, *comb. nov.**

Basionym: *Eschweilera aguilarii* S.A. Mori, Monogr. Syst. Bot. Missouri Bot. Gard. 111: 903. 2007.

TYPE: COSTA RICA. Puntarenas: Cantón de Osa, Sierpe, San Juan, cuenca superior del Río San Juan, estribaciones Cerros Chocuaco, 8°43'50"N, 83°33'05"W, 580 m, 21 July 1990 (fl), *G. Herrera 3997* (Holotype: CR; Isotypes: MO, NY).

Habitat and distribution: Wet, lowland forests at less that 600 m on the Osa Peninsula, Costa Rica, and Honduras (Batista and Mori, 2017; Mori et al., 2010 and ongoing).

Scottmoria amplexifolia (S.A. Mori) Cornejo, *comb. nov.*

Basionym: *Eschweilera amplexifolia* S.A. Mori, Fl. Neotrop. Monogr. 21(2): 210. 1990.

TYPE: PANAMA. Colón: Santa Rita Ridge Road, 26 October 1974 (fl), *S. A. Mori & J. Kallunki 2791* (Holotype: MO; Isotype: NY).

Habitat and distribution: Endemic to the wet forests from near sea level to 200 m in the Caribbean coast and lower slopes of Panama in the provinces of Colón and San Blas (Mori and Prance, 1990; Mori et al., 2010 and ongoing).

Scottmoria andina (Rusby) Cornejo, *comb. nov.**

Basionym: *Lecythis andinus* Rusby, Mem. Torrey Bot. Club 6: 37. 1896.

TYPE: BOLIVIA. Mapiri: July–August 1892 (fl), *M. Bang 1522* (Lectotype: designated by Mori and Prance, 1990, NY [accession No. 1076]; Isolectotypes: K, MO, NY [accession No. 1077]).

Homotypic synonym: *Eschweilera andina* (Rusby) J.F. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4): 246. 1941.

Habitat and distribution: In non-flooded Amazonian forests to ca. 800 m along the eastern slopes of the Andes from Colombia to Bolivia (Mori and Prance, 1990; Mori et al., 2010).

Scottmoria antioquensis (Dugand & Daniel) Cornejo, *comb. nov.*

Basionym: *Eschweilera antioquensis* Dugand & Daniel, Contr. Hist. Nat. Colomb. 2: 1–2. 1938.

TYPE: COLOMBIA. Antioquia: Laguna de Guarne, 2285 m, 26 June 1937 (fl), *H. Daniel 1201* (Holotype: Herbario del Colegio de San José de Medellín; Isotypes: COL, US).

Habitat and distribution: In unflooded forests, usually at elevations of 1000 m in northwestern Colombia in the departments of Antioquia, Chocó, and Cundinamarca and NW Venezuela in the state of Mérida (Mori and Prance, 1990; Mori et al., 2010 and ongoing) with a disjunct collection in Cerro Jefe region in central Panama (collection *R. Dressler 3508* at MO).

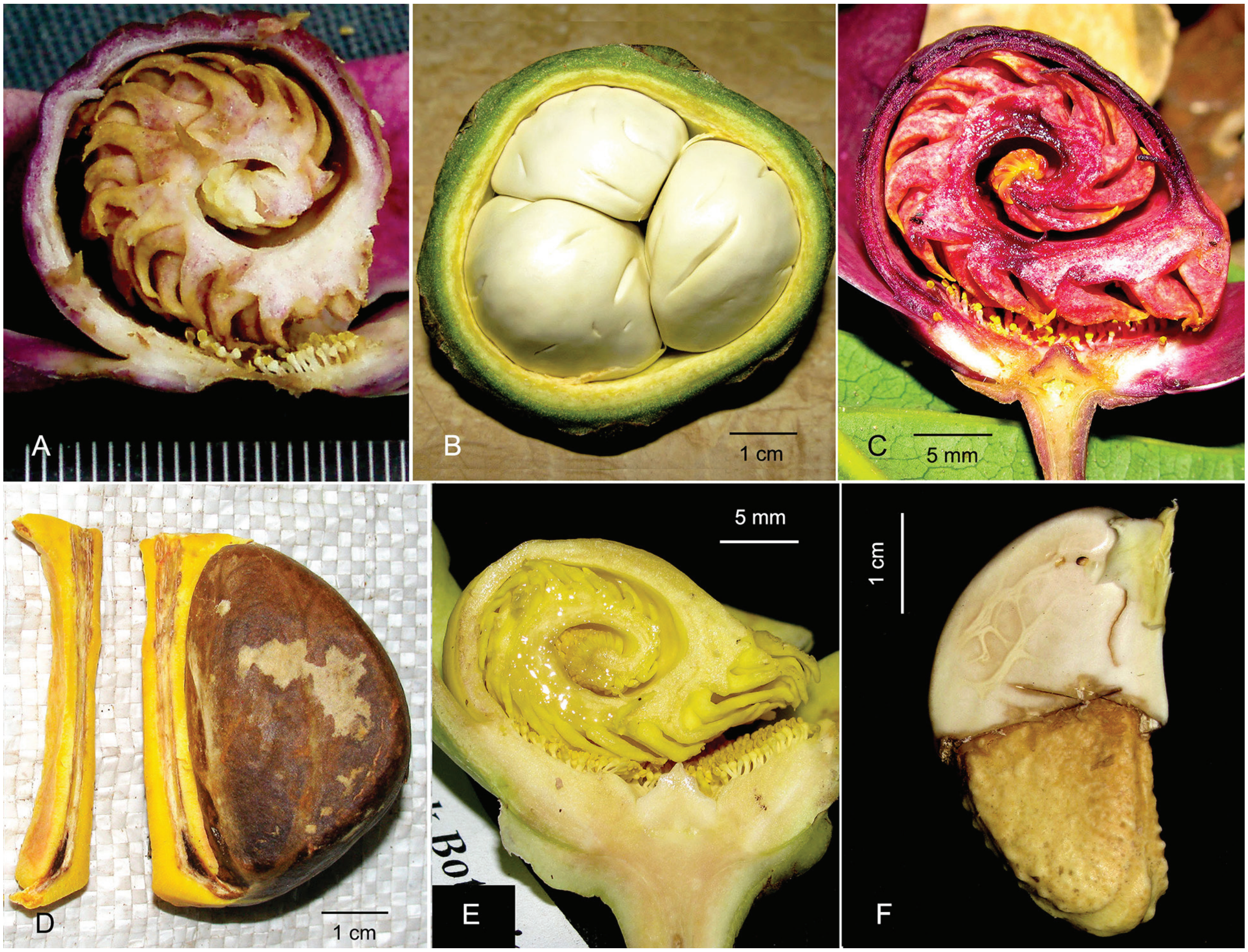


FIGURE 3. *Scotttmoria* Cornejo, morphological features. *Scottmoria integrifolia* (Ruiz & Pav. ex Miers) Cornejo: **A**, Medial section of androecial hood exhibiting a triple coil (*Cornejo & Grochowski 8057*, NY, from environs of the type area; scale in mm); **B**, Cut open fruit, the operculum removed, note three seeds fully surrounded by a fleshy white spreading aril (*Cornejo 8111*, NY). *Scottmoria rimbachii* (Standl.) Cornejo: **C**, Medial section of androecial hood exhibiting a triple coil (*Cornejo & García 8450*, NY). *Scottmoria caudiculata* (R. Knuth) Cornejo: **D**, Smooth seed with impressed nerves and a longitudinally sectioned yellow, half I-beam aril, note the funicle all the way along the interior of aril, and the irregular small relict patches of whitish thin sarcotesta (*Cornejo 8106*, NY). *Scottmoria awaensis* (S. A. Mori & Cornejo) Cornejo: **E**, Medial section of androecial hood exhibiting a triple coil; F, Seed with a white rubbery free coat, partially removed on lower half exhibiting a finely tuberculate testa (*Cornejo & Macías 8171*, NY, holotype).

Scottmoria awaensis (S.A. Mori & Cornejo) Cornejo, *comb. nov.** Fig. 3E, F.
Basionym: *Eschweilera awaensis* S.A. Mori & Cornejo, Brittonia 63: 470. 2011.
TYPE: ECUADOR. Esmeraldas: Bilsa Biological Station, Sendero Verde, 79˚44'W, 0˚21'N, 500 m, 16 October 2009 (fl, fr), *X. Cornejo & A. Macías 8171* (Holotype: NY; Isotypes: COL, GUAY, K, MO, QCNE, US, USM).

Habitat and distribution: Endemic to the wet forests on non-flooded soils from lowlands to 800 m in northwestern Ecuador (Cornejo and Mori, 2011).

Scottmoria brevipetiolata (S.A. Mori & Cornejo) Cornejo, *comb. nov.*
Basionym: *Eschweilera brevipetiolata* S.A. Mori & Cornejo, Phytotaxa 585: 288. 2023.
TYPE: COLOMBIA. Valle del Cauca: Bajo Calima; Concesión Pulpapel/Buenaventura, carretera al Dindo, 77˚00'W, 3˚55'N, ca. 100 m, 25 September 1986 (fl), *M. Monsalve 1169* (Holotype: CUVC-25917; Isotypes: MO-3701257, MO-3701347, NY-00853327).

Habitat and distribution: From 50 to 100 m elevation in wet to pluvial forests on non-flooded areas, department of Valle del Cauca, western Colombia (Cornejo, 2023b).

Scottmoria calyculata (Pittier) Cornejo, *comb. nov.*
Basionym: *Eschweilera calyculata* Pittier, Contr. U. S. Natl. Herb. 12: 97, Fig. 1, Pl. III. 1908.
TYPE: COSTA RICA. Limón: Forests between Port Limón and Moin, September 1899 (fl), *H. Pittier 16018* (Holotype: US [578009]).

Habitat and distribution: In lowland forests in *terra firme* and swamp forests at the Caribbean coast of southern Central America from a short distance N of Limón, Costa Rica to near Portobelo, Panama (Mori and Prance, 1990; Mori et al., 2010 and ongoing).

Scottmoria caudiculata (R. Knuth) Cornejo, *comb. nov.** Fig. 1D.
Basionym: *Eschweilera caudiculata* R. Knuth, Pflanzenr. (Engler) IV.219a: 95. 1939.
TYPE: COLOMBIA. Antioquia: Peñitas, 1880 (fl), *G. Kalbreyer 1860* (Holotype: B, not found or destroyed; Lectotype: designated by Mori and Prance, 1990, K, photograph NY [K neg. no. 16386]).

Eschweilera caudiculata syn. nov. was classified as a member of the Parvifolia clade in Mori and Prance (1990) but, because it has flowers with a triple coil, this species belongs in the Integrifolia clade.

Habitat and distribution: A predominantly Andean species in non-flooded forests often at 1000 to 2500 m, ranging from eastern Panama to southern Ecuador (Mori and Prance, 1990; Mori et al., 2010 and ongoing).

Scottmoria collinsii (Pittier) Cornejo, *comb. nov.**
Basionym: *Eschweilera collinsii* Pittier, Contr. U. S. Natl. Herb. 12: 97, Fig. 1, Pl. III. 1908.
TYPE: COSTA RICA. Alajuela, Plains of San Carlos, 100 m, 15 April 1903 (fr), *O. F. Cook & C. B. Doyle 95* (Holotype: US [accession No. 473872]).

Habitat and distribution: In wet forests from near sea level to 1000 m elevation, Veraguas, Panama, and on the Atlantic and Pacific slopes of Costa Rica in the Provinces of Alajuela, Puntarenas, Limón, and San José (Mori and Prance, 1990; Mori et al., 2010 and ongoing).

Scottmoria hondurensis (Standl.) Cornejo, *comb. nov.*
Basionym: *Eschweilera hondurensis* Standl., Field Mus. Nat. Hist., Bot. Ser. 9:318. 1940.
TYPE: HONDURAS. Atlantida: vicinity La Ceiba, lower slopes of Mt. Cangrejal, 6 August 1938 (fr), *T. G. Yuncker, J. M. Koepper & K. A. Wagner 8829* (Holotype: F; Isotypes: BM, K, MO, NY).

Habitat and distribution: In non-flooded primary forests, often collected on the lower slopes of low mountains at below 500 m elevation from Honduras to the Pacific coast of Panama (Cerro Hoya National Park and Coiba Island National Park) (Mori and Prance, 1990; Mori et al., 2010 and ongoing).

Scottmoria integrifolia (Ruiz & Pav. ex Miers) Cornejo, *comb. nov.** Fig. 3A, B.
Basionym: *Lecythis integrifolia* Ruiz & Pav. ex Miers, Trans. Linn. Soc. London 30(2): 225. 1874.
TYPE: ECUADOR. Guayas: Guayaquil, no date (fl), *J. Tafalla s.n.* (Lectotype: designated by Mori & Prance, 1990, MA, photograph, GH; Isolectotype: K).
Homotypic synonym: *Eschweilera integrifolia* (Ruiz & Pavón ex Miers) R. Knuth, Pflanzenr. (Engler) IV, 219a: 97. 1939.

Habitat and distribution: Persistent in secondary moist and wet forests from sea level to ca. 800 m elevation from the Pacific coast of Colombia to western Ecuador (Mori & Prance, 1990; Mori et al., 2010 and ongoing).

Scottmoria jacquelyniae (S.A. Mori) Cornejo, *comb. nov.*
Basionym: *Eschweilera jacquelyniae* S.A. Mori, Fl. Neotrop. Monogr. 21(2): 192. 1990.
TYPE: PANAMA. Panamá. Gorgas Memorial Labs. Yellow Fever Research Camp, Campamento Cuatro, 5–10 km NE of Altos de Pacora on ridge top, 600 m, 21–24 November 1974 (fl), *S. A. Mori & J. Kallunki 3440* (Holotype: NY; Isotypes: COL, K, MO, PMA, US).

Habitat and distribution: Endemic to cloud forests 600 to 1000 m elevation in central Panama (Mori and Prance, 1990; Mori et al., 2010 and ongoing).

Scottmoria jefensis (J.E. Bat. & S.A. Mori) Cornejo, *comb. nov.*
Basionym: *Eschweilera jefensis* J.E. Bat. & S.A. Mori, Phytoneuron 62: 2. 2017.
TYPE: PANAMA. Provincia de Panamá: Parque Nacional Chagres, Alrededores de Cerro Jefe, 9°12'N, 79°22'W, 900 m, 24 January 1996 (fl), *C. Galdames et al. 2414* (Holotype: PMA; Isotypes: MO, NY, SCZ).

Habitat and distribution: Endemic to the cloud forests from 800 to 1000 m in central and eastern parts of Panama Province, Panama (Batista et al., 2017).

Scottmoria ovalifolia (DC.) Cornejo, *comb. nov.*
Basionym: *Lecythis ovalifolia* DC., Prodr. (DC.) 3: 292. 1828.
TYPE: BRAZIL. Amazonas: At mouth of Rio Negro, no date (fl), *C. Martius s.n.* (Lectotype: designated by Mori & Prance, 1990, M, photo NY; Isolectotypes: G, photographs of specimen at G at A, K, M, NY [F negative. 23206]).
Homotypic synonym: *Eschweilera ovalifolia* (DC.) Nied., Nat. Pflanzenfam. 3(7): 40. 1892.

Habitat and distribution: In periodically flooded riverine forests of Central and western Amazonia in Brazil, Bolivia, and Peru (Mori and Prance, 1990; Mori et al., 2010 and ongoing).

Scottmoria pachyderma (Cuatrec.) Cornejo, *comb. nov.*
Basionym: *Eschweilera pachyderma* Cuatrec., Fieldiana, Bot. 27(2): 91. 1951.
TYPE: COLOMBIA. Valle del Cauca: Costa de Pacífico, Río Cajambre, 8 May 1944 (fl), *J. Cuatrecasas 17448* (Lectotype: designated by Mori and Prance, 1990, F [accession No.1358486]; Isolectotypes: F [accession No. 1358487], NY, U).

Habitat and distribution: Pluvial forests, Pacific coast of Colombia (Mori and Prance, 1990; Mori et al., 2010 and ongoing).

Scottmoria panamensis (Pittier) Cornejo, *comb. nov.*
Basionym: *Eschweilera panamensis* Pittier, Contr. U. S. Natl. Herb. 26(1): 12. 1927.

TYPE: PANAMA. San Blas: Hills back of Puerto Obaldia, 50–200 m, August 1911(fl, fr), *H. Pittier 4338* (Holotype: US [accession No. 679481]; Isotypes: BM, F, K, NY).

Habitat and distribution: Known only from *terra firme* forests below 500 m, from Bocas del Toro to the vicinity of Puerto Obaldia, Panama (Mori and Prance, 1990; Mori et al., 2010 and ongoing).

Scottmoria podoaquilae (Cornejo) Cornejo, *comb. nov.**
Basionym: *Eschweilera podoaquilae* Cornejo, Phytotaxa 579: 139. 2023.
TYPE: ECUADOR. Santo Domingo de los Tsáchilas: Centinela, área norte de las montañas de Ila, Parroquia El Esfuerzo, comuna Polanco, Cascadas Las Rocas, 79°11'W, 0°28'S, 560 m, 20 March 2022 (fl), *X. Cornejo, J. L. Clark & C. Restrepo 10032* (Holotype: GUAY; Isotype QCA).

Habitat and distribution: Endemic to the wet forests on *terra firme* areas in northwestern Ecuador (Cornejo, 2023a).

Scottmoria rimbachii (Standl.) Cornejo, *comb. nov.** Fig. 1C.
Basionym: *Eschweilera rimbachii* Standl., Trop. Woods 42: 31. 1935.
TYPE: ECUADOR. [probably Chimborazo]: Foot of Western Cordillera, 1931 (fr), *A. Rimbach 47* (Lectotype: designated by Mori and Prance, 1990, F [accession No. 677029]; Isolectotype: F [accession No. 677045]).

Habitat and distribution: Persistent after disturbance in *terra firme* secondary wet forests, southwestern Colombia, and western Ecuador (Mori and Prance, 1990; Mori et al., 2010 and ongoing).

Scottmoria roseocalyx (J.E. Bat., S.A. Mori, & J.S. Harrison) Cornejo, *comb. nov.*
Basionym: *Eschweilera roseocalyx* J.E. Bat., S.A. Mori, & J.S. Harrison, Phytoneuron 62: 7. 2017.
TYPE: PANAMA. Province of Panama, Parque Nacional Chagres, entrando por Altos de Cerro Azul, Cerro Jefe, bosque achaparrado dominado por *Colpothrinax aphanopetala* R. Evans (Arecaceae), 9°13'39"N, 79°23'20"W, 970 m, 28 May 2016 (fl), *J. Batista et al. 1680* (Holotype: PMA; Isotypes: MO, NY, SCZ, UCH, US).

Habitat and distribution: Endemic to Cerro Jefe, Chagres National Park, in central Panama, at elevations 900 to 1000 m (Batista et al., 2017).

In the protologue, *Eschweilera roseocalyx* was described and discussed as having androphores with a double coil; however, a closer examination of the illustration (Fig. 5 H in Batista et al., 2017) reveals an androphore with a triple coil. That character jointly with the spreading white aril design of seeds fully fits *Scottmoria*, as is also confirmed by the molecular results presented herein.

Scottmoria rotundicarpa (J.E. Bat. & S.A. Mori) Cornejo, *comb. nov.*
Basionym: *Eschweilera rotundicarpa* J.E. Bat. & S.A. Mori, Phytotaxa 296: 46. 2017.
TYPE: PANAMA. Provincia de Coclé, Corregimiento El Harino, Parque Nacional General de División Omar Torrijos Herrera, sendero de la Quebrada Yaya (Sendero Los Monos), 8°40'04"N, 80°35'53"W, 717 m, 22 September 2014 (fr), *J. Batista G., A. Espinosa, & J. Montenegro 1085* (Holotype: PMA; Isotypes: MO, NY, SCZ, UCH).

Habitat and distribution: Endemic to cloud forests at elevations 700 to 900 m and lowland rain forests at elevations 200 to 300 m in Panama (Batista and Mori, 2017).

The original description associated this species with the Integrifolia clade (Batista & Mori, 2017); however, its triple coil, and spreading aril in the seed, along with its phylogenetic position evidence the inclusion of this species in *Scottmoria*.

Scottmoria sclerophylla (Cuatrec.) Cornejo, *comb. nov.*
Basionym: *Eschweilera sclerophylla* Cuatrec., Fieldiana, Bot. 27(2): 92. 1951.
TYPE: COLOMBIA. Valle: Rio Calima (region del Choco), La Trojita, 5–50 m alt., 27 February 1944 (fl), *J. Cuatrecasas 16517* (Lectotype: designated by Mori & Prance, 1990, F [accession No. 1358508]; Isolectotypes: F [accession No. 1358509], NY).

Habitat and distribution: Known from pluvial forests near sea level to 100 m the departments of Valle and Chocó, Colombia (Mori and Prance, 1990; Mori et al., 2010 and ongoing).

Scottmoria sessilis (A.C. Sm.) Cornejo, *comb. nov.*
Basionym: *Eschweilera sessilis* A.C. Sm., Phytologia 1: 21. 1933.
TYPE: COLOMBIA. Boyacá. In forest on Mt. Chapón, 2100 m, 17 June 1932 (fl), *A. Lawrance 239* (Holotype: NY; Isotypes: BM, K, MO).

Habitat and distribution: From 350 to 2100 m elevation in wet to pluvial forests of Colombia (Mori and Prance, 1990; Mori et al., 2010 and ongoing).

Scottmoria silverstonei (Cornejo) Cornejo, *comb. nov.*
Basionym: *Eschweilera silverstonei* Cornejo, Phytotaxa 585: 290. 2023.
TYPE: COLOMBIA. Valle del Cauca: Bajo Calima; Concesión Pulpapel/Buenaventura, 77°00'W, 3°55'N, ca. 100 m, 9 August 1984 (fl), *M. Monsalve 214* (Holotype: CUVC [accession No. 19929]; Isotype: NY [accession No. 02152729]).

Habitat and distribution: At ca. 100 m elevation in wet to pluvial forests on *terra firme* areas, department of Valle del Cauca, western Colombia (Cornejo, 2023b).

Discussion

We present a phylogeny of Neotropical Lecythidaceae based on unprecedented genomic sampling of the family, with over 300 nuclear genes and a large and variable portion of the plastome genome sampled for most of the Neotropical species. We focused our sampling on the Bertholletia clade, centered in northern South America, with the aim of obtaining a robust hypothesis for the relationships among its genera. We found strong phylogenetic support for the polyphyly of *Lecythis* and *Eschweilera*—suggested but weakly supported in previous studies (Mori et al., 2007; Huang et al., 2015)—which justifies our revised classification of these two genera. The phylogenies presented here can serve as a backbone for future taxonomic and evolutionary studies of the Lecythidaceae. We provide an updated list of all described Neotropical Lecythidaceae to date (Table S3).

Taxonomic Changes

We have divided *Lecythis* and *Eschweilera* each into four genera, with a total of six new or reinstated genera. We have reduced *Lecythis* from 26 to three species, and *Eschweilera* now circumscribes only the Amazon-centered Parvifolia clade. Mori and colleagues (Huang et al., 2015; Mori et al., 2017; Mori et al., 2010 and ongoing) anticipated these taxonomic changes. For example, "*Lecythis*, as currently circumscribed, is most likely not monophyletic; thus, generic realignments are to be expected in the future…There are 26 known species, but if the genera are circumscribed differently *Lecythis sensu stricto* will consist of only three species." (*Lecythis* description in Mori et al., 2010 and ongoing). In addition to the anticipated taxonomic changes for *Eschweilera* and *Lecythis*, we detected that *Eschweilera amazoniciformis* is sister to *Corythophora* and the Tetrapetala clade (*Imbiriba*), thus justifying its elevation to a new genus, *Waimiria*. Although it was not essential to elevate to genus the Integrifolia section of *Eschweilera s.l.*, we agreed that the morphological and geographical distinctiveness of the clade merited genus-level recognition.

The alternative to splitting *Eschweilera* and *Lecythis* was to lump the entire Bertholletia clade into *Lecythis*, thereby eliminating *Eschweilera*, *Bertholletia*, and *Corythophora*. We felt that this approach would have hidden important evolutionary and biogeographic history.

Phylogenetic conflicts

We observed phylogenetic conflict among nuclear genes, as is typical of most nuclear phylogenomic analyses. We found that the monophyly of most major clades was supported by a majority of informative gene trees, whereas there was more conflict for the relationships among recently diverged species (Fig. S2). Nearly all major clades recovered in the nuclear tree were also recovered in the plastome tree (Fig. 2). An exception was the monophyly of the Parvifolia and Integrifolia clades because one sample (i.e., L302, *Eschweilera* sp.) was recovered as sister to *Scottmoria sessilis* (Integrifolia clade) in the plastome tree but was sister to *Eschweilera juruensis* R. Knuth (Parvifolia clade) in the nuclear tree. The markedly different placements of this single sample in the two trees suggests there may have been recent introgression between the Parvifolia and Integrifolia clades, since none of the other ~90 plastomes sampled from these clades share this pattern, as might be expected if this conflict was due to incomplete lineage sorting (ILS). This sampled specimen (*S. A. Mori 25642*; collected at Los Amigos biological station, Peru) was originally determined as *Eschweilera tessmannii* R. Knuth (Parvifolia clade) by S. A. Mori in 2003, but was later re-designated as *Eschweilera* sp. by Mori in 2012. This specimen was included in the sampling of a chloroplast phylogeny of the *ndhF* and *trnL-F* genes as *Eschweilera tessmannii* by Mori et al. (2007), who also found its chloroplast genome to be closely related to the Integrifolia clade. Furthermore, the chloroplast regions from that study (GenBank accessions DQ388268 and DQ417983) matched the *de novo* chloroplast assembly produced in this study with 99.9% (a single bp mismatch across the 1992 base pairs of sequence) and 100% identity, respectively (data not shown), confirming that the placement of its plastome among the Integrifolia clade is not erroneous. Notably, *Corythophora* was recovered as monophyletic in the plastome tree (Fig. 2) but was paraphyletic in the nuclear tree. We hypothesize that the non-monophyly of *Corythophora* in the nuclear data can be explained by ILS, considering that the genus is monophyletic in the plastome tree—plastome genotypes can be fixed in a population rapidly because their effective population size is one quarter relative to that of an autosomal nuclear region (Moore, 1995), thus explaining the discordance.

Evolutionary diversity uncovered

The new taxon *Waimiria*, as a monotypic genus with distinct morphology and phylogenetic isolation, is comparable to the iconic and monotypic Brazil nut tree *Bertholletia* in its position as an evolutionary outlier within the Bertholletia clade. *Waimiria amazoniciformis* is a canopy or canopy-emergent species with a distinctive cylindrical trunk. Its flowers notably have four petals (which it shares with four of the six *Imbiriba* species), and it has a distinctive elongated fruit similar to eponymous *Eschweilera amazonica*. Despite its stature and distinctive floral and fruit morphology, and its proximity to an intensively collected forest near the city of Manaus (Nelson et al., 1990) and relatively high abundance there (147 individuals in the Lecythidaceae plot; Milton et al., 2022), it was only described as a new species in 1990. This relatively recent discovery is typical of many species in Lecythidaceae and other Amazon tree families. The small geographic ranges of narrowly endemic species make them easy to overlook, and large trees of mature Amazon Forest are difficult to collect and poorly represented in herbaria. While there are exceptions, such as hyperabundant *E. coriacea* which has been collected thousands of times, the average number of global collections per Lecythidaceae species is around 24, with 82 taxa having a single specimen collected and 137 taxa having three or less specimens collected (Medellín-Zabala, in prep.). To obtain high quality (i.e., fertile) herbarium specimens, trees in mature Amazon Forest must first be identified as being distinctive and in fertile condition, requiring some local botanical knowledge, and then they must typically be climbed, which requires expertise and is a substantial investment in labor (Mori et al., 2011). In the central Amazon, mature forest tree populations may go decades without producing perceptible quantities of flowers or fruit.

Species Boundaries and Hybridization

The "Lecythidaceae Plot" within reserve 1501 of the BDFFP is a useful case study of the diversity of Lecythidaceae in the central Amazon, and it is especially relevant for this study because we sampled all of its species. Scott Mori led the identification of Lecythidaceae (>10 cm dbh) in the 100-ha forest plot beginning in 1989. The initial census yielded 7791 trees from 39 species. *Eschweilera coriacea* was the most abundant species, with n = 1529 individuals (Milton et al., 2022). Of the 39 species in the plot, 30% (13 spp.) were described since 1978; three species (*Chytroma gracieana* [n = 40], *Eschweilera romeu-cardosoi* S.A. Mori [n = 309] and *E. rankiniae* S.A. Mori [n = 16]) were first collected in the plot. Mori recognized two additional new species ("*Lecythis* 01" [n = 8] and "*Lecythis* 05" [n = 51], both species were sampled in this study and were found to belong to *Chytroma*) on the basis of field characters but didn't formally name them for lack of flower or fruit specimens. Thirty years of monitoring have not yielded a single fruit- or flower-bearing specimen from these relatively large trees. For our team, the Lecythidaceae plot was a "living herbarium" that allowed us to sample the family level diversity and explore useful field characters including aspects of bark, stature, and tree form.

We sampled multiple individuals of hyperdominant species of *Eschweilera* s.s. (Parvifolia clade) in the Lecythidaceae plot. Hyperdominant species are members of a group of 257 tree species (out of an estimated 5000 species) that comprise >50% of stem numbers and biomass in Amazonian Forest inventories (ter Steege et al., 2013). The Parvifolia clade contains three hyperdominant *Eschweilera* species in the Lecythidaceae plot, which are also dominant at the local scale: *E. coriacea* (n = 1539), *E. truncata* (n = 1321), and *E. wachenheimii* (Benoist) Sandwith (n = 926) (Mori and da Cunha 1995). *Eschweilera coriacea* was suspected to contain cryptic diversity and/or hybridize (M. Heuertz, pers. com.), and we were interested in knowing if the taxonomic boundaries corresponded with distinctive gene pools in these and the other Lecythidaceae species. Larson et al. (2021) performed more detailed population genomic analyses which supported the hypothesis of hybridization and introgression amongst *E. coriacea, E. truncata*, and *E. wachenheimii*. Hybridization and introgression are evolutionary processes that may permit ecological generalist species like *E. coriacea* to thrive in all the major Amazon Forest types (Larson et al., 2021; Heuertz et al., 2020). Further taxonomic sampling within *E. coriacea* may reveal cryptic species diversity. It is notable that, despite evidence of hybridization in the hyperdominant *Eschweilera*, Larson et al. (2021) found that the other species exhibited distinctive gene pools that corresponded with their taxonomy, suggesting that current species circumscriptions provide a meaningful description of the diversity of Neotropical Lecythidaceae, with no evidence of widespread taxonomic "over-splitting."

Implications for Ecology and Biogeography

Lecythidaceae comprise about half of all trees in mature Amazon Forest and is an important family across networks of Amazon Forest inventory plots (e.g., ter Steege et al., 2013); and in terms of tree abundance and species richness, *Lecythis s.l.* and *Eschweilera s.l.* are its two most important genera in the basin. With the BDFFP Lecythidaceae plot as our point of reference for the central Amazon forests, our revised taxonomy will not affect most of its *Eschweilera*, as the Parvifolia clade (*Eschweilera sensu stricto*) are predominant here. In the Lecythidaceae plot, 15 of the 16 *Eschweilera* species maintain their names, with only *E. amazoniciformis* transferring to the monotypic genus *Waimiria*. In contrast, the name *Lecythis* is essentially eliminated from most Amazon forests. In the Lecythidaceae plot, eight species are transferred to *Chytroma* and the remaining two are transferred to *Pachylecythis*. *Lecythis sensu stricto*, based on our revised classification, will contain only three species that are relegated to the Guiana shield region. Our revised taxonomy corresponds geographically with the centers of origin of these taxa previously suspected to be clades (Vargas and Dick, 2020). This will increase the level of genus-level turnover (beta diversity) among regions for researchers interested in continental scale biodiversity patterns.

Literature Cited

Altschul, S. F, W. Gish, W. Miller, E. W. Myers, and D. J. Lipman. 1990. Basic local alignment search tool. Journal of Molecular Biology 215: 403–410.

APG IV. 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Botanical Journal of the Linnaean Society 181: 1–20. doi: 10.1111/boj.12385

Aublet, F. 1775. *Histoire des plantes de la Guiane Francoise*. 4 vols. Didot, Paris.

Bankevich, A., S. Nurk, D. Antipov, A. A. Gurevich, M. Dvorkin, A. S. Kulikov, V. M. Lesin, S. I. Nikolenko, S. Pham, A. D. Prjibelski, A. V. Pyshkin, A. V. Sirotkin, N. Vyahhi, G. Tesler, M. A. Alekseyev, and P. A. Pevzner. 2012. SPAdes: a new genome assembly algorithm and its applications to single-cell sequencing. Journal of Computational Biology 19: 455–477.

Batista, J. E., and S. A. Mori. 2017. Two New Species of Eschweilera (Lecythidaceae) from Rainforest on the Caribbean Slope of Panama. Phytotaxa 296 (1): 041–052. https://doi.org/10.11646/phytotaxa.296.1.2.

Batista, J. E., S. A. Mori., and J. S. Harrison. 2017. New species of *Eschweilera* and a first record of *Cariniana* (Lecythidaceae) from Panama. Phytoneuron 2017: 1–16.

Brazil, Ministry of the Environment. 2022. Ordinance Nº 148 of July 7, 2022. Update of the Official List of Species of Flora Brasiliera Threatened with Extinction. Brasilia. Available at: Portaria MMA nº 148/2022

Brown, J. W., J. F. Walker, and S. A. Smith. 2017. Phyx: phylogenetic tools for Unix. Bioinformatics 33: 1886–1888.

Camacho, C., G. Coulouris, V. Avagyan, N. Ma, J. Papadopoulos, K. Bealer, and T. L. Madden. 2009. BLAST+: architecture and applications. BMC Bioinformatics 10: 421.

Capella-Gutiérrez, S., J. M. Silla-Martínez, and T. Gabaldón. 2009. trimAl: a tool for automated alignment trimming in large-scale phylogenetic analyses. Bioinformatics 25(15):1972–1973.

Caron, H, J-F. Molino, D. Sabatier, P. Léger, P. Chaumeil, C. Scotti-Saintagne, J-M. Frigério, I. Scotti, A. Franc, and R. J. Petit. 2019. Chloroplast DNA variation in a hyperdiverse tropical tree community. Ecology and Evolution 9: 4897–4905.

Chambers, J. Q, N. Higuchi, and J. P. Schimel. 1998. Ancient trees in Amazonia. Nature 391: 135–136.

Cock, P. J. A., T. Antao, J. T. Chang, B. A. Chapman, C. J. Cox, A. Dalke, I. Friedberg, T. Hamelryck, F. Kauff, B. Wilczynski, and M. J. De Hoon. 2009. Biopython: Freely available Python tools for computational molecular biology and bioinformatics. Bioinformatics 25: 1422–1423

Cornejo, X. 2023a. *Eschweilera podoaquilae*: A new species of Lecythidaceae from northwestern Ecuador. Phytotaxa 579: 139–142.

Cornejo, X. 2023b. *Eschweilera brevipetiolata* and *E. silverstonei:* Two new species of Lecythidaceae from western Colombia. Phytotaxa 585: 287–292.

Cornejo, X., and S. A. Mori. 2011. *Eschweilera awaensis* and *Grias subbullata* (Lecythidaceae), two new species from northwestern Ecuador. Brittonia 63: 469–477.

Davis, S. H. 1977. *Victims of the Miracle: Development and the Indians of Brazil*. Cambridge University Press.

Fuckel, L. 1870. Symbolae mycologicae. Beiträge zur Kenntniss der Rheinischen Pilze. Jahrbücher des Nassauischen Vereins für Naturkunde. 23–24:1–459

Heuertz, M., H. Caron, C. Scotti-Saintagne, P. Pétronelli, J. Engel, N. Tysklind, S. Miloudi, F. A. Gaiotto, J. Chave, J-F Molino, D. Sabatier, J. Loureiro, and K. B. Budde. 2020. The hyperdominant tropical tree *Eschweilera coriacea* (Lecythidaceae) shows higher genetic heterogeneity than sympatric *Eschweilera* species in French Guiana. Plant Ecology and Evolution 153(1): 67–81.

Huang, Y. Y., S. A. Mori, and L. M. Kelly. 2015. Toward a phylogenetic-based generic classification of neotropical Lecythidaceae—I. Status of *Bertholletia*, *Corythophora*, *Eschweilera* and *Lecythis*. Phytotaxa 203: 85–121. doi: 10.11646/phytotaxa.203.2.1

IPNI. 2020. International Plant Names Index. Published on the Internet http://www.ipni.org, The Royal Botanic Gardens, Kew, Harvard University Herbaria & Libraries and Australian National Botanic Gardens. [Retrieved 10 December 2020].

Jin, J. J., W. B. Yu, J. B. Yang, Y. Song, C. W. de Pamphilis, T-S. Yi, and D-Z. Li. 2020. GetOrganelle: a fast and versatile toolkit for accurate de novo assembly of organelle genomes. Genome Biology 21: 241. https://doi.org/10.1186/s13059-020-02154-5

Johnson, M. G., E. M. Gardner, Y. Liu, R. Medina, B. Goffinet, A. J. Shaw, N. J. C. Zerega, and N. J. Wickett. 2016. HybPiper: extracting coding sequence and introns for phylogenetics from high-throughput sequencing reads using target enrichment. Applications in Plant Sciences 4: 1600016.

Katoh, K., and D. M. Standley. 2013. MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. Molecular Biology and Evolution 30: 772–780. doi: 10.1093/molbev/mst010

Langmead, B., and S. Salzberg. 2012. Fast gapped-read alignment with Bowtie 2. Nature Methods 9: 357–359.

Larson, D. A., O. M. Vargas, A. Vicentini, and C. W. Dick. 2021. Admixture may be extensive among hyperdominant Amazon rainforest tree species. New Phytologist 232: 2520–2534

Li, H., and R. Durbin. 2009. Fast and accurate short read alignment with Burrows-Wheeler transform. Bioinformatics 25: 1754–1760

Li H., B. Handsaker, A. Wysoker, T. Fennell, J. Ruan, N. Homer, G. Marth, G. Abecasis, and R. Durbin. 2009. 1000 Genome Project Data Processing Subgroup. The Sequence Alignment/Map format and SAMtools. Bioinformatics 25: 2078–2079.

Lima da Venda, A. K., N. P. Smith, D. M. Judice, T. S. Almeida Penedo, and P. V. Prieto. 2013. Lecythidaceae. Pages 607–611 in G. Martinelli & M. A. Moraes, editors, *Livro vermelho da flora do Brasil*. Centro National da Conservação da Flora. Jardim Botânico do Rio de Janeiro.

Mai, U., and S. Mirarab. 2018. TreeShrink: fast and accurate detection of outlier long branches in collections of phylogenetic trees. BMC Genomics 19(Suppl 5): 272.

Miers, J. 1874. On the Lecythidaceae. Transactions of the Linnean Society of London 30(2): 157–318.

Milton, T., P. Assunção, N. Cabello, S. A. Mori, A. A. de Oliveira, P. Souza, A. Vicentini, and C. W. Dick. 2022. Biomass and demographic dynamics of the Brazil-nut family (Lecythidaceae) in a mature Central Amazon rain forest. Forest Ecology and Management 509: 120058.

Moore, W. M. 1995. Inferring phylogenies from mtDNA variation: mitochondrial-gene trees versus nuclear-gene trees. Evolution 49: 718–726.

Mori S. A., and G. T. Prance. 1981. The “sapucaia” Group of *Lecythis* (Lecythidaceae). Brittonia, 33(1): 70–80.

Mori, S. A. 1987. The Lecythidaceae of a lowland Neotropical Forest: La Fumée mountain, French Guiana. Memoirs of the New York Botanical Garden 44: 1–190

———. 1995. Observações sobre as espécies de Lecythidaceae do leste do Brasil. Boletim de Botânica, Universidade de São Paulo, 14: 1–31.

Mori S. A., and G. T. Prance. 1990. Lecythidaceae. Part II. The zygomorphic-flowered New World genera (*Couroupita*, *Corythophora*, *Bertholletia*, *Couratari*, *Eschweilera*, & *Lecythis*). Flora Neotropica Monograph 21: 1–376.

Mori, S. A., and N. M. Lepsch da Cunha. 1995. The Lecythidaceae of a central Amazonian moist forest. Memoirs of the New York Botanical Garden 75: 1–55.

Mori, S. A., C. H. Tsou, C-C. Wu, B. Cronholm, and A. A. Andergerg. 2007. Evolution of Lecythidaceae with an emphasis on the circumscription of neotropical genera: Information from combined ndhF and trnL-F sequence data. American Journal of Botany 94: 289–301. doi: 10.3732/ajb.94.3.289

Mori, S. A. and G. T. Prance. 1999. Lecythidaceae. Pages 750–779 in P. E. Berry, B. K. Holst, and K. Yatskievych, eds., Flora of the Venezuelan Guayana 5. Missouri Botanical Garden Press, St. Louis, Missouri.

Mori, S. A., N. P. Smith, X. Cornejo, and G. T. Prance. 2010 and ongoing. The Lecythidaceae Pages (http://sweetgum.nybg.org/lp/index.php). The New York Botanical Garden, Bronx, New York.

Mori, S. A., A. Berkov, C. A. Gracie, and E. F. Hecklau. 2011. *Tropical plant collecting: from the field to the internet*. NYBG Press, Bronx, NY.

Mori, S. A., E. A. Kiernan, N. P. Smith, L. M. Kelly, Y-Y. Huang, G. T Prance, and B. Thiers. 2017. Observations on the phytogeography of the Lecythidaceae clade (Brazil nut family). Phytoneuron 30: 1–85.

Nelson, B. W., C. A. C. Ferreira, M. F. da Silva, and M. L. Kawasaki. 1990. Endemism centres, refugia and botanical collection density in Brazilian Amazonia. Nature 345: 714–716.

Oldeman, R. A. A. 1971. Un *Eschweilera* (Lecythidaceae) a pneumatophores en Guyane Française. Cahiers ORSTOM, sér. Biol. 15: 21–27.

Prance, G. T., and S. A. Mori. 1979. Lecythidaceae. Part I. The actinomorphic-flowered New World Lecythidaceae (*Asteranthos*, *Gustavia*, *Grias*, *Allantoma*, & *Cariniana*). Flora Neotropica Monograph 21: 1–270.

Ribeiro, M., S. A. Mori, A. Alves-Araújo, and A. L. Peixoto. 2016a. A new species of *Eschweilera* (Lecythidaceae) from the Brazilian Atlantic Forest. Phytotaxa 255(3): 267–273. doi: 10.11646/phytotaxa.255.3.8

Ribeiro, M., S. A. Mori, A. Alves-Araújo, G. G. Siqueira, and A. L. Peixoto. 2016b. *Eschweilera compressa* (Vell.) Miers (Lecythidaceae): a new record of a threatened plant species in Espírito Santo state, Brazil. Check List 12(6): 1994. doi: http://dx.doi.org/10.15560/12.6.1994

Ribeiro, M. 2019. Filogenia e revisão taxonômica do clado *Eschweilera tetrapetala* (Lecythidaceae). Ph. D. diss., Research Institute of the Rio de Janeiro Botanical Garden, Brazil.

Rieseberg, L., and D. Soltis. 1991. Phylogenetic consequences of cytoplasmic gene flow in plants. Evolutionary Trends in Plants. 5.

Slater, G. S. C., and E. Birney. 2005. Automated generation of heuristics for biological sequence comparison. BMC Bioinformatics 6: 31.

Smith, N. P., S. A. Mori, and G. S. Siqueira. 2016a. *Lecythis marcgraaviana* (Lecythidaceae), an overlooked species from eastern Brazil. Kew Bulletin 71(1): 1–6.

Smith, N. P., S. A. Mori, W. Law, and M. Ribeiro. 2016b. Conservation assessment of Lecythidaceae from eastern Brazil. Kew Bulletin 71(14): 1–19.

Smith, S. A., M. J. Moore, J. W. Brown, and Y. Yang. 2015. Analysis of phylogenomic datasets reveals conflict, concordance, and gene duplications with examples from animals and plants. BMC Evolutionary Biology 15:150.

Stamatakis, A. 2014. RAxML Version 8: A Tool for Phylogenetic Analysis and Post-Analysis of Large Phylogenies. Bioinformatics 30(9): 1312–13. https://doi.org/10.1093/bioinformatics/btu033.

Tange, O. 2011. Gnu parallel-the command-line power tool. The USENIX Magazine 36: 42–47.

ter Steege, H., N. C. A. Pitman, D. Sabatier D., C. Baraloto, R. P. Salomão, J. E. Guevara, O. L. Phillips, C. V. Castilho, W. E. Magnusson, J-F Molino, et al. 2013. Hyperdominance in the Amazonian tree flora. Science 342: 325–342. doi: 10.1126/science.1243092

Thomson A. M., O. M. Vargas, and C. W. Dick. 2018. Complete plastome sequences from *Bertholletia excelsa* and 23 related species yield informative markers for Lecythidaceae. Applications in Plant Sciences 6: e1151. doi: 10.1002/aps3.1151

Turland, N. J., J. H. Wiersema, F. R. Barrie, W. Greuter, D. L. Hawksworth, P. S. Herendeen, S. Knapp, W-H. Kusber, D-Z. Li, K. Marhold, T. W. May, J. McNeill, A. M. Monro, J. Prado, M. J. Price, and G. F. Smith (eds.). 2018: *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017*. Regnum Vegetabile 159. Glashütten: Koeltz Botanical Books. DOI https://doi.org/10.12705/Code.2018

Vargas, O. M., E. M. Ortiz, and B. B. Simpson. 2017. Conflicting phylogenomic signals reveal a pattern of reticulate evolution in a recent high-Andean diversification (Asteraceae: Astereae: Diplostephium). New Phytologist 214(4): 1736–1750.

Vargas O. M., M. Heuertz, S. A. Smith, and C. W. Dick. 2019. Target sequence capture in the Brazil nut family (Lecythidaceae): marker selection and in silico capture from genome skimming data. Molecular Phylogenetics and Evolution 135: 98–104. doi: 10.1016/j.ympev.2019.02.020

Vargas, O. M., and C. W. Dick. 2020. Diversification history of Neotropical Lecythidaceae, an ecologically dominant tree family of Amazon rain forest. Pages 791–809 (chapter 29) in V. l Rull and A. C. Carnaval, editors, *Neotropical Diversification: Patterns and Processes*. Springer International Publishing.

Zhang, C., M. Rabiee, E. Sayyari, and S. Mirarab. 2018. ASTRAL-III: polynomial time species tree reconstruction from partially resolved gene trees. BMC Bioinformatics 19(Suppl 6):153.

Zhbannikov, I. Y., Hunter, S. S., Foster, J. A., and M. L. Settles. 2017. SeqyClean: a pipeline for high-throughput sequence data preprocessing. Pages 407–416 in Proceedings of the 8th ACM International Conference on Bioinformatics, Computational Biology, and Health Informatics.

Appendix

Supplementary materials can be accessed at https://dx.doi.org/10.7302/22806 (The supplementary tables are in the document titled "Supplementary information" at this website). Command and intermediate files can be found in the following repository: https://github.com/oscarvargash/lecy_taxo.

Supplementary Figure 1. The coalescent-consistent tree generated with ASTRAL. Branch-lengths are in coalescent units and node labels are ASTRAL local posterior probabilities.

Supplementary Figure 2. Phylogenetic conflict of gene trees with the nuclear tree, generated with phyparts. The proportion of gene trees that are concordant or discordant are represented in blue and red pies respectively. Uninformative gene trees, those with < 70% bootstrap support, are represented in gray. The number of gene trees that are concordant or discordant are also shown above and below individual branches, respectively.

Supplementary Figure 3. Plastome tree based on a concatenated matrix of 10 plastome regions. Node labels indicate standard, non-parametric bootstrap support. Branches that agree with the nuclear phylogeny are represented as thick black lines and conflicting branches are lighter gray.

Supplementary Table 1: Vouchers with their accession numbers and number of nuclear loci recovered.

Supplementary Table 2. Nuclear regions included in the phylogenetic analysis and their alignment method.

Supplementary Table 3. List of currently valid Neotropical Lecythidaceae names.

Page 180 intentionally left blank.

AMPELOCERA PERCYHERNANDEZII (ULMACEAE), AN ENDANGERED NEW TREE SPECIES FROM THE COLOMBIAN DRY FOREST REMNANTS

Boris Villanueva-Tamayo[1,2,3] and Gerardo A. Aymard-Corredor[1,4,5]

Abstract. *Ampelocera percyhernandezii,* a new tree species restricted to dry forest remnants located inside inter-Andean valleys in the upper Magdalena River basin (Cundinamarca and Tolima departments), is described and illustrated. The new taxon is proposed here based on a literature survey, examination of numerous herbarium *exssicatae*, and field observations. *Ampelocera percyhernandezii* is morphologically similar to *A. albertiae, A. longissima* and *A. macphersoni*. However, the differences between these species are contrasted in the diagnosis, discussion, Table 1, and the species key. The figures show fresh and dried material and a geographical distribution map based on occurrence records. Following the IUCN assessment tool, the conservation status of *A. percyhernandezii* is provisionally determined as endangered (EN). Additionally, habitat information, phenology, the vernacular names, and a key to the species of *Ampelocera* are provided. This new species raises to ten the number of *Ampelocera* taxa. Colombia has the highest diversity of the genus with seven species.

Keywords: Dry forest remnants, inter-Andean valleys, upper Magdalena River, endangered species, *Ampelocera*, Ulmaceae

Resumen. *Ampelocera percyhernandezii,* una nueva especie de árboles restringida a los remanentes de bosques secos localizados en los valles interandinos de la cuenca alta del río Magdalena (departamentos de Cundinamarca y Tolima), es descrita e ilustrada. Este nuevo taxon, se basó en revisiones bibliográficas, el estudio de numerosos *exsiccata* de herbarios, y observaciones en campo. *Ampelocera percyhernandezii* es morfológicamente similar a *A. albertiae, A. longissima y A. macphersoni*. Sin embargo, las diferencias con estas especies son contrastadas en la diagnosis, la tabla 1, las discusiones, y en la clave de las especies. Las figuras muestran el material fresco, seco, y un mapa distribución geográfica basado en los registros aquí presentados. De acuerdo a la evaluación de IUCN, el estado de conservación de *A. percyhernandezii* esta provisionalmente determinado como en peligro (EN). Adicionalmente, se presenta información acerca del hábitat, fenología, nombres vernaculos, y una clave para la identificación de las especies de *Ampelocera*. Esta nueva especie eleva en 10 el número de especies de *Ampelocera*. Colombia, es el país que posee la mayor diversidad del género con 7 especies.

Palabras clave: Bosques secos fragmentados, valles interandinos, alto río Magdalena, especies en peligro, *Ampelocera*, Ulmaceae

Ulmaceae (the Elm family), are a small group of deciduous and evergreen trees, shrubs, and, rarely, lianas or climbers (e.g., *Celtis* L.). The family is well known for its variety of breeding systems, its floral and fruit morph types, its use as an ornamental (e.g., *Ulmus* L.), strong wood (e.g., *Celtis* L. and *Ulmus* L.), and medicinal uses (Todzia, 1993; Sutar et al., 2016; Leme et al., 2018). The family is distributed throughout the temperate zones (Eastern Asia, mainly in China, and in the southeastern U.S.A.) and dry to wet tropical regions of the world (Africa, India, Asia, the Caribbean, Mexico, Central and South America), and currently comprises 7 genera and ca. 67 species (Fragnière et al., 2021).

Ulmaceae was proposed by the French naturalist and politician C. F. Brisseau de Mirbel (de Mirbel, 1815), who founded the science of plant cytology, histology, and physiology (Britannica, 2024). At that time the family contained two genera, *Celtis* and *Ulmus*, and, for about 150 years, it was divided into two subgroups or subfamilies (*Ulmoideae* Engler and *Celtidoideae* Engler) associated with each of the original genera (Manchester, 1989; Wiegrefe et al., 1998). Link (1831) and Grudzinskaya (1967) proposed two different families (Celtidaceae and Ulmaceae s.s.) within Ulmaceae, since many characters of the *Celtidoideae* have a greater affinity to Moraceae than to other Ulmaceae (Grudzinskaya, 1967; Chernik, 1982; Takaso and Tobe, 1990). Species of Ulmaceae exhibit an amazing diversity of breeding systems (monoecy, andromonoecy, hermaphroditism, or polygamy), a variety of floral types (staminate, pistillate, and/or perfect flowers), and a distinctive fruit morphology (for a review see: Grudzinskaya, 1967; Todzia, 1993; Leme et al., 2018; Fragnière et al, 2021).

Modern phylogenetic studies have revealed that the generic relationships in Ulmaceae form two main clades, one with three tropical genera (*Ampelocera* Klotzsch,

The authors are grateful to the scientific sub-direction of "Jardín Botánico de Bogotá José Celestino Mutis" for kindly allowing the use of their laboratory facilities and herbarium (JBB). The authors especially thank Percy Hernández for his field assistance and for his active involvement in the protection of the "Los Limones" dry forest. We also thank the curators of COAH, COL, HUA, and JAUM herbaria for their assistance, D. Rodríguez for his help with the GeoCat conservation assessment tool, and L. Niño for preparing the distribution map, M. Sanchez for the line drawing, and D. Amaya-Jimenez for the Lankester Plate. The first author is grateful to the University of Tolima for financial support that led to the discovery of the new species through the establishment of permanent plots and survey trails over the past decade. This work would not be possible without the International Plant Names Index (https://www.ipni.org/), JSTOR Global Plants (https://plants.jstor.org/), and TROPICOS (http://legacy.tropicos.org/Home.aspx). This contribution is dedicated to the memory of Alejandro Rodríguez-Leal, a promising young botanist, who tragically passed away in 2023. He extensively explored the dry forests where this new species was found.

[1] Jardín Botánico de Bogotá José Celestino Mutis, Cl. 63 #68–95, Bogotá DC., Colombia
[2] Universidad del Tolima, Grupo de Investigación de Biodiversidad y Dinámica de Ecosistemas Boscosos-GIBDET
[3] Corresponding author: bvillanueva@jbb.gov.co; bsvillanuevat@ut.edu.co
[4] UNELLEZ-Guanare, Programa de Ciencias del Agro y el Mar, Herbario Universitario (PORT), Mesa de Cavacas, estado Portuguesa 3350, Venezuela
[5] Compensation International Progress S.A. Ciprogress—Greenlife, Bogotá, D.C., Colombia; Jardín Botánico de Bogotá José Celestino Mutis, Cl. 63 #68–95, Bogotá DC., Colombia

Harvard Papers in Botany, Vol. 29, No. 1, 2024, pp. 181–190.

ISSN: 1938-2944, DOI: 10.3100/hpib.v29iss1.2024.n19, Published online: 30 June 2024

Holoptelea Planch., and *Phyllostylon* Schűch Capan. ex Benth. & Hook. f.) and 13 species, and the other with four north temperate genera (*Hemiptelea* Planch., *Planera* J.F. Gmel., *Ulmus* L., and *Zelkova* Spach) and 43 species (Neubig et al., 2012; Zhang et al., 2021). The genus *Celtis* was placed in Cannabaceae, in accordance with the modern circumscription of this family, which resulted in the integration of the majority of celtoids into Cannabaceae (e.g., *Trema* Lour.) and their exclusion from Ulmaceae (Wiegrefe et al., 1998; Yang et al., 2013). Currently, Ulmaceae, together with Cannabaceae, Moraceae, and Urticaceae, form the urticalean rosid clade (Sytsma et al., 2002; Zhang et al., 2021), which belongs to the order Rosales (APG IV, 2016).

Ampelocera is a genus endemic to the Neotropics, found throughout southern Mexico (Campeche, Chiapas, Oaxaca, Tabasco, and Veracruz states), Central America, the Caribbean, Colombia, Venezuela (including the Coastal Cordillera), the Guianas, Ecuador, Perú, Bolivia, and southern Brazil (Todzia, 1989; Fragnière et al., 2021). The genus has 10 species, including the new species described herein. According to Todzia (1989, 1993), *Ampelocera* is characterized, and differs from the other Ulmaceae genera, by its tree habit, buttressed trunk, pinnate leaves (rarely pinnipalmate), oblique leaf base, 4–16 stamens (usually 2–4 times as many as perianth parts), bifid style, and its symmetrical or asymmetrical drupaceous fruit (oblong or spherical).

Todzia (1989) published a revision of *Ampelocera*, in which he recognized nine taxa and included the description of three new species. Since Todzia's contribution, no new species have been described. The genus is included in Flora de Nicaragua (Todzia, 2001), Flora of the Venezuelan Guayana (Miller and Berry, 2005), and Manual de Plantas de Costa Rica (Todzia, 2015).

The present contribution increases to seven the number of *Ampelocera* species known from Colombia, the country with the highest diversity of the genus. This new species was discovered during fieldwork supported by the "Universidad de Tolima," while establishing permanent plots and conducting general botanical collections in dry forests located in the upper Magdalena riven basin, Tolima department, Colombia. These studies were conducted in forest remnants in one of the largest dry forest reserves (ca. 150 ha) known as "Bosque Los Limones," a region on the western side of the Magdalena River.

Materials and Methods

The new species was initially collected in the dry forest remnants of the upper Magdalena riven basin, Tolima department, Colombia. Subsequently, more individuals of the species were identified and marked while setting up permanent plots. Specimens of the new species were compared with *Ampelocera* collections deposited in the following herbaria: COAH, COL, FMB, JBB, TOLI, UDBC (acronyms follow Thiers 2024, continuously updated). Historical and current taxonomic literature on *Ampelocera* was examined: the genus revision (Todzia, 1989), treatments of Ulmaceae in "Flora de Nicaragua" (Todzia, 2001), Flora of the Venezuelan Guayana (Miller and Berry, 2005), "Manual de Plantas de Costa Rica" (Todzia, 2015), and the "Catálogo de plantas y líquenes de Colombia" (Gradstein, 2016). Additionally, *Ampelocera* collections hosted by virtual herbaria, including those maintained by the Field Museum (F; http://emuweb.fieldmuseum.org/botany/taxonomic.php), Missouri Botanical Garden (MO; http://https://tropicos.org/home), and the New York Botanical Garden (NY; https://sweetgum.nybg.org/science/vh/), were consulted. Type specimens of *Ampelocera* species involved in this study were examined using online images from JSTOR Global Plants (https://plants.jstor.org/).

The illustration was done freehand (Fig. 1), and the photographs of flowers and fruits used to prepare the Lankester Composite Digital Plate (LCDP) were taken from samples in vivo, using a Nikon D7000 camera with a 105 mm macro lens and a Raynox 250 magnifying glass. The morphological measurements were carried out using a digital caliper and ImageJ software.

The specific terminology for vegetative characters, vestiture description, inflorescences, flowers, and fruit morphology follow Todzia (1989), Font-Quer (2001), and Harris and Harris (2006).

To determine the conservation status (IUCN, 2022), the extent of occurrence (EOO) and area of occupancy (AOO) were calculated using the Red List threat assessments in GeoCAT (Bachman et al., 2011), which is continually updated (https://geocat. kew.org/). The EOO is defined by the IUCN (2022) as the minimum convex polygon encompassing all known occurrences of a species. The AOO is the area within the EOO, which comprises 2 × 2 km grid cells containing known occurrence records.

Taxonomy

Ampelocera percyhernandezii Villanueva & Aymard, *sp. nov.*

TYPE**:** COLOMBIA. Tolima: Venadillo, Vereda Salto Nuevo, Bosque Los Limones, 4°40'26"N, 74°49'22"W, 253 m, 18 septiembre 2018 (fl), *B. Villanueva-T. & A. D. Páez 4308* (Holotype: TOL; Isotypes: COL, JAUM, UDBC). Fig. 1–2.

Ampelocera percyhernandezii resembles *A. albertiae* and *A. macphersonii*, but can be distinguished from these species by its coriaceous leaves, 3.5–16.0 × 1.8–5.1 cm, with pellucid dots on the blade, the inflorescence 2–22 mm long, its floral structures that are glabrous or minutely puberulent outside, 5–9(–12) stamens, filaments that are fasciated at the base, the absence of an extended connective, a densely pubescent ovary (with erect translucent trichomes), its style branches that are white on the ventral face, and its fruit with vestigial white filaments when dried.

Tree semi-deciduous, up to 20 m tall, buttresses to 2 m high, bark striated, younger branches and branchlets reddish brown, very sparsely puberulent, older branches and branchlets gray, sparsely puberulent to glabrescent and bark flaking off when mature; stipules 0.75–1.50 mm long,

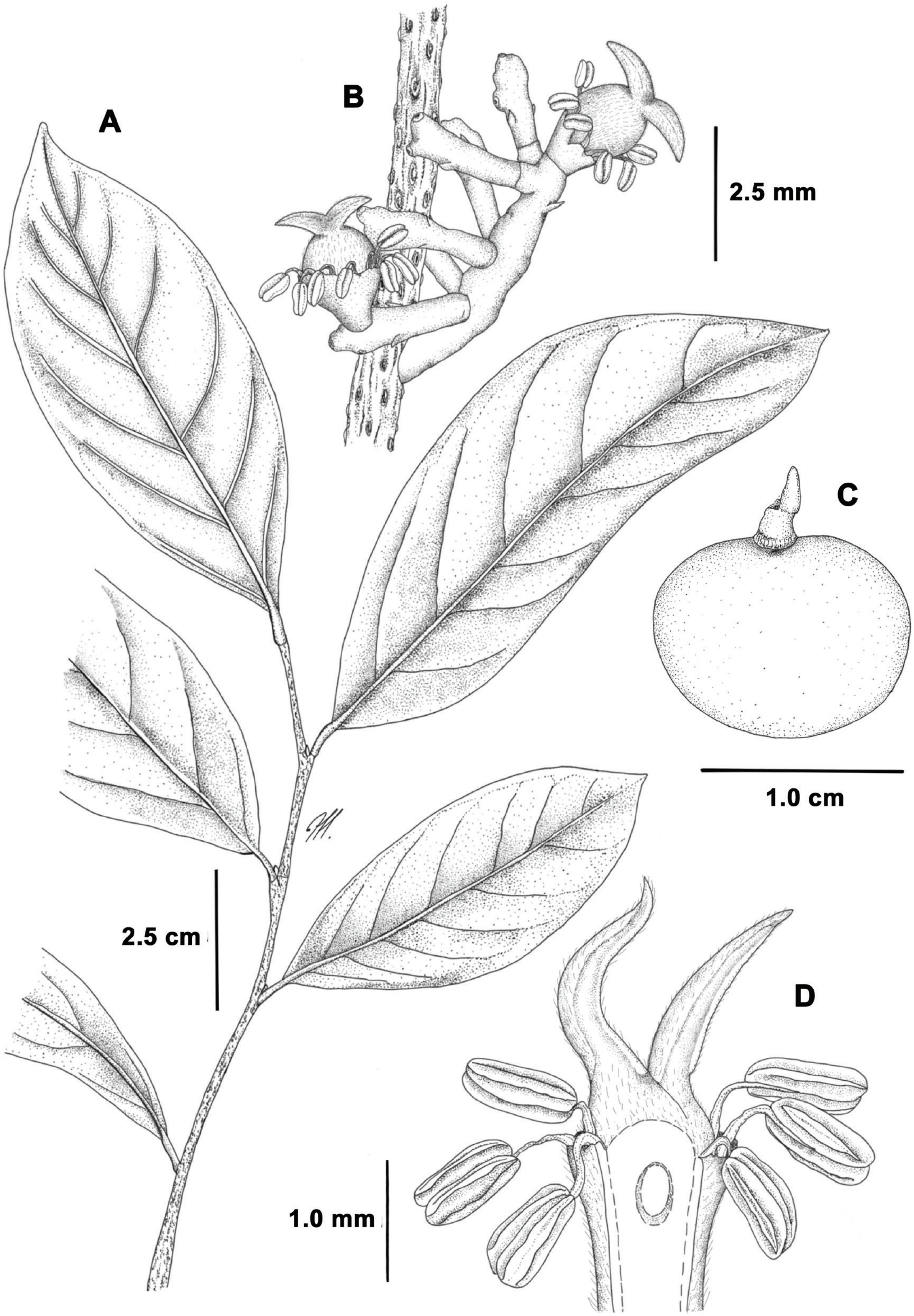


FIGURE 1. *Ampelocera percyhernandezii* Villanueva & Aymard. **A**, Habit, **B**, Perfect flower in frontal view showing the stamens, style branches, and a developed ovary, **C**, Fruit apex showing persistent style branches in anthesis, **D**, View of inflorescence. Drawn by Manuela Sánchez.

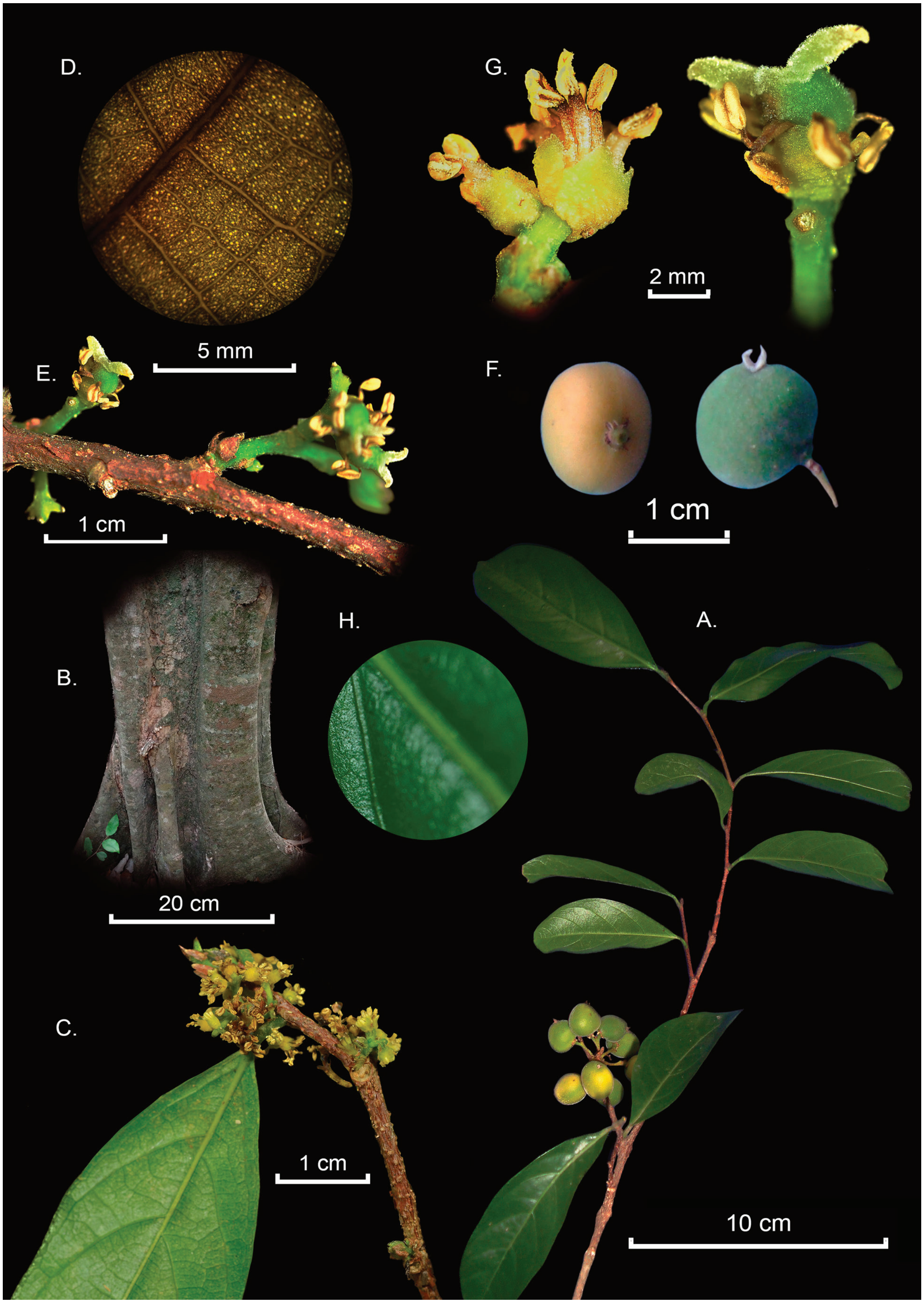


FIGURE 2. *Ampelocera percyhernandezii* Villanueva & Aymard. **A**, Habit showing branch with unripe fruit, **B**, Trunk with buttresses to 2 m high, **C** and **E**, Younger branches with lenticels and inflorescences, **D**, Leaf blade with pellucid dots (10x), **F**, Fruit with persistent stamens at the base (left): fruit with persistent style branches at the apex (right), **G**, Flower in anthesis (left); flower with a developed ovary (right), **H**, Detail of flat midvein on the upper surface. Photographs by B. Villanueva-Tamayo. Plate prepared by Daniel Amaya-Jiménez.

oblong, acute at the apex, glabrous on both sides, except at the base outside, which is covered by adpressed white trichomes, ciliate at the margins. *Leaves* elliptic to oblong, 3.5–16.0 × 1.8–5.1 cm, blades flexible (in vivo), drying coriaceous, pale green, yellow-green to pale gray, apex acute, base attenuate, subtruncate, glabrous and smooth on both surfaces, margins entire, midvein flat above, raised beneath, lateral veins 5–8 pairs, arcuate, flat adaxially, raised abaxially, inter-secondary tertiary veins strongly reticulate on both sides; petioles 4.1–6.5 mm long, canaliculate, smooth, sparsely pilose, drying tawny to reddish brown. *Inflorescence* axillary, short panicles on leafy branches, 2–22 mm long, rachis sparsely puberulent, often three-branched at the base or with a short peduncle (2–3 mm long), not densely flowered, with ca. 9 flowers, each branch 3-flowered. *Flowers*, perfect and functionally staminate, sub-sessile on the central branch, pedicellate on the lateral branches, pedicel 0.2–2.0 mm long (pubescence as on the rachis), subtended by coriaceous, ovate bracts located at the pedicel base, 1.5–1.7 × 1.2–1.4 mm, sparsely adpressed on both sides, calyx 1.0–1.2 mm long, yellow-green (in vivo), lobes 4, 0.2–0.4 mm long, glabrous or minutely puberulent outside; stamens 5–9(–12) in perfect flowers, ca. 7 in functionally staminate flowers, these with a dense, white pubescent conical pistillode, 1.0–1.5 mm long; filaments 2.0–2.5 mm long, ca. 0.38 mm wide at the base to 2/3 of its length, and ca. 0.8 mm at the apex, fasciated, canaliculate, glabrous, anthers dorsifixed, 0.9–1.2 long, glabrous, the connective not extending into a short strigose apicule; ovary oblong, green (in vivo), densely pubescent, trichomes erect, translucid 0.1–0.3 mm, style 2-branched, 1.5–1.8 mm long, free to base, dense white strigose, opening horizontal (in vivo), closed (in secco), the ovules in an apical placenta. *Fruit* yellow when mature (in vivo), 0.9–1.3 × 1.1–1.4 cm, oxidizing quickly to black or silver-brownish (in secco), asymmetrical, transversely obovoid, sparsely puberulent, with vestigial white filaments and persistent style branches (white on the ventral side) when mature. Seed not seen.

Phenology: The new species was collected with flowers in April and September (flowers in different ripening stages), and with fruit in June and September.

Etymology: *Ampelocera percyhernandezii* honors Percy Hernández (1963–), who is a prominent environmentalist and parataxonomist from the Tolima department. He has been a great defender and protector of the "Bosque Los Limones" area (4°40'26"N, 74°49'22"W, 253 m) to the extent that, if it were not for his conservation efforts, this unique dry forest of the upper Magdalena river valley would not exist.

Common names: The name "Huesito" was recorded during field work. However, in this region other taxa are also known by this common name, mainly *Casearia* spp. (Salicaceae: *C. corymbulosa* (Spruce ex Benth.) T. Samar. & M.H. Alford. and *C. thamnia* (L.) T. Samar. & M.H. Alford.).

Distribution and ecology: *Ampelocera percyhernandezii* is an endemic taxon from the upper Magdalena river valley in the Cundinamarca (San Juan de Rio Seco municipality) and Tolima (Armero, Honda, Ibagué, and Venadillo municipalities) departments, Colombia (Fig. 3). This is a region of dry forest on low hills and plains systems in inter-Andean valleys, located on the western bank of the upper Magdalena river, between 250–600 m elevation (Villanueva-Tamayo et al., 2023). These forests have a maximum slope of 45%, and the hills have an array of intermediate plains between them. They are compact, non-fragmented forests, some of which can be flooded in the rainy season. The most significant populations of *A. percyhernandezii* are found in dry plains and riparian forests along small drainage channels. This region is the same dry forest where *Cedrela gonzalopalominoi* Villanueva & M.E. Morales (Meliaceae) was found, a new species of cedar recently published (Villanueva-Tamayo et al., 2023).

Iconography: The junior author examined Celestino Mutis' watercolors of Colombian plants, made by the artists of the "Flora de la Real Expedición Botánica del Nuevo Reino de Granada," who studied the flora of Colombia under the direction of Mutis from 1783 to 1816. (These watercolors were not signed by the artists). Mutis assigned numbers to the collection specimens, but in accordance with the customs of his time he did not keep a consecutive series, but used different numerations for the different classes and genera of Linnaeus' system (Díaz-Piedrahita, 2016). The original order of the plates was modified by the great Colombian botanist José Jerónimo Triana, who visited Madrid on two occasions in 1866 and 1882 (Díaz-Piedrahita, 1990). He arranged them in 41 folders and classified them into families, tribes and genera following Endlicher's system (Endlicher, 1836–1840). This order was preserved until 1986, when a reordering was initiated following the sequence in which they appear in the 39 volumes of the Flora of the Royal Expedition that have been published since 1954. An extraordinarily artistic and accurate illustration representing a species of *Ampelocera* (Fig. 4) was found among the ca. six thousand plates. These plates are included in volume No. XIV (Duarte-Rojas and Fernández-Alonso, 2018) under numbers A-2800 (polychromatic) and 2800a,b (monochromatic). The latter volume number belongs to "Flora de la Real Expedición Botánica del Nuevo Reino de Granada." This flora was published in compliance with the Cultural Agreement between Spain and Colombia celebrated on November 4, 1952 (Pérez-Arbeláez et al. 1954).

These plates were made between 1785–1791, 19 and 52 years before Ulmaceae and the genus *Ampelocera* were described, respectively (de Mirbel, 1815; Klotzsch, 1847). It is important to emphasize in these particular plates, because no exsiccatae were found at the herbarium of the "Real Jardín Botánico," Madrid (MA). It was identified as *Ampelocera aff. albertiae* Todzia by Duarte-Rojas and Fernández-Alonso (2018). It is unfortunate that the locality for the Mutis collection is not available, but it can be assumed that this expedition mainly covered the upper Magdalena river, near Mariquita town (currently Tolima department), a region close to where *A. percyhernandezii* was found. Additionally, the plate details, such as the lenticellate branches, the leaf venation, the dense inflorescences, and the persistent style branches in the fruit, match those of the type of the new species.

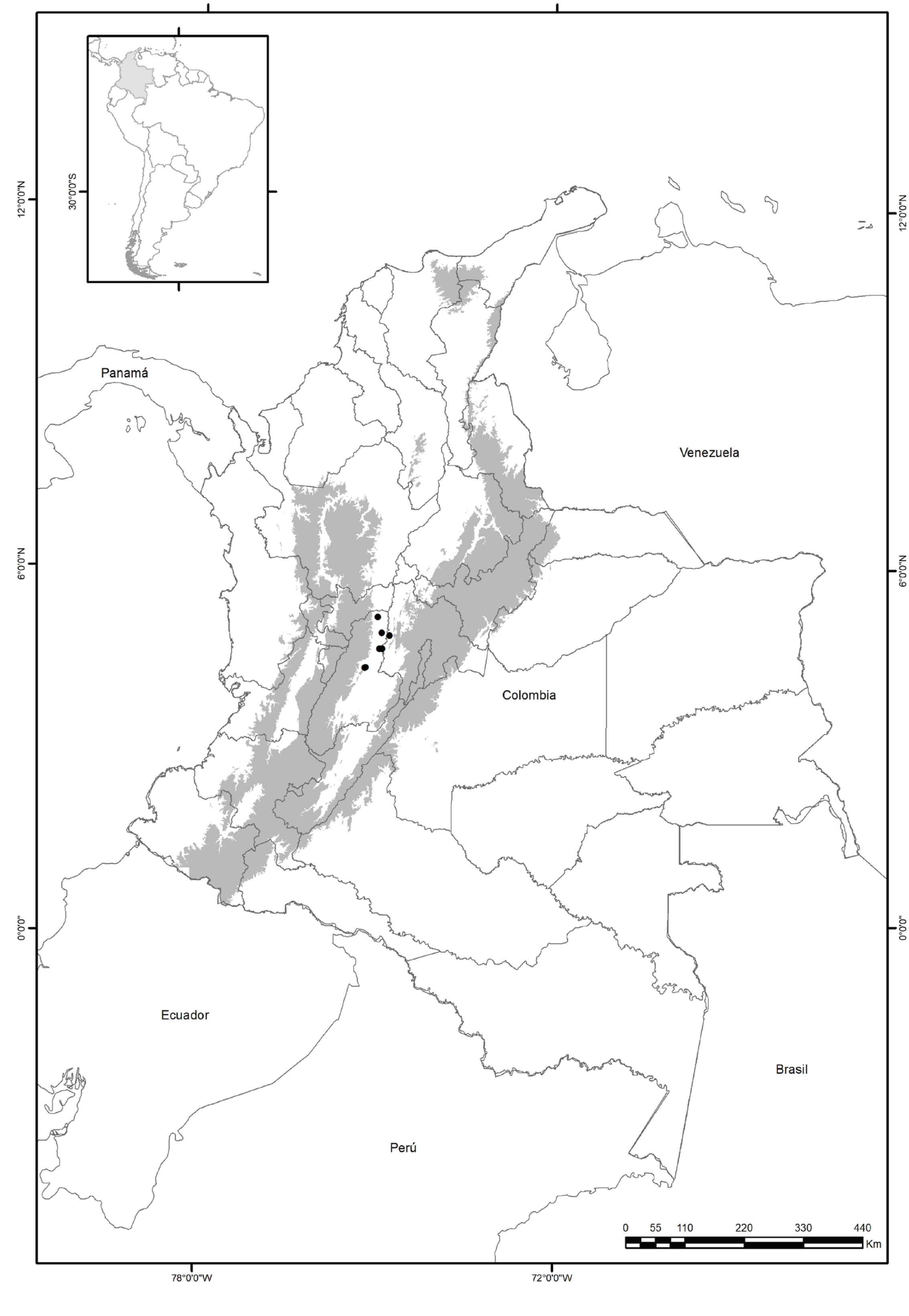


FIGURE 3. The geographical distribution of *Ampelocera percyhernandezii* Villanueva & Aymard in the Colombian Andes Cordillera. Prepared by Larry Niño.

FIGURE 4. *Ampelocera percyhernandezii* Villanueva & Aymard in *Iconografia Mutisiana*. Plate A-2800 [AJB, DIV. III A-2800 ©Real Jardín Botánico de Madrid–CSIC Archives].

Conservation status: Currently, *Ampelocera percyhernandezii* is known from the type and seven additional collections, three of which were collected near the type locality (see the additional specimens). In the type locality, 12 permanent plots, 50 × 50 m² (3 ha), were established, and all individuals with DBH greater than 10 cm were recorded (Villanueva-Tamayo et al., 2023). In this area, with a slope close to 36%, 1305 individuals were measured, 83 of which were the new species. Under IUCN (2022) guidelines, the conservation status of the new species should be Endangered. This result is based on our calculations that estimated the Area of Occupancy (AOO) as 20,000 km² and the Extent of Occurrence (EOO) as 1589.292 km² (following guidelines in IUCN, 2022). These guidelines estimate the EOO as the minimum convex polygon that includes all known occurrences of any taxon, and the AOO as the region inside the EOO that is occupied by the species (using a grid of 2 × 2 km²). For threatened species, the AOO value should be above 10,000 km² (IUCN, 2022). Although conservation status assessments can be made for species with such small numbers of collections (Rivers et al., 2011), it is difficult to determine whether the appearance of rarity in a species is due to the lack of, or outdated, data, collection artifact, loss of habitat (Verspagen and Erkens, 2022), or to its actual rarity (Zizka et al., 2018). The plot data for this taxon and the EOO and the AOO calculations are consistent with the hypothesis raised by Brown et al. (2023), who noted that species with small ranges and/or population sizes are less likely to be encountered (and thus less likely to be described) and more likely to be threatened (Gaston, 2003). The conservation of these dry forests is at risk due to continuous deforestation in and degradation of the upper Magdalena valley. The area where *A. percyhernandezii and Cedrela gonzalopalominoi* occur is unprotected by "Sistema de Parques Nacionales Naturales de Colombia" (Villanueva-Tamayo et al., 2023). However, the region "Bosque Los Limones" is a primary forest (150 ha) and it is not currently protected by regional initiatives.

Furthermore, among the neotropical Ulmaceae, *Ampelocera albertiae* is cataloged as endangered (EN) under criteria B2ab(iii) and is one of the most threatened species under this IUCN category (López-Gallego and Morales, 2020). This taxon is endemic to Colombia and is known from only five populations. It's existence is affected by cattle ranching, mining activities, and artificial forest plantations (López-Gallego and Morales, 2020).

Additional specimens examined: COLOMBIA. Cundinamarca. San Juan de Río Seco: Finca Caracoli, 4°53'46"N, 74°42'12.5"W; 462 m, 05 Feb 2018 (ste.), *Andrés Torrejano, Rene López, Karen Polania, Alex Quiasua 358* (UDBC). Tolima. Armero: Cerro Santo Tomás, 4°55'707"N, 74°49'54"W; 250 m, Nov 1995 (ste.), *Humberto Mendoza-C. & Augusto Repizzo 64* (COL). Ibague: Quebrada La Honda, bosque Laserna, bosques junto al canal de riego, 4°20'57"N, 75°06'34"W; 779 m, 06 Feb 2016 (ste.), *Boris Villanueva-Tamayo, Juan D. Peñuela, & Juan D. Franco 2799* (JBB, TOLI); Hacienda Altamira (predios donados a la Universidad del Tolima), quebrada Honda, bosques junto al canal de riego, 4°20.883'N, 75°06.651'W; 779 m, 06 Feb 2019 (ste.), *Boris Villanueva-Tamayo, Juan D. Peñuela, & Juan D. Franco* 4422 (JBB, TOLI). Venadillo: Vereda salto Nuevo, bosque Los Limones, junto al camino del centro, 4°40'25.93"N, 74°49'39.7"O, 250 m, 07 April 2012 (fr), *Boris Villanueva, Alejandra Montoya, & F. Fernández 944* (JBB, TOLI); 4°40'16.24"N, 74°51'3.81"O, 256 m, 3 Sep 2016 (fr), *Boris Villanueva-Tamayo*, *Alejandro Rodriguez-Leal, & Andrea Murillo 2799* (TOLI); 4°40'28"N, 74°49'29"O, 349 m, 08 Jun 2019 (fl), *Boris Villanueva-Tamayo, Jaime Camargo, & Semillero de Maderas SIAM 4941* (TOLI).

The new species can be recognized by its flexible and glabrous leaf blade with an attenuate base, the raised midvein on the upper surface, and pellucid dots on the blade (using 10x magnification). The latter feature is recorded for the first time in the genus (see Fig. 2D). For the inflorescences on reduced branches, the flowers are protandrous and hermaphrodite. There are 5–9(–12) stamens that are fasciated at the base; the style branches are 1.5–1.8 mm long; and the ovary is densely pubescent with erect, translucent 0.1–0.3 mm trichomes. The fruits are ca. 1.3 cm long, sparsely puberulent, with persistent style branches that are white on the ventral side.

Ampelocera percyhernandezii is morphologically related to three taxa: *A. albertiae*, *A. macphersonii* Todzia, and *A. longissima* Todzia. Nonetheless, this new species differs from these three species and others of this genus in the characters discussed in the diagnosis, in Table 1, and in the following key.

Key to the species of *Ampelocera*
(Based on Todzia, 1989)

1a. Fruit strongly asymmetrical, broader than long; filaments slender throughout 2
1b. Fruit obovoid to globose, not strongly asymmetrical, longer than broad; filaments broadened basally. 8
2a. Leaves usually dentate, occasionally entire; inflorescences borne on leafless branches; style branches 3–5 mm long 3
2b. Leaves always entire; inflorescences borne on leafy branches; style branches 1–2 mm long 5
3a. Leaf margin often revolute; calyx lobes villous; filaments ca. 2 mm long . . . . . *A. cubensis* (Cuba, Hispaniola)
3b. Leaf margin not revolute; calyx lobes sparsely puberulent to glabrous; filaments ca. 3 mm long . . . . .4 (South America)
4a. Inflorescence 0.9–1.5 cm long, with 8–23 flowers; calyx 2.0–2.5 mm long; fruit 1.0–1.2 × 1.2–1.6 cm; densely pilose . . . . . *A. ruizii* (Peru, Bolivia, Amazonian Brazil)
4b. Inflorescence 0.5–0.8 cm long, with 4–9 flowers; calyx ca. 1.5 mm long; fruit 1.5–2.0 × 2.0–2.3 cm; glabrous . . . . . *A. glabra* (southeastern and central Brazil)
5a. Leaves chartaceous, unevenly colored when dried; inflorescence with 3–5 flowers; stamens ca. 16 . . . . . *A. macphersonii* (Panama, Colombia, Venezuela)
5b. Leaves subcoriaceous or coriaceous, uniformly colored when dried; inflorescence with 9–56 flowers; stamens 4–12. 6

Key to the species of *Ampelocera* cont.
(Based on Todzia, 1989)

6a. Inflorescence (2.7–)3.5–7.8 cm long; elongate, loosely flowered; ovary sparsely puberulent . . . . *A. longissima* (Colombia, Ecuador)
6b. Inflorescence 0.2–2.8 cm long; congested, densely flowered; ovary densely strigose puberulent or densely pubescent. 7
7a. Leaves without pellucid dots; the connective extending into a short strigose apicule; ovary strigose; fruit densely pubescent, persistent style branches brown on the ventral face . . . . *A. albertiae* (Colombia)
7b. Leaves with pellucid dots; the connective not extending into a short strigose apicule; ovary densely pubescent, fruit sparsely puberulent, persistent style branches white on the ventral face . . . .*A. percyhernandezii* (Colombia)
8a. Leaves trinerved at the base; style branches ca. 4 mm long; stamens ca. 16; fruit densely brown tomentose, with longitudinal striations . . . . *A. hottlei* (Southern Mexico to Colombia)
8b. Leaves pinnately veined at the base; style branches 1–2 mm long; stamens 6–8; fruit glabrous to sparsely puberulent, without longitudinal striations 9
9a. Leaf blades elliptic to oblong-elliptic, base rounded, cuneate to oblique; stipules narrowly to broadly lanceolate, strigose, 2–6 mm long; ovary densely puberulent; fruit with a thin endocarp . . . . *A. edentula* (the Guianas, Amazon basin of Brazil, Venezuela, Colombia, Ecuador, Peru, and Bolivia)
9b. Leaf blades oblong to elliptic, base rounded to subcordate; stipules linear-lanceolate, sparsely puberulent, ca. 6 mm; ovary sparsely puberulent to glabrescent; fruit with a thick endocarp . . . . *A. macrocarpa* (Honduras to Colombia and Venezuela)

Table 1. Comparison of diagnostic morphological characters of *Ampelocera percyhernandezii* Villanueva & Aymard and closely related species.

Characters	*A. albertiae*	*A. macphersonii*	*A. longissima*	*A. percyhernandezii*
Leaf blade and midvein beneath	Subcoriaceous, 7–12 cm long uniformy colored when dried, midvein raised	Chartaceous, 7.5–21 cm long, unevenly colored when dried, midvein slightly canaliculate	Subcoriaceous, 8.5–17.4 cm long uniformly when dried, midvein raised	Coriaceous, 3.5–16.0 cm long, uniformly colored when dried, midvein raised
Pellucid points on the leaf blade	Absent	Absent	Present	Present
Inflorescence raquises length	0.6–2.8 cm	0.8–1.2 cm	(-2.7)3-5–8 cm	0.2–2.2 cm
Stamens number	4–12	ca. 16	4–10	5–9(-12)
Connective	extending into a short strigose apex	No extending	No extending	No extending
Ovary pubescence	Densely strigose	Densely pubescent	Sparsely puberulent	Densely pubescent
Fruit size and pubescence	0.9–1.2 × 1.4–1.7, densely pubescent	1.2–1.6 × 1.6–1.8 cm, densely pubescent	0.6–1 × 1–1.4, glabrous	0.9–1.3 × 1.1–1.4, sparsely puberulent

Literature Cited

APG (Angiosperm Phylogeny Group) IV. 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Botanical Journal of Linnean Society 181:1–20.

Bachman, S., J. Moat, A. W. Hill, J. de la Torre, and B. Scott. 2011. Supporting Red List threat assessments with GeoCAT: geospatial conservation assessment tool ZooKeys 150: 117126.

Britannica (The Editors of Encyclopaedia). "Charles-François Brisseau de Mirbel." Encyclopedia Britannica, udpated: 27 March 2024, https://www.britannica.com/biography/Charles-Francois-Brisseau-de-Mirbel (accessed April 18, 2024).

Brown, M. J. M., S. P. Bachman, and E. N. Lughadha. 2023. Three in four undescribed plant species are threatened with extinction. New Phytologist 240: 1340–1344. https://doi.org/10.1111/nph.19214

Chernik, V. V. 1982. Characteristics of the structural development of spermodern in some representatives of Ulmaceae and Celtidaceae. Botanicheskii Zhurnal (Moscow & Leningrad) 67: 1216–1220.

Díaz-Piedrahita, S. 2016. La botánica en Colombia, hechos notables en su desarrollo. Ministerio de Cultura–Biblioteca Nacional de Colombia. Bogotá (version electrónica).

———. 1990. Tres naturalistas del siglo XIX unidos en torno a una flora. Revista de la Academia Colombiana de Ciencias 17 (66): 415–423.

Duarte-Rojas, D. J., and J. L. Fernández-Alonso. 2018. Ulmaceae, Pages 59–69, 9 color plates (Betulaceae, Cactaceae, Cecropiaceae, Fagaceae, Moraceae, Ulmaceae, and Urticaceae) in Flora de la real expedición botánica del nuevo reino de Granada (1783–1816) XIV. Instituto Colombiano de Antropología e Historia, (ICANH), Bogotá, Colombia.

Endlicher, S. L. 1836–40. Genera Plantarum: Secundum Ordines Naturales Disposita. Fr. Beck, Wien.

Font-Quer, P. 2001. Diccionario de Botánica. Ediciones Península, Barcelona, España.

Fragnière, Y., Y.-G. Song, L. Fazan, S. R. Manchester, G. Garfì, and G. Kozlowski. 2021. Biogeographic overview of Ulmaceae: diversity, distribution, ecological preferences, and conservation status. Plants (Basel). 10(6): 1111. https://doi.org/10.3390/plants10061111

Gaston, K. J. 2003. The structure and dynamics of geographic ranges. Oxford University Press, Oxford, U.K.

Gradstein. S. R. 2016 (continuously updated). Ulmaceae. Pages 2443–2444 in R. Bernal, S. R. Gradstein, and M. Celis, eds., Catálogo de plantas y líquenes de Colombia. Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá.

Grudzinskaya, I. A. 1967. Ulmaceae and reasons for distinguishing *Celtidoideae* as a separate family Celtidaceae Link. Botanicheskii Zhurnal (Moscow & Leningrad) 52: 1723–1748.

Harris, J. G., and M. W. Harris. 2006. Plant Identification Terminology: An Illustrated Glossary. Spring Lake Publishing, Spring Lake, Utah, U.S.A.

IUCN. 2022. Guidelines for using the IUCN Red List Categories and Criteria. Version 12. Prepared by the Standards and Petitions Subcommittee (accessed March 31, 2024). https://www.iucnredlist.org/.

Klotzsch, J. F. 1847. *Artocarpeae*. Linnaea 20: 523–542.

Leme, F. M., Y. M. Staedler, J. Schönenberger, and S. P. Teixeira. 2018. Ontogeny and vascularization elucidate the atypical floral structure of *Ampelocera glabra*, a tropical species of Ulmaceae. International Journal of Plant Science 179: 461–476.

Link, J. H. F. 1831. Handbuch zur Erkennung der nutzbarsten und am haufigsten vorkommenden Gewachse. Haud & Spenersche Buchhandlung (S. J. Joseephy), Berlin, Germany.

Lopez-Gallego, C., and M. P. A. Morales. 2020. IUCN Red List of Threatened Species: *Ampelocera albertiae* ("Costillo"). Available online: https://www.iucnredlist.org/search?query=Ampelocera&searchType=species (accessed 31 March 2024).

Manchester, S. R. 1989. Systematics and fossil history of the Ulmaceae, Pages 221–251 in P. R. Crane and S. Blackmore, eds., Evolution, systematics and fossil history of the Hamamelidae. The Systematics Association Special Volume No. 40B. Clarendon Press, Oxford.

Miller, J. S., and P. E. Berry 2005. Ulmaceae, Pages 386–390 in P. E. Berry, K. Yatskievych, and B. K. Holst, eds., Flora of the Venezuelan Guayana 9 (Rutaceae–Zygophyllaceae). Missouri Botanical Garden Press, Saint Louis, Missouri, U.S.A.

Mirbel, C. F. B. de 1815. Élements de Physiologie Végétale et de Botanique; Magimel: Paris, France, Volume 1: 1–15.

Neubig, K., F. Herrera, S. R. Manchester, and J. R. Abbott. 2012. Fossils, biogeography and dates in an expanded phylogeny of Ulmaceae, Pages 7–11 in Botany 2012: Annual Meeting of the Botanical Society of America in Columbus, Columbus, Ohio, U.S.A.

Pérez-Arbeláez, E., E. Álvarez-López, L. Uribe-Uribe, E. Balguerias deQuesada and A. Sánchez-Bella. 1954. La Real expedición del Nuevo Reino de Granada. Edic. Cultura Hispanica. Madrid.

Rivers, M. C., L. Taylor, N. A. Brummitt, T. R. Meagher, D. L. Roberts and E. N. Lughadha. 2011. How many herbarium specimens are needed to detect threatened species? Biological Conservation 144(10): 2541–2547.

Sutar, R. C., S. S. Gangwar, R. N. Thakur, R. Sharma, and S. P. Krishnan. 2016. HPTLC finger printing analysis of the tannins from *Holoptelea integrifolia* (Roxb.) Planch. leaves. Journal of Pharmacognosy and Phytochemistry 5: 199–204.

Sytsma, K. J., J. Morawetz, J. C. Pires, M. Nepokroeff, E. Conti, M. Zjhra, J. C. Hall and M. W. Chase. 2022. Urticalean rosids: Circumscription, rosid ancestry, and phylogenetics based on RbcL, TrnL-F, and NdhF sequences. American Journal of Botany 89: 1531–1546.

Takaso, T., and H. Tobe. 1990. Seed coat morphology and evolution in Celtidaceae and Ulmaceae (Urticales). The Botanical Magazine (Tokyo) 103: 25–41.

Thiers, B. 2024 (continuously updated). Index Herbariorum: A Global Directory of Public Herbaria and Associated Staff. New York Botanical Garden's Virtual Herbarium. Available from: http://sweetgum.nybg.org/ih/. (accessed 31 March 2024).

Todzia, C. A. 1989. Revision of *Ampelocera* (Ulmaceae). Annals of Missouri Botanical Garden 76: 1087–1102.

———. 1993. Ulmaceae. Pages 603–613 in K. Kubitzki, J. G. Rohwer, and V. Bittrich, eds., The Families and Genera of Vascular Plants 2—Flowering plants: dicotyledons. Springer, Berlin. Germany.

———. 2001. Ulmaceae, in W. D. Stevens, C. Ulloa Ulloa, A. Pool, and O. M. Montiel, eds., Flora de Nicaragua. Monographs in Systematic Botany from the Missouri Botanical Garden 85(3): 2472–2478.

———. 2015. Ulmaceae, in B. E. Hammel, M. H. Grayum, C. Herrera, and N. Zamora, eds., Manual de Plantas de Costa Rica 8. Monographs in Systematic Botany from the Missouri Botanical Garden 131: 460–463.

Verspagen, N., and R. H. J. Erkens. 2022. A method for making Red List assessment with herbarium data and distribution models for species-rich plant taxa: Lessons from the Neotropical genus *Guatteria* (Annonaceae). Plants, People, Planet 5: 536–546.

Villanueva-Tamayo, B., M. E. Morales-Puentes, O. Melo Cruz, and G. A. Aymard-Corredor. 2023. A new species of *Cedrela* (Meliaceae) from a Colombian dry forest and an updated key for the species of the genus. Harvard Papers in Botany 28(2): 735-743.

Wiegrefe, S. J., K. J. Sytsma, and R. P. Guries. 1998. The Ulmaceae, one family or two? Evidence from chloroplast DNA restriction site mapping. Plant Systematics and Evolution 210: 249–270.

Yang, M. Q., R. van Velzen, F. T. Bakker, A. Sattarian, D. Z. Li, and T. S. Yi. 2013. Molecular phylogenetics and character evolution of Cannabaceae. Taxon 62: 73–485.

Zhang, Q., M. Deng, Y. Bouchenak-Khelladi, Z. Zhou, G. Hu, and Y. Xing. 2021. The diversification of the northern temperate woody flora—A case study of the elm family (Ulmaceae) based on phylogenomic and paleobotanical evidence. Journal of Systematics and Evolution 60(4): 1–19.

Zizka, A., H. ter Steege, M. do Céo R. Pessoa, and Alexandre Antonelli. 2018. Finding needles in the haystack: where to look for rare species in the American tropics. Ecography 41: 321–330. doi: 10.1111/ecog.02192

INDEX TO NEW NAMES AND COMBINATIONS

Harvard Papers in Botany, Vol. 29, No. 1, 2024, pp. 191–193.

ISSN: 1938-2944, DOI: 10.3100/hpib.v29iss1.2024.n20, Published online: 30 June 2024

Page 194 intentionally left blank.

(Continued from the back cover)

Harvard Papers in Botany was initiated in 1989 to consolidate the following journals published by the Harvard University Herbaria: *Botanical Museum Leaflets—Harvard University* (vols. 1–30, 1932–1986), *Contributions from the Gray Herbarium of Harvard University* N.S. (nos. 1–214, 1891–1984), and *Occasional Papers of the Farlow Herbarium of Cryptogamic Botany* (nos. 1–19, 1969–1987). Starting with no. 8, it incorporates the *Journal of the Arnold Arboretum* (vols. 1–71, 1920–1990) and the *Journal of the Arnold Arboretum Supplementary Series* (1, 1991).

Harvard Papers in Botany was published as individually paginated issues up to number 10 (April 1997). Starting with the next issue, it has been published in volumes, each volume consisting of two numbers with continuous pagination. Number 1–10, published between May 1989 and April 1997, constitute Volume 1. Volume 1, number 10, includes a cumulative, comprehensive index for the first volume. Print Copies for most volumes 1 through 18 are available. Please contact papers@oeb.harvard.edu for more information.

This issue of *Harvard Papers in Botany* was composed by Barbara Kroner Morra, using Adobe InDesign for the Macintosh. The body of the text is set in 10-point Times Roman on 11 points of leading.

Harvard Papers in Botany

Volume 29, Number 1 June 2024

A Publication of the Harvard University Herbaria Including

The Journal of the Arnold Arboretum

(Continued on the inside back cover)

Harvard Papers in Botany

Volume 29, Number 1 June 2024

A Publication of the Harvard University Herbaria Including

The Journal of the Arnold Arboretum

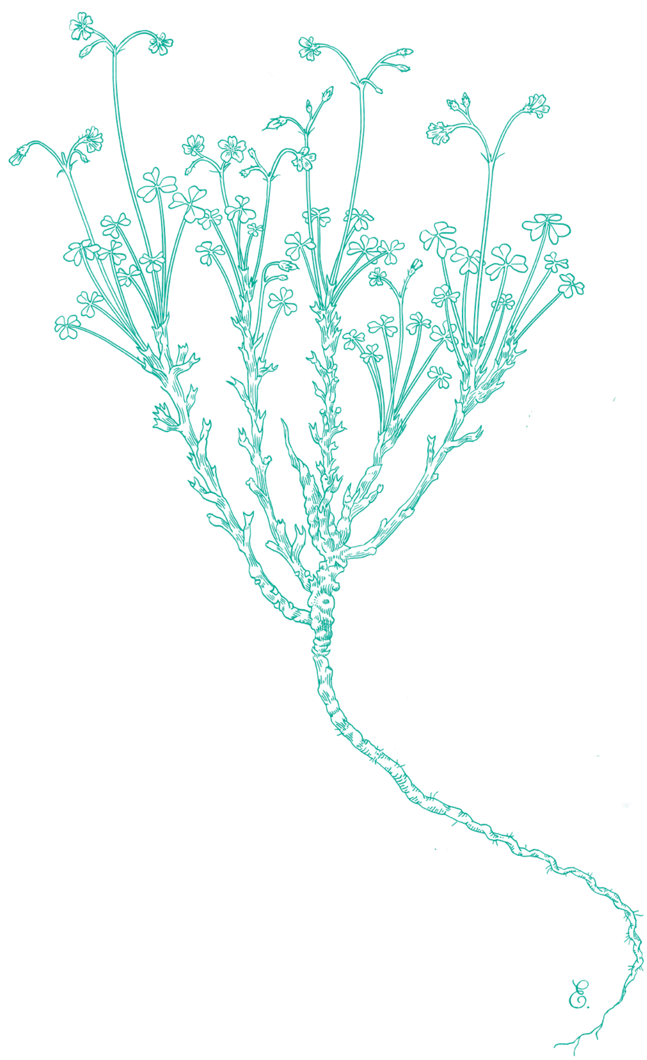
Arnold Arboretum

Botanical Museum

Farlow Herbarium

Gray Herbarium

Oakes Ames Orchid Herbarium



Harvard Papers in Botany, Vol. 29, No. 1, 2024, Front matter, Table of Contents, End matter.

ISSN: 1938-2944, DOI: 10.3100/hpib.v29iss1.2024.fmem, Published online: 30 June 2024