

GUSTAVIA MONTANA (LECYTHIDACEAE): A NEW SPECIES FROM THE ANDES IN COLOMBIA

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Abstract. *Gustavia montana*, a new species of Lecythidaceae from the montane rain forests along the western slopes of Central Cordillera and the northeastern Western Cordillera in Colombia is formally described and illustrated, and its relationship to morphologically closely related species is discussed.

Keywords: Andes, central cordillera, Colombia, Endemics, montane forest, western cordillera

Resumen. *Gustavia montana*, una nueva especie de Lecythidaceae de los bosques lluviosos montanos de las estribaciones occidentales de la cordillera Central y del noreste de la cordillera occidental de Colombia es formalmente descrita e ilustrada, se discute sus relaciones con las especies morfológicamente cercanas.

Palabras claves: Andes, bosque montano, Colombia, cordillera central, cordillera occidental, endémica

Gustavia L. is a genus of Neotropical Lecythidaceae characterized by the presence of showy actinomorphic flowers; androecium of a thin-walled staminal cup that bears numerous incurved filaments along the rim of the margin, oblong-elongate poricidal anthers; and indehiscent fruits. The genus forms a clade clearly defined by both molecular and morphological characters (Mori 1979, Mori et al. 2007, Huang et al. 2015). *Gustavia* was first studied by Mori (1979), and four additional Ecuadorian species have been described since then (Mori and Cornejo, 2013; Cornejo & Mori, 2019). With this new taxon, the genus now includes 47 species (Mori et al. 2017). Because of the beautiful, sweetly scented flowers, the members of *Gustavia* have ornamental potential and are sometimes planted as green elements in urban environments (e.g., Macas city, Ecuador).

The abundant poricidal anthers suggest bee pollination, providing food resources for native bees and also for introduced honey bees, such as *Apis mellifera* (Mori and Boom, 1987; pers. obs.). Because of the edible mesocarp, the fruit of some species, such as *Gustavia macarenensis* Philipson, known as Paso, are sold in local markets. Rodents, such as squirrels and agouties, also feed on these fruits (Sork, 1987; Mori et al. 2017; Cornejo, pers. obs.). The taxonomic study of *Gustavia* requires field work and observation of several flowering and fruiting key stages to produce useful information for recognizing species. Recent field work by the coauthors in the montane rain forests of the western cordillera in Colombia, as well as herbarium study, yielded a distinctive new species that is formally presented here.

MATERIALS AND METHODS

All relevant specimens at COL, CUVC, FAUC, HUA, HUQ, JAUM, NY, and UDBC were studied (herbarium abbreviations follow Thiers, 2022). Measurements are from herbarium specimens, rehydrated flowers, and fresh specimens. The botanical terms used in the species descriptions follow Jackson (1991) and Mori et al. (2015). Images of pollen grains were captured with a FEI-QUANTA

250 microscope-SEM in the Scanning Electron Microscopy Laboratory at the Instituto de Investigaciones en Estratigrafía-IIES, Universidad de Caldas. Terminology presented in Punt et al. (2007), Halbritter et al. (2018), Jain (2020) and Pardo-Trujillo et al. (2021) was utilized for the description of the palynomorphs. Measurements of the morphological structures were performed using ImageJ 1.51n software

We would like to express our deepest appreciation to the indigenous reservations “Territorio Ancestral Indígena San Lorenzo” and “Resguardo Indígena Nuestra Señora Candelaria de La Montaña” and their indigenous authorities and their people, for allowing us to enter to their territory and study the sacred mountains that they so zealously protect. The studies in the reservations were carried out in the framework of the court ruling 025/2018. We would like to thank Sori Morales, Carlos Betancur, Sergio Melchor, Lubian Melchor, Faiber Alarcón and Jaime Alarcón for granting us the permits, showing us more populations of the species throughout their indigenous community, hosting us for the days we were there, monitoring the phenology of the population and sharing with us the common name of this species. We are also thankful to Andrés Miguel Betancourth for his commentaries about *Gustavia romeroi* ecology. We are grateful to the staff of COL, FAUC, HUA, HUQ, JAUM and UDBC for letting us know their respective collections, and especially to the staff of FAUC for letting us prepare the specimens and for their support and advice throughout this study. We express our gratitude to Gustavo Adolfo Bolaños from the Instituto de Investigaciones en Estratigrafía-IIES, Universidad de Caldas, for granting us access to the palynology laboratory and the optical equipment, including the SEM.

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(Schindelin et al., 2012). The mean and standard deviation of the equatorial diameter in equatorial view, polar diameter in equatorial view, diameter in polar view were calculated. Specific characteristics of pollen grains, such as colpi, pores, apertures, ornamentation were described (Prance and Mori, 1979; Roubik and Moreno 1991). The Extent of Occurrence

(EOO) and Area of Occupancy (AOO) were estimated using rCAT (Moat, 2020) in the statistical software R (R Core Team, 2020) based on the geographical data from the specimens. The IUCN Red List category for the species was assessed following the guidelines of the International Union for Conservation of Nature (IUCN, 2022).

TAXONOMY

Gustavia montana Cornejo, D. Gut. & J.S. Arango-G., *sp. nov.*

TYPE: COLOMBIA. Caldas: Cordillera occidental, Mun. Ríosucio, Territorio Ancestral Indígena San Lorenzo, Comunidad Honduras, cassava and plantain crop, 1635 m, 5°28'29.9"N, 75°41'46.2"W, 8 July 2023 (fl), *D. Gutiérrez-Duque & J. S. Arango-González 645* (Holotype: FAUC; Isotypes: COL, HUA, HUQ, JAUM). Fig. 1–4.

Gustavia montana is similar to *G. sessilis* S.A. Mori by the sessile narrow leaves, ecostate hypanthium and large floral bracts, but differs from the latter species by the many branched (vs. unbranched to few-branched) growth form, leaves with 20 to 27 (vs. 40) pairs of lateral veins, a rather multiflorous inflorescence (usually 12 to 20 vs. 4- or 5-flowered), and calyces with 6 to 8 (vs. 4) sepals.

Several to many-branched trees, to 6 m tall \times 15 cm DBH. Trunk covered with lichens; bark slightly roughened, lenticellate, peeling in long strips, inner bark orangish-red. Leaves clustered at the ends of branches, subsessile, the midvein at base usually crescent-moon shaped in cross section, flattened adaxially and convex, but not carinate, abaxially; blades oblanceolate, 35–80 \times 12–20 cm, somewhat glossy adaxially, glandular-punctate, and short hyaline-pilose on veins abaxially, lower part of blade tapered to base, base cuneate to broadly obtuse, margins often inconspicuously crenulate, barely undulate, apex short-acuminate; venation brochidodromous, midrib salient adaxially and abaxially, secondary veins in 20 to 27 pairs, plain or prominulous adaxially, salient abaxially, intersecondary veins sometimes present, tertiaries more or less scalariform, higher order veins reticulate. Inflorescences terminal, racemose, bearing 12–25 flowers but one at anthesis at a time, rachis ca. 150 \times 5–7 mm, occasionally shorter, few flowered and axillary at subterminal branches; floral bract lanceolate, ca. 4 \times 1.5 cm, red to purplish-red, carinate and short pilose abaxially, soon deciduous; pedicels 80–150 mm long, short hyaline-tomentose to tomentulose, at distal half bearing 2 bracteoles, lanceolate, ca. 11–15 \times 7–8 mm, red to purplish-red, carinate and short pilose abaxially, soon deciduous. Flowers ca. 10 cm diam.; hypanthium tomentose, without costae; calyx lobes 6 to 8, broadly triangular to ovate, ca. 3–5 \times 8–11 mm, purplish towards apex, tomentose; petals 7 to 9, obovate to obovate-elliptic, ca. 50–60 \times 25–35 mm, salmon to pink and short pilose in bud, at anthesis white on both sides, salmon tinged at base abaxially; connate androecial tube ca. 5–7 mm high, outermost filaments ca. 12–17 mm long, white; anthers ca. 3 mm, light yellow; ovary 6- to 8-locular, style ca. 2 mm long, obconical; stigma with 6 to 8 stigmatic lines. Fruit subglobose, nearly smooth, broadly obtuse to almost rounded at apex, ca. 4 \times 5 cm, yellowish-brown at maturity; calycine rim persisting, inserted at summit of

fruit, infracalycine zone rounded to base, supracalycine zone prominent; pulp creamy; exocarp leathery, 3–7 mm thick. Seeds subglobose, ca. 38 \times 25 mm, seed coat thin, smooth; caruncle broadly conical, funicular aril contorted, well-developed, ca. 20 mm long, with irregular bumps, yellow, adpressed to seed.

Because the leaves are arranged in tightly congested clusters at the end of branches, and the suprafoliar terminal inflorescences with relatively large basal floral bracts and presence of pedicellary bracteoles, *Gustavia montana* resembles *G. sessilis* S.A. Mori, *G. grandibracteata* Croat & S.A. Mori, and *G. pubescens* Tafalla ex O. Berg. However, *G. montana* differs from all of those by the many-branched form (vs. unbranched or/to few-branched), more rounded seeds with distinctive developed funicular arils, and distinctive pattern of distribution, over 1600 m (versus sea level to 1000 m). Additional differences between *G. montana* and *G. sessilis* are described in the diagnosis. *Gustavia montana* differs from *G. grandibracteata* by the subsessile leaves (versus petiolate), bearing blades with fewer secondary veins (20–27 versus 45–54), and the calyx with 6 to 8 lobes (versus 4 calyx lobes). *Gustavia montana* also differs from *G. pubescens* by the smaller flowers at anthesis (ca. 10 cm in diam. versus 12 to 17 cm), bearing 7 to 9 petals (versus 6), smooth hypanthium (versus costate hypanthium), more inconspicuous pubescence and a different pattern of distribution, that is endemic to the central and western cordillera of Colombia (versus restricted to western Ecuador). By the leaves arrangement, size and shape of leaf blades, and similar number of lateral veins *Gustavia montana* may resemble *G. occidentalis* Cuatrec., but the former species differ from the later by the subsessile leaves (versus 1 to 5 cm petiolate), pedicels tomentose to tomentulose (versus glabrous), seeds with a well developed funicular aril (versus seeds without developed funicular aril), and the distinctive mentioned montane pattern of distribution over 1600 m (versus sea level to 1500 m in the Pacific slopes of southwestern Colombia and northwestern Ecuador).

Palynology: Monad; prolate; amb circular; isopolar; symmetry radial; tricolporate; pore lologate; colpi with apex acute; reticulate; heterobrochate; lumina smaller than 1 μ m; equatorial view length (polar axis) 21.1 μ m (19.3–23.8, n = 10); equatorial view width (equatorial diameter) 15.8 μ m (13.4–17.5, n = 10); polar view length 17.4 μ m (15.8–19.3, n = 10); colpi length 15 μ m (12.9–18.3, n = 10); colpi width 1.4 μ m (0.5–2.2, n = 10); pore length 2.6 μ m (2.4–2.8, n = 2); pore width 1.8 μ m (1.7–1.9, n = 2).

In some pollen grains the pore was not observed, apparently presenting a tricolpate aperture. The possible fusion of two colpi at the pole of the pollen grain was also



FIGURE 1. *Gustavia montana* Cornejo, D. Gut. & J.S. Arango-G. Based on the holotype (FAUC). Photograph by Santiago Guzmán.

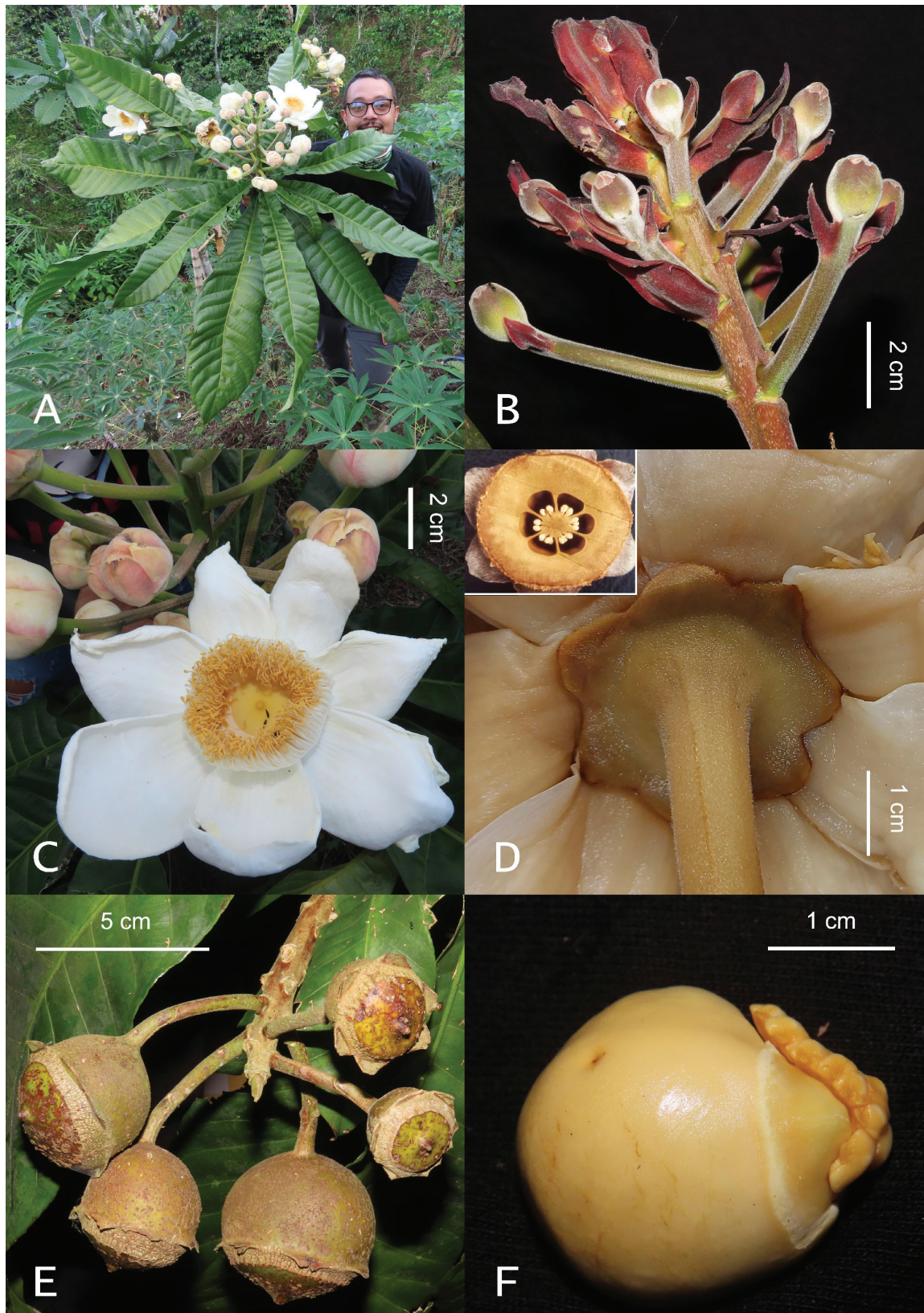


FIGURE 2. *Gustavia montana* Cornejo, D. Gut. & J.S. Arango-G. **A**, terminal leafy branch and inflorescence held by Juan Sebastián Arango, adaxial view; **B**, bracteate young inflorescence, lateral view; **C**, flower at anthesis; **D**, close-up of calyx and base of petals, with a cross-section of ovary displaying 6 locules at upper left; **E**, infructescence; **F**, seed crowned by caruncle and funicular aril. **A**, **C**, **D**, are based on the holotype *Gutiérrez-Duque & Arango-González 645* (FAUC); **B**, **E**, **F** are based on the paratype *Arango 003* (FAUC). Photographs **A**, **B**, **C**, **E**, **F** by Juan Sebastián Arango, **D** by David Gutiérrez-Duque.

observed (Fig. 3D); therefore, it is necessary to continue analyzing the pollen morphology in *G. montana* in order to determine if these characteristics occur in other populations and how it is related to other species in the genus.

Etymology: The epithet refers to the highly distinctive pattern of distribution of *Gustavia montana*, which is restricted to montane Andean forests, 1635–2176 m elevation on the slopes of the western and central cordilleras of Colombia. This montane pattern of distribution is unusual in a predominantly tropical genus.

Common names: Known as “cocolleto,” which means coconut pot in “Resguardo Indígena Nuestra Señora Candelaria de La Montaña” (Riosucio, Caldas).

Habitat and distribution: Currently known only from the Andes mountains of Colombia and distributed in the northeastern area of the Western Cordillera in the departments of Caldas and Risaralda, and throughout the Central Cordillera in the departments of Antioquia, Quindío and Risaralda. From its biogeographic affinities (see González-Orozco, 2021), it is possible that it is also found in the Western Cordillera in the department of Antioquia, and in the Central Cordillera in the department of Caldas. It grows at (1635–) 1949–2176 m of elevation, being not only the species of *Gustavia* that is distributed at the highest altitude in Colombia, but also in the entire genus. *Gustavia montana* usually inhabits secondary sub-Andean forests (Rudas et al., 2007); however, it has been found growing in

the midst of cassava and plantain crops (*Gutiérrez-Duque 645*), and planted in farm gardens (*Arango-González et al. 003*, *Vélez and L. C. Serna 7097*).

Phenology: Flowers were recorded in herbarium material and observed in the field during 2022 and 2023, from July to August and November to February, and fruits from July to October and December to February. The flowering periods can be more frequent during the dry season (Jaramillo, 2005), which is also the case in several species of the family (Prance and Mori, 1979).

Uses: Two individuals (*Arango-González et al. 003*, *C. Vélez and L. C. Serna 7097*) were found planted in farm gardens. Because of its large flowers, and the relatively short size of the trees, this species could be cultivated as an ornamental.

Conservation status: *Gustavia montana* is endemic to Colombia, currently known from 10 locations along the Central Cordillera and the northeastern sector of the Western Cordillera. Despite its restricted distribution, it was found widely distributed in a forest in Riosucio (*D. Gutiérrez-Duque and J. F. Alarcón 647*), with more than 100 individuals in less than 300 square meters. More than an ecological characteristic of the species, it could be an ecological strategy within a restricted distribution. This phenomenon, where a species with a restricted distribution has very dense populations, has been seen in other species of the genus, such as *G. parviflora* S.A. Mori (Lárez-Rivas,

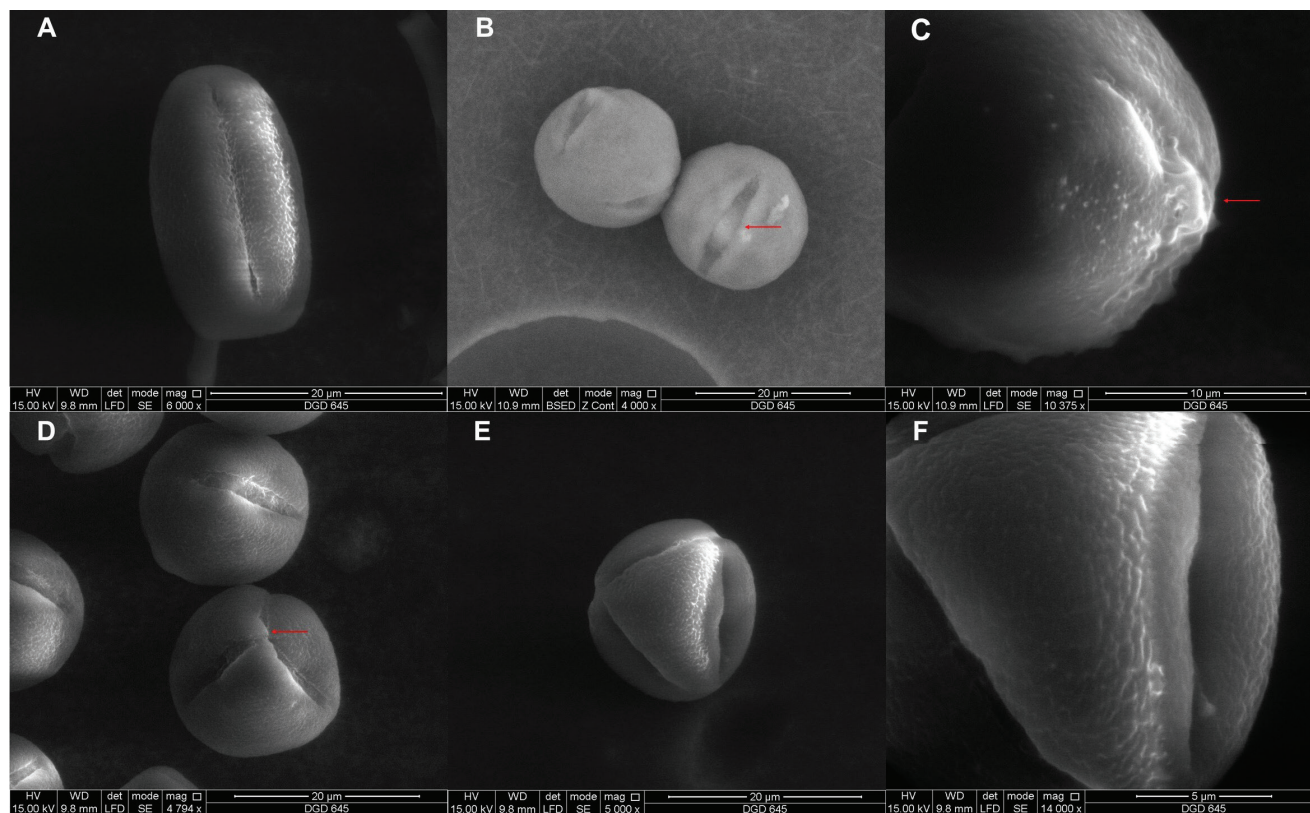


FIGURE 3. Pollen morphology in *Gustavia montana* Cornejo, D. Gut. & J.S. Arango-G. **A**, equatorial view; **B**, polar view (left) and general view (right); the red arrow indicates the colporate aperture; **C**, pore detail; **D**, possible fusion of two colpi at the pole of the pollen grain; **E**, general view; **F**, ornamentation detail. Photographs by Gustavo Bolaños.

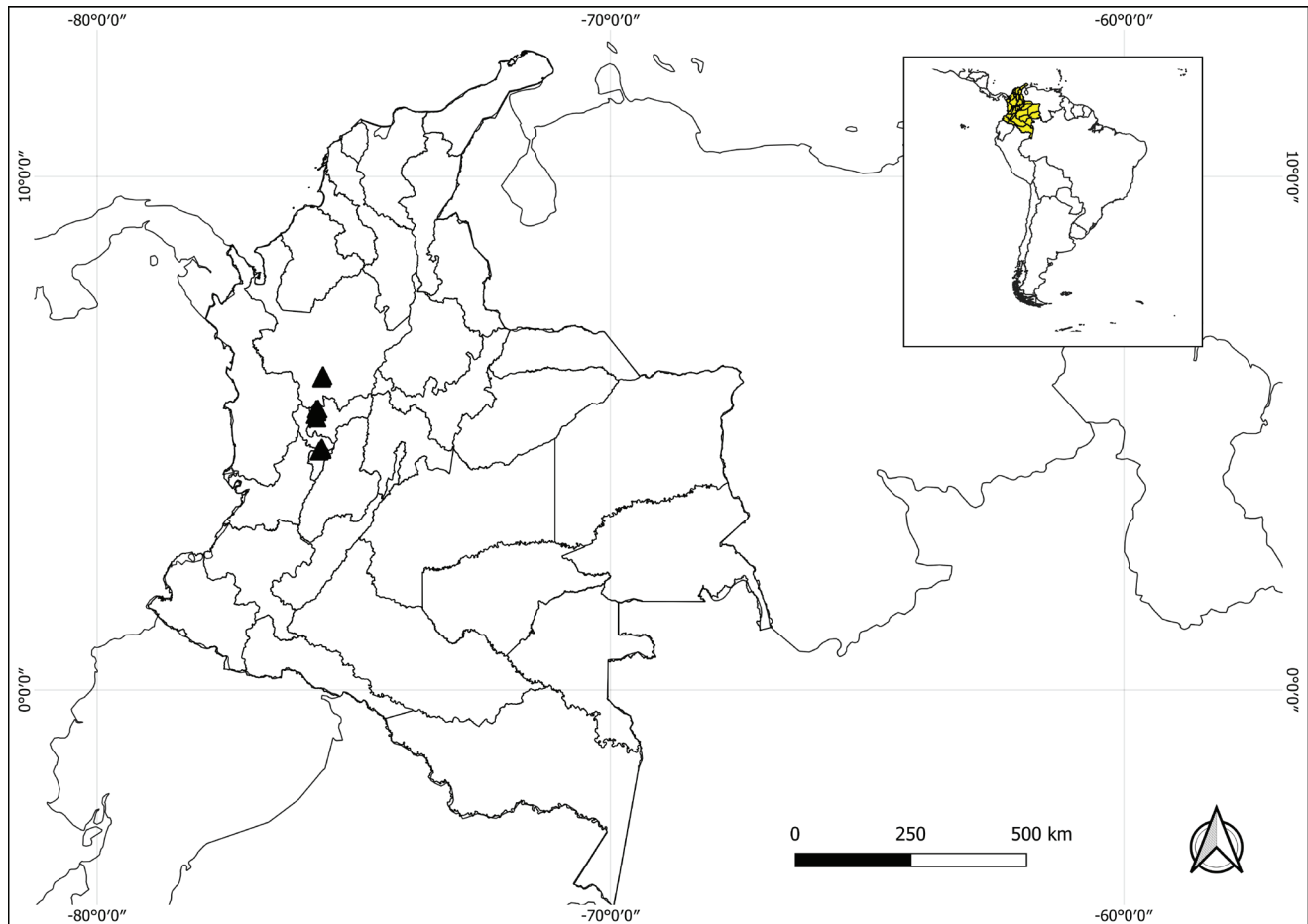


FIGURE 4. *Gustavia montana* Cornejo, D. Gut. & J.S. Arango-G. Distribution map. Prepared by Juan Sebastián Arango.

2000) and *G. romeroi* S.A. Mori & García-Barr. (A. M. Betancourth, pers. comm.). This phenomenon constitutes the risk of rapidly losing populations of the species in the few forests where it has been found. Additionally, it should also be taken into account in conservation and restoration processes.

The new species inhabits one of the most disturbed regions in Colombia, where deforestation, urban expansion, livestock and coffee plantations predominate (Rudas et al., 2007; Myster, 2020). For that reason, its populations are highly threatened by habitat loss and fragmentation. Its extent of occurrence (EOO) was estimated to be 1579.59 km², with an area of occupancy (AOO) of 44 km². The species is listed as Endangered (EN) under criteria B1ab(iii)+2ab(ii, iii, iv). Future studies on ecology, floral biology, population size and genetic diversity are needed in order to promote its long-term conservation.

Additional Specimens Examined: Antioquia: Cordillera central, Mun. Caldas, Vereda La Corrala, finca La Zarza, antes del alto de la Cruz, relicto de bosque, 1950 m, 6°4'51.9"N, 75°37'37.1"W, 27 Dec 2013 (fr), *J. Betancur and Álvaro Idárraga 18508* (COL, HUA, JAUM); Cordillera central, Mun. Sabaneta, Vía a la Romera, antes de ingresar por la portada de la reserva, 1919 m, 6°07'38.7"N, 75°36'02.7"W, 02 February 2020 (fr), *J. Mesa 10* (HUA).

Caldas: Cordillera occidental, Mun. Riosucio, Resguardo Indígena Nuestra Señora Candelaria de La Montaña, Comunidad La Cabaña, Sector La Ermita, árbol sembrado en jardín de la finca La Unión, 1949 m, 5°27'45.5"N, 75°43'08.7"W, 23 July 2023 (y. fl, fr), *S. Arango-González et al. 003* (FAUC, COL); Ibid., bosque Monte viejo, interior de bosque, 2083 m, 5°28'18.4"N, 75°43'39.4"W, 24 Jul 2023 (st), *D. Gutiérrez-Duque, J. F. Alarcón 647* (FAUC); Ibid., Cerro Ingrumá, 2176 m, 5°25'07.0"N 75°42'52.0"W, 19 Aug 2023 (fl), *J. S. Arango-González, D. Gutiérrez-Duque 004* (FAUC). Quindío: Cordillera central, Mun. Filandia, bosque aledaño a la granja Bengala, 2033 m, 4°41'06.7"N, 75°37'02.2"W, 12 Aug 2009 (fr), *C. A. Maya 69* (HUQ); vda. La Cauchera, 1900 m, 4°39'18.2"N, 75°40'29.1"W, 7 Jul 2003 (fr), *F. Viveros, C. Vélez, S. Muñoz 477* (HUQ). Risaralda: Cordillera central, Mun. Pereira, Corregimiento Arabia, Vereda El Cedral, jardín casa, 2000 m, 4°42'59.8"N, 75°37'22.9"W, 23 Sep 2000 (fr), *C. Vélez, L. C. Serna 7097* (HUQ, 2 sheets); cordillera occidental, Mun. Guática, Vereda Barroblanco, 1964 m, 5°21'40.4"N, 75°44'57.8"W, 20 February 2020 (fl), *M. A. Serna-Sánchez and S. Peláez-Vélez 325* (UDBC); Cordillera occidental, Mun. Quinchía, Vereda Matecaña, Predios de Minería Quinchía, 2020 m, 5°17'49"N, 75°42'56"W, 11 December 2021 (fr), *C. Paz 473* (UDBC).

LITERATURE CITED

- CORNEJO, X. AND S. A. MORI. 2019. *Gustavia esmeraldana* and *G. graciae*: New species of Lecythidaceae from northwestern Ecuador and a key to the species of *Gustavia* in Ecuador. *Phytotaxa* 418: 89–96.
- GONZALEZ-OROZCO, C. E. 2021. Biogeographical regionalization of Colombia: a revised area taxonomy. *Phytotaxa* 484: 247–260. DOI: 10.11646/phytotaxa.484.3.1
- HALBRITTER, A. H., H. HALBRITTER, S. ULRICH, GRIMSSON, M. WEBER, AND R. ZETTER. 2018. *Illustrated pollen terminology*. Springer, Berlin.
- 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).
- JACKSON, B. D. 1991. A Glossary of Botanic terms with their derivation and accent 4th ed. Duckworth, London.
- JAIN, S. 2020. Pollen and Spores. Pages 43–65 in *Fundamentals of Invertebrate Palaeontology*. Springer Geology. Springer, New Delhi.
- JARAMILLO, B. D. 2005. Clima andino y café en Colombia. Cenicafé, Manizales.
- LÁRES-RIVAS, A. 2000. Observaciones preliminares sobre la densidad y estructura poblacional de *Gustavia parviflora* Mori (Lecythidaceae) en la Serranía de Turimiquire, estado Monagas, Venezuela. *Acta Botanica Venezuelica* 23: 157–161.
- MOAT, J. 2020. rCAT: Conservation Assessment Tools. R package version 0.1.6. <https://CRAN.R-project.org/package=rCAT>
- MYSTER, R. W. 2020. Disturbance and Response in the Andean Cloud Forest: a Conceptual Review. *The Botanical Review* 86: 119–135. DOI: <https://doi.org/10.1007/s12229-020-09219-x>
- 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 (2): 85–121. <https://doi.org/10.11646/phytotaxa.203.2.1>
- MORI, S. A. 1979. Lecythidaceae. in G. T. PRANCE AND S. A. MORI. 1979. Lecythidaceae—Part I. The actinomorphic-flowered New World Lecythidaceae. *Flora Neotropica Monographs* 21: 128–197.
- MORI, S. A., C.-H. TSOU, C. C. WU, B. CRONHOLM, AND A. A. ANDERBERG. 2007. Evolution of Lecythidaceae: information from combined ndhF and trnL-F sequence data. *American Journal of Botany* 94(3): 289–301.
- MORI, S. A. AND B. BOOM. 1987. The forest. in S. A. MORI AND COLLABORATORS. *The Lecythidaceae of a Lowland Forest: La Fumée Mouintain, French Guiana*. *Memoirs of The New York Botanical Garden* 44: 9–29.
- MORI, S. A. AND X. CORNEJO. 2013. Two new species (*Gustavia johnclarkii* and *G. hubbardiorum*) and other contributions to the systematics of *Gustavia* (Lecythidaceae). *Brittonia* 65: 330–341. <https://doi.org/10.1007/s12228-012-9282-9>
- MORI, S. A., N. P. SMITH, X. CORNEJO, AND G. T. PRANCE. Cornejo, X. & Prance. 2015 onward. *The Lecythidaceae Pages*. The New York Botanical Garden, Bronx, New York. Available from: <http://sweetgum.nybg.org/lp/index.php> (accessed August 23, 2023).
- 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 phylogeography of the Lecythidaceae clade (Brazil nut family). 2017 (not 2016). *Phytoneuron* 30: 1–85.
- PARDO-TRUJILLO, A., A. PLATA, AND C. GÓMEZ. 2021. Palinología Colombiana: Métodos, aplicaciones y estado del conocimiento. Universidad de Caldas, Colombia.
- PRANCE, G. T. AND S. A. MORI. 1979. Lecythidaceae—Part I. The actinomorphic-flowered New World Lecythidaceae. *Flora Neotropica Monographs* 21: 1–270.
- PUNT, W., P. P. HOEN, S. BLACKMORE, S. NILSSON, AND A. LE THOMAS. 2007. Glossary of pollen and spore terminology. Review of Palaeobotany and Palynology 143(1–2): 1–81.
- R CORE TEAM. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- ROUBIK, D. AND J. MORENO. 1991. *Pollen and Spores of Barro Colorado Island*. Missouri Botanical Garden, St. Louis.
- RUDAS, G. D. MARCELO, D. ARMENTERAS, N. RODRIGUEZ, M. MORALES, L. C. DELGADO, AND A. SARMIENTO. 2007. Biodiversidad y actividad humana: Relaciones en ecosistemas de bosque subandino en Colombia. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá D. C.
- SCHINDELIN, J., I. ARGANDA-CARRERAS, E. FRISE, V. KAYNIG, M. LONGHAIR, T. PIETZSCH, S. PREIBISCH, C. RUEDEN, S. SAALFELD, B. SCHMID, J. Y. TINEVEZ, D. J. WHITE, V. HARTENSTEIN, K. ELICEIRI, P. TOMANCAK, AND A. CARDONA. 2012. Fiji: an open-source platform for biological-image analysis. *Nature methods*, 9(7): 676–682.
- SORK, V. L. 1987. Effects of predation and light on seedling establishment in *Gustavia superba*. *Ecology* 68 (5): 1341–1350. <https://doi.org/10.2307/1939218>.
- THIERS, B. 2022. *Index Herbariorum: A global directory of public herbaria and associated staff*. New York Botanical Garden's Virtual Herbarium. Available at <http://sweetgum.nybg.org/ih/> (accessed August 1, 2023).