



Lintersemina (Rubiaceae: Condamineae), a new and enigmatic genus from the Magdalena Medio Region of Colombia

HUMBERTO MENDOZA-CIFUENTES^{1,4*}, ANGELA CELIS^{2,5}, EDUARDO TOVAR^{3,6} & MAILYN A. GONZÁLEZ^{3,7}

¹ Instituto Alexander von Humboldt, Herbario FMB, Carrera 8 # 15-08, Claustro de San Agustín, Villa de Leyva, Colombia.

² Carrera 8 # 4N-15, Piedecuesta, Colombia.

³ Instituto Alexander von Humboldt, Laboratorio de Genética de la Conservación, Calle 28A # 15-09 Bogotá, Colombia.

⁴ hummendoza@gmail.com; <https://orcid.org/0000-0002-5685-9338>

⁵ angela.celis.act@gmail.com; <https://orcid.org/0000-0001-8503-7192>

⁶ etovar@humboldt.org.co; <https://orcid.org/0000-0003-2680-3904>

⁷ magonzalez@humboldt.org.co; <https://orcid.org/0000-0001-9150-5730>

*Author for correspondence

Abstract

A new genus, *Lintersemina* (Condamineae, Rubiaceae), with a single species, *L. chucuriensis* is here described, based on recent collections made during a biological exploration to the Magdalena Medio Region of Santander Department, central portion of Colombia. This region is of high interest for both the high endemism of its flora and fauna and the critical conservation status of this biodiversity due to high levels of deforestation. *Lintersemina* is unique within the tribe Condamineae for the following combination of characters: axillary, long-pedunculate inflorescences, loculicidal capsules with 1-2 seeds per locule, and large navicular seeds. Based on phylogenies obtained using plastid and nuclear sequence data, the genus is positioned in the Condamineae (subfamily Ixoroideae), as a sister group to the genera *Simira* and *Parachimarrhis*. This new genus is only known from two localities at the foothills of the Yariguíes National Park, in the municipalities of El Carmen de Chucurí and Zapatoca, at 400–800 m elevation, in forest undercanopy, near streams. Threats of deforestation and a very low population density were assessed, and this species classified as Critically Endangered (CR) following IUCN criteria. Full description and illustrations are also included.

Keywords: Conservation, flora of Colombia, Santander, Tropical humid Forest

Introduction

The Magdalena Medio Region is an extensive inter-Andean valley in the central part of Colombia, formed by the Magdalena River and dominated by tropical rainforest (Luna Uribe 2018). It constitutes a hotspot of biological diversity because it harbors a high number of species and endemism (Luna Uribe 2018). However, more than 80% of the natural cover of this region has been destroyed (Franco & Rodríguez 2005, Etter & Rodríguez 2008).

In this region, about 2000 species of vascular plants are estimated to occur (Idárraga *et al.* 2016), of which about 120 are endemic to Colombia and exclusive to the tropical humid forests of the Magdalena Medio Region (Bernal *et al.* 2015). One genus is known to be endemic to the region, *Isidodendron* J.L. Fernández-Alonso, J. Pérez-Sabala & A. Idárraga (2000: 348) (Trigonaceae; Fernández-Alonso *et al.* 2000), as well as six species of Rubiaceae: *Ciliosemina purdieana* (Weddell 1849a: 272) Antonelli (2005: 26), *Joosia antioquiensis* C.M. Taylor (2010: 475), *Ladenbergia magdalenae* L. Andersson (1997: 279), *Macrocnemum grandiflorum* (Weddell 1849b: 98) Weddell (1854: 76), *Psychotria decora* Standley (1930: 92; = *Ixora standleyana* C.M. Taylor (2018: 345), and *Simira hirsuta* C.M. Taylor (1999: 569) (Delprete & Cortés-B. 2019).

Rubiaceae is a cosmopolitan family with an estimated 609 genera and 13765 species (The Plant List 2010, Govaerts *et al.* 2020); most of the genera and species are found in humid tropical regions (Taylor 2015). About 1115 species and 118 genera of Rubiaceae are known to occur in Colombia (Delprete & Cortés-B. 2019). In the last two decades, about 20 new genera of Rubiaceae have been described or established in the World, largely from taxonomic changes based

on phylogenetic analyses and a few from specimens recently collected in unexplored tropical areas (e.g., Cabral & Bacigalupo 2001, Terrell 2001, Borhidi 2003, Andersson & Antonelli 2005, Torres-Montúfar *et al.* 2017, De Block *et al.* 2018, Cheek *et al.* 2018a, 2018b; Paudyal *et al.* 2018).

A biological expedition recently undertaken to the humid forests of the Magdalena Medio Region, Department of Santander, resulted in the discovery of the new taxon described here, as well a total of 14 new species corresponding to eight of vascular plants, two of fish, two of amphibians and two of invertebrates. This demonstrates that despite the considerable state of deterioration of this regional natural ecosystem, there are still important remnants that merit study and conservation.

Initially the new taxon of Rubiaceae could not be assigned to a genus because of its unique fruit and seed characters; nevertheless, it had been tentatively assigned to the tribe Cinchoneae A.P. de Candolle (1807: 217). We also performed a preliminary search for similarity between specimens sequences and Rubiaceae family species on the Basic Local Alignment Search Tool, BLAST (www.ncbi.nlm.nih.gov/Genbank), where this taxon resulted to be associated with *Elaeagia* Weddell (1849b: 94, adnot), of the tribe Condamineeae J.D. Hooker (in Bentham & J.D. Hooker 1873: 8). However, the characteristics of the fruits and seeds of this new taxon are not concordant with any of the genera of capsular fruits in the tribe. In this article we describe this taxon as a new monotypic genus with unique seed characters in Neotropical Rubiaceae, and a detailed phylogenetic analysis is performed to establish its tribal position in the Rubiaceae family.

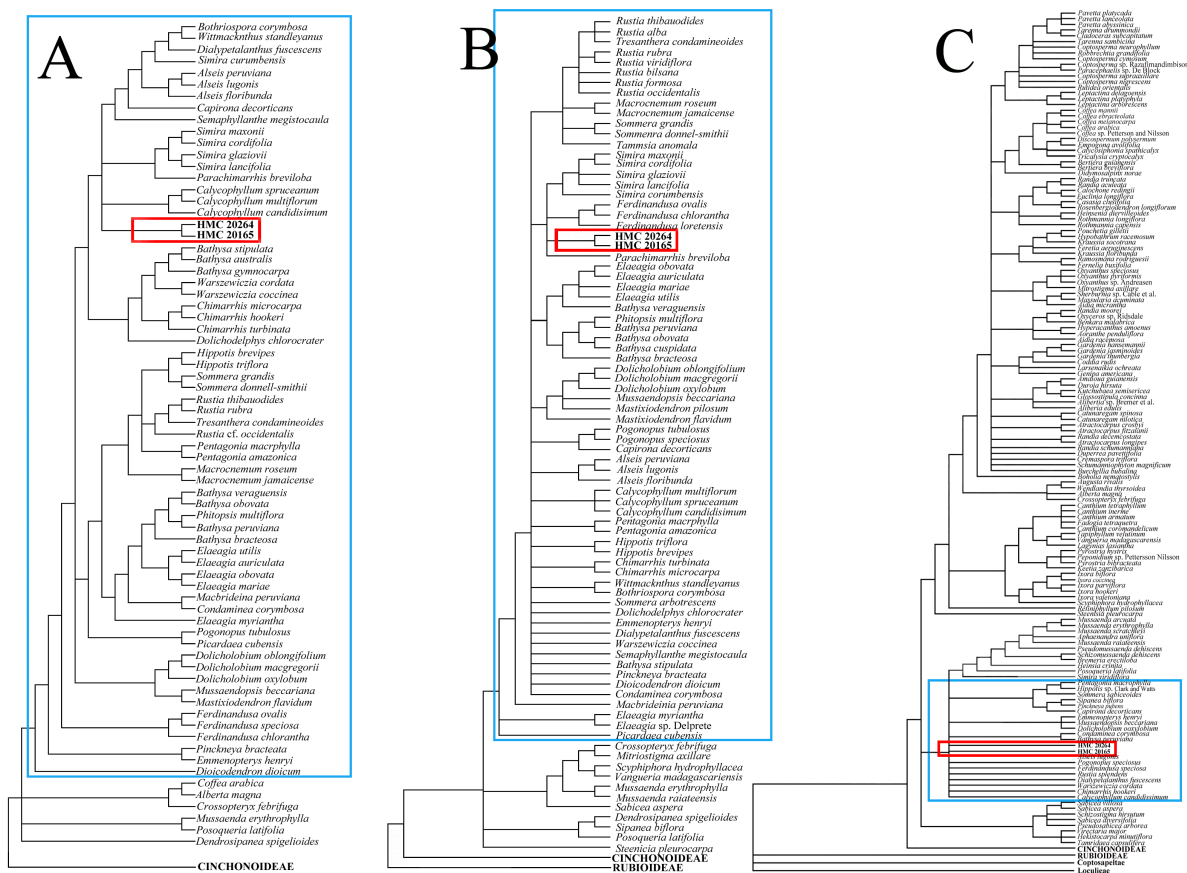


FIGURE 1. Majority rule consensus trees for each molecular marker. Light blue line boxes point out the Condamineeae tribe within the Ixoroideae subfamily. Red boxes enclose the new genus. **A**, Phylogenetic tree from ITS marker; **B**, Phylogenetic tree from matK marker; **C**, Phylogenetic tree from rbcL marker.

Material & methods

Morphology, distribution and conservation

Field collections were undertaken in El Carmen de Chucurí, near the village La Belleza, western Santander

department, in February 2018. Flowers, fruit and seeds were preserved in 70% alcohol. All collections were processed and deposited in herbarium FMB of the Instituto Alexander von Humboldt. In order to elaborate the descriptions, a digital calibrator of 0.1 mm precision was used to measure vegetative parts and the inflorescence in dry herbarium material. The measurements of the floral parts were based on fresh flowers preserved in 70% alcohol and from the specimens that were designated as types. Measurements of the floral parts and trichomes were performed with a Leica S8AP0 microscope and images were captured with a MC190 HD camera. A map of occurrence of this new taxon in Colombia, based on collection data, was generated using Arc-GIS version 10.2.1. Preliminary conservation status was assessed estimating the Area of Occupancy with GeoCat (<http://geocat.kew.org/editor>) and applying the IUCN Red List Category criteria (IUCN 2012, 2017).

DNA extraction, amplification and sequencing

Total DNA extraction of plant samples was carried out from leaf tissues using the CTAB protocol from Ivanova *et al.* (2008). DNA concentrations were estimated by quantification using the NanoDrop 1000 (Thermo Fisher Scientific). DNA was preserved at -20°C for further analysis. Amplification of DNA regions ITS, matK, and rbcL was performed using the respective universal primers in a master mixture of a final volume of 15 µL, containing 2 µL of template DNA (~10-50 ng), 1X Taq buffer ((NH₄)₂SO₄), 200 µM of each deoxynucleoside triphosphate, 2 mM MgCl₂, 0.2 µM of each primer, 0.6 µg/µL bovine serum albumin, and 1 U of Taq DNA polymerase.

The PCR cycling conditions for ITS and rbcL regions, consisted of a first cycle of denaturation at 94° C for 2 min followed by 35 cycles of 94° C for 30 s, Ta (ITS = 55 °C, rbcL = 52 °C) for 40 s, and 72° C for 2 min and a final extension cycle at 72 °C for 5 min. The PCR conditions for multiplexed primers of matK were 95° C for 2 min; 5 cycles of 95° C for 25 s, 46° C for 35 s, and 70° C for 1 min followed by 35 cycles of 95° C for 25 s, 48° C for 35 s, and 70° C for 1 min and a final extension cycle at 72° C for 5 min. PCR products were visualized on 1.5% agarose gels electrophoresis. The ExoSAP-IT protocol was used to clean PCR products, after which they were sent to La Universidad de los Andes (Bogota, Colombia) for DNA sequencing. Sequence chromatogram output files were assembled and edited manually using Geneious v10.2 software (<http://www.geneious.com>, Kearse *et al.* 2012).

Phylogenetic tree

Phylogenetic relationships of the new taxon within Rubiaceae family were retrieved through a Bayesian phylogenetic analysis using the sequence data sets previously published by Andersson & Antonelli (2005), Bremer & Eriksson (2009), and Kainulainen *et al.* (2010), available on GenBank data base (www.ncbi.nlm.nih.gov/Genbank). Data of 472 taxa from the 44 tribes in the family were gathered for the molecular markers rbcL (415 taxa), matK (127 taxa), and ITS (98 taxa) (Appendix 1). These markers provided evidence both of cpDNA and nrDNA, as well as allowed us to resolve the phylogenetic relationships at both subfamily and tribe level. Since the rbcL marker has a higher taxonomic representativeness for the tribes of Rubiaceae, we used it to resolve the phylogenetic relationships at subfamily level. To obtain an approximation of the relationships below subfamily we used matK and ITS data sets; these are more representative of the Condamineae tribe and they have a higher rate of evolution for resolving relationships at the generic and specific level.

Each molecular marker data set was aligned using MUSCLE (Edgar 2004), and the resulting alignments were edited manually on MEGA X (Kumar *et al.* 2018). jModelTest2 (Darriba *et al.* 2012) was used to select the best fitting model of molecular evolution for each molecular marker under the Akaike information criterion. The models selected were GTR + G + I for rbcL and GTR + G for matK and ITS. Characters of taxa without information for a molecular marker were scored as missing data (?) in the data set of the three molecular markers. Wiens and Moen (2008) indicated that phylogenetic relationships can be accurately reconstructed from taxa that include many missing data cells using Bayesian phylogenetic analyses. Keeping this in mind, taxa with incomplete information were not excluded from the concatenated data set. A phylogenetic tree using all markers, as well as one for each marker were reconstructed based on the Bayesian inference analysis implemented in MrBayes 3.2.2 (Ronquist *et al.* 2012). Markov Chain Monte Carlo analysis (MCMC) were configured as two independent runs each with four parallel chains. The convergence and mixing of the MCMC chains were checked by means of the average standard deviation of split frequencies. When this value was between 0.01 and 0.05 the mcmc sampling was stopped. Potential scale reduction factor and effective sample size (ESS) of parameters in the posterior probability also were checked. When the first approach a value of 1.0 and ESS were greater than 200, convergence was assumed. We discarded the first 25% of chain sampling as burn-in. A majority rule consensus tree was computed from the posterior distribution of each analysis.

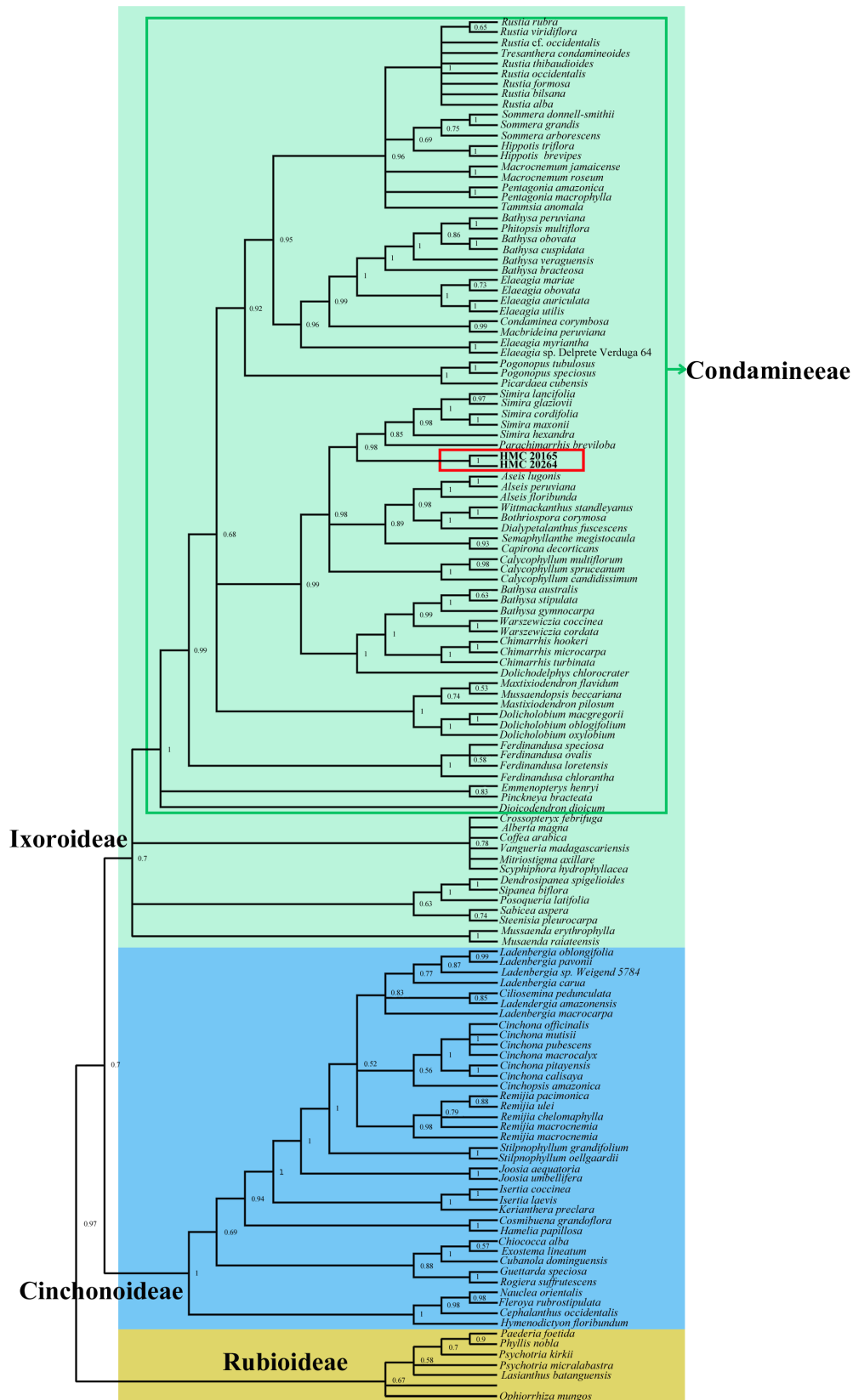


FIGURE 2. Majority rule consensus tree of ITS and matK molecular markers obtained by Bayesian analysis. Light green square points out the Ixoroideae subfamily; light blue square, the Cinchonoideae subfamily; and pale yellow square, the Rubioideae subfamily; green line box shows the Condamineeae tribe, and red line box enclose the new genus. Values on the right of the nodes correspond to the posterior probability.

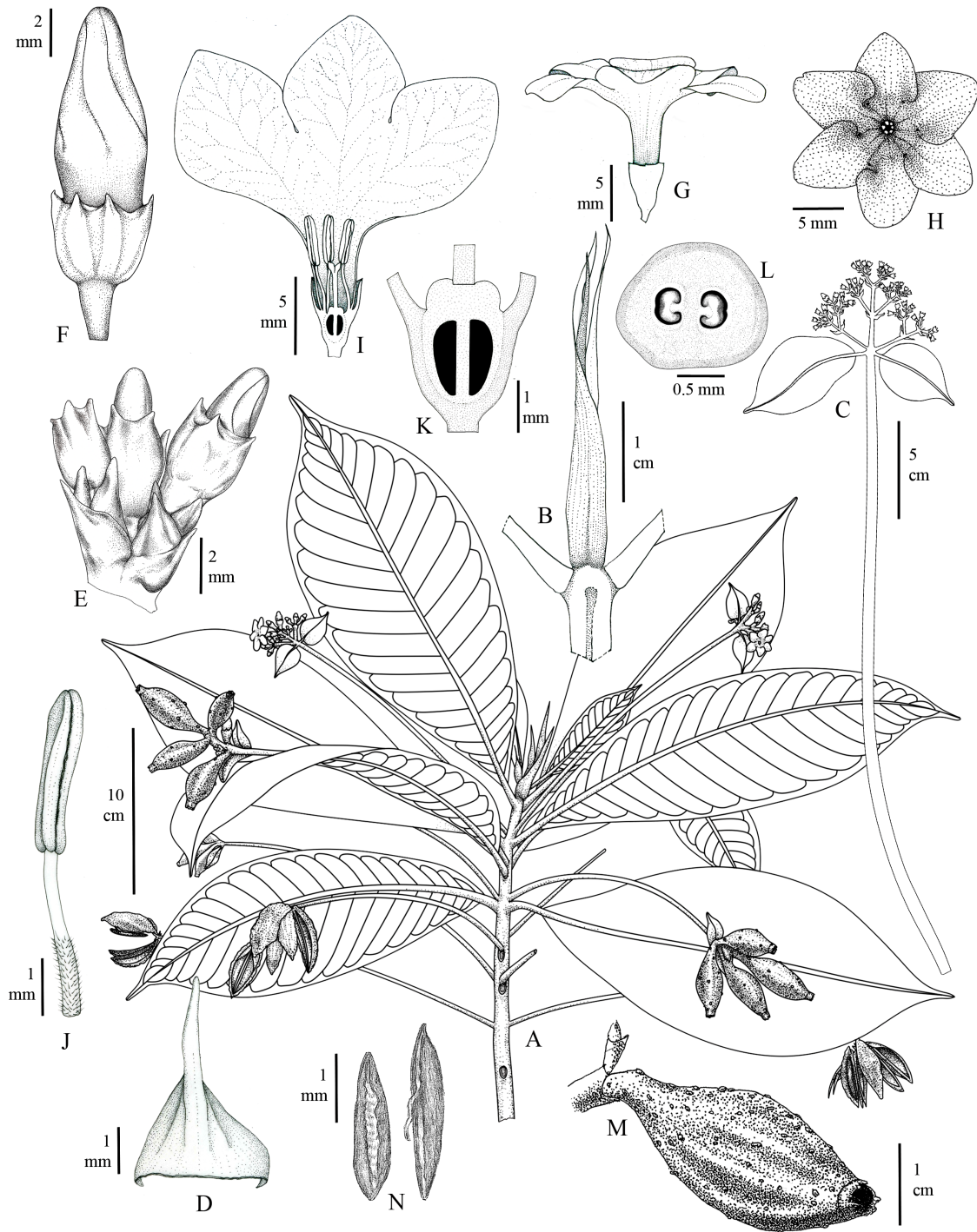


FIGURE 3. *Lintersemina chucuriensis*. **A**, Habit; **B**, Terminal stipule; **C**, Inflorescence; **D**, Bract; **E**, Apical flowering branch; **F**, floral bud; **G**, flower, side view; **H**, corolla, top view; **I**, flower, longitudinal section; **J**, Stamen; **K**, hypanthium and ovary, longitudinal section; **L**, hypanthium and ovary, horizontal section; **M**, fruit; **N**, Seeds. Based on *Mendoza et al. 20165*. Drawn by Suaty Daniela Torres.

Results

Phylogenetic analysis

Phylogenetic analyses from cpDNA and nrDNA information agreed on the location of the new genus inside the

Ixoroideae subfamily, tribe Condamineae (Figure 1). The phylogenetic analysis of the concatenated sources of information, cpDNA and nrDNA, considered the totality of the subfamilies and the majority of tribes inside Rubiaceae family with about 300 genera sampled. This phylogenetic tree located the new genus inside the subfamily Ixoroideae, tribe Condamineae, as the sister group of the genera *Simira* Aublet (1775: 170) and *Parachimarrhis* Ducke (1922: 253) with a posterior probability of 0.98 (Supplementary information). The tree obtained from rbcL data set is not clear about the phylogenetic relationships below the subfamily level, so the position of the new genus can only be established inside the Ixoroideae subfamily by this molecular marker. The tree obtained from the matK located the new genus inside the Condamineae tribe in a polytomy with the genera *Parachimarrhis*, *Ferdinandusa* Pohl (1831: 8–9), and *Simira*. The tree obtained from the ITS data set agrees on the location of the new taxon inside the Condamineae tribe as part of a polytomy. There are three groups in the polytomy, one comprises *Calycophyllum* A.P. de Candolle (1830: 367), a second *Parachimarrhis* and *Simira*, and a third *Semaphyllanthus* L. Andersson (1995: 421–422), *Capirona* Spruce (1859: 200), *Alseis* Schott (1827: 404), *Simira*, *Dialypetalanthus* Kuhlmann (1925: 363), *Bothriospora* Hooker (1870: 55) and *Wittmackanthus* Kuntze (1891: 302). The phylogenetic tree based on these two last molecular markers, matK and ITS, obtained a better resolution inside the Condamineae tribe, locating the new genus inside the Septicidal clade (Kainulainen *et al.* 2010) with a posterior probability of 0.98 (Figure 2).

Taxonomy

Lintersemina H. Mendoza-Cifuentes & A. Celis & M.A. González, *gen. nov.*

Type species:—*Lintersemina chucuriensis* H. Mendoza-Cifuentes, A. Celis & M.A. González

Diagnosis:—This new genus is unique within the tribe Condamineae by the following combination of characters: axillary, long-pedunculate inflorescences, ovary with 1–2 ovules per locule, loculicidal capsules, and large, terete, navicular (boat-shaped) seeds.

Treelet. Leaves opposite, decussate, petiolate; petioles slightly thickened at the base; blade venation brochidodromous, with secondary veins ascending and arcuate. Stipules interpetiolar, readily caducous, only found at apical buds and youngest nodes, with colleters in adaxial surface, resinous. Inflorescences axillary, subterminal, corymbose cymes, pedunculate, many-flowered; with two types of bracts, the basal ones subtending the inflorescence leaf-like, the distal ones triangular. Flowers hermaphroditic, protandrous, 5- or 6-merous, actinomorphic, pedicellate, erect. Calyx persistent in fruit. Corolla aestivation left-contorted. Stamens included; anthers opening by longitudinal slits. Ovary 2-locular, placentation axile, ovules 1 or 2 in each locule; style included, with two stigmatic branches. Fruit a loculicidal capsule. Seeds >1 cm long, terete, navicular, with membranaceous structures along the raphe.

A monospecific genus, endemic to Magdalena Medio Region of Colombia, growing in tropical rainforest.

Etymology:—The name of this genus refers to its navicular (boat-shaped) seeds.

Lintersemina chucuriensis H. Mendoza-Cifuentes, A. Celis & M.A. González, *spec. nov.* (Figs. 3–5).

Type:—COLOMBIA. Santander: El Carmen de Chucurí, vereda La Belleza, path between señor Santiago Estrada's house the Cascajales Creek, moist tropical forest with various grades of intervention, 6.585112°N, -73.575409°W, 786 m, 18 February 2018 (fl, fr), H. Mendoza-Cifuentes, A. Celis & A. Robles 20165 (holotype FMB! [Acc. No. 120626], isotypes FMB! [Acc. No. 120627], CAUP!, COAH!, COL!, CUVC!, HUA!, UDCA!, UIS!, UPTC!).

Treelet 2.5–5 m tall. Internodes oblong in cross section, laterally flattened, 0.9–2.2 cm long, glabrous. *Stipules* narrowly triangular, 26.4–30 × 3.8–6 mm, coriaceous, dark brown in dry material with entire margin, abaxially glabrous, adaxially with resin-secreting colleters in a basal triangular area, early caducous. *Leaves* clustered at the apex of branches, with warty bodies on the abaxial surface and midrib; petioles 15.7–33.6 mm long, terete towards the base, canaliculate adaxially towards the apex, glabrous; blades symmetrical, obovate, 19–33 × 6–14 cm, thinly coriaceous, glabrous except in young leaves that have margins with smooth trichomes 0.4–0.7 mm long, base obtuse, apex with acumen 7–16 mm long, margin entire; midrib slightly raised and canaliculate on adaxial side, strongly prominent on the abaxial side; with 18–24 secondary veins on each side of midrib, prominent on abaxial side, slightly conspicuous in adaxial side; tertiary veins lax and parallel, noticeable only on abaxial side. *Inflorescence* axillary on distal nodes,

corymbose cyme, 15.5–34.5 cm long, erect, with progressive reduction in length of the internodes of the branches, with 2–30 flowers; peduncle 23.5–31 cm long, oblong-flattened, puberulous, smooth trichomes 0.1–0.3 mm long; secondary branches with 2–3 branching levels; with two petiolate bracts resembling small leaves at the base of the branch, unequal in size, stalk 1.3–3.7 mm long, blades ovate, 1.8–6.2 × 0.9–3.4 cm, truncate to subcordate at base, margin ciliolate with trichomes 0.1–0.4 mm long; distal bracts 2.6–4.6 × 1.3–4.4 mm, triangular and keeled, the keel comes out at the apex, rigid and coriaceous; bracteoles 1.4–3 × 0.7–1.9 mm, similar to distal bracts. *Flowers* pedicellate; pedicels 1.5–2 mm long. *Hypanthium* obovate, 2–2.7 mm long. *Calyx* cylindrical, externally glabrous, light green, persistent in fruits; tube 2.2–2.8 mm long; lobes 5–6, broadly triangular, 0.7 × 1.5 mm, triangular and keeled. *Corolla* hypocrateriform, actinomorphic, white, externally glabrous; tube obconical, 6.6–6.9 mm long, base 1.4–1.6 mm diameter, apex 2.7–3 mm diameter, internally pubescent the first 2 mm toward the base; lobes 5–6, ovate, apex obtuse, 10–11.3 × 7–8 mm, glabrous. *Stamens* 5–6, alternate to corolla lobes, inserted near the base of corolla tube; filaments 2.4–3.9 × 0.3–0.4 mm, 2/3 basal part pubescent, trichomes subulate and smooth 0.2–0.3 mm long; anthers dorsifixed near the base, 3.3–4.5 × 0.8–1 mm, linear-oblong, opening by longitudinal splits. Nectary disk 1.7–1.9 mm diameter, 0.7–0.8 mm tall, glabrous. *Style* cylindrical, 2–2.6 mm long, 0.5–0.6 mm diameter, glabrous; stigmatic branches 2, 0.8–1 × 0.2–0.3 mm. *Infructescence* pendulous, 22–30 cm long. *Capsules* fusiform, 2.8–4.5 × 1–1.2 cm, with 2–4 seeds, crowned by the permanent calyx. *Seeds* fusiform, boat-shaped, slightly concave, 22–26.4 × 4.3–5.6 × 3.4–4 mm; seed coat 0.8–1 mm thick, internally hollow; embryo oblong, flattened, 10–11.8 × 2.4–3.4 × 0.7–0.9 mm.

Habitat:—*Lintersemina chucuriensis* grows in shady undercanopy of tropical forest, near streams (Figure 7).

Distribution:—*Lintersemina chucuriensis* is known from two localities in the Santander Department, Colombia, between 400 and 800 m elevation, in the lower part of the western foothills of the Cordillera Oriental, area associated with the ecoregion known as the Magdalena Medio (Figure 6). The forest at the site comprises the last remains of lowland inter-Andean rainforests in the Colombian Magdalena River valley region, and its condition consists of fragments in the matrix of paddocks and cocoa crops; most of the trees valuable for timber have been harvested (Figure 7).

Phenology:—Flowering and fruiting in February.

Suggested Conservation Status:—Critically Endangered (CR). The species is known from three collections at two locations where the forests had been highly disturbed by the extraction of timber trees and megaprojects (hydroelectric dams). Field observations indicate that *Lintersemina chucuriensis* is associated with riverine forests of small streams in areas with moderate slope of terrain, in forest undercanopy. These ecological conditions lead us to believe that the species has unique dispersal requirements and habitats that make it vulnerable to human intervention. Floristic inventories were carried out during eight days at the type locality, and less than five individuals were detected. This suggests that it is a species with low population densities. The second site where the species was reported is in the municipality of Zapatoca, which was recently completely inundated after the construction of the Hidrosogamoso dam. Other previous studies in the Magdalena Medio Region of the departments of Antioquia, Boyacá, Caldas, and Santander (e.g., Renteria 1977, Balcazar-Vargas *et al.* 2000, Cardona *et al.* 2011, David-H. *et al.* 2014, Idárraga *et al.* 2016) did not detect this species. The Area of Occupancy (AOO) of this species is less than 8.000 km², and its habitat specificity and the strong fragmentation and degradation of forests in the region makes it likely that the populations will continue to decline. Considering these conditions, we suggest the category of Critically Endangered (CR) under the following IUCN (2012, 2017) criteria: CR B 2ab (ii, iii, iv). In addition, urgent measures are recommended for *in situ* preservation and *ex situ* propagation.

Additional specimens examined - Paratypes:—COLOMBIA. Santander: El Carmen de Chucurí, vereda La Belleza, along the La Concordia Creek, area of moist tropical forest with different grades of intervention, 730 m, 6.581948°N, -73.583847°W, 20 February 2018 (fl, fr), H. Mendoza-Cifuentes, A. Celis & A. Robles 20264 (FMB, UIS, HUA); Zapatoca, vereda Belmonte, Belmonte farm, western slope of San Pedro peak, 400 m, 6.97646909°N, -73.40530391°W, 18 January 2011 (fl), J. Aguilar-Cano 1084 (FMB).

Discussion

Lintersemina is positioned in the Condamineae tribe in the Ixoroideae subfamily, based on the phylogenetic relationships inferred from cpDNA and nrDNA information. Within the Condamineae, *Lintersemina* is well supported inside a clade retrieved by Kainulainen *et al.* (2010), named the Septicidal clade. Despite its name, the authors clarify that this clade includes genera with loculicidal dehiscence such as *Parachimarrhis* and *Simira*. *Lintersemina* also has loculicidal

dehiscence and we positioned this genus as the sister taxon of the two cited genera with a high probability (0.98). The phylogenetic position of *Lintersemina* clearly shows that it is close to loculicidal fruits inside the Condamineae, however its unique seed characters in Neotropical Rubiaceae allowed us to establish that it as a new genus.

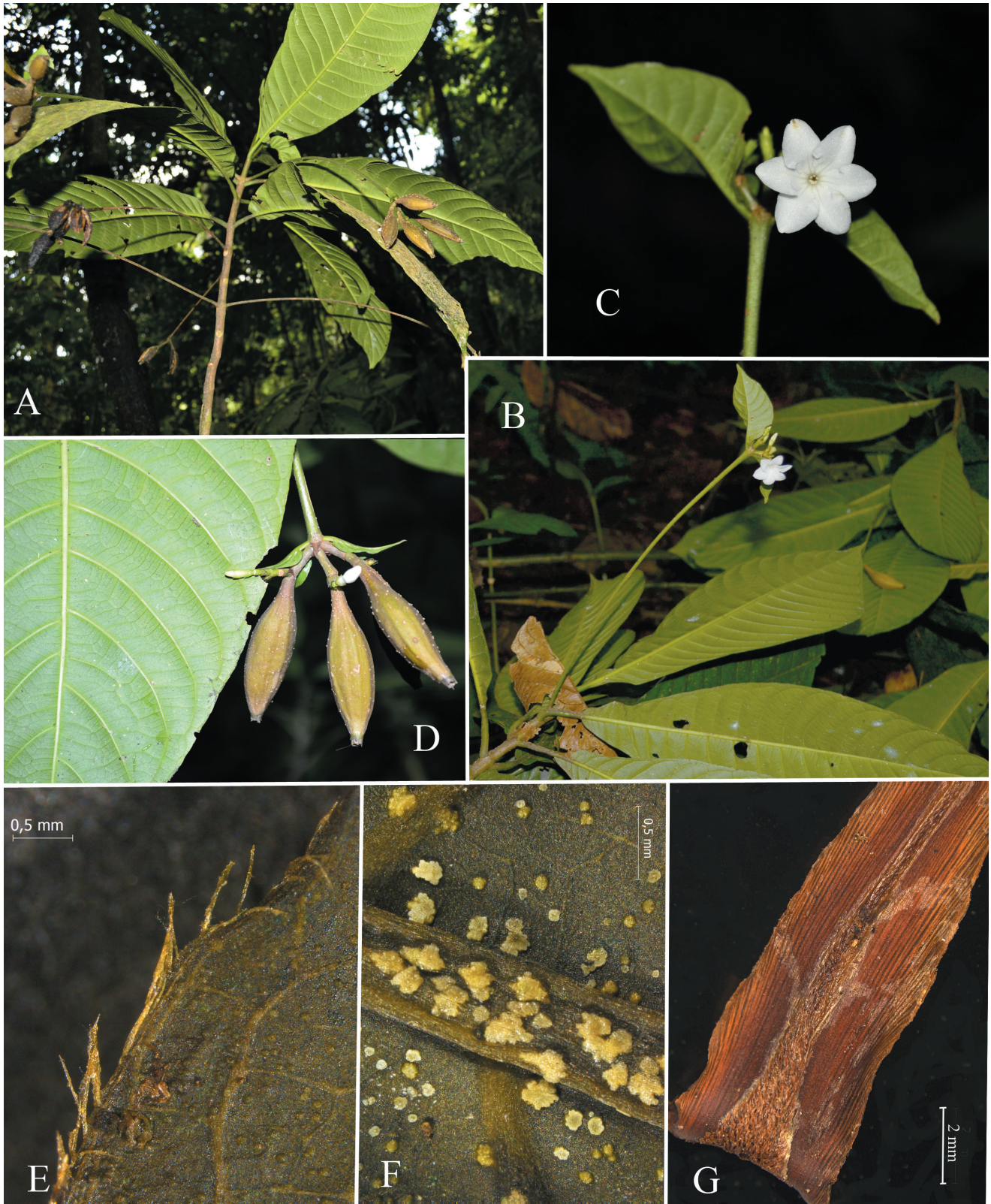


FIGURE 4. *Lintersemina chucuriensis*. **A**, habit; **B**, flowering branch; **C**, flower, front view; **D**, fruits; **E**, leaf margin (from dry material); **F**, warty bodies on abaxial leaf surface (from dry material); **G**, Stipule, adaxial surface (from dry material). Photos A, B, C, D by Angela Celis; E, F, G by Humberto Mendoza. From *Mendoza et al. 20165*.

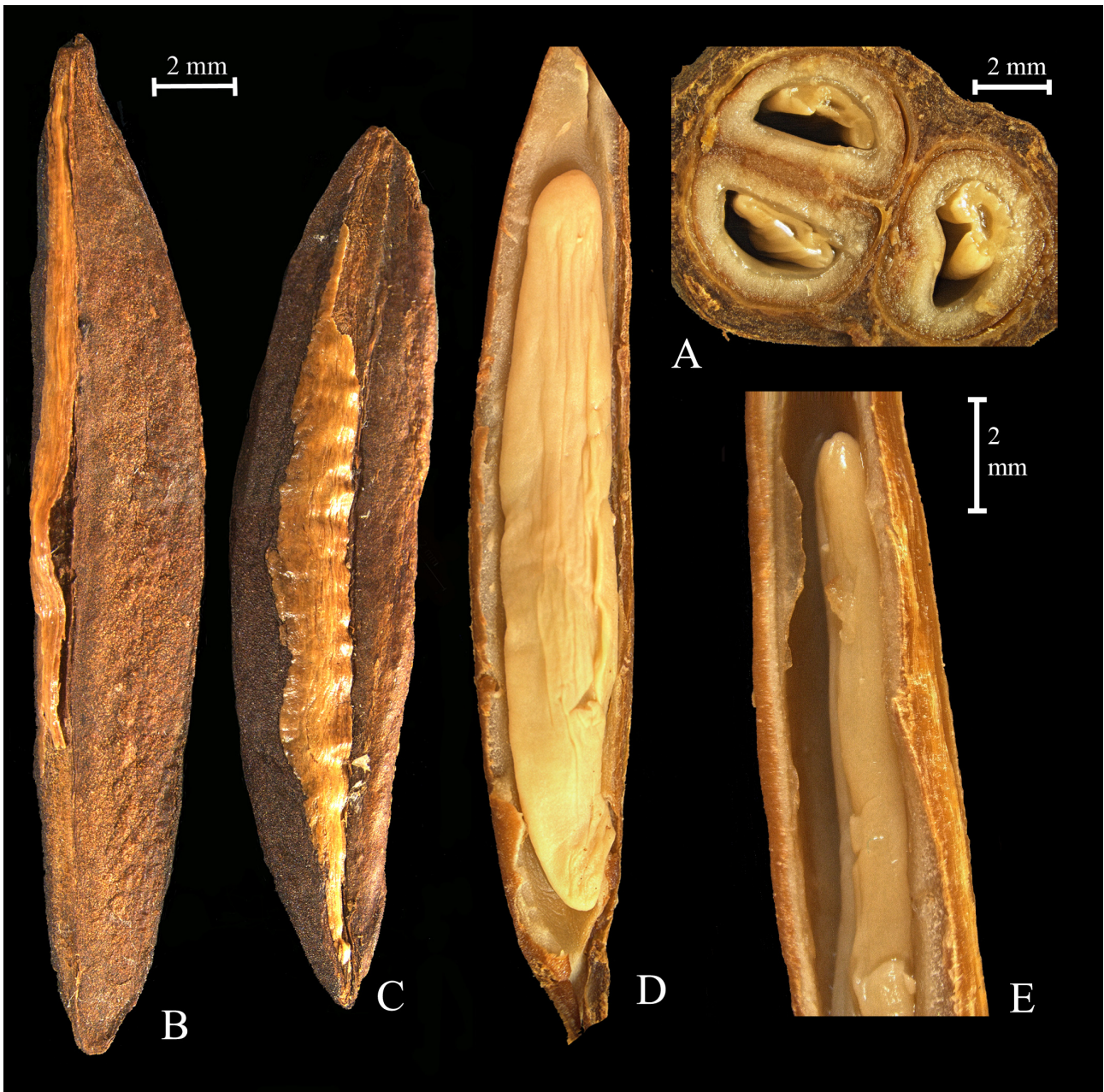


FIGURE 5. *Lintersemina chucuriensis*. **A**, cross section of capsule in the central region; **B** and **C**, seeds in lateral and ventral view; **D** and **E**, seed with partially removed pericarp. Photos by Humberto Mendoza from fresh material of *Mendoza et al. 20165* preserved in alcohol.

Taxonomy and characters

The tribe Condamineae is a monophyletic group that belongs to subfamily Ixoroideae and includes about 33 morphologically diverse genera, 10 of which monospecific, with a total of about 150 species (Kainulainen *et al.* 2010, Taylor 2016). Most of the genera are endemic to the Neotropics, but the tribe is also found in warm temperate Asia (*Emmenopterys* Oliver (1889: pl. 1823)), warm temperate North America (*Pinckneya* Michaux (1803: 103–105)), and the Pacific region (*Dolicholobium* A. Gray (1859: 308), *Mastixiodendron* Melchior (1925: 167), and *Mussaendopsis* Baillon (1879: 282)) (Taylor 2016).

The tribe is morphologically very diverse and no potential morphological synapomorphies have been detected (Kainulainen *et al.* 2010). Plants of the Condamineae are woody and range from shrubs to large trees; raphides are lacking; inflorescences are generally cymose and variously axillary and terminal; flowers are mostly hermaphroditic, protandrous or in a few genera protogynous (e.g., *Alseis*, *Chimarrhis*, *Elaeagia*); fruits are capsular or baccate, with

numerous seeds that are variously angled to flattened and winged (Taylor 2016; Table 1). Species of a number of genera have well-developed calycophylls (Delprete 2019). Several genera have quite unusual features for Rubiaceae; in particular *Dialypetalanthus* has free petals and numerous stamens in two rows, and for a long time was positioned in a distinct family (Taylor 2016).

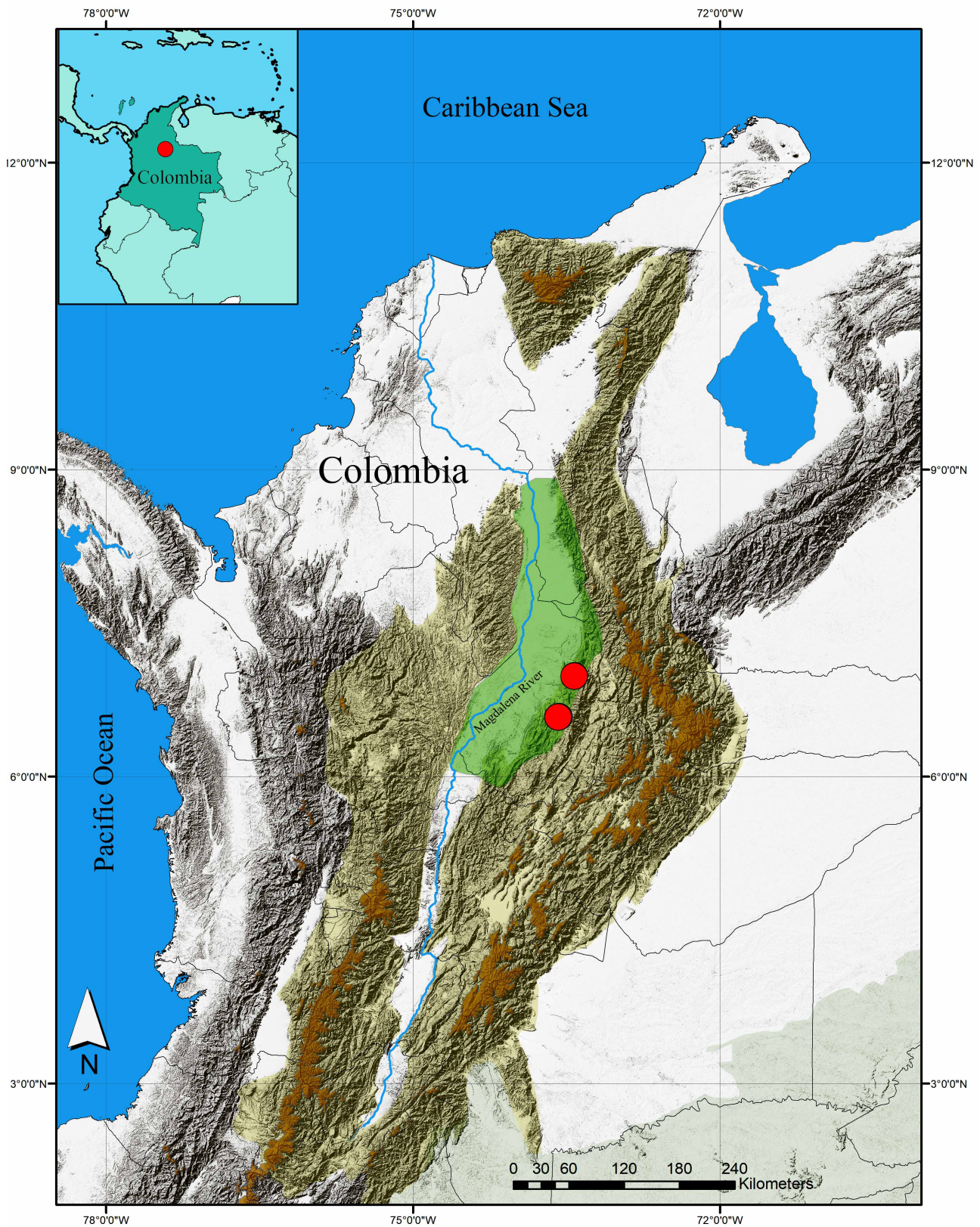


FIGURE 6. Magdalena Medio Region in Colombia (green shadow). Red dots indicate the collection localities of *Lintersemina chucuriensis*. Map made by Andres R. Acosta.



FIGURE 7. Habitat of *Lintersemina chucuriensis*. **A.** Forest interior. **B.** Edge of stream. Photos by Angela Celis

Lintersemina matches most of the general characteristics relating to the genera of the Condamineae tribe (Table 1). As in most genera of the tribe, is a treelet, although some genera of the tribe are represented by medium-sized and large trees. The interpetiolar triangular stipules (only present in the apical bud) is shared with most of the genus of the tribe so it is a character that supports its presence in the Condamineae. The presence of resin segregated by colleters on the adaxial surface of the stipule is present in 16 of the known genera for Condamineae, and it is a character present indiscriminately in several of the clades within the tribe.

The cymose inflorescences of *Lintersemina* are also a common character in the tribe with variants such as inflorescences dichotomous shortly branched, corymbiform, paniculate and spiciform. The long pedunculate, axillary, corymbose inflorescence inserted on distal nodes are shared with the genera *Chimarrhis* Jacquin (1763: 61) and *Mastixiodendron*. The corolla with contorted lobes of *Lintersemina* is shared with the genera *Capirona*, *Dolicholobium*, *Macbrideina* Standley (1929: 24), *Mussaendopsis* and *Semaphyllanthe*. The protandrous flowers are shared with 21 genera, and the included stamen with seven genera. The type of fruit in *Lintersemina* is also shared with most genera in the Condamineae; the capsular fruits are present in 19 genera of the tribe, 10 of which have loculicidal dehiscence (Table 1).

Within the Condamineae, taxa possessing fruits with numerous, small (<5 mm long), angular, ovoid or flattened seeds, with or without wings, are quite common (Table 1). Minute seeds are commonly wind-dispersed. The presence of 1–2 seeds per locule in *Lintersemina*, as well as large (> 1 cm long), naviculiform seeds are exceptional characters within the tribe, which are shared only with *Mastixiodendron* (Table 1). *Mastixiodendron* consists of 7 species occurring in Oceania, and is characterized by 4-merous flowers with nearly dialypetalous corolla, and indehiscent, baccate fruits, with large naviculiform seeds (Darwin 1977). In our phylogenetic analysis *Mastixiodendron* was not associated with *Lintersemina*, which shows that the exceptional characters of 1–2 ovules per locule and large naviculiform seeds have evolved independently within the Condamineae at least twice.

Seed morphology has been considered for a long time to be of cardinal importance in Rubiaceae systematics to the generic level (Andersson & Persson 1991, Bremer & Eriksson 1992, Delprete 1995, 1999, Andersson & Antonelli 2005). Some genera, as *Ciliosemina* Antonelli (in Andersson & Antonelli 2005: 25–26) in Cinchoneae tribe (Andersson & Antonelli 2005), have been defined, among other characters, by the features of their seeds. No genus of Neotropical Rubiaceae with capsular fruits has large naviculiform seeds, so these characters are the main morphological support for establishing *Lintersemina* as a new monospecific genus. In the tribe Psychotrieae Chamisso & Schlechtendal (1829: 4), *Coryphothamnus* Steyermark (1965: 264) is a unique Neotropical genus known with capsular fruits with 2 seeds per locule; however, its seeds are small (2.5 mm long; Steyermark 1965).

Capsular fruits with numerous seeds are considered a plesiomorphic character in the Rubiaceae while fleshy fruits are considered to be a derived character that emerged multiple times (Bremer & Eriksson 1992, Bremer & Struwe 1992). In the Condamineae indehiscent baccate fruits appear to have evolved independently at least three times (Kainulainen *et al.* 2010). The reduction of only one seed per locule is associated only with groups within the Rubiaceae when fleshy fruits occur (Bremer & Eriksson 1992), though there are exceptions, as *Coryphothamnus* and *Razafimandimbisonia* Kainulainen & Bremer (in Bremer *et al.* 2009: 765) in the tribe Psychotrieae, and *Lintersemina* in Condamineae.

TABLE 1. Morphological comparisons between *Lintersemina* and the genera in the tribe Condamineae.

Genus	No. of species	Habit	Ramification	Stipules position	Stipules form	Stick resinous exudate in vegetative buds	Inflorescence type	Inflorescence position	Flower merous	Breeding system	Aestivation	Calycophylls	Stamen insertion	Fruit type	Fruit dehiscence	Seeds number per locule	Seed type, size and form	References
<i>Lintersemina</i>	1	Shrubs	Monocaulis	Interpetiolar	Triangular	Yes	Cymose corymbiform	Lateral	5	Protandrous	Contorted	No	Inserted	Capsular	Loculicidal	1–2	Big, navicular	
<i>Alseis</i>	17	Trees	Branched	Interpetiolar	Triangular	Some spp	Spigues	Lateral	4–5	Protogynous	Imbricate	No	Exserted	Capsular	Septicidal	Numerous	Small, linear	Mendoza <i>et al.</i> 2004
<i>Bathysa</i>	10	Shrubs, trees	Branched	Interpetiolar	Triangular or calyptrate	No	Cymose paniculiform	Terminal	4–5	Protandrous	Imbricate	No, yes	Exserted	Capsular	Septicidal	Numerous	Small, angled	Germano Filho 1998, Taylor 2017
<i>Bathriospora</i>	1	Trees	Branched	Interpetiolar	Triangular	No	Cymose paniculiform	Terminal	5–6	Homostylous	Imbricate	No	Exserted	Baccate	Septicidal	2–numerous	Small, ellipsoid	Mendoza <i>et al.</i> 2004, Taylor 2015
<i>Calycophyllum</i>	10	Trees	Branched	Interpetiolar	Calyptrate	Some spp	Cymose paniculiform	Terminal	4	Homostylous, protandrous	Imbricate	No, yes	Exserted	Capsular	Septicidal	Numerous	Small, flattened winged	Andersson 1995, Mendoza <i>et al.</i> 2004
<i>Capirona</i>	2	Trees	Branched	Intrapecioliar	Triangular, deltoid	No	Cymose paniculiform	Terminal	5	Protandrous	Contorted	Yes	Inserted	Capsular	Septicidal	Numerous	Small, winged	Andersson 1995, Taylor 2015
<i>Chimarrhis</i>	14	Trees	Branched	Interpetiolar	Triangular	Some spp	Cymose corymbiform	Lateral	(4)5(6)	Protogynous	Imbricate	No, yes	Subexserted, exserted	Capsular	Septicidal	Numerous	Small, flattened, shortly winged, suborbicular or angled	Delprete 1999
<i>Condaminea</i>	2	Shrubs, trees	Branched	Interpetiolar and intrapetiolar	Triangular	Yes	Cymose corymbiform	Terminal	4–5	Protandrous	Valvate	No	Subexserted	Capsular	Septicidal	Numerous	Small, angled	Delprete 1999

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TABLE 1 (Continued)

Genus	No. of species	Habit	Ramification	Stipules position	Stipules form	Stipules exudate in vegetative buds	Inflorescence type	Inflorescence position	Flower merous	Breeding system	Aestivation	Calycohylls	Stamen insertion	Fruit type	Fruit dehiscence	Seeds number per locule	Seed type, size and form	References
<i>Dialypetalanthus</i>	1	Trees	Branched	Intrapecioliar	Triangular	No	Cymose paniculiform	Terminal	4	?	Imbricate-quinquecinal	No	Exserted	Capsular	Septicidal	Numerous	Small, winged	Piesschaert <i>et al.</i> 1997
<i>Dioicodendron</i>	2	Shrubs	Branched	interpetiolar	Wide triangular	No	Cymose paniculiform	Terminal	4	Unisexual	valvate	No	Exserted	Capsular	Septicidal	Numerous	Small, ovoid to angled	Delprete 1999
<i>Dolichodelphys</i>	1	Shrubs	Branched	Interpetiolar	Triangular	Yes	Cymose paniculiform	Terminal	5–6	Protandrous	Imbricate	No	Inserted	Capsular	Septicidal	Numerous	Small, ovoid to rhomboid	Delprete 1999
<i>Dolicholobium</i>	28	Shrubs, trees	Branched	Interpetiolar	Ovadas, triangular	No	Cymose dichasial	Lateral	4–6	Unisexual	Contorted	No	Inserted	Capsular	Septicidal	Numerous	Small, flattened to winged	Jansen & Ridsdale 1983
<i>Elaeagia</i>	16	Trees	Branched	Intrapecioliar	Cylindric, espatulate, caliptrate	Yes	Cymose paniculiform	Terminal	5–6	Protogynous	Imbricate	No	Subexserted, exserted	Capsular	Loculicidal	Numerous	Small, angled to linear	Maldonado <i>et al.</i> 2014
<i>Emmenopteris</i>	1	Trees	Branched	Interpetiolar	Triangular	No	Cymose paniculiform	Terminal	5	Protandrous	Imbricate	Yes	Inserted	Capsular	Septicidal	Numerous	Small, flattened to winged	Taylor 2015
<i>Ferdinandusa</i>	26	Shrubs, trees	Branched	Interpetiolar	Triangular	Yes	Cymose paniculiform	Terminal	4–5	Protandrous	Imbricate	No	Subexserted, exserted	Capsular	Septicidal	Numerous	Small, winged	Mendoza <i>et al.</i> 2004
<i>Hippotis</i>	12	Shrubs, trees	Branched	Interpetiolar	Triangular, ovate	Some spp	Cymose, solitary	Lateral	5	Homostylous	Valvate-reduplicate	No	Inserted	Baccate	Orbicular	Numerous	Small, ovoid to angle	Mendoza <i>et al.</i> 2014, Taylor 2015
<i>Holttonia</i>	1	Trees	Branched	Intrapecioliar	Cylindric	Yes	Cymose paniculiform	Terminal	5	Protandrous	Imbricated	No	Exserted	Capsular	Loculicidal	Numerous	Small, ellipsoids	Taylor 2015
<i>Macbrideina</i>	1	Shrubs, trees	Branched	Interpetiolar	Oblong	No	Cymose paniculiform	Terminal	5	Protandrous	Contorted	No	Inserted	Capsular	Loculicidal	Numerous	Small, angled	Mendoza <i>et al.</i> 2004
<i>Macrocneium</i>	5	Trees	Branched	Interpetiolar	Interpetiolar elliptic to obovate	Yes	Cymose paniculiform	Lateral	5	Homostylous, protandrous	Valvate-reduplicate	No	Inserted	Capsular	Loculicidal	Numerous	Small, winged	Taylor 2015
<i>Mastixiodendron</i>	7	Shrubs, trees	Branched	Interpetiolar	Triangular	No	Cymose corymbiform	Lateral	4	Protandrous	Valvate	No	Exserted	Drupaceous	Indehiscent	1–2	Big, navicular	Darwin 1977
<i>Mussaendopsis</i>	2	Shrubs, trees	Branched	Intrapecioliar	Triangular, ovate	Yes	Cymose paniculiform	Lateral	5	Protandrous	Contorted	Yes	Inserted	Capsular	Septicidal	Numerous	Very small, winged	Kainulainen <i>et al.</i> 2010

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TABLE 1 (Continued)

Genus	No. of species	Habit	Ramification	Stipules position	Stipules form	Stack resinous exudate in vegetative buds	Inflorescence type	Inflorescence position	Flower merous system	Breeding system	Aestivation	Calycophylls	Stamen insertion	Fruit type	Fruit dehiscence	Seeds number per locule	Seed type, size and form	References
<i>Parachimarrhis</i>	1	Trees	Branched	Interpetiolar	Triangular	No	Cymose corymbiform	Terminal	5	Protandrous	Imbricated	No	Exserted	Capsular	Loculicidal	Numerous	Medium, flattened, winged	Delprete 1999
<i>Pentagonia</i>	50	Shrubs, trees	Branched, monocaule	Interpetiolar	Triangular, deltoid	Some spp	Cymose corymbiform	Lateral	5–6	Protandrous	Valvate	No	Inserted	Baccate	Orbicular	Numerous	Small, angled	Mendoza <i>et al.</i> 2004
<i>Picardaea</i>	1	Shrubs, trees	Branched	Interpetiolar	Triangular	No	Cymose paniculiform	Terminal	5	Protandrous	valvate	No	Subexserted	Capsular	Loculicidal	Numerous	Small, angled	Delprete 1999
<i>Pinckneya</i>	2	Shrubs, trees	Branched	Interpetiolar	Triangular	No	Cymose paniculiform	Terminal	5	Protandrous	Valvate	Yes	Exserted	Capsular	Loculicidal	Numerous	Small, flattened, winged	Taylor 2015
<i>Pogonopus</i>	3	Shrubs, trees	Branched	Interpetiolar	Triangular, deltoid	Yes	Cymose paniculiform	Terminal	5	Protandrous	Valvate-reduplicate	Yes	Exserted	Capsular	Loculicidal	Numerous	Small, angled	Delprete 1999
<i>Rustia</i>	15	Shrubs, trees	Branched	Interpetiolar	Triangular	Some spp	Cymose paniculiform	Terminal	(4)5(6)	Protandrous	Valvate	No	Subexserted, exserted	Capsular	Loculicidal	Numerous	Small, angled or slightly flattened	Delprete 1999
<i>Schizocalyx</i>	9	Shrubs, trees	Branched	Interpetiolar	Calyptate	?	Cymose paniculiform	Terminal	5	Homostylous	Imbricate	Yes	Exserted	Capsular	Loculicidal	Numerous	Small, angled	Taylor <i>et al.</i> 2011
<i>Semaphyllanthus</i>	6	Shrubs, trees	Branched	Interpetiolar	Triangular	?	Cymose corymbiform	Terminal	4	Homostylous, protandrous	Contorted	Yes	Exserted	Capsular	Septicidal	Numerous	Small, winged	Andersson 1995
<i>Simira</i>	47	Shrubs, trees	Branched	Interpetiolar	Triangular	Some spp	Cymose paniculiform	Lateral	4–6	Protandrous	Imbricate	No	Exserted	Capsular	Loculicidal	Numerous	Big, flattened, winged	Mendoza <i>et al.</i> 2004
<i>Sommeria</i>	11	Shrubs, trees	Branched	Interpetiolar	Triangular	No	Cymose	Lateral	4–5	Homostylous	Valvate-reduplicate	No	Inserted	Baccate	Orbicular	Numerous	Small, angled	Mendoza <i>et al.</i> 2004, Taylor 2015
<i>Tammsia</i>	1	Shrubs, trees	Branched	Interpetiolar	Triangular	No	Cymose	Lateral	6	Homostylous	Valvate-reduplicate	No	Inserted	Baccate	Orbicular	Numerous	Small, angled	Taylor 2015
<i>Warszewiczia</i>	8	Shrubs, trees	Branched	Interpetiolar	Triangular	No	Cymose paniculiform	Terminal	5	Protogynous	Imbricated	Yes	Subexserted, exserted	Capsular	Septicidal	Numerous	Small, angled	Mendoza <i>et al.</i> 2004, Taylor 2015
<i>Wittmackanthus</i>	1	Trees	Branched	Interpetiolar	Short triangular	No	Cymose, racemiform to paniculiform	Terminal	(4)5(6)	Homostylous	Imbricated	Yes	Inserted	Capsular	Septicidal	Numerous	Small, winged	Mendoza <i>et al.</i> 2004, Taylor 2015

Ecological processes such as pollination by animals is strongly associated with angiosperm diversification; however, there is no relationship between diversification and dispersal mode (Eriksson & Bremer 1992). The peculiar characters of *Lintersemina*, i.e. capsular fruits with a few large seeds, can be assumed to be characters acquired as responses to ecological processes associated with seed dispersal. The dispersal mode is possibly a phenomenon of diversification in Rubiaceae, especially in tribes where capsular and baccate fruits evolved independently in different lineages.

Dispersal:—The seeds in *Lintersemina chucuriensis* have a thick seed coat and internally air spaces surrounding the embryo, conditions that allow them to float on water surface. We suggest that these seeds are dispersed by water streams, which is exceptional in Neotropical Rubiaceae, where animal or wind dispersal predominates (Bremer & Eriksson 1992). However, exceptions are found in Rubiaceae, but fairly common in rheophytic taxa as, for example, in *Augusta* Pohl (1829: 1), a rheophytic genus with seeds dispersed by wind and water currents (Delprete 1997). Water plays a limited role in the seed dispersal of land plants, but it is rather important in rheophytic plants of swamps, water courses, and shorelines (Van der Pijl 1969).

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APPENDIX 1. Taxon sampling used in phylogenetic analyses, along with GenBank sequence accession number. New sequences, provided through this research, are indicated by *. Sequences previously published were taken from the following researches: Kainulainen *et al.* (2010), Bremer & Eriksson (2009), Kainulainen *et al.* (2009), Mouly *et al.* (2009), Rydin *et al.* (2009), Samson *et al.* (2007), Alejandro *et al.* (2005), Andersson & Antonelli (2005), Delprete & Cortés-B. (2004), Lantz & Bremer (2004), Bremer *et al.* (2002), Novotny *et al.* (2002), Razafimandimbison & Bremer (2002), Backlund *et al.* (2000), Andreasen *et al.* (1999), Bremer *et al.* (1999), Oxelman *et al.* (1999), and Endress *et al.* (1996).

Supplementary information 1. ITS majority rule consensus tree with clade credibility values plot in front of nodes. *Lintersemina* taxa are labeled as HMC20165 and HMC20264.

Supplementary information 2. matK majority rule consensus tree with clade credibility values plot in front of nodes. *Lintersemina* taxa are labeled as HMC20165 and HMC20264.

Supplementary information 3. Ixoroideae subfamily in the majority rule consensus tree of rbcL marker. Values plot in front of nodes correspond to the posterior probabilities of each clade. The species *Tarenna sambucina* corresponds to the variety *buruensis*. *Lintersemina* taxa are labeled as HMC20165 and HMC20264.

Supplementary information 4. Cinchonoideae subfamily in the majority rule consensus tree of rbcL marker. Values plot in front of nodes correspond to the posterior probabilities of each clade. The species *Pausinystalia lane-polei* corresponds to the subspecies *ituriense*.

Supplementary information 5. Rubioideae subfamily in the majority rule consensus tree of rbcL marker. Values plot in front of nodes correspond to the posterior probabilities of each clade.

Supplementary information 6. Majority rule consensus tree of combined data sets (ITS, matK, and rbcL). Values plot in front of nodes correspond to the posterior probabilities of each clade. *Lintersemina* samples are labeled as HMC20165 and HMC20264.