RESEARCH ARTICLE

Integrative taxonomy recognises four species within the legume *Inga chocoensis* (Leguminosae: Caesalpinioideae)

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DOI https://doi.org/10.1002/tax.13375

Abstract The legume genus *Inga* is a significant component of Neotropical wet forests. Despite extensive study, the identities and distributions of some species remain contentious. This study focuses on the *Inga chocoensis* complex, addressing the challenges in species delimitation due to morphological similarity of closely related species. An integrative taxonomic approach was employed, combining morphological and population genetic analyses. Field and herbarium specimens of *I. chocoensis* s.l. were studied from its entire distribution range. Morphological features were documented, and DNA was extracted and sequenced from 1320 loci using a target-capture approach. Morphological analysis identified consistent differences among groups of specimens of *I. chocoensis* s.l., suggesting the presence of four distinct species. Key distinguishing features include the number and shape of nectaries on leaflets and the size and shape of fruits. Moreover, a principal component analysis and genetic ancestry admixture analysis of individuals suggest four distinct genetic groups consistent with the species delimited by morphology. Finally, a Mantel test confirms that such genetic differentiation is not due to geographic distance among populations. The four species now delimited are *I. chocoensis*, *I. coprocarpa*, and two new species described here, *I. calimensis* sp. nov. and *I. crassinectaria* sp. nov. The combination of morphological and genomic data enhanced the accuracy of species delimitation in this clade of recently diverged species. The study underscores the importance of using integrative methods to resolve taxonomic ambiguities in morphologically similar tropical tree species.

Keywords Chocó region; *Inga*; integrative taxonomy; target capture; tropical tree

Supporting Information may be found online in the Supporting Information section at the end of the article.

■ INTRODUCTION

The legume genus *Inga* Mill. (Leguminosae: Caesalpinioideae) is a common component of communities in Neotropical wet forests (Dexter & al., 2017). While there has been considerable research on *Inga*, particularly in the realms of agroforestry and insect herbivory (Brenes-Arguedas & al., 2008; Kursar & al., 2009; Marín-Gómez & al., 2016; Sinisterra & al., 2016; Coley & al., 2018), there remain important gaps in our knowledge regarding species identities and distributions despite the great contributions made on these topics by Pennington (1997). One notably underexplored region is the Chocó, renowned for its high precipitation and status as one of the world's biodiversity hotspots (Myers, 1988; Mittermeier & al., 1999; Bocanegra-González & al., 2024).

Inga species are differentiated based on combinations of several morphological characteristics including leaf lamina indumentum, leaflet number, winged or unwinged rachis, type and position of nectaries, inflorescence type, calyx and corolla size, and fruit shape (Leon, 1966; Pennington, 1997; Bocanegra-González & al., 2024). However, some of these traits are plastic and show high levels of variation within and among species, making field and herbarium identification challenging.

The most recent monograph of the genus written by T.D. Pennington (1997) compiles taxonomic, ecological and distribution data on *Inga*, covering 258 species across the

Article history: Received: 31 Jul 2024 | returned for (first) revision: 30 Sep 2024 | (last) revision received: 5 May 2025 | accepted: 6 May 2025 | published online: 10 Jun 2025 | **Associate Editor:** Domingos Cardoso | © 2025 The Author(s). *TAXON* published by John Wiley & Sons Ltd on behalf of International Association for Plant Taxonomy.
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Neotropics. Since then, 18 additional species have been described, bringing the total number of accepted *Inga* species to 276. For the Chocó region, 78 *Inga* species are recorded by Bocanegra-González & al. (2024).

One of the most common species of *Inga* in the Chocó region is *I. chocoensis* Killip ex T.S.Elias (*I.* sect. *Inga*), which is distributed from Nicaragua to Pacific Ecuador in rainforests below 500 m (Pennington, 1997). The species is easy to recognise because it has two pairs of elliptic-ovate leaflets, one set of additional nectaries on the lamina midrib of the distal leaflets and hirsute pubescence. Its inflorescences are terminal and clustered. Additionally, its fruits are coiled and pubescent. However, throughout the distribution of *I. chocoensis*, consistent differences among specimens were observed during fieldwork and visits to herbaria (K.T. Bocanegra-González, pers. obs.). These differences involve number, location and size of extrafloral nectaries, and coiled, ear-shaped versus flat or straight fruits (Fig. 1). These differences represent morphological discontinuities, which challenge the current circumscription of *I. chocoensis* (Whitehead, 1954).

Zamora Villalobos and Poveda (in Zamora Villalobos, 1990) described *Inga coprocarpa* N.Zamora & Poveda and differentiated it from *I. chocoensis* by its ear-shaped, corrugated-ribbed fruit and longer floral rachis (Fig. 1). Later, Sousa (1993) synonymised the two species, and subsequently Pennington (1997) followed this taxonomy despite doubts, especially related to fruit shape and size. In Hammel & al. (2010), Zamora Villalobos highlighted the uncertainty about the status of *I. coprocarpa*, but maintained it as a synonym of *I. chocoensis*. The decision to treat *I. chocoensis* and *I. coprocarpa* as one species may stem from the limited availability of South American collections for review. An additional reason could be that the vegetative characteristics such as the number and size of leaflets, the presence of nectaries on the midrib, and pubescence on the twigs of both species are similar. Distinguishing individuals of these species based on these vegetative characteristics is challenging, but their fruits do appear to be distinctive.

Bocanegra-González & al. (2024) identified additional consistent morphological discontinuities among individuals of *Inga chocoensis* from the central Chocó region, suggesting the potential



Fig. 1. Left, *Inga chocoensis* Killip ex T.S.Elias, *X. Cornejo, C. Bonitaz 6977* (K barcode K001475302); **Right**, *Inga coprocarpa* N.Zamora & Poveda, *C. Galdames 4322* (PMA barcode PMA20543).

existence of two new species in addition to the previously segregated *I. coprocarpa*. These putative species differ in the number and shape of the nectaries on the midrib, as well as in the shape and size of the fruits and the type of pubescence on the leaf surfaces. However, not all specimens were fertile, and many lacked fruits, which are particularly important in this group.

Species delimitation depends upon the species concept adopted, of which many have been proposed including the biological, ecological, evolutionary, and phylogenetic species concepts, among others (De Queiroz, 2007). These concepts differ in the specific criteria they emphasise for defining species, such as reproductive isolation, mate recognition systems, ecological niches, and phylogenetic relationships. De Queiroz (2007) proposed a unified species concept that integrates these alternative concepts. In this unified view, species are defined as separately evolving metapopulation lineages, emphasising that species are distinct evolutionary lineages resulting from the process of speciation (Bock, 2004; De Queiroz, 2007; Fišer & al., 2018). This is a commonly used definition and the one that we adopt here.

In this study, we employed an integrative taxonomic approach that combines morphological study of *Inga chocoensis* sensu lato (s.l.) alongside a population genetic structure analysis based on target-capture DNA sequence data. Target capture techniques allow sequencing of thousands of loci across the genome, generating a significant amount of data per individual (Peñalba & al., 2014; Maisano Delser & al., 2016). Genetic population structure analysis can aid in species delimitation by identifying patterns of genetic variation within and among populations (Knowles & Carstens, 2007; Yang & al., 2019; Franzoni & al., 2024). A population genetic approach can be useful in scenarios with many closely related, recently diverged species. This paper aims to determine the number of species in *I. chocoensis* s.l. The proposed hypothesis is that *I. chocoensis* comprises four distinct species and that genetic structure analyses support the morphological assessments.

■ MATERIALS AND METHODS

Field and herbarium work. — To determine the geographic distribution of *Inga chocoensis* s.l. (including all morphological variants), species occurrences were extracted from the Global Biodiversity Information Facility (GBIF) (Fig. 2). Seventeen specimens of *I. chocoensis* s.l. were additionally collected from six locations across the Chocó region of Colombia. Visits were made to the Buenaventura municipality in the localities of Bajo Calima (including the old and new tropical forest centres of the University of Tolima), Cajambre, and Bahía Málaga (near to Uramba Bahía Málaga National Natural Park and La Sierpe Regional Natural Park). Additional visits were made to sites in Guapi in the Department of Cauca, and Barbacoas and Tumaco in the Department of Nariño. In total, 34 specimens of *I. chocoensis* from the herbaria COL, E, F, JBB, MO, PMA, TOLI, and US, and from field collections were examined, representing the full geographic range of *I. chocoensis* s.l. (Appendix 1; Fig. 2).

Thirty-five morphological features of the specimens, both categorical and continuous, were recorded (petiole type, presence of wings on the petiole, presence of wings on the rachis, presence of appendix, pubescence type on the petiole and lamina, shape of the leaflets, shape of the leaflets apex and base, shape and location of nectaries, venation type, inflorescence type, and shape of fruits; continuous characters in suppl. Appendix S1). An analysis of variance (ANOVA) was conducted on the continuous morphological characters to determine if there were statistically significant differences among them. This analysis allowed us to assess whether the observed variations in these characters were meaningful, providing a basis for understanding the degree of morphological variation within the sample set.

DNA extraction and sequencing. — Twenty samples of *Inga chocoensis* s.l. were used for DNA extraction (13 fresh samples from the field plus 7 herbarium samples) (Appendix 1). Approximately 0.7 grams of leaf tissue was used for DNA extraction, following the QIAGEN DNeasy Plant Kit protocol. Subsequently, library preparation was performed using the NEBNext Ultra II DNA Library Prep Kit for Illumina, followed by target enrichment with the Arbor Biosciences MYbaits protocol. The prepared libraries were then sequenced on the Illumina NovaSeq 6000 platform at the University of Exeter DNA Sequencing Facility.

A set of 1320 loci composed of 276 *Inga*-specific loci (Nicholls & al., 2015), and an additional 1044 loci designed from other taxa across the Mimosoid clade (Koenen & al., 2020) were used for downstream analyses.

Sequence alignment and single nucleotide polymorphisms (SNP) calling. — All analyses were conducted on the U.K. Crop Diversity Bioinformatics HPC Resource. Sequence quality was analysed with the software FastQC v.0.11.9 (Andrews, 2010). Reads were then filtered and trimmed using Trimmomatic v.0.39 (Bolger & al., 2014) with the following parameter settings: LEADING:28 TRAILING:28 SLIDINGWINDOW:4:30 MINLEN:36. Adapter sequences were removed from the raw reads using cutadapt v.3.1 (Martin, 2011). The trimmed sequences were mapped using SAMtools v.1.19 (Li & al., 2009) against the *Inga* loci (Nicholls & al., 2015; Koenen & al., 2020). Sequence alignment map (SAM) files generated from the alignments were converted to binary alignment map (BAM) files and sorted using SAMtools v.1.19 (Li & al., 2009).

To call the variants, the Samtools mpileup tool was used to pile up the BAM files. This examines all reads at a given position and calls variants from the reads covering that position (Danecek & al., 2011). SNPs were filtered using the following criteria: first, variants with up to 10% missing data were removed using BCFtools v.1.19. Next, VCFtools v.0.1.16 (Danecek & al., 2011) was used to remove monomorphic sites, followed by filtering with a quality score > 30 and a minimum depth > 5. Additional filtering retained only SNPs with a minor allele frequency (MAF) > 0.02, and finally, SNPs that deviated significantly from Hardy-Weinberg equilibrium (P-value < 0.1%) were excluded. DNA sequences

and alignments are available in ENA under the project code PRJEB88697.

Population structure and distance calculation. — Population structure analysis was performed using principal component analysis (PCA). Initially, SNP pruning in linkage disequilibrium was carried out using PLINK v.1.9 (Purcell & al., 2007) with the filtered VCF file. This step obtained a set of SNPs in linkage equilibrium under specific parameters. The resulting files were used to compute principal components using PLINK. Subsequently, a genetic admixture analysis was carried out using Admixture v.1.3.0 with a cross validation value = 10 (Danecek & al., 2021). Finally, a Mantel test was conducted to examine the presence of an isolation-by-distance pattern. This test evaluates the overall relationship between genetic differentiation and geographic distances. Pearson's correlation coefficient was used as the correlation method, and 999 permutations were performed to assess statistical significance.

■ RESULTS

Morphological taxonomy. — Across the 34 specimens identified as *Inga chocoensis* s.l., we found distinct morphological groups with clear discontinuities amongst them. The main features that distinguish the groups are: (1) the number and location of extrafloral nectaries, (2) the size of the nectaries on the leaflet midribs and internodes, and (3) the shape (long, coiled in spiral, flat-convex or ear-shaped and ribbed) and volume (length × width × thickness) of the fruits. ANOVA was performed exclusively on continuous characters, revealing significant variation in two traits: the diameter of internode nectaries ($F = 12.41$, $P < 0.001$), and the internal diameter of leaflet nectaries ($F = 10.73$, $P < 0.001$) (suppl. Appendix S1). Further, these morphological differences are associated with the geographic area from which specimens originate. For instance, two or more pairs of extra-floral nectaries on the leaflets are only present in individuals from the

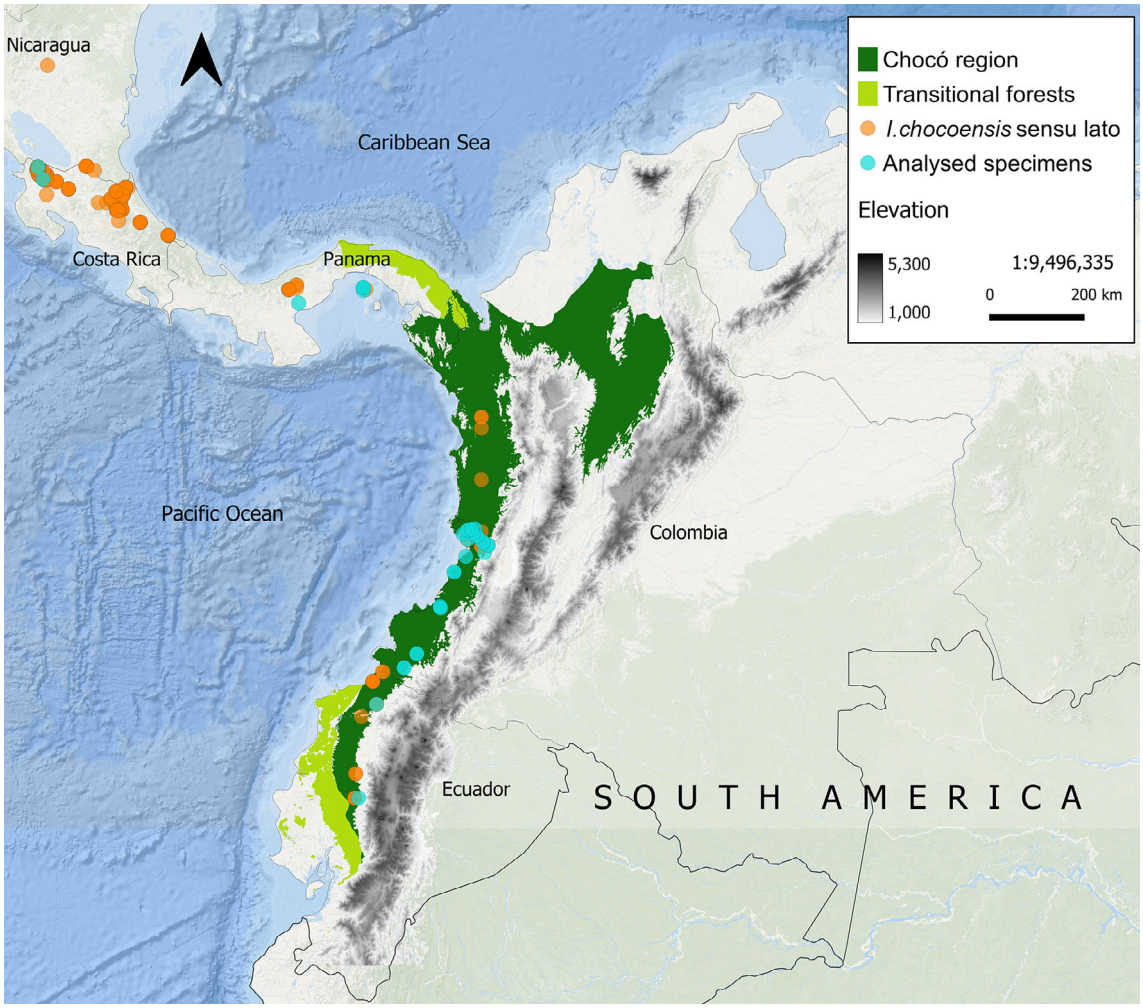


Fig. 2. Distribution of *Inga chocoensis* s.l. Orange points are records from the Global Biodiversity Information Facility (GBIF), Occurrence Download https://doi.org/10.15468/dl.x32uja. Light blue points represent specimens analysed morphologically, genetically, or both (Appendix 1). The Chocó region, along with areas at its northern and southern terminuses where the ever-wet forest of the Chocó transitions to drier forests, as proposed by Bocanegra-González & al. (2024).

central Chocó region and ear-shaped fruits only occur in the northern Chocó and Mesoamerica respectively.

Four different species were delimited based on morphology. The first is *Inga chocoensis* described by Elias (1967), of which 16 specimens were examined. The second is *I. coprocarpa*, described by Zamora Villalobos & Poveda (in Zamora Villalobos, 1990), of which seven specimens were examined. The other two species are newly described here as *I. calimensis* and *I. crassinectaria*, which are included in the population genetic analyses under those names, with four and seven accessions of each examined, respectively.

Molecular taxonomy. — After removing invariant sites, the dataset contained 5900 SNPs, and 16 of 20 accessions passed the quality controls. PCA was conducted to reduce the dimensionality of the data and visualise the variation among the different putative species. The first two principal components explained a total of 20.4% of the variation in the data, with the first principal component (PC1) explaining 11.3% and the second (PC2) explaining 9.12%. The PCA plot (Fig. 3) displays the distribution of individuals of the four proposed species in the space defined by PC1 and PC2. The individuals assigned to each species are grouped into distinct areas of this two-dimensional plot. The ancestry admixture cross-validation values are $K = 1$: 0.52; $K = 2$: 0.56; $K = 3$: 0.64; $K = 4$: 0.73; $K = 5$: 0.84; $K = 6$: 0.98, suggesting that $K = 1$ is the simplest model because it has the lowest value. However, at $K = 4$, individuals corresponding to each species form mutually exclusive groups (Fig. 4) completely congruent with the proposed morphological taxonomy. $K = 1$ is the simplest model and may reflect the recent radiation of *Inga* species, which means that they share ancestral polymorphisms, which coupled with evidence for both gene flow and extensive incomplete lineage sorting (ILS) may mean the simplest model in this context may not reflect a genetic grouping that matches real species boundaries. Regarding the Mantel test, the correlation coefficient r is very low (0.011), indicating a weak relationship of genetic and geographic distance between individuals ($P = 0.398$; see also suppl. Appendix S2).

The re-instated and new species. — The morphological and population genetic analyses support the separation of *Inga chocoensis* s.l. into four distinct species: *I. chocoensis*, distributed along the Pacific coast of the Colombian Chocó region; *I. coprocarpa* (reinstated here), distributed from the Darién Gap to Mesoamerica, and the two new species described below (*I. calimensis*, *I. crassinectaria*).

Key to species in the *Inga chocoensis* complex. — Most vegetative features of the four species are inconspicuous and difficult to distinguish by a non-expert. The combination of characteristics that is most effective for identification is the type and size of nectaries, the type of fruit, and the location.

1. One pair of nectaries in the midrib at the base of the distal leaflets 2
1. Two or more pairs of nectaries in the midrib of the distal and sometimes basal leaflets 3
2. Fruit cylindrical to irregular, ear-shaped, irregularly ribbed, ca. 12 cm long..... ***I. coprocarpa***
2. Fruit flat, convex, corrugated on the margins, ca. 15 cm long .....***I. calimensis***
3. Two or three pairs of cup-shaped nectaries 1–1.5 mm in diameter (sometimes tubular 1.8–2 mm long); fruit twisted in a spiral, sometimes coiled forming a ring, up to 35 cm long and 2–2.5 cm wide..... ***I. chocoensis***
3. Two or three pairs of thick cup-shaped nectaries 1.7–2 mm in diameter; fruit flat, convex, slightly twisted with corrugated margins, 12 cm long and 2.5 cm wide ....***I. crassinectaria***

Inga calimensis Bocanegra-González, **sp. nov.** – Holotype: COLOMBIA. Valle del Cauca, Buenaventura, Alto Anchicayá, near the hydroelectric plant, valley of Río Dagua (Tributary of the Anchicayá River), 800 m elev., 3.63 N, −76.75 W, 16 Jul 1984, *Gentry & Monsalve 48211* (COL barcode COL000189516!).

The new species is illustrated in Figs. 5 and 6.

Diagnosis. – *Inga calimensis* is similar to *I. chocoensis*, *I. coprocarpa* and *I. crassinectaria*. It can be distinguished from *I. chocoensis* and *I. coprocarpa* by its flat, convex fruit, corrugated on the margins, versus coiled in a spiral or ear-like shape. The fruit does not exceed 15 cm in length and 3 cm in width and has velvet-hirsute pubescence. It is distinguishable from *I. crassinectaria* because the nectaries in the midrib are smaller (1–1.4 mm diameter versus 1.7–2 mm diameter in *I. crassinectaria*).

Description. – Tree, up to 18 m tall. Trunk straight, bark grey, up to 50 cm diameter at breast height; twigs densely hirsute. Stipules sessile, triangular, hirsute, 5 mm long. Leaves alternate: petiole 2–7.5 cm long, marginate to winged, wings up to 0.7 mm wide, densely hirsute; rachis 6–11 cm long, winged, up to 1 cm wide; rachis appendix not present; interfoliolar nectaries cup-shaped, 1–1.4 mm diameter; additional pair of cup-shaped nectaries at the base of the midrib of the distal leaflets, 1–1.4 mm diameter, sometimes present in the basal leaflets as well and visibly smaller than the interfoliolar nectary; leaflets 2 pairs, elliptic-ovate, the basal leaflet pair 12.2–19.5 × 7.75–9.5 cm, distal leaflet pair 27–34 × 13–13.5 cm, base asymmetric, apex acuminate, reddish dense hirsute indument on both adaxial and abaxial sides; venation eucamptodromous to brochidodromous, with 9–12 pairs of secondary veins. Inflorescence not present in the analysed individuals, and flowers unknown. Fruit a flat, convex legume corrugated on the margins, ca. 15 × 3 cm, velvet-hirsute, borne singly.

Additional specimens examined. – COLOMBIA. Barbacoas, Nariño, in disturbed forest, 52.7 m elev., 1.68 N, −78.14 W, 21 Oct 2022, *Fernández-Méndez & Bocanegra-González 201* (TOLI No. 32130). Tumaco, Nariño, El Tulero, 328.6 m elev., 1.41 N, −78.38 W, 11 Nov 2022, *Fernández-Méndez & Bocanegra-González 212* & *213* (TOLI).

Distribution and habitat. – *Inga calimensis* inhabits the lowland wet forests of the central and southern Chocó region

in the departments of Valle del Cauca, Cauca, Nariño in Colombia and Esmeraldas Province in Ecuador. It occurs sympatrically with *I. chocoensis* and *I. crassinectaria*.

Phenology. – Flowering time unknown. Collected with fruit in July

Elevation. – Up to 330 m a.s.l.

Etymology. – The specific epithet "*calimensis*" derives from the Bajo Calima region in the municipality of Buenaventura, where the author first observed the species and noted distinct differences in its fruits.

Inga crassinectaria Bocanegra-González, **sp. nov.** – Holotype: COLOMBIA. Valle del Cauca, Buenaventura, Bajo Calima Km 7 vía Bahía Málaga–Las Brisas, 55 m elev., 3.98958 N, −77.060297 W, 25 Jun 2021, *Fernández-Méndez & Bocanegra-González 217* (E barcode E01080756!; isotype: TOLI No. 32111!).

The new species is illustrated in Figs. 7–9.

Diagnosis. – *Inga crassinectaria* is vegetatively similar to *I. chocoensis*, *I. coprocarpa* and *I. calimensis*. It can be distinguished from *I. chocoensis* and *I. coprocarpa* by its straight, partially convex fruit not exceeding 13 cm in length and 2–2.5 cm in width, covered by reddish-brown, abundant indumentum. *Inga crassinectaria* frequently has 2 or 3 sets of additional cup-shaped nectaries, which differ from those of *I. chocoensis* that are short stalked or tubular-shaped (up to 2 mm long) and with a slightly expanded head (up to 0.8 mm), and which are situated in the midrib of both the distal and more basal leaflets.

Description. – Tree to 18 m tall. Trunk straight, bark grey, up to 35 cm diameter at breast height, twigs quadrangular, densely hirsute. Stipules sessile, triangular, 5.5 mm long, hirsute; leaves alternate, petiole up to 3–4 cm long, quadrangular, semiterete, sometimes winged to 2 cm wide, hirsute; rachis channelled, 4.5–8.5 cm long, winged up to 2 cm wide; foliar appendix present at end of rachis; inter-foliolar nectaries

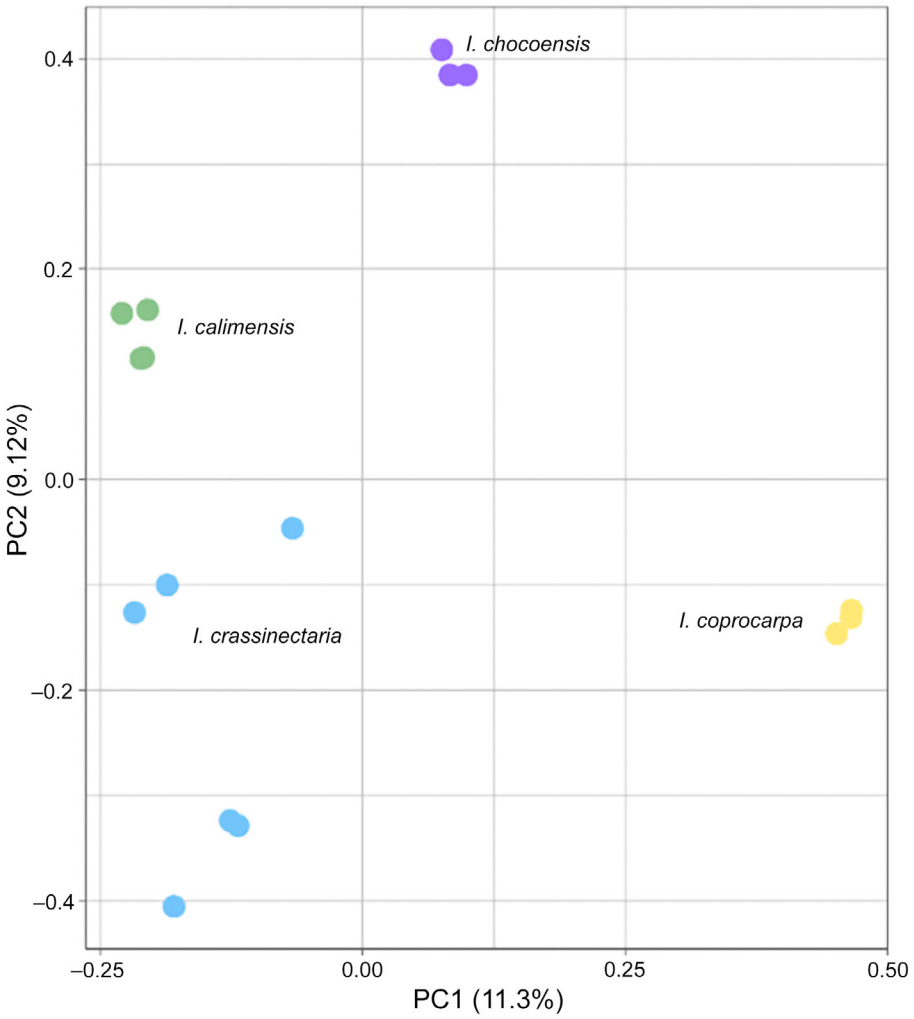


Fig. 3. Principal component analysis of population genetic diversity in *Inga chocoensis* s.l. (N = 16). In colours, the four proposed species. All yellow points corresponding to *I. coprocarpa* are from Central America, while the other points, belonging to *I. chocoensis*, *I. calimensis*, and *I. crassinectaria* are from Colombia.

cup-shaped, up to 1.7–2 mm diameter; two to three pairs of nectaries in the midrib of the distal leaflets and sometimes more basal leaflets, up to 1.7–2 mm diameter with thick edges, sometimes bigger than the inter-foliolar nectaries; leaflets 2 pairs, elliptic-ovate, the basal leaflet pair 10–15 × 5.3–7 cm, distal leaflet pair 19–29 × 10–14 cm, densely hirsute on both adaxial and abaxial surfaces, base asymmetric, apex apiculate; venation eucamptodromous to brochidodromous, with 10–14 pairs of secondary veins. Inflorescence axillary, clustered at the shoot apex, almost umbellate, axes densely hirsute; peduncle up to 3–3.5 cm long, floral rachis to 2–3 cm long; floral bracts 2.4–3 mm long, calyx 6–7.8 mm long; corolla 1.4–1.6 cm long, stamens >60; staminal tube 28 mm long. Fruit a flat, convex legume with corrugated margins, ca. 13 × 2.5 × 1.5 cm, with reddish-brown hirsute indumentum.

Additional specimens examined. – COLOMBIA. Bahía Málaga, Buenaventura, Valle del Cauca, 18 m elev., 4.05 N, −77.16 W, 2 Nov 2022, *Fernández-Méndez & Bocanegra-González 155* (TOLI 31386, 31387). Cajambre, Buenaventura, Valle del Cauca, 3.53 N, −77.19 W, 3 Sep 2021, *Fernández-Méndez & Bocanegra-González 99* (E01080747, TOLI 31329).

Distribution and habitat. – *Inga crassinectaria* has been recorded in the lowland wet forests of the central Chocó region of Colombia, in the Departments of Valle del Cauca and Cauca, in the localities of Bajo Calima, Bahía Málaga and Cajambre and Guapi. It occurs sympatrically with *I. chocoensis* and *I. calimensis*.

Elevation. – Up to 80 m a.s.l.

Phenology. – Collected with flowers and fruits in June and July.

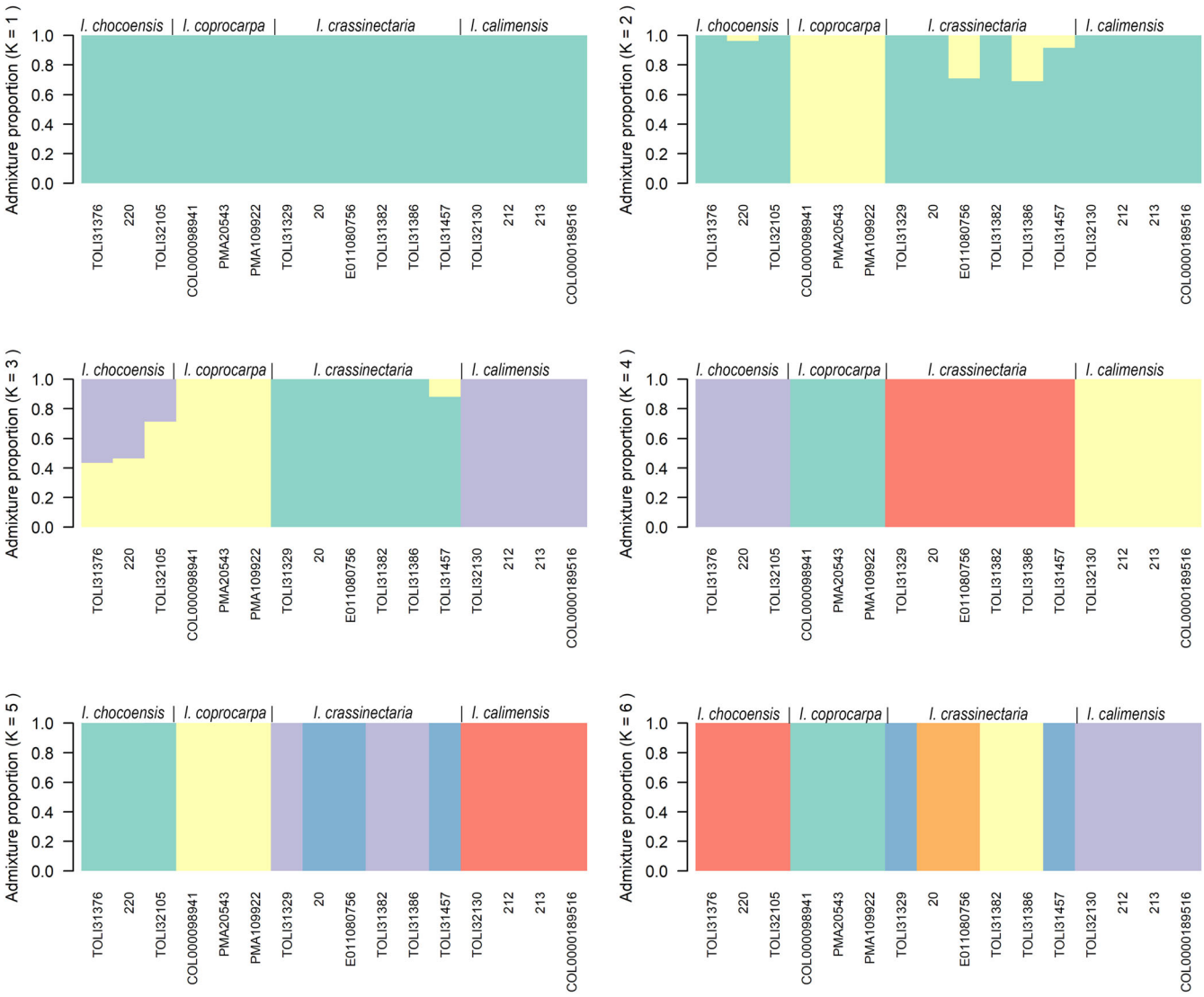


Fig. 4. Admixture analysis. *K* represents the number of genetic clusters. Sample codes and their corresponding herbarium accession numbers in Appendix 1.

Etymology. – The specific epithet "*crassinectaria*" refers to its multiple, thick nectaries in the leaflet midribs.

■ DISCUSSION

Here, using an integrative taxonomy approach, we recognise four species within the *Inga chocoensis* complex: (1) *I. chocoensis*, (2) *I. coprocarpa*; and two new species from the Chocó region, (3) *I. calimensis* and (4) *I. crassinectaria*. In this context, integrative taxonomy helped to delimit the hidden diversity of *I. chocoensis* s.l. The combination of morphological assessments and a population genetic structure analysis increased rigour in our species delimitation (Padial & al., 2010; Schlick-Steiner & al., 2010), and helped identify and define the new species.

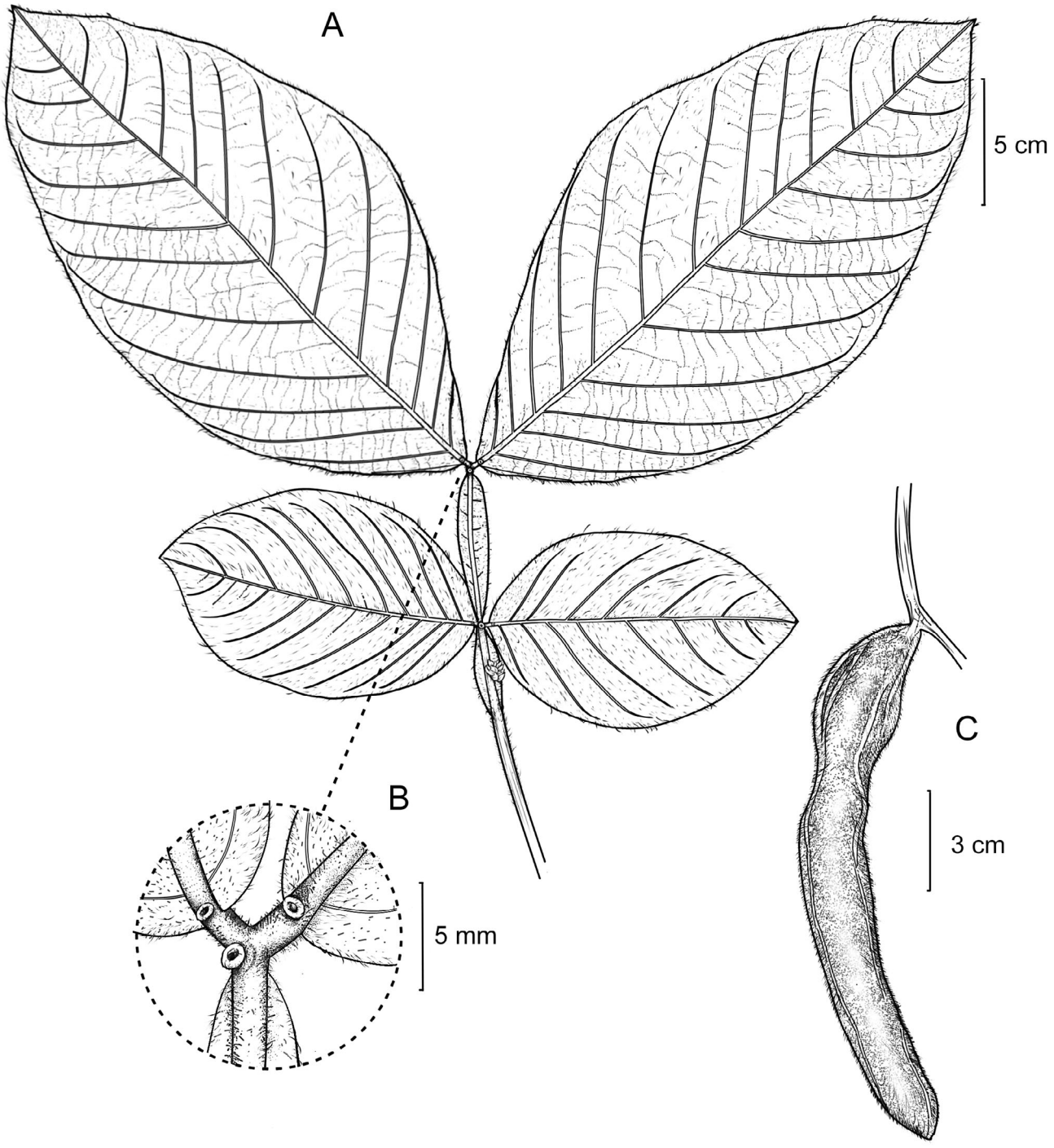


Fig. 5. *Inga calimensis*. **A**, Adaxial side of the leaf; **B**, Internode and midrib nectaries on the adaxial side of the leaf; **C**, Dry fruit. — Drawings: Manuel Montoya; based on COL000189516 and TOLI 32130 specimens.

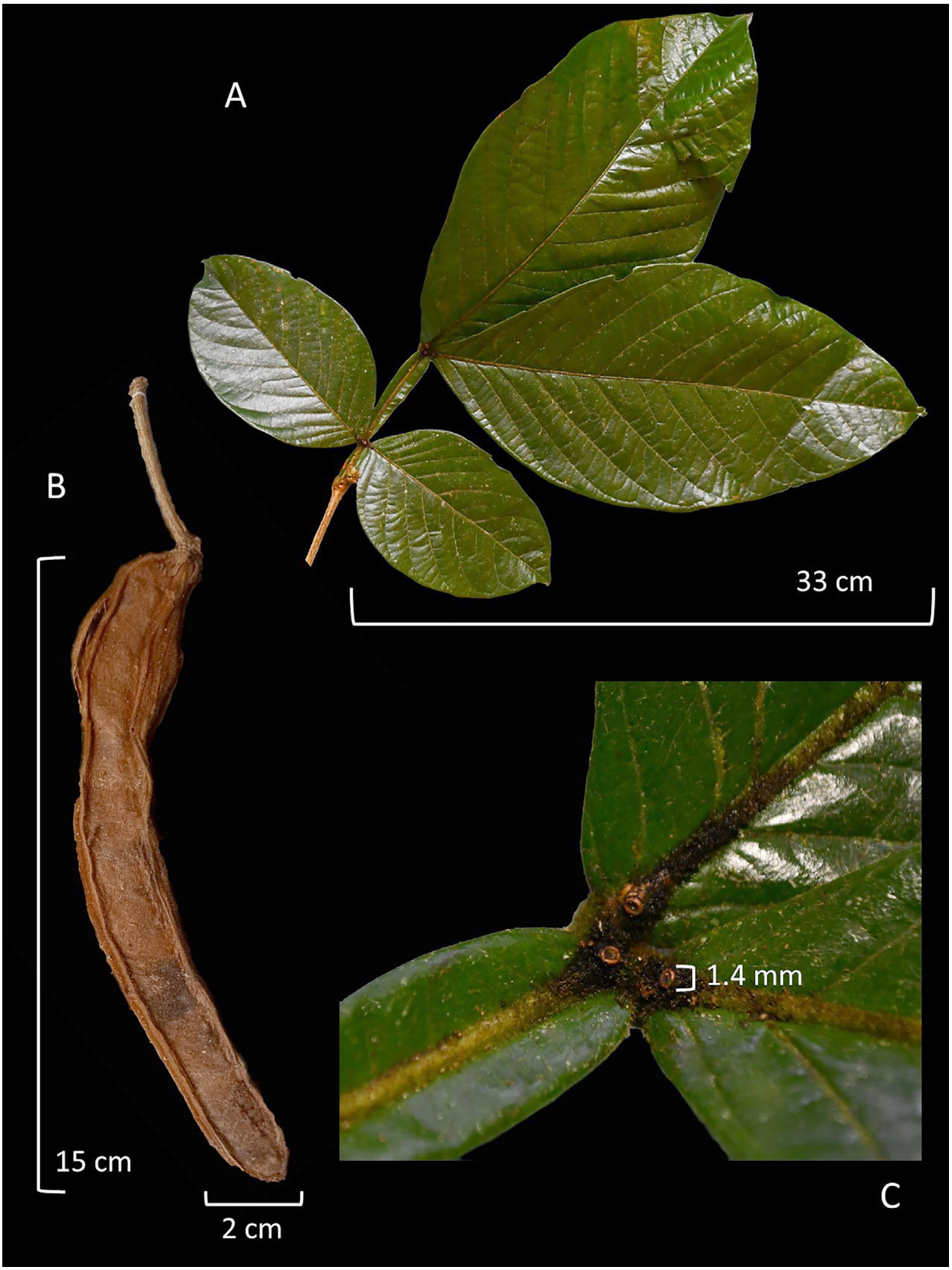


Fig. 6. *Inga calimensis*. **A**, Adaxial side of the leaf; **B**, Dry fruit; **C**, Internode and midrib nectaries. — Photos: K.T. Bocanegra-González; based on COL000189516 and TOLI 32130 specimens.

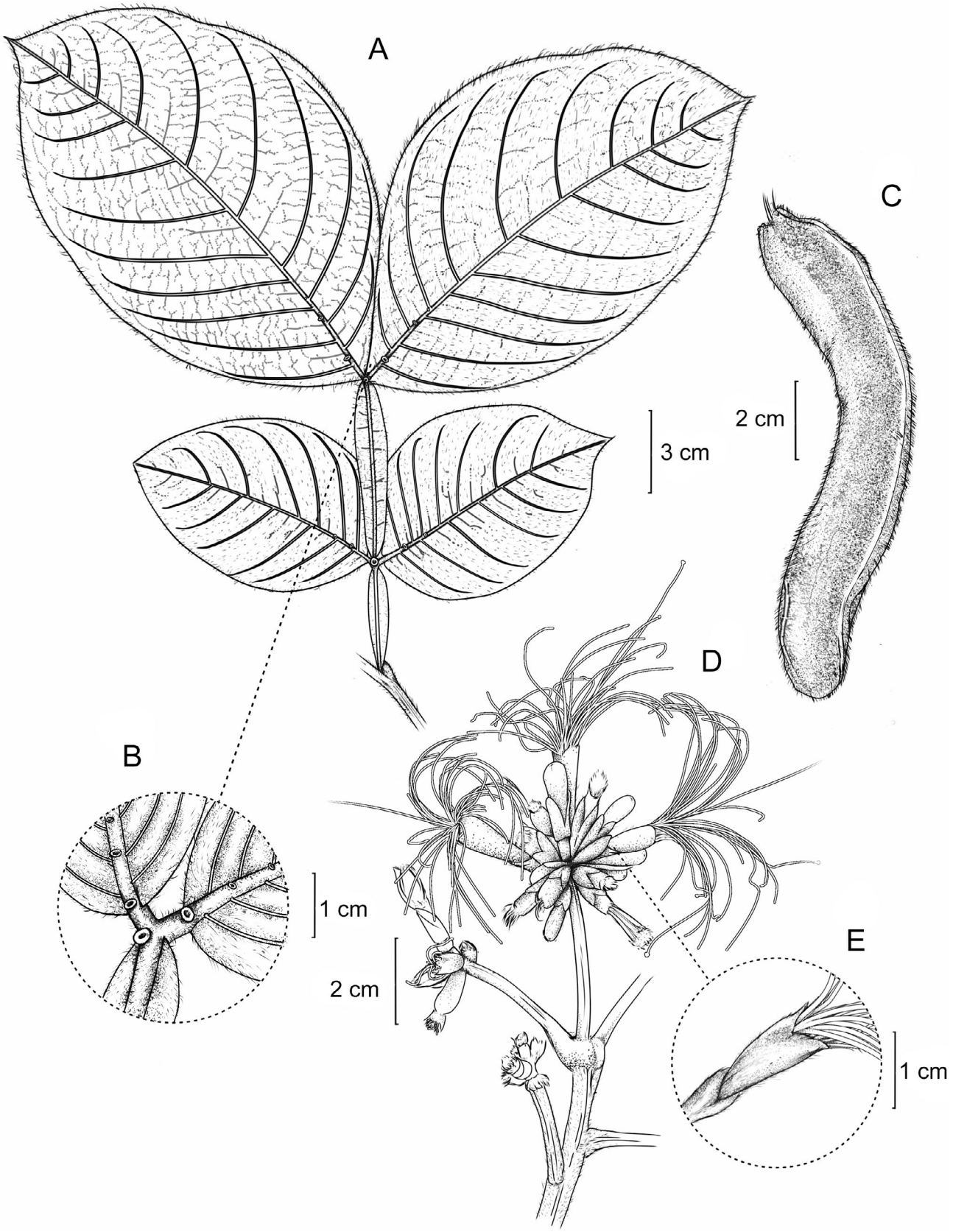


Fig. 7. *Inga crassinectaria*. **A**, Adaxial side of the leaf; **B**, Internode and midrib nectaries; **C**, Fruit; **D**, Inflorescence; **E**, Close-up of calyx. — Drawings: Manuel Montoya. Based on TOLI 32111, E01080747, and E01080756 specimens.

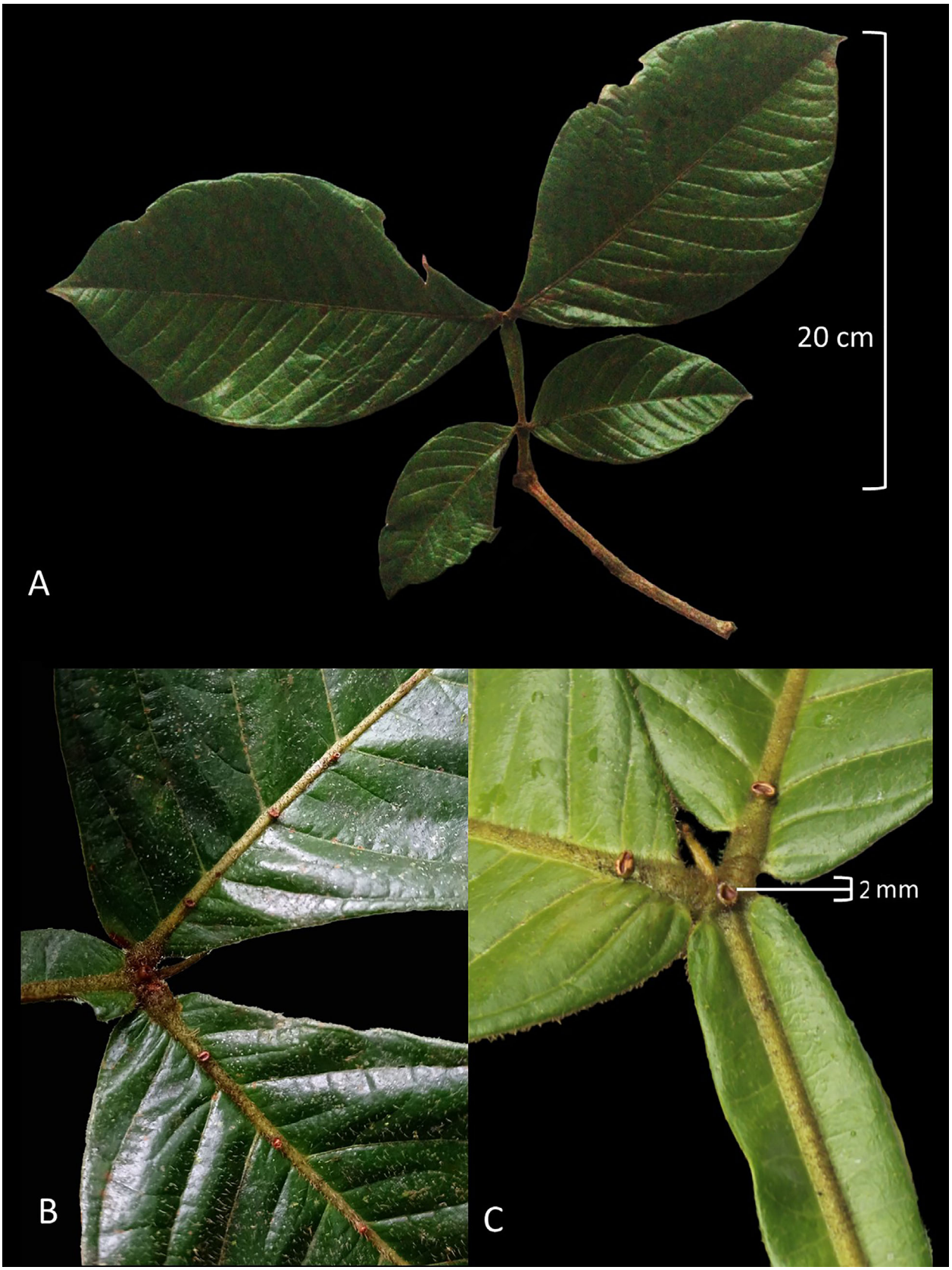


Fig. 8. *Inga crassinectaria*. **A**, Adaxial side of the leaf; **B** & **C**, Internode and midrib nectaries. — Photos: K.T. Bocanegra-González; based on TOLI 32111, E01080747, and E01080756 specimens.

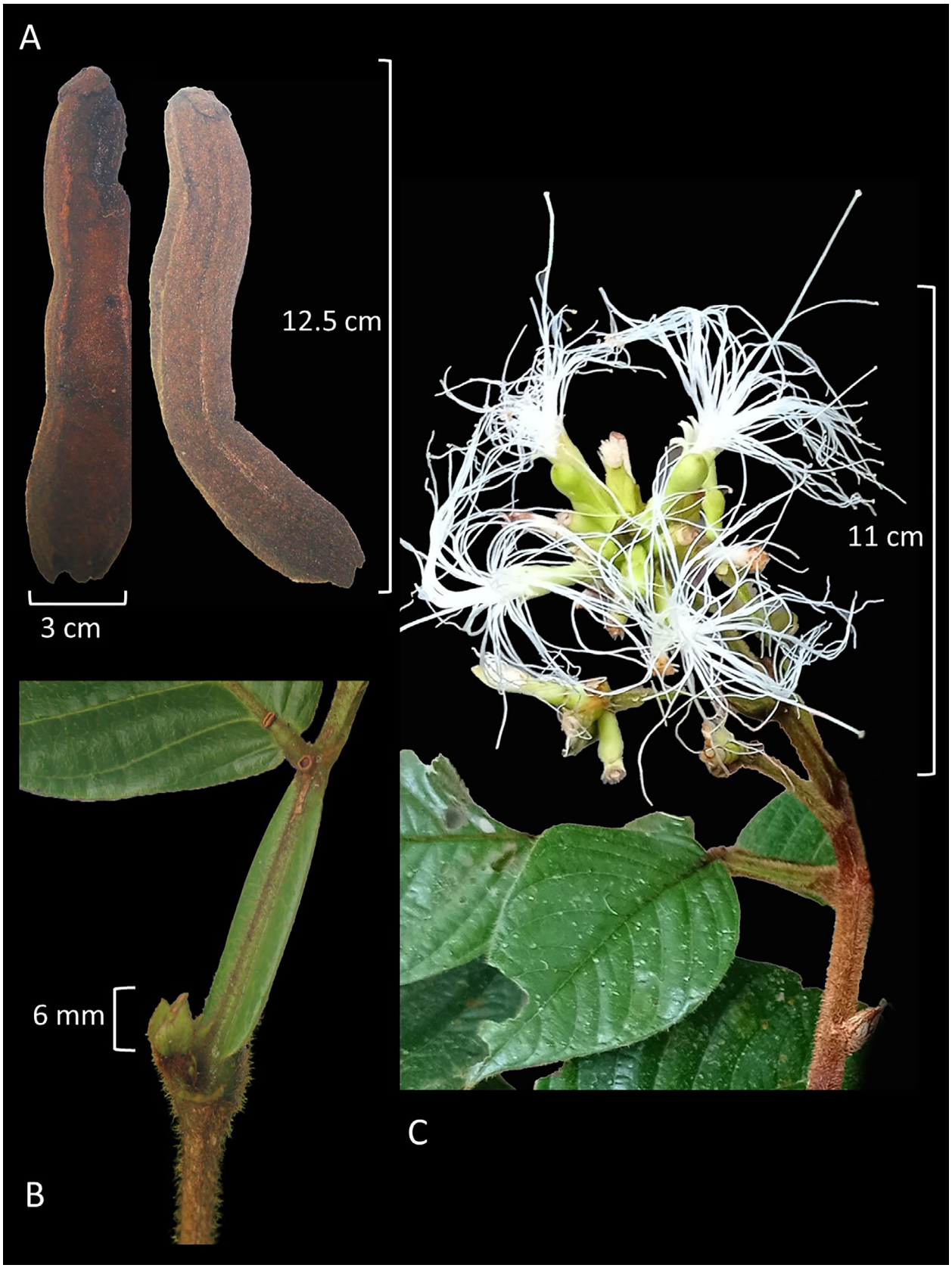


Fig. 9. *Inga crassinectaria*. **A**, Fruit; **B**, Stipule, petiole, and base of the internal leaflets; **C**, Inflorescence. — Photos: K.T. Bocanegra-González; based on TOLI 32111, E01080747, and E01080756 specimens.

The four species are vegetatively similar. The number of leaflets is always two in all species, with generally hirsute indumentum on the leaves and twigs, though tomentose on the leaves of *Inga coprocarpa*. They all have extrafloral nectaries in the midrib of the leaflets. Additionally, the inflorescence, where observed, is always short, axillary and clustered in the upper shoots. These similarities make correct identification difficult, even for experts, because some key vegetative characters for identification (i.e., nectary types and indument) are subtle and sometimes not clearly visible on herbarium specimens. Moreover, key features (i.e., fruits) are not always present. The four species can be identified by considering the combination of key characters outlined in the identification key (such as nectaries and fruits). However, in the absence of fruits, identifying the species becomes quite challenging, and misidentifications can be common.

In contrast to other species in the genus, where morphological variation within species has led to proposals for further species delineation (Dexter & al., 2010), such suggestions have been more cautious or reserved for *Inga chocoensis* s.l. (i.e., Hammel & al., 2010). Nevertheless, Dexter & al. (2010) demonstrated that incorrect segregation of rare morphological variants within common species and the erroneous grouping of geographically separated but morphologically similar species have occurred in *Inga*. Therefore, species delineations in the genus should integrate various sources such as morphology, DNA sequencing, and potentially, ecology. This research highlights clear morphological differentiation when species are in fruit but more subtle differentiation when in the vegetative state.

In the morphological assessment, we differentiated four distinct species, and population genetic analyses supported the genetic distinctness of four lineages, which coincide with the morphological species groups (Figs. 3, 4). The Mantel test showed a weak relationship of genetic variation with distance, which supports the correlation of our genetic groups with morphology rather than geography. The lack of relationship of genetic variation and distance may reflect the highly efficient historical dispersal and establishment of *Inga* in rain forest settings (Dexter & al., 2017; Nicholls & al., 2025) and is congruent with broader suggestions that legume tree distributions may be less dispersal limited in the rain forest than in dry forest biome (Pennington & al., 2009; Pennington & Lavin, 2016).

Future taxonomic studies should focus on flowers (which are currently unknown for *Inga calimensis*), anatomical characters, and chemistry that may allow for a deeper understanding of the differences within this species complex (Endara & al., 2018). Also, studies on the phylogenetic relationships of these species are needed as their close phylogenetic relatedness and geographic proximity provide an intriguing system for understanding speciation in this diverse and iconic tropical tree genus. Further field collecting is also needed not only to collect flowers of *I. calimensis*, but also to establish the conservation status of the species.

■ CONCLUSIONS

Multiple lines of evidence support the separation of *Inga chocoensis* into four species. As a result, *I. coprocarpa* has been reinstated, and *I. calimensis* and *I. crassinectaria* have been newly described. This work is based on an integrative species-validation approach that includes morphological analysis and the use of DNA sequence data as a basis for a population structure analyses, which support the separation of these species within the *I. chocoensis* complex.

■ AUTHOR CONTRIBUTIONS

KTBG conceived and initiated the research, collected samples, conducted fieldwork and wet lab work, performed data analyses, and wrote the draft of the manuscript. All other authors contributed by enhancing the data analysis, providing herbarium materials, and editing the manuscript.

■ ACKNOWLEDGMENTS

The authors thank the Chocó region communities that participated in the fieldwork. We also thank the herbaria COL, JBB, PMA, TOLI, UDBC, and E. We thank Dr. Nelson Zamora for his taxonomic advice and *Inga coprocarpa* pictures. This study was funded by the Ministry of Science and Technology of Colombia (MinCiencias), and the Davis Expedition Fund from the University of Edinburgh.

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Appendix 1. *Inga chocoensis* Killip ex T.S.Elias s.l., specimens reviewed.

Species s.str., country, department/province, municipality, elevation (m.a.s.l.), latitude longitude, collection date, collector(s) + collection number (herbarium code), ENA code. *accessions used in molecular analysis.

Inga calimensis Bocanegra-González, Colombia, Valle del Cauca, 800 m.a.s.l., 3.6333333 -76.75, 16 Jul 1984, *Gentry A.H., Monsalve M. 48211* (COL, COL000189516), ERS24002523; ****Inga calimensis*** Bocanegra-González, Colombia, Nariño, Barbacoas, 52.7 m.a.s.l., 1.685697 -78.143096, 21 Oct 2022, *Fernández-Méndez, Bocanegra-González 201* (TOLI, 32130), ERS24002508; ****Inga calimensis*** Bocanegra-González, Colombia, Nariño, Tumaco, 328.6 m.a.s.l., 1.418292 -78.386438, 27 Oct 2022, *Fernández-Méndez, Bocanegra-González 212* (TOLI), ERS24002505; ****Inga calimensis*** Bocanegra-González, Colombia, Nariño, Tumaco, 328.7 m.a.s.l., 1.417555 -78.385806, 27 Oct 2022, *Fernández-Méndez, Bocanegra-González 213* (TOLI), ERS24002506; ***Inga chocoensis*** Killip ex T.S.Elias, Colombia, Valle del Cauca, Buenaventura, 2.5 m.a.s.l., 3.253907 -77.4235, 01 Mar 1943, *Cuatrecasas J. 14319* (F, V0160533F); (US, 02187446); ***Inga chocoensis*** Killip ex T.S.Elias, Colombia, Valle del Cauca, Buenaventura, 25 m.a.s.l., 08 Feb 1944, *Cuatrecasas J. 16098* (F, V0160534F); (US, 02187444); ***Inga chocoensis*** Killip ex T.S.Elias, Colombia, Valle del Cauca, Buenaventura, 50 m.a.s.l., 4.075851 -77.080969, 10 Mar 1944, *Cuatrecasas J. 16372* (COL, COL000001624); (F, V0058140F, V0058148F; US, 00061254); ***Inga chocoensis*** Killip ex T.S.Elias, Colombia, Chocó, 5–50 m.a.s.l, 12–14 Mar 1944, *Cuatrecasas J. 16913* (US, 2187443); ***Inga chocoensis*** Killip ex T.S.Elias, Colombia, Valle del Cauca, Buenaventura, 3.88658 -76.89346, 21 May 1946, *Cuatrecasas J. 21169* (F, V0160532F); (US, 02187441); ***Inga chocoensis*** Killip ex T.S.Elias, Colombia, Valle del Cauca, Buenaventura, 50 m.a.s.l., 4.0333333, -76.2500000, 16 Dec 1985, *Gentry A.H. 53385* (MO, MO-1212569); ***Inga chocoensis*** Killip ex T.S.Elias, Ecuador, Esmeraldas, 4 m.a.s.l., -1.08333 -78.93333, *Little E.L., Dixon R.G. 21023* (MO, MO-717701); ***Inga chocoensis*** Killip ex T.S.Elias, Colombia, Valle del Cauca, Buenaventura, 130 m.a.s.l., 3.82805 -76.86944, Jan 1996, *Wilson D.A. 4596* (MO, MO-1212568); ***Inga chocoensis*** Killip ex T.S.Elias, Ecuador, Esmeraldas, 5 m.a.s.l., 1.11 -79.01, 02 Mar 2000, *Cornejo, C. Bonitaz 6967* (K, K001475302); ****Inga chocoensis*** Killip ex T.S.Elias, Colombia, Valle del Cauca, Buenaventura, 16 m.a.s.l., 4.062558 -77.163232, 15 Nov 2021, *Fernández-Méndez, Bocanegra-González 153* (TOLI, 31382), ERS24002511; ***Inga chocoensis*** Killip ex T.S.Elias, Colombia, Valle del Cauca, 42.5 m.a.s.l., 12 Dec 2021, *Cuatrecasas J. 17643* (US, 2187442); ***Inga chocoensis*** Killip ex T.S.Elias, Colombia, Cauca, Guapi, 9.8 m.a.s.l., 2.596242 -77.70135, 12 Dec 2021, *Fernández-Méndez, Bocanegra-González 215* (TOLI, 32103); ****Inga chocoensis*** Killip ex T.S.Elias, Colombia, Cauca, Guapi, 20.2 m.a.s.l., 2.562139 -77.68008, 01 Nov 2022, *Fernández-Méndez, Bocanegra-González 220* (TOLI), ERS24002509; ****Inga chocoensis*** Killip ex T.S.Elias, Colombia, Cauca, Guapi, 18.1 m.a.s.l., 2.593873 -77.692141, 01 Nov 2022, *Fernández-Méndez, Bocanegra-González 222* (TOLI, 32105), ERS24002513; ***Inga chocoensis*** Killip ex T.S.Elias, Colombia, Nariño, Barbacoas, 76.9 m.a.s.l., 1.68877 -78.142115, 02 Nov 2022, *Fernández-Méndez, Bocanegra-González 206* (TOLI); ****Inga chocoensis*** Killip ex T.S.Elias, Colombia, Valle del Cauca, Buenaventura, 17 m.a.s.l., 3.981505 -77.247635, 14 Nov 2022 *Fernández-Méndez, Bocanegra-González 150* (TOLI, 31376), ERS24002510; ****Inga crassinectaria*** Bocanegra-González, Colombia, Valle del Cauca, Buenaventura, 61 m.a.s.l., 3.952553 -76.998851, 18 Jun 2021, *Fernández-Méndez, Bocanegra-González 20* (TOLI), ERS24002522; ****Inga crassinectaria*** Bocanegra-González, Colombia, Valle del Cauca, Buenaventura, 69 m.a.s.l., 3.940167 -76.984422, 18 Jun 2021, *Fernández-Méndez, Bocanegra-González 25* (E, E01080747), ERS24002523; ****Inga crassinectaria*** Bocanegra-González, Colombia, Valle del Cauca, Buenaventura, 50 m.a.s.l., 3.98957 -77.0603, 15 Nov 2021, *Fernández-Méndez, Bocanegra-González 48* (TOLI, 31456, 31457), ERZ26868866; ****Inga crassinectaria*** Bocanegra-González, Colombia, Valle del Cauca, Buenaventura, 55 m.a.s.l., 3.98958 -77.060297, 25 Jun 2021, *Fernández-Méndez, Bocanegra-González 59* (E, E01080756), ERS24002521; ****Inga crassinectaria*** Bocanegra-González, Colombia, Valle del Cauca, Buenaventura, 55 m.a.s.l., 3.55385 -77.197696, 03 Sep 2021, *Fernández-Méndez, Bocanegra-González 99* (TOLI, 31329); (JBB, 33719), ERS24002524; ****Inga crassinectaria*** Bocanegra-González, Colombia, Valle del Cauca, Buenaventura, 17 m.a.s.l., 4.058741 -77.163058, 15 Nov 2021, *Fernández-Méndez, Bocanegra-González 155* (TOLI, 31386, 31387), ERS24002525; ***Inga crassinectaria*** Bocanegra-González, Colombia, Cauca, Guapi, 11.2 m.a.s.l., 2.574362 -77.690462, 02 Nov 2022, *Fernández-Méndez, Bocanegra-González 217* (TOLI, 32111); ****Inga coprocarpa*** Killip ex T.S.Elias, Panama, 11 Sep 1987, *Croat T.B. 67470* (PMA, PMA61626), ERS24002520; ****Inga coprocarpa*** N.Zamora & Poveda, Costa Rica, Guanacaste, 400 m.a.s.l., 11.033.333 -85.4166667, 26 May 1989, *Hammel B., Chavarría M., Herrera G., Robles R. 17415* (COL, COL000098941), ERS24002514; ***Inga coprocarpa*** N.Zamora & Poveda, Costa Rica, Guanacaste, 10.8000 -85.3167, 10 Oct 1998, *Gerardo Herrera 442* (MO, MO-128866); ****Inga coprocarpa*** N.Zamora & Poveda, Panama, Panama, Capira, 900 m.a.s.l., 8.6666666 -79.9166666, 07 Nov 1998, *Galdames C. 4322* (PMA, PMA20543), ERS24002517; ****Inga coprocarpa*** N.Zamora & Poveda, Panama, Panama, Capira, 8.7166666 -79.8666666, 05 May 2008, *De Sedas A. 741* (PMA, PMA109922), ERS24002516; ****Inga coprocarpa*** N.Zamora & Poveda, Panama, Panama, Capira, 8.716666667 -79.86666667, 22 May 2002, *Luque, D. 477* (PMA, PMA54571), ERS24002519; ****Inga coprocarpa*** N.Zamora & Poveda, Panama Coclé, 915 m.a.s.l., 8.4201897 -80.4104046, 22 Nov 2006, *Pérez R. 1676* (PMA, PMA89015), ERS24002515.