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A Common But Overlooked New Species in the Hyper-Diverse Genus *Inga* Mill. from the Northwestern Amazon

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Abstract—Inga kursarii is a new species collected in the terra firme forests of the northwestern Amazon, one of the regions with the highest tree species diversity in the world. According to morphological and phylogenetic analyses, the new species is morphologically similar and sister to *Inga gracilifolia* Ducke, but it can be distinguished by having 5–6 pairs of caducous leaflets, elliptical leaflets with acute apex and slightly asymmetrical base, spiked inflorescence, subsessile flowers, calyx tube with 4 lobes, tufts of hairs at the apex of calyx lobes, corolla tube with non-reflexed lobes, shorter staminal tubes, and capitate stigma. In addition, analyses of the chemical defensive profile (chemocoding) show that both taxa are chemically different, with *I. kursarii* having a chemistry based on gallocatechin/epigallocatechin gallates, and *I. gracilifolia* producing a series of dihydroflavonols. Finally, we present a table with a comparison of diagnostic characters that allows separation of the two species.

Keywords—Caducous, chemocoding, Ecuador, forest, phylogeny, terra firme.

Resumen—Inga kursarii es una nueva especie de árbol colectada en los bosques de tierra firme de la Amazonía noroccidental, una región caracterizada por poseer alta diversidad de especies de plantas. Se describe e ilustra este nuevo taxón y adicionalmente se discuten sus afinidades y diferencias con la especie más cercanamente relacionada *Inga gracilifolia* Ducke. Se diferencia de ésta por tener 5–6 pares de foliolos caducos y elípticos con ápice agudo y base levemente asimétrica, inflorescencia en espiga, flores sub-sésiles, tubo del cáliz con 4 lóbulos, mechones de pelos presentes en el ápice de los lóbulos del cáliz, tubo de la corola con lóbulos no recurvados, tubo estaminal más corto, y estigma capitado. Además, los análisis del perfil defensivo químico (quemo-codificación) muestran que ambos taxones son químicamente diferentes, con *I. kursarii* presentando una química basada en compuestos definidos como galatos de galocatequina / epigalocatequina, e *I. gracilifolia* produciendo una serie de dihidroflavonoles. Se incluye también una tabla con la comparación de los rasgos diagnósticos para la separación de las especies comentadas.

Palabras clave—Bosque tierra firme, deciduo, Ecuador, filogenia, quemo-codificación.

The genus *Inga* Mill. (Fabaceae) is one of the most species-rich and ecologically dominant clades in the Neotropics. This genus includes medium-sized to large trees up to 40–45 m height, although there are 5–6 species of small trees that reach 10–15 m (Pennington 1997; Pennington and Revelo 1997). Accounting for more than 300 species, this group represents one of the most documented cases of explosive and recent radiation in the Neotropics (Pennington 1997; Richardson et al. 2001; Lewis et al. 2005). Furthermore, *Inga* is one of the most species-rich groups at a local scale. For instance, 43 species coexist in a 25-ha plot in the Ecuadorian Amazon (Valencia et al. 2004). Our previous studies suggest that the adaptive radiation and the high local diversity of *Inga* might be the result of the interactions with their herbivores, probably through the diversification of their defenses, particularly secondary metabolites (Kursar et al. 2009; Coley and Kursar 2014; Endara et al. 2017).

Roughly half of all *Inga* species (ca. 160) occur in the northwestern portion of the Amazon (Ter Steege et al. 2016). This region includes the Loreto department (Peru), the Putumayo and Middle Caquetá basins (Colombia), the Ecuadorian Amazon and adjacent areas in Brazil, and harbors extraordinarily high tree and shrub diversity (Pitman et al. 2001; Valencia et al. 2004; Ter Steege et al. 2016; Guevara Andino et al. 2017). For instance, in the Ecuadorian Amazon alone, the genus *Inga* is represented by approximately 70 species (Pennington and Revelo 1997; Ter Steege et al. 2016). Most are found in terra firme forests but some specialize on temporally inundated habitats including *I. microcoma* Harms, *Inga nobilis* Willd., and *I. spectabilis* (Vahl) Willd. (Endara and Jaramillo 2011; Pitman et al. 2014). Terra firme and swamp forests are the predominant habitat types in the northwestern Amazon; these habitats cover approximately 80% and 20% of the Ecuadorian Amazon (Ministerio del Ambiente del Ecuador 2013; Pitman et al. 2014). Over the last 15 yr, we have performed long-term and large-scale floristic inventories, including terra firme, swamps, and temporarily inundated forests in different areas of the Ecuadorian and Peruvian Amazon lowlands (Pitman et al. 2008; Endara and Jaramillo 2011; Guevara Andino et al. 2017). These floristic surveys include extensive tree sampling in unexplored or poorly explored areas of both countries. After exhaustive morphological, chemical, and phylogenetic analysis, we have concluded that the species herein described and compared corresponds to a new taxon in the hyper-diverse genus *Inga.*

Materials and Methods

Since 2008, we have been researching the underlying ecological and evolutionary mechanisms for community assembly of the Amazon forests with a special emphasis on *Inga* (Kursar et al. 2009; Endara and Jaramillo

2011; Endara et al. 2017; Guevara Andino et al. 2017). As part of these studies, we made collections of *Inga* individuals in extensive tree plot inventories in Ecuador and Peru, and compared our sterile and fertile specimens with material deposited in Colombian, Ecuadorian, and Peruvian herbaria including AMAZ, COAH, COL, QAP, QCA, and QCNE; herbaria abbreviations according to Thiers (2019). In addition, we compared our specimens with those deposited in some US and European herbaria including F and K. Finally, we collected information about specimens from INPA and NY virtual herbaria.

A previously published phylogenetic reconstruction of 124 *Inga* species based on seven chloroplast regions (*rpoCI, psbA-trnH, rps16, trnL-F, trnD-T, ndhF-rpl32, and rpl32-trnL*) and the nuclear ribosomal internal transcribed spacer regions (ITS), was used to determine the closest relative of the new taxon we describe in this study (Dexter et al. 2017). The extent of occurrence (EOO) and area of occupancy (AOO) were calculated using the GeoCAT tool (Bachman et al. 2011). A principal component analysis (PCA) was performed on reproductive characters in order to determine morphological variation in relation to the closest relative to the new species.

We also performed an analysis of defense-related chemical markers via untargeted metabolomics in combination with multivariate statistics to reconstruct species-level fingerprints, which is defined as chemocoding (Endara et al. 2018). We used chemocoding to discriminate between the new taxon and its closest relative. Following methods in Endara et al. (2018), we extracted and analyzed the metabolites from five saplings from each taxon. Collection and research permits were granted by the Ministry of Environment of Ecuador, permit MAE-DNB-CM-2015–0017.

Taxonomic Treatment

Inga kursarii M.J. Endara & J.E. Guevara, ***sp. nov.*** Type: Ecuador. Parque Nacional Yasuní-ECY, Parcela de 50ha, Proyecto Dinámica del Bosque de Yasuní. Bosque húmedo tropical, áreas de tierra firme, colinado y de bajíos. Especies representativas: *Parkia nitida, Iryanthera hostmannii, Rinorea lindeniana, Iriartea deltoidea.* Árbol 30 m, sépalos verdes, estambres cremosos. Placa # 150470. 03°38′S y 76°30′ W, Alt: 200–300 m, 25 agosto 2007, fl., *A.J. Pérez & P. Alvia 3485* (holotype: QCA!; isotype: QCNE!).

Similar to *Inga gracilifolia* Ducke in possessing a flat legume and 5–6 pairs of leaflets, but differing from this species by its larger (0.9–7 × 0.4–3 cm in *I. gracilifolia*) deciduous leaflets, terete petiole, non-canaliculate rachis, foliar nectaries between leaflet pairs cyathiform, sessile, bracts lacking at the base of the inflorescence, this last with up to 20 small sessile flowers born in lax to slightly congested spike, larger corolla tube (5.5–7 mm vs. 4.7–6.3 mm in *I. gracilifolia*), and non-reflexed corolla tube lobes.

Emergent trees up to 35–40 m tall and up to 80–100 cm dbh; trunks cylindrical, external bark reddish with disperse grey irregular spots; branchlets glabrous, cylindrical, terete. Stipules 2–4 mm long, linear, caducous. Leaves alternate, paripinnate, with 6 pairs of leaflets, rarely 5, caducous; petiole 1.2–5.7 cm long, pulvinus (0.3–)0.4–1.2(–1.3) cm long, unwinged, terete and glabrous, foliar rachis non-canaliculate, unwinged, 4.4–21.5 cm long, 0.1–0.2 cm width, foliar nectaries sessile, cyathiform, 1.15–2.2 mm width; young leaves dark purple; leaflets (1.5–)2–12.1(–13) × (0.9–)1.3–4(–4.8) cm, papyraceous, subsessile, elliptical to ovate, apex acute, base obtuse and slightly asymmetrical, glabrous; secondary venation brochidodromous, prominent in the abaxial surface, slightly impressed in the adaxial surface, anastomosed 3–4 mm from the margin, green pale lustrous when live, (8) 9–10 pairs of secondary veins, ascending and forming an angle of less than 90°, numerous intersecondary veins evident and prominent on the abaxial surface, tertiary venation reticulate. Inflorescence an axillar, solitary, slightly congested spike, 20–25 flowered; peduncule 1.3–5.3 cm long, slender, glabrous, without bracts. Flowers subsessile, pedicel 0.2–0.4 mm long, flowers green-yellow when mature, 11–16.7 mm long (including exserted portion of the stamen); calyx tube green, 1–1.7 mm long, sparsely puberulent, cyathiform, slightly expanded from base to apex, 4–5 triangular lobes with tufts of small hairs at the apex; corolla tube 5.5–7 mm long, greenish yellow, glabrous and glossy, 4 triangular lobes, (0.4–)1.1–2.7 mm long, 0.4–0.5 mm wide; stamens 20–35 per flower, staminal tube white, 5.8–8 mm long and 0.6–0.7 mm wide, exserted 1.1–2.5 mm from the corolla, free filaments 5.1–7.7 mm long; ovary 1.5–1.7 mm long, 1-carpellate, glabrous, style slightly exceeding the staminal filaments, stigma head capitate, ovules ca. 25. Fruit a slender, long, and flat pod, 21.3–42.5 × 1.1–3.1 cm with cuspidate apex ca. 0.4–0.5 cm long, straight, margins strongly expanded at maturity, valves face slightly convex around seeds, covered by small lenticels, the sutures subligneous and slightly undulating around seeds, glabrous. Mature seeds not seen. Figures 1–4.

***Additional Specimens Examined*—Colombia.**—Vaupés: Mpio. Taraira, Estación Biológica Caparú, a 3 km al norte del Lago Taraira, colinas, 1°00′S, 69°49′W, 200 m., 25 agosto 1989, (fl), *S. Defler 670* (COAH, MO).—Putumayo: municipio de Mocoa, vereda San José del Pepino, Centro Experimental Amazónico (CEA), parcela permanente 2, 01°04′34.6″N, 76°37′43.5″W, 540 m, 2 marzo 2010, (fr), *J. Navarro & E. Kuiru 2366* (COAH). **Ecuador.**—Orellana: Parque Nacional Yasuní. Carretera y oleoducto de Maxus km 40. Parcela permanente de 1 hectárea. Árbol # 5.16, 00°45′S, 76°30′W, 250 m, 10–11 marzo 1994, (fr), *M. Aulestia* 1830 (QCA, QCNE); Parque Nacional Yasuní. Carretera y oleoducto de Maxus km 40. Parcela permanente #10 de 1 hectárea, 00°45′S, 76°30′W, 250 m, 10–11 marzo 1994, (fr), *M. Aulestia* 1839 (QCA, QCNE); Parque Nacional Yasuní, carretera y oleoducto de Maxus, Km 40, 00°39′S, 76°26′W, 250 m, 15–30 abril 1994, *M. Aulestia* 2173 (QCNE, MO); Orelllana Parque Nacional Yasuní, carretera y oleoducto de Maxus, Km 40, parcela permanente #10, 00°39′S, 76°26′W, 250 m, 20 julio 1994, *M. Aulestia* 2512 (QCNE, MO); Reserva Étnica Huaorani, carretera y oleoducto de Maxus en construcción km. 75–7, entre río Tivacuno y río Yasuní, 00°50′S, 76°18′W, 250 m, 17–20 febrero 1994, (fr), *M. Aulestia & O. Gonti* 1745 (QCA, QCNE, MO); Orellana, Comunidad Quichua Alta Florencia, zona de amortiguamiento del Parque Nacional Yasuní, bosque siempreverde de penillanura del Aguarico-Putumayo-Caquetá, 00°54′S, 76°26′W, *J. Guevara & H. Shiguango 1028* (QCA); Orellana, Carretera Pompeya Sur-Iro, Parque Nacional Yasuní, Km 77–79. Trocha de desbroce, 19 febrero 1994, (fr), *J. Jaramillo, X. Buitrón & M. Tapia* 16247 (QCA); Orellana, Carretera Pompeya Sur-Iro, Parque Nacional Yasuní, Km 38,4, detrás de la Estación de Monitoreo de Fauna Onkone Gare, Ecuambiente S.A., transecto C con dirección n 135° E desde el río Piraña hacia el río Tiputini, 200–220 m, 18 mayo 1994, *J. Jaramillo & X. Buitrón* 16599 (QCA); Orellana, transecto de vegetación de área de inundación temporal en la línea sísmica 9ª del Bloque 31, 00°52′S, 75°47′53″W, 250 m, 26 octubre 1997, *J. Jaramillo, I. Tapia & D. Padilla* 19546 (QCA); Estación Científica Yasuní, Km 8.2 de la carretera NPF-Tivacuno, 00°40′51″S, 76°23′12″W, 200–300 m, 13 marzo 2002, *J. Jaramillo, S. Yandún & S. Salgado* 23607 (QCA); Reserva Florística El Chuncho, 00°28′S, 77°0′W, 250 m, 3 febrero 1994, *W. Palacios 12030* (QCNE, MO); Parque Nacional Yasuní-ECY. Parcela de 50ha PDBY. 00°38′S, 76°30′W, 200–300 m, 25 febrero 2008, (fr), *A.J. Pérez & P. Alvia* 3941 (QCA); Parque Nacional Yasuní-ECY. Parcela de 50ha PDBY. 00°38′S, 76°30′W, 200–300 m, 24 septiembre 2010, (fl), *A.J. Pérez & P. Alvia* 4869 (QCA); Parque Nacional Yasuní- ECY, parcela de 50 ha, bosque siempreverde de tierras bajas del Napo-Curaray, 00°38′S, 76°30′W, 200–300 m, 27 mayo 2016, (fl), *A.J. Pérez, W. Loor & P. Alvia* 10567 (QCA); Orellana, Parque Nacional Yasuní, parcela de 50 ha, bosque siempreverde de tierras bajas del Napo-Curaray, 03°01.801′S, 77°54.932′W, 574 m, 17 julio 2014, (fl), *A. Pérez, W. Loor & P. Alvia 10567* (QCNE, QCA, F); Añangu, rain forest on well drained hilly ground in the Parque Nacional Yasuní, 00°31–32′S, 76°23′W, 260–350 m, 30 may-21 june 1982, *SEF* 9108 (AAU, QCA); Rain forest on well drained hilly ground in the Parque Nacional Yasuní, 00°31–32′S, 76°23′W, 260–350 m, 30 may-21 june 1982, *SEF* 9238 (AAU, QCA); Provincia de Orellana, Estación

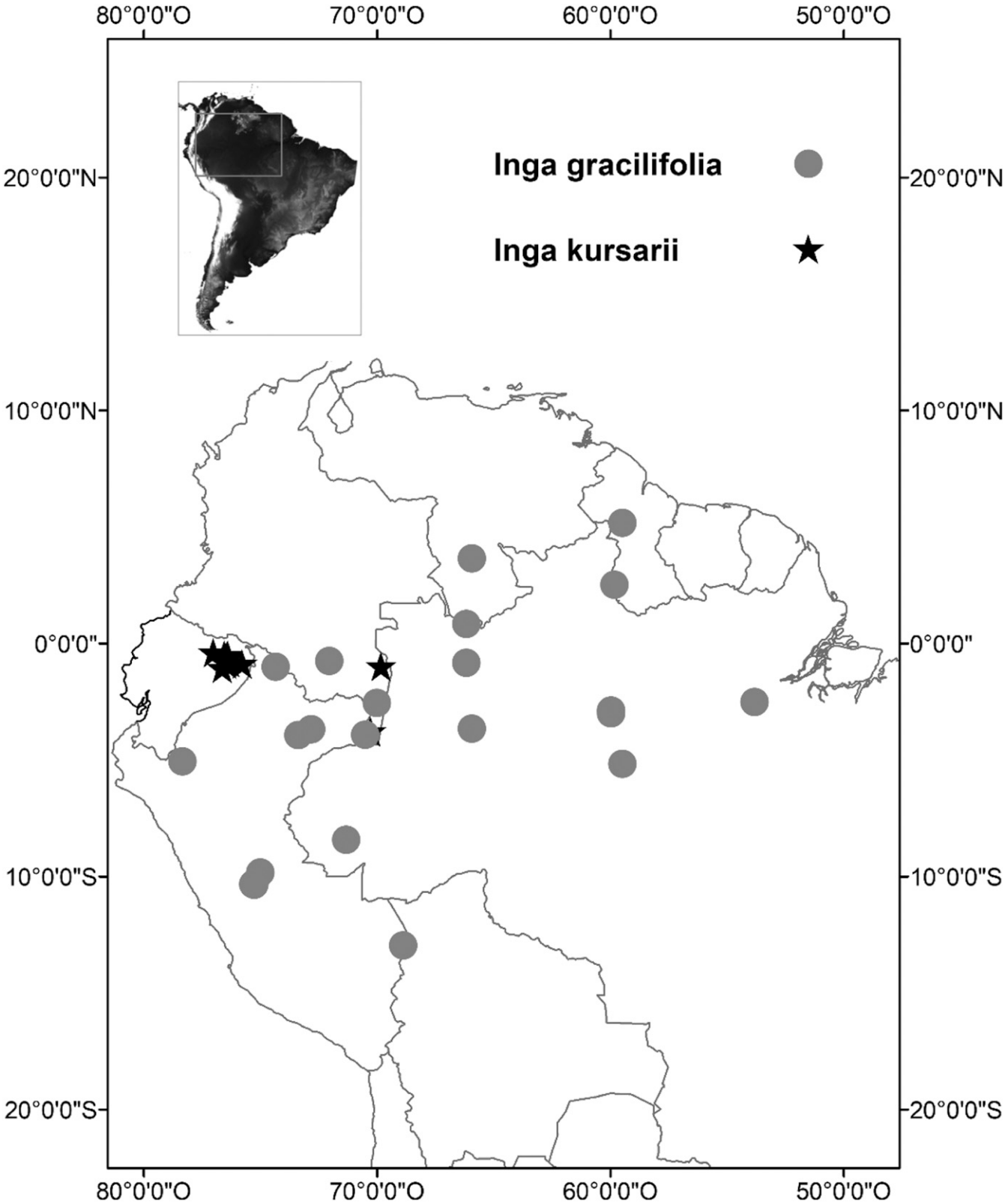

FIG. 1. Map of collections of *Inga kursarii* M.J. Endara & J.E. Guevara sp. nov. and its sister species, *Inga gracilifolia* Ducke, in the Amazon basin.

Científica Yasuní, río Tiputini, al noreste de la confluencia con el río Tivacuno, este de la carretera Repsol-YPF, km 7.9 desvío hacia el pozo Tivacuno, al margen derecho de la carretera, 00°38′S, 76°30′W, 200–300 m, 4 abril 2002, (fr), *G. Villa & P. Alvia* 1439 (QCA); Cantón Orellana, Parque Nacional Yasuní, carretera y oleoducto de Maxus en construcción, km 18–20, río Shipati, 00°32′S, 76°31′W, 250 m, 15 marzo 1993, *J. Zuleta* 302 (QCNE, MO).—MORONA SANTIAGO, Cantón Tiwintza, Centro Shuar Kaputna, cumbre del Cerro Kampa Naint, bosque siempreverde sobre mesetas de areniscas de la cordillera del Cóndor en la baja Amazonía ecuatoriana, 03°01′38″S, 77°54′50″W, 460 m, 13 abril 2011 (QCA, QCNE). **Peru.**—LORETO: Sabalillo Research Station, 3°20′3″S, 72°18′6″W, 150–180 m, *K. Dexter 813* (AMAZ, K).

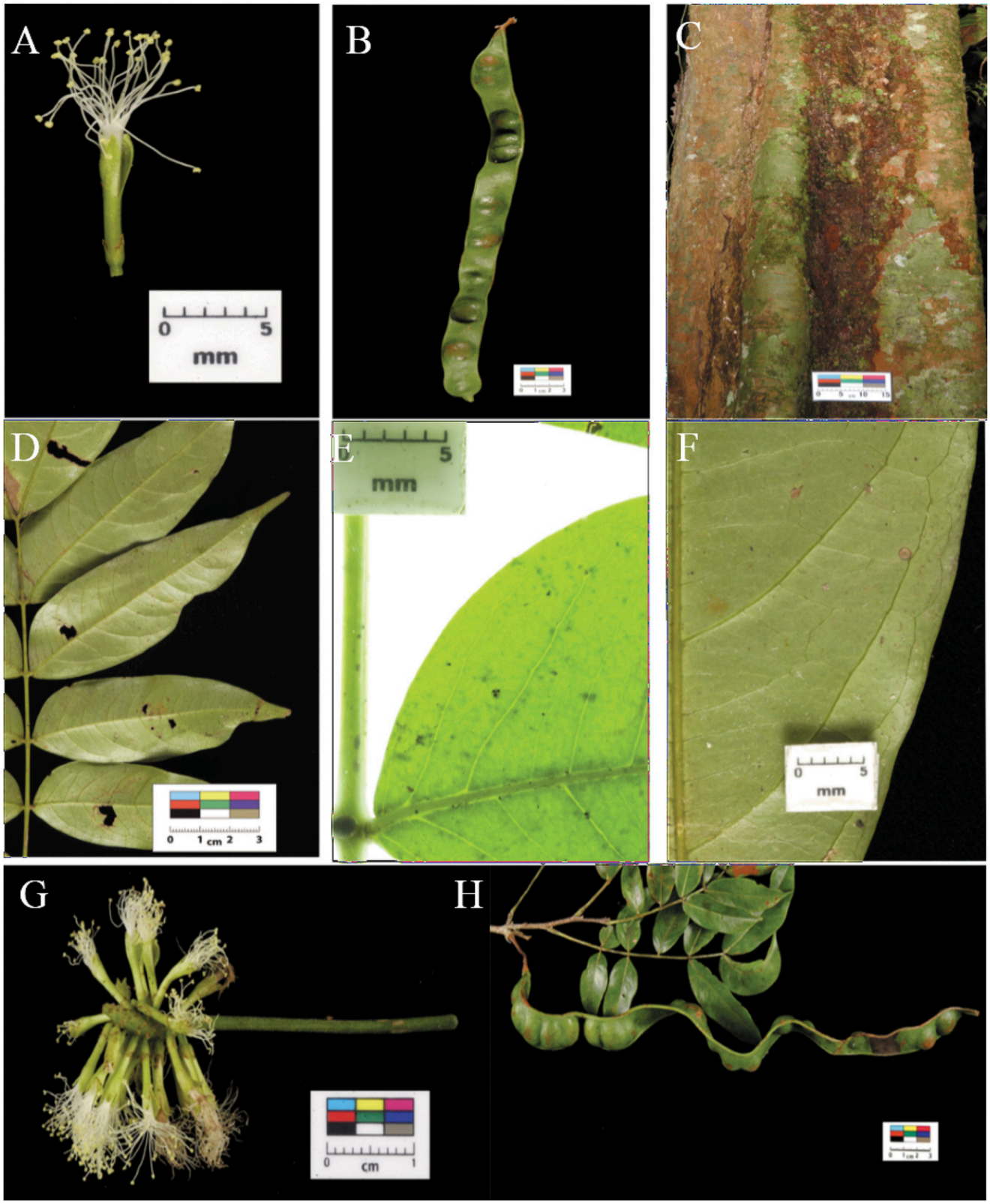

FIG. 2. *Inga kursarii* M.J. Endara & J.E. Guevara sp. nov. A. Flower. B. Fruit. C. Detail of external bark. D. Detail of adaxial leaflet morphology. E. Detail of foliar nectary and leaf rachis. F. Detail of secondary venation on the abaxial surface. G. Detail of inflorescence. H. Fruiting branch. (A, G from *G. Villa et al. 2986*; B, H from *G. Villa et al. 2546*. Photos credit: Finding Species©).

Etymology—The new taxon is named in honor of Thomas Alan Kursar (1949–2018), an evolutionary biologist renowned for his important contributions to the understanding of the ecological and evolutionary mechanisms that underlie the diversity of tropical rainforest. For more than 20 yr, his work focused on the genus *Inga.*

Habitat, Ecology, and Distribution—*Inga kursarii* is an emergent tree known to occur in the terra firme forests of

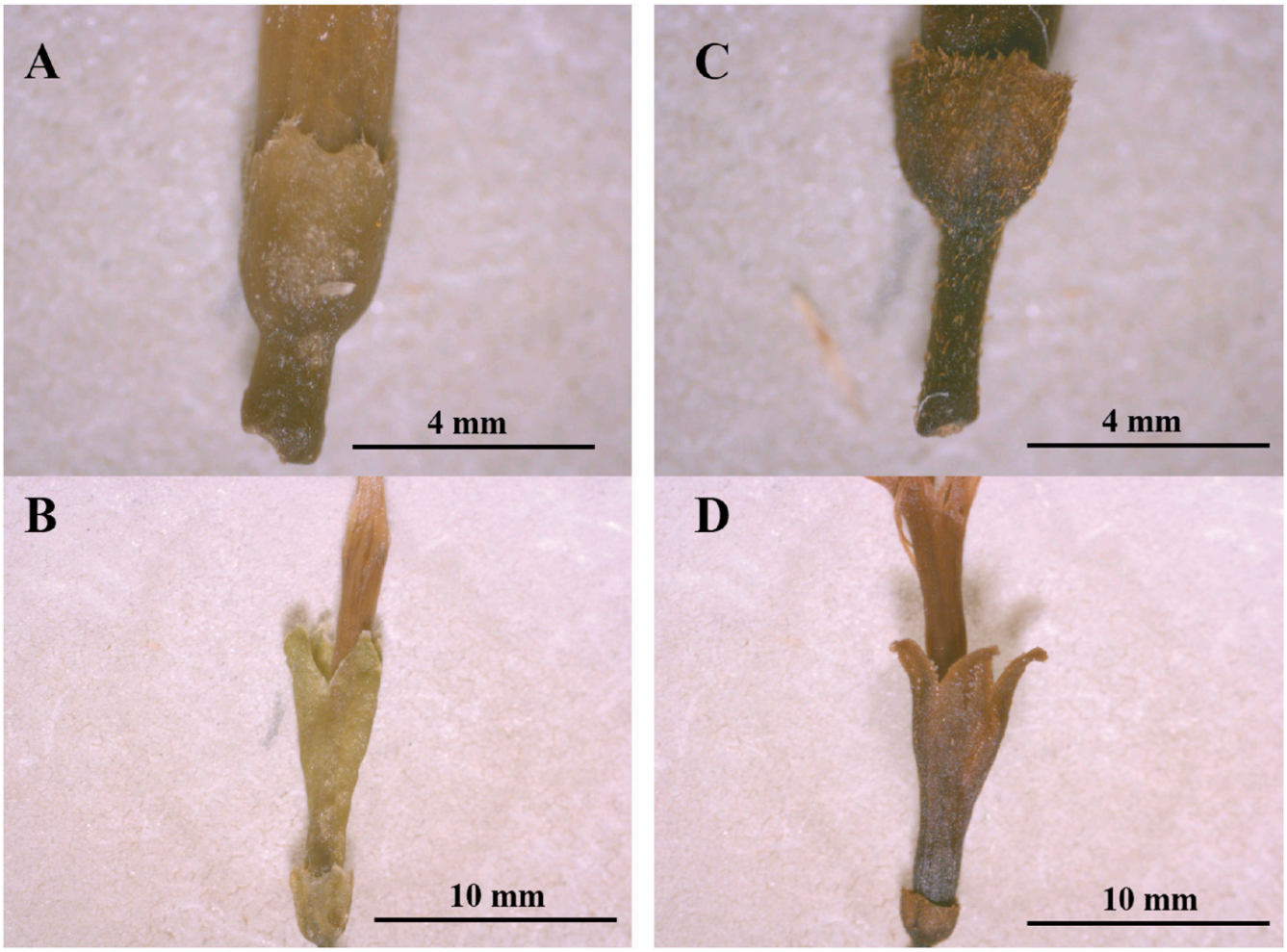

Fig. 3. A–B. *Inga kursarii* M.J. Endara & J.E. Guevara sp. nov. A. Detail of calyx. B. Detail of corolla and staminal tube exserting corolla. C–D. *Inga gracilifolia* Ducke. C. Detail of calyx. D. Detail of corolla and staminal tube (A, B from *Pérez & Alvia 3485*; C, D from *Córdoba, M.P. 1401*).

Colombia, Peru, and Ecuador, where it occurs between 200 and 600 m of elevation. The species habitat is a vast and continuous landscape of upland forests, broken by occasional strips of floodplains and swamp forests.

The largest known and best studied population of *I. kursarii* is in Yasuní National Park, Ecuador. The forests of Yasuní are characterized by high alpha-diversity of trees, with some groups such as Arecaceae, Fabaceae, Melastomataceae, Moraceae, Rubiaceae, and Sapotaceae remarkably dominant in terms of abundance and diversity. Additional species-rich genera that exhibit peaks of diversity in Yasuní are *Ocotea, Pouteria, Virola, Eugenia,* and *Calyptranthes* (Pitman et al. 2001; Valencia et al. 2004; Guevara Andino et al. 2017). In a 150 one-hectare plot network established in the Ecuadorian and Peruvian Amazon since 2001, which includes approximately 350,000 stems with a dbh ≥ 10 cm, 271 adult trees of *Inga kursarii* have been recorded (Pitman et al. 2001; Valencia et al. 2004; Pitman et al. 2014; Guevara Andino et al. 2017). *Inga kursarii* shows a habitat preference for hilly terrains, as demonstrated in its local scale spatial distribution in a 50-ha plot of Amazonian rain forest located in Yasuní National Park (Fig. 5). In this plot, 1132 individuals have been recorded, 144 with dbh ≥ 10 cm, and 988 with dbh ≤ 10 cm. In the same plot we found that the annual mortality rate of this species was 1.74% between 1995 and 2002 and 1.27% between 2002 and 2007. The annual recruitment rate was 1.73 individuals per year between 1995 and 2002 and 3.07 individuals per year between 2002 and 2007. Growth rate was lower between 1995 and 2002 (0.85 mm per year) compared with the period between 2002 and 2007 (1.021 mm per year).

I. kursarii appears to be relatively frequent and common in terra firme forests across a broad swath of western Amazonia. In a network of tree plots established in upland forests in the Ecuadorean Amazon, the species ranks second in median abundance among all *Inga* species, with 3 individuals ≥ 10 cm dbh/ha. The species is particularly common in plots in Yasuní, where it can count up to 10 individuals per plot; it is less common towards the southern and northeastern portion of Ecuadorean Amazon. It is less frequent and less common in plots in the adjacent Peruvian department of Loreto where soils are less fertile and where *I. kursarii* is reduced to simply one more of the several dozen of very rare species of *Inga* (Pitman et al. 2001; Valencia et al. 2004; Pitman et al. 2014; Guevara Andino et al. 2017).

Comparative Chemocoding Data—The profiles of secondary metabolites showed visually evident differences between species (Fig. 6), with *I. kursarii* having a chemistry based on gallocatechin/epigallocatechin gallates, and *I. gracilifolia* producing a series of dihydroflavonols. In addition, metabolomic analyses of the defensive chemistry (chemocoding, Endara et al. 2018) for five saplings each of *Inga kursarii* from Ecuador and *Inga gracilifolia* from French Guiana, delimited the samples into two distinct groups, one for each species (Fig. 7).

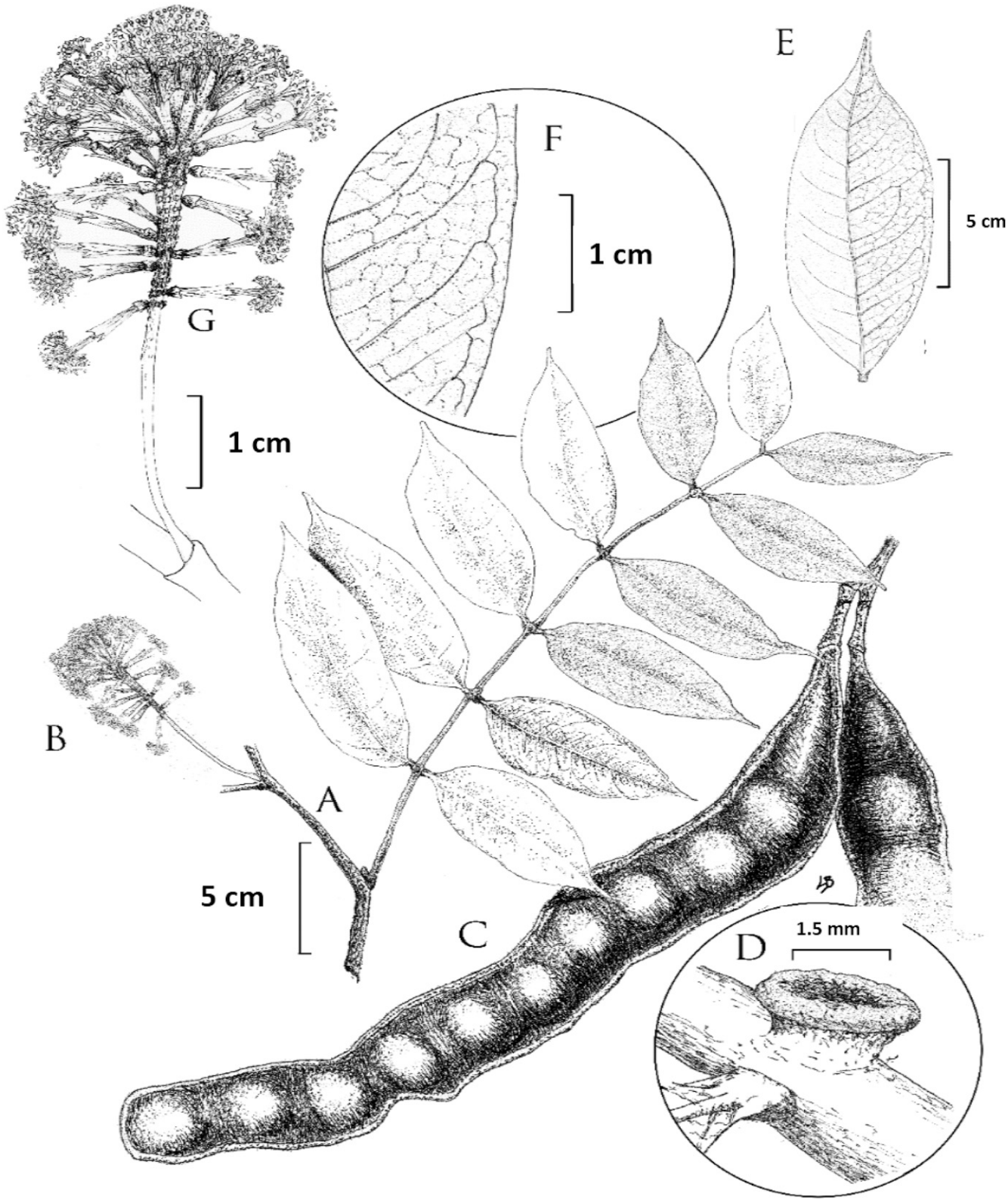

FIG. 4. *Inga kursarii.* A. General plan. B. Inflorescence. C. Pod transverse section. D. Detail of the foliar nectary. E. Individual leaflet. F. Detail of secondary and intersecondary veins on the abaxial surface of leaflets. G. Detail of inflorescence. Drawing based on *A.J. Pérez & P. Alvia 3485* (A–D) and *J. Jaramillo, X. Buitrón & M. Tapia 16247* (E–G). Drawn by Luis Baquero.

Phenology—Flowering occurs in two peaks, from May to July and between August and December; fruiting occurs between January and April.

Conservation Status—*Inga kursarii* is known from several populations in Yasuní National Park in the Ecuadorian Amazon, where it has been extensively recorded both as seedlings and juveniles, as well as adult trees. At least three populations have been recorded in the Colombian Amazon below 500 m. One is located in the surroundings of the Estación Biológica Caparú in Vaupés department. The second

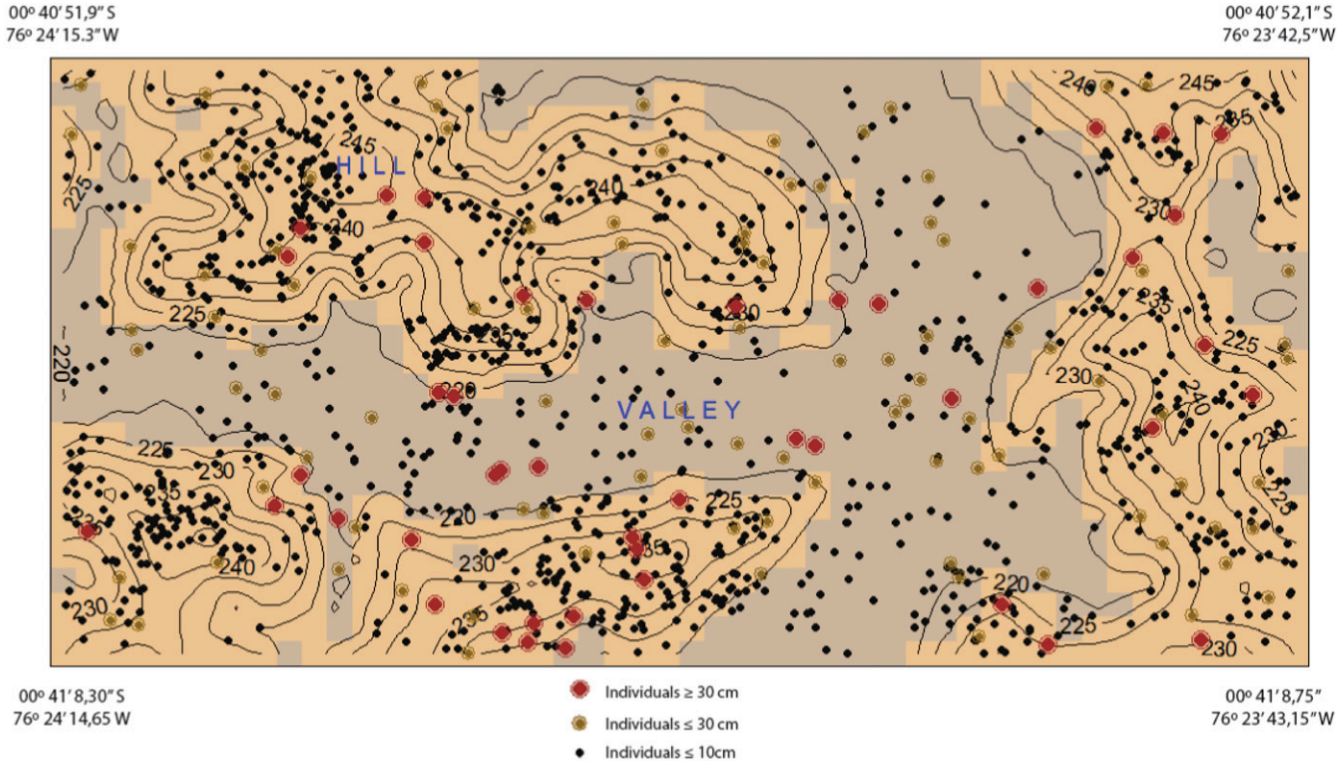

FIG. 5. Map of individuals of *Inga kursarii* M.J. Endara & J.E. Guevara sp. nov. in a 50-ha plot at Yasuní National Park, Ecuador. Three size classes are displayed: ≥ 1–10 cm (black dots); ≥ 10–30 cm (yellow dots); and ≥ 30 cm dbh (red dots). Topographic contours are at 5 m intervals, and the coordinates of each corner of the plot are given.

is at the Centro Experimental Amazónico (CEA), San José del Pepino, Putumayo department. The third corresponds to the 50-ha Center of Tropical Forest Science plot at Amacayacu National Park. In this plot, 12 individuals have been reported; only three of them are adults with a dbh ≥ 20 cm. One additional population has been recorded in the Peruvian Amazon in the upper Apayacu river area, on hilly terrain. This population grows on terra firme forests characterized by highly dissected terrain and a mixture of brown-sand and clayey soils. Using the GeoCAT tool and based on herbaria records and plot data, our estimates of extent of occurrence and area of occupancy for this species are 146,393,987 km^2 and 64,000 km^2 respectively (Bachman et al. 2011).

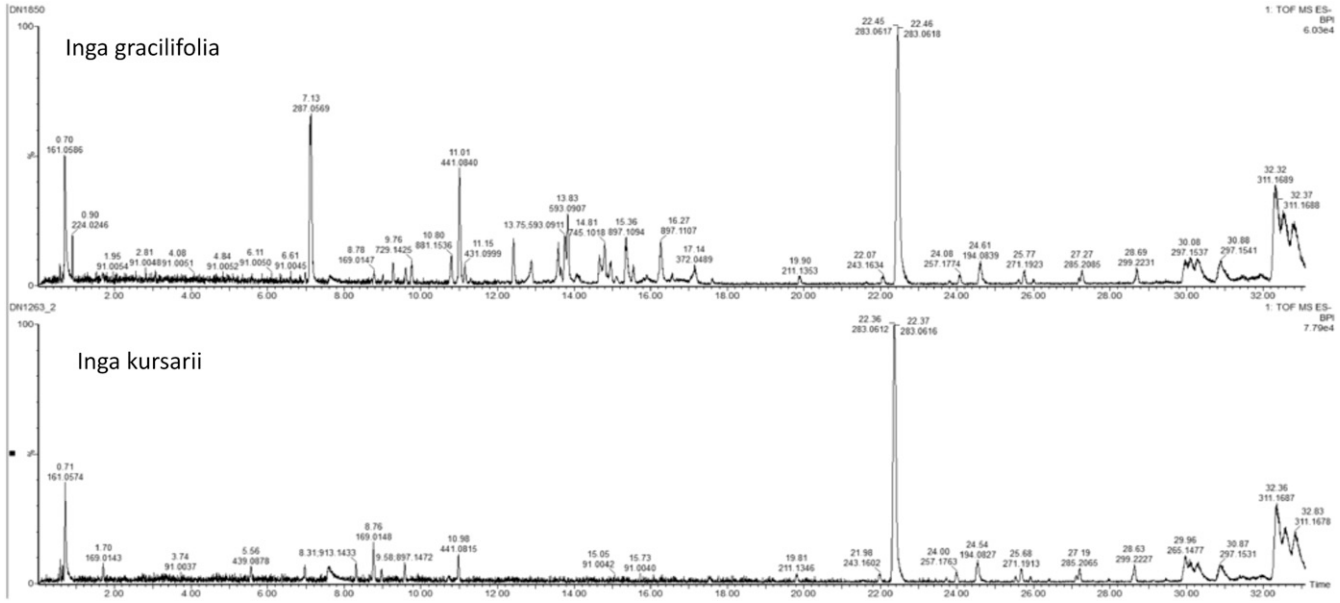

FIG. 6. Total ion chromatograms of *Inga kursarii* M.J. Endara & J.E. Guevara sp. nov. and *I. gracilifolia* Ducke, showing relative intensities of peaks from LC-QToF-MS in negative mode.

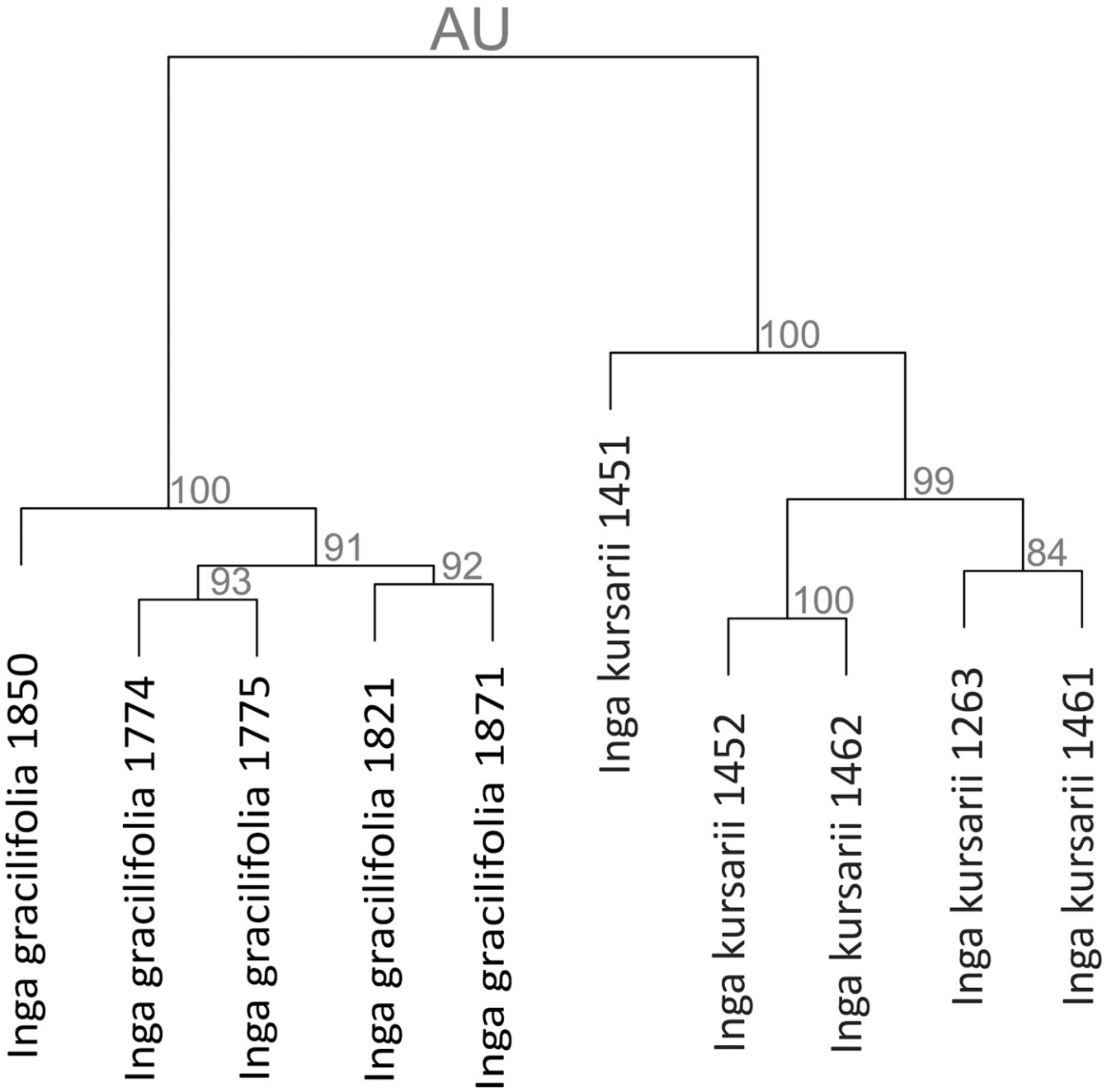

FIG. 7. Hierarchical cluster dendrogram based on relative abundances of UPLC-MS metabolites. The numbers above each branch point are the Approximately Unbiased confidence levels, which indicate the probability that the samples below that point are a cluster. Clusters with values ≥ 95 signify $p \leq 0.05$, indicating that these clusters are strongly supported by the data.

Due to the amount of available information about the ecology of the species, its large geographic range across an area of extensive and well-preserved habitat, the presence of populations in large protected areas, the lack of specific threats, the demographic data, and the potential misidentification of several specimens of this taxon as *Inga gracilifolia*, this species may be considered as Least Concern (LC) according to IUCN Red List criteria (IUCN 2014). However, extensive clear-cutting of Amazon lowland forests along the Colombia-Ecuadorian border might threaten many populations of this species in this portion of the northwestern Amazon. Thus, the conservation status of this species may require reevaluation in the near future.

Taxonomic Discussion—The overall combination of sessile foliar nectaries that are deeply cyathiform, glabrous leaflets with acute apex and slightly asymmetric bases, flowers borne in a slightly congested spike, small flowers with short campanulate calyx and short corolla, and the absence of bracts at the base of the inflorescence suggests that the new taxon must be placed in the section *Bourgonia* Benth (sensu Pennington 1997) and separates *I. kursarii* from other morphologically similar species. A maximum likelihood molecular phylogeny including more than 124 species of *Inga* reveals that the putative sister lineage of *I. kursarii* is *Inga gracilifolia* (Fig. 8), which is another 5–6-foliolate pair species, previously known to occur in Central and Western Amazonia and the Guiana Shield.

I. kursarii can be readily distinguished from its closest relative by having larger leaflets with a non-asymmetric base and acute apex, a lax to slightly congested spike inflorescence, subsessile flowers with the corolla tube lobes not reflexed, and a larger ovary (1.4–1.9 vs. 1.25–1.6 mm in *I. gracilifolia*) (Table 1; Fig. 9). *I. kursarii* is also morphologically similar to *Inga duckei* Huber, a tree species that occurs in inundated forests (e.g. varzea forests) in Brazil and Peru. Nevertheless, *I. duckei* possesses 4–5 pairs of leaflets with an asymmetric and subcordate base, a terete rachis covered with dense ferrugineous pubescence, shorter peduncles (2–3 mm vs. 1.3–5 mm in *I. kursarii*), and a globose-capitate inflorescence.

Thus, taking into consideration morphology, current DNA sequence data, and chemocoding, we propose that *Inga kursarii* is a novel taxon and that it is well differentiated from other morphologically similar species of *Inga*.

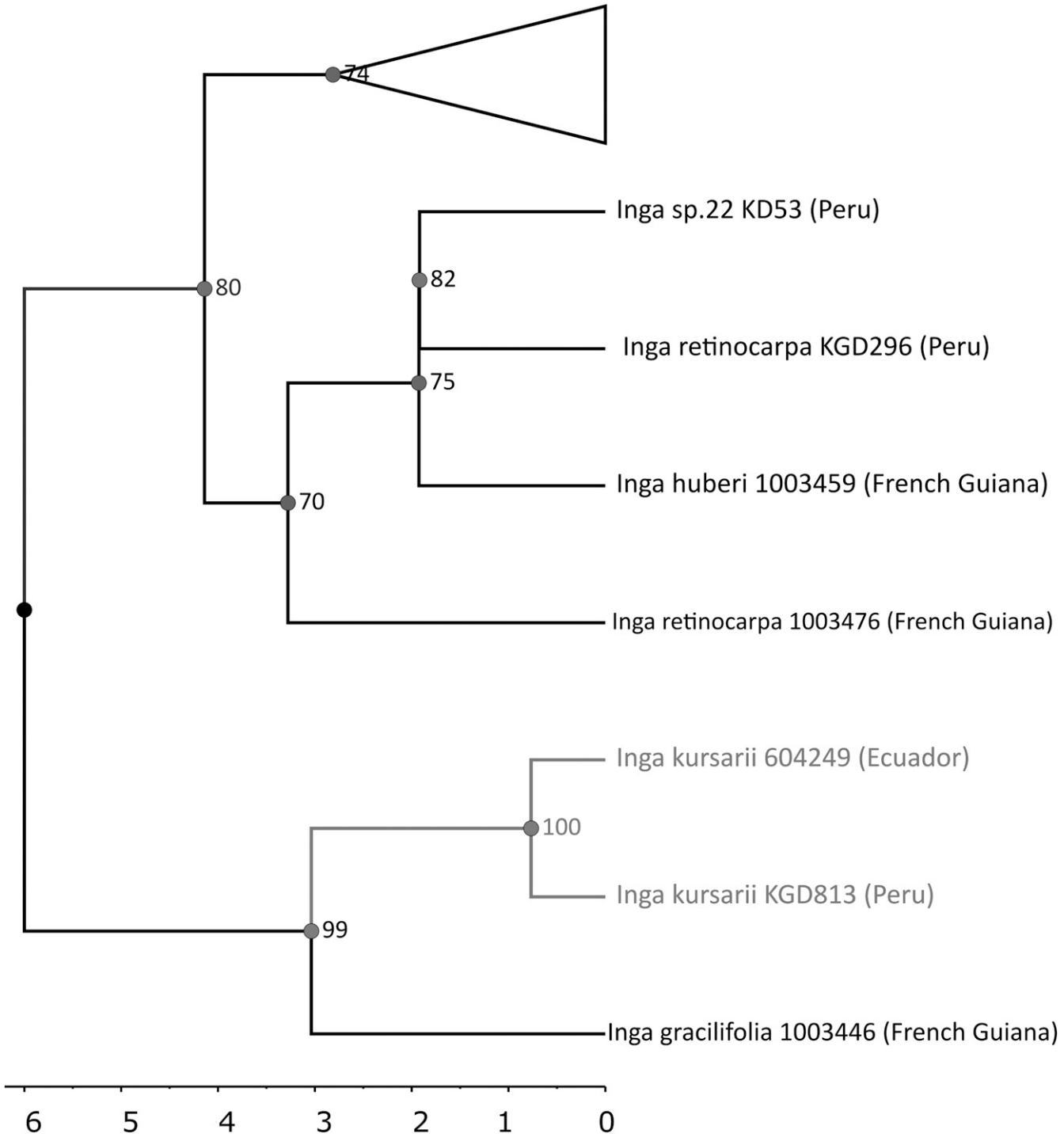

Fig. 8. Clade containing *Inga kursarii* M.J. Endara & J.E. Guevara sp. nov. and *I. gracilifolia* Ducke. This clade was adapted from a resolved maximum likelihood phylogeny for 124 species of the genus *Inga* (Dexter et al. 2017). Numbers represent bootstrap support values. Values ≥ 95 indicate that the clade is strongly supported by the data. Scale in phylogenetic tree shows lineage divergence estimated in millions of years.

TABLE 1. Diagnostic characters for *Inga kursarii* (Leguminosae, Mimosoid clade) and its closest relatives as well as their geographical distribution in the Amazon basin: North Western Amazon (NWA), Central Amazon (CA), and the Guiana Shield (GS).

Characters	*I. kursarii*	*I. gracilifolia*	*I. cylindrica*	*I. alba*	*I. duckei*
Leaflet pairs	5–6	3–8	3–5	3–6	4–5
Leaflet apex	Acute	Obtuse	Acute to attenuate	Narrowly attenuate	Narrowly acuminate or acute
Leaflet base	Obtuse and slightly asymetrical	Cuneate and strongly asymetrical	Cuneate	Acute to rounded	Cordate
Rachis	Terete or slightly canaliculate	Strongly canaliculate and slightly winged	Strongly canaliculate	Narrowly winged	Terete and slightly canaliculate
Foliar nectary	Sessile and cyathiform	Short stalked and cyathiform	Sessile and patelliform	Sessile or shortly stalked	Shortly stalked
Inflorescence structure	Spike, sessile flowers or borne on a short stalk (0.3–0.4 mm long)	Capitulate, flowers borne on a pedicel 1–1.4 mm long	Congested spike, flowers sessile	Congested spike, flowers sessile	Congested raceme, flowers borne on a pedicel 0.5–1 mm long
Corolla tube (length)	5.5–7 mm	4.7–6.3 mm	ca. 3 mm	2–3 mm	4–4.5 mm
Corolla tube lobes	4, not reflexed	5, strongly reflexed	5, not reflexed	4, strongly reflexed	5, not reflexed
Corolla tube indumentum	Glabrous and glossy	Minutely puberulous with appressed hairs	Glabrous	Sparsely appressed to glabrous	Puberulous
Calyx lobes (length)	0.2–0.5 mm, tufts of hairs at the apex	0.05–0.1 mm, sparsely pubescent	0.25 mm, puberulous	0.25 mm, puberulous	0.25 mm, sparsely puberulous
Staminal tube (length)	5.2–7.8 mm	7.3–8.9 mm	6–9 mm	6–8.5 mm	5–6 mm
Staminal tube exserting corolla tube	1.1–2.3 mm	2–3.6 mm	ca. 3 mm	3–3.5 mm	Equalling the corolla
Stigma morphology	Capitate	Simple	Simple	Simple	Simple
Geographic distribution	NWA	CA and GS	NWA, CA, and GS	NWA, CA, and GS	NWA and CA

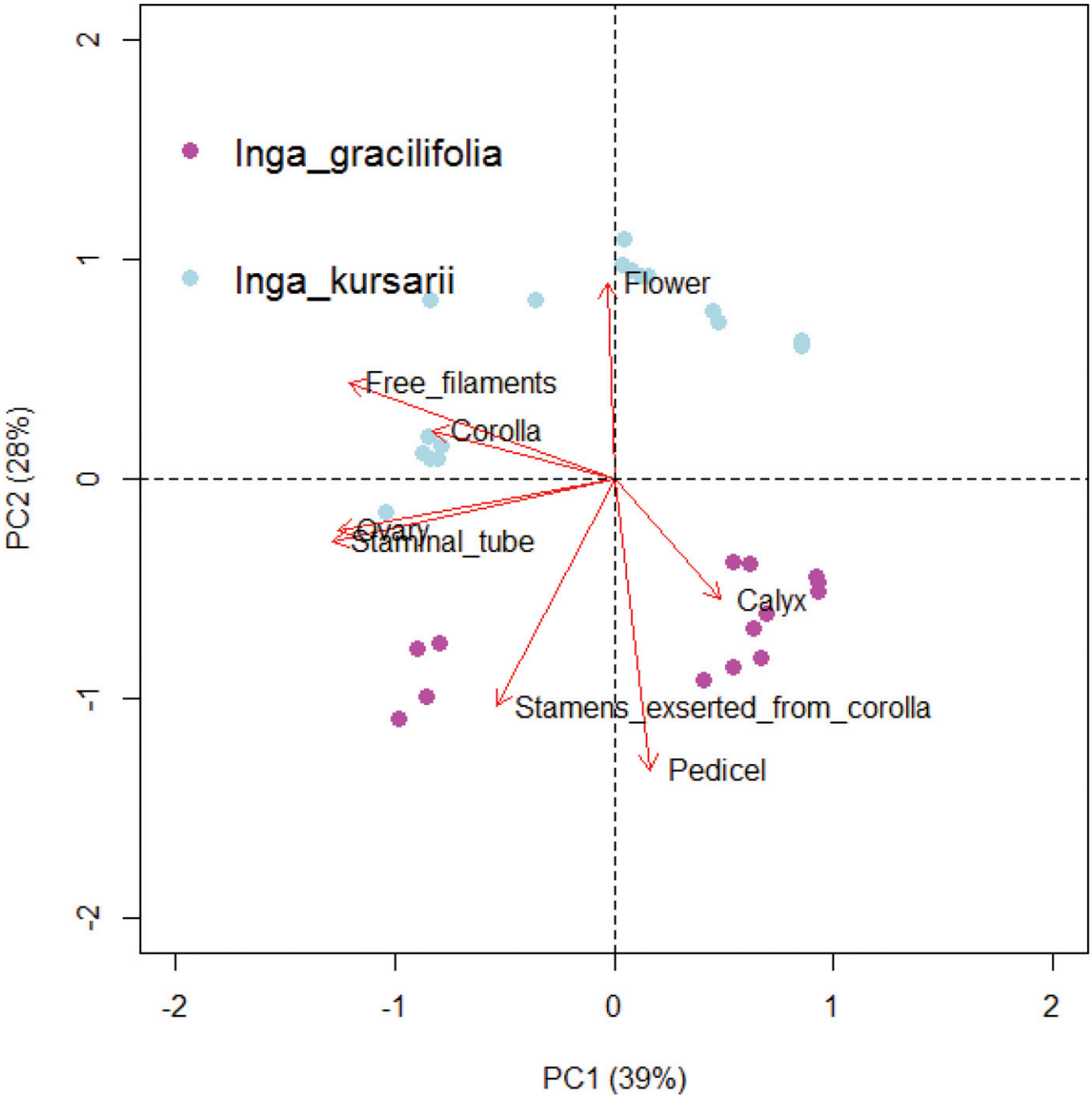

Fig. 9. Principal Component Analysis of reproductive characters for *Inga kursarii* M.J. Endara & J.E. Guevara sp. nov and *I. gracilifolia* Ducke. Each dot is an individual measure projected according to the first two axes of the PCA. The first axis is defined by values related to shorter calyces, larger pedicels, and longer staminal tubes exserting the corolla, which are characters present in *I. gracilifolia*. The second axis is defined by values associated with larger flowers, larger corollas, larger ovaries, and longer free filaments, which are diagnostic characters of *I. kursarii*. All measurements were taken in mm.

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Author Contributions

JEGA and MJE conceived the idea, reviewed voucher specimens of *Inga* deposited in Colombian, Ecuadorian and Peruvian herbaria, took measurements, analyzed data and took the lead in writing the manuscript. All other authors provided feedback and their data to the paper.

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