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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 gallatecin/epigallatecin 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 gallocatequina / epigallocatequina, 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...
unwinged, terete and glabrous, foliar rachis non-canaliculate, unwinged, 4.4 mm long, linear, caducous. Leaves alternate, paripinnate, with 6 pairs of leaflets, rarely 5, caducous; petals yellow, oblong, 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, exerted 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 cupulate 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°05′, 69°49′W, 200 m, 25 agosto 1989, (fl), S. Dífer 670 (COAH, MO).—PUTUMAYO: municipio de Mocoa, vereda San José del Peñon, 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. Kuitun 2366 (COAH).—Ecuador.—ORELLANA Parque Nacional Yasuní, Carretera y oleoducto de Maxus km 40. Parcele permanente de 1 hectárea, Árbol # 5.16, 00°45′S, 76°30′W, 250 m, 10–11 marzo 2004, (fr), M. Aulestia 1830 (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 (QCNE, QCA); 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); Orellana 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 Etnica Huaraori, carretera y oleoducto de Maxus en construcción km 75-7, entre río Ticunco y río Yasuní, 00°50′S, 76°18′W, 250 m, 17–20 febrero 1994, (fr), M. Aulestia & O. Gontier 1745 (QCNE, QCA, MO); Orellana, Comunidad Quichua Alta Florecencia, zona de amortiguamiento del Parque Nacional Yasuní, bosque semiárido de penillanura del Aguacuero-Putumayo-Caquetá, 00°54′S, 76°26′W, J. Guerra y H. Shigano 1028 (QCA); Orellana Carretera Pompeya Sur-Iro, Parque Nacional Yasuní, Km 77-79. Trocha de desbroce, 19 febrero 1994, (fr), J. Jaramillo, X. Buitron & M. Tapia 16247 (QCA); Orellana, Carretera Pompeya Sur-Iro, Parque Nacional Yasuní, Km 38, detrás de la Estación de Monitoreo de Fauna Onkone Gare, Ecuescramb S.A., transecto C con dirección n 135° E desde el río Pirahna hacia el río Tiputini, 200–220 m, 18 mayo 1994, J. Jaramillo & X. Buitron 16599 (QCA); Orellana, transecto de vegetación de área de inundación temporal en la línea sísica 9° del Bloque 31, 00°52′S, 75°47′33″W, 250 m, 26 octubre 1997, J. Jaramillo, I. Tapia & D. Padilla 19546 (QCA); Estación Científica Yasuní, Km 82 de la carretera NPE-Ticunco, 00°40′S, 76°23′12″W, 200–300 m, 13 marzo 2002, J. Jaramillo, S. Yandun & S. Salgado 23667 (QCA); Reserva Florestal El Chuncho, 00°28′S, 77°40′W, 250 m, 3 febrero 1994, W. Palacios 12030 (QCNE, MO); Parque Nacional Yasuní-ECY. Parcela de 50a PDBY. 00°38′S, 76°30′W, 200–300 m, 25 febrero 2008, (fr), A.J. Pérez y P. Alvia 3941 (QCA); Parque Nacional Yasuní-ECY. Parcela de 50a PDBY. 00°38′S, 76°30′W, 200–300 m, 24 septiembre 2010, (fr), A.J. Pérez & P. Alvia 4069 (QCA); Parque Nacional Yasuní-ECY. Parcela de 50a PDBY. bosque siempreviva de tierras bajas del Napo-Curaray, 00°31′25″S, 76°25′26″W, 250–350 m, 31 junio 1982, S.E. 9108 (AAU, QCA); Rain forest on well drained hilly ground in the Parque Nacional Yasuní, 00°31′25″S, 76°25′26″W, 250–350 m, 30 may-21 june 1982, S.E. 9238 (AAU, QCA); Provincia de Orellana, Estación...
Inga gracilifolia
Inga kursarri

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

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 $\geq 10$ 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). 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 $\geq 10$ cm, and 988 with dbh $\leq 10$ 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 $\geq 10$ 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 an 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 gallatechin/epigallatechin 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).
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

![Diagram](https://bioone.org/journals/Systematic-Botany/figs/Fig_4.png)
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 km² and 64,000 km² respectively (Bachman et al. 2011).
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 clearcutting 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.

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**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 $p < 0.05$, indicating that these clusters are strongly supported by the data.
*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*.
<table>
<thead>
<tr>
<th>Characters</th>
<th>\textit{I. kursarii}</th>
<th>\textit{I. gracilifolia}</th>
<th>\textit{I. cylindrica}</th>
<th>\textit{I. alba}</th>
<th>\textit{I. duckei}</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaflet pairs</td>
<td>5–6</td>
<td>3–8</td>
<td>3–5</td>
<td>3–6</td>
<td>4–5</td>
</tr>
<tr>
<td>Leaflet apex</td>
<td>Acute</td>
<td>Obtuse and strongly asymmetrical</td>
<td>Acute to attenuate</td>
<td>Narrowly attenuate</td>
<td>Narrowly acuminate or acute</td>
</tr>
<tr>
<td>Leaflet base</td>
<td>Obtuse or slightly canaliculate</td>
<td>Cuneate and strongly asymmetrical</td>
<td>Cuneate</td>
<td>Acute to rounded</td>
<td>Cordate</td>
</tr>
<tr>
<td>Rachis</td>
<td>Terete or slightly canaliculate</td>
<td>Strongly canaliculate and slightly winged</td>
<td>Strongly canaliculate</td>
<td>Narowly winged</td>
<td>Terete and slightly canaliculate</td>
</tr>
<tr>
<td>Foliar nectary</td>
<td>Sessile and cyathiform</td>
<td>Short stalked and cyathiform</td>
<td>Sessile and patelliform</td>
<td>Sessile or shortly stalked</td>
<td>Shortly stalked</td>
</tr>
<tr>
<td>Inflorescence structure</td>
<td>Spike, sessile flowers or borne on a short stalk (0.3–0.4 mm long)</td>
<td>Capitulate, flowers borne on a pedicel 1–1.4 mm long</td>
<td>Congested spike, flowers sessile</td>
<td>Congested spike, flowers sessile</td>
<td>Congested raceme, flowers borne on a pedicel 0.5–1 mm long</td>
</tr>
<tr>
<td>Corolla tube (length)</td>
<td>5.5–7 mm</td>
<td>4.7–6.3 mm</td>
<td>ca. 3 mm</td>
<td>2–3 mm</td>
<td>4–4.5 mm</td>
</tr>
<tr>
<td>Corolla tube lobes</td>
<td>4, not reflexed</td>
<td>5, strongly reflexed</td>
<td>5, not reflexed</td>
<td>4, strongly reflexed</td>
<td>5, not reflexed</td>
</tr>
<tr>
<td>Corolla tube indumentum</td>
<td>Glabrous and glossy</td>
<td>Minute puberulous with appressed hairs</td>
<td>Glabrous</td>
<td>Sparsely appressed to glabrous</td>
<td>Puberulous</td>
</tr>
<tr>
<td>Calyx lobes (length)</td>
<td>0.2–0.5 mm, tufts of hairs at the apex</td>
<td>0.05–0.1 mm, sparsely pubescent</td>
<td>0.25 mm, puberulous</td>
<td>0.25 mm, puberulous</td>
<td>0.25 mm, sparsely puberulous</td>
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<tr>
<td>Staminal tube (length)</td>
<td>5.2–7.8 mm</td>
<td>7.3–8.9 mm</td>
<td>6–9 mm</td>
<td>6–8.5 mm</td>
<td>5–6 mm</td>
</tr>
<tr>
<td>Staminal tube exerting corolla tube</td>
<td>2.1–3.6 mm</td>
<td>ca. 3 mm</td>
<td>3–3.5 mm</td>
<td>Equalling the corolla</td>
<td></td>
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<tr>
<td>Stigma morphology</td>
<td>Capitate</td>
<td>Simple</td>
<td>Simple</td>
<td>Simple</td>
<td>Simple</td>
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<tr>
<td>Geographic distribution</td>
<td>NWA</td>
<td>CA and GS</td>
<td>NWA, CA, and GS</td>
<td>NWA, CA, and GS</td>
<td>NWA and CA</td>
</tr>
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</table>
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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.

Literature Cited


