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Passiflora gustaviana, a New Species of Passiflora (Supersection Laurifolia) from Colombia Revealed by Multivariate Analysis

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1 OCAMPO AND MOLINARI: PASSIFLORA GUSTAVIANA, A NEW SPECIES FROM
2 COLOMBIA

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6 *Passiflora gustaviana*, a New Species of *Passiflora* (Supersection *Laurifolia*) from
7 Colombia Revealed by Multivariate Analysis

8

9 John A. Ocampo Pérez^{a,b,c} and Miguel Molinari^d

10

11 ^a Universidad Nacional de Colombia sede Palmira, Facultad de Ciencias Agropecuarias,
12 Departamento de Ciencias Biológicas. Carrera 32 No. 12-00 Chapinero, vía Candelaria
13 Palmira, Valle del Cauca, Colombia.

14 ^b International Center for Tropical Agriculture, Recta Cali-Palmira, Km. 17 –
15 CIAT/Ecosystem Services, Palmira, Valle del Cauca, Colombia.

16 ^d Universidad de los Andes, Facultad de Ciencias Forestales, Associate Curator, Herbarium
17 (MER), apartado 384, Mérida 5101, Mérida, Venezuela.

18 ^c Correspondence author (jaocampo@unal.edu.co)

19

20 *Abstract*—A new species of *Passiflora* (supersection *Laurifolia*, series *Laurifoliae*) from
21 the Andean region of Colombia is described and illustrated using morphological descriptors
22 analysis. This species is closely related to *P. popenovii* Killip and can be recognized mainly
23 by its purple stem, leaf size (12.5–16.5 × 5.0–7.9 cm), biglandular petioles, pedicel length
24 (8–10 mm), bracts light green, glandless, flowers length (28–30 mm), corona filaments in

25 five series, minute-filiform inner filaments length (1–4 mm), fimbriate purplish operculum
26 margin, staminal filaments length (6.8–7.1 mm), ovary glabrous, yellow mature fruits
27 mottled with irregular white dots, lightly pubescent, and total soluble solids content in fruit
28 juice (13.5%–14.3%). The newly identified species *P. gustaviana* grows on the slopes of
29 high mountains between 1,900 and 2,309 m above sea level, with an annual mean
30 temperature of 16.2°C. It is considered a new endemic species of Colombia and may be
31 regarded as endangered (EN) because of its limited occurrence. This new species
32 constitutes an important unexploited genetic resource useful for the improvement of
33 cultivated *Passiflora* species.

34

35 *Keywords*—Conservation, endemism, IUCN red list, *Laurifoliae*, PCA, Passifloraceae,
36 Tropical Andes.

37

38 *Passiflora* L. is the largest genus in the family Passifloraceae Juss. ex Roussel, with more
39 than 577 species of vines, lianas, shrubs, and trees. *Passiflora* is split into five subgenera
40 (*Astrophea* (DC.) Mast., *Decaloba* (DC.) Rchb., *Deidamioides* (Harms) Killip, *Passiflora*
41 L., and *Tetrapathea* (DC.) P. S. Green) distributed mainly in the Neotropics, from coastal
42 zones up to 4,300 m above sea level in the Andean slopes at páramo limits (Ulmer and
43 MacDougal 2004; Krosnick et al. 2009). Subgenus *Passiflora* includes ca. 240 species and
44 is divided into six supersections with several particular features, such as having petiolar
45 nectaries, variable leaf shape, large colorful flowers, large fruits (Killip 1938; Feuillet and
46 MacDougal 2003; MacDougal and Feuillet 2004), a chromosome number that usually is n
47 = 9, and an average genome size of 1.311 pg (Snow and MacDougal 1993; Yotoko et al.

48 2011). Pollinators include carpenter bees, bumblebees, honeybees, wasps, birds (mostly
49 short and sword-billed hummingbirds) and bats, with specific suites of floral characteristics
50 associated with each syndrome (Ulmer and MacDougal 2004; J. Ocampo pers. obs.).
51
52 Colombia has 174 reported species of *Passiflora*, being the country with the highest
53 *Passiflora* richness and with the greatest diversity in the Andean region (Ocampo et al.
54 2007; Hernández et al. 2017). The largest number of species is found between 1,000 and
55 2,000 m above sea level and the most common species thrive in disturbed habitats, such as
56 roadsides, cultivated land, and secondary forests (Ocampo et al. 2010). Thirty three
57 inventoried species are included in supersection *Laurifolia* (Cervi) Feuillet & MacDougal
58 series *Laurifoliae* Killip ex Cervi with Colombia being the center of diversity with 12
59 species, followed by Brazil and Venezuela with 10 species each (Ocampo et al. 2011).
60 *Laurifoliae* species include vigorous vines that often cover the trees used as support.
61 Species in this series are very easy to recognize by their filiform to linear stipules, one pair
62 of petiolar nectaries, and their generally long, dark green, glossy, unilobed and acuminate
63 leaves (Rome and Coppens d'Eeckenbrugge 2017). The pendent flowers have a corolla that
64 is often campanulate (except in *P. guazumaefolia* Juss., *P. odontophylla* Harms ex Glaziou,
65 and *P. kikiana* Cervi & Linsingen) and of a delicate white or cream to red and purple color,
66 frequently tinged slightly with violet (Ocampo et al. 2011). Their corona is formed of long
67 pendent filaments striated with deep violet and attached to a short hypanthium. In other
68 species, such as *P. ambigua* Hemsl., *P. popenovii* Killip, and *P. pergrandis* Holm-Nielsen
69 & Lawesson, the flowers are grouped on small branches with minute leaves and short
70 internodes, which gives the impression of a dense inflorescence (Ulmer and MacDougal
71 2004). The fruits are large (except in *P. gabrielliana* Vanderpl., 3.5–7.5 × 2.5–5.2 cm),

72 round to ovate, yellow to orange mottled with irregular white points, and with a thick
73 mesocarp. The arils present a firm consistency, and the whitish translucent pulp is strongly
74 aromatic. Most species have edible fruits and the seeds are dispersed by tree-climbing
75 arboreal mammals (e.g. monkeys and coatis), because the fruits do not fall after maturing.
76 The series *Laurifoliae* is particularly interesting for the economic development of new fruit
77 crops, while its attractive and colorful flowers also give the plant an ornamental value
78 (Ocampo et al. 2011; Rome and Coppens d'Eeckenbrugge 2017). Additionally, the
79 remarkable capacity of species in the series to grow on flooded soils (e.g. *P. riparia* Mart.
80 ex Mast., *P. gabrielliana*, *P. guazumaefolia*), as well their resistance to soil parasites (e.g.
81 *P. nitida*, *P. odontophylla*) are of interest for developing rootstocks and for transferring the
82 corresponding genes to other passion fruit species (Yockteng et al. 2011; Ocampo and
83 Coppens d'Eeckenbrugge 2017).

84

85 On the other hand, the general similarity in most organs frequently makes it difficult to
86 distinguish particular species, so as that the prominent *Passiflora* taxonomist Killip (1938)
87 and other experts of series *Laurifoliae* (Vásquez 1998; MacDougal and Feuillet 2004;
88 Rome and Coppens d'Eeckenbrugge 2017) have considered it as an "exceedingly difficult"
89 group. In several cases, both experts as well as amateurs may have underestimated the
90 infra-specific variation in widely distributed species, or even infra-individual variation,
91 splitting well known species into several new species only distinguished by a few
92 quantitative or qualitative traits, such as color. In series *Laurifoliae*, identification of
93 species into several morphological groups demands experience and caution, even for the
94 most common species such as *P. ambigua*, *P. nitida*, *P. laurifolia* and *P. tolimana* Harms,

95 which display high infra-specific variability and wide geographic distribution. For instance,
96 *P. metae* M. Bonilla, C. Aguirre & C. Caetano was recently described from Colombia
97 without taking into account the infra-specific variation; after rigorous revision based on
98 herbaria and field observations we consider it synonymous with *P. tolimana* (M. Rome and
99 G. Coppens, pers. comm.; J. Ocampo pers. obs.).

100 Multivariate analyses of morphological descriptors are a tool that can be used to solve
101 issues between closely related taxa. Despite the remarkable morphological diversity
102 described among species of series *Laurifoliae*, few studies have compared infra- and
103 interspecific variation with statistical tools. A recent and detailed list of descriptors was
104 used by Ocampo and Coppens & Eeckenbrugge (2017) to study morphological divergence
105 of 61 species of genus *Passiflora*, showing a clear separation among the subgenera
106 *Astrophea*, *Decaloba* and *Passiflora* with special emphasis on quantitative and qualitative
107 floral traits. The morphological cladistic analysis supported the delimitation of the species
108 and with particular infra-specific morphological variation in some species, such as *P.*
109 *popeonovii*, *P. nitida*, *P. maliformis* L., and *P. edulis* Sims.

110 In this paper we propose a new species, *P. gustaviana*, belonging to subgenus *Passiflora*,
111 supersection *Laurifolia*, series *Laurifoliae*, discovered in Colombia. This new species is
112 described, illustrated and compared with its closest relative *P. popeonovii*, using a phenetic
113 approach.

114

115 MATERIALS AND METHODS

116 In June 2004, Gustavo Morales of the Botanical Garden of Bogotá “José Celestino Mutis” -
117 JBB (Cundinamarca, Colombia) found a mature fruit of a *Passiflora* plant belong to
118 *Passiflora* series *Laurifoliae* along the roadside in a secondary forest in right margin in
119 Kilometer 2 between the municipalities of Pacho and Supatá (2,079-2,150 m), department
120 of Cundinamarca. Its seeds were extracted and later germinated and two seedlings were
121 planted in the JBB at 2,550 m above sea level in June 2006. Four years later, the plants
122 bloomed for the first time in August and their fruits were harvested in October of that
123 same year. Afterwards, this probable new species was compared with other species of
124 *Laurifoliae* and based on previous studies (Ocampo et al. 2011; G. Morales. pers. obs.), *P.*
125 *popenovii* was established as its morphologically closest relative species.

126

127 The morphological description was carried out *in situ* on living specimens of *P. gustaviana*
128 and the morphologically similar species *P. popeonovii*, using 42 quantitative and 51
129 qualitative vegetative and reproductive descriptors (Table 1). These descriptors were
130 assessed for individual sample taken from Colombia: two cultivated plants of *P. gustaviana*
131 planted in the JBB, and four plants of *P. popenovii* cultivated in home gardens in the
132 municipalities of Chachagui (Nariño) and Timbio (Cauca). Five measurements were taken
133 for the quantitative characters of each individual. A principal component analysis (PCA)
134 was carried out with quantitative data applying the varimax normalized rotation option, and
135 factors with an eigenvalue greater than one were retained. Additionally, Duncan's multiple
136 comparison test between means (95% confidence level) for each descriptor was used to
137 compare variation among species, using the *R* package (Pardo and Del Campo 2007). The
138 total soluble solids content (°Brix) found within the fruit's juice of quantitative characters
139 was estimated with the help of a hand held Brix refractometer (ATC). The color of the

140 qualitative characters was then recorded, using the Royal Colour Chart (Royal Horticultural
141 Society 2001). We followed the infrageneric classification of Feuillet and MacDougal
142 (2003).

143

144 Three expeditions to study highland *Laurifoliae* species in the field were carried out in
145 2010 to 2016 in 42 different localities within six departments (Antioquia, Boyacá,
146 Cundinamarca, Nariño, Tolima, and Valle del Cauca) of Colombia. Identifying data were
147 recorded for each specimen collected, which include locality, habitat, elevation and
148 geographic coordinates. Additionally, we examined specimens of series *Laurifoliae* from
149 the major herbaria in Colombia (AFP, CAUP, CDMB, CHOCO, COL, COAH, CUVC,
150 FAUC, FMB, HUA, HUQ, JBB, JAUM, MEDEL, PSO, SURCO, TOLI, TULV, VALLE,
151 and UIS) and other countries (F, GH, K, QCA, MA, MO, MOL, NY, P, TX, US, and
152 USM). Dried specimens were recorded and photographed to create a species description of
153 Colombian *Laurifoliae*. This database of field and herbaria data that we employed was
154 supplemented with specimens mentioned in various species descriptions published by
155 Killip (1938, 1960), Holm-Nielsen et al. (1988) and Ulmer and MacDougal (2004). The
156 description was created following the *Passiflora* morphological terminology proposed by
157 Tillett (1988). The data were gathered and cleaned with OpenRefine (Verborgh and de
158 Wilde 2013) to generate a dot map of the distribution of the *P. gustaviana* collections,
159 using the ArcMap 10.3 software. Finally, conservation status was assessed according to
160 IUCN (2014) categories and supported with geographic distribution data, based on the
161 extent of occurrence (EOO) and area of occupancy (AOO), found using the Geospatial
162 Conservation Assessment Tool - GeoCAT (Bachman et al. 2011).

163

164

165 RESULTS

166 Two specimens belonging to the new *P. gustaviana* were registered during the collection
167 trips, found growing mostly in disturbed habitats like road borders and secondary forest
168 margins. Regarding herbaria revisions, only four dried specimens deposited in the herbaria
169 of the Instituto de Ciencias Naturales (ICN) of the Universidad Nacional de Colombia
170 Bogotá branch (COL), and the José Celestino Mutis Botanical Garden of Bogotá (JBB)
171 were recorded as *P. gustaviana*. In relation its closest relative *P. popenovii*, 20 records from
172 herbaria (12) and field collections (8) under cultivation were registered in the departments
173 of Cauca and Nariño in the south-west of Colombia. A dot map of the spatial distribution of
174 *P. gustaviana* based on the six known records of the species, representing our recent field
175 collections and existing herbarium specimens, is shown in Fig. 1.

176

177 Multivariate analysis identified 31 quantitative descriptors with high interspecific variation.
178 Three principal components with an eigenvalue superior to one were retained, representing
179 96.1% of the total variation (Table 2). The first component (62%) is primarily associated
180 with 24 descriptors characterizing internode length, stipule length, lobe size, petiole
181 nectaries, bract size, flower length, longest inner filament of corona length, sepal length,
182 petal width, nectary chamber size, hypanthium diameter, androgynophore length, staminal
183 filaments length, ovary length, fruit size/weight/total soluble solids content in juice, and
184 seed length. The second component (26%) is represented by pedicel length, the corona's
185 outermost filament length, petal length, sepal width, hypanthium length, and styles length.
186 The third component (7.4%) is only associated with operculum length. Fig. 2 shows the

187 individuals in the principal plane (88.3% variance total), showing a clear grouping by
188 species and geographic origin. The representatives of *P. gustaviana* are placed on the right
189 side along the first axis in relation to their larger size of leaves, flowers and fruits, and
190 greater total soluble solids content in fruit juice (°Brix), in relation to individuals of *P.*
191 *popenovii*. Additionally, the 31 descriptors selected by PCA showed significant differences
192 according to Duncan's multiple comparison test between the individuals of *P. gustaviana*
193 and *P. popenovii* (Table 2).

194

195 Qualitative descriptors analysis identified 10 of the 51 descriptors evaluated on the basis of
196 their potential to discriminate among species. These descriptors were associated with stem
197 color (mature branch), and bract color and glandless, shape and color of inner filaments of
198 the corona, operculum margin, ovary pubescence, and color of mature fruits. Table 3
199 synthesizes the observations for quantitative and qualitative descriptors between *P.*
200 *gustaviana* and its closest relative *P. popenovii*.

201

202

203 TAXONOMIC TREATMENT

204 ***Passiflora gustaviana*** Ocampo & Molinari, sp. nov.—TYPE: COLOMBIA.

205 Cundinamarca: Bogotá D.C, frutales de clima frío, de semillas colectadas en Supatá vía

206 Pacho (Cundinamarca). Alt. 2,550 m.s.n.m, 17 August 2010, *Gustavo Morales 3190*

207 (holotype: JBB!);

208

209 Plant woody vine or liana. Stem terete, slender, striate, glabrous, purple colored (mature
210 branch) to green colored (young branch). Stipules narrowly linear, 8–13 mm long, 0.5 mm
211 wide, not glandular, green, soon deciduous. Tendrils glabrous, red to purple colored and up
212 to green. Petioles 1.5–2.7 cm long, slightly canaliculate adaxially, glabrous, a pair of round
213 sessile glands (about 1.5 mm long), located on the middle of the petiole, green. Leaves
214 unlobed, oblong-ovate, 12.5–16.5 cm long, 5–7.9 cm wide, mucronate and generally
215 acuminate, rounded at base, lustrous on both surfaces, penninerved (lateral nerves 7 or 8
216 pairs), subcoriaceous, margins entire, glabrous, green. Peduncles terete, slender, solitary
217 (sometimes in pairs), 10.5–12.8 cm long (including pedicel 0.8–1.0 cm long). Bracts ovate,
218 concave, 3.5–4 cm long, 2–2.4 cm wide, rounded, entire, free, glabrous, persistent (until
219 fruit maturity), light-green, glandless. Flowers pendulous, fragrant, 2.8–3.0 cm long (from
220 the base of the nectary chamber to the ovary apex) × 6.0–7.2 cm wide, sometimes seen in
221 clusters on pseudoracemes (small branches with short internodes ca. 2–3 cm, small leaves,
222 and flowers at each node). Nectary chamber glabrous, 4–5 mm long x 20–20.1 mm wide,
223 green outside and white inside. Hypanthium campanulate, 6–7.8 mm long x 22–24 mm
224 diameter (at the base of the sepals), glabrous, green outside and white inside. Sepals
225 oblong, 4–4.5 cm long x 2.0–2.3 cm wide, adaxial surface light-green, abaxial surface
226 white, slightly concave, glabrous, keeled dorsally just below the apex, the keel terminating
227 in a light-green awn about 2 mm long, glabrous. Petals white, linear-oblong, 3.8–4.1 cm
228 long x 1.4–1.8 cm wide, glabrous, reflexed. Corona filaments in five series, two major outer
229 series, white, banded (4–7 bands) purplish blue, the bands purple near base, thickened,
230 fleshy, the second outer series filaments longer (3.6–3.9 cm long) than the outermost series,
231 the three inner series 1.0–4.0 mm long, minute, filiform, purplish. Operculum
232 membranaceous, 3.6–4.5 mm long, slightly recurved, white, fimbriated-filamentous at the

233 margin, purplish. Limen none. Androgynophore white (sometimes speckled with dark
234 purple), 16–17 mm long, trochlea 5–7 mm long. Gynophore white, 1 mm long. Staminal
235 filaments white (sometimes finely speckled with dark purple), 9.0–10.0 mm long. Ovary
236 glabrous, ovoid, 5–6 mm long, olive green. Styles white (occasionally finely speckled with
237 dark purple at base), 6–7 mm long, stigmas greenish-white. Fruit ovoid, 8.1–8.5 cm long ×
238 6.5–6.7 cm diameter, lightly pubescent, immature green mottled with irregular white dots;
239 mature weights 78–120 g, yellow mottled with irregular white dots, pericarp 1.1–1.3 cm
240 thick; pulp aromatic, pleasant odor, flavor slightly sweet and acidic, total soluble solids
241 content in fruit juice 13.5–14.3 (°Brix), edible. Seeds obovate, 9–10 mm long × 4–5 mm
242 wide, dark brown, testa reticulate, acute at apex, 78–84 seeds per fruit, surrounded by a
243 translucent white aril. Figures 3, 4.

244

245 *Geographical Distribution*—Rare, endemic to the Colombian Department of Cundinamarca
246 (4,3853° to 5,0712° North and 74,2048° to 74,4339° West), Municipalities of Albán (2,309
247 m), Sylvania (1,900 and 2,000 m), Pacho (2,079 m), and Supatá (2,150 m) on the Eastern
248 flank of the Cordillera Oriental in the Andean region (Fig. 1).

249 *Etymology*—The specific epithet honors the Colombian botanist Gustavo Morales, who
250 discovered this new species, has spent most of his life enriching the knowledge of
251 Colombian botany, and has constantly fought for the conservation of plant resources,
252 especially passion flowers.

253 *Ecology*—*Passiflora gustaviana* was observed on hillsides, along roadsides and along
254 secondary cloud forest margins, climbing onto trees found in thickets, at elevations ranging
255 from 1,900 to 2,309 m above sea level in the department of Cundinamarca. This species

256 grows in areas with soils derived of volcanic ashes with middle organic matter content
257 levels, and with a sandy-clay-loam texture; the annual mean temperature is 16.2°C and the
258 annual rainfall is 1,241 mm (regular rainfall); and on average 4–5 sunshine hours per day
259 (Ideam 2016).

260 *Phenology*—This new species has been observed flowering in the months of March-April
261 to August-September, and fruiting from May-June to October-November. Carpenter bees
262 (*Xylocopa* sp.) were observed visiting open flowers and may be associated as a pollinator of
263 the species.

264 *Conservation Status*—*Passiflora gustaviana* is known only from few collections and would
265 likely be classified as endangered (EN) based on two assessment criteria, B2a and D, if we
266 had fully conducted its conservation assessment using IUCN (2014) guidelines. Within
267 category B, the new species is classified as B2a, as its area of occupancy is estimated as
268 less than 500 km² (20 km²), and its extended range of occurrence is less than 5,000 km²
269 (890.9 km²); habitats are severely fragmented and it is known to exist at five locations.
270 Regarding criterion D, the population size is estimated to be less than 50 mature
271 individuals, with just three plants observed during the collection trips.

272

273 *Additional Collections Examined*—COLOMBIA. Cundinamarca: Silvania, Cordillera
274 Oriental, vertiente occidental; estribaciones de la Cuchilla de la Cruz Grande, Km 5-6,
275 arriba de Fusagasugá, La Aguadita, 1,900-2,000 m, 28 May 1954, *J.M. Idrobo & J.*
276 *Hernández* 1660 (COL); Albán, frente a la estación del ferrocarril, 2,309 m, 1 Jul 1945, *H.*
277 *García-Barriga* 11610 (COL); Pacho, 2 km vía a Supatá, vereda la Esmeralda, 2,150 m, 20
278 June 2004, *G. Morales, M. Quintero & C. González* 2369 (JBB).

279

280 *Additional Collections Examined of Passiflora popenovii*—COLOMBIA. Cauca: El
281 Tambo, 1,700 m, 15 January 1938, *K. von Sneiden 1444* (US); Gazaabarita, 14 January
282 1965, *J.M. Idrobo 5636* (COL); entre el Tambo y el Alto del Rey, cultivada, 1,800 m, 11
283 January 1979, *L.K. Escobar & D. Escobar-Uribe 1017* (HUA); corregimiento San Joaquín,
284 vereda Pomoroso, finca los Naranjos, cultivada, 1,767 m, 6 February 2004, *C. M. Caetano,*
285 *L. Barrios, M. Restrepo & J. Ocampo 009* (VALLE); Timbío, zona urbana Barrio Boyacá,
286 cultivada, 1,875 m, 5 May 2002, *C.A. Chicangana 22* (CAUP); Vereda Santa María, n.v.
287 Granadillo de Quijos, 1,700 m, 1990, *R. Durán & J. Otálora 01* (TOLI). Cundinamarca:
288 Bogotá D.C., enredadera procedente de Timbío Cauca, cultivada, 2,550 m (4.66788 N;
289 74.09977 W), 16 August 2013, *G. Morales 3630* (JBB). ECUADOR. Rio Jamboya, 2,000
290 m, 1882, *A. Mille 223* (US); Pichincha: Quito, *L. Sodiro s.n* (P); Tunguragua: Baños, 1,850
291 m (introduced), 3 June 1921, *W. Popenoe 1271* (US, type); EL Oro, 24 January 1995, 1,400
292 m, *V. Eynden 218* (MO), Piñas, Sambotambo, cultivada, 2 September 1997, *V. Eynden 927*
293 (QCA).

294

295

296 DISCUSSION

297 A shorter list of 33 quantitative and 10 qualitative traits showed a high variability according
298 to a morphological characterization analysis (Table 3). This analysis supports the
299 classification of *P. gustaviana* as a new species of *Passiflora*, subg. *Passiflora*, supersect.
300 *Laurifolia*, series *Laurifoliae* (Ocampo et al. 2011). *Passiflora gustaviana* is distinguishable
301 from other highland *Laurifoliae* species that occur in the Andean region in Colombia

302 (>1,000 m.a.s.l.) such as *P. ambigua*, *P. pergrandis* Holm-Nielsen & Lawesson, and *P.*
303 *tolimana* Harms by the position (on the middle) and shape (round) of the petiole glands,
304 large and slender peduncles (10.5–12.8 cm long), corona filaments in five series, operculum
305 margin with short fimbriate filaments (purplish), and distinct size of the flowers (2.8–3.0
306 cm long x 6–7.2 cm wide) and fruits (8.1–8.5 cm long x 6.5–6.7 cm diameter).

307 Additionally, the new species was compared to its putative closest relative *P. popenovii*,
308 using information gathered from specimens that were recorded during collection trips and
309 herbaria visits, as well as found within the literature (Killip 1938, 1960; Holm-Nielsen et al.
310 1988; Ulmer and MacDougal 2004). *Passiflora gustaviana* is related to *P. popenovii*, but
311 differs by its stem color (mature branch, purple vs. green); stipule length (8–13 mm vs. 10–
312 17 mm); leaf size (12.5–16.5 cm long × 5.0–7.9 cm wide vs. 10.0–12.5 cm long × 3.9–5.1
313 cm wide); petiole glands (one pair vs. glandless); pedicel length (8–10 mm vs. 5–8 mm);
314 bract, sepal and petal size (see Table 3); bract color (light-green vs. reddish-purple), glands
315 (glandless vs. 3–4 pairs); corona filaments (5-series vs. 6-series), outermost longest
316 filament length (3.6–3.9 cm vs. 3.0–4.4 cm), inner longest filament length (3–4 mm vs.
317 4.0–5.5 mm), shape of the inner filament (minute-filiform vs. capillary) and color (purplish
318 vs. white and purplish-blue at apex); also in its operculum margin (fimbriated and purplish
319 vs. entire and white); staminal filaments length (9.0–10.0 mm vs. 6.8–8 mm); ovary
320 (glabrous vs. pubescent); color of mature fruits (yellow, mottled with irregular white dots
321 vs. yellow-orange); percentage of total soluble solids content in fruit juice (13.5–14.3 % vs.
322 14.8–16.8 %); and flavor (slightly sweet-acidic vs. sweet).

323 *Passiflora gustaviana* has only been encountered in the Department of Cundinamarca in
324 Colombia on the Eastern flank of Cordillera Oriental in the Andean region between 1,900

325 to 2,309 m above sea level, along roadsides, in secondary forest margins and climbing onto
326 trees found in thickets. *Passiflora popenovii* was proposed as a new species by Killip in
327 1922 based on a plant cultivated in the municipality of Baños at 1,850 m.a.s.l.
328 (Tungurahua, Ecuador), with seeds brought from the Eastern slopes of the Andes in
329 Ecuador by W. Popenoe (*W. Popenoe 1271*, US, type), but there is no record on whether
330 these seeds came from wild or cultivated plants. This species has only been found
331 cultivated in home gardens in the south-western part of Colombia (Cauca and Nariño
332 Departments) and Ecuador (El Oro, Loja, Pichincha and Tungurahua Provinces) under the
333 vernacular names of Curubejo, granadilla de Quijos or granadilla Caucana, and where it is
334 regularly propagated by cuttings (National Research Council 1989). Currently, its origin is
335 unknown and no wild representative of *P. popenovii* has been reported, so some authors
336 consider it extinct outside of cultivation (Ocampo et al. 2007; Yockteng et al. 2011).

337 The discovery of this new rare endemic species increases to 12 the number of species
338 (Table 4) belonging to the series *Laurifoliae* reported in Colombia (Ocampo et al. 2007,
339 2010, 2011), and suggests that this country concentrates the highest species diversity,
340 followed by Brazil. However, Colombia might still harbor many more unknown species,
341 given the low level of exploration in various zones of the Andes, the Caribbean, the
342 Amazon, the Orinoquia and the Pacific (Ocampo et al. 2007, 2010, 2015). Additionally, the
343 discovery of this new species in Colombian territory brings into question the putative
344 Ecuadorian origin of *P. popenovii* due to its morphological proximity and similar
345 ecological habitat to *P. gustaviana*. We here hypothesize that *P. popenovii* may be an
346 undiscovered species of Colombia that could be found growing on the slopes of high
347 mountains of the Colombian Andes.

348

349

350 *Passiflora* is considered as a biodiversity indicator in Colombia as its species have multiple
351 ecological interactions with many types of organisms (Ocampo et al. 2010), as such, it can
352 be considered to indirectly provide an ecosystem service through the regulation of
353 populations of other species. However, the species distributions have been drastically
354 affected mainly by the deforestation of rain and cloud forests in the Andean, Amazon, and
355 Pacific regions. This has occurred mainly due to extensive livestock production (pasturing),
356 plantations of illicit crops, hydroelectric dams, illegal gold mines, and agricultural practices
357 that currently support extensive coffee, sugar cane, rice, banana, and potato plantations
358 (Ocampo et al. 2007, 2010).

359 Indeed, the disappearance of *Passiflora* species from the ecosystem would entail the loss of
360 other organisms that depend on these, such as butterflies (*Heliconius* species) and many
361 nectar feeding insects, mammals (bats), and birds (Yockteng et al. 2011). In this context,
362 not only the species of the genus *Passiflora*, but also most of the Colombian Passifloraceae
363 (71%) are under some degree of threat according to the IUCN criteria (Ocampo et al.
364 2007). The discovery of *P. gustaviana* during field surveys growing on road edges in
365 severely fragmented habitats, as well as the fact that it has been classified as a probably
366 threatened species within the Endangered (ED, B2a, D) status, emphasizes the need for
367 conservation. *Ex situ* conservation techniques at botanical gardens and seed banks (e.g.
368 cryopreservation) are strategies that must be implemented in case critical habitats are
369 destroyed. These strategies have already begun to be implemented by the Botanical Garden

370 of Bogotá “José Celestino Mutis”, where individuals of the new species are under
371 cultivation.

372

373 In conclusion, statistical analysis allowed for the classification and determination of a new
374 species of *Passiflora* from 41 discriminant morphological descriptors, as well as its fruit
375 properties, *P. gustaviana* constitutes a promising new genetic resource and ecosystem
376 service as a wild relative useful for the improvement of cultivated *Passiflora* species.

377

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491

492

493 TABLE 1. List of 93 morphological descriptors evaluated in this study. Scales for qualitative characteristics: B
 494 (binary), O (Ordinal), and N (Nominal).

Organ	Qualitative characters (51)	Quantitative characters (42)
Stem	Pubescence (N) Color (N)	Internode length (mm)
Tendrill	Pubescence (N) Color (N) Anthocyanin (O)	
Stipule	Permanence (B) Color (N) Pubescence (N) Shape (N) Margin (N) Anthocyanin (O) Color (N)	Length (mm) Width (mm)
Leaf	Margin (N) Base shape (N) Apex shape (N) Presence of acumen (B) Pubescence – adaxial (N) Pubescence – abaxial (N) Anthocyanin – lamina (O) Anthocyanin – nerves (O) Color – adaxial (N) Presence of laminar nectaries (B)	Petiole length (mm) Petiole nectaries (number) Lobe length (mm) Lobe width (mm) Margin nectaries (number)
Peduncle	Pubescence (N) Color (N) Anthocyanin (O)	Length (mm) Diameter (mm) Pedicel length (mm)
Bract	Permanence (B) Pubescence (N) Color (N)	Length (mm) Width (mm) Margin nectaries (number)

	Anthocyanin (O) Shape (N)	
Flower	Color sepals (N)	Length (mm)
	Sepal awn (B)	Width (mm)
	Color petals (N)	Sepal length (mm)
	Color filaments at base (N)	Sepal width (mm)
	Color of filaments at apex (N)	Petal length (mm)
	Color hypanthium (N)	Petal width (mm)
	Hypanthium pubescence (N)	Outer filaments series of corona - radii (number)
	Color androgynophore (N)	Outer longest filament of corona length (mm)
	Color staminal filaments (N)	Inner filaments series of corona – pali (number)
	Color of ovary (N)	Inner longest filament of corona length (mm)
	Ovary pubescence (N)	Hypanthium length (mm)
	Color of styles (N)	Hypanthium diameter at base (mm)
	Color operculum (N)	Hypanthium diameter at above (mm)
	Color operculum margin (N)	Nectary chamber length (mm)
		Nectary chamber diameter (mm)
		Operculum length (mm)
		Androgynophore length (mm)
	Gynophore length (mm)	
	Staminal filaments length (mm)	
	Ovary length (mm)	
	Styles length (mm)	
Fruit	Shape (N)	Weight (g)
	Color fruit immature (N)	Length (mm)
	Color fruit mature (N)	Diameter (mm)
	Pubescence (N)	Seeds per fruit (number)
	Color aril (N)	Total soluble solids (°Brix %)
Seed	Shape seed (N)	Length (mm)
	Color seed (N)	Width (mm)

495

496 TABLE 2. Factor loadings from the principal component analysis (*varimax normalized* rotation) carried out on

497 37 quantitative descriptors. Bold values (Eigenvalues) contribute most to proportion of variance explained

Descriptors	Components		
	1	2	3
Internodes length	0.870	-0.144	0.427
Stipule length	-0.826	-0.437	0.329
Lobe length	0.888	0.387	-0.009
Lobe width	0.926	0.276	0.069
Petiole length	0.688	0.633	0.337
Petiole nectaries	0.999	-0.014	0.027
Peduncle length	0.392	-0.678	-0.606
Pedicel length	0.005	0.809	0.580
Bract length	0.962	-0.265	-0.058
Bract width	0.948	-0.307	0.024
Flower length	-0.729	-0.192	0.588
Flower width	0.097	-0.626	0.418
Outermost filament of corona length	-0.175	0.928	-0.095
Inner filaments series of corona	-0.998	-0.012	0.039

Inner longest filament of corona length	-0.999	0.014	-0.027
Petal length	0.346	0.918	0.175
Petal width	0.849	0.470	0.229
Sepal length	0.905	0.400	0.093
Sepal width	0.232	0.917	0.323
Nectary chamber length	0.815	0.105	0.561
Nectary chamber diameter	0.944	-0.327	-0.013
Hypanthium length	0.179	0.940	-0.100
Hypanthium diameter at base	0.960	-0.271	-0.017
Hypanthium diameter above	0.984	-0.156	-0.049
Operculum length	0.348	0.365	0.845
Androgynophore length	0.782	0.464	0.403
Staminal filaments length	-0.999	0.014	-0.027
Ovary length	-0.869	-0.461	-0.042
Styles length	-0.204	0.949	0.232
Fruit weight	0.999	0.023	0.011
Fruit length	0.924	0.215	0.080
Fruit diameter	0.936	0.301	0.041
Number seeds per fruit	-0.650	-0.067	-0.395
Total solid solubles content (°Brix)	-0.898	0.015	-0.275
Seed length	0.986	-0.113	0.068
% Total variance	62.425	25.964	7.740
Eigenvalue	23.097	9.607	2.864

498

499 TABLE 3. Summary and comparison of morphological characters between *P. gustaviana* (*Pg*) and *P. popenovii*

500 (*Pp*).

Organs	Descriptors	<i>Passiflora gustaviana</i>					<i>Passiflora popenovii</i>					Duncan's test (p≤0.05)				
		Minimum	Maximum	Mean	Std.Dev.	Coef.Var.	Minimum	Maximum	Mean	Std.Dev.	Coef.Var.	Pg	Pp			
Stem	Internodes length	mm	32.0	-	80.0	61.6	13.9	22.6	22.0	-	46.0	35.4	5.5	15.6	a	b
	Stem color (mature branch)				purple						green					
Stipules	Stipule length	mm	8.0	-	13.0	10.2	1.4	13.7	10.0	-	17.0	11.9	1.5	12.5	a	b
Leaves	Lobe length	mm	125.0	-	165.0	143.4	15.6	10.9	100.0	-	125.0	116.2	8.1	6.9	a	b
	Lobe width	mm	50.0	-	79.0	63.1	9.3	14.7	39.0	-	51.0	46.1	3.9	8.4	a	b
	Petiolar glands				one pair						absent - (rarely with a scarlike gland near base)					
Pedicel	Pedicel length	mm	8.0	-	10.0	9.2	0.8	8.3	5.0	-	9.0	6.9	1.2	18.1	a	b
Flowers	Flower length	mm	28.0	-	30.0	29.0	0.9	3.3	30.0	-	31.0	30.5	0.5	1.7	a	b
	Flower width	mm	60.0	-	72.0	65.5	4.3	6.5	60.0	-	80.0	71.7	7.1	9.9	a	b
	Bract length	mm	35.0	-	40.0	37.2	1.3	3.5	20.0	-	30.0	23.4	2.7	11.7	a	b
	Bract width	mm	20.0	-	24.0	21.9	1.2	5.4	11.0	-	18.0	14.8	1.9	12.9	a	b
	Bract glands				glandless						glandular					
	Color bract				light-green						reddish-purple					
	Petal length	mm	38.0	-	41.0	39.1	1.0	2.5	25.0	-	44.0	36.0	5.5	15.2	a	b
	Petal width	mm	14.0	-	18.0	15.8	1.1	7.0	10.0	-	15.0	11.8	1.7	14.3	a	b
	Sepal length	mm	40.0	-	45.0	43.0	1.3	3.1	36.0	-	42.0	40.0	1.7	4.2	a	b
	Sepal width	mm	20.0	-	23.0	21.8	0.9	4.1	16.0	-	24.0	20.6	3.2	15.4	a	b
	Outer longest filament of corona length	mm	36.0	-	39.0	37.8	0.9	2.4	30.0	-	44.0	39.0	4.2	10.8	a	b
	Inner filaments series of corona				3-seriate						4-seriate					
	Inner longest filament of corona length	mm	3.0	-	4.0	3.4	0.5	13.6	4.0	-	5.5	4.5	0.5	12.3	a	b
	Shape inner filaments				minute-filiform						capillary					
	Color of inner filaments				purplish						white and purplish-blue at apex					
	Hypanthium length	mm	12.4	-	14.0	13.1	0.5	3.8	8.2	-	11.5	9.9	1.2	11.8	a	b
	Hypanthium diameter at base	mm	20.0	-	21.0	20.7	0.4	2.2	12.0	-	16.0	13.5	1.4	10.3	a	b
	Hypanthium diameter above	mm	22.0	-	24.0	23.1	0.7	3.1	14.0	-	19.0	15.9	1.4	8.6	a	b
	Nectary chamber length	mm	7.0	-	9.0	8.2	0.6	7.0	3.0	-	5.6	4.4	0.6	14.1	a	b
	Nectary chamber diameter	mm	20.0	-	21.0	20.7	0.4	2.2	12.0	-	17.0	14.3	1.6	10.9	a	b
	Operculum length	mm	3.6	-	4.3	4.1	0.2	5.6	3.0	-	5.0	3.9	0.6	14.4	a	b
	Operculum margin				fimbriated-purplish						entire-white					
	Color operculum margin				purplish						white					
	Androgynophore length	mm	16.0	-	17.0	16.6	0.3	2.0	9.0	-	16.0	12.5	2.1	16.8	a	b
	Staminal filaments length	mm	6.8	-	7.1	6.9	0.1	1.3	6.0	-	9.9	8.4	1.2	14.5	a	b
	Ovary length	mm	5.0	-	6.0	5.7	0.3	5.4	6.0	-	7.8	6.8	0.9	12.3	a	b
	Ovary pubescence				glabrous						pubescent					
	Styles length	mm	6.0	-	7.0	6.3	0.3	5.1	5.0	-	9.0	6.9	1.6	22.9	a	b
Fruits	Fruit weight	g	199.0	-	210.0	203.3	3.1	1.5	78.0	-	120.0	100.4	12.7	12.7	a	b
	Fruit length	mm	81.0	-	85.0	82.8	1.2	1.5	63.0	-	88.0	69.9	5.6	8.0	a	b
	Fruit diameter	mm	65.0	-	67.0	66.3	0.6	0.9	50.0	-	63.0	54.3	3.2	5.9	a	b
	Color mature fruits				yellow mottled with irregular white dots						yellow-orange					
Seeds	Seeds per fruit	#	78.0	-	84.0	80.1	1.6	2.0	74.0	-	117.0	97.9	13.4	13.7	a	b
	Seed length	mm	9.0	-	10.0	9.3	2.2	1.6	7.0	-	8.0	7.2	4.8	5.1	a	b
Aril	Total soluble solids	%Brix	13.5	-	14.3	14.0	0.2	1.8	14.8	-	16.8	15.4	0.5	3.2	a	b

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503

TABLE 4. List of *Laurifoliae* species inventoried in Colombia according to Ocampo et al. (2007, 2010, 2011).

Species	Elevation m.a.s.l.	Distribution in the Biogeographic regions	Observations
<i>P. ambigua</i> Hemsl, 1902	10 – 1,500	Andean, Caribbean, Orinoquian, Pacific	Edible fruit
<i>P. sp. nov.</i>	1,800 – 1,880	Andean	Endemic, <i>D. Sánchez et al. 1378 and L. K. Escob F. J. Roldán 8662</i> (COL, CUVC, HUA, MEDEL)
<i>P. gleasonii</i> Killip, 1924	130 – 172	Amazonian	Unknown fruit, endemic
<i>P. guazumaefolia</i> Juss., 1805	6 – 70	Caribbean, Orinoquian	Edible fruit, synonymous <i>P. theobromifolia</i> DC.
<i>P. gustaviana</i> Ocampo & Molinari, 2017	1,924 – 2,309	Andean	Edible fruit, endemic
<i>P. killipiana</i> Cuatr., 1960	216	Amazonian, Orinoquian	Edible fruit, endemic
<i>P. laurifolia</i> L., 1753	79 – 237	Amazonian, Orinoquian	Edible fruit, synonymous <i>P. tinifolia</i> Juss.
<i>P. nitida</i> HBK., 1817	0 – 826	Amazonia, Andean, Orinoquian, Pacific	Edible fruit, synonymous <i>P. nymphaeoides</i> H. Ka
<i>P. pergrandis</i> Holm-Niels. & Lawesson, 1987	1,020 – 1,417	Andean	Edible fruit
<i>P. popenovii</i> Killip, 1938	1,500 – 1,900	Andean	Edible fruit, cultivated in home gardens
<i>P. riparia</i> Mart ex. Mast., 1872	180 – 300	Amazonian, Orinoquian	Edible fruit
<i>P. tolimana</i> Harms, 1894	250 – 1,800	Andean, Orinoquian	Edible fruit, synonymous <i>P. metae</i> M. Bonilla, C. Aguirre & C. Caetano

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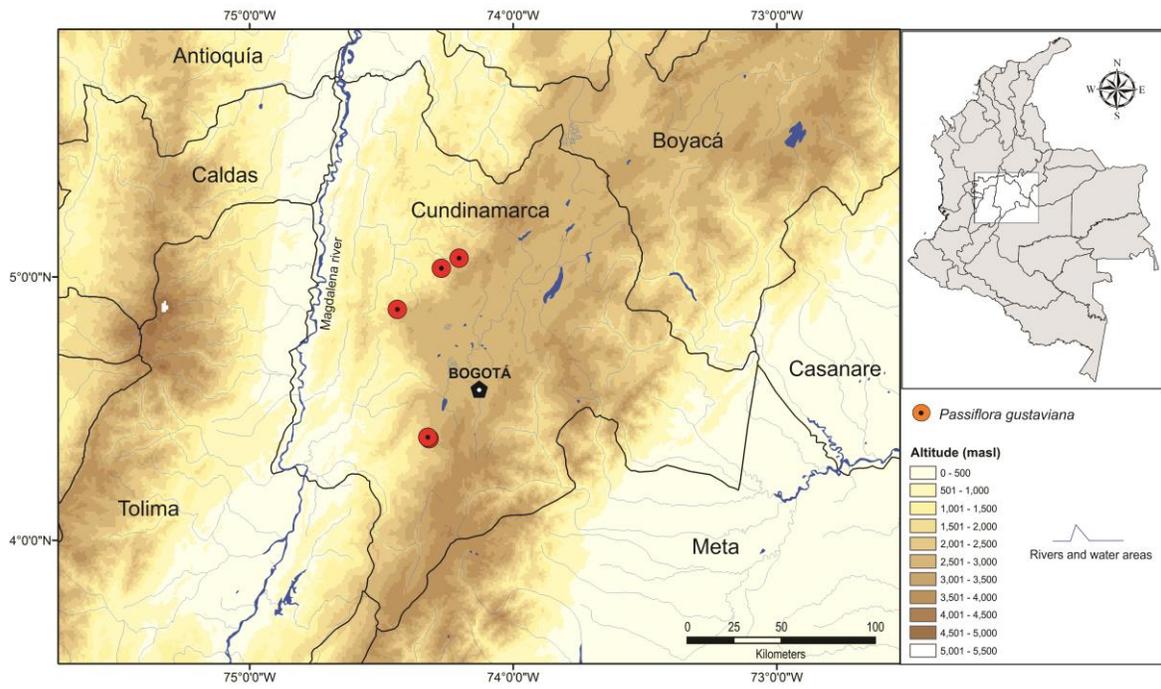
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FIG. 1. Geographical distribution of *P. gustaviana* (red dots) on Eastern Cordillera in the Colombia's Andean

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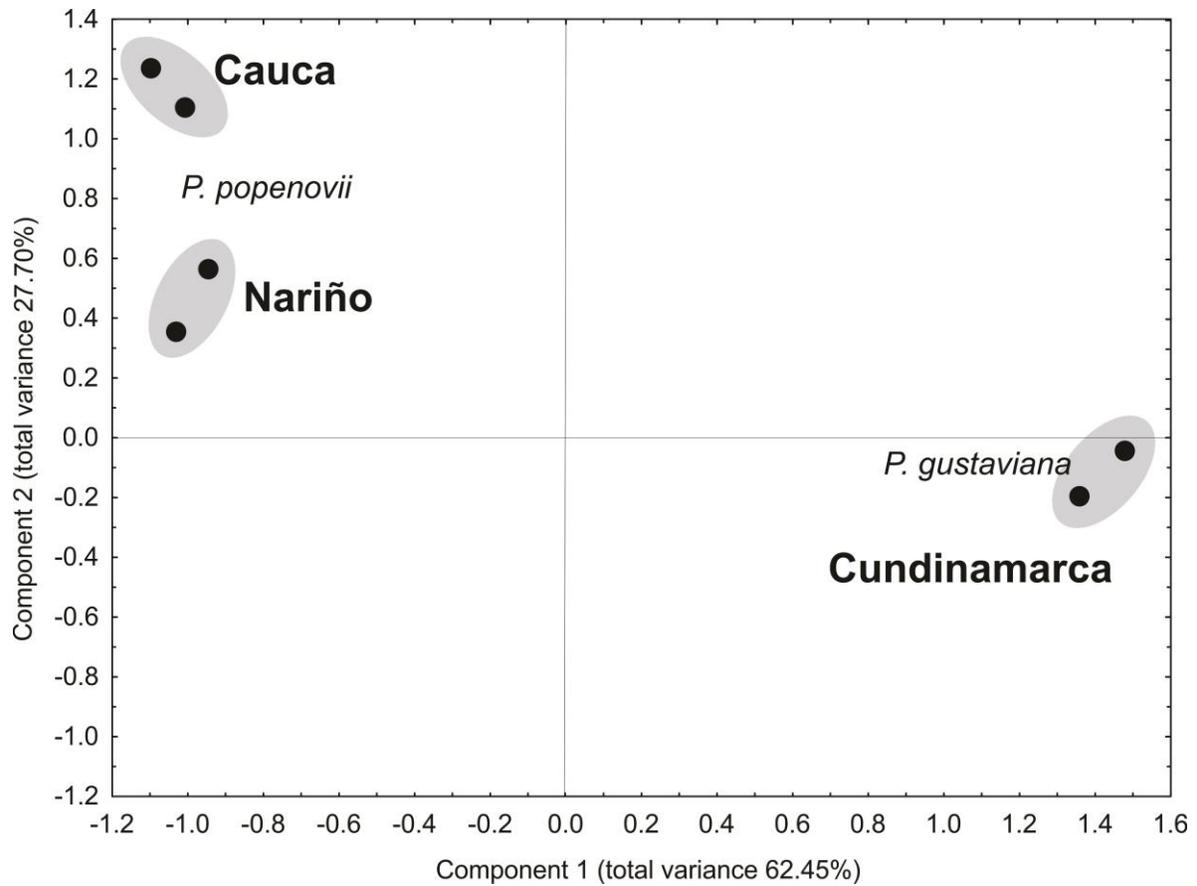
region from herbarium and field collections.

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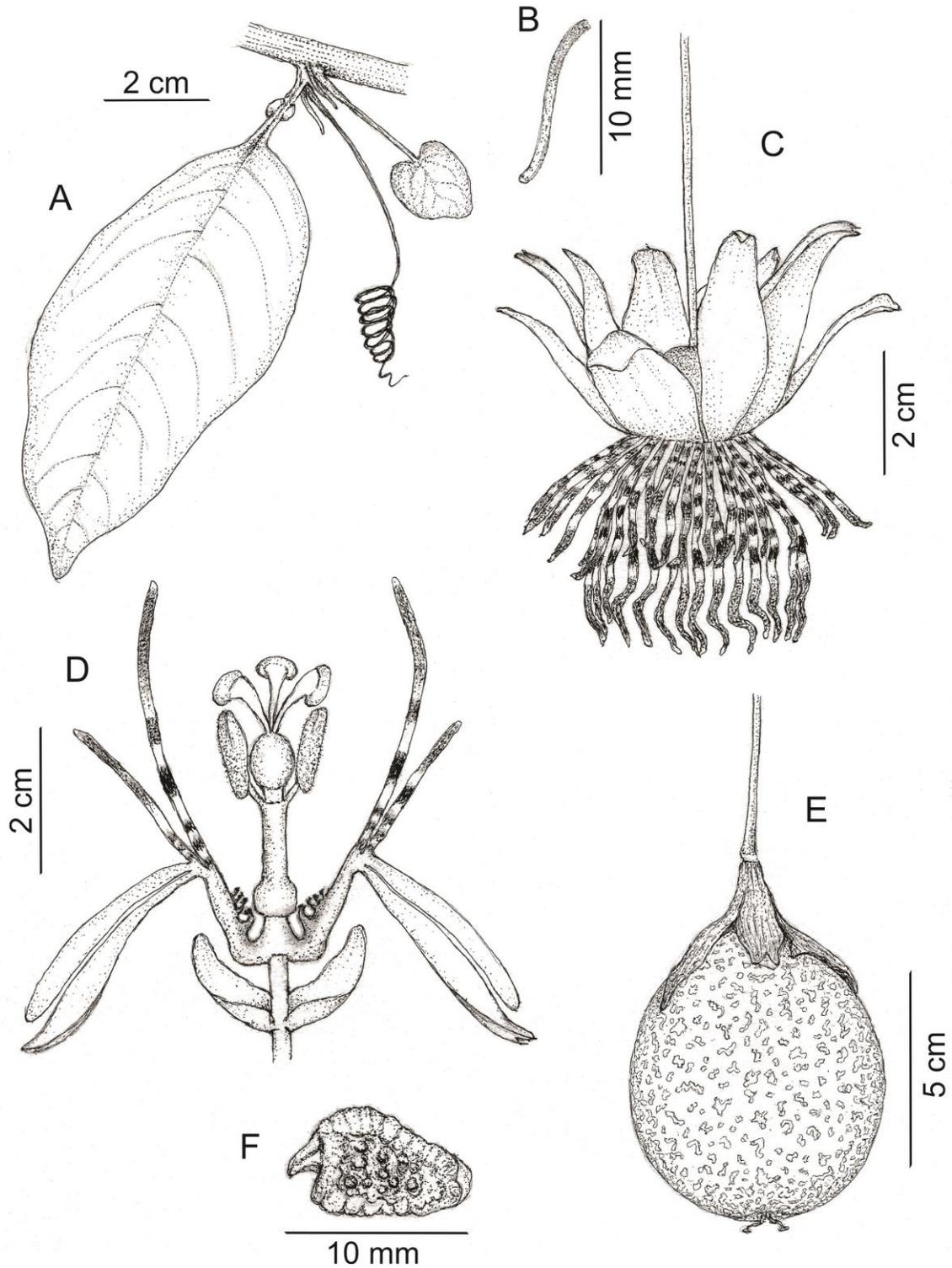
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509 FIG. 2. Plot of the scores obtained by *P. gustaviana* and *P. popenovii* accessions for the principal plane
510 quantitative variation components of the PCA.



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512 FIG. 3. *Passiflora gustaviana* Ocampo & Molinari. Drawing of a mature plant. A. Stipules, young bud, tendril,
 513 petiole, petiolar glands and leaf. B. Stipule. C. Flower, pendent. D. Longitudinal section of a flower. E. Fruit,
 514 mature. F. Seed. Drawn by Jairo Larrahondo, of the type (*Gustavo Morales 3190*, JBB).

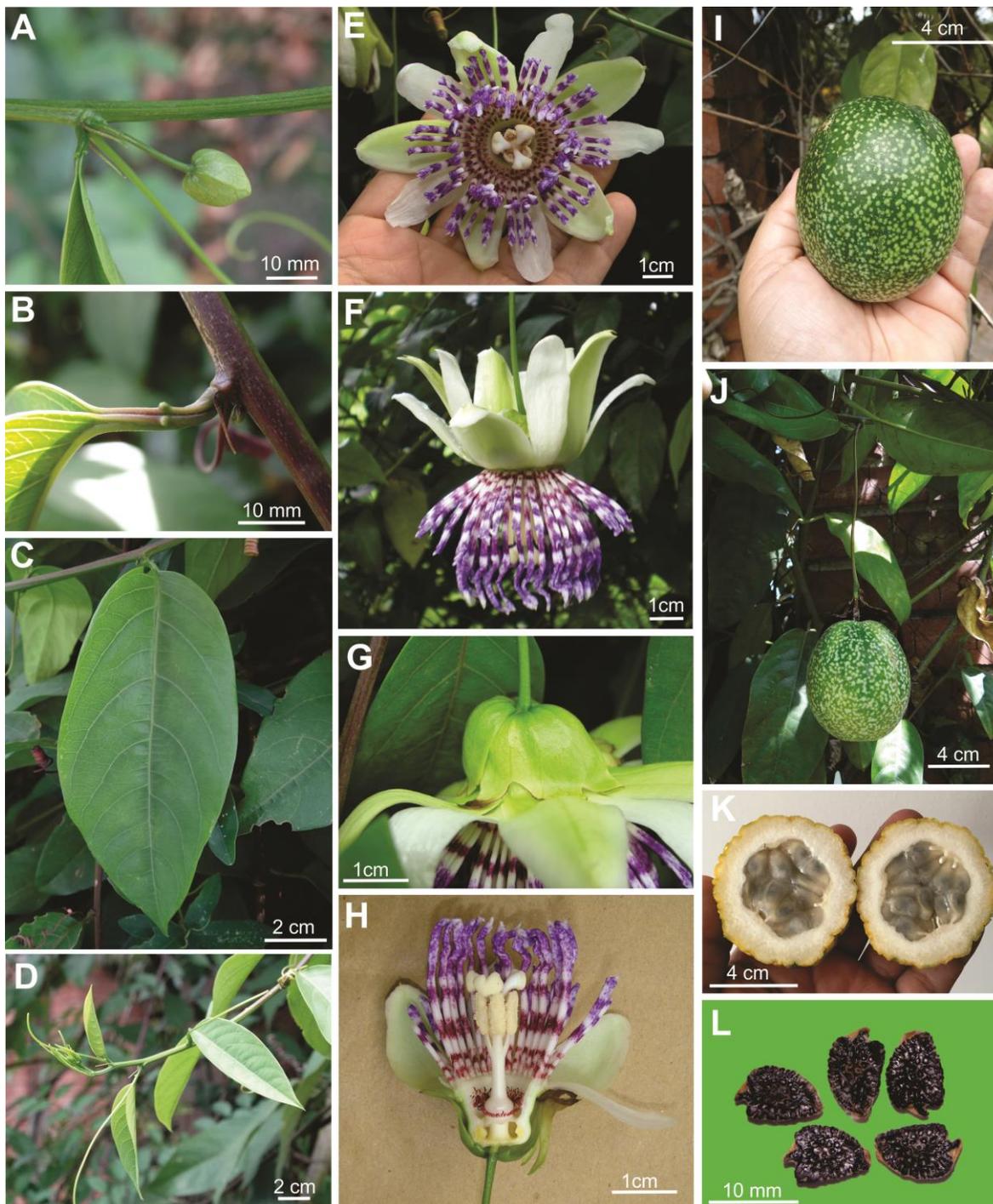


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516 FIG. 4. *Passiflora gustaviana* Ocampo & Molinari. Photographs of a mature plant. **A**, stipules, young bud and

517 tendril. **B**, petiole and petiolar glands. **C**, mature leaf. **D**, terminal branch, **E**, frontal view of a flower. **F**, flower,

518 pendent. **G**, floral bracts. **H**, longitudinal section of a flower. **I**, fruit, immature. **J**, fruit, becoming mature. **K**,
519 fruit mature, cross section showing mesocarp and pulp. **L**, seeds. Photographs by John Ocampo and Gustavo
520 Morales, of the type (*Gustavo Morales 3190*, JBB).



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