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Espeletia ocetana (Millerieae, Asteraceae), a New Tall Caulirosula from Colombia

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19 **Abstract.** A new species, *Espeletia ocatana* (Asteraceae), from about 3500 masl in Páramo de
20 Ocatá, Mongua, Boyacá department, Colombia, is described and illustrated. The new species
21 exhibits a caulescent rosette habitus (1–2 m tall), elliptic sessile leaf laminae covered with
22 greyish indumentum, robust bracteate thyrsoid capitulescences spreading laterally from rosette,
23 each holding 17–30(53) capitula with long external phyllaries and long yellow ray florets
24 arranged in less than 3 series. It is markedly different from the majority of other members of the
25 genus, and only slightly similar to *E. jaramilloi* S.Díaz, of which it can be easily distinguished by
26 its taller stems, bigger leaves with smaller length to width ratios and longer sheaths,
27 capitulescences with longer axes and longer proximal portion, involucre with longer phyllaries,
28 ray florets arranged in fewer series, with longer corollas, limbs, styles and style branches, and
29 disc florets with longer tubes, limbs and styles. In addition, *E. ocatana* is distributed allopatrically
30 in regards to *E. jaramilloi*, and differs as well in its ecological preference for humid to very
31 humid shrubby páramos. *Espeletia ocatana* is rather abundant in its type locality, which is a
32 relatively well-conserved páramo located within the limits of Parque Natural Regional Siscunsi-
33 Ocatá. However, the distribution range of *E. ocatana* remains unknown and the species is absent
34 from road margins, abandoned agriculture fields and other areas impacted by human activities.
35 Further studies will be necessary to know appropriately the extent of the geographic distribution
36 of *E. ocatana*, its ecological requirements and its phylogenetic affinities with other species.

37 **Keywords.** Andes, caulescent rosette, Compositae, frailejón, páramo.

38 *Espeletia* Mutis ex Bonpl. (Asteraceae: Millerieae: Espeletiinae) represents the best
39 example of taxonomic, morphological and ecological diversification in the Northern Andes high
40 elevation ecosystem known as páramo (Cuatrecasas 1986, 2013, Diazgranados 2012,
41 Diazgranados and Barber 2017, Mavárez 2019, Pouchon et al. 2018). The genus originated from

42 a single common ancestor in the last 2.5 MYA (Pouchon et al. 2018) and contains today 138
43 species, ranking amongst the fastest diversifying plant lineages on Earth (Madriñán et al. 2013,
44 Pouchon et al. 2018). In this relatively short period *Espeletia* generated as well a large diversity
45 of morphological types, including profusely branched, dichotomous and unbranched trees,
46 shrubs, and caulescent rosettes with short-branched or unbranched architectures. The latter type,
47 by far the most common, is a remarkable growth-form consisting of an erect stem usually tightly
48 covered by marcescent leaves, and topped by a crown of green young leaves around the apical
49 bud. The genus is also notable for its diversity of plant sizes (from 0.15–15 m), reproductive
50 strategies (monocarpy and polycarpy), and pollination syndromes (anemophily and entomophily).
51 Besides, the ample morphological variation in *Espeletia* is associated with a large ecological
52 diversity, particularly in regards to elevation ranges (2400–4800 masl), temperature and light
53 exposition (from relatively warm and shadowy gaps and borders in the upper Andean forest to
54 cold and open páramos), and environmental humidity (from very humid bogs to very dry rocky
55 outcrops) (Cuatrecasas 2013, Mavárez 2019).

56 *Espeletia* is distributed in the upper Andean forests and páramos of Venezuela, Colombia
57 and northern Ecuador, Venezuelan Cordillera de la Costa, Sierra de Perijá and Sierra Nevada de
58 Santa Marta (Cuatrecasas 2013). On a broad geographic scale, the genus exhibits two important
59 geographic centers of diversity, 50 species in the Venezuelan Cordillera de Mérida (Mavárez
60 2019) and ca. 78 species in the Colombian Cordillera Oriental, with only two species present in
61 both centers: the trees *E. neriifolia* (Bonpl. ex Humb.) Sch.Bip. ex Wedd. and *E. occulta*
62 S.F.Blake. The diversity of *Espeletia* in the latter center, and in Colombia in general, is currently
63 approximate as numerous species from this country are continuously described. For instance, 23
64 out of the 25 species described since year 2000 are from Colombia (Alzate and Giraldo-Gómez

65 2020, Díaz-Piedrahíta and Obando 2004, Díaz-Piedrahíta and Pedraza 2001, Díaz-Piedrahíta and
66 Rodríguez-Cabeza 2008, 2010, Díaz-Piedrahíta et al. 2006, Diazgranados and Morillo 2013,
67 Diazgranados and Sánchez 2013, 2017, Mavárez and Becerra 2019). 16 of these new species
68 come from the central section of Colombian Cordillera Oriental, an area composed by the páramo
69 complexes of Sierra Nevada del Cocuy, Pisba, Guantiva-la Rusia and Tota-Bijagual-Mamapacha
70 (names according to Morales et al. 2007) and that with ca. 42 species currently contains the
71 largest diversity of *Espeletia* in the country. The fact that such a large number of species has been
72 described in recent times probably reflects a delay in taxonomic research that is being rapidly
73 remedied with improvements in road infrastructure and better personal safety conditions in
74 Colombia after decades of armed conflict.

75 We recently collected an unusual *Espeletia* during a fieldtrip to Páramo de Ocetá in the
76 northern section of Parque Natural Regional Siscunsi-Ocetá, Boyacá, Colombia (Fig. 1). Park
77 officials have known this plant for some time and have identified it as *E. jaramilloi* S.Díaz,
78 although the populations of that species are found about 30–40 km northeast in Páramo de Pisba,
79 a different massif isolated from Páramo de Ocetá by the Gámeza river. In addition to allopatry,
80 individuals in the Ocetá population appear to differ from *E. jaramilloi* in the morphology of their
81 leaves and capitula, and in their preference for humid habitats. To test whether the Ocetá
82 population is co-specific with *E. jaramilloi* we performed uni- and multivariate morphometric
83 analyses of several leaf, capitulescence and capitulum traits with great taxonomic importance in
84 *Espeletia* (Cuatrecasas 2013). Our results show that the two populations do not belong to the
85 same species. The *Espeletia* from Páramo de Ocetá is described and illustrated in this work.

86

MATERIALS AND METHODS

87 ***Study sites, sampling and traits***—Twenty flowering individuals of *E. jaramilloi* were
88 collected on August and September 2020 at 3640 masl near Alto de Calarca (5.990094°N,
89 72.552189°W), at 3560 masl about 1 km W of Laguna Mesetas (5.945583°N, 72.581083°W) and
90 at 3600 masl about 2 km SW of Laguna Batanera (6.047492°N, 72.515674°W), all located in
91 Páramo de Pisba, Boyacá, Colombia (Fig. 1, filled blue circles). Twenty flowering individuals of
92 the Ocetá *Espeletia* population were collected on August 2019 and August 2020 at 3550 masl
93 near San Ignacio (5.751621°N, 72.730276°W), a northern sector of Páramo de Ocetá located
94 within the limits of PNR Siscunsi-Ocetá, Boyacá, Colombia (Fig. 1, filled red circle). From each
95 individual we measured stem height (RSH), and sampled two leaves on opposite sides of the
96 middle part of the rosette (without sheaths to avoid excessive damage), two fully developed
97 capitulescences and two mature capitula. Most leaf and capitulescence traits were measured
98 without magnification, using a tape or a ruler; whichever was most suitable for the trait being
99 measured. Leaf area (LA) was estimated using the weight of a leaf copy drawn on paper of
100 known density and a 0.01 g precision balance. Leaf density (LD) was determined by the dry
101 weight of 1.54 cm² leaf fragments obtained with a circular punch cutter and a 0.001 g precision
102 balance. Leaf lamina density (LLD) was estimated by the weight of the same leaf fragments with
103 indumentum removed using a razor blade, expressed as a percentage of LD. Leaf indumentum
104 density (LID) was estimated as 100%-LLD. Capitula were preserved in 70% ethanol and their
105 traits measured in the laboratory using a 3.5× magnification device and a vernier caliper. The ray
106 floret series trait included the fraction of incomplete whorls (e.g. 3.25, 2.50). Three replicates per
107 capitulum were obtained for some traits measured in repeated capitulum elements (e.g. phyllaries,
108 florets, paleae). In total, 46 quantitative traits were measured on each plant: 1 in rosettes, 12 in
109 leaves, 9 in capitulescences and 24 in capitula, with replicates per individual varying between 1

110 (rosette trait), 2 (leaf, capitulescence and ten capitulum traits) and 6 (fourteen capitulum traits)
111 (Table 1).

112 **Analyses**—Shapiro-Wilk tests were used to verify the normal distribution of data for each
113 trait, and a log₁₀ transformation was applied to significant deviations. Homocedasticity was
114 verified using Levene tests (no significant tests found). Differences between populations for each
115 morphological trait were evaluated using one-way analysis of variance (ANOVA), with data
116 averaged per individual. A Bonferroni correction was applied to adjust the significance cut-off
117 value for the number of tests performed, $\alpha_{\text{adj}} = 0.05/46 = 1.09\text{e-}3$ (Sokal & Rohlf 2012, p239). In
118 addition, morphological data averaged per individual were also used in a Principal Component
119 Analysis (PCA) aimed to reduce data dimensionality and facilitate the graphical representation of
120 differences between and within populations. All tests and analyses were performed in R using the
121 basic package *Stats* and visualized with packages *ggplot2* and *factoextra*.

122 **Taxonomic descriptions**—Complete leaves (with sheaths) and mature capitulescences of
123 ten additional individuals from the Ocetá population were sampled for description purposes.
124 Morphological descriptions of these samples were mostly based on dry material, although some
125 traits related to stems and rosettes were measured directly in the field, while descriptions and
126 drawings of capitula and their elements were made from samples preserved in 70% ethanol.
127 These specimens were deposited in herbarium COL, whereas duplicates will be sent to FMB,
128 JBB and UPTC (herbaria acronyms follow Thiers 2020). Terms employed in descriptions follow
129 the glossary in Roque et al. (2009).

130 RESULTS

131 Results of F-tests from one-way ANOVA are shown in Table 2. It can be seen that the

132 means of 26 out of the 46 morphological traits studied in *E. jaramilloi* and the Ocotá *Espeletia*
133 population are significantly different, and this fraction is likely an underestimate given the
134 conservative nature of the Bonferroni correction (Sokal & Rohlf 2012, p239). The magnitudes of
135 the observed differences are very high, as of those 26 significant traits, eleven differ with $p < 1.e-$
136 9 (1 leaf and 8 capitulum traits), nine with $p = 1.e-9-1.e-7$ (1 rosette, 4 leaf and 4 capitulum
137 traits) and six with $p = 1.e-6-1.e-4$ (2 leaf and 4 capitulescence traits). In regards to trait type,
138 stem height (RSH) and six out of seven traits related to leaf shape showed significant differences,
139 i.e. LA, LL, LW, LR, LMW, LBW (the exception was length at max. width, LWL, $p = 0.169$). At
140 the opposite, among the five leaf traits related to densities or angles only vein density showed
141 significant differences (LVD, $p = 4.4e-7$). Differences in capitulescence traits were relatively less
142 marked, as they are statistically significant for four out of five traits related to size and degree of
143 primary branching, i.e. CL, CPL, CBN, CBhN, while they are not for the four traits related to
144 lengths of bracts (C1BL) or bracteal internodes (C1BL, C2BL), and number of capitula (CHN).
145 For the capitulum, there were no significant differences at traits related to diameters, i.e.
146 involucre (HID), ray circle (HRD), disc circle (HDD) and receptacle (HReD), or number of
147 repeated elements, i.e. phyllaries (H1EPN, H2EPN and HIPN) and florets (HRN and HDN). In
148 the opposite, differences at all traits related to the size of repeated capitulum elements appeared
149 highly significant, with the only exception of ray floret tube length (HRTL, $p = 0.166$). Overall,
150 three traits showed no overlap in values between the two populations (H1EPL, HRS and HDSL),
151 and another six showed $< 10\%$ overlap (LA, HRL, HRLl, HRBL, HDL, and HDTL) (Table 2).
152 However, with the exception of LA and HRL, all overlaps are due to a single extreme value in
153 one of the two populations.

154 A graphical representation of the PCA results, describing the ensemble of differences

155 between and within the two populations, is shown in Fig. 2. In regards to variables, axis 1
156 explains 40.3% of total morphological variance and has an important contribution from traits
157 largely related to differences between populations, such as leaf area (LA), leaf width (LW),
158 number of ray floret series (HRS) and the lengths of capitulum elements (H...L). In the opposite,
159 axis 2 explains 10.4% of variance and is mainly composed by traits related to differences within
160 populations, such as capitulescence distal portion length (CDL) and the number of capitula
161 (CHN), ray florets (HRN) and disc florets (HDN) (Fig. 2A). For individuals, it can be seen that
162 they segregate into two clearly distinct and non-overlapping morphological clusters (Fig. 2B).
163 The average Euclidean distances in PCA space between individuals and the centroids of their
164 own population vs. the reciprocal population are 1.98 (sd. 1.03) vs. 8.20 (sd. 1.28) for *E.*
165 *jaramilloi*, and 2.30 (sd. 1.60) vs. 8.30 (sd. 1.71) for Ocetá *Espeletia*. Thus, average distances of
166 individuals between populations are at least 3.5 times larger than within populations.
167 Furthermore, without exception, each individual is both closer to its own centroid than to the
168 reciprocal one and belongs to the same group of its nearest neighbor (Fig. 2B). The ensemble of
169 these results reveals an important morphological discontinuity between *E. jaramilloi* and the
170 Ocetá *Espeletia*, indicating that they are not co-specific. The population from Ocetá is raised to
171 species level and described below.

172 TAXONOMIC TREATMENT

173 *Espeletia ocetana* M.T.Becerra & Mavárez, *sp. nov.* TYPE: COLOMBIA, Boyacá, Mongua,
174 Páramo de Ocetá, about 10.5 km in the road Mongua-Vereda Sismosa, 3550 masl,
175 5.745472°N 72.736000°W, August 18 2019, *M.T. Becerra, J. Mavárez & J. Aguirre 44*
176 (holotype: COL, isotypes: COL, FMB).

177 **Diagnosis**—Tall caulescent rosette with greyish appearance, elliptic leaf laminae,
178 bracteate thyrsoid capitulescences spreading laterally from rosette, 17–30(53) capitula with long
179 external phyllaries, long yellow ray florets arranged in less than 3 series, and long disc florets and
180 paleae. Similar to *E. jaramilloi* S.Díaz, but with taller stems; leaves with bigger laminae, smaller
181 length to width ratios and longer sheaths; capitulescences with longer axis and longer proximal
182 (unbranched) portion; involucre with longer phyllaries; ray florets arranged in fewer series, with
183 longer corollas, limbs, styles and style branches; disc florets with longer tubes, limbs and styles.

184 Caulirosula (Figs. 3A), polycarpic, stem height 0.7–1.8 m, covered with marcescent
185 leaves. Rosettes light green-greyish, diam 70–110 cm, height 50–70 cm. **Leaf** sessile (Figs. 3C,
186 4A); sheath open (Fig. 4A), trapezoid, coriaceous, 6.3–7.8 cm × 4.8–6.3 cm, with yellowish hairs
187 < 20 mm, adaxially only near lamina base; lamina elliptic, 23–43 cm × 6.5–14.0 cm, length/width
188 ratio 2.9–5.3:1, apex acute, progressively attenuated towards base, margins entire, not revolute,
189 abaxial surface with greyish velvety indumentum < 1–5 mm, midvein pale-yellow, round and
190 prominent all along, secondary veins visible, mostly craspedromous, parallel, distally curved or
191 divided, 7–11/dm apart at mid-section of lamina, angles 43°–67°; adaxial surface with whitish-
192 cinereous lanuginous indumentum < 1–5 mm, shorter, sparser and rougher in oldest leaves,
193 midvein pale-yellow, proximally prominent, distally thin to almost invisible, secondary veins
194 barely noticeable. **Capitulescence** dichasial (Figs. 3D, 4B), thyrsoid, axillary (lateral), extending
195 horizontally from rosette before ascending, axes robust, 47–98 cm long, 1.3–2.5 × longer than
196 laminae, with abundant yellow indumentum near its base, golden near its top; proximal
197 (unbranched) portion 32–61 cm long, with 3–5 opposite bract pairs decreasing in length upwards:
198 1st 16–21 cm, 2nd 14–20 cm, 3rd 12–16 cm, 4th-5th 8–12 cm; distal (branched) section 16–51 cm
199 long, with 3–5 opposite branch pairs and a terminal cyme, all subtended by triangular bract pairs,

200 lengths of branch axes (and internodes) decrease upwards: 5–10 cm (5–8 cm), 4–7 cm (3–6 cm),
201 4–5 cm (3–4 cm), cyme 2–4 cm, peduncles of capitula 3–4 cm, capitula 17–30(53), 3 in terminal
202 cyme and 1–3 in each branch. **Capitulum** radiate (Figs. 3E-F), dropping or nodding, with 159–
203 334 florets, diameters of involucre 17–25 mm, ray circle 27.5–43 mm and disc 15–29.5 mm;
204 involucre campanulate, phyllaries 24–40, in three series, tips of external phyllaries surpassing ray
205 circle; external phyllaries 4–6 (Fig. 5A-B), ovate-acuminate, 16.4–26.4 mm × 4.1–17.3 mm, 7–
206 12-veined, abaxially covered with golden curled hairs 6–12 mm long, adaxially pubescent only
207 on distal third; intermediate phyllaries 2–15 (Fig. 5D), ovate-acuminate or lanceolate-oblong,
208 8.1–24.7 mm × 3.9–11.5 mm, 5–7-veined, abaxially with yellow-golden curled hairs 3–6 mm
209 long; internal phyllaries 14–26 (Fig. 5E), lanceolate-oblong, 7.0–16.2 mm × 2.3–6.8 mm, 5–7-
210 veined, abaxially with yellow-golden hairs 1–3 mm long along central vein and distal end;
211 receptacle convex, paleaceous, diam 7.0–14.5 mm, ray paleae lanceolate (Fig. 5F), 6.5–11.4 mm
212 × 1.4–3.9 mm, 4–5-veined, abaxially with erect yellowish hairs < 1.5 mm along central vein,
213 adaxially glabrous, disc paleae oblong-acute (Fig. 5G), white-hyaline, amplexant, 7.0–10.4 mm
214 × 1.3–2.5 mm, 5–6-veined, abaxially with erect yellowish-brown hairs < 1.5 mm in the distal
215 end, adaxially glabrous. **Ray florets** 40–80 (Figs 5C), in 2.0–2.9 series; corollas liguliform,
216 bright yellow, 12.3–18.8 mm long; tubes 1.3–3.1 mm long, densely hirsute, particularly at base,
217 hairs < 0.5 mm long, eglandular, erect, transparent, uniseriate, septate, with round apex; limbs
218 oblong, 10.5–16 mm × 1.2–3.2 mm, 2–3-dentate, 3–6-veined; styles 5.1–9.7 mm long, arms 1.8–
219 3.9 mm long, apex lanceolate, papillose, base glabrous; ovaries 1.1–3.7 mm × 1.0–1.2 mm;
220 cypselae 3-ribbed (Fig. 5H), 2.1–2.9 mm × 0.7–1.0 mm, dark brown, glabrous, epappose. **Disc**
221 **florets** 107–227 (Fig. 5I), 7.0–10.2 mm long; tubes 1.5–4.4 mm, with scattered hairs < 0.5 mm
222 long, eglandular, uniseriate, septate, with round apex; limbs tubular-infundibuliform, yellow,

223 4.3–8.2 mm, lobes triangular < 0.8 mm, margins thickened, glabrous; anthers brown, 1.8–3.4 mm
224 long, often exceeding corolla, calcarate, base shortly sagittate, apical appendages ovate-acute,
225 filaments 5.2–7.6 mm long; styles 0.7–1.0 mm long, arms short, conical, glabrous, papillose,
226 nectaries tubular, 5-denticulate, 1.0–1.5 mm long.

227 ***Distribution and Habitat***—*Espeletia ocetana* is known so far from two areas in Páramo
228 de Ocetá, Boyacá dept., Colombia: near San Ignacio in the municipality of Mongua, and around
229 Laguna Siscunsi in the municipality of Sogamoso (Fig. 1). It grows above 3500 masl on flat areas
230 and gentle slopes with humid to very humid soils rich in organic matter. Occurs in open páramo
231 communities with large coverage of *Calamagrostis* sp (Poaceae) and *Chusquea* sp (Poaceae), the
232 rosettes *E. boyacensis* Cuatrec. and *E. pescana* (S.Díaz) S.Díaz, and shrubs in the genera *Aragoa*
233 Kunth (Plantaginaceae), *Baccharis* L. (Asteraceae), *Diplostephium* Kunth (Asteraceae) and
234 *Pentacalia* Cass. (Asteraceae).

235 ***Etymology***—The specific epithet refers to Páramo de Ocetá, Parque Natural Regional
236 Siscunsi-Ocetá, in which the type locality of the new species is located.

237 ***Conservation status***—Data Deficient (DD) category of the International Union for
238 Conservation of Nature (IUCN 2019) (see Discussion).

239 ***Additional Specimens Examined***—*Espeletia ocetana*—**Colombia**, BOYACÁ: Mongua,
240 Páramo de Ocetá, about 10.5 km in the road Mongua-Vereda Sismosa, 3550 masl, 5.745472°N
241 72.736000°W, *M.T. Becerra, J. Mavárez & J. Aguirre 45* (paratype: COL, JBB); *M.T. Becerra, J.*
242 *Mavárez & J. Aguirre 46* (paratype: COL, UPTC). *Espeletia jaramilloi*—**Colombia**, BOYACÁ: in
243 the road between Socha and Sacama, Páramo de Pisba, 3550–3650 masl, *Jaramillo-Mejía,*
244 *Lozano & Díaz 5049* (paratype: COL); Páramo de Pisba, western slope, 3500–3550 masl,

245 *Cuatrecasas & Jaramillo-Mejía* 28738 (COL); Páramo de Pisva [Pisba], road Socha-La Punta,
246 filo Batanera, 2 km SW Laguna Batanera, 3730 masl, *Cleef* 4763 (COL); Páramo de Pisva
247 [Pisba], road Socha-La Punta, km 61.5, Alto de Granados, East. 3700 masl, 6.01106°N
248 72.5424°W, *Cleef* 4542 (COL); Socotá, Páramo de Pisba, 3480 masl, *Camargo* 8061 (COL);
249 Socotá, Páramo de Pisba, Alto de Calarca, 3600 masl, *Stancik & Medina* 2325 (COL).

250

DISCUSSION

251 Both uni- and multivariate analyses of 46 rosette, leaf, capitulescence, and capitulum
252 traits support the recognition of *E. ocetana* as a morphologically distinct species easily
253 distinguishable from *E. jaramilloi*. The ANOVA results show that the majority of traits analyzed
254 are significantly different between the two taxa, frequently with extremely low p-values. About
255 20% of traits show no or < 10% range value overlap between *E. ocetana* and *E. jaramilloi* (Table
256 2), with overlaps usually due to a single extreme value in either species. The PCA results also
257 support strongly the recognizing of *E. ocetana*, since it appears as a distinct and non-overlapping
258 morphological cluster compared to *E. jaramilloi*. Furthermore, this analysis shows that the
259 average morphological distance between individuals of the two taxa is at least 3.5 times larger
260 than the average distances between individuals of the same population, which reveals a very
261 important morphological discontinuity. More generally, these results provide another compelling
262 example of the potential of morphometric analyses to distinguish closely related taxa in
263 Asteraceae (e.g. Cook et al. 2009, Owen et al. 2006, Sempe et al. 2019), and particularly in
264 *Espeletia*, a genus known for the close similarity between its species in which nonetheless this
265 type of tools have rarely been used (i.e. Benavides et al. 2010, Pineda et al. in press).

266 *Espeletia ocetana* exhibits a tall caulirosula habit with bracteate dichasial capitulescences
267 common in many of species in the genus. However, compared with morphologically similar
268 species distributed in the páramos of Ocetá and Pisba, *E. ocetana* can be easily distinguished
269 using vegetative traits by its sessile leaves with length/width ratios < 5 and sheaths longer than 6
270 cm, or using reproductive traits by its capitulescences with > 2 proximal bract pairs, ray florets
271 arranged in < 3 series and ray corollas longer than 12 mm with limbs longer than 10.5 mm (Table
272 3). This combination of characteristics is in fact quite unique, not seen in any other species in the
273 genus, regardless of their distribution area. Furthermore, *E. ocetana*'s arrangement of ray florets
274 in less than three series is an extremely rare condition among *Espeletia* caulirosulas with opposite
275 capitulescences. It has been observed so far only in *E. aristeguietana* Cuatrec. from Venezuelan
276 Cordillera de Mérida, *E. cabrerensis* Cuatrec. from the south section of Colombian Cordillera
277 Oriental and *E. frontinoensis* Cuatrec. from the north section of Colombian Cordillera Occidental
278 (Cuatrecasas 2013).

279 Despite its distinctiveness, *E. ocetana* exhibits certain resemblances in gross morphology
280 with *E. jaramilloi*, as both species have rather large greyish rosettes with sessile leaves and
281 robust bracteate thyrsoïd yellow capitulescences spreading laterally from its lower portion. The
282 morphological similarities between *E. ocetana* and *E. jaramilloi* and their geographic
283 distributions suggest that the two species could be closely related and the result of a relatively
284 recent speciation event, a suggestion that nonetheless would require confirmation using
285 molecular phylogenetics (e.g. Pouchon et al. 2018). Given that the largest differences between the
286 two species are related to reproductive (e.g. size of capitulum elements) rather than vegetative
287 traits (e.g. size and shape of leaves), if the speciation scenario suggested above turns out to be
288 correct, it would provide further support to recent findings showing that morphological change

289 for reproductive traits in *Espeletia* can be very rapid and tends to be concentrated at the tips of
290 the phylogenetic tree, i.e. between closely related species (Pouchon et al. in press).

291 At this time there is not enough information to evaluate adequately the conservation status
292 of *E. oacetana*. The species is abundant in its natural habitat, which seems relatively well
293 conserved and protected by the Parque Natural Regional Siscunsi-Ocetá. However, it is absent
294 from the dryer areas within its type locality, as well as from areas under influence of human
295 activities, such as road margins, abandoned agricultural fields and localities impacted by past
296 fires. Thus, although *E. oacetana* must for now be categorized as data deficient (DD) according to
297 the IUCN criteria (IUCN 2019), its fine scale spatial distribution indicates that this species could
298 have narrow ecological tolerances that make it highly sensitive to habitat and climate changes.
299 We strongly recommend national research institutes and environmental authorities to conduct
300 local evaluations to gather more information about the ecology and demography of this species
301 and take the measures needed to guarantee its conservation.

302 Most recently described species in *Espeletia* have relatively small distribution ranges,
303 come from poorly sampled areas and have been described using material previously
304 unrepresented in herbaria, all of which indicates that their descriptions are the result of first time
305 encounters with taxa that until then had escaped discovery. Other species will presumably be
306 discovered in the near future, with the increase in scientific explorations to páramos planned as
307 part of national and regional management strategies for this ecosystem (e.g. Sarmiento et al.
308 2013), the establishment of new conservation areas and the improvements in road infrastructure
309 and personal safety conditions. This is particularly true for the central section of Colombian
310 Cordillera Oriental, where an important number of regional natural parks with páramo habitats
311 have been created during the last few years (e.g. Guantiva-La Rusia in 2008, Rabanal in 2009,

312 Siscunsi-Ocetá in 2011, Cortadera in 2015, El Valle in 2015 and Pan de Azúcar in 2018). The
313 census of biodiversity in these areas is currently under study as part of ongoing research projects
314 based on scientific explorations (e.g. Colombia BIO 2016), which has led to the discovery the
315 several new paramo and sub-paramo plant taxa (e.g. Aguilar-Cano and Hind 2020, Malagón et al.
316 2019, Mendoza-Cifuentes et al. 2019). There is no doubt that these actions will also help to
317 enhance the overall knowledge about *Espeletia* and provide further support to the trend that
318 páramos in this section of Cordillera Oriental hold the highest diversity of this genus in
319 Colombia.

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329 AUTHOR CONTRIBUTIONS

330 MTB provided morphological data, line drawings (Fig. 5) and photographs, and was the
331 primary author of the new species description. JM performed statistical analyses, provided maps
332 and line drawings (Fig. 4), and was the primary author for the rest of the manuscript.

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426

427 TABLE 1. List of traits analyzed and results of ANOVA in the two *Espeletia* populations
 428 evaluated. Superscripts on plant parts and traits represent the number of replicates per individual
 429 and per trait, respectively. Grey background indicates traits significantly different between the
 430 two populations as determined by the ANOVA and Bonferroni correction (see Table 2).

Rosette¹	Capitulum²
1. Stem height (RSH) ¹	1. Involucre diameter (HID) ¹
Leaf²	2. Ray circle diameter (HRD) ¹
1. Leaf area (LA) ¹	3. Disc diameter (HDD) ¹
2. Leaf length (LL) ¹	4. Receptacle diameter (HReD) ¹
3. Leaf max. width (LW) ¹	5. Number of external phyllaries in 1 st row (H1EPN) ¹
4. Length/width ratio (LR) ¹	6. Length of external phyllaries in 1 st row (H1EPL) ³
5. Length at max. width (LWL) ¹	7. Number of external phyllaries in 2 nd row (H2EPN) ¹
6. Midpoint width (LMW) ¹	8. Length of external phyllaries in 2 nd row (H2EPL) ³
7. Base width (LBW) ¹	9. Number of internal phyllaries (HIPN) ¹
8. Veins/dm at midsection (LVD) ¹	10. Length of internal phyllaries (HIPL) ³
9. Vein angles at midsection (LVA) ¹	11. Number of ray florets (HRN) ¹
10. Leaf density (LD) ¹	12. Ray floret series (HRS) ¹
11. Leaf lamina density (LLD) ¹	13. Ray floret length (HRL) ³
12. Leaf indumentum density (LID) ¹	14. Ray floret limb length (HRLL) ³
Capitulescence²	15. Ray floret tube length (HRTL) ³
1. Length (CL) ¹	16. Ray floret style length (HRSL) ³
2. Proximal section length (CPL) ¹	17. Ray floret style branch length (HRBL) ³
3. Distal section length (CDL) ¹	18. Ray palea length (HRPL) ³
4. Number of bract pairs (CBN) ¹	19. Number of disc florets (HDN) ¹
5. 1 st bract length (C1BL) ¹	20. Disc floret length (HDL) ³
6. 1 st bracteal internode length (C1BIL) ¹	21. Disc floret limb length (HDLL) ³
7. 2 nd bracteal internode length (C2BIL) ¹	22. Disc floret tube length (HDTL) ³
8. Number of branch pairs (CBhN) ¹	23. Disc floret style length (HDSL) ³
9. Number of capitula (CHN) ¹	24. Disc palea length (HDPL) ³

431

432 TABLE 2. Minimum, mean (sd) and maximum values of morphological traits averaged per
 433 individual in *E. jaramilloi* and *Ocetá Espeletia*. P-value refers to F-tests from one-way ANOVA.
 434 Significant differences after Bonferroni correction are highlighted with grey background.
 435 Asterisks indicate degree of trait value overlap between populations: ***: no overlap, **: 0–5%
 436 overlap, *: 5–10% overlap Trait acronyms given in Table 1.

Trait (unit)	Min / Mean (sd) / Max		P-value
	<i>E. jaramilloi</i>	<i>Ocetá Espeletia</i>	
RSH (cm)	56.0 / 79.9 (17.7) / 122.0	70.0 / 129.9 (32.5) / 182.0	3.1e-7
*LA (cm ²)	82.8 / 125.2 (24.4) / 174.0	136.7 / 243.4 (77.6) / 477.9	8.7e-10
LL (cm)	23.8 / 28.6 (2.3) / 32.0	24.0 / 34.1 (5.0) / 43.0	7.8e-5
LW (cm)	4.7 / 5.9 (1.0) / 7.9	6.5 / 9.1 (1.8) / 13.9	3.8e-9
LR	3.9 / 4.9 (0.7) / 6.3	2.9 / 3.8 (0.6) / 5.0	9.2e-6
LMW (cm)	4.3 / 5.6 (1.0) / 7.9	6.3 / 8.8 (1.8) / 13.9	2.5e-9
LBW (cm)	1.1 / 1.7 (0.3) / 2.4	1.7 / 2.6 (0.6) / 3.8	5.9e-7
LWL (cm)	13.4 / 17.6 (2.0) / 20.5	12.3 / 18.9 (3.2) / 26.5	0.169
LVD (#/dm)	9 / 12.1 (2.5) / 17	7 / 8.6 (1.2) / 11	4.4e-7
LVA (°)	51 / 58.4 (4.6) / 66	43 / 53.5 (5.1) / 62	0.003
LD (mg/cm ²)	20 / 24.85 (3.95) / 36	19 / 23.20 (2.76) / 29	0.130
LID (%)	7.3 / 18.2 (6.1) / 36.4	7.7 / 26.2 (9.6) / 46.0	0.009
LLD (%)	63.6 / 81.8 (6.1) / 92.7	54.0 / 73.8 (9.6) / 92.3	0.003
CL (cm)	44.5 / 58.3 (11.3) / 80.3	50.5 / 70.1 (9.7) / 95.5	7.4e-4
CPL (cm)	17.0 / 33.0 (9.0) / 49.5	34.5 / 44.6 (5.3) / 56.5	1.8e-5
CDL (cm)	16.0 / 25.2 (6.6) / 40.0	16.0 / 25.5 (7.6) / 51.0	0.976
CBN (#)	2 / 3.1 (0.7) / 6	3 / 4.0 (0.6) / 5	3.4e-5
CBhN (#)	3 / 4.7 (0.5) / 6	3 / 3.8 (0.6) / 5	2.2e-5
C1BL (cm)	12.8 / 19.3 (3.7) / 26.3	4.0 / 21.1 (5.6) / 29.0	0.658
C1BIL (cm)	3.0 / 7.2 (2.8) / 13.0	2.0 / 6.4 (4.2) / 19.0	0.182
C2BIL (cm)	4.5 / 10.4 (2.6) / 15.5	5.5 / 10.1 (2.5) / 14.5	0.748
CHN (#)	18 / 26.6 (4.9) / 39	17 / 24.1 (7.8) / 53	0.103
HID (mm)	15.75 / 19.53 (2.22) / 25.70	17.70 / 20.50 (2.03) / 24.85	0.138
HRD (mm)	24.00 / 32.91 (4.26) / 39.00	30.85 / 35.69 (3.15) / 42.50	0.023
HDD (mm)	14.20 / 18.26 (2.69) / 25.80	15.20 / 18.46 (2.28) / 24.35	0.736
HReD (mm)	6.79 / 10.56 (2.02) / 14.45	8.55 / 11.35 (1.75) / 14.45	0.167
H1EPN (#)	4 / 4.13 (0.28) / 5	4 / 4.33 (0.41) / 6	0.071
H2EPN (#)	3 / 6.50 (2.24) / 11	2 / 4.83 (1.68) / 10	0.014
HIPN (#)	13 / 17.55 (1.99) / 21	14 / 19.00 (2.65) / 26	0.059
HRN (#)	53 / 67.6 (7.5) / 78	44 / 62.5 (9.1) / 80	0.056
HDN (#)	104 / 179.35 (35.63) / 245	119 / 164.95 (31.61) / 221	0.209
***H1EPL (mm)	8.78 / 12.77 (1.73) / 15.55	16.37 / 20.27 (2.76) / 26.35	8.2e-13
H2EPL (mm)	8.04 / 10.20 (1.12) / 11.98	10.99 / 14.25 (1.87) / 17.80	2.1e-10
HIPL (mm)	6.37 / 8.38 (0.87) / 9.89	8.60 / 10.41 (1.10) / 12.42	1.3e-7
***HRS (#)	3.2 / 3.39 (0.20) / 3.9	2.2 / 2.37 (0.25) / 2.9	1.2e-15
*HRL (mm)	11.90 / 13.95 (1.24) / 16.03	15.62 / 17.63 (1.07) / 18.90	1.0e-11
**HRL (mm)	7.73 / 9.70 (0.98) / 11.42	11.15 / 13.05 (0.96) / 14.23	9.2e-13
HRTL (mm)	1.38 / 2.15 (0.27) / 2.49	1.75 / 2.26 (0.24) / 2.64	0.166
HRSL (mm)	4.31 / 5.07 (0.51) / 6.31	5.72 / 6.88 (0.50) / 7.78	1.9e-13
**HRBL (mm)	1.22 / 1.61 (0.19) / 2.09	2.09 / 2.52 (0.24) / 2.97	8.9e-16
HRPL (mm)	6.51 / 7.47 (0.55) / 8.46	7.57 / 8.79 (0.60) / 9.92	1.2e-8
**HDL (mm)	6.34 / 6.84 (0.29) / 7.33	7.18 / 8.34 (0.48) / 9.30	9.4e-15
HDLL (mm)	3.57 / 4.59 (0.35) / 5.17	4.52 / 5.44 (0.44) / 6.65	5.8e-8
*HDTL (mm)	1.76 / 2.25 (0.34) / 2.68	2.55 / 2.95 (0.27) / 3.72	7.5e-12
***HDSL (mm)	6.20 / 6.90 (0.38) / 7.68	7.98 / 8.65 (0.44) / 9.42	3.5e-16
HDPL (mm)	5.96 / 7.22 (0.53) / 8.28	7.47 / 8.52 (0.61) / 9.73	1.3e-8

437 TABLE 3. Morphological comparison among *Espeletia* species with bracteate opposite capitulescences distributed in the páramos of
 438 Pisba and Siscunsi-Ocetá. Grey background indicates traits showing no overlap with *E. ocetana*. Sources: *E. ocetana* and *E. jaramilloi*
 439 (this study), *E. boyacensis*, *E. curialensis* and *E. oswaldiana* (Cuatrecasas 2013), *E. mirabilis* (Díaz-Piedrahíta and Rodríguez-Cabeza
 440 2010), *E. soroca* and *E. pulcherrima* (Díaz-Piedrahíta and Rodríguez-Cabeza 2010).

Trait (unit)	<i>E. ocetana</i>	<i>E. jaramilloi</i>	<i>E. boyacensis</i>	<i>E. oswaldiana</i>	<i>E. curialensis</i>	<i>E. mirabilis</i>	<i>E. soroca</i>	<i>E. pulcherrima</i>
Max. stem height (m)	1.8	1.2	0.5	2(5)	10	ca. 1.2	ca. 3	ca. 2.3
Leaf length/width ratio	2.8–5.0:1	3.7–6.6:1	7–17:1	6–9:1	5–7:1	> 6	ca. 3.8–4.8	ca. 4.8–5.5
Leaf type	sessile	sessile	pseudopet.	sessile	sessile	pseudopet.	pseudopet.	pseudopet.
Sheath length (cm)	6.3–7.8	5.5–6.0	3.0–5.5	7–10	5.5–7.0	5.5–6.0	7.5–9.0	7.5–8.0
# Bract pairs	3–5	2–3(6)	3–5	3–4	(3)4–6	2	1–2	1
Outer phyllary length (mm)	14.0–31.0	7.7–17.4	6.0–11.0	10.0–13.0	15.0–17.0	8.5–19.0	22.0–24.0	21.0–24.0
Ray floret series	2.2–2.9	3.2–3.9	3–4	3–4	3	6	4	4
R. corolla length (mm)	12.3–18.8	8.1–14.6	7.0–12.0	7.6–15.0	9.0–15.0	11.8–14.5	9.0–10.0	10.0–13.3
R. cor. limb length (mm)	10.5–16.0	6.5–12.0	5.5–10.5	6.0–8.4	6.8–12.8	10.1–12.6	7.0–8.0	7.6–10.9
R. cor. style length (mm)	5.1–9.7	3.8–7.2	3.0–4.0	4.5–5.0	6.0–8.0	4.3–5.5	6.5–7.0	7.0–8.0

442 FIG. 1. Maps of the Colombian Cordillera Oriental showing the known localities of
443 *Espeletia jaramilloi* S.Díaz in Páramo de Pisba (blue) and the *Espeletia* from Páramo de
444 Ocetá (red). Filled dots indicate localities analyzed in this study.

445 FIG. 2. Results of the PCA analysis. **A.** Biplot graph for all traits (variables) studied.
446 Traits with values within the extreme 15% are highlighted in red (axis 1) or blue (axis 2).
447 **B.** Biplot graph for individuals. Red: *E. jaramilloi*, blue: Ocetá *Espeletia*. Ellipses: 90%
448 of population variation, larger dots: centroids.

449 FIG. 3. **A.** *Espeletia ocetana*. **B.** *Espeletia jaramilloi*. **C.** *E. ocetana*, lateral view of
450 rosette. Note the sessile leaves with elliptic outline and greyish indumentum, and the
451 robust bracteate capitulescences spreading laterally from lower portion of rosette. **D.** *E.*
452 *ocetana*, distal portion of capitulescence. **E-F.** *E. ocetana*, capitulum. Note the
453 arrangement of ray florets in < 3 series.

454 FIG. 4. *Espeletia ocetana*. **A.** Schematic representation of leaf (right: abaxial surface with
455 lamina indumentum removed to highlight secondary venation, left: adaxial surface). **B.**
456 Diagrams of variations in capitulescence structure.

457 FIG. 5. *Espeletia ocetana*. **A, B.** Outer phyllaries (right: abaxial surface, left: adaxial
458 surface). **C.** Ray floret, **D.** Intermediate phyllary (right: abaxial surface, left: adaxial
459 surface). **E.** Inner phyllary (abaxial surface). **F.** Ray floret palea (abaxial surface). **G.**
460 Disc floret palea (abaxial surface). **H.** Cypsela. **I.** Disc floret.







