# Taxonomic novelties in páramo plants. *Espeletia ramosa* (Asteraceae), a new species from Colombia Jesús Mavárez

Laboratoire d'Écologie Alpine, UMR UGA-USMB-CNRS. Université Grenoble Alpes. BP 53, 2233 rue de la Piscine, 38041 Grenoble Cedex 9, France. jesus.mavarez@univ-grenoble-alpes.fr

and

#### María Teresa Becerra

Instituto Universitario de Investigación CIBIO, Universidad de Alicante, 03690 San Vicente del Raspeig, Alicante, España

### ABSTRACT

A new species *Espeletia ramosa* (Espeletiinae, Asteraceae) is described and illustrated. This species is not apparently allied to any other, however its morphological relationships with the most similar *Espeletia* species are discussed. It is currently only known from a small subpáramo area near "Laguna de Tota", Boyacá department, Cordillera Oriental, Colombia. *Espeletia ramosa* is the only Colombian species growing as a compact colony of rosettes branched near the ground, and harbours an array of morphological traits relatively plesiomorphic in comparison with other Espeletinae members, which make it one of the living species phenotypically closest to the presumed ancestor of the subtribe. In addition, *E. ramosa* represents a notable addition to the diversity of *Espeletia* growth forms in Colombia, a country where *Espeletia* spp. with consistently and profusely branched rosettes were so far unknown. Unfortunately, *E. ramosa* must be considered as an "Endangered" or even "Critically Endangered" species, since its only known population occupies an area < 0.2 km<sup>2</sup>. Moreover, the ensemble of areas with relatively undisturbed habitats potentially suitable for the species in the same mountain range likely represents < 10 km<sup>2</sup>, is already highly fragmented and seriously threatened by the expansion of the agricultural frontier. Published on-line www.phytologia.org *Phytologia 101(4): 222-230 (Dec 21, 2019)*. ISSN 030319430.

KEY WORDS: Andes, Asteraceae, Caulescent Rosette, Colombia, Espeletia, Páramo.

The subtribe Espeletiinae (Asteraceae) represents the best example of taxonomic, morphological and ecological diversification in the high elevations of the Northern Andes, particularly in the grassland habitat known as páramo (Cuatrecasas, 1976, 1986, 2013; Diazgranados, 2012; Diazgranados and Barber, 2017; Pouchon et al., 2018; Mavárez, 2019). The ca. 140 species in the group, broadly distributed in the upper Andean forests and páramos of Venezuela and Colombia, with one species in northern Ecuador (E. pycnophylla Cuatrec.), have two important diversity centres in the Colombian Cordillera Oriental (ca. 80 spp.) and the Venezuelan Cordillera de Mérida (54 spp.). Espeletiinae exhibit a remarkable degree of morphological diversity, which includes trees with profusely branched, dichotomous or unbranched stems, shrubs, and rosettes that can be sessile, short-branched or, notably, giant caulescent. The latter is a remarkable growth-form that produces an erect stem usually tightly covered by the bases of old and dead leaves, and topped by a crown of green young leaves around the apical bud. The group also exhibits diversity in reproductive strategies; with polycarpic species that reproduce repeatedly across adult life and monocarpic species that reproduce only once before death (Smith, 1981; Cuatrecasas, 2013), and in pollination syndromes; with entomophilous and anemophilous species (Berry and Calvo, 1989). In addition, Espeletiinae are noteworthy by their degree of ecological diversity in regards with tolerance to (a) elevation: ranging from mountain cloud forests at about 1300 m to the very edge of glaciers at 4800 m, (b) humidity: from wet páramo bogs to xeric periglacial talus slopes and rocky outcrops, and (c) solar irradiation: from gaps in the forest to open vegetation such as páramo grasslands. In contrast, these plants show very limited dispersal capacities, as the achenes in all but one species lack pappus (the exception is the scale-like pappus of E. Chardonii A.C.Sm.). They are therefore transported by gravity, with longdistance dispersal events hypothesised to have occurred only in a few tree lineages from lower elevations

(Pouchon et al., 2018). Another interesting fact about Espeletiinae is that they frequently become ecologically dominant in the páramos of Northern Ecuador, Colombia and Venezuela in terms of abundance and biomass (Luteyn, 1999). For instance, adult densities of *E. schultzii* Sch.Bip ex Wedd in Venezuela varies between 0.57–2.97 plants/m<sup>2</sup> (Smith, 1981), while local densities of *E. grandiflora* Mutis ex Bonpl in Colombia vary between 0.45–1.43 plants/m<sup>2</sup> (Fagua and González, 2007). Indeed, Espeletiinae usually contribute so largely to the characteristic physiognomy of páramos that for the general public they are the very defining element of this beloved ecosystem, a fact celebrated in countless postcards, books, webpages and even Colombia and Venezuelan national banknotes.

Given the diversity and ecological dominance of Espeletiinae in the páramos, it is not surprising that this group had been subjects of many taxonomic studies. Taxonomic research started with the formal publication of the genus *Espeletia* Mutis ex Bonpl. and the descriptions of three Colombian species (*E. argentea* Bonpl., *E. corymbosa* Bonpl. and *E. grandiflora* Bonpl.) by A. J. A. Bonpland (Humboldt and Bonpland, 1809). Since then, the number of species in the subtribe has been growing considerably, particularly to the extraordinary work due by J. Cuatrecasas (75 spp), but also by S. Díaz-Piedrahita and his collaborators (20 spp), A. C. Smith (9 spp), H. A. Weddell (8 spp), P. C. Standley (6 spp) and L. Aristeguieta (4 spp), among others. One would expect taxonomic research to be nearly complete after more than two centuries of study in a group like Espeletiinae, with its morphological distinctiveness, its association with the comparatively small páramo habitat (ca. 35.000 km<sup>2</sup>), and the great attraction they generate to the people, yet the truth is that much taxonomic research remains to be done. For instance, several species are known by only a handful of specimens, while many localities are desperately underrepresented or not at all in collections, particularly in Colombia, where access to certain páramos has been hampered by the scarcity of roads and decades of armed conflict.

Here we describe a remarkable new Espeletiinae species from near Laguna de Tota, in the Colombian Cordillera Oriental. The new species was found during a series of fieldtrips set up to some relatively poorly explored páramos in the central section of the Boyacá department in Colombia, a region that nonetheless holds the highest Espeletiinae diversity in the country (Diazgranados, 2012; Cuatrecasas, 2013), and where several new species have been described in the last decade (Díaz-Piedrahita and Rodríguez-Cabeza, 2010).

### **MATERIALS AND METHODS**

Hereafter we follow the classification system for the subtribe Espeletiinae proposed by Mavárez (2019), which considers as taxonomically valid the genus *Espeletia*, while the other genera included in the subtribe by Cuatrecasas (1976, 1995) are treated as heterotypic synonyms of *Espeletia*.

The material described below was collected in August 2019 near el Alto, km 4–5 in the road Pesca-Tota, Boyacá, Colombia (Fig. 1). Most traits were measured on dry samples. However, morphological traits associated with the plant habitus (e.g., stem size and architecture, rosette diameter, number of leaves, number of capitulescences) were measured directly in the field (10 plants). On the other hand, capitulum elements (e.g., phyllaries, disc flowers, ray flowers) were drawn from samples preserved in 50% ethanol. Collected plants of the new species were preserved and distributed to herbarium COL (duplicates will be distributed to herbaria FMB, JBB y UPTC). Collections of somehow similar species already present in other herbaria were also studied (see 'Specimens examined' below). Herbaria acronyms follow Thiers (2019).

## TAXONOMIC TREATMENT

Espeletia ramosa Mavárez & Becerra, sp. nov.

TYPE: COLOMBIA, Boyacá, near El Alto, about 4.5 km in the road Pesca-Tota, 3060 m., 5.546853 N, -

73.031896 W, August 17 2019, *M.T. Becerra, J. Mavárez* and *J. Aguirre 35* (Holotype: COL; Isotypes: COL). Additional collections from the same type locality (paratypes): *M.T. Becerra, J. Mavárez* and *J. Aguirre 36* (COL), *37* (COL).

**Diagnosis.** *Espeletia ramosa* is unlike any other species. It is somehow similar to *E. jahnii* Standl., from which it differs by having polycarpic rosettes, much broader leaves, lateral capitulescences and ligulate capitula. It also resembles Colombian *E. pleiochasia* Cuatrec. and *E. garciae* Cuatrec., but differs by having stems profusely branched at ground level, rigidly coriaceous leaves, bracteate capitulescences and ligulate capitula.

**Habitus** (Fig. 2A): branched polycarpic caulescent rosettes with short, thick stems. Stems are usually divided at ground level into several alternate, prostrate or subterranean branches. Some individuals, usually of small size, appear as undivided and isolated rosettes. Branches usually divided into robust branchlets that can divide again or become terminal, erect and crowned by a rosette. Branches and branchlets are shorter than the rosette diameter, so the latter overlap to a large extent with each other, giving the plant the appearance of a compact colony of up to 15 rosettes. The diameter of terminal branchlets is 7–10 cm at the base of the rosette and their height is frequently smaller than 25 cm, occasionally up to 50 cm. Terminal branchlets are covered by the remains of marcescent leaves and/or their sheaths. Fully grown rosettes are 30–60 cm in diameter, 25–35 cm in height, and are composed by 25–35 green leaves.

Leaf (Fig. 2B, 3A): coriaceous, sessile. Laminae oblanceolate, attenuate towards the base, with acute apex, erect, rigid, total length 23–27 cm, maximum width 4.5–6.5 cm (at 16–18 cm from the base), length to width ratio 3.5–5.7:1, width at mid-length 4.0–5.5 cm, width above base 0.75–1.10 cm. Margins entire, revolute, occasionally undulate. Young leaves loosely covered by a thin veil of light yellow straight hairs up to 4 mm long; becoming paler or whitish, deciduous and shorter with age. Adaxial sides of mature leaves are green, sparsely covered by whitish hairs that are denser and longer near the base, where they can reach up to 4 mm. Very old leaves are almost entirely glabrous adaxially and rough at touch. The costa is visible all along, pale-yellow, mostly flat but prominent at the slightly enlarged base. Abaxial sides of mature leaves are pale-green, covered by a yellowish-creamy indument longer than on the adaxial side and that can reach up to 8 mm near the base. The costa is visible, pale-yellow, round and prominent all along. Secondary nerves mostly parallel but becoming distally irregular (curved or divided), frequently not reaching the leaf margin, adaxially visible although faint, much more prominent abaxially, deviation angles 30°–60°, bases separated by 0.6–1.9 cm at the mid-section of the leaf. Sheaths open, semi-circular, coriaceous, 1.90–2.40 cm long, 3.30–4.40 cm wide, adaxially glabrous, whitish, abaxially woolly, with yellowish hairs up to 1.8 mm long.

**Capitulescence** (Fig. 2B, C): 1–10 per rosette, coetaneous, corymbose, axillary (lateral), erect, robust, straight or slightly curved, 39–47 cm long, 1.5–2.0x longer than leaves; covered by abundant whitish, villous indument, longer at the capitulescence base, becoming gradually shorter along the axis. Vegetative section 28–34 cm long, ebracteate at the base but with 2–5 alternate bracts along the axis. Reproductive section 8–15 cm long, formed by 9–11 compound branches (i.e., further divided into branchlets), plus several simple branches (undivided) at the top of the axis. Lengths of branches and internodes decrease gradually along the axis, giving the capitulescence the appearance of an almost perfect corymb. Terminal branches and branchlets end with 2–6 capitula.

**Capitulum** (Fig. 2D, 3B–F): radiate, sub-globbose, small, 6–8 mm in diameter, each with 32–50 flowers, discs 6.5–8.0 mm in diameter, ligular circles 12.5–15.0 mm in diameter. 4–5 external (sterile) phyllaries, thickly herbaceous, adaxially glabrous with 2–5 visible nerves, abaxially villous with hairs < 1 mm long, the outermost pair ovate-triangular, attenuate distally, 3.8–5.2 mm x 2.0–2.2 mm; the others ovate, acuminate, 3.4–5.0 mm x 2.0–3.2 mm. Internal (sterile) phyllaries in two rows, herbaceous, oblong, 3.2–

4.6 mm x 1.6–2.2 mm, adaxially glabrous with 3–4 visible nerves, abaxially villous, hairs < 1 mm long. Fertile phyllaries membranaceous, transparent, oblong, 3.2–3.8 mm x 1.4–1.6, adaxially glabrous, abaxially villous on the distal end. Paleae oblong, 3.1–4.0 mm x 1.2–1.4 mm, distal margin villous. Receptacles convex, glabrous.

**Ray flowers** (Fig. 3G, H): 10–16 ray flowers per capitulum, in one series. Corollas ligulate; tubes 1.0–1.1 mm long (excluding the ovaries), 0.9-1.0 mm in diameter, densely hirsute, hairs up to 1 mm long; ligules bright yellow, oblong, 3.4-5.2 mm x 1.8–2.5 mm, bi or three-dentate, with a few scattered adaxial hairs. Styles bifid, 1.0–1.5 mm long. Achenes heart-shaped, triangulate, glabrous, dark brown, 1.9-2.1 mm long, 1.1-1.9 m wide. **Disc flowers** (Fig. 3I): 21–36 disc flowers per capitulum, 3.4-4.5 mm long (excluding anthers); tubes 1.8-2.1 mm long, 0.5-0.8 mm in diameter, with a few scattered hairs < 1.0 mm long; limbs 2.0-2.5 mm long when fully open, densely hirsute at the base, hairs up to 1.2 mm long, lobes sparsely hairy; anthers brown, shorter than corolla.

**Distribution.** Hitherto only known from the type locality.

**Ecology.** Grows on dry crests, slopes and soils covered by a shrubby sub-páramo vegetation with presence of other rosettes (e.g., *Eryngium*, *Puya*), sclerophyllous shrubs (e.g., *Hesperomeles*, *Monnina*, *Stevia*), herbs (e.g., *Castilleja*, *Halenia*) and some grasses.

Etymology. Refers to the branched stems of the species.

**Similar species.** Venezuelan *E. jahnii* Standl. also produces branched stems with prostrated or subterranean branches, but their rosettes are monocarpic with strictly linear leaves (length:width ratio 50–100:1), their capitulescences are terminal with profusely bracteate axes, and their capitula are larger (12–18 mm) with eligulate ray flowers. Colombian *E. pleiochasia* Cuatrec. sometimes produces branched caulescent rosettes, but their stems are straight, erect, taller (3–6 m) and divided distally (2–4 rosettes per plant), their oblanceolate leaves are flexible, and their capitulescences are ebracteate. Colombian *E. garciae* Cuatrec. occasionally also produces plants with a branched caulescent rosette habit similar to *E. pleiochasia*, but their capitula are agglomerate and eligulate.

**Conservation status.** The only known population of *E. ramosa* occupies an area  $< 0.2 \text{ km}^2$  and is probably composed by a few hundreds of individuals. Its habitat, the shrubby sub-páramo, is seriously threatened by the expansion of the agricultural frontier. The species should for now be included into the IUCN "endangered (EN)" category, until detailed population studies will be done to reach or achieve its conservation status.

Additional specimens examined. E. ramosa: M.T. Becerra, J. Mavárez & J. Aguirre 36, 37 (Paratypes: COL). E. jahnii: J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28414 (COL), 28414B (IVIC), A. Fernández, J. Mavárez, S. Aubert & S. Lavergne 31739 (IVIC), 31759 (IVIC), J. Cuatrecasas, L. Ruiz-Terán & L. Marcano-Berti 28007 (MERF), M. López-Figueiras 9149 (MERF). E. pleiochasia: B. V. Rodríguez-Cabeza, R. Galindo-Tarazona & L. Velasco BVR 2012 (COL), H. García-Barriga & R. Jaramillo-Mejía 20279 (COL), L. Uribe-Uribe 1068 (COL), S. Díaz-Piedrahita 17 (COL), 35 (COL). E. garciae: L. Uribe-Uribe 6491 (COL), 6491 (COL), H. García-Barriga & R. Jaramillo-Mejía 20264 (COL), H. García-Barriga 20369 (COL).

### DISCUSSION

*Espeletia ramosa* is a truly unique species in the subtribe, growing as a compact colony of rosettes branched near the ground. Its habitus is superficially similar to *Espeletia jahnii*, a Venezuelan species that also grows as a compact colony of rosettes branched near the ground or a prostrate shrub. However, *E. ramosa* is different in many important aspects: its rosettes are polycarpic, its leaves are much broader and with less indument, its capitulescences are lateral and its capitula are ligulate. The morphological traits listed above for *E. ramosa* are relatively plesiomorphic in comparison with other members of the genus, which allow us to hypothesize that this new taxon could be one of the living species phenotypically closest to the presumed ancestor of all *Espeletia* (Pouchon et al., 2018). On the

other hand, branching in *E. ramosa* could be character state evolutionarily derived; perhaps acquired through the development of branching in an ancestor with unbranched stems. Indeed, Pouchon et al. (2018) have shown that branching/unbranching are traits relatively plastic in *Espeletia*, which have evolved repeatedly during the history of these plants. The latter suggests that evolutionary inferences based solely on morphological evidence could be misleading in this group, and that formal testing of the alternative scenarios mentioned above will certainly require the analysis of molecular-based phylogenetic reconstructions.

The presence of a constantly and profusely branched rosette in Colombia represents a notable addition to the diversity of Espeletia growth forms in this country. Until now, the genus was considered to be represented in Colombia by a large majority of unbranched rosettes, two rosette species in the páramos of Boyacá that may occasionally be sparsely branched, and a few tree species in the north of the Cordillera Oriental, Sierra de Perijá and Sierra Nevada de Santa Marta (Cuatrecasas, 2013; Mavárez, 2019). The much lower diversity of branched forms in Colombia and their geographic proximity to Venezuela motivated the hypothesis of an evolutionary origin for Espeletia in Venezuela, with a subsequent dispersal to Colombia, such as suggested by Smith and Koch (1935) and Cuatrecasas (1986, 2013). However, Pouchon et al. (2018) have shown that the radiations of Espeletia in Colombia and Venezuela arose rather independently from a common ancestor about 2.5 mya, with relatively recent events of long-distance dispersal between the Andes of the two countries in a few low elevation tree lineages (e.g., E. neriifolia (Bonpl. ex Humb.) Sch.Bip. ex Wedd., E. occulta S.F.Blake, E. chardonii), but not among rosettes. Under the scenario proposed by Pouchon et al. (2018), E. ramosa should be phylogenetically closer to other Colombian rosettes, whereas under the scenario of Smith and Koch (1935) and Cuatrecasas (1986), it should be closer to some Venezuelan branched taxa (i.e., E. jahnii). However, this matter should be resolved by detailed phylogenetic analyses before a firm statement in this regard can be made.

The demographic and distribution information available indicates that *E. ramosa* must be considered in the IUCN "Endangered (EN)" category. However, although its conservation status of has not been definitely evaluated, preliminary evidence allow us to believe that it could indeed be "Critically endangered (CR)" (IUCN, 2019). First, its only known population occupies an area  $< 0.2 \text{ km}^2$  and is probably composed by a few hundreds of individuals. On the other hand, the ensemble of areas with relatively undisturbed sub-páramo habitat potentially suitable for the species within the same mountain range likely represents  $< 10 \text{ km}^2$ , is already highly fragmented into a series of small and isolated patches of suitable habitat immersed within a widespread matrix of farmland, and is seriously threatened by the expansion of the agricultural frontier and climate change (Mavárez et al., 2018). In any case, whatever the appropriate threat category for this species, it is clear that some urgent measures are required to guarantee its conservation.

### ACKNOWLEDGEMENTS

We are very grateful for the help provided during fieldwork by Julián Aguirre. We are also very grateful to the staff in herbarium COL for the support provided for this work. We thank Gerardo Aymard (PORT) and Angel Fernández (IVIC) for the reviews they made to a previous version of this work. JM thanks Universidad Jorge Tadeo Lozano for the support provided during his sabbatical leave in Bogotá during 2019. Collections were made under Permiso Marco de Recolección de Especímenes, resolución 01435 del 3 de septiembre de 2018 de la Autoridad Nacional de Licencias Ambientales (ANLA) to J. Aguirre. This work is part of MTB's Ph.D. dissertation.

### LITERATURE CITED

Berry, P. E. and R. N. Calvo. 1989. Wind Pollination, Self-Incompatibility, and Altitudinal Shifts in Pollination Systems in the High Andean genus *Espeletia* (Asteraceae). Amer. J. Bot. 76: 1602– 1614. doi: 10.2307/2444398.

- Cuatrecasas, J. 1976. A new subtribe in the Heliantheae (Compositae): Espeletiinae. Phytologia 35: 43–61.
- Cuatrecasas, J. 1995. A new genus of Compositae: *Paramiflos* (Espeletiinae) from Colombia. Proc. Biol. Soc. Wash. 108: 748–750.
- Cuatrecasas, J. 1986. Speciation and radiation of the Espeletiinae in the Andes. *in* High Altitude Tropical Biogeography, F. Vuilleumier and M. Monasterio, eds., Oxford University Press, New York.
- Cuatrecasas, J. 2013. A Systematic Study of the Subtribe Espeletiinae (Heliantheae, Asteraceae). Mem. New York Bot. Gard. Vol. 107. The New York Botanical Garden Press, New York.
- Díaz-Piedrahita, S. and B. V. Rodríguez Cabeza. 2010. Nuevas Especies Colombianas de *Espeletiopsis* Cuatrec. y de *Espeletia* Mutis ex Humb. & Bonpl. (Asteraceae, Heliantheae, Espeletiinae). Rev. Acad. Col. Ci. Exact. 34: 441–454.
- Diazgranados, M. 2012. A nomenclator for the frailejones (Espeletiinae Cuatrec., Asteraceae). PhytoKeys 16: 1–52. doi: 10.3897/phytokeys.16.3186.
- Diazgranados, M. and J. C. Barber. 2017. Geography shapes the phylogeny of frailejones (Espeletiinae Cuatrec., Asteraceae): a remarkable example of recent rapid radiation in sky islands. PeerJ 5: e2968. doi:10.7717/peerj.2968.
- Fagua, J. and V. González. 2007. Growth Rates, Reproductive Phenology, and Pollination Ecology of *Espeletia grandiflora* (Asteraceae), a Giant Andean Caulescent Rosette. Plant Biol. 9(1): 127– 135.
- Humboldt, A. and A. Bonpland. 1809[1808]. Plantae Aequinoctiales 2(9): 10. F. Schoell, Paris.
- IUCN Standards and Petitions Committee. 2019. Guidelines for Using the IUCN Red List Categories and Criteria. Version 14. Available at: http://www.iucnredlist.org/documents/RedListGuidelines.pdf.
- Luteyn, J. L. 1999. Páramos: A Checklist of Plant Diversity, Geographical Distribution, and Botanical Literature. Mem. New York Bot. Gard. Vol. 84. The New York Botanical Garden Press, New York.
- Mavárez, J., Bézy, S., Goeury, T., Fernández, A., and S. Aubert. 2018. Current and future distributions of Espeletiinae (Asteraceae) in the Venezuelan Cordillera de Mérida based on statistical downscaling of climatic variables and niche modelling. Plant Ecol. & Divers. Doi: 10.1080/17550874.2018.1549599.
- Mavárez, J. 2019. A Taxonomic revision of *Espeletia* (Asteraceae). The Venezuelan Radiation. Harv. Pap. Bot. 24(2), in press.
- Pouchon, C., Fernández, A., Nassar, J. M., Boyer, F., Aubert, S., Lavergne, S. and J. Mavárez. 2018. Diversification of the Giant Rosettes of the *Espeletia* complex (Asteraceae). A Phylogenomic Analysis of an Explosive Adaptive Radiation in the Andes. Syst. Biol. 67: 1041–1060. Doi: 10.1101/gr.074492.107.
- Smith, A. P. 1981. Growth and population dynamics of *Espeletia* (Compositae) in the Venezuelan Andes. Smithson. Contrib. Bot. Vol. 48.
- Smith, A. C., and M. F. Koch. 1935. The genus *Espeletia*: A study in phylogenetic taxonomy. Brittonia 1: 479–530. doi: 10.2307/2804673.
- Thiers, B. 2019+ (continuously updated). Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium, http://sweetgum.nybg.org/science/ih/ (accessed: May 1 2019).

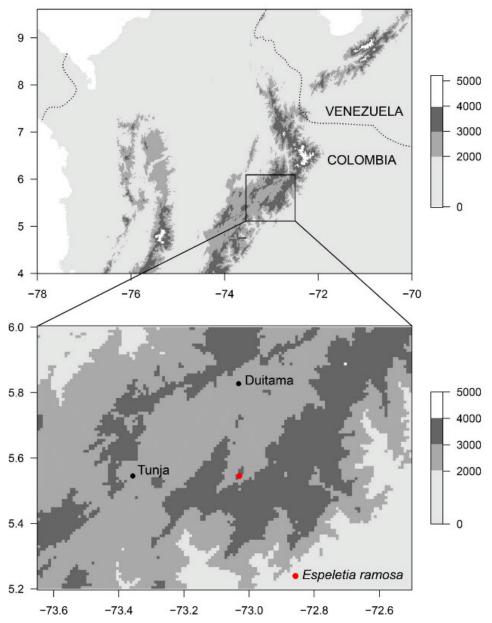
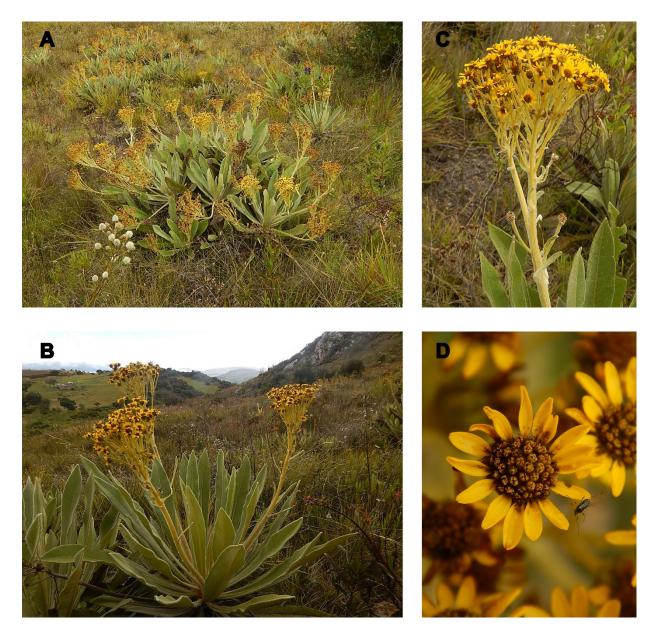
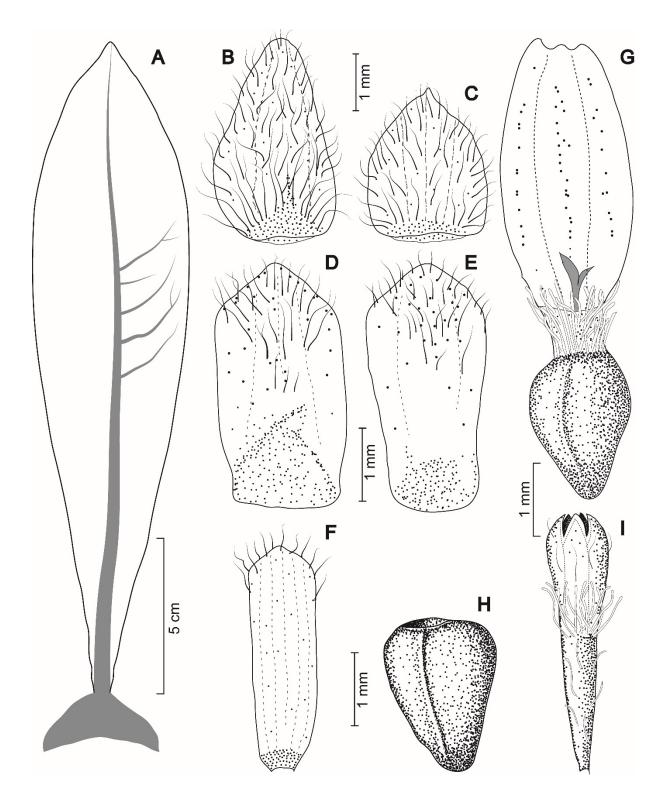


Figure 1. Maps of the Colombian Cordillera Oriental showing the collection locality of *E. ramosa*.



**Figure 2**. *Espeletia ramosa*. **A**. Example of branched caulescent habit. **B**. Lateral view of individual rosette (note the oblanceolate leaves and alternate bracts along the inflorescence axis). **C**. Lateral view of corymbose inflorescence. **D**. Upper view of capitulum (note the single row and small number of ligulate ray flowers).



**Figure 3**. **A**. Leaf outline with secondary nerves from its mid-section. **B** and **C**. External sterile phyllaries. **D**. Internal sterile phyllary. **E**. Fertile phyllary. **F**. Palea. **G**. Ray flower. **H**. Mature achene. **I**. Disc flower (anthers not shown).