A TAXONOMIC REVISION OF *ESPELETIA* (ASTERACEAE). THE VENEZUELAN RADIATION

Jesús Mavárez[1,2,3]

Abstract. Subtribe Espeletiinae (Asteraceae) represents the best example of morphological and ecological diversification in the Northern Andes high-elevation ecosystem known as *páramo*. These plants, formerly considered as belonging to a single genus, *Espeletia*, were later referred to eight genera defined mainly according to their habit, branching pattern, and inflorescence position and structure. However, several molecular phylogenetic analyses have shown that this classification system is artificial since the larger genera, regrouping ca. 85% of the species, are polyphyletic. Here, a return to the previous classification system of the subtribe at the generic level is proposed, adopting the view that only *Espeletia* should be recognized, with the other seven genera considered as (heterotypic) synonyms. At the species level, a taxonomic revision is made of the nomenclature, morphology, and distribution of the taxa in the Venezuelan clade of *Espeletia*, one of the two major clades that compose the genus. Fifty-four species are accepted, 48 entirely endemic to the Venezuelan Cordillera de Mérida, 2 broadly distributed in this range and nearby areas in Colombia and Venezuela, and 4 endemic to the northern section of the Colombian Cordillera Oriental and Sierra de Perijá. Distribution maps for all species are proposed, along with brief morphological descriptions and lists of diagnostic features that facilitate their identification against similar species. Thirteen hybrid taxa and their putative parental species are also given, eight of them proposed here for the first time.

Keywords: Andes, Asteraceae, caulescent rosette, Cordillera de Mérida, *Espeletia*, páramo, Venezuela

The plants in subtribe Espeletiinae (Asteraceae) represent perhaps the best example of taxonomic, morphological, and ecological diversification among tropical high-elevation taxa (Diazgranados, 2012; Cuatrecasas, 2013; Diazgranados and Barber, 2017; Pouchon et al., 2018). The ca. 140 species in the group are distributed in the high Andes of Venezuela, Colombia, and Northern Ecuador, with two important diversity centers in the Colombian Cordillera Oriental (ca. 76 species, Fig. 1A) and the Venezuelan Cordillera de Mérida (ca. 50 species, Fig. 1B). These plants originated from a single ancestor about 2.5 mya (Pouchon et al., 2018), after the final uplift of the Northern Andes, which facilitated environmental conditions for the rise of the tropical high-elevation grassland ecosystem known as *páramo* to which the subtribe is endemic (Hooghiemstra et al., 2006; Torres et al., 2013). The diversification of Espeletiinae occurred very rapidly indeed, particularly during the intensification of climatic variability after the middle Pleistocene transition, 1.25–0.70 mya (Clark et al., 2006), and it is now considered one of the fastest-evolving plant groups in the world (Madriñán et al., 2013; Pouchon et al., 2018). In this short time Espeletiinae generated a notable degree of ecological diversity with regard to (1) elevation, ranging from montane cloud forests at about 2000 m.a.s.l. to the very edge of glaciers at 4800 m.a.s.l.; (2) humidity, from wet páramo bogs to xeric periglacial talus slopes and rocky outcrops; and (3) solar irradiation, from gaps in the montane forest to open vegetation such as páramo grasslands. However, what has attracted the greatest attention to these plants is their large disparity in morphological types, which includes profusely branched, dichotomous, and unbranched trees; shrubs; short-branched rosettes; sessile rosettes; and, notably, giant caulescent rosettes. The latter is a growth form that produces an erect and unbranched stem usually tightly covered by the bases of old and dead leaves and crowned by a rosette of green young leaves around the apical bud (Fig. 1B). 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).

Given the diversity and ecological dominance of Espeletiinae in the páramos, particularly in Colombia and Venezuela, it is not surprising that they have been the subject of many scientific studies, mainly in population and community ecology, eco-physiology, and, of course, taxonomy. Taxonomic research in particular started more than two centuries ago with the formal publication of *Espeletia* Mutis ex Bonpl. and descriptions of three Colombian species in Humboldt and Bonpland (1809: 10). *Espeletia* was attributed by the authors to José Celestino Mutis, director of the "Expedición Botánica del Nuevo Reino de Granada," who first named the genus at the end of the 18th century (see the detailed chronological account of systematic studies in Cuatrecasas, 2013). In 1814 Bonpland

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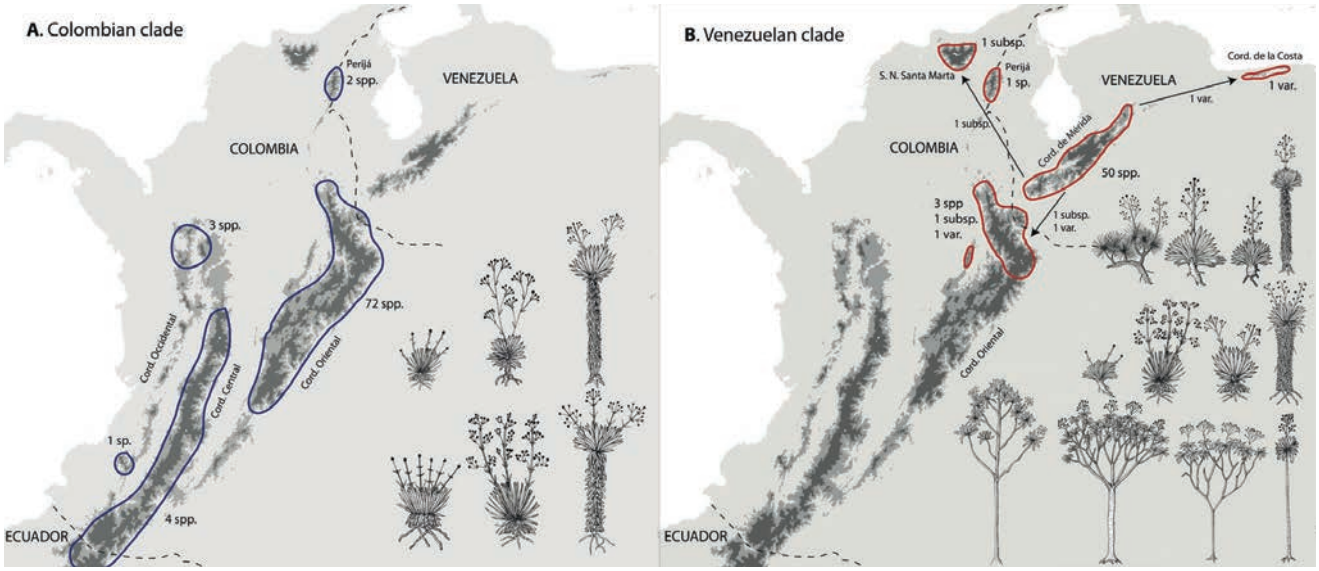


FIGURE 1. **A**, species diversity and distribution in the Colombian clade of Espeletiinae. Plants: upper row—examples of polycarpic rosette plants with monochasial inflorescences; lower row—examples of polycarpic rosette plants with dichasial inflorescences. **B**, species diversity and distribution in the Venezuelan clade of Espeletiinae. Arrows give the number of shared taxa between geographic sections. Plants: upper row—examples of monocarpic rosette plants with monochasial inflorescences; middle row—examples of polycarpic rosette plants with inflorescences monocephalous (left), dichasial (2nd) or monochasial (3rd, right); lower row—examples of trees with branched and unbranched stems.

described a new species with arborescent habit collected by him and Humboldt in La Silla de Caracas, Venezuela, as *Trixis neriifolia* Bonpl. ex Humb. The same species was renamed as *Baillieria? neriifolia* (Bonpl. ex Humb.) Kunth (Humboldt et al., 1820), and later as *Clibadium? neriifolium* (Bonpl. ex Humb.) DC. According to Weddell (1855: 68), Schultz Bipontinus was the first to notice that this species with branched stems belonged to *Espeletia* and renamed it as *Espeletia neriifolia* (Bonpl. ex Humb.) Sch. Bip. ex Wedd. The genus remained undivided in almost all subsequent taxonomic treatments of the group: 11 species in Weddell (1855), 17 species in Standley (1915), 30 species (18 from Venezuela, 12 from Colombia) in Smith and Koch (1935), 71 species (26 from Venezuela, 42 from Colombia with 1 reaching Ecuador, 3 in Venezuela and Colombia) in Cuatrecasas (1949), and 45 species from Venezuela in Aristeguieta (1964). The only exception to this single genus system came from Ernst (1870), who, probably unaware of Weddell's work, placed *E. neriifolia* in a new genus as *Libanothamnus neriifolius* (Bonpl. ex Humb.) Ernst. In 1976 the 124 species known at the time were raised to subtribe Espeletiinae and split into seven genera in Cuatrecasas (1976, 1986b), after which an additional genus was added in Cuatrecasas (1995). The eight-genera system has been used in recent treatments of the group; 141 species in Diazgranados (2012) and 126 species in Cuatrecasas (2013). The latter work, unfortunately published posthumously in an unfinished state (one genus and ca. 20 species missing), represents an impressive monographic masterpiece of the subtribe. Therein, among many other topics, Cuatrecasas fully developed the classification and nomenclature system of this group sketched in his 1976 and 1986 works, which defined the genera mainly according to the plant habitus and the position and structure of the inflorescence, summarized here:

A. Rosette plants: a compact crown of green leaves arranged spirally around the apical meristem, each leaf possessing a flat sheath tightly imbricated under and over the sheaths of nearby leaves. Stem with a large central pith surrounded by secondary vascular tissues, entirely covered in its apical part by the sheaths of the green leaves. The stem is usually unique and unbranched, but some species can be slightly branched near ground level, each branch producing a terminal crown of rosette leaves.

A.1. *Coespeletia* Cuatrec. Unbranched stem. Lateral inflorescences with monochasial structure: botryoid, botryoid-paniculate, or monocephalous. Endemic to Cordillera de Mérida.

A.2. *Espeletia* Mutis ex. Bonpl. Unbranched stem. Lateral inflorescences with dichasial structure: thyrsoid, oligocephalous, or monocephalous. Cordillera de Mérida, Sierra de Perijá, Colombian Andes, and Northern Ecuador (1 sp. shared with Colombia).

A.3. *Espeletiopsis* Cuatrec. Unbranched stem (some occasionally branched). Lateral inflorescences with monochasial structure: corymboid or corymboid-paniculate, rarely monocephalous. Cordillera de Mérida and Colombian Cordillera Oriental.

A.4. *Paramiflos* Cuatrec. Unbranched stem. Lateral inflorescences with monochasial structure: corymboid. Involucre with sharp separation between outer and inner phyllaries. Monotypic. Endemic to Colombian Cordillera Oriental.

A.5. *Ruilopezia* Cuatrec. Unbranched stem (one species frequently branched, some occasionally branched). Terminal inflorescences with monochasial structure: corymboid or corymboid-paniculate. All species but one endemic to

Cordillera de Mérida, the exception is endemic to Páramo de Tamá in Colombian Cordillera Oriental.

B. Trees: have a distinct woody trunk with a small or no pith in comparison with the surrounding wood. Branched at a considerable distance from the ground (one species unbranched). Little or no overlapping of consecutive leaf sheaths, although some leaf crowding is frequent at the ends of the branches. Leaf sheaths are either curved with free margins and embracing most of the branch, or tubular and encircling the branch entirely (one species with open and flat sheaths).

B.1. *Carramboa* Cuatrec. Monopodial branching. Lateral inflorescences with primary structure dichasial: corymboid. Endemic to Cordillera de Mérida.

B.2. *Libanothamnus* Ernst. Main branching monopodial, peripheral branching sympodial (one species unbranched). Terminal inflorescences with monochasial structure: corymboid. Most species endemic to Cordillera de Mérida, some occurring as well in nearby areas in Colombia, and two endemic to either the Tamá region or Sierra de Perijá.

B.3. *Tamania* Cuatrec. Main branching sympodial. Open and flat leaf sheaths. Terminal inflorescences with monochasial structure: corymboid. Monotypic. Endemic to Páramo de Tamá and nearby areas in Colombian Cordillera Oriental.

At the generic level, all six nonmonotypic genera are found in Cordillera de Mérida in Venezuela, two of them entirely endemic to this range (*Carramboa* and *Coespeletia*) and two others nearly so (*Ruilopezia* and *Libanothamnus*). This observation motivated the hypothesis of a center of origin and diversification for the group in Venezuela (Smith and Koch, 1935; Cuatrecasas, 1986b), with multiple subsequent dispersal events towards the Colombian Andes in *Espeletia*, *Espeletiopsis*, *Libanothamnus*, *Ruilopezia*, and *Tamania*.

Molecular Phylogenetic Studies in the Subtribe Espeletiinae

The subtribe Espeletiinae has become the subject of a certain number of recent molecular studies aiming to understand its closest relatives and positioning within the tribe Heliantheae (Panero et al., 1999; Rauscher, 2002), internal phylogenetic relationships (Sánchez-Andrade, 2005; Diazgranados and Barber, 2017; Pouchon et al., 2018), diversification dynamics (Madriñán et al., 2013; Pouchon et al., 2018), and the metabolic similarities among its taxa (Padilla-González et al., 2017). These studies have provided unequivocal evidence for several phylogenetic relationships in Espeletiinae, some of them supporting previous hypotheses for the evolution of this group, such as its monophyly, recent origin, and close affinities with Melampodiinae and Milleriinae, while others are novel and somehow in contradiction with previous ideas (see examples in Diazgranados and Barber, 2017; Pouchon et al., 2018). Two important results in the second category, particularly relevant to the theme of this work, are the following:

(1) There have been two geographically delimited and mostly disconnected radiations in the Venezuelan and Colombian Andes, respectively, instead of an initial radiation in Venezuela followed by multiple colonizations of Colombia, as proposed by Smith and Koch (1935) and Cuatrecasas (1986b, 2013). The "Venezuelan Espeletiinae clade" comprises all species living in the Venezuelan Cordillera de Mérida, plus a few lineages that colonized the Tamá region and nearby areas in the Colombian Cordillera Oriental, Sierra de Perijá, and Sierra Nevada de Santa Marta. The "Colombian Espeletiinae clade" comprises all remaining species in the subtribe living in the Colombian Andes, Sierra de Perijá, and Northern Ecuador.

(2) As currently circumscribed, most genera in Cuatrecasas's classification system of Espeletiinae are poly- or paraphyletic (Fig. 2). For instance, the phylogenomic analysis by Pouchon et al. (2018), based on whole plastomes and 1877 fragments covering about a million bp of the nuclear genome, has shown that the three largest genera in the subtribe—*Espeletia*, *Espeletiopsis*, and *Ruilopezia*—representing ca. 85% of the species, are clearly polyphyletic. Each of the former two genera comprises at least two distantly related clades, one in Venezuela and one in Colombia, a number that could increase on analysis of more taxa from the latter country. The polyphyly of *Ruilopezia* is even greater, since it embraces at least three unrelated clades in Venezuela. *Coespeletia* is paraphyletic with regard to *Espeletia semiglobulata* Cuatrec., while the monotypic *Tamania* and *Paramiflos* are nested within one clade of *Ruilopezia* and the Colombian *Espeletiopsis*, respectively. Only *Carramboa* and *Libanothamnus* appeared to be monophyletic. This pattern of extensive polyphyly/paraphyly among Espeletiinae genera could be even worse, as suggested by Diazgranados and Barber (2017), whose phylogenetic analysis of a larger taxonomic sample of the subtribe indicates that the clade of Colombian *Espeletia* could be nested within the Colombian *Espeletiopsis*.

The Need for a New Classification System of the Subtribe Espeletiinae

The classification system with eight genera of Espeletiinae (Cuatrecasas, 1976, 2013) is therefore largely artificial and must be modified. One such modification, following a "splitter approach," could include (1) preserving the seemingly monophyletic genera *Carramboa* and *Libanothamnus*, (2) modifying the definition of *Coespeletia* so that it can accept *Espeletia semiglobulata*, (3) creating a new genus for the Venezuelan *Espeletiopsis*, (4) creating a new genus for the Venezuelan *Espeletia*, (5) deciding whether *Tamania* is preserved or merged into *Ruilopezia*, (6) splitting *Ruilopezia* into three or four genera depending on the decision made in (5), (7) deciding whether *Paramiflos* is preserved or merged into *Espeletiopsis*, and (8) splitting the Colombian *Espeletiopsis* into two or more genera depending on the decision made in (7). The number of genera in the subtribe would thus increase to 10–15, according to the actions taken. The problem with this approach is that it would require a considerable amount of time and effort to identify the synapomorphies that define the new genera, as well as the creation of many new name combinations.

A more workable and stable solution is proposed here, adopting the view that only the genus *Espeletia* should be recognized in the subtribe, with the other seven genera considered as (heterotypic) synonyms. In this case, the

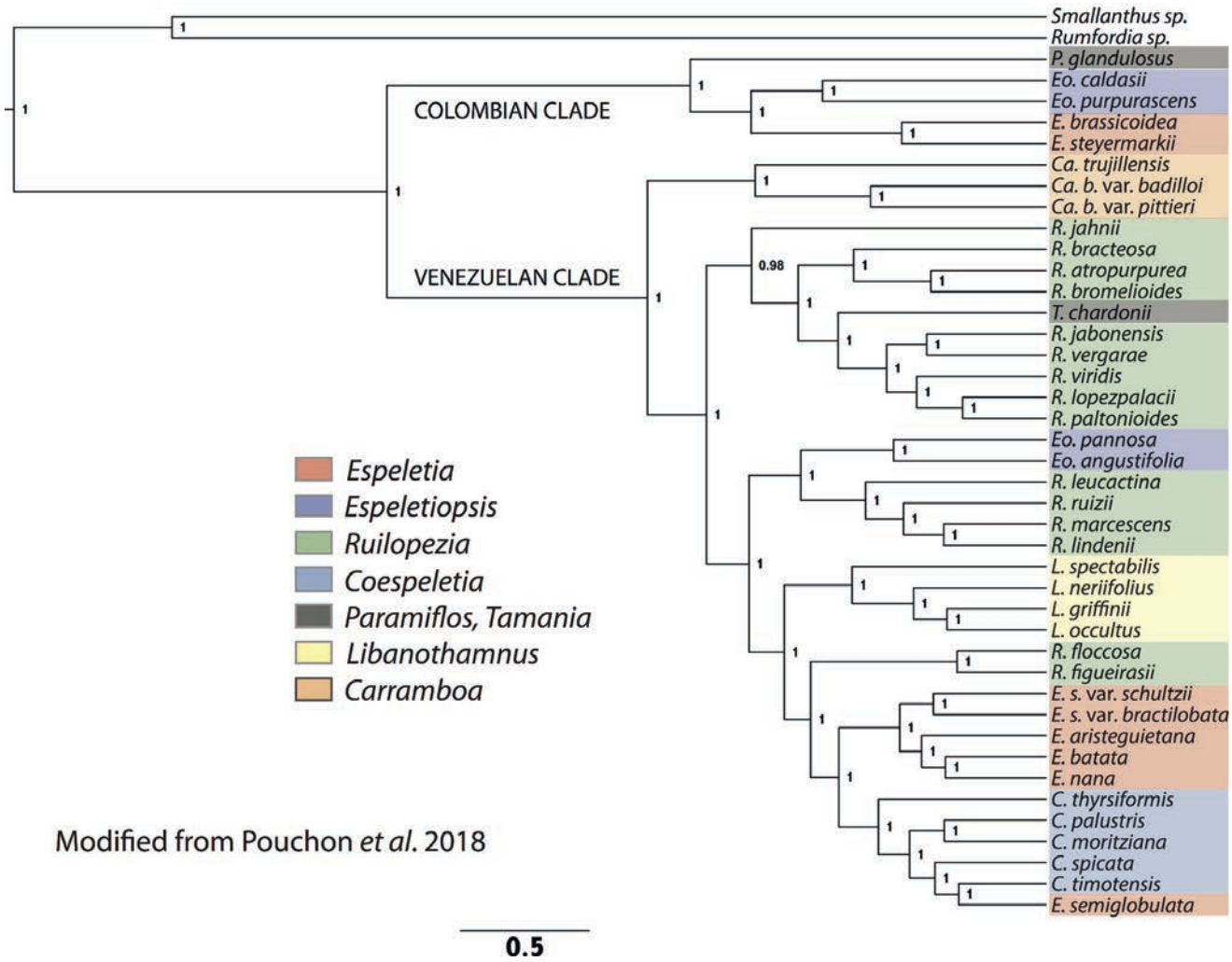


FIGURE 2. Molecular phylogeny of Espeletiinae genera sensu Cuatrecasas (1976, 2013), based on a maximum-likelihood (ML) analysis of nuclear data. Numbers on nodes give ML support values. Modified from Pouchon et al. (2018).

genus *Espeletia* would recover its original definition, currently employed for the subtribe Espeletiinae, without the need for additional morphological definitions for new groupings. Another advantage of this solution is that since the majority of the species in the subtribe were originally described under the genus *Espeletia* (ca. 130 species), the proposed change implies essentially the restoration of species names discarded by Cuatrecasas (1976, 1996, 2013) and 12 new combinations for some species described after 1976: 2 in *Coespeletia* (Cuatrecasas, 2013; Diazgranados and Morillo, 2013), 5 in *Espeletiopsis* (Diaz-Piedrahita and Obando, 2004; Diaz-Piedrahita et al., 2006; Diaz-Piedrahita and Rodríguez-Cabeza, 2008, 2010; Diazgranados and Sánchez, 2013), 2 in *Libanothamnus* (Cuatrecasas, 1980b), and 3 in *Ruilopezia* (Cuatrecasas, 1986a).

In this work, the proposed changes in the nomenclature are applied to the ensemble of the Venezuelan clade of Espeletiinae. Six species found within Venezuela's political borders but belonging to the clade of Colombian Espeletiinae will not be treated here but in a taxonomic revision of that clade to be published in the near future. A succinct but diagnostic description is also given for each species, together with distribution maps, most of them provided here for the first time.

MATERIALS AND METHODS

A total of 2264 samples were analyzed for this study: 1450 samples deposited in herbaria B, BC, BR, COL, F, G, GH, HAL, IVIC, K, LD, MER, MERF, MO, MY, NY, P, S, U, US, and W (according to Thiers, 2019), and 814 plants identified during fieldwork by the author and some colleagues (250 of which are now deposited at herbarium IVIC) (see Supplementary Material). Several diagnostic morphological traits were measured in the fresh samples, with an emphasis on traits of the leaf, inflorescence, and capitulum, which can also be measured nondestructively in dry specimens, either directly on sheets or on high-quality photographs. However, to avoid possible biases due to differences between fresh and dry material, comparisons between capitula from different species were done for traits

measured only on dry samples from herbarium sheets (IVIC, MERF, MY) and new field-dried specimens. The majority of traits used are visible to the naked eye and can be measured without the need for sophisticated equipment; however, for some minute details such as disc corolla's tube length or the presence of glands, a small optical magnification device was necessary. It should be mentioned that the purpose of these morphological descriptions is not to provide a complete portrayal of the taxa but to facilitate their identifications in the field. Readers interested in more-detailed morphological accounts of these taxa should consult their original descriptions and other appropriate works.

Plant samples collected in this study were geo-referenced with a GPS during fieldwork, whereas for herbarium sheets this information was either retrieved directly from labels when inferred from the descriptions of collection sites and 1:25,000 maps of Colombia and Venezuela. The geographic coordinates were used to produce distribution maps of each species using R package raster v2.3-33.

The ensemble of the information gathered for each taxon was summarized as follows:

Valid name, followed by the appropriate reference or *status*. Taxa below the rank of species are also given; subspecies (subsp.), variety (var.), and forma (f.), even if the validity of most of these secondary ranks remains to be verified. Autonyms are provided as well, for databasing purposes. TYPE information: whenever possible, given as COUNTRY. State. Locality, elevation, collection date, *collection number* (herbaria acronyms).

List of all names associated with the taxon. Information about the TYPE is provided for basionyms and heterotypic synonyms.

A brief and standardized morphological description is provided for (1) Growth form: *habitus*, type of stem branching, size; (2) *Leaf* shape, pseudopetiole length, type and degree of adaxial pubescence, leaf length, leaf width, length-to-width ratio, shape and distribution of secondary nerves; (3) *Inflorescence* position, structure (simple or compound), branchlet organization (monochasial or dichasial; Fig. 3), inflorescence length, number and distribution of bracts; (4) *Capitulum* shape, diameters of capitulum, ligular circle and disc, color of ray ligules. The key morphological characteristics that allow the identification of the taxon with respect to similar taxa are also provided.

Information on distribution is provided as confirmed presence of the taxon on the major geographic units of páramo traditionally considered for Venezuela and Eastern Colombia (Fig. 4). Recorded minimum and maximum elevations are also given, together with a description of the main habitat types in which the taxon is found: (1) the páramo proper, located between ca. 3500 and ca. 4200 m.a.s.l., composed mostly of small sclerophyllous shrubs, herbs, grasses, and rosette plants; (2) an upper transition zone, the superpáramo, from ca. 4200 m.a.s.l. to the limits of glaciers, characterized by a mixture of bare soil, low-height vegetation (mostly grasses, herbs), and some caulescent rosette plants; and (3) a lower transition zone, the subpáramo, from the upper Andean forest to ca. 3500 m.a.s.l., characterized mainly by a shrubby vegetation mixed with patches of meadows and small trees that are usually isolated or in thickets (Hooghiemstra et al., 2006).

A list of some representative samples of each taxon is given, with an emphasis on exsiccata that include both vegetative and reproductive material, and that are available in online herbarium databases.

A list of interspecific hybrid taxa in Venezuelan Espeletiinae is provided at the end of the Taxonomy section. The status of some of these taxa had already been proposed or at least conjectured (Morillo and Briceño, 2007; Diazgranados, 2012; Cuatrecasas, 2013), while others are proposed here for the first time. Inferences about the hybrid nature of these taxa are mostly based on the study of living plants, which allows the analysis of the evidence for hybridization on important diagnostic traits that are usually unavailable in dried specimens, such as habit, size, branching structure, pubescence organization, and different instances of color. Furthermore, inferences of hybridization based on living plants also permit the gathering of important morphological and ecological data from the sympatric putative parental species. Parents in hybrid formulae are provided in alphabetical order.

Both Diazgranados (2012) and Cuatrecasas (2013) provided lists of Spanish names that appear on the labels of herbarium samples and that are supposedly attributed to some Espeletiinae species. However, it is unclear to what extent those names represent common uses by local populations or attempts by scientists to socialize the knowledge about these plants. To explore this issue, adult people living near collection sites were asked to provide the names they give to the plants, directly in the field whenever possible, or using good quality photographs or fresh samples.

Results

Taxonomic Changes

The type of *Espeletia pannosa* Standl. contains a mixture of that species and *Espeletia floccosa* Standl. A lectotype is designated here for the part that corresponds most with the original description of *E. pannosa*. Seven new combinations are proposed for taxa at the species level, and 10 for taxa below species. New status is proposed for eight taxa now considered to be interspecific hybrids. Changes in the spelling of four epithets are proposed in accordance with rules of the International Code of Nomenclature for algae, fungi, and plants, hereafter ICN (Turland et al., 2018).

Diversity

The analysis of morphological data in both herbarium samples and living plants formerly considered to belong to the Venezuelan *Espeletia* clade revealed that this group is composed of 54 species, which, together with the 6 other species found within Venezuela's political borders but phylogenetically affiliated with the clade of Colombian *Espeletia*, elevate the total diversity of the genus in Venezuela to 60 species The remaining 13 species were found to represent the product of interspecific hybridization; 4 between rosette parents, 3 between tree parents, and 6

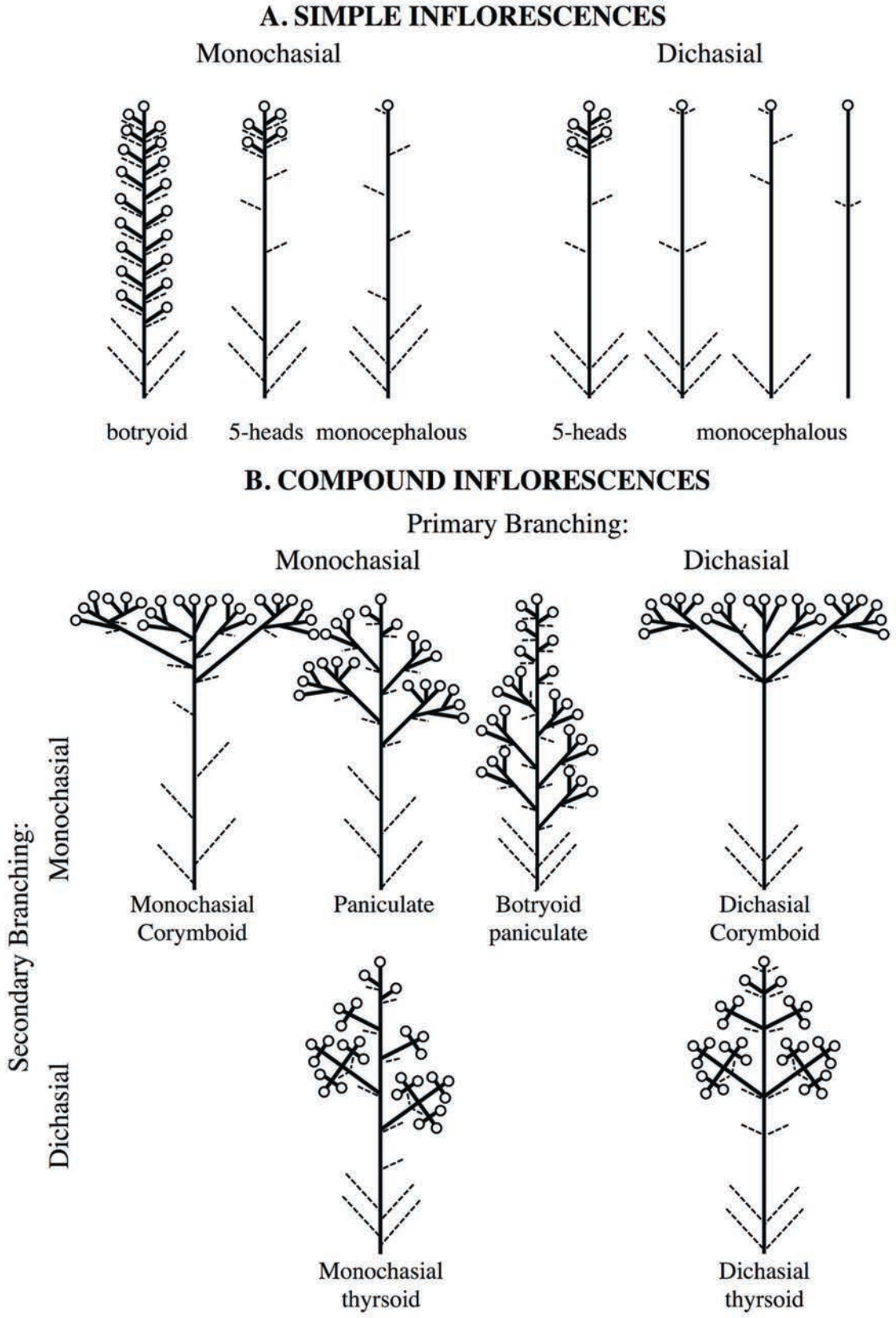


FIGURE 3. Schematic representation of main types of inflorescence structure in the Venezuelan clade of *Espeletia* Mutis ex Bonpl.

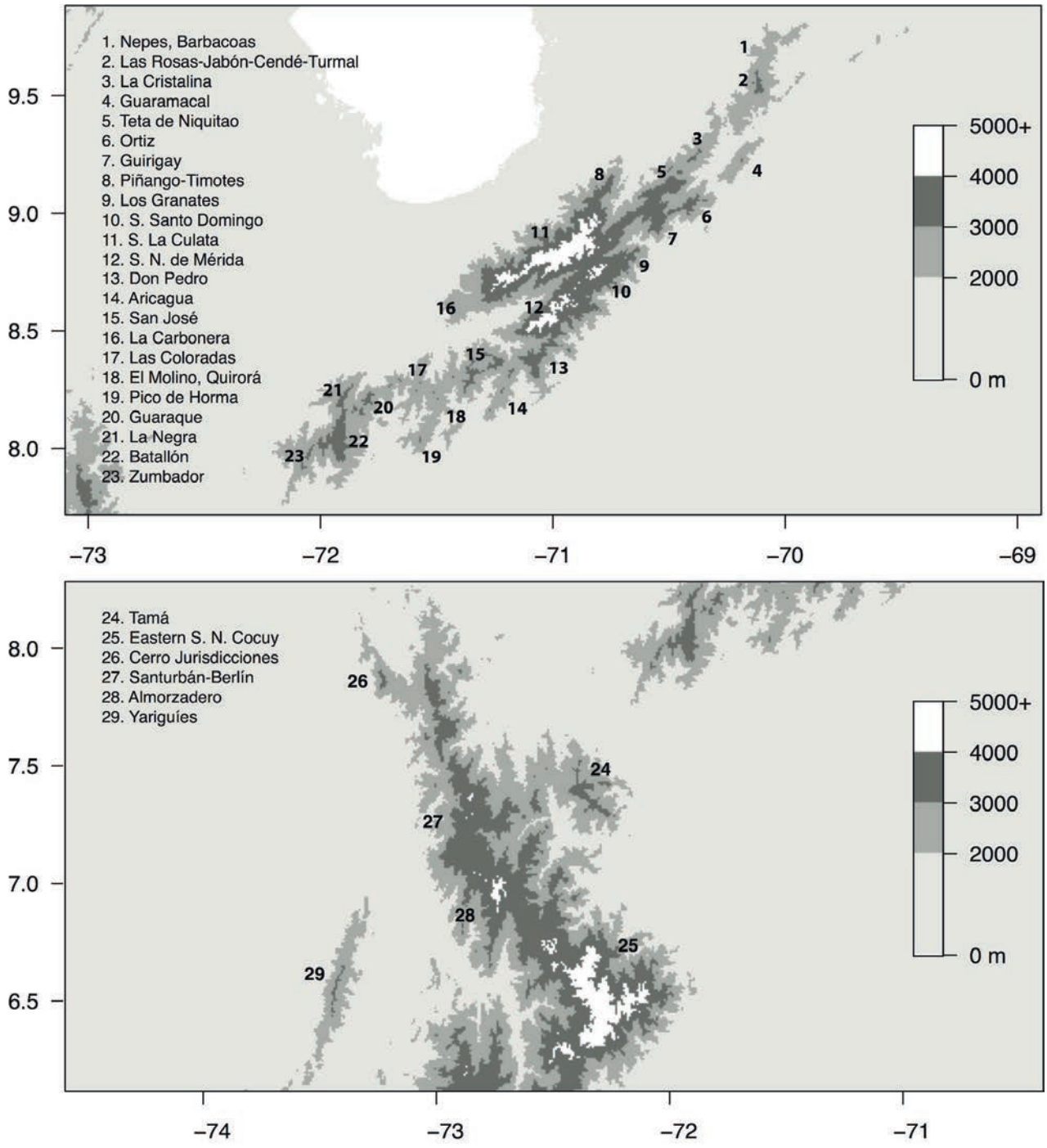


FIGURE 4. Maps of the Venezuelan Cordillera de Mérida (upper panel) and northern section of the Colombian Cordillera Oriental (lower panel) with locations of main páramo areas.

between a rosette and a tree parent (see Fig. 5 and Hybrid Taxa section). Eight of these hybrid taxa are proposed here for the first time.

Distribution

Of the 54 species in the Venezuelan *Espeletia* clade, (1) 48 are endemic to Cordillera de Mérida, (2) two are broadly distributed in this range, in nearby areas in the Colombian Cordillera Oriental and even out of the Andes: *E. neriifolia* and *E. occulta* S.F. Blake, and (3) four are distributed outside Cordillera de Mérida: *E. cardonae* Cuatrec., *E. chardonii* A.C. Sm., and *E. tamana* Cuatrec. in the eastern extreme of the Colombian Cordillera Oriental, and *E. divisoriensis* (Cuatrec.) Mavárez in Sierra de Perijá. It is worth noting that five out the six species nonendemic to Cordillera de Mérida are trees, which implies higher dispersal ability in this growth form, probably as a consequence of their preference for lower elevation habitats.

Of the 48 species endemic to Cordillera de Mérida, 30 are found in the central core, composed of Sierra de la Culata, Sierra Nevada de Mérida, Sierra de Santo Domingo, and mountains around Guirigay and Teta de Niquitao. Despite its comparatively smaller area, the northern section of Cordillera de Mérida (i.e., Guaramacal and the complex Las Rosas-Jabón-Cendé-Turmal) harbor 12 species, 8 of them endemic to these páramos and 4 shared with the central core. Sixteen species are found in the southern section of Cordillera de Mérida (i.e., Aricagua, San José, Las Coloradas, El Molino-Quirorá, Guaraque, and the complex Batallón-la Negra-Zumbador), 10 of them endemic to these páramos and 4 shared with the central core. None of the endemic species to Cordillera de Mérida is found in all three geographic sections, but *Espeletia schultzii* Wedd. is found all over the central core, to the south in Páramo de San José and to the north in Páramo de la Teta de Niquitao and Páramo de la Cristalina.

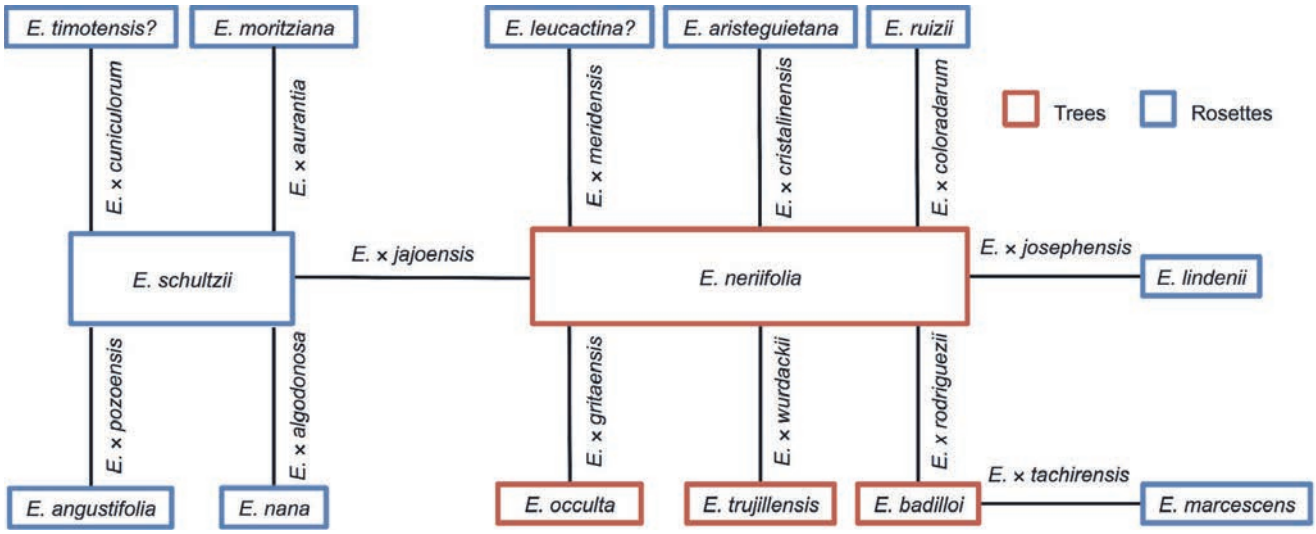


FIGURE 5. Hybrid taxa and their parental combinations in the Venezuelan clade of *Espeletia* Mutis ex Bonpl.

Microendemism and Conservation

According to the IUCN guidelines, most if not all species endemic to the Cordillera de Mérida must be considered at least in the "Endangered" category because they forcibly occupy an area smaller than 5000 km^2 (the total area of páramo in this range is ca. 3000 km^2; Josse et al., 2009) with a significant projected decline in the extent of their suitable habitat due to climate change (Mavárez et al., 2018). However, about a third of the species inhabit single páramo units in the north or south sections, or relatively isolated areas within the central core, which probably makes them qualify for the "Critically Endangered" category. For instance, three endemics to the highest elevations in Páramo de Cendé—*Espeletia liscanoana* Cuatrec., *E. parvula* (Cuatrec.) Mavárez, and specially *E. ulotricha* Cuatrec.—are known from single populations covering an area probably smaller than 10 km^2, and that will certainly disappear or be deeply modified by global warming in the near future. The same extinction risk is likely faced as well by the two endemics to Páramo de Guaramacal, *E. griffinii* Ruiz-Terán & López-Fig. and *E. lopezpalacii* Ruiz-Terán & López-Fig., and by some of the endemics to the low-elevation páramos in the south sections, such as *E. bromelioides* Cuatrec. and *E. ruizii* Cuatrec. Whatever the appropriate threat category for these taxa, it is clear that some urgent measures are required to guarantee their conservation.

Morphology

Growth form (Fig. 6A). There are 14 trees and 40 rosette plants in the Venezuelan *Espeletia* clade. On average, rosette plants tend to occupy higher elevations than trees, notably above 3900 m.a.s.l., which appears to be the upper elevation limit to the tree growth form in this group. On the other hand, the rosette plants are not exclusively associated with the higher elevations, since about half of species with this growth form have been found below 3000 m.a.s.l. and five have not been collected above this elevation.

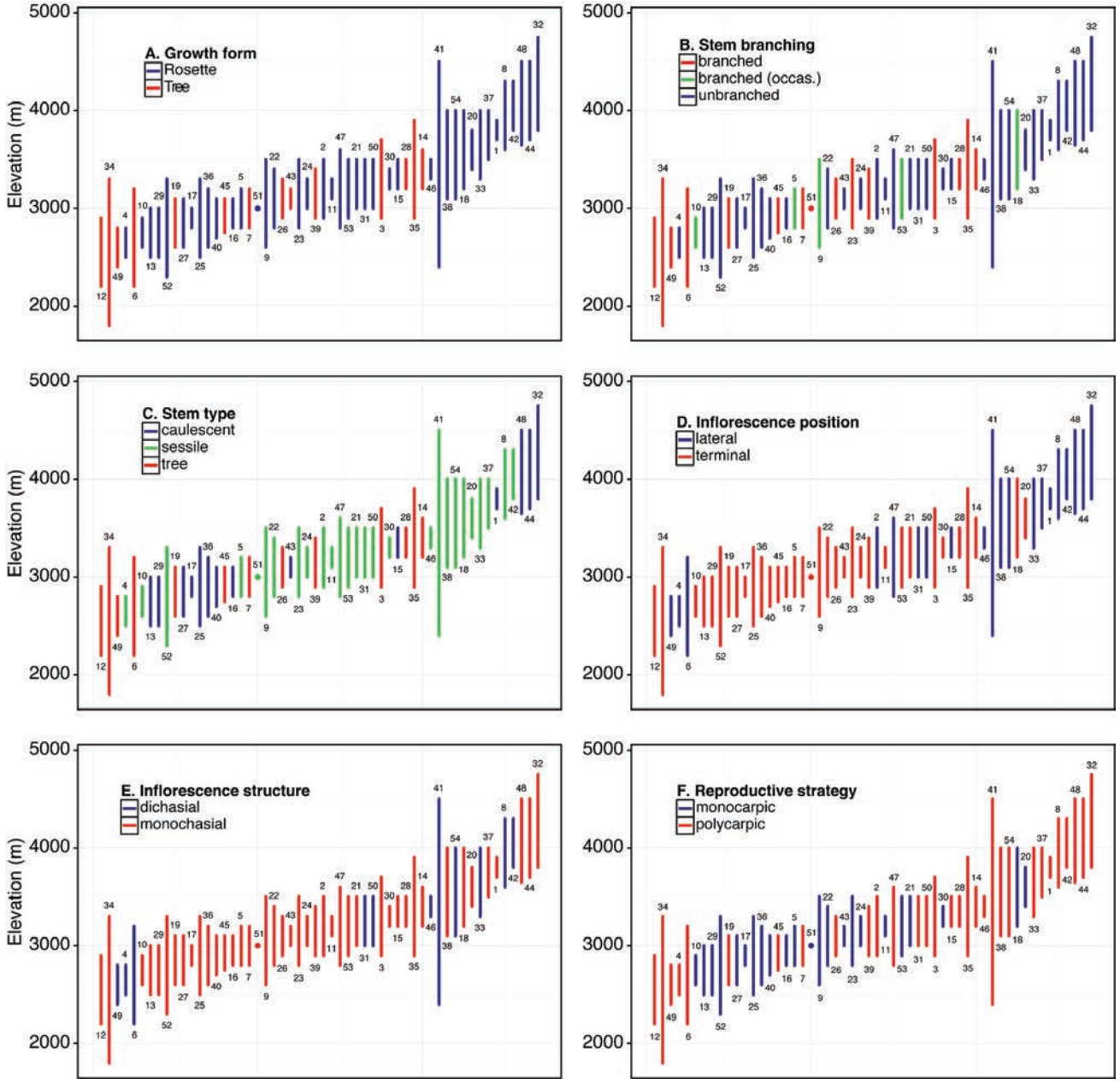


FIGURE 6. Minimum and maximum elevation limits of the 54 species in the Venezuelan clade of *Espeletia* Mutis ex Bonpl., organized according to: **A**, growth form; **B**, stem branching; **C**, stem type; **D**, inflorescence position; **E**, inflorescence structure; and **F**, reproductive strategy. Species labels: 1. *E. albarregensis* (Cuatrec.) Mavárez. 2. *E. angustifolia* Cuatrec. 3. *E. arborea* Aristeg. 4. *E. aristeguietana* Cuatrec. 5. *E. atropurpurea* A.C. Sm. 6. *E. badilloi* Cuatrec. 7. *E. banksiifolia* Sch. Bip. & Ettingsh. ex Wedd. 8. *E. batata* Cuatrec. 9. *E. bracteosa* Standl. 10. *E. bromelioides* Cuatrec. 11. *E. cardonae* Cuatrec. 12. *E. chardonii* A.C. Sm. 13. *E. cuatrecasasii* Ruiz-Terán & López-Fig. 14. *E. divisoriensis* (Cuatrec.) Mavárez. 15. *E. elongata* A.C. Sm. 16. *E. emmanuelis* (Cuatrec.) Mavárez. 17. *E. figueirasii* Cuatrec. 18. *E. floccosa* Standl. 19. *E. griffinii* Ruiz-Terán & López-Fi 20. *E. grisea* Standl. 21. *E. hanburyana* Cuatrec. 22. *E. jabonensis* Cuatrec. 23. *E. jahnii* Standl. 24. *E. leucactina* Cuatrec. 25. *E. lindenii* Sch. Bip. ex Wedd. 26. *E. liscanoana* Cuatrec. 27. *E. lopezpalacii* Ruiz-Terán & López-Fig. 28. *E. lucida* Aristeg. 29. *E. marcescens* S.F. Blake. 30. *E. margarita* Cuatrec. 31. *E. marthae* Cuatrec. 32. *E. moritziana* Sch. Bip. & Ettingsh. ex Wedd. 33. *E. nana* Cuatrec. 34. *E. neriifolia* (Bonpl. ex Humb.) Sch. Bip. ex Wedd. 35. *E. occulta* S.F. Blake. 36. *E. paltonioides* Standl. 37. *E. palustris* (Diazgr. & Morillo) Mavárez. 38. *E. pannosa* Standl. 39. *E. parvula* (Cuatrec.) Mavárez. 40. *E. ruizii* Cuatrec. 41. *E. schultzii* Wedd. 42. *E. semiglobulata* Cuatrec. 43. *E. spectabilis* Cuatrec. 44. *E. spicata* Sch. Bip. ex Wedd. 45. *E. tamana* Cuatrec. 46. *E. tenorae* Aristeg. 47. *E. thyrsiformis* A.C. Sm. 48. *E. timotensis* Cuatrec. 49. *E. trujillensis* Cuatrec. 50. *E. ulotricha* Cuatrec. 51. *E. usubillagae* (Cuatrec.) Mavárez. 52. *E. vergarae* (Cuatrec. & López-Fig.) Mavárez. 53. *E. viridis* Aristeg. 54. *E. weddellii* Sch. Bip. ex Wedd.

Stem branching (Fig. 6B). Among trees, 13 species are branched and one is unbranched (*Espeletia spectabilis* Cuatrec.). Among rosette plants, seven species are branched: one frequently, *E. jahnii* Standl.; five occasionally; and one known only from the type collection, *E. usubillagae* (Cuatrec.) Mavárez. The remaining 33 rosette species are almost invariably unbranched, although some rare branched individuals have been observed in some species, most likely resulting from accidental division of the apical bud.

Stem type (Fig. 6C). There are about two orders of magnitude of variation in stem height among rosette plants, from ca. 15 cm to ca. 15 m. Most sessile and short-stemmed rosette plants (< 1 m) live in páramo habitats between 3000 and 4000 m.a.s.l., some in relatively humid areas within superpáramos, such as *Espeletia batata* Cuatrec. and *E. semiglobulata*, and some in open places in subpáramos, such as *E. aristeguietana* Cuatrec. and *E. bromelioides*. On the other hand, caulescent rosette plants (> 1 m) occupy two very different habitat types: either the coldest and more exposed areas in páramos and superpáramos, such as *E. moritziana* Sch. Bip. ex Wedd., *E. spicata* Sch. Bip. ex Wedd., and *E. timotensis* Cuatrec.; or the relatively warmer and shrubby subpáramos, such as *E. cuatrecasasii* Ruiz-Terán & López-Fig., *E. paltonioides* Standl., and *E. spectabilis*. The giant stems in the Venezuelan *Espeletia* clade could therefore be the response to two rather different selective pressures imposed by the habitats in which these species live: the positioning of the apical bud as far as possible from the ground, where the temperatures are lowest in the superpáramos; and the competition for light, pollinators, or both in the structurally more complex habitat of the subpáramos.

Inflorescence position (Fig. 6D). Twelve tree species have terminal inflorescences, whereas they are placed in lateral position in the remaining two, *Espeletia badilloi* Cuatrec. and *E. trujillensis* Cuatrec. Among rosette plants the proportion is more equilibrated, with terminal inflorescences in 22 species and lateral in 18 species. Rosette plants with lateral inflorescences clearly tend to occupy higher elevations than those with terminal inflorescences, with an important exception to this pattern in *E. aristeguietana*.

Inflorescence structure (Fig. 6E). Among trees, 12 species have inflorescences with monochasial and alternate structure, whereas they are dichasial and opposite in the remaining 2, *Espeletia badilloi* and *E. trujillensis*. The same trend is observed among rosette plants, with monochasial and alternate inflorescences in 31 species, and dichasial and opposite in 9 species. However, if the 7 rosette species with monocephalous inflorescences are excluded, the proportion of monochasial/alternate to dichasial/opposite becomes 29 to 4. It is worth mentioning that the opposite trend is observed among the Colombian *Espeletia* clade, in which taxa with dichasial/opposite inflorescence structure are much more diverse than those with monochasial/alternate inflorescence structure (Cuatrecasas, 2013).

Monocarpy/polycarpy (Fig. 6F). Strict monocarpy—death of the plant after the single reproduction event—is found among *Espeletia* in unbranched plants with terminal inflorescences. This combination of morphological features is observed in 1 tree, *E. spectabilis*, and 16 rosette species. However, monocarpy is also observed frequently among rosette plants with branching capacity, either by lack of branching after reproduction in individuals with single stems or as the simultaneous reproduction of all rosettes in multibranched individuals. Interestingly, the latter phenomenon has also been observed in some trees (e.g., *E. neriifolia*).

Spanish Names

After more than 10 years of extensive fieldwork in the Venezuelan Andes and interviewing about 100 people with regard to Spanish names, I have noticed that these plants, notably the rosette plants with dense indumentum on leaves, are indeed collectively known as *frailejón* (plural, *frailejones*), a name that nonetheless is also applied to some species of *Senecio* and *Orithrophium*. Branched forms are simply known as *árbol*, and I have rarely or never seen the use of the supposedly common names *incienso*, *anime*, or *carrambo*. Those names must therefore today be very rare or extremely localized. As noted by Diazgranados (2012) and Cuatrecasas (2013), there are some Spanish names that appear relatively more specific, particularly among rosette plants, but none is used bi-univocally. For instance, *frailejón (f.) amarillo* is used indistinctly for *Espeletia moritziana* (also known as *f. dorado*) and *E. schultzii* (also known as *f. de octubre*). The six dwarf *Espeletia* species are known as *f. pata de burro, f. batato*, or *f. chijí*, while *f. plateado* is used for all species with silvery indumentum: *E. jabonensis* Cuatrec., *E. floccosa, E. pannosa* (also known as *f. lanoso* and *f. chirique*) and *E. angustifolia* Cuatrec. (also known as *f. chirique*). Spanish names therefore seem to be rare or inconsistent in this plant group and, contrary to the practice promoted by Diazgranados (2012) and Cuatrecasas (2013), they will not be provided in this work. New Spanish names will not be proposed either. I share the view expressed in Diazgranados (2012) that giving common names helps in "socializing the knowledge of these species and instilling a feeling of responsibility among local inhabitants to protect these resources," but I also believe that these names would have a greater chance of being accepted and used if chosen by or in agreement with local communities.

Taxonomy

Espeletia Mutis ex Bonpl., Plant. Aeq. 2: 10. 1809.

Type species: *Espeletia grandiflora* Bonpl., Plant. Aeq. 2: 11. 1809. COLOMBIA. Santa Fe de Bogotá i Quindio, *Herbier de l'Amérique équatoriale, donné par M. A. Bonpland, s.n.* (Holotype: P [MNHN-P-P00320272]; Isotypes: P [MNHN-P-P00320273, MNHN-P-P00307378, MNHN-P-P00680447]).

Synonyms: *Carramboa* Cuatrec., Phytologia 35: 54. 1976. Type species: *Espeletia pittieri* Cuatrec., Ciencia (México) 6: 262. 1945. VENEZUELA. Mérida: forest between El Molino and ridge above San Isidro Alto, 2430–2895 m.a.s.l., 14 May 1944, *J. Steyermark 56532* (Holotype: VEN [not seen]; Isotypes: F, NY, US).

FIGURES 7–8. *Espeletia albarrengensis* (Cuatrec.) Mavárez. Laguna Albarregas, Mérida, Venezuela. **7**. Photograph by S. Aubert. **8**. Photograph by L. Gámez.

Coespeletia Cuatrec., Phytologia 35: 56. 1976. Type species: *Espeletia spicata* Sch. Bip. ex Wedd., Chlor. Andina: 65. 1855. VENEZUELA. Mérida: Sierra Nevada de Mérida, 14,000 pieds, August 1842, *J. Linden 400* (Holotype: P; Isotypes: F, FI [not seen], K, P).

Espeletiopsis Cuatrec., Phytologia 35: 54. 1976. Type species: *Espeletia jimenezquesadae* Cuatrec., Rev. Acad. Col. Ci. Exact. 3: 247. 1940a. COLOMBIA. Boyacá: Cordillera Oriental, Nevado del Cocuy, hacia la Cueva, en la Zanja, 3700 m.a.s.l., 13 Septiembre 1938, *J. Cuatrecasas & H. García-Barriga 1635* (Holotype: COL; Isotype: US).

Libanothamnus Ernst, Vargasia 7: 186. 1870. Type species: *Espeletia neriifolia* (Bonpl. ex Humb.) Sch. Bip. ex Wedd., Chlor. Andina: 67. 1855. VENEZUELA. Caracas: Silla de Caracas, 3 Janvier 1800, *Herbier donné par M. Bonpland en 1833 N° 652* (Lectotype: P [MNHN-P-P04086343]; Isolectotype: P [MNHN-P-P04086342]).

Ruilopezia Cuatrec., Phytologia 35: 51. 1976. Type species: *Espeletia figueirasii* Cuatrec., Phytologia 20: 475. 1971. VENEZUELA. Mérida: Sierra Nevada de Santo Domingo, Páramo de los Granates, Loma de Paja, las Escaleras, 3240 m.a.s.l., 11 October 1969, *J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28068* (Holotype: US; Isotypes: F, IVIC, MERF, U, US).

Paramiflos Cuatrec., Proc. Biol. Soc. Wash. 108: 748. 1995. Type species: *Espeletia glandulosa* Cuatrec., Rev. Acad. Col. Ci. Exact.: 434. 1940b. COLOMBIA. Boyacá: Cordillera Oriental, Alto de Canutos, Páramo de Guantiva, vertiente sur, 3200–3400 m.a.s.l., *J. Cuatrecasas 10360* (Holotype: COL; Isotypes: COL, F, P, US).

Tamania Cuatrec., Phytologia 35: 53. 1976. Type species: *Espeletia chardonii* A.C. Sm., Bol. Soc. Ven. Ci. Nat. 7: 237. 1942. VENEZUELA. Táchira: Páramo de Tamá, El Paramito, 2550 m.a.s.l., 15 August 1939, *C. E. Chardon 78* (Holotype: US; Isotypes: NY, VEN [not seen]).

1. Espeletia albarregensis (Cuatrec.) Mavárez, *comb. nov.* Basionym: *Coespeletia albarregensis* Cuatrec., Mem. New York Bot. Gard. 107: 588. 2013. TYPE: VENEZUELA. Mérida: Laguna Albarregas, Páramo de los Conejos, Sierra de la Culata, 3850 m.a.s.l., 27 March 1972, *L. Ruiz-Terán 7050* (Holotype: US; Isotype: MERF). Fig. 7–9.

Rosette polycarpic, caulescent, stem height up to 1.0 m, entirely covered by marcescent leaves. *Leaf* open sheath, sessile, adaxially densely pubescent, lanuginose, length 30–45 cm, width 2.8–5.0 cm, ratio 9–10:1, secondary nerves parallel, 5–10 mm apart. *Inflorescence* lateral, simple, monochasial, botryoid, axes 60–80 cm, 9–11 monocephalous peduncles, vegetative part usually with 4–6 alternate bracts. *Capitulum* diam. 35–55 mm, ligular circle equal or slightly shorter than the involucre, disc 20–25 mm, ray ligules yellow. *Espeletia albarregensis* can be distinguished from other Venezuelan rosette plants for its botryoid inflorescences with large capitula (diam. > 35 mm). It resembles *E. timotensis*, from which it can be distinguished for its smaller stem

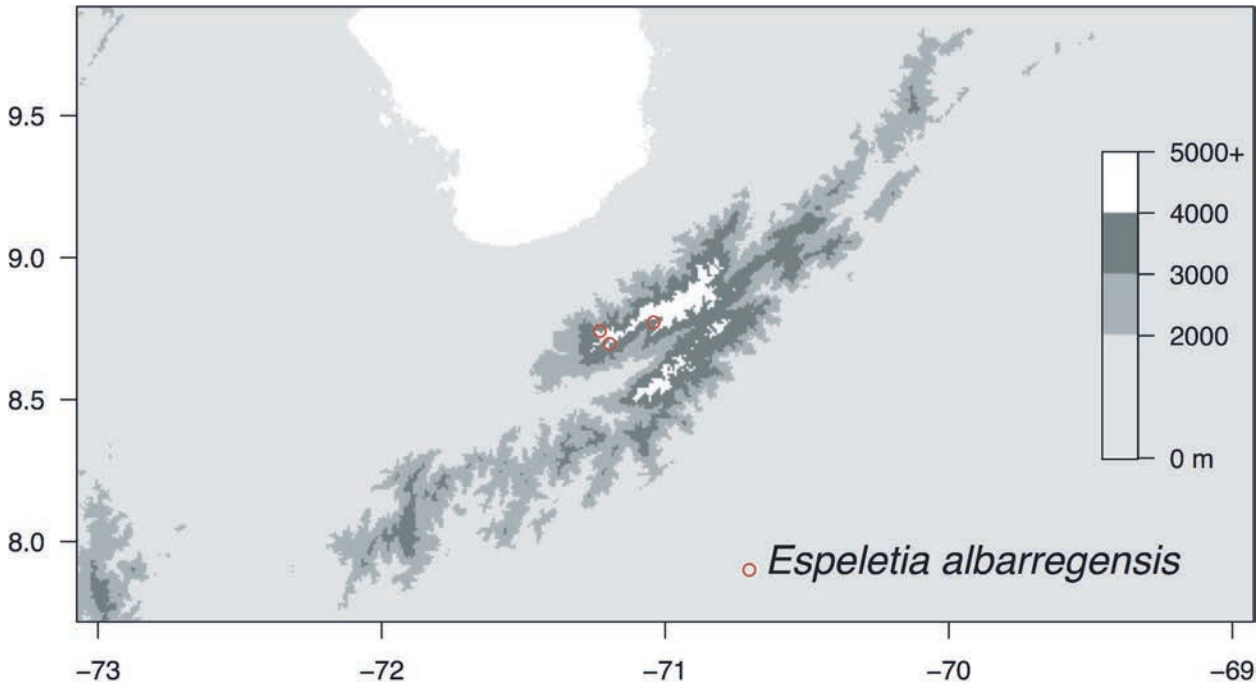
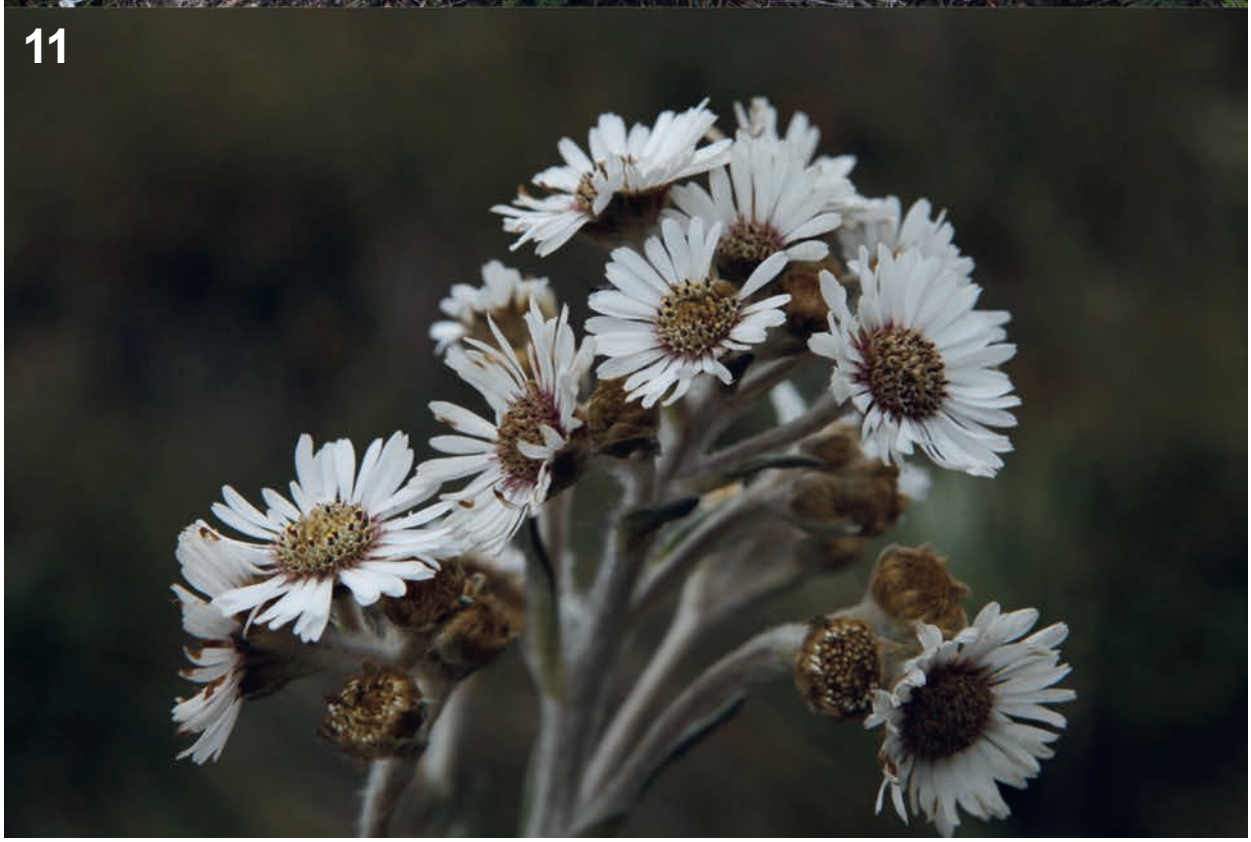


FIGURE 9. Distribution of *Espeletia albarregensis* (Cuatrec.) Mavárez.



FIGURES 10–11. *Espeletia angustifolia* Cuatrec. Páramo de San José, Mérida, Venezuela (Photographs by S. Aubert).

(< 1.0 m vs. > 1.0 m), smaller length-to-width leaf ratio (< 10:1 vs. > 10:1), shorter inflorescences (< 80 cm vs. > 85 cm), fewer capitula (9–11 vs. 8–15). and longer ray corollas (> 11.0 mm vs. < 9.0 mm).

Distribution: VENEZUELA. Mérida: originally known only from the type locality. However, I have recently found a few isolated individuals 3 km NW of the town of la Culata (8°46'19.1"N 71°02'30.9"W), about 20 km NW of the type locality. 3700–3900 m.a.s.l., on steep and rocky páramo slopes, and down to the lakeshore in the type locality (Fig. 9).

Additional specimens examined (selection): *L. Ruiz-Terán 7050* (US), *L. Ruiz-Terán 7051* (US), *López-Figueiras 30545* (US). *P. Berry 3852* (US) is probably a hybrid: *E. albarregensis* × *E. schultzii* or *E. schultzii* × *E. timotensis*.

2. *Espeletia angustifolia* Cuatrec., Bol. Soc. Ven. Ci. Nat. 17: 80. 1956a. TYPE: VENEZUELA. Mérida: Páramo de Mijará, 3300 m.a.s.l., 18 March 1922, *A. Jahn 973* (Holotype: US; Isotypes: G, NY). Fig. 10–12.

Homotypic synonym: *Espeletiopsis angustifolia* (Cuatrec.) Cuatrec., Phytologia 35: 55. 1976.

Rosette polycarpic, sessile. *Leaf* open sheath, sessile, adaxially densely pubescent, lanuginose, length 15–30 cm, width 0.7–1.5 cm, ratio 20–25:1, secondary nerves obsolete or thin, 1–3 mm apart when visible. *Inflorescence* lateral, compound, primary branching monochasial, corymboid, length 50–70 cm, vegetative part with several alternate bracts. *Capitulum* diam. 15–20 mm, ligular circle 25–35(40) mm, disc 12–15 mm, ray ligules white. *Espeletia angustifolia* differs from other species for its sessile polycarpic rosette habit and its capitulum with white ray ligules. It resembles *E. pannosa*, from which it can be distinguished for its leaves with smaller ratios (< 25:1 vs. > 30:1) and lanuginose indumentum on both sides (vs. silvery/sericeous adaxially).

Distribution: VENEZUELA. Mérida: Páramo de Mijará, de San José, and de la Veguilla. 2900–3500 m.a.s.l., in open grass páramos and well-drained slopes (Fig. 12).

Additional specimens examined (selection): *A. Jahn 973* (US, G, NY), *C. Sobrevila & M. Guariguata 1534* (US), *P. Berry*, *C. Sobrevila & C. Estrada 4291* (US), *P. Berry & R. Calvo 4396* (US), *J. Cuatrecasas*, *M. López-Figueiras & L. Marcano-Berti 28098* (US).

J. Steyermark 56279 in F is not an isotype but a paratype.

3. *Espeletia arborea* Aristeg., Bol. Soc. Ven. Ci. Nat. 20: 286. 1959. TYPE: VENEZUELA. Trujillo: Guirigay, hacia Peña Blanca, 3200 m.a.s.l., August 1958, *L. Aristeguieta & E. Medina 3635* (Holotype: VEN [not seen]; Isotypes: NY, US). Fig. 13–15.

Homotypic synonym: *Libanothamnus arboreus* (Aristeg.) Cuatrec., Phytologia 35: 50. 1976.

Tree profusely branched, height up to 5 m. *Leaf* tubular sheath, pseudopetiolate (length 1.5–2.5 cm), leaf length 15–25 cm, width 3.0–7.0 cm, ratio 3.0–4.0:1, secondary nerves parallel, 1–2(3) mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, at about the same level as the surrounding leaves, length 15–30 cm, branched near the base. *Capitulum* diam. 12–18 mm, ligular circle 24–30 mm, disc 14–18 mm, ray ligules cream or greenish. *Espeletia arborea* differs from other tree

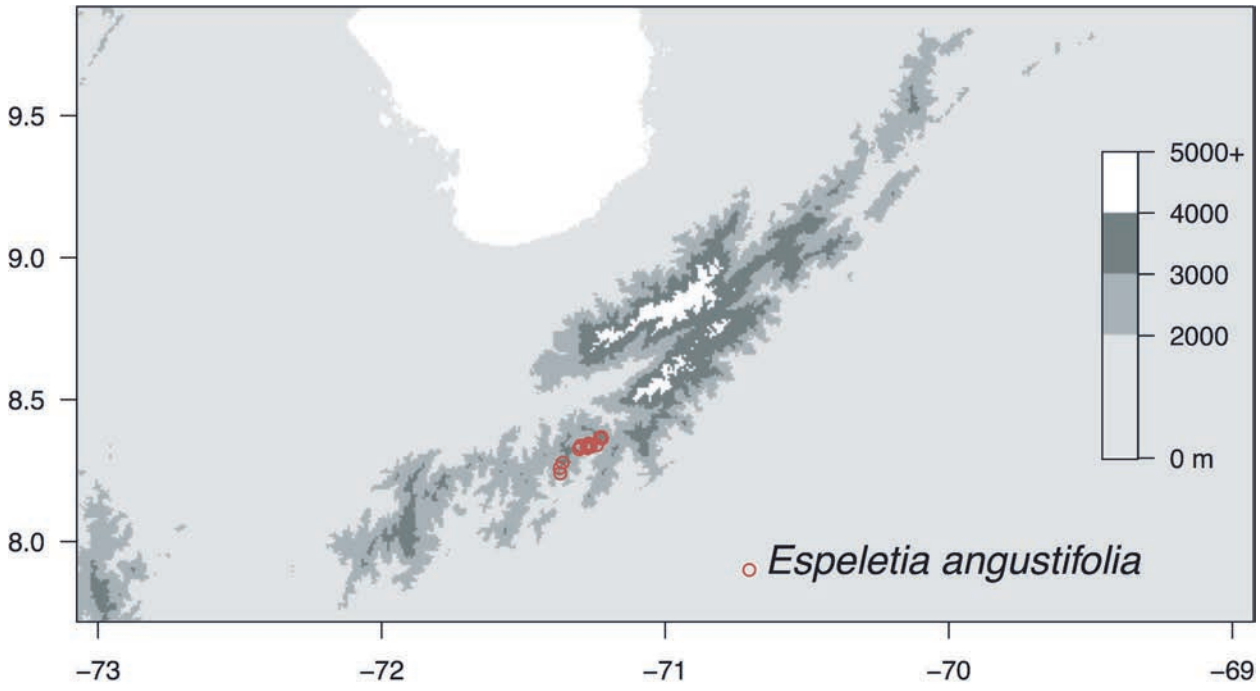


FIGURE 12. Distribution of *Espeletia angustifolia* Cuatrec.

FIGURES 13–14. *Espeletia arborea* Aristeg. Laguna de Santo Cristo, Mérida, Venezuela (Photographs by S. Aubert).

species for its pseudopetiolate leaves with sheaths adaxially glabrous, closely packed parallel secondary nerves (< 3 mm apart), and its ligulate capitulum with diam. > 12 mm.

Distribution: VENEZUELA. Trujillo: Páramo de Guirigay, in the upper basins of rivers Aracay and Burate. Mérida-Barinas border: Páramo de los Granates, de Gavidia, and around Laguna de Santo Cristo in Sierra Nevada de Mérida. Northern populations (var. *arborea*) found 2900–3200 m.a.s.l. in the upper level of the Andean forest below the timberline, whereas southern populations (var. *lancifolia*) found 3300–3700 m.a.s.l., usually in subpáramo habitats above the timberline, as well as in humid páramos near rivers and lakes (Fig. 15).

Additional specimens examined (selection): *L. Aristeguieta & E. Medina 3635* (US, NY), *L. Ruiz-Terán & López-Figueiras 13081* (US), *R. Riina*, *R. Duno*, *R. Ghinaglia & R. Gonto 635* (US), *López-Figueiras & H. Rodríguez 8823* (US), *López-Figueiras 14520* (US).

Only "L. Aristeguieta" (E. Medina missing) appears as collector in the labels of the isotypes at NY and US.

3.1. *Espeletia arborea* Aristeg. var. ***arborea***

Distribution: Venezuela. Trujillo: Páramo de Guirigay, in the upper basins of rivers Aracay and Burate. 2900–3200 m.a.s.l., found in the upper level of Andean forest below the timberline, as well as in low-elevation shrubby subpáramo habitats.

3.2. Espeletia arborea Aristeg. var. ***lancifolia*** (Cuatrec.) Mavárez, *comb. nov*.

Basionym: *Libanothamnus arboreus* (Aristeg.) Cuatrec. var. *lancifolius* Cuatrec., Mem. New York Bot. Gard. 107: 438. 2013. TYPE: VENEZUELA. Mérida-Barinas border: Laguna Azul o del Corazón, arriba de Loma de Paja, Páramo de los Granates, unos 18 km al E. de Sierra Nevada de Santo Domingo, 3350 m.a.s.l., 17 September 1971, *L. Ruiz-Terán 6348* (Holotype: US; Isotype: MERF).

Differs from *Espeletia arborea* var. *arborea* for its acutely lanceolate leaves and its involucre completely covered by the last row of outer phyllaries (*vs*. with several imbricated levels).

Distribution: VENEZUELA. Mérida-Barinas border: Páramo de Los Granates, de Gavidia, and Laguna de Santo Cristo in Sierra Nevada de Mérida. 3300–3700 m.a.s.l., found in subpáramo habitats above the timberline, as well as in humid páramos near rivers and lakes.

Additional specimens examined (selection): *L. Ruiz-Terán 6348* (US), *L. Ruiz-Terán 8462* (US), *L. Dorr & L. Barnett 5632* (US).

Collection date given as "17 October 1971" in Cuatrecasas (2013: 438).

4. *Espeletia aristeguietana* Cuatrec., Phytologia 27: 174. 1973b. TYPE: VENEZUELA. Trujillo: la Cañada, Páramo de la Cristalina, 2500–2600 m.a.s.l., 30 October 1969. *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28194* (Holotype: US; Isotype: US). Fig. 16–18.

Rosette polycarpic, sessile. *Leaf* open sheath, sessile, adaxially densely pubescent, tomentose-velvety, greenish, length 40–55 cm, width 7.5–14.0 cm, ratio 4.0–5.7:1, bases of secondary nerves parallel, unevenly distributed, 8–20 mm apart. *Inflorescence* lateral, compound, primary branching dichasial, thyrsoid, length 70–90 cm, vegetative part with 2 pairs of opposite bracts. *Capitulum* diam. 10–14 mm, ligular circle 24–28 mm, disc 10–11 mm, ray ligules yellow.

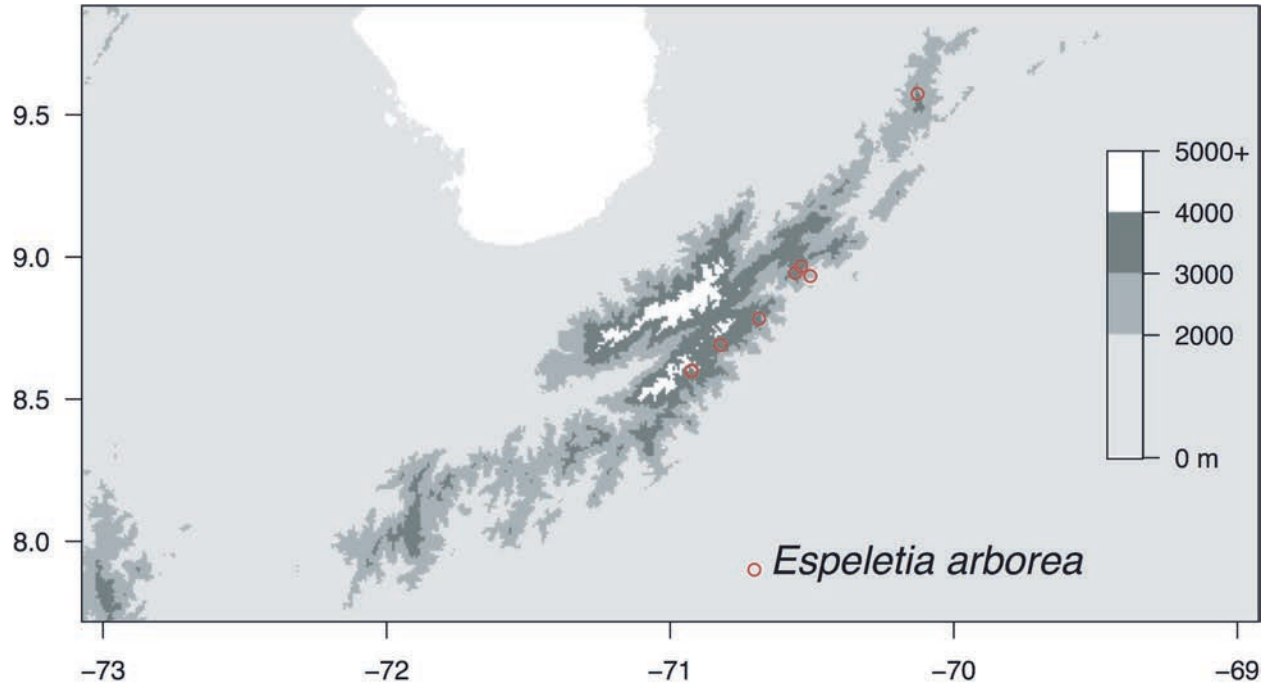


FIGURE 15. Distribution of *Espeletia arborea* Aristeg.

FIGURES 16–17. *Espeletia aristeguietana* Cuatrec. Páramo de la Cristalina, Trujillo, Venezuela (Photographs by S. Aubert).

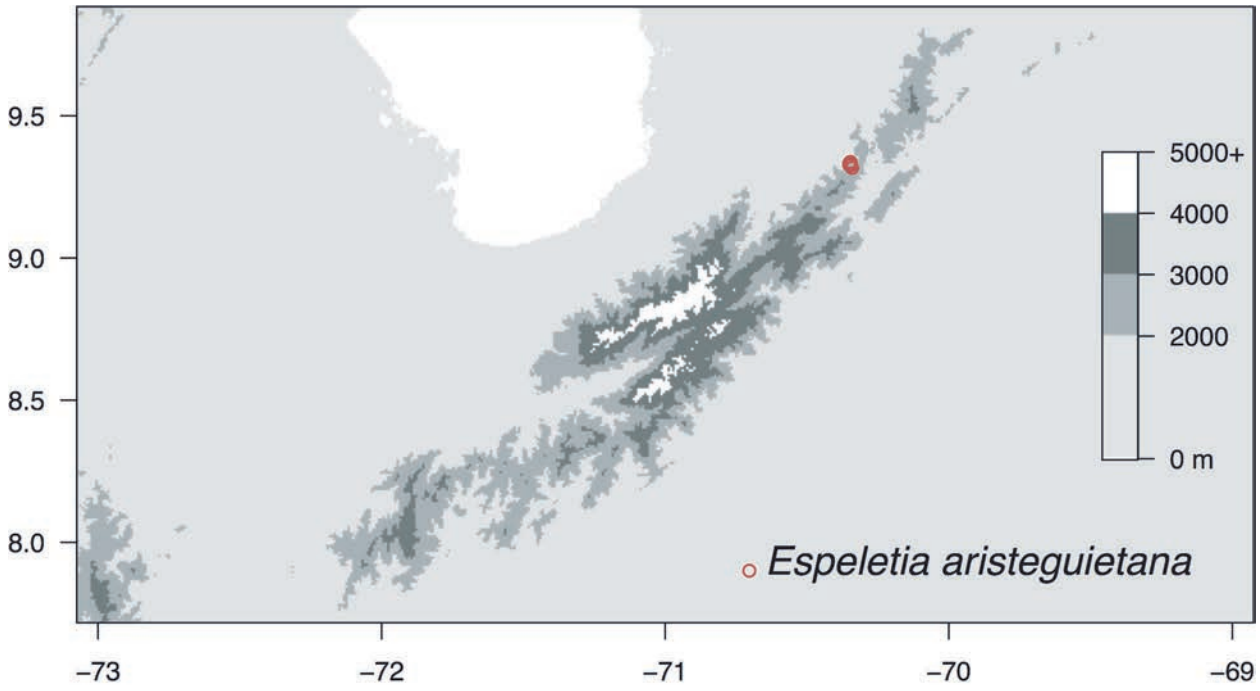


FIGURE 18. Distribution of *Espeletia aristeguietana* Cuatrec.

Espeletia aristeguietana can be easily distinguished from other species with dichasial thyrsoid inflorescences for its unique tomentose, velvety indumentum on both sides of leaves and for its small capitulum (diam. < 15 mm).

Distribution: VENEZUELA. Trujillo: known only from the type locality. 2500–2800 m.a.s.l., found in open locations within a relatively low-elevation subpáramo habitat, and in clearings in the highly degraded upper level of the Andean forest (Fig. 18).

Additional specimens examined (selection): *J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28194* (US); *id. 28559* (F, U, US), *J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28560* (US), *J. Cuatrecasas, M. López-Figueiras & H. Rodríguez 28994* (US), *L. Ruiz-Terán & M. López-Figueiras 2258* (US).

5. *Espeletia atropurpurea* A.C. Sm., Brittonia 1: 508. 1935. TYPE: VENEZUELA. Mérida: Páramo de Quirorá, 3200 m.a.s.l., 8 October 1971, *A. Jahn 731* (Holotype: US; Isotypes: F, G, GH, NY, US, VEN [not seen]). Fig. 19–21.

Homotypic synonym: *Ruilopezia atropurpurea* (A.C. Sm.) Cuatrec., Phytologia 35: 52. 1976.

Rosette monocarpic, sometimes with smaller rosettes budding at the base of the main rosette, sessile. *Leaf* open sheath, strongly pseudopetiolate (length 5–25 cm), adaxially glabrous, glossy green, length 20–45 cm, width 4.0–9.0 cm, ratio 4–8(11):1, margins sometimes dentate, teeth 4–10 mm apart, secondary nerves filiform, parallel, 3–10 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, paniculate, length 100–200 cm, usually branched from near the base, although rather loosely. *Capitulum* diam. 10–14 mm, up to 20 mm when dry, eligulate. *Espeletia atropurpurea* can be easily distinguished from other species for its sessile monocarpic rosette habit, strongly pseudopetiolate and oblong leaves glabrous on the adaxial side, and eligulate ray corollas.

Distribution: VENEZUELA. Mérida: widespread in the southern páramos of Sierra Nevada de Mérida (e.g., Don Pedro, Aricagua, San José, Quirorá), and of Sierra de la Culata (e.g., los Conejos). Also found in the western slopes of Pico Bolívar, between cable car stations La Aguada and Loma Redonda. Border Mérida-Táchira: Páramo de Guaraque, hills above El Portachuelo and Las Porqueras (above La Grita) and Páramo de la Negra. Táchira: Páramo del Batallón. Usually 2800–3200 m.a.s.l., but the population west of Pico Bolívar can reach 3700 m.a.s.l. Found in shrubby subpáramo habitats and in forest clearings near the timberline (Fig. 21).

Additional specimens examined (selection): *A. Jahn 731* (F, G, GH, NY, US), *J. L. Panero, C. E. Benítez & V. M. Badillo 2702* (US), *C. Sobrevila, A. Weitzman & D. Solbrig 1560* (US), *J. Cuatrecasas, M. López-Figueiras & L. Marcano-Berti 28013* (F, U, US), *J. Cuatrecasas, M. López-Figueiras & L. Marcano-Berti 28001* (F, U, US).

6. *Espeletia badilloi* Cuatrec., Ciencia (México) 6: 261. 1945. TYPE: VENEZUELA. Mérida: Páramo de Don Pedro, 2900 m.a.s.l., 18 July 1944, *V. Badillo 991* (Holotype: VEN). Fig. 22–25.

Homotypic synonym: *Carramboa badilloi* (Cuatrec.) Cuatrec., Phytologia 35: 54. 1976.

Heterotypic synonyms: *Espeletia littlei* Aristeg., Fl. Venez. 10(1): 434. 1964. TYPE: VENEZUELA. Mérida: La Carbonera, 2700 m.a.s.l., October 1953, *Little 15592* (Holotype: VEN).

Carramboa littlei (Aristeg.) Cuatrec., Phytologia 35: 54. 1976.

FIGURES 19–20. *Espeletia atropurpurea* A.C. Sm. Páramo de San José, Mérida, Venezuela (Photographs by S. Aubert).

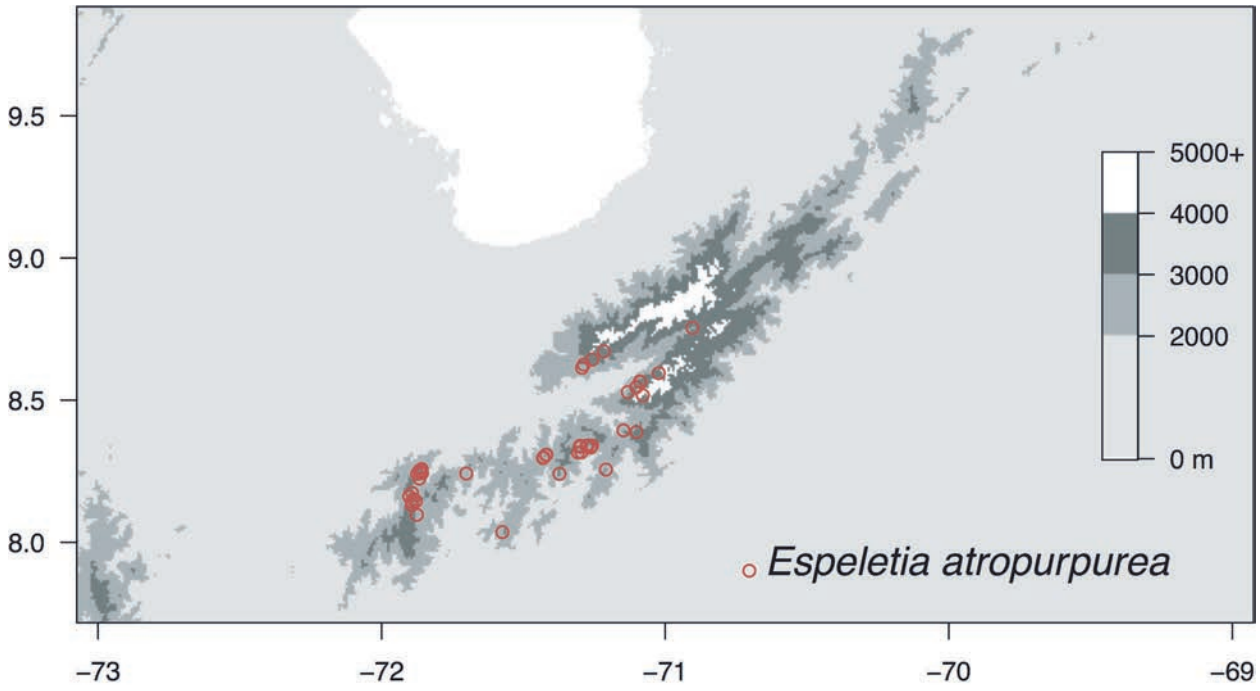


FIGURE 21. Distribution of *Espeletia atropurpurea* A.C. Sm.

Tree profusely ramified, height up to 20 m. *Leaf* tubular sheath, pseudopetiolate (length 2.5–9.0 cm), adaxially glabrous or loosely short-hirsute, dark green, length 25–60 cm, width 15–35 cm, ratio 1.3–2.2:1, bases of secondary nerves parallel, unevenly distributed, 10–40 mm apart. *Inflorescence* lateral, compound, primary branching dichasial, corymboid, length 20–70 cm, at the same level or slightly surpassing the surrounding leaves, vegetative part leafless, about half of total length. *Capitulum* diam. 6–9 mm, ligular circle 12–22 mm, disc 5–8 mm, ray ligules yellow. *Espeletia badilloi* can be distinguished from other tree species for its profusely ramified habit, pseudopetiolate leaves with low length-to-width ratio (< 2.2:1), and dichasial corymboid inflorescences with vegetative part aphyllous.

Distribution: VENEZUELA. Border Barinas-Trujillo: forested hills in Páramo de Guirigay and de Ortiz. Mérida: forested areas in the southern slopes of Sierra Nevada de Mérida, toward Páramo de Don Pedro and the hills above Aricagua, Páramo de las Coloradas (above El Molino), de Quirorá, de Guaraque, and Pico de Horma. Southern slopes of Sierra de la Culata in the valley of Río Capaz and slopes of Pico Campanario. Mérida-Táchira: forested hills above Pregonero, El Portachuelo, and Las Porqueras (la Grita) and below Páramo de la Negra and del Batallón. 2400–3200 m.a.s.l., locally down to 2200 m.a.s.l., usually found in gregarious populations in forests clearings and along trails/roads (Fig. 25).

Additional specimens examined (selection): *M. López-Figueiras*, *R. Ovando & F. Ricardi 14120* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28149* (F, U, US), *M. López-Figueiras & L. Ruiz-Terán 14013* (US).

6.1. *Espeletia badilloi* Cuatrec. var. ***badilloi***

Distribution: VENEZUELA. Border Barinas-Trujillo: forested hills in Páramo de Guirigay and de Ortiz. Mérida: forested areas in the southern slopes of Sierra Nevada de Mérida, towards Páramo de Don Pedro and the hills above Aricagua. Southern slopes of Sierra de la Culata in the valley of Río Capaz and slopes of Pico Campanario. Between 2400 and 3200 m.a.s.l., sometimes down to 2200 m.a.s.l., usually found in gregarious populations in forest clearings and along trails/roads.

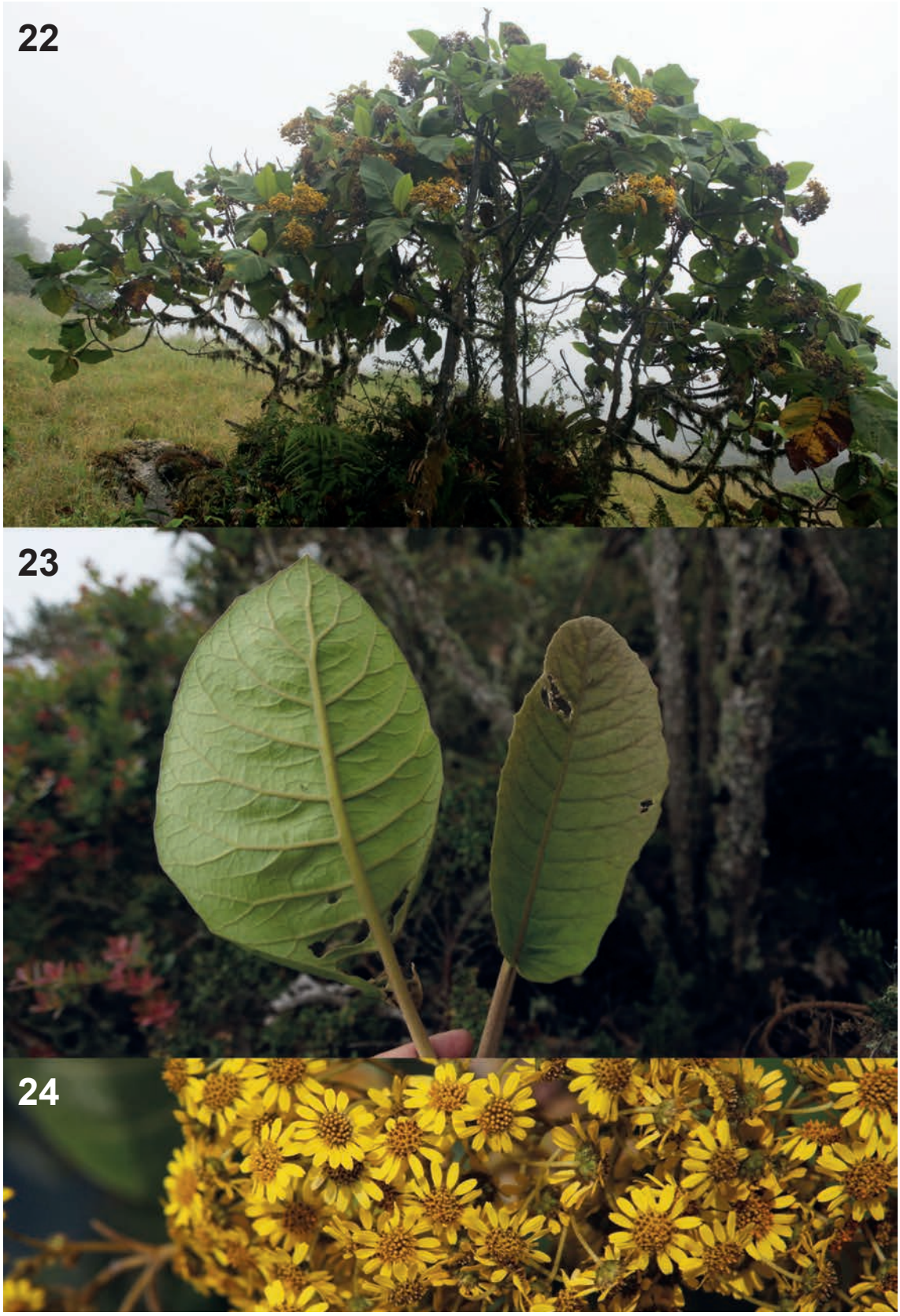
6.2. Espeletia badilloi Cuatrec. var. ***pittieri*** (Cuatrec.) Mavárez, *comb. nov.*

Basionym: *Espeletia pittieri* Cuatrec., Ciencia (México) 6: 262. 1945. TYPE: VENEZUELA. Mérida: forest between El Molino and ridge above San Isidro Alto, 2430–2895 m.a.s.l., 14 may 1944, *J. A. Steyermark 56532* (Holotype: VEN [not seen]; Isotypes: F, NY, US).

Homotypic synonyms: *Carramboa pittieri* (Cuatrec.) Cuatrec., Phytologia 35: 54. 1976.

Carramboa badilloi (Cuatrec.) Cuatrec. var. *pittieri* Cuatrec., Mem. New York Bot. Gard. 107: 396. 2013.

According to Cuatrecasas (2013: 396), *Espeletia badilloi* var. *pittieri* can be distinguished from *E. badilloi* var. *badilloi* for its rigidly coriaceous leaves (vs. chartaceous), scarcely pilose adaxially and rough to the touch (vs. softly hirsute), with shorter pseudopetioles (1.5–5.5 cm vs. 2.5–9.0 cm) and with many conspicuous transverse nerves near the base (vs. none or few). However, these differences are subtle and depend largely on subjective criteria, making



FIGURES 22–24. *Espeletia badilloi* Cuatrec. Páramo de Don Pedro, Mérida, Venezuela (Photographs by S. Aubert).

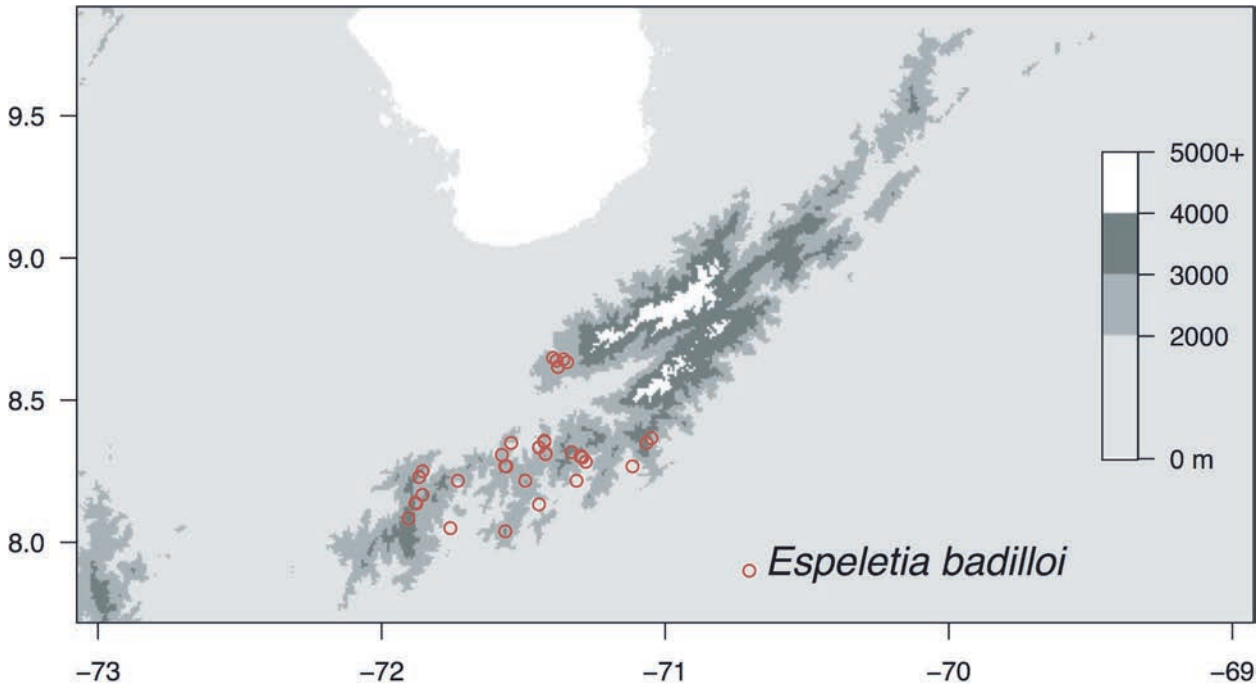


FIGURE 25. Distribution of *Espeletia badilloi* Cuatrec.

the identification of *E. badilloi* var. *pittieri* quite difficult. Besides, individuals with intermediate or mosaic characters are relatively common. More studies will be necessary to determine the validity of this taxon.

Distribution: VENEZUELA. Mérida-Táchira: forested hills in the southern end of Sierra Nevada de Mérida, in Páramo de las Coloradas (between Santa Cruz de Mora and El Molino), de Quirorá, de Guaraque, de la Negra, and del Batallón; Pico de Horma; hills above Pregonero; and El Portachuelo (La Grita). 2400–3200 m.a.s.l., usually found in gregarious populations in forest clearings and along trails/roads.

Additional specimens examined (selection): *J. Steyermark 56532* (F, NY, US), *L. Ruiz-Terán & M. López-Figueiras 9320* (US), *L. Ruiz-Terán & M. López-Figueiras 1468* (US), *L. Ruiz-Terán & M. López-Figueiras 541* (U, US).

7. *Espeletia banksiifolia* Sch. Bip. & Ettingsh. ex Wedd., Chlor. Andina: 67. 1855. TYPE: VENEZUELA. Mérida: Sierra Nevada de Mérida, 10,000 pieds, Juin 1847, *N. Funck & L. J. Schlim 1550* (Holotype: P; Isotypes: BR, F, G, GH, LD, P). Fig. 26, 27.

Homotypic synonym: *Libanothamnus banksiifolius* (Sch. Bip. & Ettingsh. ex Wedd.) Cuatrec., Phytologia 35: 50. 1976.

The final epithet of this species was originally spelled "*banksiaefolia*." According to ICN Art. 60.10, the correct spelling is "*banksiifolia*." Also, collectors are given as "*V. A. Funck & L. J. Schlim*" in Diazgranados (2012: 35).

7.1. *Espeletia banksiifolia* Sch. Bip. & Ettingsh. ex Wedd. subsp. ***banksiifolia***

Tree size and architecture unknown. *Leaf* tubular sheath, pseudopetiolate (length 2.5–5.0 cm), adaxially glabrous, green, length 15–30 cm, width 4.5–6.5 cm, ratio 3.5–5.0:1, margins clearly dentate, teeth 0.5–1.0 mm long, 2–5 mm apart, secondary nerves parallel, 1–2 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, barely surpassing the surrounding leaves, length 18–30 cm, branched near the base. *Capitulum* diam. 18–22 mm, ligular circle 25–35 mm, disc 13–18 mm, ray ligules white. *Espeletia banksiifolia* can be distinguished from other tree species for its oblong leaves with dentate margins and sheaths adaxially barbate. Other trees occasionally show some teeth in their leaves, but with lower density and smaller size, and not as a consistent feature of the species.

Distribution: VENEZUELA. Mérida-Barinas: known only from the type collection, without precise locality.

Specimens examined: *N. Funck & L. J. Schlim 1550* (P, BR, F, G, GH, LD).

7.2. Espeletia banksiifolia Sch. Bip. & Ettingsh. ex Wedd. subsp. ***granatesiana*** (Cuatrec.) Mavárez, *comb. nov.*

Basionym: *Espeletia granatesiana* Cuatrec., Phytologia 27: 44. 1973a. TYPE: VENEZUELA. Mérida: Sierra de Santo Domingo, Páramo de Los Granates, Loma de Paja, 3100 m.a.s.l., 11 October 1969, *J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28063* (Holotype: US; Isotypes: COL, F, MERF, U, US).

Homotypic synonyms: *Libanothamnus granatesianus* (Cuatrec.) Cuatrec., Phytologia 35: 50. 1976.

Libanothamnus banksiifolius Sch. Bip. & Ettingsh. ex Wedd. subsp. *granatesianus* Cuatrec., Mem. New York Bot. Gard. 107: 443. 2013.

Tree profusely branched, height up to 10 m. *Leaf* tubular sheath, pseudopetiolate (length 2.5–6.0 cm), adaxially

FIGURES 26–27. *Espeletia banksiifolia* Sch. Bip. & Ettingsh. ex Wedd. Páramo de los Granates, Mérida, Venezuela (Photographs by S. Aubert).

glabrous, green, length 20–40 cm, width 7.0–15.0 cm, ratio 2.0–3.5:1 (young individuals may have bigger leaves), margins clearly dentate, teeth 0.5–1.0 mm long, 2–6 mm apart, secondary nerves parallel, 1.5–3.0 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, surpassing the surrounding leaves, length 25–60 cm, width 15–30 cm, vegetative part with several alternate bracts, about half of total length. *Capitulum* diam. 10–12 mm, ligular circle 15–25 mm, disc 8–12 mm, ray ligules white or greenish-creamy. *Espeletia banksiifolia* subsp. *granatesiana* can be distinguished from other tree species for its leaves with dentate margins. It differs from the *E. banksiifolia* subsp. *banksiifolia* in its broader leaves (width > 7.0 cm) and its much smaller capitulum (diam. < 12 mm).

Distribution (Fig. 28): VENEZUELA. Mérida-Barinas: all along the eastern slopes of Sierra Nevada de Mérida, in Páramo de Don Pedro, Filo la Vagabunda (between El Morro and Aricagua), Las Lajas (Mucutuy), Los Aranguren, and Minungú (approx. 10 km E. of Tabay). Also found in Páramo de Los Granates in Sierra de Santo Domingo, and in Páramo de Guirigay. 2800–3200 m.a.s.l., in humid locations in the upper levels of the Andean forest below the timberline.

Additional specimens examined (selection): *J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28063* (US, F, U), *M. López-Figueiras 21973* (U, US), *L. Ruiz-Terán & M. López-Figueiras 9393* (US), *L. Ruiz-Terán & M. López-Figueiras 9394* (US).

Cuatrecasas, Ruiz-Terán & López-Figueiras 28063 in F should be labelled as isotype.

8. *Espeletia batata* Cuatrec., Phytologia 40: 27. 1978. TYPE: VENEZUELA. Mérida: Alto del Morato, Páramo de los Granates, Sierra Nevada de Santo Domingo, 3600 m.a.s.l., 10 October 1969, *J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28058* (Holotype: US; Isotypes: F, MERF, US). Fig. 29–31.

Rosette polycarpic, sessile, dwarf. *Leaf* open sheath, sessile, adaxially densely pubescent, lanate-lanuginose, white-cinereous, length 6.5–14.5 cm, width 0.8–2.0 cm, ratio 5–15:1, bases of secondary nerves parallel, 2–4 mm apart. *Inflorescence* lateral, simple, dichasial, monocephalous, length 25–55 cm, with 2–3 pairs of opposite bracts. *Capitulum* diam. 18–24 mm, ligular circle 30–40 mm, disc 12–15 mm, yellow ligules. *Espeletia batata* can be distinguished from other Venezuelan rosette plants with monocephalous inflorescences by its leaf sheaths densely barbate abaxially and its inflorescences with 2–3 pairs of opposite bracts (vs. 1, rarely 2 opposite basal pairs and 5–12 alternate in *E. ulotricha*). *Espeletia batata* also resembles some uncommon individuals of *E. weddellii* with monocephalous inflorescences, from which it can be distinguished by its broader leaves (0.8–2.0 cm vs. 0.3–1.0 cm), with oblong or spatulate shape (vs. linear) and covered by a lanate indumentum on both sides (vs. villous and subappressed adaxially).

Distribution: VENEZUELA. Mérida: Sierra de la Culata, Sierra Nevada de Mérida and Sierra de Santo Domingo. 3600–4300 m.a.s.l., in humid locations close to swamps and streams, also in seasonally humid places where some water can be retained within apparently dry rocky areas (Fig. 31).

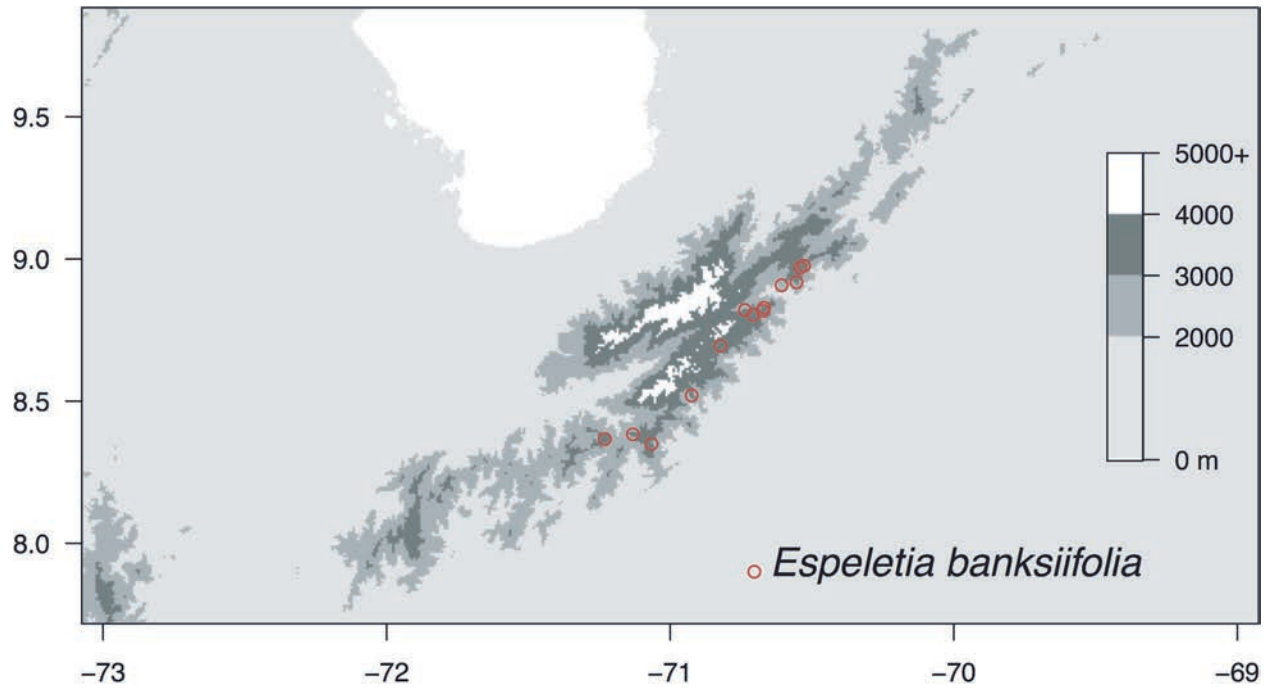


FIGURE 28. Distribution of *Espeletia banksiifolia* Sch. Bip. & Ettingsh. ex Wedd.

FIGURES 29–30. *Espeletia batata* Cuatrec. Páramo de Piedras Blancas, Mérida, Venezuela (Photographs by S. Aubert).

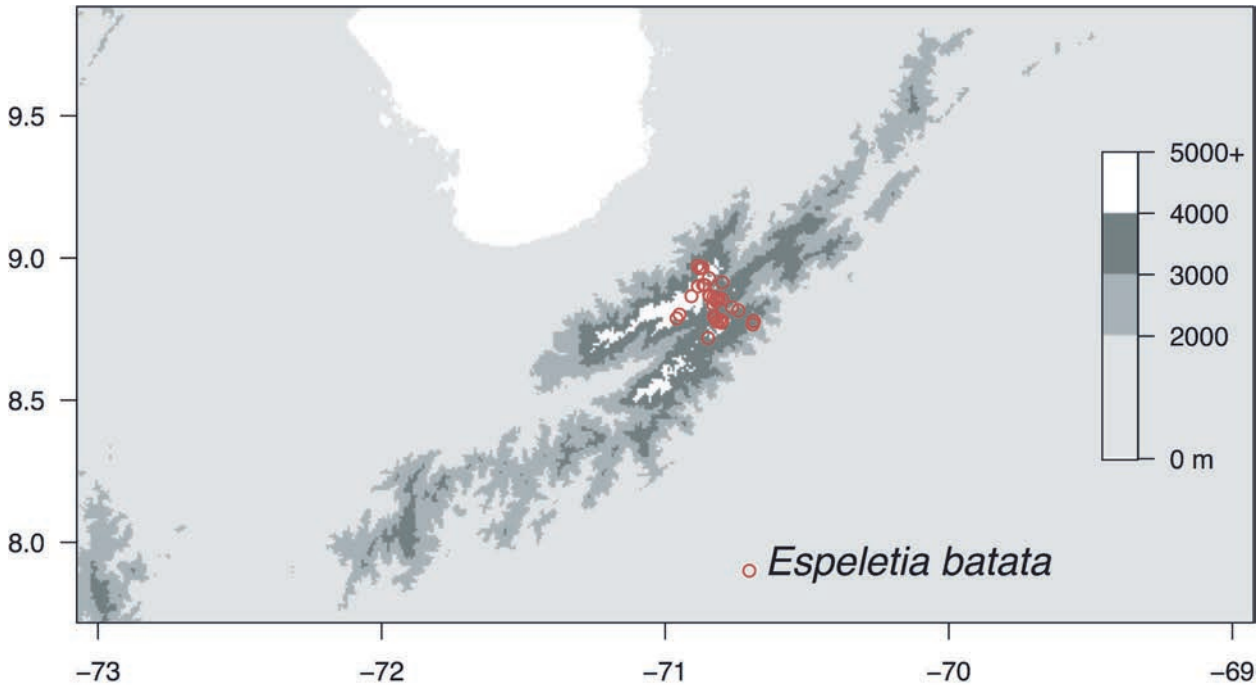


FIGURE 31. Distribution of *Espeletia batata* Cuatrec.

Additional specimens examined (selection): *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28058* (F, U, US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28081* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras. 28036* (F, U, US), *P. Berry 3860* (US), *L. Ruiz-Terán & M. López-Figueiras 1071* (US).

Cuatrecasas, *Ruiz-Terán & López-Figueiras 28058* in F should be labelled as an isotype.

9. *Espeletia bracteosa* Standl., Amer. J. Bot. 2: 484. 1915. TYPE: VENEZUELA. Trujillo: Páramo de la Cristalina, 2900 m.a.s.l., 20 December 1910, *A. Jahn 156* (Holotype: US; Isotype: VEN [not seen]). Fig. 32–34.

Homotypic synonym: *Ruilopezia bracteosa* (Standl.) Cuatrec., Phytologia 35: 52. 1976.

Heterotypic synonyms: *Espeletia frailejonota* Aristeg., Bol. Soc. Ven. Ci. Nat. 20: 284. 1959. TYPE: VENEZUELA. Trujillo: Páramo de Guirigay, hacia Laguna la Parida, 3400 m.a.s.l., August 1958, *L. Aristeguieta & E. Medina 3576* (Holotype: VEN [not seen]; Isotypes: NY, US).

Ruilopezia frailejonota (Aristeg.) Cuatrec., Phytologia 35: 52. 1976.

Rosette monocarpic, sometimes branched at the base, sessile. *Leaf* open sheath, strongly pseudopetiolate (length 3–10 cm), adaxially glabrous, length 20–75 cm, width 2.0–10.0 cm, ratio 7–15:1, secondary nerves parallel, 4–12 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 50–200 cm, vegetative part copiously bracteate, about half of total length. *Capitulum* diam. 12–15 mm, ligular circle 20–30(35), disc 10–14 mm, ray ligules yellow. *Espeletia bracteosa* can be easily distinguished from other species by its monocarpic sessile rosette habit, strongly pseudopetiolate obate-elliptic leaves, and capitulum with yellow ray ligules.

Distribution: VENEZUELA. Trujillo: Páramo de la Cristalina, Filo la Cañada (4.5 km SW of Burbusay), and Páramo de Guirigay. Border Trujillo-Barinas: Páramo de Ortiz. Border Mérida-Trujillo: Páramo del Arenal (between Pueblo Llano and Tuñame). Usually 3000–3500 m.a.s.l., locally down to 2600 m.a.s.l., found in páramo habitat and relatively open subpáramos (Fig. 34).

Additional specimens examined (selection): *A. Jahn 156* (NY, US), *B. Stergios*, *L. Dorr & K. Wurdack 20582* (US), *J. Cuatrecasas*, *M. López-Figueiras & L. Marcano-Berti 28173* (F, U, US), *López-Figueiras 13948* (US), *López-Figueiras & H. Rodríguez 8835* (US).

10. *Espeletia bromelioides* Cuatrec., Phytologia 29: 369. 1975. TYPE: VENEZUELA. Mérida: Potreros de San Rafael, Páramo de las Coloradas, Distrito Sucre, 2600 m.a.s.l., 18–20 July 1974, *M. López-Figueiras & H. Rodríguez 9054* (Holotype: US; Isotypes: F, MERF). Fig. 35–37.

Homotypic synonym: *Ruilopezia bromelioides* (Cuatrec.) Cuatrec., Phytologia 35: 52. 1976.

Rosette monocarpic, sometimes branched at the base, sessile. *Leaf* open sheath, sessile, adaxially glabrous, green, length 20–30 cm, width 1.2–2.5 cm, ratio 10–15:1, with 3–4 secondary basal nerves parallel to the costa. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 50–80 cm, vegetative part copiously bracteate, about half of total length. *Capitulum* diam. 7–13 mm, ligular circle shorter than the involucre,

FIGURES 32–33. *Espeletia bracteosa* Standl. Páramo de Ortiz, Barinas-Trujillo, Venezuela (Photographs by S. Aubert).

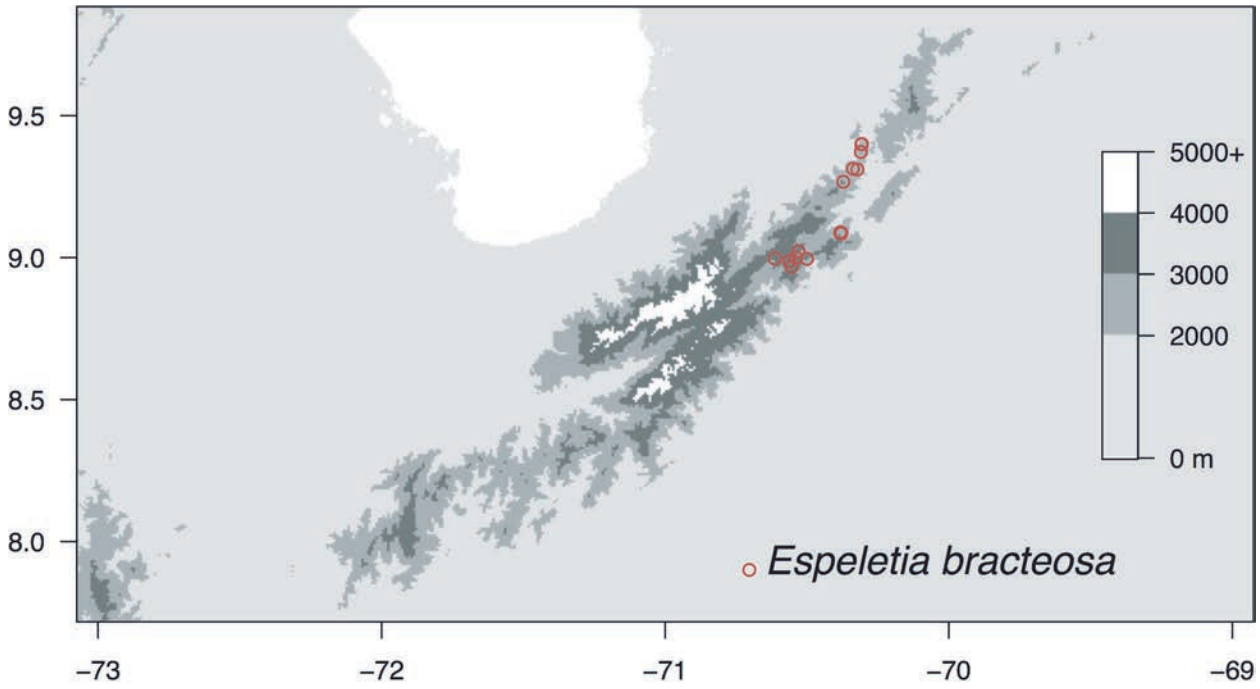


FIGURE 34. Distribution of *Espeletia bracteosa* Standl.

disc 5–10 mm, frequently eligulate or with very small yellowish/greenish ray ligules. *Espeletia bromelioides* can be easily distinguished from other species by its monocarpic short-branched sessile rosette habit, its linear-cuneate green leaves exhibiting longitudinally parallel basal nerves, its inflorescences with axis almost entirely covered by many erect bracts, and its eligulate or shortly-radiate capitulum.

Distribution: VENEZUELA. Mérida: known only from Páramo de las Coloradas, between Santa Cruz de Mora and El Molino. 2600–2900 m.a.s.l., in well drained and rather dry/rocky open subpáramo habitats (Fig. 37).

Additional specimens examined (selection): *M. López-Figueiras & H. Rodríguez 9054* (F, US), *M. López-Figueiras & H. Rodríguez 9042* (US), *M. López-Figueiras & H. Rodríguez 9044* (US), *M. López-Figueiras & L. Ruiz-Terán 14017* (US), *López-Figueiras & M. Keogh 9106* (US).

FIGURE 35. *Espeletia bromelioides* Cuatrec. Páramo de las Coloradas, Mérida, Venezuela (Photograph by S. Aubert).

FIGURE 36. *Espeletia bromelioides* Cuatrec. Páramo de las Coloradas, Mérida, Venezuela (Photograph by S. Aubert).

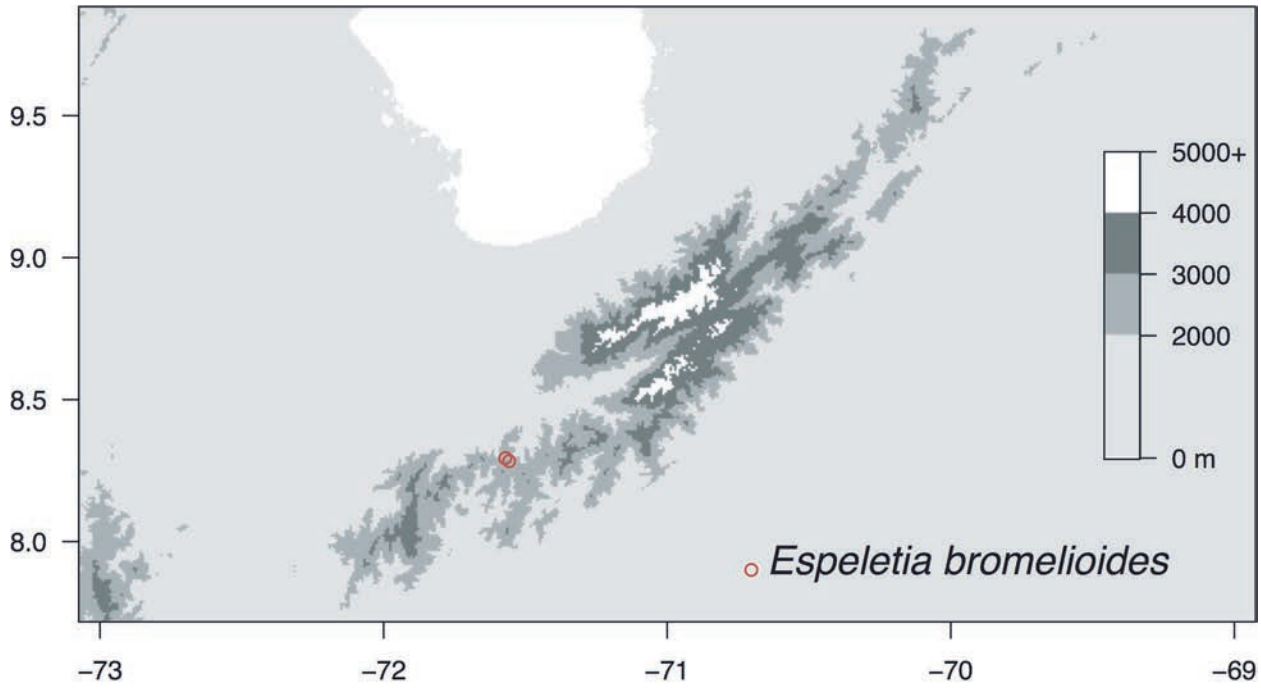


FIGURE 37. Distribution of *Espeletia bromelioides* Cuatrec.

11. ***Espeletia cardonae*** Cuatrec., Rev. Acad. Col. Ci. Exact. 5: 20. 1942. TYPE: VENEZUELA. Táchira: Páramo de Tamá, cabeceras del Río Oirá, 3100–3300 m.a.s.l., July 1939, *F. Cardona 304* (Holotype: VEN [not seen]; Isotypes: COL [fragment], F, US). Fig. 38–39.

Homotypic synonym: *Ruilopezia cardonae* (Cuatrec.) Cuatrec., Phytologia 35: 52. 1976.

Rosette monocarpic, caulescent, stem height usually up to 0.5 m, rarely up to 1.0 m, entirely covered by marcescent leaves and sheaths. *Leaf* open sheath, pseudopetiolate

FIGURE 38. *Espeletia cardonae* Cuatrec. Páramo de Tamá, Norte de Santander, Colombia (Photograph by M. Diazgranados).

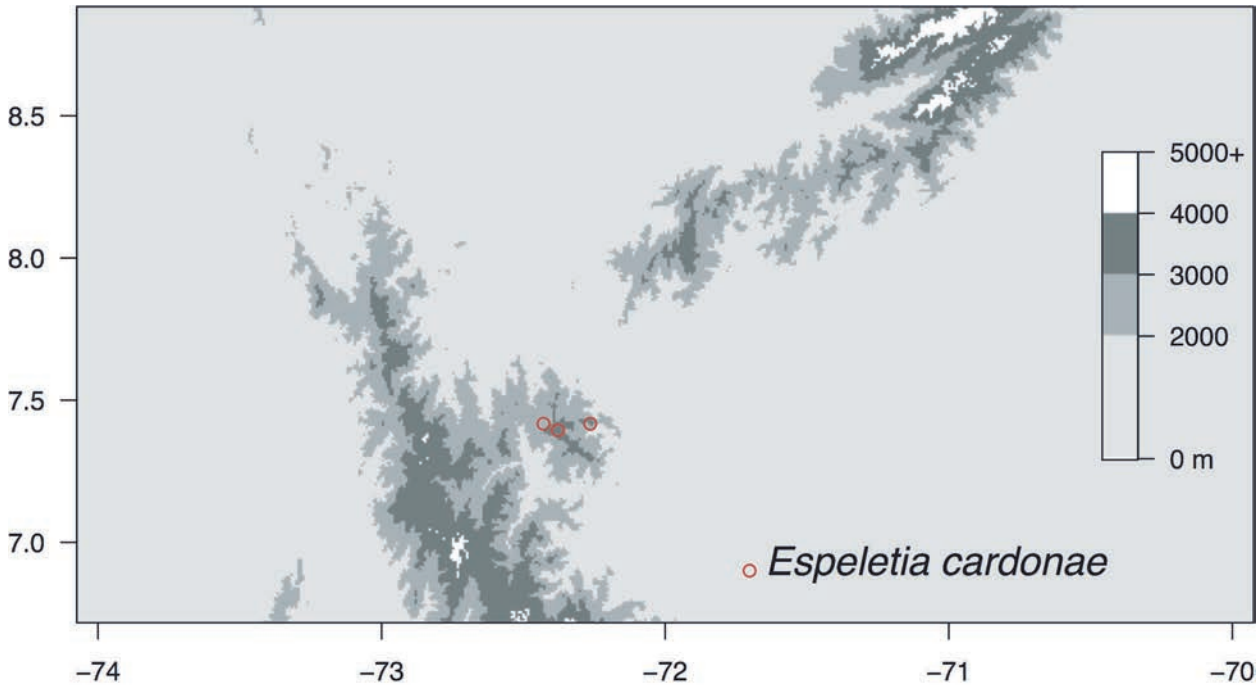


FIGURE 39. Distribution of *Espeletia cardonae* Cuatrec.

(length 5–8 cm), adaxially glabrous, green, length 25–50 cm, width 1.5–3.0 cm, ratio 15–20:1, secondary nerves parallel, 1.5–2.5 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 50–100 cm, branched near the base. *Capitulum* diam. 10–12 mm, ligular circle 20–25 mm, disc 8–11 mm, ray ligules white, turning pinkish/purplish with age according to Diazgranados (2012). *Espeletia cardonae* can be distinguished from other species by its unbranched caulescent monocarpic rosette habit, adaxially glabrous pseudopetiolate leaves, and capitulum with white ray ligules.

Distribution: VENEZUELA. Táchira: Páramo de Tamá, in the headwaters of Río Oirá, extending locally across the border with Colombia in Norte de Santander (Diazgranados, 2012: 46). 3100–3300 m.a.s.l., on well-drained slopes in subpáramo and grassy páramo habitats (Fig. 39).

Additional specimens examined (selection): *F. Cardona 304* (F, US), *Ruiz-Terán & M. López-Figueiras 8820* (US), *Ruiz-Terán & M. López-Figueiras 8820A* (US), *M. López-Figueiras 30238* (US).

12. *Espeletia chardonii* A.C. Sm., Bol. Soc. Ven. Ci. Nat. 7: 237. 1942. TYPE: VENEZUELA. Táchira: Páramo de Tamá, El Paramito, 2550 m.a.s.l., 15 August 1939, *C. E. Chardon 78* (Holotype: US; Isotypes: NY, VEN [not seen]). Fig. 40–42.

Homotypic synonym: *Tamania chardonii* (A.C. Sm.) Cuatrec., Phytologia 35: 53. 1976.

Heterotypic synonym: *Espeletia leporina* Cuatrec., Rev. Acad. Col. Ci. Exact. 5: 17. 1942. TYPE: COLOMBIA. Norte de Santander: Alto del Venado, between Samaria and Toledo, 2300–2400 m.a.s.l., 31 October 1941, *J. Cuatrecasas*, *R. E. Schultes & E. Smith 12813* (Holotype: COL; Isotypes: COL, F, GH, U, US).

Tree sparingly branched, sympodial branching giving pseudodichotomous aspect, height up to 10 m. *Leaf* open sheath, pseudopetiolate (length 1.0–4.0 cm), adaxially glabrous, green, length 12–30 cm, width 4.0–12.0 cm, ratio 3.2–5.2:1, bases of secondary nerves parallel, 4–6(8) mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, largely surpassing the surrounding leaves, length 30–80 cm, vegetative part about half of total length, usually with 1–3 bracts. *Capitulum* diam. 7–10(11) mm, ligular circle 12–18 mm, disc 6–8 mm, ray ligules yellow, turning orange or reddish when old. *Espeletia chardonii* is a unique species that can be easily distinguished by its pseudodichotomous tree habit and leaves with open sheaths.

Distribution: VENEZUELA. Táchira: Páramo de Tamá. COLOMBIA. Norte de Santander: Southern slopes of Páramo de Tama around Margua valley. Santander: Cordillera (or Cuchilla) de Los Cobardes, area known as El Picacho, near Galán. 2200–3000 m.a.s.l., in the upper level of the Andean forest, particularly in climatically wet areas (Fig. 42).

Additional specimens examined (selection): *C. E. Chardon 78* (NY, US), *J. Cuatrecasas*, *R. E. Schultes & E. Smith 12813* (COL, F, GH, U, US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28375* (F, US), *J. Cuatrecasas*, *L. Ruiz-Terán & J. Araque-Molina 28247* (F, U, US), *S. Díaz-Piedrahita 89* (US), *S. Díaz-Piedrahita 95* (US).

Isotype at NY labelled as "A. Escalona (Chardon 78), Aug. 25, 1939."

FIGURES 40–41. *Espeletia chardonii* A.C. Sm. Páramo de Tamá, Táchira, Venezuela (Photographs by S. Aubert).

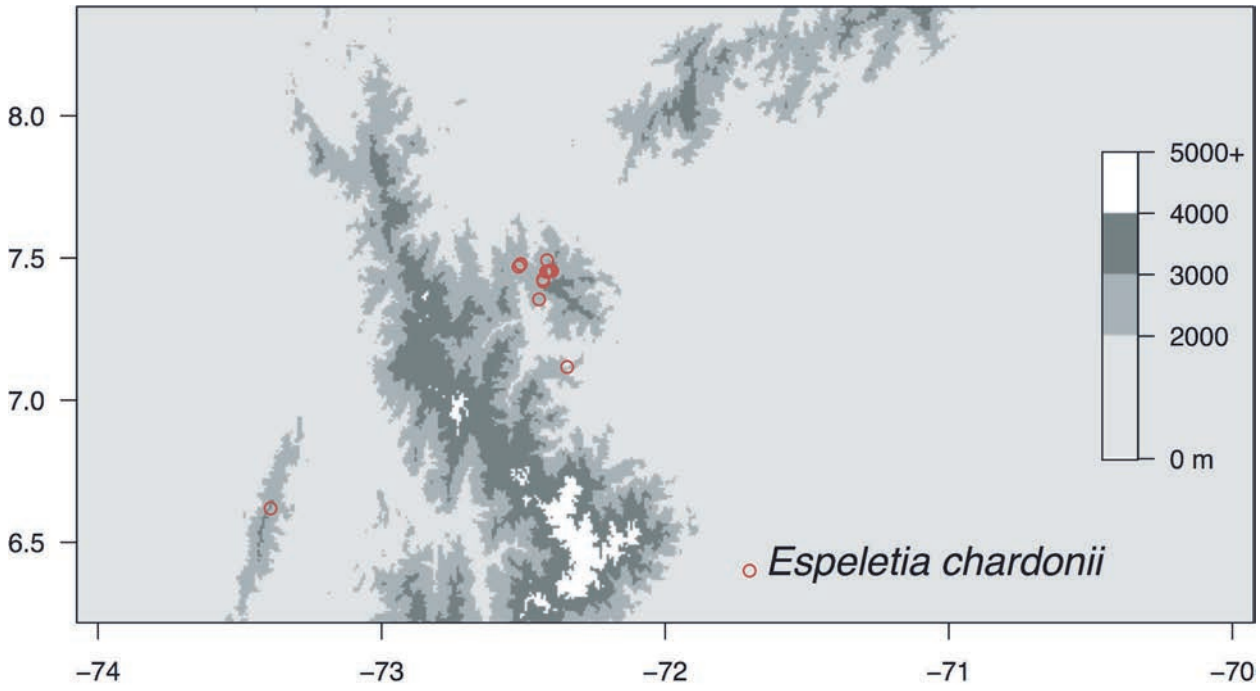


FIGURE 42. Distribution of *Espeletia chardonii* A.C. Sm.

13. *Espeletia cuatrecasasii* Ruiz-Terán & López-Fig., Rev. Fac. Farm. Univ. Andes. 14: 5. 1974. TYPE: VENEZUELA. Mérida: Laguna Tapada, antes del Portachuelo, junto a la carretera entre El Morro y Aricagua, Distrito Libertador, 2630 m.a.s.l., 9 June 1973, *L. Ruiz-Terán & M. López-Figueiras 8738* (Holotype: MERF; Isotype: US). Fig. 43–45. Homotypic synonym: *Ruilopezia cuatrecasasii* (Ruiz-Terán & López-Fig.) Cuatrec., Phytologia 35: 52. 1976.

Rosette monocarpic, caulescent, stem height up to 8 m, mostly naked, with marcescent leaves only below the rosette. *Leaf* open sheath, sessile, usually auriculate-amplectant above sheaths, adaxially glabrous or loosely hirsute, green, length 25–60 cm, width 4.5–10.0 cm, ratio 5–6:1, margins dentate, teeth 3–6 mm apart, bases of secondary nerves parallel, 3–8 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 35–70 cm, branched near the base, branches and sheaths of bracts reddish-purplish. *Capitulum* outer phyllaries herbaceous, diam. 12–18 mm, ligular circle 24–35 mm, disc 11–13 mm, rose, reddish or purplish ray ligules. *Espeletia cuatrecasasii* can be distinguished from other species for its tall caulescent monocarpic rosette habit, sessile green leaves with small length-to-width ratio (< 7:1) and capitula with herbaceous outer phyllaries and rose, reddish, purplish ray ligules. *Espeletia cuatrecasasii* resembles *E. marcescens*, but besides the numerous color differences, *E. cuatrecasasii* has leaf bases more prominently auriculate, lower density of secondary nerves (4–8 mm vs. 2–5 mm apart), smaller deviation angles (60–65° vs. 70–90°), smaller capitulum diam. (< 18 mm vs. > 20 mm), and shorter ray corollas (7–9 mm vs. 12–17 mm).

Distribution: VENEZUELA. Mérida: known only from Páramo de Aricagua and the western slopes of Páramo de Don Pedro. 2500–3000 m.a.s.l., found in very humid clearings and stream margins in the upper level of the Andean forest (Fig. 45).

Additional specimens examined (selection): *L. Ruiz-Terán & M. López-Figueiras 8738* (US), *M. López-Figueiras & C. Torres 13926* (U), *M. López-Figueiras 12581* (US), *V. M. Badillo 6538* (US).

14. Espeletia divisoriensis (Cuatrec.) Mavárez, *comb. nov.* Basionym: *Libanothamnus divisoriensis* Cuatrec., Phytologia 47: 1. 1980b. TYPE: VENEZUELA. Zulia: Environs of "Campamento Frontera II" (10°00'13"N, 72°58'25"W), mesa below international boundary on main ridge, headwaters of Río Negro, Sierra de Perijá, Serranía de los Motilones, 3000 m.a.s.l., 27 June to 5 July 1974, *S. Tillett & W. Hönig 746–746* (Holotype: US; Isotypes: MY, US, VEN [not seen]). Fig. 46–47.

Tree profusely branched, height up to 5 m. *Leaf* tubular sheath, pseudopetiolate (length 1.0–3.0 cm), adaxially glabrous, green, length 20–35 cm, width 5.0–8.0 cm, ratio 3.5–5.0:1, secondary nerves parallel, 2–4 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, surpassing the surrounding leaves, length 30–50 cm, branched near the base. *Capitulum* diam. 8–11 mm, ligular circle 14–21 mm, disc 8–10 mm, ray ligules white or cream. *Espeletia divisoriensis* can be distinguished from other tree species for its pseudopetiolate leaves with sheaths adaxially glabrous, densely packed secondary nerves (< 4 mm apart) and small capitula (diam. < 12 mm).

Distribution: VENEZUELA-COLOMBIA border. Sierra de Perijá. 3200–3600 m.a.s.l., at the timberline or right below in the upper level of the Andean forest (Fig. 47).

FIGURES 43–44. *Espeletia cuatrecasasii* Ruiz-Terán & López-Fig. Páramo de Don Pedro, Mérida, Venezuela (Photographs by S. Aubert).

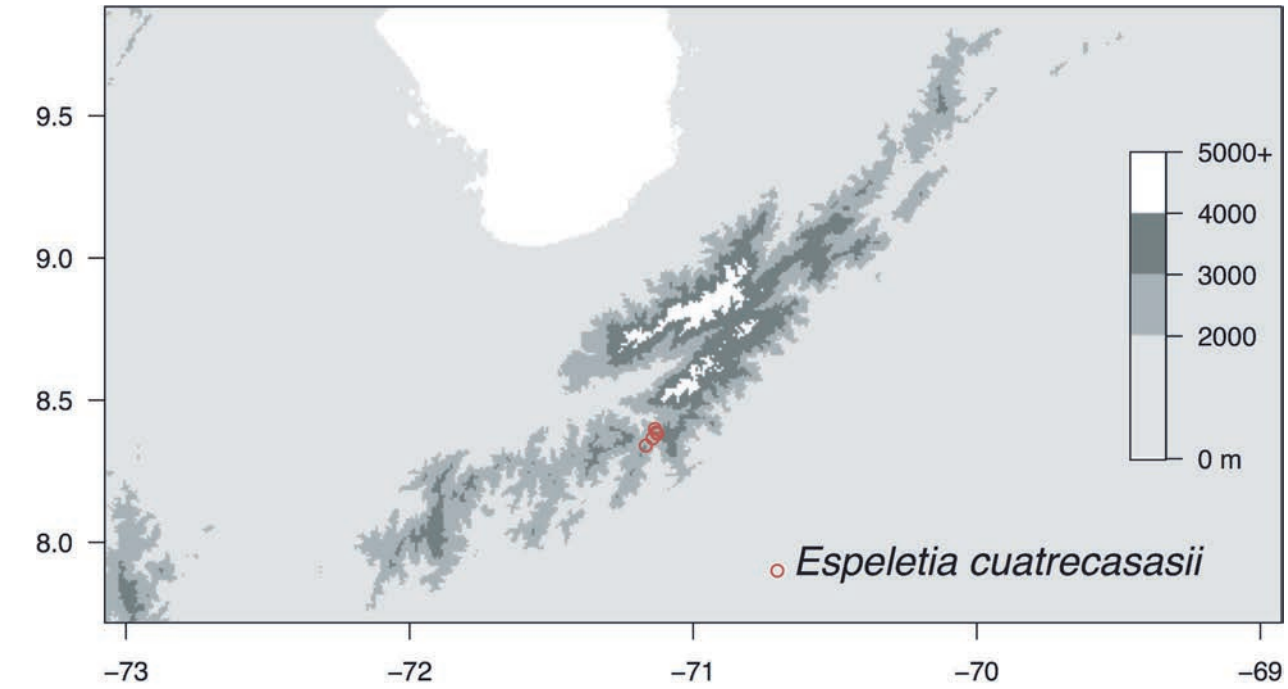


FIGURE 45. Distribution of *Espeletia cuatrecasasii* Ruiz-Terán & López-Fig.

FIGURE 46. *Espeletia divisoriensis* (Cuatrec.) Mavárez. Páramo de Sabana Rubia, Cesar, Colombia (Photograph by J. O. Rangel).

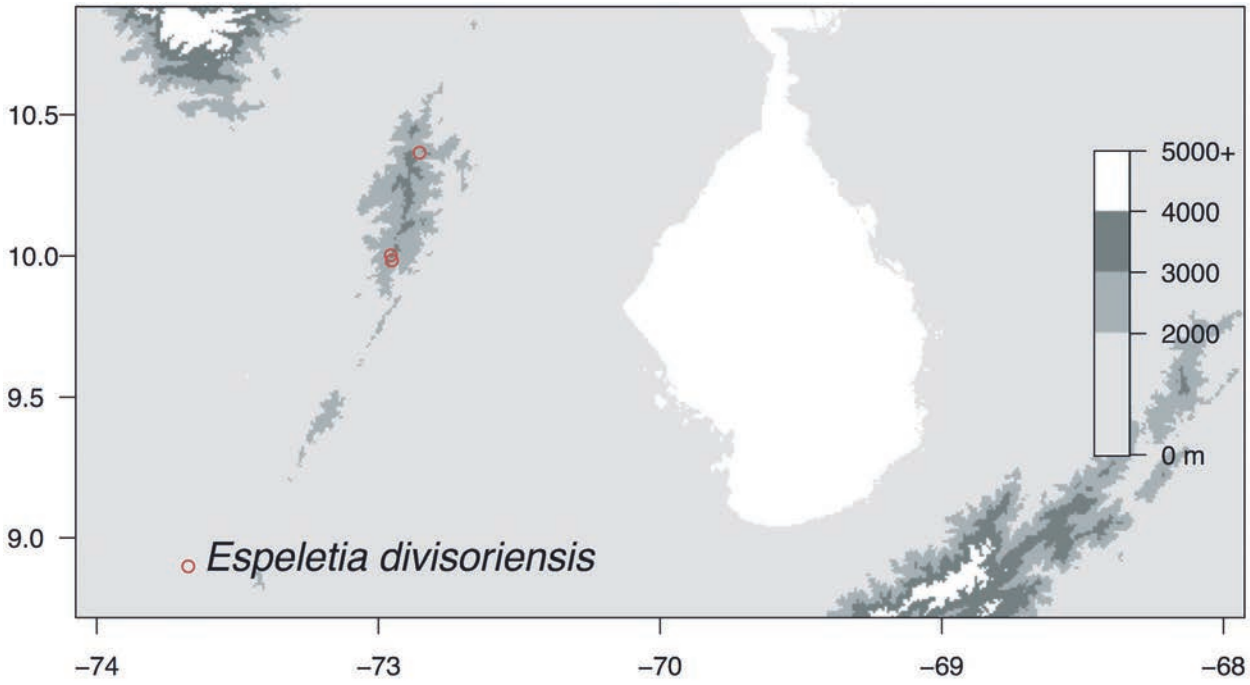


FIGURE 47. Distribution of *Espeletia divisoriensis* (Cuatrec.) Mavárez.

Additional specimens examined (selection): *S. Tillett & W. Hönig 746–746* (US), *S. Tillett & W. Hönig 747-921* (US), *M. L. Grant 10965* (US), *O. Rangel-Ch. 13706* (US), *O. Rangel-Ch 13616* (US).

15. *Espeletia elongata* A.C. Sm., Amer. J. Bot. 27: 546. 1940. TYPE: VENEZUELA. Mérida: Páramo de los Conejos, 13,000 ft, 10 September 1938, *J. Hanbury-Tracy 83* (Holotype: NY; Isotype: K). Fig. 48–50.

Homotypic synonym: *Coespeletia elongata* (A.C. Sm.) Cuatrec., Phytologia 35: 57. 1976.

Rosette polycarpic, caulescent, stem height up to 2.5 m, entirely covered by marcescent leaves. *Leaf* open sheath, pseudopetiolate (length 5–10 cm), adaxially densely pubescent, lanate-lanuginose, length 50–70 cm, width 3.5–5.0 cm, ratio 9–18:1, secondary nerves parallel, 5–7 mm apart. *Inflorescence* lateral, compound, primary branching monochasial, botryoid-paniculate, axes 75–110 cm, 30–60 peduncles, proximal polycephalous (3–5 capitula), vegetative part with 3–5 alternate bracts. *Capitulum* diam. 15–25 mm, ligular circle about the same size or slightly shorter than the involucre, disc 14–15 mm, ray ligules bright yellow. *Espeletia elongata* can be distinguished from all other Venezuelan rosette plants for its caulescent and entirely marcescent polycarpic rosette habit, its pseudopetiolate leaves, and its botryoid-paniculate inflorescences with large number of peduncles (30–60), the proximal ones polycephalous.

Distribution: VENEZUELA. Mérida: páramos in Sierra de la Culata. Between 3200–3500 m.a.s.l., especially in humid locations (Fig. 50).

Additional specimens examined (selection): *J. Hanbury-Tracy 83* (K, NY), *P. Berry & R. Calvo 4395* (US), *López-Figueiras 23698* (US), *López-Figueiras 23699* (US), *L. Ruiz-Terán & J. Dugarte 12418* (US).

Collection year given as "1983" in Diazgranados (2012: 7) and Cuatrecasas (2013: 603).

16. Espeletia emmanuelis (Cuatrec.) Mavárez, *comb. nov.*

Basionym: *Ruilopezia emmanuelis* Cuatrec., Phytologia 61: 56. 1986a. TYPE: VENEZUELA. Trujillo: Páramo de las Rosas, en las lajas de Barro Amarillo, 2900–3000 m.a.s.l., 8 March 1985, *M. López-Figueiras & D. Griffin 32405* (Holotype: US; Isotypes: F, G, K, MERF, NY, US). Fig. 51–52.

Rosette monocarpic, caulescent, stem height up to 1.5 m, entirely covered by marcescent leaves. *Leaf* open sheath, pseudopetiolate (length 1–4 cm), adaxially pubescent, villous-velvety, length 35–50 cm, width 3.5–5.5 cm, ratio 9–10:1, secondary nerves parallel, 5–8 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 50–70 cm, branched near the base. *Capitulum* diam. 10–12 mm, ligular circle 20–25 mm, disc 9–10 mm, ray ligules yellow. *Espeletia emmanuelis* can be distinguished from other species by its caulescent-marcescent monocarpic rosette habit with pseudopetiolate leaves and its capitulum with yellow ray ligules.

Distribution: VENEZUELA. Border Lara-Trujillo: páramos in the northern end of the Cordillera de Mérida: Páramo de Los Nepes, de la Nariz, de las Rosas, de Cendé, and del Turmal. 2800–3100 m.a.s.l., usually in flat and rather humid locations within subpáramo habitats (Fig. 52).

Additional specimens examined (selection): *M. López-Figueiras & D. Griffin 32405* (F, G, K, NY, US), *M. López-Figueiras & H. Rodríguez 26234* (US), *M. López-Figueiras 32490* (US), *R. Riina*, *R. Duno*, *R. Ghinaglia & R. Gonto 729* (US).

Distribution given as on the border Trujillo-Barinas in Cuatrecasas (2013: 555).

FIGURES 48–49. *Espeletia elongata* A.C. Sm. Páramo de la Culata, Mérida, Venezuela (Photographs by S. Aubert).

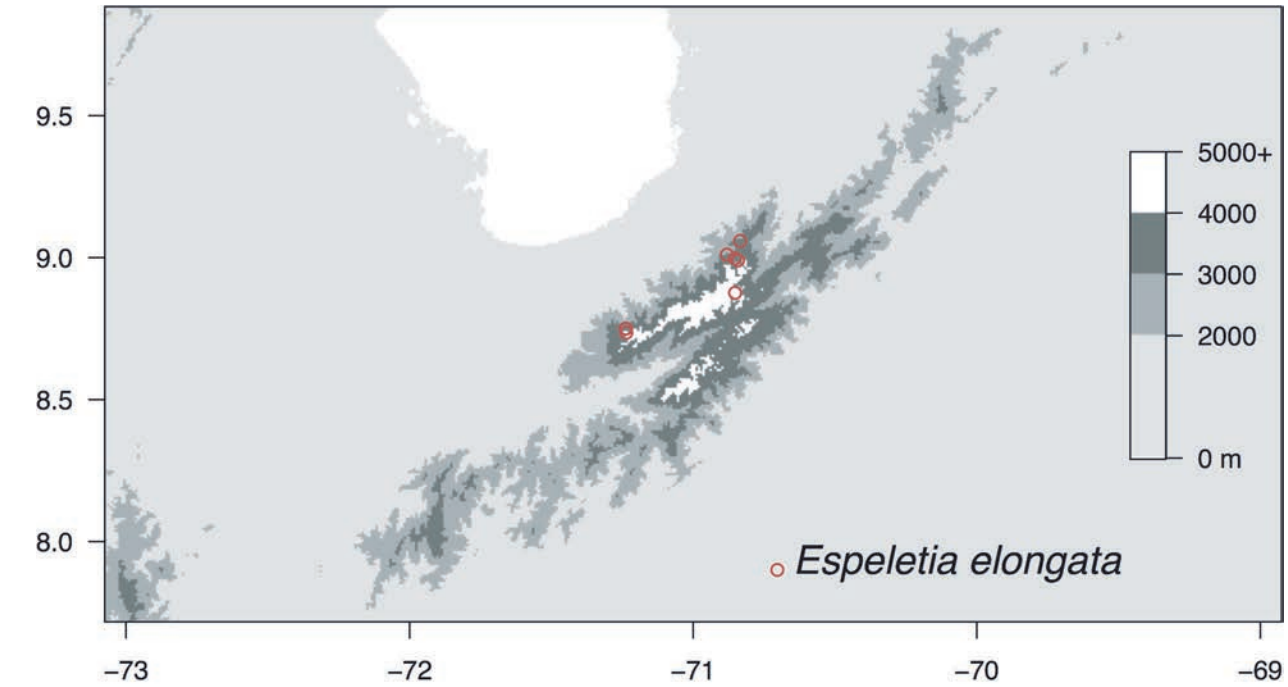


FIGURE 50. Distribution of *Espeletia elongata* A.C. Sm.

FIGURE 51. *Espeletia emmanuelis* (Cuatrec.) Mavárez. Páramo de los Nepes, Lara-Trujillo, Venezuela (Photograph by M. Quiroga).

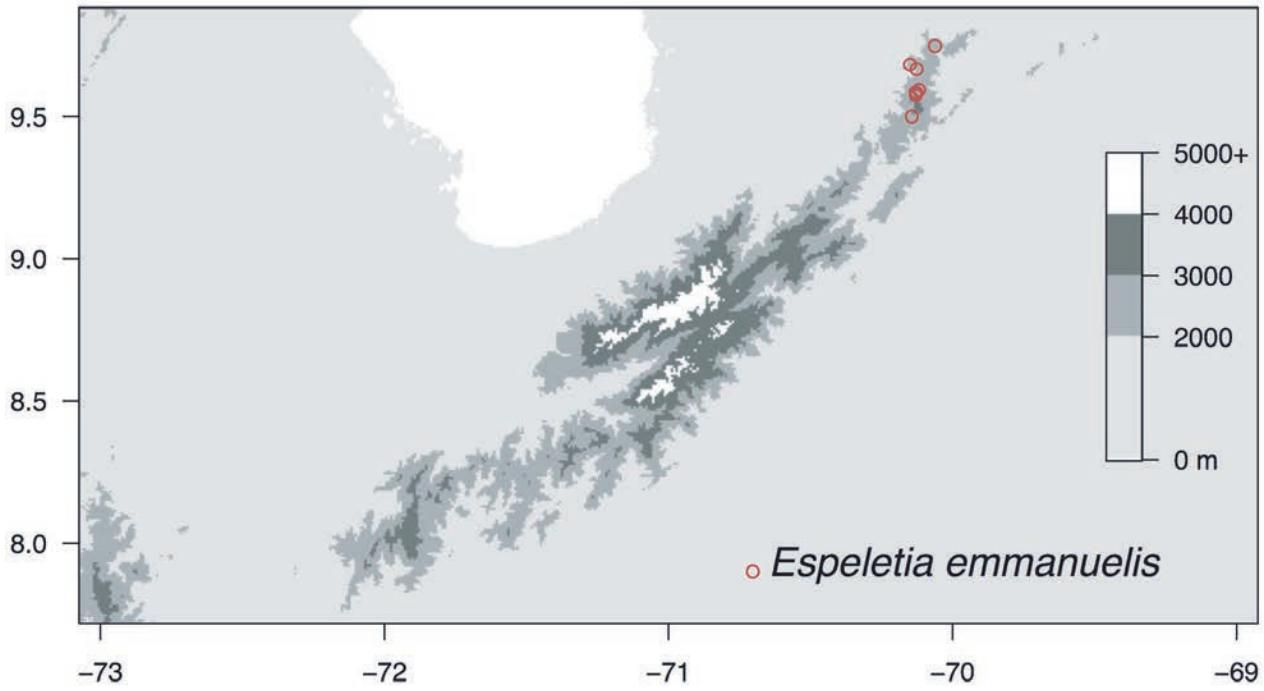


FIGURE 52. Distribution of *Espeletia emmanuelis* (Cuatrec.) Mavárez.

17. *Espeletia figueirasii* Cuatrec., Phytologia 20: 475. 1971. TYPE: VENEZUELA. Mérida: Sierra Nevada de Santo Domingo, Páramo de los Granates, Loma de Paja, las Escaleras, 3240 m.a.s.l., 11 October 1969, *J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28068* (Holotype: US; Isotypes: F, IVIC, MERF, U, US). Fig. 53–56.

Homotypic synonym: *Ruilopezia figueirasii* (Cuatrec.) Cuatrec., Phytologia 35: 52. 1976.

Rosette monocarpic, caulescent, stem height up to 2.0 m, entirely covered by marcescent leaves. *Leaf* open sheath, sessile, adaxially glabrous, green, length 25–40 cm, width 0.7–2.5 cm, ratio 20–30:1, apex with a sharp teeth, 1.0–2.0 mm long, secondary nerves obsolete. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 100–250 cm, vegetative part profusely bracteate, about a third of total length. *Capitulum* diam. 12–22 mm, eligulate. *Espeletia figueirasii* can be distinguished from other species by its caulescent-marcescent monocarpic rosette habit with long, sessile, flexible, green leaves and its eligulate semiglobose capitulum.

Distribution: VENEZUELA. Mérida: slopes of Sierra Nevada de Santo Domingo, Páramo de Los Granates and Páramo de Guirigay, Sierra de la Culata in the slopes above Piñango, Páramo de la Sal, and Páramo de Palmira. 2800–3000 m.a.s.l., in the upper level of the Andean forest below the timberline (Fig. 56).

Additional specimens examined (selection): *J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28068* (F, U, US), *J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28619* (F, U, US), *J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28620* (F, U, US), *L. Dorr & L. Barnett 5597* (US), *L. Ruiz-Terán 6449* (F, U, US).

18. *Espeletia floccosa* Standl., Amer. J. Bot. 2: 481. 1915. TYPE: VENEZUELA. Mérida: Páramo de Timotes, 3300–4000 m.a.s.l., and Sierra Nevada de Mérida, 4000 m.a.s.l., October 1910, *A. Jahn 154* (Holotype: US). Fig. 57–59.

Homotypic synonym: *Ruilopezia floccosa* (Standl.) Cuatrec., Phytologia 35: 52. 1976.

Rosette monocarpic, sometimes branched at the base, sessile. *Leaf* open sheath, sessile, adaxially pubescent, silvery-sericeous, length 25–30 cm, width 1.5–2.5 cm, ratio 15–20:1, secondary nerves almost obsolete, 2–4 mm apart when present. *Inflorescence* terminal, compound, primary branching monochasial, multiple branches spreading radially from the base, each one botryoid-paniculate or corymboid-paniculate with length 50–120 cm, proximal part about half of the branch's total length, with several alternate bracts. *Capitulum* diam. 15–20 mm, ligular circle 40–50 mm, disc 13–17 mm, ray ligules yellow. *Espeletia floccosa* can be distinguished from other species for its sessile monocarpic rosette habit with densely pubescent silvery-sericeous leaves, its inflorescences with extremely short or no central axis, and its large yellow-rayed capitulum.

Distribution: VENEZUELA. Mérida: widespread in páramos of Sierra de la Culata (e.g., Mucuchíes, Piedras Blancas, Piñango, Timotes), and through the Nudo de Apartaderos to the páramos in the Sierra Nevada de Santo Domingo (e.g., Gavidia, Laguna de Mucubají, Laguna Negra, and Laguna Victoria). Trujillo: Páramo de Teta de Niquitao, de Cabimbú, and de Tuñame. 3200–4000 m.a.s.l., in open and humid páramos (Fig. 59).

Additional specimens examined (selection): *A. Jahn 154* (US), *J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28110* (F, U, US), *L. Ruiz-Terán & M. López-*

FIGURES 53–55. *Espeletia figueirasii* Cuatrec. **53**. Piñango, Mérida, Venezuela (Photograph by S. Aubert). **54–55**. Páramo de los Granates, Mérida, Venezuela (Photographs by S. Aubert).

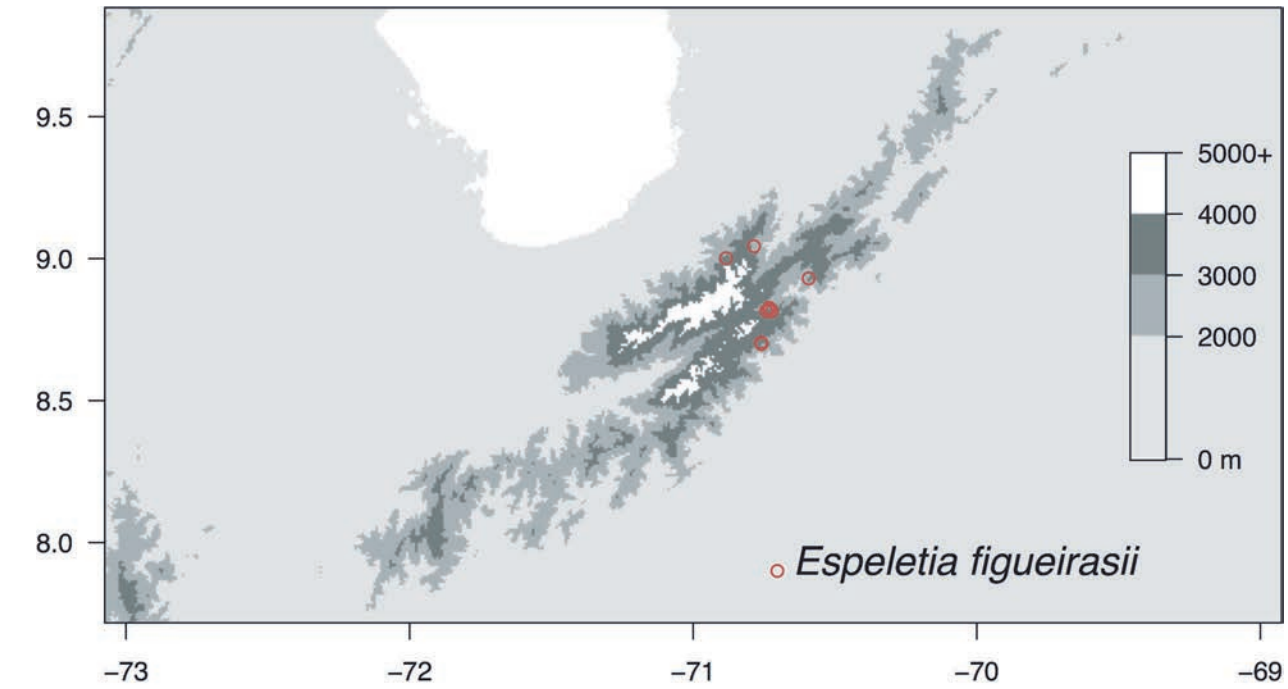


FIGURE 56. Distribution of *Espeletia figueirasii* Cuatrec.

FIGURES 57. *Espeletia floccosa* Standl. Laguna de Mucubají, Mérida, Venezuela (Photograph by S. Aubert).

FIGURES 58. *Espeletia floccosa* Standl. Laguna de Mucubají, Mérida, Venezuela (Photograph by S. Aubert).

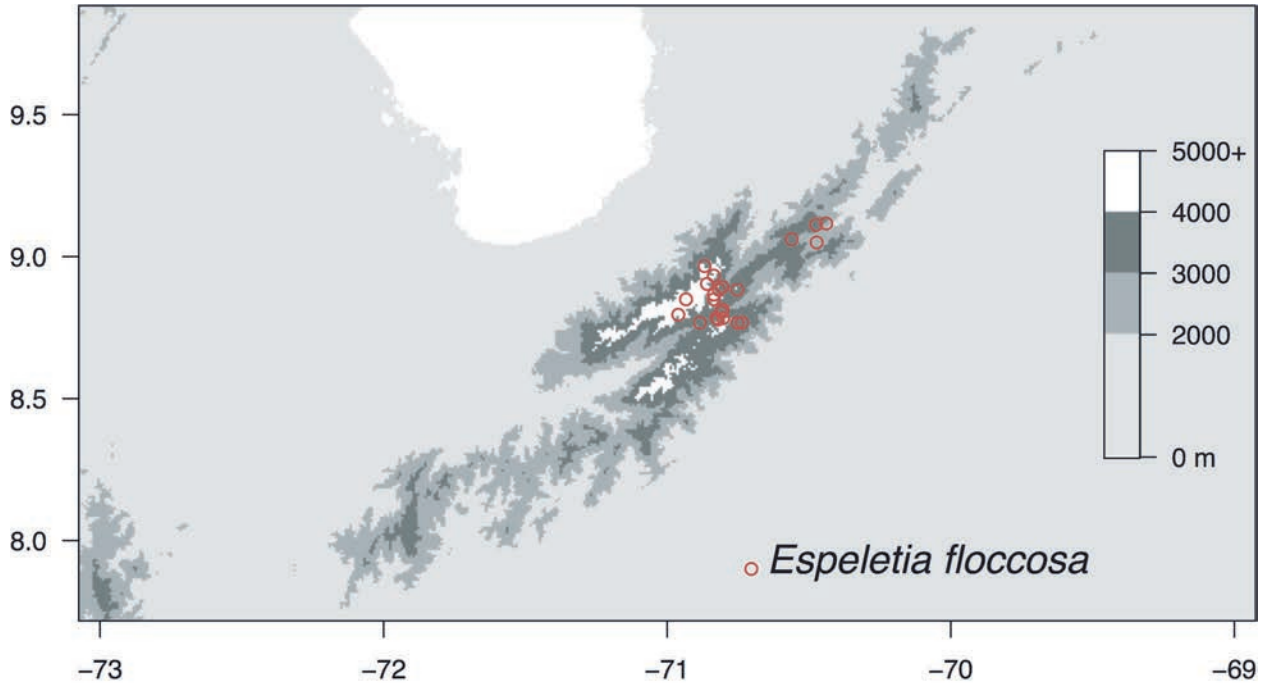


FIGURE 59. Distribution of *Espeletia floccosa* Standl.

FIGURES 60–61. *Espeletia griffinii* Ruiz-Terán & López-Fig. Páramo de Guaramacal, Trujillo, Venezuela (Photographs by S. Aubert).

Figueiras 371 (US), *L. Ruiz-Terán & M. López-Figueiras 184* (U, US), *L. Ruiz-Terán & M. López-Figueiras 2218* (US).

As noted by Cuatrecasas (2013: 565), the locality "Páramo del Jabón" and the description "white flowers" in *Jahn 154* are certainly confusions with *E. jabonensis* and *E. pannosa*, two species that also have sessile rosette habit and long linear leaves covered with silvery-sericeous indumentum. The type locality of *E. floccosa* should be Páramo de Timotes and Sierra Nevada de Mérida.

19. *Espeletia griffinii* Ruiz-Terán & López-Fig., Rev. Fac. Farm. Univ. Andes 17: 27. 1976. TYPE: VENEZUELA. Trujillo: Páramo de Guaramacal, aprox. 15 km E. de Boconó, 2600 m.a.s.l., 9 August 1975, *L. Ruiz-Terán*, *M. López-Figueiras*, *D. Griffin & N. Griffin 12606* (Holotype: MERF; Isotype: US). Fig. 60–62.

Homotypic synonym: *Libanothamnus griffinii* (Ruiz-Terán & López-Fig.) Cuatrec., Phytologia 35: 50. 1976.

Shrub or *small tree* profusely branched, height up to 4 m. *Leaf* tubular sheath, pseudopetiolate (length 1.0–3.0 cm), adaxially glabrous, green, length 7–15 cm, width 2.5–4.5 cm, ratio 2.5–3.5:1, secondary nerves parallel, 1–2(3) mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, largely surpassing the surrounding leaves, length 10–20 cm, branched near the base. *Capitulum* diam. 10–12(13) mm, ligular circle 15–20 mm, disc 8–12 mm, ray ligules white or cream. *Espeletia griffinii* can be distinguished from other tree species by its distinctly pseudopetiolate small leaves (< 15 cm). Only two other tree taxa have leaves with somewhat similar lengths, but they have either a sessile outline (*E. parvula*) or short pseudopetioles < 1 cm long and a capitulum diam. < 10 mm (*E. neriifolia* var. *cristamontis*).

Distribution: VENEZUELA. Trujillo: Páramo de Guaramacal. 2600–3100 m.a.s.l., above the timberline in shrubby subpáramo habitat (Fig. 62).

Additional specimens examined (selection): *L. Ruiz-Terán*, *M. López-Figueiras*, *D. Griffin & N. Griffin 12606* (US), *H. Werff & F. Ortega 6081* (US), *J. Cuatrecasas & L. Ruiz-Terán 28811* (F, U, US), *L. Ruiz-Terán & J. Dugarte 12771* (US), *J. L. Panero*, *C. E. Benítez & V. M. Badillo 2643* (US).

Collectors and date given as "*L. Ruiz-Terán*, *M. López-Figueiras & D. Griffin*" (*N. Griffin* missing) and "3 August 1975" in Diazgranados (2012: 35) and Cuatrecasas (2013: 446).

20. *Espeletia grisea* Standl., Amer. J. Bot. 2: 477. 1915. TYPE: VENEZUELA. Mérida: Chorro Blanco, Sierra Nevada de Mérida, 3000–4000 m.a.s.l., January 1911, *A. Jahn 157* (Holotype: US). Fig. 63–65.

Homotypic synonym: *Ruilopezia grisea* (Standl.) Cuatrec., Phytologia 35: 52. 1976.

Rosette monocarpic, caulescent, stem height up to 1.0 m, entirely covered by marcescent leaves. *Leaf* open sheath, sessile, adaxially loosely hirsute, green aspect, length 20–35 cm, width 1.0–2.5 cm, ratio 12–15:1, secondary nerves parallel, 1.5–3.0 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 50–120 cm, branched near the base. *Capitulum* diam. 12–15 mm, ligular circle 15–22 mm, disc 11–14 mm, ray ligules short and white. *Espeletia grisea* can be distinguished from other species for its caulescent-marcescent monocarpic rosette habit, its sessile

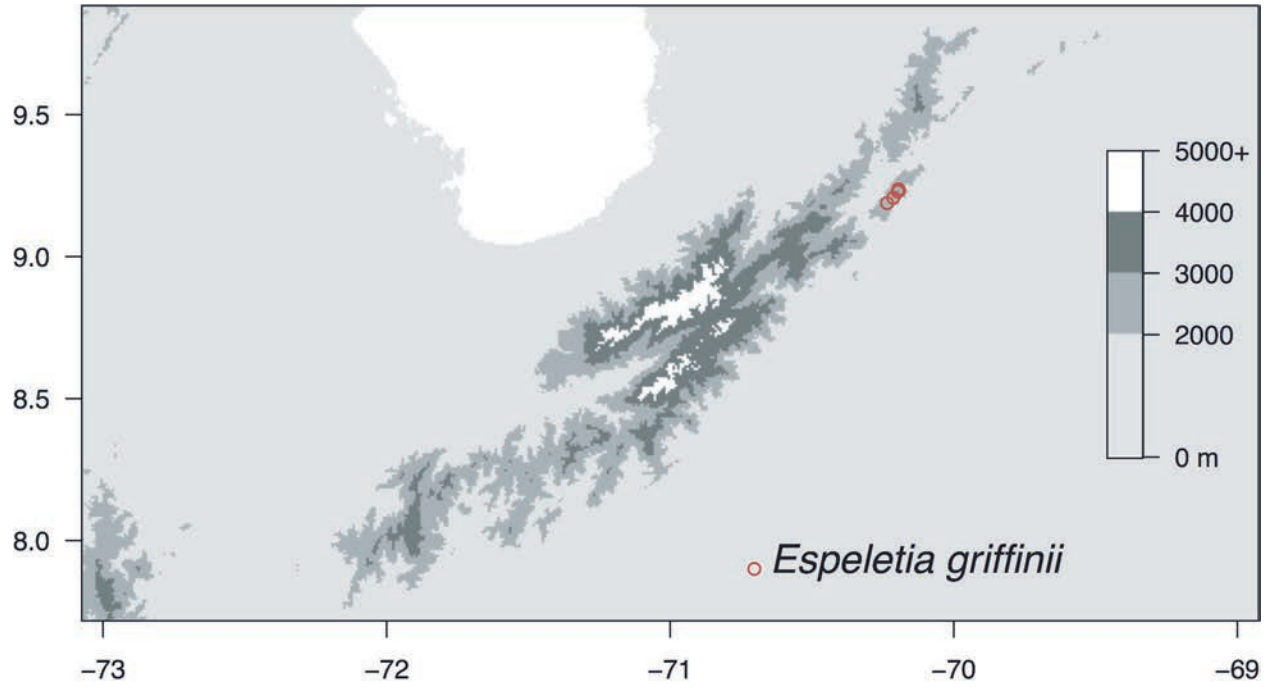


FIGURE 62. Distribution of *Espeletia griffinii* Ruiz-Terán & López-Fig.

FIGURES 63–64. *Espeletia grisea* Standl. Páramo de los Nevados, Mérida, Venezuela (Photographs by S. Aubert).

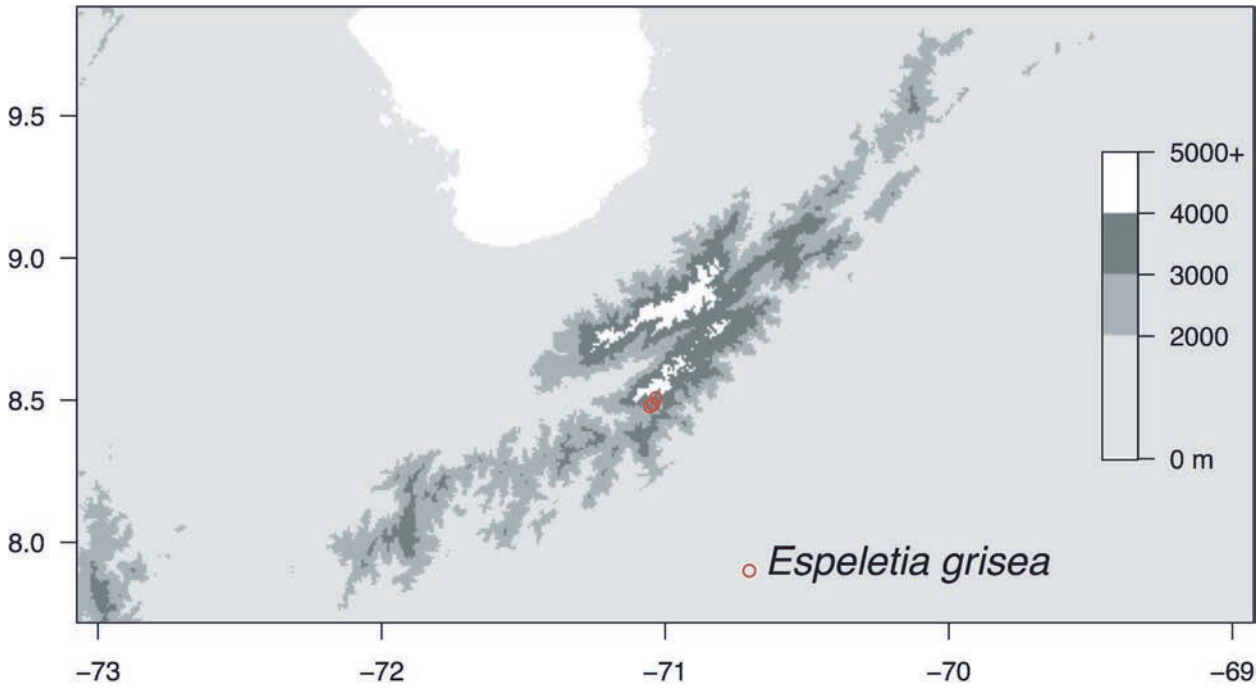


FIGURE 65. Distribution of *Espeletia grisea* Standl.

thinly hirsute leaves, secondary nerves < 3 mm apart with deviation angles > 50°, and its subglobose capitulum with short white ray ligules (corolla length < 7 mm).

Distribution: VENEZUELA. Mérida: known only from the southern slopes of Sierra Nevada de Mérida to the N of town Los Nevados. Between 3400–3800 m.a.s.l., in humid páramos along streams and ravines (Fig. 65).

Additional specimens examined (selection): *A. Jahn 157* (US), *L. Ruiz-Terán 6809* (US); *id. 6745* (US).

21. *Espeletia hanburyana* Cuatrec., Bol. Soc. Ven. Ci. Nat. 17: 86. 1956a. TYPE: VENEZUELA. Mérida: Páramo de Acequias, 12,000 ft, 18 October 1938, *J. Hanbury-Tracy 130* (Holotype: K; Isotypes: NY, US). Fig. 66–67.

Homotypic synonym: *Ruilopezia hanburyana* (Cuatrec.) Cuatrec., Phytologia 35: 52. 1976.

Rosette monocarpic, caulescent, stem height up to 1.0 m, entirely covered by marcescent leaves, densely leafy rosette. *Leaf* open sheath, sessile, adaxially glabrous, green, length 20–45 cm, width 1.2–2.2 cm, ratio 14–23:1, secondary nerves parallel, 1.5–2.0 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 50–60 cm, branched near the base. *Capitulum* diam. 15–20 mm, ligular circle 32–42 mm, disc 14–17 mm, ray ligules white. *Espeletia hanburyana* can be distinguished from other species by its caulescent-marcescent monocarpic rosette habit with a large number of straight and narrow green leaves, which gives a globose aspect to the rosette, and for its capitulum with long white ray ligules. The species resembles caulescent individuals of *E. lindenii*, but it has adaxially glabrous and slender leaves (ratio > 14:1 vs. < 12:1) and narrower sterile phyllaries (width 3–5 mm vs. 5–12 mm) with membranaceous texture and without glands (vs. foliaceous and copiously glanduliferous).

Distribution: VENEZUELA. Mérida: known only from the region Pueblos del Sur in the southern end of the Sierra Nevada de Mérida (e.g., Páramo de Acequias, de San José, and de Aricagua). 3000–3500 m.a.s.l., in humid subpáramos near depressions, streams, and lakes (Fig. 67).

Additional specimens examined (selection): *J. Hanbury-Tracy 130* (K, NY, US), *M. López-Figueiras*, *H. Rodríguez*, *J. Wurdack & M. Wurdack 8937* (US), *M. López-Figueiras 30158* (US), *M. López-Figueiras 30159* (US).

This taxon honors N. F. J. Hanbury-Tracy (Cuatrecasas, 2013: 550). According to ICN Art. 60.8, the correct spelling for the derived substantival epithet is "*hanburyana*" (not "*hanburiana*").

22. *Espeletia jabonensis* Cuatrec., Phytologia 23: 360. 1972. TYPE: VENEZUELA. Trujillo: Tres Pozos, un sector del Páramo del Turmal, unos 14,4 km al E. de la población de Carache, distrito Carache, 2800–2850 m.a.s.l., 8 June 1971, *L. Ruiz-Terán & M. López-Figueiras 1995* (Holotype: US; Isotypes: MERF, NY, US). Fig. 68–70.

Homotypic synonym: *Ruilopezia jabonensis* (Cuatrec.) Cuatrec., Phytologia 35: 52. 1976.

Rosette monocarpic, sessile, densely leafy rosette. *Leaf* open sheath, sessile, rigid, linear, adaxially pubescent, shiny silvery-sericeous, length 10–30 cm, width 0.3–0.8 cm, ratio 30–40:1, secondary nerves obsolete. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 40–80 cm, branched near the base, vegetative part profusely bracteate. *Capitulum* diam. 12–16

FIGURE 66. *Espeletia hanburyana* Cuatrec. Páramo de Acequias, Mérida, Venezuela (Photograph by S. Aubert).

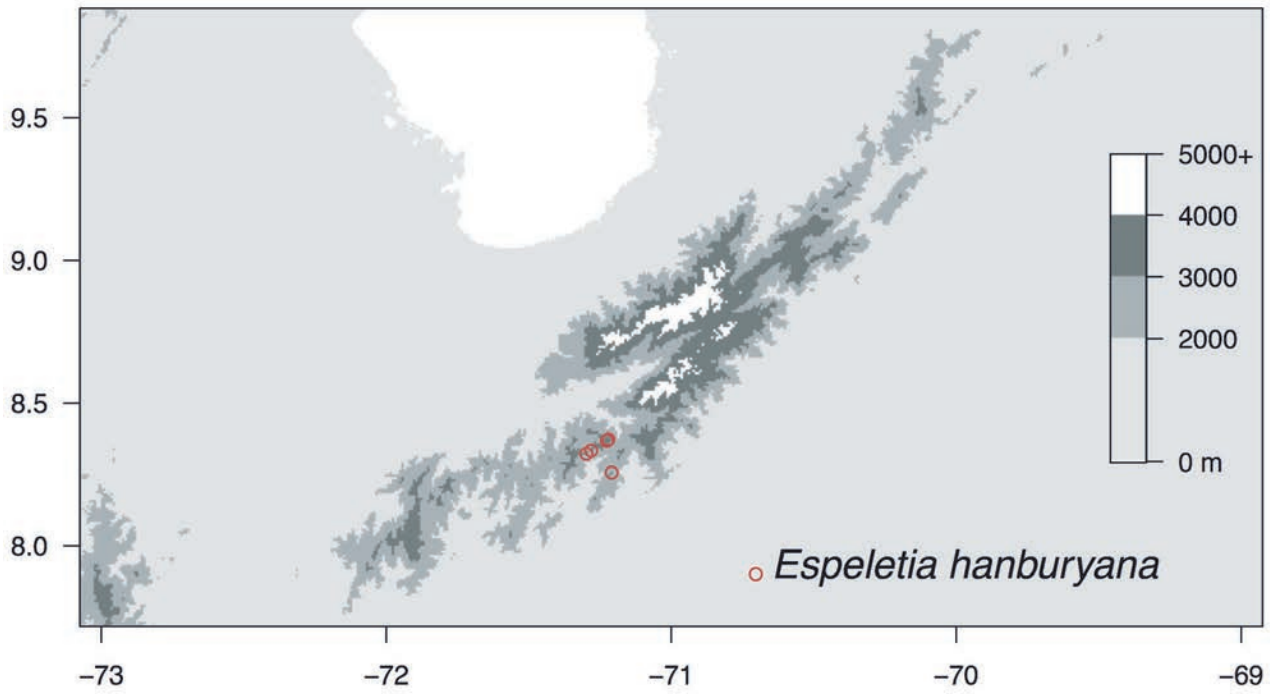


FIGURE 67. Distribution of *Espeletia hanburyana* Cuatrec.

FIGURES 68–69. *Espeletia jabonensis* Cuatrec. **68**. Páramo de Guaramacal, Trujillo, Venezuela (Photograph by S. Aubert). **69**. Páramo del Jabón, Lara-Trujillo, Venezuela (Photograph by S. Aubert).

mm, ligular circle 25–35 mm, disc 10–15 mm, yellow ray ligules. *Espeletia jabonensis* can be distinguished from other species for its sessile monocarpic rosette habit with a large number of straight and narrow silvery-shiny leaves, and its axial inflorescence with yellow-ligulate capitula. Flowering individuals are however relatively rare, suggesting some form of reproductive synchrony, so the identification of *E. jabonensis* must frequently be achieved using vegetative characters alone. The species can be distinguished from other taxa with silvery-sericeous indumentum by its strictly linear leaves with small rectangular sheaths (2.0–2.5 cm × 0.5–0.8 cm).

Distribution: VENEZUELA. Trujillo: Páramo de Guaramacal. Border Trujillo-Lara: Páramo de Cendé, del Jabón, and del Turmal. 2800–3400 m.a.s.l., in open subpáramos and páramos, particularly in exposed and windy slopes, summits, and crests (Fig. 70).

Additional specimens examined (selection): *L. Ruiz-Terán & M. López-Figueiras 1995* (NY, US), *L. Ruiz-Terán & M. López-Figueiras 2101* (US), *G. Aymard*, *F. Ortega & R. Morán 2924* (US), *M. López-Figueiras 13940* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28541* (F, US).

23. *Espeletia jahnii* Standl., Amer. J. Bot. 2: 479. 1915. TYPE: VENEZUELA. Táchira: Páramo del Batallón, 3000 m.a.s.l., March 1911, *A. Jahn 155* (Holotype: US; Isotype: VEN [not seen]). Fig. 71–74.

Homotypic synonym: *Ruilopezia jahnii* (Standl.) Cuatrec., Phytologia 35: 53. 1976.

Rosette monocarpic, the axis frequently divided into prostrate branches, each one entirely covered with marcescent leaves or sheaths and ending with a densely leafy rosette. *Leaf* open sheath, sessile, linear, adaxially glabrous, green, length 15–35 cm, width 0.2–0.4 cm, ratio 50–100:1, secondary nerves obsolete. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, length 50–80 cm, vegetative part profusely bracteate, about half of total length. *Capitulum* diam. 12–18 mm, eligulate. *Espeletia jahnii* can be distinguished from other species by its multibranched monocarpic rosette habit with a large number of straight and linear green leaves, and its inflorescence with eligulate capitula.

Distribution: VENEZUELA. Táchira: Páramo del Batallón and del Zumbador. 2800–3500 m.a.s.l., in open and exposed páramo slopes, summits, and crests (Fig. 74).

Additional specimens examined (selection): *A. Jahn 155* (US), *J. L. Panero*, *C. E. Benítez & V. M. Badillo 2705* (US), *P. Berry & R. Calvo 4415* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28414* (F, U, US), *J. Cuatrecasas*, *L. Ruiz-Terán & L. Marcano-Berti 27992* (F, U, US).

24. *Espeletia leucactina* Cuatrec., Phytologia 29: 377. 1975. TYPE: VENEZUELA. Táchira: Páramo del Batallón, 3000 m.a.s.l., 13 August 1974, *M. López-Figueiras 9151* (Holotype: US; Isotypes: MY, MERF, US). Fig. 75–77.

Homotypic synonym: *Ruilopezia leucactina* (Cuatrec.) Cuatrec., Phytologia 35: 52. 1976.

Rosette monocarpic, mostly sessile, rarely with a stem up to 0.3 m. *Leaf* open sheath, sessile, adaxially pubescent, densely appressed, cinereous-ashy, length 35–45 cm, width 2.0–3.3 cm, ratio 15–30:1, secondary nerves parallel, 1.5–4.0 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 50–100 cm, branched near the base. *Capitulum* diam. 15–16 mm,

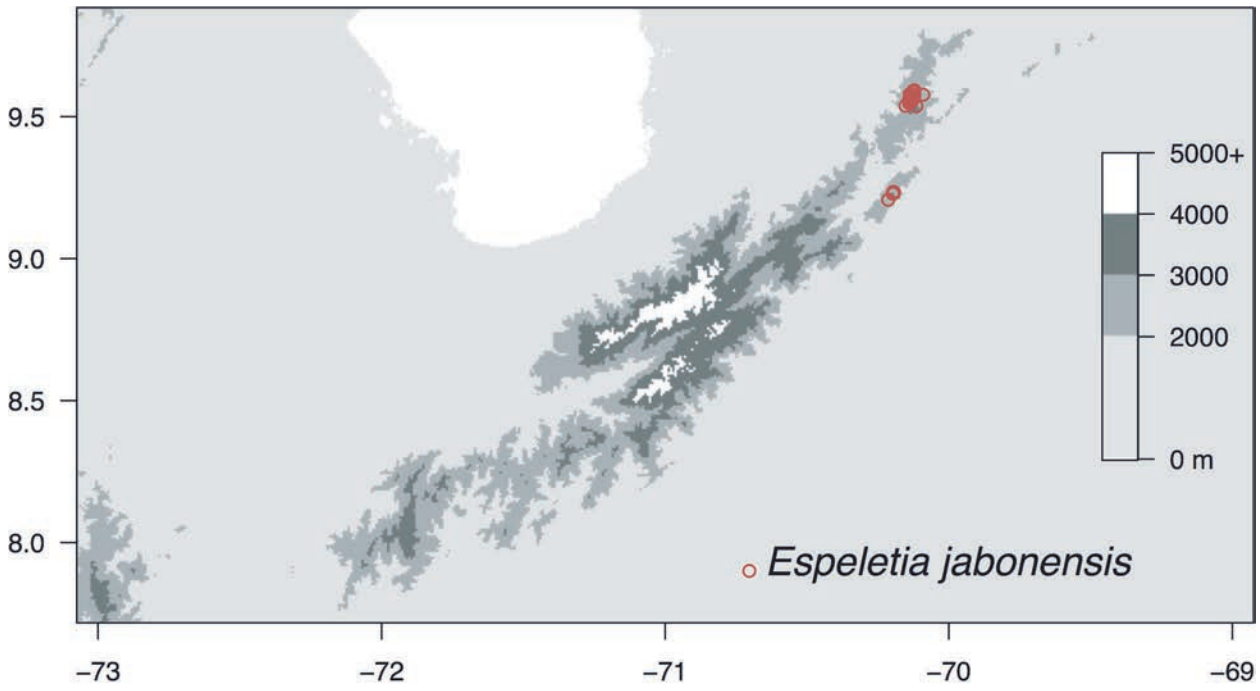
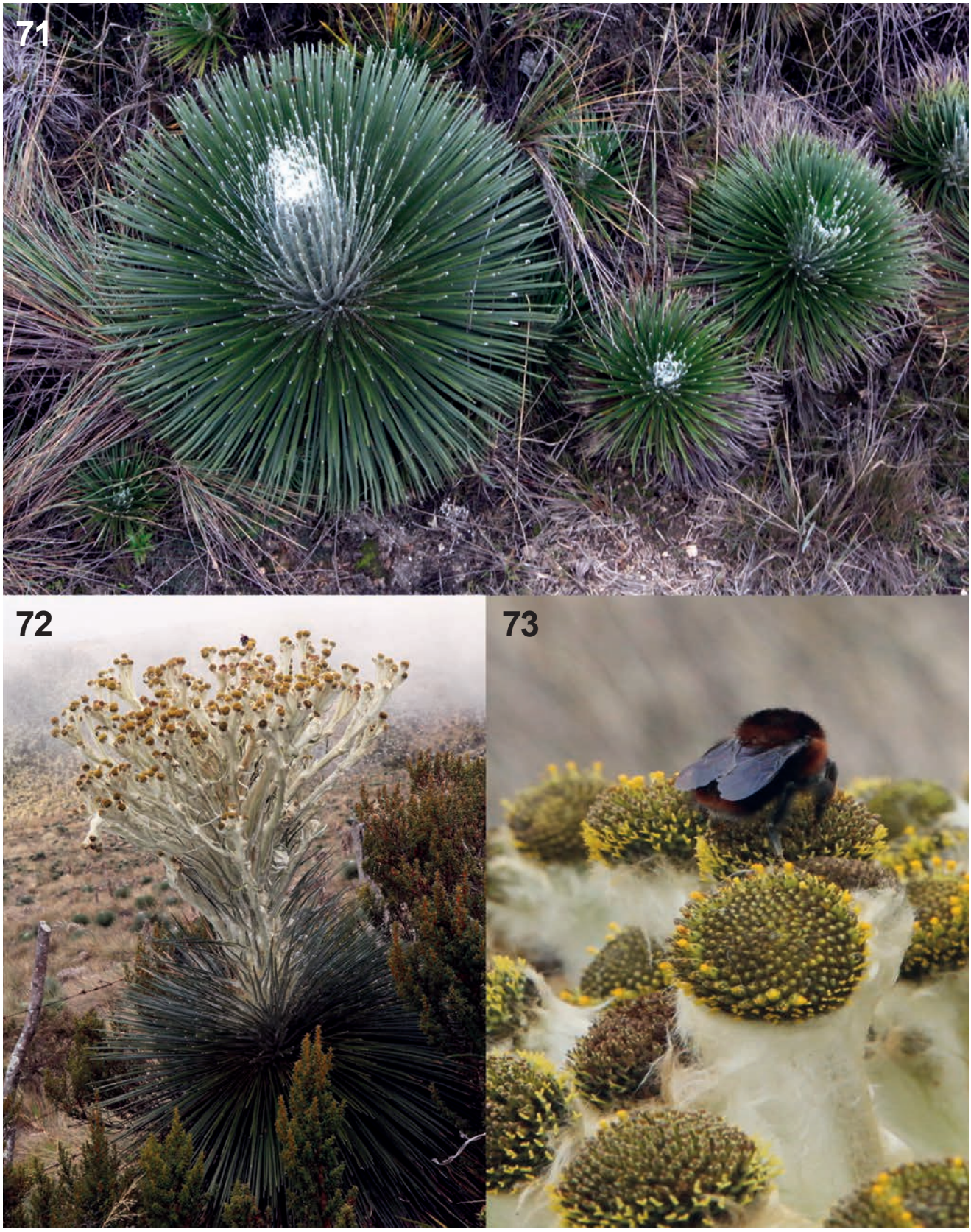


FIGURE 70. Distribution of *Espeletia jabonensis* Cuatrec.



FIGURES 71–73. *Espeletia jahnii* Standl. Páramo del Batallón, Táchira, Venezuela (Photographs by S. Aubert).

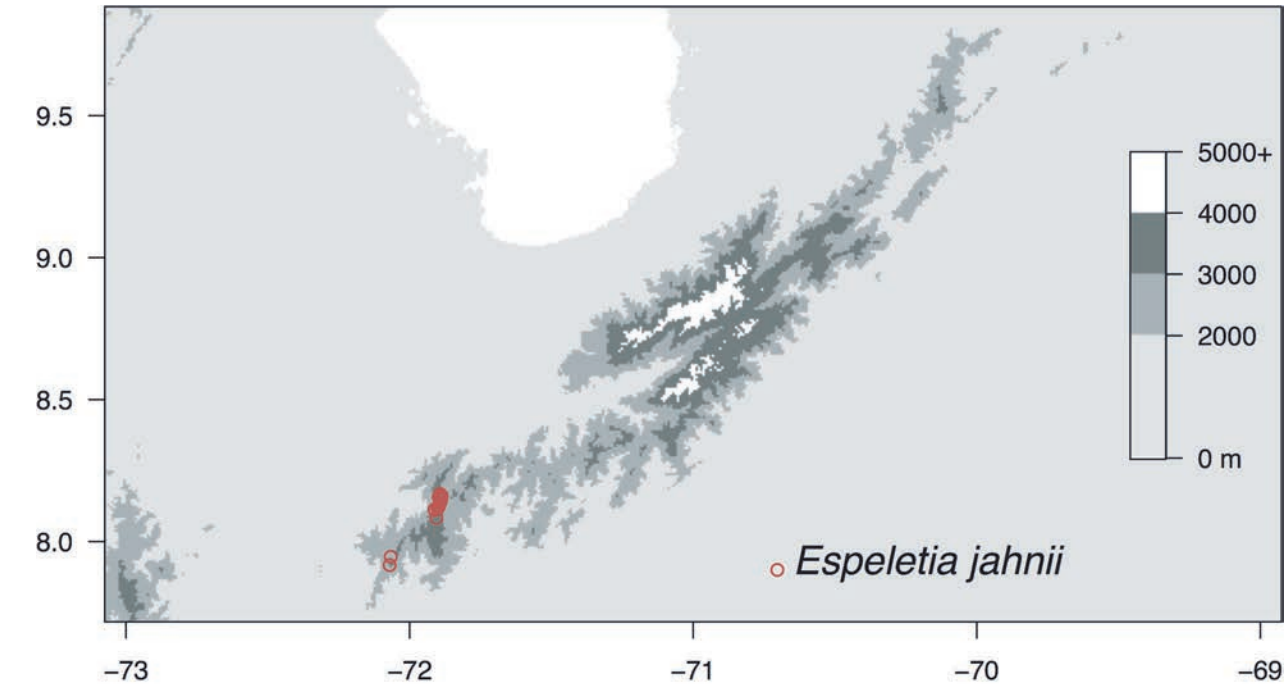


FIGURE 74. Distribution of *Espeletia jahnii* Standl.

FIGURE 75. *Espeletia leucactina* Cuatrec. Páramo del Batallón, Táchira, Venezuela (Photograph by S. Aubert).

FIGURE 76. *Espeletia leucactina* Cuatrec. Páramo del Batallón, Táchira, Venezuela (Photograph by S. Aubert).

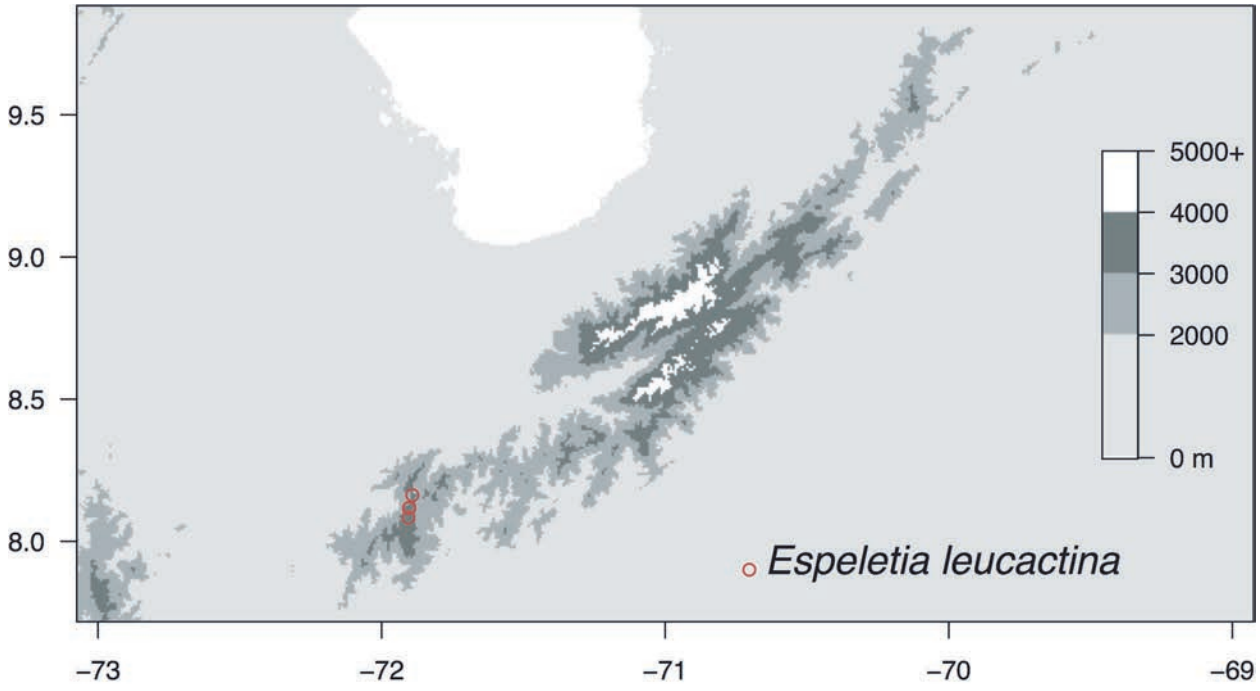


FIGURE 77. Distribution of *Espeletia leucactina* Cuatrec.

ligular circle 22–25 mm, disc 11–12 mm, ray ligules white. *Espeletia leucactina* can be distinguished from other species by its large sessile monocarpic rosette habit with long adaxially pubescent leaves, and its capitulum with white ray ligules. The species resembles *E. margarita* Cuatrec., from which it can be distinguished by its broader leaves (width 2.0–3.3 cm vs. 0.8–1.4 cm), secondary nerves with much larger deviation angle (60˚–80˚ vs. 20˚–25˚ when present), and its shorter ray corollas (8–10 mm vs. 13–17 mm).

Distribution: VENEZUELA. Táchira: Páramo del Batallón and del Portachuelo (between La Grita and Bailadores). 3000–3300 m.a.s.l., in open páramo, particularly in humid depressions and along streams (Fig. 77).

Additional specimens examined (selection): *M. López-Figueiras 9151* (US), *M. López-Figueiras 9152* (US), *M. López-Figueiras*, *H. Rodríguez & B. Rock 24651* (US), *L. Ruiz-Terán*, *M. López-Figueiras*, *D. Griffin & N. Griffin 12594* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28408* (F, US).

25. *Espeletia lindenii* Sch. Bip. ex Wedd., Chlor. Andina: 66. 1855. TYPE: VENEZUELA. Mérida: Province de Mérida, 10,000 pieds, July 1843, *J. Linden 1414* (Holotype: P; Isotypes: BR, F, FI [not seen], G, K, P). Fig. 78–80.

Homotypic synonym: *Ruilopezia lindenii* (Sch. Bip. ex Wedd.) Cuatrec., Phytologia 35: 53. 1976.

Rosette monocarpic, sessile in Sierra Nevada de Mérida, caulescent with a stem height up to 2.0 m and entirely covered by marcescent leaves in Páramo El Tambor. *Leaf* open sheath, sessile, adaxially thinly villous-sericeous, green-grey aspect, length 15–30 cm, width 1.5–4.0 cm, ratio 7–9:1 (in Páramo El Tambor: leaf length up to 50 cm, width up to 5 cm, ratio up to 11.5:1), secondary nerves parallel, 1.5–4.0 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 50–80 cm (up to 240 cm in Páramo El Tambor), vegetative part profusely bracteate, about half of total length. *Capitulum* outer phyllaries foliaceous, diam. 18–25 mm, ligular circle 20–30(35) mm, disc 10–17 mm, ray ligules white, cream, or pale green. *Espeletia lindenii* from south of Sierra Nevada de Mérida can be distinguished from other species by its sessile monocarpic rosette habit, sessile adaxially green lanceolate leaves with ratio 7–9:1, and capitula with rather large herbaceous outer phyllaries and creamy/greenish ligules. The population from south of Sierra de la Culata differs for its tall caulescent and marcescent monocarpic rosette habit with longer leaves and inflorescences.

Distribution: VENEZUELA. Mérida: páramos in the southern ends of both Sierra Nevada de Mérida (e.g., Aricagua, Quirorá, San José, Las Coloradas) and Sierra de la Culata (e.g., Páramo El Tambor at the SW of La

FIGURE 78. *Espeletia lindenii* Sch. Bip. ex Wedd. Páramo de San José, Mérida, Venezuela (Photograph by S. Aubert).

FIGURE 79. *Espeletia lindenii* Sch. Bip. ex Wedd. Páramo de San José, Mérida, Venezuela (Photograph by S. Aubert).

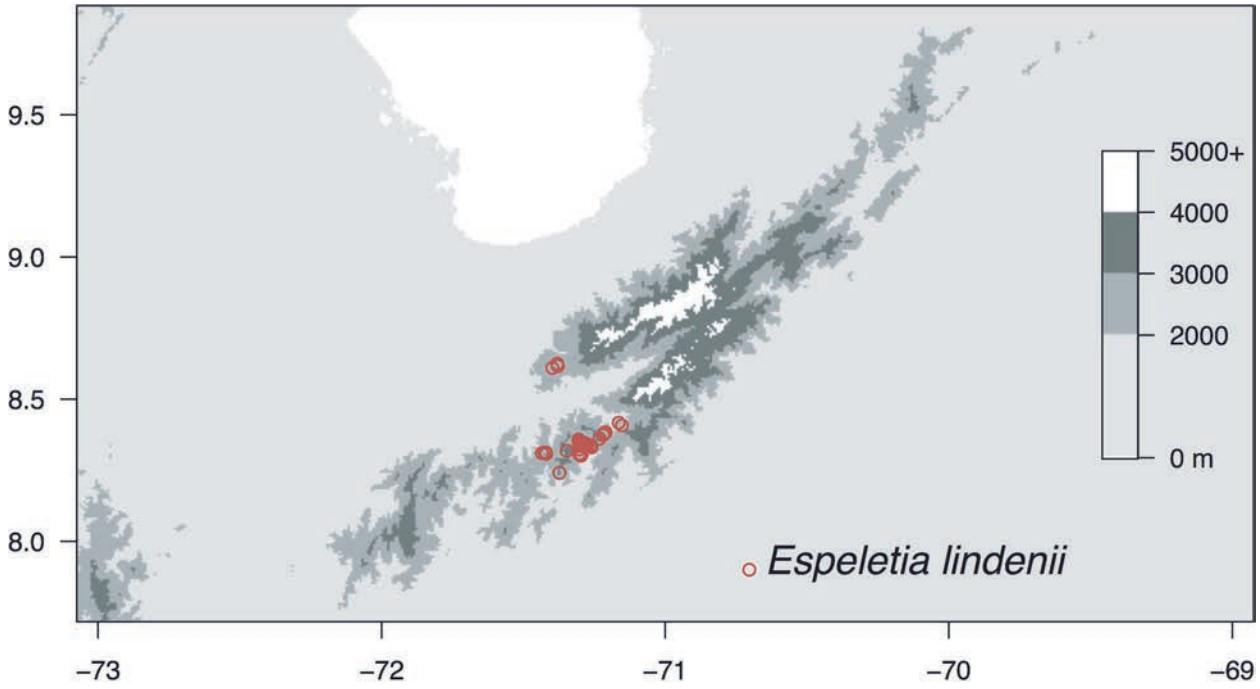


FIGURE 80. Distribution of *Espeletia lindenii* Sch. Bip. ex Wedd.

FIGURES 81–82. *Espeletia liscanoana* Cuatrec. Páramo del Jabón, Lara-Trujillo, Venezuela (Photographs by S. Aubert).

Carbonera). The two allopatric populations of this species grow in rather different habitats: 2600–2800 m.a.s.l., in flat and rather humid subpáramo habitat in Páramo el Tambor, and 2500–3300 m.a.s.l., in open subpáramo slopes with dry/rocky soils in Sierra Nevada de Mérida (Fig. 80).

Additional specimens examined (selection): *J. Linden 1414* (BR, F, G, K, P), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28477* (F, U, US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28478* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28479* (U, US). Páramo el Tambor: *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28157* (F, U, US).

26. *Espeletia liscanoana* Cuatrec., Phytologia 27: 41. 1973a. TYPE: VENEZUELA. Lara: Páramo del Jabón, vertiente oriental, 3100–3400 m.a.s.l., 2 November 1969, *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28206* (Holotype: US; Isotypes: MERF, US). Fig. 81–83.

Homotypic synonym: *Libanothamnus liscanoanus* (Cuatrec.) Cuatrec., Phytologia 35: 51. 1976.

Tree profusely branched, height up to 10 m. *Leaf* tubular sheath, sessile, adaxially glabrous, green, length 15–30 cm, width 3.5–9.0 cm, ratio 3.2–5.5:1 (young individuals may have bigger leaves), secondary nerves parallel, (4)5–10 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, at the same level or slightly surpassing the surrounding leaves, length 20–35 cm, branched near the base. *Capitulum* diam. 15–20 mm, ligular circle 25–30 mm, disc 10–15 mm, ray ligules cream, greenish, or pale-yellow. *Espeletia liscanoana* can be easily distinguished from other tree species by its sessile leaves with loosely packed secondary nerves (> 4 mm apart).

Distribution: VENEZUELA. Border Lara-Trujillo: Páramo del Jabón, de Cendé, and del Turmal. 2900–3300 m.a.s.l., in humid locations in the upper level of the Andean forests usually below the timberline. Also found in subpáramo habitats, in places locally protected from winds, such as stands of tall trees, big rocks, and along ravines (Fig. 83).

Additional specimens examined (selection): *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28206* (US), *R. Duno & R. Riina 765* (US), *Monasterio 3525* (US), *R. Riina*, *R. Duno*, *R. Ghinaglia & R. Gonto 634* (US), *L. Ruiz-Terán & M. López-Figueiras 957* (US).

27. *Espeletia lopezpalacii* Ruiz-Terán & López-Fig., Rev. Fac. Farm. Univ. Andes 17: 13. 1976. TYPE: VENEZUELA. Trujillo: Páramo de Guaramacal, unos 15 km al E. de Boconó, distrito Boconó, 2600 m.a.s.l., 9 August 1975, *L. Ruiz-Terán*, *M. López-Figueiras*, *D. Griffin & N. Griffin 12619* (Holotype: MERF; Isotype: US). Fig. 84–86.

Homotypic synonym: *Ruilopezia lopezpalacii* (Ruiz-Terán & López-Fig.) Cuatrec., Phytologia 35: 53. 1976.

Rosette monocarpic, caulescent, stem height up to 1.0 m, entirely covered by marcescent leaves. *Leaf* open sheath, sessile, usually narrowed toward the base in an apparent pseudopetiole (length 1–4 cm), adaxially pubescent, appressed-sericeous, greenish-ashy aspect, length 25–38 cm width 1.5–2.3 cm, ratio 14–23:1, secondary nerves parallel, irregular length, long ones 4–10 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 120–180 cm, vegetative part

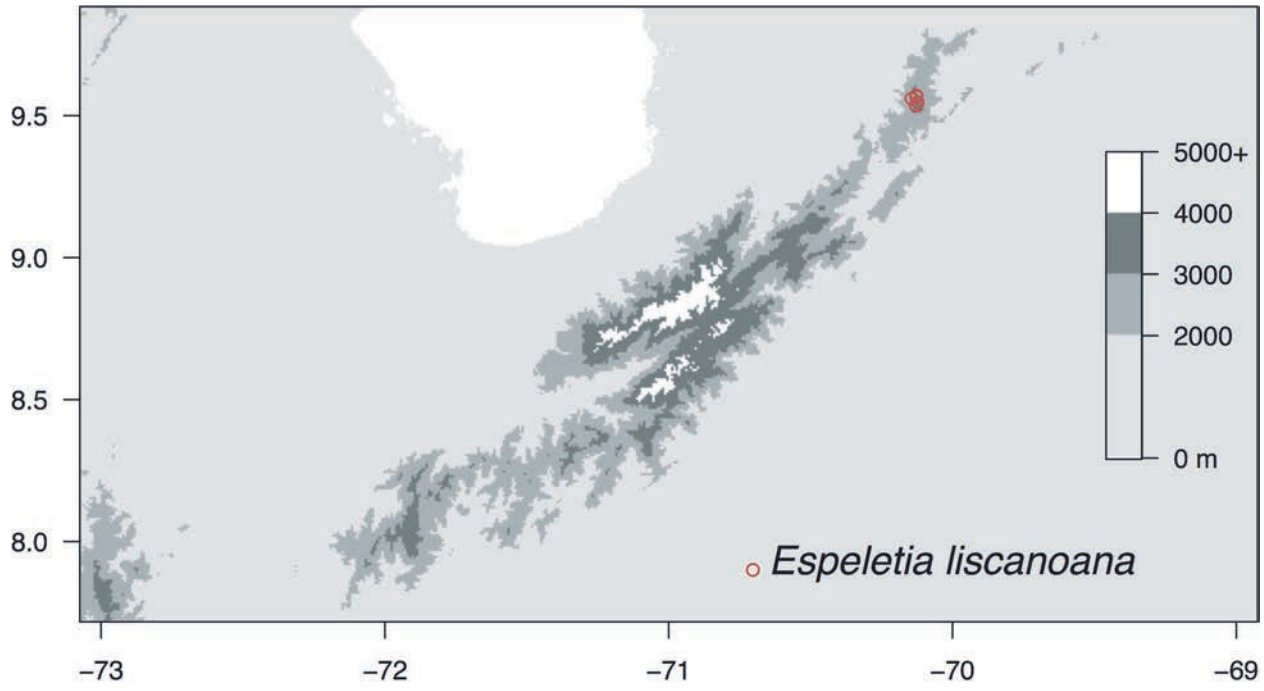


FIGURE 83. Distribution of *Espeletia liscanoana* Cuatrec.

FIGURES 84–85. *Espeletia lopezpalacii* Ruiz-Terán & López-Fig. Páramo de Guaramacal, Trujillo, Venezuela (Photographs by S. Aubert).

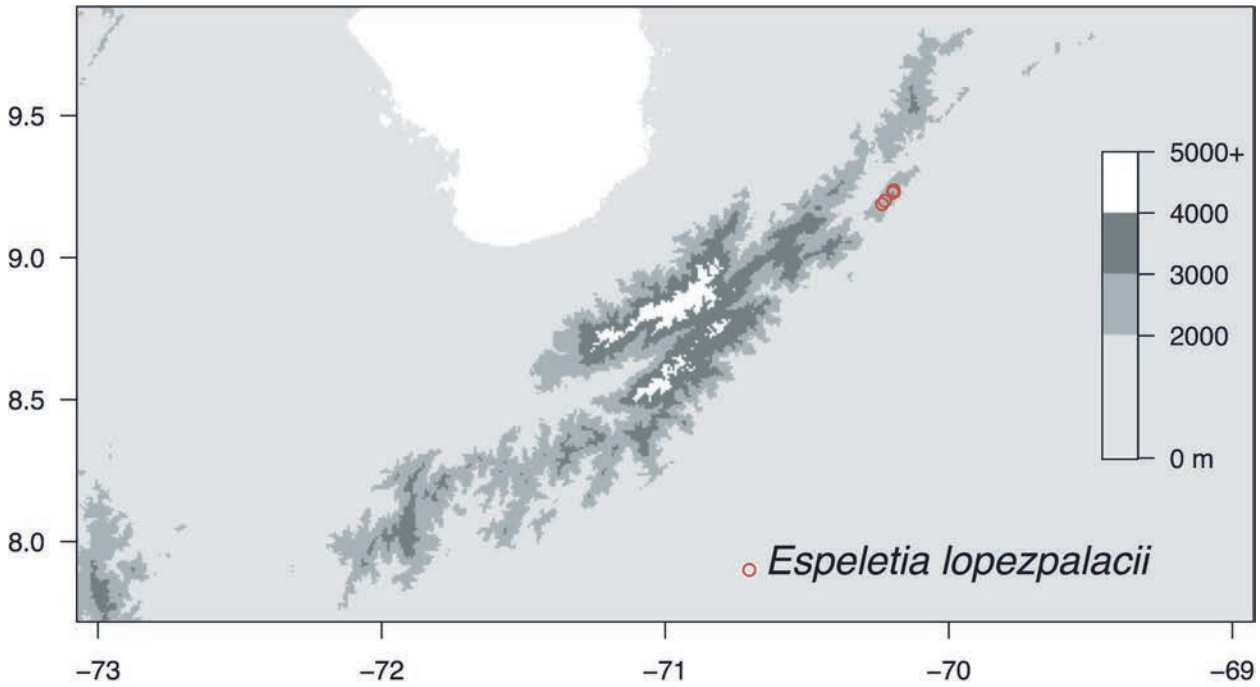


FIGURE 86. Distribution of *Espeletia lopezpalacii* Ruiz-Terán & López-Fig.

bracteate, about a third of total length. *Capitulum* diam. 7–10 mm, ligular circle 12–15 mm, disc 6–9 mm, ray ligules white. *Espeletia lopezpalacii* can be distinguished from other species by its caulescent-marcescent monocarpic rosette habit, lanceolate and pubescent leaves, secondary nerves > 4 mm apart with deviation angles < 40°, and long inflorescence with rather small white-ligulate capitula.

Distribution: VENEZUELA. Trujillo: Páramo de Guaramacal. Between 2600–3100 m.a.s.l., in humid locations within shrubby subpáramo habitats (Fig. 86).

Additional specimens examined (selection): *L. Ruiz-Terán*, *M. López-Figueiras*, *D. Griffin & N. Griffin 12619* (US), *J. Cuatrecasas & L. Ruiz-Terán 28812* (F, US), *J. Cuatrecasas & L. Ruiz-Terán 28813* (US), *M. López-Figueiras 13941* (US), *G. Aymard*, *F. Ortega & R. Morán 2920* (US).

This taxon honors S. López Palacios (Cuatrecasas, 2013: 531). According to ICN Art. 60.11, the correct spelling for the derived substantival epithet is "*lopezpalacii*" (not "*lopez-palacii*"). Also, collectors given as "*L. Ruiz-Terán*, *M. López-Figueiras & D. Griffin*" (*N. Griffin* missing) in Diazgranados (2012: 41) and Cuatrecasas (2013: 529).

28. *Espeletia lucida* Aristeg., Fl. Venez. 10(1): 420. 1964. TYPE: VENEZUELA. Mérida: Camino al Pico Bolívar, 3800 m.a.s.l., 9 April 1951, *ULA-1001* (Holotype: VEN [not seen]; Isotype: MER). Fig. 87–89.

Homotypic synonym: *Libanothamnus lucidus* (Aristeg.) Cuatrec., Phytologia 35: 51. 1976.

Tree profusely branched, height up to 10 m. *Leaf* tubular sheath, pseudopetiolate (length 10–25 cm), adaxially glabrous, lucid green, length 15–30 cm, width 3.5–5.0 cm, ratio 4.0–5.5:1, secondary nerves parallel, (1.5)2–3(4) mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, at the same level or slightly surpassing the surrounding leaves, length 20–30 cm, branched near the base. *Capitulum* diam. 9–12 mm, eligulate. *Espeletia lucida* can be easily distinguished from other tree species by its eligulate ray corollas.

Distribution: VENEZUELA. Mérida: restricted to a limited area in the western slopes of the Sierra Nevada de Mérida, between la Aguada cable-car station and lagunas la Coromoto and Verde to the SE of Tabay. 3200–3500 m.a.s.l., in the upper level of the Andean forest near the timberline and in secondarily open or disturbed vegetation (Fig. 89).

Additional specimens examined (selection): *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28591* (US), *M. López-Figueiras & S. López-Palacios 8692* (US), *L. Ruiz-Terán & S. López-Palacios 1674* (US), *H. Barclay & P. Juajibioy 9945* (US).

29. *Espeletia marcescens* S.F. Blake, Contr. U.S. Nat. Herb. 20: 536. 1924. TYPE: VENEZUELA. Mérida: Southern slopes of Páramo de Quirorá, 2950 m.a.s.l., 24 February 1922, *A. Jahn 875* (Holotype: US; Isotypes: G, GH, K, NY, US, VEN [not seen]). Fig. 90–93.

Homotypic synonym: *Ruilopezia marcescens* (S.F. Blake) Cuatrec., Phytologia 35: 53. 1976.

Rosette monocarpic, caulescent, stem height up to 10 m, usually covered by marcescent leaves in the distal half, sometimes only below the rosette. *Leaf* open sheath, sessile, usually with small folding at the base, adaxially glabrous, bright green, length 20–50 cm, width 3.5–8.0 cm, ratio 5.5–6.2:1, margins dentate, teeth 1–5 mm apart, bases of

FIGURES 87–88. *Espeletia lucida* Aristeg. Estación la Aguada, Mérida, Venezuela (Photographs by S. Aubert).

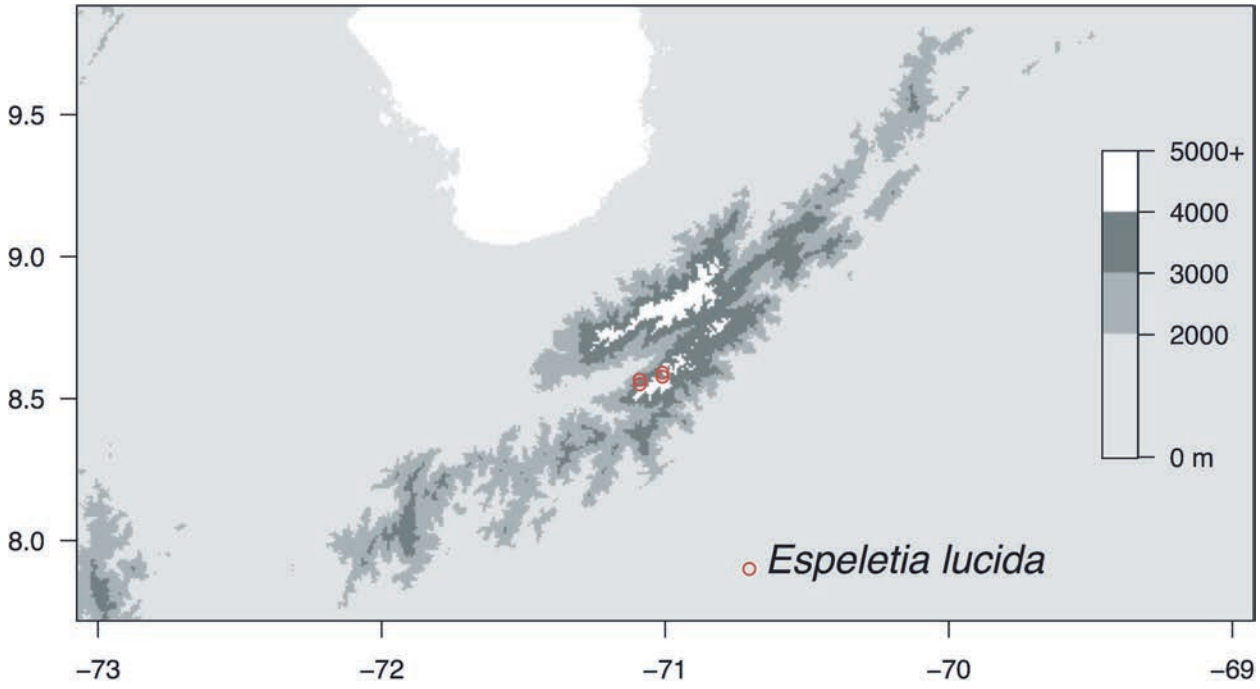


FIGURE 89. Distribution of *Espeletia lucida* Aristeg.

secondary nerves parallel, unevenly distributed, 2–5 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 40–80 cm, branched near the base, branches and sheaths of bracts pale green. *Capitulum* outer phyllaries herbaceous, diam. 20–25 mm, ligular circle 30–45 mm, disc 15–20 mm, ray ligules white, cream, or pale green. *Espeletia marcescens* can be distinguished from other species by its tall caulescent monocarpic rosette habit, sessile green leaves with small length-to-width ratio (< 7:1), and capitula with herbaceous outer phyllaries and creamy/greenish ligules. *Espeletia marcescens* resembles *E. cuatrecasasii*, but in addition to numerous color differences, *E. marcescens* has leaves with less prominent auriculate bases, greater density of secondary nerves (2–5 mm vs. 4–8 mm apart), greater deviation angles (70–90˚ vs. 60–65˚), larger capitulum diam. (> 20 mm vs. < 18 mm), and longer ray corollas (12–17 mm vs. 7–9 mm).

Distribution: VENEZUELA. Mérida: páramos in the southern end of Sierra Nevada de Mérida (e.g., Aricagua, Quirorá, San José, Las Coloradas) toward the border with Táchira state (e.g., Portachuelo, La Grita). Táchira: Páramo de la Negra and Páramo del Batallón. 2500–3000 m.a.s.l., found in humid clearings and margins of the upper level of the Andean forest below the timberline (Fig. 93).

Additional specimens examined (selection): *A. Jahn 875* (G, GH, K, NY, US), *M. López-Figueiras 12579* (US), *J. L. Panero*, *C. E. Benítez & V. M. Badillo 2699* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28398* (F, U, US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28500* (F, US), *M. López-Figueiras*, *H. A. Rodríguez & J. Wurdack & M. Wurdack 8916* (US).

30. *Espeletia margarita* Cuatrec., Phytologia 27: 49. 1973a. TYPE: VENEZUELA. Mérida: Alrededores inmediatos de la Laguna Brava, Páramo de Los Granates, Sierra Nevada de Santo Domingo, 3300 m.a.s.l., 20 May 1971, *M. López-Figueiras 8720* (Holotype: US; Isotypes: BC, F, K, MERF, NY, U, US, VEN [not seen]). Fig. 94–96.

Homotypic synonym: *Ruilopezia margarita* (Cuatrec.) Cuatrec., Phytologia 35: 53. 1976.

Rosette monocarpic, sessile. *Leaf* open sheath, sessile, linear, adaxially pubescent, villous-sericeous, green-ashy aspect, length 25–40 cm, width 0.8–1.4 cm, ratio 20–40:1, secondary nerves frequently obsolete, distributed unevenly when visible. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 50–100 cm, branched near the base. *Capitulum* diam. 15–18 mm, ligular circle 30–40, disc 12–15, ray ligules white. *Espeletia margarita* can be distinguished from other species by its sessile monocarpic rosette habit with long-linear adaxially pubescent leaves, and its capitulum with white ray ligules. The species resembles *E. leucactina*, from which it can be distinguished by its thinner leaves (width 0.8–1.4 cm vs. 2.0–3.3 cm), scarcity of secondary nerves with smaller deviation angles when visible (20˚–25˚ vs. 60˚–80˚), and its capitulum with longer ray corollas (13–17 mm vs. 8–10 mm).

Distribution: VENEZUELA. Mérida: Páramo de Los Granates in Sierra Nevada de Santo Domingo. 3200–3400 m.a.s.l., in open páramo near lakes (Fig. 96).

Additional specimens examined (selection): *M. López-Figueiras 8720* (F, K, NY, U, US), *B. Vergara 1* (US), *B. Vergara 1A* (US), *L. Ruiz-Terán 6346* (US).

FIGURES 90–92. *Espeletia marcescens* S.F. Blake. Páramo de San José, Mérida, Venezuela (Photographs by S. Aubert).

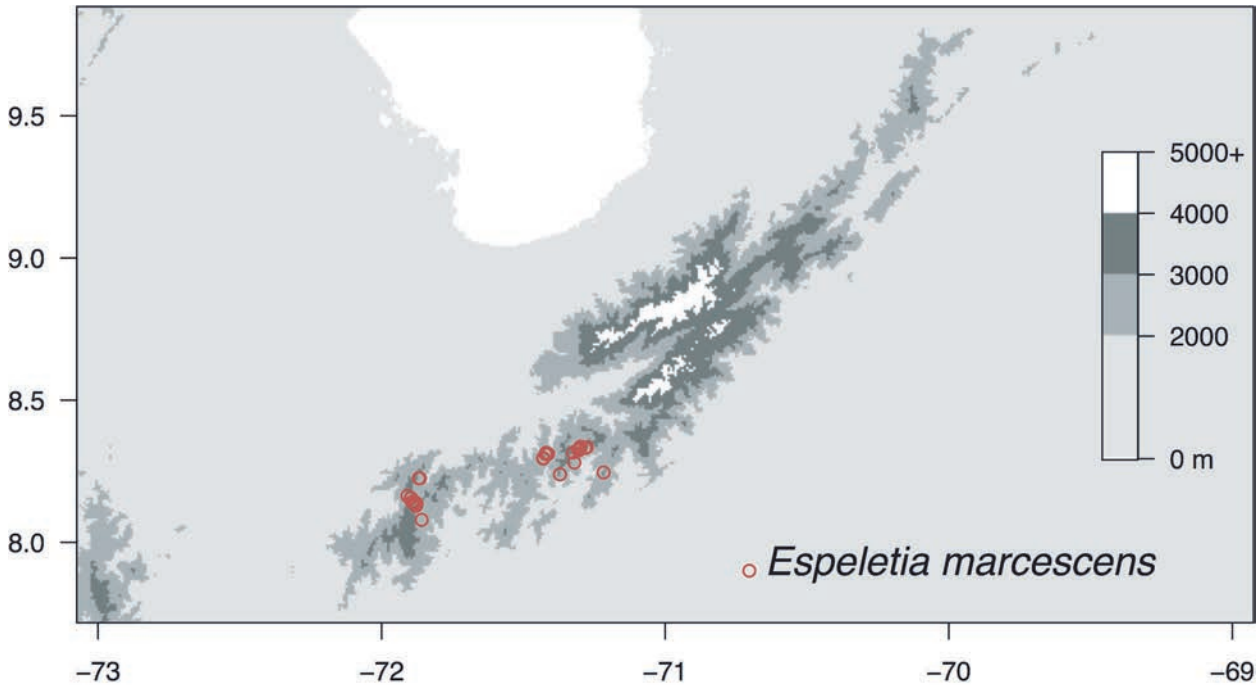


FIGURE 93. Distribution of *Espeletia marcescens* S.F. Blake.

FIGURE 94. *Espeletia margarita* Cuatrec. Páramo de Ortiz, Barinas-Trujillo, Venezuela (Photograph by S. Aubert).

FIGURE 95. *Espeletia margarita* Cuatrec. Páramo de Ortiz, Barinas-Trujillo, Venezuela (Photograph by S. Aubert).

31. ***Espeletia marthae*** Cuatrec., Phytologia 36: 20. 1977. TYPE: VENEZUELA. Mérida: Llano Corredor, Páramo de Guirigay, 3300 m.a.s.l., 25 October 1969. *J. Cuatrecasas, M. López-Figueiras & L. Marcano-Berti 28162* (Holotype: US; Isotypes: F, MERF). Fig. 97–99.

Rosette polycarpic, sessile, dwarf. *Leaf* open sheath, sessile, adaxially pubescent, silvery-sericeous, length 4.0–6.5 cm, width 0.4–0.5 cm, ratio 10–14:1, secondary nerves reticulate. *Inflorescence* lateral, simple, dichasial, monocephalous, length 25–40 cm, with 3–5 pairs of opposite bracts. *Capitulum* diam. 19–21 mm, ligular circle 30–35 mm, disc 9–12 mm, yellow ray ligules. *Espeletia marthae* can be distinguished from all other Venezuelan dwarf rosette plants with monocephalous inflorescences by its leaf sheaths glabrous on both sides and its inflorescences with 3–5 pairs of basal opposite bracts plus one or more solitary, alternate leaves. The species resembles *E. nana*, but it has smaller leaves covered with silvery-sericeous indumentum (vs. villous-lanate) and a smaller capitulum disc (< 12 mm and < 125 flowers).

Distribution: VENEZUELA. Border Mérida-Trujillo: Páramo de Guirigay. 3000–3500 m.a.s.l., in swampy areas, very humid depressions, and ponds (Fig. 99).

Additional specimens examined (selection): *J. Cuatrecasas, M. López-Figueiras & L. Marcano-Berti 28162* (F, US), *L. Ruiz-Terán & M. López-Figueiras 12979* (US), *M. López-Figueiras & H. Rodríguez 8873* (US), *M. López-Figueiras & H. Rodríguez 8879* (US), *L. Aristeguieta 3571* (US).

Cuatrecasas, López-Figueiras & Marcano-Berti 28162 in F should be labelled as isotype.

32. ***Espeletia moritziana*** Sch. Bip. ex Wedd., Chlor. Andina: 65. 1855. TYPE: VENEZUELA. Mérida: Sierra Nevada de Mérida, 13,000 à 14,000 pieds, August 1842, *J. Linden 399* (Syntype: P [MNHN-P-P04086194]; Isosyntypes: P [leaves in MNHN-P-P02441522]). Mérida: Sierra Nevada de Mérida, 1852, *J. W. K. Moritz 1416* (Syntype: B destroyed [photo 15156 in F]). Fig. 100–102.

Homotypic synonym: *Coespeletia moritziana* (Sch. Bip. ex Wedd.) Cuatrec., Phytologia 35: 57. 1976.

Rosette polycarpic, usually sessile, occasionally caulescent with stem height up to 1.0 m and entirely covered by marcescent leaves. *Leaf* open sheath, sessile, linear, adaxially densely pubescent, lanate-lanuginose, yellowish-greenish aspect, length 25–50 cm, width 0.5–1.5 cm, ratio 20–40:1, secondary nerves parallel, (2.0)2.5–4.0 mm apart. *Inflorescence* lateral, simple, monochasial, monocephalous, axes 60–80 cm, with several alternate bracts. *Capitulum* diam. 40–60(–80) mm, ligular circle shorter than the involucre, disc 27–37(–40) mm, ray ligules bright yellow, orange, reddish. *Espeletia moritziana* can be easily recognized by its polycarpic rosette habit, long linear leaves, and monocephalous inflorescences with very large capitula (the largest in the subtribe). It resembles *E. palustris*, from which it can be distinguished by its yellowish–greenish indumentum (vs. whitish), smaller sheaths (5.0–7.0 cm × 0.9–2.2 cm vs. 7.0–10.0 cm × 2.2–2.5 cm), bracteate inflorescences (vs. aphyllous), sterile phyllaries with orderly pubescence (vs. dishevelled), and capitula with higher number of both disc (600–860 vs. 215–280) and ray (400–740 vs. 95–200) flowers.

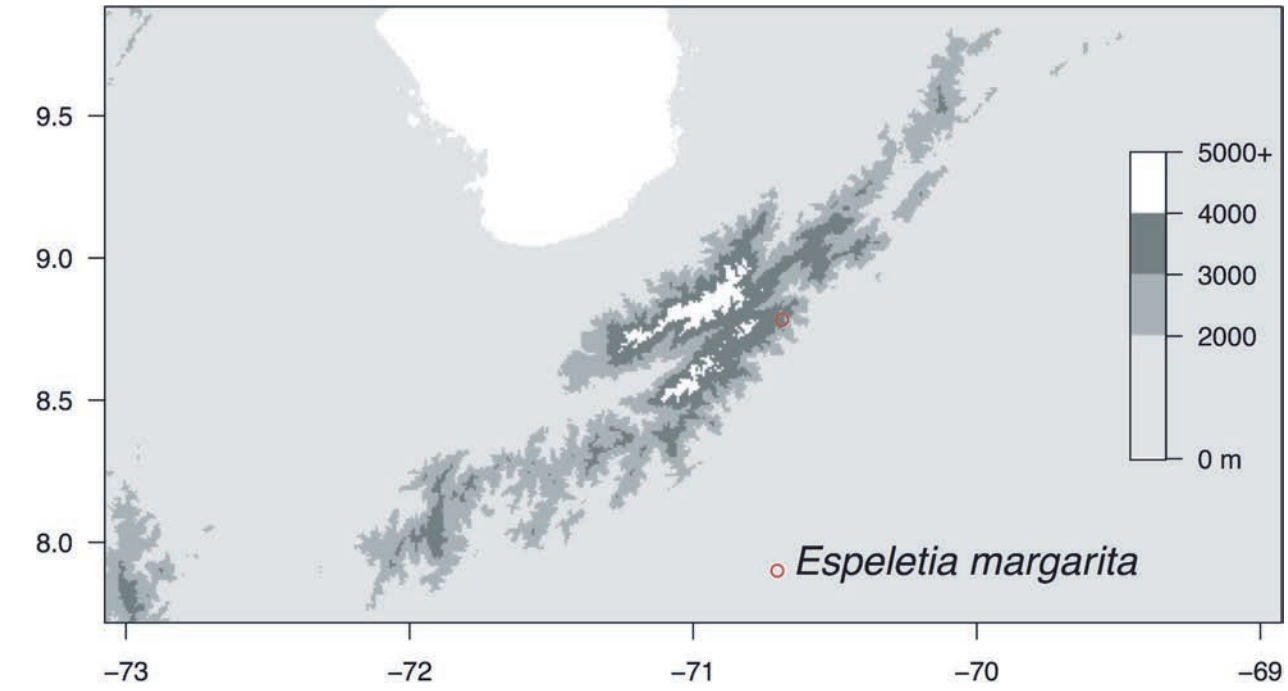


FIGURE 96. Distribution of *Espeletia margarita* Cuatrec.

FIGURE 97. *Espeletia marthae* Cuatrec. Páramo de Guirigay, Trujillo, Venezuela (Photograph by S. Aubert).

FIGURE 98. *Espeletia marthae* Cuatrec. Páramo de Guirigay, Trujillo, Venezuela (Photograph by S. Aubert).

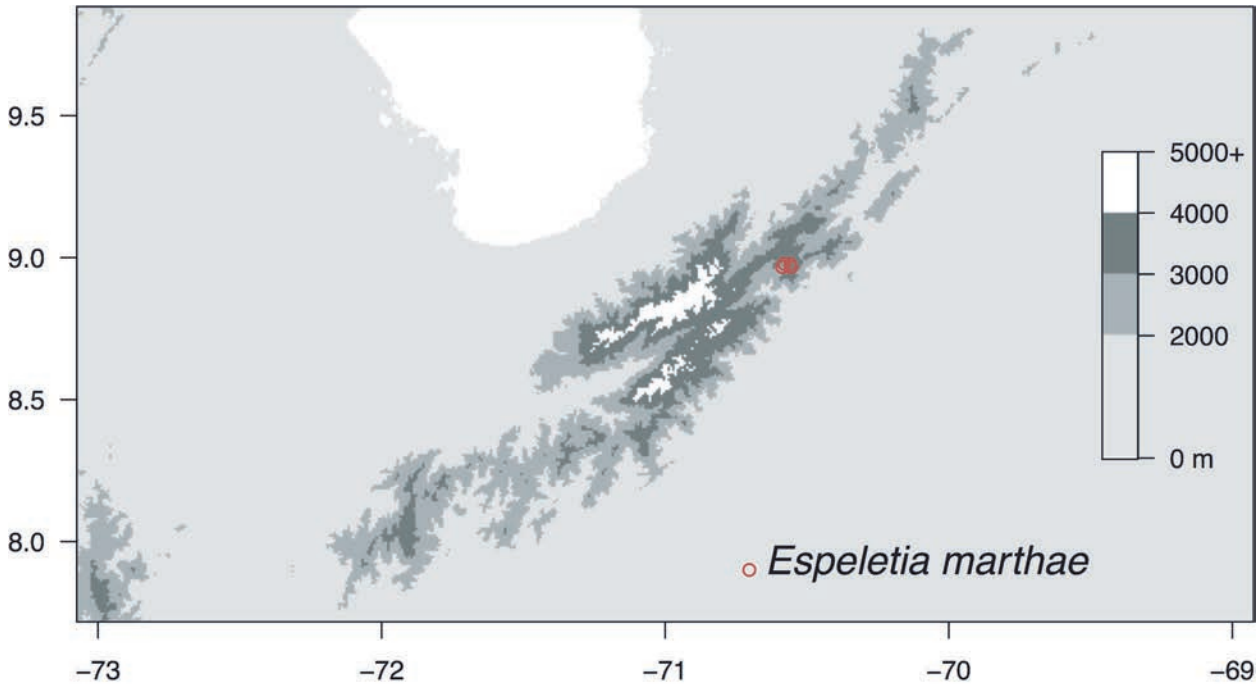


FIGURE 99. Distribution of *Espeletia marthae* Cuatrec.

FIGURES 100–101. *Espeletia moritziana* Sch. Bip. ex Wedd. Sierra de la Culata, Mérida, Venezuela (Photographs by L. Gámez).

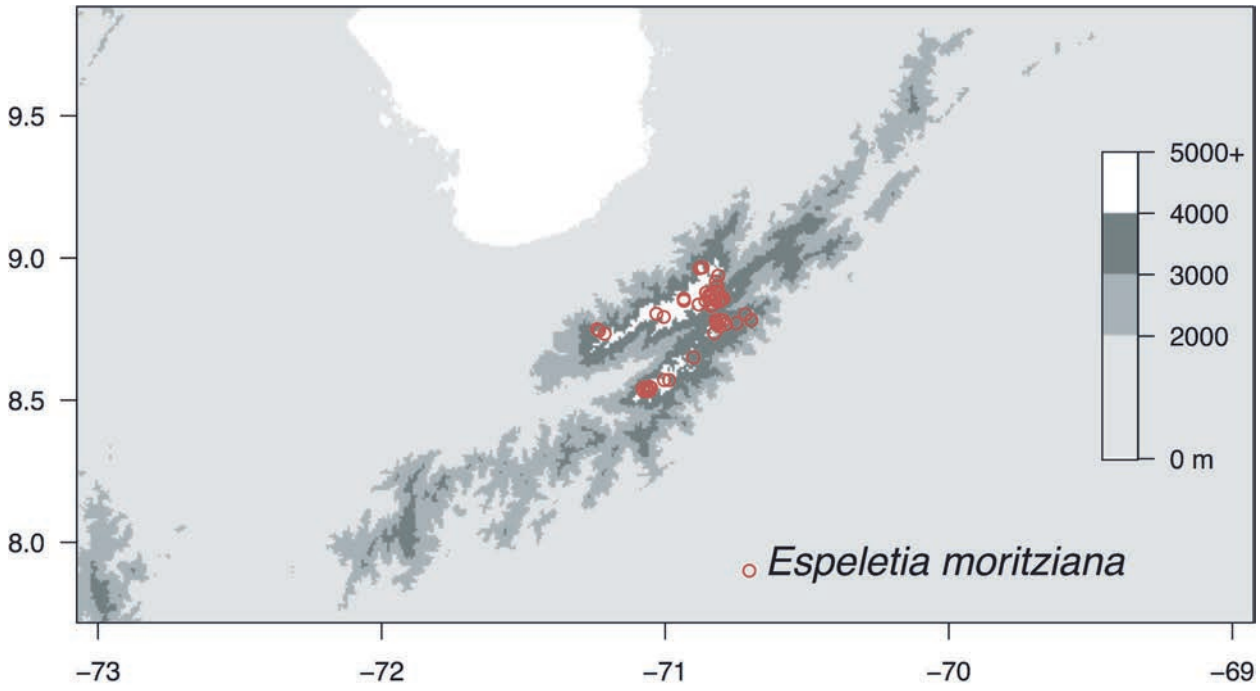


FIGURE 102. Distribution of *Espeletia moritziana* Sch. Bip. ex Wedd.

Distribution: VENEZUELA. Mérida: Sierra de la Culata and Sierra Nevada de Mérida. Usually 3800–4500 m.a.s.l., occasionally up to 4750 m.a.s.l. below Pico Espejo and Pico Bolívar, higher than any other Espeletiinae. Found in cold and windy superpáramos, usually on rocky crests (Fig. 102).

Additional specimens examined (selection): *J. L. Panero*, *C. E. Benítez & V. M. Badillo 2669* (US), *Barclay & P. Juajibioy 10043* (US), *L. Ruiz-Terán & M. López-Figueiras 369* (US), *L. Ruiz-Terán 6882* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28031* (F, U, US).

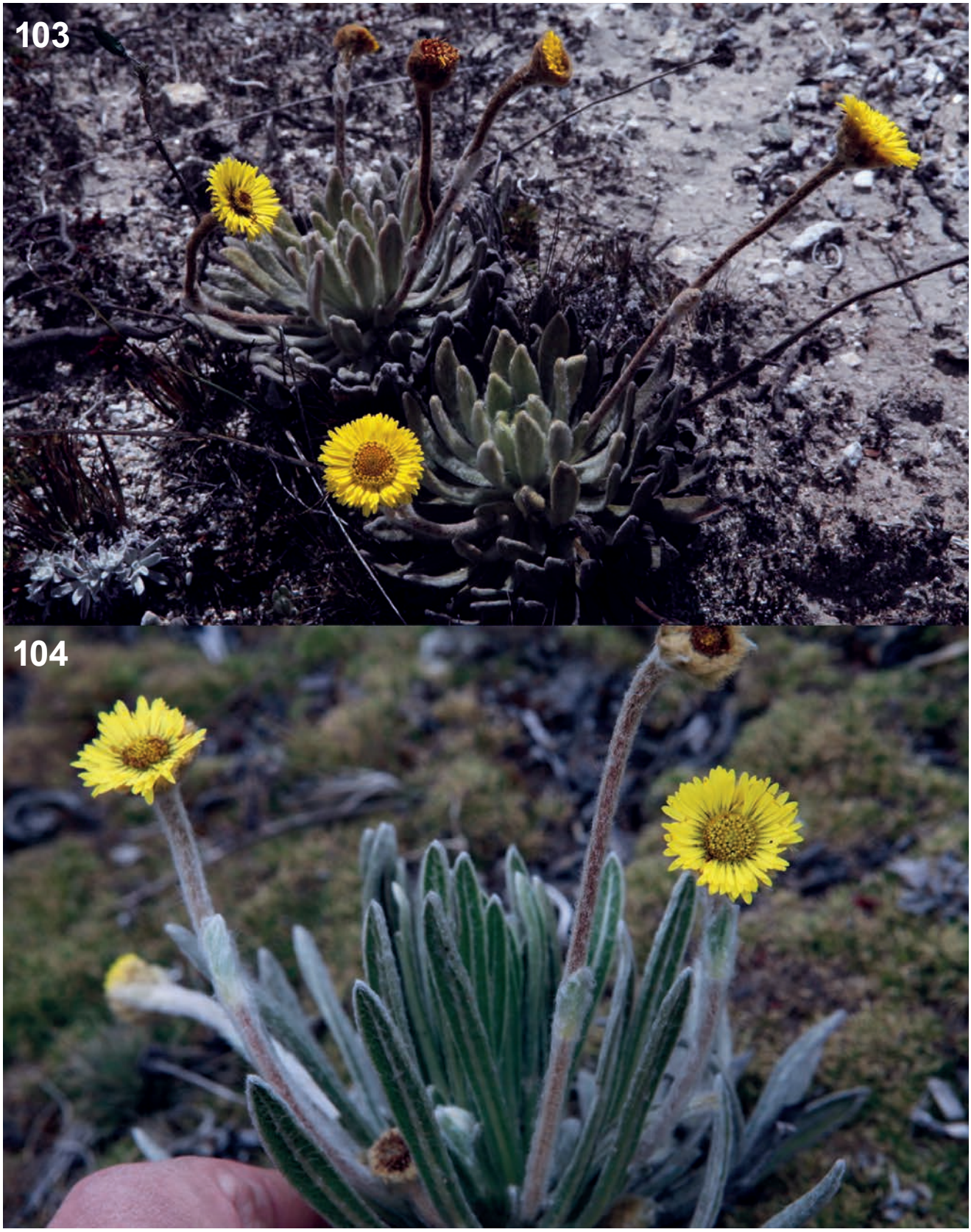
Weddell (1855: 65) mentioned two specimens in the protologue of *E. moritziana*: *J. Linden 399* and *Moritz 1416*. However, both Weddell (1855: 63) and Cuatrecasas (2013: 579) noticed that some confusion took place in the labelling of the Linden collections, with some numbers including a mixture of *Espeletia moritziana* and *E. semiglobulata*. I revised the Linden collections in P and noticed that *Linden 399* (MNHN-P-P04086194) contains only *E. moritziana* and should be considered as a syntype, whereas *Linden 399* (MNHN-P-P02441522) is a mixture of *E. moritziana* leaves and *E. semiglobulata* inflorescences, and therefore only the leaves should be considered as an isosyntype. Cuatrecasas (2013: 579) also suggested that *Linden 368* and *Linden 398* probably are duplicates of *Linden 399*. I revised these collections and noticed that *Linden 368* (MNHN-P-P04086193 in P), *Linden 398* (MNHN-P-P02441483 in P), and *Linden 398* (catalogue number 1473203 in US) contain only *E. moritziana*, but *Linden 398* (MNHN-P-P04086312 in P) is a mixture of *E. moritziana* leaves and *E. semiglobulata* inflorescences. If Cuatrecasas's suggestion is correct, all the material in the former three, but only the leaves in the last one, could be considered as isosyntypes.

33. *Espeletia nana* Cuatrec., Phytologia 40: 29. 1978. TYPE: VENEZUELA. Trujillo: Distrito Urdaneta, la Morita, cresta arriba de la capilla, entre el caserío de Tuñame y la población de Jajó, 3000 m.a.s.l., 13 July 1971, *L. Ruiz-Terán & M. López-Figueiras 2204* (Holotype: US; Isotype: MERF). Fig. 103–105.

Rosette polycarpic, sessile, dwarf. *Leaf* open sheath, sessile, adaxially pubescent, lanate-lanuginose, length 4–13 cm, width 0.4–1.1 cm, ratio 8–14:1, secondary nerves obsolete or unevenly distributed when visible. *Inflorescence* lateral, simple, dichasial, monocephalous, length 25–45 cm, usually with 2 pairs of opposite basal bracts, plus 1–5 alternate bracts along the axis. *Capitulum* diam. 20–26 mm, ligular circle 24–35 mm, disc 12–16 mm, ray ligules yellow. *Espeletia nana* can be recognized from other dwarf rosette plants by its leaf sheaths glabrous on both sides and its monocephalous inflorescences with 2 pairs of basal opposite bracts. *Espeletia nana* resembles *E. marthae*, but it has bigger leaves covered with villous-lanate indumentum (vs. silvery-sericeous) and larger capitulum discs (> 12 mm and > 125 flowers).

Distribution: VENEZUELA. Trujillo: Páramo de Tuñame, de Cabimbú, de Guirigay, de Ortiz, de Niquitao, and de la Cristalina. 3300–4000 m.a.s.l., frequently found in humid and swampy locations, but also in dryer ridges and slopes (Fig. 105).

Additional specimens examined (selection): *L. Ruiz-Terán & M. López-Figueiras 2204* (US), *L. Ruiz-Terán & M. López-Figueiras 2221* (US), *M. López-Figueiras 11885* (US), *L. Ruiz-Terán & M. López-Figueiras 11886* (US), *L. Ruiz-Terán 8996* (US).



FIGURES 103–104. *Espeletia nana* Cuatrec. Páramo del Arenal, Mérida, Venezuela (Photographs by S. Aubert).

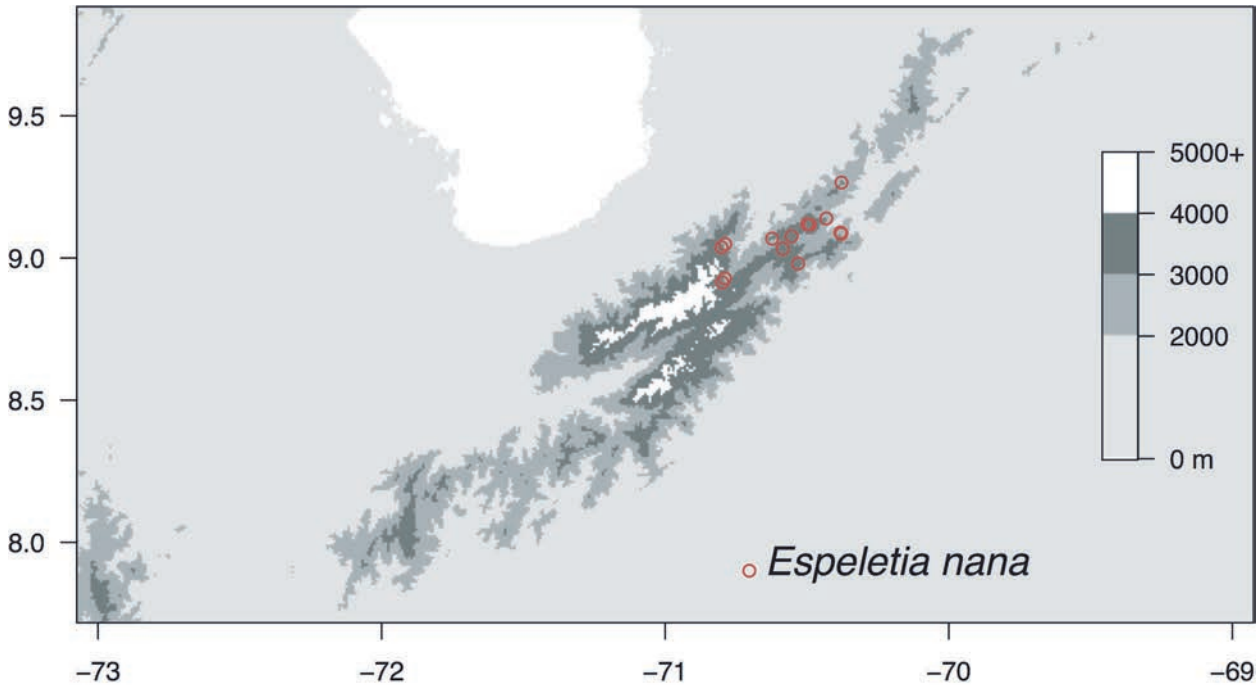


FIGURE 105. Distribution of *Espeletia nana* Cuatrec.

34. *Espeletia neriifolia* (Bonpl. ex Humb.) Sch. Bip. ex Wedd., Chlor. Andina: 67. 1855. TYPE: VENEZUELA. Caracas: Silla de Caracas, [3] January 1800, *Herbier donné par M. Bonpland en 1833 N° 652* (Lectotype: P [MNHN-P-P04086343]; Isolectotype: P [MNHN-P-P04086342]). Fig. 106–108.

Homotypic synonyms: *Trixis neriifolia* Bonpl. ex Humb., Voy. Reg. Aeq. Rel. Hist. 1: 605. 1814.

Baillieria neriifolia (Bonpl. ex Humb.) Kunth, Nov. Gen. Sp. 4: 289. 1820.

Clibadium neriifolium (Bonpl. ex Humb.) DC., Prodr: 507. 1836.

Libanothamnus neriifolius (Bonpl. ex Humb.) Ernst, Vargasia 7: 186. 1870.

Tree profusely branched, height up to 10 m. *Leaf* tubular sheath, pseudopetiolate (length 1.0–3.0[4.0] cm), adaxially glabrous, green, length 15–30(40) cm, width 4.0–8.0 cm, ratio 4.0–6.5:1 (young individuals may have bigger leaves), margins frequently entire, sometimes with teeth up to 0.5 mm long and 3–10 mm apart, secondary nerves parallel, (3)4–10 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, frequently longer than surrounding leaves, length 15–25 cm, branched near the base. *Capitulum* diam. 7–10 mm, ligular circle 14–20 mm, disc 6–10 mm, ray ligules white or cream. *Espeletia neriifolia* can be distinguished from other tree species by its distinctly pseudopetiolate leaves with loosely packed parallel secondary nerves (> 4[3] mm apart).

Distribution: VENEZUELA. Widespread: all over the Cordillera de Mérida, from hills south of Páramo de las Rosas (Táchira) to Sierra de Barbacoas (Lara). Also found in the highest elevations in Cordillera de la Costa (Aragua, Distrito Federal, and Miranda). Border Colombia-Venezuela: Páramo de Tamá. Colombia. Norte de Santander: Páramos de Pamplona and de Ocaña. Frequently 2200–3000 m.a.s.l., but can also be found down to 1800 m.a.s.l. or as high as 3300 m.a.s.l. *Espeletia neriifolia* is a very common tree in the uppermost level of the Andean forest and can even be the dominant element in the timberline. It is also found naturally in more exposed places such as shrubby subpáramos and dry/windy mountaintops and crests, and is an aggressive colonizer of upper Andean forests recently opened by fire or deforestation (Fig. 108).

Additional specimens examined (selection): *Williams 10903* (US), *H. Pittier 6240* (US), *M. López-Figueiras 25148* (US).

The lectotype of *Espeletia neriifolia* was designated by Smith and Koch (1935: 503) as "Venezuela. Federal District: Silla de Caracas, *Bonpland* (P, type)" for material collected by Aimé Bonpland and Alexander von Humboldt and described as *Trixis neriifolia*. Two herbarium samples in P match this description (MNHN-P-P04086343 and MNHN-P-P04086342), holding labels "lecto-holotypus" and "lecto-isotypus," respectively, added by José Cuatrecasas. The herbarium samples in B (B -W 16672) and HAL (HAL0113153, HAL0112801) are not lectotypes, as stated in Diazgranados (2012: 36) and Cuatrecasas (2013: 419).

Neither *Moritz 372* nor *Cuatrecasas, Schultes & Smith 12721* are types of *L. neriifolius* or *E. neriifolia* as stated in Diazgranados (2012: 35). *Moritz 372* was not collected in Colombia as stated in Diazgranados (2012: 35) but in Venezuela.

FIGURES 106–107. *Espeletia neriifolia* (Bonpl. ex Humb.) Sch. Bip. ex Wedd. Páramo de los Conejos, Mérida, Venezuela (Photographs by S. Aubert).

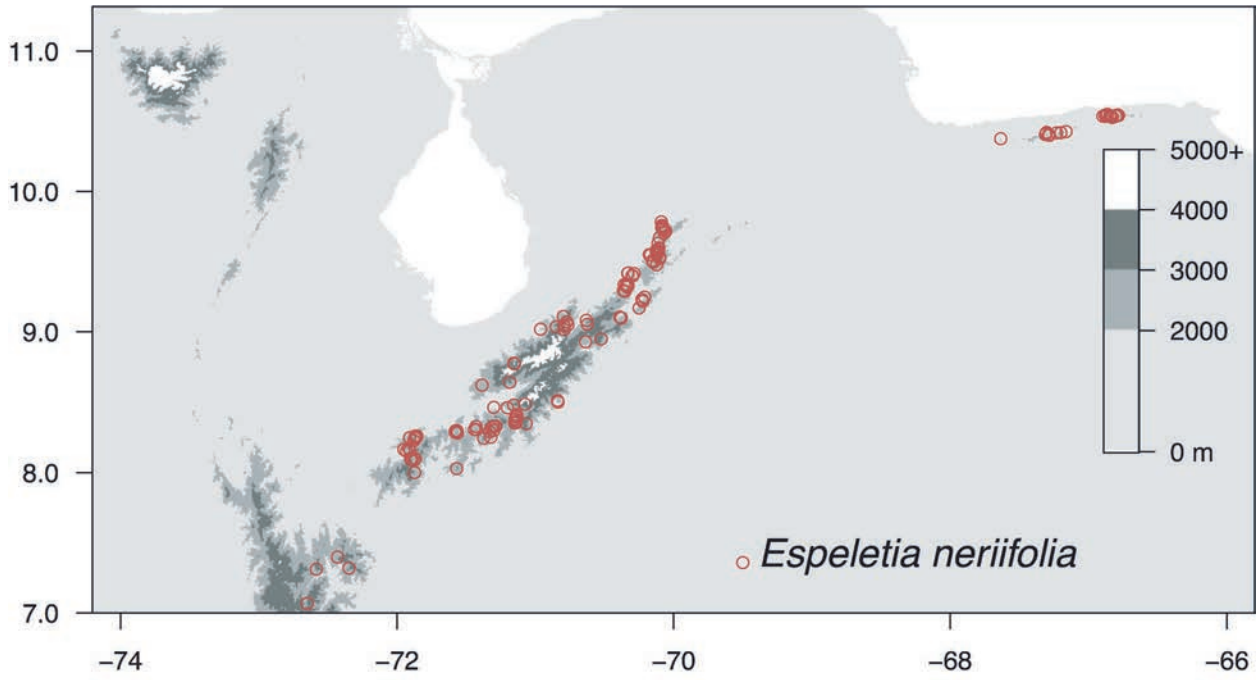


FIGURE 108. Distribution of *Espeletia neriifolia* (Bonpl. ex Humb.) Sch. Bip. ex Wedd.

Over its broad geographic distribution *E. neriifolia* has been found to hybridize with *E. angustifolia*, *E. aristeguietana*, *E. badilloi*, *E. bromelioides*, *E. lindenii*, *E. marcescens*, *E. occulta*, *E. ruizii*, *E. schultzii*, *E. vegarae*, *E. thyrsiformis*, and *E. trujillensis* (see Hybrid Taxa section).

34.1. *Espeletia neriifolia* (Bonpl. ex Humb.) Sch. Bip. ex Wedd. var. ***neriifolia***.

Distribution: VENEZUELA. Distrito Federal: along the crest that connects Lagunazo and Pico Naiguatá. Aragua: Pico Codazzi and nearby areas around Colonia Tovar. Usually found above 2200 m in dry and windy locations on mountaintops and crests, occasionally down to 1800–2000 m.a.s.l., in the upper level of the Andean forest below the timberline.

34.2. *Espeletia neriifolia* (Bonpl. ex Humb.) Sch. Bip. ex Wedd. var. ***columbica*** Cuatrec., Rev. Acad. Col. Ci. Exact. 5: 19. 1942. TYPE: COLOMBIA. Norte de Santander: Páramo de Tamá, vertiente hacia Samaria, 2600–2900 m.a.s.l., 29 October 1941, *J. Cuatrecasas*, *R. E. Schultes & E. Smith 12721* (Holotype: COL; Isotypes: BC, COL, F, GH, MO, NY, U, US).

Homotypic synonyms: *Libanothamnus neriifolius* (Bonpl. ex Humb) Ernst var. *columbicus* Cuatrec., Mem. New York Bot. Gard. 107: 429. 2013.

According to Cuatrecasas (1942, 2013: 428), *E. neriifolia* var. *columbica* can be distinguished from any other variety by its more prominent secondary nerves in the abaxial side of leaves and, particularly, its longer tubes of disc corollas (0.5–1.2 mm vs. 0.3–0.5 mm).

Distribution: VENEZUELA. Widespread: found in all mountains in the Andes, from Páramo de Tamá (Táchira) to de Timotes (Trujillo) and de Los Granates (Mérida-Barinas). COLOMBIA. Norte de Santander: Páramo de Tamá and de Pamplona. 2500–3000 m.a.s.l., occasionally as low as 2200 m.a.s.l., in the upper level of the Andean forest, in the timberline, and in shrubby subpáramos.

Additional specimens examined (selection): *J. Cuatrecasas*, *R. E. Schultes & E. Smith 12721* (F, GH, MO, NY, U, US), *J. L. Panero*, *C. E. Benítez & V. M. Badillo 2669* (US), *C. Sobrevila & A. Weitzman 1349* (US).

34.3. Espeletia neriifolia (Bonpl. ex Humb.) Sch. Bip. ex Wedd. var. ***cristamontis*** (Cuatrec.) Mavárez, *comb. nov*.

Basionym: *Libanothamnus neriifolius* (Bonpl. ex Humb) Ernst var. *cristamontis* Cuatrec., Mem. New York Bot. Gard. 107: 428. 2013. TYPE: VENEZUELA. Trujillo: Entre el Alto y los Pocitos, en la fila o cresta del cerro paralela al camino hacia Humocaro Alto, divisoria entre los estados Lara y Trujillo, a 15 km al E. de Carache, 3150 m.a.s.l., 5 October 1970, *L. Ruiz-Terán & M. López-Figueiras 1034a* (Holotype: US; Isotypes: MERF, US).

Homotypic synonym: *Libanothamnus cristamontis* Cuatrec., Phytologia 47: 5. 1980b.

Espeletia neriifolia var. *cristamontis* can be distinguished from other varieties of *E. neriifolia* by its inflorescences covered with thick indumentum and its small leaves (length 10–15 cm, width 3.0–4.0 cm), very short pseudopetioles (length 0.1–0.8 cm), and relatively denser secondary nerve packing (2–4 mm apart). Individuals with very small leaves

can look superficially similar to sympatric *E. parvula*, from which they differ by the lower density of secondary nerves (2–4 mm vs. 1–2 mm apart), smaller deviation angles (70–75˚ vs. 75–90˚), and smaller sterile phyllaries (3.5–4.0 mm × 2.3–2.8 mm vs. 4.5–5.5 mm × 4.0–5.5 mm). The morphological ressemblance and sympatry between *E. neriifolia* var. *cristamontis* and *E. parvula* suggests that the former might be the results of hybridization between lower elevation *E. neriifolia* and higher elevation *E. parvula*.

Distribution: VENEZUELA. Border Lara-Trujillo: along the mountain crest that connects the summits Cajingo, El Jabón, Cendé, and El Turmal. 3000–3200 m.a.s.l., at the timberline, in dry and windy locations on mountaintops and crests.

Additional specimens examined: *L. Ruiz-Terán & M. López-Figueiras 1034a* (US).

The other two varieties of *Espeletia neriifolia* described by Cuatrecasas (1980b: 6–7) are morphologically very close to each other and to *E. neriifolia* var. *columbica*. Furthermore, their identification can be difficult because some of the supposedly distinctive traits in the keys and descriptions provided in Cuatrecasas (2013: 428) can be rather subjective, hard to measure in the wild with the required precision, or show overlapping values among taxa. The two varieties will nonetheless be listed below, but their status must remain uncertain until more comprehensive studies are performed.

34.4. Espeletia neriifolia (Bonpl. ex Humb.) Sch. Bip. ex Wedd. var. ***boconensis*** (Cuatrec.) Mavárez, *comb. nov*.

Basionym: *Libanothamnus neriifolius* (Bonpl. ex Humb) Ernst var. *boconensis* Cuatrec., Phytologia 47: 6. 1980b. TYPE: VENEZUELA. Trujillo: Páramo de la Cristalina, 2250–2300 m.a.s.l., 30 October 1969, *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28190* (Holotype: US; Isotypes: F, MERF, U, US).

Morphologically close to *E. neriifolia* var. *columbica*, but with secondary nerves abaxially less prominent and with shorter tubes of disc corollas (0.3–0.5 mm vs. 0.5–1.2 mm). Also very similar to *E. nerifolia* var. *turmalensis*, from which it can be distinguished by its larger leaves (15–30 × 3.5–7.5 cm vs. 12–18 cm × 2.5–4.5 cm).

Distribution: VENEZUELA. Lara: Páramo de los Nepes and Alto del Filo (near Agua de Obispo) in Sierra de Barbacoas. Trujillo: Páramo de Tuñame, de Teta de Niquitao, de Cabimbú, de Guaramacal, de la Morita (above Jajó), de las Siete Lagunas (above Monte Carmelo), and de la Cristalina. Trujillo-Barinas border: Páramo de Guirigay and de Ortiz. 2200–3000 m.a.s.l., in the upper level of the Andean forest and small forest stands below the timberline, occasionally in subpáramo habitat in association with other large shrubs and trees.

Additional specimens examined (selection): *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28190* (F, U, US), *J. Cuatrecasas*, *M. López-Figueiras & H. Rodríguez 28972* (US), *J. Cuatrecasas*, *M. López-Figueiras & H. Rodríguez 28976* (US).

34.5. *Espeletia neriifolia* (Bonpl. ex Humb.) Sch. Bip. ex Wedd. var. ***turmalensis*** (Cuatrec.) Mavárez, *comb. nov*.

Basionym: *Libanothamnus neriifolius* (Bonpl. ex Humb) Ernst var. *turmalensis* Cuatrec., Phytologia 47: 7. 1980b. TYPE: VENEZUELA. Trujillo: Páramo del Turmal, hacia el Páramo del Jabón y Páramo de las Rosas (vertiente occidental), hoya del Río Turmal, al E. de Carache, 2800–2900 m.a.s.l., 3 November 1969, *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28239* (Holotype: US; Isotypes: F, MERF, U, US).

Morphologically close to *E. neriifolia* var. *columbica*, but with secondary nerves less prominent abaxially and with shorter tubes of disc corollas (0.3–0.5 mm vs. 0.5–1.2 mm). Also very similar to *E. nerifolia* var. *boconensis*, from which it can be distinguished by its smaller leaves (12–18 cm × 2.5–4.5 cm vs. 15–30 × 3.5–7.5 cm).

Distribution: VENEZUELA. Lara: Páramo de Los Nepes and Alto del Filo (near Agua de Obispo) in Sierra de Barbacoas. Border Trujillo-Lara: Páramo de las Rosas, del Jabón, de Cendé, and del Turmal. 2100–3300 m, in the upper level of the Andean forest and in subpáramo habitats above the timberline, occasionally in relatively open and exposed páramo hills.

Additional specimens examined (selection): *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28239* (F, U, US), *M. López-Figueiras 32304* (US), *M. López-Figueiras & H. Rodríguez 26231* (US).

35. *Espeletia occulta* S.F. Blake, Contr, U.S. Nat. Herb. 20: 537. 1924. TYPE: VENEZUELA. Mérida: Páramo de Quirorá, 3000 m.a.s.l., 8 October 1921, *A. Jahn 730* (Holotype: US; Isotypes: MERF, US). Fig. 109–111.

Homotypic synonym: *Libanothamnus occultus* (S.F. Blake) Cuatrec., Phytologia 35: 51. 1976.

Libanothamnus occultus (S.F. Blake) Cuatrec. var. *salomonii* Cuatrec. & López-Fig., Phytologia 61: 51. 1986a. TYPE: VENEZUELA. Táchira: Laderas occidentales alrededor de Pico de Horma, 7.5 km SE. de Mesa de Quintero, 3100 m.a.s.l., 11 January 1985, *M. López-Figueiras*, *H. Rodríguez & N. Rengifo 31344* (Holotype: US; Isotypes: F, MERF, NY, US).

Tree profusely branched, height up to 15 m. *Leaf* tubular sheath, sessile, rarely with short pseudopetiole (length < 0.3 cm), adaxially glabrous, green, length 18–40 cm, width 4.5–10.0 cm, ratio (2.5)3.0–4.5:1 (young individuals may have bigger leaves), margins frequently entire, occasionally with teeth up to 0.5 mm long and 5–10 mm apart, secondary nerves parallel, 2.5–4(5) mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, at about the same level as or slightly surpassing surrounding leaves, length 20–40 cm, branched near the base. *Capitulum* diam. 14–22 mm, ligular circle 20–30(35) mm, disc 9–15 mm, ray ligules white, cream, or yellowish. *Espeletia occulta* can be distinguished from other tree species by its large sessile leaves (> 18 cm), with sheaths barbate only in the abaxial side and with densely packed secondary nerves (< 5 mm apart).

FIGURES 109–110. *Espeletia occulta* S.F. Blake. Páramo del Batallón, Táchira, Venezuela (Photographs by S. Aubert).

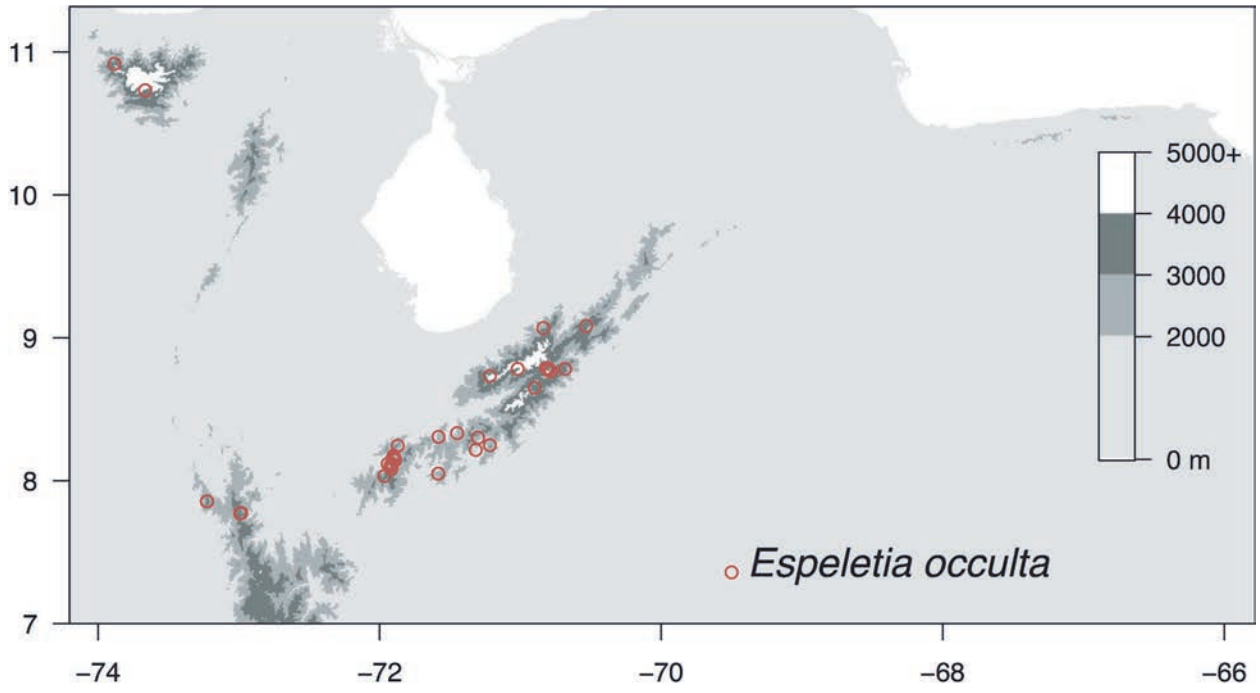


FIGURE 111. Distribution of *Espeletia occulta* S.F. Blake.

Distribution: VENEZUELA. Mérida: mountains in the southern end of the Sierra Nevada de Mérida: Aricagua, Chacantá, El Molino, and the area known as "Pueblos del Sur" (subsp. *occulta*). Páramos along the central and north sections of the Sierra Nevada de Mérida, Sierra de Santo Domingo and Páramo de Los Granates. Sierra de la Culata, from Páramo de los Conejos to the páramos between Piñango and Timotes (subsp. *humbertii*). Táchira: Pico de Horma, mountains nearby La Grita, Las Porqueras, Páramo del Batallón, and Páramo de las Rosas. Trujillo: El Paramito, between Jajó and Tuñame (subsp. *occulta*). COLOMBIA. Magdalena: Sierra Nevada de Santa Marta (subsp. *glossophylla*). Norte de Santander-Cesar: Las Jurisdicciones, Cerro de Oroque (subsp. *oroquensis*). 2900–3800 m.a.s.l., from the uppermost level of the Andean forest just below the timberline to shrubby subpáramo, extensions of forest growing at higher elevations along streams and some relatively humid and protected locations within open páramo habitat (Fig. 111).

35.1. *Espeletia occulta* S.F. Blake subsp. ***occulta***

Distribution: VENEZUELA. Mérida: mountains in the southern end of the Sierra Nevada de Mérida: Aricagua, Chacantá, El Molino, and the area known as "Pueblos del Sur." Táchira: Pico de Horma, mountains nearby La Grita, Las Porqueras, Páramo del Batallón, and Páramo de las Rosas. Trujillo: El Paramito, between Jajó and Tuñame. 2900–3400 m.a.s.l., from the uppermost level of the Andean forest just below the timberline to shrubby subpáramo, also in extensions of forest growing at higher elevations along streams within otherwise open páramo habitat.

Additional specimens examined (selection): *A. Jahn 730* (US), *J. L. Panero*, *C. E. Benítez & V. M. Badillo 2701* (US), *C. Sobrevila & A. Weitzman 1542* (US), *M. López-Figueiras 13992* (US).

35.2. Espeletia occulta S.F. Blake subsp. ***glossophylla*** (Mattf.) Mavárez, *comb. nov.*

Basionym: *Libanothamnus occultus* (S.F. Blake) Cuatrec. subsp. *glossophyllus* (Mattf.) Cuatrec., Mem. New York Bot. Gard. 107: 465. 2013. TYPE: COLOMBIA. Magdalena: Mamancanaca valley, Sierra Nevada de Santa Marta, 3450 m.a.s.l., 8 March 1928, *A. Schultze 1300* (Holotype: B [destroyed], photo 15153 in F).

Homotypic synonyms: *Espeletia glossophylla* Mattf., Notizbl. Bot. Gart. Berlin-Dahlem 10: 702. 1929.
Libanothamnus glossophyllus (Mattf.) Cuatrec., Phytologia 35: 50. 1976.

Heterotypic synonyms: *Espeletia subneriifolia* Cuatrec., Mutisia 16: 3. 1953. TYPE: COLOMBIA. Magdalena: Sierra Nevada de Santa Marta, about 30 km inland from Dibulla, 3850 m.a.s.l., July 1932, *W. Seifriz 440* (Holotype: US; Isotype: COL).
Libanothamnus subneriifolius (Cuatrec.) Cuatrec., Phytologia 35: 51. 1976.

Espeletia occulta subsp. *glossophylla* can be distinguished from other subspecies by its leaves with large length-to-width ratios (> [6]8:1), smaller disc corollas (< 5.0 mm), and copiously glanduliferous fertile phyllaries and pales (Cuatrecasas, 2013: 456).

Distribution: COLOMBIA. Magdalena: Sierra Nevada de Santa Marta. 3400–3800 m.a.s.l., in open páramo. According to Cuatrecasas (2013: 470), this taxon can also be found as low as 2550 m.a.s.l., in shrubby subpáramo habitat (although probably not anymore due to habitat destruction), and as high as 4000 m.a.s.l. along streams.

Additional specimens examined (selection): *W. Seifriz 440* (US), *H. Cuadros & A. Gentry 2729* (US), *S. White & W. Alverson 622* (US), *J. Hanbury-Tracy 312* (US).

35.3. Espeletia occulta S.F. Blake subsp. ***humbertii*** (Cuatrec.) Mavárez, *comb. nov.*

Basionym: *Libanothamnus occultus* (S.F. Blake) Cuatrec. subsp. *humbertii* Cuatrec., Mem. New York Bot. Gard. 107: 461. 2013. TYPE: VENEZUELA. Mérida: Sierra Nevada de Santo Domingo, versant NW, Laguna Negra, 3600 m.a.s.l., 21 September 1952, *H. Humbert 26441* (Holotype: P; Isotypes: COL, F, P, US, VEN [not seen]).

Homotypic synonyms: *Espeletia humbertii* Cuatrec., Notul. Syst. 15: 233. 1956b.

Libanothamnus humbertii (Cuatrec.) Cuatrec., Phytologia 35: 50. 1976.

Tree profusely branched, height up to 10 m. *Leaf* tubular sheath, sessile, adaxially glabrous, green, length 18–35 cm, width 3.5–6.0 cm, ratio (4.0)4.5–6.0(7.0):1 (young individuals may have bigger leaves), margins frequently dentate, teeth 0.2–0.4 mm long and 2–5 mm apart, secondary nerves parallel, 1.0–2.5(3.0) mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, usually not exceeding the surrounding leaves, length 15–30 cm, branched near the base. *Capitulum* diam. 13–16 mm, ligular circle 22–30 mm, disc 12–15 mm, ray ligules white, cream, greenish, or yellowish. *Espeletia occulta* subsp. *humbertii* can be distinguished from subsp. *occulta* for its larger length-to-width leaf ratios, smaller capitulum diam. (13–16 mm vs. 14–22 mm), and slender sterile phyllaries (8–13 mm × 5.0–6.5 mm vs. 12–20 mm × 6.0–9.0 mm).

Distribution: VENEZUELA. Mérida: páramos along the central and north sections of the Sierra Nevada de Mérida, Sierra de Santo Domingo, and Páramo de Los Granates. Sierra de la Culata, from Páramo de Los Conejos to the páramos between Piñango and Timotes. 3300–3800 m.a.s.l., from the uppermost level of the Andean forest just below the timberline to shrubby subpáramo, extensions of forest growing at higher elevations along streams, and some relatively humid and protected locations within open páramo habitat.

Additional specimens examined (selection): *H. Humbert 26441* (F, P, US), *M. López-Figueiras 8741* (US), *L. Ruiz-Terán 6276* (US), *L. Ruiz-Terán 7008* (US).

35.4. Espeletia occulta S.F. Blake subsp. ***oroquensis*** (Cuatrec.) Mavárez, *comb. nov.*

Basionym: *Libanothamnus occultus* (S.F. Blake) Cuatrec. subsp. *oroquensis* Cuatrec., Mem. New York Bot. Gard. 107: 471. 2013. TYPE: COLOMBIA. Norte de Santander-Cesar: Las Jurisdicciones, Cerro de Oroque, 20 km al S. de Abrego, 3700–3900 m.a.s.l., 22–27 July 1974, *H. García-Barriga & R. Jaramillo-Mejía 20600* (Holotype: US; Isotypes: COL, U, US).

Espeletia occulta subsp. *oroquensis* is morphologically very close to subsp. *occulta*, from which it can be distinguished by its larger receptacle diam. (8–9 mm vs. 5–6 mm) and the presence of numerous glands on the surface of its fertile phyllaries and pales (Cuatrecasas, 2013: 471). These differences are nonetheless rather subtle and based on the inspection of a few samples. Further studies will be necessary before the status of *E. occulta* subsp. *oroquensis* can be firmly validated.

Distribution: COLOMBIA. Norte de Santander-Cesar: known only from the type locality. According to Cuatrecasas (2013: 471), this taxon can be found at 3700–3900 m.a.s.l., growing close to the locally high-elevation limit between the upper Andean forest and the subpáramo habitat in sandstone hills.

Additional specimens examined (selection): *H. García-Barriga & R. Jaramillo-Mejía 20600* (U, US), *H. García-Barriga & R. Jaramillo-Mejía 20601, H. García-Barriga & R. Jaramillo-Mejía 19731* (U, US), *19771* (U, US).

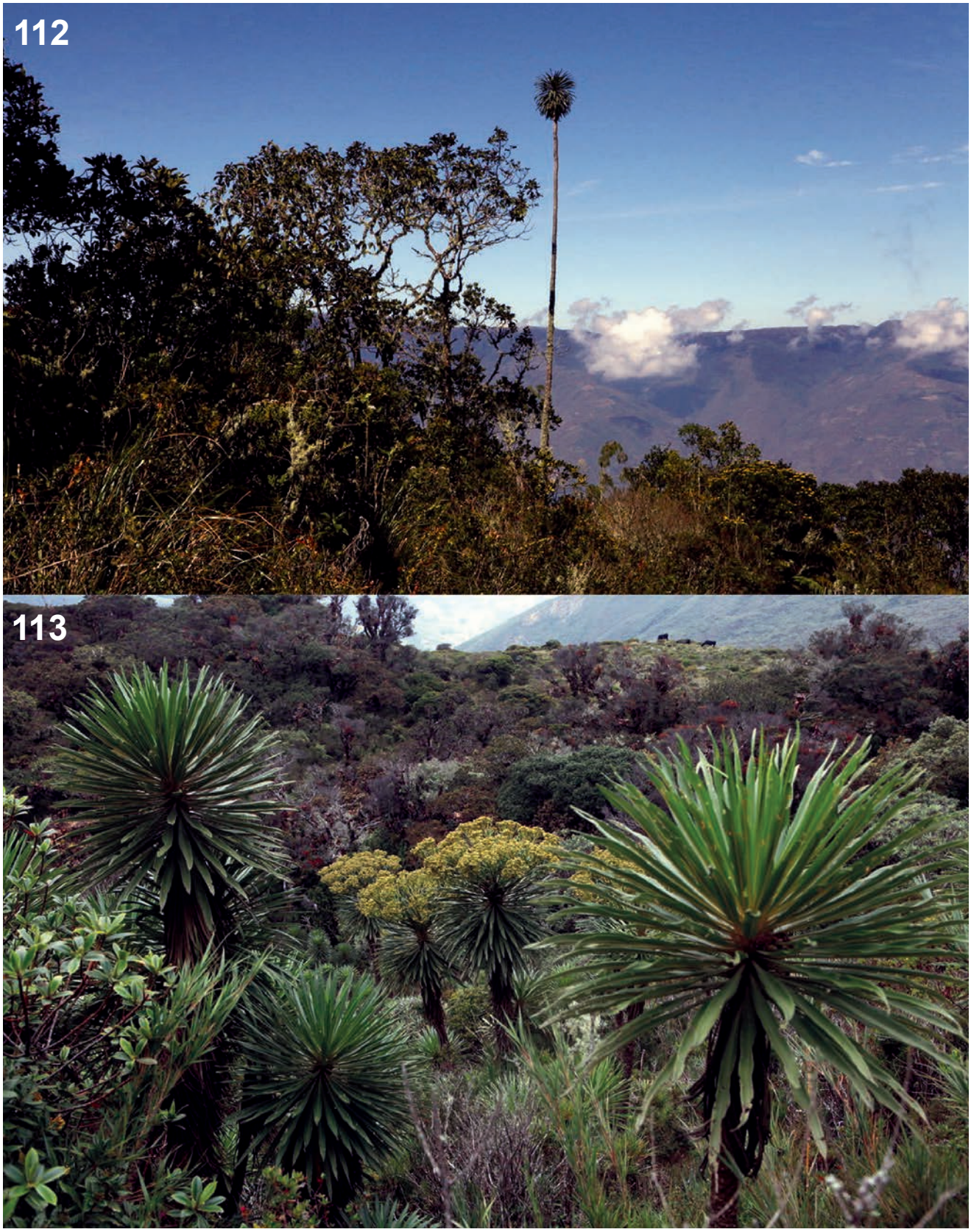
36. *Espeletia paltonioides* Standl., Amer. J. Bot. 2: 482. 1915. TYPE: VENEZUELA. Trujillo: Páramo de las Rosas, 3200 m.a.s.l., October 1912, *A. Jahn 159* (Holotype: US; Isotype: VEN [not seen]). Fig. 112–115.

Homotypic synonym: *Ruilopezia paltonioides* (Standl.) Cuatrec., Phytologia 35: 53. 1976.

Rosette monocarpic, caulescent, stem height up to 10 m, mostly leafless, occasionally with marcescent leaves below the rosette. *Leaf* open sheath, sessile (but strongly attenuated at the base), adaxially with short pubescence, strigose, greenish-greyish aspect, length 30–45 cm, width 1.4–3.0 cm, ratio 12–20:1, secondary nerves frequently obsolete or thin, 6–8 mm apart when visible. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, length 30–50 cm, branched near the base. *Capitulum* diam. 8–12 mm, ligular circle 14–15 mm, disc 7–10 mm, short ray ligules pale green or pale yellow. *Espeletia paltonioides* can be distinguished from other species by its tall leafless monocarpic rosette habit, its greenish leaves strongly attenuated at the base and with large length-to-width ratio (> 12:1), and its shortly radiated capitulum with yellowish/greenish ligules.

Distribution: VENEZUELA. Trujillo: Páramo de Guaramacal, de la Cristalina, and de Cabimbú. Border Trujillo-Lara: Páramo de las Rosas, de Cendé, and del Turmal. Border Trujillo-Barinas-Mérida: Páramo de Guirigay. Mérida: Páramo de Los Granates in Sierra Nevada de Santo Domingo and Páramo de Palmira (NE of Piñango). 2600–3200 m.a.s.l., in the upper level of the Andean forest below the timberline (Fig. 115).

Additional specimens examined (selection): *A. Jahn 159* (US), *M. López-Figueiras & J. Dugarte 29413* (US), *H. Werff & F. Ortega 6085* (US), *M. López-Figueiras 13943* (US), *L. Ruiz-Terán & J. Dugarte 12419* (US).



FIGURES 112–113. *Espeletia paltonioides* Standl. **112**. Páramo de Guaramacal, Trujillo, Venezuela (Photograph by S. Aubert). **113**. *Espeletia paltonioides*, Páramo de Cendé, Trujillo, Venezuela (Photograph by S. Aubert).

FIGURE 114. *Espeletia paltonioides* Standl. Páramo de Cendé, Trujillo, Venezuela (Photograph by S. Aubert).

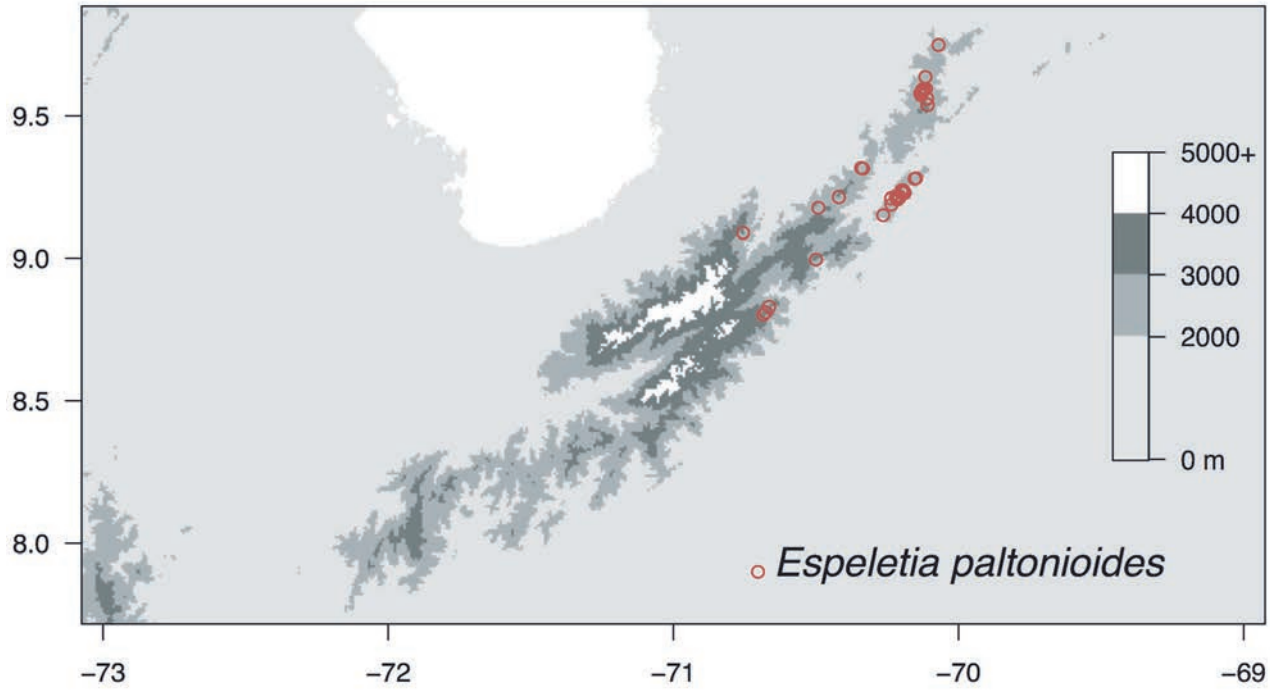


FIGURE 115. Distribution of *Espeletia paltonioides* Standl.

37. Espeletia palustris (Diazgr. & Morillo) Mavárez, *comb. nov*.

Basionym: *Coespeletia palustris* Diazgr. & Morillo, Phytokeys 28: 9. 2013. TYPE: VENEZUELA. Mérida: Páramo de Santo Domingo, alrededores de laguna de los Patos, en zona de turbera, 3729 m, 8.77522 N, -70.80349 E, 29 September 2011, *G. Morillo*, *M. Diazgranados*, *L. Gámez*, *S. Rodríguez & J. Parra 14155* (Holotype: MER; Isotype: VEN [not seen]). Fig. 116–118.

Rosette polycarpic, usually sessile, rarely with a short stem up to 0.2 m. *Leaf* open sheath, pseudopetiolate (length 2 cm), adaxially densely pubescent, lanuginose, whitish-grayish aspect, length 28–38 cm, width 0.7–1.3 cm, ratio 28–35:1, secondary nerves parallel, (2.0)2.5–4.0 mm apart. *Inflorescence* lateral, simple, monocephalous, axes 60–80 cm, aphyllous. *Capitulum* diam. 45–65 mm, ligular circle about the same size as the involucre, disc 22–24 mm, ligules bright yellow, becoming brownish/reddish toward the apex. *Espeletia palustris* can be easily recognized by its polycarpic rosette habit with long linear leaves and monocephalous inflorescences with large capitula. It resembles *E. moritziana*, from which it can be distinguished for its whitish indumentum (vs. yellowish–greenish), bigger sheaths (7.0–10.0 cm × 2.2–2.5 cm vs. 5.0–7.0 cm × 0.9–2.2 cm), aphyllous inflorescences (vs. bracteate), sterile phyllaries with dishevelled pubescence (vs. relatively ordered), and capitula with smaller number of both disc (215–280 vs. 600–860) and ray (95–200 vs. 400–740) flowers.

Distribution: VENEZUELA. Mérida: Páramo de Santo Domingo, de Los Granates, and de Gavidia in Sierra Nevada de Mérida, and Páramo El Banco in Sierra de la Culata. 3500–4000 m.a.s.l., in swampy and wet locations nearby marshes, lakes, and streams (Fig. 118).

Additional specimens examined (selection): *H. Barclay & P. Juajibioy 9741* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28055* (F, US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28057* (F, US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28584* (US), *L. Aristeguieta 2445* (US).

FIGURE 116. *Espeletia palustris* (Diazgr. & Morillo) Mavárez. Páramo el Banco, Mérida, Venezuela (Photograph by S. Aubert).

FIGURE 117. *Espeletia palustris* (Diazgr. & Morillo) Mavárez. Laguna de los Patos, Mérida, Venezuela (Photograph by L. Gámez).

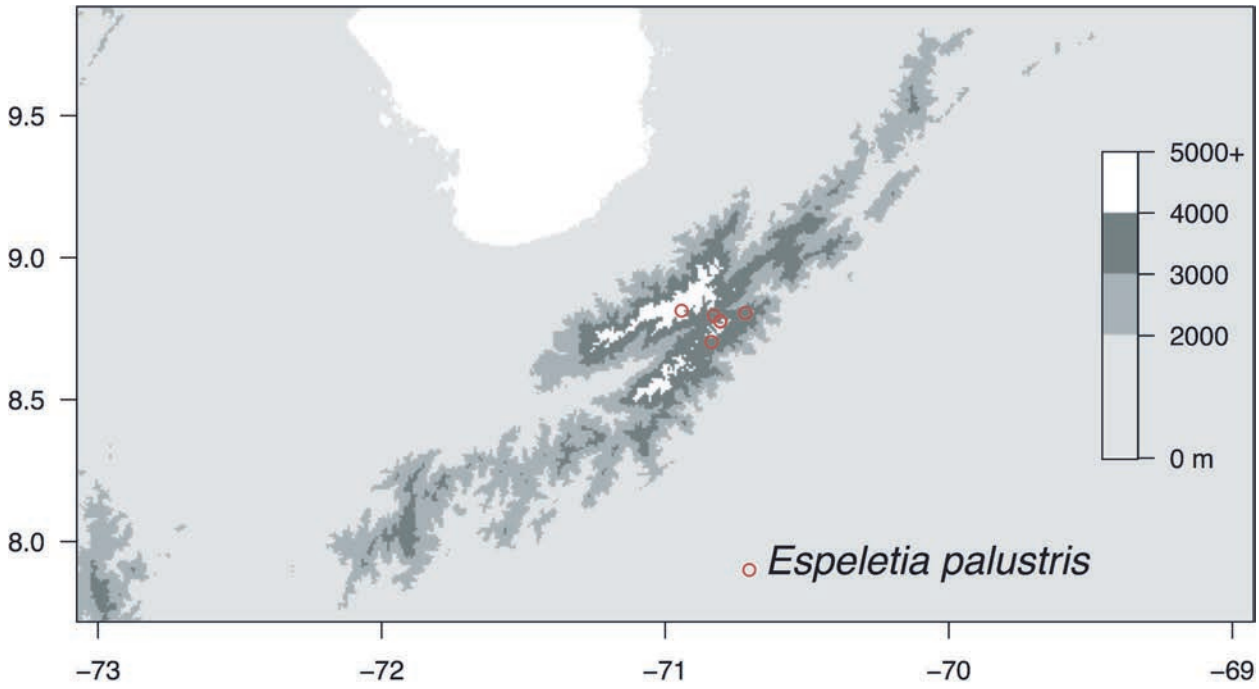


FIGURE 118. Distribution of *Espeletia palustris* (Diazgr. & Morillo) Mavárez.

38. ***Espeletia pannosa*** Standl., Amer. J. Bot. 2: 480. 1915. TYPE: VENEZUELA. Trujillo: Páramo del Jabón, 3000–3200 m.a.s.l., October 1910, *A. Jahn 165* (Lectotype: US, designated here). Fig. 119–121.

Homotypic synonym: *Espeletiopsis pannosa* (Standl.) Cuatrec., Phytologia 35: 56. 1976.

Heterotypic synonym: *Espeletia sericea* Cuatrec., Ciencia (México) 6: 263. 1945. TYPE: VENEZUELA. Mérida: Mucurubá, 3500–4000 m.a.s.l., 18 July 1930, *W. Gehriger 342* (Holotype: VEN [not seen]; Isotypes: F, G, MO, US).

Rosette polycarpic, sessile. *Leaf* open sheath, sessile, adaxially pubescent, appressed silvery-sericeous, length 25–45 cm, width 0.4–1.0 cm, ratio 30–40:1, secondary nerves obsolete or very thin, 1–3 mm apart when visible. *Inflorescence* lateral, compound, primary branching monochasial, corymboid, 45–60 cm, vegetative part about half the total length, with several alternate bracts. *Capitulum* diam. 15–20 mm, ligular circle 25–30 mm, disc 12–15 mm, ray ligules white. *Espeletia pannosa* can be distinguished from all other species for its polycarpic rosette habit, leaves adaxially covered with shiny silvery-sericeous indumentum and capitula with white ligules. It closely resembles *E. angustifolia*, from which it differs in its more slender leaves (ratio 30–40:1 vs. 20–25:1), adaxially covered with silvery/sericeous indumentum (*vs.* lanuginose).

Distribution: VENEZUELA. Mérida: widespread in páramos of Sierra de la Culata and Sierra Nevada de Mérida. 3100–4000 m.a.s.l., in open páramo meadows and well-drained slopes (Fig. 121).

Additional specimens examined (selection): *A. Jahn 165* (US), *C. Sobrevila*, *A. Weitzman & D. Solbrig 1551* (US), *M. López-Figueiras 23689* (US), *L. Ruiz-Terán 7914* (US), *L. Ruiz-Terán & M. López-Figueiras 1607* (US) .

The original type of *Espeletia pannosa* Standl. is *A. Jahn 165*, from Páramo del Jabón, 3000–3200 m.a.s.l., Trujillo, Venezuela, October 1910 (US). However, *A. Jahn 165* is a mixture of two taxa, *E. pannosa* Standl. and *E. floccosa* Standl. José Cuatrecasas noticed the mixing in *A. Jahn 165* and added a handwritten note to the specimen, designating part of it as the holotype of *Espeletiopsis pannosa* (Standl.) Cuatrec. According to Art. 9.14 of the ICN, when a type contains parts that belong to more than one taxon, a lectotype must be designated for the part that corresponds most with the original description or diagnosis.

39. Espeletia parvula (Cuatrec.) Mavárez, *comb. nov.*

Basionym: *Libanothamnus parvulus* Cuatrec., Phytologia 47: 3. 1980b. TYPE: VENEZUELA. Border Lara-Trujillo: Laja del Díctamo, un sector de la vertiente oriental del Páramo de Cendé, 2900 m.a.s.l., 10 June 1971, *L. Ruiz-Terán & M. López-Figueiras 2036* (Holotype: US; Isotype: MERF). Fig. 122–124.

Shrub or *small tree* profusely branched, height up to 1 m. *Leaf* tubular sheath, sessile or with short pseudopetiole (length < 0.1 cm), adaxially glabrous, green, length 6–10(15) cm, width 2.5–4.5 cm, ratio 2.2–4.0(4.5):1, margins entire, secondary nerves parallel, 1.0–1.5(2.0) mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, at the same level or slightly surpassing the surrounding leaves, length 5–10 cm, branched near base. *Capitulum* diam. 10–11(12) mm, ligular circle 15–21 mm, disc 9–10 mm, ray ligules white. *Espeletia parvula* can be distinguished from other species by its shrubby/tree habit with small size and its small sessile leaves (< 10(15) cm). It can look superficially similar to some small individuals of *E. neriifolia* var. *cristamontis*, but *E. parvula* has higher density of secondary nerves (1–2 mm vs. 2–4 mm apart), larger deviation angle (75–90° vs. 70–75°), and larger sterile phyllaries (4.5–5.5 mm × 4.0–5.5 mm vs. 3.5–4.0 mm × 2.3–2.8 mm).

Distribution: VENEZUELA. Border Lara-Trujillo. Páramo de las Rosas, del Jabón, and de Cendé. 2900–3400 m.a.s.l., above the timberline, in the subpáramo habitat located in the eastern slopes of hills and crests exposed to the strong winds that predominate in the region (Fig. 124).

Additional specimens examined (selection): *L. Ruiz-Terán & M. López-Figueiras 2036* (US), *L. Dorr*, *L. Barnett*, *R. Rivero & W. Díaz 5323* (US), *M. López-Figueiras 32306* (US, this sample has leaves with pseudopetioles).

40. ***Espeletia ruizii*** Cuatrec., Phytologia 23: 362. 1972. TYPE: VENEZUELA. Mérida: Loma de la Libertad, Páramo de las Coloradas, unos 500 m después del Portachuelo (el Ramal) entre las poblaciones de Santa Cruz de Mora and el Molino, 2750–2800 m.a.s.l., 16 January 1971, *L. Ruiz-Terán & M. López-Figueiras 1457* (Holotype: US; Isotypes: MERF, NY, US). Fig. 125–127.

Homotypic synonym: *Ruilopezia ruizii* (Cuatrec.) Cuatrec., Phytologia 35: 53. 1976.

Rosette monocarpic, caulescent, stem height up to 1.5 m, most individuals with the upper half of the stem covered by marcescent leaves, some entirely marcescent, a few entirely naked. *Leaf* open sheath, sessile, linear, adaxially glabrescent, glossy green aspect, length 15–40 cm, width 0.5–1.8 cm, ratio 20–45:1, secondary nerves parallel, 1.5–2.5 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, length 30–80 cm, branched from the base. *Capitulum* diam. 15–18 mm (densely cottony), ligular circle 16–22 mm, covered by the tips of the sterile phyllaries, disc 8–12 mm, young ray ligules white, turning pink or reddish when old. *Espeletia ruizii* can be distinguished from other species by its caulescent monocarpic rosette habit, its sessile, linear, glossy green leaves, and its capitulum with long cottony sterile phyllaries conspicuously surpassing the ligular circle and pinkish/reddish old ray ligules.

Distribution: VENEZUELA. Mérida: Páramo de las Coloradas, in the southern end of Sierra Nevada de Mérida. Between 2700–3100 m.a.s.l., in dry and exposed rocky slopes within subpáramo habitat (Fig. 127).

Additional specimens examined (selection): *L. Ruiz-Terán & M. López-Figueiras 1457* (NY, US), *P. Berry*, *R. Calvo & S. Beaujon 4374* (US), *M. López-Figueiras & H. Rodríguez 9045* (US), *L. Ruiz-Terán & S. López-Palacios 1869* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28510* (F, US).

FIGURES 119–120. *Espeletia pannosa* Standl. Estación la Aguada, Mérida, Venezuela (Photographs by S. Aubert).

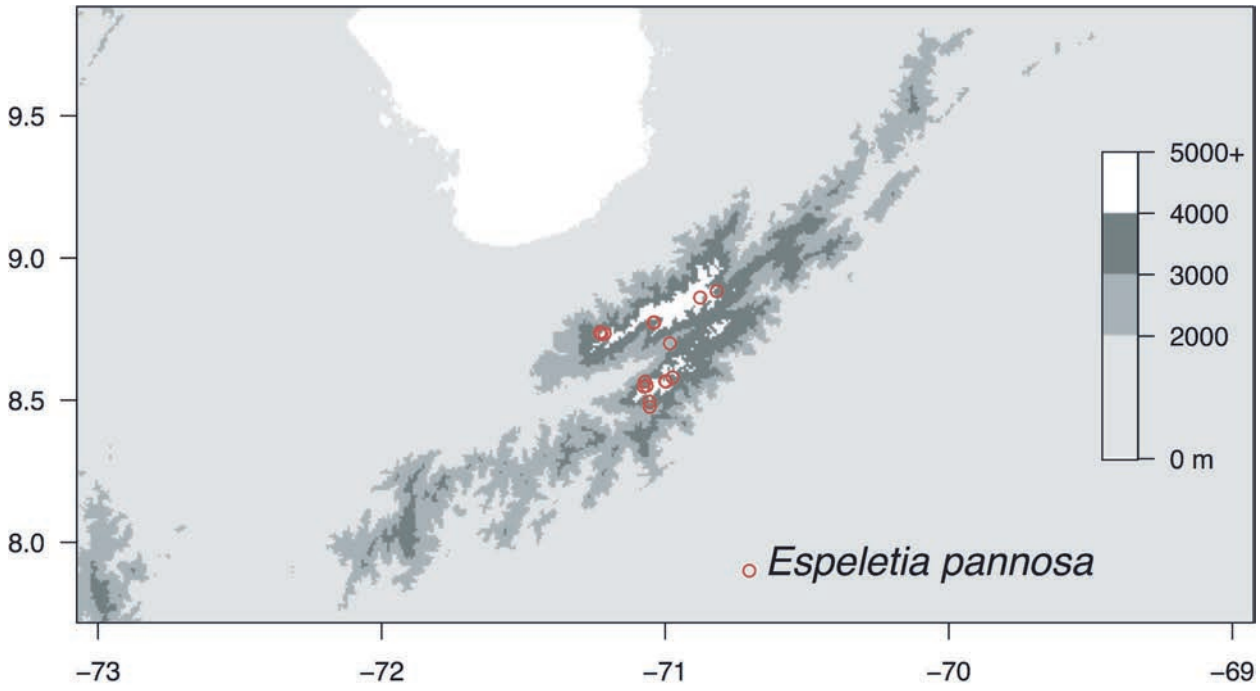


FIGURE 121. Distribution of *Espeletia pannosa* Standl.

FIGURE 122. *Espeletia parvula* (Cuatrec.) Mavárez. Páramo del Jabón, Lara-Trujillo, Venezuela (Photograph by S. Aubert).

FIGURE 123. *Espeletia parvula* (Cuatrec.) Mavárez. Páramo del Jabón, Lara-Trujillo, Venezuela (Photograph by S. Aubert).

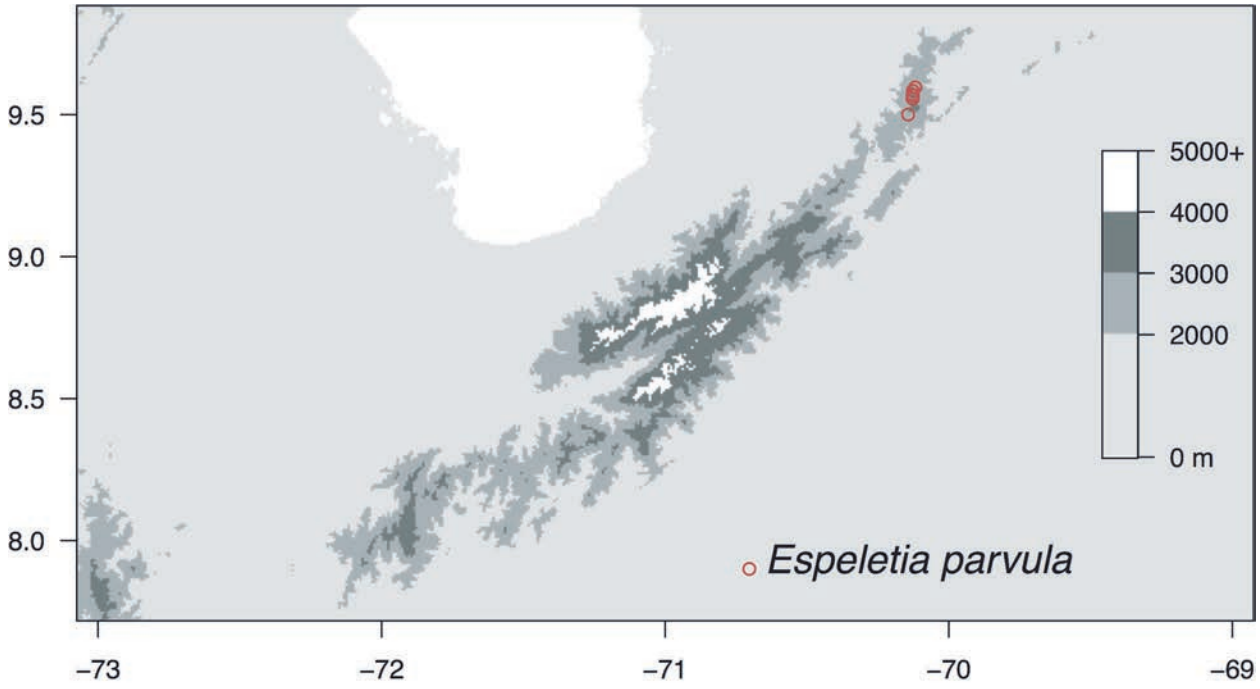
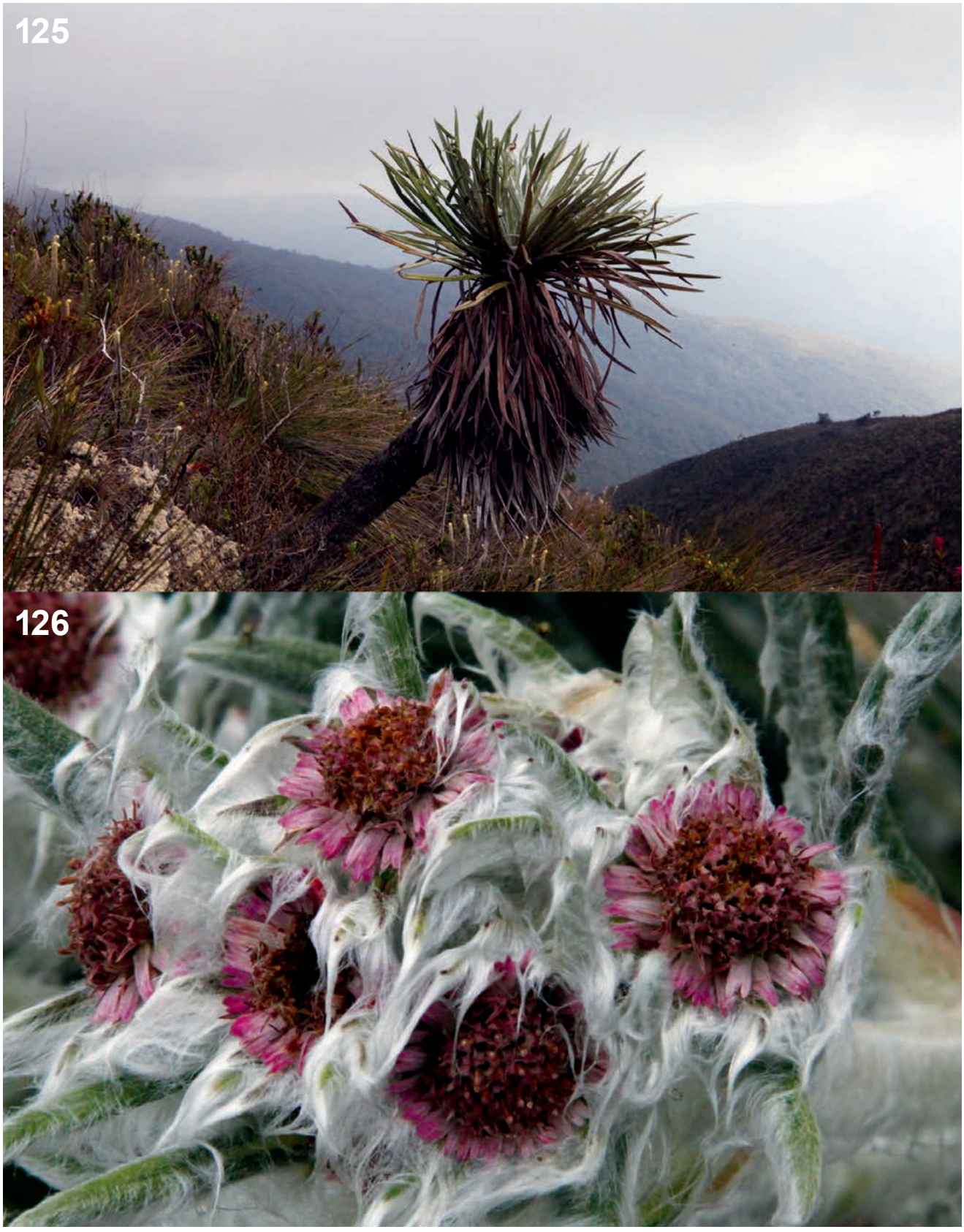


FIGURE 124. Distribution of *Espeletia parvula* (Cuatrec.) Mavárez.



FIGURES 125–126. *Espeletia ruizii* Cuatrec. Páramo las Coloradas, Mérida, Venezuela (Photographs by S. Aubert).

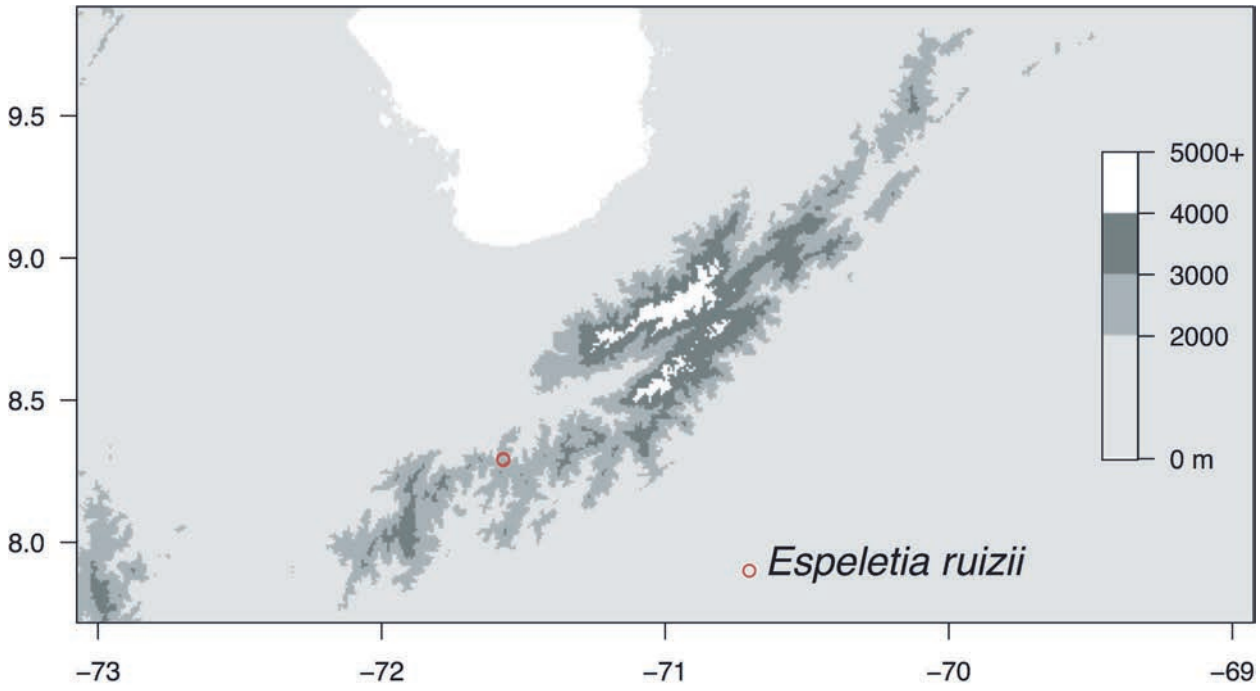


FIGURE 127. Distribution of *Espeletia ruizii* Cuatrec.

41. *Espeletia schultzii* Wedd., Chlor. Andina: 63. 1855. TYPE: VENEZUELA. Mérida: Páramos dans la province de Mérida, 10.000 à 11.000 pieds, Juin 1842(1843), *J. Linden 370* (Syntype: P; Isosyntypes: BR, F, FI [not seen], G, P, US, W), *Moritz 1419* (Syntype: P; Isosyntypes: BR, G, K, P, W). Fig. 128–130.

Rosette polycarpic, usually sessile, occasionally caulescent with a stem height up to 1.0 m, entirely covered by marcescent leafs. *Leaf* open sheath, sessile, adaxially densely pubescent, lanate-lanuginose, whitish-grayish aspect, length 25–50 cm, width 3.0–8.0 cm, ratio 4.7–12.0:1, bases of secondary nerves parallel, unevenly distributed, 4–12 mm apart. *Inflorescence* lateral, compound, primary branching dichasial, thyrsoid, length 70–180 cm, vegetative part usually with 2–3 pairs of opposite bracts. *Capitulum* diam. (12)20–30 mm, ligular circle (22)30–50 mm, disc (9)12–18 mm, ray ligules yellow. *Espeletia schultzii* is easily recognizable by its polycarpic rosette habit, sessile leaves and dichasial thyrsoid inflorescences. It superficially resembles *E. aristeguietana*, from which it can be distinguished by its larger capitulum and leaves with whitish/grayish lanuginose indumentum (vs. greenish tomentose-velvety).

Distribution: VENEZUELA. Mérida: widespread in Sierra Nevada de Mérida, Sierra de la Culata, Sierra de Santo Domingo, and southward to Páramo de San José and Páramo de Mijará. Trujillo: Páramo de Tuñame, de Teta de Niquitao, de Cabimbú, and de la Cristalina. Border Trujillo-Barinas: Páramo de Guirigay and de Ortiz. *Espeletia schultzii* has the broadest elevation span of any Espeletiinae, ca. 2400–4500 m.a.s.l. (Fig. 6), and the second largest geographic distribution among rosette plants (after Colombian *E. hartwegiana* Cuatrec.) The species is found near the upper limit of the Andean forest, in shrubby subpáramo, in proper páramo, and in protected spots in the superpáramo. It thrives particularly well in the undisturbed open páramos, but also in more disturbed locations such as recent forest clearings, road margins, and abandoned agricultural fields. In fact, *E. schultzii* is only absent from the extremely cold and dry superpáramo locations and the very humid areas around swamps, ponds, and streams (Fig. 130).

Additional specimens examined (selection): *J. Linden 370* (BR, F, G, P, US, W), *P. Berry 4621* (US), *P. Berry 4411* (US), *M. López-Figueiras 30155* (US), *L. Dorr*, *L. Barnett & B. Stergios 9283* (US).

Weddell (1855: 64) cited two specimens in the protologue of *E. schultzii*: *Linden 370* and *Moritz 1419*, without designation of either as the nomenclatural type. According to the ICN (Art. 9.5), these specimens must be considered as syntypes; however, most herbaria treat *Linden 370* as the holotype and *Moritz 1419* as a paratype. This should be corrected wherever necessary.

Espeletia schultzii has been found to hybridize with *E. angustifolia*, *E. banksiifolia*, *E. batata*, *E. floccosa*, *E. grisea*, *E. lindenii*, *E. margarita*, *E. moritziana*, *E. nana*, *E. neriifolia*, *E. occulta*, *E. pannosa*, *E. spectabilis*, *E. spicata*, *E. tenorae*, *E. timotensis*, and *E. weddellii*.

As do other Espeletiinae with broad distributions, *Espeletia schultzii* exhibits large morphological diversity, particularly with regard to leaf shape, inflorescence size and architecture, and capitulum size. Cuatrecasas (2013: 345–347) examined this variation and concluded that it is best described as representing four varieties within a single species: a widespread nominal variety (*E. schultzii* var. *schultzii*), plus three varieties with somehow restricted geographic distributions: *E. schultzii* var. *bractilobata*

FIGURES 128–129. *Espeletia schultzii* Wedd. Páramo de Piedras Blancas, Mérida, Venezuela (Photographs by S. Aubert).

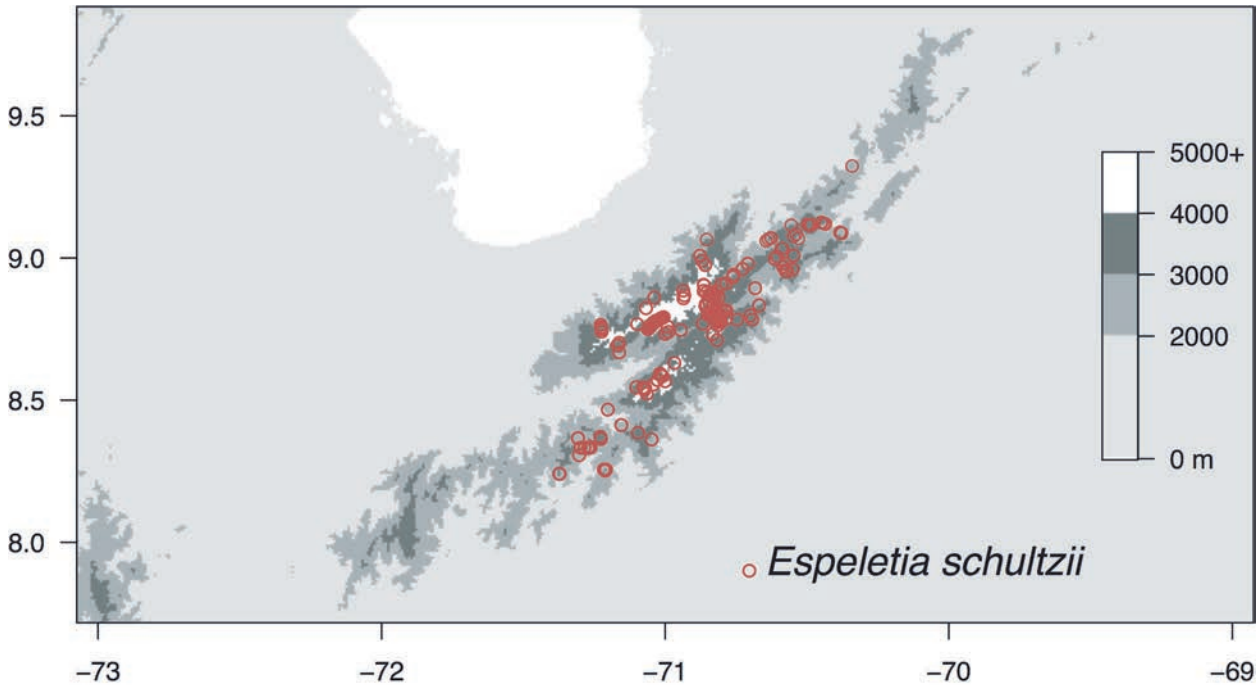


FIGURE 130. Distribution of *Espeletia schultzii* Wedd.

Cuatrec. (subpáramo between Jajó and Tuñame in Trujillo), *E. schultzii* var. *mucurubana* Cuatrec. (subpáramo above Mucurubá in Sierra de la Culata), and *E. schultzii* var. *subparamuna* Cuatrec. (subpáramos de la Cristalina in Trujillo and San José/la Veguilla in Mérida). I believe that some of the taxa represent in fact the extremes of morphological variation distributed continuously along elevational gradients. For instance, individuals from lower elevations frequently show the broader leaves, longer inflorescences, and larger capitula characteristic of *E. schultzii* var. *subparamuna*. On the other hand, over its broad distribution area, *E. schultzii* coexists in sympatry with more than 30 other *Espeletia*, hybridizing with at least 17 of them, which certainly contributes to the variation observed in this species (see note below). Thus, in places where hybridization is frequent between *E. schultzii* and other species with monochasial inflorescences and smaller capitula (e.g., *E. floccosa*), certain hybrids have the rosette appearance and leaf shapes of *E. schultzii* but exhibit inflorescence structures and capitulum sizes intermediate between the two parental species, looking very similar to *E. schultzii* var. *mucurubana*.

41.1 *Espeletia schultzii* Wedd. var. ***schultzii***.

41.2 *Espeletia schultzii* Wedd. var. ***bractilobata*** Cuatrec., Phytologia 45: 27. 1980a. TYPE: VENEZUELA. Trujillo: Paramillo above Jajó via Tuñame, 3100 m.a.s.l., 29 October 1969, *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28189* (Holotype: US; Isotypes: F, MERF, U).

Vegetative part of the inflorescence with some 2- or 3-lobed bracts.

Distribution: VENEZUELA. Trujillo: the type locality in the Morita-Paramito region between Jajó and Tuñame. Mérida: area between Los Frailes and Santo Domingo.

Additional specimens examined (selection): *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28189* (F, U, US), *C. Sobrevila 1513* (US), *L. Ruiz-Terán 2141* (US).

41.3 *Espeletia schultzii* Wedd. var. ***mucurubana*** Cuatrec., Phytologia 45: 28. 1980a. TYPE: VENEZUELA. Mérida: Páramo de Mucurubá, 3250 m.a.s.l., 20 October 1969, *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28148* (Holotype: US; Isotypes: F, MERF, U).

Inflorescences with predominant monochasial branching and smaller capitula (diam. 12–20 mm, ligular circle 22–28 mm, disc 9–13 mm).

Distribution: VENEZUELA. Widespread between 3000 and 3500 m.a.s.l., but relatively rare.

Additional specimens examined (selection): *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28148* (F, U, US), *M. López-Figueiras* 23696 (US), *C. Sobrevila*, *A. Weitzman & C. Estrada 1569* (US).

41.4 *Espeletia schultzii* Wedd. var. ***subparamuna*** Cuatrec., Phytologia 45: 29. 1980a. TYPE: VENEZUELA. Trujillo: Páramo de la Cristalina, 2500–2600 m.a.s.l., 17 February 1973, *J. Cuatrecasas*, *L. Ruiz-Terán*, *M. López-Figueiras 28557* (Holotype: US; Isotypes: BC, F, G, NY, MERF, US).

With broad leaves (ratio 4.7–6.5:1), a large number of flowers (ray: 100–170, disc: 150–340), and outer phyllaries abruptly acuminate.

Distribution: VENEZUELA. Widespread at the lower elevation ranges of the species, 2400–3200 m.a.s.l.

Additional specimens examined (selection): *J. Cuatrecasas*, *L. Ruiz-Terán*, *M. López-Figueiras 28557* (F, G, NY, US), *L. Ruiz-Terán & J. Dugarte 12248* (US), *L. Ruiz-Terán 9141* (US).

42. *Espeletia semiglobulata* Cuatrec., Ciencia (México) 6: 264. 1945. TYPE: VENEZUELA. Mérida: Páramo de Piedras Blancas, 3800 m.a.s.l., 17 May 1944, *V. M. Badillo 821* (Holotype: VEN [not seen]; Isotype: VEN [not seen]). Fig. 131–132.

Heterotypic synonym: *Espeletia rufescens* Cuatrec., Bol. Soc. Ven. Ci. Nat. 17: 88. 1956a. TYPE: VENEZUELA. Mérida: Sierra Nevada de Mérida, 12,000 pieds, August 1842, *J. J. Linden 398* (Holotype: P [inflorescences in MNHN-P-P04086312]; Isotype: NY [inflorescences in barcode number 579543]).

Rosette polycarpic, usually sessile, sometimes caulescent, stem height up to 0.5 m, entirely covered by marcescent leaves. *Leaf* open sheath, pseudopetiolate (length 15–25 cm), adaxially densely pubescent, appressed lanate, whitish-cinereous, length 35–50 cm, width 2.0–4.5 cm, ratio 10–20:1, secondary nerves parallel, 2–4 mm apart. *Inflorescence* lateral, compound, primary branching dichasial, thyrsoid, length 1.5–2.0 m, vegetative part with 4–5 pairs of opposite bracts. *Capitulum* diam. 15–20 mm, ligular circle not exceeding the involucre (14–18 mm), disc 10–14 mm, ray ligules yellow. *Espeletia semiglobulata* can easily be distinguished from the other Venezuelan species with dichasial thyrsoid inflorescences by its long and thin pseudopetiolate leaves and its short-radiate capitula.

Distribution: VENEZUELA. Mérida: Sierra Nevada de Mérida, Sierra de Santo Domingo and Sierra de la Culata. 3800–4300 m.a.s.l., in very humid locations such as wet depressions and along the margins of streams, ponds, and small lakes (Fig. 132).

Additional specimens examined (selection): *L. Ruiz-Terán & M. López-Figueiras 272* (US), *L. Ruiz-Terán & M. López-Figueiras 351* (US); *id. 370* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28583* (F, U, US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28598* (F, U, US).

Other samples of *Linden 398* (MNHN-P-P02441483 in P, catalog number 1473203 in US) contain only material belonging to *E. moritziana* and should be considered as isosyntypes of that species (see notes on *E. moritziana*).

43. *Espeletia spectabilis* Cuatrec., Phytologia 27: 46. 1973a. TYPE: VENEZUELA. Mérida: Páramo de San José, Zanjón del Cupís, orillas de la carretera San José-Mucutuy, a 7 km de San José, 3100 m.a.s.l., 18–21 November 1972,

FIGURE 131. *Espeletia semiglobulata* Cuatrec. Páramo de Piedras Blancas, Mérida, Venezuela (Photograph by S. Aubert).

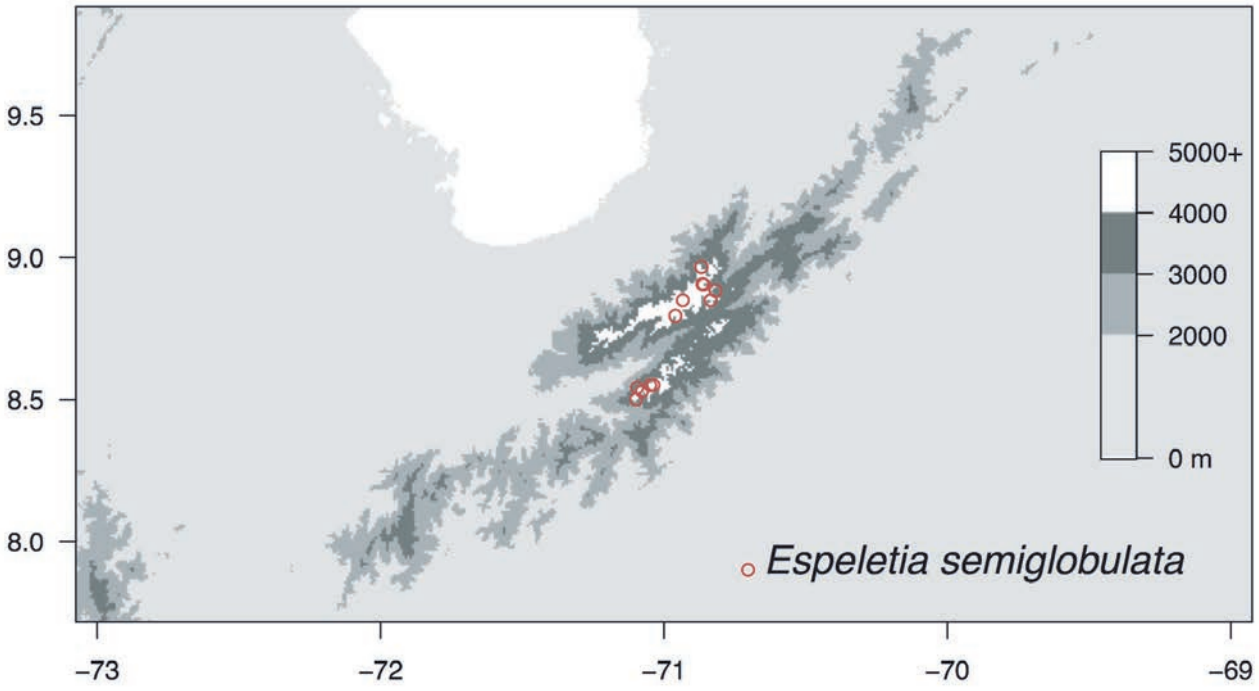


FIGURE 132. Distribution of *Espeletia semiglobulata* Cuatrec.

M. López-Figueiras, H. A. Rodríguez, J. Wurdack & M. Wurdack 8912 (Holotype: US; Isotypes: BC, F, G, K, MERF, MO, NY, US). Fig. 133–136.

Homotypic synonym: *Libanothamnus spectabilis* (Cuatrec.) Cuatrec., Phytologia 35: 51. 1976.

Tree monocarpic, unbranched stem, stem height up to 10 m, mostly leafless, marcescent leaves only below the apical rosette of green leaves. *Leaf* tubular sheath, sessile, adaxially glabrous, green, length (25)40–65 cm, width 7.5–15.0 cm, ratio (3.5)4.0–5.0(6.5):1, margins frequently entire, sometimes with small teeth up to 1.0 mm long, secondary nerves parallel, 1.5–3.0(4.0) mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, largely surpassing the surrounding leaves, length 40–60 cm, branched near the base. *Capitulum* diam. 15–20 mm, ligular circle (25)30–35 mm, disc (12)14–18 mm, ray ligules cream or yellowish. *Espeletia spectabilis* is a truly exceptional species that can be easily distinguished from any other by its unique combination of tall monocarpic caulescent rosette habit and leaves with tubular sheaths. More generally, *E. spectabilis* exhibits a mixture of several ecological and morphological features characteristic of both trees and rosette plants, which suggests that this taxon could be the result of a hybrid speciation event involving branched and unbranched parental species (Pouchon et al. 2018).

Distribution: VENEZUELA. Mérida: Apparently restricted to the Páramo de San Jose and some nearby areas in the south of Sierra Nevada de Mérida. 3000–3200 m.a.s.l., limited to the belt within the uppermost level of the Andean forest and the subpáramo habitat (Fig. 136).

Additional specimens examined (selection): *M. López-Figueiras, H. Rodríguez & J. Wurdack & M. Wurdack 8912* (F, G, K, MO, NY, US), *J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28457* (US), *J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28458* (F, U, US), *J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28458A* (U, US), *L. Ruiz-Terán & S. López-Palacios 6651* (US).

44. *Espeletia spicata* Sch. Bip. ex Wedd., Chlor. Andina: 65. 1855. TYPE: VENEZUELA. Mérida: Sierra Nevada de Mérida, 14,000 pieds, August 1842, *J. Linden 400* (Holotype: P; Isotypes: F, FI [not seen], K, P). Fig. 137–139.

Homotypic synonym: *Coespeletia spicata* (Sch. Bip. ex Wedd.) Cuatrec., Phytologia 35: 57. 1976.

Heterotypic synonyms: *Espeletia alba* A.C. Sm., Brittonia 1: 512, 1935. TYPE: VENEZUELA. Mérida: Páramo de Mucurubá, cabeceras de la quebrada del pueblo (El Rincón, El Colorado, Fila de Estití), Sierra Nevada de Mérida, 3900 m.a.s.l., April 1930, *W. Gehriger 125* (Holotype: G; Isotypes: F, MO, PH [not seen], NY, VEN [not seen]).

Coespeletia alba (A.C. Sm.) Cuatrec., Phytologia 35: 57. 1976.

Rosette polycarpic, caulescent, stem height up to 2.5 m, entirely covered by marcescent leaves. *Leaf* open sheath, sessile, adaxially densely pubescent, lanate, whitish-cinereous, length 35–50 cm, width 1.2–2.0 cm, ratio 20–35:1, secondary nerves parallel, 4–6 mm apart. *Inflorescence* lateral, simple, monochasial, botryoid, axes 75–130 cm, (14)20–38 monocephalous peduncles, vegetative part with several alternate bracts. *Capitulum* diam. 15–25 mm, ligular circle shorter than the involucre, ray ligules yellow. *Espeletia spicata* can be easily distinguished from other species with strictly botryoid inflorescences by its leaves

FIGURES 133–135. *Espeletia spectabilis* Cuatrec. Páramo de San José, Mérida, Venezuela (Photographs by S. Aubert).

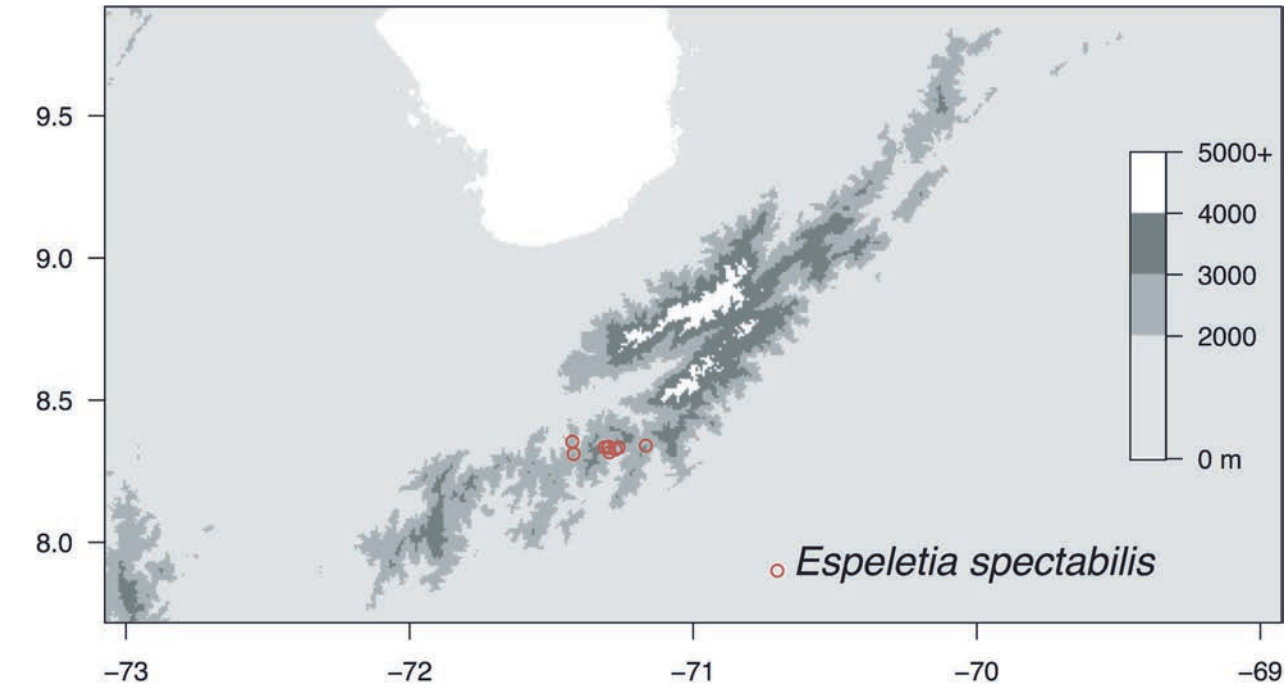


FIGURE 136. Distribution of *Espeletia spectabilis* Cuatrec.

FIGURE 137. *Espeletia spicata* Sch. Bip. ex Wedd. Páramo de Piedras Blancas, Mérida, Venezuela (Photograph by S. Aubert).

FIGURE 138. *Espeletia spicata* Sch. Bip. ex Wedd. Páramo de Piedras Blancas, Mérida, Venezuela (Photograph by S. Aubert).

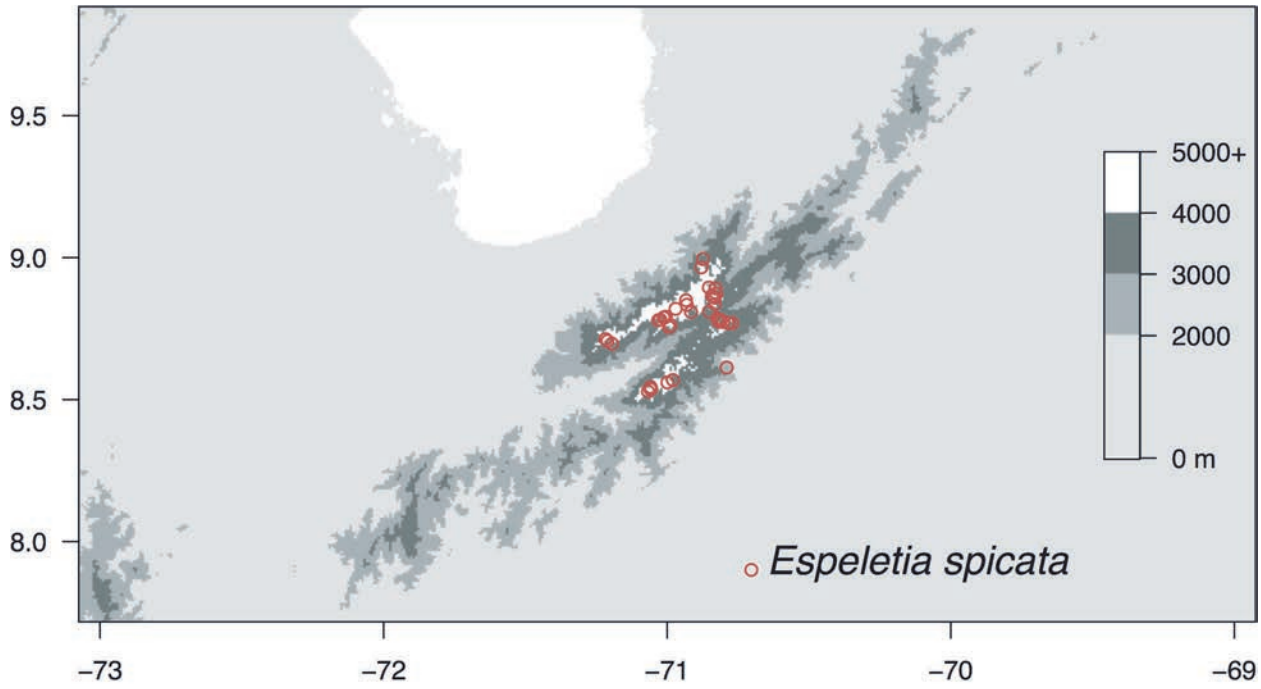


FIGURE 139. Distribution of *Espeletia spicata* Sch. Bip. ex Wedd.

with large length-to-width ratios (> 20:1), large number of peduncles (>[14]20), and small capitulum diam. (< 25 mm).

Distribution: VENEZUELA. Mérida: Sierra de la Culata and Sierra Nevada de Mérida. Superpáramos 3800–4300 m.a.s.l., locally reaching 4500 m.a.s.l. Frequently associated with *E. timotensis*, with *E. spicata* usually occupying the lower and more humid sections of the slopes (Fig. 139).

Additional specimens examined (selection): *J. Linden 400* (F, K, P), *L. Ruiz-Terán & M. López-Figueiras 203* (U, US), *L. Ruiz-Terán 6976* (US), *L. Ruiz-Terán 7770* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28117* (F, U, US).

Linden 400 in F labelled as from "Colombia."

45. *Espeletia tamana* Cuatrec., Phytologia 27: 171. 1973b. TYPE: VENEZUELA. Táchira: Cabeceras semiboscosas de la Quebrada El Reposo, 6–7 km N de Villa Páez, en el Páramo de Tamá, 2800 m.a.s.l., 28 June 1973, *L. Ruiz-Terán & M. López-Figueiras 8915* (Holotype: US; Isotype: MERF). Fig. 140–142.

Homotypic synonyms: *Libanothamnus tamanus* (Cuatrec.) Cuatrec., Phytologia 35: 51. 1976.

Tree moderately branched, height up to 5 m. *Leaf* tubular sheath, sessile or with short pseudopetiole (length 2.0–4.0 cm), adaxially glabrous, green, length 25–50 cm, width 3.0–6.5 cm, ratio 6–9:1, margins entire or with small teeth concealed under the indumentum, secondary nerves parallel, 1–2 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, surpassing the surrounding leaves, length 40–80 cm, vegetative part profusely bracteate, about a quarter of the total length. *Capitulum* diam. 10–12 mm, ligular circle 20–25 mm, disc 8–10 mm, ray ligules white. *Espeletia tamana* can be distinguished from other tree species for its pseudopetiolate leaves with lanceolate outline and sheaths barbate adaxially. *Espeletia tamana* can look similar to *E. banksiifolia*, but it has slender leaves (ratio > 6:1 vs. < 5:1) and shorter disc corollas (< 4 mm vs. > 4 mm).

Distribution: VENEZUELA. Táchira: Páramo de Tamá (extending towards Norte de Santander, Colombia). COLOMBIA. Arauca: headwaters of Río Casanare, on the eastern slopes of Sierra Nevada del Cocuy. 2700–3100 m.a.s.l., in the upper level of the Andean forest, below the timberline (Fig. 142).

Additional specimens examined (selection): *L. Ruiz-Terán & M. López-Figueiras 8915* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28322* (U, US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28353* (F, U, US), *M. López-Figueiras & M. E. Hale 9255* (US), *L. Ruiz-Terán, M. López-Figueiras & D. Griffin 12571* (US).

Collection date given as "2 June 1973" in Diazgranados (2012: 37) and Cuatrecasas (2013: 444).

FIGURE 140. *Espeletia tamana* Cuatrec. Páramo de Tamá, Táchira, Venezuela (Photograph by S. Aubert).

FIGURE 141. *Espeletia tamana* Cuatrec. Páramo de Tamá, Táchira, Venezuela (Photograph by S. Aubert).

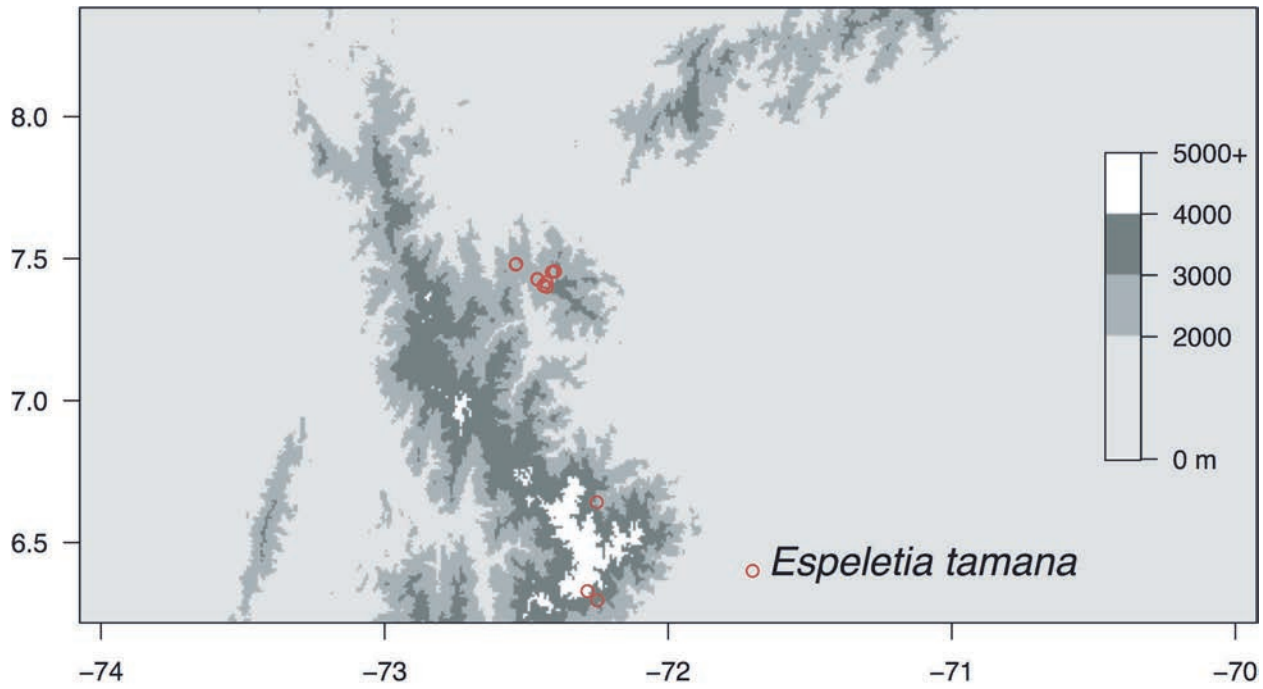


FIGURE 142. Distribution of *Espeletia tamana* Cuatrec.

46. ***Espeletia tenorae*** Aristeg., Bol. Soc. Ven. Ci. Nat. 20: 275. 1959. TYPE: VENEZUELA. Trujillo: Páramo del Guirigay, hacia Laguna la Parida, 3500 m.a.s.l., August 1958, *L. Aristeguieta & E. Medina 3572* (Holotype: VEN [not seen]; Isotypes: NY, US). Fig. 143–145.

Rosette polycarpic, sessile, dwarf. *Leaf* open sheath, sessile, adaxially densely pubescent, lanate, whitish-cinereous, length 4–7 cm, width 0.4–0.7 cm, ratio 10–14:1, secondary nerves reticulate. *Inflorescence* lateral, simple, monocephalous, length 25–50 cm, usually without bracts, sometimes with 1–2 opposite or alternate bracts near the distal part. *Capitulum* diam. 40–50 mm (densely cottony), ligular circle shorter than the floccose involucre (20–30 mm), disc 16–18 mm, ray ligules yellow. *Espeletia tenorae* can be distinguished from all other Venezuelan dwarf rosette plants with monocephalous inflorescences by its leaf sheaths glabrous on both sides and its inflorescences usually aphyllous or with 1–2 distal bracts. *Espeletia tenorae* is also the Venezuelan dwarf rosette with the largest proportion of ray flowers (53%–57%).

Distribution: VENEZUELA. Border Mérida and Trujillo: known only from the type locality and nearby areas in Páramo de Guirigay. 3300–3500 m.a.s.l., in swampy areas, humid depressions, and ponds (Fig. 145).

Additional specimens examined (selection): *L. Aristeguieta & E. Medina 3572* (NY, US), *B. Stergios, L. Dorr & K. Wurdack 20327* (US), *L. Ruiz-Terán & M. López-Figueiras 13127* (US), *L. Ruiz-Terán & M. López-Figueiras 13128* (US), *J. Cuatrecasas, M. López-Figueiras & L. Marcano-Berti 28167* (F, U, US).

47. ***Espeletia thyrsiformis*** A.C. Sm., Brittonia 1: 513. 1935. TYPE: VENEZUELA. Mérida: Páramo de Mucuchíes, December 1927, *R. Gutzwiller 36* (Holotype: US; Isotypes: G, NY). Fig. 146–148.

Homotypic synonym: *Coespeletia thyrsiformis* (A.C. Sm.) Cuatrec., Phytologia 35: 57. 1976.

Rosette polycarpic, usually sessile, sometimes caulescent, stem height up to 0.5 m, entirely covered by marcescent leaves. *Leaf* open sheath, sessile, adaxially densely pubescent, lanate, whitish-cinereous, length 25–50 cm, width 4.5–8.0 cm, ratio 4–10:1, bases of secondary nerves parallel, 5–10 mm apart. *Inflorescence* lateral, compound, monochasial, botryoid-paniculate, axes 70–130 cm, 17–35 peduncles, proximal polycephalous (3–7 capitula), proximal part with several alternate bracts. *Capitulum* diam. 15–20 mm, ligular circle about the same size or slightly shorter than the involucre, disc 10–12 mm, ray ligules yellow. *Espeletia thyrsiformis* can be distinguished from all other Venezuelan species for its sessile or subsessile leaves with low length/width ratio (4–10:1) and botryoid-paniculate inflorescences with a moderate number of peduncles (17–33).

Distribution: VENEZUELA. Northern Táchira and nearby Mérida: south-western end of the Cordillera de Mérida in Páramo del Batallón, de la Negra, del Rosal and del Zumbador. Between 2800–3600 m.a.s.l., in grassy and dry páramos with rocky soils, but also in some humid depressions (Fig. 148).

Additional specimens examined (selection): *R. Gutzwiller 36* (G, NY, US), *J. Cuatrecasas, M. López-Figueiras & L. Marcano-Berti 28002* (F, U, US), *J. Cuatrecasas, M. López-Figueiras & L. Marcano-Berti 28017* (F, US), *J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28430* (F, U, US), *M. López-Figueiras 13993* (US).

The type locality "Páramo de Mucuchíes" in *Gutzwiller 36* is certainly a mistake. The species is endemic to the region around Páramo del Batallón, de la Negra, and del Zumbador, more than 70 km to the south of Páramo de Mucuchíes. Other numbers in R. Gutzwiller collections suggest that the correct type locality for the type of *E. thyrsiformis* should be "Páramo de la Negra, Mérida, Venezuela" (e.g., *R. Gutzwiller 34*). Also, Gutzwiller spelled "Gutzviller" in Diazgranados (2012: 8) and Cuatrecasas (2013: 597).

47.1. ***Espeletia thyrsiformis*** A.C. Sm. f. ***thyrsiformis***

47.2. Espeletia thyrsiformis A.C. Sm. f. ***marcanoana*** (Cuatrec.) Mavárez, *comb. nov.*

Basionym: *Coespeletia thyrsiformis* (A.C. Sm.) Cuatrec. f. *marcanoana* Cuatrec., Mem. New York Bot. Gard. 107: 603. 2013. TYPE: VENEZUELA. Táchira: Páramo del Colorado, continuación del Páramo del Zumbador, 3100–3200 m.a.s.l., 1 October 1969, *J. Cuatrecasas, M. López-Figueiras & L. Marcano-Berti 27993* (Holotype: US; Isotypes: F, MERF, U, US).

Homotypic synonyms: *Espeletia marcanoana* Cuatrec., Phytologia 20: 476. 1971.

Coespeletia marcanoana (Cuatrec.) Cuatrec., Phytologia 35: 57. 1976.

Heterotypic synonyms: *Espeletia racemosa* Cuatrec., Ciencia (México) 6: 266. 1945. TYPE: VENEZUELA. Mérida: Páramos de Apartaderos, *Fortanier s.n.* (Holotype: VEN [not seen]).

Espeletia thyrsiformis f. *marcanoana* resembles the nominal form but shows no polycephalous peduncles, or only a few restricted to the most basal section of the inflorescence.

Distribution: VENEZUELA. Northern Táchira and nearby Mérida: Páramo del Zumbador and del Batallón.

Additional specimens examined (selection): *J. Cuatrecasas, M. López-Figueiras & L. Marcano-Berti 27993* (F, U, US), *J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28376* (US), *L. Ruiz-Terán & M. López-Figueiras 8297* (US).

This taxon was dedicated to Luis Marcano (Cuatrecasas, 2013: 603). According to ICN Art. 60.8, the correct spelling for the derived adjectival epithet is "*marcanoana*" (not "*marcana*").

48. ***Espeletia timotensis*** Cuatrec., Bol. Soc. Ven. Ci. Nat. 17: 84. 1956a. TYPE: VENEZUELA. Mérida: Páramo de Piñango-Timotes, Sierra Nevada de Mérida, 4000 m.a.s.l., 9 December 1938, *J. Hanbury-Tracy 193* (Holotype: K; Isotypes: K, NY). Fig. 149–151.

Homotypic synonym: *Coespeletia timotensis* (Cuatrec.) Cuatrec., Phytologia 35: 57. 1976.

FIGURES 143–144. *Espeletia tenorae* Aristeg. Páramo de Guirigay, Trujillo, Venezuela (Photographs by S. Aubert).

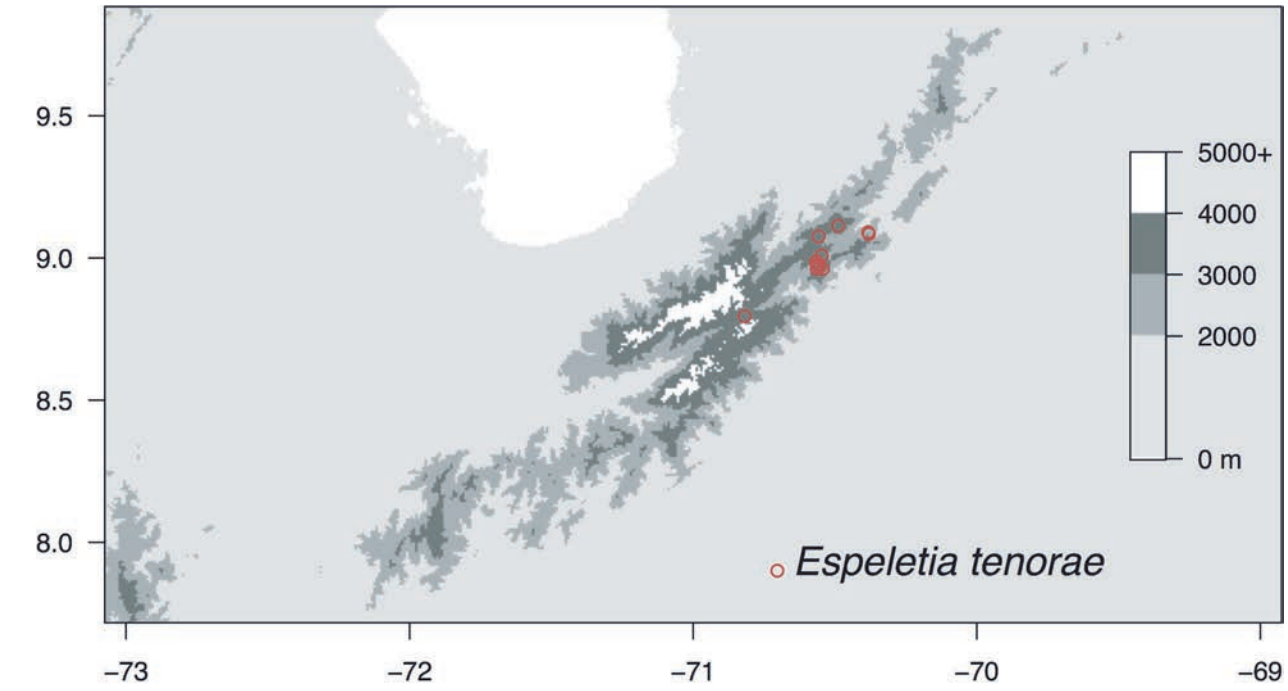


FIGURE 145. Distribution of *Espeletia tenorae* Aristeg.

FIGURE 146. *Espeletia thyrsiformis* A.C. Sm. Páramo del Batallón, Táchira, Venezuela (Photograph by S. Aubert).

FIGURE 147. *Espeletia thyrsiformis* A.C. Sm. Páramo del Batallón, Táchira, Venezuela (Photograph by S. Aubert).

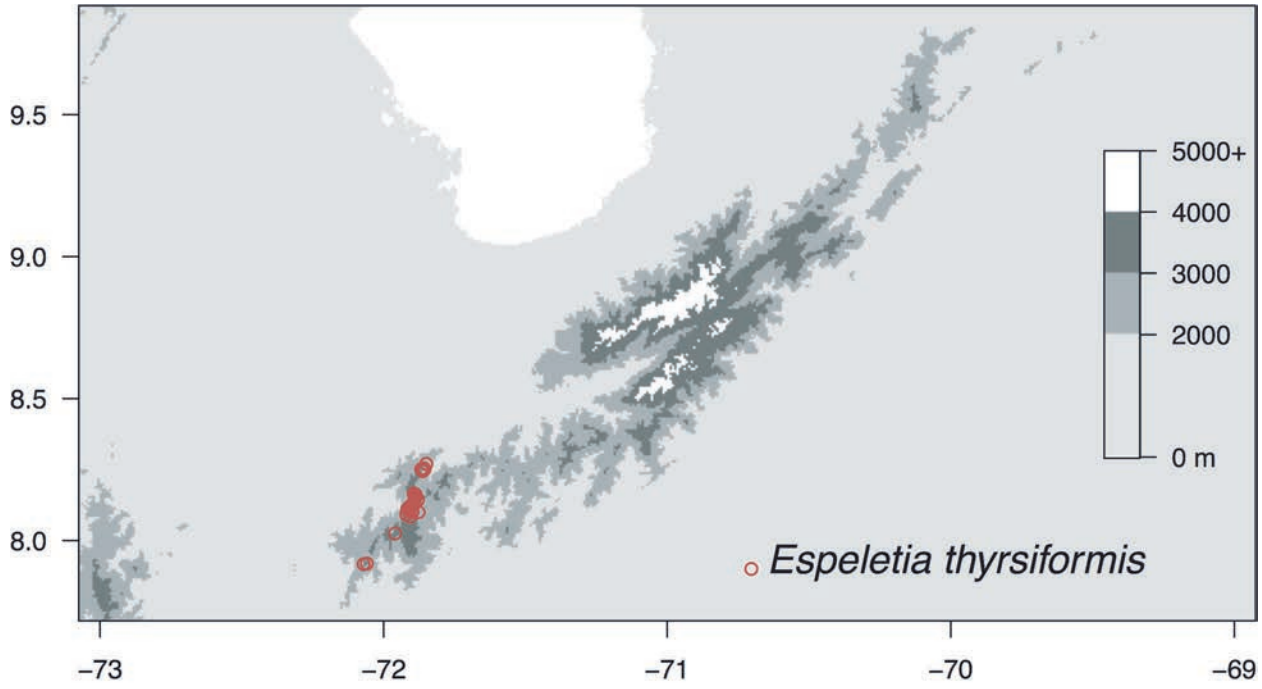


FIGURE 148. Distribution of *Espeletia thyrsiformis* A.C. Sm.

FIGURES 149–150. *Espeletia timotensis* Cuatrec. Páramo el Banco, Mérida, Venezuela (Photographs by S. Aubert).

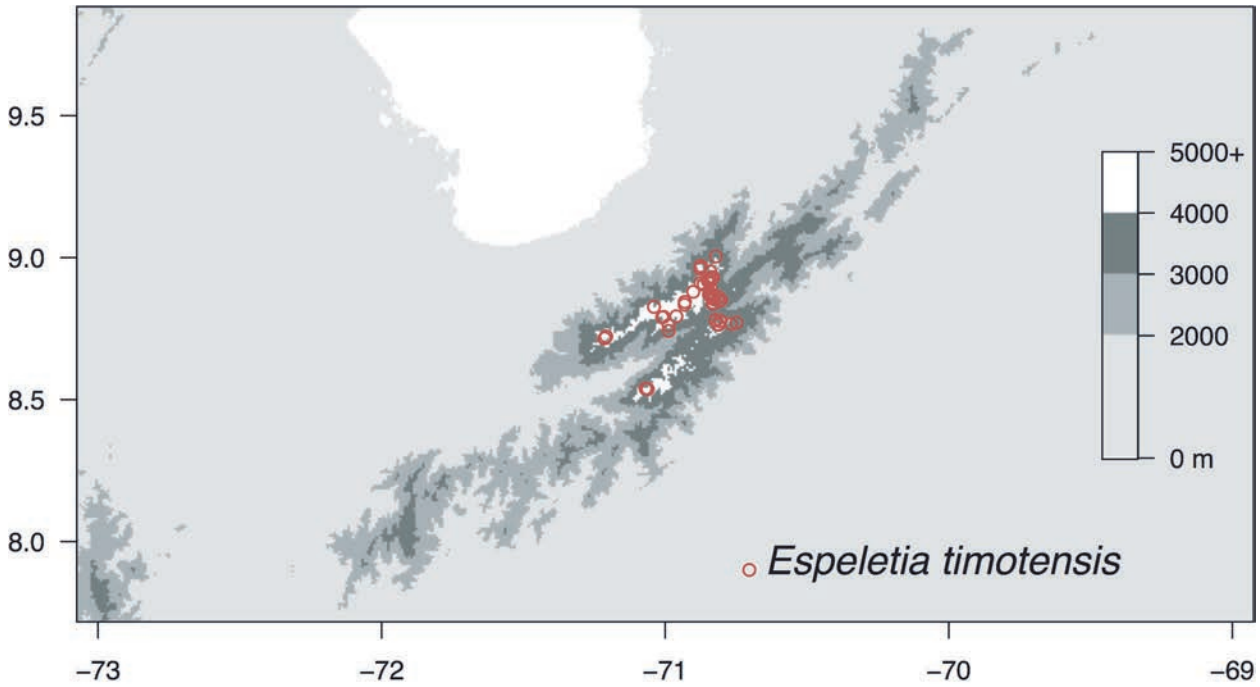


FIGURE 151. Distribution of *Espeletia timotensis* Cuatrec.

Heterotypic synonym: *Espeletia lutescens* Cuatrec. & Aristeg., Fl. Venez. 10(1): 443. 1964. TYPE: VENEZUELA. Mérida: Páramo de Timotes, 3000–3500 m.a.s.l. [4000 m on added tag], December 1910, *A. Jahn 149* (Holotype: US; Isotypes: G, VEN [not seen]).

Coespeletia lutescens (Cuatrec. & Aristeg.) Cuatrec., Phytologia 35: 57. 1976.

Rosette polycarpic, caulescent, stem height up to 3.5 m, entirely covered by marcescent leaves. *Leaf* open sheath, sessile or with short pseudopetiole (length 2–6 cm), adaxially densely pubescent, lanate, white-cinereous, length 40–55 cm, width 2.5–4.0 cm, ratio 10–18:1, bases of secondary nerves parallel, 4–6 mm apart. *Inflorescence* lateral, simple, monochasial, botryoid, axes 85–150 cm, 8–15 monocephalous peduncles, vegetative part with several alternate bracts. *Capitulum* diam. 35–55 mm, ligular circle shorter than the involucre (30–38 mm), disc 23–30 mm, ray ligules bright yellow or orange, turning brownish with age. *Espeletia timotensis* can be distinguished from other Venezuelan rosette plants by its botryoid inflorescences with large capitula (diam. > 35 mm). It closely resembles *E. albarregensis*, but *E. timotensis* has taller stems (1.0–3.5 m vs. 0.5–1.0 m), longer inflorescences (85–150 cm vs. 60–80 cm), and larger number of capitula (8–15 vs. 9–11).

Distribution: VENEZUELA. Mérida: Sierra de la Culata and Sierra Nevada de Mérida. 4000–4500 m.a.s.l., locally down to 3650 m.a.s.l., in dry superpáramos (Fig. 151).

Additional specimens examined (selection): *J. Hanbury-Tracy 193* (K, NY), *A. Jahn 149* (G, US), *L. Ruiz-Terán 227* (US), *P. Berry 4213* (US), *M. López-Figueiras & A. Usubillaga 14022* (US), *L. Ruiz-Terán & M. López-Figueiras 1128* (US).

49. *Espeletia trujillensis* Cuatrec., Mutisia 16: 5. 1953. TYPE: VENEZUELA. Trujillo: Quebrada del Cortijo, above Humocaro Bajo, 2600–2800 m.a.s.l., 6 February 1944, *J. Steyermark 55341* (Holotype: F; Isotype: F). Fig. 152–154.

Homotypic synonym: *Carramboa trujillensis* (Cuatrec.) Cuatrec., Phytologia 35: 54. 1976.

Tree profusely ramified, up to 20 m. *Leaf* tubular sheath, sessile, adaxially glabrous, green, length 30–60 cm, width 12–25 cm, ratio 2.3–3.5:1, bases of secondary nerves parallel, unevenly distributed, 10–30 mm apart. *Inflorescence* lateral, compound, primary branching dichasial, corymboid, length 35–60 cm, vegetative part about half of total length, with 1–2 pairs of opposite bracts. *Capitulum* diam. 6–9 mm, ligular circle 16–21 mm, disc 6–9 mm, ray ligules yellow. *Espeletia trujillensis* can be distinguished from all other species by its profusely ramified tree habit, sessile leaves with low length-to-width ratio (2.3–3.5:1), and primarily dichasial corymboid inflorescences with proximal part bracteate.

Distribution: VENEZUELA. Trujillo: forested hills in Páramo de la Cristalina and Guaramacal. Lara: forested hills around Humocaro Bajo. 2400–2800 m.a.s.l., found in rather humid locations and along forest streams (Fig. 154).

Additional specimens examined (selection): *J. Steyermark 55341* (F), *L. Ruiz-Terán 9214* (US), *L. Ruiz-Terán 9215* (US), *M. López-Figueiras 12956* (US), *J. Cuatrecasas*, *M. López-Figueiras & H. Rodríguez 28979* (US).

FIGURES 152–153. *Espeletia trujillensis* Cuatrec. Páramo de Guaramacal, Trujillo, Venezuela (Photographs by S. Aubert).

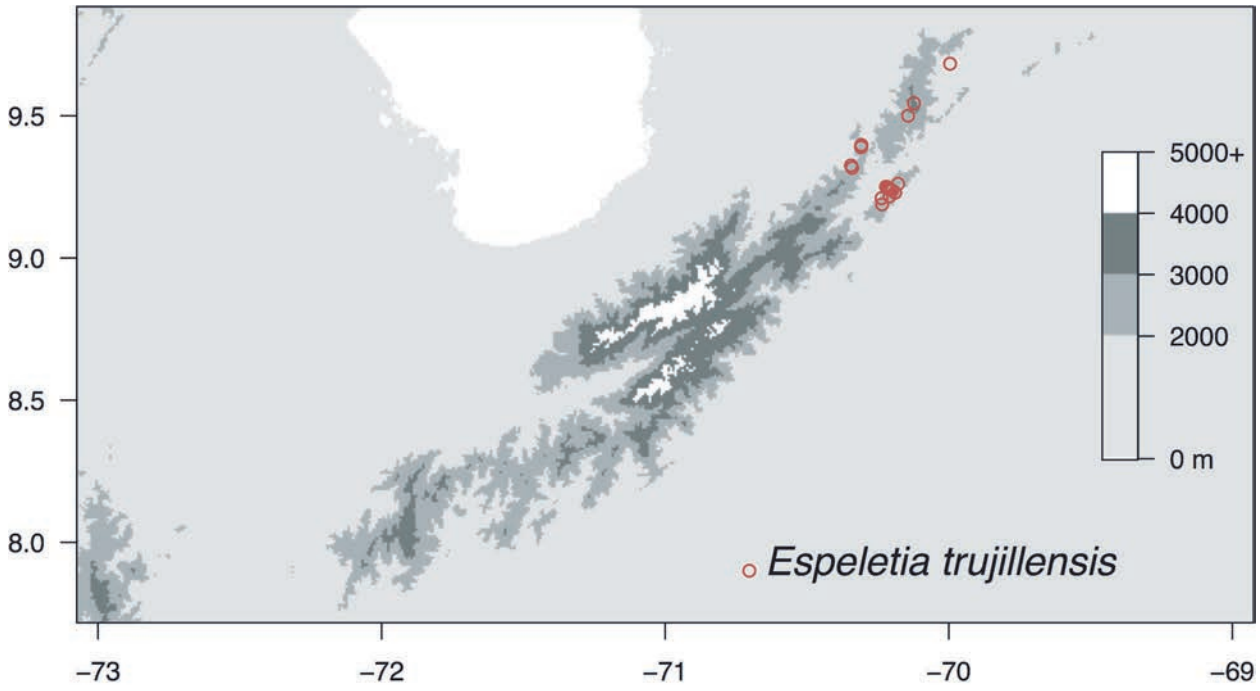


FIGURE 154. Distribution of *Espeletia trujillensis* Cuatrec.

50. *Espeletia ulotricha* Cuatrec., Phytologia 23: 364. 1972. TYPE: VENEZUELA. Lara: Páramo del Jabón, vertiente oriental, 3100–3400 m.a.s.l., 2 November 1969, *J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28220* (Holotype: US; Isotypes: F, MERF, US). Fig. 155–156.

Rosette polycarpic, sessile, dwarf. *Leaf* open sheath, sessile, adaxially densely pubescent, crispy lanate, whitish-cinereous, length 10–25 cm, width 0.7–1.2 cm, ratio 15–28:1, secondary nerves filiform, parallel, 3–6 mm apart. *Inflorescence* lateral, simple, dichasial, monocephalous, rarely with 2 or 3 capitula, length 30–70 cm, with 1 pair (rarely 2) of opposite bracts near the base and 5–12 alternate along the inflorescence. *Capitulum* diam. 24–32 mm, ligular circle 40–45 mm, disc 20–25 mm, ray ligules yellow. *Espeletia ulotricha* can be distinguished from all other Venezuelan dwarf rosette plants with monocephalous inflorescences by its leaf sheaths barbate abaxially, lamina with cylindrical outline and thick crispy-lanate indumentum, and inflorescences with 5–12 alternate bracts.

Distribution: VENEZUELA. Border Lara-Trujillo: Páramo del Jabón, de Cendé, and del Turmal. 3000–3500 m.a.s.l., in open and windy páramos on top of hills and rocky ridges (Fig. 156).

Additional specimens examined (selection): *J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28220* (F, US), *M. López-Figueiras & H. Rodríguez 26235* (US), *L. Ruiz-Terán & M. López-Figueiras 929* (US), *L. Ruiz-Terán & M. López-Figueiras 2055* (US), *Monasterio 3518* (US).

51. Espeletia usubillagae (Cuatrec.) Mavárez, *comb. nov.* Basionym: *Ruilopezia usubillagae* Cuatrec., Phytologia 61: 53. 1986a. TYPE: VENEZUELA. Mérida: Páramo de Aricagua, 3000 m.a.s.l., 31 March 1922, *A. Jahn 1021* (Holotype: US; Isotypes: US, VEN [not seen]). Fig. 157.

Rosette stem divided, each branch short, erect, ending with a leafy rosette. *Leaf* open sheath, subsessile, or with a short "winged" pseudopetiole, oblong, adaxially glabrous, green, length 12–20 cm, width 3.0–3.3 cm, ratio 4–6:1, secondary nerves parallel, 2–4 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 56 cm, vegetative part profusely bracteate, about half of the total length. *Capitulum* diam. 15–18 mm, ligular circle 25 mm, disc 12–14 mm, ray ligules white, with purplish blotches. *Espeletia usubillagae* can be distinguished from other species by its multibranched rosette habit, oblong subsessile leaves, and radiate capitula with white ray ligules.

Distribution: VENEZUELA. Mérida: known only from the type collection. Given the locality and elevation, the habitat probably corresponds to a shrubby subpáramo (Fig. 157).

Additional specimen examined: *A. Jahn 1021* (US).

Collection date given as "3 November 1922" in Diazgranados (2012: 42) and Cuatrecasas (2013: 494).

A handful of Espeletiinae rosette plants exhibit branched stems, with the best example of this growth form found in *Espeletia jahnii*, and to a lesser extent in a few related species (e.g., *E. bracteosa*, *E. bromelioides*, or *E. viridis*), which frequently produce multiple sessile or prostrate rosette plants connected through a common stem. Multi-branched rosette plants with erect branches or stems, such

FIGURE 155. *Espeletia ulotricha* Cuatrec. amid *E. jabonensis* Cuatrec. Páramo del Jabón, Lara-Trujillo, Venezuela (Photograph by S. Aubert).

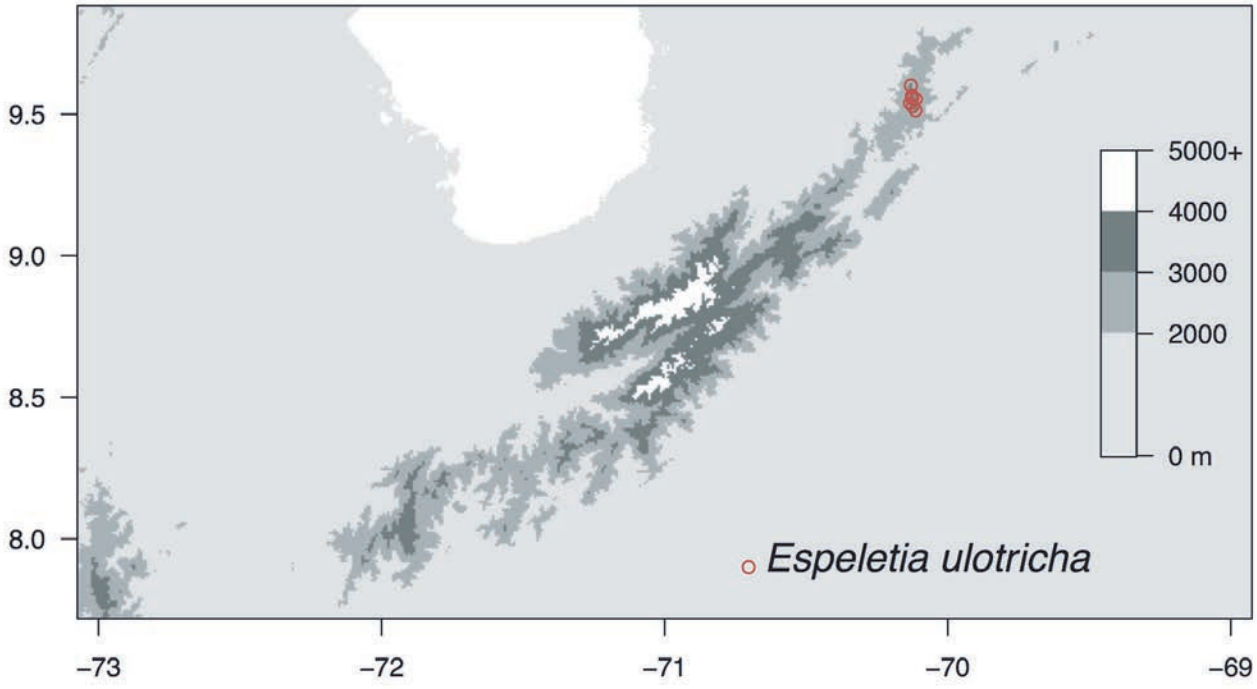


FIGURE 156. Distribution of *Espeletia ulotricha* Cuatrec.

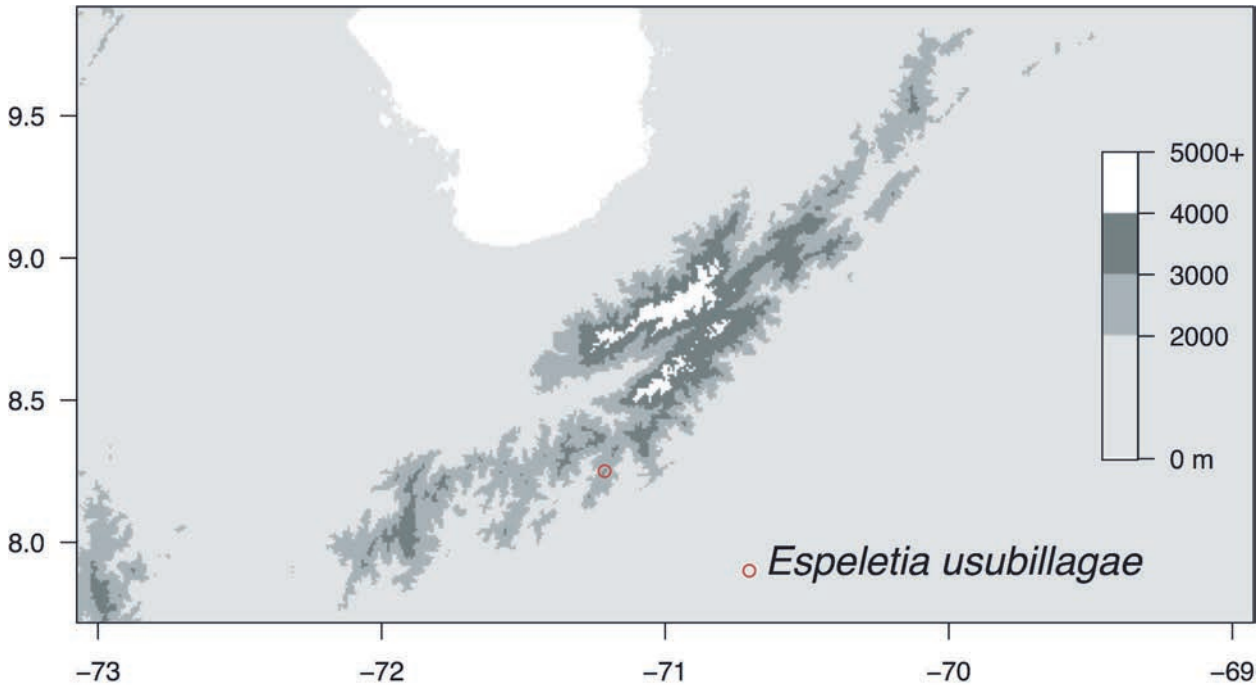


FIGURE 157. Distribution of *Espeletia usubillagae* (Cuatrec.) Mavárez.

as *E. usubillagae*, have also been observed but much more rarely, and with all examples representing cases of interspecific hybridization between rosette and tree species (e.g., *E. cristalinensis* and *E. meridensis*; see below). The type of branching in *E. usubillagae* and its extreme scarcity suggest that this taxon probably represents an interspecific hybrid instead of a good species with a primitive growth form, but more studies will be necessary before a conclusion can be reached in this regard.

52. Espeletia vergarae (Cuatrec. & López-Fig.) Mavárez, *comb. nov*.

Basionym: *Ruilopezia vergarae* Cuatrec. & López-Fig., Phytologia 61: 58. 1986a. TYPE: VENEZUELA. Trujillo: la Palma [Las Palmas], 10–15 km [NE] de Carache, en la carretera hacia Agua de Obispo, 2390 m.a.s.l., 4 April 1976, *M. López-Figueiras 12960* (Holotype: US; Isotypes: F, K, MA [not seen], MERF, NY, U, US, VEN [not seen]). Fig. 158–160.

Rosette monocarpic, sessile. *Leaf* open sheath, sessile, adaxially densely pubescent, appressed sericeous, whitish-cinereous, length 20–40 cm, width 1.1–3.0 cm, ratio 10–20:1, secondary nerves parallel, 10–15 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 80–100 cm, branched near the base. *Capitulum* diam. 12–17 mm, ligular circle 25–35 mm, disc 10–16 mm, ray ligules yellow. *Espeletia vergarae* can be distinguished from other species for its sessile monocarpic rosette, leaves adaxially appressed-sericeous, and capitula with bright-yellow ray ligules. The species resembles sympatric *E. jabonensis*, from which it can be distinguished by its appressed-sericeous leaves (vs. shiny-silvery), with smaller length-to-width ratio (10–20:1 vs. 30–40:1), visible secondary nerves (vs. obsolete), and ovate sheaths 2.5–3.0 cm × 3.5–4.0 cm (vs. rectangular sheaths 2.0–2.5 cm × 0.5–0.8 cm).

Distribution: VENEZUELA. Border Trujillo-Lara: páramos in the northern end of the Cordillera de Mérida, Sierra de Barbacoas, Los Nepes, and the complex Las Rosas-Jabón-Cendé-Turmal. 2300–3300 m.a.s.l., in open subpáramo and páramo slopes, also in deforested spots in former upper Andean forest (Fig. 160).

Additional specimens examined (selection): *M. López-Figueiras 12960* (F, K, NY, U, US), *M. López-Figueiras 12951* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28547* (US), *L. Ruiz-Terán & M. López-Figueiras 1029* (US), *L. Ruiz-Terán & M. López-Figueiras 1997* (US), *L. Ruiz-Terán & M. López-Figueiras 2058* (US).

53. *Espeletia viridis* Aristeg., Bol. Soc. Ven. Ci. Nat. 20: 278. 1959. TYPE: VENEZUELA. Trujillo: Páramo de Guirigay, hacia Laguna la Parida, 3500 m.a.s.l., August 1958, *L. Aristeguieta & E. Medina 3570* (Holotype: VEN [not seen]; Isotypes: NY, US, VEN [not seen]). Fig. 161–163.

Homotypic synonym: *Ruilopezia viridis* (Aristeg.) Cuatrec., Phytologia 35: 53. 1976.

Rosette monocarpic, frequently short-branched at the base, sessile. *Leaf* open sheath, sessile, adaxially glabrous, glossy green, length 25–45 cm, width 0.7–2.0 cm, ratio 15–50:1, minimum width located in the proximal half above the base, apex with a sharp teeth, 1.0–1.5 mm long, secondary nerves obsolete or fused into a reticulum. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, length 100–150 cm, vegetative part profusely bracteate,

FIGURES 158–159. *Espeletia vergarae* (Cuatrec. & López-Fig.) Mavárez. Páramo de Cendé, Trujillo, Venezuela (Photographs by S. Aubert).

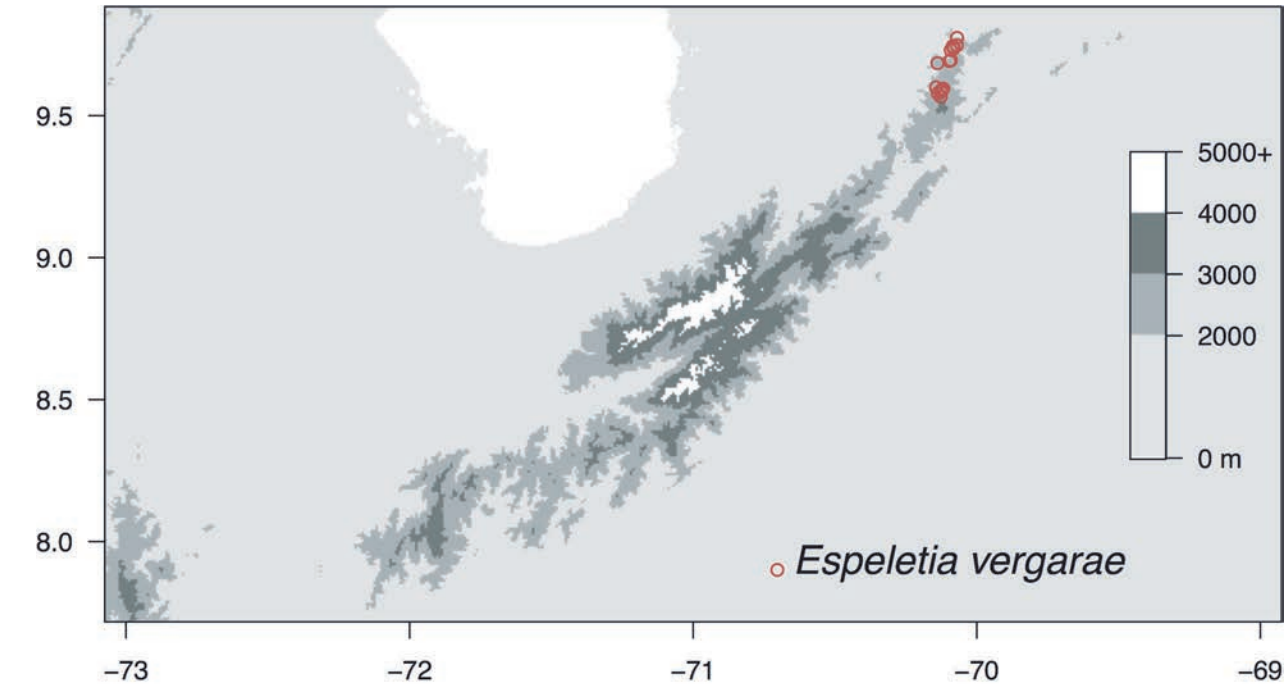


FIGURE 160. Distribution of *Espeletia vergarae* (Cuatrec. & López-Fig.) Mavárez.

FIGURES 161–162. *Espeletia viridis* Aristeg. Páramo de Guaramacal, Trujillo, Venezuela (Photographs by S. Aubert).

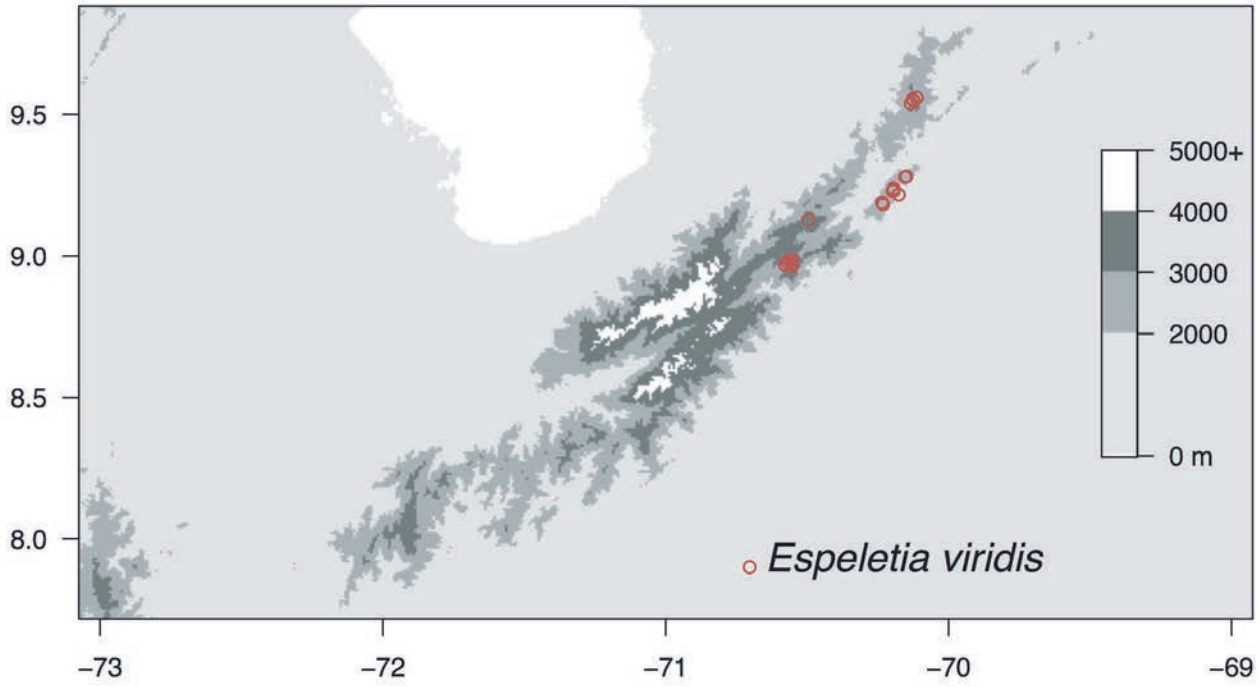


FIGURE 163. Distribution of *Espeletia viridis* Aristeg.

about half of total length. *Capitulum* diam. 14–17 mm, ligular circle 22–35 mm, disc 12–16 mm, bright yellow ray ligules. *Espeletia viridis* can be distinguished from other species by its sessile monocarpic rosette habit with long, sessile, flexible, green leaves, and its capitulum with yellow ray ligules.

Distribution: VENEZUELA. Border Trujillo-Lara: Páramo de Cendé, Páramo del Jabón, and Páramo del Turmal. Trujillo: Páramo de Guaramacal. Border Trujillo-Barinas-Mérida: Páramo de Guirigay. 2900–3500 m.a.s.l., found in humid locations within open subpáramo and páramo habitats (Fig. 163).

Additional specimens examined (selection): *L. Aristeguieta & E. Medina 3570* (NY, US), *J. Cuatrecasas & L. Ruiz-Terán 28814* (F, US), *M. López-Figueiras & H. Rodríguez 8803* (US), *B. Stergios*, *L. Dorr & K. Wurdack 20436* (US), *J. Cuatrecasas*, *M. López-Figueiras & L. Marcano-Berti 28168* (F, U, US).

54. ***Espeletia weddellii*** Sch. Bip. ex Wedd., Chlor. Andina: 66. 1855. TYPE: VENEZUELA. Trujillo: Páramo de Niquitao, 12,500 pieds, July 1843, *Linden 1443* (Holotype: P; Isotypes: BR, F, G, K, P, US, W). Fig. 164–166.

Rosette polycarpic, sessile, dwarf. *Leaf* open sheath, sessile, adaxially densely pubescent, appressed villous-lanate, whitish-cinereous, length 5–15 cm, width 0.3–1.0 cm, ratio 10–25:1, secondary nerves obsolete or filiform, irregularly fused into a reticulum. *Inflorescence* lateral, simple, botryoid, with 2–5 alternate monocephalous peduncles, rarely a single one, length 15–70 cm, with 2 pairs (rarely 1 or 3) of opposite bracts near the base and 1–3 alternate along the inflorescence. *Capitulum* diam. 15–25 mm, ligular circle 20–30 mm, disc 10–15 mm, yellow ray ligules. *Espeletia weddellii* can be distinguished from all other Venezuelan dwarf rosette plants by its polycephalous inflorescences. Some atypical individuals of *E. weddellii* with monocephalous inflorescences look similar to *E. batata*, but they can be recognized by their slender leaves (width 0.3–1.0 cm vs. 0.8–2.0 cm), with rather linear shape (vs. oblong or spatulate) and covered adaxially by a subappressed-villous indumentum (vs. lanuginose).

Distribution: VENEZUELA. Mérida: Páramo de Los Granates in Sierra de Santo Domingo. Trujillo: Páramo de Tuñame, de Cabimbú, de Guirigay, de Ortiz, and de Niquitao. 3100–4000 m.a.s.l., in páramo meadows and relatively open places within subpáramo habitats (Fig. 166).

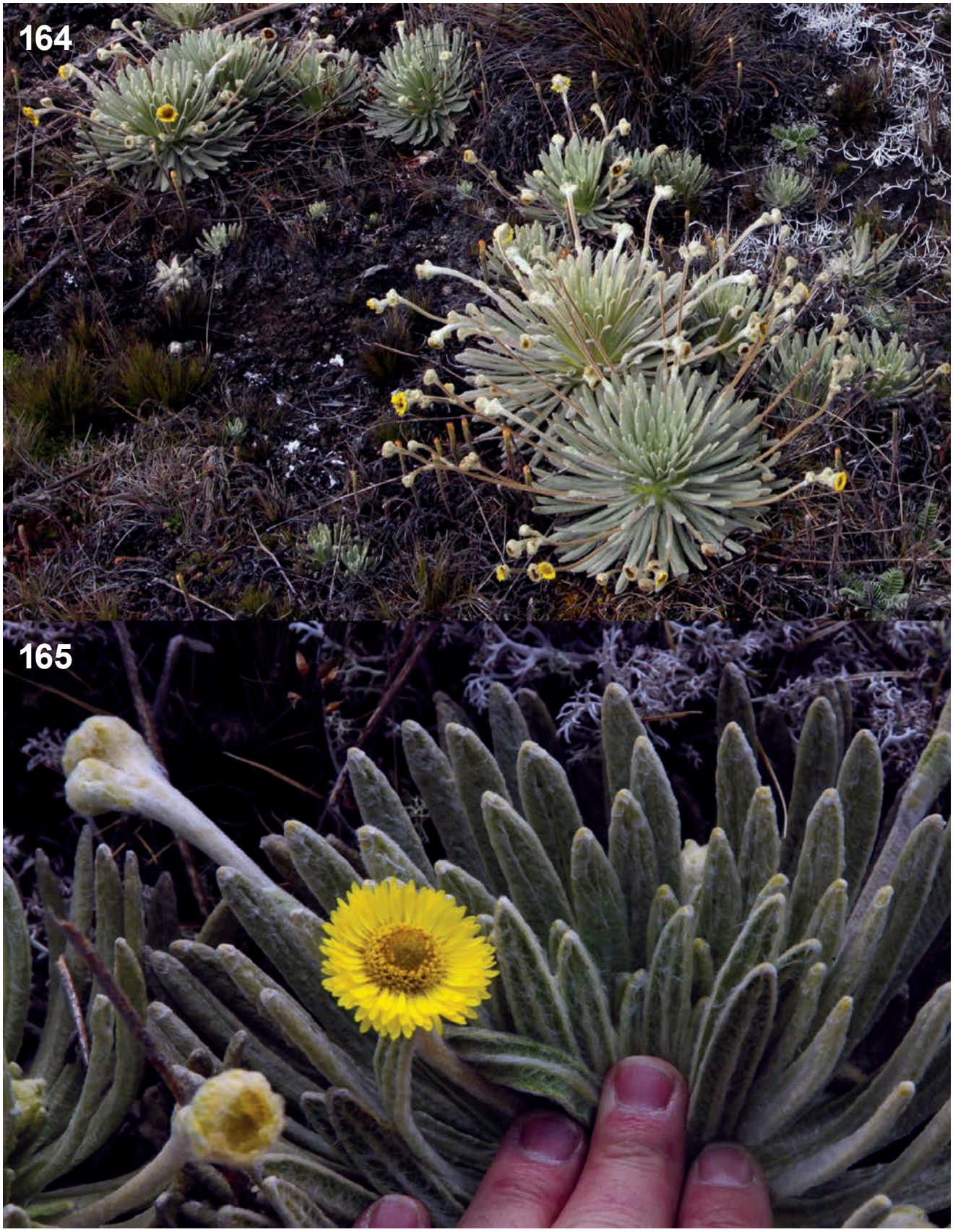
Additional specimens examined (selection): *Linden 1443* (BR, F, G, K, P, US, W), *B. Stergios 19884* (US), *L. Dorr & L. Barnett 9182* (US), *M. López-Figueiras 8716* (US), *M. López-Figueiras & H. Rodríguez 8877* (US).

Hybrid Taxa

H1. ***Espeletia*** **×** ***algodonosa*** Aristeg., Bol. Soc. Ven. Ci. Nat. 20: 282. 1959. (= *E. nana* × *E. schultzii*), hybrid status in Cuatrecasas (2013: 349). TYPE: VENEZUELA. Trujillo: El Paramito, hacia Tuñame, vía Jajó-la Morita, ca. 3000 m.a.s.l., August 1958, *L. Aristeguieta & E. Medina 3453* (Holotype: VEN [not seen]; Isotypes: NY, US).

Distribution: VENEZUELA. Trujillo: in areas where *E. schultzii* and *E. nana* occur in syntopy (i.e., Cabimbú, Guirigay, Tuñame).

Additional specimens examined (selection): *L. Aristeguieta & E. Medina 3453* (NY, US), *L. Ruiz-Terán & M. López-Figueiras 2223* (US), *M. López-Figueiras & H. Rodríguez 8868* (US), *M. López-Figueiras 11895* (US).



FIGURES 164–165. *Espeletia weddellii* Sch. Bip. ex Wedd. Páramo de Guirigay, Trujillo, Venezuela (Photographs by S. Aubert).

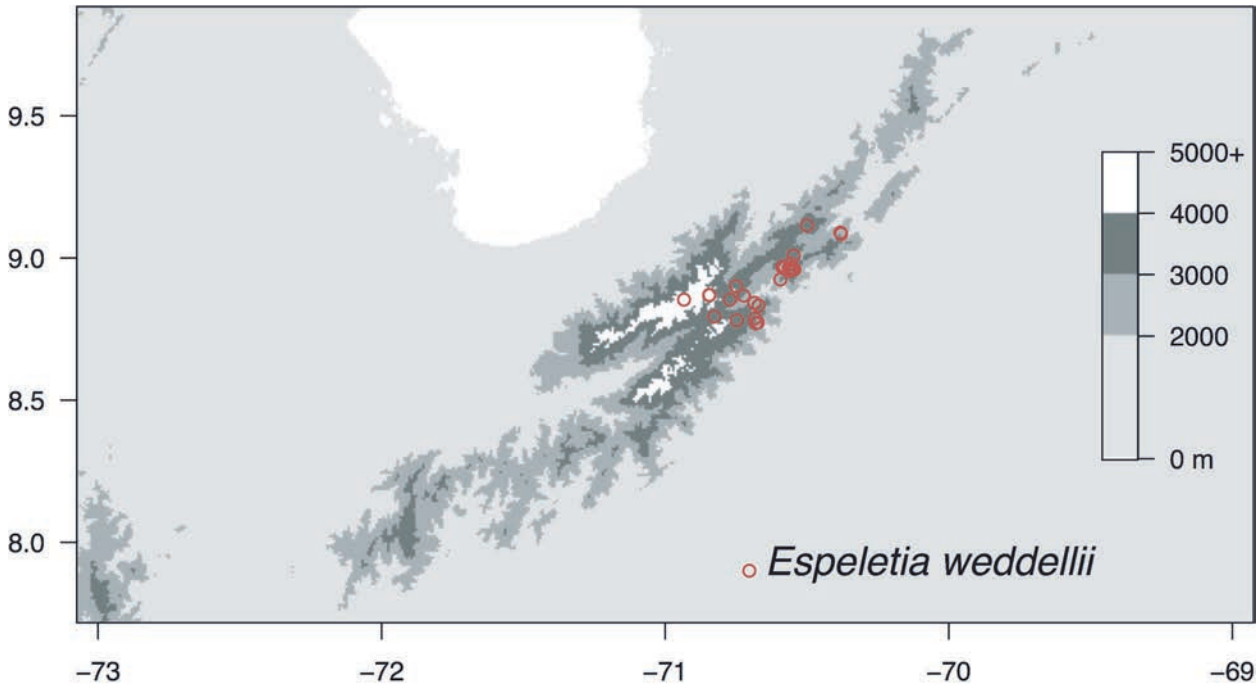


FIGURE 166. Distribution of *Espeletia weddellii* Sch. Bip. ex Wedd.

H2. *Espeletia* × *aurantia* Aristeg., Fl. Venez. 10(1): 448. 1964. (= *E. moritziana* × *E. schultzii*), hybrid status in Cuatrecasas (2013: 579). TYPE: VENEZUELA. Mérida: Laguna Verde, 4100 m.a.s.l., 1 October 1956, *L. Aristeguieta 2613* (Holotype: VEN [not seen]; Isotypes: GOET [not seen], K, US).

Distribution: VENEZUELA. Mérida: a relatively common hybrid found in areas where *E. schultzii* and *E. moritziana* occur in sympatry.

Additional specimens examined (selection): *L. Aristeguieta 2613* (K, US), *P. Berry 4188* (US), *P. Berry 4189* (US), *J. L. Panero*, *C. E. Benítez & V. M. Badillo 2670* (US).

H3. *Espeletia* × *coloradarum* Cuatrec., Phytologia 29: 372. 1975. (= *E. neriifolia* × *E. ruizii*). TYPE: VENEZUELA. Mérida: potrero de San Rafael, Páramo de las Coloradas, 2700 m.a.s.l., 3 July 1974, *M. López-Figueiras & M. Keogh 9108* (Holotype: US; Isotypes: F, MERF, NY, US).

Homotypic synonym: *Ruilopezia coloradarum* (Cuatrec.) Cuatrec., Phytologia 35: 52. 1976.

Espeletia × *coloradarum* represents an interspecific hybrid between an *E. neriifolia* tree and an *E. ruizii* monocarpic rosette. All known specimens of this taxon have been collected exclusively in a restricted area within Páramo de las Coloradas, in which I have observed that hybridization between *E. neriifolia* and *E. ruizii* is very active. The leaves of *E.* × *coloradarum* are clearly intermediate between its putative parental species with regard to size, shape, color, nerve structure, and pubescence. Its inflorescences are also rather intermediate in size and structure, although the long subtending bracts and small capitula are closer to *E. neriifolia*. The hybrid nature of *E.* × *coloradarum* is even more evident when studied directly in the *E. neriifolia*/*E. ruizii* hybrid zone at Las Coloradas, where several individuals in the morphological continuum from *neriifolia*-like to *ruizii*-like can usually be compared at once.

Distribution: VENEZUELA. Mérida: known only from the type locality.

Additional specimens examined (selection): *M. López-Figueiras & M. Keogh 9108* (F, NY, US), *J. L. Panero*, *C. E. Benítez & V. M. Badillo 2694* (US), *M. López-Figueiras & H. Rodríguez 9046* (US), *M. López-Figueiras & H. Rodríguez 9047* (US).

H4. *Espeletia* × *cristalinensis* Cuatrec., Phytologia 27: 169. 1973b. (= *E. aristeguietana* × *E. neriifolia*), hybrid status in Diazgranados (2012: 38). TYPE: VENEZUELA. Trujillo: Distrito Boconó, Páramo de la Cristalina, 2500–2600 m.a.s.l., 17 February 1973, *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28556* (Holotype: US; Isotypes: MERF, U, US).

Homotypic synonym: *Espeletiopsis cristalinensis* (Cuatrec.) Cuatrec., Phytologia 35: 55. 1976.

This taxon exhibits a mixture of vegetative and reproductive traits that strongly suggest it represents a case of hybridization between *Espeletia aristeguietana* rosette plants and *E. neriifolia* trees. For instance, *E.* × *cristalinensis* are frequently branched, but their open leaf sheaths are characteristic of rosette plants. Their foliose, alternate and corymboid inflorescences structurally resemble *E. neriifolia*, but their large size and dense pubescence is similar to *E. aristeguietana*. Their capitula are also, in many ways, intermediate between the two parental species. Finally, individuals of this taxon are scarce, morphologically variable, and found only in close syntopy with *E. aristeguietana* and *E. neriifolia*.

Distribution: VENEZUELA. Trujillo: known only from Páramo de la Cristalina, in syntopy with *E. aristeguietana* and *E. neriifolia*.

Additional specimens examined (selection): *J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28556* (U, US), *M. López-Figueiras 13949* (US), *M. López-Figueiras 13950* (US), *L. Ruiz-Terán & M. López-Figueiras 2257* (US), *J. Cuatrecasas, M. López-Figueiras & H. Rodríguez 28993* (US).

H5. *Espeletia* × *cuniculorum* Cuatrec., Phytologia 40: 25. 1978. (= *E. schultzii* × *E. timotensis*). TYPE: VENEZUELA. Mérida: Páramo de los Conejos, Cañada de los Puentes, Sierra de la Culata, 3350 m.a.s.l., 19 October 1972, *L. Ruiz-Terán 7722* (Holotype: US; Isotypes: MERF, MY, US).

Espeletia × *cuniculorum* represents an interspecific hybrid between *E. schultzii* and another rosette species with lanceolate leaves from Sierra de la Culata, most likely *E. timotensis*, or perhaps *E. albarregensis*. This taxon not only exhibits a series of morphologic traits that appear intermediate with regard to those taxa, but that also match the variation observed in interspecific hybrids between the aforementioned taxa. For instance, the long lanceolate leaves with white/shiny pubescence of *E.* × *cuniculorum* are quite similar to *E. timotensis*. Its relatively small ligular circle in comparison with a rather large capitulum is also reminiscent of this species. On the other hand, the dichasial inflorescence of *E.* × *cuniculorum* is structurally similar to *E. schultzii*, although a possible influence of *E. timotensis* is found in the number of capitula per branch (3 in the proximal, 2 in the middle, and 1 in the terminal), as well as in the copiously hirsute receptacles (Cuatrecasas, 2013: 351). Besides, *E.* × *cuniculorum* is still known only from the type collection despite the many visits I and other researchers have made to the type locality and nearby areas. Demographic scarcity is a predominant feature of several interspecific hybrids that were initially described as species in *Espeletia* (e.g., *E.* × *cristalinensis*).

Distribution: VENEZUELA. Mérida: known only from the type collection.

Additional specimens examined (selection): *L. Ruiz-Terán 7722* (US). Specimen *P. Berry 3852* (US) looks similar to *E.* × *cuniculorum*. This sample was initially considered by Paul Berry to be a hybrid, *E. schultzii* × *E. timotensis*, and later identified by José Cuatrecasas as *E. albarregensis*.

H6. Espeletia × gritaensis (Cuatrec.) Mavárez, *comb. nov.* (= *E. neriifolia* var. *columbica* × *E. occulta*), hybrid status in Cuatrecasas (1980b: 7).

Basionym: *Libanothamnus* × *gritaensis* Cuatrec., Phytologia 47: 7. 1980b. TYPE: VENEZUELA. Táchira: Llano de Campoalegre, cercanías de La Grita, hacia Páramo del Batallón, 2520 m.a.s.l., 2 October 1969, *J. Cuatrecasas, M. López-Figueiras & L. Marcano-Berti 27999* (Holotype: US; Isotypes: F, MERF, U, US).

Distribution: the taxon has been known only from the type locality. However, hybrids between *E. neriifolia* var. *columbica* and *E. occulta* are frequently found wherever the two species coexist in sympatry.

Specimens examined (selection): *J. Cuatrecasas, M. López-Figueiras & L. Marcano-Berti 27999* (F, U, US).

H7. *Espeletia* × *jajoensis* Aristeg., Fl. Venez. 10(1): 424. 1964. (= *E. neriifolia* × *E. schultzii*). TYPE: VENEZUELA. Trujillo: el Paramito, hacia Tuñame, vía Jajó-la Morita, 3000 m.a.s.l., Aug. 1958, *L. Aristeguieta & E. Medina 3452* (Holotype: VEN [not seen]; Isotypes: NY, US).

Homotypic synonym: *Espeletiopsis jajoensis* (Aristeg.) Cuatrec., Phytologia 35: 56. 1976.

The combination of morphological traits in this taxon is so unique that Cuatrecasas (2013: 375) created a new group within *Espeletia* just for it, with the revealing name "Group Aberrantes." Indeed, *E.* × *jajoensis* is the only polycarpic rosette species in the subtribe whose inflorescences exhibit monochasial (alternate) primary branching but with secondary branching frequently dichasial (opposite). Cuatrecasas was visibly puzzled by this architecture, which explains why he moved this taxon from *Espeletia* to *Espeletiopsis* (Cuatrecasas, 1976: 56) and then back to *Espeletia* (Cuatrecasas, 1996: 377). Cuatrecasas also noted an unusual leaf polymorphism in this taxon; with most individuals exhibiting sessile leaves with rather parallel and dense secondary nerves, while others have clearly pseudopetiolate leaves with bent and more loosely packed secondary nerves. He proposed that "these variations indicate instability and a probably hybrid origin (…) the result of a cross pollination probably between *Espeletia schultzii* and *Espeletiopsis cristalinensis*." Cuatrecasas's final insight in this sense was partially correct, since *E.* × *jajoensis* is the product of hybridization between *E. neriifolia* and *E. schultzii*, where it represents the fraction of the morphological spectrum of the hybrids closest to the rosette plants, probably as a consequence of backcrossing toward *E. schultzii*.

Distribution: VENEZUELA. Trujillo: páramos in the Jajó-Tuñame and Timotes-Piñango areas. Mérida: found sporadically in most páramos Sierra Nevada de Santo Domingo, Sierra de la Culata, and Sierra Nevada de Mérida, where *E. neriifolia* and *E. schultzii* coexist in sympatry.

Additional specimens examined (selection): *L. Aristeguieta & E. Medina 3452* (NY, US), *M. López-Figueiras & B. Vergara 14514* (US), *M. López-Figueiras & B. Vergara 14515* (US); *14516* (US), *L. Ruiz-Terán*, *M. López-Figueiras & M. Hale 10436* (US).

Aristeguieta (1964: 424) used the suffix *-ense* (neuter) in the original spelling of the epithet of this taxon. Cuatrecasas (1976: 56) changed the suffix to *-ensis* (masc./fem.) to match the epithet with the feminine gender of both *Espeletia* and *Espeletiopsis*.

H8. *Espeletia* × *josephensis* Cuatrec., Phytologia 29: 374. 1975. (= *E. lindenii* × *E. neriifolia*). TYPE: VENEZUELA. Mérida: Páramo de San José de Acequias, arriba de Veguilla, distrito Arzobispo Chacón, 2600 m.a.s.l., 18–20 June 1974, *M. López-Figueiras & H. A. Rodríguez 9073* (Holotype: US; Isotypes: F, MERF, MY, US).

Homotypic synonym: *Ruilopezia josephensis* (Cuatrec.) Cuatrec., Phytologia 35: 52. 1976.

Espeletia × *josephensis* represents an interspecific hybrid between an *E. lindenii* monocarpic rosette and an *E. neriifolia* tree. All known specimens of this taxon have been collected in two restricted areas in Sierra Nevada de Mérida (Páramo de San José and Páramo de Acequias) and Sierra de la Culata (Páramo el Tambor), in which I have observed that hybridization between *E. lindenii* and *E. neriifolia* is very active. Most vegetative and reproductive traits in this taxon are indeed intermediate between its putative parental species, including growth form, since there are branched and unbranched individuals in *E.* × *josephensis*. The latter fact is particularly suggestive of an origin from hybridization and backcrossing toward both tree and rosette parental species.

Distribution: known until recently only from the type locality and nearby areas in the S. of Sierra Nevada de Mérida, I have found a few isolated individuals in Páramo el Tambor in the S. end of Sierra de la Culata.

Additional specimens examined (selection): *M. López-Figueiras & H. A. Rodríguez 9073* (F, US), *M. López-Figueiras & J. Dugarte 29536* (US), *M. López-Figueiras & J. Dugarte 29537* (US), *M. López-Figueiras & J. Dugarte 29538* (US), *M. López-Figueiras & J. Dugarte 29541* (US).

Correct spelling of the epithet is "*josephensis*," not "*joséphensis*" as in Diazgranados (2012: 41). Collection date given as "18–20 July" in Diazgranados (2012: 41) and Cuatrecasas (2013: 551).

Although the habit of the typus of *E.* × *josephensis* was described as "Arbolito de 2–2,5 m de alto" (i.e., small tree 2.0–2.5 m tall) in Cuatrecasas (1975: 377), the species was characterized as "Caulirosula" in the original description provided in the same work (p374). In his last treatment of this taxon, Cuatrecasas maintained the categorization as caulirosula (Cuatrecasas, 2013: 551), but he changed the description of the habit of the typus to "Caulirosula 2.0–2.5 m" (p660), without further explanations. This change appears unjustified since the labels in the holotype and isotypes clearly say "Arbolito."

H9. *Espeletia* × *meridensis* Cuatrec., Mutisia 16: 4. 1953. (= *E. leucactina* × *E. neriifolia*). TYPE: VENEZUELA. Mérida: Carretera Andina, Páramo de la Negra, 3000 m.a.s.l., 26 November 1948, *H. García-Barriga 13297* (Holotype: US; Isotypes: COL, MEDEL [not seen], NY, VEN [not seen]).

Homotypic synonym: *Espeletiopsis meridensis* (Cuatrec.) Cuatrec., Phytologia 35: 56. 1976.

Espeletia × *meridensis* is undoubtedly the result of interspecific hybridization between a tree and a rosette species. The tree parent is most likely *E. neriifolia*, an abundant species in the distribution area of *E.* × *meridensis* and whose contribution to this taxon is clearly noticeable in the shape and structure of both its leaves and inflorescences. Indeed, the similarities between *E.* × *meridensis* and *E. neriifolia* are so important that Cuatrecasas considered the reassignment of the former to *Libanothamnus* (Cuatrecasas, 2013: 434). The rosette parent of *E.* × *meridensis* is relatively harder to identify, as individuals arising from more than one interspecific hybrid combination have probably been included in this taxon. Thus, some specimens have corymboid-paniculate inflorescences with white/cream ray ligules, while others have racemiform inflorescences with pale-yellow ray ligules. One good candidate parent for the former hybrid type is *E. leucactina*, the only local rosette species with corymboid-paniculate inflorescences and white ray ligules, frequently found in close sympatry with *E. neriifolia*. Several diagnostic traits in *E.* × *meridensis* are intermediate between *E. leucactina* and *E. neriifolia*, such as leaf size and shape, capitulum size, ray corollas length and color, and outer phyllaries shape and size. For the second hybrid type, the best parent candidate is *E. thyrsiformis*, the only rosette species in the area with botryoid-paniculate inflorescences and yellow ray ligules.

Distribution: VENEZUELA. Mérida and Táchira: Páramos de la Negra, del Batallón and del Rosal.

Additional specimens examined (selection): corymboid-paniculate inflorescences with white/cream ray ligules: *H. García-Barriga 13297* (NY, US), *J. Cuatrecasas*, *M. López-Figueiras & L. Marcano-Berti 28018* (US). Racemiform inflorescences with pale yellow ray ligules: *J. Cuatrecasas*, *M. López-Figueiras & L. Marcano-Berti 28006* (US), *C. Smith & R. Jorgensen 3533* (US).

According to Art. H.4 of the ICN, hybrid names should be circumscribed so as to include only one particular hybrid formula. In this case, the typus of *E.* × *meridensis* probably represents an *E. leucactina* × *E. neriifolia* cross. If this turns to be correct and the name *E.* × *meridensis* is conserved, another hybrid name would be needed for the hybrid combination *E. neriifolia* × *E. thyrsiformis*.

H10. *Espeletia* × *pozoensis* Cuatrec., Ciencia (México) 6: 266. 1945. (= *E. angustifolia* × *E. schultzii*). TYPE: VENEZUELA. Mérida: Páramo de Pozo Negro, entre San José and Beguilla [la Veguilla], 2950–3220 m.a.s.l., 3 May 1944, *J. A. Steyermark 56278* (Holotype: VEN [not seen]; Isotypes: F, NY).

Homotypic synonym: *Espeletiopsis pozoensis* (Cuatrec.) Cuatrec., Phytologia 35: 56. 1976.

Espeletia × *pozoensis* represents an interspecific hybrid between two polycarpic rosette plants, *E. angustifolia* and *E. schultzii*. All known specimens of this taxon have been collected in the páramos in the "Pueblos del Sur" region in which both parental species coexist in sympatry and hybridize rather frequently. As for other hybrids in *Espeletia*, quantitative traits in this taxon are clearly intermediate between *E. angustifolia* and *E. schultzii*, most notably with regard to the size, shape, and structure of leaves, which differ greatly in the parental species. The branching of the inflorescence, as in other crossings between species with alternate and opposite architectures, is alternate in *Espeletia* × *pozoensis*. Flowering individuals of this taxon can also be easily recognized by their pale-yellow ray ligules, a color quite intermediate between white in *E. angustifolia* and bright yellow in *E. schultzii*.

Distribution: VENEZUELA. Mérida: Páramos de Mijará, de San José and de la Veguilla.

Additional specimens examined (selection): *J. A. Steyermark 56278* (F, NY), *M. López-Figueiras 30160* (US), *L. Ruiz-Terán & S. López-Palacios 6562* (US), *C. Sobrevila & M. Guariguata 1533* (US), *P. Berry & R. Calvo 4387* (US). Several specimens identified as *Espeletia* × *pozoensis* appear instead to be the morphologically similar hybrid *E. pannosa* × *E. schultzii* (e.g., *L. Ruiz-Terán 7723* US).

H11. ***Espeletia* × *rodriguezii*** Cuatrec., Phytologia 29: 379. 1975. (= *Espeletia badilloi* × *E. neriifolia*). TYPE: VENEZUELA. Mérida: Betania, entre el Páramo de las Coloradas y el Molino, 2400 m.a.s.l., 18–20 June 1974, *M. López-Figueiras & H. Rodríguez 9050* (Holotype: US; Isotypes: F, MERF, US).

Homotypic synonym: *Carramboa rodriguezii* (Cuatrec.) Cuatrec., Phytologia 35: 54. 1976.

Espeletia × *rodriguezii* represents an interspecific hybrid between two trees with very different leaves and inflorescences, *E. badilloi* and *E. neriifolia*. *Espeletia* × *rodriguezii* leaves are somehow closer to *E. neriifolia*, since they tend to be clustered at the end of branches, have similar length-to-width ratios, and have secondary nerves relatively straight, parallel, and evenly distributed. The opposite trend can be observed in the inflorescences of *E.* × *rodriguezii*, much closer to *E. badilloi* given their lateral positioning, dichasial (opposite) organisation of sterile bracts and main branches, and capitula with yellow ray ligules.

Distribution: VENEZUELA. Mérida: found in all páramos in the S. end of Cordillera de Mérida where *E. badilloi* and *E. neriifolia* coexist in sympatry, particularly in Páramo de San José and Páramo de las Coloradas. *Espeletia* × *rodriguezii* is a relatively common hybrid, particularly in degraded areas of former upper Andean forest that have been aggressively colonized by *E. neriifolia*, such as in the "Pueblos del Sur" region, where flowering individuals of *E.* × *rodriguezii* can be recognized by their resemblance to an *E. neriifolia* tree with yellow capitula.

Additional specimens examined (selection): *M. López-Figueiras & H. Rodríguez 9050* (F, US), *M. López-Figueiras & H. Rodríguez 9049* (US), *P. Berry 4367* (US), *P. Berry 4368* (US), *P. Berry & R. Calvo 4560* (US).

H12. ***Espeletia* × *tachirensis*** Aristeg., Fl. Venez. 10(1): 427. 1964. (= *E. badilloi* var. *pittieri* × *E. marcescens*), hybrid status in Morillo and Briceño (2007). TYPE: VENEZUELA. Táchira: Páramo del Batallón, hacia Pregonero, 2800 m.a.s.l., 26 Sept 1956, *L. Aristeguieta 2533* (Holotype: VEN [not seen]; Isotype: US).

Homotypic synonyms: *Espeletiopsis tachirensis* (Aristeg.) Cuatrec., Phytologia 35: 56. 1976.

Carramboa tachirensis (Aristeg.) Cuatrec., Phytologia 52: 158. 1982.

Distribution: VENEZUELA. Mérida: páramos in the southern end of Sierra Nevada de Mérida (e.g., Aricagua, Quirorá, San José, Las Coloradas) toward the border with Táchira state (e.g., Portachuelo, La Grita). Táchira: Páramo de la Negra and Páramo del Batallón.

Additional specimens examined (selection): *L. Aristeguieta 2533* (US), *M. López-Figueiras 13988* (US), *V. Badillo 5271* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28418* (US).

H13. ***Espeletia* × *wurdackii*** Ruiz-Terán & López-Fig., Rev. Fac. Farm. Univ. Andes 17: 1. 1976. (= *Espeletia neriifolia* × *E. trujillensis*). TYPE: VENEZUELA. Trujillo: Finca Florencia, Páramo del Turmal, cercanías de Carache, ca. 2450 m.a.s.l., 3 April 1976, *M. López-Figueiras 12957* (Holotype: MERF; Isotypes: NY, US).

Homotypic synonyms: *Libanothamnus wurdackii* (Ruiz-Terán & López-Fig.) Cuatrec., Phytologia 35: 51. 1976.

Carramboa wurdackii (Ruiz-Terán & López-Fig.) Cuatrec., Phytologia 52: 158. 1982.

Espeletia × *wurdackii* represents another example of interspecific hybridization between two trees with very different leaves and inflorescences, *E. neriifolia* and *E. trujillensis*. *Espeletia* × *wurdackii* leaves are very close to *E. neriifolia*, since they tend to be clustered at the end of branches, are pseudopetiolate, have a lanceolate outline with similar length-to-width ratios, and have secondary nerves straight, parallel, and 5–10 mm apart. In fact, the only obvious contributions of *E. trujillensis* to *E.* × *wurdackii* leaves are found in their relatively large size (compared to *E. neriifolia*) and their velvety-felty abaxial indumentum. On the other hand, an important contribution of *E. trujillensis* to *E.* × *wurdackii* is evident in the lateral position of the inflorescences, as well as in the dichasial (opposite) organization of some sterile bracts and main branches, and the yellow ray ligules. The inflorescences of *E.* × *wurdackii* are nonetheless variable, particularly with regard to their structure, with some specimens exhibiting predominant alternate branching. These combinations of vegetative and reproductive characteristics make it difficult to fully fit *E.* × *wurdackii* into any of the tree genera proposed by Cuatrecasas, which explains why he first classified this taxon as a *Libanothamnus* (Cuatrecasas, 1976: 51) and latter as a *Carramboa* (Cuatrecasas, 1982: 158).

Distribution: VENEZUELA. Trujillo: known only from the type locality and nearby areas below Páramo del Turmal.

Additional specimens examined (selection): *M. López-Figueiras 12957* (NY, US), *J. Cuatrecasas*, *M. López-Figueiras & H. Rodríguez 28980* (F, US), *J. Cuatrecasas*, *M. López-Figueiras & H. Rodríguez 28983* (US).

Supplementary Material

An Excel file with information on Taxon, Sample type, Collectors, Collection number, Herbarium, Country, Province, Locality, Latitude, Longitude, and Elevation of all plants examined is available at: https://www.researchgate.net/publication/336369055_Mavarez_Espeletia_I_Appendix.

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