

A nomenclator for the frailejones (Espeletiinae Cuatrec., Asteraceae)

Mauricio Diazgranados^{1,2}

1 Department of Biology, Saint Louis University, 3507 Laclede Ave., St. Louis, MO 63103 **2** Missouri Botanical Garden, 4344 Shaw Boulevard, Saint Louis, MO 63110

Corresponding author: Mauricio Diazgranados (espeletias@gmail.com)

Academic editor: Vicki Funk | Received 3 April 2011 | Accepted 10 August 2012 | Published 21 August 2012

Citation: Diazgranados M (2012) A nomenclator for the frailejones (Espeletiinae Cuatrec., Asteraceae). PhytoKeys 16: 1–52. doi: 10.3897/phytokeys.16.3186

Abstract

The páramos and high Andean forests of the tropical Andes are largely dominated by frailejones (Espeletiinae Cuatrec., Asteraceae). These plants are ecologically and culturally essential for both ecosystems and local inhabitants. The frailejones have been studied for over two centuries, but the taxonomic knowledge is still sparse and incomplete. The inedited monograph by Cuatrecasas contains only ca. 70% of the species known today, and publications in the last decade disagree regarding the number of taxa within the group, with estimates ranging from 3 genera and 90 species to 8 genera and 154 species. Moreover the literature contains inexact information about their distribution. As part of a study of the phylogenetic and biogeographic relationships of the group, a thorough revision of the nomenclature was needed as a first step. Currently the subtribe has 8 recognized genera, 141 species, 17 subspecies, 22 varieties, 8 forms, 33 recognized hybrids, 142 synonyms and 5 invalid names, for a total of 368 names (autonyms not counted). The most current list of taxa is presented here, along with some notes and Spanish names. *Tamananthus crinitus* V.M.Badillo is not included within the subtribe. Various previous species or infraspecific taxa (i.e. *Carramboa tachirensis* (Aristeg.) Cuatrec., *Espeletia algodonosa* Aristeg., *E. aurantia* Aristeg., *E. brassicoidea* var. *macroclada*, *E. brassicoidea* var. *pedunculata*, *E. garcibarrigae* Cuatrec. and *Espeletiopsis cristalinensis* (Cuatrec.) Cuatrec.) are proposed or confirmed as hybrids. Two new records for Colombia are mentioned: *Ruilopezia cardonae* (Cuatrec.) Cuatrec., which is the first report of *Ruilopezia* for that country, and *Espeletia steyermarkii* Cuatrec. Observations regarding the frequency of hybrids in the subtribe are also given.

Keywords

Andean forest, *Carramboa*, *Coespeletia*, *Espeletia*, *Espeletiopsis*, frailejón, *Libanothamnus*, Páramo, *Paramiflos*, *Ruilopezia*, *Tamania*

Introduction

José Celestino Mutis, founder and director of the “Expedición Botánica del Nuevo Reino de Granada” wrote two short diagnoses for the first species of frailejones to be collected, described and illustrated; this material is currently preserved at the Royal Botanical Garden of Madrid, Spain. A manuscript with a four-page description, dated March 7 1792, was found in the Institute of France, Paris. This document was presumably written by Juan Bautista Aguilar, calligrapher for the Mutis expedition, and included detailed morphological information and uses. These earliest works are evidence of the admiration that these plants caused in the members of the botanical expedition. Among all the plants collected in over a decade in the New Kingdom of Granada, Mutis chose these plants to honor the viceroy José de Ezpeleta, dedicating the genus *Espeletia* to him. The genus was published officially by Humboldt and Bonpland in *Plantae Aequinoctiales* (1809 [1808]) de Cumana et de Barcelone, aux Andes de la Nouvelle Grenade, de Quito et du Pérou, et sur les bords du rio-Negro de Orénoque et de la rivière des Amazones. This was the beginning of two centuries of prolific but complex scientific research on this group.

Today new species are still being discovered and the taxonomy of some genera is still unfinished. Dr José Cuatrecasas (1903–1996), a prominent Spanish botanist, spent nearly 60 years studying the group, and published in 1976 the subtribe Espeletiinae Cuatrec. with seven genera: *Carramboa* Cuatrec., *Coespeletia* Cuatrec., *Espeletia* Mutis ex Humb. & Bonpl., *Espeletiopsis* Cuatrec., *Libanothamnus* Ernst, *Ruilopezia* Cuatrec. and *Tamania* Cuatrec. (Cuatrecasas 1976). The eighth genus, *Paramiflos* Cuatrec., was added almost 20 years later (Cuatrecasas 1995). The subtribe has numerous synapomorphies, such as spiral leaf phyllotaxis; obpyramidal to prismatic shape of the epappose cypselae; fertile female ray flowers and functionally male disc flowers; pluriseriate involucre and persistent pales of the receptacle; thick and woody stems; xeromorphic structure; specialized life-forms; and a static chromosome number ($n=19$) (Cuatrecasas 1976; Cuatrecasas in press).

The frailejones are very abundant and dominant in the páramos, subpáramos and high Andean forests (Cuatrecasas 1986). They are of critical ecological importance because they contribute to regulating the hydrologic cycle, produce most of the biomass in these ecosystems, prevent soil erosion, and have key associations with more than 125 animal species (García et al. 2005). Much like the astonishing dendrosenecios of the African mountains, frailejones have intrigued naturalists and botanists, not just for their appealing beauty but also for their remarkable adaptations to the extremely harsh environmental conditions of the páramo. Their morphological diversity is impressive. Plant sizes range from diminutive fist-sized species to plants more than 15 m high. Leaves vary from grass-like and glabrous to some of the most densely pubescent found in flowering plants. Reproductive structures exhibit a similarly spectacular level of variation and hybridization occurs between almost all sympatric species.

In the last decades hundreds of works have been produced on the páramo ecosystem, mainly on ecology, evolution, ethnobotany, and phytochemistry. A quick search

in Google Scholar (accessed in March 28 2012) yields 1290 biological papers mentioning one or more of the genera of the subtribe, and 104 papers include these names in their titles. However, the lack of clarity regarding the correct nomenclature and taxonomy of the Espeletiinae, the obligate point of reference in almost all studies on páramos, is a serious handicap. Cuatrecasas worked until his last day on the revision of the subtribe. This revision is based on his extremely detailed morphological observations and extensive field experience of decades, and treats seven of the eight genera (excluding *Espeletiopsis*) and 105 species. The revision includes new taxa and combinations, and some of these unpublished names have been used in the literature for more than a decade. The manuscript, however, is still in press at the New York Botanical Garden, and valid publication of these names is forthcoming.

In 1996 Cuatrecasas published a key for 20 species of *Espeletiopsis*, knowing that he would not be able to finish the treatment for this genus (Cuatrecasas 1996). Since then, nearly 19 new species and one variety have been published, one species was reestablished and one hybrid proposed (Díaz-Piedrahita and Obando 2004; Díaz-Piedrahita and Pedraza 2001; Díaz-Piedrahita and Rodríguez 2008; Díaz-Piedrahita et al. 2006; Díaz-Piedrahita and Rodríguez-Cabeza 2010; Morillo and Briceño 2007); the author is currently working on the description of 17 additional new species.

Furthermore, there is no agreement regarding Cuatrecasas' classification, and many of the genera were not resolved as monophyletic in earlier studies. Even the number of published species is unclear in recent publications. Based on molecular evidence (nrITS), Rauscher (2002) concluded that the subtribe is monophyletic and that the closest relatives are *Rumfordia* DC., *Ichthyothere* Mart. and *Smallanthus* Mack.; he proposed to replace the subtribe Espeletiinae by the "*Espeletia* complex" and mentioned that the group has approximately 100 species. Díaz-Piedrahita et al. (2006) indicated a total of 154 species for Espeletiinae. Fagua and González (2007) mentioned ca. 100 species. Panero (2007) described the subtribe with only three genera (*Carramboa*, *Espeletia* and *Tamananthus*) and 90 species, and Baldwin (2009) reported 90 species as well. The Plant List (Missouri Botanical Garden and Royal Botanic Gardens in Kew 2010), however, shows in total 145 species (*Carramboa* 7 spp., *Coespeletia* 6 spp., *Espeletia* 69 spp., *Espeletiopsis* 24 spp., *Libanothamnus* 14 spp., *Ruilopezia* 24 spp. and *Tamania* 1 sp.), and mentions 4 hybrids, 88 synonyms, 36 scientific plant names of infraspecific rank, and 24 unassessed names. The subtribe has been recently circumscribed within the tribe Millerieae Lindl, as part of the Heliantheae Alliance (Baldwin 2009; Panero 2007).

Methods

The taxonomy of the subtribe was carefully examined. A total of 4408 specimens from personal collections and different herbaria (A, AAU, ANDES, CAS, COL, CUVC, DS, ECON, F, FMB, G, GB, GH, H, HECASA, HUA, K, M, MA, MEDEL, MER, MERF, MIN, MO, MY, MYF, NEU, NY, P, PSO, QCA, QCNE, S, U, UC, US, VALLE, VEN and WAG) were studied. A database was built and 3408 totally iden-

tified specimens were georeferenced. Plants from 1685 photographs taken during fieldwork by the author were identified and georeferenced as well, for a total of 5093 mapped individuals. Maps were generated in ArcGIS10 (ESRI) and DIVA-GIS 7.5 (Hijmans et al. 2012).

A list of all valid names including infraspecific taxa is provided here, with synonyms and basionyms. Autonyms are not included here; these are automatically established with the first instance of valid publication of a name of an infraspecific taxon under a legitimate species, in conformity with the Art. 26.3 of the ICBN (McNeill et al. 2006). To preclude valid publication in this paper of the new taxa and combinations from Cuatrecasas' manuscript, no type information, description, diagnosis or full and direct references were added for these names (in conformity with Art. 33.4 and 33.8 of the ICBN, in McNeill et al. 2006). In addition, the abbreviation “*ined.*” was added after the names, as well as a note about the forthcoming publication. The information for these names will be updated in the online version after the publication of the Cuatrecasas manuscript.

Hybrids are listed at the end of each genus. The dominant morphology of the hybrid corresponds to the first species listed in the hybrid formula. Therefore hybrids are arranged alphabetically by the first species in the formula.

There is no English name for these plants. In Spanish they are usually called frailejones (pronounced fry-lay-ho-ness; in singular frailejón, pronounced fry-lay-hón), which means “big monk”, due to the resemblance of these plants to medieval monks when seen in the typically foggy weather of the páramo. This name is applied to all the species of the group. Some of the smallest species are also called chijí. The arboreal species often receive equivocal (applied to more than one species) names like anime, carrambo and quíñon (*Carramboa* spp.), punta de lanza, tabaco and its derived names, trementino or incienso (*Libanothamnus* spp. and *Tamania chardonii*). Punta de lanza refers to the spear-like shape of the leaves. Tabaco and derived homonymy (tabaque-ro, tabaquillo, tabacote, tabacón, etc.) were probably given by the resemblance of the leaves of some species to tobacco leaves. The names trementino and incienso originated from a common use for these plants. Resin from all the frailejones is abundant and aromatic, and can be used as incense or to extract oil of turpentine, which is used as a solvent for paints and varnishes. This was a common practice in the eighteenth century, as reported in the first description of the genus *Espeletia* by Mutis' expedition in 1792.

There are other common names used, mainly in Venezuela, where the group shows its maximum morphological variation. A list of all common names found on specimens and in the literature (Bernal et al. 2012) contained a total of 49 different names used for all 141 species and some hybrids. There are 16 univocal names (applied only to a single species), but there are no biunivocal names (applied only to a single species, which does not receive any other common name). One species receives six common names and four species are referred to by five names.

The red list for the frailejones of Colombia (García et al. 2005) proposed new Spanish names for all the species included in the publication, with the aim of socializing the knowledge of these species and instilling a feeling of responsibility among local inhabitants to protect these resources. This strategy has been applied successfully in the

past, and remarkable examples exist today, especially with birds, where some endangered species that are well-known today were virtually unknown to the public two decades ago. Frailejones are common motifs in posters, postcards and T-shirts, and most Colombians, northern Ecuadorians and Venezuelans from the mountain regions have seen or heard of frailejones. However, their knowledge about the diversity of this group is extremely low, and most people believe that there is only one species, the frailejón.

In this work, all common names reported for each taxon are included, and the respective countries of origin are indicated in parenthesis (C: Colombia, E: Ecuador, V: Venezuela). When names are in indigenous tongue, the name of the tongue is reported (e.g. Kamsá). Names for intraspecific taxa are reported only when they differ from the names used for the species. For species that lack univocal names, new univocal Spanish names are proposed to create the consciousness, appropriateness and responsibility for conservation among locals (marked with *). Recommended names to use (univocal names) are emphasized in bold.

Systematics

1 *Carramboa* Cuatrec., Phytologia 35(1): 54. 1976. **TYPE:** *Espeletia pittieri* Cuatrec. (= *Carramboa badilloi* var. *pittieri* (Cuatrec.) Cuatrec.)

1.1 *Carramboa badilloi* (Cuatrec.) Cuatrec., Phytologia 35(1): 54. 1976. *Espeletia badilloi* Cuatrec., Ciencia (Mexico) 6(7–9): 261. 1945. **TYPE. VENEZUELA: Mérida:** Páramo de Don Pedro, 2900 m, small tree, yellow ligules, 18 Jul 1944, V.M.Badillo 991 (holotype: VEN).

Carramboa littlei (Aristeg.) Cuatrec., Phytologia 35(1): 54. 1976. *Espeletia littlei* Aristeg., Fl. Venez. 10(1): 433–435, fig. 67, p. 434. 1964. **TYPE. VENEZUELA: Mérida:** La Carbonera, 2700 m, Oct 1953, E.L.Little 15592 (holotype: VEN; isotype: VEN).

Common names. **Anime amarillo** (V), anime montañero (V), carrambo (V), carrambo paramero (V), frailejón amarillo (V), frailejón anime (V).

Note. *C. badilloi* includes now former *C. littlei* and *C. pittieri* was proposed as a variety of *C. badilloi* (below). However some individuals show contrasting morphological differences, especially in the morphology of the leaves. More ecological, morphological, anatomical and genetic studies are needed to determine if these entities are indeed different taxa.

***Carramboa badilloi* var. *pittieri* (Cuatrec.) Cuatrec.**, *ined.* (Forthcoming publication in Cuatrecasas in press.)

Carramboa pittieri (Cuatrec.) Cuatrec.

Espeletia pittieri Cuatrec.

Common names. Carrambo (V), anime amarillo (V), **anime montañero** (V).

1.2 *Carramboa rodriguezii* (Cuatrec.) Cuatrec., *Phytologia* 35(1): 54. 1976. *Espeletia rodriguezii* Cuatrec., *Phytologia* 29(5): 379–382. 1975. **TYPE. VENEZUELA: Mérida:** Betania, between Páramo de Las Coloradas and El Molino, 2400 m, Jun 1974, M.López-Figueiras & H.Rodríguez 9050 (holotype: US!; isotypes: FI, MERFI!).

Common names. Carrambo (V), **carrambo de las Coloradas***.

Note. No large populations of this species have been observed and it might be an intergeneric hybrid.

1.3 *Carramboa trujillensis* (Cuatrec.) Cuatrec., *Phytologia* 35(1): 54. 1976. *Espeletia trujillensis* Cuatrec., *Mutisia* 16: 5–7, figs. 4, 5T. 1953. **TYPE. VENEZUELA: Trujillo:** Quebrada del Cortijo, above Humocaró Bajo, 2600–2800 m, 6 Feb 1944, J.Steyermark 55341 (holotype: FI; isotype: FI!).

Common names. Anime (V), carrambo (V), **quiñón** (V).

1.4 *Carramboa wurdackii* (Ruiz-Terán & López-Fig.) Cuatrec., *Phytologia* 52(3): 158. 1982. *Espeletia wurdackii* Ruiz-Terán & López-Fig., *Rev. Fac. Farm. Univ. Andes Mérida* 17: 1–5, figs. 1–2. 1976. *Libanothamnus wurdackii* (Ruiz-Terán & López-Fig.) Cuatrec., *Phytologia* 35(1): 51. 1976. **TYPE. VENEZUELA: Trujillo:** Finca Florencia, 2450 m, near Carache, 3 Apr 1976, M.López-Figueiras 12957 (holotype: MERFI; isotype: NY!, US!).

Common names. Carrambo (V), **carrambo de Carache***.

Note. This species is known from only a few collections; it may be an intergeneric hybrid.

Hybrids

***Carramboa* × *tachirensis* (Aristeg.) Cuatrec.** (= *Carramboa badilloi* var. **pittieri** (Cuatrec.) Cuatrec. × *Ruilopezia marcescens* (S. F. Blake) Cuatrec.), *Phytologia* 52(3): 158. 1982 (hybrid status in *Rev. Fac. Agron.* 1:475–481. 2007). *Espeletia tachirensis* Aristeg., *Fl. Venez.* 10(1): 427–428. 1964. **TYPE. VENEZUELA: Táchira:** Páramo del Batallón, 26 Sep 1956, L.Aristeguieta 2523 (holotype: VEN; isotype: US!).

Espeletiopsis tachirensis (Aristeg.) Cuatrec., *Phytologia* 35(1): 56. 1976.

Common names. Carrambo (V), **carrambo de Táchira***.

Note. Molecular analyses of ITS and ETS regions by the author confirm the hybrid nature of this combination (Diazgranados 2012). Anatomical and morphological studies support this conclusion (Morillo and Briceño 2007).

2 *Coespeletia* Cuatrec., *Phytologia* 35(1): 55–56, fig. 4, pl. 61. 1976. **TYPE. *Coespeletia spicata*** (Sch. Bip. ex Wedd.) Cuatrec.

2.1 *Coespeletia albarregensis* Cuatrec., *ined.* (Forthcoming publication in Cuatrecasas in press.)

Common names. Albarragüero (V), frailejón (V).

2.2 *Coespeletia elongata* (A. C. Sm.) Cuatrec., Phytologia 35(1): 57. 1976. *Espeletia elongata* A. C. Sm., Amer. J. Bot. 27: 546. 1940. **TYPE. VENEZUELA: Mérida:** Páramo de los Conejos, 4000 m, 10 Sep 1983, J.Hanbury-Tracy 83 (holotype: NY!; isotype: K).

Common names. Frailejón (V), frailejón amarillo (V), **frailejón florón***.

2.3 *Coespeletia laxiflora* (S. Díaz & Rodr.-Cabeza) S. Díaz & Rodr.-Cabeza, Revista Acad. Colomb. Ci. Exact. 35(137): 422, 424. 2011. *Espeletiopsis laxiflora* S. Díaz & Rodr.-Cabeza, Revista Acad. Colomb. Ci. Exact. 34 (133): 441–454, figs. 1, 3A–B. 2010. **TYPE. COLOMBIA: Santander:** Santuario de Fauna y Flora Guanentá Alto Río Fonce, Municipio de Encino, Vda. Avendaños Tres, sector Páramo de Las Playas, 19 Oct. 2008, B. V. Rodríguez-Cabeza 1993 (holotype: COL; isotypes: COL, HUA, UIS, UPTC).

Common names. Frailejón (C), **frailejón laxo***.

2.4 *Coespeletia moritziana* (Sch. Bip. ex Wedd.) Cuatrec., Phytologia 35(1): 57. 1976. *Espeletia moritziana* Sch. Bip. ex Wedd., Chlor. And. 1: 65–66. 1856. **TYPE. VENEZUELA: Mérida:** Sierra Nevada, 4000–4500 m, 1842, J.J.Linden 399 (lectotype: P; J.J.Linden 368 and 398 isoelectotypes: P, US!).

Espeletia rufescens Cuatrec., Bol. Soc. Venez. Ci. Nat. 17 (85): 88–91, figs. 5, 6. 1956. **TYPE. VENEZUELA: Mérida:** Sierra Nevada de Mérida, 12000 ft, J.J.Linden 398, (lecto-holotype: P, only leaves; J.J.Linden 399 paratype: P, only leaves pro parte).

Common names. Frailejón (V), frailejón amarillo (V), **frailejón cabello de ángel** (V), frailejón dorado (V), frailejón morado (V).

Note. *E. rufescens* is an herbarium mixture and only the leaves of the type collection of *E. rufescens* correspond to *C. moritziana* (see *E. rufescens* below).

2.5 *Coespeletia spicata* (Sch. Bip. ex Wedd.) Cuatrec., Phytologia 35(1): 57. 1976. *Espeletia spicata* Sch. Bip. ex Wedd., Chlor. And. 1: 65. 1856. **TYPE. VENEZUELA: Mérida:** Sierra Nevada de Mérida, 14000 ft, Aug 1842, J.J.Linden 400 (lectotype: P; isoelectotypes K!, FI).

Coespeletia alba (A. C. Sm.) Cuatrec., Phytologia 35(1): 57. 1976. *Espeletia alba* A. C. Sm., Brittonia 1(7): 512–513. 1935. **TYPE. VENEZUELA: Mérida:** Sierra Nevada de Mérida, Cordillera del Norte, Páramo de Mucurubá El Rincon, El Colorado Fila de Estiti, 3900 m, Apr 1930, W.Gehriger 125 (holotype: NY!; isotypes: F!, G!, MO!, US!, VEN, photo holotype 4789: F).

Common names. Frailejón (V), frailejón amarillo (V), frailejón blanco (V), frailejón gris (V), frailejón morado (V), **frailejón pincho***.

2.6 *Coespeletia thyrsoformis* (A. C. Sm.) Cuatrec., Phytologia 35(1): 57. 1976. *Espeletia thyrsoformis* A. C. Sm., Brittonia 1(7): 513. 1935. **TYPE. VENEZUELA: Táchi-**

ra: wrongly cited from “Páramo de Mucuchíes”, Dec 1927, R.Gutzwiller 36 (holotype: US!; isotypes: G!, NY!).

Common names. Frailejón (V), **frailejón amarillo del batallón***.

Coespeletia thyrsoformis* f. *marcana* (Cuatrec.) Cuatrec., *ined. (Forthcoming publication in Cuatrecasas in press.)

Coespeletia marcana (Cuatrec.) Cuatrec.

Espeletia marcana Cuatrec.

Espeletia racemosa Cuatrec.

2.7 *Coespeletia timotensis* (Cuatrec.) Cuatrec., *Phytologia* 35(1): 57. 1976. *Espeletia timotensis* Cuatrec., *Bol. Soc. Venez. Ci. Nat.* 17(85): 84, figs. 1, 2. 1956. **TYPE. VENEZUELA: Mérida:** Sierra Nevada, Páramo de Timotes–Piñango, 4000 m, open páramo, 9 Dec 1938, J.Hanbury-Tracy 193 (holotype: K; isotypes: NY!, US!).

Coespeletia lutescens (Cuatrec. & Aristeg.) Cuatrec., *Phytologia* 35(1): 57. 1976. *Espeletia lutescens* Cuatrec. & Aristeg., *Fl. Venez.* 10(1): 443–444. 1964. **TYPE. VENEZUELA: Mérida:** Páramo de Timotes, 3000–3500 m, 4000 m on tag, Dec 1910, A. Jahn 149 (holotype: US!; isotypes: G, VEN).

Common names. Frailejón (V), frailejón amarillo (V), frailejón blanco (V), **frailejón bravo** (V), frailejón morado (V).

Hybrids

***Espeletia* × *aurantia* Aristeg. (= *Coespeletia moritziana* (Sch. Bip. ex Wedd.) Cuatrec. × *Espeletia schultzii* Wedd.),** *Fl. Venez.* 10(1): 448. 1964. **TYPE. VENEZUELA: Mérida:** Laguna Verde, 4100 m, Oct 1956, L.Aristeguieta 2613 (holotype: VEN).

Note. Only a few individuals of this hybrid combination can be seen in the topolocality in the surroundings of Laguna Verde, where *C. moritziana* and *E. schultzii* have abundant populations. Morphological characters described for *E. aurantia* are not consistent and are certainly a mix between the parental species proposed here. The large capitula with carnose and rather short orange ray flowers is typical for *C. moritziana*. The leaves, which are broader than in *C. moritziana*, the large opposite branchlets of the synflorescence and the hirsute ray corollas suggest introgression from *E. schultzii*.

***Coespeletia moritziana* (Sch. Bip. ex Wedd.) Cuatrec. × *C. timotensis* (Cuatrec.) Cuatrec. Representative specimens. VENEZUELA: Mérida:** alrededores del Picacho de El Águila, 12 Nov 1952, L.Aristeguieta 1076 (US!); ibidem: Sierra Nevada, páramos alrededores de Picos Bolívar y Espejo, 4600 m, 15 Dec 1959, H.G.Barclay 10187 (US!); ibidem: Páramo de Las Cruces (Páramo de Mucuchíes), a 6,3 km de El Águila por la carretera a Piñango, Distritos Rangel y Justo Briceño, 4220 m, caulirrosula de 1/2 m de altura. sinflorescencias axilares, racemosas, capítulos con lígulas rojizas, hojas amarillas en la base, 11 Jun 1983, P.E.Berry 4293 (US!, MO!); ibidem: Páramo de Mucuchíes, el Águila, 4200 m, 5 Oct 1969, J.Cuatrecasas 28029 (US!); ibidem: Páramo

de Mucuchíes, cabeceras del río Chama, cercanías del Pico El Águila, Cordillera de los Andes, 3900–4000 m, 5 Oct 1977, M.López-Figueiras 14023 (US!).

***Coespeletia spicata* (Sch. Bip. ex Wedd.) Cuatrec. × *C. timotensis* (Cuatrec.) Cuatrec. Representative specimens. VENEZUELA: Mérida: Miranda, páramo en las cabeceras de la Quebrada El Turmero (afluente del Río Motatán), a 11.7 km de El Águila por la carretera a Piñango, 4160 m, 12 Nov 1984, P.E.Berry 4399 (US!); ibidem: a 10.8 km de El Águila por la carretera a Piñango, 4180 m, 12 Nov 1984, P.E.Berry 4400 (US!); ibidem: a 11.5 km de El Águila por la carretera a Piñango, 4180 m, 12 Nov 1984, P.E.Berry 4401 (US!).**

***Coespeletia timotensis* (Cuatrec.) Cuatrec. × *Espeletia schultzei* Wedd. Representative specimens. VENEZUELA: Mérida: Páramo de Las Cruces (Páramo de Mucuchíes), a 6,3 km de El Águila por la carretera a Piñango, Distritos Rangel y Justo Briceño, 4300 m, 17 Dec 1982, P.E.Berry 3996(a) (US!).**

3 *Espeletia* Mutis ex Humb. & Bonpl., Pl. Aequinoc. 2: 10. 1808. TYPE. *Espeletia grandiflora* Humb. & Bonpl.

3.1 *Espeletia annemariana* Cuatrec., Phytologia 32(4): 315–317. 1975. TYPE. COLOMBIA: Boyacá: Alto de Mogotes, from Vadohondo to Labranzagrande, subpáramo, 3300 m, 2 Apr 1973, A.M.Cleef 9296 (holotype: US!; isotypes: COL!, U).

Common names. Frailejón (C), **frailejón blanco***.

***Espeletia annemariana* var. *rupicola* Cuatrec., Phytologia 32(4): 317. 1975. TYPE. COLOMBIA: Boyacá: Peña del Arnical headwaters of Quebrada Candelas, rocky cliffs, 3600 m, 6 Apr 1973, A.M.Cleef 9466 (holotype, US!; isotypes: COL!, U).**

Common names. Frailejón (C), **frailejón blanco de las rocas***.

3.2 *Espeletia arbelaezii* Cuatrec., Revista Acad. Colomb. Ci. Exact. 3(11): 247–248, figs. 2, 6E, pl. B. 1940. TYPE. COLOMBIA: Boyacá: Páramo de Güina (o de Huínas), 3300 m, 19 Sep 1938, J.Cuatrecasas & H.García-Barriga 1964 (holotype: COL!; isotypes: COL!, F!, US!).

Common names. Frailejón (C), frailejón de Pérez-Arbeláez (C), **frailejón orejudo***.

Note. This is a polymorphic species that needs to be revised.

3.3 *Espeletia argentea* Humb. & Bonpl., Pl. Aequinoc. 2: 14–15, pl.7, Nov. 1808. TYPE. COLOMBIA: Cundinamarca: Zipaquirá, reg. Novae Granatae, ano 1801, Humboldt & Bonpland (holotype: P, herb Bonpland; fragment in F).

Espeletia nivea Moritz ex Wedd., nom. illeg. Chlor. And. 1: 65. 1856 [1855 publ. 30 Jun 1856].

Common names. Frailejón de hoja lisa (C), Frailejón plateado (C), **frailejón plateado de Cundinamarca***.

***Espeletia argentea* f. *phaneractis* (S. F. Blake) Cuatrec.**, *Phytologia* 27(3): 179. 1973. *Espeletia argentea* subsp. *phaneractis* S. F. Blake, *Contr. U.S. Natl. Herb.* 22(8): 603–604. 1924. *Espeletia phaneractis* (S. F. Blake) A. C. Sm., *Brittonia* 1(7): 525–526, Pl. 2, figs. 49–50. 1935. **TYPE. COLOMBIA: Cundinamarca:** Zipaquirá, dry Páramo on Mt. Águila West of city, 3100–3300 m, 20–24 Oct 1917, f.W.Pennell 2522 (holotype: US!; isotypes: F!, GH, MO!, NY!).

Common names. Frailejón de hoja lisa (C), frailejón plateado (C), **frailejón plateado de Cundinamarca***.

3.4 *Espeletia ariana* S. Díaz & Rodr.-Cabeza, *Revista Acad. Colomb. Ci. Exact.* 30 (16): 343–345 figs. 7, 8C–D. 2006. **TYPE. COLOMBIA: Boyacá:** Municipio de Socotá, Vereda Comeza Hoyada, sector Pantano Hondo, lado izquierdo arriba de la quebrada Pantano Hondo, 3600 m alt., 19 oct 2005. B. V. Rodríguez-Cabeza, L. Velasco & E. Benítez 1454 (holotype: COL; isotype: UIS).

Common names. Frailejón (C), **frailejón del caminante***.

3.5 *Espeletia aristeguietana* Cuatrec., *Phytologia* 27(3): 174–176. 1973. **TYPE. VENEZUELA: Trujillo:** Páramo La Cristalina, La Cañada 2500–2600 m, J.Cuatrecasas, L.Ruiz-Terán & M.López-Figueiras 28194 (holotype: US!).

Common names. Frailejón (V), **frailejón de la Cristalina***.

3.6 *Espeletia azucarina* Cuatrec., *Phytologia* 47(1): 12–13. 1980. **TYPE. COLOMBIA: Boyacá:** Cerro Pan de Azúcar, north of Belén, 4000 m, A.M.Cleef 9835 (holotype: US!; isotypes: COL!, HPUJ!, U!, US!).

Common names. Frailejón (C), **frailejón de Pan de Azúcar (C).**

3.7 *Espeletia barclayana* Cuatrec., *Phytologia* 38(1): 8–12. 1977. **TYPE. COLOMBIA: Cundinamarca:** Represa del Neusa, hill at NW, 3650 m, 26 May 1972, A.M.Cleef & Jaramillo 4174 (holotype: US!; isotypes: COL!, U).

Common names. Frailejón (C), **frailejón repollo de Cundinamarca***.

3.8 *Espeletia batata* Cuatrec., *Phytologia* 40(1): 27–29. 1978. **TYPE. VENEZUELA: Mérida:** Páramo de Los Granates, Alto del Morato, 3600 m, 10 Oct 1969, J.Cuatrecasas, L.Ruiz-Terán, M.López-Figueiras 28058 (holotype: US!; isotypes: MERF!, US!).

Common names. **Frailejón batato** (V), frailejón patata (V), pata de burro (V).

3.9 *Espeletia boyacensis* Cuatrec., *Phytologia* 27(3): 176–179. 1973. **TYPE. COLOMBIA: Boyacá:** Alto de Canutos, open páramo, 3350 m, J.Cuatrecasas & Rodríguez 27759 (holotype: US!; isotype: COL).

Espeletia phaneractis subsp. *boyacensis* Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(14): 167, figs. 9, 12J. 1941. **TYPE. COLOMBIA: Boyacá:** near Las Gaitas, 3300 m, Boyacá, COLOMBIA: J.Cuatrecasas 10364A (holotype: COL).

Common names. Frailejón plateado (C), **frailejón plateado boyacense***.

3.10 *Espeletia brachyaxiantha* S. Díaz, Mutisia 37: 5–10, fig. 2. 1972. **TYPE. COLOMBIA: Boyacá:** Páramo Alto de Las Cruces, NW of Belén, 3800 m, 6 Mar 1972, A.M.Cleef 2326 (holotype: COL!; isotypes: U, US!).

Common names. Frailejón (C), **frailejón de Belén** (C).

3.11 *Espeletia brassicoidea* Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(15–16): 337–338, figs. 1, 6A, 6B, pl. I, II. 1941. **TYPE. COLOMBIA: Norte de Santander:** Páramo de Fontibón, 2700 m, 21 Jun 1940, J.Cuatrecasas & H.García-Barriga 10096 (holotype: COL!; isotypes: COL!, US!).

Espeletia brassicoidea f. *pamplonensis* Cuatrec., Revista Acad. Colomb. Ci. Exact. 5(17): 338. 1942. *Nomen nudum*.

Common names. Frailejón (C, V), **frailejón arrepollado** (C).

Espeletia brassicoidea subsp. *angusta* Cuatrec., Phytologia 47(1): 13. 1980. **TYPE. COLOMBIA: Norte de Santander:** Páramo between Pamplona and Berlín, 3050 m, 23 Sep 1969, J.Cuatrecasas & L.Rodríguez 27916 (holotype: US!; isotype: COL).

Espeletia brassicoidea subsp. *constricta* (Cuatrec.) Cuatrec., Revista Acad. Colomb. Ci. Exact. 5(17): 23. 1942. *Espeletia brassicoidea* f. *constricta* Cuatrec., Revista Acad. Colomb. Ci. Exact. 5(17): 23. 1942. **TYPE. COLOMBIA: Norte de Santander:** Páramo de Tamá, toward La Cueva, 3100 m, 28 Oct 1941, J.Cuatrecasas, R.E.Schultes & E.Smith 12653B (holotype: COL!; isotypes: F!, US!).

Espeletia brassicoidea f. *minorifolia* Cuatrec., Revista Acad. Colomb. Ci. Exact. 5(17): 23, pl. II. 1942. **TYPE. COLOMBIA: Norte de Santander:** Páramo de Tamá ca. La Cueva, 3100–3200 m, 28 Oct 1941, J.Cuatrecasas, Schultes & Smith 12653 (holotype: COL; isotypes: F!, US!).

3.12 *Espeletia cabrerensis* Cuatrec., Phytologia 32(4): 318–320. 1975. **TYPE. COLOMBIA: Cundinamarca:** Cabrera, to Páramo de Sumapaz 3200 m, 23 Feb 1970, Uribe-Uribe 6400 (holotype: US!; isotype: COL).

Common names. Frailejón (C), **frailejón de Cabrera** (C).

3.13 *Espeletia cachaluensis* Rodr.-Cabeza & S. Díaz, Revista Acad. Colomb. Ci. Exact. 32(125): 459–462 figs. 2d, 3. 2008. **TYPE. COLOMBIA: Santander:** Santuario de Fauna y Flora Guanentá Alto Río Fonce. Municipio de Encino Vereda Avendaños, sector Los cuadros. 3744 m alt., 12 oct 2007. B.V.Rodr.-Cabeza, H.Palacios, R.Rivero & J.Velasco 1897 (holotype: COL; isotypes: COL!, UIS).

Common names. Frailejón (C), **frailejón de Cachalú***.

3.14 *Espeletia canescens* A. C. Sm., Brittonia 1(7): 516–517. 1935. **TYPE. COLOMBIA: Boyacá:** Páramo del Romeral, sobre La Baja, 3800–4200 m alt. 30 Ene 1927. E.P.Killip & A. C. Smith 18624 (holotype: NY!; isotypes: GH, PH, US!).

Common names. Frailejón (C), **frailejón blanco de Santurbán***.

Note. This species is known only from the type collection, and it might be a hybrid of *E. conglomerata*. Unfortunately the páramo where the species is found is currently threatened by mining.

3.15 *Espeletia cayetana* Cuatrec., Phytologia 52(3): 159. 1982. *Espeletia grandiflora* var. *cayetana* Cuatrec., Phytologia 32(4): 323. 1975. **TYPE. COLOMBIA: Cundinamarca:** Páramo between Cogua and San Cayetano, near Laguna Seca, east slope of Filo del Santuario, valley 2 km south of Laguna Seca, subpáramo scrub, 3650 m alt., 17 Nov 1972, A.M.Cleef 6508 (holotype, US!; isotypes: COL!, HPUJ!, NY!, U!, US!).

Common names. Frailejón (C), frailejón de San Cayetano (C).

3.16 *Espeletia chocontana* Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(14): 164, figs. 4, 12G, pl. III. 1941. **TYPE. COLOMBIA: Cundinamarca:** Páramo de Chocontá, 2800 m, J.Cuatrecasas 9658 (holotype: COL; isotypes: F!, US!).

Common names. Frailejón (C), frailejón de Chocontá (C).

3.17 *Espeletia chontalensis* Rodr.-Cabeza & S. Díaz, Revista Acad. Colomb. Ci. Exact. 32(125): 462–464 figs. 2e–f, 4. 2008. **TYPE. COLOMBIA: Santander:** Santuario de Frauna y Flora Guanentá Alto Río Fonce. Municipio de Encino, Vereda Río Negro, camino sector Chontales–Páramo de la Rusia. 28 jun. 2007. B.V.Rodr.-Cabeza & H.Palacios 1874 (holotype: COL; isotypes: COL!, UIS).

Common names. Frailejón (C), frailejón de Chontales*.

3.18 *Espeletia cleefii* Cuatrec., Phytologia 32(4): 312–314. 1975. **TYPE. COLOMBIA: Boyacá:** Sierra Nevada de Cocuy, Boqueron de Cusiri, A.M. Cleef & P.A. Florschütz 5922 (holotype: US!; isotypes: COL!, U).

Common names. Frailejón (C), frailejón del Cocuy*.

3.19 *Espeletia congestiflora* Cuatrec., Revista Acad. Colomb. Ci. Exact. 3(12): 434–435, figs. 19, 23J, pl. IV. 1940. **TYPE. COLOMBIA: Boyacá:** Páramo de Guantiva near Las Gaitas, 3300 m, J.Cuatrecasas 10366 (holotype: COL!; isotypes: F!, P, US!).

Common names. Frailejón (C), frailejón de bastón*.

3.20 *Espeletia conglomerata* Cuatrec., Brittonia 1(7): 515–516. 1935. **TYPE. COLOMBIA: Norte de Santander:** Páramo del Romeral, 3800–4200 m, 30 Jan 1927, E.P.Killip & A.C.Smith 18635 (holotype: NY!; isotypes: F!, GH, PH, S, US!).

Espeletia brassicoidea f. *contracta* Cuatrec., Revista Acad. Colomb. Ci. Exact. 5(17):23–24. 1942. **TYPE. COLOMBIA: Norte de Santander:** Páramo de Tamá at

La Cueva, 3200 m, 28 Oct 1941, J.Cuatrecasas, Schultes & Smith 12653D (holotype: COL; isotype: F).

Common names. Frailejón (C, V), frailejón aglomerado (C).

3.21 *Espeletia cuniculorum* Cuatrec., Phytologia 40(1): 25–27. 1978. **TYPE. VENEZUELA: Mérida:** Páramo de los Conejos, Cañada de los Puentes, 3350 m, 19 Oct 1972, L.Ruiz-Terán 7722 (holotype: US!; isotypes: HPUJ!, MERF!).

Common names. Frailejón (V), frailejón de los conejos*.

3.22 *Espeletia curialensis* Cuatrec., Phytologia 20(8): 473–475. 1971. **TYPE. COLOMBIA: Boyacá:** Páramo entre Chita y Sacama, vertiente oriental (tributaria del Río Casanare), J.Cuatrecasas & L.Rodríguez 27790 (holotype: US!; isotype: COL!).

Common names. Frailejón (C), frailejón del Curial*.

***Espeletia curialensis* var. *exigua* Rodr.-Cabeza & S. Díaz,** Revista Acad. Colomb. Ci. Exact. 30 (16): 347–349 figs. 10, 12C–D. 2006. **TYPE. COLOMBIA: Casanare:** Parque Nacional Natural El Cocuy, Municipio de La Salina, sector El Ahogadero, 3200 m **alt.**, 12 dic 2005. B.V.Rodríguez-Cabeza, J.M.Valderrama & O.E.López 1537 (holotype: COL; isotypes: COL!, UIS).

3.23 *Espeletia discoidea* Cuatrec., Revista Acad. Colomb. Ci. Exact. 3(12): 437–438, figs. 21, 22, 23M, pl. IV. 1940. **TYPE. COLOMBIA: Boyacá:** Páramo de Guantiva below Alto de Canutos, 3200 m, 3 Aug 1940, J.Cuatrecasas 10358 (holotype: COL!; isotypes: COL!, F!, P, US!).

Common names. Frailejón (C), frailejón discoideo (C).

***Espeletia discoidea* var. *brevis* Cuatrec.,** Revista Acad. Colomb. Ci. Exact. 3(12): 437–438, figs. 21, 22, 23 M, pl. IV. 1940. **TYPE. COLOMBIA: Boyacá:** Páramos NW of Belen, headwaters of Quebrada Laguna Grande, NW slope of the dividing ridge with dry graminetum of Calamagrostis effusa, 3830 m, 6 May 1973, A.M.Cleef 9774 (holotype: US!; isotypes: COL!, U).

Common names. Frailejón (C), frailejón discoideo (C).

3.24 *Espeletia dugandii* Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(14): 163–164, figs. 3, 12H, pl. III. 1941. **TYPE. COLOMBIA: Santander:** Peralonso, Páramo del Almorzadero, 3200 m, 19 Jul 1940, J.Cuatrecasas & H.García-Barriga 9889 (holotype: COL!; isotypes: F!, US!).

Common names. Frailejón (C), frailejón de Cerrito*, frailejón de Dugand (C).

3.25 *Espeletia episcopal* S. Díaz & Rodr.-Cabeza, Revista Acad. Colomb. Ci. Exact. 30 (16): 341–343 figs. 6, 8C–D. 2006. **TYPE. COLOMBIA: Boyacá:** Municipio de Socotá, Vereda Comeza Hoyada, sector río Arzobispo, parte alta, Los Corazones,

alrededores de las lagunas Larga y Peña Negra. 3700 m **alt.**, 21 Oct. 2005. B.V.Rodr.-Cabeza, L.Velasco & E.Benitez 1498 (holotype: COL; isotype: UIS).

Common names. Frailejón (C), frailejón del Arzobispo*.

3.26 *Espeletia estanislana* Cuatrec., Revista Acad. Colomb. Ci. Exact. 3(12): 429, figs. 10, 23–A, pl. I. 1940. **TYPE. COLOMBIA: Santander:** Páramo del Almorzadero, 3700–3800 m, Hno. A.Miguel s.n. (holotype, US!).

Common names. Frailejón (C), frailejón de Estanislao (C), frailejón unifloro*.

3.27 *Espeletia formosa* S. Díaz & Rodr.-Cabeza, Revista Acad. Colomb. Ci. Exact. 30 (16): 336–339 figs. 3, 4E–F. 2006. **TYPE. COLOMBIA: Boyacá:** Parque Nacional Natural Pisba. Municipio de Socotá, Vereda Chipa viejo, ruta libertadora, sector El Santuario. 3414m alt. 16 Jun 2005. B.V.Rodríguez-Cabeza & L.Velasco 1407 (holotype: COL; isotype: COL!).

Common names. Frailejón (C), frailejón elegante*.

3.28 *Espeletia frontinoensis* Cuatrec., Phytologia 38(1): 15–17. 1977. **TYPE. COLOMBIA: Antioquia:** Cordillera Occidental, Páramo de Frontino near Llano Grande, J.D.Boeke & J.B.McElroy 234 (holotype: US!; isotype: NY!).

Common names. Frailejón (C), frailejón de Frontino*.

3.29 *Espeletia grandiflora* Humb. & Bonpl., Pl. Aequinoc. 2: 11–13. 1808. 1809 (t.p.). **TYPE.** Plant Aequinoc, Santa Fe de Bogotá et Quindio, Herbar de l’Amerique equatoriale, donné par M.A.Bonpland, Humboldt & Bonpland in “Herb. HBK” (holotype: P (fiche 112); isotype: P; photo FM-15154: US, B, from destroyed isotype, no more extant).

Espeletia grandiflora f. *longiligulata* Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(14): 169, fig. 12C. 1941. **TYPE. COLOMBIA: Cundinamarca:** Páramo de Cruz Verde–Bogotá, 3400–3500 m, J.Cuatrecasas 10467 (holotype: COL!; isotype: US!).

Espeletia grandiflora f. *multiflora* Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(14): 169, pl. 4. 1941. **TYPE. COLOMBIA: Cundinamarca:** Páramo de Zipaquirá, 3100–3200 m, J.Cuatrecasas 9527 (holotype: COL!; isotypes: F!, US!).

Espeletia grandiflora f. *reducta* Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(14): 169. 1941. **TYPE. COLOMBIA: Cundinamarca:** Páramo de Zipaquirá, 3100–3200 m, J.Cuatrecasas 9527A (holotype: COL!; isotype: US!).

Common names. Frailejón (C), frailejón mayor*.

***Espeletia grandiflora* subsp. *boyacana* (Cuatrec.) Cuatrec.**, *ined.* (Forthcoming publication in Cuatrecasas in press.)

Espeletia grandiflora var. *boyacana* Cuatrec.

Espeletia grandiflora subsp. *subnivalis* (Cuatrec.) Cuatrec., *ined.* (Forthcoming publication in Cuatrecasas in press.)

Espeletia grandiflora var. *subnivalis* Cuatrec.

Espeletia grandiflora var. *attenuata* Cuatrec., Phytologia 32(4): 325–326. 1975.

TYPE. COLOMBIA: Cundinamarca: Lagunas de Chisacá, Macizo de Bogotá, 3650–3700 m, 29 Dec 1959, J.Cuatrecasas & R. Jaramillo 25748 (holotype: US!; isotypes: BC!, F!, COL!, HPUJ!).

3.30 *Espeletia hartwegiana* Sch. Bip. ex Cuatrec., Trab. Mus. Nac. Ci. Nat., Ser. Bot. 26: 17, pl. I, II-2. 1933. Ibid. 27: 105–114, pl. 23–25. 1934. Ibid. 33: 140. 1936. **TYPE. COLOMBIA: Cauca:** Páramo de Guanacas, 1841–42, C.T.Hartweg 1137 (lectotype: G (photo FM-28724); isolectotypes: P, FI, G, K!, LE, W).

Espeletia hartwegiana Sch. Bip., in Wedd., Chlor. And. 1: 62. 1856. Pro syn. sub *Espeletia grandiflora* Humb. & Bonpl., Pl. Aequinoc. 2: 11–13. 1808. 1809 (t.p.).

Espeletia grandiflora var. *hartwegiana* (Cuatrec.) Benoist, Bull. Soc. Bot. France 92: 139. 1945.

Common names. Frailejón (C), frailejón amarillo (C), frailejón de Los Nevados*.

Espeletia hartwegiana subsp. *barragensis* Cuatrec., Phytologia 45(1): 23–24. 1980.

TYPE. COLOMBIA: Valle del Cauca: Páramo de Santa Lucía, above Barragán, 3600–3680 m, 16 Mar 1946, J.Cuatrecasas 20076 (holotype: COL!; isotypes: BC!, F!, HPUJ!, P, US!).

Common names. Frailejón (C), frailejón de Barragán*.

Espeletia hartwegiana subsp. *centroandina* Cuatrec., Phytologia 45(1): 21–33. 1980.

TYPE. COLOMBIA: Caldas: Nevado del Ruiz, El Aprisco, 3600–3800 m, 5 May 1940, J.Cuatrecasas 9312 (holotype: COL!; isotypes: F!, HPUJ!, US!).

Espeletia centroandina Cuatrec., pro syn. sub *Espeletia hartwegiana* Sch. Bip. ex Cuatrec., Trab. Mus. Nac. Ci. Nat., Ser. Bot. 26: 17. 1933.

Common names. Frailejón (C), frailejón de Los Nevados*.

Espeletia hartwegiana var. *morarum* Cuatrec., Phytologia 45(1): 25–27. 1980.

TYPE. COLOMBIA: Cauca: Páramo de Moras, 3600 m, 19 Mar 1973, J.Cuatrecasas & Lehmann 28638 (holotype: US!; isotypes: COL!, US!).

Common names. Frailejón (C), frailejón de Moras*.

Espeletia hartwegiana var. *vegasana* Cuatrec., Phytologia 45(1): 24–25. 1980.

TYPE. COLOMBIA: Valle del Cauca: Páramo de Las Vegas, in Páramo de Las Hermosas, 3800 m, 22 Mar 1946, J.Cuatrecasas 20285 (holotype: US!; isotypes: COL!, HPUJ!, F!).

Common names. Frailejón (C), frailejón de Las Hermosas*.

3.31 *Espeletia idroboi* Cuatrec., *Phytologia* 38(1): 12–15. 1977. **TYPE. COLOMBIA: Cauca:** Valle de Las Papas, 2910 m, Idrobo, Pinto & Bischler 3372 (holotype: COL; isotype: P).

Common names. Frailejón (C), frailejón del Cauca*, frailejón de Idrobo (C).

3.32 *Espeletia incana* Cuatrec., *Revista Acad. Colomb. Ci. Exact.* 3(12): 435–436, figs. 20, 23–K, pl. IV. 1940. **TYPE. COLOMBIA: Boyacá:** Páramo de la Rusia, NW slopes, 3500 m, 4 Aug 1940, J. Cuatrecasas 10430 (holotype: COL; isotypes: COL, F!, P, US!).

Common names. Frailejón (C), frailejón blanco (C), frailejón de los incas*.

***Espeletia incana* f. *prolifcens* Cuatrec.**, *Revista Acad. Colomb. Ci. Exact.* 3(12): 435, figs. 20A–E, 23K. 1940. **TYPE. COLOMBIA: Boyacá:** Páramo de la Rusia, NNW of Duitama, Serranía de Peña Negra, cerca de Las Torres, 3900 m alt, caulirósula 3 m, hojas oscuro-grisáceas, 12 Dec 1972, A.M. Cleef 7124 (Holotype, US!; isotypes: COL!, U)

Common names. Frailejón (C).

3.33 *Espeletia jajoensis* Aristeg., *Fl. Venez.* 10(1): 424–425. 1964. **TYPE. VENEZUELA: Trujillo:** El Paramito, between Jajó and Tuñame, 3000 m, Aug 1958, L. Aristeguieta & Medina 3452 (holotype: VEN; isotypes: VEN, US!).

Espeletiopsis jajoensis (Aristeg.) Cuatrec., *Phytologia* 35(1): 56. 1976.

Common names. Frailejón (V), frailejón de Jajó*, frailejón peludo blanco (V), frailejón punta de lanza pequeño de hoja ancha (V).

3.34 *Espeletia jaramilloi* S. Díaz, *Mutisia* 37: 1–5. 1972. **TYPE. COLOMBIA: Boyacá:** Páramo de Pisba, 3500–3600 m, 9 Oct 1971, R. Jaramillo, G. Lozano & S. Díaz 5047 (holotype: COL; isotype: US!).

Common names. Frailejón (C), frailejón de Jaramillo (C).

3.35 *Espeletia killipii* Cuatrec., *Revista Acad. Colomb. Ci. Exact.* 3(12): 425–426, figs. 2, 3, 4–D, E, pl. 1. 1940. **TYPE. COLOMBIA: Cundinamarca:** Páramo de Guasca, eastern slope, 3200–3300 m, 11 Oct 1939, H. García-Barriga 8117 (holotype: COL; isotype: US!).

Common names. Frailejón (C), frailejón de Chisacá*.

***Espeletia killipii* var. *chisacana* Cuatrec.**, *Phytologia* 32(4): 326. 1975. **TYPE. COLOMBIA: Cundinamarca:** Páramo de Chisacá, 3680–3700 m, 16 Sep 1961, J. Cuatrecasas & Jaramillo 25986 (holotype: US!; isotypes: COL!, F!, MA, P).

Common names. Frailejón (C), frailejón de Chisacá*.

3.36 *Espeletia lopezii* Cuatrec., *Revista Acad. Colomb. Ci. Exact.* 3(11): 248–249, figs. 3, 4, 6D, pl. C. 1940. **TYPE. COLOMBIA: Boyacá:** Las Lagunillas, in Nevado

del Cocuy, 4100 m, 12 Sep 1938, J. Cuatrecasas & H. García-Barriga 1540 (holotype, COL!; isotypes: F!, P, US!).

Common names. Frailejón (C), frailejón perrito (C).

Espeletia lopezii subsp. *ursina* Cuatrec., *ined.* (Forthcoming publication in Cuatrecasas in press.)

Common names. Frailejón del oso*.

Espeletia lopezii var. *escobalensis* Cuatrec., Phytologia 45(1): 21. 1980. **TYPE. COLOMBIA: Boyacá:** Alto del Escobal, Páramo between Soatá and Cocuy, 3800 m, 8 Sep 1938, J. Cuatrecasas & H. García-Barriga 1236 (holotype: US!; isotypes: COL!, F).

Espeletia lopezii var. *major* Cuatrec., Phytologia 31(4): 325–327. 1975. **TYPE. COLOMBIA: Boyacá:** Quebrada del Curial, Nevado del Cocuy, Páramo on the eastern slope, 3350 m, Boyacá, COLOMBIA: 15 Sep 1969, J. Cuatrecasas & Rodríguez 27791 (holotype: COL!; isotype: US!).

Espeletia lopezii f. *alticola* Cuatrec., Phytologia 31(4): 327–328. 1975. **TYPE. COLOMBIA: Boyacá:** Páramo Cóncavo, Nevado del Cocuy, superPáramo 4335 m, 26 Feb 1973, A.M. Cleef 8547 (holotype: US!; isotypes: COL!, HPUJ!, U).

3.37 *Espeletia marnixiana* S. Díaz & Pedraza, Revista Acad. Colomb. Ci. Exact. 25(94): 12–15, figs. 3, 4. 2001. **TYPE. COLOMBIA: Cauca:** Mpio. de Argelia, vereda El Naranjal, Río Plateado, Páramo de la Soledad, M.L. Becking 1042 (holotype: COL!).

Common names. Frailejón (C), frailejón de Argelia*.

3.38 *Espeletia marthae* Cuatrec., Phytologia 38(1): 20–22. 1977. **TYPE. VENEZUELA: Mérida:** Páramo del Guirigay–Llano Corredor, swampy ground, 3300 m, Mérida, VENEZUELA, 25 Oct 1969, J. Cuatrecasas, M. López-Figueiras & Marciano-Berti 28162 (holotype: US!; isotype: MERF!).

Common names. Frailejón (V), frailejoncito plateado (V).

3.39 *Espeletia mirabilis* S. Díaz & Rodr.-Cabeza, Revista Acad. Colomb. Ci. Exact. 34 (133): 441–454, figs. 3F, 4. 2010. **TYPE. COLOMBIA: Boyacá:** Parque Nacional Natural Pisba, Municipio de Socotá, Vereda Corral de Piedra, sector Río Arzobispo, parte alta de Los Estupendos, 3550 m de alt., 05° 58' 33"N 72° 33' 47"W, 14 sep 2008, B. V. Rodr.-Cabeza & L. Velasco 2001 (holotype: COL; isotypes: COL!, HUA, UIS, UPTC).

Common names. Frailejón (C), frailejón de Los Estupendos*.

3.40 *Espeletia miradorensis* (Cuatrec.) Cuatrec., Phytologia 52(3): 158. 1982. *Espeletia grandiflora* var. *miradorensis* Cuatrec., Phytologia 32(4): 324. 1975. **TYPE.**

COLOMBIA: Cundinamarca: El Mirador, Páramo de Sumapaz, 3560 m, A.M.Cleef 8421 (holotype: US!; isotypes: COL!, U).

Common names. Frailejón (C), frailejón del Mirador*.

3.41 *Espeletia murilloi* Cuatrec., Revista Acad. Colomb. Ci. Exact. 3(12): 425–426, Figs. 4-A, B, C, pl. I. 1940b. Ibid. 4(14): 168. 1941. **TYPE. COLOMBIA: Boyacá:** Páramo de Arcabuco, 2800–2950 m, 22 Feb 1940, E.Pérez-Arbeláez & J.Cuatrecasas 8098 (holotype: COL!; isotypes: F!, US!).

Espeletia murilloi var. *rusiana* Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(14): 168. 1941. **TYPE. COLOMBIA: Boyacá:** Páramo de La Rusia, 3500 m, 4 Aug 1940, J.Cuatrecasas 10429 (holotype: COL!; isotypes: F!, US!).

Espeletia murilloi var. *subcoriacea* Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(14): 168, figs. 11, 12-B, pl. 4. 1941. *Espeletia murilloi* subsp. *subcoriacea* Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(14): 168. 1941. **TYPE. COLOMBIA: Boyacá:** Páramo de la Rusia, 3300–3400 m, 4 Aug 1940, J.Cuatrecasas 10411 (holotype: COL!; isotype: COL!).

Common names. Frailejón (C), frailejón de Murillo (C).

3.42 *Espeletia mutabilis* S. Díaz & Rodr.-Cabeza, Revista Acad. Colomb. Ci. Exact. 30 (16): 345–347 figs. 9, 12A–B. 2006. **TYPE. COLOMBIA: Boyacá:** Municipio de Socha, Vereda El Mortiñal (parte alta), sector El Alizal, sitio El Frailejonal, finca de la Alcaldía, 3700 m alt., 28 Jul 2006. B.V.Rodríguez & P.Velasco 1675 (holotype: COL; isotypes: COL!, UIS).

Common names. Frailejón (C), frailejón mutante*.

3.43 *Espeletia nana* Cuatrec., Phytologia 40(1): 29–31. 1978. **TYPE. VENEZUELA: Trujillo:** La Morita, between Tuñame and Jajó, open páramo, 3000 m, 13 Jul 1971, L.Ruiz-Terán & M.López-Figueiras 2204 (holotype: US!; isotype: MERF!).

Common names. Frailejón (V), frailejón enano (V), frailejoncito (V).

3.44 *Espeletia nemekenei* Cuatrec., Revista Acad. Colomb. Ci. Exact. 3(12): 430–431 figs. 12, 24-C, pl. II. 1940. **TYPE. COLOMBIA: Boyacá:** Alto de Canutos below Páramo de Guantiva, 3200 m, 3 Aug 1940, J.Cuatrecasas 10348 (holotype: COL!; isotypes: COL!, F!, US!).

Common names. Frailejón (C), frailejón de Nemequené (C).

3.45 *Espeletia occidentalis* A. C. Sm., Brittonia 1(7): 520–521. 1935. **TYPE. COLOMBIA: Antioquia–Córdoba:** Cordillera Occidental, Páramo de Chaquiro, 3000–3200 m, f.W.Pennell 4266 (holotype: NY!; isotypes: GH, US!).

Common names. Frailejón (C), frailejón de occidente*.

Espeletia occidentalis subsp. *antioquiensis* (Cuatrec.) Cuatrec., *ined.* (Forthcoming publication in Cuatrecasas in press.)

Espeletia occidentalis var. *antioquensis* Cuatrec.

Common names. Frailejón (C), frailejón de Antioquia*.

3.46 *Espeletia oswaldiana* S. Díaz, Mutisia 32: 1–5, figs. 1, 2. 1970. **TYPE. COLOMBIA: Boyacá:** Vado Hondo, Valle del Río Cusiana, 2880 m, 2 Jul 1968, S.Díaz 74 (holotype COL!; isotype: US!).

Common names. Frailejón (C), frailejón de la Sarna*, frailejón de Oswaldo (C).

3.47 *Espeletia paipana* S. Díaz & Pedraza, Revista Acad. Colomb. Ci. Exact. 25(94): 12–15, figs. 3, 4. 2001. **TYPE. COLOMBIA: Boyacá:** Mpio. de Paipa, Cuchilla El Páramo, 3300 m, D.Stancik 1507 (holotype: COL; isotype: COL!).

Common names. Frailejón (C), frailejón de Paipa (C).

3.48 *Espeletia perijaensis* Cuatrec., Phytologia 38(1): 17–20. 1977. **TYPE. COLOMBIA: Cesar:** Sierra de Perijá, east of Manaure, 2800 m, 10 Nov 1959, J.Cuatrecasas & R.Romero-Castañeda 25192 (holotype: US!; isotype: COL).

Common names. Frailejón (C, V), frailejón de Perijá*.

3.49 *Espeletia pescana* (S. Díaz) S. Díaz, Revista Acad. Colomb. Ci. Exact. 32 (125): 459. 2008. *Espeletia brachyaxiantha* subsp. *pescana* S. Díaz, Mutisia 61: 8–10, fig. 3. 1985. **TYPE. COLOMBIA: Boyacá:** Páramo La Cortadera, Pesca, 3750 m, 21 Aug 1982, M.Bejarano 257 (holotype: COL; isotype: US!).

Common names. Frailejón (C), frailejón de Pesca (C).

3.50 *Espeletia pisbana* S. Díaz & Rodr.-Cabeza, Revista Acad. Colomb. Ci. Exact. 30 (16): 332–334 figs. 1.4 A–B. 2006. **TYPE. COLOMBIA: Boyacá:** Parque Nacional Pisba. Municipio de Socotá, Vereda Pueblo Viejo, ruta libertadora, sector La Australia, sitio el Alto del Almorzadero, 3406 m alt., 16 jun 2005. B.V.Rodr.-Cabeza & L.Velasco 1389 (holotype: COL; IT; COL!).

Common names. Frailejón (C), frailejón de Pisba*.

3.51 *Espeletia praefrontina* Cuatrec., Phytologia 47(1): 10–12. 1980. **TYPE. COLOMBIA: Antioquia:** Cordillera Occidental, Páramo de Frontino ca. Llano Grande, J.D. Boeke & J.M. McElroy 273 (holotype: US!; isotype: NY!).

Common names. Frailejón (C), frailejón del Sol*.

3.52 *Espeletia pulcherrima* Rodr.-Cabeza & S. Díaz, Revista Acad. Colomb. Ci. Exact. 30 (16): 339–341 figs. 5, 8A–B. 2006. **TYPE. COLOMBIA: Boyacá:** Municipio de Chita, Vereda Minas, Páramo de Los Venados, carretera hacia Sácama, km 86, desvío a Chita, 3300 m alt., 23 Oct 2005, B.V.Rodríguez-Cabeza & L.Velasco 1520 (holotype: COL; isotype: UIS).

Common names. Frailejón (C), frailejón pulcro*.

3.53 *Espeletia pycnophylla* Cuatrec., Revista Acad. Colomb. Ci. Exact. 5(17): 24–25, figs. 11–I, 12. 1942. **TYPE. COLOMBIA: Nariño–Putumayo:** Páramo de San Antonio del Bordoncillo (Páramo de Quilinsayaco), 3200 m, 4 Jan 1941, J.Cuatrecasas 11736 (holotype: COL!; isotypes: BC!, F!, US!).

Common names. Frailejón (C, E), frailejón del sur*.

***Espeletia pycnophylla* subsp. *angelensis* Cuatrec.**, Phytologia 45(1): 18–20. 1980. **TYPE. ECUADOR:** Carchi: Páramo del Angel, 3400 m, 21 Jun 1939, E.Asplund 7078 (holotype: US!; isotypes: G, K!, US!).

***Espeletia cochensis* Cuatrec.**, Revista Acad. Colomb. Ci. Exact. 5(17): 25–26, figs. 11J, 13. 1942. **TYPE. COLOMBIA: Putumayo:** Quebrada de Santa Lucía, south side of Laguna de La Cocha, 2850 m, 4 m high, 8 Jan 1941, J.Cuatrecasas 11820 (holotype: COL!; isotypes: F!, US!).

Common names. Frailejón (C, E), frailejón del sur*.

***Espeletia pycnophylla* subsp. *llanganatensis* Cuatrec.**, Phytologia 45(1): 20–21. 1980. **TYPE. ECUADOR:** Tungurahua: Cordillera de los Llanganates, near Las Torres, 3700–3800 m, 23 Nov 1939, E.Asplund 9944 (holotype: S).

Common names. Frailejón (E), singurima (E).

***Espeletia pycnophylla* var. *galerana* Cuatrec.**, Phytologia 45(1): 17. 1980. **TYPE. COLOMBIA: Nariño:** Volcán Galeras, Páramo 3900 m, 7 Feb 1965, J.Cuatrecasas & L.E.Mora 26931 (holotype: US!; isotype: COL).

***Espeletia pycnophylla* var. *lacinulata* Cuatrec.**, Phytologia 45(1), 17–18. 1980. **TYPE. COLOMBIA: Nariño:** Páramo de Quilinsayaco, 3200–3250 m, 21 Mar 1973, J.Cuatrecasas, E.Hernández & A.Estrada 28653 (holotype: US!; isotypes: COL!, PASTO).

3.54 *Espeletia raquirensis* S. Díaz & Rodr.-Cabeza, Revista Acad. Colomb. Ci. Exact. 34 (133): 441–454, fig. 2, 3C–D. 2010. **TYPE. COLOMBIA: Boyacá:** Municipio de ráquira, Vereda Firita, Peña Arriba, Páramo de Rabanal, en límites con el Municipio de Guachetá, vereda San Antonio (Cundinamarca), 3200 m alt., 05° 24'N 73° 36'W, 12 Aug 2008, B.V.Rodríguez-Cabeza, R.Galindo-T, & I.Cortez 1973 (holotype: COL; isotypes: COL!, HUA, UIS, UPTC).

Common names. Frailejón (C), frailejón de Ráquira*.

3.55 *Espeletia robertii* Cuatrec., Phytologia 38(1): 7–10. 1977. **TYPE. COLOMBIA: Norte de Santander–Cesar:** linea divisoria, Cerro de Las Jurisdicciones, H.García-Barriga & R.Jaramillo M. 20648 (holotype: US!; isotype: COL!).

Common names. Frailejón (C), frailejón de Jurisdicciones (C), frailejón de Oroque*, frailejoncito (C).

3.56 *Espeletia rositae* Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(14): 164–165, figs. 5, 12I, pl. III. 1941a. Ibid. 4(15–16): 341. 1941. **TYPE. COLOMBIA: Boyacá:** Páramo de Santa Rosita 3300–3400 m, 3 Aug 1940, J.Cuatrecasas 10371 (holotype: COL!; isotypes: COL!, F!, US!).

Common names. Frailejón (C), frailejón de Santa Rosita (C).

Espeletia rositae* subsp. *macrocephala* (Cuatrec.) Cuatrec., *ined. (Forthcoming publication in Cuatrecasas in press.)

Espeletia rositae var. *macrocephala* Cuatrec.

Common names. Frailejón (C), frailejón de Santa Rosita (C).

3.57 *Espeletia schultesiana* Cuatrec., Revista Acad. Colomb. Ci. Exact. 5(17): 26–27, figs. 14, 11F, G, H, pl. II. 1942. **TYPE. COLOMBIA: Putumayo:** Páramo del Tambillo, 2700–2800 m, 13–14 Dec 1941, R.E.Schultes & C.E.Smith 3096 (holotype: COL!; isotypes: BR, C, COL!, F!, F, FI, G, GH, HPUJ!, MO!, NCU, NY!, P, U!, US!, W).

Common names. Frailejón (C), frailejón de Schultes (C), frailejón “ush” (C, Kamsá).

Espeletia schultesiana* f. *alternifolia* (Cuatrec.) Cuatrec., *ined. (Forthcoming publication in Cuatrecasas in press.)

Espeletia alternifolia Cuatrec.

Common names. Frailejón (C).

3.58 *Espeletia schultzii* Wedd., Chlor. And. 1: 63–64. 1855. **TYPE. VENEZUELA: Mérida:** Páramos prov. Mérida, 3300–3600 m, Jun 1842, J.J.Linden 370, lectotype P; isotypes: BM, BR, F!, FI, G, LE, P, US!, W).

Espeletia corymbosa Sch. Bip. ex Wedd., nom. illeg. Chlor. And. 1: 63. 1856 [1855 publ. 30 Jun 1856].

Common names. Frailejón (V), frailejón amarillo (V), frailejón común (V), frailejón lanudo (V), frailejón manso (V), frailejón octubre (V).

***Espeletia schultzii* var. *bractilobata* Cuatrec.,** Phytologia 45(1): 27. 1980. **TYPE. VENEZUELA: Trujillo:** Paramillo above Jajó via Tuñame, 3100 m, 29 Oct 1969, J.Cuatrecasas, L.Ruiz-Terán & M.López-Figueiras 28189 (holotype: US!; isotype: MERF!).

***Espeletia schultzii* var. *mucurubana* Cuatrec.,** Phytologia 45(1): 28. 1980. **TYPE. VENEZUELA: Mérida:** Páramo de Mucurubá, 3250 m, 20 Oct 1969, J.Cuatrecasas, L.Ruiz-Terán & M.López-Figueiras 28148 (holotype: US!; isotypes: MERF!).

***Espeletia schultzii* var. *subparamuna* Cuatrec.,** Phytologia 45(1): 29. 1980. **TYPE. VENEZUELA: Trujillo:** Páramo de La Cristalina, 2500–2600 m, 17 Feb 1973,

J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28557 (holotype: US!; isotypes: BCI, F!, G!, MERF!, NY!, US!).

Note. Specimens of this taxon have been annotated with the name *Espeletia cristalina* Cuatrec. However, this combination was never published.

3.59 *Espeletia semiglobulata* Cuatrec., *Ciencia* (Mexico) 6(7–9): 264, fig. 5. 1945.

TYPE. VENEZUELA: Mérida: Páramo de Piedras Blancas, 3800 m, V.M. Badillo 821 (holotype: VEN; isotype: VEN).

Espeletia oppositifolia Sch. Bip., mscr. pro parte ex Wedd., *Chlor. And.* 1: 62. 1855. *Nomen nudum*.

Espeletia rufescens Cuatrec., *Bol. Soc. Venez. Ci. Nat.* 17 (85): 88–91, figs. 5, 6. 1956. **TYPE. VENEZUELA: Mérida:** Sierra Nevada de Mérida, 12000 ft, J.J. Linden 398, (lecto-holotype: P, only inflorescence; J.J. Linden 399 paratype: P, pro parte, only inflorescence).

Common names. Frailejón (V), frailejón semigloboso*.

Note. *E. rufescens* is an herbarium mixture and only the synflorescences of the type collection of *E. rufescens* correspond to *E. semiglobulata* (see *E. rufescens* below).

3.60 *Espeletia soroca* S. Díaz & Rodr.-Cabeza, *Revista Acad. Colomb. Ci. Exact.*

30 (16): 334–336 figs. 2, 4C–D. 2006. **TYPE. COLOMBIA: Boyacá:** Municipio de Chita, Vereda Minas, Páramo de Los Venados, carretera hacia Sácama, km 86, desvío a Chita. 3200 m **alt.**, 23 oct 2005. B. V. Rodr.-Cabeza & L. Velasco 150 (holotype: COL; isotype: COL!).

Common names. Frailejón (C), frailejón soroco*.

3.61 *Espeletia standleyana* A. C. Sm., *Brittonia* 1(7): 514–515, Pl. I, 17–21. 1935.

TYPE. COLOMBIA: Santander: Páramo de Santurbán, 3800 m, E.P. Killip & A.C. Smith 19558 (holotype: NY!; isotypes: COL!, GH, P, PHIL, US!).

Common names. Frailejón (C), frailejón de Bucaramanga*, frailejón de Standley (C).

***Espeletia standleyana* subsp. *ampla* (Cuatrec.) Cuatrec.**, *ined.* (Forthcoming publication in Cuatrecasas in press.)

Espeletia standleyana var. *ampla* Cuatrec.

***Espeletia standleyana* subsp. *laxior* (Cuatrec.) Cuatrec.**, *ined.* (Forthcoming publication in Cuatrecasas in press.)

Espeletia standleyana var. *laxior* Cuatrec.

3.62 *Espeletia steyermarkii* Cuatrec., *Ciencia* (México) 6(7–9): 265–266, fig. 6.

1945. **TYPE. VENEZUELA: Táchira:** Quebrada del Palmar, 2500 m, Páramo de Tamá, J. Steyermark 57217 (holotype: VEN; isotypes: F!, NY!, US!).

Espeletia brassicoidea var. *contracta* sensu Aristeg., *Fl. Venez.* 10(1): 449, 451. 1964.

Common names. Frailejón (C, V), frailejón ramoso*.

3.63 *Espeletia summapacis* Cuatrec., Phytologia 31(4): 331–333. 1975. **TYPE. COLOMBIA: Cundinamarca:** Macizo de Sumapaz, near Pico de San Mateo, 3950–4000 m, 7 Feb 1975, L.Uribe-Uribe & R.Jaramillo 6895 (holotype: US!; isotypes: COL!, HPUJ!, G!).

Common names. Frailejón (C), frailejón de Sumapáz*.

3.64 *Espeletia tapirophila* Cuatrec., Phytologia 32(4): 320–322. 1975. **TYPE. COLOMBIA: Cundinamarca:** Puerta de las Dantas, Páramo de Sumapaz, 3400 m, A.M.Cleef 8301 (holotype: US!; isotypes: COL!, U).

Common names. Frailejón (C), frailejón de las dantas (C).

3.65 *Espeletia tenorae* Aristeg., Bol. Soc. Venez. Ci. Nat. 20(93): 275–279. 1959. **TYPE. VENEZUELA: Trujillo:** Páramo del Guirigay, ca. Laguna La Parida, 3500 m, Aug 1958, L.Aristeguieta & Medina 3572 (holotype: VEN; isotypes: NY!, US!).

Common names. Frailejón (C), frailejoncito (C), frailejoncito de Guirigay*.

3.66 *Espeletia tibamoensis* S. Díaz & Rodr.-Cabeza, Revista Acad. Colomb. Ci. Exact. 34 (133): 441–454, figs. 3E, 5. 2010. **TYPE. COLOMBIA: Boyacá:** Límites entre los municipios de Siachoque y Toca, veredas Cormechoque arriba y Tubenecos, Páramo La Cortadera, sector Alto Tibamoa, 3600 m alt, 16 May 2008, B.V.Rodr.-Cabeza & A.Burgos 1959. (holotype: COL; Isotypes: COL, HUA, UIS, UPTC).

Common names. Frailejón (C), frailejón de Tibamoa*.

3.67 *Espeletia tillettii* Cuatrec., Phytologia 47(1): 8–10. 1980. **TYPE. VENEZUELA: Zulia:** Sierra de Perijá, 3100 m, S.S.Tillett 747–1126 (holotype: US!; isotypes: MYF!, VEN).

Common names. Frailejón (C, V), frailejón de Zulia*.

3.68 *Espeletia tunjana* Cuatrec., Revista Acad. Colomb. Ci. Exact. 3(12): 433–434, figs. 16, 23H, G, pl. III. 1940. **TYPE. COLOMBIA: Boyacá:** Páramo de Santa Rosa de Viterbo, El Portachuelo, 3000 m, 3 Aug 1940, J.Cuatrecasas 10338 (lectotype: COL; isotypes: F!, US!; photo of holotype (Cuatrecasas C-1727): US!).

Common names. Frailejón (C), frailejón de Tunja (C).

3.69 *Espeletia ulotricha* Cuatrec., Phytologia 23(4): 364–365. 1972. **TYPE. VENEZUELA: Lara–Trujillo:** Páramo del Jabón, 3000 m, in open grass Páramo, 2 Nov 1969, J.Cuatrecasas, L.Ruiz-Terán & M.López-Figueiras 28220 (holotype: P; isotypes: MERF!, US!).

Common names. Frailejón (V), frailejón salchicha*, frailejoncito (V).

3.70 *Espeletia uribei* Cuatrec., Mutisia 16: 1–2, fig. 1. 1953. Ibid. 19: 9. 1954. **TYPE. COLOMBIA: Cundinamarca:** Páramo de La Siberia mun. La Calera 3500 m, 26 Oct 1952, L.Uribe-Uribe 2475 (holotype: F!; isotypes: P, US!).

Common names. Frailejón (C), frailejón de Chingaza*.

3.71 *Espeletia weddellii* Sch. Bip. ex Wedd., Chlor. And. 1: 66, Pl. 15-B. 1856. **TYPE. VENEZUELA: Trujillo:** Páramo de Niquitao, La Teta, 4000 m, Jul 1843, J.J.Linden 1443 (lectotype: P; lectoisotypes: BR, F!, FI, G, K!, LE, US!, W).

Common names. Chijí (V), chijí chiquito (V), frailejón (V), frailejón batata (V), frailejón chijí (V), frailejón casco de burro (V), frailejón pata de burro (V).

Hybrids

***Espeletia* × *garcibarrigae* Cuatrec.** (= *Espeletia argentea* f. *phaneractis* (S. F. Blake) Cuatrec. × *E. grandiflora* H. & B.), Revista Acad. Colomb. Ci. Exact. 3(12): 426–427. 1940. **TYPE. COLOMBIA: Cundinamarca:** Páramo de Guasca, 3000–3500 m alt., 2 Oct 1939 H.García-Barriga 08108 (holotype: COL).

Espeletia × *pachoana* Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(14): 165. figs. 6, 12E, tab. 4. 1941. **TYPE. COLOMBIA: Cundinamarca:** Cordillera Oriental, Páramo de Zipaquirá, entre Zipaquirá y Pacho, 3100–3200 m alt., 16 Jun de 1940, J.Cuatrecasas 9563 (holotype: COL; isotype: US!).

Espeletia × *pachoana* f. *brevifolia* Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(14): 166. 1941. **TYPE. COLOMBIA: Cundinamarca:** Cordillera Oriental, Páramo de Zipaquirá, entre Zipaquirá y Pacho, 3100–3200 m alt., 16 Jun de 1940, J.Cuatrecasas 9561 (holotype: COL; isotype: US!).

***Espeletia* × *verdeana* Cuatrec.** (= *Espeletia argentea* H. & B. × *E. grandiflora* H. & B.), Revista Acad. Colomb. Ci. Exact. 4(14): 166, figs. 8, 12F. 1941. **TYPE. COLOMBIA: Cundinamarca:** Cordillera Oriental, Páramo de Cruz Verde, 3400–3500 m alt., 15 Sep 1940, J.Cuatrecasas 10477 (holotype: COL; isotype: US!).

***Espeletia* × *guascensis* Cuatrec.** (= *Espeletia argentea* f. *phaneractis* × *E. killipii* Cuatrec.), Revista Acad. Colomb. Ci. Exact. 4(14): 166, figs. 7, 12K. 1941. **TYPE. COLOMBIA: Cundinamarca:** Páramo de Guasca, Cordillera Oriental, 3200–3300 m, 2 Jun 1940, J.Cuatrecasas 9493 (holotype: COL; isotypes: COL!, US!).

***Espeletia batata* Cuatrec. × *E. schultzii* Wedd. Representative specimens.** **VENEZUELA: Mérida:** páramo de Los Granates, Sierra nevada de Santo Domingo, Alto del Morato, 3670 m, rósula, hojas blancas o blanco verdosas, escapos ramosos con 3–5 capítulos, 12 Oct 1969, J.Cuatrecasas 28083 (US!); ibidem: Páramo de Piedras Blancas, después de las Cruces, carretera vía Piñango, 3600 m, subfrútice más pequeño que *Espeletia schultzii* y más grande que *Espeletia batata*, con hábitos morfológicamente intermedios entre esas dos especies, en general presenta más de 3 inflorescencias por eje, de colores llamativos (amarillo), 22 Sep 1984, J.M.Moreno-Alvarez 170 (US!); ibidem: Rangel, Páramo de Mucuchíes, alrededores de la Piedra Grietada, junto a la carretera hacia la población de Piñango, cordillera de los Andes, 4300 m, acaulirroruleto de 50–55 cm de altura total, roseta foliar de 40 cm de alto x 26 cm de diámetro, hojas oblanceoladas, crespo-lanosas en ambas caras, los pelos blanquecinos, hojas tiernas con

pelos blancos, muy largos, seríceos, que se entrelazan con los de las hojas adyacentes, formando a modo de una telaraña cuando se mira la roseta desde arriba, ejes inflorescenciales alrededor de 7, axilares, erectos, cimoso-ramificados distalmente, cilíndricos con indumento lanoso, denso marrón, presenta también en el involucro, capítulos heterógamo-radiados, péndulos, 4 cm de diámetro total y 13 mm en el disco, lígulas numerosas, suberectas, intensamente amarillas, flósculos amarillos, 18 Nov 1970, L.Ruiz-Terán 1081 (US!, F!).

***Espeletia conglomerata* Cuatrec. × *E. brassicoidea* Cuatrec.**

Espeletia conglomerata var. *macroclada* Cuatrec., Revista Acad. Colomb. Ci. Exact. 5(17): 23. 1942. **TYPE. COLOMBIA: Santander:** Páramo del Almorzadero northern slopes, 3600–3800 m, 28 Nov 1941, J.Cuatrecasas 13494A (holotype: COL; isotypes: F!, US!).

Espeletia conglomerata var. *pedunculata* Cuatrec., Revista Acad. Colomb. Ci. Exact. 5(17):23. 1942. **TYPE. COLOMBIA: Santander:** Páramo del Almorzadero, eastern slopes, 3600–3800 m, 28 Nov 1941, J.Cuatrecasas 13494 (holotype: COL; isotypes: F!, US!).

Note. There are a few scattered individuals of this hybrid in the topolocality, between the abundant populations of *E. brassicoidea* and *E. conglomerata*. *E. brassicoidea* is found generally in lower elevations than *E. conglomerata*, which is more abundant in the Páramo del Almorzadero, especially on the north side. The hybrid presents different levels of introgression, being *E. conglomerata*-dominant in its morphology. In some specimens (e.g. those corresponding originally to *E. conglomerata* var. *macroclada*) the synflorescences are more similar to those of *E. brassicoidea*, while the narrowly oblong leaves are typical of *E. conglomerata*. The short tube of the ray corollas also matches with those in *E. conglomerata*. In other specimens (e.g. those identified as *E. conglomerata* var. *pedunculata*) the general appearance of the synflorescence is similar in shape and size to *E. conglomerata*, with regular dense cymes, but with a pair of two long straight peduncles at the base, probably as an introgression with *E. brassicoidea* in which the first two pairs of peduncles are well developed.

***Espeletia congestiflora* Cuatrec. × *E. murilloi* Cuatrec. Representative specimens.**

COLOMBIA: Boyacá: Páramo de La Rusia, NW–N de Duitama: aislada, cerca del empalme de la carretera, 3540 m, acaulirósula hojas grisáceas, lígulas amarillas, 13 Dec 1972, A.M.Cleef 7184a (US!, MO!).

***Espeletia conglomerata* Cuatrec. × *E. dugandii* Cuatrec. Representative specimens.**

COLOMBIA: Norte de Santander: between Pamplona and Malaga, on highway, arborescent, 6 inches to 4 feet high, stem diameter 6 inches or more, photo: SI 3243, used to make cushions and mattresses, 24 Mar 1935, W.A.Archer 3243 (US).

***Espeletia grandiflora* H. & B. × *E. killipii* var. *chisacana* Cuatrec. Representative specimens. COLOMBIA, CUNDINAMARCA: Páramo de Sumapaz, Chisacá near**

the road-marker 30, 3700 m, caulirosula 1 m, associated with *Puya*, *Calamagrostis* and *Arcytophyllum*, 5 Aug 1974, Grabant & J. Idrobo 86 (U, US!); ibidem: Páramo de Chisacá, 17 Mar 1970, R.E. Schultes & I. Cabrera 26009 (GH).

***Espeletia schultzii* Wedd. × *Coespeletia moritziana* (Sch. Bip. ex Wedd.) Cuatrec.**

Representative specimens. VENEZUELA: Mérida: Rangel, vía El Aguila–Piñango, entre la Quebrada de Mifafi y la mina abandonada de caolín, 4170 m, caulirrósula de ca 1 m de altura, tallo de 50 cm. Hojas con pelos blancuzcos, lanosos, sinflorescencias axilares de ca 1 m de altura, con 3–5 capítulos por eje, dispuestos en forma racemosa, pedúnculo erecto en su base y recurvado en su ápice, capítulos más o menos en plano vertical o algo nutantes, lígulas amarillas en la base, rojizas en el ápice, estilos morado oscuro, flores del disco moradas con polen amarillo, 5 Sep 1983, P.E. Berry 4188 (US!, MO!); ibidem: Páramo de las Cruces, a 6.3 km de El Aguila, del otro lado de la fila, 4250 m, monocaule arrosetada sin tronco evidente, sinflorescencias axilares con racimos de capítulos semi-péndulos, lígulas amarillas teñidas de morado, estilos morados, 9 Sep 1983, P.E. Berry, 4200 (US!, MO!), ibidem: a 6.3 km de El Aguila, del otro lado de la fila, 4250 m, monocaule arrosetada sin tronco evidente, sinflorescencias axilares con racimos de capítulos semi-péndulos, lígulas amarillas teñidas de morado, estilos morados, disco pardo–morado, polen amarillo, 9 Sep 1983, P.E. Berry 4201 (US!, MO!).

***Espeletia schultzii* Wedd. × *Coespeletia spicata* (Sch. Bip. ex Wedd.) Cuatrec.**

Representative specimens. VENEZUELA: Mérida: Rangel, base del Pico de Piedras Blancas, 4000 m, caulirrósula de 1 m de alto, parte aérea del tallo poco desarrollada, vaina foliar marrón clara, lígulas cortas, amarillas, 15 Sep 1984, P.E. Berry 4379 (US!).

Espeletia schultzii* Wedd. × *Coespeletia timotensis* (Cuatrec.) Cuatrec. **Representative specimens.*

VENEZUELA: Mérida: Justo Briceño, Páramo y chirivital en la vertiente NW del Alto del Totumo, hoya del Río Chirurí, a 19.5 km de El Aguila por la carretera a Piñango, 3900–4000 m, caulirrósula de 1/2 m de alto, sinflorescencias axilares, racemosas, capítulos levemente inclinados hacia abajo, lígulas amarillas, estigmas rojo–morados, flores del disco amarillas, 8 Jan 1983, P.E. Berry 3999 (US!, MO!); ibidem: sinflorescencias axilares, ramosas, capítulos divergentes, lígulas amarillas, flores del disco amarillas, estigmas morados, 12 Oct 1983, P.E. Berry 4233 (US!, MO!); ibidem: Miranda, páramo en las cabeceras de la Quebrada El Turmero (afuentes del Río Motatán), a 6.3 km de El Aguila por la carretera a Piñango, 4280 m, caulirrósula de 1 m de alto, sinflorescencias axilares, dicasiales, capítulos orientados hacia el lado, lígulas amarillas por el haz, rojo–anaranjado por el envés, estigmas morados, polen amarillo, 12 Nov 1984, P.E. Berry 4398 (US!, MO!).

***Espeletia ×algodonosa* Aristeg. (= *Espeletia schultzii* Wedd. × *E. nana* Cuatrec.),**

Bol. Soc. Venez. Ci. Nat. 20(93): 282–283, figs., 1959a. **TYPE. VENEZUELA: Trujillo:** El Paramito, toward Tuñame, Jajó–La Morita Rd, 3000 m, Aug 1958, L. Aristeguieta & Medina 3543 (holotype: VEN; isotypes: NY!, US!); additional collec-

tions: **VENEZUELA: Trujillo:** Páramo de Tuñame, El Paramito, un sector del Páramo de Tuñame, vía Jajó–La Morita, 3000 m, planta arrosetada, cabezuelas amarillas, 1 Aug 1958, L.Aristeguieta 3449 (US!); ibidem: Páramo de Cabimbú, alrededores de la Teta de Niquitao, un sector del páramo de Cabimbú, 4000 m, planta acaule de 25–30 cm de altura, ejes inflorescenciales axilares, ramificados, capítulos con lígulas amarillas, 2 Feb 1976, M.López-Figueiras 11883 (US!); ibidem: Mérida: Rangel, Páramo de Guirigay, Llano Corredor, 3000 m, hierba acaule hojas de 27 cm x 2–3 cm de largo, vaina de 2.5 x 2.6 cm, inflorescencias axilares ca de 78 cm de largo, capítulos con lígulas amarillas, 16 Oct 1972, M.López-Figueiras 8868 (US!).

Note. Specimens of this proposed hybrid have been collected at El Paramito, between Jajó and Tuñame, and in the páramo of Guirigay–Teta de Niquitao. *E. nana* and *E. schultzii* have large sympatric populations in both localities. The morphological characteristics (e.g. size and shape of leaves and synflorescences) of the specimens of *E. xalgodonosa* are intermediate between the parental species, with different levels of introgression.

***Espeletia schultzii* Wedd. × *Ruilopezia lindenii* (Sch. Bip. ex Wedd.) Cuatrec. Representative specimens.** **VENEZUELA: Mérida:** Campo Elías, páramo de San José, vía a Mucutuy, a 6.5 km de San José, 2970 m, hierba arrosetada, con varias rosetas juntas, sinflorescencia terminal, racemosa, lígulas y flores del disco amarillas, 22 Aug 1984, P.E.Berry 4358 (US!).

***Espeletia tenorae* Aristeg. × *E. schultzii* Wedd. Representative specimens.** **VENEZUELA: Mérida:** Páramo de Guirigay, Llano Corredor, camino del Arenal, 3200 m, acaulirrosuleto, inflorescencias axilares, capítulos con lígulas amarillas, 10 Jan 1978, M.López-Figueiras, 14517 (US!).

***Espeletia weddellii* Sch. Bip. ex Wedd. × *Espeletia marthae* Cuatrec. Representative specimens.** **VENEZUELA: Mérida:** Llano corridor between Las Piedras and Guirigay, 3300 m, 25 Oct 1969, J.Cuatrecasas, M.López-Figueriras & L.Marcano-Berti 28163 (holotype: US!; isotypes: US!, MERF).

***Espeletia weddellii* Sch. Bip. ex Wedd. × *Espeletia schultzii* Wedd. Representative specimens.** **VENEZUELA: Mérida:** Páramo de Los Granates, near Laguna Brava, 3300 m, 20 May 1971, M.López-Figueriras 8725 (holotype: US!; isotypes: US!, MERF).

Herbarium mixture

***Espeletia rufescens* Cuatrec. (= *Coespeletia moritziana* (Sch. Bip. ex Wedd.) Cuatrec. (leaves) + *Espeletia semiglobulata* Cuatrec. (inflorescences)), Bol. Soc. Venez. Ci. Nat. 17(85): 88, figs. 5–6. 1956. TYPE. **VENEZUELA: Mérida:** Sierra Nevada de Mérida, 12000 ft, J.J.Linden 398 (lectoholotype: P; J.J.Linden 399 paratype: P).**

Note. As suggested by Weddell (1855[1857]: 64–65) and later by Cuatrecasas (in press), the two mounted specimens that exist (Linden 398 and 399) show clearly the leaves from *C. moritziana*, except for one that is probably from *E. semiglobulata*, and the synflorescences from *E. semiglobulata*.

4 *Espeletiopsis* Cuatrec., *Phytologia* 35(1): 54–56. 1976. **TYPE.** *Espeletiopsis jimenez-quesadae* (Cuatrec.) Cuatrec.

4.01 *Espeletiopsis angustifolia* (Cuatrec.) Cuatrec., *Phytologia* 35(1): 55. 1976. *Espeletia angustifolia* Cuatrec., *Bol. Soc. Venez. Ci. Nat.* 17 (85): 80. 1956. **TYPE.** **VENEZUELA: Mérida:** Páramo de Mijara, 3300 m alt.; 18 Mar 1922, A.Jahn 973 (holotype: US!; isotype: G!).

Common names. Frailejón (V), frailejón blanco (V), frailejón plateado (V), frailejón plateado de Mérida*.

4.02 *Espeletiopsis betancurii* Rodr.-Cabeza, S. Díaz & Gal.-Tar., *Revista Acad. Colomb. Ci. Exact.* 30 (16): 349–352 figs. 11, 12C–D. 2006. **TYPE.** **COLOMBIA: Boyacá:** Municipio de Chita, Vereda Minas, Páramo de Los Venados, carretera hacia Sácama, km 86 desvío a Chita, 3200 m alt., 23 Oct 2005. B.V.Rodr.-Cabeza & L.Velasco 1515 (holotype: COL; isotype: UIS).

Common names. Frailejón (C), frailejón de los venados*.

4.03 *Espeletiopsis caldasii* (Cuatrec.) Cuatrec., *Phytologia* 35(1): 55. 1976. *Espeletia caldasii* Cuatrec., *Revista Acad. Colomb. Ci. Exact.* 3(11): 431. 1940. **TYPE.** **COLOMBIA: Norte de Santander:** Páramo de Santurbán, extremo occidental, 3400 m alt., 27 Aug 1940, J.Cuatrecasas & H.García-Barriga 10317 (holotype: US).

Common names. Frailejón (C), frailejón enano (C), frailejón enano de Caldas*, frailejoncito (C).

4.04 *Espeletiopsis colombiana* (Cuatrec.) Cuatrec., *Phytologia* 35(1): 55. 1976. *Espeletia colombiana* Cuatrec., *Revista Acad. Colomb. Ci. Exact.* 3(11): 249. 1940. **TYPE.** **COLOMBIA: Boyacá:** Cordillera Oriental, Nevado del Cocuy; Las Lagunillas, Pozo Azul; páramo 4.110 m alt., 11 Sep 1938, J.Cuatrecasas & H.García-Barriga 1432 (holotype: US!; isotype: FI!).

Common names. Frailejón (C), frailejón colombiano*.

4.05 *Espeletiopsis corymbosa* (Humb. & Bonpl.) Cuatrec., *Phytologia* 35(1): 55. 1976. *Espeletia corymbosa* Humb. & Bonpl., *Pl. Aequinoc.* 2: 16. 1809. **TYPE.** **COLOMBIA: Cundinamarca:** Nous avons trouvé l'*Espeletia corymbosa* dans la Cordillère des Andes, près la ville d'Almaguer, à 1163 toises (2268 mètres) d'élévation au-dessus du niveau de l'Océan, c'est le seul endroit où nous ayons rencontré cette plante, elle s'élève à cinq à six pieds (2 mètres) de hauteur, et fournit une aussi grande quantité

de résine que l'*Espeletia grandiflora*, ces deux plantes pourroient donc être cultivées en Amérique et en Europe, et la résine qu'elles produisent seroit employée utilement dans les arts (from a Cuatrecasas draft: "Type: Humboldt & Bonpland in 'Herb. H.B.K.' holotype, ficha No. ? 'Cordillera los Andes pre la Ville d'Almaguer a 1163 toises (2268 m) elevation.'"), (holotype: P).

Espeletia corymbosa var. *foliosa* Duse, Nuovo Giorn. Bot. Ital., Nuova ser. 12: 294. 1905. **TYPE. COLOMBIA: Cundinamarca:** Neuva Grenada: Bogota, locis frigidis, Goudot, Mar 1844.

Espeletia corymbosa subsp. *zipaquirana* Cuatrec., Revista Acad. Colomb. Ci. Exact. 4: 168, figs. 10, 12a, tab. 3. 1941. **TYPE. COLOMBIA: Cundinamarca:** Páramo de Zipaquirá, 3100–3200 m, 16 Jan 1940, J.Cuatrecasas 9564 (holotype: F; isotypes: COL!, US!, MA!).

Espeletia rigida Humb. & Bonpl., Pl. Aequinoc. 2(9): t. 72. 1808 [1809 publ. Nov 1808]. *Nomen nudum*.

Espeletia platylepis Sch. Bip. ex Wedd., Chlor. And. 1: 64. 1856 [1855 publ. 30 Jun 1856]. **TYPE. NOUVELLE GRENADE: Cordillères de Bogota:** h. 2250 mètres, Goudot & J.J.Linden 1291; environs d'Almaguer!, h. 2050 mètres, Humb. & Bonpl.

Common names. Frailejón (C), frailejón liso*, oreja de mula (C).

4.06 *Espeletiopsis funckii* (Sch. Bip. ex Wedd.) Cuatrec., Phytologia 35(1): 55. 1976. *Espeletia funckii* Sch. Bip. ex Wedd., Chlor. And. 1: 64. 1856 [1855 publ. 30 Jun 1856]. **TYPE. COLOMBIA: Norte de Santander:** Hab. Nouvelle grenade: Andes de Pamplona, à une élévation de 3400 mètres, Jan 1847, V.A.Funck & L.J.Schlim 1290 (holotype: P; isotypes: F, G!).

Espeletia smithiana Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(14): 339, figs. 3, 4. 1941. **TYPE. COLOMBIA: Santander:** Cordillera Oriental: Páramo de Santurbán entre Cuesta Boba y el extremo oeste, 3400 m alt., 27 Jul 1940, J.Cuatrecasas & H.García-Barriga 10315 (holotype: COL!; isotypes: COL!, F!, HPUJ!, P, US!).

Common names. Frailejón (C), frailejón de Funk (C), frailejón de oro*.

Note. *E. smithiana* was not included in the last publications of Cuatrecasas (Cuatrecasas 1976; Cuatrecasas 1996; Cuatrecasas in press), probably because he was uncertain regarding the position of this species. Certainly it was an *Espeletiopsis*, although he never published the new combination. The comparison between numerous specimens of *E. funckii* and *E. smithiana* shows no difference between the two. High morphological variation between specimens suggests also that this species might have frequent hybridization.

4.07 *Espeletiopsis garciae* (Cuatrec.) Cuatrec., Phytologia 35(1): 55. 1976. *Espeletia garciae* Sch. Bip. ex Wedd., Phytologia 23(4): 358–360. 1972. Et in Ciencias 27(6): 176. 1972. **TYPE. COLOMBIA. Boyacá:** Leiva, vereda de Capilla, encima del km 21, en el monte, 2640 m alt., tallo liso de 4 m alt × 6 cm diám que culmina en tres cortas ramificaciones, flores amarillas, 2 Dec 1970, L.Uribe-Uribe 6491 (holotype: US!; isotypes: MO!); ibidem: vereda de Capilla, monte sobre km 21, 2640 m, mata

6 m, tallo muy duro bifucado a 1 m sobre el suelo, cada rama terminada en cortas ramificaciones apicales, inflorescencias erguidas con flores amarillas, crece en matorral alto, 2 Dec 1970, L.Uribe-Uribe 6492 (paratype: US!); ibidem: Arcabuco, al NE de la poblacion, cerca límite con Santander, 2650 m, 4 m, erecta, tallo 5 cm diam, nervios foliares color oro, pelos amarillos, flores amarillas, cuando se corta se ramifica, 12 Oct 1966, H.García Barriga 18764 (paratype: US!).

Common names. Frailejón (C), frailejón de Arcabuco*, frailejón de García-Barriga (C).

4.08 *Espeletiopsis guacharaca* (S. Díaz) Cuatrec., *Phytologia* 35(1): 55. 1976. *Espeletia guacharaca* S. Díaz, *Caldasia* 11(53): 19. 1975. *Espeletiopsis jimenez-quesadae* var. *guacharaca* (S. Díaz) Cuatrec., *Anales Jard. Bot. Madrid* 54(1): 374. 1996. **TYPE.** **COLOMBIA: Boyacá:** Páramo de la Rusia, cerca a la cima, carretera Duitama–Charalá, 3.500 m alt., caulirrosuleto 1.50 m, envés con indumento dorado blanquecino, hojas jóvenes con indumento blanco amarillento, inflorescencias péndulas, lígulas amarillas, hojas secas cubriendo el tallo, poblaciones abundantes en suelo seco, el ejemplar presenta huellas de quema, 13 May 1968, S. Díaz 42 (holotype: COL; isotype: US!).

Common names. Frailejón guacharaco (C), guacharaco (C).

4.09 *Espeletiopsis insignis* (Cuatrec.) Cuatrec., *Phytologia* 35(1): 55. 1976. *Espeletia insignis* Cuatrec., *Revista Acad. Colomb. Ci. Exact.* 3(11): 432. 1940. **TYPE.** **COLOMBIA: Norte de Santander:** Hoya del río Chitagá, abajo de Quebrada de Presidente, junto a “Vega Colombia”, bosques 2900–3000 m alt., 21 Jul 1940, J.Cuatrecasas & H.García-Barriga 10071 (holotype: COL; isotypes: BC!, F!, US!).

Common names. Frailejón (C), frailejón de Chitagá (C).

4.10 *Espeletiopsis jimenez-quesadae* (Cuatrec.) Cuatrec., *Phytologia* 35(1): 56. 1976. *Espeletia jimenez-quesadae* Cuatrec., *Revista Acad. Colomb. Ci. Exact.* 3(11): 247. 1940. **TYPE.** **COLOMBIA: Boyacá:** Cordillera Oriental: Sierra Nevada del Cocuy, hacia La Cueva en La Zanja, Páramo 3700 m alt., 13 Sep 1938, J.Cuatrecasas & H.García-Barriga 1635 (holotype: COL; isotype: US!).

Common names. Frailejón (C), frailejón negro (C).

4.11 *Espeletiopsis meridensis* (Cuatrec.) Cuatrec., *Phytologia* 35(1): 56. 1976. *Espeletia meridensis* Cuatrec., *Mutisia* 16: 4. 1953. **TYPE.** **VENEZUELA: Mérida:** Carretera Andina, Páramo de la Negra, 3000 m alt., planta de 0.50 m, tallo floral 1 m, flores amarillas, Nov 1948, H.García-Barriga 13297 (holotype: US!; isotypes: COL, NY, VEN).

Common names. Frailejón (V), frailejón de Mérida*.

Note. Based on examination of herbarium specimens I suspect that, as with *Espeletiopsis ×cristalinensis* (see section of hybrids for *Libanothamnus*), this is another interge-

neric hybrid, probably between *L. neriifolius* and a species of *Espeletia*. However, more material is needed to confirm this hypothesis.

4.12 *Espeletiopsis muiska* (Cuatrec.) Cuatrec., Phytologia 35(1): 56. 1976. *Espeletia muiska* Cuatrec., Revista Acad. Colomb. Ci. Exact. 3(11): 429. 1940. **TYPE. COLOMBIA: Boyacá:** Páramo de Guantiva, Alto de Canutos, vert. sur, 3300 m alt., 3 Aug 1940, J. Cuatrecasas 10359 (holotype: US!; isotype: COL!); additional collections: ibidem: Páramo de Guantiva, Alto de Canutos, 3200 m alt., 17 Jul 1940, J. Cuatrecasas & H. García-Barriga 9748 (COL!, US!); ibidem: Páramo de la Rusia, vert. SE, en Boca del Monte, 3300–3400 m alt., 4 Aug 1940, J. Cuatrecasas 10409 (COL!, US!); ibidem: Páramo de Arcabuco (entre Arcabuco y Tunja), 2950 m alt., 5 Jul 1940, J. Cuatrecasas 10440 (COL!, US!).

Common names. Frailejón (C), frailejón de los muiskas*.

4.13 *Espeletiopsis pannosa* (Standl.) Cuatrec., Phytologia 35(1): 56. 1976. *Espeletia pannosa* Standl., Amer. J. Bot. 2: 480. 1915. **TYPE. VENEZUELA: Trujillo:** Páramo del Jabón, 3,000–3,200 m, Oct 1910, A. Jahn 165 (holotype: US!).

Espeletia sericea Cuatrec., Ciencia (Mexico) 6: 263, fig. 4. 1945. **TYPE. VENEZUELA: Mérida:** Mucurubá, 3500–4000 m alt., n. v. Frailejón chirique, 18 Jul 1930, W. Gehrig 342 (holotype: VEN; isotype: G!).

Common names. Frailejón (V), frailejón chirique (V), frailejón plateado (V).

4.14 *Espeletiopsis petiolata* (Cuatrec.) Cuatrec., Phytologia 35(1): 56. 1976. *Espeletia petiolata* Cuatrec., Revista Acad. Colomb. Ci. Exact. 4: 338. 1941. **TYPE. COLOMBIA: Santander:** Cordillera Oriental: Páramo del Almorzadero, región media, 3500 m alt.; 20 Jul 1940, J. Cuatrecasas & H. García-Barriga 9973 (holotype: BC!, US!; isotypes: COL!, F!).

Espeletia petiolata f. *paniculata* Cuatrec., Revista Acad. Colomb. Ci. Exact. 5: 22. 1942. **TYPE. COLOMBIA: Santander:** Cordillera Oriental: Páramo del Almorzadero, región media, 3500 m alt., 20 Jul 1940, J. Cuatrecasas & H. García-Barriga 9973 (holotype: US!; isotypes: BC!, COL!, F!).

Common names. Frailejón (C), frailejón de Almorzadero*.

***Espeletiopsis petiolata* var. *escobensis* (Cuatrec.) M. Diazgranados, comb. nov.** *Espeletia petiolata* var. *escobensis* Cuatrec., Revista Acad. Colomb. Ci. Exact. 5: 22. 1942. **TYPE. COLOMBIA: Boyacá:** Cordillera Oriental, entre Soatá y Cocuy en el Alto de Escobal, páramo 3900 m alt., 15 Sep 1938, J. Cuatrecasas & H. García-Barriga 1760 (holotype: COL!; isotype: US!).

***Espeletiopsis petiolata* f. *corymbosa* (Cuatrec.) M. Diazgranados, comb. nov.** *Espeletia petiolata* f. *corymbosa* Cuatrec., Revista Acad. Colomb. Ci. Exact. 5: 22. 1942. **TYPE. COLOMBIA: Norte de Santander:** quebrada de Presidente en la alta hoja del río Chitagá, 3100 m alt., panícula valde reducta, corymbum *Espeletia corymbosae*

simulans, folia typo similia sed generaliter angustiora, 28 Nov 1941, J. Cuatrecasas 13479 (holotype: COL!; isotypes: US!, F!).

***Espeletiopsis petiolata* f. *media* (Cuatrec.) M. Diazgranados, comb. nov.** *Espeletia petiolata* f. *media* Cuatrec., Revista Acad. Colomb. Ci. Exact. 5: 22. 1942. **TYPE. COLOMBIA: Santander:** Páramo del Almorzadero, vertiente norte, 3600–3800 m alt., panícula typo minus evoluta, folia minus elongata, ligulae breviores (9 mm), 28 Nov 1931, J. Cuatrecasas 13497 (holotype: COL!; isotypes: US!, F!).

***Espeletiopsis petiolata* f. *reducta* (Cuatrec.) M. Diazgranados, comb. nov.** *Espeletia petiolata* f. *reducta* Cuatrec., Revista Acad. Colomb. Ci. Exact. 4: 338. 1941. **TYPE. COLOMBIA: Santander:** Cordillera oriental, Páramo del Almorzadero, region media, 3500–3700 m, acaulirrosuletum, 20 Jul 1940, J. Cuatrecasas 9987-A (lectotype: COL!, here designated).

4.15 *Espeletiopsis pleiochasia* (Cuatrec.) Cuatrec., *Phytologia* 35(1): 56. 1976. *Espeletia pleiochasia* Cuatrec., Revista Acad. Colomb. Ci. Exact. 3: 432. 1940. **TYPE. COLOMBIA: Boyacá:** Quebrada de Becerra, al NW de Duitama, bosques y matorrales, 3000–3100 m alt., 4 Aug 1940, J. Cuatrecasas 10399 (holotype: COL!; isotypes: BC!, COL!, F!, HPUJ!, U, US!).

Common names. Frailejón (C), frailejón de Duitama*.

***Espeletiopsis pleiochasia* var. *socotana* (Cuatrec.) M. Diazgranados, comb. nov.** *Espeletia pleiochasia* var. *socotana* Cuatrec., *Phytologia* 31(4): 328. 1975. **TYPE. COLOMBIA: Boyacá:** Municipio de Socha, subpáramo seco, 2900–3000 m alt, Apr 1973, A.M. Cleef 9870 (holotype: US!; isotypes: COL!, U, US!). Additional collections: ibidem: hoyá del río Socotá (afluente del río Chicamocha), cerros áridos, rocosos en el flanco izquierdo, arriba de la carretera después del empalme tronco 1 m alto 4 cm diam, cubierto de hoja marcescente, hoja clara, algo ruda haz, más clara envés; jóvenes verde amarillento–blanquecino seríceo, inflorescencias secas excepto algun raro cortas, marcescentes, reflejas, 4 Apr 1973, J. Cuatrecasas & R. Jaramillo 28730 (COL!, US!); id., 2940 m, rósulas y caulirrósulas verdoso–grisáceo claras, tronco hasta 30 cm, involucro verde, lígulas amarillas, hojas distales y cogollo cinéreo blanquecinos, densamente tomentoso–vellosos y algo seríceos, las viejas rudas en la haz con vello mas escaso; barbas de la vaina blanca, 5 Apr 1973, J. Cuatrecasas & R. Jaramillo 28734 (US!); id., 2900 m, ladera seca, caulirrosuleto 1.5 m, hojas con indumento blanco, capítulos 7 mm diam, brácteas invol. verde limón, brácteas ligulíferas verde oscuro, lígulas amarillas, 9 Oct 1971, R. Jaramillo, G. Lozano & S. Díaz 5017 (COL!, US!).

4.16 *Espeletiopsis pozoensis* (Cuatrec.) Cuatrec., *Phytologia* 35(1): 56. 1976. *Espeletia pozoensis* Cuatrec., *Ciencia (Mexico)* 6: 266. 1945. **TYPE. VENEZUELA: Mérida:** between San José and Beguilla, Páramo de Pozo Negro, 8500–10500 ft, leaves in dense rosette, gray white on both sides; rays pale yellow, disk dull yellow, 3 May

1944, J.Steyermark 56278 (holotype: VEN; isotypes: FI, NY!; photos of VEN and F specimens in US!; photo NY 4564A).

Common names. Frailejón (V), frailejón chirique (V), frailejón plateado (V), frailejón plateado chico (V).

4.17 *Espeletiopsis purpurascens* (Cuatrec.) Cuatrec., Phytologia 35(1): 56. 1976. *Espeletia purpurascens* Cuatrec., Revista Acad. Colomb. Ci. Exact. 5: 16. 1942. **TYPE. COLOMBIA: Norte de Santander:** Cordillera Oriental, Páramo de Tamá, alrededores de La Cueva, 3000–3200 m alt., entre arbustos en subpáramo, caulirrósula, tallo de 3 m, flores liguladas púrpura, reflejas, flores del disco rojizas, 28 Oct 1941, J.Cuatrecasas, R.E.Schultes & E.Smith 12689 (holotype: COL!; isotypes: BC!, COL!, FI, US!).

Common names. Frailejón (C, V), frailejón purpúreo (C, V), frailejón de árbol (C, V).

4.18 *Espeletiopsis rabanalensis* S. Díaz & Rodr.-Cabeza, Revista Acad. Colomb. Ci. Exact. 32 (125): 456–458 figs 1, 2A–B. 2008. **TYPE. COLOMBIA: Boyacá:** Municipio de Samacá, Páramo del Rabanal, 3412 m de alt., 3–5 Oct 2007, B.V.Rodr.-Cabeza, f.Márquez 1895 (holotype: COL; isotypes: COL!, UIS).

Common names. Frailejón (C), frailejón de Rabanal*.

4.19 *Espeletiopsis sanchezii* S. Díaz & Obando, Revista Acad. Colomb. Ci. Exact. 28(108): 324, fig. 1. 2004. **TYPE. COLOMBIA: Norte de Santander:** Pamplona, sector de La Lejía, Páramo de Tierranegra, 3200–3300 m L.R.Sánchez, M.A.Murcia & W.Valencia 7281 (holotype: COL; isotype: COL!).

Common names. Frailejón (C), frailejón de Tierranegra*.

4.20 *Espeletiopsis santanderensis* (A. C. Sm.) Cuatrec., Phytologia 35(1): 56. 1976. *Espeletia santanderensis* A. C. Sm., Brittonia 1(7): 527. 1935. **TYPE. COLOMBIA: Santander:** Páramo de Vetás, alt. 3400–4000 m, 16 Jan 1927, E.P.Killip & A.C.Smith 17422 (holotype: NY!; isotypes: G, NY); additional collections: ibidem: edge of Páramo de Santurbán, near Vetás, E.P.Killip & A. C. Smith 17587 (G, N, Y); ibidem: Páramo de Mogotocoro, near Vetás, E.P.Killip & A.C.Smith 17603 (G, N, Y), 17622 (G, N, Y); ibidem: páramo Rico, near Vetás, E.P.Killip & A.C.Smith 17667 (G, N, Y); ibidem: Páramo de Santurbán, above Tona, E.P.Killip & A.C.Smith 19552 (G, N, Y); Norte de Santander: Páramo Viejo, Purdie (G, K!, P); ibidem: Páramo near Ocaña, L.J.Schlim 332 (P).

Common names. Frailejón (C), tache (C).

4.21 *Espeletiopsis sclerophylla* (Cuatrec.) Cuatrec., Phytologia 35(1): 56. 1976. *Espeletia sclerophylla* Cuatrec., Revista Acad. Colomb. Ci. Exact. 3: 436. 1940. **TYPE. COLOMBIA: Santander:** Páramo del Almorzadero, extremo sur, Peralonso, 3200 m alt., 19 Jul 1940, J.Cuatrecasas & H.García-Barriga 9929 (holotype: COL!; isotypes: FI, US!).

Common names. Frailejón (C), frailejón hojiduro*.

4.22 *Espeletia trianae* (Cuatrec.) Cuatrec., *Phytologia* 35(1): 56. 1976. *Espeletia trianae* Cuatrec., *Revista Acad. Colomb. Ci. Exact.* 5: 18. 1942. **TYPE. COLOMBIA: Norte de Santander:** páramos de Pamplona, 3000 m alt., árbol, Jun 1851, Triana 2476-5 (holotype: COL!).

Common names. Frailejón (C), frailejón de Triana*.

Hybrids

***Espeletia* × *almorzana* (Cuatrec.) Cuatrec. (= *Espeletia petiolata* (Cuatrec.) Cuatrec. × *E. sclerophylla* (Cuatrec.) Cuatrec.)**

Espeletia almorzana Cuatrec., *Revista Acad. Colomb. Ci. Exact.* 4(14): 340, figs. 5, 6H. 1941. **TYPE. COLOMBIA: Santander:** Cordillera Oriental: Páramo del Almorzadero, región media 3.500 m alt., 20 Jul 1940, J.Cuatrecasas & H.García-Barriga 9987 (holotype: US!).

Espeletia almorzana f. *latifolia* Cuatrec., *Revista Acad. Colomb. Ci. Exact.* 4(14): 340, figs. 5, 6H. 1941. **TYPE. COLOMBIA: Santander:** Páramo del Almorzadero, vertiente norte, 3600–3800 m alt., 28 Nov 1941, J.Cuatrecasas 13503 (holotype: COL!).

Common names. Frailejón (C).

***Espeletia* × *bogotensis* (Cuatrec.) Cuatrec. (= *Espeletia corymbosa* (Humb. & Bonpl.) Cuatrec. × *Espeletia grandiflora* Humb. & Bonpl.)**

Espeletia bogotensis Cuatrec., *Revista Acad. Colomb. Ci. Exact.* 3(11): 427. 1940. **TYPE. COLOMBIA: Cundinamarca:** Macizo de Bogota en Cerro de Monserrate, vert. orient., páramo 3000 m alt., 28 Jan 1940, J.Cuatrecasas 7998 (holotype: COL!; isotypes: COL!, FI, US!); et ibidem: Páramo de Usaquén, 3000 m alt., 20 Jan 1940, J.Cuatrecasas 7995 (paratype: US!); additional collections: ibidem: Páramo de Guasca, 3000–3400 m alt., tallo simple de 1'5 m alt., cubierto por denso estuche de hojas secas persistentes y terminado por un rosetón de hojas lanudas, E.P.Killip 34056 (COL).

Common names. Frailejón (C), frailejón de Bogotá*.

5 *Libanothamnus* Ernst, *Vargasia* 7: 186. 1870. **TYPE.** *Libanothamnus neriifolius* (Bonpl. & Humb.) Ernst. (= *Trixis neriifolia* Bonpl. & Humb.)

5.01 *Libanothamnus arboreus* (Aristeg.) Cuatrec., *Phytologia* 35(1): 50. 1976. *Espeletia arborea* Aristeg., *Bol. Soc. Venez. Ci. Nat.* 20(93): 286–287. 1959. **TYPE. VENEZUELA: Trujillo:** Guirigay, near Peña Blanca, 3200 m, Aug 1958, L.Aristeguieta & Medina 3635a (holotype: VEN).

Common names. Incienso (V), punta de lanza grande (V).

Libanothamnus arboreus* var. *lancifolius* Cuatrec., *ined. (Forthcoming publication in Cuatrecasas in press.)

5.02 *Libanothamnus banksiaefolius* (Sch. Bip. & Ettingsh.) Cuatrec., Phytologia 35(1): 50. 1976. *Espeletia banksiaefolia* Sch. Bip. & Ettingsh. ex Wedd., Chlor. And. 1: 67. 1856. **TYPE. VENEZUELA: Mérida:** Sierra Nevada de Mérida, 10000–10500 ft, arbuste fl. blanches, Jun 1847, V.A.Funck & L.J.Schlim 1550 (holotype: P (Preté No. 736); isotypes: G, GH, LE, P).

Common names. Frailejón de árbol (V), frailejón punta de lanza grande (V), incienso (V), punta de lanza (V), tabacón (V).

Libanothamnus banksiaefolius* subsp. *granatesianus* (Cuatrec.) Cuatrec., *ined. (Forthcoming publication in Cuatrecasas in press.)

Espeletia granatesiana Cuatrec.

Libanothamnus granatesianus (Cuatrec.) Cuatrec.

Common names. Frailejón de árbol (V), incienso (V), punta de lanza (V), punta de lanza grande (V), tabacón (V).

5.03 *Libanothamnus divisoriensis* Cuatrec., Phytologia 47(1): 1–3. 1980. **TYPE. VENEZUELA: Zulia:** Sierra de Perijá, boundary with COLOMBIA: 3000 m, flowers dirty cream white, 27 Jun–5 Jul 1974, S.S.Tillett & K.W.Hönig 746–746 (holotype: US!; isotypes: UCV, VEN).

Common names. Incienso (V), tabaquillo de la frontera (C, V).

5.04 *Libanothamnus griffinii* (Ruiz-Terán & López-Fig.) Cuatrec., Phytologia 35(1): 50. 1976. *Espeletia griffinii* Ruiz-Terán & López-Fig., Rev. Fac. Farm. Univ. Andes Mérida 17: 7–13, figs. 3–6. 1976. **TYPE. VENEZUELA: Trujillo:** Páramo de Guaramacal, Boconó, 2600 m, 3 Aug 1975, L.Ruiz-Terán, M.López-Figueiras & D.Griffin 12606 (holotype: MERF!; isotype: US!).

Common names. Incienso (V), incienso de Guaramacal*.

5.05 *Libanothamnus liscanoanus* (Cuatrec.) Cuatrec., Phytologia 35(1): 51. 1976. *Espeletia liscanoana* Cuatrec., Phytologia 27(1): 41–44. 1973. **TYPE. VENEZUELA: Lara:** Páramo del Jabón, 3100–3200 m, tree 8–10 m, 20–25 cm diameter, 2 Nov 1969, J.Cuatrecasas, L.Ruiz-Terán & M.López-Figueiras 28206 (holotype: US!; isotype: MERF!).

Common names. Incienso (V), incienso de Carache*.

5.06 *Libanothamnus lucidus* (Aristeg.) Cuatrec., Phytologia 35(1): 51. 1976. *Espeletia lucida* Aristeg., Fl. Venez. 10(1): 420–421. 1964. **TYPE. VENEZUELA: Mérida:** without collector and exact locality, 3800 m, ULA-1001 (holotype: VEN); ibidem: camino al Pico Bolívar, 9 Apr 1951, Uscátegui 1001 (isotype: MER).

Common names. Frailejón de madera (V), incienso (V).

5.07 *Libanothamnus neriifolius* (Bonpl. ex Humb.) Ernst, Vargasia 7: 186. 1870. **TYPE. COLOMBIA:** Moritz 372 (B). *Baillieria nereifolia* (Kunth) Bonpl. ex Kunth,

Nov. Gen. Sp. Pl. 4: 289. 1820; Folio. 4: 227. 1818. *Clibadium neriifolium* (Bonpl. ex Kunth) DC., Prodr. Syst. Nat. Reg. Veg. 5: 507. 1836. *Espeletia neriifolia* (H.B.K.) Sch. Bip. ex Wedd., Chlor. And. 1: 67–68. 1856. **TYPE. COLOMBIA: Norte de Santander:** Páramo de Tamá, Hoya de Samaria, 2600–2900 m, rays white, 29 Oct 1941, J.Cuatrecasas, R.E.Schultes & E.Smith 12721 (holotype: COL!; isotypes: BC!, COL!, F!, GH, HPUJ!, US!).

Trixis neriifolia Bonpl. ex Humb., Voy. Reg. Equin. Rel. 1: 605. 1814. As *T. neriifolia*, typographic error. **TYPE. VENEZUELA:** Syngenesia necessaria, *Trixis neriifolia* foliis lanceolatis integerrimis subtus laniculatis, habitat in Caracas, incienso, Silla de Caracas, Humboldt s.n. (Willdenow 16672 lectotype: B, photo 16103: F); ibidem: Caracas, incienso, Buphthalmum, Silla de Caracas, in other label “*Andromachia?* *Trixis neriifolia* Willd! *Espeletia neriifolia* Sch. Bip. 19/10/55, Silla de Caracas, Herbar donné par M.Bonpland in 1833, Jan 1800, No. 652, (isolectotype: P).

Common names. Frailejón de árbol (C, V), frailejón de resina (V), frailejón resino (V), incienso (C, V), oreja de burro (C), resino (V), tabaquillo trementino (C), trementino (C).

***Libanothamnus neriifolius* var. *boconensis* Cuatrec.,** Phytologia 47(1): 6. 1980. **TYPE. VENEZUELA: Trujillo:** Páramo de La Cristalina, 2300 m, tree 6–10 m, rays white, 30 Oct 1969, J.Cuatrecasas, L.Ruiz-Terán & M.López-Figueiras 28190 (holotype: US!; isotype: MERF!).

Common names. Incienso (V), incienso de Boconó*.

***Libanothamnus neriifolius* var. *columbicus* (Cuatrec.) Cuatrec.,** *ined.* (Forthcoming publication in Cuatrecasas in press.)

Espeletia neriifolia var. *columbicus* Cuatrec.

Common names. Incienso (C), incienso colombiano*, oreja de burro (C), tabaquillo trementino (C), trementino (C).

***Libanothamnus neriifolius* var. *cristamontis* Cuatrec.,** *ined.* (Forthcoming publication in Cuatrecasas in press.)

Libanothamnus cristamontis Cuatrec.

Common names. Incienso (V), incienso de Dinira*.

***Libanothamnus neriifolius* var. *turmalensis* Cuatrec.,** Phytologia 47(1): 7. 1980. **TYPE. VENEZUELA: Trujillo:** Páramo del Turmal, east of Carache, 2800–2900 m, tree 5 m, rays creamy–white, 3 Nov 1969, J.Cuatrecasas, L.Ruiz-Terán & M.López-Figueiras 28239 (holotype: US!; isotype: MERF!).

Common names. Incienso (V), incienso del Turmal*.

5.08 *Libanothamnus occultus* (S. F. Blake) Cuatrec., Phytologia 35(1): 51. 1976.

Espeletia occulta S. F. Blake, Contrib. U.S. Nat. Herb. 20: 537. 1924. **TYPE. VENEZUELA: Mérida:** Páramo de Quirorá, 3000 m, 8 Oct 1921, Jahn 730 (holotype: US!; isotype: MERF!).

Libanothamnus occultus var. *salomonii* Cuatrec. & López-Fig., Phytologia 61(1): 51–53. 1986. **TYPE. VENEZUELA: Táchira:** Pico de Horma, 7.5 Km SE of Mesa de Quintero, 3100 m, western slopes, subpáramo, tree up to 5 m, ligules pale–yellowish, leaves tawny beneath, Táchira, VENEZUELA, 11 Jan 1985, M.López-Figueiras, Rodríguez & Rengifo 31344 (holotype: US!; isotypes: F!, HPUJ!, MERF!, NY!).

Common names. Incienso (V), tabaquillo (C), tabaquillo oscuro*.

Libanothamnus occultus subsp. *glossophyllus* (Mattf.) Cuatrec., *ined.* (Forthcoming publication in Cuatrecasas in press.)

Espeletia glossophylla Mattf.

Espeletia subneriifolia Cuatrec.

Libanothamnus glossophyllus (Mattf.) Cuatrec.

Libanothamnus subneriifolius (Cuatrec.) Cuatrec.

Common names. Frailejón (C), incienso (C), nabalda (Kogi), tabaco de la sierra*.

Libanothamnus occultus subsp. *humbertii* (Cuatrec.) Cuatrec., *ined.* (Forthcoming publication in Cuatrecasas in press.)

Espeletia humbertii Cuatrec.

Libanothamnus humbertii (Cuatrec.) Cuatrec.

Common names. Frailejón de árbol (V), frailejonote (V), incienso (V), punta de lanza (V), punta de lanza amarillo (V), punta de lanza pequeño (V), tabacote (V).

Libanothamnus occultus subsp. *oroquensis* Cuatrec., *ined.* (Forthcoming publication in Cuatrecasas in press.)

Common names. Incienso (C), tabaquillo de Oroque (C).

5.09 *Libanothamnus parvulus* Cuatrec., Phytologia 47(1): 3–4. 1980. **TYPE. VENEZUELA: Lara:** Páramo de Cendé, 2900 m at Laja del Dícamo, short tree, 10 Jun 1971, L.Ruiz-Terán & M.López-Figueiras 2036 (holotype: US!; isotype: MERF!).

Common names. Incienso (V), incienso hojipequeño*.

5.10 *Libanothamnus spectabilis* (Cuatrec.) Cuatrec., Phytologia 35(1): 51. 1976. *Espeletia spectabilis* Cuatrec., Phytologia 27(1): 46–49. 1973. **TYPE. VENEZUELA: Mérida:** Zanjón del Cupís, in Páramo de San José, Andean silva, 3100 m, caulirosula 8–10 m, 18–21 Nov 1972, M.López-Figueiras, H.A.Rodríguez & J.&M.Wurdack 8912 (holotype: US!; isotypes: BC!, F!, G!, HPUJ!, K!, MERF!, NY!, VEN!).

Common names. Frailejón de monte (V), incienso (V).

5.11 *Libanothamnus tamanus* (Cuatrec.) Cuatrec., Phytologia 35(1): 51. 1976. *Espeletia tamana* Cuatrec., Phytologia 27(3): 171–173. 1973. **TYPE. VENEZUELA: Táchira:** Páramo de Tamá, NW end, Quebrada del Reposo, timberline, 2800 m, tree 4 m, white ligules, 2 Jun 1973, L.Ruiz-Terán & M.López-Figueiras 8915 (holotype: US!; isotype: MERF!).

Common names. Incienso (C, V), tabaquillo de Tamá*.

Hybrids

***Espeletia* × *cristalinensis* (Cuatrec.) Cuatrec. (= *Libanothamnus neriifolius* (Bonpl. ex Humb.) Ernst × *Espeletia aristeguietana* Cuatrec.),** *Phytologia* 35(1): 55. 1976.

Espeletia cristalinensis Cuatrec., *Phytologia* 27(1): 169. 1973. **TYPE. VENEZUELA: Trujillo:** Distrito de Boconó, Páramo de la Cristalina, 2500–2600 m alt., en lomas semi clareadas de monte andino, porte gris verdoso claro o ceniciento verdoso, cogollo blanquecino, tronco erecto hasta 60 cm, 7 cm de diám., cubierto de hoja marcescente, simple o ramoso sobre la base con varios grandes rosetones, 8–12 sinflorescencias axilares robustas, hojas coriáceas flexibles o rígidas, verdoso grisáceas haz, claras envés, vainas semiamplectantes, lígulas amarillo vivo, flósculos amarillos, círculo ligular 30 mm, disco 13 mm, 17 Feb 1973, J.Cuatrecasas, L.Ruiz-Terán & M.López-Figueiras 28556 (holotype: US!; isotype: MERF).

Common names. Frailejón (V), incienso cenizo de la Cristalina*.

Note. Both molecular and morphological evidence suggest the hybrid nature of *E. ×cristalinensis*. Based on the author's field observations in the topolocality, only a few sparse individuals were found in the contact zone of two large populations of the species suggested in the hybrid formula (Fig. 1A). *E. ×cristalinensis* has characteristics of both *Libanothamnus* and *Espeletia*, which probably confused Cuatrecasas, who was never convinced about the position of this form, and had placed it within *Libanothamnus* in his notes. Leaves with open sheaths and abundant hairs are more similar to *Espeletia* species, while numerous characteristics from *Libanothamnus* are expressed in the synflorescences. A photograph at US of the live paratype (L.Ruiz-Terán & M.López-Figueiras 2257) shows the plant growing between *L. neriifolius* plants, and having leaves with undulate margin and unhealthy appearance, which I have seen as frequent characters in other hybrids of the group. Another photograph taken by Cuatrecasas in the topolocality (photo I-4976, coll. J.Cuatrecasas 28994) shows an individual of *E. ×cristalinensis* growing isolated in a population of *E. aristeguietana* (Fig. 1B).

***Libanothamnus ×gritaensis* Cuatrec. (= *Libanothamnus neriifolius* var. *columbicus* Cuatrec. × *L. occultus* (S. F. Blake) Cuatrec.),** *Phytologia* 47(1): 7 (–8). 1980. **TYPE. VENEZUELA: Tachira:** Llano de Campoalegre, cercanías de La Grita hacia Páramo del Batallón, 2500 m, árbol 5 m, hoja coriácea, crasiúscula, verde amarillenta haz, verde cenicienta envés, pedúnculos verde claros, lígulas blancas (blanco crema), photos K 2705–2712, I, 2 Oct 1969, J.Cuatrecasas, M.López-Figueiras, L.Marcano-Berti 27999 (holotype: US!; isotypes: US!, MERF).

6 *Paramiflos* Cuatrec., *Proc. Biol. Soc. Wash.* 108: 748–750. 1995. **TYPE.** *Espeletia glandulosa* Cuatrec. (= *Paramiflos glandulosus* (Cuatrec.) Cuatrec.)

6.01 *Paramiflos glandulosus* (Cuatrec.) Cuatrec., *Proc. Biol. Soc. Wash.* 108: 749. 1995. *Espeletia glandulosa* Cuatrec., *Revista Acad. Colomb. Ci. Exact.* 3(11): 434, figs.

17, 18, 23, pl. III. 1940. **TYPE. COLOMBIA: Boyacá:** Alto de Canutos, Páramo de Guantiva, southern slope, 3200–3400 m, 3 Aug 1940, J. Cuatrecasas 10360 (holotype: COL; isotypes: COL!, FI, P, US!); additional collections: ibidem: Páramo de Arcabuco, 2950 m alt., 5 Aug 1940, J. Cuatrecasas 10444 (COL, US).

Espeletia glandulosa var. *scaberrima* Cuatrec., Brittonia 8(3): 185. 1956. **TYPE. COLOMBIA: Norte de Santander:** Andes de Pamplona, 2800 m, Jun 1851, Triana 1327 (holotype: P; isotypes: P, COL).

Espeletiopsis glandulosa (Cuatrec.) Cuatrec., Phytologia 35(1): 55. 1976.

Common names. Frailejón (C), frailejón glanduloso (C).

7 *Ruilopezia* Cuatrec., Phytologia 35(1): 51, fig. 2. 1976. **TYPE. *Ruilopezia figueirasii* (Cuatrec.) Cuatrec.**

7.01 *Ruilopezia atropurpurea* (A. C. Sm.) Cuatrec., Phytologia 35(1): 52. 1936. *Espeletia atropurpurea* A. C. Sm., Brittonia 1(7): 508. 1935. **TYPE. VENEZUELA: Mérida:** Páramo de Quirorá, 3200 m, 8 Oct 1971, Jahn 731 (holotype: US!; isotypes: FI, G, GH, NY!, VEN).

Common names. Frailejón (V), frailejón tostado (V).

7.02 *Ruilopezia bracteosa* (Standl.) Cuatrec., Phytologia 35(1): 52. 1976. *Espeletia bracteosa* Standl., Amer. J. Bot. 2: 484. 1915. **TYPE. VENEZUELA: Trujillo:** Páramo de la Cristalina, between Boconó and Trujillo, 2900 m, 20 Dec 1910, Jahn 156 (holotype: US!; isotype: VEN).

Espeletia frailejonota Aristeg., Bot. Soc. Venez. Ci. Nat. 20(93): 284–285. 1959. **TYPE. VENEZUELA: Trujillo:** Sierra de Guirigay near the Laguna Parida, 3400 m, Aug 1958, L. Aristeguieta & Medina 3576 (holotype: VEN; isotypes: NY!, US!).

Ruilopezia frailejonota (Aristeg.) Cuatrec., Phytologia 35(1): 52. 1976.

Common names. Frailejón (V), frailejón de potrero*.

7.03 *Ruilopezia bromelioides* (Cuatrec.) Cuatrec., Phytologia 35(1): 52. 1976. *Espeletia bromelioides* Cuatrec., Phytologia 29(5): 369–372. 1975. **TYPE. VENEZUELA: Mérida:** Páramo de Los Colorados, potreros de San Rafael, 2600–2700 m, 18–20 Jul 1974, M. López Figueiras & H. A. Rodríguez 9054 (holotype: US!; isotype: MERF!).

Common names. Frailejón (V), frailejón bromelia*.

7.04 *Ruilopezia cardonae* (Cuatrec.) Cuatrec., Phytologia 35(1): 52. 1976. *Espeletia cardonae* Cuatrec., Revista Acad. Col. Ci. Exact. 5(17): 20–21, fig. 8. 1942. **TYPE. VENEZUELA: Táchira:** Cordillera de Los Andes, Páramo de Tamá, headwaters of Río Oirá, 3100–3300 m, Jul 1939, Cardona 304 (holotype: VEN; isotypes: FI, US!).

Common names. Frailejón (V), frailejón de cardo*.

7.05 *Ruilopezia coloradarum* (Cuatrec.) Cuatrec., Phytologia 35(1): 52. 1976. *Espeletia coloradarum* Cuatrec., Phytologia 29(5): 372–374. 1975. **TYPE. VENEZUELA: Mérida:** potrero de San Rafael in Páramo de Las Coloradas, 2700 m,

3 Jul 1974, M.López-Figueiras & M.Keogh 9108 (holotype: US!; isotypes: F!, MERF!, NY!).

Common names. Frailejón (V), frailejón de las Coloradas*.

7.06 *Ruilopezia cuatrecasii* (Ruiz-Terán & López-Fig.) Cuatrec., *Phytologia* 35(1): 52. 1976. *Espeletia cuatrecasii* Ruiz-Terán & López-Fig., *Rev. Fac. Farm. Univ. Andes Mérida* 14: 5–13. 1974. **TYPE. VENEZUELA: Mérida:** between El Morro & Aricagua, at the border of Laguna Tapada, 2630 m, 9 Jun 1973, L.Ruiz-Terán & M.López-Figueiras 8738 (holotype: MERF!; isotype: US!).

Common names. Frailejón (V), frailejón de Cuatrecasas*.

7.07 *Ruilopezia emmanuelis* Cuatrec., *Phytologia* 61(1): 56–58. 1986. **TYPE. VENEZUELA: Trujillo:** Páramo de Las Rosas, between Las Lajas and Barro Amarillo, 2900–3000 m, 8 Mar 1985, M.López-Figueiras & D.Griffin 32405 (holotype: US!; isotypes: F!, G!, K!, MERF!, NY!, US!, VEN!).

Common names. Frailejón (V), frailejón de Las Rosas*.

7.08 *Ruilopezia figueirasii* (Cuatrec.) Cuatrec., *Phytologia* 35(1): 52. 1976. *Espeletia figueirasii* Cuatrec., *Phytologia* 20(8): 475–476. 1971. **TYPE. VENEZUELA: Mérida:** Páramo de Los Granates, in Loma de Paja, 3240 m, 11 Oct 1969, J.Cuatrecasas, L.Ruiz-Terán & M.López-Figueiras 28068 (holotype: US!; isotype: MERF!).

Common names. Frailejón guarura (V), frailejón maguey (V), frailejón negro (V).

7.09 *Ruilopezia floccosa* (Standl.) Cuatrec., *Phytologia* 35(1): 52. 1976. *Espeletia floccosa* Standl., *Amer. J. Bot.* 2: 481. 1915. **TYPE. VENEZUELA: Mérida:** Páramo de Timotes, 3300–4000 m, frailejón plateado, Oct 1910, Jahn 154 (holotype: US!).

Common names. Frailejón (V), frailejón brillante (V), frailejón muñeco (V), frailejón niño (V), frailejón plateado (V).

7.10 *Ruilopezia grisea* (Standl.) Cuatrec., *Phytologia* 35(1): 52. 1976. *Espeletia grisea* Standl., *Amer. J. Bot.* 2: 477–478. 1915. **TYPE. VENEZUELA: Mérida:** Sierra Nevada de Mérida, southern slopes, Chorro Blanco, 3800 m, Jan 1911, Jahn 157 (holotype: US!).

Common names. Frailejón (V), frailejón gris (V).

7.11 *Ruilopezia hanburiana* (Cuatrec.) Cuatrec., *Phytologia* 35(1): 52. 1976. *Espeletia hanburiana* Cuatrec., *Soc. Venez. Cienc. Nat.* 17(85): 86–88, figs. s.n. 1956. **TYPE. VENEZUELA: Mérida:** Páramo de Acequias, 3500 m, 18 Oct 1938, Hanbury-Tracy 130 (holotype: K!; isotypes: NY!, US!).

Common names. Frailejón (V), frailejón de Campo Elías*.

7.12 *Ruilopezia jabonensis* (Cuatrec.) Cuatrec., *Phytologia* 35(1): 52. 1976. *Espeletia jabonensis* Cuatrec., *Phytologia* 23(4): 360–362. 1972. **TYPE. VENEZUELA:**

Trujillo–Lara: Páramo del Turmal, Tres Pozos, close to border with state of Lara and Páramo del Jabón, 2800–2850 m, 8 Jun 1971, L.Ruiz-Terán & M.López-Figueiras 1995 (holotype: US!; isotype: MERF!).

Common names. Frailejón blanco (V), frailejón plateado (V), frailejón plateado de hoja fina*.

7.13 *Ruilopezia jahnii* (Standl.) Cuatrec., Phytologia 35(1): 53. 1976. *Espeletia jahnii* Standl., Amer. J. Bot. 2: 479–480, fig. 5. 1915. **TYPE. VENEZUELA: Táchira:** Páramo del Batallón, 3000 m, Mar 1911, Jahn 155 (holotype: US!; isotype: VEN).

Common names. Frailejón (V), frailejón de Táchira*.

7.14 *Ruilopezia joséphensis* (Cuatrec.) Cuatrec., Phytologia 35(1): 52. 1976. *Espeletia joséphensis* Cuatrec., Phytologia 29(5): 374–377. 1975. **TYPE. VENEZUELA: Mérida:** Páramo de San José de Acequias, 2600 m, 18–20 Jul 1974, M.López-Figueiras & H.A.Rodríguez 9073 (holotype: US!; isotype: MERF!).

Common names. Frailejón (V), frailejón de Don José*.

7.15 *Ruilopezia leucactina* (Cuatrec.) Cuatrec., Phytologia 35(1): 52. 1976. *Espeletia leucactina* Cuatrec., Phytologia 29(5): 377–379. 1975. **TYPE. VENEZUELA: Táchira:** Páramo del Batallón, 3000 m, 13 Aug 1974, M.López-Figueiras 9151 (holotype: US!; isotypes: FI, MERF!).

Common names. Frailejón (V), frailejón blanco del Batallón*.

7.16 *Ruilopezia lindenii* (Sch. Bip. ex Wedd.) Cuatrec., Phytologia 35(1): 53. 1976. *Espeletia lindenii* Sch. Bip. ex Wedd., Chlor. And. 1: 66–67. 1856. **TYPE. VENEZUELA: Mérida:** Páramo del Tambor, 11000–12000 ft, Jul 1843, J.J.Linden 1414 (holotype: P; isotypes: BR, FI, FI, G, KI, LE, P, W).

Common names. Frailejón (V), frailejón macho (V), frailejón morado (V).

7.17 *Ruilopezia lopez-palacii* (Ruiz-Terán & López-Fig.) Cuatrec., Phytologia 35(1): 53. 1976. *Espeletia lopez-palacii* Ruiz-Terán & López-Fig., Rev. Fac. Farm. Univ. Andes Mérida 17: 13–19, figs. 31–34. 1976. **TYPE. VENEZUELA: Trujillo:** Páramo de Guaramacal, 15 km East of Boconó, 2600 m, 9 Aug 1975, L.Ruiz-Terán, M.López-Figueiras & D.Griffin 12619 (holotype: MERF!; isotype: US!).

Common names. Frailejón (V), frailejón piña de Guaramacal*.

7.18 *Ruilopezia marcescens* (S. F. Blake) Cuatrec., Phytologia 35(1): 53. 1976. *Espeletia marcescens* S. F. Blake, Contrib. U.S. Nat. Herb. 20: 536–537. 1924. **TYPE. VENEZUELA: Mérida:** Páramo de Quirorá, 2950 m, 24 Feb 1922, Jahn 875 (holotype: US!; isotype: VEN).

Common names. Frailejón (V), frailejón marcescente (V).

7.19 *Ruilopezia margarita* (Cuatrec.) Cuatrec., *Phytologia* 35(1): 53. 1976. *Espeletia margarita* Cuatrec., *Phytologia* 27(1): 49–51. 1973. **TYPE. VENEZUELA: Mérida:** Páramo de Los Granates near Laguna Brava, more or less East of Sierra Nevada de Santo Domingo, near Laguna Brava, 3300 m, 20 May 1971, M.López-Figueiras 8720 (holotype: US!; isotypes: BC!, F!, HPUJ!, K!, MERF!, NY!, U!, VEN!).

Common names. Frailejón (V), frailejón perla (V).

7.20 *Ruilopezia paltonioides* (Standl.) Cuatrec., *Phytologia* 35(1): 53. 1976. *Espeletia paltonioides* Standl., *Amer. J. Bot.* 2: 482–483. 1915. **TYPE. VENEZUELA: Trujillo:** Páramo de las Rosas, 3200 m, Oct 1912, Jahn 159 (holotype: US!; isotype: VEN).

Common names. Frailejón (V), frailejón piña (V), frailejón piñón (V).

7.21 *Ruilopezia ruizii* (Cuatrec.) Cuatrec., *Phytologia* 35(1): 53. 1976. *Espeletia ruizii* Cuatrec., *Phytologia* 23(4): 362–363. 1972. **TYPE. VENEZUELA: Mérida:** Loma de La Libertad in Páramo de Las Coloradas, about 500 m from El Portachuelo (El Ramal) between Santa Cruz de Mora and El Molino, 2750–2800 m, 16 Jan 1971, L.Ruiz-Terán & M.López-Figueiras 1457 (holotype: US!; isotypes: F!, MERF!, NY!).

Common names. Frailejón (V), frailejón lanudo (V).

7.22 *Ruilopezia usubillagae* Cuatrec., *Phytologia* 61(1): 53–55. 1986. **TYPE. VENEZUELA: Mérida:** Páramo de Aricagua, 3000 m, 3 Nov 1922, Jahn 1021 (holotype: US!; isotype: VEN).

Common names. Frailejón (V), frailejón de Aricagua*.

7.23 *Ruilopezia vergarae* Cuatrec. & López-Fig., *Phytologia* 61(1): 58–61. 1986. **TYPE. VENEZUELA: Trujillo:** Sierra de Barbacoas, La Palma, 2390 m, 4 Apr 1976, M.López-Figueiras 12960 (holotype: US!; isotypes: BC!, F!, K!, MA!, MERF!, NY!, U!, VEN!).

Common names. Frailejón (V), frailejón blanco (V), frailejón plateado (V), frailejón plateado hojiancho (V).

7.24 *Ruilopezia viridis* (Aristeg.) Cuatrec., *Phytologia* 35(1): 53. 1976. *Espeletia viridis* Aristeg., *Bol. Soc. Venez. Ci. Nat.* 20(93): 278–281, figs. s.n. 1959. **TYPE. VENEZUELA: Trujillo:** Sierra de Guirigay, towards Laguna Parida, 3500 m, Aug 1958, L.Aristeguieta & Medina 3570 (holotype: VEN; isotypes: NY!, US!, VEN).

Common names. Frailejón (V), frailejón morado (V), frailejón piñón (V).

Hybrids

***Ruilopezia jabonensis* (Cuatrec.) Cuatrec. × *R. vergarae* Cuatrec. & López-Fig.** **VENEZUELA: Trujillo:** Quebrada del Río Turmal, upwards to Páramo del Jabón, subpáramo zone, 3000 m, rosette sessile, leaves shiny sericeous, ray and disc corollas

yellow, chromosome no. $n = ca. 19$, “frailejón plateado”, 3 Nov 1969, J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28237 (MERF!, US!).

***Ruilopezia vergarae* Cuatrec. & López-Fig. × *R. jabonensis* (Cuatrec.) Cuatrec.**
VENEZUELA: Trujillo: Páramo del Turmal, Tres Pozos, 2800–2850 m, acaulirosula, leaves silvery-sericeous, sterile, 8 Jun 1971, L. Ruiz-Terán & M. López-Figueiras 1996 (MERF!, US!); Id., Tres Pozos, 2850–2800 m, acaulirosula, leaves 1 cm latitude, sericeous but less shiny than 28541, incipient inflorescence, 21 cm long, 5.5 cm diam. at the middle, seldom at the ecotonical zone between communities of *R. vergarae* and *R. jabonensis*, “frailejón plateado hojiancho”, 15 Feb 1973, J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28545 (MERF!, US!).

8 *Tamania* Cuatrec., Phytologia 35(1): 53. 1976. **TYPE.** *Espeletia chardonii* A.C. Sm. (= *Tamania chardonii* Cuatrec.)

8.01 *Tamania chardonii* (A. C. Sm.) Cuatrec., Phytologia 35(1): 53–54. 1976. *Espeletia chardonii* A. C. Sm., Bol. Soc. Venez. Ci. Nat. 7(50): 237–238. 1942. **TYPE.**
VENEZUELA: Táchira: Páramo de Tamá, El Paramito, 2550 m, Frontera Colombo-Venezolana, 25 Aug 1939, A. Escalona & Chardon 78 (holotype: US!; isotypes: NY!, VEN, fragm. isotype: COL; photo 4555A, 4556A: NY!, BG).

Espeletia leporina Cuatrec., Revista Acad. Colomb. Ci. Exact. 5(17): 17–18, figs. 3–5; 9C, D; pl. I. 1942. **TYPE. COLOMBIA: Norte de Santander:** Alto del Venado, between Samaria and Toledo, in forest 2300–2400 m, 31 Oct 1941, J. Cuatrecasas, R.E. Schultes & E. Smith 12813 (holotype: COL!; isotypes: A, COL!, F!, HPUJ!, US!).

Common names. Frailejón (V), frailejón grande (V), tabaquero (C, V).

Excluded names

Some herbarium specimens hold names that have never been published: *Coespeletia aurantia* (Aristeg.) Cuatrec., *Espeletia brassicoidea* var. *lancifolia* Cuatrec., *Espeletia conglomerata* var. *lanceolata* Cuatrec., *Espeletia cristalina* Cuatrec., *Espeletia rosea* Cuatrec., *Espeletia tunjana* f. *magnificens* Cuatrec. and *Espeletia xhaughtii* Cuatrec.

Other excluded names are:

***Espeletia amplexicaulis* Nutt.,** J. Acad. Nat. Sci. Philadelphia 7: 38. 1834 (= *Wyethia amplexicaulis* (Nutt.) Nutt.).

***Espeletia helianthoides* Nutt.,** J. Acad. Nat. Sci. Philadelphia 7: 39. 1834 (= *Balsamorhiza sagittata* (Pursh) Nutt.).

***Espeletia sagittata* Nutt.,** J. Acad. Nat. Sci. Philadelphia 7: 39. 1834 (= *Balsamorhiza sagittata* (Pursh) Nutt.).

***Tamananthus crinitus* V.M. Badillo,** Ernstia 30: 25–28. 1985. Explanation follows.

Exclusion of *Tamananthus* V.M.Badillo

The inclusion of the monotypic genus *Tamananthus* V.M.Badillo within the subtribe *Espeletiinae* was proposed by Panero (2007). There is only one collection for the described species in the genus:

Tamananthus crinitus V.M.Badillo, *Ernstia* 30: 25–28. 1985, and *Ernstia* (2 Etapa) 1–2(2): 17–19. 1992. **TYPE. VENEZUELA: Táchira:** distrito Junín, hacia el extreme nor-occidental del gran Páramo de Tamá, cabecera semi-boscosa de la quebrada El Reposo, unos 6–7 km al norte de Villa Páez, 2800 m, hierba o arbusto, ramitas rojo–purpúrea, involucro verde intenso con zonas rojo intenso, ligulas amarillo–intenso, L.Ruiz-Terán & M.López-Figueiras 8930 (holotype: MERF; isotypes: MY, US!).

The specimen was poorly preserve and glued to the herbarium sheet, and does not allow a comprehensive examination. The following characteristics do not fit within the synapomorphies of the *Espeletiinae*: herbaceous or shrubby habit, alternate leaves, bilabiate corolla with the 2-lobed-lip well developed, bidentate style, 7–8 ray flowers in total, isomorphic uncompressed cypselae with prominent carpodium, and fertile disk flowers. Some species (*Coespeletia* spp. and a few *Espeletia* spp.) in *Espeletiinae* show bilabiate ray flowers, sometimes with one or two lobes, although this seems to be an inconsistent character within the species. However, the lip in *Espeletiinae* species, when present, is never as developed as in *T. crinitus*, and lobes in *Espeletiinae* are in general shorter, deeper and more divergent from each other. The morphological characteristics in the specimen and in the description do not conclusively place this taxon with the *Espeletiinae*. DNA amplifications have not been successful until now, but AFLP data suggest that this species is closer to *Ichthyothere* Mart. and *Smallanthus* Mack. than to the *Espeletiinae*. I propose excluding this genus from the subtribe until more material can be studied morphologically and genetically.

Frequency of hybrids in the subtribe *Espeletiinae*

A total of 27 hybrids are included here. From the 4408 herbarium specimens examined, 122 (2.8%) were hybrids. However these numbers do not represent the frequency of hybridization events. It is unquestionable that hybridization is an important process in the subtribe. During my field observations, I was able to collect and photograph dozens of putative hybrids, which occur typically in contact zones of two parapatric populations (e.g. between the usually low-elevation populations of *Libanothamnus* and the high-elevation populations of *Espeletia*), or in areas where sympatric species have large populations (e.g. páramos with *E. grandiflora* and *E. argentea*, or with *E. schultzii* and *E. weddellii*). However, the frequency of hybridization is overemphasized in the botanical collections, because hybrids are the “different ones” and are usually more often collected by inexpert collectors who believe they are novelties to science.

It is interesting to note that hybridization appears to be more frequent at both extremes of the altitudinal range. In the superpáramos it is relatively frequent between *Coespeletia* species and other sympatric taxa of the subtribe (e.g. *E. schultzii*). In the

subpáramos it is common between *Carramboa*, *Espeletiopsis*, lower-elevation *Espeletia* (e.g. *E. aristeguietana*, *E. argentea*, *E. boyacensis*, etc.), *Libanothamnus* and lower-elevation *Ruilopezia* species (e.g. *R. marcescens*, *R. jabonensis*, *R. vergarae*, etc.).

Even more intriguing is that when hybridization in these altitudinal extremes occurs, the synflorescence of the hybrids are often more similar to the species that is adapted to lower elevations, while the leaves are more similar to the species adapted to higher elevations. For instance, *Espeletiopsis* $\times$ *cristalinensis* is found in the upper range of *Libanothamnus neriifolius* and the lower range of *Espeletia aristeguietana*. It has very pubescent thick leaves like those of *E. aristeguietana*, whereas its synflorescence has the branching patterns and shape of *L. neriifolius*. The same pattern can be seen when hybridization occurs between the lower-elevation *E. brassicoidea* and the higher-elevation *E. conglomerata*, or with other hybrids. A possible explanation is that the leaves of the higher-elevation parental species are more adapted to the colder conditions than those of a parental species adapted to warmer conditions, and therefore the expression of this character is selected. In the same way, synflorescences of lower-elevation parental species may be more effective in attracting potential pollinators than those adapted to higher-elevation pollinators. What is clear is that there is a fertile field of research on hybridization within the subtribe.

Based on my personal observations and collections of Espeletiinae, collectors should be always suspicious about a hybrid individual when any of the following conditions occurs:

- Isolated individuals with no abundant populations: Espeletiinae have no pappus in their cypselae, and seeds are dispersed mainly by gravity; therefore collectors should expect to find several individuals of the same species, all related in some degree, and a few sporadic hybrids of sympatric or parapatric species.
- Generally the hybrids have leaves with undulate margins, and often unhealthy appearance.
- Pubescence of hybrids frequently looks disheveled.

First report of two species and one genus for Colombia

***Espeletia steyermarkii* Cuatrec. Representative specimens. COLOMBIA: Norte de Santander:** en vía a Chitagá, antes del desvío hacia Cornejo, subpáramo y páramo azonal del Carbón, 2798 m, 7°4.13'N, 72°39.25'W, acaule, altura total 1.7 m (individuos en la población de hasta 2 m), altura hasta la roseta 0.6 m, 5 inflorescencias frescas y 2–3 secas, todas largas y bien desarrolladas, con ramas florales extremadamente largas alternas (aunque individuos en la población las presentan también opuestas), un par de brácteas estériles en sección media del escapo, pubescencia de aspecto dorado-leonado, población muy densa, con todos los individuos en flor, 3 Oct 2009, M. Díazgranados & R. Sánchez 3860 (ANDES!, COL!, HECASA!, MO!, US!); ibidem, 2801 m, 7°4.10'N, 72°39.15'W, acaule, altura total 1.8 m (individuos en la población de hasta 2 m), altura hasta la roseta 0.6 m, 5 inflorescencias frescas con 5–10 capítulos cada una, todas largas

y bien desarrolladas, con ramas florales extremadamente largas opuestas (a diferencia de la colección MD 3860), un par de brácteas estériles en sección media del escapo, pubescencia de aspecto dorado-leonado, población muy densa, con todos los individuos en flor, 3 Oct 2009, M.Diazgranados & R.Sánchez 3862 (ANDES!, COL!, HECASA!, MO!, US!; photo: Fig. 1C-E).

Note. A very dense population of this species was found for the first time in this country, in an azonal (atypical) páramo for the area, on soils of poor drainage. This is the same environment in which the species is usually found in Venezuela. Some individuals had extremely long opposite floral branches starting in the first portion of the scape of the synflorescences, while others plants had alternate branches, which is a characteristic reported for *E. steyermarkii*. A second population in Colombia has been found in another azonal páramo in the area of the Vereda el Azul (Mun. Toledo).

***Ruilopezia cardonae* (Cuatrec.) Cuatrec. Representative specimens. COLOMBIA: Norte de Santander:** Municipio Toledo, gran Páramo de Tamá, Parque Nacional Natural Tamá, Cuenca del Río Oirá, al comienzo del Cañón del Oirá, sobre la ladera escarpada en el lado colombiano, 7°23.56'N, 72°22.95'W, 3257 m, población abundante de unos 500 individuos maduros, la mayoría con floración pasada o infértiles y unos pocos con flores frescas, altura total 1.3 m, altura hasta la roseta 0.5 m, altura del caule 0.3 m, inflorescencia terminal copiosa, con 16 ramas florales, flores jóvenes blancas que se tornan rosadas cuando maduras y púrpura en la senescencia, 15 Oct 2009, M.Diazgranados & R.Sánchez 3257 (ANDES!, COL!, HECASA!, MO!, US!; photo: Fig. 1F-I).

Note. The species had been reported in the Venezuelan slopes of the gran Páramo de Tama, especially along the basin of the Oirá river. One large population was found on the Colombian side. This is the first record of *Ruilopezia* for Colombia.

Notes about the geographic distribution

The frailejones are widely distributed and abundant in the high Andean forest and páramos of Colombia, Venezuela and, to a lesser extent, Ecuador, where only one species occurs in the north of the country and in the Sierra de Llanganates (Fig. 2A). The northernmost population (-73.8°W, 11°N) grows in the Sierra Nevada de Santa Marta, at -73.8°N. Even though the author has been told about reports of *L. neriifolius* in the state of Sucre in Venezuela (approx. -63.5°W, 10.5°N), which would be the extreme NE of the geographic range, no herbarium specimens from this locality have been seen. The southernmost species is *Espeletia pycnophylla*, which grows in the border region between Colombia and Ecuador and has a separate isolated population far south in the Llanganates National Park (-78.5°W, 1.2°S) (Fig. 2B). Nearly 80% of the species occur between -70.5 and -73°W and 5.5 and 9.0°N, along the Eastern Cordillera in Colombia and the Venezuelan Andes. The frailejones grow in 21 states (64%) of Colombia, six in Ecuador (24%) and 12 in Venezuela (52%).

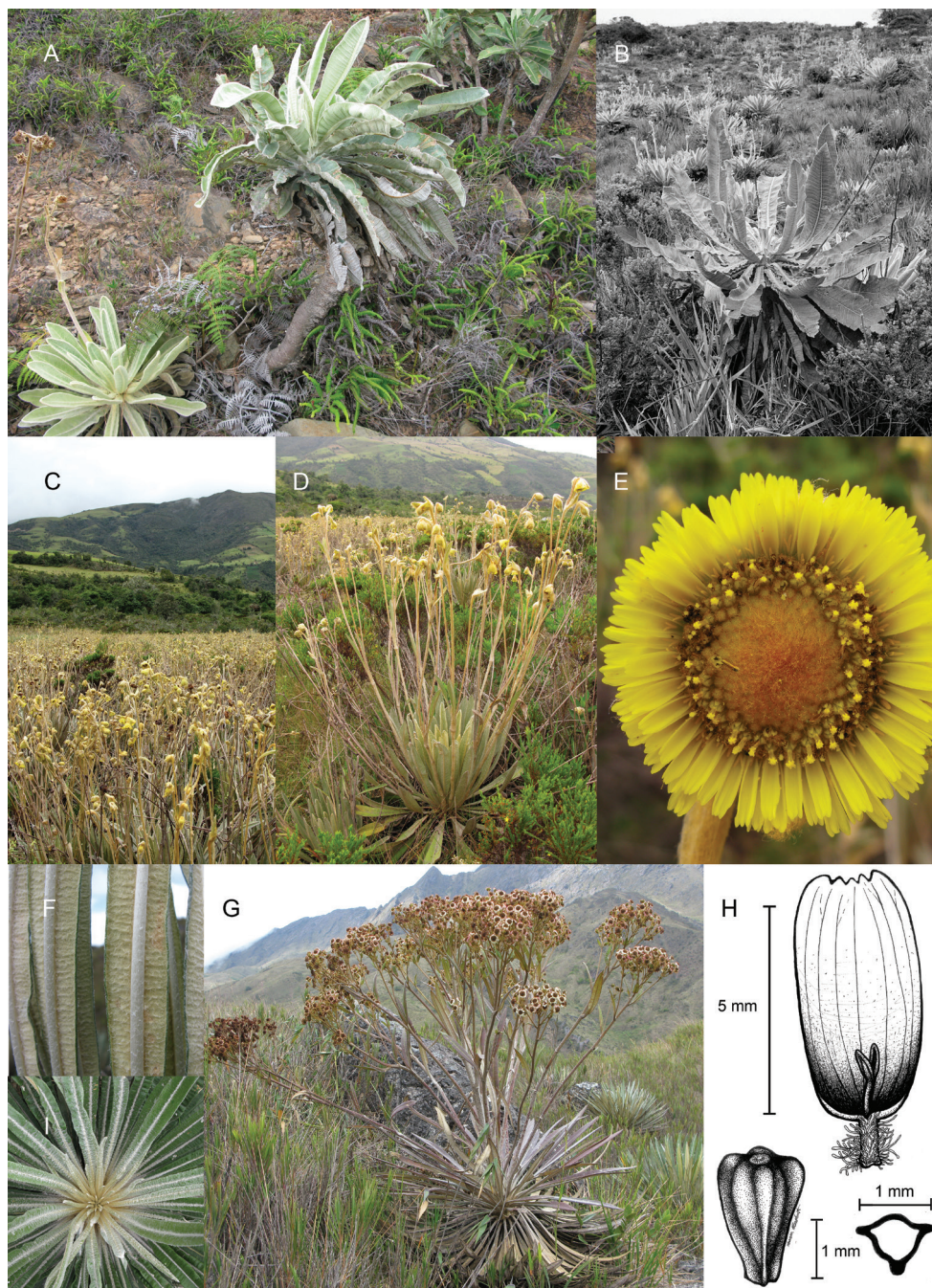


Figure 1. **A–B** *Espeletiopsis x cristalinensis* in the topolocality (**A** coll. M.Díazgranados 4088 (center), growing between *Espeletia aristeguietana* (bottom left corner) and *Libanothamnus neriifolius* (top right corner) **B** coll. J.Cuatrecasas 28994) **C–E** first record of *Espeletia steyermarkii* for Colombia (coll. M.Díazgranados 3862) **F–I** first record of *Ruilopezia cardonae* for Colombia (coll. M.Díazgranados & R.Sánchez 3922). Photographs **A**, **C–G**, **I** by M.Díazgranados, **B** by J.Cuatrecasas; illustrations in **H** by Lauren Merchant.

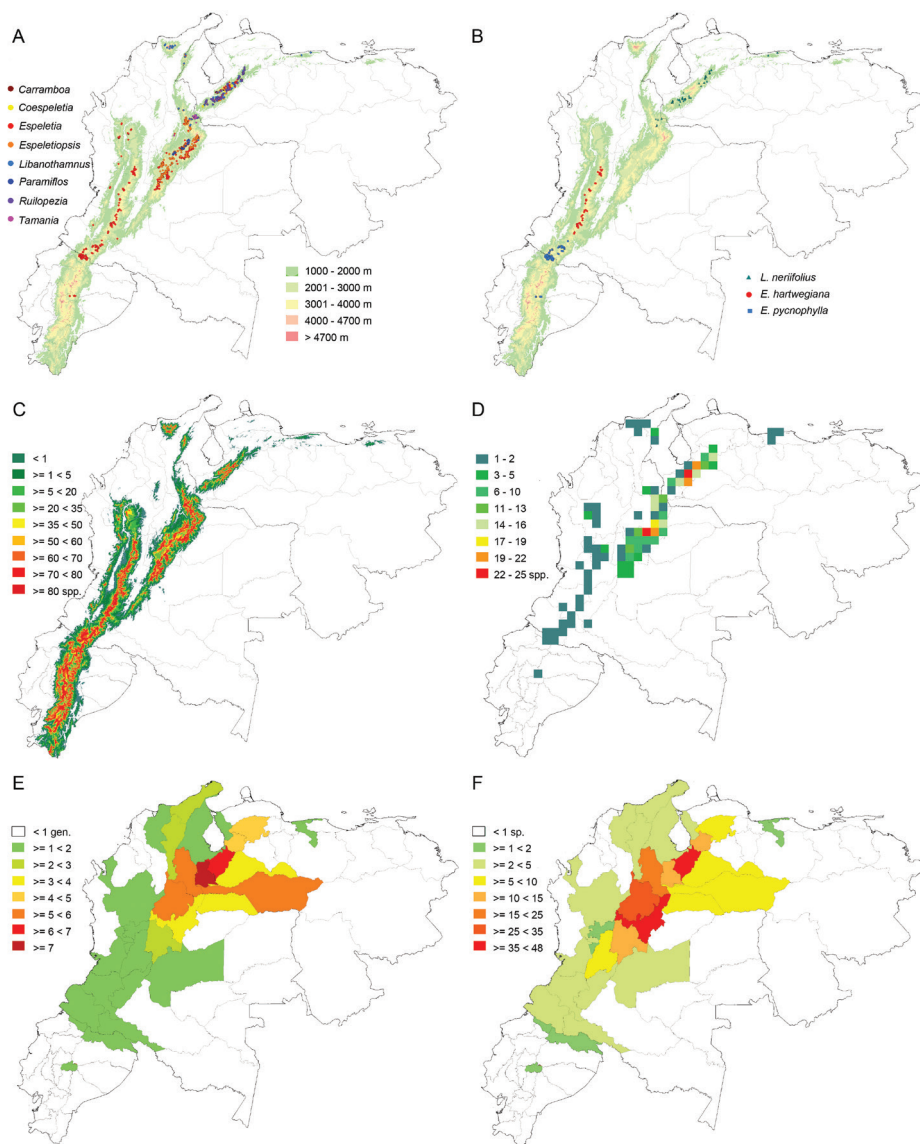


Figure 2. Geographic distribution and species richness of the subtribe Espeletiinae. **A** geographic distribution of the genera (colored dots); background color denotes mountains over 1000 m of elevation **B** distribution of three widespread species **C** species richness throughout the elevation, with classes every 200 m **D** species richness by area (squares: $0.4^{\circ} \times 0.4^{\circ}$); **E** richness of genera by state **F** species richness by state.

Most of the species of Espeletiinae are restricted to a single topographic páramo complex. Similar to island species, they have lost the ability for long-distance dispersal. Seeds lack pappus (except for the scale-like pappus of *Tamania*) and are dispersed by gravity, with no long-distance dispersers known. Only nine species are shared between Colombian and Venezuela, and a few species occur in multiple páramo localities, includ-

ing *L. neriifolius* (in Venezuela), *E. hartwegiana* (in Colombia) and *E. pycnophylla* (in Colombia and Ecuador) as some of the species with the broadest distributions (Fig. 2B). It is notable that these all have various infraspecific taxa, without counting the auto-nyms (*L. neriifolius* has four varieties, and both *E. hartwegiana* and *E. pycnophylla* have two subspecies and two varieties), which denotes a notable morphological variation.

The frailejones grow abundantly above the tree line of the tropical Andes. Although there are some species endemic from the high Andean forests, and a few that can succeed at elevations as low as 1300 m (i.e. *L. neriifolius* var. *turmalensis*, coll. J.Steyermark 105028), most of the taxa (104 species) are found between 3200–3400 m of elevation (Fig. 2C, 3). A few species grow in the superpáramo, close to the snow line, and the highest elevation ever reported is for a *Coespeletia timotensis* (coll. L.Ruiz-Terán 851) growing at 4780 m (Appendix 1). In general, *Carramboa* and *Tamania* grow below 3500 m of elevation, *Coespeletia* grows above 2800 m while the remaining genera have a more or less normal distribution throughout the entire range between 2000–4600 m (Fig. 3, Appendix 1).

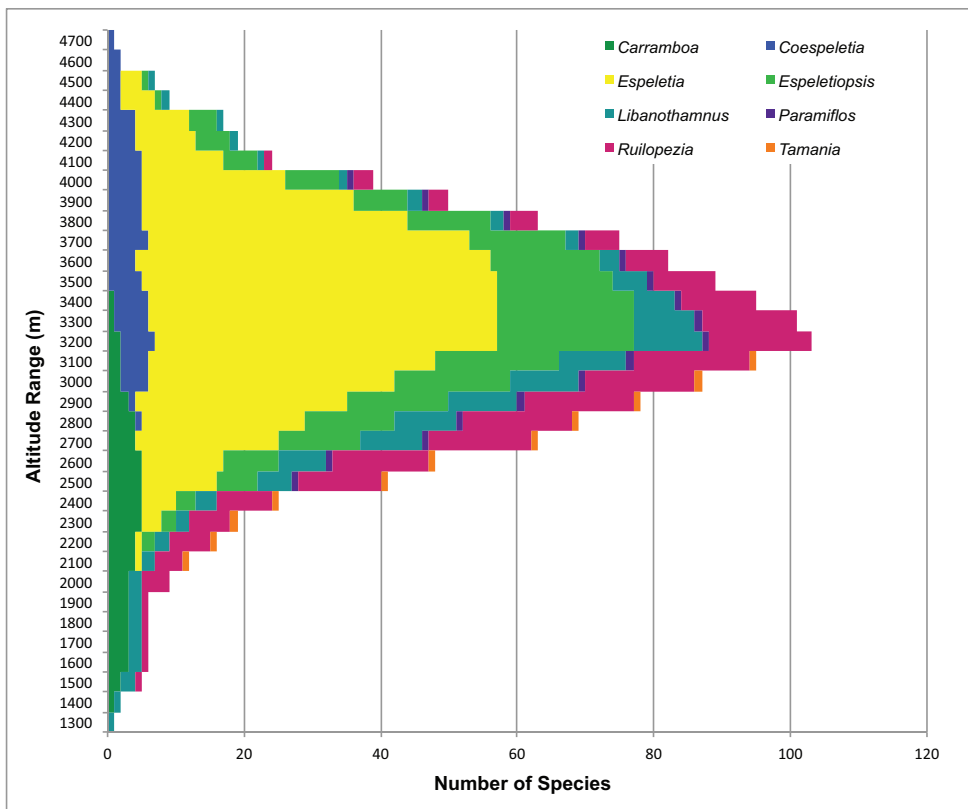


Figure 3. Richness of species throughout the elevation gradient. Each color represents species of each of the genera. *L. neriifolius* has been reported as low as 1300 m, while *C. timotensis* has been found at 4780 m. Most of the species (104) grow in elevations between 3200 and 3400 m.

There are three apparent centers of radiation: Mérida (with 44 spp.) in Venezuela, Santander–Norte de Santander (39 spp. combined) and Boyacá (45 spp.) in Colombia (Fig. 2E–F). An analysis of richness by area (squares of $0.4^{\circ} \times 0.4^{\circ}$ km²) highlights two areas with the highest number of species (> 22 spp.), one in central Mérida and the other in Boyacá with limits of Santander (Fig. 2D). Táchira, a Venezuelan state bordering with Colombia, has the highest richness of genera, followed by Mérida (Fig. 2E). Overall, Colombia has the highest richness of species (86 spp.), followed by Venezuela (67 spp.) and Ecuador (1 spp.). These numbers include one presumable species in Colombia (i.e. *E. tillettii*), found on the Sierra de Perijá in the Venezuelan border with Colombia.

The author is currently describing 17 new taxa of frailejones. The phylogeny will provide new insights into understanding the relationships between species and genera, and will generate further changes in the taxonomy of the group. The systematic list here provides a taxonomic base for all these changes and for any other study related to frailejones.

Acknowledgements

Special thanks to my advisor, Janet C. Barber, and the members of my dissertation committee, Gerardo Camilo, Vicki Funk, Allison Miller, Jason Knouft and Peter Raven, for all their comments and support. I gratefully acknowledge the comments of Christina Flann, Warren L. Wagner and one anonymous reviewer. My most sincere appreciations for the students who contributed to building the database for Espeletii-nae: Camilo Cadena, Matthew DeAngelo, Eduardo García Milagros, Hannah King, Aleksandar Radosavljevic and Lila Wahidi. I want to thank Harold Robinson for his always wise advice. Thanks to Petr Sklenář and Filip Kolar from Czech Republic, and to Gilberto Morillo and Luis 'Kike' Gamez for their immense help in Venezuela. All my acknowledgments to the field assistants: Camilo Cadena, Andrés Diavanera, Elí Flores, Carlos Gómez, Jennifer Gruhn, Rachel Jabaily, César Alirio Leal, Llizeth Mantilla, Clara Quintero, Diego Rodríguez, Nicolás Rodríguez, Susana Rodríguez, César Sanabria, Roberto Sánchez, Jessica Sarmiento, the park rangers of Pisba, Chingaza, Tamá and Denira, and many others. I want to thank the team of the Missouri Botanical Garden, especially Monica Carlsen, Mick Richardson and Peter Hoch. Thanks to Santiago Madriñán and his lab students at the ANDES herbarium, to Santiago Díaz-Piedrahita and to Carlos Parra from COL. Special thanks to the institutions and herbaria that allow me to study their collections, especially: ANDES, CAS, COL, CUVC, F, FMB, HECASA, HUA, K, MER, MO, NY and US. This project has been funded by Saint Louis University, a DDIG grant from NSF (DEB 1011624), a grant from the Committee for Research and Exploration of the National Geographic Society (Grant No. 8613-09), the Missouri Botanical Garden, the Smithsonian Institution (SI) graduate fellowship, the SI Cuatrecasas Fellowship, the SI Latino Initiative, the Society for Systematic Biologists, the American Society of Plant Taxonomist, the Botanical Society of America, the Idea-Wild Foundation, the Neotropical Grassland Conservancy and the Fondo Colombia Biodiversa of the Fundación Alejandro Ángel Escobar.

References

- Baldwin BG (2009) Heliantheae alliance. In: Funk VA, Susanna A, Stuessy T, Bayer RT (Eds) Systematics, Evolution and Biogeography of Compositae. International Association for Plant Taxonomy, Vienna, Austria, 689–711.
- Bernal R, Galeano G, Sarmiento H, Gutiérrez M (2012) Nombres Comunes de las Plantas de Colombia. <http://www.biovirtual.unal.edu.co/nombrescomunes/>
- Cuatrecasas J (1976) A New Subtribe in the Heliantheae (Compositae): Espeletiinae. *Phytologia* 35: 43–59.
- Cuatrecasas J (1986) Speciation and radiation of the Espeletiinae in the Andes. In: Vuilleumier F, Monasterio M (Eds) High Altitude Tropical Biogeography. Oxford University Press, New York, USA, 267–303.
- Cuatrecasas J (1995) A new genus of the Compositae: *Paramiflos* (Espeletiinae) from Colombia. *Proceedings of the Biological Society of Washington* 108: 748–750.
- Cuatrecasas J (1996) Clave provisional de las especies del género *Espeletiopsis* Cuatrec. (Espeletiinae, Compositae). *Anales del Jardín Botánico de Madrid* 54: 370–377.
- Cuatrecasas J (in press) A Systematic Study of the Subtribe Espeletiinae (Heliantheae, Asteraceae). *Memoirs of The New York Botanical Garden*.
- Díaz-Piedrahita S, Obando S (2004) Una nueva especie de *Espeletiopsis* (Asteraceae, Heliantheae) de Colombia. *Revista Acad Colomb Ci Exact* 28: 323–326.
- Díaz-Piedrahita S, Pedraza P (2001) dos Nuevas Especies de *Espeletia* (Asteraceae - Heliantheae) de Colombia. *Revista Acad Colomb Ci Exact* 25: 11–15.
- Díaz-Piedrahita S, Rodríguez BV (2008) Novedades en los géneros *Espeletia* Mutis ex Humb. & Bonpl. y *Espeletiopsis* Cuatrec. (Asteraceae, Heliantheae, Espeletiinae). *Revista Acad Colomb Ci Exact* 32: 455–464.
- Díaz-Piedrahita S, Rodríguez BV, Galindo-Tarazona R (2006) Interesantes Novedades en Espeletiinae (Asteraceae-Heliantheae) de Colombia. *Revista Acad Colomb Ci Exact* 30: 332–352.
- Díaz-Piedrahita S, Rodríguez-Cabeza BV (2010) Nuevas Especies Colombianas de *Espeletiopsis* Cuatrec. y de *Espeletia* Mutis ex Humb. & Bonpl. (Asteraceae, Heliantheae, Espeletiinae). *Revista Acad Colomb Ci Exact* 34: 441–454.
- Díazgranados M (2012) Phylogenetic and biogeographic relationships within the Espeletiinae (family Asteraceae), an endemic subtribe of the South American Páramos (Doctoral Dissertation). PhD Thesis, Saint Louis University, USA.
- Fagua JC, Gonzalez VH (2007) Growth rates, reproductive phenology, and pollination ecology of *Espeletia grandiflora* (Asteraceae), a giant Andean caulescent rosette. *Plant biology* (Stuttgart, Germany) 9: 127–135. doi: 10.1055/s-2006-924544
- García N, Calderón E, Galeano G (2005) Frailejones. In: Calderón E, Galeano G, García N (Eds) Libro Rojo de Plantas de Colombia. Bogotá D.C., Colombia, 225–385.
- Hijmans RJ, Guarino L, Bussink C, Mathur P, Cruz M, Barrentes I, Rojas E (2012) DIVA-GIS 7.5. A geographic information system for the analysis of species distribution data. Manual available at: <http://www.diva-gis.org>

- Humboldt A, Bonpland A (1809 [1808]) *Plantae Aequinoctiales recueillies au Mexique :dans l'île de Cuba, dans les provinces de Caracas, de Cumana et de Barcelone, aux Andes de la Nouvelle Grenade, de Quito et du Pérou, et sur les bords du rio-Negro de Orénoque et de la rivière des Amazones.*
- Mcneill J, Barrie FR, Burdet HM, Demoulin V, Hawksworth DL, Marhold K, Nicolson DH, Prado J, Silva PC, Skog JE, Wiersema JH, Members, Turland NJ, Secretary of The Editorial Committee (2006) International Code of Botanical Nomenclature (VIENNA CODE). Electronic version of the original English text, adopted by the Seventeenth International Botanical Congress. Vienna, Austria, July 2005. International Association for Plant Taxonomy, online at <http://ibot.sav.sk/icbn/main.htm>
- Missouri Botanical Garden, Royal Botanic Gardens in Kew (2010) The Plant List, Version 1. Published on the internet. <http://www.theplantlist.org>
- Morillo G, Briceño B (2007) Estudio sobre *Carramboa tachirensis* (Aristeg.) Cuatrec. (Asteraceae) y sus afines. *Rev Fav Agron (LUZ)* 24: 475–481.
- Panero J (2007) Tribe Millerieae Lindl. (1829). In: Kubitzki K (Ed) *The Families and Genera of Vascular Plants*. Springer, Berlin Heidelberg New York, 477–492.
- Rauscher J (2002) Molecular phylogenetics of the *Espeletia* complex (Asteraceae): evidence from nrDNA ITS sequences on the closest relatives of an Andean adaptive radiation. *American Journal of Botany* 89: 1074–1084. doi: 10.3732/ajb.89.7.1074
- Weddell HA (1855[1857]) *Chloris Andina*, 1: 212.

Appendix

Geographic distribution of the species of the subtribe Espeletiinae. (doi: 10.3897/phytokeys.16.3186.app) File format: MS Excell spreadsheet (xlsx).

Explanation note: Data based on the evaluation of 3794 herbarium specimens.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Citation: Diazgranados M (2012) A nomenclator for the frailejones (Espeletiinae Cuatrec., Asteraceae). *PhytoKeys* 16: 1–52. doi: 10.3897/phytokeys.16.3186.app

Two new species of forget-me-nots (*Myosotis*, Boraginaceae) from New Zealand

Carlos A. Lehnebach¹

¹ Museum of New Zealand Te Papa Tongarewa, POBOX 467, Wellington, New Zealand

Corresponding author: Carlos A. Lehnebach (CarlosL@tepapa.govt.nz)

Academic editor: James Miller | Received 27 June 2012 | Accepted 13 August 2012 | Published 21 August 2012

Citation: Lehnebach CA (2012) Two new species of forget-me-nots (*Myosotis*, Boraginaceae) from New Zealand. PhytoKeys 16: 53–64. doi: 10.3897/phytokeys.16.3602

Abstract

Two new species of forget-me-nots, *Myosotis chaffeyorum* C.A.Lehnebach **sp. nov.** and *Myosotis mooreana* C.A.Lehnebach **sp. nov.** are described and illustrated. These species are endemic to New Zealand and restricted to the mountains of north-west Nelson (South Island). Both species are uncommon and *M. mooreana* is known from the type locality only. Their conservation status is rated as “Nationally Critical”. A table listing differences between these two new species and other similar species and an identification key are provided.

Keywords

Boraginaceae, Kahurangi National Park, *Myosotis*, *Myosotis chaffeyorum*, *Myosotis mooreana*, new species, New Zealand, New Zealand Flora

Introduction

The genus *Myosotis* L. is found in the Northern and Southern Hemisphere. Phylogenetic analyses of nuclear and chloroplast sequences suggest *Myosotis* originated in the Northern Hemisphere (Winkworth et al. 2002) and is nested within the tribe Cynoglosseae along with *Trigonotis* Steven (Weigend et al. 2010). In the Southern Hemisphere, New Zealand is the centre of diversity for the genus *Myosotis*, and 39 species have been listed for the country (Breitwieser et al. 2012). These species occupy a great diversity of habitats ranging from coastal cliff faces and sand dunes to stream banks in

forests, tussock grasslands, tarns, limestone and marble outcrops, and scree-slopes on the mountains of the Southern Alps. This ecological diversification is matched by an equally remarkable diversification of habit (cushion, single rosette, creeping/trailing stems), plant size (less than a centimetre to up to 40 cm height), and vegetative (leaf shape, indumentum type) and reproductive characters (white, yellow, brown-bronze, blue flowers and automatic selfing and out-crossing species).

Despite the many phenotypic differences exhibited by New Zealand *Myosotis*, identification at the species level can be challenging, especially when dealing with rare or under-collected species or poorly press-dried specimens in which flower and leaf characters have become distorted. The former situation, in particular, is commonly encountered by students of this genus, as many species have a highly restricted distribution with small-size populations (Brandon 2001). In fact, some of the currently recognised species are known only from a single locality (e.g. *M. alboseric*a Hook.f., *M. laeta* Cheeseman) or, in more extreme cases, the type collection is the only collection ever made (e.g. *M. laingii* Cheeseman).

Currently, a revision of the genus *Myosotis* in New Zealand is underway and species limits for a number of widespread and critically endangered species are under assessment. Also, phylogenetic affinities within New Zealand species are being studied using DNA sequences of both nuclear and chloroplast markers and AFLP fingerprinting data (Meudt et al. in preparation). Towards this end, a number of collecting trips to sub-alpine and alpine areas of the North and South Island of New Zealand have taken place between 2009 and 2012. An expedition to Kahurangi National Park in north-west Nelson (South Island, 41°11'26"S, 172°44'52"E), one of the diversity hotspots for *Myosotis* in the country, uncovered the existence of two morphologically and ecologically distinct entities, which are illustrated and described here as new species. An identification key and a table summarising morphological differences between these two new species and other morphologically similar species are included.

Methods

Specimens were press-dried in the field as soon as they were collected. Flowers, when available, were collected and preserved in 70% ethanol for later examination. Some samples were kept fresh and later photographed under a dissecting microscope. To test whether phenotypic differences observed in the field were due to phenotypic plasticity, some samples were cultivated for two seasons, under common garden conditions. Vegetative and reproductive characters were observed and measured from fresh and press-dried material. These records were later compared with descriptions in Moore (1961, 1988), Moore and Simpson (1973), and with fresh and dried material of morphologically similar species, i.e. *M. brockiei* L.B.Moore & M.J.A.Simpson, *M. forsteri* Lehm., *M. matthewsii* L.B.Moore, and *M. spathulata* G.Forst. (Table 1). Collections of *Myosotis* from the Allan Herbarium (CHR), the Department of Conservation Nelson-

Table 1. Morphological comparison of *M. chaffeyorum*, *M. mooreana* with other species of *Myosotis*. Data for *M. brockiei*, *M. forsteri*, *M. matthewsii*, and *M. spathulata* are from Moore (1961, 1988), Moore and Simpson (1973) and representative voucher specimens (Appendix 1).

Character	<i>M. chaffeyorum</i>	<i>M. matthewsii</i>	<i>M. spathulata</i>	<i>M. mooreana</i>	<i>M. brockiei</i>	<i>M. forsteri</i>
Rosette leaf lamina shape	orbicular	orbicular	orbicular to broadly elliptic	obovate	narrow-elliptic	orbicular to broadly elliptic
Rosette leaf lamina size (mm)	8.1 – 8.9 × 7.7 – 9.2	16.8 – 21 × 15.3 – 20.3	10.1 – 16.3 × 9 – 12.2	32.4 – 56 × 15.8 – 20.5	60 – 120 × 10 – 15	25 – 30 × 31 – 39
Leaf indumentum	strigose	hispid	hispid	hispid	tomentose	hispid
Hairs on leaf margin	appressed	appressed	arcuate	arcuate/straight	arcuate/erect	arcuate
Rosette leaf petiole width (mm)	0.2 – 0.3	0.5 – 0.6	0.3 – 0.4	1.4 – 1.8	1.8 – 1.9	1.9 – 3
Hairs on petiole	appressed	appressed	erect/arcuate	arcuate	arcuate	erect/arcuate
Stem habit	decumbent	decumbent	creeping	ascending	erect	ascending
Hairs on stem	appressed only	appressed only	erect/arcuate	appressed, arcuate, erect	appressed, arcuate, erect	arcuate/appressed
Stem rooting at nodes	no	no	yes	no	no	no
Flower arrangement	solitary, usually opposite to leaf	ill-defined cyme, on stem below/above leaf	solitary, on stem above/below leaf	cyme	cyme	cyme
Pedicle at fruiting (mm)	1.5 – 3	4.6 – 8.4	2.3 – 3.7	2.5 – 2.9	3.6 – 4.3	2.6 – 3
Corolla diameter (mm)	3.7 – 4	5 – 8	3	3.8 – 4.8	9 – 10	3.2 – 4.6
Position of anthers	within corolla tube	outside corolla tube	within corolla tube	within corolla tube	outside corolla tube	within corolla tube
Fruiting calyx (mm)	2.3 – 3	3.5 – 4.2	2.1 – 2.7	2.7 – 2.8	3.9 – 4.4	4.5 – 5
Nutlet shape	ovoid-ellipsoid	ovoid-ellipsoid	ovoid	ovoid-ellipsoid	ovoid	ovoid
Nutlet size (mm)	1.2 × 0.7 – 0.8	1.2 – 1.8 × 0.8 – 1.2	1 – 1.3 × 0.6 – 1	1.4 – 1.5 × 0.7 – 0.9	1.7 – 1.9 × 1.1	1.2 – 1.8 × 0.9 – 1.1
Known distribution	South Island	North Island	North & South Island	South Island	South Island	North & South Island
Representative specimen	CHR 311719	WELT SP093687	WELT SP090633	WELT SP092756	WELT SP090249	WELT SP092226

Marlborough Conservancy (NM) and the Museum of New Zealand Te Papa Tongarewa (WELT) were checked for previous collections of these two entities. Type material of known *Myosotis* species stored at the Auckland Museum (<http://www.aucklandmuseum.com/57/botany>) and Museum of New Zealand (<http://collections.tepapa.govt>).

nz/search.aspx?term=Myosotis types) were also studied and compared with the new material collected at Kahurangi National Park.

Taxonomy

Myosotis chaffeyorum C.A.Lehnebach, sp. nov.

urn:lsid:ipni.org:names:77121627-1

http://species-id.net/wiki/Myosotis_chaffeyorum

Figs 1–2

Diagnosis. Similar to *M. spathulata* and *M. matthewsii*, but differs from *Myosotis spathulata* by its well-defined, slender petiole; appressed, straight hairs on stem, petiole, leaf lamina and margin; and its decumbent stem not rooting at nodes. It differs from *M. matthewsii* by its strigose indumentum on leaf upper surface; smaller flowers (3.7 – 4 mm across vs 5 – 8 mm across); stamens included in the corolla tube and fruiting calyx on shorter pedicel (1.5 – 3 mm vs 4.6 – 8.4 mm).

Type. NEW ZEALAND. South Island, north-west Nelson: Takaka Valley, under overhanging limestone rock in forest, alt. ca 730 m, February 1977, A.P.Druce s.n. (Holotype: CHR [CHR 311719]; Fig. 1).

Plant perennial, 1.4 – 4.6 cm tall. Rosette leaves 6 – 9, lamina orbicular, 8.1 – 8.9 × 7.7 – 9.2 mm, apex mucronate, mucro ca 1 mm long. Leaf indumentum strigose, hairs on upper and lower surface sparsely distributed, non overlapping, appressed and antrorse. Hairs on leaf margin appressed. Petiole well-defined, 11.9 – 13.5 × 0.2 – 0.3 mm; hairs appressed, antrorse, sparsely distributed. Stem light brown, decumbent, not rooting at nodes, 59 – 100 × 0.3 – 0.5 mm. Stem hairs appressed as for leaves, hairs 0.2 – 0.6 mm long. Stem leaves elliptic or orbicular, 7.2 – 8.8 × 4.4 – 6.2 mm, mucronulate, shortly petiolate or sessile towards distal end of stem. Indumentum as for rosette leaves. Calyx lobes lanceolate, 1.5 – 2 mm long, hairs in upper half of the lobe only. Fruiting calyx 2.3 – 3 mm long; hairs appressed, straight, overlapping, not uniform in size. Flowers borne along the trailing stem, each usually opposite to a leaf. Pedicel at fruiting 1.5 – 3 mm long. Corolla white with yellow scales, 3.7 – 4 mm across. Corolla lobes obovate, not overlapping, 1.4 – 1.8 × 1.2 – 1.6 mm, apex rounded or irregularly notched. Corolla tube 2 – 2.2 mm long. Stamens included in the corolla, with only the anther's appendage slightly above the scales. Filament attached below scales. Anther 0.5 × 0.2 mm. Style 1.8 mm long, stigma clavate. Nutlet smooth, light brown, ovoid to ellipsoid, 1.2 × 0.7 – 0.8 mm, ventral surface rounded.

Specimens examined. New Zealand, South Island: north-west Nelson. Kahurangi National Park, upper Takaka River track, under overhang of limestone outcrop, alt. 857 m, 8 January 2011, C.A.Lehnebach & A.Zeller s.n. (WELT SP092173). Track along Takaka River, under overhang of limestone, alt. 736 m, 8 January 2011, C.A.Lehnebach & A.Zeller s.n. (WELT SP092172). Takaka Valley, alt. 900 m, under overhanging limestone rock in forest, February 1977, A.P. Druce s.n. (CHR 311720).

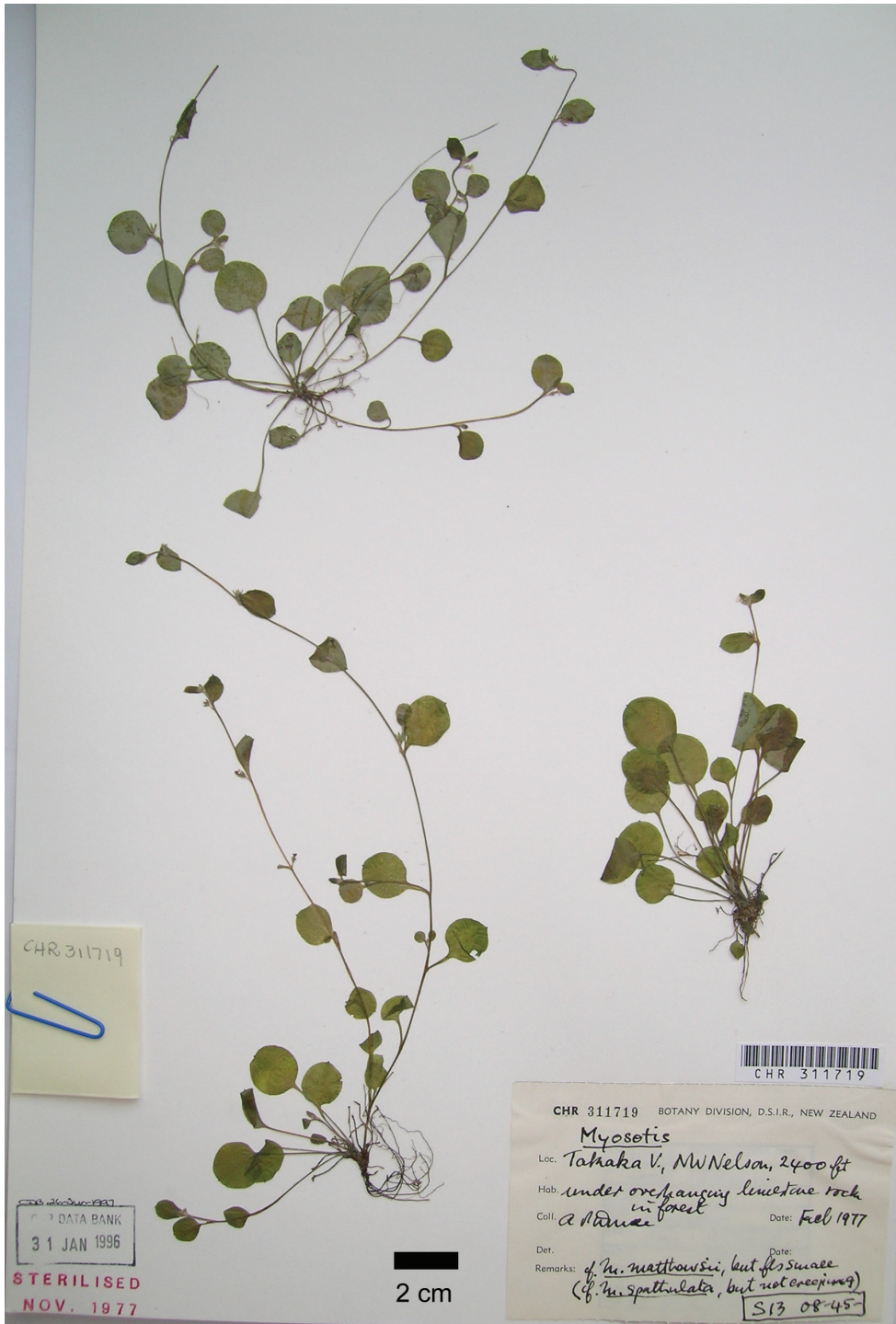


Figure 1. Photograph of the holotype of *Myosotis chaffeyorum* C.A. Lehnebach. (A.P.Druce s.n., CHR 311719). Copyright Allan Herbarium (CHR), Landcare Research. New Zealand.

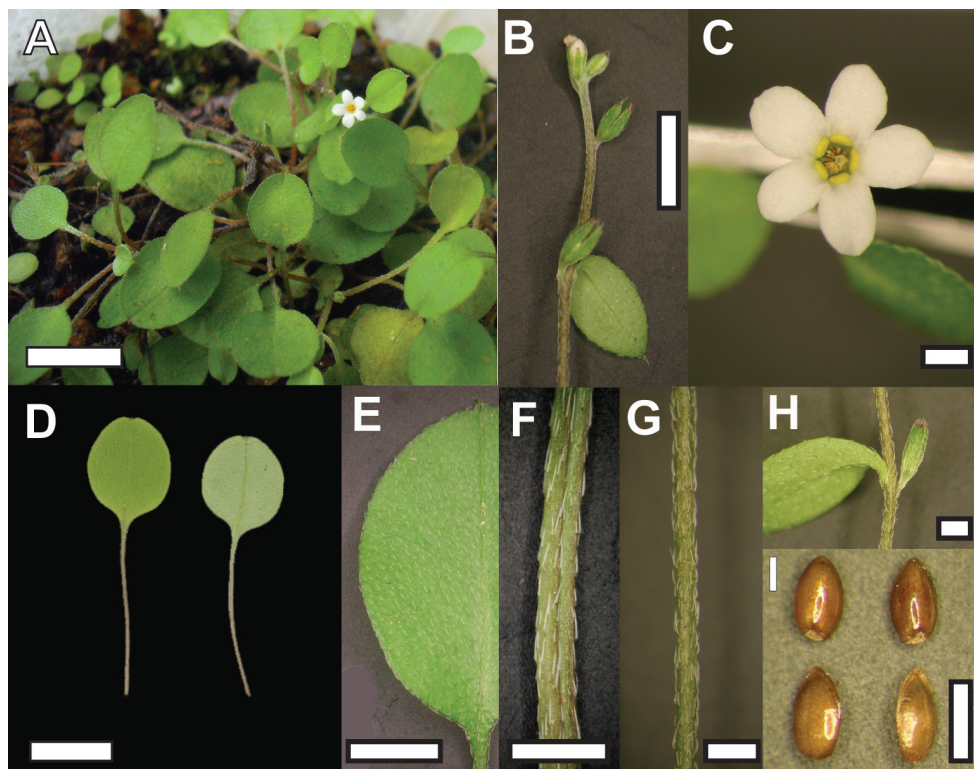


Figure 2. Plant of *Myosotis chaffeyorum* (A) and close-up view of vegetative and reproductive structures (B Flowering stem C Flower D Rosette leaves E Rosette leaf indumentum F Petiole G Stem H Node with flower and stem leaf I Nutlets). Bar = 1 cm in A & D, 5 mm in B & E, 1 mm in C, F, G, H, I. Material from WELT SP092173 (D, E, F, G, H) and WELT SP094151 (A, B, C, I).

Takaka River, near Ghost Creek Saddle, alt. 840 m, under overhang of limestone outcrop on dry loose fine soil, 22 April 2005, S. Courtney s.n. (NM 2688). Takaka Valley, Paynes Ford, at a base of limestone bluff, 30 October 2010, S. Courtney s.n. (NM 4835). Aniseed Valley. Valley down which Roding River, tributary of the Wairoa River, runs, 26 November 1967, R.H.S. (CHR 269160).

Etymology. This species is named after Annie and Henry Chaffey (<http://www.teara.govt.nz/en/biographies/4c15/1>), who lived from ca 1913, for almost 40 years, as self-sustained, pioneers/exiles in this mountainous area of Kahurangi National Park. The tiny cottage they lived in still remains in place and served me as shelter during the expedition in which this new species was collected.

Distribution. Endemic to New Zealand, only found in north-west Nelson (South Island). Detailed geographic coordinates are not shown to protect this species from illegal collection but are available from the author on request.

Conservation status. Currently the existence of only five populations of this species can be confirmed. Two of them are within Kahurangi National Park where they occupy an approximate area of 6 m² and 1 m². The number of individuals at each site is

low, ca 20 and 3, respectively. Three other populations are found outside the park, two of them in smaller protected areas which are regularly monitored by the Department of Conservation. At all these sites the species occupies a similar habitat and a small area (Shannel Courtney, personal communication). Considering this information and following the New Zealand Threat Classification System (Townsend et al. 2008), *M. chaffeyorum* should be considered as “Nationally Critical”.

Ecology. This is a perennial, self-pollinating species. It is habitat-specific and restricted to dry loose fine soil under shelters formed by limestone overhangs.

Discussion. The earliest known collection of *M. chaffeyorum* dates from 1967 (CHR 269160). Its distinctiveness from other species of *Myosotis*, however, was only noticed ca 10 years later when Anthony (Tony) Druce collected it while surveying the flora associated with Palaeogene calcareous rocks in north-west Nelson (Druce, unpublished). Druce noticed the overall similarity of this species to *M. matthewsii* and *M. spathulata* but also differences between them, which he wrote on the labels of the herbarium sheets of these collections (see Fig. 1). These notes read “cf. *M. matthewsii*, but the flowers are smaller” and “cf. *M. spathulata*, but stem not creeping”.

Myosotis matthewsii and *M. spathulata* are the only forget-me-nots in New Zealand with orbicular rosette leaves with which *M. chaffeyorum* could be confused. The small flower with stamens within the corolla tube, the absence of roots at the nodes of the decumbent flowering stem and the strigose indumentum of the leaf lamina, petiole and stems of *M. chaffeyorum* are key diagnostic characters to distinguish it from *M. matthewsii* or *M. spathulata*. In the absence of flowers, *M. matthewsii* can be distinguished from *M. chaffeyorum* by the presence of arcuate and erect hairs on the upper surface of the rosette leaves, larger leaves and a longer pedicel at fruiting (see Table 1). As for *M. spathulata*, if no stems are present, it can be readily distinguished from *M. chaffeyorum* by the hispid indumentum on the leaf petiole and larger leaf lamina (see Table 1).

***Myosotis mooreana* C.A.Lehnebach, sp. nov.**

urn:lsid:ipni.org:names:77121628-1

http://species-id.net/wiki/Myosotis_mooreana

Figs 3–4

Diagnosis. Similar to *M. forsteri* and *M. brockiei*, but differs from *M. forsteri* by its obovate rosette leaves; larger leaves at base of the cyme and smaller calyx at fruiting. It differs from *M. brockiei* by its smaller flowers (3.8 – 4.8 mm vs 9 – 10 mm); stamens included within the corolla tube; fruiting calyx with shorter pedicel (2.5 – 2.9 mm vs 3.6 – 4.3 mm); and hispid indumentum on leaves and petiole.

Type. NEW ZEALAND. South Island, north-west Nelson: Kahurangi National Park, Cobb Reservoir, among leaf litter accumulated by the side of large boulders in forest, alt. ca 867 m, 6 January 2011, C.A.Lehnebach & A.Zeller s.n. (Holotype: WELT [WELT SP092756/A]; Fig. 3).



Figure 3. Photograph of the holotype of *Myosotis mooreana* C.A. Lehnebach. (C.A. Lehnebach & A. Zeller s.n., WELT SP092756/A).

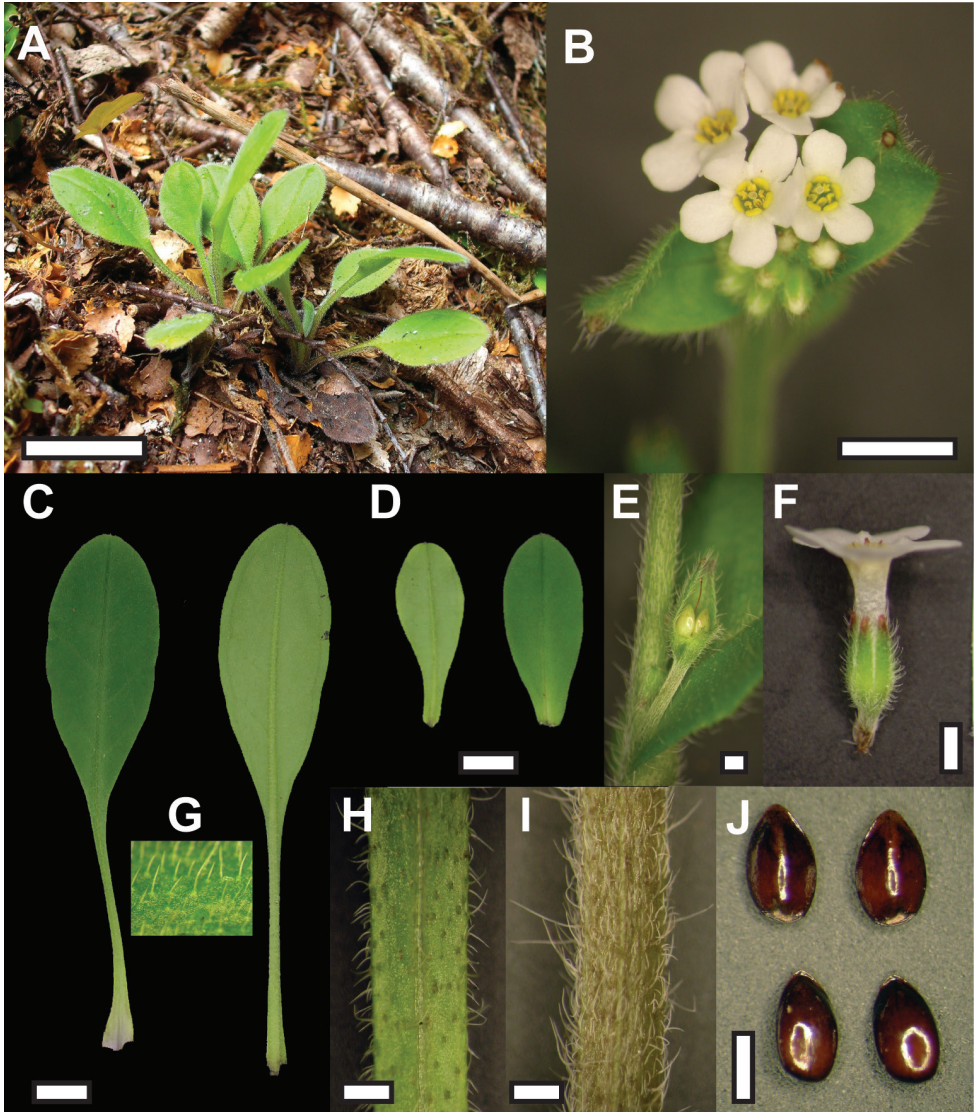


Figure 4. Plant of *Myosotis mooreana* in situ (**A**) and close-up view of vegetative and reproductive structures (**B** Inflorescence **C** Rosette leaves **D** Stem leaves **E** Fertilised flower at leaf axil **F** Flower **G** Rosette leaf indumentum, upper surface **H** Rosette leaf petiole **I** Stem **J** Nutlets). Bar = 1 cm in A, C & D, 5 mm in B, 1 mm in E, F, H, I, J. Material from WELT SP092756/A.

Plant perennial, ca 20 cm tall. Rosette leaves 5 – 12, obovate, $32.4 - 56 \times 15.8 - 20.5$ mm; apex mucronulate, ca 0.4 mm long. Leaf lamina base attenuate to petiole. Leaf indumentum hispid, hairs on upper surface sparsely distributed, antrorse, arcuate or erect. Hairs on the lower surface sparsely distributed, retrorse, arcuate or erect. Hairs arcuate or straight on margin. Petiole $26 - 40 \times 1.4 - 1.8$ mm, hispid, hairs erect, arcuate, antrorse or retrorse on margins. Flowering stem ascending, dark green to brown,

210 × 1.5 – 1.9 mm. Hairs, appressed, arcuate or erect, 0.8 – 2.1 mm long. Stem leaves elliptic-obovate, mucronulate, 15.3 – 35.4 × 6.4 – 14 mm, either shortly petiolate or sessile towards distal end of the inflorescence. Indumentum as for rosette leaves. Cyme with 15 – 31 flowers. Pedicel at fruiting, 2.5 – 2.9 mm. Calyx lobes lanceolate, 2.3 – 2.8 mm long, hairs inside calyx in upper half or along entire lobe. Fruiting calyx 2.7 – 2.8 mm long, hairs densely distributed, overlapping and hooked or straight. Corolla white with yellow scales, 3.8 – 4.8 mm across, lobes ovate, 2 × 1.6 – 1.8 mm; not overlapping, apex rounded or irregularly notched. Corolla tube 3 mm long. Stamens included within the corolla tube, with only the anther's appendage above the scales. Filament attached below the scales. Anther 0.8 × 0.2 mm. Style 3 mm long, stigma clavate. Nutlet smooth, dark brown, ovoid to ellipsoid, 1.4 – 1.5 × 0.7 – 0.9 mm, ventral surface keeled.

Etymology. This species is named in honour of Lucy Beatrice Moore, New Zealand botanist (<http://www.teara.govt.nz/en/biographies/5m55/1>) who described several species of endemic *Myosotis* and revised this genus for the Flora of New Zealand (Allan 1961).

Distribution. Endemic to New Zealand. Known from a single location in Kahurangi National Park, north-west Nelson (South Island). Detailed geographic coordinates are not shown to protect this species from illegal collection but are available from the author on request. It is likely *M. mooreana* also occurs at two other sites within the Park (Shannel Courtney, personal communication) but this cannot be confirmed at this stage.

Conservation status. Considering the small population size for this species (six individuals only), low number of mature individuals observed in the population and the small area of occupancy (less than 1 m²), and following the New Zealand Threat Classification System (Townsend et al. 2008), *M. mooreana* should be rated as “Nationally Critical”.

Ecology. This is a perennial, fertile, self-pollinating species. It grows among the twigs and leaf-litter accumulated among large boulders under red beech (*Nothofagus fusca*) forest.

Discussion. There are only two species of forget-me-nots in New Zealand that can be mistaken with *M. mooreana*; i.e. *M. brockiei* and *M. forsteri*. These two are the only species growing in a similar habitat, under forest or scrub in north-west Nelson and throughout New Zealand, respectively. The main differences between *M. mooreana* and *M. brockiei* are the large flowers with stamens fully exerted beyond the corolla tube in the latter species. Flowers in *M. mooreana* are only ca 5 mm across and stamens are always included within the corolla tube. In contrast, *M. brockiei* bears flowers ca 1 cm across and anthers with long filaments (ca 4 mm). When not fertile, indumentum and leaf shape are useful characters to distinguish between these two species. *Myosotis mooreana* bears oblanceolate rosette leaves and wide cauline leaves covered by a combination of arcuate, erect, antrorse and retrose hairs. *Myosotis brockiei*, in contrast, has narrowly elliptic leaves with a distinct tomentose almost greyish indumentum. Leaf shape is the most useful character to differentiate *M. mooreana* from *M. forsteri*. The latter species possess orbicular to broadly elliptic leaves with a well-defined petiole. The

flowers of both species are very similar in size (see Table 1) but the calyx of *M. forsteri* at fruiting is almost twice the size of the fruiting calyx of *M. mooreana*.

Key to *Myosotis chaffeyorum*, *M. mooreana* and other white flowered and laxly tufted species of *Myosotis* found in forest areas of New Zealand

- 1 Rosette leaf lamina obovate to narrowly elliptic **2**
- Rosette leaf lamina orbicular to broadly elliptic..... **3**
- 2 Leaf and petiole indumentum tomentose; stem erect; calyx 3.9 – 4.4 mm at fruiting; stamens fully exserted from corolla tube..... ***M. brockiei***
- Leaf and petiole indumentum hispid; stem ascending; calyx ca 2.8 mm at fruiting; stamens included in corolla tube ***M. mooreana***
- 3 Petiole of rosette leaves 1.9 – 3 mm wide; stem ascending; cyme well-defined; calyx ca 5 mm long at fruiting ***M. forsteri***
- Petiole of rosette leaves 0.2 – 0.6 mm wide; stem prostrate; cyme ill-defined; calyx < 4.5 mm at fruiting **4**
- 4 Indumentum on leaf margin, petiole and stem hispid; stem creeping, rooting at nodes ***M. spathulata***
- Indumentum on leaf margin, petiole and stem strigose; stem decumbent, no roots at the nodes..... **5**
- 5 Indumentum on leaf surface hispid; pedicel 4.6 – 8.4 mm long at fruiting; calyx hairs arcuate; stamens fully exserted from corolla tube.... ***M. matthewsii***
- Indumentum on leaf surface strigose; pedicel 1.5 – 3 mm long at fruiting; calyx hairs straight; stamens included in corolla tube ***M. chaffeyorum***

Acknowledgments

I would like to thank Andreas Zeller and Barry Sneddon for their help in the field, Andrea Brandon and Shannel Courtney for sharing their knowledge on *Myosotis* in the Kahurangi National Park, the staff of AK, CHR and WELT for their assistance with loans, and Patrick Brownsey, Phil Garnock-Jones and Barry Sneddon and two anonymous reviewers for comments on an earlier version of this manuscript and Phil Garnock-Jones for advice on Latin names. This research was supported by the New Zealand Ministry of Science and Innovation through the Defining New Zealand's Land Biota Programme.

References

- Allan HH (1961) Flora of New Zealand. Vol. I. Wellington: Government Printer. liv + 1885
<http://floraseries.landcareresearch.co.nz/pages/Index.aspx>

- Brandon A (2001) Breeding systems and rarity in New Zealand *Myosotis*. PhD Thesis, Massey University, Palmerston North. New Zealand.
- Breitwieser I, Brownsey P, Garnock-Jones P, Perrie L, Wilton A (2012) In: Gordon D (Ed) New Zealand inventory of biodiversity. Phylum Tracheophyta, vascular plants. Vol. 3. Kingdoms Bacteria, Protozoa, Chromista, Plantae, Fungi. Canterbury University Press, 411–459.
- Druce A (unpublished) Plant checklist for Tertiary calcareous areas, NW Nelson. <http://www.nzpcn.org.nz>
- Moore LB (1961) *Myosotis*. In: Allan HH (Ed) Flora of New Zealand. Vol. I. Wellington: Government Printer, 807–833.
- Moore LB (1988) *Myosotis*. In: Webb CJ, Sykes WR, Garnock-Jones PJ (Eds) Flora of New Zealand. Vol. IV. Naturalised pteridophytes, gymnosperms, dicotyledons. Botany Division, DSIR. Christchurch, 377–390.
- Moore LB, Simpson MJ (1973) A new *Myosotis* from north-west Nelson. New Zealand Journal of Botany 11: 163–170. doi: 10.1080/0028825X.1973.10430270
- Townsend A, de Lange P, Duffy C, Miskelly C, Molloy J, Norton D (2008) New Zealand Threat Classification System Manual. Science & Technical Publishing, Department of Conservation. New Zealand.
- Weigend M, Gottschling M, Selvi F, Hilger HH (2010) Fossil and extant Western Hemisphere Boraginaceae, and the polyphyly of “Trigonotideae” Riedl (Boraginaceae: Boraginoideae). Systematic Botany 35: 409–419. doi: 10.1600/036364410791638423
- Winkworth RC, Grau J, Robertson AW, Lockhart PJ (2002) The origins and evolution of the genus *Myosotis* L. (Boraginaceae). Molecular Phylogenetics and Evolution 24: 180–193. doi: 10.1016/S1055-7903(02)00210-5

Appendix I

Representative material listed in Table 1.

- Myosotis brockiei*: New Zealand. South Island: north-west Nelson, Kahurangi National Park, base of the cliff behind Growler Rock Shelter, alt. 1003 m, 4 January 2011, C.A. Lehnebach & A.Zeller s.n. (WELT SP090249).
- Myosotis forsteri*: New Zealand, North Island: Pureora Forest Park, Whenuakura, January 2011, T.Emmitt s.n. (WELT SP092226).
- Myosotis matthewsii*: New Zealand, North Island: Warawara Forest, 8 March 2012, J.Prebble et al. JMP12-010g (WELT SP093687).
- Myosotis spathulata*: New Zealand, North Island: Waipuna Station, south end of Te Waka Range, alt. 835 m, 13 December 2011, H.Meudt et al. HMM 334 A (WELT SP090633).

A new tetraploid species of *Solanum* L. sect. *Solanum* (Solanaceae) from Tanzania

Mkabwa L. K. Manoko^{1,4}, Gerard M. van der Weerden²,
Ronald G. van den Berg³, Celestina Mariani⁴

1 Department of Botany, University of Dar es Salaam, Box 35060, Dar es Salaam, Tanzania **2** Experimental Garden and Genebank, IWWR, Radboud University Nijmegen, Toernooiveld 11, 6525 ED Nijmegen, The Netherlands **3** Biosystematics Group, Wageningen University, Radix building, Droevendaalsesteeg 1, 6708 PB Wageningen, The Netherlands **4** Department of Molecular Plant Physiology, IWWR, Radboud University Nijmegen, Huygens building, Heyendaalseweg 135, 6525 AJ Nijmegen, The Netherlands

Corresponding author: Ronald G. van den Berg (Ronald.vandenberg@wur.nl)

Academic editor: Sandra Knapp | Received 8 February 2012 | Accepted 13 August 2012 | Published 24 August 2012

Citation: Manoko MLK, van der Weerden GM, van den Berg RG, Mariani C (2012) A new tetraploid species of *Solanum* L. sect. *Solanum* (Solanaceae) from Tanzania. *PhytoKeys* 16: 65–74. doi: 10.3897/phytokeys.16.2884

Abstract

Solanum umalilaense Manoko **sp. nov.** (Solanaceae) is described from the Umalila area, in the southern highlands of Tanzania. Its novelty is supported with both morphological and AFLP data. Phenetic and phylogenetic analyses place *S. umalilaense* as a unique and well-supported taxon among tetraploid species of *Solanum* sect. *Solanum* from Africa. It can be distinguished from other African species by its extremely developed branching, each branch producing many multi-flowered inflorescences, flowers with short calyx lobes and its persistent, small, light yellowish brown fruits.

Keywords

New species, *Solanum umalilaense*, *Solanum* sect. *Solanum*, Tanzania, tetraploid, Umalila

Introduction

Solanum L. section *Solanum* is a pantropical group of about 55 species, most of which are found in the New World, and about 10 in Africa; the group forms part of the Morelloid clade of Bohs (2005). *Solanum nigrum* L. is the type species for the section, and of the genus. Species in the section *Solanum* are herbs, sometimes suf-

frutescent and occasionally small shrubs. They also have simple, unbranched, uniseriate, multicellular hairs with or without glandular heads. Their ploidy levels range from diploid to hexaploid. Species with branched or stellate hairs do not fall in this section as traditionally circumscribed (Gray 1968). In Africa, section *Solanum* species form one of the largest groups of leafy vegetables.

The most thorough account of the African species of the section *Solanum*, with good morphological descriptions and keys, was published by Edmonds and Chweya (1997). Their list of native and introduced members of the section found in Africa includes *S. americanum* Mill., *S. chenopodioides* Lam., *S. nigrum* L., *S. physalifolium* Rusby var. *nitidibaccatum* (Bitter) Edmonds, *S. retroflexum* Dunal, *S. sarrachoides* Sendtn., *S. scabrum* Mill., *S. villosum* Mill. and other taxa such as *S. florulentum* Bitter, *S. grossidentatum* A. Rich., *S. hirsutum* (Vahl) Dunal and *S. tarderemotum* Bitter, which may represent good species and need taxonomic revision. Delimitation of species based on morphological data alone is complicated by phenotypic plasticity, polyploidy, natural hybridization and discordant variation in this group (Edmonds and Chweya 1997). Jacoby (2003) and Olet (2004) studied accessions of some species of the section *Solanum* found in Africa using also a molecular approach (Amplified Fragment Length Polymorphism, AFLP). Jacoby found that 15 morphological characters reflected the genetic variation observed in the AFLP analysis, and Olet defined species of the section *Solanum* found in Uganda by using morphological characterization and AFLP on living accessions. Whereas eight species were defined by morphological characters, only five were recognized using AFLPs.

While studying accessions of *Solanum* section *Solanum* from Africa at the Radboud University Nijmegen, it became apparent that plants grown from seeds of accession A24750133 collected from the Umalila area in the southern highlands of Tanzania were strikingly different from other African accessions. Chromosome counts revealed that they had 48 chromosomes, in common with some other species of the section in Africa (Manoko 2007). The plants were temporarily designated as “species A” in Schippers (2004).

During a herbarium visit in Dar es Salaam, Tanzania, we found a specimen of the same taxon (*R.E. Gereau et al.* 5084, DSM) collected on the 14th of November 1992 from Umalila forest reserve. Duplicate specimens were present in NHT, MO and K. Annotation labels on these specimens indicated that they were identified by W.G. D’Arcy as *S. aff. americanum* Mill. and by L.B. Mwasumbi (DSM) as *S. nigrum* L.

We also located an additional specimen collected as a weed in maize field in Uyole (Mbeya) in the DSM herbarium (*A.A. Mwambunga A.A.M.6*). Fieldwork (July 2010) in Tanzania enabled us to collect a number of accessions of this species and here we formally describe it. Voucher specimens have been deposited at the Experimental Garden and Genebank herbarium of the Radboud University Nijmegen, DSM and WAG.

Taxonomic treatment

Solanum umalilaense Manoko, sp. nov.

urn:lsid:ipni.org:names:77121698-1

http://species-id.net/wiki/Solanum_umalilaense

Figs 1, 3

Diagnosis. *Solanum umalilaense* can be distinguished from other African species of *Solanum* sect. *Solanum* by its extremely developed branching, each branch producing many multi-flowered inflorescences, flowers with short calyx lobes and producing persistent, small, light yellowish brown fruits.

Type. Tanzania. Mbeya: Mbeya District, Umalila Forest Reserve, ca. 7 km W of Ruanda II on road to Izumbwe, 2 km SSE of Mbogo Mtn. main peak, 09°11'S, 33°18'E, 2180 m, on bushy south-facing slopes with scattered shrubs. 14 Nov 1992. R.E. Gereau, D.K. Harder, C.J. & M.J. Kayombo 5084 (holotype, DSM!; isotypes: K, not seen, MO, not seen, NHT!).

Description. Herb, up to ± 0.5 m, erect, predominantly with many erect or spreading branches from the base; stems dark purple, angular with well marked ridges, teeth on ridges very small, glabrescent to sub-glabrous with sparse, long, appressed, eglandular hairs. Leaf simple, petiolate, ovate to elliptic with wings running to petiole base, margins entire, apex acuminate to acute, base truncate; petiole 0.6–1.3 cm; leaf blade 1.8–2.8 $\times$ 0.1–1.4 cm, widest 1–1.7(–2.1) cm from apex. Inflorescences numerous, up to 100 per plant, consisting of simple, rarely forked cymes, 2–9(–11) flowered; peduncle (0.5–)1.1–3.2, erect; pedicels 5–7(–9) mm, pendent. Calyx pentagonal, 3–3.2(–4) mm diam., lobes short (± 1 mm), broadly triangular, equal and adherent to mature berries; corolla stellate, 7–11 mm diam. white, margins occasionally tinged with purple, style protruding the anthers, straight or sometimes hooked with eglandular hairs at the base, 3.1–3.5(–4.2) mm; anthers equal, yellow, 1.8–2 mm, filaments 0.5–1 mm; fully hydrated pollen 24.6–26.3 μ m diam. Berries globose, changing from green to dull yellowish green, at mature stage light yellowish brown, texture soft, persistent and aromatic, 3–4(–5) mm diam.; sclerotic granules present; seeds obovate, brownish, 9 to 22 per berry. 1.6–2.1 $\times$ 1.3–1.8 mm.

Chromosome counts on accession A24750133 using standard cytological methods and flow cytometry on root and leaf cells respectively, showed that *S. umalilaense* had 48 chromosomes ($2n=4x=48$). The same was found for related African species such as *S. florulentum*, *S. tarderemotum*, *S. hirsutum*, *S. grossidentatum* and *S. retroflexum*, indicating that all these species are tetraploid.

In phenetic and cladistic analyses of an AFLP (Vos et al. 1995) dataset of the tetraploid species from Africa, including *S. villosum*, *S. retroflexum*, *S. florulentum*, *S. tarderemotum*, *S. grossidentatum* and *S. hirsutum*, *S. umalilaense* had 100% jack-knife support in the neighbour joining and maximum parsimony analyses (Manoko



Figure 1. Holotype specimen of *Solanum umalilaense* Manoko sp. nov. (DSM)

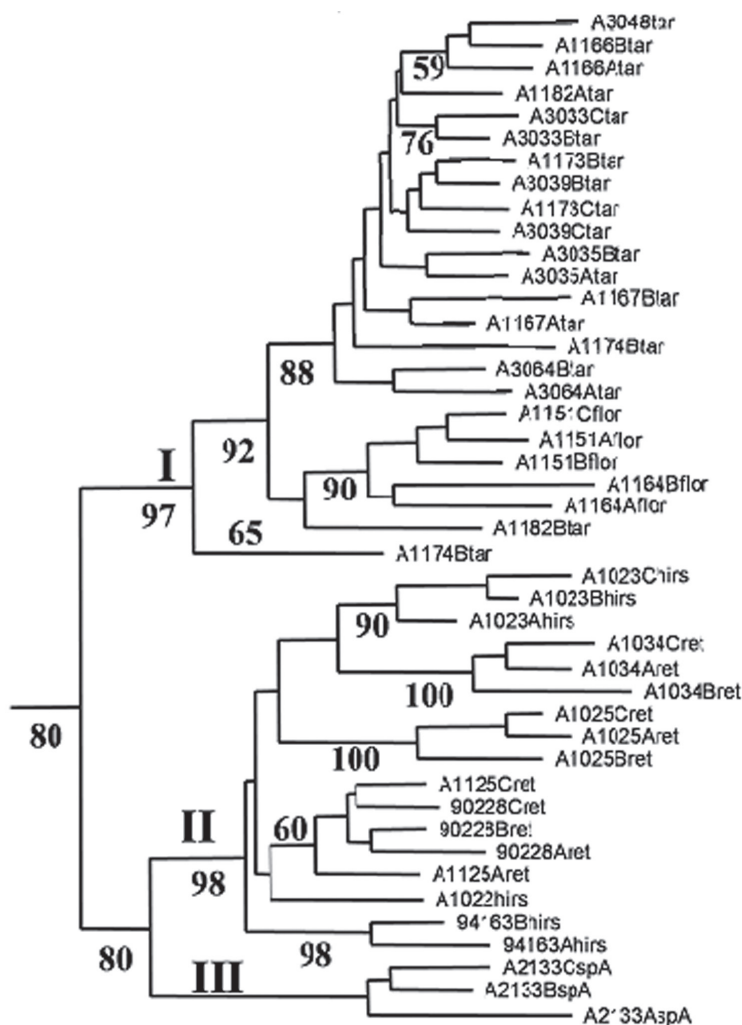


Figure 2. Part of the NJ tree from Manoko (2007). Numbers at the nodes are NJ Jackknife support values. Cluster I contains *S. tarderemotum* and *S. florulentum*. In cluster II are *S. retroflexum* and *S. hirsutum*. Cluster III is composed of individuals of *S. umalilaense*

2007). A NJ tree was constructed using 435 polymorphic AFLP loci generated from 102 tetraploid individuals. Here only results for 44 individuals are shown, representing about 50% of the tree (Fig. 2; Manoko 2007), with *S. umalilaense* indicated as “sp A”. Cluster I was made up of individuals morphologically similar but not identical (Manoko 2007). Part of the material conformed to *S. tarderemotum* forms A and B described by Olet (2004), and two remaining accessions were *S. florulentum*. Individuals that conformed to *S. tarderemotum* forms A and B in this cluster shared morphological characteristics not only with *S. florulentum*, but also with *S. tarderemotum* form C. Cluster II was composed of *S. retroflexum* and a taxon that we identified as *S.*



Figure 3. Pictures A,B,C,D taken from plants grown at the Experimental Garden, Radboud University Nijmegen (A24750133). Pictures E,F,G,H taken from plants growing in Mbeya region, Tanzania (E,F: Manoko et al. 2010-2; G,H: Manoko et al. 2010–14).

hirsutum (Manoko 2007). Both taxa have ovate calyx lobes, covering only half of the fruit during development, but reflexed away from mature fruits. The globose fruits, turning from green to purple/black, remain with the pedicel on the plant and are not aromatic. Cluster III is composed only of individuals of accession A24750133, which we describe here as the new species *S. umalilaense* (Fig. 2).

Distribution. Mbeya region, Tanzania, at elevations between 1952 and 2052 m (Fig. 4).

Ecology. During our collecting trip in the Umalila area (July 7–10, 2010) we found many plants in cultivated fields (Fig. 3E,F) on the slope of mountains, or left in abandoned cultivated plots (Fig. 3H), which also contained maize and beans.

According to the information on Gereau *et al.* 5084 the species is frequent on the ash layer in charcoal-burning areas. The Umalila area is located in the Mbeya region, in the South West of Tanzania at the border with Malawi and Zambia (Figure 3). Because of its elevation, the region is also known as the Southern Highlands of Tanzania, with volcanic type of soil, temperatures ranging from 12 to 23°C, and annual rainfall levels from 1500 to 2700 mm. The vegetation is mountainous, with cool temperature grasslands and the region is good for cultivation of coffee, maize, beans and vegetables (Anon. 1997).

Etymology. The name *S. umalilaense* refers to the area the species was found. Umalila (Malila or Umalila) is the highland area of the Malila, a relatively unknown ethnic group in south-west Tanzania (Walsh 1998).

Conservation status. Based on the information on the type specimen, *S. umalilaense* grows in the Umalila forest reserve. We visited the villages of Maganjo, Isangati, Igala, and different wards and found that the species was cultivated as an important and well known leafy vegetable. It has been cultivated for many generations and farmers collect fruits and keep dried seeds for the next growing season. Since this species is cultivated as a food crop and has become almost domesticated, its preliminary conservation status can be considered to be of Least Concern (LC, IUCN 2001) although its very narrow distribution may be cause for further analysis.

Local names. Insungwe, so called by the Malila (Schippers 2004).

Uses. Used as a leafy vegetable. Leaves can be picked from the plant until the plant starts flowering. Using leaves when the plant is in flower is not attractive because of their bitter taste (Latham 2006).

Specimens examined. **Tanzania. Mbeya Rural District:** Maganjo village (Lwindi ward), 09°02'29"S, 033°23'54"E, July 8, 2010, *Manoko et al.* 2010–11 (DSM, WAG, and Radboud University Experimental Garden and Genebank herbarium); Isangati village (Iyunga ward), 09°04'12"S, 033°25'25"E, July 8, 2010, *Manoko et al.* 2010–2 (DSM, WAG, and Radboud University Experimental Garden and Genebank herbarium); Igala village (Holondo ward), 09°03'21"S, 033°26'44"E, July 8, 2010, *Manoko et al.* 2010–8 (DSM, WAG, Radboud University Experimental Garden and Genebank herbarium); Isangati village (Iyunga Mapinduzi ward), 09°05'03"S, 033°25'53"E, July 9, 2010, *Manoko et al.* 2010–11 (DSM, WAG, Radboud University Experimental Garden and Genebank herbarium); Isangati village (Iyunga Mapinduzi ward), 09°05'03"S, 033°25'53"E, July 9, 2010, *Manoko et al.* 2010–12 (DSM, WAG, Radboud University Experimental



Figure 4. Map courtesy of the University of Texas Libraries, The University of Texas at Austin.

Garden and Genebank herbarium); field plot near Umalila Forest reserve, 09°11'26"S, 033°20'46"E, July 9, 2010, *Manoko et al.* 2010–14 (DSM, WAG, Radboud University Experimental Garden and Genebank herbarium); Uyole (Mbeya), 5500 ft, 22 May 1968, *A.A. Mwambunga A.A.M.6* (DSM). **The Netherlands.** Accession A24750133 from the Umalila area cultivated at Radboud University Experimental Garden and Genebank, *Anon. s.n.* (Radboud University Experimental Garden and Genebank herbarium).

Discussion. *Solanum umalilaense* differs from all other species that have been described or studied so far from Africa (Bitter 1912; 1913; Bukenya and Hall 1988; D'

Arcy and Rakotozafy 1994; Edmonds and Chweya, 1997; Bosser et al. 2000; Jacoby 2003; Olet 2004; Gonçalves 2005; Edmonds 2006 a, b). The new species produces a large number of inflorescences such that at full anthesis the plant appears to be covered with white flowers, strikingly different from other species in the section. Seeds of “species A”, as it was provisionally labeled, were received from the Southern Highlands of Tanzania where this taxon is a common leafy vegetable. Morphologically, it could not be assigned to any known species, therefore Schippers (2004) had given it the name species A. Herbaria surveys at NHT and DSM in Tanzania produced comparable material, all collected from Umalila Forest Reserve in Mbeya by R.E. Gereau et al. in 1992 (*R.E. Gereau, D.K. Harder, C.J. & M.J. Kayombo 5084*, the DSM specimen of which we designate as holotype). They had found these plants ‘frequent on ash, in charcoal-burning area’. During our collection-trip in Tanzania in the same region, however, we always found this species in cultivated plots, never in ash. Gereau’s material had been first determined by the late W.G. D’Arcy (MO) in 1993 as *S. aff. americanum* Mill. Later, L.B. Mwaumbi (DSM) changed the name to *S. nigrum* L. These names refer to a diploid and to a hexaploid species, respectively, whereas *S. umalilaense* is tetraploid. This clearly demonstrates that the suggested affinities with *S. americanum* and *S. nigrum* were not correct.

Edmonds’s opinion (JM Edmonds pers. comm.) that it might be a hybrid between two tetraploid species was investigated. We found that for the three generations we grew the plants (between 2002–2004) none of the characters showed segregation.

All together, the distinct morphology, chromosome number different from *S. americanum* and *S. nigrum*, and a clear separate clustering from other species of the section, make this African species unique in section *Solanum* in Africa.

Acknowledgements

We thank the support of Nuffic, through the MHO-ENVIRONS program, COSTECH for permission to perform field work in the Mbeya region, the Faculty of Science of the Radboud University Nijmegen and the National Herbarium of the Netherlands for funding this study. We also wish to extend our thanks to the staff at the Radboud University Experimental Garden and Genebank for looking after the plants, and to Dr. E. Pierson for her assistance during seed and pollen measurements. We thank the reviewers of this paper for critical comments, specially reviewer 2 for adding new information regarding section *Solanum*.

References

- Anonymous (1997) Mbeya District socio-economic profile. Joint publication by The Planning Commission Dar es Salaam and Mbeya District Council, Mbeya, Mbeya District. <http://www.tzonline.org/pdf/Mbeyadis.pdf>
- Bitter G (1912) *Solana nova vel minus cognita*. I. Repert. Spec. Nov. Regni. Veg. 10: 529–565.

- Bitter G (1913) *Solana Africana*. I. Bot. Jahrb. Syst. 49(5): 560–569.
- Bosser J, Cadet T, Gueho J, Marais W (2000) *Flore des Mascareignes: La Réunion, Maurice and Rodrigues*. The Royal Botanical Gardens, Kew.
- Bohs L. (2005) Major clades in *Solanum* based on *ndhF* sequence data. Pages 27–49 In: Keating RC, Hollowell VC, Croat TB (Eds) *A festschrift for William G. D'Arcy: the legacy of a taxonomist*. Monographs in Systematic Botany from the Missouri Botanical Garden, Vol. 104. Missouri Botanical Garden Press, St. Louis, MO.
- Bukenya ZR, Hall JB (1988) *Solanum* (Solanaceae) in Ghana. *Bothalia* 18: 79–88.
- D'Arcy WG, Rakotozafy A (1994) Famille 176. Solanaceae. In: Morat P (Ed) *Flore de Madagascar et des Comores*. Museum Nationale d'Histoire Naturelle, Paris.
- Edmonds JM (2006a) *Solanum* L. section *Solanum*. In: Thulin M (Ed) *Flora Somalia*, Vol.3, Royal Botanic Gardens, Kew, 207–208.
- Edmonds JM (2006b) *Solanum* L. section *Solanum*. In: Hedberg I, Edwards S (Eds) *Flora of Ethiopia and Eritrea* 5: 13–21.
- Edmonds JM, Chweya JA (1997) Black nightshades. *Solanum nigrum* L. and related species. Institute of Plant Genetics and Crop Plant Research Gatersleben / International Plant Genetic Resources Institute, Rome, Italy, 5–113.
- Gonçalves AE (2005) Solanaceae. In: Pope GV, Polhill RM, Martin ES (Eds) *Flora Zambesiaca*, Royal Botanic Gardens, Kew, 8 (4).
- Gray JM (1968) The taxonomy of the *Morella* section of the genus *Solanum* L. within South America. PhD thesis, University of Birmingham, Birmingham, U.K.
- IUCN Species Survival Commission (2001) *IUCN Red List Categories: Version 3.1*. IUCN Gland and Cambridge.
- Jacoby A (2003) Genetic variability in the *Solanum nigrum* L. complex and related species in South Africa. PhD thesis, University of Free State Bloemfontein, South Africa.
- Latham P (2006) *Plants visited by bees and other useful plants of Umalila, Southern Tanzania*. Third edition, 174.
- Manoko MLK (2007) A systematic study of African *Solanum* section *Solanum* (Solanaceae). PhD thesis, Radboud University Nijmegen. <http://dare.ubn.kun.nl/bitstream/2066/30032/1/30032.pdf>
- Olet EA (2004) Taxonomy of *Solanum* L. section *Solanum* in Uganda. PhD thesis, Agricultural University of Norway.
- Schippers RR (2004) *Légumes Africains Indigènes: présentation des espèces cultivées*. Margraf Publishers GmbH, Scientific books, Weikersheim, 369–407.
- Vos P, Hogers R, Bleeker M, Reijans M, van der Lee T, Hornes M, Frijters A, Pot J, Peleman J, Kuiper M, Zabeau M (1995) AFLP: a new technique for DNA fingerprinting. *Nucl. Acids Res.* 23: 4407–4414. doi: 10.1093/nar/23.21.4407
- Walsh M (1998) *The Malila: Preliminary notes on language, history and ethnography*. Unpublished paper. <http://www.scribd.com/doc/14539285/The-Malila-Preliminary-Notes-on-language-History-and-Ethnography>