AN ILLUSTRATED DIAGNOSTIC KEY OF THE SPECIES IN THE VENEZUELAN CLADE OF
ESPELETIA (ASTERACEAE).

JESÚS MAVÁREZ^{1,2}

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¹ Laboratoire d’Écologie Alpine, UMR UGA-USMB-CNRS 5553 Université Grenoble Alpes, 38000 Grenoble, France.

² Address for correspondence: LECA, BP 53, 2233 rue de la Piscine, 38041 Grenoble Cedex 9, France; jesus.mavarez@univ-grenoble-alpes.fr

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Abstract. An illustrated key is presented for the species in the Venezuelan clade of *Espeletia* (Asteraceae), based on herbarium specimens, virtual herbaria and fresh samples from field collections. The fifty-four *Espeletia* species in this clade are documented: (i) 48 entirely endemic to the Venezuelan Andes, (ii) two found as well in the Venezuelan Cordillera de la Costa, the eastern section of the Colombian Cordillera Oriental and the Sierra Nevada de Santa Marta, and (iii) four endemic to eastern Colombian Cordillera Oriental and Sierra de Perijá. Schematic representations of leaves of all species are provided, including important

diagnostic characters such as length-to-width ratios, and the shape, density or angles of secondary nerves. Additional diagnostic characters are also described or illustrated for some species, such as the type of indumentum on leaves, the structure of the inflorescence, the size of the capitulum, and the colour of ray ligules. The key has been shown to allow identification of species using both herbarium samples and fresh material, and given the predominant use of vegetative characters it is also useful on some monocarpic rosettes species that are frequently found in the vegetative stage.

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

The plants in the genus *Espeletia* Mutis ex Bonpl (Humboldt and Bonpland, 1809) represent the best example of taxonomic, morphological and ecological diversification in the tropical high-elevation grassland ecosystem of the Northern Andes known as páramo (Diazgranados, 2012; Cuatrecasas, 2013; Diazgranados and Barber, 2017; Pouchon et al., 2018; Mavárez, 2019). The genus evolved from a single ancestor quite recently, about 2.5 My ago (Pouchon et al. 2018), after the final uplift of the Northern Andes that facilitated the environmental conditions for the páramo habitat (Hooghiemstra et al., 2006; Torres et al., 2013). The ca. 140 *Espeletia* species are distributed phylogenetically in two major groups (Diazgranados and Barber, 2017; Pouchon et al., 2018; Mavárez, 2019): (i) a north-eastern clade of 54 species, a.k.a. “Venezuelan clade”, almost entirely restricted to the Venezuelan Cordillera de Mérida, with some species found in the Venezuelan Cordillera de la Costa, the eastern section of the Colombian Cordillera Oriental, the Sierra de Perijá and the Sierra Nevada de Santa Marta, and (ii) a south-western clade of ca. 80 species, a.k.a. “Colombian clade”, distributed across the Colombian Andes, the Sierra de Perijá and northern Ecuador. The Venezuelan clade is morphologically more diverse, since it includes shrubs and unbranched, dichotomous or profusely branched trees, and also monocarpic and polycarpic rosettes that can be sessile, short-branched or unbranched. The Colombian clade, richer in species, is composed exclusively by polycarpic rosettes, almost all of them unbranched, plus one species that always is profusely branched (Mavárez and Becerra, 2019) and two that can occasionally be sparsely branched (Cuatrecasas, 1996).

The identification of *Espeletia* species can sometimes be a real challenge, most particularly when attempted directly in the field. An important number of taxa are indeed very similar morphologically, differing mainly on quantitative traits associated with the shape and

size of leaves, inflorescences and capitula. On the other hand, sympatry is also particularly common among members of this genus and it is not unusual to find several species living near each other in some locations, as for instance in Sierra de la Culata, Venezuela, where up to eleven rosette species can be found in close sympatry (Mavárez pers. obs.). Furthermore, inter-specific hybridisation can be relatively frequent between certain species pairs, contributing thereby to the morphological variation observed within some taxa (Berry et al., 1988; Pouchon et al., 2018; Mavárez, 2019). Researchers studying *Espeletia* are therefore often confronted to situations in which groups of morphologically similar and closely-related species in this genus coexist in sympatry and, in some cases, hybridise. This identification challenge can receive an additional difficulty in Venezuela, where about half of the rosette species are monocarpic, spending many years in a vegetative state before flowering for a few days or weeks, after which they die. The identification of these taxa must often rely on vegetative traits of the rosettes, yet available identification keys for these plants usually depend strongly on reproductive traits (Cuatrecasas, 1996, 2013).

In this work I present an illustrated diagnostic key for the 54 species in the Venezuelan clade of *Espeletia* (Mavárez, 2019), leaving the analysis of the species in the Colombian clade for another work to be presented in the near future. The key is mainly aimed at the identification of live plants directly in the field, but several of the diagnostic traits used can also be retrieved from dry samples, so that they key may be used as well to identify herbarium specimens.

MATERIALS AND METHODS

Samples: the key is based on the analysis of 2264 samples reliably identified to the species level: 1450 samples deposited in herbaria B, BC, BR, COL, F, G, GH, HAL, IVIC, K, LD, MER, MERF, MO, MY, NY, P, S, U, US and W (Thiers, 2019), and 814 plants identified during fieldwork by the author and some colleagues (250 of which are now deposited at herbarium IVIC). These samples include all 54 species currently known to belong to the Venezuelan clade of *Espeletia* and thirteen inter-specific hybrid taxa that have received binomials in the past (Mavárez, 2019). However, hybrid taxa will not be treated in this key.

Morphological characters: The key used the inter-specific variation observed at several diagnostic macroscopic morphological attributes of the plants' stem, leaves,

inflorescences and capitula, all of which can be easily measured on both living plants and herbarium samples without need for sophisticated equipment:

a) Growth-form. Habitus (tree or rosette), type of stem branching (branched or unbranched, monopodial or sympodial), stem size and aspect (naked or covered by marcescent leaves).

b) Leaf. Sheath type (open or closed) and shape, pubescence on sheaths (present or absent). Lamina type (sessile or pseudopetiolate), shape (linear, lanceolate, oblong, etc.), length, width, length-to-width ratio, type of adaxial pubescence (absent, sericeous, lanuginous, etc.). Pseudopetiole length. Angle and density of secondary nerves.

c) Inflorescence. Position (lateral or terminal), structure (simple or compound), organisation of main branches (monochasial or dichasial), axis length, number and distribution of bracts in the vegetative section.

d) Capitulum. Diameters of capitulum, ligular circle and disc, number or proportion of ray and disc flowers, length and colour of ray corollas, shape and texture of sterile phyllaries.

Key testing: the key was tested blindly, *i.e.* without knowing previously the identity of the individual, on living plants of the *Espeletia* species shown in Figure 1. Whenever possible, the key was tested on adult individuals that were in reproduction at the moment of the test or hold remnants of past reproduction events (dry inflorescences with attached capitula). However, tests of the key performance were also tried in juvenile/sterile individuals when fertile ones were exceedingly rare in the population assayed.

The key was also tested on herbarium samples of species *E. angustifolia*, *E. arborea*, *E. aristeguietana*, *E. atropurpurea*, *E. badilloi*, *E. banksiifolia*, *E. batata*, *E. bracteosa*, *E. bromelioides*, *E. chardonii*, *E. cuatrecasasii*, *E. elongata*, *E. figueirasii*, *E. floccosa*, *E. griffinii*, *E. grisea*, *E. hanburyana*, *E. jabonensis*, *E. jahnii*, *E. leucactina*, *E. lindenii*, *E. lopezpalacii*, *E. lucida*, *E. marcescens*, *E. margarita*, *E. moritziana*, *E. nana*, *E. neriifolia*, *E. occulta*, *E. paltonioides*, *E. palustris*, *E. pannosa*, *E. ruizii*, *E. schultzii*, *E. semiglobulata*, *E. spectabilis*, *E. spicata*, *E. tamana*, *E. tenorae*, *E. thyrsoformis*, *E. timotensis*, *E. trujillensis*, *E. vergarae*, *E. viridis* and *E. weddellii*. Specimens of these species were collected by the author and some colleagues and are now deposited at herbarium IVIC, in which the identification tests were performed blindly by IVIC staff that did not participate in the sampling.

RESULTS

Almost all living plants were correctly identified with this key. The few failures corresponded to some juvenile or sterile individuals with no remnants of past reproduction events, which did not allow the determination of diagnostic traits such as the position and structure of the inflorescence or the size of the capitula. This occasional difficulty did not prevent the correct identification of any species, since in all populations evaluated there were always individuals with inflorescences and capitula from on-going or past reproduction events. However, fertile individuals can be relative rare in certain monocarpic species, e.g. < 1% in *E. jabonensis* or *E. paltonioides* (Mavárez pers. obs), probably as a consequence of a high degree of reproductive synchronisation. The identification of individuals in this type of species was attempted using vegetative traits alone, with complete success.

The rate of correct identification for herbarium samples was also relatively high, about 90%. The failures occurred in some herbarium sheets in which diagnostic information, such as the description of the pubescence of sheaths, the position of the inflorescence, or the length and colour of ray corollas, cannot be retrieved from the specimens or their labels.

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TAXONOMIC KEY

- 1a. Trees 2
- 2a. Inflorescence structure primarily dichasial and in lateral position in regards with branch axis 3 (plate 1A)
- 3a. Pseudo-petiolate leaves. Vegetative part of the inflorescence leaf-less *E. badilloi*
- 3b. Sessile leaves. Vegetative part of the inflorescence with 1–2 pairs of opposite leaves *E. trujillensis*
- 2b. Inflorescence structure primarily monochasial and in terminal position in regards with branch axis 4
- 4a. Sessile leaves 5 (plate 1B)
- 5a. Secondary nerves > 4 mm apart *E. liscanoana*
- 5b. Secondary nerves < 4 mm apart 6
- 6a. Leaf length > 15 cm *E. occulta*
- 6b. Leaf length < 15 cm *E. parvula*
- 4b. Pseudo-petiolate leaves 7 (plate 2)
- 7a. Sparsely branched, sympodial (pseudo-dichotomous). Sheaths open, semi-amplectant. Ray ligules bright yellow *E. chardonii*
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- 8b. Secondary nerves < 4 mm apart 9

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9b. Ray corollas ligulate	10
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11a. Sheaths adaxially barbate	12
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17b. Leaves with linear or cuneiform outline	19
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19b. Ray corollas eligulate	20
20a. Leaves with flat margins and basal nerves parallel to axis	<i>E. bromelioides</i>
20b. Leaves with revolute margins and obsolete secondary nerves	<i>E. jahnii</i>
16b. Caulescent rosettes with unbranched stems	21 (plate 3B)
21a. Leaves broadly oblong (ratio < 6.5:1)	22

22a. Tubular sheaths. Leaves with unfolded margin and obtuse apex, secondary nerves 1–3 mm apart, deviation angles 70–90°	<i>E. spectabilis</i>
22b. Open sheaths. Leaves with folded margin and acute apex	23
23a. Leaf usually with small basal folding, secondary nerves 2–5 mm apart, deviation angles 70–90°, capitulum diameter > 20 mm. Ray ligules pale-yellow or greenish	<i>E. marcescens</i>
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21b. Leaves with linear or linear-lanceolate outline (ratio > 14:1)	24
24a. Ray corollas eligulate	<i>E. figueirasii</i>
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27a. Sessile rosettes or with short stems	28 (plate 4A)
28a. Ray corollas white, cream or pale-yellow	29
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30a. Leaves with linear outline (ratio 20–40:1), secondary nerves obsolete or scarce, deviation angles 20–30°. Length of ray corollas > 13 mm	<i>E. margarita</i>
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32a. Leaves with silvery-sericeous indumentum, secondary nerves obsolete or thin, 2–4 mm apart, deviation angles 25–50°. Ligular circles > 40 mm	<i>E. floccosa</i>
32b. Leaves with appressed-sericeous indumentum, secondary nerves 10–15 mm apart, deviation angles 15–30°. Ligular circles < 35 mm	<i>E. vergarae</i>
27b. Caulescent rosettes with unbranched stems	33 (plate 4B)
33a. Length of ray corollas > 8 mm	34
34a. Leaves pseudo-petiolate, secondary nerves 5–8 mm apart, deviation angles 45–75°. Ray corollas yellow	<i>E. emmanuelis</i>
34b. Leaves sessile, secondary nerves 2–4 mm apart, deviation angles 70–85°. Ray corollas white or pale-yellow, outer phyllaries broad, green, foliaceous and reticulate	<i>E. lindenii</i>
33b. Length of ray corollas < 8 mm	35
35a. Secondary nerves 1–3 mm apart, deviation angles 50–70°. Capitulum diameter > 12 mm, ligular circle > 15 mm	<i>E. grisea</i>
35b. Secondary nerves > 4 mm apart, deviation angles < 40°. Capitulum diameter < 12 mm, ligular circle < 15 mm	36
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36b. Stems mostly leaf-less, up to 10 m high. Capitulum short-radiate, ray corollas 2.0–3.5 mm long, ligules pale-yellow	<i>E. paltonioides</i>
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37a. Inflorescences mono- or oligocephalous (< 5 capitula)	38 (plate 5)
38a. Large rosettes (leaf length > 25 cm)	39
39a. Sheath length 5.0–7.0 cm, sheath width 0.9–2.2 cm. Leaves with yellowish–greenish indumentum. Inflorescences bracteate. Capitulum with 600–860 disc flowers and 400–740 ray flowers	<i>E. moritziana</i>
39b. Sheath length 7.0–10.0 cm, sheath width 2.2–2.5 cm. Leaves with white indumentum. Inflorescences aphyllous. Capitulum with 215–280 disc flowers and 95–200 ray flowers	<i>E. palustris</i>
38b. Small rosettes (leaf length < 15(25) cm)	40
40a. Sheaths abaxially glabrous	41

- 41a. Leaves usually cub-shaped, with lanuginous indumentum. Inflorescences frequently aphyllous, sometimes with 1–2 alternate or opposite bracts in the upper half. Capitulum densely pubescent, diameter 40–50 mm, ligular circle smaller than the involucre (20–30 mm), disc diameter 16–18 mm. Capitulum with 53–57% ray flowers *E. tenorae*
- 41b. Leaves lanceolate, with silvery-sericeous indumentum. Inflorescences with 3–5 pairs of opposite bracts. Capitulum diameter 19–21 mm, ligular diameter 30–35 mm, disc diameter 16–18 mm. Capitulum with 35–45% ray flowers *E. marthae*
- 41c. Leaves oblong-lanceolate, with lanuginous indumentum. Inflorescences with 2 pairs of opposite bracts. Capitulum diameter 20–26 mm, ligular diameter 24–35 mm, disc diameter 12–16 mm. Capitulum with 45–52% ray flowers *E. nana*
- 40b. Sheaths abaxially barbate..... 42
- 42a. Leaves oblong-lanceolate, with lanuginous indumentum. Inflorescences with 2–3 pairs of opposite bracts. Capitulum diameter 18–24 mm, ligular diameter 30–40 mm, disc diameter 12–15 mm. Capitulum with 50–52% ray flowers *E. batata*
- 42b. Leaves with revolute margins and cylindrical outline, with crispy-lanuginous indumentum. Inflorescences frequently monocephalous, rarely with 2–3 capitula, also with 1–2 pairs of opposite bracts. Capitulum diameter 24–32 mm, ligular diameter 40–45 mm, disc diameter 20–25 mm. Capitulum with 30–35% ray flowers *E. ulotricha*
- 42c. Leaves lanceolate, with sub-appressed villous indumentum. Inflorescences frequently with 2–5 capitula, rarely 1, also with 2 pairs of opposite bracts (rarely 1 or 3). Capitulum diameter 15–25 mm, ligular diameter 20–30 mm, disc diameter 10–15 mm. Capitulum with 37–47% ray flowers *E. weddellii*
- 37b. Inflorescences polycephalous (> 5 capitula) 43
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- 44a. Inflorescences monochasial, corymboid-paniculate. Ray corollas white 45
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- 45b. Leaves with linear-lanceolate outline (ratio 20–25:1) and lanuginous indumentum *E. angustifolia*
- 44b. Inflorescences dichasial, thyrsoïd. Ray corollas yellow 46
- 46a. Leaves with oblong outline (ratio 4.0–5.7:1) and green tomentose-velvety indumentum. Capitulum diameter 10–14 mm, ligular diameter 24–28 mm, disc diameter 10–11 mm *E. aristeguietana*

- 46b. Leaves with oblong outline (ratio 4.7–12.0:1) and whitish-greyish lanuginose indumentum. Capitulum diameter 20–30 mm, ligular diameter 30–50 mm, disc diameter 12–18 mm *E. schultzei*
- 43b. Capitula dropping or nodding. Ligular circles usually smaller than the involucre, occasionally equal or slightly larger 47 (plate 7)
- 47a. Inflorescences simple, monochasial (strict botryoid) 48
- 48a. Leaves with linear-lanceolate outline (ratio 20–35:1). Inflorescences with 14–38 monocephalous peduncles. Capitulum diameter 15–25 mm *E. spicata*
- 48b. Leaves with lanceolate outline (ratio 10–18:1). Inflorescences with 8–15 monocephalous peduncles. Capitulum diameter 35–55 mm *E. timotensis*
- 48c. Leaves with lanceolate outline (ratio 9–10:1). Inflorescences with 9–11 monocephalous peduncles. Capitulum diameter 35–55 mm *E. albarregensis*
- 47b. Inflorescences compound (at least basal peduncles polycephalous), monochasial or dichasial 49
- 49a. Leaves with oblong outline (ratio 4–10:1), sessile, with secondary nerves 5–10 mm apart. Inflorescences monochasial, with 17–35 peduncles, basal ones usually polycephalous (rarely monocephalous) *E. thyrsoformis*
- 49b. Leaves with lanceolate outline (ratio 9–20:1), distinctly pseudo-petiolate 50
- 50a. Secondary nerves 5–7 mm apart. Inflorescences monochasial, with 30–60 peduncles, basal one polycephalous *E. elongata*
- 50b. Secondary nerves 2–4 mm apart. Inflorescences dichasial, thyrsoid *E. semiglobulata*

Figure 1. *Espeletia* species used for tests of key performance in living plants and their geographic locations (páramo names given in boldface). The three species marked with (*) are found in Páramo de Tamá but do not belong to the Venezuelan *Espeletia* clade.

Plates legends: Schematic representations of leaf outlines and inflorescences of species in the Venezuelan *Espeletia* clade. Leaf sheaths not shown unless otherwise stated. Abbreviations: r: leaf length to width ratio, Ø: capitulum diameter, LC: ligular circle diameter, disc: disc diameter, %RF: proportion of ray flowers.

1A. Trees with dichasial inflorescences

1B. Trees with monochasial inflorescences, sessile leaves

2. Trees with monochasial inflorescences, pseudopetiolate leaves

3A. Monocarpic rosettes, sessile or short-branched, adaxially glabrous leaves

3B. Monocarpic unbranched caulescent rosettes, adaxially glabrous leaves

4A. Monocarpic rosettes, sessile or short-branched, adaxially pubescent leaves

White, cream or pale-yellow ray ligules

Yellow ray ligules

4B. Monocarpic unbranched caulescent rosettes, adaxially pubescent leaves

Ray corollas > 8 mm

Ray corollas < 7 mm

5. Polycarpic rosettes, mono- or oligocephalous inflorescences

6. Polycarpic rosettes, polycephalous, ligular circles larger than involucre

Monochasial inflorescences, white ray corollas

Dichasial inflorescences, yellow ray corollas

7. Polycarpic rosettes, polycephalous, ligular circles smaller than involucre

Simple inflorescences (strict botryoid)

Compound inflorescences