



<https://doi.org/10.11646/phytotaxa.518.2.3>

Touch me carefully: a step towards understanding morphological diversity in the South American spiny sunflowers (Compositae, Barnadesioideae)

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Abstract

The subfamily Barnadesioideae (Compositae) is endemic to South America, comprising 10 genera and 80 species of mostly spiny herbs, subshrubs, shrubs, trees, or woody vines distributed from Venezuela to Argentina. Three genera, *Dasyphyllum* (27 species), *Chuquiraga* (22 spp.) and *Barnadesia* (19 spp.) contain 85% of the species, while the other seven genera (*Archidasyphyllum*, *Arnaldoa*, *Doniophyton*, *Dusenilla*, *Fulcaldea*, *Huarpea*, and *Schlechtendalia*) are represented by up to three species each. Most species are found in xeric areas in the Andean and Patagonian regions—as in the Páramos, Puna and Patagonian steppe vegetation—with a secondary center of diversity in eastern South America. Previous phylogenetic hypotheses have clarified the relationships within the subfamily, showing that there are many non-monophyletic groups in different taxonomic ranks. As a result, taxonomic changes have been proposed over recent decades in order to reflect classifications comprising only monophyletic groups. In the present study, we provide a generic synopsis of the subfamily Barnadesioideae based on the most recent generic circumscriptions, including a key, expanded morphological descriptions, information on geographical distribution and habitat, photographs and taxonomic notes for all genera.

Keywords: Asteraceae, distribution, Neotropical flora, morphology, taxonomy

Introduction

The Compositae subfamily Barnadesioideae (D. Don) K. Bremer & R. K. Jansen (Bremer & Jansen 1992: 415) comprises ten genera and 80 South American species of perennial or annual herbs, subshrubs, shrubs, trees, or woody vines distributed from Venezuela to Argentina (Fig. 1). Most taxa are found in xeric areas in the Andean and Patagonian regions (Bremer 1994, Stuessy *et al.* 2009), but also in the *Nothofagus* forest (broadleaf and mixed beech forest) of central Chile and adjacent central-western areas of Argentina. A secondary center of diversity spans in Brazil, Bolivia, Paraguay, Uruguay and northeastern Argentina. The subfamily is characterized by having axillary spines, rarely solitary, in pairs or fascicles, straight or curved, convergent (when the spines follow the same direction) or divergent (when the spines follow different directions), and by the “barnadesioid trichomes”—a pubescence of unbranched three-celled hairs on the corollas, cypselae and pappus (Cabrera 1959, Urtubey 1999, Erbar & Leins 2000, Stuessy *et al.* 2009).

Barnadesioideae was first recognized as a group by Don (1830), who described the tribe Barnadesieae (Don 1830: 273), classifying 12 species in two genera, *Barnadesia* and *Chuquiraga*. Later, the genera of Barnadesioideae were recognized in different taxonomic ranks (Lessing 1832, Candolle 1838, Bentham 1873, Hoffmann 1893, Cabrera 1961). With the advent of DNA technologies, phylogenetic studies recovered the subtribe Barnadesiinae as sister group to the rest of the family (Jansen & Palmer 1987, 1988, Jansen *et al.* 1992), and the subtribe was elevated to the subfamilial rank, as Barnadesioideae (Bremer & Jansen 1992).

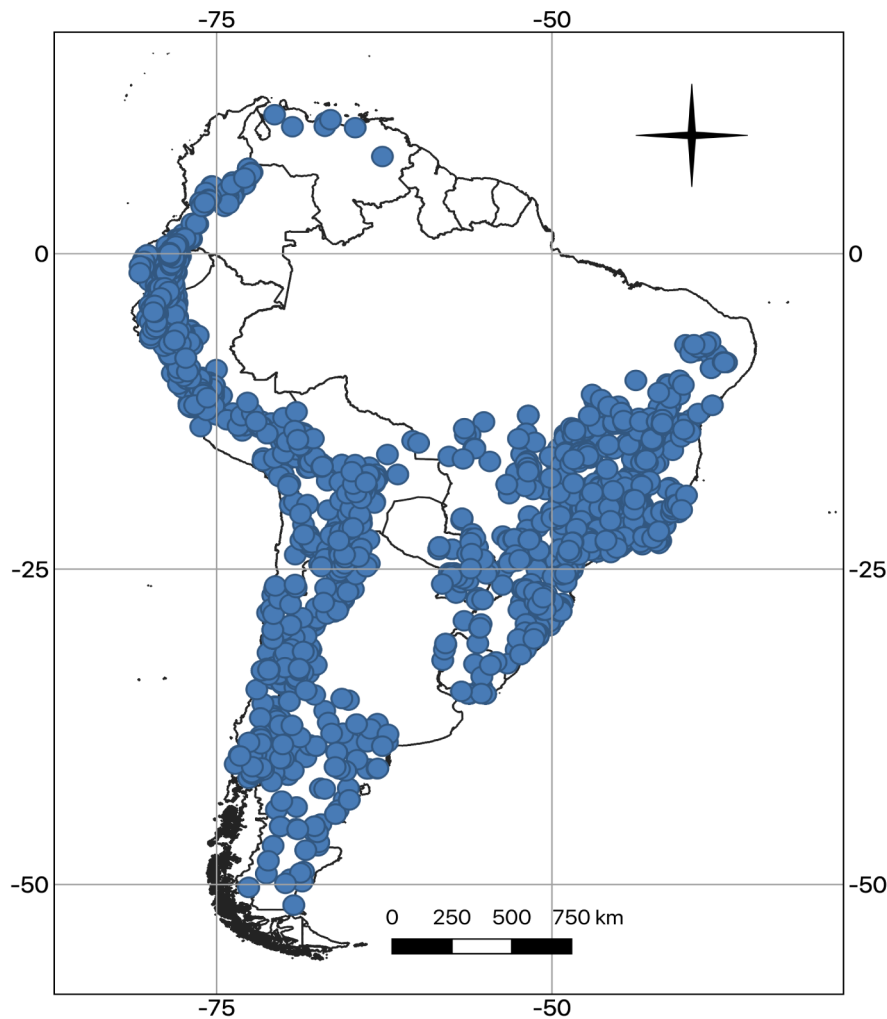


FIGURE 1. Distribution of the South American subfamily Barnadesioideae (Compositae).

Although Barnadesioideae comprises less than 1% of the species currently accepted in Compositae, the subfamily presents a great diversity in many aspects, such as morphology (Ezcurra 1985, Urtubey 1999, Padin *et al.* 2015a, Stuessy & Urtubey 2006, Stuessy *et al.* 2009, Svoma *et al.* 2019), chemical compounds (Bohm & Stuessy 1995, Mediando *et al.* 1997, 2000, Bohm & Stuessy 2001, Ccana-Ccapatina *et al.* 2018), pollen (Skvarla *et al.* 1977, Hasen 1991, Urtubey 1997, Urtubey & Telléria 1998, DeVore *et al.* 2000, Zhao *et al.* 2000, Suessy & Urtubey 2007, Telléria *et al.* 2015), chromosome counts (Diers 1961, Heiser 1963, Olsen 1980, Ciadella & López 1981, Wulff 1984, Cristóbal 1986, Wulff 1990, Stuessy & Sagástegui 1993, Strother & Panero 1994), and habitats, (Stuessy *et al.* 2009) which makes the subfamily an interesting group for the study of evolutionary trends in the Neotropics. Moreover, since Barnadesioideae is proposed as the sister group to the rest of the Compositae (Jansen & Palmer 1987, 1988), evolutionary studies allied to morphology, taxonomy, nomenclature and historical biogeography can shed light into the early evolution of the family.

Despite previous studies on the evolution of Barnadesioideae, understanding the relationships within the subfamily remains a challenge. Today, there is no doubt that the subfamily is monophyletic (Gustafsson *et al.* 2001, Gruenstaeudl *et al.* 2009, Padin *et al.* 2015b, Ferreira *et al.* 2019, Mandel *et al.* 2019). However, previous phylogenetic analyses have provided different hypotheses regarding the monophyly of the subfamily, the relationships between genera, infrageneric classification, and also species delimitation (Bremer 1994, Stuessy *et al.* 1996, Gustafsson *et al.* 2001, Urtubey & Stuessy 2001, Gruenstaeudl *et al.* 2009, Padin *et al.* 2015b, Ferreira *et al.* 2019). Previous phylogenetic results could have been affected by the taxa selected, choice of the molecular regions, and the phylogenetic reconstruction method

(Nabhan & Sarkar 2012). With the advance of high-throughput sequencing, phylogenies including thousands of molecular markers and species, using new statistical models and coalescence methods, could provide better insights into this group.

This work aims to increase the understanding of this diverse subfamily, providing updated generic circumscriptions in addition to a key, morphological descriptions, photographs, geographical distribution, maps, habitat, and notes for all genera currently circumscribed in Barnadesioideae.

Material and methods

This study is based on a bibliographic review of Barnadesioideae (Cabrera 1959, Ezcurra 1985, Hansen 1991, Harling 1991, Sagástegui & Sánchez 1991, Stuessy & Sagástegui 1993, Ferreyra 1995, Bremer 1994, Granda 1997, Katinas & Stuessy 1997, Urtubey 1999, Hind 2001, Ulloa *et al.* 2002, Urtubey & Stuessy 2001, Stuessy & Urtubey 2006, 2007, Stuessy *et al.* 2009, Funk & Roque 2011, Saavedra 2011, Saavedra *et al.* 2014, 2018, Ferreira *et al.* 2019, Svoma *et al.* 2019), examination of ca. 3,500 voucher materials from 36 herbaria: ALCB, B, BHCB, CEN, CESJ, COL, E, EAC, ESA, F, FURB, GB, HJ, HRCB, HUEFS, HUFU, IBGE, ICN, K, LP, MBM, MO, NY, NYBG, P, QCA, QCNE, RB, RFA, SI, SJRP, SPF, SPFR, UEC, US, WU (acronyms according to Thiers 2019), and observations of living plants during fieldwork conducted in Brazil and Ecuador between 2012 and 2018. Information on pollen and chromosome numbers present in the taxonomic treatment were directly extracted from the literature (Diers 1961, Heiser 1963, Olsen 1980, Cialdella & López 1981, Wulff 1990, Stuessy & Sagástegui 1993, Strother & Panero 1994, Stuessy *et al.* 1996, Stuessy & Urtubey, 2007, Watanabe *et al.* 2007).

We present a taxonomic key that reflects the recent modifications on generic circumscriptions and morphological diversity within Barnadesioideae. Morphological terms follow Radford *et al.* (1974) for indument and shapes, whereas corolla types follow Stuessy & Urtubey (2006), except for the genus *Chuquiraga*, which follows Ezcurra (1985). Geographical distribution information was obtained from herbarium specimens and a review of the literature cited above. For the maps, when the coordinates were not available, we added georeferences using the municipality coordinates provided by NASA (<https://mydasdata.larc.nasa.gov/>, last accessed December 2018); the records were plotted using QGIS version 3.2.1 (QGIS Development Team 2019).

Results

Taxonomic treatment

Barnadesioideae (D. Don) K. Bremer & R. K. Jansen (1992: 415). **Type:** *Barnadesia* Mutis ex L. f.

Annual, or perennial herbs, subshrubs, shrubs, trees, or woody vines, up to 30 m tall. *Stems* erect, decumbent or scandent, single- to much-branched, with or without lenticels, cylindrical or rarely flat, with or without scales at base, glabrous or with diverse types of trichomes, unarmed or armed with axillary spines—rarely solitary, in pairs or fascicles, straight or curved, divergent or convergent (Fig. 2), glabrous, pubescent, villous or tomentose at the base and becoming glabrous towards the apex. *Leaves* simple, alternate, opposite, or fasciculate, rarely rosulate, sessile to petiolate, persistent or deciduous, blade linear, oval, elliptic, obovate or orbicular, chartaceous, coriaceous or succulent, pale or lustrous, glabrous or with diverse types of trichomes, leaf base acute or obtuse, sometimes amplexicaul, margin entire, flat, revolute or involute, rarely plicate, glabrous or commonly ciliate apex unarmed, mucronate or spiny; nervation brochidodromous, eucamptodromous, actinodromous (with 3–5 basal or supra-basal veins), acrodromous, parallelodromous or hyphodromous, venation immersed in the mesophyll and barely visible in succulent leaves. *Capitulescence* (the secondary arrangement of capitula) terminal or axillary, monocephalous, cymose, corymbiform, paniculiform, racemiform, spiciform or umbelliform. *Capitula* 1–135-flowered, homogamous or heterogamous, discoid, disciform or radiate, sessile to pedunculate, involucre cylindrical to campanulate, 3–14-seriate, phyllaries imbricate, scarious to coriaceous, commonly colorful, erect to reflexed, glabrous to densely villous, triangular-ovate to linear, apex unarmed, mucronate or spiny, margin flat or reflexed, glabrous or commonly ciliate. *Receptacle* flat, rarely convex, pilose, rarely glabrous. *Flowers* isomorphic or dimorphic, bisexual or pistillate by the androecium atrophy or staminate by the suppression of the style, corolla bilabiate (3+2), subbilabiate (4+1, 3+1), tubular (5+0, 4+0, 3+0), or

ligulate (5+0), 3–5-lobed, cream, white, yellow, orange, red, pink to purple, glabrous to villous on both surfaces. *Anthers* 5, rarely 3 or 4, apical appendage acute, bilobed, apiculate, emarginated, obtuse, lanceolate, basal appendage ecaudate or caudate, ecalcarate or calcarate, inserted from the base to the throat of corolla, filaments free, glabrous, rarely partial connate or connate into a staminal tube, villous; staminodes shorter than the stamens or indistinct from these. *Style* cylindrical or rarely swollen below the branching point, cream, white, yellow, red, purple or orange; pistillodes usually shorter than the fertile pistils. *Cypsela* cylindrical, fusiform or turbinate, villous or rarely glabrous. *Pappus* barbellate, plumose, scaly, setaceous, rarely absent, 1-seriate, connate at base, shorter or equal to the corolla length, glabrous or with bristles pink or red. *Pollen* with or without intercolpal depressions, psilate, lophate, microechinate, sparsely microechinate, scabrate-microechinate (Stuessy & Urtubey 2007). *Chromosome number* (haploid numbers) = 8, 12, 24, 25, 26, 27, 31, 48, 50, 54 (Diers 1961, Heiser 1963, Olsen 1980, Cialdella & López 1981, Wulff 1990, Stuessy & Sagástegui 1993, Strother & Panero 1994, Stuessy *et al.* 1996, Watanabe *et al.* 2007).

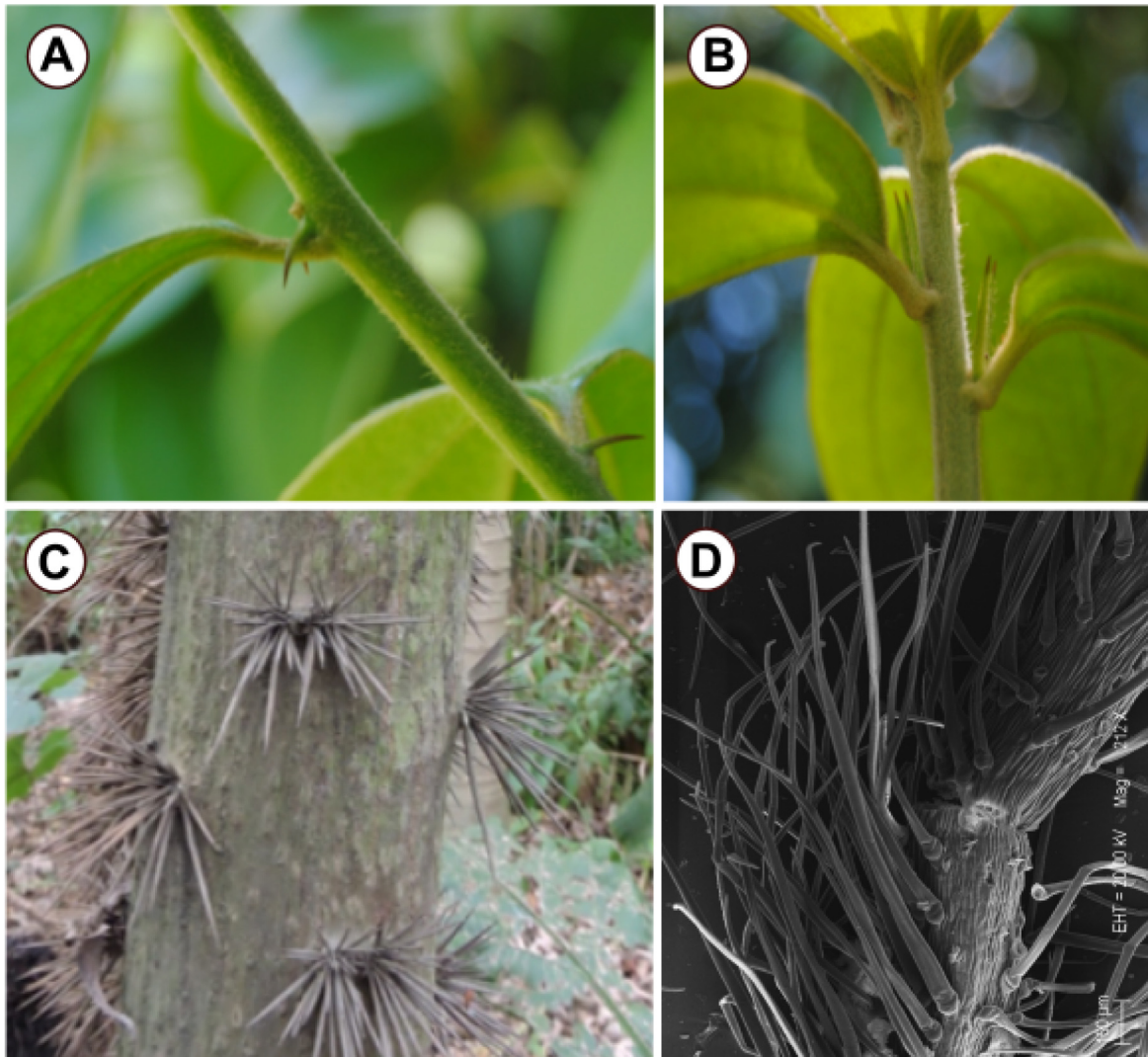


FIGURE 2. Synapomorphies of Barnadesioideae. **A–C:** Diversity of spines. **D:** Barnadesioid trichomes. **A–B:** *Dasyphyllum vagans*. **A:** Spines in pairs, curved, and convergent. **B:** Spines in pairs, straight, and convergent. **C:** *Barnadesia parviflora*. Spines in fascicles, straight, and divergent. **D:** SEM photograph of Barnadesioid trichomes.

Barnadesioideae comprises 10 genera and 80 species endemic to South America. Three genera, *Dasyphyllum* (27 species), *Chuquiraga* (22 spp.) and *Barnadesia* (19 spp.), contain 85% of the species, while the other seven genera (*Archidasiphyllum*, *Arnaldoa*, *Doniophyton*, *Dusenilla*, *Fulcaldea*, *Huarpea*, and *Schlechtendalia*) are represented by up to three species each. Most species are found in the Andes, especially in montane, xeric vegetations in the Páramos (alpine meadows), the Puna (highland and lowland steppe), and in the Patagonian steppe and semidesert, but also in the Andean tropical and subtropical mixed (deciduous-evergreen) forests (especially species of *Barnadesia*). A secondary center of diversity spans in Brazil, Bolivia, Paraguay, Uruguay and northeastern Argentina, with species of

Dasyphyllum occurring in many types of vegetation, *Schlechtendalia* occurring in the Pampas (grassland in south Brazil and adjacent areas in Uruguay and Argentina), and *Archidasphyllum* restricted to the *Nothofagus* forest (broadleaf and mixed beech forest) of central Chile and adjacent central-western areas of Argentina (Fig. 1).

Species of Barnadesioideae are mainly perennial or annual herbs, subshrubs, or shrubs, but there are also trees (some up to 30 m high, as in *Archidasphyllum*) or woody vines. Representatives of the subfamily are characterized by morphological synapomorphies that include the presence of axillary spines (in pairs or fascicles, rarely solitary), and by the “barnadesioid trichomes”—a pubescence of unbranched three-celled hairs on the corollas, cypselae and pappus (Cabrera 1959, Urtubey 1999, Erbar & Leins 2000, Stuessy *et al.* 2009, see Fig. 2).

Key to genera of Barnadesioideae

1.	Herbs or subshrubs	2
-	Shrubs, trees or woody vines	5
2.	Axillary spines present	<i>Doniophyton</i>
-	Axillary spines absent	3
3.	Capitula discoid; leaves with parallelodromous nervation	<i>Schlechtendalia</i>
-	Capitula disciform or radiate; leaves with hypodromous or actinodromous nervation; nervation immersed in the mesophyll and barely visible in succulent leaves	4
4.	Leaves succulent, capitula with marginal flowers female and corolla tubular 10–40, disc flowers hermaphroditic and corolla tubular 30–95, anthers caudate	<i>Dusenilla</i>
-	Leaves not succulent; capitula with marginal flowers female and corolla subbilabiate 5, disc flower hermaphroditic and corolla tubular 1, anthers ecaudate	<i>Huarpea</i>
5.	Capitula unflowered; style swollen below the branching point	<i>Fulcaldea</i>
-	Capitula multflowered; style not swollen below the branching point	6
6.	Capitula radiate	<i>Barnadesia</i>
-	Capitula discoid	7
7.	Leaves with brochidodromous or eucamptodromous venation; anthers with apical appendage emarginated	<i>Archidasphyllum</i>
-	Leaves with actinodromous or hypodromous venation; anthers with apical appendage acute, bilobed, lanceolate or obtuse	8
8.	Corolla orange, red, purple, yellow, or rarely white (<i>A. argentea</i>); anthers with apical appendage acute, lanceolate or obtuse	9
-	Corolla white or yellow; apical appendage bilobed	<i>Dasyphyllum</i>
9.	Corolla subbilabiate; anthers with filaments inserted at the corolla throat	<i>Arnaldoa</i>
-	Corolla tubular; anthers with filaments inserted at the base of the corolla	<i>Chuquiraga</i>

1. *Archidasphyllum* (Cabrera) P.L.Ferreira, Saavedra & Groppo (2019: 13)

Type:—*Archidasphyllum diacanthoides* (Less.) P.L.Ferreira, Saavedra & Groppo

Trees, up to 30 m tall, multi-stemmed. *Stems* erect or decumbent, much-branched, lenticelate, cylindrical, scales imbricate at base, glabrous, strigose, villous, or velutinous, unarmed or with axillary spines in pairs of fascicles, straight, convergent or rarely divergent, glabrous or rarely sparse pubescent at base and becoming glabrous towards the apex. *Leaves* alternate, spiral, sessile to petiolate, persistent or deciduous, blade narrow elliptic, elliptic, obovate or orbiculate, coriaceous, pale or lustrous, glabrous or pubescent in both surfaces, base acute or obtuse, margin flat, ciliate, apex mucronate or spiny; venation brochidodromous or eucamptodromous. *Capitulescence* terminal or axillary, monocephalous or spiciform. *Capitula* 20–35-flowered, homogamous, discoid, sessile to pedunculate, involucre campanulate, 3–4-seriate, phyllaries coriaceous, green or brown, erect or rarely slightly reflexed, glabrous or densely villous, ovate-triangular grading to lanceolate, apex unarmed or mucronate, margin flat, ciliate. *Receptacle* flat, pilose. *Flowers* isomorphic, bisexual, or pistillate by the gynoeceum atrophy, corolla tubular (5+0), ligulate (5+0), subbilabiate (4+1) or bilabiate (3+2), 5-lobed, white to cream, externally sericeous at lobes apex. *Anthers* 5, apical appendage emarginated, basal appendage lanceolate, acute to rounded, caudate, calcarate or ecalcarate, inserted at the throat of the corolla, filaments free, glabrous. *Style* cylindrical, cream to yellow. *Cypselae* fusiform, densely villous. *Pappus* plumose, slightly shorter or equal to corolla length, bristles whitish. *Pollen* with intercolpal depressions (Suessy & Urtubey 2007). *Chromosome number* unknown.

Fig. 3a–b; 10e.

Distribution and habitat:—*Archidasphyllum* comprise two species restricted to the *Nothofagus* (southern beech) forest (broadleaf and mixed beech forest) of central Chile and adjacent central-western areas of Argentina from above an altitude of 1,200 m a.s.l. (Cabrera 1959, Ferreira *et al.* 2019).

Notes:—*Archidasyphyllum* can be distinguished from the rest of Barnadesioideae by a set of characters: monoecious or gynodioecious trees reaching 30 m tall, discoid capitula, and anthers with emarginated apical appendages. Cabrera (1959), in the taxonomic revision of *Dasyphyllum*, considered *Archidasyphyllum* as a subgenus due to the high morphological similarity, because both genera have discoid capitula, a monoecious or gynodioecious breeding system, pollen with intercolpar depressions, and similar corolla shape and color. Moreover, Cabrera (1959) believed that *Dasyphyllum*, especially the subgenus *Archidasyphyllum* (*Archi*—from the ancient Greek ἀρχι- chief, early + *Dasyphyllum*—a genus of Barnadesioideae) was the most primitive group and therefore the ancestor of the other genera within the subfamily. However, molecular phylogenies recovered *Dasyphyllum* subgenus *Archidasyphyllum* as sister to the *Arnaldoa* and *Fulcaldea* clade (Gustafsson *et al.* 2001, Gruenstaeudl *et al.* 2009, Ferreira *et al.* 2019). Therefore, Ferreira *et al.* (2019) elevated the subgenus *Archidasyphyllum* to the rank of genus based on molecular phylogenetic, morphology, and biogeographical evidence. Although all phylogenetic analyses based on molecular data recover *Archidasyphyllum* as sister to *Fulcaldea* and *Arnaldoa*, this clade is morphologically diverse and synapomorphies that support the relationships are still unknown (Funk & Roque 2011, Ferreira *et al.* 2019).

Iconography:—Poeppig & Endlicher (1835–1836), Cabrera (1959).

Accepted species:—**1.1.** *Archidasyphyllum diacanthoides* (Less.) P.L.Ferreira, Saavedra & Groppo; **1.2.** *Archidasyphyllum excelsum* (D. Don) P.L.Ferreira, Saavedra & Groppo.

Selected specimens examined:—ARGENTINA. Río Negro: Bariloche, near Blest, 800 m, 41°02'S, 71°49'W, 03 March 1979, *K. Rahn 4643* (MO; 1.1). Parque Nacional Nahuel Huapi, January 1968, *Esk 150* (MBM; 1.1). CHILE. Araucanía: Cautín, 3 km E of Melipeuco, 600 m, 38°51'S, 71°42'W, 03 February 1990, *M.F. Gardner 4704* (E; 1.1). Malleco, Camino entre Curacautín y Malalcahuello, 3 km antes de Manzanar, 700 m, 38°28'S, 71°47'W, 07 January 1977, *C. Marticorena 1225* (B; 1.1). Caracautín, Estrada para Parque Nacional Tolhuaca, próximo a Terma de Tolhuaca, na beira da estrada, no lado esquerdo, 1065 m, 38°14'43''S, 71°44'44.2''W, 25 September 2013, *C.L. Silva-Luz 200* (SPFR, SPF; 1.1). Bío-bío: Recinto, N from Hotel Lleuques, toward small hill, 750 m, 14 January 1993, *T.F. Stuessy 12703* (WU; 1.1). Los Lagos: Llanquihue, Lago de todos los santos, 41°13'S, 72°16'W, *K.W. Wolffhügel s.n.* (B; 1.1). Osorno, Parque Nacional Puyehue, Termas de Puyehue, 560 m, 40°40'S, 72°20'W, 01 February 1988, *M.F. Gardner 4045* (E; 1.1). Los Rios: Valdivia, Cordillera de la Costa, road to Curiñanco on the way to Parque Oncol., 379 m, 30°46'16.9''S, 73°19'W, 18 January 2003, *M.F. Gardner 8* (E; 1.1). Valparaíso: Quillota, Olmué, Cordillera de la Costa, Parque Nacional La Campana (sector Granizo), 700 m, 32°57'S, 71°05'W, 01 February 1998, *P. Baxter 2* (E; 1.2). Quillota, Parque Nacional Cerro Campana, 17 January 1993, *T.F. Stuessy 12749* (WU; 1.2).

2. *Arnaldoa* Cabrera (1962: 39)

Type:—*Arnaldoa weberbaueri* (Muschl.) Ferreyra

Arching shrubs, up to 4 m tall, multistemmed. *Stems* erect or decumbent, much-branched, lenticelate, cylindrical, glabrous, velutinous or densely tomentose, axillary spines in pairs, straight, convergent or divergent, glabrous or tomentose at base and becoming glabrous towards the apex. *Leaves* alternate, petiolate, persistent or deciduous, blade elliptic, ovate or oblate, coriaceous, pale or lustrous, adaxially glabrous to tomentose, abaxially glabrous to densely tomentose, villous, floccose, lanose, apex acute or obtuse, margin flat or slightly revolute, glabrous or ciliate, apex mucronate or spiny; venation actinodromous with 3 basal suprabasal nerves. *Capitulescence* terminal, monocephalous. *Capitula* 30–95-flowered, homogamous, discoid, sessile, involucre campanulate, 8–15 series, phyllaries coriaceous, brown or black, erect or reflexed, glabrous to densely tomentose, ovate—triangulate grading to lanceolate, apex mucronate or spiny, margin flat, ciliate. *Receptacle* flat, pilose. *Flowers* isomorphic, bisexual, corolla subbilabiate (4+1), 5-lobed, red, purple, orange or white, villous. *Anthers* 5, apical appendage lanceolate or obtuse, basal appendage truncate, caudate, calcarate, inserted at the throat of the corolla, filaments free, glabrous or villous. *Style* cylindrical, red, purple, orange, white. *Cypselae* turbinate or cylindrical, densely villous. *Pappus* plumose, slightly shorter or equal to

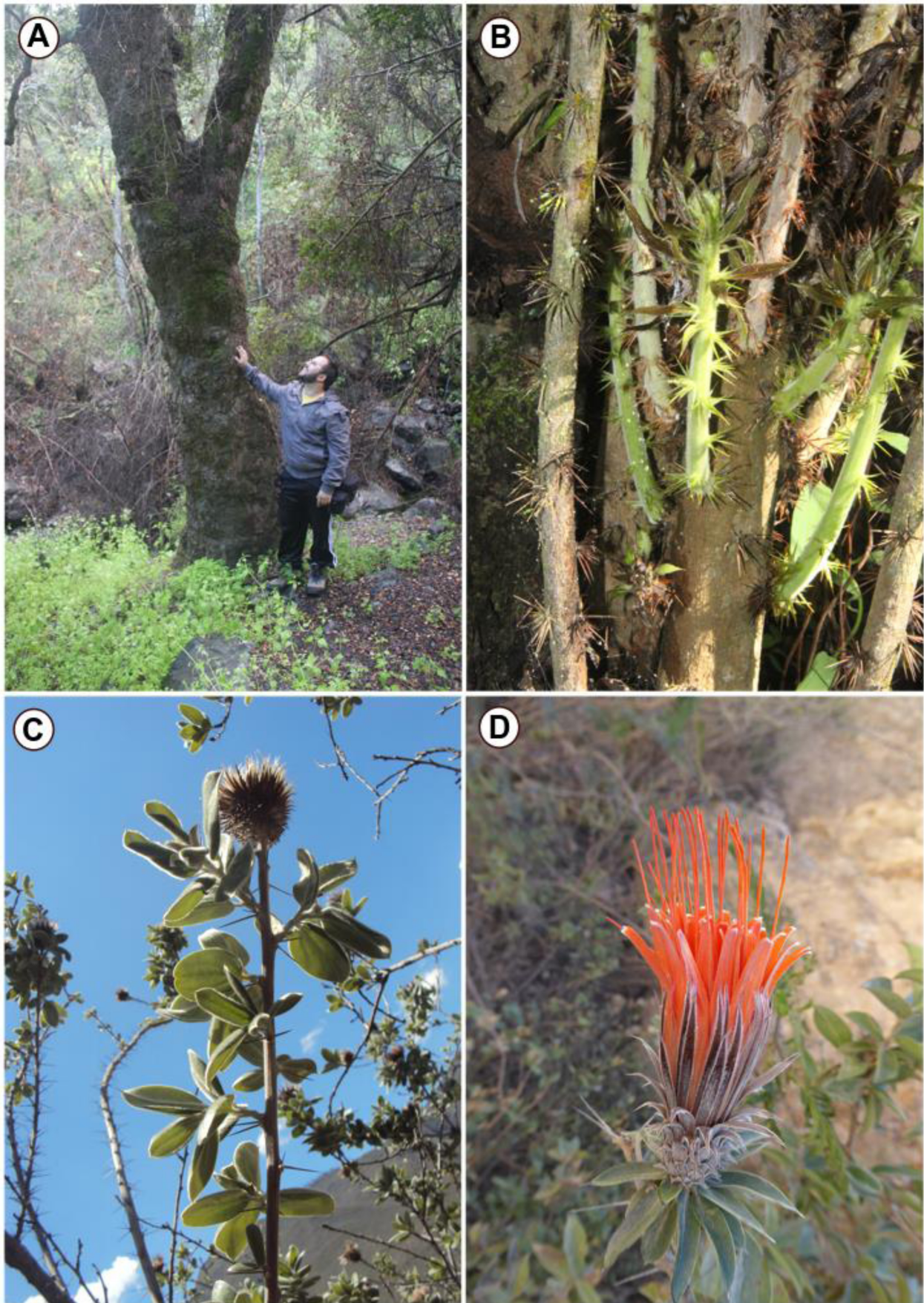


FIGURE 3. *Archidasyphyllum* and *Arnaldoa*. **A–B:** *Archidasyphyllum diacanthoides*. **A:** Habit. **B:** Multi-stemmed tree with fasciculate spines. **C–D:** *Arnaldoa weberbaueri*. **C:** Habit. **D:** Capitulum. Photos by Marcelo Monge (A–B), Gari Ccana-Ccapatinta (C), and Daniel Montesinos (D).

corolla length, bristles whitish. *Pollen* with intercolpal depression, microechinate (Suessy & Urtubey 2007). *Chromosome number* = 24–27 (Stuessy & Sagástegui 1993).

Fig. 3c–d; 10f.

Distribution and habitat:—*Arnaldoa* comprise three shrubby species found in Monte Bajo Puna vegetation (shrubby dry slopes) above an altitude of 1,500 m in northern Peru and southern Ecuador (Stuessy & Sagástegui-Alva 1993, Ulloa *et al.* 2002).

Notes:—*Arnaldoa* is morphologically close to *Chuquiraga*, sharing the shrubby habit, discoid capitula, colorful corollas and stigma, long caudate anthers, and microechinate pollen. However, *Arnaldoa* is distinguished by the subbilabiate corolla (*vs.* tubular in *Chuquiraga* *sensu* Ezcurra 1985) and stamens inserted on the throat of corolla tube (*vs.* base of corolla in *Chuquiraga*). Phylogenetic hypotheses based on molecular data recovered *Arnaldoa* as closely related to *Fulcadea* (Gustafsson *et al.* 2001, Gruenstaeudl *et al.* 2009, Funk & Roque 2011, Ferreira *et al.* 2019). Although the morphological differences between *Arnaldoa* and *Fulcaldea* are remarkable, *Arnaldoa* by having solitary capitula with 30–95-flowered, subbilabiate corollas, caudate anthers, microechinate pollen, cylindrical style *vs.* capitula arranged in synflorescence with 1-flowered, tubular corollas, ecaudate anthers, spinulose pollen, and swollen style below the branching point in *Fulcaldea*, they share the arching shrubby habit, red corollas, and geographical distribution in southern Ecuador and Northern Peru.

Iconography:—Stuessy & Sagástegui-Alva (1993), Ferreyra (1995), Ulloa *et al.* (2002).

Accepted species:—**2.1** *Arnaldoa argentea* C. Ulloa, P. Jørg. & M.O. Dillon; **2.2.** *Arnaldoa macbrideana* Ferreyra; **2.3.** *Arnaldoa weberbaueri* (Muschl.) Ferreyra.

Selected specimens examined:—ECUADOR. Loja: Amaluza, road to the antennas above town, at the top, 2400 m, 4°33'58"S, 79°26'26"W, 05 November 2000, *P.M. Jørgensen 2234* (QCNE, MO, WU; 2.1). Bellavista, Vicinity of Bellavista, at “Las Antenas” (7 km from Amaluza), 2400 m, 04°33'S, 79°26'W, 14 August 2001, *J.E. Madsen 8341* (MO; 2.1). Vicinity of Bellavista, at “Las Antenas” (6–7 km from Amaluza), 2200–2300 m, 04°33'S, 79°27'W, 31 May 2001, *J.E. Madsen 8175* (MO; 2.1). PERU. Amazonas: Chachapoyas, western base of the Cerros Calla Calla, 22 km east of Balsas on the road to Leymebamba, 1940 m, 30 May 1964, *P.C. Wright 5454* (K, MO; 2.3). Cordillera de Calla Calla, Balsas-Leymebamba road near km 359, 6400 ft. (c. 1951m) 9 July 1977, *T. Ducan 2602* (MO; 2.3). Ancash: Chingas, north of the village of Llamellin, on the west flanks of the Rio Marañón, 2669 m, 09°04'08"S, 76°59'39"W, 27 May 2011, *E. Gagnon 3157* (K; 2.3). Huari, Falda de los Cerros de los rios Mosna y Puchca, 2400–2800 m, 27 May 1962, *M.Z. Agnes 41* (MO; 2.3). Cajamarca: Celendín, Rio Marañón valley, Celedín-Balsas road, 25 km, and onward from Celendín, 1000–2500 m, 06°51'S, 78°05'W, 16 July 1983, *D.N. Smith 4323* (MO; 2.3). Celendín, Had. El Limón (Celedín-Balsas), 2150 m, 5 May 1970, *A. Sagástegui A. 7410* (US; 2.3). Celendín, Hacienda Limon, 33 kms E of Celendín on road to Rio Marañón, 2050 m, 10 July 1992, *T.F. Stuessy 12524* (WU; 2.3). Lambayeque: Lambayeque, Alredores del Cuello Porculla, 1800 m, 24 July 1991, *J. Mostacero L. 2296* (MO; 2.2). Lambayabeque, Road from Olmos to Abra Porculla, 1500 m, 22 February 1976, *T. Plowman 5516* (US; 2.2). Lambayabeque, west side Abra Porculla Km. 35 east of Olmos. Mesones-Muro Highway between Olmos y Río Marañón, 1650 m, 26 September 1957, *C. Hutchison 1379* (US; 2.2). Libertad: Pataz, road Buldibuyo to Tayabamba, dryish inner andean valley, mostly cultivated, but steeper slopes with scrub forest, 3141 m, 08°12.571'S, 77°19.665'W, 24 April 2004, *M. Weigend 8031* (B; 2.3). Pataz, Huancaspata-Puente Mamahuaje, 3000 m, 26 June 1974, *A. López M. 8218* (MO; 2.3). Bolivar, District La Longotea, section Pampa Colorada, 1914 m, 13 May 2011, 07°02'31"S, 77°55'08"W, *R.W. Bussman 16871* (MO; 2.3). Piura: Abra de Porculla, entre Olmos y Jaen, 2100–2200 m, 28 June 1959, *R. Ferreyra 13731* (MO; 2.2). Bajando Abra de Porculla y Jaen, cerca del Abra, 1800–1900 m, 26 June 1959, *R. Ferreyra 13628* (MO; 2.2).

3. *Barnadesia* Mutis ex Linnaeus f. (1782: 55)

Type:—*Barnadesia spinosa* L. f.

Arching shrubs or trees, up to 20 m tall, multistemmed. *Stems* erect, decumbent or sometimes scandent, much-branched, lenticelate, cylindrical or rarely flat, with or without scales imbricate at base, glabrous, tomentose, villous, velutinous, sericeous, rarely dendritic, unarmed or with axillary spines in pairs or fascicles, straight or curved, convergent or divergent, glabrous, villous or pubescent at base and becoming glabrous towards the apex. *Leaves* alternate or in fascicles, sessile to petiolate, persistent or deciduous, blade elliptical, oblanceolate, or obovate, chartaceous to coriaceous, pale or lustrous, glabrous to densely villous, tomentose or sericeous on both surfaces, apex mucronate or spiny, margin flat, glabrous or ciliate, base acute or obtuse; venation eucamptodromous or actinodromous with 3 suprabasal nerves. *Capitulescence* terminal or axillary, monocephalous, corymbose or racemose. *Capitula* 9

or 16-flowered, heterogamous or homogamous, radiate, sessile to pedunculate, involucre cylindrical, turbinate or campanulate, 6–14-seriate, phyllaries scarious to coriaceous, green, brown, reddish-brown to purple, erect or reflexed, glabrous or pubescent, ovate grading to lanceolate, apex unarmed, mucronate or spiny, margin flat, ciliate. *Receptacle* flat, pilose. *Flowers* dimorphic or isomorphic. *Ray flowers* 8 or 13, bisexual, corolla subbilabiate (4+1), 5-lobed, red to purple, pink or rarely white, externally villous, internally glabrous or sericeous on throat, rarely sericeous on tube. *Disc flowers* 1 or 3, bisexual or pistillate by the androecium atrophy or staminate by the suppression of the style (only in *Barnadesia* subgenus *Bacasia*), corolla tubular (5+0, 4+0, 3+0), subbilabiate (4+1, 3+1) or ligulate (5+0), 3–5-lobed, purple, pink or rarely white, externally and internally glabrous or villous. *Anthers* 5 (ray flowers) or 3–5 (disc flowers), apical appendage lanceolate to obtuse, basal appendage obtuse or shortly sagittate, ecaudate, ecalcarate, stamens inserted at the throat (ray flowers) or at the base or between the base and the throat (disc flowers), filaments glabrous, free, partially connate or totally connate into a staminal tube, (ray and disc flowers), or rarely connate in disc flowers, (only in *B. spinosa*) *Style* cylindrical, purple. *Cypsela* (ray flowers) cylindrical or rarely turbinate, villous, or (disc flowers) turbinate, densely villous. *Pappus* (ray flowers) plumose, shorter than the corolla length, or (disc flowers) plumose, barbellate or setaceous, when barbellate or setaceous usually recurved at maturity, glabrous to villous, equal to or shorter than the corolla, bristles whitish. *Pollen* lophate, radially symmetric or asymmetric, smooth (Suessy & Urtubey 2007). *Chromosome number* = 12, 24, 25, 31, ca. 48, ca. 50, 62 (Heiser 1963, Olsen 1980, Strother & Panero 1994, Stuessy *et al.* 1996).

Fig. 4; 10c.

Distribution and habitat:—*Barnadesia* is the third largest genus of Barnadesioideae, comprising 19 species distributed mainly along the Andes from Colombia to Argentina, with the highest number of species found in Peru (Urtubey 1999, Hind 2001, Stuessy *et al.* 2009). The species occur at the edges of tropical and subtropical mixed (deciduous-evergreen) montane forests, and gallery forests; there are also records in the Páramos (alpine meadows) and in the Puna (highlands and steppe), c. 3,700 m a.s.l. One species, *Barnadesia caryophylla* (Vell.) S.F. Blake occurs in Brazil, in the Cerrado (Brazilian savanna) and in the Atlantic Forest (tropical or subtropical evergreen-semideciduous forest) (Saavedra 2020).

Notes:—The species of the genus are classified in two subgenera (following Urtubey 1999): *Barnadesia* subg. *Barnadesia*, with 17 species from Colombia to Argentina and one species in Brazil (*B. caryophylla*), characterized by sessile or subsessile leaves disposed in fascicles, sessile or shortly pedunculate capitula, disc flowers with subbilabiate or ligulate corolla with pappus simple or barbellate; and *Barnadesia* subg. *Bacasia*, with two species distributed from Colombia to Bolivia, characterized by alternate and petiolate leaves, pedunculate capitula, disc flower with tubular corolla and plumose pappus.

Barnadesia is the type genus of the subfamily and can be distinguished from the other genera by the following set of characters: arching shrub or trees, radiate capitula, 8 or 13 ray flowers, 1 or 3 disc flowers, colorful corolla (pink, red, purple, white), ecalcarate and ecaudate anthers, obtuse apical appendage, free filaments, partial or connate into a staminal tube, the pappus of the disc flower usually setaceous or barbellate that recurves at maturity, and lophate pollen.

Iconography:—Chung (1965), Harling (1991), Urtubey (1999), Ferreyra (1995), Hind (2001).

Accepted species:—*Barnadesia* subgenus *Barnadesia*: **3.1** *Barnadesia aculeata* (Benth.) I.C. Chung; **3.2** *Barnadesia arborea* Kunth; **3.3** *Barnadesia blakeana* Ferreyra; **3.4** *Barnadesia caryophylla* (Vell.) S.F. Blake; **3.5** *Barnadesia dombeyana* Less; **3.6.1** *Barnadesia glomerata* Kuntze var. *glomerata*; **3.6.2** *Barnadesia glomerata* var. *mucronata* I.C. Chung; **3.7** *Barnadesia horrida* Muschl.; **3.8** *Barnadesia jelskii* Hieron.; **3.9.1** *Barnadesia lehmannii* var. *angustifolia* I.C. Chung; **3.9.2** *Barnadesia lehmannii* var. *ciliata* I.C. Chung; **3.9.3** *Barnadesia lehmannii* Hieron var. *lehmannii*; **3.9.4** *Barnadesia lehmannii* var. *villosa* (I.C. Chung) Urtubey; **3.10** *Barnadesia macbridei* Ferreyra; **3.11** *Barnadesia macrocephala* Kuntze; **3.12** *Barnadesia odorata* Griseb.; **3.13** *Barnadesia polyacantha* Wedd.; **3.14** *Barnadesia pycnophylla* Muschl.; **3.15** *Barnadesia reticulata* D. Don; **3.16** *Barnadesia spinosa* L. f.; **3.17** *Barnadesia woodii* D.J.N. Hind. *Barnadesia* subg. *Bacasia* (Ruiz & Pav.) Urtubey: **3.18** *Barnadesia corymbosa* (Ruiz & Pav.) D. Don; **3.19** *Barnadesia parviflora* Spruce ex Benth. & Hook.f.

Selected specimens examined:—ARGENTINA. Jujuy: Capital, Lozano-Tiraxi, 11 November 1978, *S.A. Renvoize* 3439 (B; 3.12). Salta: Capital, Castellanos, Arroyo Castellanos 5 Km al W del puente a Yacone, 1500–1800 m, 15 September 1988, *L.J. Novara* 8098 (B, 3.12). Santa Victoria, Los toldos, Quebrada del Artillera, 4–7 km al E de la Municipalidad, 1500–1700 m, 17 March 1986, *L. Novara* 5225 (B; 3.12). Tucumán: Tafí Viejo, Cumbres de San Javier, Ruta Provincial 340, 04 November 1978, *S.A. Renvoize* 3340 (B; 3.12). BOLIVIA. Cochabamba: Ayopaya, Independencia, in the second valley north of La Mina on road to Sailapata, c 48 km N of Independencia, 2800 m, 16°56.35'S, 66°57.05'W, 15 May 2002, *J.R.I. Wood* 18477 (K; 3.6.1). Carrasco, Siberia-Cochabamba, 2800 m, March

1959, *Cárdenas 5736* (US; 3.12). Carrasco, Dianpampa, 2160 m, 17°40'53''S, 64°40'55''W, 09 September 2003, *S. Duran 6* (MO; 3.18). Carrasco, Siberia, Chua Kocha, 2195 m, 17°48'56''S, 64°42'27''W, 22 June 2003, *E. Fernández 1943* (MO; 3.6.2). Cochabamba, Quebradas von Tiraque, 2900 m, 13 November 1928, *J. Steinbach 8723* (MO, K; 3.11); Chapare road, 36 km from Cochabamba, roadside, 12,000 ft (c. 3,557 m alt.), 22 August 1964, *W.J. Badcock 296* (K; 3.11). Tapacari, kilo 86 (near Sarari) on the road from Cochabamba to Oruro, 4000 m, 22 June 1997, *J.R.I. Wood 12323* (K, 3.11). Chuquisaca: Luis Calvo, comunidad Chuya Yaco, a 3 km aproximadamente al Sur-este de la comunidad de Chuya Yaco, 1239 m, 19°45'12''S, 63°52'36''W, 20 October 2005, *A. Lliully 461* (MO; 3.18). Sud Cinti, ca. 11 km al NW de la Comunidad de Las Abras caminho hacia la comunidad de El Palmar, pendiente superior cerro Alto de Rosas, 862 m, 21°02'24''S, 64°13'08''W, 10 June 2005, *R. Lozano 1380* (MO; 3.18). La Paz: Franz Tamayo, Parque Nacional Madidi entre Piñalito y Cuchiwani, 2140 m, 14°30'44''S, 68°16'28''W, 21 July 2012, *A.F. Fuentes 17401A* (MO; 3.18). Inquisivi, along the trail between Loma El Abra and Cerro Negro Kkota, a 6 km hike, ca. 6 km N from Inquisivi, 2900–3000 m, 16°50'S, 67°08'W, 22 August 1988, *M. Lewis 881108* (MO; 3.6.2). Murillo, valle del río Zongo, 21.1 km al N de la cumbre, 3200 m, 16°09'S, 68°07'W, 04 April 1987, *J.C. Solomon 16453* (MO, K; 3.14). Saavedra, Rio Comata valley, on descent from Charazani on road to Apolo, 1600 m, 06 August 2000, *J.R.I. Wood 16594* (K; 3.17). Potosí: Charcas, Toro Toro, Siti Wilta caminho de Toro Toro a San Pedro de Buena vista, 3418 m, 18°07.99'S, 65°50.25'W, 27 February 2003, *J.R.I. Wood 19251* (K; 3.14). Santa Cruz: Comaropa, Jungas de San Mateo, 2500 m, 22 October 1928, *J. Steinbach 8400* (K; 3.6.2). Florida, Comunidad de Bella Vista, 1600–1900 m, 18°14'S, 63°39'W, 18 June 2006, *L. Arroyo 3406* (K; 3.18). Samaipata, Bella Vista, sendero Ecologico el Cañadon, 1487 m, 42°80'38''S, 79°83'15.4''W, 08 September 2005, *D. Villarreal 151* (MO; 3.18). Vallegrande, Huasacañada, 5 km al S de la ciudad de Vallegrande, 2050 m, 18°31.5'S, 64°5.8'W, 05 August 1991, *I.G. Vargas 1071* (US; 3.12). Tarija: Entre Ríos, Tarija road, c.km. 40, 19 July 1964, *W.J. Badcock 273* (K, 3.12). BRAZIL. Goiás: Sylvania, Área de influência da AHE Corumbá IV, 23 May 2003, *A.A. Santos 2053* (CEN; 3.4). Serranópolis, RPPN Pousada das Araras, 18°26'22''S, 51°59'43''W, *L.F. Souza 2980* (HJ; 3.4). Mato Grosso: Juína, ca 40 km WNW (em linha reta) de Juína, 11°18'S, 59°05'W, 06 July 1997, *V.C. Souza 18251* (UEC; 3.4). Minas Gerais: Carandaí, Pedra do Sino Hotel Fazenda, BR 040 Km 6, Trilha da matinha atrás da cas., 1000–1200 m, 15 July 2005, *N.F.O. Mota 286* (BHCB; 3.4). Lima Duarte, arraial de Conceição do Ibitipoca, Parque Estadual do Ibitipoca e Pedra do Gavião, 20 May 2001, *R.M. Castro 393* (CESJ; 3.4). Santana do Garambeu, Trecho do Alto Rio Grande adjacente a zona urbana de Santana de Garambeu, 1100–1150 m, 21°36'12.6''S, 44°07'25.3''W, 08 June 2001, *A. Salino 7007* (BHCB; 3.4). São Paulo: Cunha, 20 April 1939, *J. Kiehl 3711* (US; 3.4). São José do Rio Preto, Mirassol, 07 August 1991, *N. Taroda-Ranga s.n.* (SJRP; 3.4). COLOMBIA. Boyacá: Cordillera Oriental, Sierra Nevada del Cocuy, Quebrada de San Paulino próximo Alto Ritacuva, 3500 m, *H.G. Barclay 7305* (MO; 3.16). Cauca: Puracé, márgen derecha Río Vinagre, corregimiento Chibchiguará, 3250 m, 02°23'47'' S, 76°50'21'' W, 15 January 1991, *R. Ruiz 1232* (MO; 3.16). Cudinamarca: Above Guasca, 10,000 ft. (c. 3058m), 16 December 1938, *E.K. Balls 85767* (K; 3.16). Salto de Tequendama, 25 km west-southern of Bogotá, western margin Cordillera Oriental, 17 June 1950, *S. Galen Smith 1091* (K; 3.16). Meta: Puerto López, 3000 m, 12 August 1946, *M. Jaramillo Mejia 402* (US; 3.16). Nariño: Near top of divide on Tuquerres-Ricaurte road, roadside subparamo, 3000 m, 22 November 1981, *Al. Gentry 34833* (MO; 3.16). Putamayo: Valle de Sibundoy, Sibundoy, ca. 2200 m, *M.L. Bristol 858* (US; 3.16). Quindío: Salento, Paraje Cocora, orilla del río Quindío, 2470 m, 11 June 1983, *S. Royos 203* (MO; 3.19). Risaralda: La Pastora, Reserva Ucumari, 2610 m, 11 October 1989, *D. Rangel 5406* (MO; 3.19). Santander: Páramo de las Puentes, above La Baja, 3500–3700 m, 25 January 1927, *E.P. Killip 18250* (US; 3.16). Valle del Cauca: Tuluá, Corregimiento Santa Lucía, finca San Luis, 2800 m, 22 September 1984, *W. Devia 724* (MO; 3.16). ECUADOR. Azuay: 8–10 km. S of Cumbe on the road to Loja, 9050–9400 ft. (c. 2758–2865 m), 22 January 1979, *R.M. King 7762* (MO; 3.2). Bolívar: Simiatug, Hacienda Talahua, 3200 m, 28 April; 1939, *C.W. Penland 547* (US; 3.2). Carchi: Wooded hills about 5 miles south of Tulcán, 2500 m, 10 August 1923, *A.S. Hitchcock 21012* (US; 3.16). Cañar: 20 km S of Cañar on the road to Cuenca, along railroad tracks, 9000 ft. (c. 2743m), 21 January 1979, *R.M. King 7742* (MO; 3.2). Cotopaxi: Corazón, *E.F. André K-271* (K; 3.2). Imbabura: Cotacachi, Hda. La Florida, 1900–2500m, 00°23'S, 78°28'W; 27 August 1992, *A. Alvarez 614* (QCA; 3.19). Guayas: Guayaquil Canton, Bosque Protector Cerro Blanco, carretera a Salinas, km 15, 350 m, 02°10'S, 79°58'W, 15 August 1991, *D. Rubio 1790* (MO; 3.9.4). Loja: Old road to Catamayo (La Toma)-Loja, km 7, c. 18 km from Catamayo, 2600 m, 04°00'S, 79°16'W, 21 May 1997, *G.P. Lewis 3329* (MO; 3.1). Cordillera de Las Lagunitas, Amaluza-Jimbura-Zumba, km 41, 3270 m, 4°44'55''S, 79°25'13''W, 23 November 1994, *P.M. Jørgensen 792* (MO; 3.1). Napo: Baeza, 2 km antes de Baeza, carretera Papallacta-Baeza parte alta de "Y", 2000 m, 00°28'S, 77°54'W, 11–14 July 1992, *R. Valencia 2461* (QCA; 3.19). Quijos, Serra Azul, Agrícola Industrial Río Aragón, Colinas del Tundal, 2200 m, 00°40'S, 77°54'W, 30 April 1992, *A. Alvarez 300* (MO, QCA; 3.19). Cerca de baños termales, dos kms. Al N. de Papallacta, 22 March 1977, *S. González 17* (MO; 3.2). Pichincha: Along road from Santo Domingo de los Colorados and Alóag, ca. 14 km W of



FIGURE 4. *Barnadesia*. **A and E:** *Barnadesia pycnophylla*. **A.** Habit. **E.** Divergent and fasciculate spines on stem. **B:** *Barnadesia caryophylla*. Capitulum. **C:** *Barnadesia odorata*. Capitulum. **D:** *Barnadesia arborea*. Capitula. Photos by Gari Ccana-Ccapatinta (A and E), Gustavo Shimizu (B), Claudia Martin (C), Carmen Ulloa (D).

Alóag, 2250 m, 00°26'54"S, 78°42'44"W, 01 August 2004, *T.B. Croat 92841* (MO; 3.19). Quito, carretero Nono-Guarumos-Tandayapa, colecciones en sendero entre Guarumos y Cerro Guarumos, derecho de vía del Oleoducto de Crudos Pesados, 2400–2700 m, 00°03'S, 78°38'W, 01 September 2001, *A.F. Fierro 3148* (MO; 3.19). Tabacundo,

Quebrada Verdetola, km 2.8, 3000 m, 00°12'S, 78°23'W, 09 July 2000, *B. Cuamacás* 623 (MO; 3.8). Tambilho, 2700 m, 25 May 1939, *E. Asplund* 6439 (K; 3.2). Tungurahua: Bãnos-puyo road 6 km, South of Bãnos, trail leading disturbed wet montane forest, 2500 m, 01°22'S, 78°25'W, 10 December 1983, *A. Barfod* 49003 (QCA; 3.19). PERU. Ancash: Bolognesi, cerros al E. de Chiquian, 3700 m, 10 May 1950, *E. Cerrate* 523 (MO; 3.5). Amazonas: Chacapoyas, 28 kms along road from Leimebamba SW towards Celendín, 9700 ft. (c. 2956m), *R.M. King* 9254 (MO; 3.2). Bongará, banda frente a Pomacochas, en trocha, 2200–2300 m, 17 August 1963, *R. Ferreyra* 15201 (MO; 3.9.3). Mendoza, 1400 m, August 1963, *F. Woytkowski* 8121 (MO; 3.4). Partly along main road Jumbilla-Pedro Ruiz, partly along road to Tialango, 05°52'31"S, 76°46'36"W, 03 November 2012, *H. van der Werff* 24976 (MO; 3.9.3). Apurímac: Valley of Rio Colcachaca at Cotarusi-Colce ca. 1 km above junction w Rio Chalhuanca ca. 15 km (air) S of Chalhuanca, 3000–3100 m, 16 December 1962, *H.H. Iltis* 541 (US; 3.7). Ayacucho: Humanguilla, ca. 15 km before Ayacucho left of road Huanta-Ayacucho, 10,000 ft. (c. 3048m), 01 January 1962, *S.G.E. Saunders* 725 (K; 3.7). La mar, commonest of dry puna scrub along roadside from Ayacucho to San Francisco, shortly after crossing over the 2nd high pass, 34 km S of Tambo, c. 10 km from Rirconado at 3 am in the morning, 3500 m, 13°S, 74°W, 07 June 1968, *T.R. Dudley* 9053 (US; 3.14). Cajamarca: Celendín, on roado to Celendín, 3 km east of Encañada, 3200 m, 16 May 1964, *P.C. Hutchison* 5120 (MO; 3.5). Celendín, cerca a Celendín, 3400–3500 m, 21 June 1963, *R. Ferreyra* 15032 (MO; 3.8). Contumazá, arriba de Trinidad, 2200 m, 06 July 1977, *A. Sagástegui* A. 8945 (MO; 3.9.3). Cutervo, entre Cutervo y Cochabamba, 2500–2600 m, 01 August 1946, *R. Ferreyra* 838 (MO; 3.8). entre Llama y Chongoyape, 2200–2500 m, 02 August 1946, *R. Ferreyra* 862 (MO; 3.9.3). Cusco: Cusco, road to Pisac, ca 1 km after ruins of Sacsayhuaman, 3700 m, 13°30'07"S, 71°58'50"W, 10 September 2002, *M. Ackermann* 262 (B; 3.7). Qorao, abra de Qorao, 3817 m, 13°29'S, 71°56'W, 21 March 2003, *W. Galiano* 4793 (MO; 3.7). Urubamba, trilha para a lagoa Yanacocha, 3449 m, 13°18'01.7"S, 72°03'13.6"W, 11 January 2016, *G. Cappatinta* 54 (SPFR; 3.7). Huacavelica: Paucartambo, 11,500 ft. (c. 3505m), 03 May 1939, *B. Balls* 6683 (K; 3.7). Huánuco: Ambo, Tomayaquichua, a caminho de Estanco, 3609 m, 76°08'52.0"W, 10°03'52.9"S, 27 January 2016, *G. Cappatinta* 49 (SPFR; 3.14). on open slope of ravine, 3 km east of Acomayo, 26 July 1946, *F. Woytkowski* 34335 (MO; 3.10). Huánuco, km 474 on Lima-Tingo Maria road, 1650 m, 02 June 1981, *K. Young* 632 (MO; 3.18). Llata, about 7000 ft. (c. 2133m), 21 August 1922, *Macbride* 2250 (US; 3.5). Huaraz: Recuay, aos redores de Cátaç, 12 February 2016, *G. Cappatinta* 48 (SPFR; 3.5). Junín: Tarma, entre La Merced y Quimiri, valle del Chanchamayo, 800–900 m, 27 June 1948, *R. Ferreyra* 3696 (MO; 3.4). San Luíz, 14 August 1944, *C. Ridoutt* 14564 (MO; 3.4). Yucapata, 1400 m, 16, July 1961, *F. Woytkowski* 6637 (MO; 3.4). Ica: Pisco, Arriba de Pisco, 2900 m, 20 March 1954, *W. Rauh* 386 (MO; 3.15). La Libertad: Otuzco, 9 km west of and below Shorey toward Trujillo, 3590 m, 11 August 1964, *P.C. Hutchison* 6289 (MO; 3.5). Lima: Canta, alrededores de Canta, 2900–2950 m, 16 March 1950, *R. Ferreyra* 6914 (MO; 3.15). Canta, cerca a San Juan, Valle de Chancay, 3000–3200 m, 29 May 1974, *R. Ferreyra* 18415 (MO; 3.5). Huarochirí, Monte de Zárate, encima de San Bartolomé, 2900 m, *R. Ferreyra* 10427 (MO; 3.3). Moyobamba, *Mathews* 1389 (K; 3.9.1); above Huamantanga and Obrajilla, *Mathews* 643 (K; 3.9.1). Pasco: Oxapampa, road from Paucartambo to Oxapampa, towards Tingo Chontabamba, km 82, 2280 m, 10°38'S, 75°25'W, 04 April 2001, *M. Weigend* 5485 (B; 3.18). Daniel Carrión, 16 km NE of Yanahuanca 1 km NW of Páucar, along fencerow, 3450, 01 August 1965, *R. Bird* 1258 (MO; 3.5). Piura: Huancabamba, Mitopampa (Huancabamba-Cuello del Indio), 2650 m, 22 July 1975, *A. Sagástegui* A. 8239 (MO; 3.8). Huancabamba, arriba de Palamba, 1300 m, 13 September 1981, *A. Lopez M.* 8802 (MO; 3.9.3). Puno: Carabaya, Ollachea, across San Gaban river from town, 23 August 1980, *J.D. Boeke* 3171 (MO; 3.18). Carabaya, 3 km South of Ollachea, roadside puna, 13 August 1980, *J.D. Boeke* 2997 (US; 3.14). Sandia, San Juan del Oro, 1300 m, 06 August 1965, *C. Vargas C.* 16401 (US; 3.4). Sandia, entre Sandia y Cuyocuyo, 3200–3300 m, 16 May 1966, *R. Ferreyra* 16740 (MO; 3.7). San Martín: Near to Moyobamba, 890 m, 22 June 1947, *F. Woytkowski* 35300 (MO; 3.4). Tumbes: Zarumilla, El Caucho, 300–400 m, September 1960, *Maekava s.n.* (MO; 3.9.3).

4. *Chuquiraga* Jussieu (1789: 178)

Type:—*Chuquiraga jussieui* J.F. Gmel.

Shrubs or dwarf cushion-forming shrubs, up to 2 m tall. *Stems* erect, much-branched, without lenticels, cylindrical, rarely scales imbricate at base, glabrous, tomentose, strigose, villous, sericeous, unarmed or with axillary spines in pairs or fascicles, straight, convergent or divergent, glabrous, villous or pubescent at base and becoming glabrous towards the apex. *Leaves* alternate or opposite, sessile or subsessile, persistent or deciduous, blade acicular, linear, or ovate, coriaceous, pale or commonly lustrous, glabrous to densely sericeous on both surfaces, base acute or obtuse, margin flat or involute, glabrous or ciliate, apex mucronate or spiny; venation hyphodromous or actinodromous with 3

basal supra-basal nerves. *Capitulescence* terminal, monocephalous. *Capitula* 5–100-flowered, homogamous, discoid, sessile, involucre cylindrical, turbinate or campanulate, 4–14-seriate, phyllaries scarious or commonly coriaceous, green, brownish, yellow to orange, erect or reflexed, glabrous to densely sericeous, triangular-ovate to lanceolate, apex mucronate or spiny, margin flat or reflexed, glabrous or ciliate. *Receptacle* flat, pilose. *Flowers* isomorphic, bisexual, tubular (5+0), 5-lobed often unequal and deep incisions between lobes, yellow, orange, villous. *Anthers* 5, apical appendage lanceolate, obtuse or acute, basal appendage rounded or acute, caudate, calcarate or ecalcarate, inserted at the base of the corolla, filaments free, glabrous. *Style* cylindrical, yellow to orange. *Cypselae* turbinate, densely villous. *Pappus* plumose, shorter than or equal to corolla length, bristles whitish. *Pollen* without intercolpar depressions, microechinate (Suessy & Urtubey 2007). *Chromosome number* = 24–27 (Diers 1961, Wulff 1990).

Fig. 5; 10b.

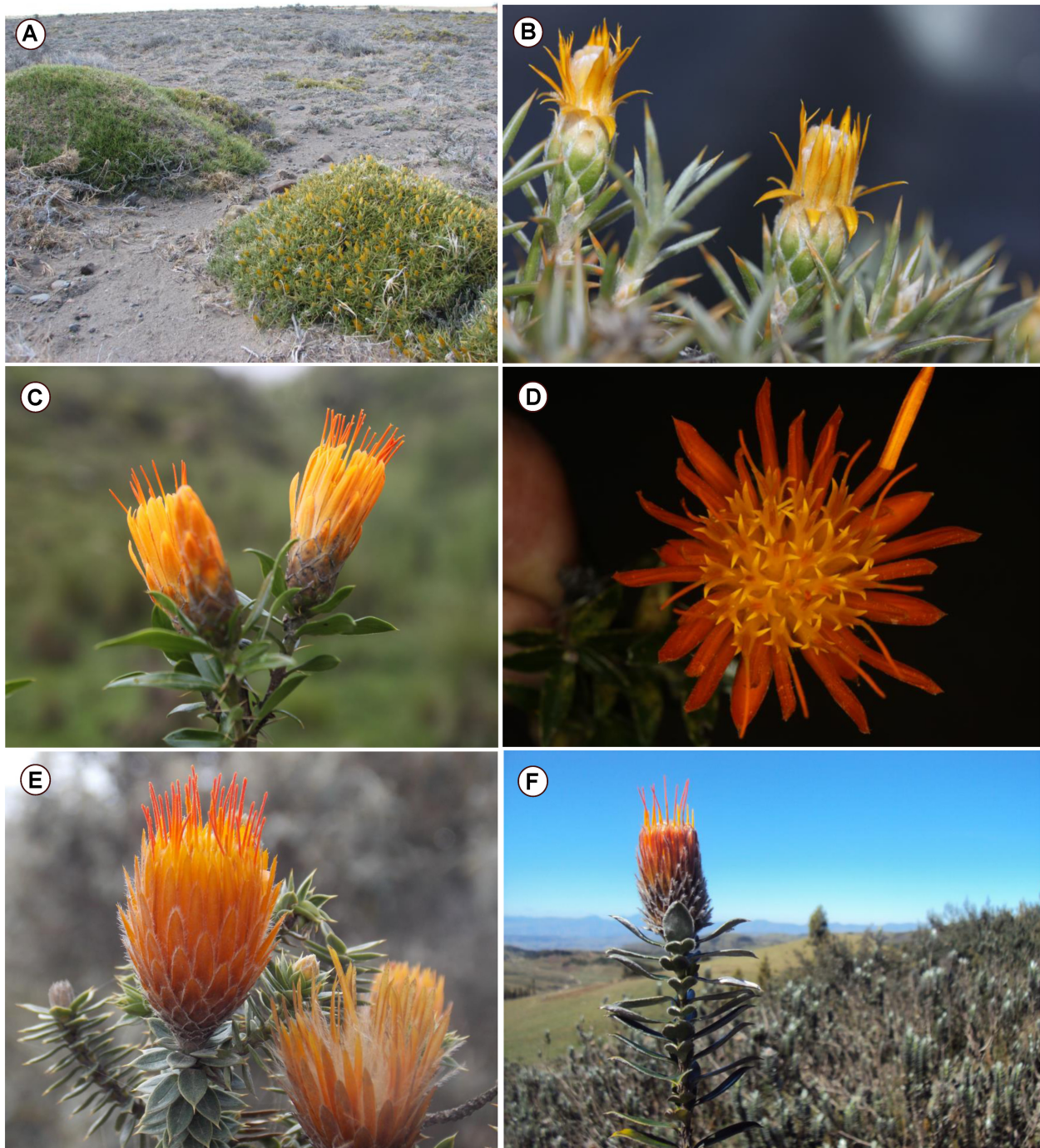


FIGURE 5. *Chuquiraga*. **A–B:** *Chuquiraga aurea*. **A:** “Cushion” Habit. **B:** Capitulum. **C–D:** *Chuquiraga longiflora*. **D:** Capitulum. **D:** Tubular corolla. **E:** *Chuquiraga jussieui*. Capitulum. **F:** *Chuquiraga weberbaueri*. Shrub Habit. Photos by Darwinion Institute (A–D), Paola Ferreira (E), Gari Ccana-Ccpatinta (F).

Distribution and habitat:—*Chuquiraga* is the second largest genus of Barnadesioideae, comprising 22 species (Ezcurra 1985, Harling 1991, Sagástegui & Sánchez 1991, Granda 1997). The species are found in the Andes and Patagonia, from Colombia to Argentina, in the Páramos (alpine meadows), in the Puna (Highlands and steppe), and open woodlands. Some species can be found at 4,200 m. a.s.l, but there are also records in lowland Puna near sea level.

Notes:—Species of *Chuquiraga* contain several medicinal properties commonly used into the phytopharmaceutical industry and commercialized by European countries. In addition, *Chuquiraga* is largely commercialized in some medicinal marketplaces in Peru and Ecuador and it is indicated for the treatment of several conditions (Ccana-Ccapatinta *et al.* 2018).

The species of *Chuquiraga* are classified into two sections (following Ezcurra 1985): *Chuquiraga* sect. *Acanthophylla*, comprising nine species distributed from northwest Bolivia to Chile and Argentina (Fig. 5a, b) and characterized by leaves with the margin involute, naviculate or cymbiform (Fig. 5b), abaxial surface without the prominent midvein, and absence of axillary spines; and *Chuquiraga* sect. *Chuquiraga*, the most species-rich in the genus, comprising 13 species distributed from Colombia to Argentina (Fig. 5 c–e) and characterized by flat leaves, the abaxial surface with prominent midvein and by the presence of axillary spines, rarely reduced or absent. Within the *Chuquiraga* section *Chuquiraga*, two series are recognized: *Chuquiraga* and *Parviflorae*, distinguished by the length of capitula (>3cm vs. 0–3cm), corolla (>17mm vs. <16mm) and anthers (15–20mm vs. 8–12mm), and by the geographical distribution (from Colombia to northwest Argentina vs. western Bolivia to Argentinean Patagonia).

The great morphological variation in habit, leaf shape, venation, trichomes, spines, involucre shape, size, bract colors, and others, makes *Chuquiraga* the most taxonomically complex group of Barnadesioideae. After analyzing hundreds of specimens and other material from this genus, we decided to follow the corolla classification *sensu* Ezcurra (1985), and do not use the classification *sensu* Suessy & Urtubey (2006). Although the study by Suessy & Urtubey (2006) represents a significant step towards understanding corolla evolution in Barnadesioideae, in *Chuquiraga* it is difficult to apply a corolla classification, since this genus has different lengths of corolla incisions splitting the lobes. Therefore, we prefer to classify the corolla as tubular with different incision lengths (see Sagástegui & Sánchez 1991, Figure 1.I; for the corolla line drawing).

The most comprehensive phylogeny at species-level for *Chuquiraga* was performed based on molecular data by Padin *et al.* (2015b). The results were incongruent regarding the monophyly of the genus in relation to the position of *Doniophyton* or *Dusenilla*. Within the genus, the sections were found to be monophyletic, but the results do not corroborate the series of *Chuquiraga* sect. *Chuquiraga*, a finding that was also corroborated by phylogenomic studies (Ferreira *et al.* in prep.). Further taxonomical and morphological studies are therefore needed in order to propose a new classification and species circumscription.

Iconography:—Ezcurra (1985), Harling (1991), Sagástegui & Sánchez (1991), Ferreyra (1995), Granda (1997).

Accepted species:—*Chuquiraga* section *Acanthophylla* C. Ezcurra: **4.1** *Chuquiraga acanthophylla* Wedd.; **4.2** *Chuquiraga atacamensis* Kuntze; **4.3** *Chuquiraga aurea* Skotts.; **4.4** *Chuquiraga echegarayi* Hieron.; **4.5.1** *Chuquiraga erinacea* subsp. *erinacea* D. Don; **4.5.2** *Chuquiraga erinacea* subsp. *hystrix* (D. Don) C. Ezcurra; **4.6** *Chuquiraga kuschelii* Acevedo; **4.7** *Chuquiraga rosulata* Gaspar; **4.8** *Chuquiraga ruscifolia* D. Don; **4.9.1** *Chuquiraga ulicina* subsp. *acicularis* (D. Don) C. Ezcurra.; **4.9.2** *Chuquiraga ulicina* subsp. *ulicina* Hook. *Chuquiraga* section *Chuquiraga* series *Chuquiraga*: **4.10** *Chuquiraga arcuata* Harling; **4.11** *Chuquiraga calchaquina* Cabrera; **4.12** *Chuquiraga jussieui* J.F. Gmel.; **4.13** *Chuquiraga longiflora* (Griseb.) Hieron; **4.14** *Chuquiraga oblongifolia* Sagást. & Sánchez Veja; **4.15** *Chuquiraga raimondiana* A. Granda; **4.16.1** *Chuquiraga spinosa* subsp. *australis* C. Ezcurra; **4.16.2** *Chuquiraga spinosa* subsp. *huamanpinta* C. Ezcurra; **4.16.3** *Chuquiraga spinosa* subsp. *rotundifolia* (Wedd.) C. Ezcurra; **4.16.4** *Chuquiraga spinosa* subsp. *spinosa* D. Don; **4.17** *Chuquiraga weberbaueri* Tovar. *Chuquiraga* sect. *Chuquiraga* series *Parviflorae* C. Ezcurra: **4.18** *Chuquiraga avellanadae* Lorentz; **4.19** *Chuquiraga morenonis* (Kuntze) C. Ezcurra; **4.20** *Chuquiraga oppositifolia* D. Don; **4.21** *Chuquiraga parviflora* (Griseb.) Hieron; **4.22** *Chuquiraga straminea* Sandwith.

Selected specimens examined:—ARGENTINA. Catamarca: Andalgalá, Las Niñas, 05 March 1916, *P. Jörgensen* 1671 (US; 4.5.1). Andalgalá, Rio Potrero sup., Cuenca Pelada, 2750 m, 27 February 1951, *H. Sleumer* 1959 (B; 4.13). Chubut: 25 kms N of Comodoro Rivadavia on rte 3 (ca. 5 kms S of Estancia Begonia), 220 m, 16 February 1993, *T.F. Stuessy* 12928 (MO; 4.3). Florentino Ameghino, Ruta 3, Sarmiento, *A.L. Cabrera* 33267 (SI; 3.5.2). Río Senguerr, Rio Mayo, 17 December 1981, *A.L. Cabrera* 33187 (SI; 4.19). Sarmiento, Ruta 26, 50 km al E de Sarmiento, 17 December 1981, *A.L. Cabrera* 33245 (SI; 4.19). Sierra de San Bernardo, 15 December 1981, *A.L. Cabrera* 33225 (SI; 4.3). 25 kms N of Comodoro Rivadavia on rte 3, ocean can be seen in the distance, 200 m, 16 February 1993, *T.F. Stuessy* 12929 (WU; 4.18). 96 kms E of Sarmiento on rte 26 to Comodoro Rivadavia (ca. 56 kms W of Comodoro Rivadavia),

600 m, 17 February 1993, *T.F. Stuessy 12940* (WU; 4.19). Jujuy: Abra de Pipes, 11 November 1973, *A.L. Cabrera 24037* (SI; 4.16.1). Rinconada, desde la Ciénaga a Lipan, 2800 m, 23°41'8.74"S, 65°33'058"W, 08 January 2001, *P.M. Simon 512* (MO; 4.5.1). Santa Catalina, Ruta provincial 5, 20 km de la Quiaca camino a Santa Catalina, Cuesta de Toquero, 3660 m, 22°07'S, 65°45'W, 16 February 1998, *O. Morrone 2671* (MO; 4.1). Tumbaya, along rte 40 to El Moreno ca. 7 km S of its intersection with rte 16, 3310 m, 23°42'01"S, 65°50'22"W, 15 March 1994, *C.M. Taylor 11189* (MO; 4.2). Tumbaya, Ruta Nac. 9.4 km de Volcán camino a S.S. de Jujuy, cantera sobre el Río Grande, 2040 m, 23°56'S, 65°27'W, 10 December 1998, *O. Morrone 3173* (MO; 4.21). Valle Grande, entre três morros y Cerro Hermoso, Serranía Callileagua, 2700 m, 23°37'15.02"S, 64°54'35.78"W, 18 April 2016, *C.M. Martín 736* (SPFR; 4.13). Yavi, La Quiaca, 2km antes de llegar al aeropuerto, 3400 m, 28 January 1999, *A. Chapin 25951* (MO; 4.1). Yavi, cerca de La Quiaca, 20 January 1942, *A.L. Cabrera 7780* (K; 4.1). La Pampa: Monte em Laguna Amarga, 17 February 1948, *A. Burkart 15951* (SI; 4.5.1). Zwischen Santa Isabel und 25 de Llago, 19 November 1965, *H. Walter 456* (B; 4.7). La Rioja: Chilecito, camino a mina el Oro (cerca de Chilecito), 2000 m, 29°05'7.81"S, 67°41'8.76"W, 23 January 2001, *P.M. Simon 720* (MO; 4.21). General Lamadrid, Ruta providencial 76 de Punta de Agua a Laguna Brava, 3300 m, 28°30'23"S, 68°47'51"W, 24 January 2012, *F.O. Zuloaga 13753* (MO; 4.5.2). Río Amarillo, sierra de Famatina, 3900 m, 15 January 1947, *J.H. Hunziker 1959* (MO; 4.8). Mendoza: Along route #143, ca 150 kms generally NW of San Rafael, 2700 ft. (c. 822m), 15 January 1985, *R.M. King 9436* (MO; 4.5.1). Caracoles de Villavicencio, cerca del empalme a la Quebrada del Toro, 2700 m, 11 May 1980, *O. Bottino 85* (WU; 4.8). High desert near Uspallata, route to Mina Monya (talca) 18 km E of Uspallata, 2800 m, 32°37'S, 69°32'W, 12 January 1996, *R.R. Brooks MS32* (MO; 4.5.2). Marlargüe, Valle de Río Salado, a 13 km de Los Molles hacia las Leñas, puente sobre el Arooyo el Deshecho, 2000 m, 12 January 1988, *B. Leunberger 3813* (B; 4.20). San Rafael, cerca de Cerro Bola, 17 January 1982, *A.L. Cabrera 33319* (SI; 4.7). Ruta 40 a 24 km S de Calmuco, 01 February 1963, *O. Boelcke 10421* (SI; 4.18). Neuquén: Añelo, Ruta Prov. 17, 6 km al E de Añelo em la meseta, 11 November 1981, *J.J. Valla 27* (MO; 4.7). Chos Malal: 27 km de Chos Malal, por ruta prov. 43, em dirección a Andacollo, em Cañadón, 1200 m, 37°15'37"S, 70°29'32"W, 27 February 1994, *H. Fortunato 4322* (US; 4.20). Pehuenches, Laguna Auquinco, January 1984, *A. Wulff 359* (SI; 4.18). Along the gravel road to route #40, ca 68 kms from route #40, 4700 ft. (c. 1432m), 12 January 1985, *R.M. King 9404* (US; 4.20). Along route #40. Ca. 26 kms from route #237, 1800 ft. (c. 548m), 09 January 1985, *R.M. King 9378* (MO; 4.22). Río Negro: Adolfo Alsina, road to San Antonio 100km west of Viedma, growing along roadside in clay sand, 30 m, 19 December 1938, *W.J. Eyerdam 23496* (MO; 4.18). 25 de Mayo, 9 km al W de Ing. Jacobacci em dirección a Bariloche, 800 m, 41°19'59"S, 69°40'09"W, 04 March 1994, *H. Fortunato 4373* (US; 4.22). General Roca, 250–360 m, Sep 1914–February 1915, *W. Fischer 11* (MO; 4.7). Manuel Choique, Winderosionsfläche in Talgrund am westlichen Ortsausgang, 800 m, 41°45'S, 70°10'W, 13 November 1984, *Hager 1008* (B; 4.3). Along the route #22m ca 36 kms W of Río Colorado, 200 ft. (c. 60.9m), 05 February 1985, *R. M. King 9336* (MO; 4.5.1). Salta: Chicoana, Quebrada de Escoipe, entre Escoipe y San Fernando, 1900–2000 m, 15 December 1987, *L. Novara 9200* (B; 4.21). San Antonio de Los Cobres, 21 October 1948, *H. Humbert 21072* (P; 4.2). San Antonio de Los Cobres, 3800 m, 13 December 1946, *A. Krapovickas 3131* (MO; 4.2). Chicoana x Cachi, Valle Encantado, 3000–3400 m, 24 June 1980, *I. Novara 1109* (B; 4.11). Valle Encantado (Mirador), 3273 m, 25°10'55.3"S, 65°51'11.9"W, 29 February 2016, *C.M. Martín 608* (SPFR; 4.13). San Juan: Calingasta, Reserva El Leoncito, subiendo el Cordón del Naranja por la Quebrada de Las Minas, 17 km al este de la Ruta Prov N. 412, paraje llamado Pampa de Los Pozos, 3325 m, 20 March 1999, *F. Biurrun 5749* (SI; 4.4). Calingasta, de confluencia a Alojjo Las minitas, 2500–3000 m, 17 February 1988, *R. Kiesling 6857* (SI; 4.4). Calingasta, Reserva El Leoncito, Rancho del Cura, 2802 m, 31°46'S, 69°13'W, 15 March 2005, *R. Kiesling 10206* (SI; 4.4). Calingasta, limite com Mendoza, Yalguaraz, 21 January 1987, *R. Kiesling 6514* (SI; 4.5.2). Calingasta, Qda. De Santa Clara, 1700 m, 32°06'49"S, 68°57'44"W, 17 February 2000, *T.S. Tombesi 79* (SI; 4.7). Iglesia, Quebrada del Agua Negra, 3000 m, 23 February 1979, *A.L. Cabrera 30131* (SI; 4.8). Zonda, camino a estancia maradona, 1300 m, 27 January 1981, *R. Kiesling 3310* (SI; 4.5.1). Zonda, Cno. a Estancia Maradona, 2100 m, 12 November 1982, *R. Kiesling 4079* (SI; 4.7). Santa Cruz: Deseado, SW Cañadon Seco, 350 m, 03 January 1991, *B. Leunberger 4095* (B; 4.3). Deseado, em la estepa, 25 November 1979, *R. Méndez 9868* (SI; 4.19). Corpen Aike, Laguna Grande a Gob Gregores, 8 km, 49°34'S, 70°14'W, 24 January 1967, *O. Boelcke 12770* (SI; 4.3). Tucumán: Tafí, Tafí del Valle, Cerro Pelado, 2250 m, 24 January 1950, *H. Sleumer 132* (B; 4.11). Tafí, subida al Infiernillo, 07 November 1978, *A.L. Cabrera 29699* (SI; 4.11). Tafí, quebrada del Río blanco, cerca del Valle Tafí, 2600 m, 26 January 1950, *H. Sleumer 105* (B; 4.13). Tafí, 3000 m, 24 April 1926, *S. Venturi 4180* (US; 4.21). BOLIVIA. Chuquisaca: Cinti, 4000 m, January 1846, *A. Weddel 3974* (P; 4.1). Oropesa, between Tipoyo y Cerro Obispo on Sucre—Quila Quila road, 2900 m, 24 January 1999, *J.R.I. Wood 14397* (SPF; 4.21). Cochabamba: Carrasco, El Churo-Sunchal, ca. de 10 km. Hacia Pojo, lado del camino carretero Comparapa-Cochabamba, 2780 m, 17°47'50.5"S, 64°47'24.3"W, *I.G. Vargas 7051* (B; 4.21). La Paz: Murillo 9.5 km al oeste de Ventilla por el camino entre Palca y Calacoto (La Paz),

4200 m, 16°32'S, 67°58'W, 15 March 1987, *J.C. Solomon 16358* (MO; 4.12). La Paz, 10,000 ft. (c. 3048m), 1889, *A.M.B. Lectae 138* (K; 4.21). Potosí: Above Quechisla (Palcahuasi), 3600 m, November 1946, *M. Cárdenas 3725* (US; 4.2). Daniel Campos, Llica, 45 km. Hacia el salar de Uyuni, 19°52'57"S, 68°13'15"W, 22 September 2006, *S.G. Beck 32409* (US; 4.2). Miraflores, 3250 m, 19°27'4"S, 65°15'W, 04 December 1986, *S. Riera 668* (B; 4.21). Sud Chicas, Mina Usca-Isca above the village of La Torre, north of Tupiza, 3875–3880 m, 02 December 1967, *B. Vuilleumier* (SI; 4.16.1). Santa Cruz: Vallegrande, entre Las Lajas y Abra Grande, 2741 m, 18°16'57"S, 64°17'59"W, 05 December 2011, *G.A. Parada 4084* (MO; 4.21). Tarija: Cercado, ladera sur, 2260 m, 15 February 2006, *F. Zenterro 3739* (US; 4.21). Tarija, de Tarija a Iscayachi, 2000–3000 m, 20 March 1982, *R. Kiesling 3847* (US; 4.13). CHILE. Antofagasta: Ascotan, 3900 m, 08 March 1992, *O. Kuntze s.n.* (US; 4.2). Guatín, San Pedro de Atacama, Provincia Loa, 3500 m, 22°43'9.20"S, 68°00'7.95"W, 05 February 2001, *M. Ackermann 50* (B; 4.2). El Loa, NE of Calama, along the road from near Chiu Chiu to Caspana, ca. 46 km from its turnoff from the Calama-Chiu Chiu road, 3500 m, 22°20'36"S, 68°15'30"W, 10 April 1994, *C.M. Taylor 11548* (MO; 4.2). Coquimbo: Elqui, Río Turbío, road from Rivadavia to Laguna Dam, ca 75 km, 2000 m, 05 November 1938, *C.R. Worth 16404* (SI; 4.9.2). Illapel, Loma Negra in the Andes between La Veja Escondida and Cuncumen, 2300 m, 27 February 1939, *J.L. Morrison 17438* (MO; 4.9.1). Rivadavia, 800 m, November 1923, *E. Werdermann 102* (MO; 4.9.1). Maule: Talca, Upper valley of Río Maule, 1500 m, 35°55'S, 70°43'W, 26 January 1990, *M.F. Gardner 4579* (E; 4.20). Metropolitana: La Parva, just 0.3 km up from village towards ski slopes, 2800 m, 16 January 1993, *T.F. Stuessy 12727* (WU; 4.20). 3.7 km W of Farellones, on rd back to Santiago, 2000 m, 16 January 1993, *T.F. Stuessy 12726* (WU; 4.20). O'Higgins: Copada, 1750–2000 m, *F.W. Pennel 12271* (US; 4.20). Tarapacá: Arica, 90 km E of the Panamericana on Ruta 11 towards Putre, just before the frontier to Prov. Parinacota, 2950–3000 m, 18°24.27'S, 69°39.22'W, 17 September 1997, *U. Eggli 2813* (B; 4.6). Arica, antes de Zapahuira, 3000 m, 22 February 1978, *H. Escobar A. X232* (SI; 4.6). Parinacota, Putre, Cordillera de Los Andes, Ch11—road to Putre at kilometer 102, 3300 m, 18°19'49"S, 69°34'41"W, 15 December 1999, *M.F. Gardner 6261* (E; 4.16.3). COLOMBIA. Nariño: Cumbal, Arriba de Cumbal, alto de Machines, 3200 m, 02 September 1962, *L.E. Mora 2346* (COL; 4.12). Quindío: Génova, vereda Pedregales, predio Valle Lindo, 3500 m, March 2004, *E. Méndez 3042* (COL; 4.12). Tolima: Cajamarca, Valle del río Anaime, Páramo de los Valles, 3550–3800 m, 11 February 1991, *J.I. Barrera 07* (COL; 4.12). Valle del Cauca: Cordillera Central, Cerro de Pan de Azúcar, páramo, 3700 m, 26 February 1969, *J. Cuatrecasas 27561* (COL; 4.12). ECUADOR. Azuay: Road Cuenca–Loja road, km 31 from Cuenca outskirts, 3150 m, 03°08'S, 79°02'W, 30 November 1996, *G.P. Lewis 2869* (US; 4.12). Bolívar: Cordillera Occidental, high country at headwaters of Río Gradass, 15 km s. of Chimborazo Volcano, 4000 m, 01°35'S, 78°51'W, 10 January 1945, *F.R. Fosberg 22484* (US; 4.12). Cañar: between Biblián and Cañar, 3250 m, 21 September 1955, *E. Asplund 17679* (S; 410). Vicinity of Cañar, near paramo, 15 September 1918, *J.N. Rose 1918* (US; 4.12). Carchi: Mira Cantón, 30 km al oeste de San Isidro, 3000 m, 00°35'S, 78°05'W, 22 July 1990, *E. Gudiño 420* (MO; 4.12). Chimborazo: ca 7 kms up road toward Chimborazo (Mt.) from main road N of Riobamba (ca. 20 kms NW of Riobamba), 3700 m, *T.F. Stuessy 12432* (WU; 4.12). Cotopaxi: 25 km W of Pujilí on road to Quevedo, 3850 m, 20 August 1991, *T.F. Stuessy 12411* (WU; 4.12). Imbabura: side of Cayambo mountain, 13,500 ft. (c. 4,115m), 12 June 1961, *P.C.D. Cazalet 5700* (B; 4.12). Loja: Road to Jimbura to Zumba, páramo de Cordillera de Las Lagunitas km 19, 3380 m, 04°43'34"S, 79°26'00"W, 06 November 2000, *P.M. Jørgensen 2251* (WU; 4.12). Napo: Rd from Quito to Baeza, just at the pass., 3000 m, 22 February 1992, *V. Funk 11026* (US; 4.12). Pichincha: Cerro Pichincha, up from Quito, on road to microondas towers above city, 3700 m, *T.F. Stuessy 12417* (WU; 4.12). Tungurahua: Near Calamaca, app. 20 km W of Ambato along old road Amabato–Guaranda, 3400–3900 m, 01°16'S, 78°48'W, 22 June 1985, *S. Laegaard 54562* (MO; 4.12). PERU. Amazonas: along road Jumbilla—Molinopampa until ca 1 ½ hours by car from Jumbilla, 2500–3000 m, 06°04'44" S, 77°39'47" W, 07 November 2012, *H. van der Werff 25304* (MO; 4.17). Ancash: collected near road Km. 25 towards Carpa, 4260 m, 24 August 1977, *K.A. de Mayolo 332* (US; 4.16.2). Arequipa: Arequipa, South slopes of Nevado Chachani, on the road to Sumbay, ca 10 km north of Arequipa, 3500 m, 30 November 1964, *P.C. Hutchison 7234* (K; 4.16.3). Ayacucho: amostra comercial comprada no mercado "Central de Huamanga", January 2015, *G. Ccapatinta 24* (SPFR; 4.16.2). Huanta, north of Huanta, near Huaillay, 4900–4000 m, 13–14 March 1926, *A. Weberbauer 7593* (US; 4.16.4). Cajamarca: Celendín, Jalca de Jumulca (Ruta a Celendín), 3800 m, 19 August 1984, *A. Sagástegui A. 12268* (MO; 4.17). San Miguel, sobre el desvío a Tongod, em el lugar llamado Toropampa, Antes de Quilcata, 3300 m, 13 September 1991, *I. Sánchez Veja 5761* (MO; 4.14). San Miguel, sobre el desvío a Tongod, a 10 km de la Carretera Cajamarca–Hualgayoc, 3300 m, 06 November 1991, *I. Sánchez Vega 6076* (MO; 4.14). San Miguel, 76 kms NNW of Cajamarca on road toward Hualgayoc, detour to Tongod, 3320 m, 15 July 1992, *T.F. Stuessy 12625* (WU; 4.14). Cuzco: Combepala, 26 January 1969, *Soukup 6342/6132* (US; 4.16.2). Junín: entre Carhuamayo y Junín, 4100–4200 m, 09 January 1949, *R. Ferreyra 5237* (K; 4.16.2). Tarma, Tarma, Carretera La Oroya, 28 January 2015, *G. Ccapatinta 51* (SPFR; 4.16.2). Huancayo, amostra comercial comprada no mercado "Modelo", January 2015, *G. Ccapatinta 22*

(SPFR; 4.16.3). Huancayo, road from Huancayo to Huancavelica, 3543 m, 12°23'38" S, 74°54'15" W, 16 September 2001, *M. Weigend* 5807 (B; 4.16.4).

Huancavelica: Ccaullapa, a 5 km. O. de Comaica, 4100–4150 m, 18 March 1951, *O. Tovar* 230 (US; 4.16.2). Huancavelica, Amostra comercial comparada no mercado de “Abastos”, January 2015, *G. Ccapatinta* 32 (SPFR; 4.16.4). Tayacaja, quebrada, 3 km north of Salcabamba Village, 3500 m, 09 January 1939, *H.E. Stork* 10329 (K; 4.17). Huánuco: Ambo, Tomayquichua, camino de Estanco, aos arredores de lagoa, 27 January 2016, *G. Ccapatinta* 48 (SPFR; 4.15). Huanuco, amostra comercial comprada no mercado “Modelo”, January 2015, *G. Ccapatinta* 17 (SPFR; 4.16.2). Quina, October 1927, *M. Sawada* P84 (US; 4.16.4). Huaraz: Recuay, Cátaç, a caminho de Pastoruri, 4206 m, 09°53'02.3" S, 77°17'36.1" W, 25 January 2015, *G. Ccapatinta* 46 (SPFR; 4.16.2). La Libertad: Sanchez Carrión, señal Huaylliyas, NW-facing, 4200 m, 07°53'S, 78°02'W, 21 August 1982, *D.N. Smith* 2269 (MO; 4.17). Uuncha, fila de Andosa, 3802 m, 07°06'52" S, 77°49'30" W, 12 November 2013, *C.V. Ocaña* 45 (MO; 4.17). Lima: Lima, amostra comercial comprada no mercado “La Parada”, January 2015, *G. Ccapatinta* 15 (SPFR; 4.16.2). Pasco: Cerro de Pasco, amostra comercial comprada no mercado “Central”, *G. Ccapatinta* 26 (SPFR; 4.16.2). Piura: Huacabamba, trilha para as lagoas de Las Huarinas, January 2015, *G. Ccapatinta* 10 (SPFR; 4.12). Puno: Azángaro, Watasani, 4100 m, 04 April 1959, *C. Vargas* 812539 (US; 4.12).

5. *Dasyphyllum* Kunth (1820: 17)

Type:—*Dasyphyllum argenteum* Kunth

Shrubs, trees or woody vines, up to 15 m tall, commonly mutistemmed. *Stems* erect, decumbent or scandent, much-branched, lenticelate, cylindrical, with or without scales imbricate at base, glabrous, villous, sericeous, tomentose or velutinous, unarmed or with axillary spines in pairs or fascicles, straight or curved, convergent or divergent, glabrous or sparse pubescent at base and becoming glabrous towards the apex. *Leaves* alternate, spiral, rarely in fascicles, subsessile or petiolate, persistent or deciduous, blade narrow elliptical, obovate or orbiculate, chartaceous or coriaceous, pale or lustrous, glabrous or pubescent, villous, tomentose, lanose in both surfaces, base acute or obtuse, margin flat or revolute, glabrous or ciliate, apex unarmed, mucronate or spiny; venation actinodromous with 3 or more basal or suprabaasal main nerves. *Capitulescence* terminal or axillary, monocephalous, racemose, paniculiform, corymbiform or umbelliform. *Capitula* 5–60-flowered, homogamous, discoid, sessile to pedunculate, involucre cylindrical to campanulate, 6–14-seriate, phyllaries scarious or commonly coriaceous, green, yellow-golden, brown or black, erect or reflexed, glabrous or densely villous, ovate—triangulate grading to lanceolate, apex unarmed, mucronate or spiny, margin flat, ciliate. *Receptacle* flat, pilose. *Flowers* isomorphic, bisexual or pistilate by the gynoecium atrophy, corolla tubular (5+0), ligulate (5+0), subbilabiate (4+1), or bilabiate (3+2), 5-lobed, white to cream, externally glabrous or sericeous, internally sericeous. *Anthers* 5, apical appendage bilobed, basal appendage lanceolate, acute to rounded, caudate or ecaudate, calcarate, inserted at the base or between the base and the throat, filaments free, glabrous. *Style* cylindrical, cream to yellow. *Cypsela* cylindrical or fusiform, densely villous or rarely glabrous. *Pappus* plumose, shorter than or equal to corolla length, bristles whitish. *Pollen* with or rarely lacking intercolpal depressions, sparsely microechinate (Suessy & Urtubey 2007). *Chromosome number* = 27 (Watanabe *et al.* 2007).

Fig. 6; 10a.

Distribution and habitat:—*Dasyphyllum* is the largest genus of Barnadesioideae, comprising 27 species. The last revision of the genus was by Saavedra (2011), who recognized 33 species—two of them were later transferred to *Archidasyphyllum* (Ferreira *et al.* 2019, see above), plus four probably new species remain undescribed (not counted here). Species of the genus are distributed throughout South America in two main centers of diversity: the first, in the Andes, from Venezuela to northern-western Argentina, occurring in environments such as the Puna (highlands and steppe, till 3,700 m high) or in dry to tropical to subtropical mixed (deciduous-evergreen) montane forests; and the second, in Brazil, Bolivia, and Paraguay, in savannas, such as the Brazilian Cerrado, in dry to tropical to subtropical mixed (deciduous-evergreen) forests, such as the Atlantic Forest, in the Caatinga (Brazilian thorn forest and shrubs), in the Chaco (dry forests and open woodland), in the Brazilian Campos Rupestres (open vegetation in rocky outcrops), in gallery forests (Cabrera 1959, Sagástegui 1980, Sagástegui & Dillon 1985, Saavedra *et al.* 2014, Ferreira *et al.* 2019, Saavedra 2020)

Notes:—*Dasyphyllum* can be distinguished from the other genera by the following characters: arching shrubs, trees, or woody vines, discoid capitula, cream to white corolla, bisexual or pistilate by the gynoecium atrophy and bilobed apical appendage.

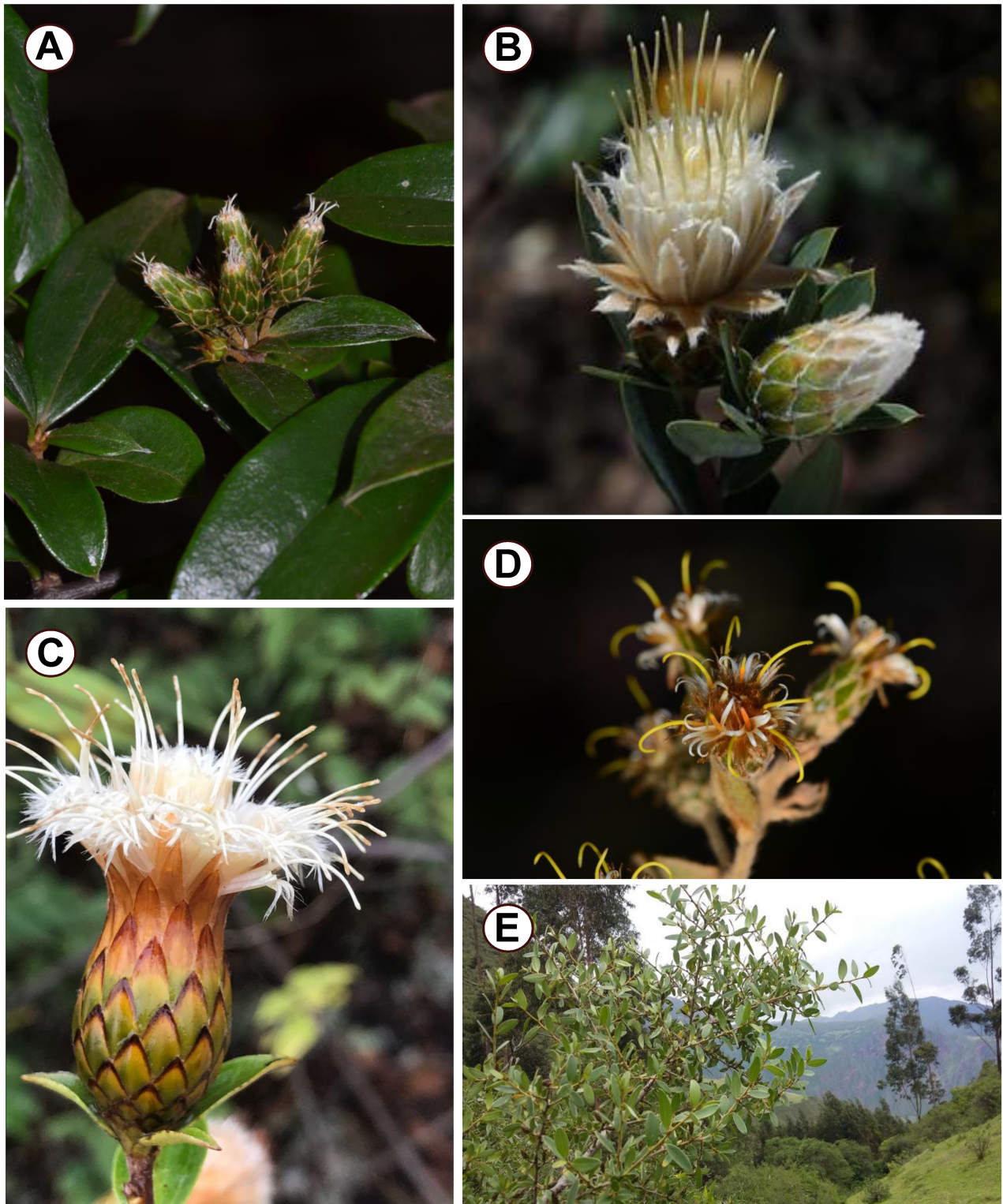


FIGURE 6. *Dasyphyllum*. **A:** *Dasyphyllum lanceolatum*. Capitulescence. **B:** *Dasyphyllum reticulatum*. Capitulum. **C:** *Dasyphyllum sprengelianum*. Capitulum. **D:** *Dasyphyllum vagans*. Capitulescence. **E:** *Dasyphyllum leiocephalum*. Habit. Photos by Carolina Ferreira (A and D), Mauricio Mercadante (B), Paola Ferreira (C), and Gari Ccana-Ccapatinta (E).

The circumscription of *Dasyphyllum* presented here correspond to the species of *Dasyphyllum* subgenus *Dasyphyllum* (*Dasyphyllum* “*sensu stricto*”) since the other subgenus—*Dasyphyllum* subgenus *Archidasyphyllum*—was erected to the generic rank after Ferreira *et al.* (2019). Differences between these two groups are discussed above under *Archidasyphyllum*.

Cabrera (1959) recognized two sections in his *Dasyphyllum* subgenus *Dasyphyllum* (*Dasyphyllum* “*senso stricto*”): sections *Microcephala* (23 species) and *Macrocephala* (11 species). Saavedra *et al.* (2018) recognized only six species in section *Macrocephala*. The two sections are distinguished by their involucre size and capitula arrangement, with section *Macrocephala* having involucre longer than 20 mm in length and arranged in a solitary or small group of heads and section *Microcephala* having heads arranged in synflorescence (corymbiform cymes) smaller than 18 mm in length. Ferreira *et al.* (2019) investigated the phylogenetic relationships of *Dasyphyllum* based on molecular data. In this study, both sections were rejected and further studies are necessary to propose a new infrageneric classification.

Iconography:—Cabrera (1959), Harling (1991), Ferreyra (1995), Saavedra *et al.* (2014, 2018).

Accepted species (Saavedra 2011):—**5.1** *Dasyphyllum argenteum* Kunth; **5.2** *Dasyphyllum armatum* (J.Kost.) Cabrera; **5.3** *Dasyphyllum brasiliense* (Spreng.) Cabrera; **5.4** *Dasyphyllum brevispinum* Sagást. & Dillon; **5.5** *Dasyphyllum colombianum* (Cuatr.) Cabrera; **5.6** *Dasyphyllum cryptocephalum* (Baker) Cabrera; **5.7** *Dasyphyllum diamantinense* Saavedra & M.Monge; **5.8** *Dasyphyllum donianum* (Gardner) Cabrera; **5.9** *Dasyphyllum ferox* (Wedd.) Cabrera; **5.10** *Dasyphyllum flagellare* (Casar.) Cabrera; **5.11** *Dasyphyllum floribundum* (Gardner) Cabrera; **5.12** *Dasyphyllum fodinarum* (Gardner) Cabrera; **5.13** *Dasyphyllum hystrix* (Wedd.) Cabrera; **5.14** *Dasyphyllum inerme* (Rusby) Cabrera; **5.15** *Dasyphyllum lanceolatum* (Less.) Cabrera; **5.16** *Dasyphyllum leiocephalum* (Wedd.) Cabrera; **5.17** *Dasyphyllum leptacanthum* (Gardner) Cabrera; **5.18** *Dasyphyllum maria-lianae* Zardini & Soria; **5.19** *Dasyphyllum popayanense* (Hieron.) Cabrera; **5.20** *Dasyphyllum reticulatum* (DC.) Cabrera; **5.21** *Dasyphyllum retinens* (S.Moore) Cabrera; **5.22** *Dasyphyllum spinescens* (Less.) Cabrera; **5.23** *Dasyphyllum sprengelianum* (Gardner) Cabrera; **5.24** *Dasyphyllum trichophyllum* (Baker) Cabrera; **5.25** *Dasyphyllum vagans* (Gardner) Cabrera; **5.26** *Dasyphyllum varians* (Gardner) Cabrera; **5.27** *Dasyphyllum vepreculatum* (D.Don) Cabrera.

Selected specimens examined:—ARGENTINA. Misiones: Cainguás, ruta 14, 5 km E de Aristóbulo del Valle, 29 July 1987, R. Vanni 836 (K; 5.3). BRASIL. Bahia: Caraíbas, próximo à cancela, 13°05'S, 41°22'W, 15 August 2005, E.C. Oliveira III (HUEFS; 5.23). Coribe, estrada vicinal partindo da estrada São Félix do Coribe-Coribe, ca. 28km de São Félix do Coribe, cerca de 4km após o distrito de Colônia do Formoso, entrar a direita por 2km até as margens do Rio Formoso, 448 m, 13°34'53"S, 44°19'36"W, 20 July 2009, M.M. Saavedra 997 (RB; 5.11). Entre Rios, Fazenda do Rio do Negro, área antropizada, próximo a plantio de eucalipto, 143 m, 12°01'04"S, 38°02'56"W, 04 September 2009, M.M. Saavedra 934 (RB; 5.15). Érico Cardoso, localidade da porteira, estrada para Capão, ca. 15 km de Érico Cardoso, 851 m, 13°18'5"S, 42°08'31"W, 23 July 2009, M.M. Saavedra 1000 (RB, SPFR; 5.3). Jacaraci, 18 September 2010, J.G. Carvalho-Sobrinho 2864 (RB; 5.8). Mucugê, Capão do Correia, estrada vicinal saindo de Caraíba a 17.5 Km da BA-142, base de campo rupestre com solo pedregoso, 1221 m, 13°6'38"S, 41°22'39"W, 11 July 2009, M.M. Saavedra 968 (RB; 5.7). Palmeiras, Morro do Pai Inácio, ao redor da trilha iniciada para a torre de transmissão, 1103 m, 12°27'21.6"S, 41°28'23"W, 17 May 2013, P.L. Ferreira 09 (SPFR; 5.7). Piatã, Fazenda Dragão Verde, 1318 m, 13°05'45"S, 41°51'12"W, 07 July 2017, N. Roque 5012 (ALCB; 5.23). Rio dos Pires, beira do riacho da Forquilha, 1500 m, 13°54'S, 42°29'W, 24 July 1993, W. Ganey 1945 (HUEFS, K; 5.7). São Desidério, assentamento Thainá, ca. 40 km da BA-467, 732 m, 12°35'46"S, 44°50'28"W, 16 July 2009, M.M. Saavedra 993 (RB, SPFR; 5.8). Ceará: Crato, estrada para casa do guarda, Belmonte, 1010 m, 07°16'27"S, 39°27'03"W, 26 October 2010, M. Mata 2241 (HUEFS; 5.23). Crato, Estrada Crato-Exu, Carrasco, 964 m, 07.1457 S, 39.2940 W, 13 October 2011, M.I.B. Loiola 1372 (EAC; 5.23). Distrito Federal: Áreas da FERCAL, A 6,7 km da fábrica de cimento da CIPLAN, na DF-250 Leste, 850 m, 26 July 1990, L.B. Bianchetti 891 (HUFU; 5.25). Brasília, Bacia do Rio São Bartolomeu, 06 May 1981, E.P. Heringer 6908 (RB; 5.15). Recanto das EMAS, Núcleo Rural Monjolo, 11 August 2009, A.E. Ramos 1903 (RB; 5.8). Brasília, condomínio Mini Chácaras, próximo à barragem do Paranoá, 1100 m, 15°48'20"S, 41°47'32"W, 05 October 2001, G. Pereira da Silva 5507 (CEN; 5.23). Brasília, Brasilândia, Fazenda do Sr. Pereira, 1200 m, 15°36'19"S, 48°06'02"W, 08 October 2015, B.T.P.M. Goes 87 (IBGE; 5.23). Brasília, bacia do Rio São Bartolomeu, 05 August 1981, E.P. Heringer 7323 (MO; 5.3). Espírito Santo: Afonso Cláudio, três pontões, 1018 m, 20°31'28"S, 41°07'14"W, 09 September 2007, M.M. Saavedra 520 (RB, SPFR; 5.3). Castelo, Distrito de Forno Grande, localidade Rio Manso, 1480 m, 20°31'28"S, 41°07'14"W, 20 September 2008, M.M. Saavedra 825 (RB; 5.22). Castelo, Forno Grande, localidade Balança, 1250–1600 m, 20°31'37"S, 41°06'06"W, 18 July 2008, M.M. Saavedra 796 (RB; 5.10). Várzea Alegre, mata do Fausto, próximo ao colégio, 27 September 2000, V. Demuner 1305 (RB; 5.15). Goiás: Caiaponia, Rio Borá, 24 July 1977, G. Hatschbach 40069 (MO; 5.3). Corumbaíba, margem esquerda do rio Corumba, 300 m montante da alternativa 4, 24 April 1993, S.P. Cordovil 289 (UEC; 5.25). Doverlândia, Conglomerado, GO-561, subunidade 2, subparcela 1, individuo 11, 12 June 2018, G. Allegretti IFN 522 (CEN; 5.23). Niquelândia, Macedo, ca 18 km de Niquelândia, 24 August 1994, T.S. Filgueiras (RB; 5.8). Piranhas, Serra do São João, estrada para a cachoeira São Domingos a partir da zona urbana de Piranhas, 35.6 km da zona urbana, 748 m, 16°35'44.5"S, 51°55'57.7"W, 06 November 2012, B. Loeuille 770 (SPF; 5.23). Pirenópolis, Parque Estadual dos Pirineus, 15 km da base da Serra.

Cerrado com campo rupestre, afloramentos de quartzito, 1273 m, 15°48'8"S, 48°51'11"W, 19 July 2007, *M.M. Saavedra 425* (RB; 5.8). Mato Grosso: Chapada dos Guimarães: road to radarstation, 11 July 1994, *B. Dubs 1502* (K; 5.21). Nobres, cerca de 30 km NE, em linha reta, BR-242, ca. 2 km do entroncamento com a linha BR 364/163, crista da serra do Caixa Furada, 14°42' S, 56°11'W, 19 May 1997, *V.C. Souza 16463* (ESA; 5.23). Mato Grosso do Sul: Três Lagoas, Km 85 da estrada para o alto Sucuriu, Fazenda Barreirinho, 24 July 1983, *F. Barros 858* (UEC; 5.25). Minas Gerais: Alto do Caparaó, Parque Nacional campo de altitude ao lado da trilha, 2200 m, *L.S. Leoni 3970* (RB; 5.10). Araporã, Reserva vegetal da usina Alvorada, 07 June 2001, *A.A. Arantes s.n.* (RB; 5.25). Baependi, Toca dos Urubus, face sudeste da serra de Sta. Maria, 08 October 2006, *F.M. Ferreira 1167* (RB; 5.15). Botumirim, no barranco à beira da estrada de retorno da Serra do Botumirim, próximo a cidade, 1021 m, 16°51'59"S, 43°00'52"W, 10 July 2007, *M.M. Saavedra 578* (RB, SPFR; 5.24). Botumirim, trilha para o Cruzeiro, na entrada da cidade, pelo acesso a partir de Cristália, 16°51'26"S, 43°00'46"W, 07 July 2001, *P. Fiaschi 851* (SPFR; 5.24). Brazilândia de Minas-MG, 17°04'24"S, 45°54'16"W, 11 July 2000, *J.A. Lombardi 3963* (SPF; 5.3). Cata altas, RPPN Santuário do Caraça, trilha para o tanque grande, 1166 m, 20°06'10"S, 43°29'38"W, 26 April 2010, *L.L. Giacomini 1139* (RB; 5.12). Cristália, Morro da Antena de Televisão, 1200 m, 16°43'28"S, 42°55'42"W, *V.C. Souza 25816* (ESA; 5.24). Diamantina, Estrada Diamantina-Datas, próximo ao km 602 da estrada, 1367 m, 18°18'26"S, 43°41'04"W, 26 May 2009, *M.M. Saavedra 888* (RB; 5.20). Felício dos Santos, APA Felício dos Santos, Interior de Mata semidecídua, 27 August 2008, *N.F.O. Mota 1414* (RB; 5.12). Jaboticatubas, PARNA Serra do Cipó, cachoeira da farofa, portaria do retiro, coletas realizadas ao longo da encosta após a bifurcação para a cachoeira da farofa até o riacho, 883 m, 19°20'56"S, 43°34'38"W, 16 October 2013, *M. Verdi 6717* (SPFR; 5.20). Lima Duarte, Distrito de Conceição do Ibitipoca, Serra do Ibitipoca, estrada para o Parque Estadual do Ibitipoca, próximo a Pousada dos Manacas, 1370 m, 21°42'32"S, 43°54'12"W, 09 May 2002, *R. Marquete 3258* (RB; 5.10). Mato Verde, estrada Mato verde—Rio Pardo de Minas, ca de 8 km de entrocamento Rio Pardo/Mato verde/Mentezuma em direção a Rio Pardo, 1030 m, 15°26'08"S, 42°39'36"W, 20 July 2005, *R.C. Forzza 4110* (RB, SPFR; 5.8). Ouro Preto, Serra de Ouro Preto, Fazenda brigida, 1538 m, 20°21'51"S, 43°31'02"W, 17 May 2011, *R.C. Forzza 6343* (RB; 5.12). Santa Bárbara, Serra do Caraça, estrada para a Capelinha, 23 May 1983, *J.R. Pirani 716* (SPF; 5.24). Santana do Pirapama, Serra do Cipó, acesso pela fazenda Inhame, afloramento rochoso e mata seca ao norte da fazenda Inhame, 750 m, 18°55'54"S, 43°48'33"W, 14 March 2009, *D.C. Zappi 2124* (RB; 5.25). Santana do Riacho, estrada para Conceição do Mato Dentro (MG 10), lado esquerdo do morrote, 940 m, 19°18'31.8"S, 43°36'23"W, 23 August 2006, *R. Marquete 3806* (RB; 5.20). Santana do Riacho, morro de calcário na base da Serra do Cipó, 24 May 2009, *M.M. Saavedra 869* (RB; 5.25). Santana do Riacho, Serra do Cipó, Morro da Pedreira, 3° grupo de calcário, 935 m, 19°18'18.4"S, 43°36'47.9"W, 17 June 2007, *M. Groppo 1452* (SPFR; 5.23). São Roque de Minas, Parque Nacional da Serra da Canastra, 1307 m, 20°15'13.7"S, 46°24'17.2"W, 29 October 2016, *P.L. Ferreira 57* (SPFR; 5.23). Paraná: Arapoti, Rio das Perdizes, 06 April 1970, *G. Hatschbach 24104* (RFA; 5.10). Bituruna, Faxinal, 12 February 1966, *G. Hatschbach 13853* (MBM; 5.22). Campina Grande do Sul, Serra do Capivari, 14 July 1986, *J.M. Silva 121* (MBM; 5.22). Curitiba, Jardim das Américas, próximo à fábrica da Coca-Cola, esquina das ruas S. Saza Lattes e Dr. Paulo Assumpção, *M.M. Saavedra 521* (RB, SPFR; 5.3). Morretes, Zoador, 20–50 m, 21 July 1987, *G. Hatschbach 51270* (WU; 5.3). Pernambuco: Moreilândia, Mata Agreste, 07 August 1999, *F.S. Cavalcante 528* (EAC; 5.23). Moreilândia, Serra do Catolé, refúgio das abelhas Professor Paulo Nogueira Neto, 880 m, 7.2751 S, 39.28132 W, *V.M. Mascena 54C* (EAC; 5.23). Rio de Janeiro: Itatiaia, Sítio Vista linda, 750 m, 22°15'00"S, 44°34'00"W, 13 September 1994, *M.P.M. de Lima 278* (RB; 5.17). Itatiaia, Parque Nacional do Itatiaia, Três picos, área perturbada, 1200 m, 22°15'00"S, 44°34'00"W / 22°28'00"S, 44°45'00"W, 37 March 1995, *R.R. Guedes 2533* (NY; 5.22). Nova Friburgo, subida para o Pico da Caledônia, trilha de acesso ao Pico, 2190 m, 22°21'11.56"S, 42°35'4.83"W, 20 April 2009, *L.L. Giacomini 951* (RB; 5.17). Nova Friburgo, Reserva Ecológica Municipal de Macaé de Cima, estrada para Sítio Sophronites, 1000 m, 22°00'S, 42°03'W, 03 June 1990 *S.V.A. Pessoa 522* (NY; 5.22). Paraty, pico do Cairuçu, acesso pela Praia Negra, 25 November 1990, *C. Farney 2558* (RB; 5.10). Petrópolis, Vale das Videiras, Morro do Cuca, 1500–1750m, 10 October 1979, *G. Martinelli 6148* (RB; 5.6). Petrópolis, Araras, Pico da Maria Comprida, Vertente NE, 1900 m, 22°24'22"S, 43°12'62"W, *G. Martinelli 10696* (RB, SPFR; 5.6). Petrópolis, Vale das Videiras, Morro do Cuca, esqueda da trilha próximo ao topo do morro, 1636 m, 22°24'57.9"S, 43°16'09.6"W, 03 May 2013, *P.L. Ferreira 01* (SPFR; 5.17). Petrópolis, entre Araras e Vale das Videiras, morro do cuca, 1050–1200 m, 02 June 1984, *G. Martinelli 9884* (RB; 5.10). Reserva Biológica de Araras, Vale das Videiras, Pedra Comprida, 22°25'25"S, 43°15'58"W, 28 March 2018, *T.M. Portugal 139* (RB; 5.6). Rio de Janeiro, 1874, *A.F.M. Glaziou 7697* (NY; 5.25). Teresópolis, Parque Nacional da Serra dos Órgãos, trilha para a Pedra do Sino, 2118 m, 22°27'54"S, 43°01'56"W, 19 November 2006, *E.J. Lucas 556* (RB, K; 5.17). Rio Grande do Sul: Bom Jesus, Fazenda do Cilho, 1050 m, 28°31'45"S, 50°26'37"W, 25 February 1999, *M. Rossato 24* (NY; 5.22). Encruzilhada do Sul, fazenda Xafri, ca. 20 km distante do centro da cidade, 17 April 2004, *C. Giongo 353* (ICN; 5.22). Jaquirana, beira da mata, 800 m, 01 July 1989, *R. Wasum*

s.n. (MO; 5.3). Santa Catarina: Anita Garibaldi, Portão de entrada da UHE Barra Grande, sentido Anita Garibaldi, 1006 m, 27°46'21''S, 51°10'36''W, 02 February 2006, *E.S.G. Guarino 972* (CEN; 5.22). Lages, 10 April 2008, *M. Verdi 22695* (FURB; 5.22). São Paulo: Altinópolis, Morro do Forno, 762 m, 21°05'47.3''S, 47°20'01.0''W, 18 August 2014, *P.L. Ferreira 34* (SPFR; 5.23). Anhembi, sítio Ribeirão Bonito, 22°48'43.5''S, 48°12'51.6''W, 22 March 1994, *K.D. Barreto 2194* (SPF; 5.25). Campinas, Santa Genebra Forest Reserve, Barão Geraldo near Campinas, 22°52'S, 46°05'W, 550 m, 26 August 1987, *A. Gentry 58680* (MO; 5.3). Campos do Jordão, Horto Florestal, 22°42'31''S, 45°27'58''W, 22 September 1993, *K.D. Barreto 1240* (ESA; 5.22). Cunha, Parque Estadual da Serra do Mar, picada do rio bonito, 18 August 1994, *G.A.D.C. Franco 1242* (HRCB; 5.12). Cruzeiro, estrada da fazenda Boa Vista, 22°29'02''S, 45°02'00''W, 05 April 1995, *J.L.A. Moreira 32* (UEC; 5.22). Jundiá, Reserva Biológica Municipal da Serra do Japi, trilha Base/Mirante/DAE/Rua Bauru/Cidinho/Base, 850–1178 m, 23°13'49''S, 46°56'8''W, 24 June 2008, *J.A. Lombardi 7443* (RB; 5.10). Ilha Solteira, Fazenda São José, 05 August 1995, *M.R. Pereira-Noronha 1379* (HRCB; 5.26). Itaporanga, Patrimônio do Mosteiro Santa Cruz, 19 July 1949, *A.B. Joly s.n.* (SPF; 5.25). Ribeirão Preto, Estação Ecológica de Santa Tereza, 582m, 21°13'30.5''S, 47°50'57.7''W, 13 September 2016, *P.L. Ferreira 67* (SPFR; 5.15). São Paulo, cidade jardim, August 1941, *W. Hoehne s.n.* (SPF; 5.15). Tocantins: Dianópolis, Serra do Ouro, fazenda Cachoeira do Sr. Martins, 15 July 1963, *A.L. Costa s.n.* (RB; 5.21). BOLIVIA. Chuquisaca: Padilla, ca. 10 km west of Padilla, 9 April 1994, *J.R.I. Wood 8219* (K; 5.2). Zudañez, on ascent c. 20 km SE of Icla on road to Cordillera de los Sombreros and Azurduy, 3000 m, 13 March 1999, *J.R.I. Wood 14663* (SPF, K; 5.13). Cochabamba: Ayopaya, ca. 1 km above Independencia in wooded valley above ford and footbridge, 2500 m, 11 March 2000, *J.R.I. Wood 16012* (K; 5.2); Pasorapa, ca. 36 km de Pasorapa, y unos 4 km antes de Buena Vista, 2426 m, 18°31'S, 64°33'W, 24 March 2003, *J.R.I. Wood 19461* (K; 5.2). La Paz: Calamarca, on Antiplano, 55 km South of La Paz, 4200 m, 16°59'S, 68°07'W, 28 September 1947, *F.R. Fosberg 28698* (MO; 5.9). Larecaja, along road Caranavi-Guanay, outskirts of Guanay, 600m, 05 August 1998, *D.C. Wasshausen 2204* (K; 5.21). Trail from Cota Cota to Muela del Diablo, 3500–3800 m, 16°32'S, 68°03'W, 13 April 1982, *J.C. Solomon 7473* (MO; 5.9). Potosi: Charcas, Toro Toro, Sendero bajando al Cañon del Vergel, 2558m, 18°07'S, 65°46'W, 26 February 2003, *J.R.I. Wood 19231* (K; 5.16). Cornélio Saavedra, Betanzos area, in the valley NW of Ticoya, 3500–3700 m, 28 December 1994, *J.R.I. Wood 9046* (SPF, K; 5.13). Santa Cruz: Andres Ibanez, along road from Santa Cruz to Samaipata, 2–4 km SW of Angostura, 700 m, 18°10'S, 63°32'W, 12 July 1987, *M. Nee 35138* (GB; 5.3). Caballero, Comarapa, ca. 2 km E de Comunidad Candelaria, subiendo unos 200m hacia cerro Empinao, 2275 m, 17°54'S, 64°34'W, 27 March 2004, *M. Mendoza 936* (K, NY). Ñuflo de Chávez, ca. 3–4 km SW of San Javier on road to San Ramon, 500 m, 24 July 2000, *J.R.I. Wood 16507* (K; 5.21). Tarija: Tarija, 3000–3500 m, 04 February 1904, *K. Fiebrig 3038* (K; 5.13). COLOMBIA. Boyacá: Valle del Cocuy, toward southeast, 2880–3000 m, *J. Cuatrecasas 1735* (P; 5.5). Norte de Santander: Between Mutiscua and Pamplona, 2700–3400 m, 23 February 1927, *E.P. Killip 19690* (US; 5.5). Valle del Cauca: Cordillera Central, vertiente occidental, hoya del río Bugalagrande, Loma de Barragám, Hacienda de San José, 2580–2600 ft. (c. 786–792m), 15 March 1946, *J. Cuatrecasas 20005* (F; 5.5). Cordillera Central, vertiente occidental, márgenes del río Bugalagrande, entre El Puente y Salinas, 2000 m, 27 March 1946, *J. Cuatrecasas 20468* (F; 5.5). ECUADOR. Azuay: 7 kms N of Nabon on road toward Cuenca, 2720 m, 26 August 1991, *T.F. Stuessy 12464* (US; 5.1). Km 86 out of Cuenca en route to Loja, 3000 m, 25 September 1959, *B. Maguire 44308* (GB; 5.1). Between Oña and Cuenca, 2700–3300 m, 9–10 September 1923, *A.S. Hitchcock 21589* (US; 5.1). Vicinity of Nabón, 26 September 1918, *A. Pachano 23055* (US; 5.1). Carchi: El Angel, Carretera entre San Isidro y Chulte, 3200 m, 00°36'S, 78°02'W, 08 April 1991, *W. Palacios 7016* (MO; 5.19). Imbabura: Selva Alegre-Otavallo, W side of pass, 2800–3000 m, 00°15'S, 78°25'W, 04 December 1988, *P.M. Jørgensen 65606* (QCA; 5.19). Loja: on road from Loja to Cuenca, 2900 m, 01 October 1961, *C.H. Dodson 858* (MO; 5.1). Loja-Gonzanama, 8 km SW of Gonzanama, 1 km along track from sign to PREDESUR, 1750 m, 04°14'9.09''S, 79°28'5.91''W, 13 May 1997, *G.P. Lewis 3277* (QCA; 5.19). Pichincha: Camino al Hospital entre el Mauca Quito y el Sincholagua, 2400–2750 m, 00°05'S, 78°30'W, 21 May 1988, *C.E. Cerón 3769* (MO; 5.19). Ca 2 kms W of Calacali on dirt rd to Nebli, Just outside Reserva Pululahua, 3020 m, 14 August 1991, *T.F. Stuessy 12308* (WU; 5.19). Piura: Ayabaca, 3.6 kms W of Arreipite Norte, 16.6 kms W of Ayabaca, 21 July 1992, *T.F. Stuessy 12700* (WU; 5.19). PARAGUAY. Amambay: Parque Nacional Cerro Corá, cerro Trébol, table mountain, 22°37'10''S, 56°02'36''W, 13 June 1996, *E.M. Zardini 45013* (MO; 5.23). Cordillera: in regione lacus Ypacaray, *E. Hassler 11862* (MO; 5.26). Guairá: Mbocayaity-Melgarejo, cerro Naville, 25°43'S, 56°21'W, 06 July 1992, *E.M. Zardini 32470* (MO; 5.18). Paraguari: Pirajú, 25°30'S, 57°15'W, 15 May 1984, *W. Hahn 2572* (MO; 5.3). Ybicui, Parque Nacional Ybycu'i, alrededores de la administración, 15–20 m, 15 August 1984, *L. Pérez 257* (MO; 5.3). San Pedro: Laguna Blanca, 23°48'46''S, 56°16'39''W, 01 August 1996, *E.M. Zardini 45480* (MO; 5.18). PERU. Ancash: Sihuas, road from Sihuas to Yanac, before Pomabamba turnoff, 3500–3800 m, 10 March 2001, *M. Weigend 5078* (B; 5.9). Huaraz, 10 km by road from Cachabamba, 2870 m, 09°27'S, 77°51'W, 6–8 June 1985, *D.N. Smith 10850* (MO; 5.9). Recuay, en ladera abierta, 3300 m, 25 May 1970, *A. Lopez M. 7488* (MO;

5.9). Apurímac: Andahuaylas: 2 km south of Chincheros, 26 February 1939, *H.E. Stork 10737* (K; 5.16). Cajamarca: Contumazá, 16 kms S of Contumazá, 2530 m, 17 July 1992, *T.F. Stuessy 12689* (WU; 5.4). Desvío al Bosque de Cachil (Cascas-Contumazá), 2200–2300 m, 25 June 1982, *A. López M. 9136* (F; 5.4). Cajamarca, Namora, Ladera oeste que converge a La Laguna San Nicolás, 2800 m, 05 March 2002, *I. Sánchez Veja 11276* (US; 5.13). Cusco: Canchis, Sicuani, beira da Estrada a caminho de Uyumiri, 06 February 2016, *G. Ccapatinta 58* (SPFR; 5.9). Urubamba, Urubamba, trilha para a lagoa Yanacocha, 3372 m, 13°18'04.4''S, 72°03'08.4''W, 10 January 2016, *G. Ccapatinta 55* (SPFR; 5.16). km 34, road between Cusco and Urcos (near town of Huaró), along Río Urubamba, 3100 m, 25 May 1977, *J.C. Solomon 3091* (MO; 5.9). Vilcabamba, Chuanquiri camino a resistencia, 1000 m, 12°50'30''S, 73°09'10''W, 19 October 2006, *J. Farfán 1117* (MO; 5.3). Junín: Tarma, 3200 m, 27 January 1968, *H.W. Schwabe s.n.* (B; 5.9). La Libertad: Otuzco, Abajo de José Balta, ruta hacia Agallpampa, 2540 m, 09 June 1994, *S. Leiva G. 1133* (GB; 5.9). VENEZUELA. Anzoátegui: forested rocky slopes along Río Querecual southwest of Bergantín, 500 m, 14 March 1945, *J.A. Steyermark 61489* (US; 5.27). Bolívar: Pira, Isla en el Lago de Guri, Sector Danto Machado, 40 km al S de la Presa R. Leoni, 270 m, 07°35'S, 62°58'W, 24 February 1992, *G. Aymard 10166* (NYBG; 5.27). Distrito Capital: lado norte de la Cordillera de La Costa, Osmá, 7 km de distancia aérea al este de Los Caracas, a lo largo del río, 200 m, Mayo 1992, *W. Meier 2107* (B; 5.27).

6. *Doniophyton* Weddell (1855: 7)

Type:—*Doniophyton anomalum* (D. Don) Kurtz

Subshrubs, up to 40 cm tall. *Stems* erect or decumbent, much-branched, lenticellate, cylindrical, scales imbricated at base, tomentose, velutinous, axillary spines in fascicles, straight, divergent or convergent, glabrous or rarely pubescent at base. *Leaves* alternate, sessile, persistent or deciduous, blade linear-lanceolate, chartaceous or coriaceous, pale or lustrous, glabrous or tomentose on both surfaces, base truncate, leaf margin revolute or plicate, ciliate, abaxial with prominent midvein, apex spiny; nervation hypodromous. *Capitulescence* terminal, monocephalous. *Capitula* 40–135-flowered, heterogamous, disciform, sessile or shortly pedunculate, involucre hemispherical or campanulate, 4–7-seriate, phyllaries scarious, yellow or yellow and purple, erect or reflexed, hirsute or velutinous, lanceolate grading to linear, apex spiny, margin flat, ciliate. *Receptacle* flat or convex, alveolate or tuberculate, pubescent. *Flowers* heteromorphic. *Ray flowers* 10–40, pistillate, corolla narrowly tubular (5+0), 5-lobed, yellow, villous. *Style* cylindrical, yellow. *Disc flowers* 30–95, bisexual, corolla tubular (5+0), 5-lobed, yellow, villous. *Anthers* 5, apical appendage acute or rarely apiculate, basal appendage acute, ecalcarate, caudate, inserted at base of the corolla, filaments free, glabrous. *Style* cylindrical, yellow. *Cypselas* turbinate, densely villous. *Pappus* plumose, shorter than or equal to corolla length, bristles whitish. *Pollen* without intercolpal depression, scabrate-microechinate. (Suessy & Urtubey 2007). *Chromosome number* = 24, 25 (Wulff 1990).

Fig. 7a–b; 10d.

Distribution and habitat:—*Doniophyton* comprises two species found in dry open areas from northern Chile to Patagonian Argentina up to an altitude of 4,000 m (Katinas & Stuessy 1997). The species occur in the Puna vegetation (highland and steppe) and in the Patagonian steppe and semidesert.

Notes:—*Doniophyton* is a xeromorphic genus that has always been proposed as being closely related to *Chuquiraga* and *Duseniella* by sharing drier habitats, long caudate anthers, yellow corolla, and pollen without intercolpal depression. However, this group has long been enigmatic, since previous phylogenetic studies have not resolved the relationships among these genera, recovering *Doniophyton* as either nested in *Chuquiraga* (Gruenstaedl *et al.* 2009, Padin *et al.* 2015b), or as sister to *Chuquiraga* (Gustaffson *et al.* 2001). Morphologically, *Doniophyton* can be distinguished from *Chuquiraga* by the subshrub habit (*vs.* shrub), chartaceous leaves (*vs.* coriaceous), heterogamous and disciform capitula (*vs.* homogamous and discoid capitula), and female marginal flowers (*vs.* all flowers in the capitula are hermaphroditic), and from *Duseniella* by its chartaceous or coriaceous leaves (*vs.* succulent leaves in *Duseniella*), by its perennial subshrubs habit, up to 40 cm tall (*vs.* annual herbs up to 10 cm in *Duseniella*) and by the pappus scaly overlapped (*vs.* a plumose pappus in *Duseniella*).

Iconography:—Katinas & Stuessy (1997).

Accepted species:—**6.1** *Doniophyton anomalum* (D. Don) Kurtz; **6.2** *Doniophyton weddellii* Katinas & Stuessy.

Selected specimens examined:—ARGENTINA. Chubut: Laguñeño, 12 December 1981, *A.L. Cabrera 33104* (SI; 6.1). 96 kms E of Sarmiento on rte 26 to Comodoro Rivadavia (ca. 56. kms W of Comodoro Rivadavia), 600 m, *T.F. Stuessy 12939* (WU; 6.1). Jujuy: Cochinoca, Abra pampa, 20 January 1976, *A.L. Cabrera 27396* (MO, SI; 6.2). La Pampa: Utracán, General Acha, 05 November 1953, *A. Burkart 19219* (SI; 6.1). Mendoza: Malargüe, camino a la

mina la Valenciana, 20 January 1982, *A.L. Cabrera 33461* (SI; 6.1). San Rafael, hotel Termas del Sosneado, 2180 m, 34°46'12"S, 70°03'33"W, 22 November 2010, *F.O. Zuloaga 12385* (SI; 6.1). Puente del Inca, 2700 m, 20 December 1946, *B. Sparre 1515* (K). Neuquén: Collon Curá, RN 40 between bridge over Embalse Piedra de Aguila and Collon Curá, 640 m, 40°21'27"S, 70°39'46"W, 13 January 2002, *M. Weigend 5871* (B; 6.1). Zapala, 01 November 1925, *H.F. Comber III* (K; 6.1). Río Negro: General Roca, Vicinity of General Roca, 250–360 m, September 1914–February 1915, *W. Fischer 7* (MO; 6.1). Ñorquinco, entre Ruta Ruin y Manuel Chique, 11 December 1981, *A.L. Cabrera 33045* (SI; 6.1). Santa Cruz: Deseado, Caleta Olivia, 250 m, 20 November 1929, *A. Donat 127* (MO; 6.1). Ruta 40, 38 km al ESSE de la intersección con ruta 37, 3 km al sur de Ruta 40, 47°58'23.3"S, 70°58'45.8"W, 18 January 2002, *M. Bonifacino 481* (LP; 6.1). San Juan: Iglesia, quebrada del Agua Negra, 3800 m, 10 January 1976, *A.L. Cabrera 27070* (SI; 6.2). Pie de Palo, then 2 kms N toward the hills and sand dunes (Médanos), 600 m, *T.F. Stuessy 12887* (WU; 6.1). Calingasta, Manatiales, 27 March 1971, *Zardini 175* (MO; 6.2). CHILE. Atacama: Copiapó, Río Turbío, Co. Cadillal, 3.000 m, January 1926, *E. Werdermann 953* (K; 6.2). Vallenar, Vicinity of Laguna Valeriano, 4.000 m, 29°03'S, 69°52'W, *I.M. Johnston 6073* (K; 6.2). Coquimbo: Baños del Toro, 3500 m, December 1923, *E. Werdermann 201* (K; 6.2). Elquí, Baños del Toro, 3200–3300 m, 05 February 1939, *J.L. Morrison* (K; 6.2). Cordillera Doña Ana, Cancha de Sky, 3400 m, 29°51'S, 70°03'W, 06 January 1988, *F.A. Squeo 88001* (MO; 6.2). 21.4 kms N of Junta del Toro (aduana chilena) on road to Baños del Toro, 3100 m, 20 January 1993, *T.F. Stuessy 12780* (WU; 6.2).

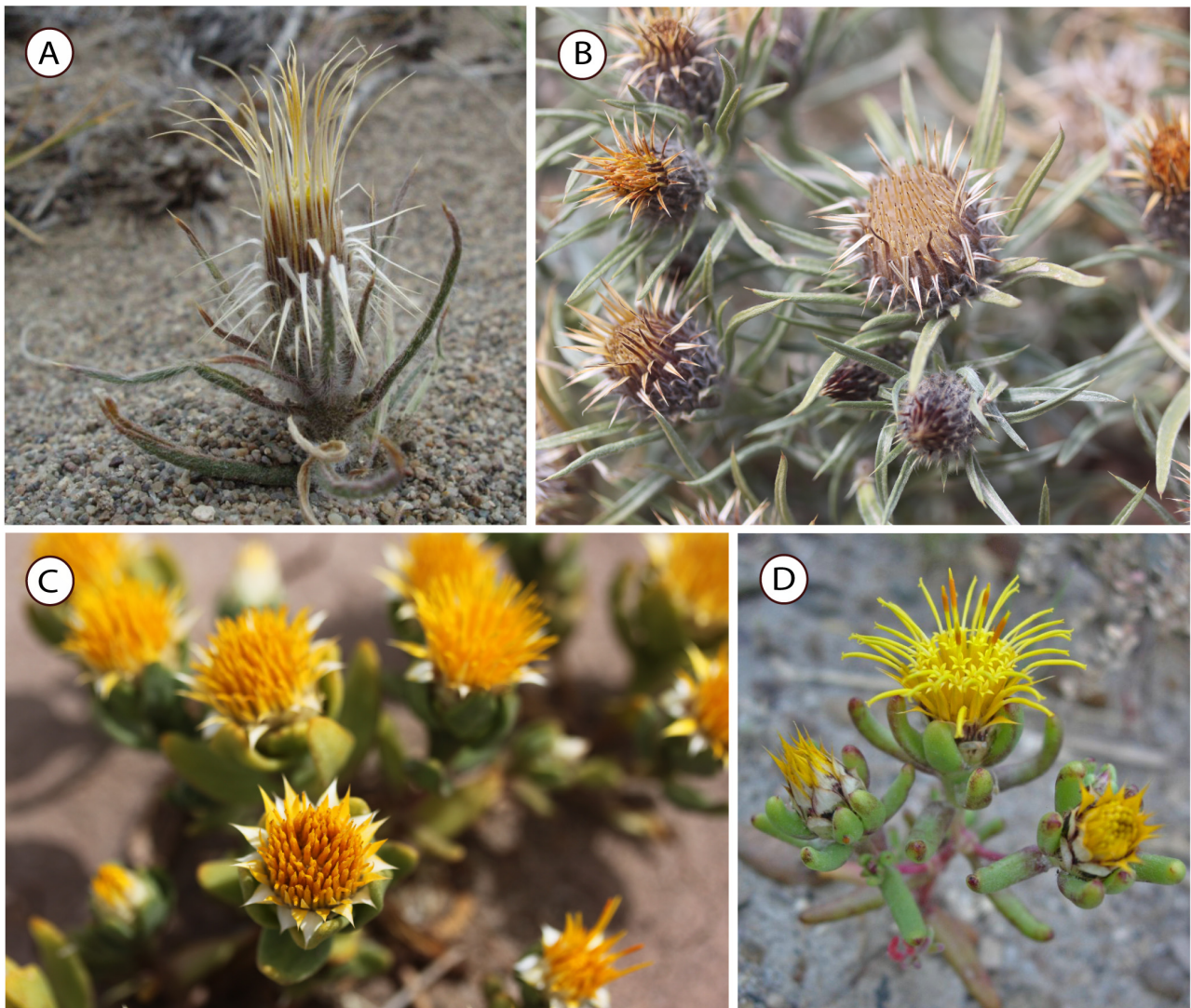


FIGURE 7. *Doniophyton* and *DusenIELLA*. **A–B:** *Doniophyton*. **C–D:** *DusenIELLA*. **A:** *Doniophyton anomalum*. **B:** *Doniophyton weddellii*. **C–D:** *DusenIELLA patagonica*. Photos by Darwinion Institute.

7. *Duseniella* Schumann (1902: 475)

Type:—*Duseniella patagonica* (O.Hoffm.) K.Schum.

Annual herbs, up to 10 cm tall, unarmed. *Stems* erect, much-branched, lenticellate, cylindrical or flat, scales imbricated at base, sparsely sericeous. *Leaves* opposite at base, alternate in the upper parts, sessile, persistent, blade linear, succulent, lustrous, adaxially glabrous or sparsely sericeous, adaxially sericeous, leaf margin flat, ciliate, apex mucronate; venation actinodromous, with 3 basal nerves, not evident and immersed in the mesophyll. *Capitulescence* terminal, monocephalous. *Capitula* heterogamous, disciform, 9–41-flowered, sessile, surrounded by subinvolucral bracts, involucre campanulate, 4–5-seriate, phyllaries scarious, erect, glabrous, ovate–oblong grading to linear, apex spiny, margin flat, ciliate. *Receptacle* convex, glabrous. *Flowers* heteromorphic. *Ray flowers* 4–16, pistillate, corolla tubular (5+0), 5-lobed, yellow, villous at apex. *Style* cylindrical, yellow. *Disc flowers* 5–25, bisexual, corolla tubular (5+0), 5-lobed, externally sericeous at base of corolla and apical lobes, internally sericeous at tube margin petals. *Anthers* 5, apical appendage lanceolate or obtuse, basal appendage acute, caudate, calcarate, inserted between the base and the throat, filaments free, glabrous. *Style* cylindrical, yellow. *Cypsela* cylindrical to turbinate, densely villous. *Pappus* scaly lanceolate, overlapped, shorter than the corolla tube, sericeous, ciliate. *Pollen* without intercolpal depression, microechinate (Suessy & Urtubey 2007). *Chromosome number* $2n = 54$ (Baeza *et al.* 2019).

Fig. 7c–d; 10e.

Distribution and habitat:—*Duseniella* is monotypic, represented only by *D. patagonica*, which is endemic to xeric areas in Argentinean Patagonia and Monte vegetation up to an altitude of 1,500 m. It occurs in semi-desert and steppe vegetation in Patagonia.

Notes:—*Duseniella* is a morphologically distinctive genus in the subfamily Barnadesioideae, being the only genus of annual herbs with unarmed branches, succulent leaves, and disciform capitula with pappus scales overlapped and ciliate. Because of its distinctive morphology, Cabrera (1959, 1961) did not recognize the genus as a member of the subtribe Barnadesiinae (tribe Mutiseae); instead, he placed *Duseniella* in the subtribe Gochnatiinae (Cabrera 1977). Phylogenetically, *Duseniella* is recovered in a clade with *Doniophyton* and *Chuquiraga*, but its relationship to these two genera is still unclear (see discussion above under *Doniophyton*). A phylogenomic study including a large number of taxa from this clade could provide better insights into the evolution of this group.

Iconography:—Flora del Conosur available at <http://www.darwin.edu.ar/Proyectos/FloraArgentina/DetalleEspecie.asp?forma=&variedad=&subespecie=&especie=patagonica&genero=Duseniella&espcod=16513>

Accepted species:—7.1 *Duseniella patagonica* (O. Hoffm.) K. Schum.

Selected specimens examined:—ARGENTINA. Chubut: Escalante, Pico Salamanca, 21 January 1965, *E. De Marco de Kreibohm* 223 (SI). Escalante, Comodoro Rivadavia, punta Borgia, 08 February 1903, *M.S. Pennington* 128 (SI). Ruta 20, 20 km al este de Sarmiento, 45°38' 33.4"S, 68°57'01.0"W, 14 January 2002, *J.M. Bonifacio* 0437 (US). Neuquén: Picún Leufú, 08 November 1972, *E.M. Zardini* 142 (MBM). Río Negro: Aguada Cecilio, 20 November 1980, *Z.A. Manuel s.n.* (SI). General Roca and vicinity, 250–360 m, 16 November 1914, *W. Fischer* 173 (MO). Camino de Cinco Saltos a Lago Pellegrini, *E.M. Zardini* 149 (MBM). General Roca, Labio S del Valle, frente a General Roca, 15 km, 16 February 1944, *E.G. Nicora* 4061 (SI). Santa Cruz: La Angostura, 300m, 13 January 1930, *A. Donat* 238 (MO). Corpen Aike, Laguna Grande hacia Gregores, 49°34'S, 70°14'W, 24 January 1967, *O. Boelcke* 12772 (SI). Deseado, 35 km de Jaramillo caminho al bosque petrificado, 10 January 1967, *O. Boelcke* 12169 (SI).

8. *Fulcaldea* Poirét (1817: 375)

Type:—*Fulcaldea laurifolia* (Bonpl.) Poir.

Arching shrubs or small trees, up to 10 m tall. *Stems* erect, much-branched, lenticellate, cylindrical or flat, scales imbricate at base, glabrous, pubescent or rarely strigose, unarmed or with axillary spines in pairs, straight, convergent or divergent, glabrous or rarely pubescent at base. *Leaves* alternate, spiral, subsessile or petiolate, persistent or deciduous, blade elliptic or ovate, coriaceous, pale or rarely lustrous, glabrous, base acute or obtuse, margin flat, glabrous, apex acute, mucronate; venation eucamptodromous or actinodromous with 3 basal nerves. *Capitulescence* terminal or axillary, in corymbose or paniculate cymes. *Capitula* 1-flowered, homogamous, sessile or subsessile, involucre narrow cylindrical to cylindrical, 5–13-seriate, phyllaries scarious, green or pale brown, apex purple, erect or reflexed, glabrous or villous, ovate–triangulate grading to lanceolate, apex mucronate, margin flat, ciliate. *Receptacle* convex, glabrous, or pilose. *Flowers* bisexual, corolla tubular (5+0), 5-lobed, white, red, purple, externally densely

villous. *Anthers* 5, apical appendage lanceolate, or obtuse, basal appendage decurrent, ecaudate, ecalcarate, inserted between the base and the throat, filaments free, glabrous. *Style* cylindrical but with a swollen portion below the branching point, white to cream or purple, apex purple. *Cypsel*a cylindrical, densely sericeous. *Pappus* plumose, longer than the corolla length, white, pink or red bristles. *Pollen* without intercolpal depressions, spinulose (Suessy & Urtubey 2007). *Chromosome number* unknown.

Fig. 8a; 10f.

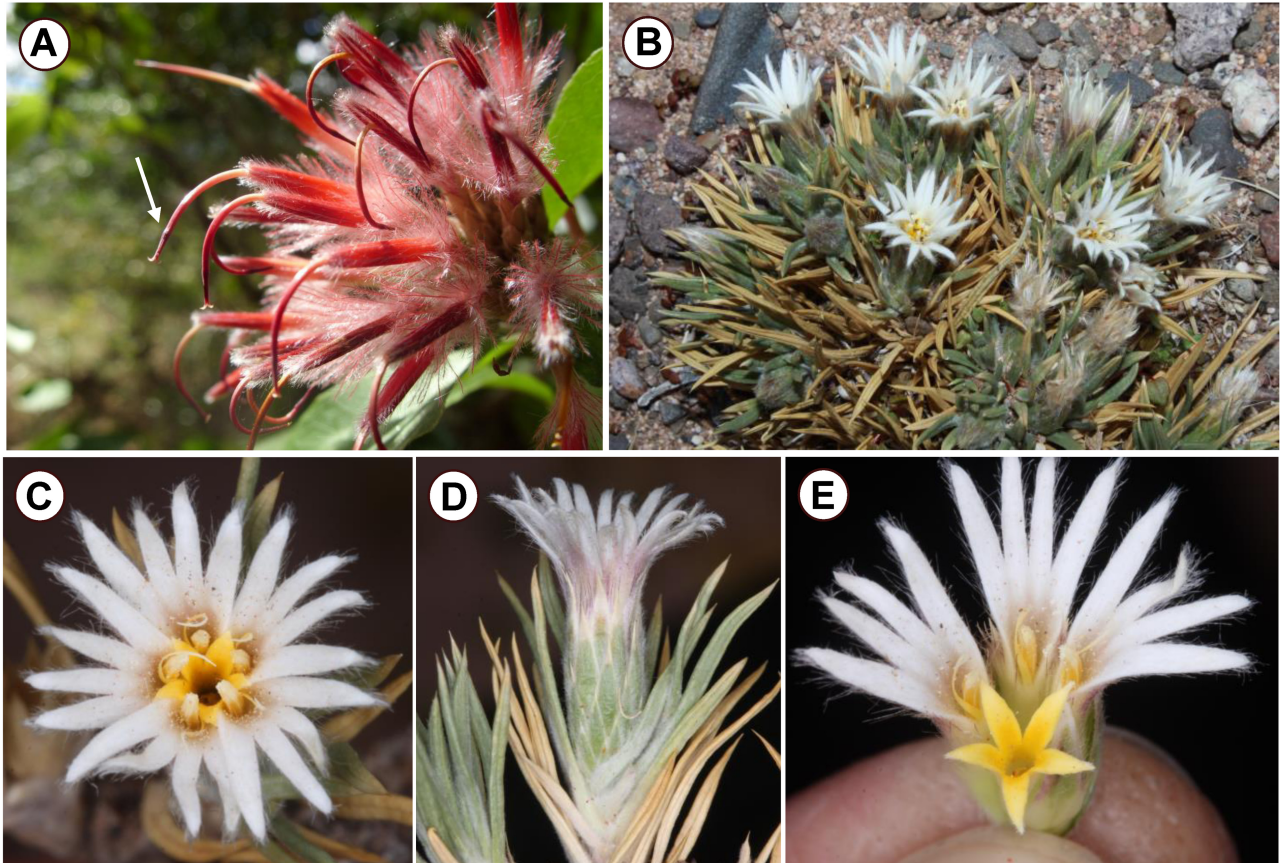


FIGURE 8. *Fulcaldea* and *Huarpea*. **A:** *Fulcaldea*. **B–E:** *Huarpea*. **A:** *Fulcaldea stuessyi*. Inflorescence with a white arrow showing swollen style below the branching point. **B:** *Huarpea andina*. Habit. **C:** Capitulum showing five ray flowers and a disc flower. **D:** Lateral view from the capitula. **E:** Dissected capitula showing three ray flowers (white) and a disc flower (yellow). Photos by Ivan Abreu (A) and Darwinion Institute (B–E).

Distribution and habitat:—*Fulcaldea* comprises two species with a remarkable 4,000 km disjunct distribution (Funk & Roque 2011). *Fulcaldea laurifolia* (Bonpl.) Poir. is restricted to the dry forest in intermontane regions of southern Ecuador and northern Peru (Ferreira 1995), and *Fulcaldea stuessyi* is restricted to seasonally deciduous forest in northeastern Brazil in the Chapada Diamantina rocky chain (Funk & Roque 2011).

Notes:—*Fulcaldea* is easily distinguished from the other Barnadesioideae genera by having a single-flower capitulum, and by the swollen style below the branching point (Fig. 8a). The genus is part of a strongly supported clade together with *Archidasphyllum* and *Arnaldoa*, being sister (also with strong support) to the latter according to Ferreira *et al.* (2019); however, this clade is morphologically diverse and synapomorphies that support the relationships among the genera are still to be determined (Funk & Roque 2011, Ferreira *et al.* 2019). Funk & Roque (2011) hypothesized that the remarkable disjunction distribution (4,000 km) may be the result of vicariance or long-distance dispersal, thus being inconclusive on this subject.

Iconography:—Ferreira (1995), Roque & Funk (2011).

Accepted species:—**8.1** *Fulcaldea laurifolia* (Bonpl.) Poir.; **8.2** *Fulcaldea stuessyi* N. Roque & V.A. Funk.

Selected specimens examined:—BRASIL. Bahia, Chapada Diamantina, Rio de Contas, distrito de Arapiranga, Fazenda Brandão, 5 August 2010, *I.S. Abreu 123* (ALCB; 8.2). Rio das Contas, antiga estrada do Brandão, sentido do sítio Marcela, 716 m, 13°28'11"S, 41°46'32"W, July 2014, *N. Roque 4386* (ALCB; 8.2). ECUADOR. Loja: Catacocha

to Loma Quemada, km 8.5, 1600 m, 04°06'95"S, 79°36'312"W, 16 April 1996, *G.P. Lewis 2247* (MO, K; 8.1). Sozoranga, km 4 along track from Sozoranga-Macará road to Reserva natural El Tundo, propiedad de fundación ARCOIRIS, 1850 m, 04°19'S, 79°49'W, 19 August 1997, *G.P. Lewis 3497* (MO; 8.1). Sozoranga outskirts, 1 km along track to Utuaña, 1700 m, 04°20'S, 70°47'W, 5 March 1977, *G.P. Lewis 3038* (MO, K; 8.1). Km 2 road Sororanga-Yaramine, 1750 m, 04°18'S, 79°48'W, 17 June 1997, *B.B. Klitgaard 203* (QCA, K; 8.1). Manabí: Jama, 24 km south of Pedernales (as the crow flies) northwest off coastal highway; 1.5 km east of Eudaldo (Don Lalo; 8.1) Loor's farm, 30–150 m, 00°04'31"S, 80°09'22"W, 9 October 1999, *T. Delinks 399* (MO; 8.1). Jama Cantón, Cerro del Matal, 3km northwest of Jama, 1 km inland from seashore, 100 m, 00°11'S, 80°18'W, *D. Neill 11621* (MO; 8.1). Machalilla National Park, 01°39'S, 80°41'W, *C. Josse 1063* (GB, QCA; 8.1). Pedernales, Estación Biológica Lalo Loor, a 22 km al sur de Pedernales por la carretera costera, 2 km de la costa, 150 m, 00°05'07"S, 80°09'05"W, October 2005, *J. Cevallos 213* (MO; 8.1). San Vicente, thicket, 07 June 1955, *E. Asplund 16595* (K; 1.1). PERU. Piura: Ayabaca, on road to Ayabaca, 18 km above Puente Tandopa (Río Quiroz), 1700 m, *P.C. Hutchison 6685* (MO, K; 8.1). Ayabaca, 12.7 kms up from Puente Tandopa over Río Quiroz, 1.540 m, 20 July 1992, *T.F. Stuessy 12693* (WU; 8.1). Huacabamba, bajo de Cachaque, 1100–1200m, 02 May 1955, *R. Ferreyra 10932* (MO; 8.1). Paimas, Ayabaca road, ca. 15 km W of Ayabaca, 1900 m, 20 September 1991, *A.H. Gentry 74930* (MO; 8.1).

9. *Huarpea* Cabrera (1951: 129)

Type:—*Huarpea andina* Cabrera

Rhizomatous subshrubs, up to 4.5 cm tall, unarmed; underground system formed by thickened rhizomatous stems, occurring at ground level and below. *Stems* erect, single- to much-branched, lenticelate, cylindrical, scales imbricated at base, tomentose. *Leaves* alternate, subrosulate, sessile, persistent, blade linear, coriaceous, lustrous, adaxial face glabrous, abaxial lanate, base truncate, margin revolute, ciliate, apex spiny, venation hypodromous. *Capitulescence* terminal, monocephalous. *Capitula* 6-flowered, heterogamous, radiate, sessile, hidden by the leaves, involucre cylindrical–campanulate, 5–7-seriate, phyllaries coriaceous, lanceolate, erect, lanate, apex spiny, margin flat, ciliate. *Receptacle* flat, pilose. *Flowers* dimorphic. *Ray flowers* 5, bisexual, subbilabiate (4+1), 5-lobed, with the inner lobe shorter than the outer lobes, externally hirsute-sericeous, white, internally glabrous, yellow. *Disc flower* 1, male, tubular (5+0), externally sericeous-pilose, pistil not seen. *Anthers* 5, apical appendage lanceolate to obtuse, inserted at the throat of the corolla (ray flowers) or inserted between the base and the throat (disc flowers), filaments free, glabrous. *Style* cylindrical, yellow (ray flowers), not seen in disc flowers; *Cypselae* turbinate (ray flowers) or cylindrical (disc flowers), densely villous. *Pappus* plumose or single villous bristle or absent, equal to the corolla length. *Pollen* lophate, radially symmetrical, smooth (Suessy & Urtubey 2007). *Chromosome number* unknown.

Fig. 8b–e; 10c.

Distribution and habitat:—*Huarpea* is a monotypic genus restricted to the department of Iglesia in San Juan province, Argentina (Cabrera 1951). The sole species, *H. andina*, is found in the dry Monte vegetation above an altitude of 3,300 m (Suessy *et al.* 1996).

Notes:—*Huarpea* can be distinguished from the other Barnadesioideae genera by being unarmed subshrubs up to 4.5 cm tall, capitula hidden by the leaves, with 5 ray flowers, hermaphroditic and subbilabiate corollas and one-disc flower with tubular corollas and atrophied gynoecium (Cabrera 1951, Suessy *et al.* 2009). Phylogenetically, *Huarpea* is always recovered as sister to *Barnadesia* (Bremer 1994, Suessy *et al.* 1996, Gustafsson *et al.* 2001, Gruenstaedl *et al.* 2009, Ferreira *et al.* 2019). This clade is distinguished by the radiate and heterogamous capitula, slightly sagittate or decurrent anther bases, lophate pollen, and atrophied gynoecium in the disc flowers (only in *Barnadesia* subgenus *Bacasia*).

Iconography:—Cabrera (1951).

Accepted species:—9.1 *Huarpea andina* Cabrera

Selected specimens examined:—ARGENTINA. San Juan: Iglesia, Reserva de San Guillermo, Cordón del Infiernillo, 17 January 1083, *E. Nicora 8573* (MO). Iglesia, Reserva de San Guillermo, alrededores del refugio de San Guillermo, al Sur, 11 November 1982, *E.A. Ulibarri 1499* (US). Iglesia, Reserva de San Guillermo, Reserva de San Guillermo, detras del refugio de Agua del Godo, 3000 m, *R. Kiesling 4555* (MO).

10. *Schlechtendalia* Lessing (1830: 242–243)

Type:—*Schlechtendalia luzulifolia* Less.

Perennial herbs, up to 1 m tall, unarmed. *Leaves* opposite on stems, rosulate at base, amplexicaul, sessile, persistent, blade linear, chartaceous, pale or lustrous, sericeous or lanate, margin flat or slightly revolute, ciliate, apex spiny; nervation parallelodromous. *Capitulescence* terminal or axillary, monocephalous, cymose, corymbiform, racemose, or umbellate. *Capitula* homogamous, discoid, 50–100 flowered, pedunculate, involucre turbinate or hemispherical, 5–7-seriate, phyllaries chartaceous, green, brownish, erect or reflexed, sericeous, lanceolate, apex spiny, margin flat, ciliate. *Receptacle* flat, pilose. *Flowers* isomorphic, bisexual, corolla subbilabiate (4+1), 5-lobed, yellow, externally and throat villous. *Anthers* 5, apical appendage obtuse, basal appendage acute, short-sagittate, ecalcarate, ecaudate, inserted between the base and the throat, filaments free, glabrous. *Style* cylindrical, yellow. *Cypselae* turbinate, densely villous. *Pappus* scaly, lanceolate, shorter than the corolla, scarious, glabrous. *Pollen* with one depression per mesocolpus, sparsely microechinate (Suessy & Urtubey 2007. *Chromosome number* = 8 (Cialdella & López 1981).

Fig. 9; 10d.

Distribution and habitat:—The genus *Schlechtendalia* is monotypic, represented only by *S. luzulifolia*, and occurs in the Pampa vegetation (grassland) in southern Brazil, Uruguay, and adjacent areas of Argentina (Stuessy *et al.* 1996, 2009). In Brazil, *Schlechtendalia luzulifolia* is classified as an endangered species, since the Pampas biome has lost almost 54% of its original vegetation (Nakajima *et al.* 2013).

Notes:—*Schlechtendalia* is clearly a member of Barnadesioideae since it displays the “barnadesioids trichomes” and subbilabiate corollas (Gustafsson *et al.* 2001). However, it has a set of morphological features that diverge from the rest of the subfamily, including the unarmed habit, and the opposite leaves on stems, basally rosulate leaves with parallelodromous venation. Besides these traits, the pappus is glabrous and narrow-scaly (also found in *Duseniella*) without the pappus bristles (Gustafsson *et al.* 2001). Moreover, it is the only genus totally absent in xeric areas (Stuessy *et al.* 2009).

The phylogenetic position of *Schlechtendalia* within Barnadesioideae remains uncertain. It has been proposed as the sister group to the rest of the subfamily (Stuessy *et al.* 1996, Urtubey & Stuessy, 2001, Gruenstaudl *et al.* 2009, Ferreira *et al.* 2019, Ferreira *et al.* in prep.), and as sister to the *Doniophyton* and *Duseniella* clade (Bremer 1994); *Chuquiraga* and *Doniophyton* (Gustafsson *et al.* 2001); the *Archidasphyllum*, *Arnaldoa* and *Fulcaldea* clade (Gustafsson *et al.* 2001); or the *Barnadesia* and *Huarpea* clade (Gruenstaudl *et al.* 2009). New ongoing studies focusing on Barnadesioideae phylogeny (Ferreira *et al.* in prep.) may clarify the phylogenetic position of *Schlechtendalia*.

Iconography:—Suessy & Urtubey (2007).

Accepted species:—*Schlechtendalia luzulifolia* Less.

Selected specimens examined:—ARGENTINA. Entre Ríos: Colón, paraje la Calera, márgenes del Río Uruguay, desembocadura del arroyo Perucho Vema em Río Uruguay, 21–22 December 1998, *P.M. Simon 88* (WU). Colón, Parque Nacional El Palmar, Palmar de Butia Yatay, Sendero La Glorieta, 31°53'08", 58°16'22"W, 14 December 2014, *M.S. Ferrucci 3196* (HUEFS). Confederación, Confederación, 18 December 1963, *A. Burkart 24972* (SI). BRAZIL. Rio Grande do Sul: Alegrete, Estância Cerro do Tigre, cerro da ponte, 141 m, 29°39'48"S, 55°23'40"W, 25 October 2012, *G. Heiden 2008* (SPF). Itapoã, Chacara Weber, 18 December 1948, *B. Rambo SJ 38950* (B). Jaguarão, BR 116, entre Arroio Grande e Jaguarão, 44 m, 32°30'2"S, 53°19'15"W, 03 January 2011, *G. Heiden 1455* (SPF). Livramento, Cerro Palomas, *D.F.M. Valls 1379* (RB). Porto Alegre, Morro da Policia, 18 January 1964, *E. Pereira 8490* (RB). São Lourenço do Sul, BR116, main road from Pelotas to Porto Alegre, between arroio S. Isabel & R. Camaqua (km 167), 02 December 1979, *T.M. Pedersen 12612* (MBM). URUGUAY. Maldonado, Sierra Ballena, 23 December 1964, *Del Puerto 3867/4348* (US). Maldonado, Punta Ballena, Bosque Lussich, 09 February 1943, *Rosengurtt B4507* (US). Maldonado, Cerro San Antonio, just above Puerto Antonio, 0.9 km SE of Piriápolis (jct. rd to Punta del Este), 09 February 1993, *T.F. Stuessy 12810* (WU). Maldonado, Punta Ballena (La Bellena), about ½ distance from Piriápolis and Punta del Este (ca. 28 km E of Piriápolis), 09 February 1993, *T.F. Stuessy 12820* (WU). San José, Balneario Kiyú al E, 14 November 1991, *D. Bayce s.n.* (US).

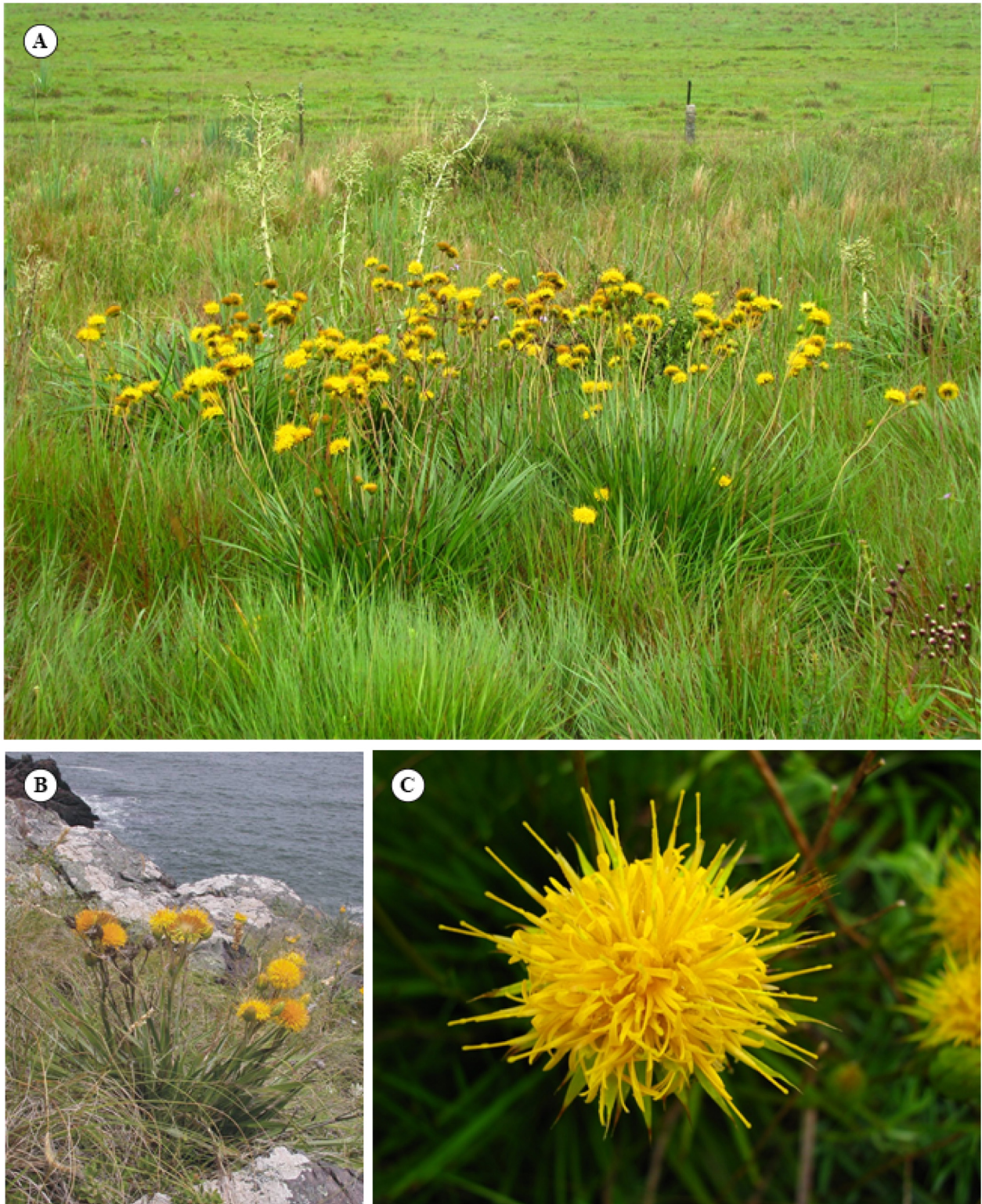


FIGURE 9. *Schlechtendalia luzulifolia*. **A:** Brazilian Pampas. **B:** Grassy-like habit. **C:** Capitulum with subbilabiate corollas. Photos by Gustavo Heiden (A and C) and Mauricio Bonifacino (B).

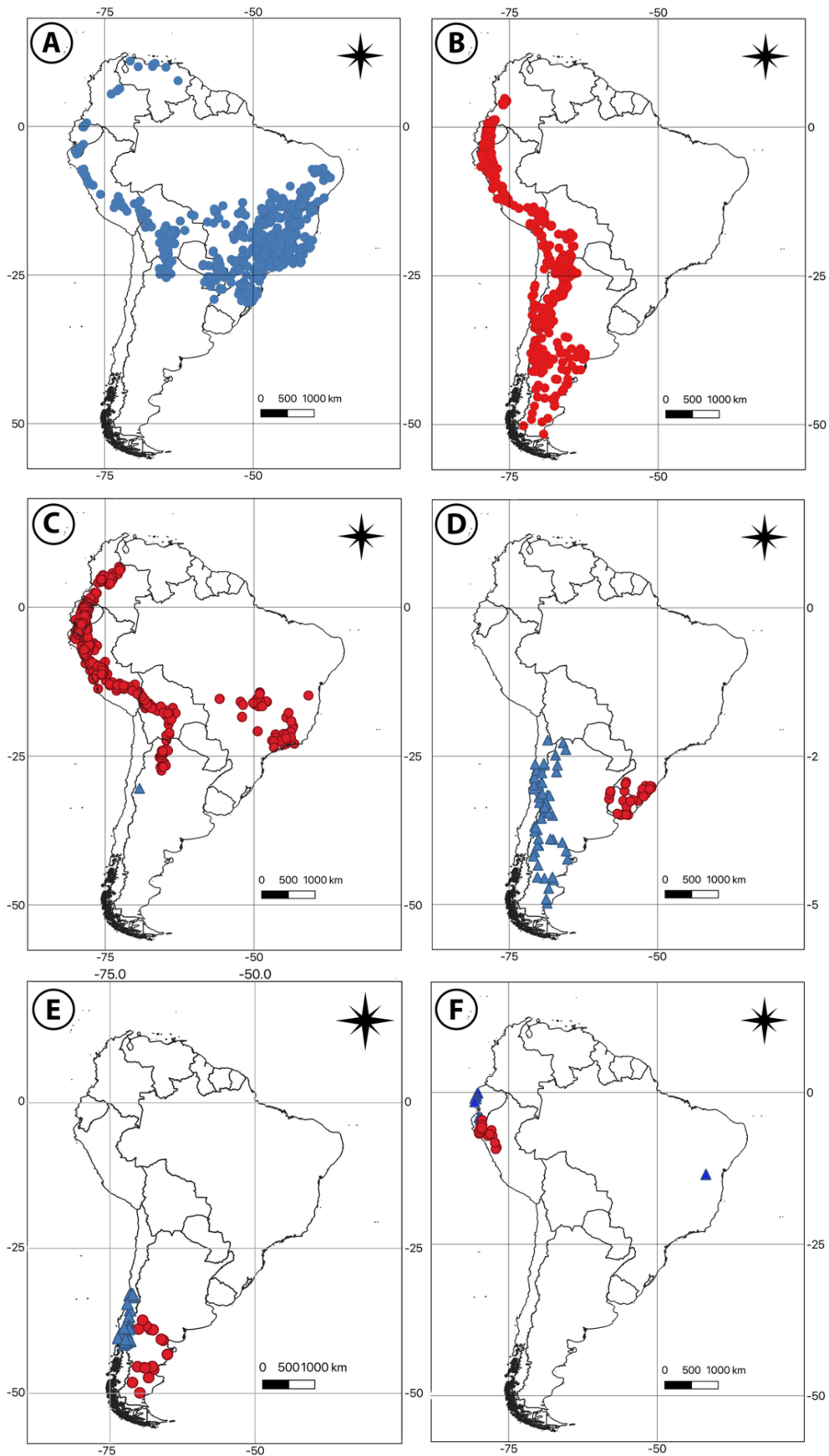


FIGURE 10. Geographical distribution for the genera of Barnadesioideae. **A:** *Dasyphyllum*. **B:** *Chuquiraga*. **C:** *Barnadesia* (red dots) and *Huarpea* (blue triangle). **D:** *Doniophyton* (blue triangles); **E:** *Archidasyphyllum* (blue triangles); *Fulcaldea* (blue triangles)—these words (triangle) in plural (triangles).

Conclusions and Prospects

Taxonomy is one of the oldest branches of plant science, dating back to the Greek and Roman civilizations ca. 370–285 BC. Since then, taxonomic classifications have been radically improved, changing from descriptions mostly based on morphology to integrated monographies using as many sources of information as possible (Grace *et al.* 2021). Such integrative methods provide a better understanding of evolution and species delimitation.

Previous taxonomic studies in Barnadesioideae generally comprised short descriptions of genera and did not highlight the great diversity in this group. Taxonomic revisions at generic level display a more detailed understanding (Ezcurra 1985, Katinas & Stuessy 1997, Urtubey 1999, Saavedra 2011), but these are genus-specific and not comparable across genera as they were not proposed using the same morphological characters. In this work, we assembled data from previous studies and analyzed thousands of herbarium collections in order to present an integrated monography of Barnadesioideae, providing extended descriptions including morphology, pollen, chromosome counts, taxonomic and phylogenetic relationship comments, distribution maps, photos and a key for all ten genera circumscribed in this subfamily.

Given the advances in molecular techniques this century, we now have a much better understanding of the phylogenetic relationships, classification and evolution of morphological characters in the subfamily (Gustaffson *et al.* 2001, Stuessy & Urtubey 2006, Gruenstaudl *et al.* 2009, Padin *et al.* 2015b, Ferreira *et al.* 2019, Svoma *et al.* 2019). Although generic relationships are roughly stable (exceptions are found in the *Chuquiraga/Doniophyton/Duseniella* clade and *Schlechtendalia*), infrageneric relationships and species delimitations often remain unclear, and additional in-depth studies—for example using phylogenomics—will be required to shed further light on the evolution of Barnadesioideae and the entire family.

Acknowledgments

This research was supported by FAPESP (grant #2016/06260-2) and CNPq to M.G.; the Swedish Foundation for Strategic Research, the Swedish Research Council, the Knut and Alice Wallenberg Foundation and the Royal Botanic Gardens, Kew to A.A.; a Doctoral Fellowship (CAPES, Finance Code 001) and a Fellowship for Internship abroad from Coordination for the Improvement of Higher Education Personnel (CAPES, PDSE proc. 88881.132410/2016-01), Missouri Botanical Garden Elisabeth E. Bascom scholarship, MEMOVA project (EU Operational Programme Research, Development and Education No. CZ.02.2.69/0.0/0.0/18_053/0016982), and an International Association for Plant Taxonomy Granted in 2017 to P.L.F. The authors thank all the herbarium curators and staff who have enabled the development of this work. Special thanks to John Pruski for his invaluable support and enthusiasm during a period at Missouri Botanical Garden. Thanks also to Gari V. Ccana-Ccapatinta, Cíntia Luz, Marcelo Monge, Mariana Saavedra, Claudia Martín for sending herbarium samples that greatly contributed to this work; Laura Afonso for helping with the distributional data and maps; Fernando Zuloaga for allowing us the use of the Darwinion Institute photos; Carolina Siniscalchi, Danilo Marques, José Pirani, Marcelo Monge, and Vanessa Rivera for critically reading this manuscript; and Rhian Smith for English editing and proofreading.

References

- Bentham, G. (1873) Notes on the classification, history, and geographical distribution of Compositae. *Journal of the Linnean Society, Botany* 13: 335–577.
<https://doi.org/10.1111/j.1095-8339.1873.tb02575.x>
- Bohm, B.A. & Stuessy, T.F. (1995) Flavonoid chemistry of Barnadesioideae (Asteraceae). *Systematic Botany* 20: 22–27.
<https://doi.org/10.2307/2419629>
- Bohm, B.A. & Stuessy, T.F. (2001) *Flavonoids of the Sunflower Family (Asteraceae)*. Springer-Verlag Wien, Vienna, 831 pp.
<https://doi.org/10.1007/978-3-7091-6181-4>
- Bremer, K. (1994) *Asteraceae: cladistics and classification*. Timber Press, Portland, 752 pp.
- Bremer, K. & Jansen, R.K. (1992) A new subfamily of the Asteraceae. *Annals of the Missouri Botanical Garden* 79: 414–415.
<https://doi.org/10.2307/2399777>

- Cabrera, A.L. (1951) *Huarpea*, nuevo genero de Compuestas. *Boletín de la Sociedad Argentina de Botánica* 4: 129–132.
- Cabrera, A.L. (1959) Revisión del género *Dasyphyllum* (Compositae). *Revista del Museo de La Plata, Sección botánica* 38: 21–100.
- Cabrera, A.L. (1961) Compuestas Argentinas. Clave para la determinación de los géneros. *Revista del Museo Argentino de Ciencias Naturales. Botánicas* 2: 291–362.
- Cabrera, A.L. (1962) Compuestas andinas nuevas. *Boletín de la Sociedad Argentina de Botánica* 10: 21–45.
- Cabrera, A.L. (1977) Mutisieae—systematic review. In: Heywood, V.H., Harborne, J.B. & Turner, B.L. (Eds.) *The Biology and Chemistry of the Compositae*, vol. 2. Academic Press, London, pp. 1039–1066.
- Candolle, A.P. de (1838) *Prodromus Systematis Naturalis Regni Vegetabilis*, vol. 7. Treuttel & Würtz, Paris, 801 pp.
- Ccana-Ccapatinta, G.V., Monge, M., Ferreira, P.L. & Da Costa, F.B. (2018) Chemistry and medicinal uses of the subfamily Barnadesioideae (Asteraceae). *Phytochemistry Reviews* 17: 471–489.
<https://doi.org/10.1007/s11101-017-9544-y>
- Chung, I.C. (1965) *Revision of Barnadesia*. Published by the author, Chicago, Illinois.
- Cialdella, A.M. & López de Kiesling, A.G. (1981) Cariología de *Schlechtendalia luzulaefolia* (Compositae). *Darwiniana* 23: 357–360.
- Cristóbal, C.L. (1986) El número cromosómico de dos Compositae–Mutisieae. *Boletín de la Sociedad Argentina de Botánica* 24: 363–380.
- DeVore, M.L., Zhao, Z., Jansen, R.K. & Skvarla, J.J. (2000) Utility of trends in pollen morphology for phylogenetic analyses: an example using subfamilies Barnadesioideae and Cichorioideae (Asteraceae). In: Harley, M.M., Morton, C.M. & Blackmore, S. (Eds.) *Pollen and Spores: morphology and biology*. Kew Royal Botanic Gardens, London, pp. 399–412.
- Diers, L. (1961) Der Anteil an Polyploidien in den Vegetationsgürteln der Westkordillera Perus. *Zeitschrift für Botanik* 49: 437–488.
- Don, D. (1830) Descriptions of the new Genera and Species of the Class Compositae belonging to the Floras of Peru, Mexico, and Chile. *Transactions of the Linnean Society of London* 16: 169–304.
<https://doi.org/10.1111/j.1095-8339.1829.tb00136.x>
- Erbar, C. & Leins, P. (2000) Some interesting features in the capitulum and flower of *Arnaldoa macbrideana* Ferreyra (Asteraceae, Barnadesioideae). *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 122: 517–537.
- Ezcurra, C. (1985) Revisión del género *Chuquiraga* (Compositae–Mutisieae). *Darwiniana* 26: 219–284.
- Ferreira, P.L., Saavedra, M.M. & Groppo, M. (2019) Phylogeny and circumscription of *Dasyphyllum* (Asteraceae: Barnadesioideae) based on molecular data with the recognition of a new genus, *Archidasyphyllum*. *PeerJ* 7: e6475.
<https://doi.org/10.7717/peerj.6475>
- Ferreyra, R. (1995) Family Asteraceae: Part IV, Tribe Mutiseae. In: Macbride, J.F. et al. (Eds.) *Flora of Peru*. Fieldiana Botany. N.S. 35: 1–101.
- Funk, V.A. & Roque, N. (2011) The monotypic Andean genus *Fulcaldea* (Compositae, Barnadesioideae) gains a new species from Northeastern Brazil. *Taxon* 60: 1095–1103.
<https://doi.org/10.1002/tax.604012>
- Grace, O.M., Pérez-Escobar, O.A., Lucas, E.J., Vorontsova, M.S., Lewis, G.P., Walker, B.E., Lohmann, L.G., Knapp, S., Wilkie, P., Särkinen, T., Darbyshire, I., Lughadha, E.N., Monro, A., Woudstra, Y., Demissew, S., Muasya, A.M., Díaz, S., Baker, W.J. & Antonelli, A. (2021) Botanical Monography in the Anthropocene. *Trends in Plant Science* 26: 433–441.
<https://doi.org/10.1016/j.tplants.2020.12.018>
- Granda, P.A. (1997) Una nueva especie de *Chuquiraga* (Asteraceae–Mutiseae) del Perú. *Kurtziana* 25: 151–156.
- Gruenstaedl, M., Urtubey, E., Jansen, R.K., Samuel, R., Barfuss, M.H.J. & Stuessy, T.F. (2009) Phylogeny of Barnadesioideae (Asteraceae) inferred from DNA sequence data and morphology. *Molecular Phylogenetics and Evolution* 51: 572–587.
<https://doi.org/10.1016/j.ympev.2009.01.023>
- Gustafsson, M.H.G., Pepper, A.S.R., Albert, V.A. & Källersjö, M. (2001) Molecular phylogeny of the Barnadesioideae (Asteraceae). *Nordic Journal of Botany* 21: 149–160.
<https://doi.org/10.1111/j.1756-1051.2001.tb01352.x>
- Hansen, H.V. (1991) Phylogenetic studies in Compositae tribe Mutisieae. *Opera Botanica* 109: 1–50.
- Harling, G. (1991) Compositae–Mutisieae. In: Harling, G. & Andersson, L. (Eds.) *Flora of Ecuador*. University of Gothenburg, Gothenburg, pp. 1–105.
- Heiser, C.B. (1963) Numeración cromosómica de plantas ecuatorianas. *Ciencia y Naturaleza* 6: 2–6.
- Hind, D.J.N. (2001) A New Species of *Barnadesia* (Compositae: Barnadesioideae) from Bolivia. *Kew Bulletin* 56: 705–710.
<https://doi.org/10.2307/4117698>
- Hoffmann, O. (1893) Tubuliflorae–Mutisieae. In: Engler, A. & Prantl, K. (Eds.) *Die natürlichen Pflanzenfamilien*, vol. 4 (5). Engelmann, Leipzig, pp. 333–350.
- Jansen, R.K. & Palmer, J.D. (1987) Chloroplast DNA from lettuce and *Barnadesia* (Asteraceae): structure, gene localization, and

- characterization of a large inversion. *Current Genetics* 11: 553–564.
<https://doi.org/10.1007/BF00384619>
- Jansen, R.K. & Palmer, J.D. (1988) Phylogenetic implications of Chloroplast DNA restriction site variation in the Mustiseae (Asteraceae). *American Journal of Botany* 75: 753–766.
<https://doi.org/10.1002/j.1537-2197.1988.tb13496.x>
- Jansen, R.K., Michaels, H.J., Wallace, R.S., Kim, K.-J., Keeley, S.C., Watson, L.E. & Palmer, J.D. (1992) Chloroplast DNA Variation in the Asteraceae: Phylogenetic and Evolutionary Implications. In: Soltis, P.S., Soltis, D.E. & Doyle, J.J. (Eds.) *Molecular Systematics of Plants*. Springer, Boston, pp. 252–279.
https://doi.org/10.1007/978-1-4615-3276-7_11
- Jussieu, A.L. (1789) *Genera Plantarum Secundum Ordines Naturales Disposita*. Hérissant & Barrois, Paris, 498 pp.
- Katinas, L. & Stuessy, T.F. (1997) Revision of *Doniophyton* (Compositae, Barnadesioideae). *Plant Systematics and Evolution* 206: 33–45.
<https://doi.org/10.1007/BF00987939>
- Kunth, C.S. (1820) Compositae. In: Humboldt, F.W.H.A., Bonpland, A.J.A. & Kunth, K.S. (Eds.) *Nova genera et species plantarum*, vol. 4. Librariae Graeco-Latino-Germanico, Paris, 312 pp. + 113 tab.
- Lessing, C.P. (1832) *Synopsis generum compositarum*. Duncker & Humblot, Berlin.
- Mandel, J.R., Dikow, R.B., Siniscalchi, C.M., Thapa, R., Watson, L.E. & Funk, V.A. (2019) A fully resolved backbone phylogeny reveals numerous dispersals and explosive diversifications throughout the history of Asteraceae. *Proceedings of the National Academy of Sciences* 116: 14083 LP-14088.
<https://doi.org/10.1073/pnas.1903871116>
- Mendiondo, M.E., Juárez, B.E. & Seeligmann, P. (1997) Flavonoid patterns of some Barnadesioideae (Asteraceae). Eventual chemosystematic significance. *Biochemical Systematics and Ecology* 25: 673–674.
[https://doi.org/10.1016/S0305-1978\(97\)00060-4](https://doi.org/10.1016/S0305-1978(97)00060-4)
- Mendiondo, M.E., Juárez, B.E. & Seeligmann, P. (2000) Flavonoid profiles of some Argentine species of *Chuquiraga* (Asteraceae). *Biochemical Systematics and Ecology* 28: 283–285.
[https://doi.org/10.1016/S0305-1978\(99\)00061-7](https://doi.org/10.1016/S0305-1978(99)00061-7)
- Mutis, J.C.B. (1781) Polyadelphia Pentandria. In: Linné, C. (Ed.) *Supplementum Plantarum*. Brunsvigae, pp. 55.
- Nabhan, A.R. & Sarkar, I.N. (2012) The impact of taxon sampling on phylogenetic inference: a review of two decades of controversy. *Briefings in bioinformatics* 13: 122–134.
<https://doi.org/10.1093/bib/bbr014>
- Nakajima, J.N., Dematteis, M., Loeuille, B., Teles, A.M., Heiden, G., Schneider, A., Ritter, M., Oliveira, C.T., Hattori, E.K.O., Roque, N., Ferreira, S.C., Magenta, M., Bringel, J.B.A., Esteves, R., Almeida, G.S.S., Saavedra, M.M., Monge, M., Soares, N.P., Sancho, G., Mondin, C.A., Fernandes, A.C., Pereira, A.C.M., Kutschenko, D.C., Filho, L.A.F.S., Prieto, P.V., Borges, R.A.X., Penedo, T.S.A., Messina, T., Moraes, M.M.V., Moraes, M.A. & Coelho, M.A.C. (2013) Asteraceae. In: Martinelli, G. & Moraes, M.A. (Eds.) *Livro vermelho da Flora do Brasil*. Centro Nacional de Conservação da Flora, Rio de Janeiro, pp. 203–286.
- Olsen, J. (1980) Chromosome number reports LXVII. *Taxon* 29: 366–367.
<https://doi.org/10.1002/j.1996-8175.1980.tb00607.x>
- Padin, A.L., Calviño, C.I. & Ezcurra, C. (2015a) Morfología y anatomía foliar comparada de *Chuquiraga* y géneros afines (Asteraceae). *Brittonia* 67: 150–165.
<https://doi.org/10.1007/s12228-015-9364-6>
- Padin, A.L., Calviño, C.I. & Ezcurra, C. (2015b) Molecular Phylogeny of *Chuquiraga* (Asteraceae-Barnadesioideae): Infrageneric Classification and Generic Affinities. *Systematic Botany* 40: 316–326.
<https://doi.org/10.1600/036364415X686602>
- Poeppig, E.F. & Endlicher, S.L. (1835–1836) *Nova genera ac species plantarum*, vol. 1. F. Hofmeister, Leipzig, 62 pp.
- Poiret, J.L.M. (1817) *Fulcaldea* [under *Turpinia*]. In: Lamarck, M. & Poiret, J.L.M. (Eds.) *Encyclopedie Methodique*, Botanique, suppl., vol. 5. Paris, pp. 575.
- QGIS Development Team (2019) QGIS Geographic Information System, version 3.4. Open Source Geospatial Foundation Project. Available from: <http://qgis.osgeo.org> (accessed 20 February 2019)
- Radford, A.E., Dickson, W.C., Massey, W.C. & Bell, C.R. (1974) *Vascular Plant Systematics*. Harper & Row, New York, 891 pp.
- Saavedra, M.M. (2011) *Sistemática de Dasyphyllum (Asteraceae)*. Phd Thesis. Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Rio de Janeiro, pp. 1–247.
- Saavedra, M.M. (2020) *Dasyphyllum* in Flora do Brasil 2020. Jardim Botânico do Rio de Janeiro. Available from: <http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB5291> (accessed 20 March 2021)

- Saavedra, M.M., Guimarães, E.F., Loeuille, B. & Forzza, R.C. (2018) Taxonomic Revision of *Dasyphyllum* sect. *Macrocephala* (Asteraceae: Barnadesioideae). *Systematic Botany* 43: 297–315.
<https://doi.org/10.1600/036364418X696888>
- Saavedra, M.M., Monge, M., Guimarães, E.F. (2014) *Dasyphyllum diamantinense* (Asteraceae, Barnadesioideae): A new species from the Chapada Diamantina, Bahia State, Brazil. *Phytotaxa* 174 (4): 231–236.
<https://doi.org/10.11646/phytotaxa.174.4.4>
- Sagástegui, A.A. (1980) Compuestas andinas peruanas nuevas para la ciencia. *Boletín de la Sociedad Argentina de Botánica* 19 (1–2): 61–68.
- Sagástegui, A.A. & Dillon, M. (1985) Four new species of Asteraceae from Peru. *Brittonia* 37 (1): 6–13.
<https://doi.org/10.1007/BF02809659>
- Sagástegui, A.A. & Sánchez, V.I. (1991) Una nueva especie de *Chuquiraga* (Asteraceae-Mutisieae) del Norte del Peru. *Arnaldoa* 2: 1–4.
- Schumann, K.M. (1902) Neue Arten des Siphonogamen. *Just's botanischer Jahresbericht* 28 (Abt. 1): 410–498.
- Skvarla, J.J., Turner, B.L., Patel, V.C. & Tomb, A.S. (1977) Pollen morphology in the Compositae and in morphologically related families. In: Heywood, V.H., Harborne, J.B. & Turner, B.L. (Eds.) *The Biology and Chemistry of the Compositae*. Academic Press, London, pp. 141–248.
- Strother, J.L. & Panero, J.L. (1994) Chromosome studies: Latin American Compositae. *American Journal of Botany* 81: 335–577.
<https://doi.org/10.2307/2445657>
- Stuessy, T.F. & Sagástegui, A.A. (1993) Revision de *Arnaldoa* (Compositae, Barnadesioideae) género endémico del norte del Peru. *Arnaldoa* 1: 9–21.
- Stuessy, T.F. & Urtubey, E. (2006) Phylogenetic implications of corolla morphology in subfamily Barnadesioideae (Asteraceae). *Flora: Morphology, Distribution, Functional Ecology of Plants* 201: 340–352.
<https://doi.org/10.1016/j.flora.2005.07.009>
- Stuessy, T.F. & Urtubey, E. (2007) Barnadesioideae. In: Kadereit, J.W. & Jeffrey, C. (Eds.) Kubitzki, K., *The Families and genera of vascular plants*, vol. 8. Springer-Verlag, Berlin & Heidelberg, pp. 87–90.
- Stuessy, T.F., Sang, T. & DeVore, M.L. (1996) Phylogeny and biogeography of the subfamily Barnadesioideae with implications for early evolution of the Compositae. In: Hind, D.J.H. & Beentje, H.J. (Eds.) *Compositae: Systematics. Proceedings of the International Compositae Conference, Kew, 1994*, vol. 1. Royal Botanical Garden, Kew, pp. 463–490.
- Stuessy, T.F., Urtubey, E. & Gruenstaedl, M. (2009) Barnadesioideae (Barnadesioideae). In: Funk, V.A., Susanna, A., Stuessy, T. & Bayer, R.J. (Eds.) *Systematics, evolution, and biogeography of Compositae*. IAPT, Vienna, pp. 215–228.
- Svoma, E., Mayer, V., Stuessy, T.F. & Urtubey, E. (2019) Staminal features in Barnadesioideae (Asteraceae): description, evolution and function. *Botanical Journal of the Linnean Society* 192: 474–497.
<https://doi.org/10.1093/botlinnean/boz091>
- Tellería, M.C., Palazzesi, L. & Barreda, V. (2015) Evolutionary significance of exine ultrastructure in the subfamily Barnadesioideae (Asteraceae) in the light of molecular phylogenetics. *Review of Palaeobotany and Palynology* 221: 32–46.
<https://doi.org/10.1016/j.revpalbo.2015.05.008>
- Thiers, B. (2019) Index Herbariorum: A Global Directory of Public Herbaria and Associated Staff. New York Botanical Garden's Virtual Herbarium. Available from: <http://sweetgum.nybg.org/science/ih/> (accessed 20 February 2019)
- Ulloa Ulloa, C., Jørgensen, P.M. & Dillon, M.O. (2002) *Arnaldoa argentea* (Barnadesioideae: Asteraceae), a new species and a new generic record for Ecuador. *Novon* 12: 415–419.
<https://doi.org/10.2307/3393091>
- Urtubey, E. & Stuessy, T.F. (2001) New hypotheses of phylogenetic relationships in Barnadesioideae (Asteraceae) based on morphology. *Taxon* 50: 1043–1066.
<https://doi.org/10.2307/1224720>
- Urtubey, E. (1997) Morfología del pólen de *Barnadesia* (Asteraceae, Barnadesioideae). *Boletín de la Sociedad Argentina de Botánica* 33: 69–75.
- Urtubey, E. (1999) Revisión del género *Barnadesia* (Barnadesioideae, Asteraceae). *Annals of the Missouri Botanical Garden* 86: 57–111.
<https://doi.org/10.2307/2666218>
- Urtubey, E. & Tellería, M.C. (1998) Pollen morphology of the subfamily Barnadesioideae (Asteraceae) and its phylogenetic and taxonomic significance. *Review of Palaeobotany and Palynology* 104: 19–37.
[https://doi.org/10.1016/S0034-6667\(98\)00049-9](https://doi.org/10.1016/S0034-6667(98)00049-9)
- Watanabe, K., Yahara, T., Hashimoto, G., Nagatani, Y., Soejima, A., Kawahara, T. & Nakazawa, M. (2007) Chromosome numbers and karyotypes in Asteraceae. *Annals of the Missouri Botanical Garden* 94: 643–654.

[https://doi.org/10.3417/0026-6493\(2007\)94\[643:CNAKIA\]2.0.CO;2](https://doi.org/10.3417/0026-6493(2007)94[643:CNAKIA]2.0.CO;2)

Weddell, H.A. (1855) *Chloris andina: essai d'une flore de la région alpine des Cordillères de l'Amérique de Sud*. Bertrand, Paris.

<https://doi.org/10.5962/bhl.title.217>

Wulff, A.F. (1984) Estudios cromosómicos en Compuestas de las floras patagónica y bonaerense. *Darwiniana* 25: 17–26.

Wulff, A.F. (1990) Estudios cromosómicos en Barnadesiinae (Mutisieae, Asteraceae). I. *Chuquiraga* y *Doniophyton*. *Darwiniana* 30: 185–193.

Zhao, Z., Skvarla, J.J., Jansen, R.K. & DeVore, M.L. (2000) Phylogenetic implications of pollen morphology and ultrastructure in the Barnadesioideae (Asteraceae). *Lundellia* 3: 26–40.

<https://doi.org/10.25224/1097-993X-3.1.26>