

New combinations in *Belloa* J. Rémy and new diagnoses for Andean *Lucilia* Cass. and *Mniodes* (A.Gray) Benth. (Gnaphalieae, Asteraceae)

Nuevas combinaciones en *Belloa* J. Rémy y nuevos diagnósticos de *Lucilia* Cass. y *Mniodes* (A. Gray) Benth. (Gnaphalieae, Asteraceae) de los Andes



Abstract

Changes in the generic boundaries, as suggested by DNA sequence data, have altered concepts of Andean Asteraceae, specifically *Belloa* J. Rémy, *Lucilia* Cass., and *Mniodes* (A.Gray) Benth. (Gnaphalieae, Asteraceae). Over the past 30 years, numerous changes in classification and the resulting transfers have generated confusion. This paper provides a short history of these changes and current information for these genera as they exist in Andean South America. Further, other transfers are provided as suggested by results of sequence analysis data and newly proposed generic concepts: *Belloa eriophora* (J. Rémy) M. O. Dillon, comb. nov., and *Belloa nivea* (Phil.) M. O. Dillon, comb. nov. Changes in the diagnosis of *Mniodes* necessitates the following transfers: *Mniodes argentea* (Wedd.) M. O. Dillon, comb. nov., *M. spathulifolia* (Sagást. & M. O. Dillon) M. O. Dillon, comb. nov. and *M. turneri* (Sagást. & M. O. Dillon) M. O. Dillon, comb. nov.

Keywords: Asteraceae, Gnaphalieae, Chile, Peru, Andean flora.

Resumen

Los cambios en los límites genéricos, como sugieren los datos de secuenciación de ADN, han alterado conceptos en las asteráceas andinas, específicamente en *Belloa* J. Rémy, *Lucilia* Cass. y *Mniodes* (A. Gray) Benth. (Gnaphalieae, Asteraceae). En los últimos 30 años, numerosos cambios en la clasificación y las transferencias resultantes han generado confusión. Este documento proporciona una breve historia de estos cambios y la información actual para estos géneros tal como existen en los Andes de América del Sur. Además, se proporcionan varias transferencias como lo sugieren los resultados de análisis de secuenciación y nuevos conceptos genéricos propuestos: *Belloa eriophora* (J. Rémy) M. O. Dillon, comb. nov., y *Belloa nivea* (Phil.) M. O. Dillon, comb. nov. Los cambios en el diagnóstico de *Mniodes* requieren las siguientes transferencias: *Mniodes argentea* (Wedd.) M. O. Dillon, comb. nov., *Mniodes spathulifolia* (Sagást. & M. O. Dillon) M. O. Dillon, comb. nov. y *Mniodes turneri* (Sagást. & M. O. Dillon) M. O. Dillon, comb. nov.

Palabras clave: Asteraceae, Gnaphalieae, Chile, Perú, flora andina.

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Introduction

The Gnaphalieae (Cass.) Lecoq & Juill. (Asteraceae) is a small tribe comprising ca. 185 genera (Ward *et al.*, 2009) and perhaps 2000 species. In South America, some 20 genera and over 100 species are recorded with highest diversity in the tropical and subtropical Andean Cordillera (Dillon & Sagástegui 1991), and some have proliferated in upper elevation or alpine habitats (Dillon, 2005). These genera overwhelmingly possess at least some members with reduced habits form small cushions of tightly clustered pubescent stems and densely canescent leaves. Some genera look remarkably similar, both in

the field and as collections on herbarium sheets. Experience within these groups has suggested that inspection of capitular and floral microcharacters are necessary for generic identity to be confirmed with certitude.

Biologists often distinguish between 'convergent' and 'parallel' evolution (Arendt & Reznick, 2008). The distinction between these two usually assumes that phenotypes are the result of the underlying genetic mechanisms; when the mechanisms are different and in distantly related taxa it is convergent, but when mechanisms are similar and in more closely related taxa it is termed parallel. Convergent evolution, such

as the formation of cushion plants in high-elevation habitats within several different families, for example, *Azorella compacta* Phil. (Apiaceae), *Mniodes aretioides* (Schultz-Bip.) Cuatrec. (Asteraceae), and *Pycnophyllum peruvianum* Muschl. (Caryophyllaceae). The formation of cushions within different clades of the subtribe Gnaphaliinae could be viewed as parallel, similar forms in *Mniodes* (A. Gray) Benth. (South America), *Pterygopappus* Hoof.f. (Tasmania), and *Raoulia* Hook.f. (New Zealand), with each having derived from related genetic origins (Luebert *et al.*, 2017, Nie *et al.*, 2013). The distinction within the tribe would be best viewed as a continuum of convergence.

Generic boundaries have been controversial and none more so than the recognition and relationships of a suite of genera in the *Lucilia*-group, an informal gathering first proposed by Merxmüller *et al.* (1977). The recognition and constitution of *Belloa* J. Rémy and *Lucilia* Cass. has been an ongoing classification saga (Dillon 1990, Luebert *et al.*, 2017). The description of additional genera, e.g., *Luciliocline* Anderb. & S. E. Freire and *Gamochoetopsis* Anderb. & S. E. Freire, has been confusing even to the most astute student of the Asteraceae. Further, in response to sequence data, Friere *et al.* (2014) transferred all *Luciliocline*, and some *Lucilia* and some *Belloa* into a greatly expanded *Mniodes* Wedd. The generic delimitation or boundaries of *Belloa* and *Lucilia* have been expanded (Cabrera, 1958; Freire, 1986; 1987a,b) and contracted (Anderberg & Freire 1991, Dillon, 2003; Freire *et al.*, 2014). Recently, on the strength of molecular studies (Urtubey *et al.*, 2016), *Lucilia alpina* (i.e., *Gamochoetopsis*) has been transferred to *Gamochoeta* Wedd.

Materials and methods

Herbarium material was investigated

from the following herbaria: including B, BM, COL, CONC, F, GH, HAO, HSP, HUT, K, M, MO, NY, P, SGO, TEX, US, and W. Dried herbarium material was used for measurements and descriptions of achene surface structures. Vouchers were listed in Luebert *et al.*, 2017 (cf. Appendix 2). Herbarium acronyms follow Thiers (2017).

Results and discussion

A. Chilean *Belloa* J. Rémy (1847)

In 1835, William Joseph Hooker and George Walker Arnott published *Lucilia chilensis* Hook. & Arn. based upon a collection by Hugh Cumming 342 from Chile. De Candolle (1838) recognized the distinctness of *Lucilia chilensis* when he established *Lucilia* section *Lucilioides* based upon *Lucilia chilensis*. J. Rémy (1847) described the genus *Belloa* to contain *Belloa (Lucilia) chilensis*, a single species with pubescent achenes but with much smaller trichomes, only 40–50 µm long. He was aware of the genus *Lucilia*, also having described *Lucilia eriophora* J. Rémy (1847) from central Andean Chile in the same publication. The latter species has achenes pubescent with elongate twin hairs or *Zwillingshaares* (Hess 1938), the type and size of trichomes more similar to other *Lucilia* species with twin hairs > 150 µm long.

Cabrera (1958) recognized *Belloa* as distinct from *Lucilia* Cass. and transferred six species that had been in *Gnaphalium* L., *Lucilia* or *Merope* Wedd. Subsequently, Cabrera (1958) expanded his concept of *Belloa*, transferring two more species and describing two new species from Peru and Argentina. He commented that *Belloa* was distinct and easily distinguishable from *Lucilia* principally through their achenial trichomes. In addition to the strikingly different pubescence of the achenes, several other important characteristics separated

these two genera, including the apices of the style branches of hermaphroditic florets and pappus characteristics. One of the species that Cabrera initially recognized as a *Belloa*, *B. erythraetis* (Wedd.) Cabrera, was subsequently transferred to *Gamochoaeta* Wedd. on the basis of its unique, sessile achenial trichomes (Cabrera 1978, Urtubey *et al.*, 2016).

Freire (1986) provided a monograph for *Lucilia* and expanded its generic limits to include all taxa previously accorded to *Belloa* (Cabrera 1958; Sagástegui & Dillon 1985) with the statement that the type of achenial trichomes had no phylogenetic significance and provided no distinction between *Belloa* and *Lucilia*. She had based her classification system upon phenetic cladistic analysis (Freire 1984) and subsequently published another phenetic cladistic analysis (Freire 1987b) to support her expanded *Lucilia*. Freire (1987a) published a paper where she synonymized several of the newly described species proposed by Sagástegui & Dillon (1985). She argued for an expanded generic concept for *Lucilia*; a diagnosis that allowed for a genus with component species containing at least two fundamentally different types of achenial trichomes, i.e., some species possessing biseriate, capitate-glandular trichomes and others possessing elongate twin hairs or *Zwillingshaares* (Hess, 1938). Under the discussion, Freire maintained that the types of achenial trichomes were trivial and had no importance in the systematics of the group.

Dillon (1988, 1990) presented data suggesting that the two different types of trichomes represented in some *Belloa* (*pro parte*) and those of *Lucilia* (*sensu stricto*) were the products of quite complex ontogenetic patterns that were fundamentally different. These ontogenetic developments are not

reversible ontogenetic endpoints, i.e., one type of trichomes could not revert or transform into the other. There appears to be no capacity to reverse ontological developments as illustrated by Hess (1938).

During morphological investigations, Dillon and Sagástegui (1991) provided the observation that a unique type of achenial trichomes was to be found in both *Mniodes* and in some members of *Belloa* (*sensu lato*), i.e., not like those of the type species but rather like those eventually become *Luciliocline* Anderb. & S. E. Freire and more recently *Mniodes* (Freire *et al.*, 2014). Dillon (2003) accepted *Luciliocline*, concluding that Chilean *Belloa* (*B. chilensis*) were distinct and easily separated from *Luciliocline*. Further, Dillon (2003) suggested that *Mniodes* and *Luciliocline* shared close relationships, as both possessed similar habits, leaves, and floral morphology as well as the achenial trichomes.

Anderberg and Freire (1991) published a morphological cladistic analysis where *Lucilia* was dismantled, parsing the various species into four genera, i.e., *Lucilia* (8 spp.), *Belloa* (9 spp.), *Luciliocline* (5 spp.), and *Gamochoetopsis* (1 sp.). Surprisingly, their generic diagnosis for both *Belloa* and *Luciliocline* contained clearly non-parsimonious mixtures of achenial trichome types by maintaining *Lucilia* species within their concept of *Belloa*, [e.g. *Lucilia kunthiana* (DC.) Zardini, *L. lehmannii* Hieron.]. They amended the generic description of *Belloa* to include a mixture of the types of achenial trichomes with six *Luciliocline* species considered as *Belloa*.

Dillon (2003) provided transfers for eight *Belloa* species to *Luciliocline*. In Dillon's generic diagnosis, all species *Luciliocline* were diagnosed by achenes covered with capitate-glandular trichomes or rarely, with trichomes only near the carpopodium.

He recognized *B. kunthiana* as a legitimate member of *Lucilia* and placed *B. lehmannii* under the synonymy of the former species; both these taxa have achenes possessing elongate, twin hairs > 150 µm long. Dillon (2003) had considered *Belloa chilensis* (Hook. & Arn.) J. Rémy to be monotypic and with trichomes representing greatly reduced twin hairs and not similar to the capitateglandular achenial trichomes possessed by *Luciliocline* and some *Mniodes*. However, these two species have well-developed twin hairs.

Although, gross morphology was not unlike other *Lucilia* species, *L. eriophora* and *L. nivea*, are here transferred to *Belloa* on the strength of DNA results and biogeography (Luebert *et al.*, 2017; Nie *et al.*, 2013). The Chilean species previously attributed to *Lucilia*, i.e., *L. nivea* and *L. eriophora* are recovered in well-supported clade with *Belloa chilensis*. The apical cells of the trichomes of *Belloa chilensis* are uniformly less than 50 µm long (Dillon 2003).

These Chilean taxa are isolated from the clade containing *Lucilia s.s.* Freire *et al.* (2014) interpreted *Belloa* as monotypic and placed *L. araucana* Phil., *L. eriophora* and *L. nivea* into synonymy of an expanded *Belloa*. Luebert *et al.* (2017) maintained these morphologically distinct taxa and *Lucilia eriophora* and *L. nivea* are here transferred to join a re-circumscribed *Belloa*. The new diagnosis of *Belloa* includes the presence of two sizes of trichomes, elongate, twin hairs >150 µm long in *L. eriophora* and *L. nivea*, and smaller twin hairs uniformly <50 µm long in *Belloa chilensis*.

Lucilia araucana Phil. (1895) is perhaps best placed in the synonymy of *L. nivea* on the strength of overall comparative morphology. It may be observed that *L. araucana* tends to form more compact cushions, however, field observations

have confirmed that growing positions can affect overall phenotypes and especially shortening or expanding internode length. These two species share elongated achenial trichomes and further studies are needed to confirm taxonomic status.

1. *Belloa chilensis* (Hook. & Arn.) J. Rémy, Basionym: *Lucilia chilensis* Hook & Arn., *Comp. Bot. Mag.* 1: 102. 1835. TYPE: Chile, Región V (Valparaíso), Valparaíso, *H. Cuming* 342 (lectotype: K000500443; isolectotypes: K00050439, P00704659). Fig. 1, 2.

2. *Belloa eriophora* (J. Rémy) M. O. Dillon, comb. nov., Basionym: *Lucilia eriophora* J. Rémy, *Fl. Chil.* 3 (3): 335. 1847. TYPE: Chile, Región VI (Libertador General Bernardo O'Higgins), Prov. Colchagua, Yaquil, "april 1839", *C. Gay* 243 (holotype: P, FM neg. 37818). Fig. 3.

3. *Belloa nivea* (Phil.) M. O. Dillon, comb. nov., Basionym: *Chevreulia nivea* Phil., *Anales Univ. Chile* 21: 380. 1862. TYPE: Chile, Región VIII (Bio-Bio), Concepcion, Nevado de Chillan, Cerro de Azufre, *R.A. Philippi s.n.* (holotype: SGO#64455). *Lucilia nivea* (Phil.) Cabrera, *Notas Mus. La Plata, Bot.* 7: 118. 1942.

B. Andean *Lucilia* Cass. (1817)

Molecular studies (Luebert *et al.*, 2017, Nie *et al.*, 2013) confirm that Andean *Lucilia*, i.e., *L. kunthiana* and *L. conoidea*, are recovered in a clade with other members of the genus from Brazil, and *Berroa*, *Facelis*, and *Micropsis*. These high-elevation taxa with greatly reduced habits have been recorded from throughout the Andean Cordillera from Venezuela to Argentina and Chile. Therefore, *Lucilia* is a genus of nine species distributed throughout South America, but with a center of diversity in Argentina, Bolivia, southeast Brazil, Uruguay and Paraguay; two are known from Peru and

a single species *Lucilia kunthiana* recorded from Venezuela, Colombia, Ecuador, Peru, Bolivia, Argentina, and Chile.

The generic limits between *Lucilia* and *Belloa* have been controversial (see above). The gross appearance of some members of each genus is quite similar and especially those which occupy high elevation Andean habitats. Cassini's original description of *Lucilia* described sericeous achenes; however, Freire (1986; 1987a) expanded the genus and transferred several species possessing achenes with biseriate, multicellular, capitate-glandular trichomes into *Lucilia*. Sagástegui & Dillon (1985) removed from *Lucilia* all members with glandular achenes and placed them in *Belloa*. Eventually, the genus *Luciliocline* was proposed for the majority of species in *Belloa* (Dillon, 2003). In the present treatment, only those taxa with consistently sericeous achenes are included in *Lucilia*. The extra-Andean taxa are restricted to more eastern South America and at altitudes below 3000 m; *Lucilia acutifolia* (Poir.) Cass., *L. ferruginea* Bak., *L. linearifolia* Bak., *L. lycopodioides* (Less.) S. E. Freire, *L. nitens* Less., and *L. tomentosa* Wedd.

Key to Species of Andean *Lucilia*

1. Habit not cespitose; stems weakly erect, 6-18 cm tall, leaves linear-oblong, 2-6 mm long, 0.7-1 mm wide, recurved; capitula 9-11 mm tall *L. recurva*

1'. Habit cespitose; stems in dense cushions, linear-obovate to spatulate, 5-20 mm long, 0.8-2 mm wide, blades not recurved but occasionally plane to falcate; capitula (5-)7-8 mm tall2

2. Leaves spatulate, plane to falcate, 10-20 mm long, 1-2 mm wide, both surfaces tomentose *L. kunthiana*

2'. Leaves linear, pleated or canaliculate,

5-15 mm long, 0.8-1 mm wide, lower surface arachnoid-tomentose, glabrescent, upper surface densely silvery-tomentose *L. conoidea*

1. *Lucilia conoidea* Wedd., Chlor. Andina 1: 154. 1856. TYPE: Peru, Dept. Cuzco, "Cordilleres du departement de Cuzco," C. Gay 1355 (holotype: P00704661, fragment, F). Fig. 4, 5.

Lucilia conoidea is known from southern Peru and northern Bolivia. It approaches *L. kunthiana* in general appearance but is distinctive in having leaves that are pubescent on the upper surface and glabrescent below, the reverse of the usual condition in *Lucilia*. This morphological distinction has a restricted geographic range in southern Peru and adjacent Bolivia. *Lucilia conoidea* was reduced to synonymy of *L. kunthiana* (as *L. pusilla*) by Freire (1986).

2. *Lucilia kunthiana* (DC.) Zardini, Ann. Missouri Bot. Gard. 74: 431. 1987.

Conyza kunthiana DC., Prodr. 5: 379. 1836. (nomen novum for *Conyza pusilla* Kunth). *Gnaphalium kunthianum* (DC.) Kuntze, Revis. Gen. PL, 3: 152. 1898. *Mniodes kunthiana* (DC.) S. E. Freire, Chemisquy, Anderb. & Urtubey, Pl. Syst. Evol. 301 (4): 1245. 2014.

Conyza pusilla Kunth, Nov. Gen. Sp. (fol.) 4: 54. 1820. TYPE: Ecuador, Prov. Pichincha, "crescit regione alpina Regni Quitensis," A. Humboldt & A. Bonpland s.n. (holotype: P00322293; isotype: P00704669, FM neg. 15126). Non Houuttuyn (1779). *Lucilia pusilla* (Kunth) Hieron., Bot. Jahrb. Syst., 29. 29. 1900. Fig. 6.

Gnaphalium depressum Nutt., Trans. Amer. Philos. Soc., n.s. 7: 405. 1841. TYPE: Ecuador, Prov. Pichincha, W. Jameson s.n. (holotype: PH-01085444, img 00012252).

Lucilia lehmannii Hieron., Bot. Jahrb. Syst. 19: 51. 1895. TYPE: Ecuador, Prov.

Azuay, Paramo del Cajas, 3600-4200 m, F. C. *Lehmann* 4649 (holotype: B, probably destroyed, F neg. 15126; isotype: NY00214769). *Mniodes lehmannii* (Hieron.) S. E. Freire, *Chemisquy*, *Anderb. & Urtubey*, *Pl. Syst. Evol.* 301 (4): 1245. 2014.

Lucilia affinis Wedd., *Chlor. Andina* 1: 230. 1857. TYPE: Bolivia, La Paz, Cordilleres du departement de la Paz, *H. Mandon* 168 (lectotype: K000500449; isolectotypes: G00223212, G00223213, P02533964, P02533965, P02533966, P02533958).

Lucilia violacea Wedd., *Chlor. Andina* 1: 155. 1855[1856]. TYPE: Bolivia, Cordillera de Sorata, *Weddell s.n.* [biz 3000] (holotype: P00704674).

Lucilia venezuelensis Steyer., *Fieldiana, Botany* 28: 644, f. 140. 1953. TYPE: Venezuela, Merida, below El Aguila and Chachopo, 3650-3965 m, 13 Mar 1944, *J. A. Steyermark* 55657 (holotype: F-1390433; isotypes: NY00214771, US-2046674, VEN).

Lucilia kunthiana is distributed throughout high elevation Andean habitats from Venezuela, Colombia, Ecuador, Peru, Bolivia, and extreme northern Chile; 3000-4800 m. Many regional species have described for cespitose, highly reduced plants with canescent leaves and achenes densely pubescent.

Schultz-Bip. (1856) proposed *Gnaphalium evacooides* based upon a plant collected from Venezuela by *Moritz* 1407 (P); however, the name was not validly published. Steyermark (1953) concluded that it was identical to *Gnaphalium radians* Benth. At the same time, Steyermark transferred *Gnaphalium radians* Benth. to *Lucilia*, placing *G. evacooides* Schultz-Bip. under its synonymy; Bentham's type material was collected by *K.T. Hartweg* 1146 (K) in Colombia. Steyermark mentioned that *G. radians* had been confused with *Lucilia kunthiana* (as *L. pusilla*), a species

originally collected in Ecuador by Bonpland and Humboldt and described in *Conyza*. De Candolle (1836) provided a new name, *Conyza kunthiana* due to the presence of an earlier homonym, *Conyza pusilla* Houtt 1779.

Weddell (1855) misinterpreted Bentham's Colombian *Gnaphalium radians* and Knuth's Ecuadorian species, *Conyza pusilla*, combining them under one name, *Merope kunthiana* (DC.) Wedd. The same error was perpetrated by Hieronymus (1900) as he combined all under one name, *Lucilia pusilla*.

Steyermark (1953) stated that Bentham's *Gnaphalium radians* and *Conyza pusilla* Kunth were entirely different species and recognized by their achenes, with the former being glabrous and the latter being densely pubescent with elongate, biseriate trichomes (*Zwillingshaares*). From this material, Steyermark described *Lucilia venezuelensis* and related it to *Lucilia kunthiana*, a species with densely pubescent achenes with elongate (>150 µm) biseriate trichomes distributed from Colombia to Argentina.

2. *Lucilia recurva* Wedd., *Chl. Andina*, 1: 156, tab. 25B, 1856. TYPE: Bolivia. Dept. Chuquisaca, Prov. Tomina, "sur les rochers nus, près du sommet du mont Curi", 3500 m, *H. Weddell* 3742 (lectotype: P00704670; isolectotype: P00704671). Fig. 7.

Lucilia recurva is recorded from dry sites in Bolivia (Cochabamba, Chuquisaca, Tarija) and Argentina (Salta), most frequently at 2500-2800 m. As the species epithet implies, its oblong leaves are strongly recurved. It is noteworthy that unlike the close relationship between *L. conoidea* and *L. kunthiana* (sister taxa), the relationship of *L. recurva* apparently with Brazilian taxa, i.e., *L. acutifolia* and *L. lycopodioides* (Luebert et al., 2017, Nie et al., 2013).

C. *Laennecia alpina* Poepp. (1845)

Laennecia alpina was proposed by Poeppig (1845) for a small herb with obovate or suborbicular leaves and achenes with pilose pubescence collected in southern Chile (Araucanía, Los Lagos, Magallanes and Chilean Antarctica). Cabrera (1961) considered it to be congeneric with *Lucilia* [i.e., *L. alpina* (Poepp.) Cabrera]. He stated that it could be confused vegetatively with *Gamochaeta nivalis* (Phil.) Cabrera, but suggested that it was easily distinguished from the latter taxon by its pubescent achenes.

Anderberg and Freire (1991) based their new genus, *Gamochaetopsis* Anderb. & S. E. Freire, upon *Laennecia alpina*. In an examination of the type collection at W, it was observed that the achenial trichomes elaborated in *Gamochaetopsis* are essentially reduced clavate trichomes (ca. 60 µm long) and quite unlike the sessile, biseriate trichomes elaborated in all authentic *Gamochaeta* (< 20 µm). In the analysis of resulting from sequence data, both Urtubey *et al.* (2016) and Luebert *et al.* (2017) found *Gamochaetopsis* as resolved as nested in a clade also including *Gamochaeta* and *Stuckertiella* Urtubey *et al.* (2016) transferred *L. alpina* from *Gamochaetopsis* to *Gamochaeta*. In an effort to document the morphology of reproductive characters of authentic material, the holotype collection housed at W (Vienna, Austria) E. F. Poeppig 889 (W0028920, Fig. 8) was investigated. Achenes were prepared for SEM photographs, including pappus and achenial trichomes (Fig. 9). Our observations point to inconsistencies between the morphology of the type collection, the protolog for the species by Poeppig (1845), and subsequent generic description by Anderberg and Freire (1991).

***Gamochaeta alpina* (Poepp.) S. E. Freire & Anderb.**, In: E. Urtubey, *et al.*, 2016. New circumscription of the genus *Gamochaeta* (Asteraceae, Gnaphalieae) inferred from nuclear and plastid DNA sequences. Pl. Syst. Evol. 302: 1062. Basionym: Chile. "Chile australis rupium fissuris montis Pico de Pilque in Andibus Antuensium, Januario florebat", 1829, E.F. Poeppig 889 (holotype: W0028920; isotype: G-DC, G00499745).

D. *Mniodes* (A.Gray) Benth. (1873)

Freire *et al.* (2014) found *Mniodes* and *Luciliocline* Anderb. & S. E. Freire in the same clade, and transferred an array of species into *Mniodes*, a genus traditionally composed of strictly dioecious species. Luebert *et al.* (2017) also recovered members of *Mniodes* and *Luciliocline*, a connection that had been suggested by similarity in achenial trichomes (Dillon & Sagástegui 1991). This new generic concept requires additional taxa from *Luciliocline* be transferred into monophyletic group circumscribed by both morphological and molecular markers. While the *Lucilia*-group is recovered in the same large New World clade, neither *Mniodes* nor *Luciliocline* are closely related to *Lucilia* or *Belloa*. A few highly reduced *Mniodes* species approach *Raouliopsis* S. F. Blake (Colombia) in general compact habit and reduced tightly clustered leaf arrangements. The latter genus is recorded from extreme northern South America and diagnosed with compact habits and strictly dioecious breeding systems; molecular systematic studies have not been successful.

With a monograph of *Mniodes* in preparation, including several new species, the following combinations are necessary as a new diagnosis of *Mniodes* is adopted.

1. ***Mniodes argentea* (Wedd.) M. O. Dillon, comb. nov.** Basionym: *Merope argentea* Wedd., Chl. And. 1: 163. 1856.

TYPE: Bolivia, Dept. La Paz, Quebrada de Chuquiaguillo, *H. Weddell s.n.* (holotype: P00704580). Fig. 10.

Freire (1986) placed *Belloa argentea* into the synonymy of *Belloa schultzii* with the statement that the presence of papillose achenes was not sufficient to recognize the species. Ariza (1989) accepted *Belloa schultzii* and distinguished it from all other Argentine species as having a cushion-form habit and glabrous achenes. While potentially related to *M. schultzii*, a position supported by molecular sequence data (Luebert *et al.*, 2017), morphological differences allow discrimination of *M. argentea* from its sister species, *M. schultzii*; the former species has glabrous upper leaf surfaces.

Weddell (1855) described *Meropargentea*, *M. schultzii* Wedd., *M. virescens* Wedd., and *M. caespititia* Wedd. consecutively and in this order (p. 163–164). The first two, *L. argentea* and *L. schultzii*, are each accepted and treated as distinct; the former with smaller habit and achenes pubescent with capitate-glandular trichomes. Cabrera (1978) recognized *L. argentea* as distinct from *L. virescens* (a synonym of *L. schultzii*) based upon the latter's larger leaves and pubescent achenes. In molecular studies, nrDNA data suggests these two species are sister taxa (Luebert *et al.*, 2017).

2. *Mniodes spathulifolia* (Sagást. & M. O. Dillon) M. O. Dillon, **comb. nov.** Basionym: *Belloa spathulifolia* Sagást. & Dillon, *Phytologia* 58 (6): 394. 1985. TYPE: Peru, Dept. La Libertad, Prov. Santiago de Chuco, A. Sagástegui A., J. Mostacero L., & M. Diestra Q. 11695 (holotype: HUT; isotypes: F1947608, FM neg. 061880, MO). Fig. 11.

Freire (1987b) placed *Belloa spathulifolia* under the synonymy of *Lucilia santanica* (Cabrera) S. E. Freire, overlooking differences in habit, capitulescence, floral

number, ecological preferences, and geographic distribution (Sagástegui & Dillon 1985). It is perhaps difficult for systematists to evaluate species without herbarium and field observations. Based upon data from several sources, we reject the suggestion by Freire that this distinctive taxon is a synonym of *Mniodes (Luciliocline) santanica*, a species with distinct morphology and distributed nearly 2500 kms to the south in northern Argentina.

While discussing *Mniodes santanica*, it is noteworthy that Anderberg and Freire (1991) also listed *Gnaphalium depressum* Nutt. and *Gnaphalium sarmentosum* Klatt as synonyms of *M. santanica*. An examination of type material shows these taxa are essentially unrelated to *Mniodes (Luciliocline) santanica* or any member of *Mniodes*. *Gnaphalium depressum* (W. Jameson *s.n.*, PH00012252) from Andean Ecuador, is a synonym of *Lucilia kunthiana* (DC.) Zardini; it possesses achenes with elongate trichomes typical for *Lucilia*, i.e. 250–850 μ m long. Gray (1862) also commented that the Ecuadorian *Gnaphalium depressum* Nutt. was not synonymous with *Gnaphalium radians* (i.e., *Mniodes radians* (Benth.) S. E. Freire, Chemisquy, Anderb. & Urtubey, 2014), and Gray suggested it best related to *Lucilia kunthiana* or *L. conoidea* Wedd.

Freire annotated an isotype of *Gnaphalium sarmentosum* Klatt (C. B. Pringle 4249, S-G-2896) as *Luciliocline santanica*. An examination of isotype material of Pringle 4249 (MEXU01216408) from Mexico shows it to be the type of *Mexerion* Nesom (1990). Its achenes possess reduced twin hairs with enlarged adaxial basal cells and short, blunt, apical cells ca. 50 μ m long, very different from the capitate-glandular achenial trichomes found in *Mniodes santanica* and most *Mniodes* species. Not only does the Mexican material not correspond to the morphology

of *M. santanica*, the two populations would exhibit an amphitropical disjunction of over 6000 kms. The published results of Nie *et al.* (2013) and Luebert *et al.* (2017) both recover this taxon in a clade with *Gnaphaliothamnus* Kirp., far removed from *Mniodes* (Dillon & Luebert 2015).

3. *Mniodes turneri* (Sagást. & M. O. Dillon) M. O. Dillon, comb. nov.
Basionym: *Belloa turneri* Sagást. & Dillon, Phytologia 58 (6): 392. 1985. TYPE: Peru. Dept. Cajamarca, Prov. Contumazá, A. Sagástegui A., E. García A., S. López M., & J. Mostacero L. 10087 (holotype: HUT; isotypes: F1906100, FM neg 061881, MO, TEX). Fig. 12.

Freire (1987b) placed *B. turneri* under the synonymy of *B. lopezmirandae* with the statement that nothing separated them except the length of the corollas, number of phyllaries, and number of florets per capitula. Freire mentioned that these characters were of no significance and likely represented populational variability. I have examined these species in detail, both in the herbarium and in the field, and I continue to accept our *Belloa turneri* as distinct species, just as when it was originally published (Sagástegui & Dillon 1985). It is a species that represents a morphologically and ecologically distinct entity and, as with several other of her efforts at synonymy, we reject Freire's contention that these species are conspecific. It is moved yet again to satisfy current generic concepts.

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sharing information that suggested the taxonomic changes presented here and his SEM photographs of *Poeppig* 889 from W. I thank Daniel Le for providing the digital images of Field Museum collections. I thank Daniel Montesinos for the use of the photograph of *Lucilia conoidea* (Figure 5) taken in the field near Abra Málaga, Department of Cusco.

Contribution of the authors

M.D.: Redaction of the text, evaluation methodology, fieldwork, taxonomic determination of the species, review and approval of the final text.

Conflicts of interest

The author declares not to have conflicts of interest.

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Fig. 1. Image of lectotype for *Lucilia chilensis* Hook. & Arn. collected by H. Cumming 342 (K000500441).

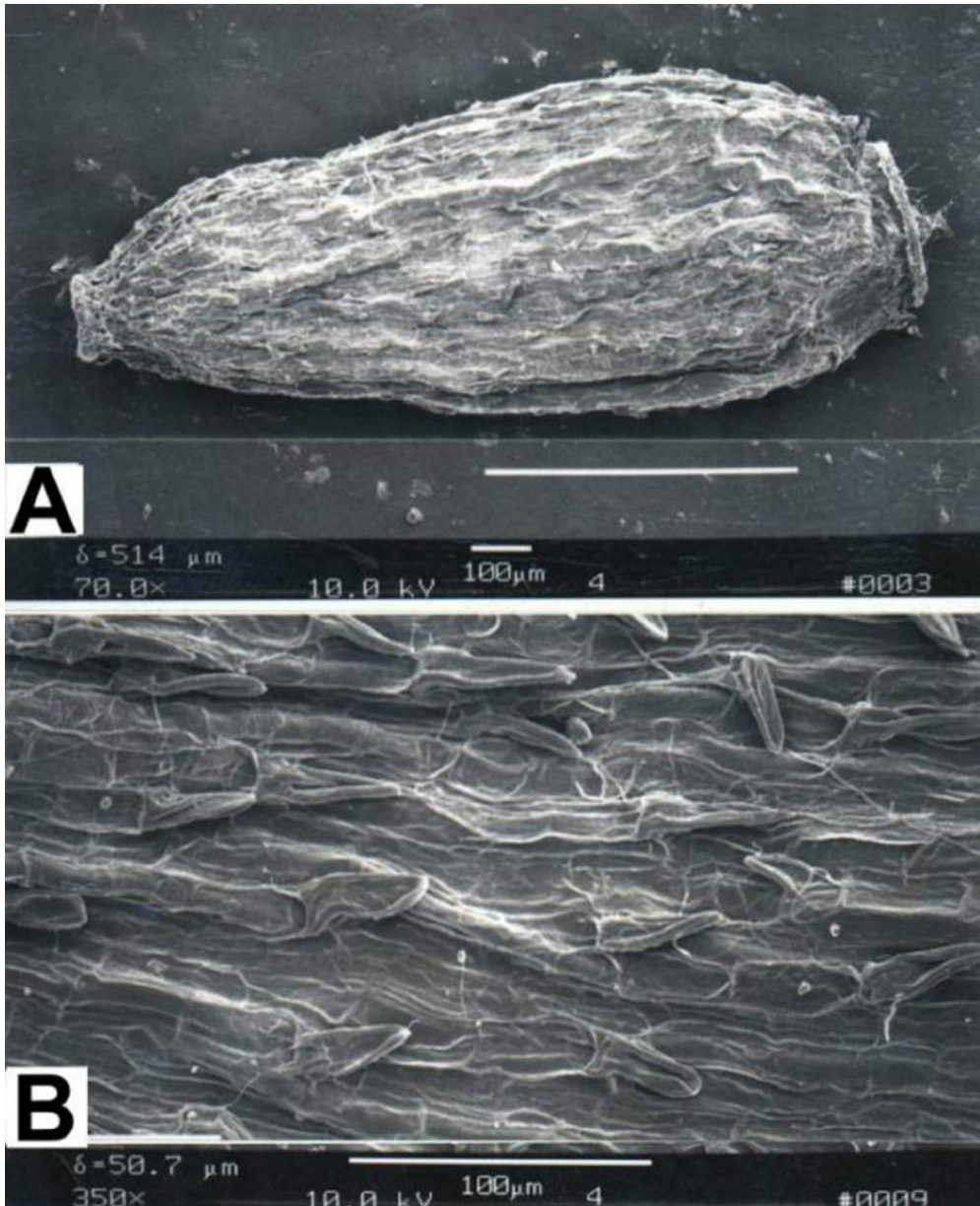


Fig. 2. Scanning electron microscope image of *Lucilia chilensis*. A. Achene. B. Enlargement of surface trichomes.

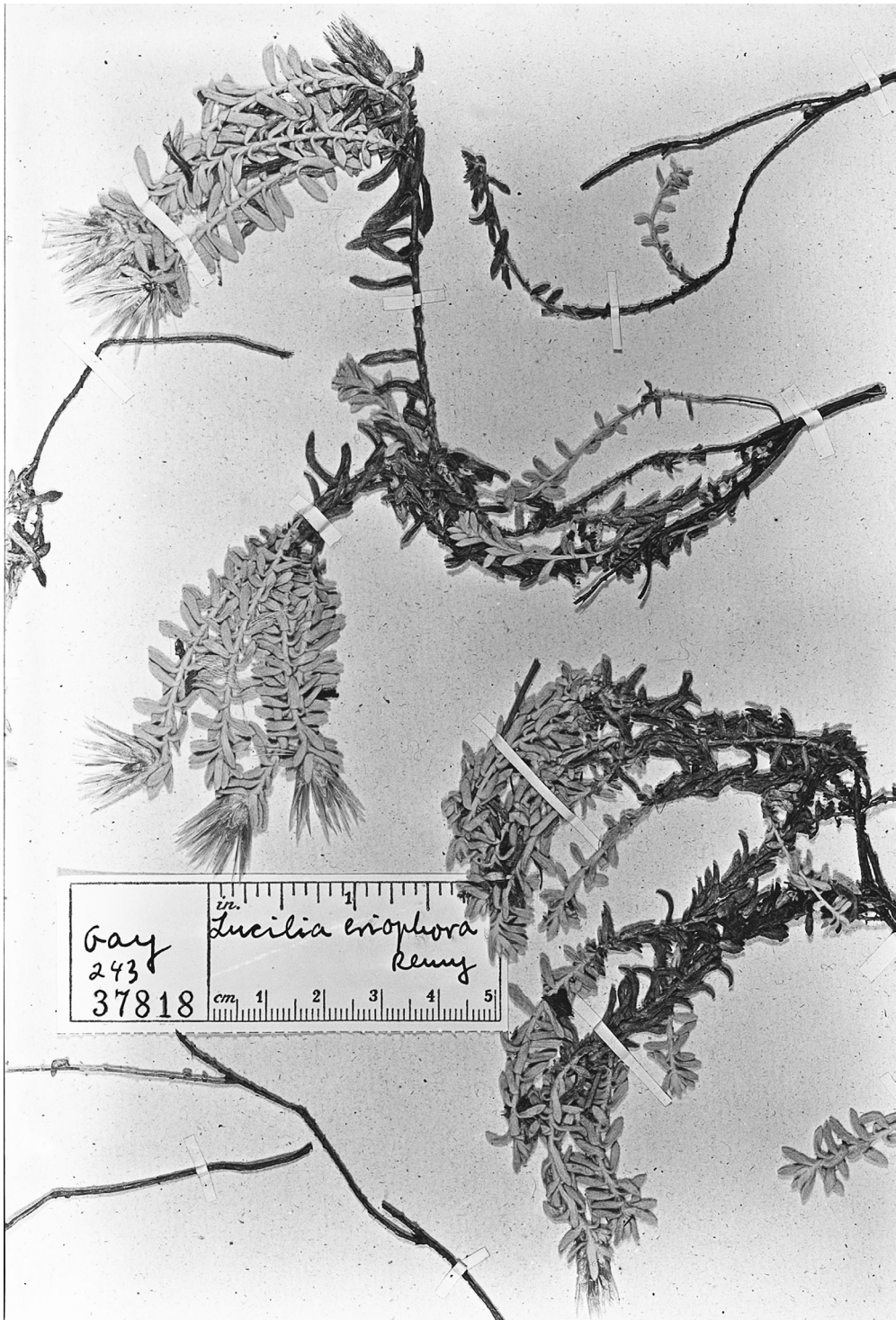


Fig. 3. Image of holotype of *Lucilia eriophora* J. Rémy collected by C. Gay 243 (FM neg. 37818) from P.

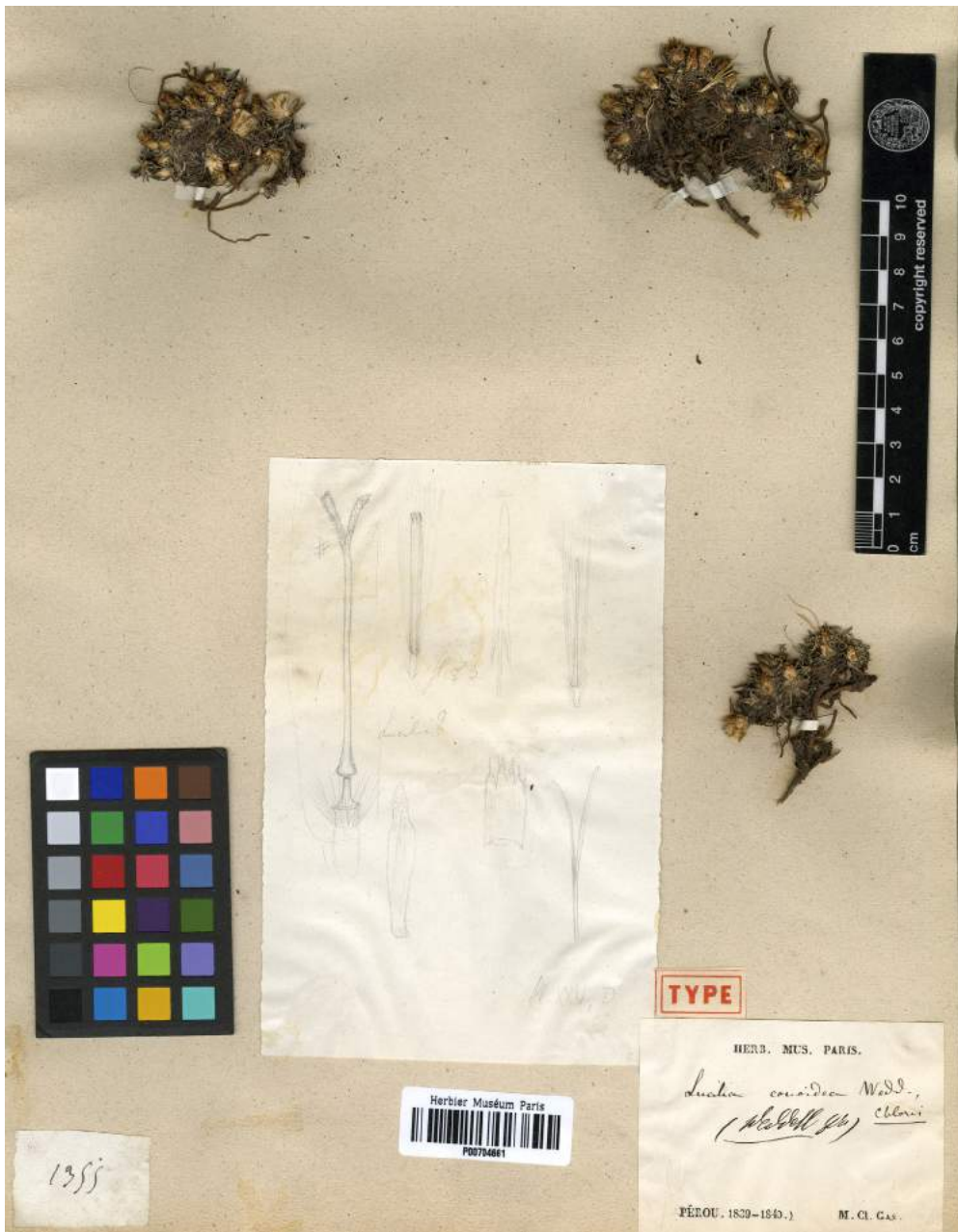


Fig. 4. Image of holotype for *Lucilia conoidea* Wedd. collected by C. Gay 1355 (P00704661).

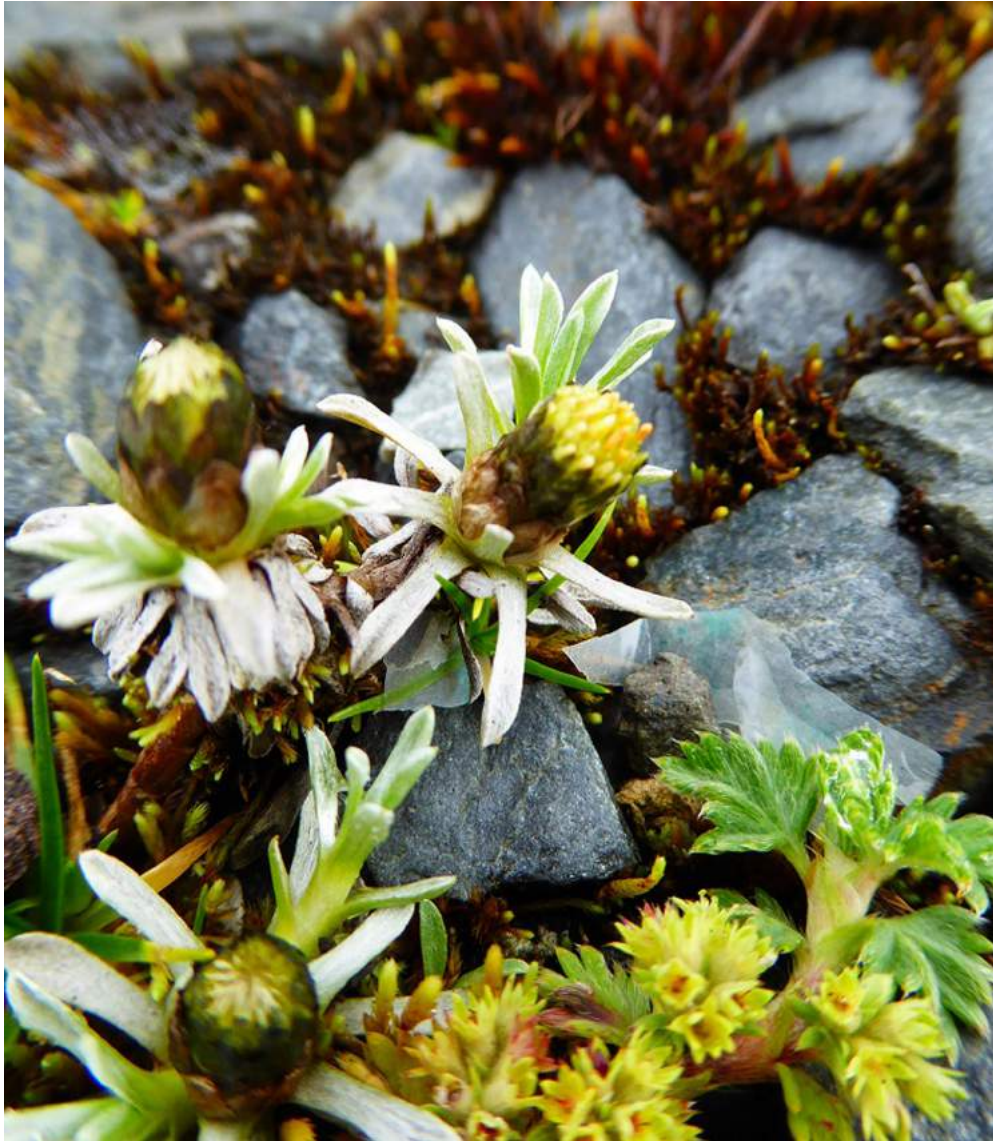


Fig. 5. *Lucilia conoidea* (note pubescent adaxial leaf surfaces and glabrescent abaxial leaf surfaces).



Fig. 6. *Lucilia kunthiana* (DC.) Zardini. *Conyza kunthiana* a replacement name for *Conyza pusilla* Kunth collected by A. Humboldt & A. Bonpland s.n., P00322293.

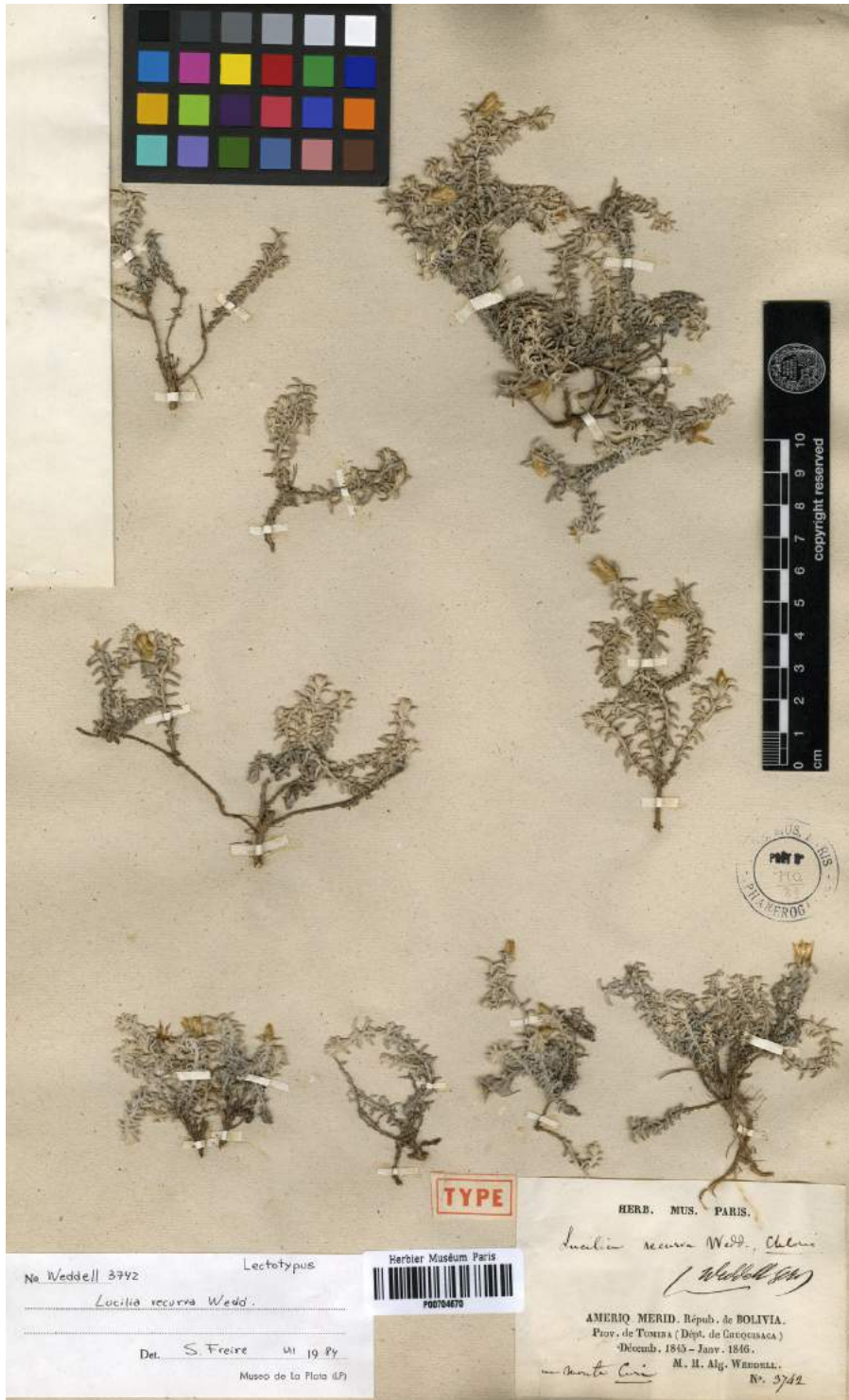


Fig. 7. *Lucilia recurva* Wedd. Lectotype collection by H. Weddell 3742 (P00704670).



Fig. 8. *Laennecia alpina* Poepp. Holotype collection by E.F. Poeppig 899 (W0028920).

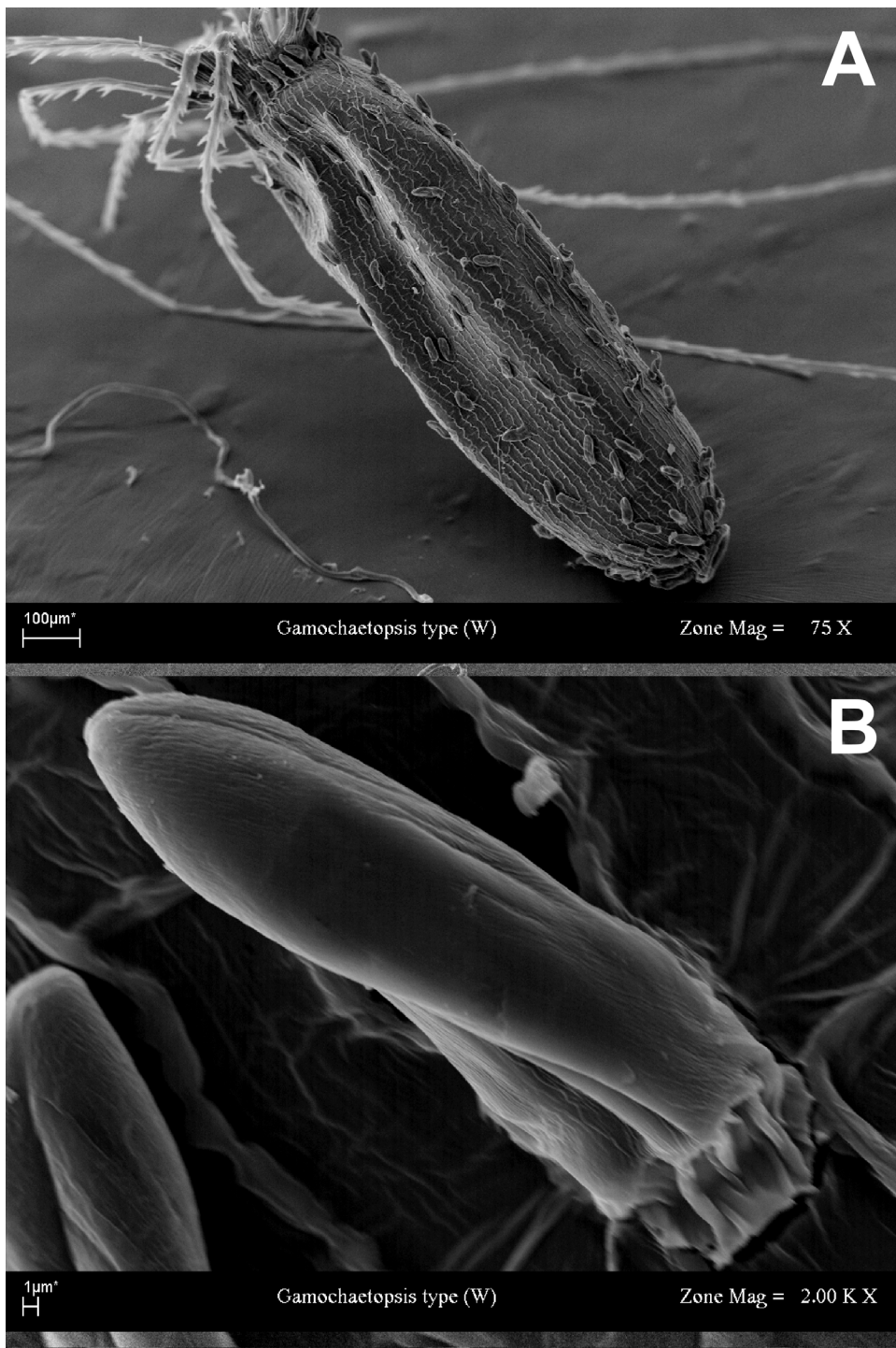


Fig. 9. Scanning electron microscope images of *Laennecia alpina* achenes from type collection by *E.F. Poeppig* 899 (W0028920). A. Achene with attached pappus, scale bar = 100 µm. B. Individual clavate achenial trichome, scale bar = 1 µm.

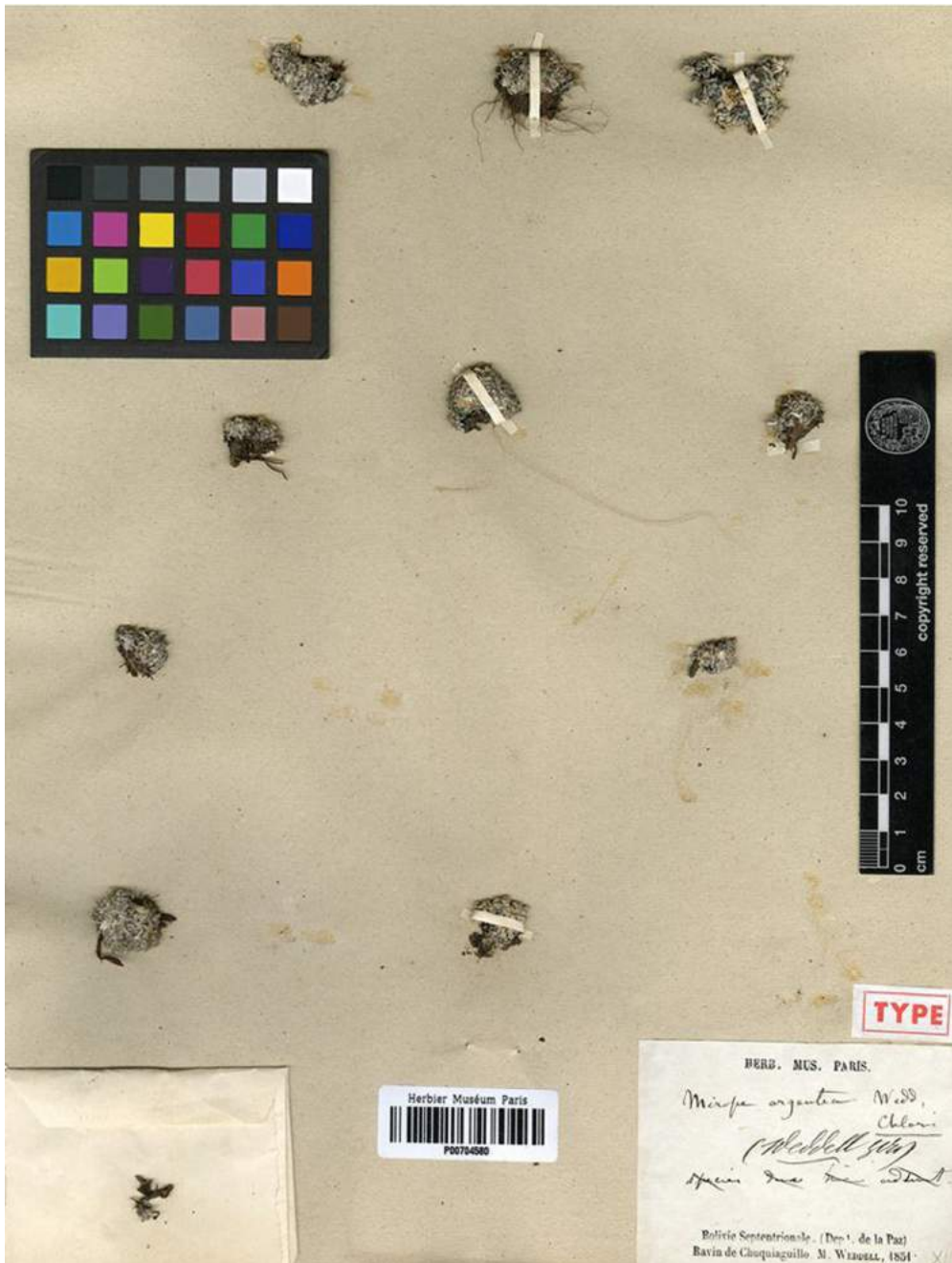


Fig. 10. *Merope argentea* Wedd.. Holotype collection by H. Weddell s.n. (P00704580).

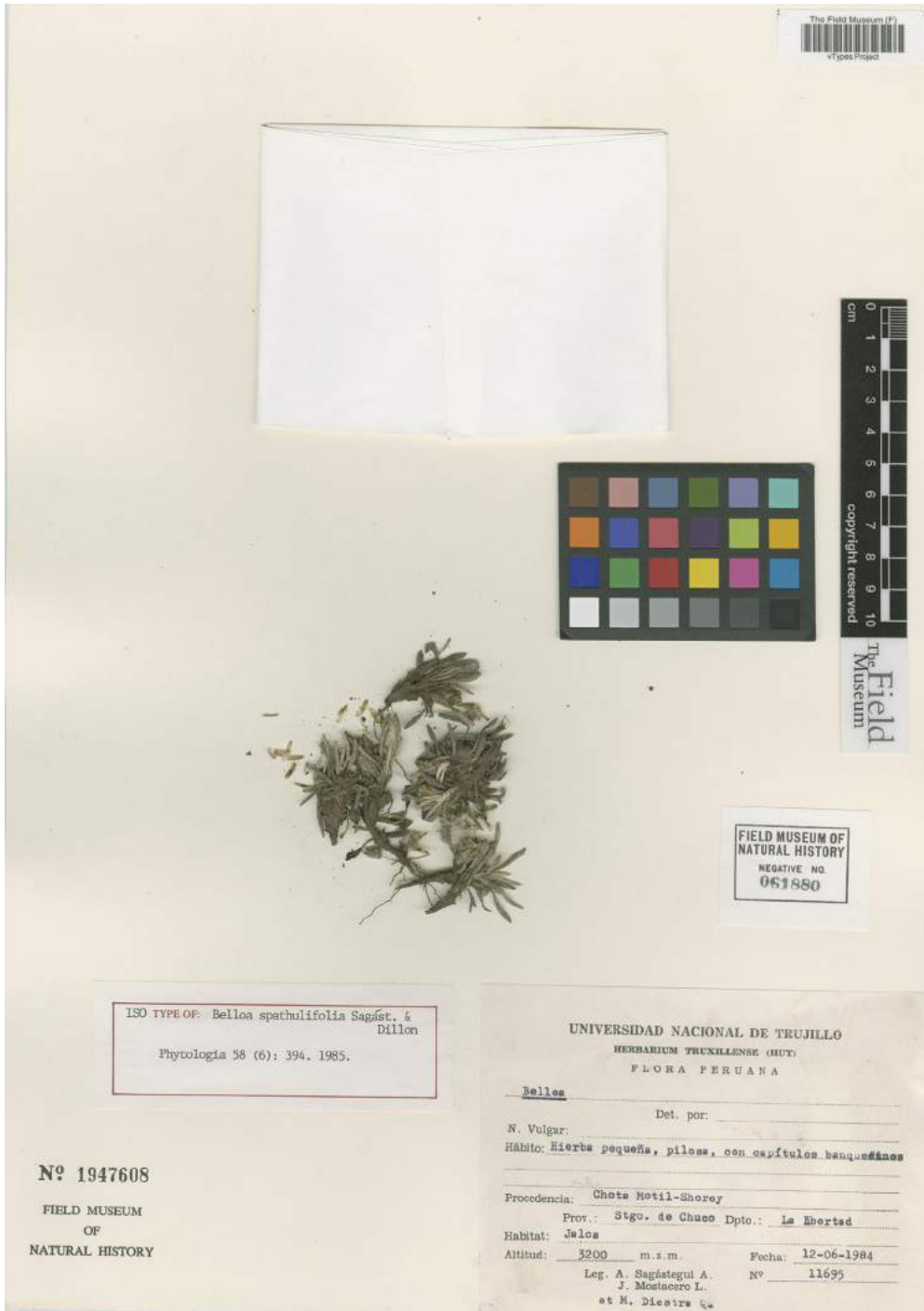


Fig. 11. *Belloa spathulifolia* Sagást. & M.O.Dillon. Isotype collection by A. Sagástegui A. et al. 11695 (F1947608, FM neg 061880).

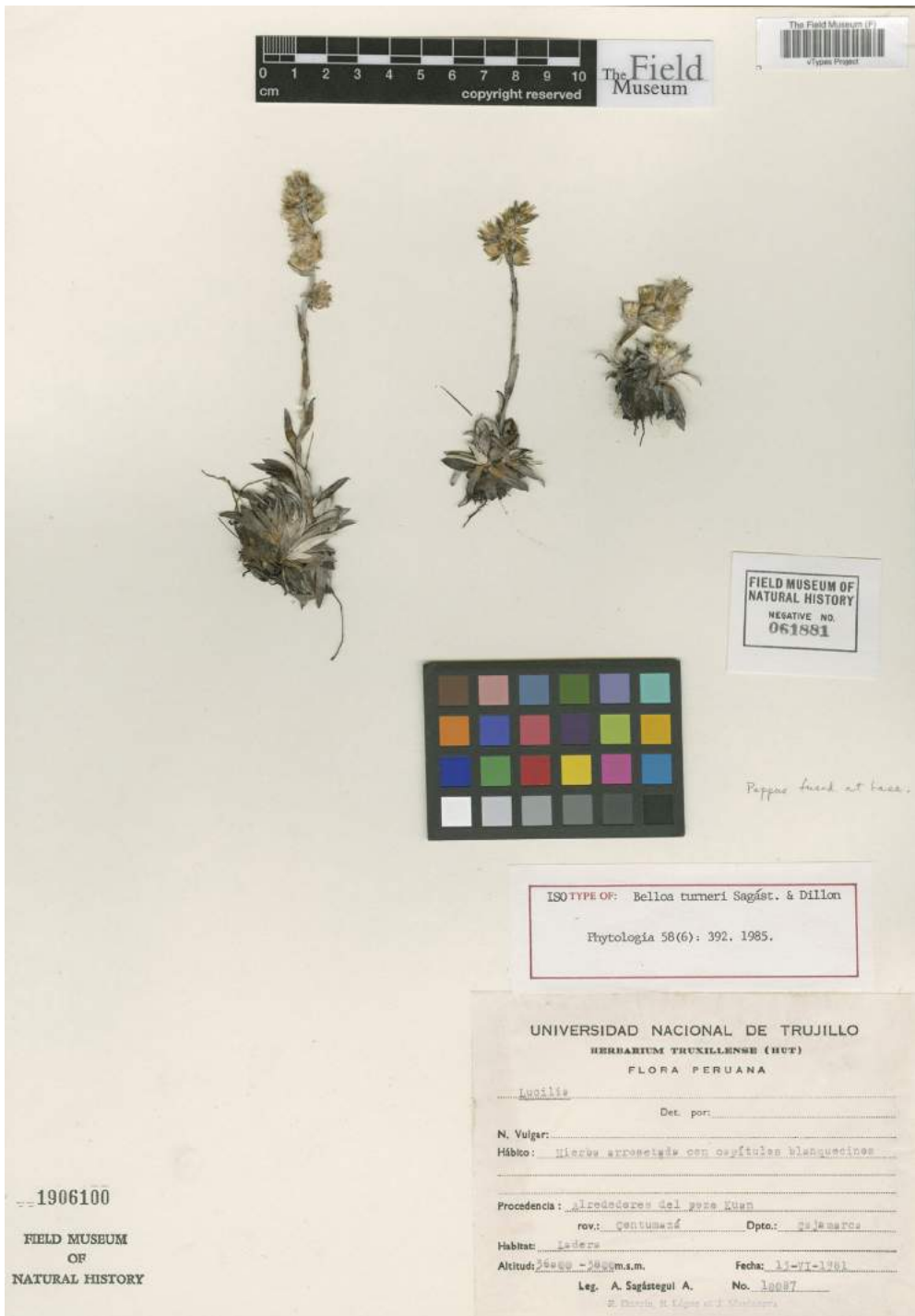


Fig. 12. *Belloa turneri* Sagást. & M.O.Dillon. Isotype collection by A. Sagástegui et al. 10087 (F1906100, FM neg 061881).

