

**NEW SPECIES OF AMERICAN PSEUDOGNAPHALIUM  
(ASTERACEAE: GNAPHALIEAE). I.  
SPECIES WITH AN INVERTED RATIO  
OF BISEXUAL TO PISTILLATE FLORETS**

**GUY L. NESOM**

Research Associate

Academy of Natural Sciences of Drexel University

Philadelphia, Pennsylvania 19103

guynesom@sbcglobal.net

**ABSTRACT**

Heads with a greater number of bisexual florets than pistillate have been considered diagnostic of the Old World genus *Helichrysum*, in distinction to the primarily American *Pseudognaphalium*, where the ratio is reversed. In the Guatemalan *Pseudognaphalium leucostegium* Pruski (2012), however, the ratio is like that of *Helichrysum*, and five additional American species are described here with a similarly "inverted" ratio — ***Pseudognaphalium alquitranum* Nesom, sp. nov.**, ***Pseudognaphalium candelabrum* Nesom, sp. nov.**, ***Pseudognaphalium hadroflorum* Nesom, sp. nov.**, ***Pseudognaphalium hidalgoense* Nesom, sp. nov.**, and ***Pseudognaphalium hyperandros* Nesom, sp. nov.** These new species are from Mexico and probably closely related to *P. chartaceum* and *P. ehrenbergianum*, which produce a relatively large number of bisexual florets. The genus is estimated here to comprise 137 species from the USA, Mexico, Central America, Caribbean, South America, Asia/Pacific Islands, and Africa, although molecular data show the South American species to constitute a separate clade.

"The genera *Stenophalium*, *Pseudognaphalium*, and *Achyrocline* ... have divided stereomes and seem to be poorly delimited from *Helichrysum*" (Anderberg 1991, p. 17). The ratio of bisexual to pistillate florets is the only character used in Anderberg's cladistic analysis to separate *Helichrysum* and *Pseudognaphalium* — the latter characterized by a greater number of pistillate florets. Anderberg noted, however (p. 18), that "this is a technical character and can as such be suspected to have evolved several times" ... as in "*Vellereophyton* and *Troglophyton*, two genera which have both character states." Hilliard and Burt (1981) earlier noted this distinction between *Pseudognaphalium* and *Helichrysum* and pointed out that exceptions exist in *Helichrysum* (e.g., the African *H. athrixiifolium*, *H. basalticum*, *H. callicomum*, *H. forskahlii* (some populations), *H. polycladum*, *H. roseum*, and *H. rugulosum* have a greater number of pistillate florets).

Exceptions can now be pointed out in American *Pseudognaphalium* — *P. leucostegium* Pruski (2012), endemic to Dept. Huehuetenango in Guatemala, has a greater number of bisexual florets than pistillate, and five Mexican species with a similarly 'reversed' ratio are newly described in this manuscript.

**Recent taxonomic studies by Freire et al.**

Freire et al. (2022b) have published a "taxonomic revision of *Pseudognaphalium* from North America" (Mexico and the USA), basing some of their taxonomic decisions on a morphometric analysis (2022a). The clusterings in the latter were used to relegate three USA species to synonymy, *P. beneolens* (to *P. thermale*), *P. microcephalum* (to *P. canescens*) and *P. micradenium* (to *P. helleri*) — in contrast, the reality of each of these is supported by geographical and morphological evidence (e.g., Nesom 2001, 2004, 2006). The dendrogram groupings of Freire et al. appear to be artificial — an accurate portrayal of evolutionary relationships among these often subtly identified species presumably awaits a molecular analysis. Contrasts in identifications between mine and those in the Freire et al. study suggest that their descriptions and distribution maps should be used with circumspection.

The Freire et al. revision includes 37 species of *Pseudognaphalium* — several Mexican species published slightly earlier perhaps understandably were not included — *P. rebmanii* Nesom and *P. cacachilense* Nesom (2022) and *P. stereovirens* Nesom and *P. priscum* Nesom (2021). No new taxa were described by Freire et al., suggesting that perhaps their study was intended mostly as a summary of current knowledge, using only existing names. But in a series of studies beginning here, at least 25 previously undescribed species from Mexico and Central America will be recognized, including narrowly endemic to wide-ranging species.

### Taxonomic overview of the genus

The number of species in *Pseudognaphalium* was estimated as ca. 90 by Anderberg (1991). Perhaps following Anderberg, Chen and Bayer (2011) also estimated about 90 species. I estimated 100 species (Nesom 2016). The estimate of Freire et al (2022a) was about 60 species. The estimate here is 137 (as below) — the final number in bold is the figure for unique species, combining to 137.

USA - 21 species (12\* also occurring in Mexico, see Nesom 2016 and 2023b — *\*P. arizonicum* (A. Gray) Anderb., *P. austrotexanum* Nesom, *\*P. beneolens* (Davidson) Anderb., *\*P. biolettii* Anderb. ex Nesom, *\*P. californicum* (DC.) Anderb., *\*P. canescens* (DC.) Anderb., *P. helleri* (Britt.) Anderb., *\*P. jaliscense* (Greenm.) Anderb., *\*P. leucocephalum* (A. Gray) Anderb., *\*P. luteoalbum* (L.) Hilliard & Burt, *P. macounii* (Greene) Kartesz, *P. micradenium* (Weatherby) Nesom, *P. microcephalum* (Nutt.) Anderb., *P. obtusifolium* (L.) Hilliard & Burt, *\*P. pringlei* (A. Gray) Anderb., *\*P. priscum* Nesom, *P. ramosissimum* (Nutt.) Anderb., *\*P. roseum* (Kunth) Anderb., *P. saxicola* (Fassett) Ballard & Feller, *\*P. stramineum* (Kunth) Anderb., *P. thermale* (E. Nels.) Nesom. **9 species** My annotation in 2000 of a collection from Brevard Co., Florida (*Small & DeWinkeler 9458-US*), as the Caribbean *P. domingense* was in error and occasioned the inclusion of that species in various databases — the plant is *P. obtusifolium*, as originally identified.

Mexico - ca. 65 species, including ca. 20 overlapping with the USA and Central America). Many of these, perhaps conservatively estimated here, are to be described in forthcoming publications, beginning here. **65 species** — this includes overlapping species excluded from the total counts of the USA, Central America, the Caribbean, South America and Asia.

Central America - ca. 19 species (ca. 9\* overlapping with Mexico and/or South America — species accepted here from Pruski (2018): *P. alatocaulis* (Nash) Anderb., *\*P. brachyphyllum* (Greenm.) Anderb., *\*P. elegans* (Kunth) Kartesz, *P. leucostegium* Pruski, *\*P. liebmanni* (Sch.Bip. ex Klatt) Anderb., *\*P. luteoalbum* (L.) Hilliard & Burt, *P. rhodarum* (Blake) Anderb., *\*P. roseum* (Kunth) Anderb., *\*P. stramineum* (Kunth) Anderb., *P. subsericeum* (Blake) Anderb., *\*P. viscosum* (Kunth) Anderb.; taxa from Pruski (2018) that are (or perhaps represent) undescribed species: *\*brachypterum*, *chartaceum*, *\*greenmannii*, *liebmanni* var. *monticola* (= *monticola*), *oxyphyllum*, *semiamplexicaule*, *"aff. paramorum"*, and *"sp. A."* *Pseudognaphalium stolonatum* = *Mexerion stolonatum* (Nesom 2023a). **10 species**

Caribbean - 10 species (3\* also occurring in Mexico and/or South America; *\*P. attenuatum* (DC.) Anderb., *P. domingense* (Lam.) Anderb., *P. eggersii* (Urb.) Anderb., *\*P. elegans* (Kunth) Kartesz, *\*P. luteoalbum* (L.) Hilliard & Burt, *P. rosillense* (Urb.) Anderb., *P. selleanum* (Urb. & Ekman) Anderb., *P. tortuanum* (Urb. & Ekman) Anderb., and 2 previously undescribed species. **7 species** A taxonomic summary of the Caribbean species is in preparation.

South America - ca. 40 species (3 also occurring in Central America and North America, *P. elegans* and *P. luteoalbum*) — as counted and inferred from Freire et. al (2018 and references therein). *Pseudognaphalium elegans* is in the North American clade. **37 species** The Venezuelan *P. moritzianum* is part of the North American clade — Venezuelan species not yet included in molecular analyses are *P. badillanum*, *P. caeruleocanum*, *P. meridanum*, and *P. paramoranum*.

Asia/Pacific Islands - *P. hypoleucum* (DC.) Hilliard & Burt, *P. flavescens* (Kitam.) Anderb. Molecular data place these two species, both with bright yellow involucre, in the North American *Pseudognaphalium* clade — it seems plausible that at least one other similar southeast Asian species (Chen & Bayer 2011) is closely related: *P. chrysocephalum* Hilliard & Burt, which was

noted by Hilliard and Burtt (1981) as closely similar to *P. hypoleucum*. *Pseudognaphalium affine* also has yellow involucre but molecular data place it as closely related to *P. luteoalbum*. The affinities of *P. adnatum* (DC.) Y.S. Chen are obscure — it occurs widely in southeastern Asia, from Pakistan through India and the Himalayas into Taiwan, Philippines, and southeastern China. *P. sandwicensium* is counted here as a single species, although molecular data indicate that four species are present (Smitsen et al. 2023). **6 species**

**Africa** - Hilliard and Burtt (1981) transferred three African species to *Pseudognaphalium*: *P. oligandrum* (DC.) Hilliard & Burtt, *P. richardianum* (Cufod.) Hilliard & Burtt, and *P. undulatum* (L.) Hilliard & Burtt. Although anomalous in its undivided stereome, *P. oligandrum* is consistently aligned in molecular studies with North American *Pseudognaphalium*. *Pseudognaphalium richardianum* has not been included in molecular studies. *Pseudognaphalium undulatum* is placed among species of *Gnaphalium* sensu stricto (Nie et al. 2016; Smitsen et al. 2020), but because "*Gnaphalium oxyphyllum*" (the type of *Pseudognaphalium*) also is placed as *Gnaphalium* sensu stricto (Nie et al. 2016; Smitsen et al. 2020), it seems probable that GenBank vouchers of "*G. undulatum*" and "*G. oxyphyllum*" have been misidentified. **3 species**

### Insights from molecular analyses

North American and South American *Pseudognaphalium* constitute two separate clades (Fig. 1), their morphology thus apparently convergent. Each is most closely related to a group of *Helichrysum* species from southern Africa — plants in both *Helichrysum* groups produce solitary heads, the *H. aureum* group with mostly yellow involucre, the *H. reflexum* group and mostly white

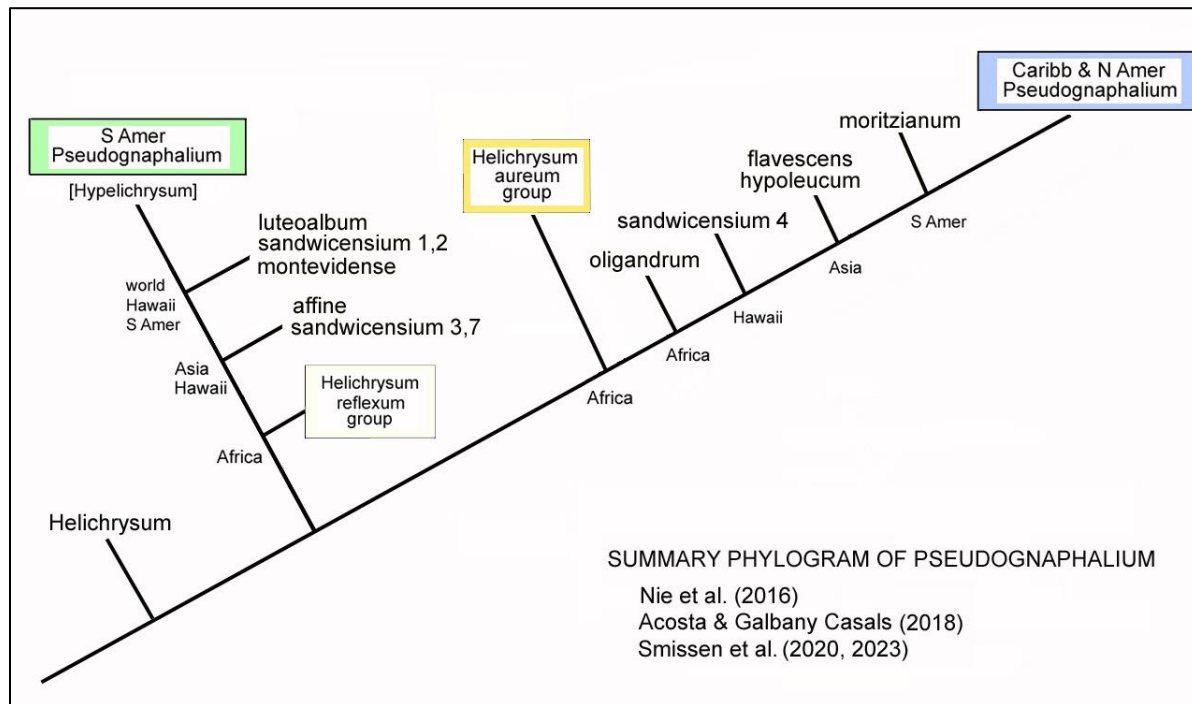
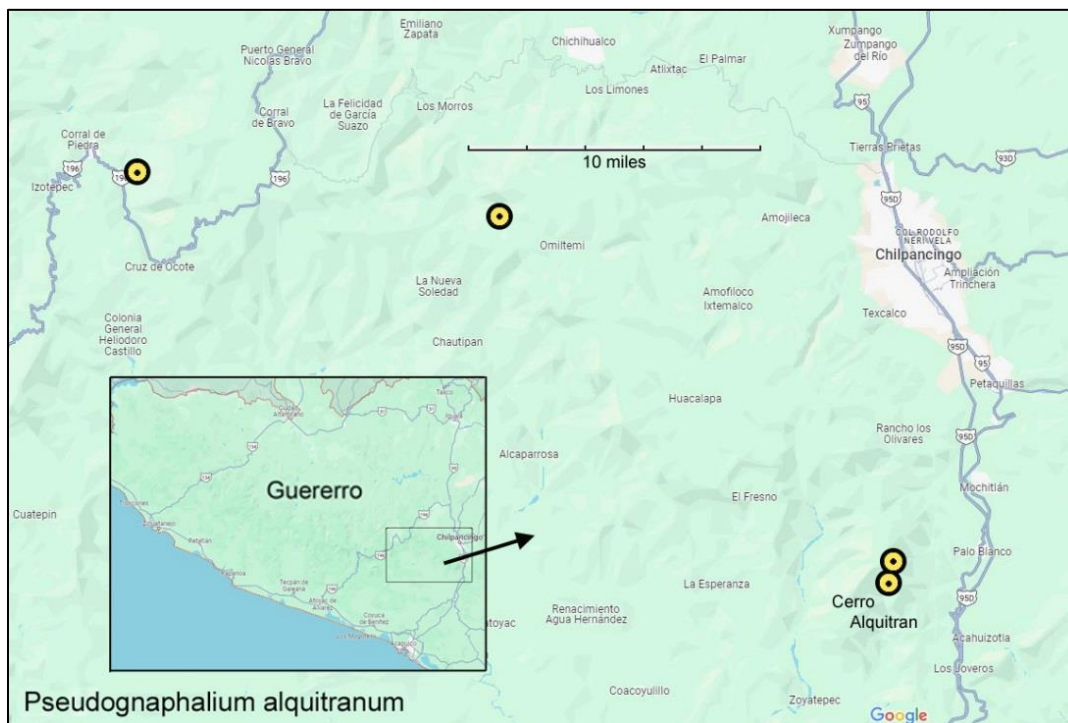


Figure 1. Summary phylogram of *Pseudognaphalium*. Topology derived from Nie et al. (2016), Acosta & Galbany Casals (2018), and Smitsen et al. (2020, 2023). The position of the African *P. oligandrum* varies but is always within the Caribbean & North American clade. The analysis of Smitsen et al. (2023) indicates that samples of *P. luteoalbum* comprise two species — plants endemic to New Zealand have been named as *P. lanatum* (G. Forst) Smitsen et al. *Pseudognaphalium sandwicensium* (samples numbered here as from Smitsen et al. 2023) apparently comprises four separate species. The only Caribbean species included in molecular analyses has been *P. eggertii*, which is positioned among Mexican species. The two African *Helichrysum* species groups are morphologically distinct and cladistically separate.

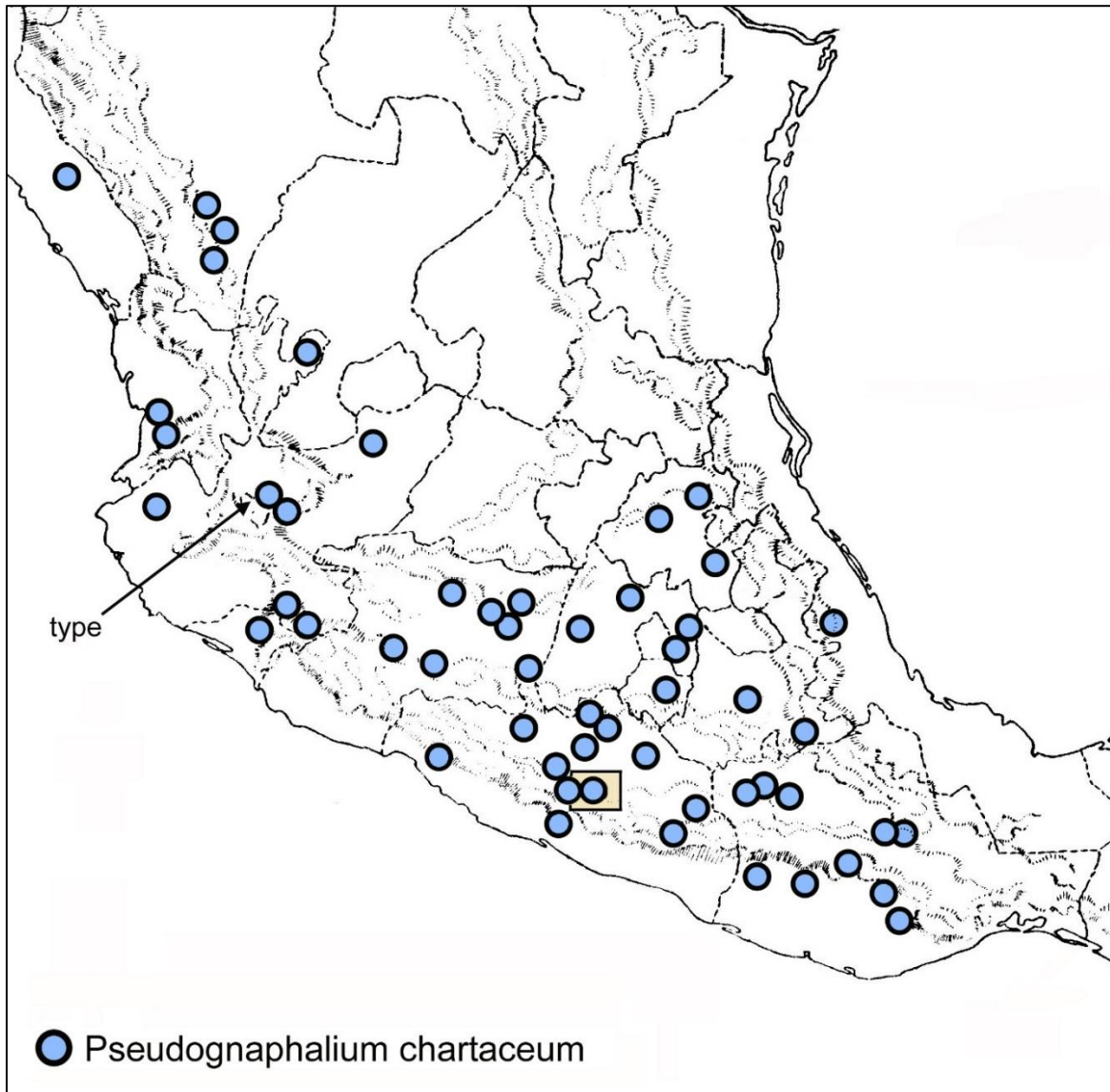
involucres. If this topology is further confirmed, the two *Pseudognaphalium* groups perhaps will be recognized as separate genera (the South American as *Hypelichrysum* Kirpichn.). Such implies also the formal segregation of the *H. reflexum* and *H. aureum* groups, as well as other *Helichrysum* segregates. The diametric alternative would be to enlarge *Helichrysum* by including the *Pseudognaphalium* clades.

#### KEY TO THE INVERTED-RATIO SPECIES OF MEXICO AND GUATEMALA

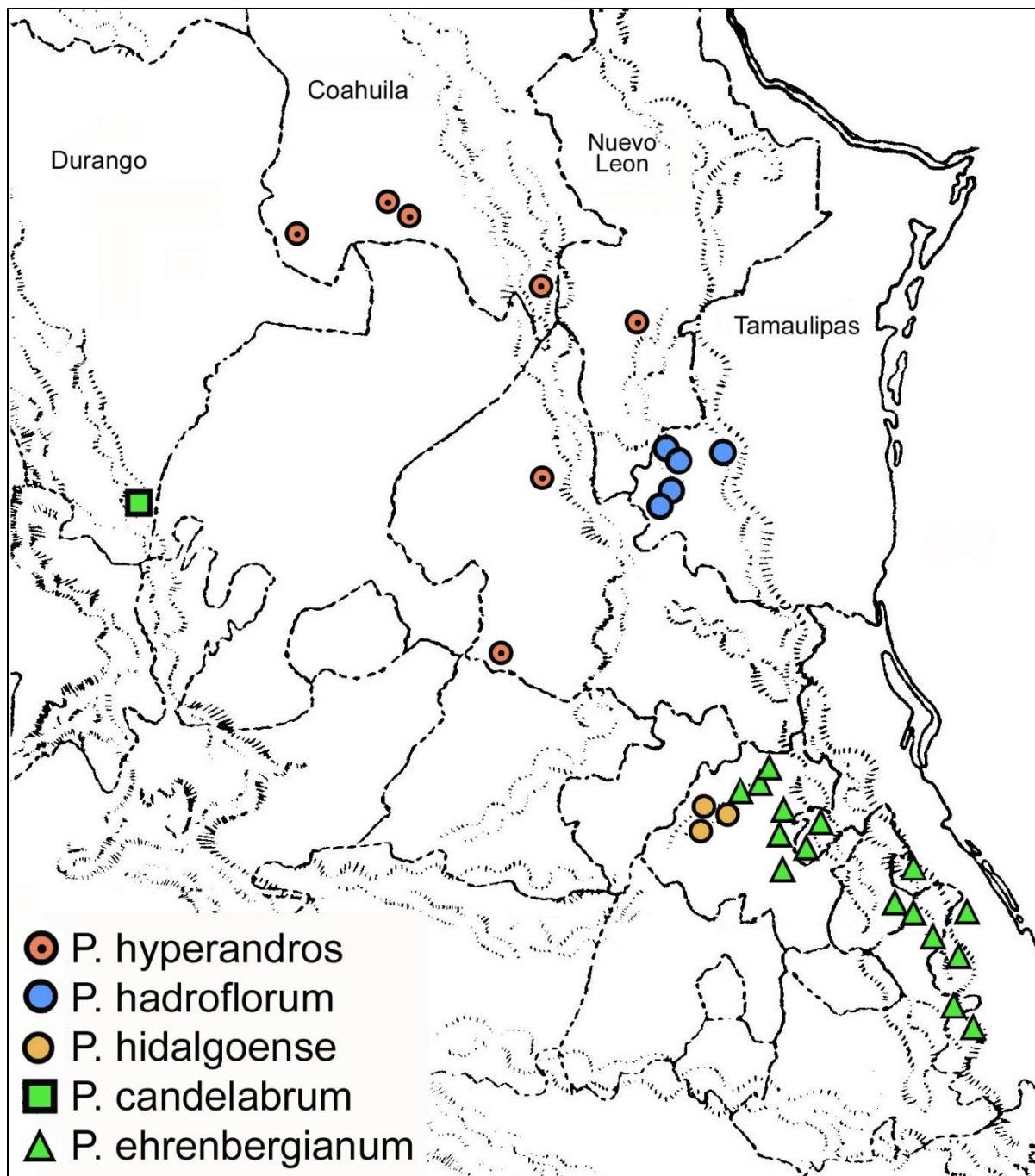
1. Leaves mostly linear; Guatemala ..... ***Pseudognaphalium leucostegium***
1. Leaves oblong to oblanceolate, obovate, or spatulate; Mexico.
  2. Leaves mostly 5–7 cm long, narrowed to a subpetiolar base, surfaces eglandular; Durango ..... ***Pseudognaphalium candelabrum***
  2. Leaves mostly 1.5–5 cm long; adaxial surface glandular; Guerrero and northeastern Mexico.
    3. Leaves 6–10 mm wide; pistillate florets 40–45; Guerrero ..... ***Pseudognaphalium alquitranum***
    3. Leaves 3–8(–10 in *P. hidalgoense*) mm wide; pistillate florets 6–23; northeastern Mexico.
      4. Leaves concolor, persistently white-tomentose on both surfaces, minutely sessile-glandular beneath the tomentum; Tamaulipas ..... ***Pseudognaphalium hadroflorum***
      4. Leaves bicolor, white-tomentose abaxially or somewhat glabrescent, green and densely stipitate-glandular adaxially.
        5. Leaves obovate-oblong to obovate-spatulate, cauline hardly reduced in size distally; phyllary apex rounded to obtuse, midrib not thickened; Hidalgo ..... ***Pseudognaphalium hidalgoense***
        5. Leaves oblong to narrowly lanceolate; cauline becoming bracteate distally; phyllary apex acute to acuminate, midrib thickened (keeled); Coahuila, Nuevo León, San Luis Potosí ..... ***Pseudognaphalium hyperandros***



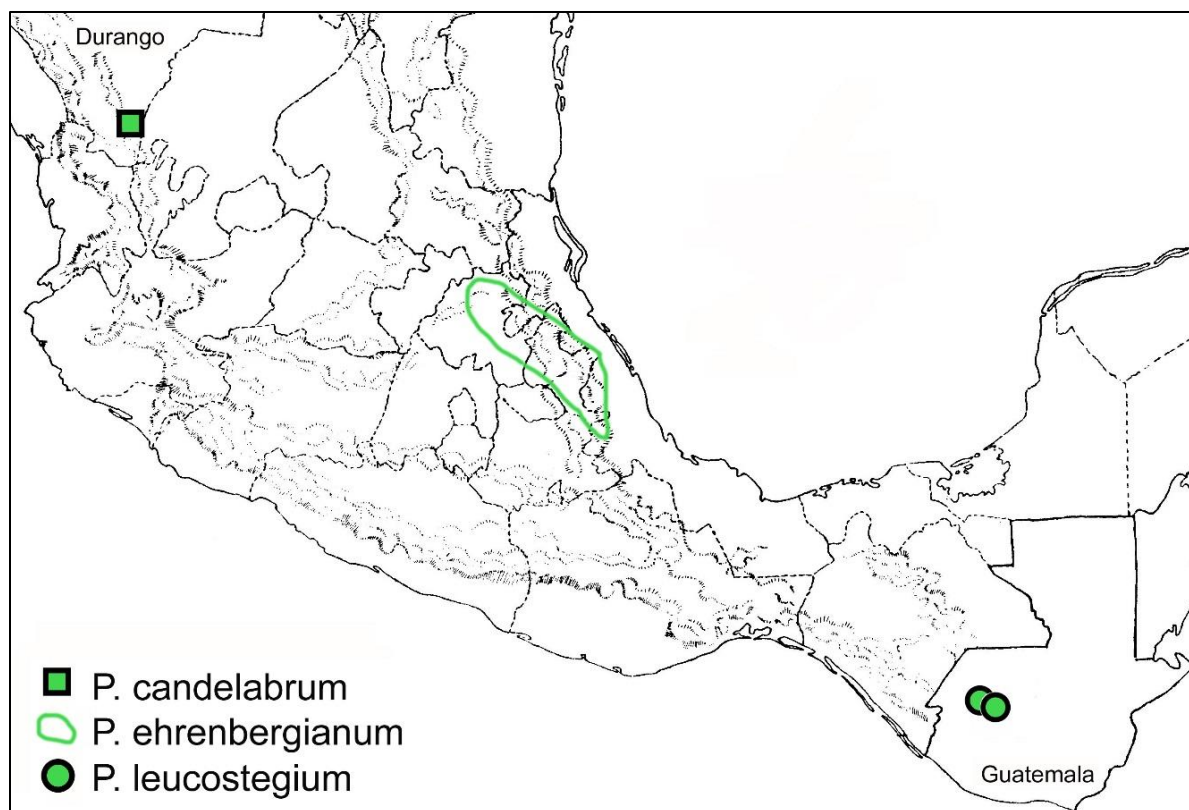
Map 1. Distribution of *Pseudognaphalium alquitranum*. Endemic to central Guerrero.



Map 2. Distribution of *Pseudognaphalium chartaceum*. The inset in Guerrero shows the range of *P. alquitranum*.



Map 3. Distribution of *hyperandros*, *P. hadroflorum*, *P. hidalgoense*, *P. candelabrum*, and *P. ehrenbergianum*. The ratio of bisexual/pistillate florets in *P. ehrenbergianum* is ca. 1/1.6-2, but the relatively large number of bisexual florets suggests that it is related to the other four, which have an "inverted" ratio.



Map 4. Distribution of *Pseudognaphalium leucostegium*, *P. ehrenbergianum*, and *P. candelabrum*. *Pseudognaphalium ehrenbergianum* and *P. candelabrum* are hypothesized here to be close evolutionary relatives — the relationship of *P. leucostegium* to the other two is speculative (see comments below).

1. **PSEUDOGNAPHALIUM LEUCOSTEGIUM** Pruski, *Phytoneuron* 2012-1: 1. 2012. **TYPE:** GUATEMALA. Dept. Huehuetenango. Ravine near the ruins of Zacaleu, mixed forest area near Huehuetenango, 1800 m, 5 Dec 1962, *L.O. Williams et al.* 22433 (holotype: NY; isotype: F). Figures 1-3.

**Perennial** (probably), roots not seen. **Stems** ca. 25–50 cm long, erect or ascending, closely sericeous-tomentose, eglandular. **Leaves** linear to linear-triangular, 1–3 cm long, 1–2 mm wide, distal strongly ascending, midrib impressed adaxially, bicolor, adaxially green to gray-green, eglandular and arachnoid-lanate, abaxially grayish, closely sericeous-tomentose, base slightly dilated and subclasping, not decurrent or barely so (ca. 1 mm), margins entire, narrowly revolute, apex acute, short-apiculate. **Phyllaries** white-opaque, broadly triangular-ovate, not keeled, apex broadly obtuse to rounded, graduate in 4–6 series, inner 4–5 mm long, stereome pale green, glabrous. **Pistillate florets** 18–23. **Bisexual florets** 23–25, corollas 2.5–3 mm long, lobes papillose-glandular. **Achenes** glabrous, mature size not seen. [Description abbreviated mostly from Pruski 2012.] Known from the type collection and one other.

**Additional collection.** GUATEMALA. Dept. Huehuetenango. E of Huehuetenango, about Laguna de Ocubilá, dry open bank, ca. 1900 m, 7 Jan 1941, *Standley* 82702 (US).

Both collections are from the vicinity of Cd. Huehuetenango, Guatemala. Recognized by its linear, bicolor, eglandular stems and leaves, bright white-opaque phyllaries, and slightly greater number of bisexual florets than pistillate. Although evidence is scanty, the geography of the three inverted-ratio species of northwestern Mexico and the similarity of *P. ehrenbergianum* to *P. candelabrum* (comments below) suggest that the relatively large number of bisexual florets may be heritable.

**2. PSEUDOGNAPHALIUM ALQUITRANUM** Nesom, **sp. nov.** **TYPE: MEXICO. Guerrero.** Mpio. Chilpancingo, 1.6 km by air W of Cruz de Ocote on road to Yextla, toward Yextla 0.1-0.3 km from the jct with the main road out of Chichihualco, limestone rock outcrops covered with low shrubs, 1930 m, 17° 35' 50" N, 99° 54' 56" W, 23 Jul 1991, *M. Mayfield 1017* (holotype: TEX, annotated as voucher for chromosome count of "n = 14 II" by B.L. Turner, as *P. chartaceum*). Figures 4-5.

Similar to *Pseudognaphalium chartaceum* in its stipitate-glandular stems and leaves, broadly ampliate-clasping leaves, and bright white-opaque phyllaries; distinct in its denser abaxial leaf vestiture, heads in compact clusters of 4-8, and ca. 1/1 ratio of bisexual to pistillate florets.

**Perennial**, taproot thickened, woody or lignescent. **Stems** 25-60 cm long, loosely and persistently sericeous-villous and prominently and densely glandular with long, spreading, viscid hairs from a thickened base and with an orange-glandular but not swollen apex. **Leaves** mostly oblong-lanceolate, mostly 2.5-4.5 cm long, 5-10 mm wide, ampliate basally and clasping, not decurrent, margins not revolute, apex acute, cauline becoming shorter and bracteate distally, distinctly bicolor, dark green adaxially, gray-white abaxially, margins and adaxial surfaces densely glandular with erect, viscid, multicellular hairs, abaxially with densely matted, gray-white hairs, eglandular. **Heads** short-pedicellate in compact terminal clusters of 4-8. **Phyllaries** bright white-opaque, strongly graduate, broadly ovate, not keeled, inner 4-4.5 mm long, stereome light green, eglandular, apex rounded-obtuse to obtuse-attenuate, often slightly apiculate. **Pistillate florets** ca. 40-45. **Bisexual florets** 43-46, sexual ratio ca. 1/1, corollas 3 mm long, lobes glandular. **Mature achenes** not seen. Figures 6-11.

**Additional collections. Guerrero.** Mpio. Chilpancingo, falda E de Cerro Alquitrán, 17° 23' 10" N, 99° 31' 00" W, bosque alterado, con pradero, 2040 m, 2 Nov 1968, *Kruse 2230* (MEXU); Mpio. Chilpancingo, falda E de Cerro Alquitrán, 17° 23' 10" N, 99° 31' 00" W, 1350 m, 2 May 1969, *Kruse 2474* (MEXU); 6 km [3.7 mi] NW de Omiltemi, brecha Chilpancingo-Omiltemi-Las Joyas, bosque mesófilo de montaña, 2530 m, 11 Nov 1982, *Tenorio L. 2628* (MEXU).

I have studied first-hand only the holotype, but my attention was first drawn to the species by images of the MEXU collections. The inflorescence morphology is distinctive and there seems good confidence that the inverted sexual ratio of florets is characteristic of all.

These plants might justifiably be regarded as a localized variant of the widespread *Pseudognaphalium chartaceum* (Figs. 12-15), which they resemble in most features and which produces a relatively large number of bisexual florets (the bisexual/pistillate ratio is 0.5-0.6(-0.7) / 1, from collections over the whole range). Formal recognition of *P. alquitrán* emphasizes the geographical coherence of these variants and the inverted sexual ratio, which perhaps is of biological significance. I found no other plants of *P. chartaceum* from Guerrero with a sexual ratio approaching that of *P. alquitrán* (e.g., Mpio. Chilpancingo — *Saunders 1455* (TEX); Mpio. Apaxtla — *Mexia 8989* (LL); Mpio. Teloloapan — *Prather 1216* (TEX); Mpio. Iguala de la Independencia — *Prather 1171* (TEX); Mpio. Leonardo Bravo — *Rzedowski & McVaugh 303* (TEX). *Pseudognaphalium chartaceum* and possibly related, further undescribed species will be discussed in a forthcoming manuscript.

Besides *Pseudognaphalium chartaceum*, other Mexican species produce a relatively large number of bisexual florets (but not greater than the pistillate) — *P. ehrenbergianum* (25-42 florets), *P. jaliscense* (mostly 8-12), and *P. leucocephalum* (29-44) — and opaque-white phyllaries. It seems plausible that these may be closely related among themselves.



- 3. PSEUDOGNAPHALIUM CANDELABRUM** Nesom, **sp. nov.** **TYPE: MEXICO. Durango.** Mpio. Mezquital, 45 km NW of Huejuquilla El Alto, Jalisco, steep slope with *Pinus* and *Quercus*, 1830–2150 m, 23 Oct 1983, *D.E. Breedlove* 59227 (holotype: TEX; isotype: UCR). Figures 16–18.

Similar to *Pseudognaphalium ehrenbergianum* in its eglandular vestiture, persistently villous-sericeous stems, large, oblanceolate, subpetiolate leaves slightly ampliate and subclasping at the base and its white-opaque phyllaries. Distinct in its tawny and less strongly bicolor leaves and its fewer florets with ratio of bisexual/pistillate florets slightly greater than 1.

**Perennial** (probably, roots not seen), stems and leaves tawny (light golden orange), more from the color of the epidermis than the vestiture, eglandular. **Stems** ca. 30–75 cm long, thick, closely villous-sericeous with fine hairs. **Leaves** oblong-oblanceolate, (2.5–3) 5.5–7 cm long, (2–3) 9–18 mm wide, reduced in size distally to narrowly lanceolate bracts in the inflorescence, slightly ampliate or not basally and subclasping, not decurrent, margins not revolute, apex broadly acute, weakly bicolor, densely and closely tomentose with fine hairs arising from a short, thickened base, abaxially more densely matted-tomentose and slightly lighter in color than the adaxial, hairs without a thickened base. **Phyllaries** bright white-opaque, graduate in 4–5(–6) series, broadly ovate-lanceolate, not keeled, apex mostly blunt to rounded or obtuse, without an apiculum, inner 5–6 mm long, stereome light tawny (outer), villous, eglandular. **Pistillate florets** ca. 26. **Bisexual florets** 27–31, corollas 3.5–3.8 mm long, lobes yellow, glandular. **Achenes** ridged, not papillate, mature size not seen.

Known only from the type collection. The epithet alludes to the convex array of bright white heads.

Similarities between *Pseudognaphalium candelabrum* and *P. ehrenbergianum* (Figs. 19–23) — particularly their subpetiolate leaves and high number of bisexual florets, suggest that they are sister species. In the latter, bisexual florets are 25–42, pistillate 48–68.

- 4. PSEUDOGNAPHALIUM HADROFLORUM** Nesom, **sp. nov.** **TYPE: MEXICO. Tamaulipas.** [Mpio. Miquihuana]: Ca. 52 air km WNW of Juamave, ca. 10 km NW of Miquihuana, ca. 10 km N of La Perdida on top of ridge along high road to Marcela, near 23° 38' N, 99° 52' W, chaparral with *Cercocarpus*, *Mortonia*, *Dasyllirion*, *Hechtia*, *Quercus pringlei*, *Rhus virens*, *Gochmatia*, *Agave lecheguilla*, *Leucophyllum*, *Berberis*, *Bouteloua*, *Orthosphenia*, *Pinus nelsonii*, *Opuntia*, *Vauquelinia*, *Ceanothus gregii*, infrequent, particularly along graded road, ca. 2200 m, 9 Oct 1982, *J. Henrickson* 19180 (holotype: TEX; isotype: MEXU). Figures 29–30.

Distinct in its persistently tomentose, eglandular stems, distinctly ampliate and subclasping leaves slightly bicolor and glandular adaxially beneath the tomentum, heads at the apex of long peduncle-like branches with reduced (bracteate), appressed-ascending leaves, narrowly ovate-lanceolate phyllaries, and bisexual florets outnumbering the pistillate.

Perennial, taproot woody. **Stems** basally ascending, apparently several from the base, 40–110 cm long, woody at the base, ascending, loosely but persistently whitish-tomentose, eglandular. **Leaves** weakly bicolor, persistently gray-white tomentose on both surfaces or sometimes tardily glabrescent adaxially, minutely sessile-glandular beneath the tomentum, proximal leaves narrowly oblong-lanceolate, 2–4 cm long, 4–7 mm wide, subclasping, slightly basally ampliate, decurrent 0–2 mm, gradually reduced in size distally, and, distal leaves (upper third) linear-lanceolate, closely ascending-appressed, 0.5–1.5 cm long and bracteate below the inflorescence, not decurrent. **Phyllaries** opaque-white, narrowly ovate-lanceolate with acute to obtuse apex, keeled with a narrow, thickened midrib, sessile-glandular at the stereome apices, strongly graduate in 5–6 series, inner 6–7 mm long. **Pistillate florets** 9–15, corollas 3 mm long. **Bisexual florets** 28–35, bisexual/pistillate ratio 2–4/1, corollas 3.5 mm long, lobes glandular. **Achenes** ridged, smooth (not papillate).

Tamaulipas. Limestone slopes, ridge tops, canyons, chaparral, thorn scrub; 1700-3100 m; August-December.

**Additional collections. Tamaulipas.** 63 mi SW of Cd. Victoria on Mexico 101 toward San Luis Potosi [between Palmillas and Tula], limestone rocky slopes in thorn-scrub with *Agave*, *Yucca*, *Dasyllirion*, and *Juniperus*, 1720 m, occasional, herbs to 0.5 m tall, 9 Oct 1989, *King & Peterson 9953* (US, Figs. 31-33); ca. 10 road mi SW of Victoria on Hwy 101, just below and NE of La Libertad at crossing of transmission line on N-facing bluffs above hwy, oak-palm association, 1200 m, common on steep slope in open, 10 Oct 1993, *Mayfield 1855* (LSU, MEXU, TEX, UTEP); [Mpio. Tula, see comments below], "En route from San Luis Potosi to Tampico," Dec 1878-Feb 1879, *E. Palmer 423 1/2* (GH); 4 km W of Miquihuana in canyon with luxuriant vegetation, 3110 m, 4 Aug 1941, *Stanford et al. 666* (GH, MO).

At the end of his 1878-1879 trip, Edward Palmer travelled from the city of San Luis Potosí to Tampico, reaching the latter on 3 February 1879 (McVaugh 1956). On the way, he went north into Tamaulipas and arrived at Tula on 1 December 1878, "made a trip to Sierra Naola (3-6 December), made some collections near Tula," then left on return toward San Luis Potosí on 9 December. The Palmer's specimen was annotated "Vera" in Asa Gray's hand, but it seems certain (judging from the other localities for the species) that it was collected in the vicinity of Tula.

*Pseudognaphalium hadroflorum* is recognized by its persistently tomentose, eglandular stems, weakly bicolor, relatively short, narrowly but distinctly ampliate and subclasping leaves, capitulescences on long, peduncle-like branches with reduced distal leaves, narrowly ovate-lanceolate phyllaries, and bisexual florets twice as numerous as the pistillate. The epithet alludes to the dense concentration of bisexual florets in each head.

Several of these collections were initially annotated by me in ca. 1990 as "*Pseudognaphalium cylindralbum*," alluding to the narrow involucre.

**5. PSEUDOGNAPHALIUM HIDALGOENSE** Nesom, **sp. nov.** **TYPE: MEXICO. Hidalgo.** Barranca de San Vicente near KM 238 on hwy between Zimapán and Jacala, limestone ledges along roadside, 1800-2000 m, 13 Jul 1948, *H.E. Moore 3990* (holotype: MEXU, Figs. 34, 36; isotype: GH).

Distinct in its obovate to obovate-spatulate, subclasping, strongly bicolor, adaxially green and stipitate-glandular leaves, white-opaque phyllaries, and bisexual florets outnumbering the pistillate.

**Perennial.** **Stems** 4–6 dm long, initially white-tomentose but glabrescent, becoming greenish and densely stipitate-glandular (glands beneath the tomentum). **Leaves** (basal and midcauline) obovate-oblong to obovate-spatulate, 2.5–5 cm long, 5–10 mm wide, sometimes slightly tapered to a subpetiolar base, narrowly ampliate, subclasping, not decurrent, distal becoming narrowly oblanceolate to lanceolate, strongly bicolor, green and densely stipitate-glandular adaxially, white-tomentose and eglandular abaxially. **Phyllaries** white-opaque, strongly to weakly graduate, ovate, keeled, apex short-apiculate, inner 5 mm long, middle and inner with an apically glandular stereome. **Pistillate florets** 16–23. **Bisexual florets** 26–39, bisexual/pistillate ratio 1.5–2/1, corollas 3–3.2 mm long. **Achenes** shallowly longitudinally ridged, epidermal surface smooth (not papillate).

Hidalgo. Rocky slopes and limestone ledges, oak and pine woods; ca. 1700-2150 m; July-August.

**Additional collections examined. MEXICO. Hidalgo.** 10-15 mi S of Jacala, precipitous rocky slope, 7000 ft, 24 Jul 1938, *Hodgdon et al. 5644* (GH, NHA-Fig. 35); [Mpio. Zimapán], 3 mi N of Puerto Ing. San Isidro Díaz along Hwy 85, 21 Aug 1971, *Vaughn et al. 1064* (MO); 17 mi N of Zimapán, steep mountainside with oaks and pines, 20 Aug 1957, *Waterfall 14147* (SMU, US).

The type collection (*Moore 3990*) was identified and cited by Freire et al. (2022a) as *Pseudognaphalium chartaceum*. A collection of *P. hidalgoense*, unambiguous in identity, was made by James S. Wilson in 1967, but the label describes it as an "orchid hellow with brown spots" from south of Cd. Mante, Tamaulipas (*Wilson 12325*, TEX) — this surely is an instance of confusion in labeling.

**6. PSEUDOGNAPHALIUM HYPERANDROS** Nesom, *sp. nov.* **TYPE: MEXICO. Coahuila.** Sierra de Parras, Arroyo Seco en el rancho del Tunal entre las sierras San Jose y El Tunal, E de Parras de la Fuente, veg. de *Pinus pinceana*, *Juniperus flaccida*, *Cowania plicata*, *Cercocarpus mojadensis*, *Gochnatia*, y *Quercus*, 2050 m, 14 Aug 1983, A. Rodríguez & M.A. Carranza 1084 (holotype: TEX).

Distinct in its narrowly oblong to narrowly oblong-lanceolate, subclasping, strongly bicolor, adaxially green and stipitate-glandular leaves, distally becoming bracteate and appressed to the stem, white-opaque phyllaries, and bisexual florets outnumbering the pistillate.

**Perennial**, taproot thick and woody. **Stems** 3–7 cm long, woody at base, densely and persistently white-woolly-villous, stipitate-glandular beneath the tomentum. **Leaves** narrowly oblong to narrowly oblong-lanceolate, 1.5–3 cm long, 3–8 mm wide, subclasping and narrowly or not at all ampliate, not decurrent, becoming linear-bracteate distally and to 1–1.5 cm long, strongly to weakly bicolor, green and densely stipitate-glandular adaxially, sometimes sessile-glandular, the tomentum not persistent, densely and persistently white-tomentose abaxially. **Phyllaries** ovate with acute apices, white-opaque, strongly graduate, the inner 3.5–4 mm long, distinctly keeled and short-apiculate. **Pistillate florets** 6–14. **Bisexual florets** 33–40, bisexual/pistillate ratio 2.5–4/1, corollas 3–3.5 mm long, lobes glandular. **Achenes** 0.6 mm long, shallowly longitudinally 6–8-ridged, epidermal surface smooth (not papillate).

Coahuila, Nuevo León, San Luis Potosí. Grassy, limestone slopes, matorral of *Agave-Dasyilirion-Yucca*, *Arctostaphylos* scrub, oak-chaparral; 1650–2650 m; August–November.

The plants from Nuevo León (*Dorr 2122*) are persistently gray-tomentose on adaxial leaf surfaces; others (Coahuila) are mostly green adaxially, glandular only.

**Additional collections examined. MEXICO. Coahuila.** Mpio. Torreon, Sierra de Jimulco and up to 3 km N of Mina San Jose, 8 km NE of Estacion 'OTTO," steep slopes of limestone, matorral or chaparral on higher slopes, 1800–3138 m, 27 Sep 1972, *Chiang et al. 9551* (LL, MEXU); Mpio. Parras, Sierra de Parras, N slope and top, approached from Ejido Cerro Colorado, ca. 10 km W of Parras de la Fuente, 4 Nov 1972, *Chiang et al. 10066* (ARIZ, LL, MEXU); General Cepeda, ledges, 5500 ft, 8 Oct 1905, *Pringle 13557* (GH, LL-2 sheets, NMC); Sierra de Parras, 8000–9000 ft, Oct 1910, *Purpus 4663* (F, GH, MO, US); Cerro San Pedro, ca. 50 m below summit on W side, near Nuevo León line (Sierra del Puerto de Jesús María on AMS-DCM top map), 21 Aug 1974, *Wendt 618* (TEX, MEXU, RSA, TEX). **Nuevo León.** Mpio. Galeana, 4.0 mi S of Pablillo on Hwy 51 toward Dr. Arroyo, 26 Oct 1981, *Dorr et al. 2112* (TEX). **San Luis Potosí.** Mpio. Charcas, Sierra de Monte Grande, Arroyo de Carbonerías, al NE del cerro de Juan Chape, matorral rosetófilo con *Dasyilirion*, *Yucca carnerosana*, *Agave stricta*, *Lindleyella*, 175 m, 14 Sep 1989, *Reyes 450* (TEX); ca. 5 km E of Laguna Seca, Cerro Chiquihuitillo, 21 Oct 1956, *Rzedowski 8235* (MEXU). Figures 24–28.



Figure 1. *Pseudognaphalium leucocephalum*. Guatemala, Williams *et al.* 22433, isotype (F).



Figure 2. *Pseudognaphalium leucostegium*. Detail from Williams *et al.* 22433, isotype (F).



Figure 3. *Pseudognaphalium leucostegium*. Detail from Williams *et al.* 22433, isotype (F).



Figure 4. *Pseudognaphalium alquitranum*. Guerrero, Mayfield 1017, holotype (TEX).



Figure 5. *Pseudognaphalium alquitranum*. Detail from holotype, Figure 4.



Figure 6. *Pseudognaphalium alquitranum*. Guerrero, Kruse 2474 (MEXU).

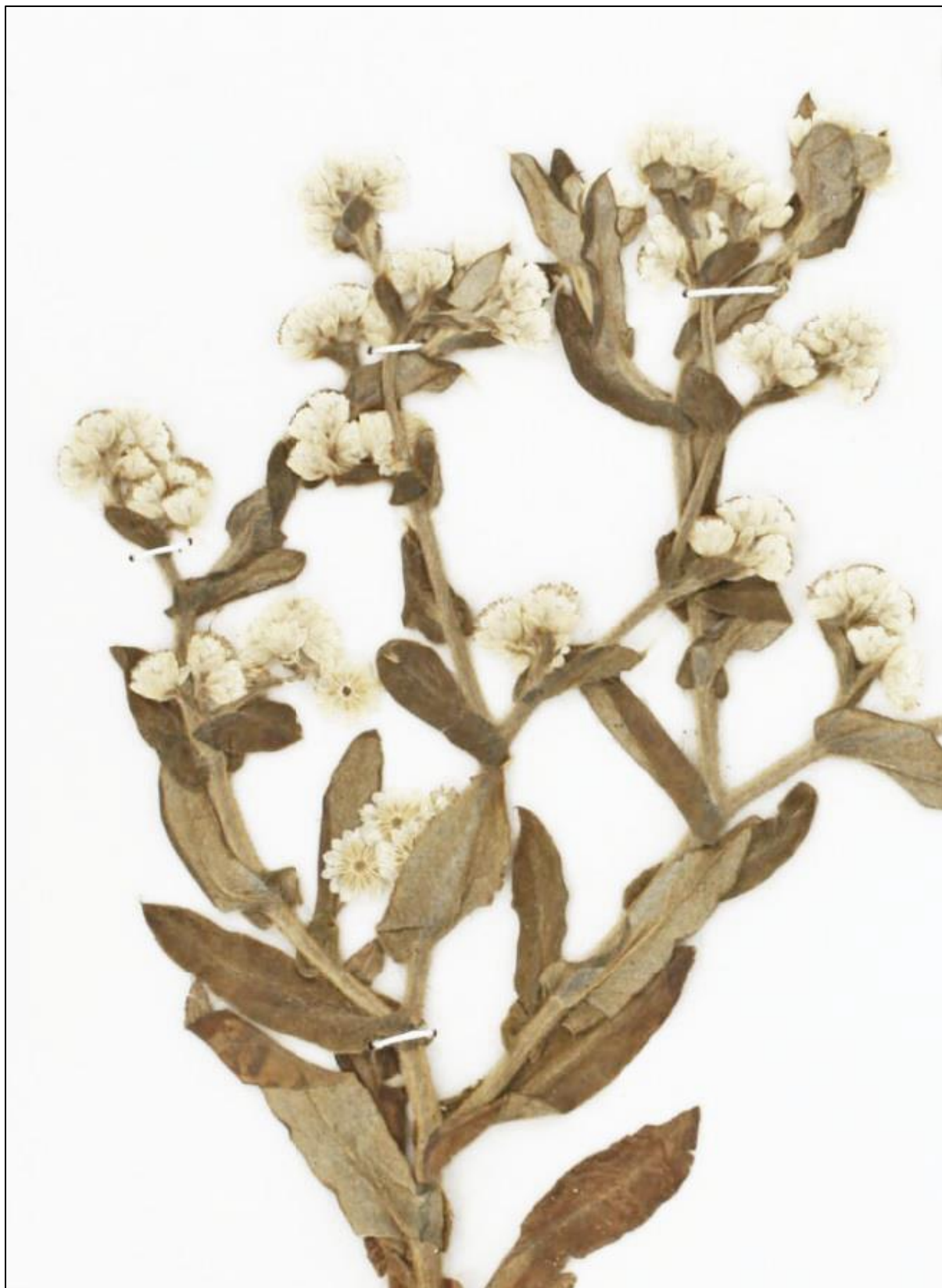


Figure 7. *Pseudognaphalium alquitranum*. Detail from Kruse 2474 (MEXU).



Figure 8. *Pseudognaphalium alquitrantum*. Guerrero, Kruse 2203 (MEXU).



Figure 9. *Pseudognaphalium alquitranum*. Detail from Kruse 2203 (MEXU).



Figure 10. *Pseudognaphalium alquitranum*. Guerrero, Tenorio L. 2628 (MEXU).



Figure 11. *Pseudognaphalium alquitranum*. Detail from Tenorio L. 2628 (MEXU).



Figure 12. *Pseudognaphalium chartaceum*. Jalisco, McVaugh & Koelz 280 (MICH).



Figure 13. *Pseudognaphalium chartaceum*. Nayarit, E. Palmer s.n. (US).





Figure 14. *Pseudognaphalium chartaceum*. Nayarit, E. Palmer s.n. (US).



Figure 15. *Pseudognaphalium chartaceum*. Puebla, de Gante C. 339 (HUAP).

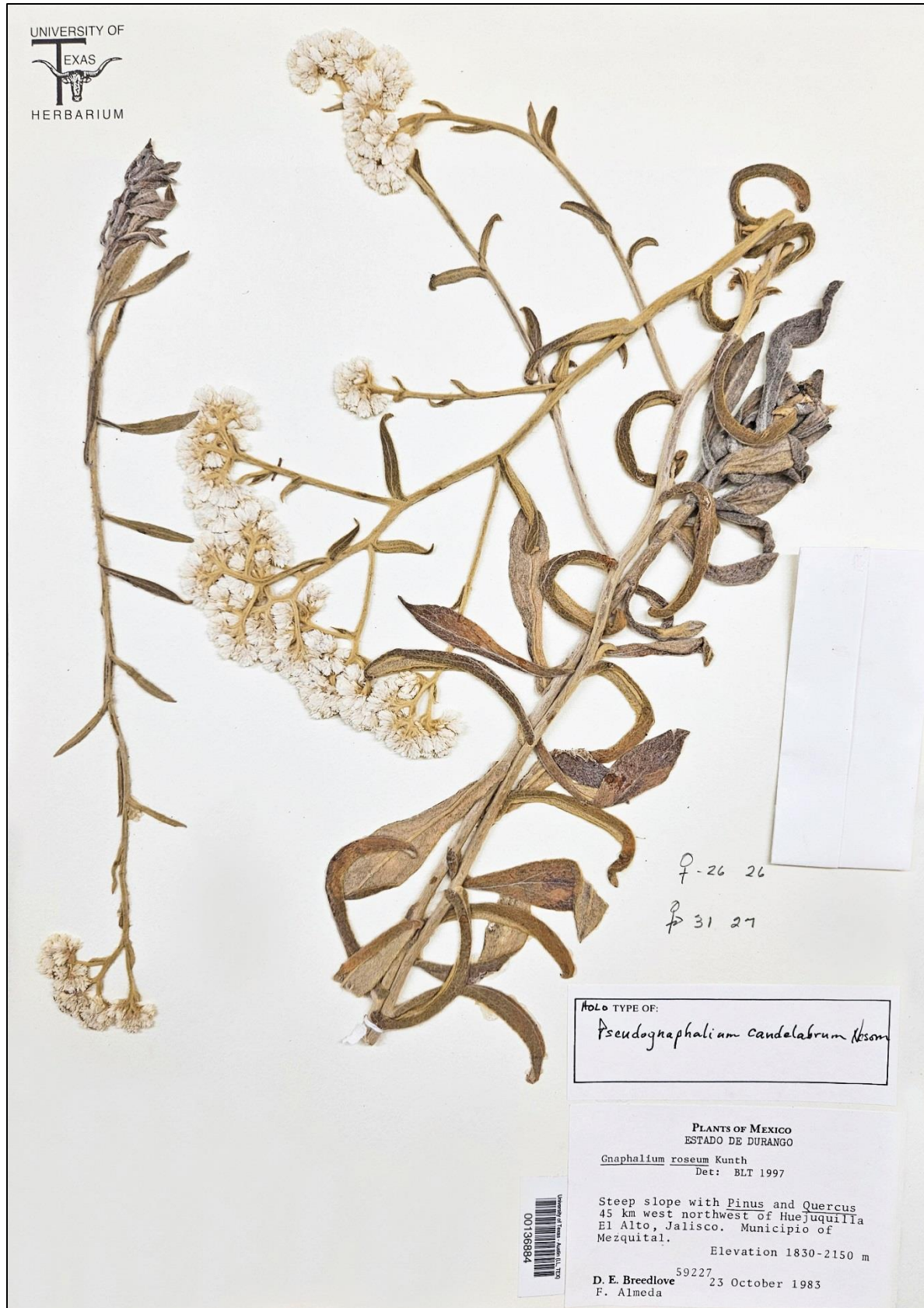


Figure 16. *Pseudognaphalium candelabrum*. Durango, Breedlove 59227, holotype (TEX).



Figure 17. *Pseudognaphalium candelabrum*. Detail from *Breedlove 59227* (TEX).



Figure 18. *Pseudognaphalium candelabrum*. Detail from *Breedlove 59227* (TEX).



**HERBARIO DE LA BENEMÉRITA UNIVERSIDAD  
AUTÓNOMA DE PUEBLA (HUAP)**

*Gnaphalium* L.  
 Familia: Asteraceae  
 Edo. PUEBLA Mpio. TETELA DE OCAMPO  
 Loc. .5 Km. al O de Chalahuico  
 Lat. 19.00° 52.00' 18" Lon. 97.00° 40.00' 42" Alt. 1,650.00 msn  
 Habitat: Bosque mesófilo de montaña  
 Descr. Hierba de .40 m de altura, bractea crema.  
 Colector: J. L. Contreras J. Nº. 6759  
 Fecha: 10.00/12.00/1998.00 Det. J. L. Contreras J. (8,157.00)

HERBARIO DE LA BENEMÉRITA UNIVERSIDAD  
AUTÓNOMA DE PUEBLA (HUAP)

*Pseudognaphalium semiamplexicaule* (DC) Anderb.  
 Det. J. L. Villaseñor from Huap. Fecha: 2014  
 MEX

Figure 19. *Pseudognaphalium ehrenbergianum*. Puebla, Contreras 6759 (HUAP).



Figure 20. *Pseudognaphalium ehrenbergianum*. Puebla, Contreras 9350 (HUAP).



Figure 21. *Pseudognaphalium ehrenbergianum*. Puebla, Caamaño O. 6436 (HUAP).



Figure 22. *Pseudognaphalium ehrenbergianum*. Puebla, Contreras 6796 (HUAP).



Figure 23. *Pseudognaphalium ehrenbergianum*. Puebla, Contreras 7038 (HUAP). Unusually narrow leaves, perhaps from distal branches of a large plant.

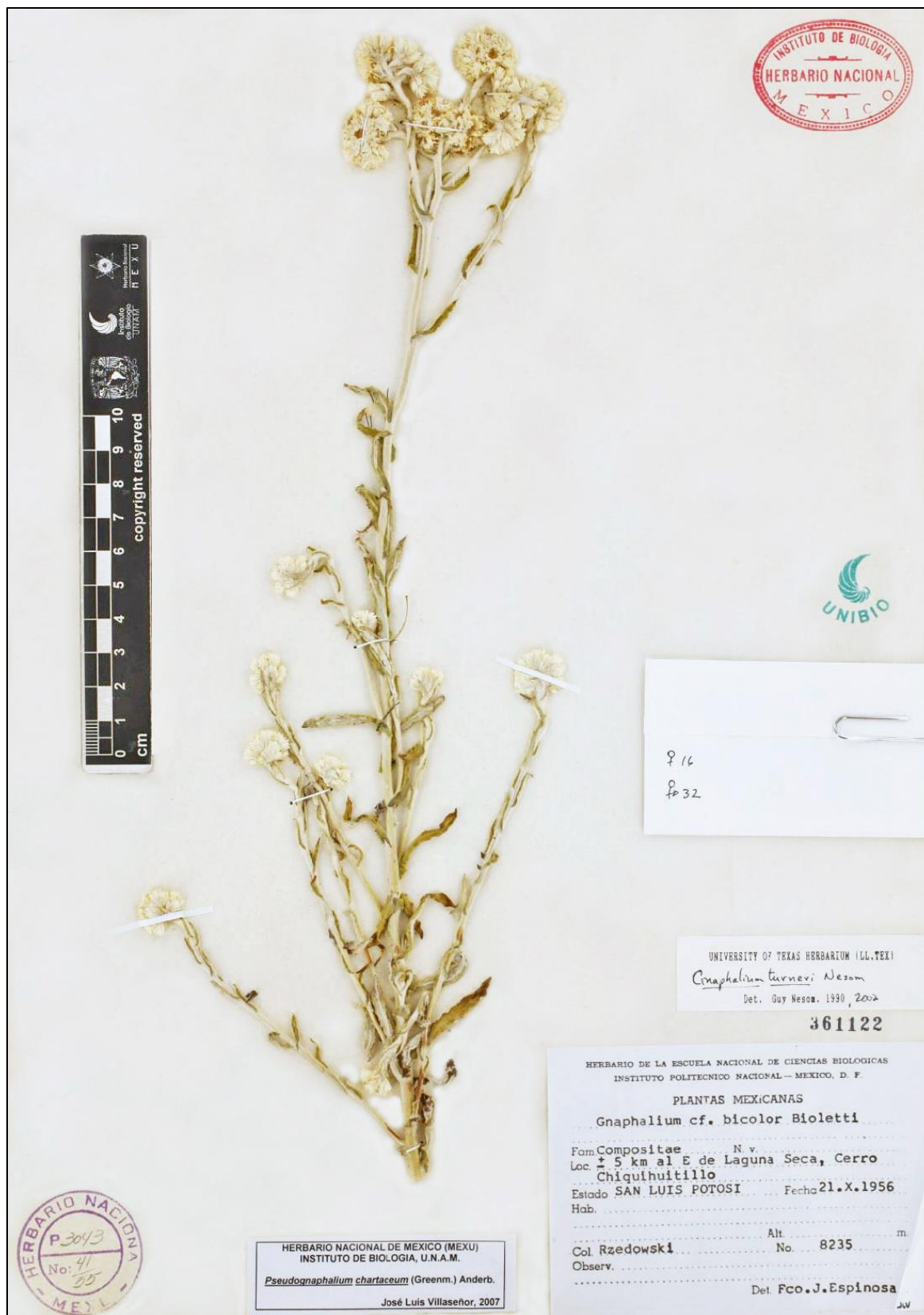


Figure 24. *Pseudognaphalium hyperandros*. San Luis Potosi, Rzedowski 8235 (MEXU). "*Gnaphalium turneri*" (annotation) is an unpublished name.

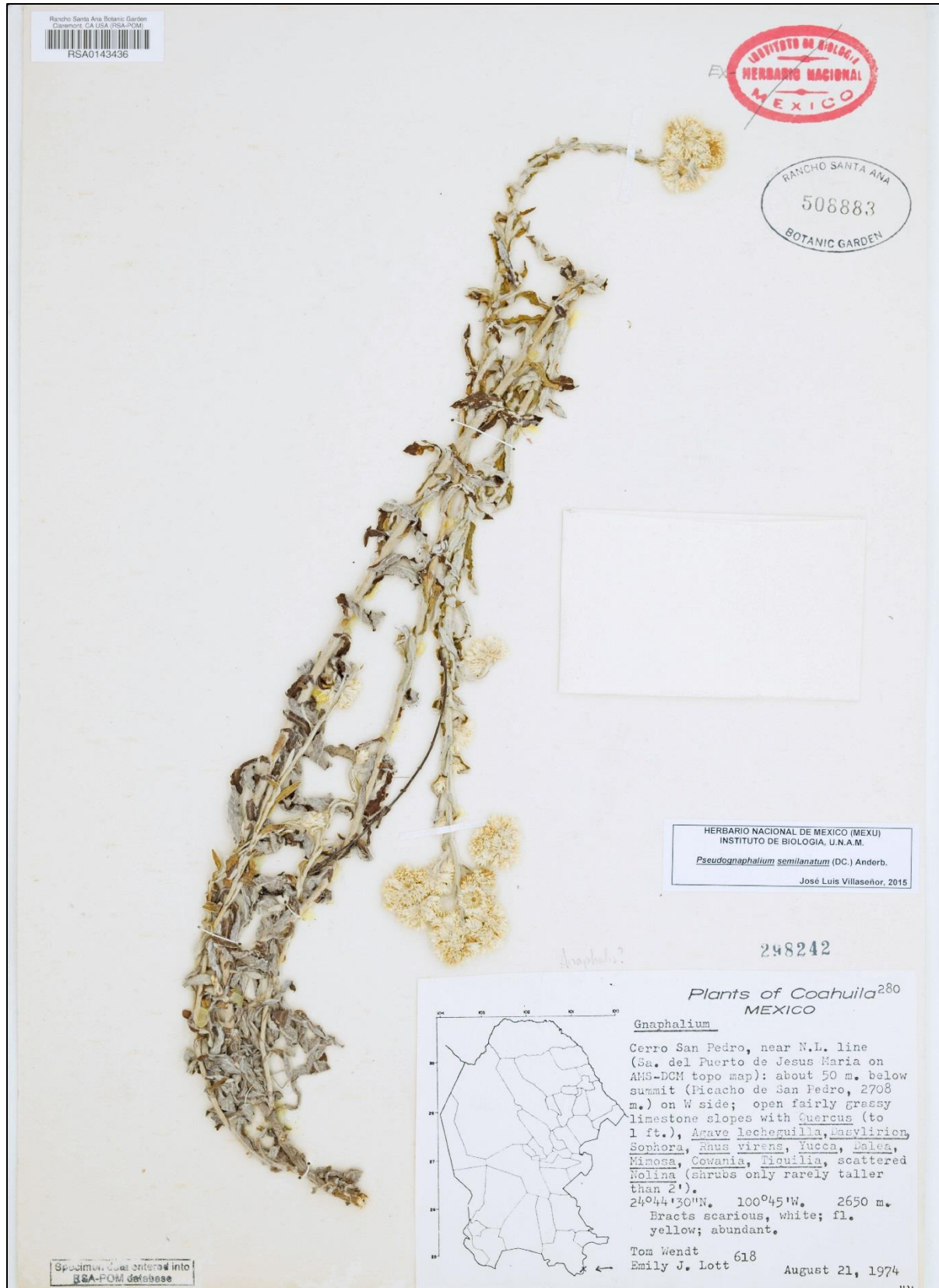


Figure 25. *Pseudognaphalium hyperandros*. Coahuila, Wendt 618 (RSA).

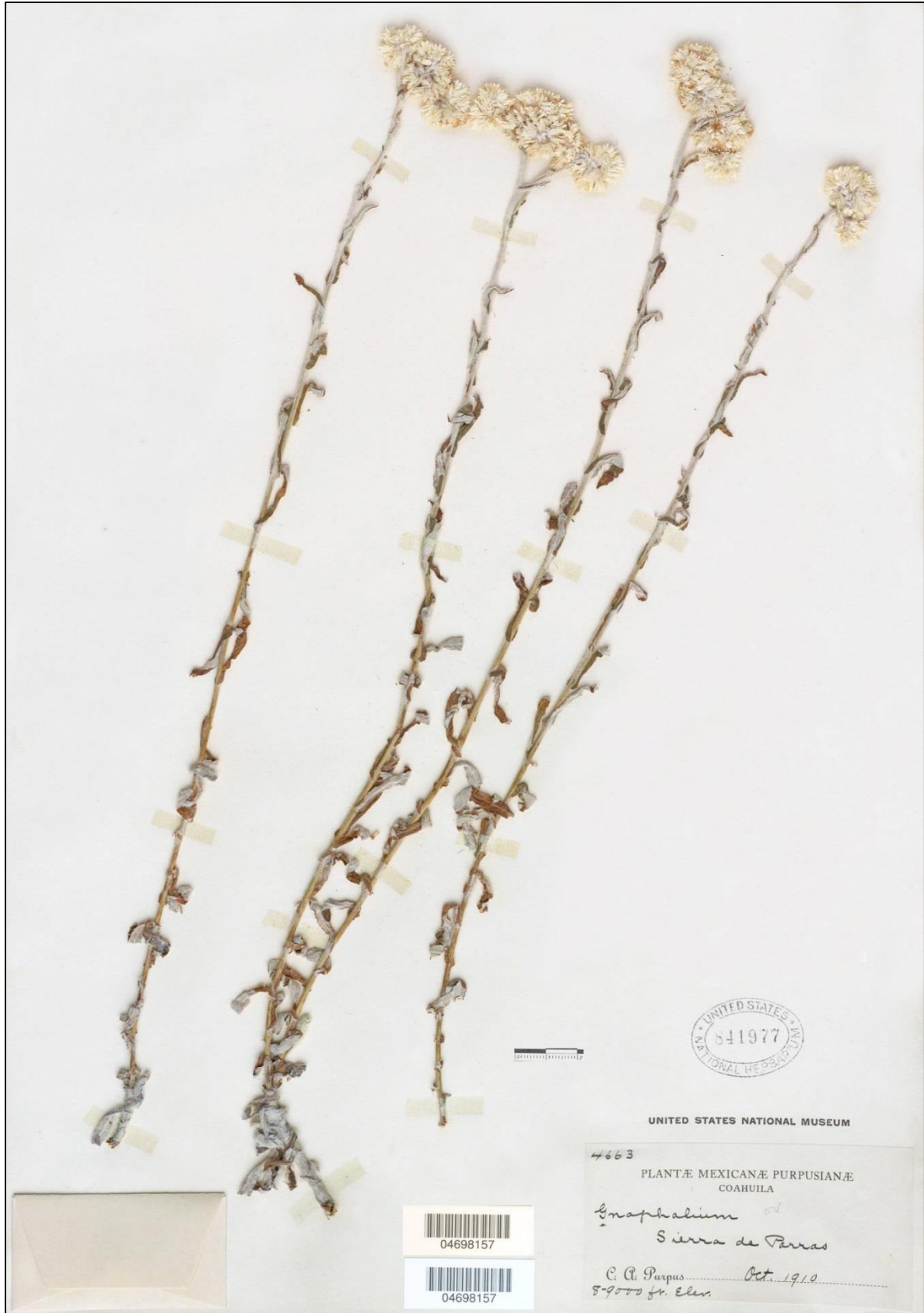


Figure 26. *Pseudognaphalium hyperandros*. Coahuila, Purpus 4663 (US).



Figure 27. *Pseudognaphalium hyperandros*. Detail from *Purpus 4663* (US).



Figure 28. *Pseudognaphalium hyperandros*. Details of leaf insertion.



Figure 29. *Pseudognaphalium hadroflorum*. Tamaulipas, Henrickson 19180, isotype (MEXU).





Figure 30. *Pseudognaphalium hadroflorum*. Detail from *Henrickson 19180* (MEXU)

Figure 31. *Pseudognaphalium hadroflorum*. Tamaulipas, King & Peterson 9953 (US).



Figure 32. *Pseudognaphalium hadroflorum*. Details from King & Peterson 9953 (US).



Figure 33. *Pseudognaphalium hadroflorum*. Detail from King & Peterson 9953 (US).



Figure 34. *Pseudognaphalium hidalgoense*. Hidalgo, Moore 3990, isotype (MEXU).



Figure 35. *Pseudognaphalium hidalgoense*. Hidalgo, Hodgdon 5644 (NHA).



Figure 36. *Pseudognaphalium hidalgoense*. Detail from Moore 3990 (MEXU).

#### ACKNOWLEDGEMENTS

I'm grateful to the staff of TEX,LL and US for help and hospitality there during recent study and for loans (to TEX) from F, GH, MEXU, US, and others, to the Missouri Botanical Garden library for help with literature, George Hinton for images of collections in herbarium GBH, John Pruski for observations on MO collections, and Allan Coombes (HUAP) for images of the cudweed collections there. Access to images of MEXU collections through the Portal de Datos Abiertos UNAM has been invaluable.

Editor's note: In the originally posted version, pages of informal notes beyond the end of the paper at page 48 were included — they are removed here. No other change has been made.

## LITERATURE CITED

- Acosto-Maindo, A. and M. Galbany-Casals. 2018. *Pseudognaphalium aldunateoides* back in *Gnaphalium* (Compositae: Gnaphalieae). *Collectanea Bot.* 37: e012 <<http://doi.org/10.3989/collectbot.2018.v37.012>>
- Anderberg, A.A. 1991. Taxonomy and phylogeny of the tribe Gnaphalieae (Asteraceae). *Opera Bot.* 104: 1–195.
- Aristeguieta, L. 1964. Compositae, Tribus I-V. Flora of Venezuela, Vol. X, Parte Primera. Edicion Especial del Instituto Botanico, Caracas.
- Chen, Y. and R.J. Bayer. 2011. *Pseudognaphalium*. Pp. 815–817, in Flora of China, Vol. 20-21. Science Press (Beijing) and Missouri Botanical Garden Press (St. Louis).
- Freire, S.E., C. Monti, N.D. Bayón and M.A. Migoya. 2018. Taxonomic studies in *Pseudognaphalium* Kirp. (Asteraceae, Gnaphalieae) from Peru. *Syst. Bot.* 43: 325–343.
- Freire, SE, J.L. Villaseñor, C. Monti, N.D. Bayón, and M.A. Migoya. 2022a. Taxonomic revision of *Pseudognaphalium* (Asteraceae, Gnaphalieae) from North America. *Ann. Missouri Bot. Gard.* 107: 314–404.
- Freire, S.E., M.A. Grossi, N.D. Bayón, and C. Monti. 2022b. Morphometric analysis and synopsis of *Pseudognaphalium* (Gnaphalieae, Asteraceae) in North America. *Anais Acad. Brasil. Ci.* 94(4).
- Galbany Casals, M, M. Unwin, N. Garcia-Jacas, R. Smissen, A. Susanna, and R. Bayer. 2014. Phylogenetic relationships in *Helichrysum* (Compositae, Gnaphalieae) and related genera: Incongruence between nuclear and plastid phylogenies, biogeographic and morphological patterns, and implications for generic delimitation. *Taxon* 63: 608–624.
- Hilliard, O.M. and B.L. Burtt. 1981. Some generic concepts in Compositae–Gnaphaliinae. *Bot. J. Linn. Soc.* 82: 181–232.
- Nesom, G.L. 2001. Notes on variation in *Pseudognaphalium obtusifolium* (Asteraceae: Gnaphalieae). *Sida* 19: 615–619.
- Nesom, G.L. 2004. *Pseudognaphalium canescens* (Asteraceae: Gnaphalieae) and putative relatives in western North America. *Sida* 21: 781–790.
- Nesom, G.L. 2006. *Pseudognaphalium*. Pp. 415–425, in Flora of North America North of Mexico, Vol. 19. Oxford Univ. Press, New York and Oxford.
- Nesom, G.L. 2021. Taxonomic review of the *Pseudognaphalium pringlei* group (Asteraceae: Gnaphalieae). *Phytoneuron* 2021-70: 1–33.
- Nesom, G.L. 2022. Four new Gnaphalieae (Asteraceae) from Baja California Sur. *Phytoneuron* 2022-14: 1–30.
- Nesom, G.L. 2023. Taxonomic summary of *Gnaphaliothamnus* and *Mexerion* (Asteraceae: Gnaphalieae). *Phytoneuron* 2023-50: 1–86.
- Nesom, G.L. 2023. New species of American *Pseudognaphalium* (Asteraceae: Gnaphalieae). II. Miscellaneous. *Phytoneuron* 2023-52: 1–53.
- Nie, Z.-L., V.A. Funk, Y. Meng, T. Deng, H. Sun, and J. Wen. 2016. Recent assembly of the global herbaceous flora: Evidence from the paper daisies (Asteraceae: Gnaphalieae). *New Phytol.* 209: 1794–1806.
- Pruski, J.F. 2012. Studies of Neotropical Compositae–IV. *Pseudognaphalium leucostegium*, a new species from Huehuetenango, Guatemala, and a new combination in *Chionolaena* (Gnaphalieae). *Phytoneuron* 2012-1: 1–5.
- Pruski, J.F. 2018. Flora Mesoamericana. Volumen 5, Parte 2. Asteraceae. Univ. Nacional Autónoma de México, Missouri Botanical Garden, and The Natural History Museum (London). [*Pseudognaphalium*, pp. 222–231]
- Smissen, R.D., R.J. Bayer, N.G. Bergh, I. Breitwieser, S.E. Freire, M. Galbany-Casals, A.N. Schmidt-Lebuhn, and J.M. Ward. 2020. A revised subtribal classification of Gnaphalieae (Asteraceae). *Taxon* 69: 778–806.
- Smissen, R.D., I. Breitwieser, and P.J. De Lange. 2023. *Pseudognaphalium* (Asteraceae, Gnaphalieae) diversity in New Zealand revealed by DNA sequences with notes on the phylogenetic relationships of Hawaiian Islands plants referred to *Pseudognaphalium sandwicense*. *New Zealand J. Bot.* 61: 304–331.