



CELLULAR AND MOLECULAR BIOLOGY

Morphometric Analysis and Synopsis of *Pseudognaphalium* (Gnaphalieae, Asteraceae) in North America

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Abstract: *Pseudognaphalium* Kirp. (Asteraceae, Gnaphalieae) consist of about 60 species mainly distributed in South, Central, and North America. As a first contribution toward a comprehensive taxonomic review of *Pseudognaphalium*, we perform here the first morphometric analysis of North American species, using UPGMA method for the construction of the dendrogram. Based upon these results we present a synopsis including a key to identify species and their associated synonymy. Thirty-seven species are recognized, two taxa are newly synonymized, *Pseudognaphalium microcephalum* under the name *P. canescens* and *Pseudognaphalium semilanatum* under the name *P. semiamplexicaule*, and two other names are confirmed as synonymous as previously proposed, *Pseudognaphalium micradenium* as a synonym of *P. helleri* and *Pseudognaphalium crenatum* as a synonym of *P. viscosum*. Lectotypes are newly designated for *Gnaphalium beneolens*, *G. berlandieri* (= *Pseudognaphalium stramineum*), *Gnaphalium decurrens* (= *Pseudognaphalium macounii*), *G. leucocephalum*, *G. oxyphyllum*, *G. oxyphyllum* var. *semilanatum* (= *P. semiamplexicaule*), *G. semiamplexicaule*, *G. sulphurescens* (= *P. stramineum*), *G. thermale*, and second-step lectotypifications are proposed for *G. helleri* and *G. wrightii* (= *P. canescens*). In addition, the first illustrations of *Pseudognaphalium helleri* and *P. semiamplexicaule*, and a colour figure of *P. canescens* and *P. beneolens* emphasizing the results of the morphometric analysis are provided.

Key words: Cluster analysis/UPGMA dendrogram, compositae, morphology, phenetics, taxonomy.

INTRODUCTION

Pseudognaphalium Kirp. (Asteraceae, Gnaphalieae) was segregated from *Gnaphalium* L. by Kirpichnikov & Kuprijanova (1950). Estimates of the number of species ranges between about 90 (Anderberg 1991, Bayer et al. 2007) and 150 (Dillon 2005), and they are mainly distributed in South, Central, and North America, but some species also occur in Asia and Africa. However, as treated in recent revisions of the South American species (Freire et al. 2014a, b, 2018), the number of taxa accepted in *Pseudognaphalium* has been reduced to ca. 60. The genus is mainly

characterized by its herbaceous habitat and the presence of disciform, heterogamous capitula in clusters arranged in corymbs or panicles, the possession of monochromous phyllaries with a divided stereome, truncate style branches with apical sweeping hairs, achenes either glabrous or with short oblong myxogenic duplex hairs, and pappus bristles free at the base. Studies of detailed morphological characters (Hilliard & Burtt 1981) and phylogenetic analysis inferred from morphology (Anderberg 1991) and molecular data (Bayer et al. 2007, Ward et al. 2009, Smissen et al. 2011, Galbany-Casals et al. 2010, 2014) have been interpreted as providing

support for recognizing *Pseudognaphalium* as a distinct genus. However, the most recent molecular phylogenies (e.g. Nie et al. 2016, Acosta Maindo & Galbany-Casals 2018) recover *Pseudognaphalium* as polyphyletic in two independent clades: a clade containing mainly North American species (Canada, United States of America, and Mexico), and the other clade including mainly South American species. The generitype, *Pseudognaphalium oxyphyllum* (DC.) Kirp., was included in the North American clade with the other North American species. Both clades were nested within the southern African HAP clade (*Helichrysum*, *Anaphalis*, *Pseudognaphalium*, etc.) showing a southern African origin of *Pseudognaphalium* (Nie et al. 2016).

Taxonomic treatments and catalogues of North American species of *Pseudognaphalium* were carried out by Espinosa-García (1985, 2005, sub *Gnaphalium*), and Villaseñor (2016) for Mexican species, and by Nesom (2006) for North American North Mexican species. These treatments include several taxonomically critical groups of closely related species, as well as polymorphic species with complex intraspecific variation. As an example, the species *Gnaphalium beneolens* Davison, *G. microcephalum* Nutt., *G. thermale* E.E.Nelson, and *G. wrightii* A.Gray, were accepted by Ferris (1960), Munz & Keck (1959), and Munz (1968, 1974). On the other hand, Cronquist (1950) recognized *Gnaphalium thermale* as a variety of *G. microcephalum* while Douglas (1986) considered it as a subspecies. Stebbins & Keil (1992) and Stebbins (1993) merged all these species into a single polymorphic species, *Gnaphalium canescens*, recognizing *G. beneolens*, *G. microcephalum*, and *G. thermale* as subspecies, and placing *G. wrightii* into synonymy. Meanwhile, Nesom (2004) considered these four taxa as species under *Pseudognaphalium*, accepting *Gnaphalium*

wrightii as a synonym of *P. canescens*. This taxonomic instability affects the identification of specimens of these and other species, and this prompted an investigation based on multivariate analysis to shed light on the delimiting morphologically close, infraspecific taxa or species classification. Cluster analysis and other multivariate techniques have been useful for solving taxonomic problems and circumscribing taxa from morphometric variability data. Several authors have used this type of study to identify entities based on morphology in diverse groups of plants (Owen et al. 2006, Lopez Laphitz et al. 2011, Grossi et al. 2011, Robbiati et al. 2014, Fernández et al. 2017).

The purpose of this study is to examine the current circumscription of the North American *Pseudognaphalium* taxa to define which species should be recognized based on the variation of morphological characters, including diagnostic characters, using cluster analysis for delimitation of species.

MATERIALS AND METHODS

Sample collection

A total of 297 specimens (including type material), representing 41 of the 43 North American species of *Pseudognaphalium* recognized in previous studies (Nesom 2006, Villaseñor 2016, Villarreal-Quintanilla et al. 2020), were chosen for the morphometric analysis (Appendix 1). Only two species, *Pseudognaphalium altamiranum* and *Gnaphalium oaxacanum* could not be included in the analysis since no material was available from these species. Herbarium material was examined from G, GH, M, MEXU, MO, NY, S, and UC (acronyms following Thiers 2020). Type images at high resolution from BM, C, G-DC, GH, L, LINN, MEXU, MICH, NDG, OS, P, RM, TEX, UC, US, and WIS were also examined (<http://plants.jstor.org/>).

Morphological data and cluster analysis

We analyzed a total of 36 characters: 13 vegetative and 23 reproductive. A list of the characters and their states can be seen in the Table I. All characters used to separate the North American species of *Pseudognaphalium* by former authors were included in our analysis. The measurements were performed on mature specimens. All specimens were studied by direct observation and by using a WILD Heerbrugg M5-26799 stereoscope; measurements were taken using a calibrated ocular micrometer. The leaf-blade observations were limited to the mid-section of flowering branches. Three florets per capitulum at same stage of anthesis from 2 or 3 capitula in each specimen were dissected. When the availability of specimens made it possible, replicates of three measurements for each character were obtained and the average was used in the ensuing statistical analyses.

We carried out a cluster analysis on all the OTUs. The similarity between two OTUs was calculated on the basis of Gower's general similarity coefficient (Gower 1971) and the UPGMA method was used for the construction of the dendrogram (Sneath & Sokal 1973).

The multivariate analyses with Gower's (1971) coefficient are suitable for the analysis of mixed characters, e.g., qualitative (binary and ordinal) and quantitative characters to generate a distance/dissimilarity matrix (Mapaya & Cron 2016). Likewise, UPGMA is an accurate and spread method to deduce similarity/dissimilarity among OTUs (Radford 1986, Ward 1993). The qualitative characters were coded accordingly as binary (presence/absence) or a code was assigned for each character state (see Table I for the list of characters and coding). Cluster analysis was performed on all the OTUs using all 36 characters, to obtain information about general relationships and similarities between them. The analyses were carried out using the software's PAST (Hammer & Harper 2006).

Concepts of species delimitation

The treatment here reported is based on the conservative and widely accepted morphological species concept. According to this concept, continuous variation of characters is allowed within the species, while discontinuous variation in more than one character define distinct species (Davies & Heywood 1967).

Table I. Morphological characters and character states evaluated in the study.

Vegetative characters:
1. plant height (cm); 2. stem (1 = 0, 2 or 3 = 1, 4 or more = 2); 3. winged stem (absent = 0, present = 1); 4. filiform stems (absent = 0, present = 1); 5. stem pubescence (woolly = 0, lanuginose = 1, glandular = 2); 6. leaf length (cm); 7. leaf width (cm); 8. leaf apex (acute = 0, acuminate = 1, obtuse to rounded = 2); 9. leaf base (attenuate = 0, rounded = 1, decurrent = 2, clasping = 3); 10. leaf margins (flat = 0, undulate = 1); 11. leaf adaxial surface (lanuginose = 0, wolly = 1, glandular = 2); 12. leaf abaxial surface (lanuginose = 0, wolly = 1, glandular = 2); 13. basal rosette of leaves at flowering (whitered = 0, fresh/persistent = 1).
Reproductive characters:
14. capitula arrangement (lax corymbs = 0, dense corymbs = 1, paniculiform corymbs = 2); 15. involucre height (mm); 16. involucre diameter (mm); 17. number of series of phyllaries (3 or 4 = 0, 5 or 6 = 1, 7 or more = 2); 18. phyllary number (#); 19. outer phyllary length (mm); 20. outer phyllary width (mm); 21. outer phyllary apex (acute = 0, obtuse = 1); 22. inner phyllary length (mm); 23. inner phyllary width (mm); 24. inner phyllary apex (acute or acuminate = 0, obtuse to rounded = 1); 25. inner phyllary color (white or creamy = 0, brownish = 1, yellowish or stramineous = 2, pinkish or purple = 3); 26. inner phyllary transparency (shiny = 0, opaque = 1); 27. marginal florets number (#); 28. marginal floret corolla length (mm); 29. disc florets number (#); 30. disc corolla length (mm); 31. disc corolla lobes (yellowish = 0, dark = 1); 32. disc corolla lobes pubescence (smooth = 0, papillose = 1); 33. achenes length (mm); 34. achenes diameter (mm); 35. achenes epidermis (smooth = 0, papillose = 1); 36. pappus length (mm).

RESULTS AND DISCUSSION

The cluster analysis (UPGMA) (Figure 1a) showed that most of the specimens of each species grouped together in separated clusters. A few specimens were intermingled in four main groups (Figure 1b), each with little metric distance suggesting high similarity between the species of each group.

The first group (I) includes *Pseudognaphalium canescens* (Figure 2a, b) and *P. microcephalum*. These species are morphologically similar with weakly discolored leaves, which are oblanceolate, not decurrent and eglandular, and corymbiform capitulescences. Both are confined to United States of America and Mexico and are sympatric in part of their distributions, i.e. they are found together in Chihuahua (Mexico) and California (USA). Stebbins & Keil (1992), suggested that *Pseudognaphalium beneolens* (= *G. beneolens*), *P. microcephalum* (= *G. microcephalum*), and *P. thermale* (= *G. thermale*) could be treated as subspecies within a single polymorphic species, *P. canescens* (= *G. canescens*). Nesom (2004) considered these four taxa as separate species mainly by leaf base, shape of leaves, nature of tomentum, apex of phyllaries, capitulescence, number of florets, and size of capitula. Our results recovered *P. beneolens* and *P. thermale* in separate clusters. *Pseudognaphalium beneolens* (Figure 2c, d) is characterized by its linear to linear-oblanceolate leaves and paniculate capitulescences, and *P. thermale* characterized by its concolorous oblanceolate leaves, decurrent leaf base, and corymbiform capitulescences. However, the specimens of *P. microcephalum* and *P. canescens* appear intermingled. Consequently, based on this study, we consider *Pseudognaphalium microcephalum* as a synonym of *P. canescens*.

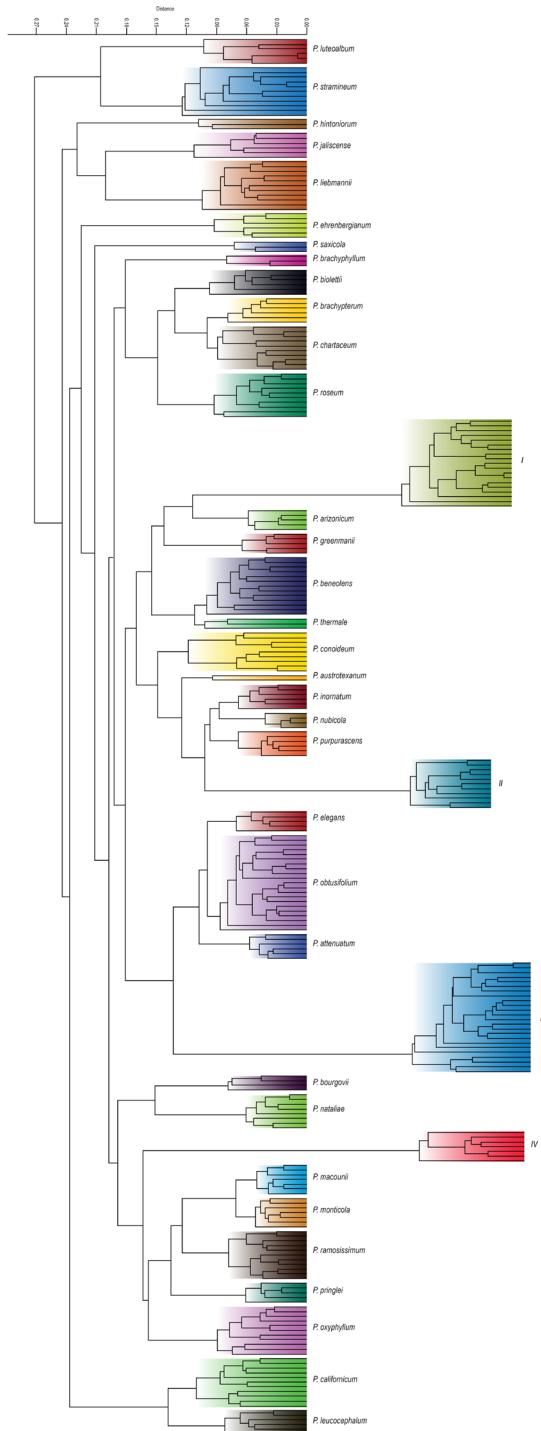


Figure 1a. UPGMA cluster analysis of the whole set of 297 specimens of the North American species of *Pseudognaphalium*, using a matrix calculated from 36 characters (Gower's coefficient of similarity). I: *P. canescens* and *P. microcephalum*; II: *P. semilanatum* and *P. semiamplexicaule*; III: *P. helleri* and *P. micradenium*; IV: *P. crenatum* and *P. viscosum*.

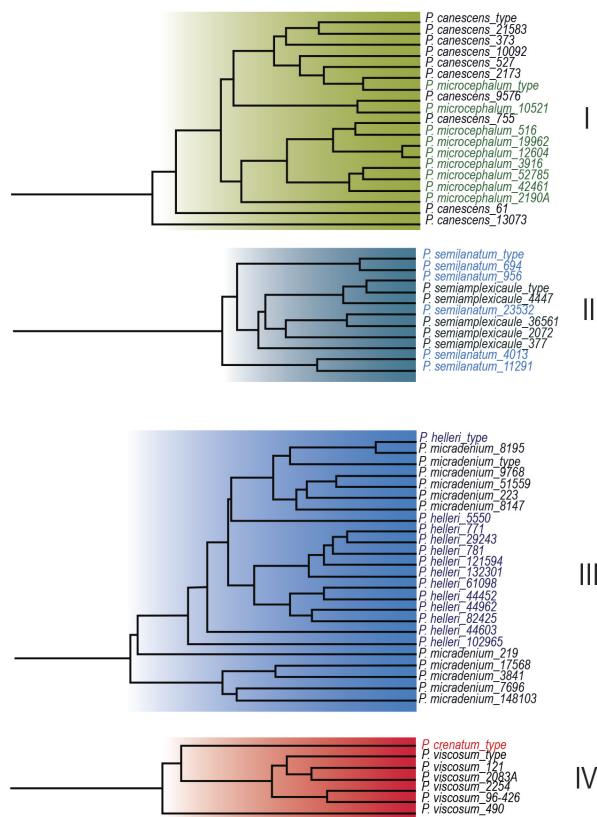


Figure 1b. Groups I-IV of the UPGMA cluster analysis of the North American species of *Pseudognaphalium* (continued from Fig. 1a). I: *P. canescens* and *P. microcephalum*; II: *P. semilanatum* and *P. semiamplexicaule*; III: *P. helleri* and *P. micradenium*; IV: *P. crenatum* and *P. viscosum*.

The second group (II) includes *Pseudognaphalium semiamplexicaule* (Figure 4a-g) from Mexico and Mesoamerica and *P. semilanatum*, endemic to Mexico. These two species have discolorous lanceolate leaves, clasping leaf bases, white shiny phyllaries and corymbiform to paniculate capitulescences. Villaseñor (2016) accepted both names as valid species. Espinosa-García (2005) considered *Pseudognaphalium semiamplexicaule* as a valid species and *P. semilanatum* as a dubious species. According to Pruski (2018) the identity of *Pseudognaphalium semilanatum* would be based on its adaxially stipitate-glandular leaves (vs. arachnid-tomentose in *P. semiamplexicaule*). The present analysis shows

specimens with glandular and eglandular leaves of *Pseudognaphalium semilanatum* and *P. semiamplexicaule* intermingled. Consequently, based on this study, we consider *Pseudognaphalium semilanatum* as a synonym of *P. semiamplexicaule*.

The third group (III) includes *Pseudognaphalium hellerii* (Figure 3 a-h) and *P. micradenium* from East of United States of America, characterized by narrow oblong-lanceolate leaves. *Pseudognaphalium hellerii* (= *Gnaphalium helleri*) was mainly described based on its densely glandular-pubescent stems and obtuse phyllaries. According to Weatherby (1923), the identity of *Pseudognaphalium micradenium* (= *Gnaphalium obtusifolium* var. *micradenium*) was based on its glandular-puberulent stems (vs. glandular-villous in *P. helleri*), linear or linear-lanceolate leaves (vs. leaves oblong-lanceolate in *P. helleri*), and acute phyllaries (vs. obtuse phyllaries in *P. helleri*). Mahler (1975), considered *Pseudognaphalium micradenium* (= *Gnaphalium obtusifolium* var. *micradenium*) as a variety of *P. hellerii* (= *G. helleri*; i.e. *G. helleri* var. *micradenium*). Cronquist (1980) distinguished *Pseudognaphalium obtusifolium* (= *Gnaphalium obtusifolium*) from *P. helleri* (= *G. helleri*, including *G. obtusifolium* var. *micradenium* as its synonym) by its wooly pubescence (vs. principally glandular in *P. helleri*). Nesom (2006) considered *Pseudognaphalium obtusifolium*, *P. helleri*, and *P. micradenium* as separate species, using leaf shape, pubescence, and the number of florets as a way to distinguish them. The present cluster analysis shows the specimens of *Pseudognaphalium obtusifolium* in a separate cluster, but those of *P. helleri* and *P. micradenium* appear intermingled. Consequently, based on this study, we consider *Pseudognaphalium micradenium* as a synonym of *P. helleri* as was previously suggested by Cronquist (1980).



Figure 2. *Pseudognaphalium canescens*. a. Habit; b. Detail of the inflorescence. c, d. *Pseudognaphalium beneolens*. c. Habit; d. Detail of the habit.
(Photographs: a, b. John Avise, Asteraceae of Orange Co., California; C. Neal Kramer, CalPhotos-University of California, Berkeley; d. Michael Mitchell, montereywildflowers.com).

The fourth group (IV) includes *Pseudognaphalium crenatum* from Mexico and *P. viscosum*, from United States of America (Texas), Mexico, and Mesoamerica, characterized by its stipitate-glandular stems, linear-lanceolate leaves, white shiny phyllaries, and numerous pistillate florets. Villaseñor (2016) accepted *Pseudognaphalium crenatum* as a valid species, but McVaugh (1984) and Pruski (2018) placed *P. crenatum* into synonymy of *P. viscosum*. The present cluster analysis shows the type specimen of *P. crenatum* grouped together with the specimens of *P. viscosum* and confirms previously proposed synonymy.

Therefore, in agreement with our results *Pseudognaphalium* consists of 37 North

American species (Figures 1a, b), and the corresponding synonyms for the three newly circumscribed species are indicated in the taxonomic treatment provided below.

Taxonomic Treatment of *Pseudognaphalium* in North America

Pseudognaphalium Kirp. (1950: 33).

Type: *Gnaphalium oxyphyllum* DC. \equiv *Pseudognaphalium oxyphyllum* (DC.) Kirp.

Hypelichrysum Kirp. (1950: 33). **Type:** *Gnaphalium heterotrichum* Phil. *Hypelichrysum heterotrichum* (Phil.) Kirp. \equiv *Pseudognaphalium heterotrichum* (Phil.) Anderb.

Gnaphalium L. sect. *Calolepis* Kirp. (1960: 309). **Type:** *Gnaphalium luteoalbum* L. *Pseudognaphalium luteo-album* (L.) Hilliard & Burtt. *Pseudognaphalium* subgen. *Laphangium* Hilliard & Burtt (1981): 205 \equiv *Laphangium* (Hilliard & Burtt 1981) Tzvelev (1993[1994]: 105) ‘*Gnaphalium* Kirp. subgen. *Laphangium* (Hilliard & Burtt 1981), (Sell 2006): 555. **Type:** *Gnaphalium luteo-album* L. ‘*Pseudognaphalium luteo-album* (L.) Hilliard & Burtt 1981.

Annual, biennial or perennial herbs, woolly or glandular woolly. Leaves alternate, entire, sessile, often stem-clasping and decurrent. Capitula small, heterogamous, disciform, sessile or short pedunculate, in small clusters arranged in corymbs or panicles; involucre often campanulate; phyllaries in 3-many-series, papery, phyllary lamina monochromous opaque or hyaline and shiny, white, yellowish, brownish, straw, pinkish or purple coloured, stereome divided; receptacle smooth or honeycombed. Florets many, pistillate florets usually outnumbering bisexual; pistillate florets corollas filiform or narrowly tubular; bisexual florets corollas tubular, scarcely broadened above, 5-lobed, all corollas yellowish or whitish, lobes glandular and often yellowish or whitish; anthers with a small obtuse apical anther appendage;

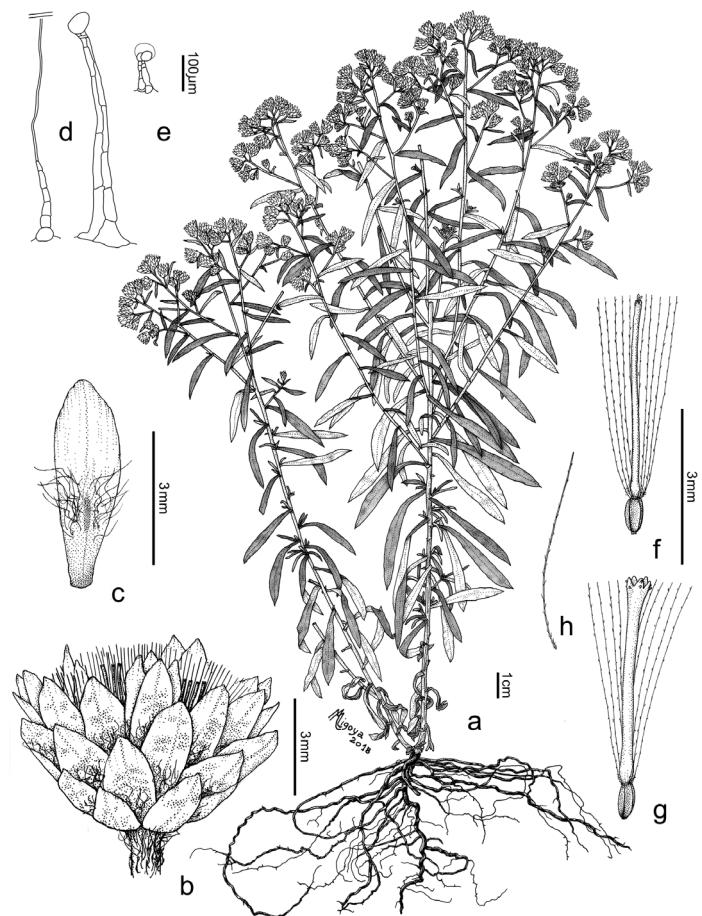


Figure 3. *Pseudognaphalium helleri*. a. Plant; b. Capitulum; c, Inner phyllary; d-e, Foliar and stem trichomes; f. Pistillate floret; g. Bisexual floret; h. Bristle pappus [a-c, f-h. Fernald & Bayard Long 7696, PH; d. Bush 1000, MO; e. Demaree 16387, GH].

tails slightly longer or shorter than the filament collar; style branches truncate and penicillate. Achenes glabrous smooth or with imbricate microscopic papillae, rarely setuliferous with short duplex myxogenic hairs; carpopodium symmetrical, continuous; pappus monomorphic, of free capillary, barbellate bristles, apical cells sometimes inflated, bases cohering by patent cilia.

Worldwide distribution, mostly American, some African and Asian species. About 60 species of which 37 grow in North America.

Key to Species of *Pseudognaphalium* in North America

1. Leaves \leq 1.5 cm long ***P. brachyphyllum***
 1'. Leaves \geq 2 cm long 2

- 2(1'). Stem leaves strongly decurrent on stem (wings extending down beyond middle of internode)..... 3
 2'. Stem leaves not to moderately decurrent on stem (wings never extending down beyond middle of internode) 4
 3(2). Leaves linear-oblong, adaxial surface arachnoid ***P. bourgovii***
 3'. Leaves lanceolate, adaxial surface stipitate-glandular ***P. nataliae***
 4(2'). Leaves pseudopetiolate (long-attenuate at the base) ***P. ehrenbergianum***
 4'. Leaves sessile (shortly or not attenuate at base)..... 5
 5(4'). Adaxial surface of leaf blades glandulose, arachnoid or lanuginose, abaxial surface white-lanuse 6

- 5'. Adaxial and abaxial surface of leaf blades glandulose, lanuginose, glandular-lanuginose or lanose 23
- 6(5). Adaxial surface of leaf blades conspicuously stipitate-glandular 7
- 6'. Adaxial surface of leaf blades not stipitate-glandular 16
- 7(6). Bases of leaf blades not clasping 8
- 7'. Bases of leaf blades clasping 13
- 8(7). Leaves narrowly linear to linear-lanceolate, margins strongly revolute 9
- 8'. Leaves lanceolate, oblong-oblanceolate or elliptic, margins slightly revolute 11
- 9(8). Phyllaries acute ***P. austrotexanum***
- 9'. Phyllaries obtuse to rounded 10
- 10(9'). Phyllaries shiny; pistillate florets 200–400; achenes papillose ***P. viscosum***
- 10'. Phyllaries opaque; pistillate florets ≤ ca. 125; achenes smooth ***P. leucocephalum***
- 11(8'). Stems lanose; leaves lanceolate to elliptic ***P. elegans***
- 11'. Stems glandular; leaves lanceolate to oblong-oblanceolate 12
- 12(11'). Stem leaves moderately decurrent ***P. macounii***
- 12'. Stem leaves not decurrent ***P. helleri***
- 13(7'). Phyllaries brownish ***P. monticola***
- 13'. Phyllaries white 14
- 14(13'). Involucre narrowly campanulate, 2.5–3 mm diam; capitula ≤ 40-flowered ***P. pringlei***
- 14'. Involucre obconic, 3–6 mm diam; capitula ≥ 70-flowered 15
- 15(14'). Stems lanose; involucre 4–5(–5.5) mm high ***P. biolettii***
- 15'. Stems glandular-lanuginose; involucre (5–)5.5–6 mm high ***P. brachypterum***
- 16(6'). Leaves narrowly linear 1–2.5 mm wide, 30–50 times as long as wide ***P. greenmanii***
- 16'. Leaves linear, linear-oblanceolate, linear-oblanceolate or lanceolate > 2.5 (rarely 2) mm wide, up to 23 times as long as wide 17
- 17(16'). Phyllaries purple ***P. purpurascens***
- 17 '. Phyllaries white, yellowish, purple, pinkish, brownish or straw coloured 18
- 18(17'). Bases of leaf blades not clasping, not decurrent 19
- 18'. Bases of leaf blades clasping or moderately decurrent 20
- 19(18). Leaves lanceolate or linear-lanceolate, acute-acuminate ***P. attenuatum***
- 19'. Leaves linear-oblanceolate, acute or subobtuse ***P. obtusifolium***
- 20 (18'). Phyllaries white, occasionally pinkish 21
- 20'. Phyllaries brownish 22
- 21(20). Leaves lanceolate, apex acuminate ***P. semiamplexicaule***
- 21'. Leaves lanceolate-oblanceolate to linear-oblanceolate, apex acute ***P. roseum***
- 22(20'). Capitula arranged in corymbs; leaf blade margins flat ***P. arizonicum***
- 22'. Capitula arranged in panicles; leaf blade margins undulate ***P. inornatum***
- 23(5'). Annual herbs 24
- 23'. Perennial herbs 25
- 24(23). Achenes setuliferous; leaves linear-oblanceolate; stems 15–70 cm high ***P. luteoalbum***
- 24'. Achenes glabrous; leaves oblong-obovate; stems 5–30 cm high ***P. saxicola***
- 25(23'). Capitula arranged in elongate to broadly columnar panicles ***P. ramosissimum***
- 25'. Capitula arranged in corymbs or paniculiform corymbs 26
- 26(25'). Phyllaries brownish 27
- 26'. Phyllaries white, whitish, pinkish, yellowish or straw coloured 28
- 27(26). Leaves apices acute; basal rosette of leaves usually persisting at flowering ***P. liebmanni***
- 27'. Leaves apices attenuate; basal rosette of leaves withered at flowering ***P. conoideum***
- 28(26'). Stem leaves obovate 29

- 28'. Stem leaves predominantly lanceolate or linear 31
- 29(28). Leaves oblong-obovate, 5–10(–20) mm wide, margins undulate *P. nubicola*
- 29'. Leaves linear-obovate, 4–10 mm wide, margins flat 30
- 30(29'). Leaves concolorous, glandular-pubescent under wool *P. thermale*
- 30'. Leaves weakly discolored, eglandular or with few short glandular trichomes hidden under wool *P. canescens*
- 31(28'). Stem leaves predominantly lanceolate 32
- 31'. Stem leaves predominantly linear 34
- 32(31). Phyllaries opaque, white 33
- 32'. Phyllaries shiny, whitish, yellow-greenish or purple *P. oxyphyllum*
- 33(32). Leaves lanceolate, glandular-stipitate on both surfaces; pistillate florets 7–15 (24) times as many as bisexual florets *P. californicum*
- 33'. Leaves oblong-lanceolate, glandular-lanuginose on abaxial surface; pistillate florets 1–1.5 times as many as bisexual florets *P. chartaceum*
- 34(31'). Phyllaries yellowish *P. stramineum*
- 34'. Phyllaries white or whitish 35
- 35 (34'). Leaves glandular on both surfaces, margins undulate *P. hintoniorum*
- 35'. Leaves lanuginose on both surfaces or with short glandular trichomes hidden under the woolly trichomes on adaxial surface, margins flat 36
- 36(35'). Leaf apices acute, capitula 45–ca. 100-flowered *P. beneolens*
- 36'. Leaf apices attenuate; capitula ca. 140–270-flowered *P. jaliscense*
1. ***Pseudognaphalium arizonicum* (A. Gray)** Anderb. (Anderberg 1991: 147). *Gnaphalium arizonicum* A. Gray (1883: 1884: 3. **Type:** UNITED STATES OF AMERICA. Arizona, Huachuca Mts., “near Fort Huachuca along exsiccated beds of streams” [Cochise Co.], J. G. Lemmon 2757

(holotype: GH 00008290!; isotype: K 000978290! by Lemmon in 1882).

Distribution: Mexico and United States of America.

2. ***Pseudognaphalium attenuatum* (DC.) Anderb.** (Anderberg 1991: 147).

2a. ***Pseudognaphalium attenuatum* (DC.) Anderb.** var. ***attenuatum***. *Gnaphalium attenuatum* DC. (Candolle 1838: 228). **Type:** MEXICO. Tamaulipas, Tampico de Tamaulipas, 1827, J. L. Berlandier 70 (holotype: G-DC G-00312671!; isotypes: G 00301179!, P 00704492!).

Distribution: Mexico and Mesoamerica [Belice, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, Panama (Pruski 2018)].

2b. ***Pseudognaphalium attenuatum* (DC.) Anderb.** var. ***sylvicola*** (McVaugh) Hinojosa-Espinosa & Villaseñor (2014: 490). *Gnaphalium attenuatum* DC. var. *sylvicola* McVaugh (1972: 465). **Type:** MEXICO. Jalisco: Sierra de Cuale SW of Talpa de Allende, 1800–2250 m, 19–21 Nov 1952, R. McVaugh 14283 (holotype: MICH 1107414!; isotypes: BM 000574758!, BRIT 23669!, DUKE 10000803!, MEXU 00149481!; probable isotype: NY 00169487! by R. McVaugh and J. Sooby, Jr. 14283).

Distribution: Mexico.

3. ***Pseudognaphalium austrotexanum* Nesom** (2001a): 507. **Type:** UNITED STATES OF AMERICA. Texas. Jim Wells Co. 10.1 mi S of Alice, railroad right of way Santa Gertrudis Division of King Ranch, 24 Nov 1954, M. C. Johnston 542108 (holotype: TEX 00008978!; isotype: BRIT 23963!).

Distribution: Mexico and United States of America.

4. ***Pseudognaphalium beneolens* (Davidson)** Anderb. (Anderberg 1991: 147). *Gnaphalium beneolens* Davidson (1918: 17). *Gnaphalium canescens* DC. subsp. *beneolens* (Davidson) Stebbins & Keil (1992: 437). *Pseudognaphalium canescens* (DC.) Anderb. subsp. *beneolens* (Davidson) Kartesz (1999: no. 25. **Type:** UNITED STATES OF AMERICA. [California] Los Angeles Co.,

Crescenta, Sep 1917, F. E. Burlew 3275 (**lectotype, designated here: GH 00008291!**; isolectotypes: RSA 0001209!, RSA 0001210!). **Figure 2c, d.**

Observation: Nesom (2004): 782 indicated the type of *Gnaphalium beneolens* Davidson as ‘Type: U.S.A. California. [Los Angeles Co.]: Crescenta, 1 Sep 1917, E.E. Burlew 3275 (Isotype: GH!)’. This citation of an ‘isotype’ (after 1 January 2001) cannot be corrected to a designation of a lectotype (Art. 9.10 of the ICN, Shenzhen Code; Turland et al. 2018), because they did not use the phrase ‘designated here’ or an equivalent (ICN, Art. 7.11, Shenzhen Code; Turland et al. 2018) in their associated statement. Consequently, Nesom’s typification for the name *G. beneolens* was not effective (ICN, Art. 9.23, Shenzhen Code; Turland et al. 2018). The specimen GH 00008291 which presents the most complete plant is designated here as the lectotype of *G. beneolens*.

Distribution: Mexico and United States of America.

5. ***Pseudognaphalium biolettii*** Anderb. ex G.L.Nesom (Nesom 2002): 149, replacement name for *Gnaphalium bicolor* Bioletti (1893: 16), hom. illeg., non *G. bicolor* (Lindl.) Sch.Bip. 1845 [= *Xerochrysum bicolor* (Lindl.) R.J.Bayer], nec Franch. 1896 [= *Anaphalis bicolor* (Franch.) Diels]. *Pseudognaphalium biolettii* Anderb. (Anderberg 1991: 147), nom. inval. **Type:** UNITED STATES OF AMERICA. California, San Diego, 25 Mar 1891, G. W. Dunn s.n. (holotype: UC 31964!).

Distribution: Mexico and United States of America.

6. ***Pseudognaphalium bourgovii*** (A.Gray) Anderb. (Anderberg 1991: 147). *Gnaphalium bourgovii* A. Gray (1883): 1884: 3. **Type:** MEXICO. Veracruz: Valley of Cordova, 7 Feb 1866, E. Bourgeau 1852 (holotype: GH 00008317!; isotypes: K 000500363!, L 0001972!, MSC 0091946!, P 00704482!, P 00704483!, P 00704484!).

Distribution: Mexico.

7. ***Pseudognaphalium brachyphyllum*** (Greenm.) Anderb. (Anderberg 1991: 147). *Gnaphalium brachyphyllum* Greenm. (Greenman 1907: 267). **Type:** GUATEMALA. Quetzaltenango: Cerro Quemada, 9000 ft, 8 Feb 1906, W. A. Kellerman 5301 (holotype: F, not seen; isotypes: OS 0000179!, US 00129533!).

Distribution: Mexico and Mesoamerica [Guatemala].

8. ***Pseudognaphalium brachypterum*** (DC.) Anderb. (Anderberg 1991: 147). *Gnaphalium brachypterum* DC. (Candolle 1838: 226). **Type:** MEXICO. Circà Victoriam, Nov. 1830, J. L. Berlandier 2189 (holotype: G-DC G-00469610!; isotypes: GH 00008318!, P 00704485!, PH 00012282!).

Distribution: Mexico and Mesoamerica [El Salvador, Guatemala, Honduras, Nicaragua (Pruski 2018)].

9. ***Pseudognaphalium californicum*** (DC.) Anderb. (Anderberg 1991: 147). *Gnaphalium californicum* DC. (Candolle 1838: 224). **Type:** UNITED STATES OF AMERICA. California: year 1833, D. Douglas 57 ‘... v. s. comm. ab hon. soc. hortic. Londin.’ (holotype: G-DC G-00469618!; isotype: BM 000839374!, probable isotypes: [D. Douglas s.n.] GH 00008292!, K 000978292!).

Distribution: Mexico and United States of America.

10. ***Pseudognaphalium canescens*** (DC.) Anderb. (Anderberg 1991: 147). *Gnaphalium canescens* DC. (Candolle 1838: 228). **Type:** MEXICO. Guanajuato, León, year 1829, J. Mendez s.n. (holotype: G-DC G-00312669!; isotype: P 00704486!). **Figure 2a, b.** *Gnaphalium microcephalum* Nutt. (Nuttall 1841): 404. 1841. *Gnaphalium canescens* DC. subsp. *microcephalum* (Nutt.) Stebbins & Keil (1992): 437. *Pseudognaphalium canescens* (DC.) Anderb. subsp. *microcephalum* (Nutt.) Kartesz (1999): no. 26. *Pseudognaphalium microcephalum* (Nutt.) Anderb. (Anderberg 1991: 147). **Type:** UNITED STATES OF AMERICA. California, San Diego, T. Nuttall s.n. (holotype: BM 001010942!), **syn. nov.**

Gnaphalium wrightii A. Gray (1882): 214. **Type:** UNITED STATES OF AMERICA. Texas, [El Paso or Hudspeth Co.] between El Paso and Guadalupe Mts., Oct 1849, C. Wright 394 (lectotype [first step], designated by Nesom (2004): 783: GH; **lectotype [second step], designated here: GH 00008314!**; isolectotypes: GH 00008313!, US 00129567!).

Gnaphalium albatum Osterh. (Osterhout 1906): 141. **Type:** UNITED STATES OF AMERICA. Colorado. Larimer Co., canyon of Thompson River, [between the foothills and Estes Park], 16 Aug 1905, G. E. Osterhout 3158 (holotype: RM 0001102!; isotype: NY 00169466!).

Gnaphalium sonorae I.M.Johnst. (Johnston 1923): 99. **Type:** MEXICO. Sonora, Hermosillo, 1888, M. A. Crawford s.n. (holotype: GH 00008349!; isotype: US 00129558!-fragment and photograph of the holotype).

Gnaphalium texanum I.M.Johnst. (Johnston 1924): 86. **Type:** UNITED STATES OF AMERICA. Texas, Brewster Co., Mouth of Tarlinga Creek, Sep 1883, V. Havard 26 (holotype: GH 00008310!; probable isotype: US 00129562! [s.n.]).

Gnaphalium viridulum I.M.Johnst. (Johnston 1924): 86. **Type:** UNITED STATES OF AMERICA. New Mexico, Grant Co., Bear Mts., near Silver City, 2400 m, 19 Sep 1903, O. B. Metcalfe 742 (holotype: GH 00008312!; isotype: US 00129565!).

Gnaphalium albidum I.M.Johnst. (Johnston 1924): 84. **Type:** UNITED STATES OF AMERICA. California, San Diego Co., granite, in chaparral, 1850 ft [550 m], 11 Jul 1916, M. F. Spencer 69 (holotype: GH 00008288!; isotype: US 00129528!).

Observations:

1. According to the protologue, *Gnaphalium canescens* was based on the specimen 'in Mexico ad Leonem ultrà Guanaxuato legit cl. Mendez'. We found at G-DC, where the original herbarium of Candolle is deposited, the sheet G 00312669 'Mexiq. (Léon à l'ouest de Guanajuato), 1829, M. Mendez' [sheet 1], which is in accordance

with the protologue and is considered as the holotype of *Gnaphalium canescens*.

2. According to the protologue, *Gnaphalium microcephalum* was based on the specimen 'St. Diego, Upper California'. We found at BM, where the original herbarium of Nuttall is mainly deposited, the sheet Nuttall s.n. BM 001010942, which is in accordance with the protologue and matches the locality. Since Nuttall mentioned in the protologue '(I have seen but a single specimen)' this specimen is almost surely the holotype. There are other two collections on the same sheet BM 001010942, i.e. Suksdorf s.n. and Macoun s.n.

3. Nesom (2004): 782 indicated the type of *Gnaphalium wrightii* A. Gray as 'Type. U.S.A. Texas [El Paso or Hudspeth Co.] valley between El Paso and the Guadalupe Mts., Oct [1849], C. Wright 394 (Lectotype, designated here: GH!; Isolectotypes: GH!, US!)'. This constitutes a valid [first-step] lectotypification. Since we located two sheets of this collection at GH, 'second-step' lectotypification is required (ICN, Art. 9.17. Shenzhen Code; Turland et al. 2018). The specimen GH 00008314 which presents the most complete plant is here designated as the lectotype of *G. wrightii*. Furthermore, this is the specimen that was labelled as the 'lectotype' by Kittredge in 2009, and shows that Nesom did not annotate either of the two sheets in GH.

4. The types of new species described by Osterhout were deposited in his private herbarium and, upon his death, all his sheets were bequeathed to the Rocky Mountain Herbarium in Laramie, Wyoming. Consequently, the only collection kept at RM (RM 0001102) is considered as the holotype of *Gnaphalium albatum*.

Distribution: Mexico and United States of America.

11. ***Pseudognaphalium chartaceum* (Greenm.) Anderb.** (Anderberg 1991: 147). *Gnaphalium*

chartaceum Greenm. (Greenman 1904: 95). **Type:** MEXICO. Jalisco: Hillsides and banks near Guadalajara, 22 Nov 1888, C. G. Pringle 1827 (lectotype, designated by Pruski (2018: 225): GH 00008319!, isolectotypes: BR 0000005317776!, K 000500362!, M 0029851!, MEXU 01215400!, MICH 1107416!, NDG 59113!, UC 88344!, US 00129536!; syntype: Puebla, near Tehuacan, 22 Dec 1895, C. G. Pringle 7033, GH 00008320!).

Distribution: Mexico and Mesoamerica [Guatemala (Pruski 2018)].

12. ***Pseudognaphalium conoideum*** Anderb. (Anderberg 1991: 147), nom. nov. *Gnaphalium conoideum* Kunth (1818, folio edition): 67; (1820, quarto edition): 85 p., hom. illeg. non *G. conoideum* Lam. 1788. **Type:** MEXICO. ‘Crescit prope urbem Mexici, alt. 1170 hex. Floret Majo’, F. W. H. A. Humboldt & A. J. A. Bonpland s.n. [4157] (holotype: P 00322315!; isotypes: P 00704488!, P 00704489-fragment!).

Distribution: Mexico.

13. ***Pseudognaphalium ehrenbergianum*** (Sch. Bip. ex Klatt) Hinojosa-Espinosa & Villaseñor (2014): 490. *Gnaphalium ehrenbergianum* Sch. Bip. ex Klatt (1878): 127. **Type:** MEXICO. [Hidalgo] Zamaltepan [=Zacualtipán], Ehrenberg 24 (P-fragment 00704465! ex herb. Schultz Bipontinus 1845).

Distribution: Mexico.

Observation. Since the material, ex herb. (Schultz Bipontinus 1856) is not annotated by Klatt one could assume that he saw material in B, now destroyed, in order to provide some parts of the description.

14. ***Pseudognaphalium elegans*** (Kunth) Kartesz (1999): no. 28. *Gnaphalium elegans* Kunth (1818, folio edition): 63; (1820, quarto edition): 81, p. 30 **Type:** ECUADOR. Pichincha, 2450 m, Jun 1802, F. W. H. A. Humboldt & A. J. A. Bonpland 3001 (lectotype, designated by Freire et al. (2018): 330: P-HBK 00322306!; isolectotypes: P 00704547!, P 00704548!).

Gnaphalium poeppigianum DC. (Candolle 1838: 227). **Type:** PERU. Dpto. Huánuco, Cuchero, Sep 1829, E. F. Poeppig n. 34 diar. 1368 (lectotype, designated by Freire et al. (2018: 330): G-DC G-00469598!; isolectotypes: F 881500!, F 970435!-fragment, B† photo FOBN015138!, GH 00008361! fragment, GH 00008362!, HAL 112159!, NY 00169513!, P 00704530!, P 00704531!).

Distribution: Mexico, Mesoamerica [Costa Rica, Guatemala, Honduras, Nicaragua, Panama (Pruski 2018)] and South America [Colombia, Ecuador, Peru, Venezuela (Freire et al. 2018), Guyanas (Boggan et al. 1997)].

15. ***Pseudognaphalium greenmanii*** (S.F.Blake) Anderb. (Anderberg 1991: 147). *Gnaphalium greenmanii* S.F.Blake (1931): 329, nom. nov. for *Gnaphalium linearifolium* Greenm. (Greenman 1897): 308, hom. illeg. non *G. linearifolium* (Wedd.) Franch. 1892. [= *Quasiantennaria linearifolia* (Wedd.) R.J.Bayer & M.O.Dillon]. **Type:** MEXICO. Jalisco, rocky hills near Guadalajara, 7 Oct 1889, C. G. Pringle 2342 (lectotype, designated by McVaugh (1984): 455: GH 00008329!; isolectotypes: CAS 0002858!, CM 2400!, GOET 001569!, MEXU 01215406!, NDG 59124!, UC 88345!, US 00129543!, UVMVT 027543!, UVMVT 027544!).

Distribution: Mexico and Mesoamerica [Guatemala, Honduras (Pruski 2018)].

16. ***Pseudognaphalium helleri*** (Britton) Anderb. (Anderberg 1991: 147). *Gnaphalium helleri* Britton (1893: 280). *G. polyccephalum* Michx. var. *helleri* (Britton) Fernald (1908: 94). *G. obtusifolium* L. var. *helleri* (Britton) S.F.Blake (1918: 72). **Type:** UNITED STATES OF AMERICA. Virginia: Southeast Virginia, Norfolk Co., 23 Sep 1892, A. A. Heller s.n. (lectotype [first step], designated by Mahler (1975): 30: NY 00169470!; probable isolectotypes: E 00385958!, GH 00008294!, MO 2168385!, NY 00169472!, PH 00012602!, PH 00012603!, PH 00012604!, US 00129539! [all these probable isolectotypes bear the number 741]. **Figure 3a-h.**

Gnaphalium obtusifolium L. var. *micradenium* Weath. (Weatherby 1923): 22. *G. helleri* Britton var. *micradenium* (Weath.) Mahler (1975): 32. *Pseudognaphalium helleri* (Britton) Anderb. subsp. *micradenium* (Weath.) Kartesz (1999): n 29. *Pseudognaphalium micradenium* (Weath.), Nesom (2001b): 618. **Type:** UNITED STATES OF AMERICA. Massachusetts: Barnstable Co., 7 Oct 1917, M. L. Fernald 15870 (holotype: GH 00008300!; isotype: NEBC 00231216!).

Observation: Mahler (1975): 30 indicated the type of *Gnaphalium helleri* Britton as 'Lectotype selected. Northwest Norfolk County, Virginia, A. A. Heller s.n., 23 Sep 1892, annotated by Britton (NY). Syntypes. Northwest Norfolk County, Virginia, A. A. Heller s.n., 23 Sep 1892, annotated by Britton (NY, MO) ...'. By referring to the collection at NY as 'lectotype', this constitutes a valid [first-step] lectotypification. Since Mahler (1975) mentioned two sheets of this collection at NY, 'second-step' lectotypification is required (ICN, Art. 9.17. Shenzhen Code; Turland et al. 2018). The specimen NY00169470 which has two complete plants with inflorescences and a label of 1974 in which Mahler annotated 'lectotype' is here designated as the lectotype of *G. helleri*.

Distribution: Eastern United States of America.

17. ***Pseudognaphalium hintoniorum* (G.L.Nesom)**
Hinojosa-Espinosa & Villaseñor (2014): 490.
Gnaphalium hintoniorum Nesom (1990): 414.

Type: MEXICO. Nuevo León: Mpio. Galeana, Cerro Potosí, pine forest, 3350 m, 15 Sep 1969, G. B. Hinton et al. 17263 (holotype: TEX 00373729!; isotypes: ANSM 094528!, CIIDIR 017091!, GBH 017263!, MICH 1107417!).

Gnaphalium flavocephalum Nesom (1990): 413.

Type: MEXICO. Coahuila, Mpio. Arteaga. Sierra del Coahuilón, open limestone hillsides, 3200 m, 28 Jul 1985, G. B. Hinton et al. 18902 (holotype: TEX 00373728!; isotypes: ANSM 064097, CIIDIR 022434, GBH 018902).

Distribution: Mexico.

18. ***Pseudognaphalium inornatum* (DC.) Anderb.** (Anderberg 1991: 147). *Gnaphalium inornatum* DC. (Candolle 1838: 225). **Type:** MEXICO. Morelos: 'Cordillère de Guchilaque, 8bre 1827', J. L. Berlandier 1146 (lectotype, designated by McVaugh (1984): 456: G-DC G-00312682!; isolectotypes: G 00301178!, P 00704472!, P 00704473!; syntypes: J. L. Berlandier 309 G-DC G-00312681!, J. L. Berlandier 740 G-DC G-00312660!, J. L. Berlandier 1195 G-DC G-00312680!; isosyntypes: J. L. Berlandier 309 HAL 0112155!, P 00704469!, P 00704470!, J. L. Berlandier 740 HAL 0112154!, J. L. Berlandier 1195 P 00704472!).

Distribution: Mexico.

19. ***Pseudognaphalium jaliscense* (Greenm.)** Anderb. (Anderberg 1991: 147). *Gnaphalium jaliscense* Greenm. (Greenman 1904: 96). **Type:** MEXICO. Jalisco. Gravelly soil near Guadalajara, 9 Aug 1902, C. G. Pringle 8628 (lectotype, designated by Nesom (2001c): 1187: GH not seen; isolectotypes: C 10007405!, CAS 0002857!, CM 2399!, E 00433304!, ENCB 003704!, JE 00000746!, K 000500360!, LL 00373730!, M 0029852!, MEXU 01215402!, MEXU 01215403!, MICH 1107418!, MIN 1001224!, MSC 0091947!, NY 00169490!, P 00704477!, P 00704478!, PH 00012605!, RSA 0001212!, UC 88403!, US 01101249!, UVMVT 027540!, S 07-11985!).

Distribution: Mexico and United States of America.

20. ***Pseudognaphalium leucocephalum* (A.Gray)** Anderb. (Anderberg 1991: 147). *Gnaphalium leucocephalum* A. Gray (1853): 99. **Type:** MEXICO. Sonora: Bed of mountain torrents near Santa Cruz, 23 Sept. 1851, C. Wright 1285 (lectotype, designated here: GH 00254927!; isolectotypes: GH 00008297!, K 000978299!, NY 00169474!, NY 00169475!; syntype: Texas, Pecos County, Western Texas to El Paso, New Mexico [80 miles beyond the Pecos], 21 Aug 1849, C. Wright 393, GH 00008296!, GH 00008299!, GH 00282538!, K not seen).

Observation. In the protologue of *Gnaphalium leucocephalum*, Gray (1853) mentioned 'G.

polycephalum Gray, *Pl. Wright* p. 124. no. 393, non Michx.- Bed of mountain torrents near Santa Cruz, Sonora; Sept. (1285)'. Stafleu & Cowan (1976) stated that the herbarium types of Asa Gray are at GH. We located at GH two specimens of *C. Wright* 1285 (GH 00254927 and GH 00008297) and three other specimens of *C. Wright* 393 (GH 00008296, GH 00008299 and GH 00282538). Only two of these specimens, *Wright* 1285-GH 00254927 and *Wright* 393-GH 00008296, were there when Asa Gray described the species, the remaining are duplicates transferred to GH from the Boston Natural History Society at a later date. We selected the specimen *C. Wright* 1285 GH 00008297 as lectotype of *Gnaphalium leucocephalum*, because it bears the name of the new species written on it in Gray's own hand with the annotation 'n. sp' and it is better preserved. There are other two collections on the same sheet GH 00254927, i.e. *Thurber* 924 GH 00254926 and *Xantus* 66 GH 00008298.

Distribution: Mexico and United States of America.

21. ***Pseudognaphalium liebmannii*** (Sch.Bip. ex Klatt) Anderb. (Anderberg 1991: 147). *Gnaphalium liebmannii* Sch.Bip. ex Klatt (1887): 89. **Type:** MEXICO. [Veracruz], Pico de Orizaba, 10.000 ped., F. M. Liebmann 310. (holotype: C 10007406!, isotype: GH 00008328-fragment! together with a pencil sketch (by Klatt) of the holotype and a full Latin description as appearing in Leopoldina).

Gnaphalium vulcanicum I.M.Johnst. (Johnston 1923): 100. **Type:** MEXICO. [Veracruz], Citlaltepetl (=Pico de Orizaba), near timber line, Sep 1907, C. A. Purpus 2782 (holotype: GH 00008352!; isotype: US 00129566!).

Distribution: Mexico and Mesoamerica [Guatemala (Pruski 2018)].

22. ***Pseudognaphalium luteoalbum*** (L.) Hilliard & Burtt (1981): 206. *Gnaphalium luteoalbum* L. (Linnaeus 1753): 851. *Gnaphalium conglobatus*

Lam. (Lamarck 1779, 1788): 64. *Helichrysum luteoalbum* (L.) Rchb. (Reichenbach 1829): 1460. *Filaginella luteoalba* (L.) Opiz (1852): 44. *Gnaphalium luteoalbum* L. var. *incanum* A.Rich. ex Endl. (Endlicher 1833: 50), nom. illeg. *Dasyanthus conglobatus* (Lam.) Bubani (1900: 199), nom. illeg. *Laphangium luteoalbum* (L.) Tzvelev (1994): 105. **Type:** EUROPA. 'Habitat in Helvetia, G. Narbonensi, Hispania, Lusitania' A. van Royen s.n. (lectotype, designated as holotype by Hilliard & Burtt (1981): 206: L, sheet 900. 286-294).

Gnaphalium trifidum Thunb. (Thunberg 1800): 150. **Type:** SOUTH AFRICA. Cape of Good Hope, C. P. Thunberg s.n. (UPS 19278!).

Gnaphalium multiceps Wall. ex DC. (Candolle 1838: 222). *Gnaphalium luteoalbum* L. var. *multiceps* (Wall. ex DC.) Hook.f. (Hooker 1881: 288). **Type:** NEPAL. Mar 1821, N. Wallich 2949-59A, (lectotype, designated by Freire et al. (2018): 339: K 001118249!; isolectotype: BM 000521869!, probable isolectotype E 00531206!).

Gnaphalium luteofuscum Webb (1849): 143.

Syntypes: 'Hab. In petrosis supra medium Montis Verede ins. S. Vincentii (Vogel, n. 38. 55. 56. Junio, 1841, sp. florida et fructifera.)' (Vogel 55, 56, K).

Gnaphalium luteoalbum L. var. *pallidum* Hook.f. (Hooker 1881): 288. **Type:** INDIA. 'G. pallidum, Ham. in Wall. Cat. 2953.' (lectotype, designated by Freire et al. (2018): 339: K 001118256!; isolectotypes: K 001118255!, K 001118257!).

Gnaphalium luteoalbum L. var. *compactum* Kirk (1899): 298. **Type:** [New Zealand] 'Lake Lyndon, Enys and Kirk'.

Observation. In the protologue of *Gnaphalium luteoalbum* var. *compactum*, Kirk (1899) mentioned 'Lake Lyndon, Enys and Kirk'. We located one specimen at K [...of Lake Lyndon, 2800 p, New Zealand, T. Kirk 1093 com. 9/1884] K 000975815, which totally corresponds to the protologue in its detail, including agreement for the locality. However, since we were able to see

only one sheet, we prefer not to lectotypify the name at the moment.

Distribution: Eurasian species with cosmopolitan distribution, being adventitious in Mexico and United States of America (Pruski 2018).

23. ***Pseudognaphalium macounii* (Greene)** Kartesz (1999): no. 30. *Gnaphalium macounii* Greene (1902): 278. **Type:** CANADA. British Columbia, Chilliwack Valley, B.C., 2500 ft, 29 Jul 1901, J. M. Macoun 26487 [26847 in lit.] (holotype: NDG 59133!).

Gnaphalium ivesii A.Nelson & J.F.Macbr. (Nelson & Macbride 1916): 46 as nom. nov. for *Gnaphalium decurrens* Ives (1819: 380), hom illeg., non *G. decurrens* L. 1759. **Type:** Plate s.n. sub. 'Gnaphalium decurrens' (Ives 1819) (**lectotype, designated here**).

Observations. The protologue of *Gnaphalium decurrens* Ives does not include any reference to the collector: 'This plant was observed by me in company with Mr. C. Whitlow, in July, 1817, by the margin of a brook, a few rods north of Mr. E. Whitney's gun manufactory, near New Haven. It it is also found on the margin of the Housatonick about thirty miles from Long Island soun where it was observed by Dr. Alfred Monson, the last summer'. The name of this species is accompanied by an illustration, which is here selected as the lectotype.

Distribution: Canada and United States of America.

24. ***Pseudognaphalium monticola* (McVaugh)** Villarreal, Estrada & Encina (2020): 5. *Gnaphalium vulcanicum* I.M.Johnst. var. *monticola* McVaugh (1972): 466. *Gnaphalium liebmannii* Sch.Bip. ex Klatt var. *monticola* (McVaugh), Nash (1974): 74. *Pseudognaphalium liebmannii* (Sch.Bip. ex Klatt) Anderb. var. *monticola* (McVaugh) Hinojosa-Espinosa & Villaseñor (2014): 490. **Type:** MEXICO. Jalisco. Sierra de Manantlán, 25-30 km SE of Autlan, pine forest near summits between El Chante and Cuzalapa, 19°35'N, 104°8'-15'W, 2750

m, 20-21 Mar 1965, R. McVaugh 23126 (holotype: MICH 1107419!; isotypes: CAS 0002859!, ENCB 003706!, NY 00169500!).

Distribution: Mexico and Mesoamerica [Guatemala (Pruski 2018)].

25. ***Pseudognaphalium nataliae* (F.J.Espinosa)** Villarreal, Estrada & Encina (2020): 6. *Gnaphalium oxyphyllum* (DC.) var. *nataliae* F.J.Espinosa (1983: 17). *Pseudognaphalium oxyphyllum* (DC.) Anderb. var. *nataliae* (F.J.Espinosa) Hinojosa-Espinosa & Villaseñor (2014): 491. **Type:** MEXICO. Mexico, Municipio de Amecameca, San Pedro Nexcapa, 3000 m, 21 Sep 1979, F. J. Espinosa 766 (holotype: MEXU 00343482!; isotypes: ANSM 030402!, ENCB 003705!).

Distribution: Mexico.

26. ***Pseudognaphalium nubicola* (I.M.Johnst.)** Anderb. (Anderberg 1991: 147). *Gnaphalium nubicola* I.M.Johnst. (Johnston 1923): 98. **Type:** MEXICO. Rocks above timber-line, Mt. Ixtacuhuatl, Nov 1905, C. A. Purpus 1524 'type' (holotype: GH 00008332!; isotypes: GH 00008333!, UC 134562!, US 00129545!).

Distribution: Mexico.

27. ***Pseudognaphalium obtusifolium* (L.)** Hilliard & Burtt (1981): 205. *Gnaphalium obtusifolium* L. (Linnaeus 1753): 851. **Type:** UNITED STATES OF AMERICA. [Habitat in Virginia, Pennsylvania] Kalm, Herb. Linn. No. 989.64 (lectotype, designated by Reveal (1998: 362): LINN).

Gnaphalium obtusifolium L. var. *praecox* Fernald (1936: 231). TYPE. United States of America. Maine: York Co., 2 miles east of Walterboro, 17 July 1927, K. M. Wiegand & W. E. Manning 3301 (holotype: GH 00008301!).

Distribution: United States of America and adjacent Canada.

28. ***Pseudognaphalium oxyphyllum* (DC.)** Kirp. (Kirpichnikov 1960): 33. *Gnaphalium oxyphyllum* DC. (Candolle 1838: 225). **Type:** MEXICO. Villalpando au Sud est de Guanajuato, J. Mendez s.n. (**lectotype, designated here**:

G-DC G00469505! sheet 4, isolectotypes: G-DC G00469505! sheet 1-left hand plants, sheet 2-left hand plants, sheet 3).

Observation: The specimen G-DC G00469505 consists of four sheets. However, on sheet 1 and 2 the three plants on right of sheet correspond to *Gnaphalium oxyphyllum* var. *semilanatum*. Because the sheet 4-G-DC G-00469505 has a label on it, identifying it as the type and matches the locality provided in the protologue, it is here formally designated as the lectotype of *Gnaphalium oxyphyllum* DC.

Distribution: Mexico and Mesoamerica [Guatemala (Espinosa-García 2005)].

29. ***Pseudognaphalium pringlei*** (A.Gray) Anderb. (Anderberg 1991: 147). *Gnaphalium pringlei* A. Gray (1886): 387. **Type:** MEXICO. Chihuahua: cool shades slopes, rocky hills near Chihuahua, 25 Oct 1885, C. G. Pringle 305 (holotype: GH 00008341!; isotypes: AC 00319433!, BR 0000005317783!, CM 2402!, COLO 00368399!, CORD 00004577!, E 00433303!, FI 005289!, GOET 001573!, JE 00000749!, K 000500355!, MEXU 01215407!, MO 191020!, NY 00169497!, NY 00169498!, P 00704570!, P 00704571!, P 00704572!, PH 00012614!, RSA 0001213!, TEX 00373731!, UC 88343!, US 00129552!, US 00930967!, UVMVT 027542!).

Distribution: Mexico and United States of America.

30. ***Pseudognaphalium purpurascens*** (DC.) Anderb. (Anderberg 1991: 147). *Gnaphalium purpurascens* DC. (Candolle 1838: 225). **Type:** MEXICO. 1833, M. Mairet s.n. (holotype: G-DC G-0469517!; probable isotype: P 00704573!, without collector).

Distribution: Mexico.

31. ***Pseudognaphalium ramosissimum*** (Nutt.) Anderb. (Anderberg 1991: 147). *Gnaphalium ramosissimum* Nutt. (Nuttall 1848): 20, non *G. ramosissimum* Sch.Bip. 1856, hom. illeg. [=Achyrocline ramosissima Britton ex Rusby].

Type: UNITED STATES OF AMERICA. California.

Monterrey ("Monterey"), W. Gambel s.n., -Types: GH 00008306!, GH 00008307!, K 001096583! "Nuttall from Gambel", written on sheet.

Observation. Stafleu & Cowan (1981) stated that the types of Nuttall are mainly deposited in BM and PH with additional specimens or duplicates in GH, K, MO, NY, OXF. Since we not able to see Nuttall specimen at PH and BM, we prefer not to lectotypify the name at the moment.

Distribution: United States of America.

32. ***Pseudognaphalium roseum*** (Kunth) Anderb. (Anderberg 1991: 147). *Gnaphalium roseum* (1818, folio edition): 63; (1820, quarto edition): 81, p. 33.

Type: MEXICO. 'Crescit in covalli Guanaxuatensi, alt. 1700 hex. (Regno Novae Hispaniae) Floret Septembri' Guanajuato, F. W. H. A. Humboldt & A. J. A. Bonpland s.n. (holotype: P 00322305!).

Distribution: Mexico, Mesoamerica [Belice, Guatemala, Honduras, Nicaragua (Pruski 2018)], and United States of America.

33. ***Pseudognaphalium saxicola*** (Fassett) H.E.Ballard & Feller (2004: 777). *Gnaphalium saxicola* Fassett (1931: 75). *Gnaphalium obtusifolium* L.var. *saxicola* (Fassett) Cronquist (1946: 121). *Pseudognaphalium obtusifolium* (L.) Hilliard & Burtt 1981 subsp. *saxicola* (Fassett) Kartesz (1999): no. 32. **Type:** UNITED STATES OF AMERICA. Wisconsin: Adams Co., sandstone ledges, cold water canyon, Dells of the Wisconsin River, 22 Sep 1929, N. C. Fassett, F. M. Uhler & W. T. McLaughlin 9590 (holotype: WIS v0011634!; isotypes: F 0050259F!, GH 00008308!, NY 00169480!).

Distribution: United States of America.

34. ***Pseudognaphalium semiamplexicaule*** (DC.) Anderb. (Anderberg 1991: 148). *Gnaphalium semiamplexicaule* DC. (Candolle 1838: 228).

Type: MEXICO. 'Vittoria a Tula, Nov 1830', J. L. Berlandier 2188 (**lectotype, designated here: G-DC G-00469541!**; isolectotypes: G 00223947!, G-DC G-00469542!, GH 00008348!, K 000500347!, P 00704575!, PH 00012624!). **Figure 4a-g.**

Gnaphalium oxyphyllum DC. var. *semitanatum* DC. (Candolle 1838: 225). *Gnaphalium semitanatum* (DC.) McVaugh (1972): 465. *Pseudognaphalium semitanatum* (DC.) Anderb. (Anderberg 1991: 148). **Type:** MEXICO. Villalpando, au Sud est de Guanajuato, J. Méndez s.n. (**lectotype, designated here: G-DC G-00469505!** sheet 1-right hand plants; isolectotypes: G-DC G-00469505! sheet 2-right hand plants, probable isolectotype: G-DC G-00469537!), **syn. nov.**

Observations:

1. According to the protologue, *Gnaphalium semiamplexicaule* was based on the specimen 'in Mexico inter Vittoria et Tula legit cl. Berlandier pl. exs. n. 2188'. We found two sheets at G-DC, G-DC G-00469541 [sheet 2] and G-DC G-00469542 [sheet 1]. We propose the specimen G-DC G-00469541

which bears the number '2' written in pencil in the top right hand corner, as the lectotype of *Gnaphalium semiamplexicaule*, since this is the only one that bears the annotations provided by Candolle.

2. Candolle (1838:225) mentioned 'β. *semitanatum*, foliis subtūs albo-lanatis,— Cum var. α mixtum in pl. Mendezianis. (v.s.)'. We located at G-DC, where the original herbarium of Candolle is deposited, the collection 'Villalpando, au Sud est de Guanajuato, J. Mendez s.n.' G-DC G-00469505 of four sheets (see observation of *Pseudognaphalium oxyphyllum*). On sheet 1 and 2 the three plants on right have discolored lanceolate leaves, with abaxial surface white lanate. We propose the sheet 1- G-DC G-00469505

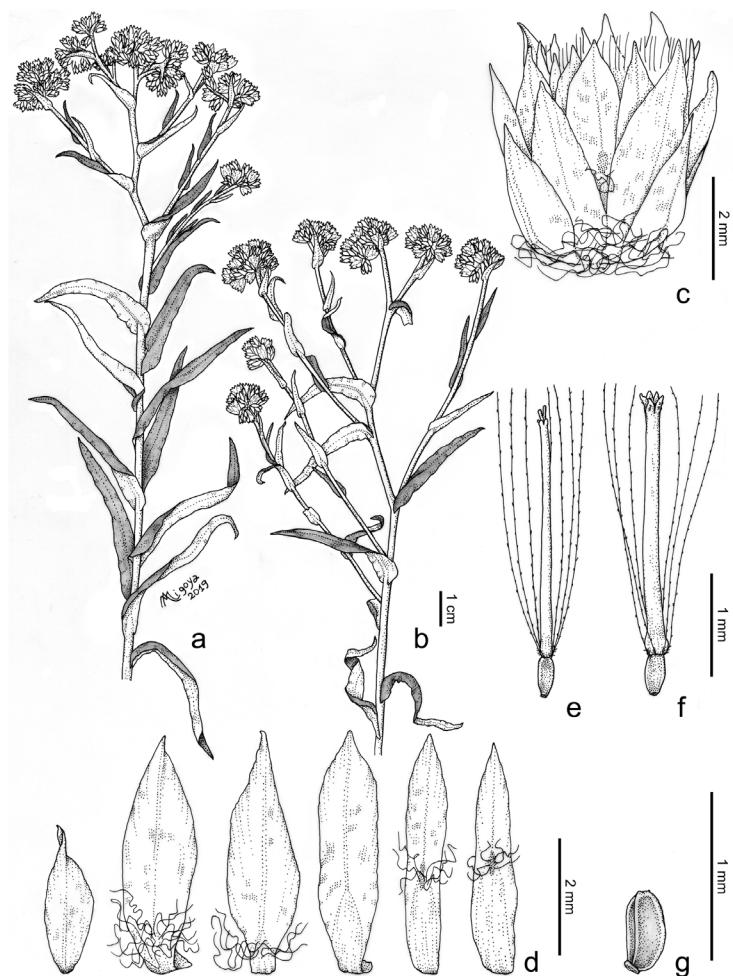


Figure 4. *Pseudognaphalium semiamplexicaule*. a, b. Flowering branches; c. Capitulum; d. Phyllaries; e. Pistillate floret; f. Bisexual floret; g. Achene [a-g. Rzedowski 36561, MEXU].

as the lectotype of *Gnaphalium oxyphyllum* var. *semilanatum*.

Distribution: Mexico and Mesoamerica [Belice, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, Panama (Pruski 2018)].

35. ***Pseudognaphalium stramineum* (Kunth) Anderb.** (Anderberg 1991: 148). *Gnaphalium stramineum* Kunth (1818, folio edition): 64; (1820, quarto edition): 82. **Type:** MEXICO. ‘Crescit locis temperatis inter Moran et Omitlan Mexicanorum, alt. 1300 hex.’, F. W. H. A. Humboldt & A. J. A. Bonpland 4108 (holotype: P 0322314!; isotype: P 00704565!).

Gnaphalium berlandieri DC., Prodr. 6: 223. 1838.

Type: MEXICO: 30 Jun 1827, J. L. Berlandier 471 (**lectotype, designated here: G-DC G-00469612!**; isolectotypes: G-DC G-00469600! 24 Jun 1827, HAL 0112152! 29 Jun 1827, LP 001900! 24 Jun 1827, MICH 1107415!, 30 Jun 1827?, P 00704481! 24 Jun 1827, P 00704479!, P 00704480! Jun 1827, P 00704481!, 24 Jun 1827).

Gnaphalium gossypinum Nutt. (Nuttall 1841): 403. **Type:** UNITED STATES OF AMERICA. Oregon [Río Columbia], 1834–1835, T. Nuttall s.n. (not seen).

Gnaphalium chilense Spreng. var. *confertifolium* Greene (1897): 400. **Type:** UNITED STATES OF AMERICA. California. San Francisco, 27 May 1893, E. L. Greene (holotype, NDG 59239!).

Gnaphalium sulphurescens Rydb. (Rydberg 1900: 415). **Type:** UNITED STATES OF AMERICA. Yellowstone Park, Lower Geyser Basin, 7500 ft, 4 Aug 1897, P. A. Rydberg & E. A. Bessey 5135 (**lectotype, designated here: NY 00169483!**; isolectotypes: E 00433320!, GH 00008309!, K 000978305!, NDG 59192!, NEB-v-0000112!, NEB-v-0000111!, PH 00012625!, RM0001109!, US 00129561!, US 00130793!).

Gnaphalium lagopodioides Rydb. (Rydberg 1900: 416). **Type:** UNITED STATES OF AMERICA. Yellowstone Park, Lower Geyser Basin, 7500 ft, 4 Aug 1897, P. A. Rydberg & E. A. Bessey 5134

(holotype: NY00169473!; isotypes: GH 00008295!, NDG 59122!, NEB-v-0000110!, US 00129542!).

Gnaphalium proximum Greene (1902): 279. **Type:** UNITED STATES OF AMERICA. Wyoming. In moist ground about warm springs, Mammoth Hot Springs, Yellowstone Park, 21 Jul 1899, A. Nelson & E. Nelson 6036 (holotype: NDG 59162; isotypes: NY 00169479!, RM 0001107!, RM 0001108!, US 00129553!).

Observations:

1. Rydberg (1900: 415) mentioned in the protologue of *Gnaphalium sulphurescens*: ‘Yellowstone Park: Lower Geyser Basin, August 4, 1897, Rydberg & Bessey, 5135; Hot Springs, 1884, Tweedy, 172; Mud Springs, 1871, Hayden Survey’. We propose as the lectotype of *G. sulphurescens* the collection Rydberg & Bessey 5135 kept at NY which is a widely distributed collection (duplicates seen at E, GH, K, NDG, NEB, PH, RM, and US), and the specimen kept at NY, NY 00169483, because, according to the preface to Rydberg’s paper, ‘Rydberg & Bessey, 1897’ type materials are found in this herbarium.

2. Candolle (1838: 223) mentioned for *Gnaphalium berlandieri*: ‘circa urbem Mexico media aestate legit cl. Berlandier pl. exs. n. 471! ... (v.s.)’. We found two sheets at G-DC of the collection Berlandier 471 G-DC G-00469600 [sheet 1], 24 Jun 1827 and G-DC G-00469612 [sheet 2], 30 Jun 1827. We selected as the lectotype of *G. berlandieri*, the specimen G-DC G-00469612 with the pencil number ‘2’ in the top right hand corner, which is the only one annotated by de Candolle and has a annotation on the original Berlandier label indicating there were ‘14 ex’ [= duplicates].

Distribution: Canada (Pruski 2018), Mexico, United States of America and Mesoamerica [Guatemala, Honduras (Pruski 2018)].

36. ***Pseudognaphalium thermale* (Nelson 1900, 2004): 781. *Gnaphalium thermale* Nelson (1900): 121. *Gnaphalium microcephalum* Nutt. var. *thermale* (Nelson 1900) Cronquist (1950):**

47). *Gnaphalium microcephalum* Nutt. subsp. *thermale* (Nelson 1900) G.W. Douglas (1986: 2726). *Gnaphalium canescens* DC. subsp. *thermale*, (Nelson 1900) Stebbins & Keil (1992): 437. *Pseudognaphalium canescens* (DC.) Anderb. subsp. *thermale* (Nelson 1990) Kartesz (1999): no. 27. *Pseudognaphalium microcephalum* (Nutt.) Anderb. var. *thermale* (Nelson 1900) Dorn (2001: 375). **Type:** UNITED STATES OF AMERICA. Yellowstone National Park, Norris Geyser Basin, 25 Jul 1899, A. Nelson & E. E. Nelson 6139 (**lectotype, designated here:** RM 0001110!); isolectotypes: GI!, GH 00008311!, K 000978306!, NDG 59193!, NEB-v-0000113!, NY 00169484!, P 00704566!, RM 0001111!, US 00129563!).

Gnaphalium johnstonii. Jones (1938): 159, 176. **Type:** UNITED STATES OF AMERICA. Washington. [Thurston Co.], upper valley of the Nesqually, open, barren ground, 15 Sep 1896, O. D. Allen 223 (isotype: WTU-V-001136!).

Observation: Nesom (2004): 781 indicated the type of *Gnaphalium thermale* E.E.Nelson as 'Type. U.S.A. Wyoming [Park Co.]: Yellowstone Park, geyser... A. Nelson & E. Nelson 6139 (Holotype; RM; Isotypes: GH!, US!)'. This citation of a 'holotype' (after 1 January 2001) cannot be corrected to a designation of a lectotype (Art. 9.10 of the ICN, Shenzhen Code; Turland et al. 2018), because they did not use the phrase 'designated here' or an equivalent (ICN, Art. 7.11, Shenzhen Code; Turland et al. 2018) in their associated statement. Consequently, Nesom's typification for the name *G. beneolens* was not effective (ICN, Art. 9.23, Shenzhen Code; Turland et al. 2018). The specimen RM 0001110 which presents the most complete plant is designated here as the lectotype of *G. thermale*.

Distribution: United States of America.

37. *Pseudognaphalium viscosum* (Kunth) Anderb. (Anderberg 1991): 148. *Gnaphalium viscosum* Kunth (1818, folio edition): 64; (1820, quarto edition): 82. **Type:** MEXICO. [Distrito

Federal] 'Crescit in radicibus montis Chapaltepec juxta urbem Mexici', F. W. H. A. Humboldt & A. J. A. Bonpland 4153 (holotype: P-HBK, not seen; isotype, P-00704569!).).

Gnaphalium hirtum Kunth (1818, folio edition): 64; (1820, quarto edition): 82. **Type:** MEXICO. 'Crescit in radicibus montis Chapaltepec juxta urbem Mexici, alt. 1170 hex. Floret Aprili' F. W. H. A. Humboldt & A. J. A. Bonpland s.n. (holotype: P 00322309!; isotype: P 00704568!).

Gnaphalium gracile Kunth (1818, folio edition): 65; (1820, quarto edition): 83. **Type:** MEXICO. 'Crescit in Regno Mexicano in declivitate montis Serenae, Guanaxuatum inter et fodinam Belgradensem alt. 1100 hex. Floret Septembri', F. W. H. A. Humboldt & A. J. A. Bonpland s.n. (holotype: P 00322310!).

Gnaphalium tenue Kunth (1818, folio edition): 65; (1820, quarto edition): 83. **Type:** MEXICO. 'Crescit in Nova Hispania', F. W. H. A. Humboldt & A. J. A. Bonpland s.n. (holotype: P 00322311!; isotype: P 00714567!).

Gnaphalium leptophyllum DC. (Candolle 1838: 226). **Type:** MEXICO. 1831, L. Alaman s.n. (holotype: G-DC G-00469611!).

Gnaphalium crenatum Greenm. (Greenman 1904): 96. *Pseudognaphalium crenatum* (Greenm.) Anderb. (Anderberg 1991): 147. **Type:** MEXICO. Jalisco, near Guadalajara, 5000 ft, 15 May 1901, C. G. Pringle 9524 (holotype: GH 00008322!; isotypes: CM 2398!, ENCB 003703!, K 000500361!, MEXU 01215401!, NY 00169489!, TEX 00000466!, UV MVT027538!).

Pruski (2018: 230) indicated the type of *Gnaphalium viscosum* Kunth as 'Holotipo: Mexico, Distrito Federal, Humboldt y Bonpland 4153', erroneously as 'P-Bonp', pers. comm.

Distribution: Mexico, United States of America, and Mesoamerica [Guatemala, Honduras (Pruski 2018)].

Excluded species

Gnaphalium chilense Spreng. (1826: 480). *Gnaphalium sprengelii* Hook. & Arn. (1841[1833]: 150), nom. superfl. TYPE. 'Chili. Chamisso. Peru?' (P 00704592!).

Gnaphalium sprengelii Hook. et Arn. (1841[1833]: 150) is a nomen superfluum because this name was used to replace Sprengel's *Gnaphalium chilense* (1826: 480), adopted by Lessing (1831): 525 for Californian plants. Rémy (1849): 228, mentioned *Gnaphalium chilense* Hook. & Arn. (1841[1833]: 31), non *G. chilense* Spreng. (1826), as a synonym of *G. falcatum* Lam. [= *Gamochaeta falcata* (Lam.) Cabrera]. One sheet of *Gnaphalium chilense* Spreng., 'Chili. Chamisso. Peru?', that bears the label 'Sprgl. herb. no.: 827, Syt. III, 480... 168', was located at P, P 00704592, where most of the original material used by Sprengel for his new taxa, in *Systema Vegetabilium*, is deposited. According to the digital image, the two plans on the sheet correspond to *Gamochaeta falcata* by having capitula arranged in spikes, pappus bristles basally connate, and linear obovate to obovate leaves.

Names of Dubious Identity

Pseudognaphalium altamiranum (Greenm.) Anderb. (1991: 147). *Gnaphalium altamiranum* Greenm. (Greenman 1904): 95. **Type:** MEXICO. Morelos, Mountains above Cuernavaca, 2640 m, 2 Feb 1899, C. G. Pringle 8041 (holotype: GH 00008316!; isotypes: CM 2397!, E 00433305!, G 00301190!, G 00301191!, GOET 001566!, K 000500364!, LL 00373727!, M 0029850!, MEXU 01215398!, MEXU 01215399!, MIN 1001223!, MSC 0091945!, NY 00169486!, P 00704490!, P 00704491!, PH 00012284!, RSA 0001208!, S07-11955!, UC 88249!, US 00129529!, US 01101248!, UVMVT 027539!).

Gnaphalium nubicola (I.M.Johnst.) Anderb. var. ***panniforme*** (S.F.Blake) F.J.Espinosa (1983: 20). *Gnaphalium panniforme*, Blake (1943): 268,

replacement name for *Gnaphalium pannosum* A.Gray, hom. illeg., non *Gnaphalium pannosum* (DC.) Sch.Bip. 1845. **Syntypes:** MEXICO. 'In the mountains near San Luis de Potosi, Schaffner 227, Parry & Palmer 420' (both collections on sheet GH 00008339!; isosyntypes Parry & Palmer 420: NY 00169496 and US 00811084).

Gnaphalium oaxacanum Greenm. (Greenman 1904): 96. **Type:** MEXICO. Oaxaca. 1750 m, Jul-Aug 1900, C. Conzatti & V. González 1012 (holotype: GH 00008334!, isotypes: MEXU 00525673!, TEX 00000467!).

Since we were able to see only the images of type specimens of *Pseudognaphalium altamiranum*, *Gnaphalium oaxacanum* and *G. nubicola* var. *panniforme*, and we have seen no other material that can be assigned to these species, the identity of them is not clear to us.

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SEF planned and designed the research and led the writing of the paper. MAG conducted the morphometric analysis and produced figures 1a, b. SEF, NDB, and CM, examined morphological characters of taxonomic relevance. All authors contributed to literature review, interpretation of the analysis, discussion of the taxonomy of North American *Pseudognaphalium*, participated in decisions about the placement of particular taxa, and approved the final draft.

