

GNAPHALIOTHAMNUS NESOMII (ASTERACEAE: GNAPHALIEAE),  
A NEW SPECIES FROM GUATEMALA AND NOMENCLATORIAL CHANGES

Michael O. Dillon

Botany Department  
The Field Museum  
1400 South Lake Shore Drive  
Chicago, IL 60605, U.S.A.  
mdillon@fieldmuseum.org

Federico Luebert

Universität Bonn  
Nees-Institut für Biodiversität der Pflanzen  
Meckenheimer Allee 170  
D-53115 Bonn, GERMANY

ABSTRACT

**Gnaphaliothamnus nesomii** M.O. Dillon & Luebert (Asteraceae: Gnaphalieae) is a new species from the Sierra de los Cuchumatanes, Department Huehuetenango, Guatemala. The generic boundaries within the Gnaphalieae have been controversial and the genus *Gnaphaliothamnus* has not been universally accepted. New molecular phylogenetic studies support the acceptance of *Gnaphaliothamnus* as distinct from *Chionolaena*, which is congruent with cypselar trichome morphology. Two *Gnaphalium* species are transferred as **Pseudognaphalium stolonatum** (S.F. Blake) M.O. Dillon and **P. paramorum** (S.F. Blake) M.O. Dillon.

KEY WORDS: *Chionolaena*, *Gamochoeta*, *Gnaphaliothamnus*, *Gnaphalium*, *Pseudognaphalium*, Asteraceae, Gnaphalieae, Gnaphaliinae, Guatemala, *Lucilia*-group, comb. nov., sp. nov., Sierra de los Cuchumatanes, taxonomy

RESUMEN

**Gnaphaliothamnus nesomii** M.O. Dillon & Luebert (Asteraceae: Gnaphalieae), es una nueva especie proveniente de Sierra de los Cuchumatanes, Departamento Huehuetenango, Guatemala. Los límites genéricos en Gnaphalieae son controvertidos y el género *Gnaphaliothamnus* no ha sido universalmente aceptado. Nuevos estudios filogenéticos moleculares apoyan la aceptación de *Gnaphaliothamnus* como un género diferente de *Chionolaena*, lo que es congruente con la morfología de los tricomas de las cipselas. Dos especies de *Gnaphalium* son transferidas como **Pseudognaphalium stolonatum** (S.F. Blake) M.O. Dillon y **P. paramorum** (S.F. Blake) M.O. Dillon.

PALABRAS CLAVE: *Chionolaena*, *Gamochoeta*, *Gnaphaliothamnus*, *Gnaphalium*, *Pseudognaphalium*, Asteraceae, Gnaphalieae, Gnaphaliinae, Guatemala, *Lucilia*-group, comb. nov., sp. nov., Sierra de los Cuchumatanes, taxonomy

INTRODUCTION

*Gnaphaliothamnus* Kirp. (Asteraceae, Gnaphalieae) comprises around 11 species distributed from Mexico to Costa Rica. It has been accepted (Nesom 1990a,b; 1994) or subsumed in the South American *Chionolaena* DC. (Anderberg & Freire 1989, 1991; Freire 1993; Nesom 2001; Freire et al. 2015). Based upon differences in cypselar (acheneal) trichomes, Dillon (2003) argued that *Gnaphaliothamnus* was a monophyletic group not necessarily close to *Chionolaena*. The cypselar trichomes in *Gnaphaliothamnus* are described (Hess 1938) as short clavate (*zwillingshaars*) with an enlarged adaxial basal cell (*schwellpolster*) and myxogenic apical cells 65–125 µm long. The two apical cells in the cypselar trichomes in *Chionolaena* are much longer (250–850 µm long) and not myxogenic (Dillon & Sagástegui 1991; Loeuille et al. 2011).

Pruski (2012) transferred a Guatemalan species, *Gnaphalium stolonatum* S.F. Blake, to *Chionolaena*, with the comment that it resembled other Mexican and Central American members. He apparently did not examine the type material of *G. stolonatum*, providing a new description drawn from a herbarium collection that he termed a “topotype” (*A. Molina et al. 1644I*, NY). From this voucher, he described the plants as reduced subshrubs to 30 cm tall with clusters of capitula each having 30–70+ pistillate florets and 11–25 hermaphroditic disc florets. He described the cypselas as setose with elongate trichomes, a condition very different from that described for the type by Blake, i.e., minutely hispidulous with conical, bluntish, few-celled, dark-based hairs (Blake 1937). An examination of the holotype of *Gnaphalium stolonatum* (*A.F. Skutch 1098*, GH) has shown it to be distinct from other collections from the same general region annotated as *G. stolonatum*. *Gnaphalium stolonatum* is here treated as a *Pseudognaphalium* Kirp. and transferred to that genus. The other morphologically different collec-

tions (e.g., *A. Molina et al. 16441*) are described here as a new species of *Gnaphaliothamnus* from the Sierra de los Cuchumatanes.

In the ultimate offering from H. Robinson (2015), he relegates *Pseudoligandra* M.O. Dillon & Sagást. (1990) and *Gnaphaliothamnus* to the synonymy of *Chionolaena*. He states that the publications by Freire (1993) and Nesom (2001) have “totally resolved that problem by reducing all three genera to synonymy under the name *Chionolaena*.” While we have been unsuccessful in extracting DNA from the samples representing *Pseudoligandra* at our disposal, we are confident that our nrDNA results have more definitively resolved the problem of the recognition of *Gnaphaliothamnus* as distinct from *Chionolaena*.

#### TAXONOMY

***Gnaphaliothamnus nesomii*** M.O. Dillon & Luebert, sp. nov. (**Fig. 1**). TYPE. GUATEMALA. Huehuetenango: common on moist bank along road to San Juan Ixcay, Sierra Cuchumatanes, 12–23 Jan 1966, *A. Molina R., W.C. Burger, and B. Wallenta 16441* (HOLOTYPE: F1637117; ISOTYPE: NY, n.v.)

Similar to *Gnaphaliothamnus salicifolius* (Bertol.) G.L. Nesom but habit considerably smaller (to 15 cm tall), capitulescences glomerulate, obscured in dense arachnoid-tomentose indumentum, cypselar trichomes ca. 100 µm long

Subshrubs, 5–10(–15) cm tall; stems ascending, basally-branched from lignified base. **Leaves** sessile, oblanceolate to spatulate, 10–42 mm long, 2–4 mm wide, abaxial surfaces white-tomentose, adaxial surfaces darker, weakly arachnoid-tomentose, apices acute, apiculate, proximal leaves marcescent. **Capitulescences** densely glomerulate with 7–11(–20) tightly grouped capitula, pedicels obscured by dense arachnoid-tomentose indumentum. **Capitula** 5–7 mm long, 2–3 mm diam.; involucre narrowly campanulate, graduated, submerged in dense arachnoid-tomentose indumentum; phyllaries 4–6-seriate, the outer with arachnoid-tomentose bases; the inner with white-opaque, oblong apical lamina, 5–7 mm long, ca. 2 mm wide; outer florets 20–32, pistillate, fertile; central disc florets 13–15, hermaphroditic, ovary sterile. **Cypselas** oblong, ca. 1 mm long, trichomes 4-celled, clavate, ca. 100 µm long, the apical cells myxogenic, not rupturing (Fig. 2A); pappus of ca. 20, setose bristles, 2.8–3.2 mm long, apical cells of bristles of hermaphroditic florets expanded, apical cells of pistillate florets obtuse, not expanded.

**Etymology.**—*Gnaphaliothamnus nesomii* is dedicated to Dr. Guy L. Nesom, noted synanthrologist and systematist, one of the first botanists to accept *Gnaphaliothamnus* in modern usage, and first to provide a detailed revision for Mexican and Central American taxa. Over the years, Dr. Nesom has been generous with his detailed knowledge of Mexican and Central American Asteraceae and particularly the Gnaphalieae. He also commented on the uniqueness of some of the sheets examined within his loan of material from Field Museum in 1990.

**Distribution and Ecology.**—The type locality is within the Sierra de los Cuchumatanes in the Department of Huehuetenango, Guatemala [15°31'S, 91°32'W]. This is the highest non-volcanic mountain range in Central America and has the most extensive highlands above 3000 m. The region is home to a variety of different biomes, including montane pine-oak forest, intermittent shrublands, and grasslands. *Gnaphaliothamnus nesomii* is found in alpine habitats at ca. 3700 m, notably different from the environments associated with the “llanos” or plains where *Gnaphalium stolonatum* occurs (see below).

**Conservation status.**—*Gnaphaliothamnus nesomii* deserves a preliminary status of Critically Endangered (CR) because total area of its known distribution is less than 100 km<sup>2</sup> and only three populations are known (IUCN 2001).

**Discussion.**—Recent molecular phylogenetic studies (nrDNA) have provided results that suggest the great majority of New World genera of Gnaphalieae are associated with the *Lucilia*-group within the FLAG clade (Freire et al. 2015; Luebert et al., unpubl.). The *Lucilia*-group has been expanded to include *Gnaphaliothamnus*, *Chionolaena*, and *Antennaria* Gaertn. from the subtribe Cassiniinae Anderb. (Anderberg 1991). These results support the hypothesis that the gross morphological similarity between *Gnaphaliothamnus* and *Chionolaena* is convergence; they are found in distant well-supported clades within the *Lucilia*-group (Fig. 3). *Gnaphaliothamnus* is phylogenetically related to *Antennaria*, while *Chionolaena* appears to be sister to a group including the type species of *Lucilia* Cass., which is in agreement with their similarity in cypselar trichomes.



Fig. 1. *Gnaphaliothamnus nesomii*. Photograph of holotype collection, A. Molina R. et al. 16441 (F1637117, imgV0093984F).

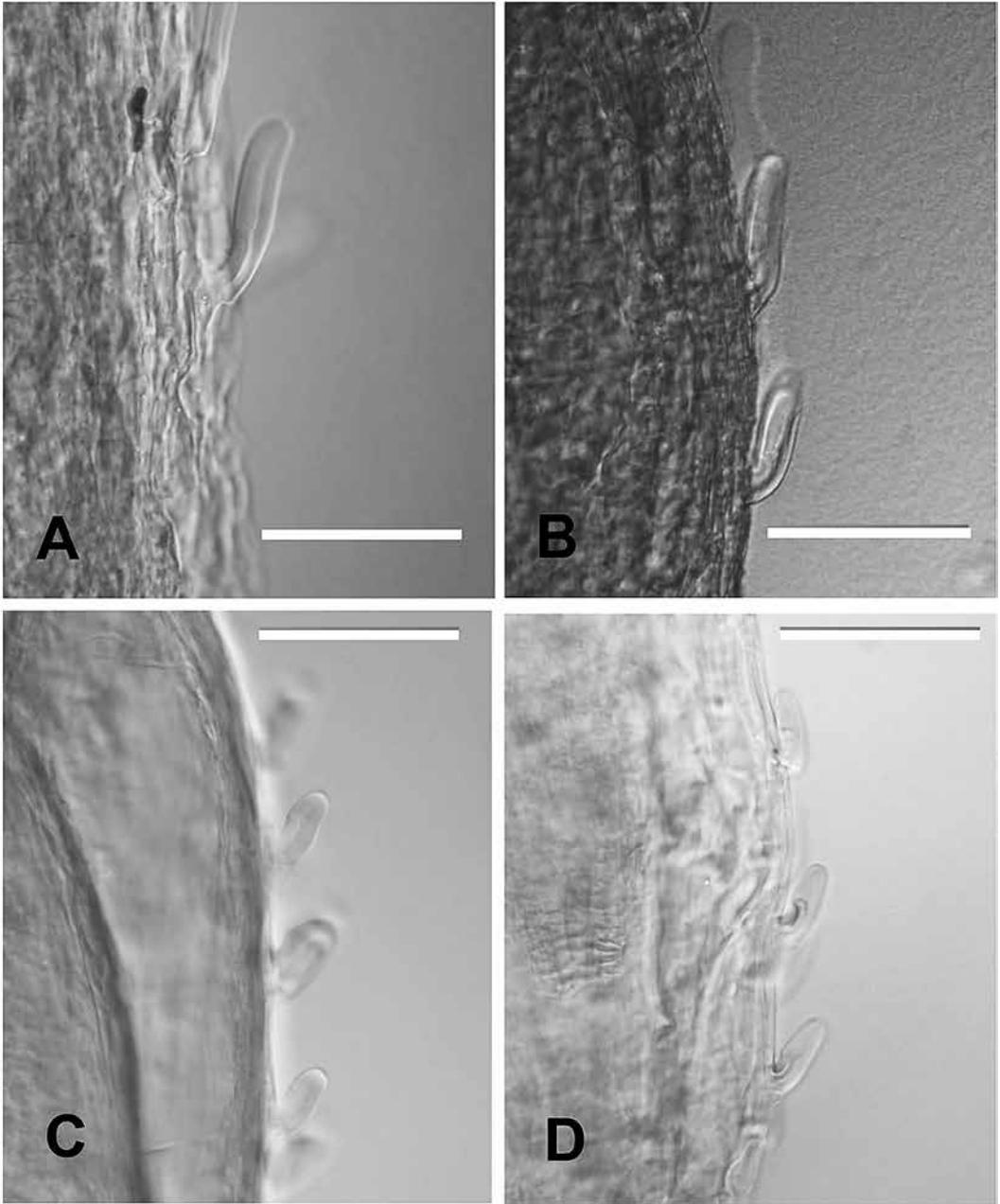


FIG. 2. Cypselar trichomes, white scale bar = 100  $\mu$ m. **A.** *Gnaphaliothamnus nesomii* (F1637117), **B.** *G. salicifolius* (F1639348), **C.** *Pseudognaphalium stolonatum* (GH00008351), **D.** *P. antennarioides* (F1148157).

Nesom (1990a) provided a detailed taxonomic history for *Gnaphaliothamnus* and his rationales for its acceptance (Nesom 1990b, 1994). Interestingly, Nesom also discussed the putative relationships for *Gnaphalium stolonatum* as outside of *Gnaphaliothamnus* (Nesom 1990a, p. 367). He commented that this taxon did have white-tipped phyllaries, but it had more florets per capitulum in general (+100) and fertile central disc florets,

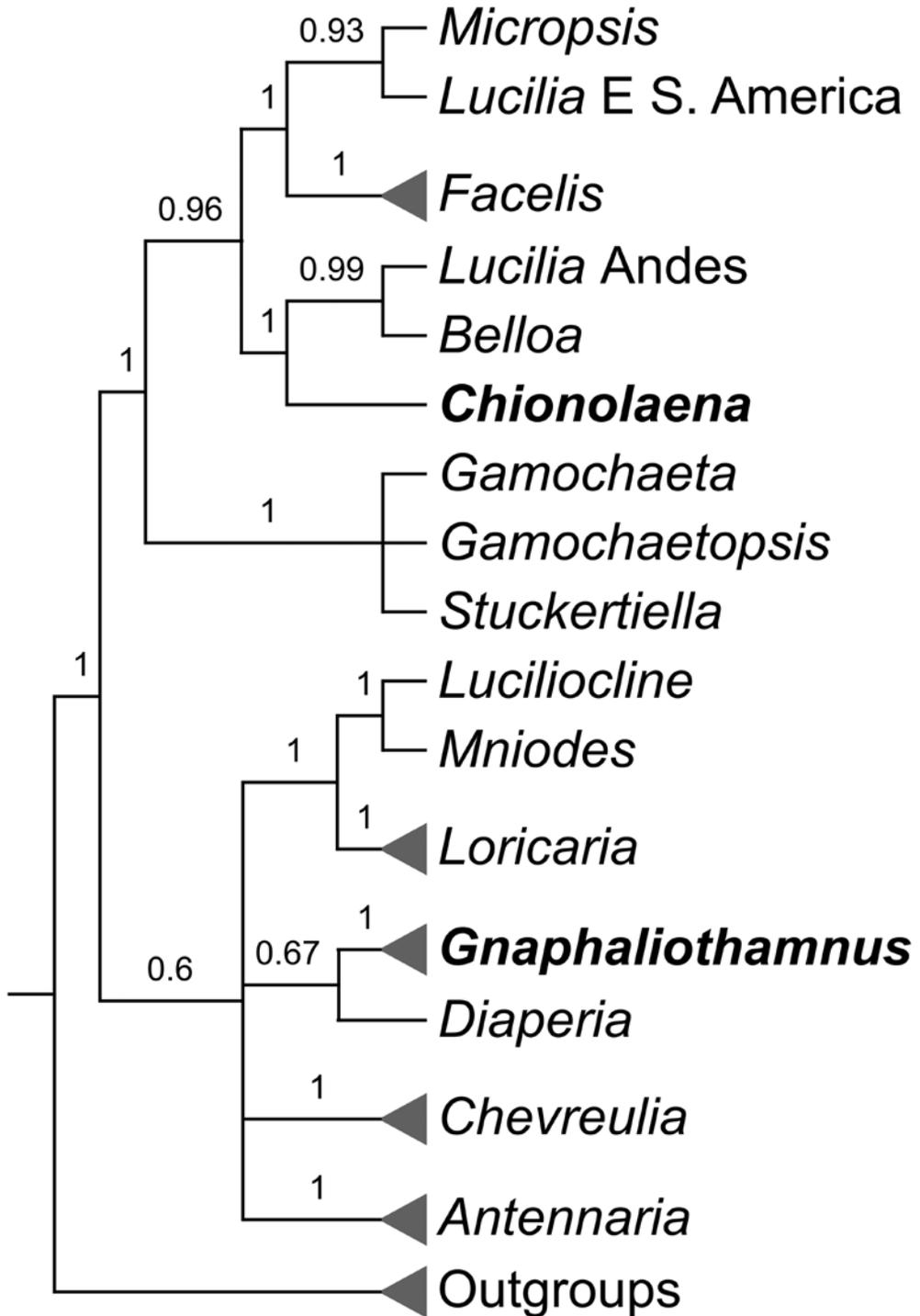


FIG. 3. Simplified cladogram of the *Lucilia*-group derived from preliminary result of a Bayesian analysis of Gnaphalieae with nrDNA sequence data (ITS+ETS) carried out in MrBayes v.3.1.2 (Ronquist & Huelsenbeck 2003). The numbers above branches are Bayesian posterior probabilities. The results are congruent with those reported by Freire et al. (2015). *Chionolaena* and *Gnaphaliothamnus* do not form a clade.

TABLE 1. Comparison of salient morphological characters in the species of *Gnaphaliothamnus* and *Pseudognaphalium* discussed here. Cypselar trichomes are illustrated in Figure 2.

Character	<i>G. nesomii</i>	<i>G. salicifolia</i>	<i>P. stolonatum</i>	<i>P. antennarioides</i>
Habit	subshrubs to 15 cm	subshrubs to 100 cm	perennial herbs	perennial herbs
Stolons	none	none	present	present
Capitula height	5–7 mm	6–7	4.5–5.5 mm	6–7 mm
Pistillate florets	20–32	(22–)34–55	44–92	(50–)75–190
Hermaphroditic florets	13–15	3–4(–7)	7–14	7–16
Cypselar trichomes	ca. 100 µm long, Fig. 2A	62–78 µm long, Fig. 2B	38–40 µm long, Fig. 2C	ca. 50 µm long, Fig. 2D

and suggested it was probably best maintained in *Gnaphalium* L. s.s. There has been acceptance of *Pseudognaphalium* and the majority of New World species previously classified as *Gnaphalium* were transferred there (Anderberg 1991).

*Gnaphaliothamnus nesomii* was originally treated as *Gnaphalium stolonatum*. In a note from Guy Nesom (16 Feb 1990) accompanying the return of his Field Museum loan, he mentioned the presence of some unusual or atypical specimens with fewer pistillate florets. When Pruski (2012) encountered what he considered conspecific material (*A. Molina* 16441, NY), he transferred the species to *Chionolaena* and described its floral morphology exactly as it is in *Gnaphaliothamnus*. He related it to other Mexican and Central American species, including *C. eleagnoides* Klatt, *C. lavandulifolia* (Kunth) Benth & Hook. f., *C. concinna* (A. Gray) Anderb. & S. E. Freire (as *C. mexicana* S. E. Freire), and *C. salicifolia* (Bertol.) G.L. Nesom, all species considered here to belong within *Gnaphaliothamnus*.

*Gnaphaliothamnus nesomii* is distinctive among members of *Gnaphaliothamnus*. It has a dwarf woody vegetative habit with stems only 5–10(–15) cm long, the basal leaves are marcescent and cloaking the lower portions of the stems, and the glomerulate capitulescences with the heads immersed in dense, white, arachnoid-tomentose indumentum, is a combination of characteristics unmatched in the genus. It has oblanceolate to spatulate leaves to 42 mm long, white-opaque phyllary apices, and capitula with 20–32 pistillate florets, and 13–15 hermaphroditic florets, Nesom's (1990a) key would lead to *G. salicifolius*; which is the only other member of *Gnaphaliothamnus* to be recorded from Guatemala, and it has a widespread distribution extending north from Guatemala to central Mexico.

*Gnaphaliothamnus salicifolius* has a distribution quite unlike all other species, which tend to be narrowly endemic and geographically restricted (Nesom 1990a,b, 1994). In Guatemala, it inhabits the edge of pine-oak forests at about 3000 m and is also found in the Sierra de los Cuchumatanes, recorded on the road between Paquix and San Juan Ixcay (*A. Molina* R. 21293, F1661761; *A. Molina* R. et al. 30031, F1734420; *A. Molina* R. et al. 16550, F1639348) and N of Santa Eulalia (*F. Almeda and J.L. Luteyn* 1686, F1733978).

Table 1 allows for comparison of the salient morphological characteristics of three of the Gnaphalieae taxa known to occur in region around the Sierra de los Cuchumatanes.

Additional material examined: **GUATEMALA. Huehuetenango:** Sierra Cuchumatanes between Paquix and San Juan Ixcay, 8 Jan 1974, 3000–3350 m, *A. Molina* R., *A.R. Molina*, and *J.A. Molina* 30055 (F1734422); between Tojquiá and Caxin bluff, summit of Sierra de los Cuchumatanes, 3700 m, 6 Aug 1942, *J.A. Steyermark* 50159 (F1148150).

#### KEY TO GNAPHALIOTHAMNUS SPECIES

The following annotated key will allow for identification of *Gnaphaliothamnus* species (adapted from Nesom 1990a):

1. Inner phyllaries lacking prominent, white lamina; pappus bristles monomorphic (Chiapas - Mexico) \_\_\_\_\_ **G. cryptocephalus**  
G.L. Nesom
1. Inner phyllaries with prominent, white lamina.
  2. Adaxial leaf surfaces with stipitate glandular trichomes beneath the arachnoid-tomentum.
    3. Pistillate florets 5–10; pappus bristles strongly dimorphic, caducous; cypselas glabrous (Costa Rica) \_\_\_\_\_ **G. costaricensis**  
G.L. Nesom

3. Pistillate florets 12–24; pappus bristles monomorphic to weakly or strongly dimorphic, basally persistent; cypselas with trichomes.
4. Pistillate florets 12–18, usually equal the number of hermaphroditic; pappus bristles strongly dimorphic (Oaxaca - Mexico) \_\_\_\_\_ **G. macdonaldii** G.L. Nesom
4. Pistillate florets 21–24, usually about twice as many as the hermaphroditic; pappus bristles monomorphic to very weakly dimorphic (Veracruz, Puebla, Tlaxcala, Morelos - Mexico) \_\_\_\_\_ **G. lavandulifolius** (Kunth) G.L. Nesom
2. Adaxial leaf surfaces arachnoid-tomentose to glabrate, eglandular.
5. Leaves 7–8 mm long; phyllaries subequal (Oaxaca - Mexico) \_\_\_\_\_ **G. sartorii** (Klatt) G.L. Nesom
5. Leaves shorter than 5 mm or longer than 10 mm long; phyllaries strongly graduated.
6. Heads few in tight clusters at tips of leafy stems.
  7. Plants dioecious; leaves 2.5–5 mm long; phyllaries with reddish midregion (Oaxaca - Mexico) \_\_\_\_\_ **G. aecidiocephalus** (Grierson) G.L. Nesom
  7. Plants polygamodioecious; leaves 10–20 mm long; phyllaries without a red midregion (San Luis Potosí - Mexico) \_\_\_\_\_ **G. concinnus** (A. Gray) G.L. Nesom
6. Heads numerous in corymbs above the leaves.
8. Leaves elliptic to elliptic-oblancoelate; pappus bristles weakly dimorphic.
  9. Leaves elliptic to elliptic-oblancoelate, 15–42 mm long, 4–8 mm wide (Hidalgo, Oaxaca - Mexico) \_\_\_\_\_ **G. eleagnoides** (Klatt) G.L. Nesom
  9. Leaves elliptic-obovate, 10–20 mm long, 3–5 mm wide (Durango - Mexico) \_\_\_\_\_ **G. durangensis** G.L. Nesom
8. Leaves linear to oblanceolate or spatulate; pappus bristles strongly dimorphic.
  10. Leaves 20–80 mm long, 1–3(–5) mm wide; pistillate florets (22–)34–55; hermaphroditic florets 3–4(–7) (Guatemala, Mexico) \_\_\_\_\_ **G. salicifolius** (Bertol.) G.L. Nesom
  10. Leaves 10–42 mm long, 2–4 mm wide; pistillate florets 20–32; hermaphroditic florets 13–15 (Guatemala) \_\_\_\_\_ **G. nesomii** M.O. Dillon & Luebert

NEW COMBINATIONS IN *PSEUDOGNAPHALIUM*

***Pseudognaphalium stolonatum*** (S.F. Blake) M.O. Dillon, comb. nov. (**Fig. 4**). *Gnaphalium stolonatum* S.F. Blake, *Brittonia* 2:341. 1937. TYPE: GUATEMALA. HUEHUETENANGO: llanos of the Sierra Cuchumatanes, 10,500 ft [3200 m], 24 Aug 1934, A. F. Skutch 1098 (HOLOTYPE: GH00008351; ISOTYPE: TEX-LL00373732, n.v.).

*Chionolaena stolonata* (S.F. Blake) Pruski, *Phytoneuron* 2012-1:4. 2012.

Perennial herbs 10–25 mm tall, roots fibrous; stolons from the base, filiform; stems erect, usually simple, rarely branched, thinly arachnoid-tomentose, purplish. **Leaves** oblanceolate to linear, 2–4.5 mm long, 0.5–1 mm wide, abaxial surfaces gray with dense tomentose indumentum, adaxial surfaces obscurely stipitate-glandular under thinly arachnoid-tomentose indumentum, apices apiculate, bases slightly decurrent. **Capitulescences** glomerulate, crowded at apices. **Capitula** campanulate, sessile, 4.5–5.5 mm tall, 4.5–5.5 mm diam.; phyllaries ca. 4-seriate, graduated, thinly arachnoid-tomentose; outer ovate to oblong-lanceolate, obtuse to acute, inner narrowly lanceolate, narrowed to an obtuse apex; pistillate florets 85–92, the corollas filiform, white, ca. 2.5 mm long, pappus bristles ca. 3 mm long, apices acute; hermaphroditic florets (7–)11(–14), the corollas cylindrical, white with rose-color lobes, the styles apically subtruncate, ovary sterile; pappus bristles ca. 3 mm long, apically obtuse, slightly expanded. **Cypselas** ca. 1 mm long, minutely hispidulous, the trichomes clavate, 38–40 µm long (Fig. 2C).

*Pseudognaphalium stolonatum* has been collected within the Sierra de los Cuchumatanes from alpine meadows on rock outcrops, 3200–3750 m. It was included in *Gnaphalium* s.s. by Anderberg (1991). Inspection of the type has shown it to have floral morphology consistent with *Pseudognaphalium* (Anderberg 1991).

Blake (1937) specifically related *Pseudognaphalium stolonatum* to *P. antennarioides* (DC.) Anderb., a rosulate, stoloniferous herb distributed from Colombia to Bolivia with capitula having (50–)75–190 pistillate and 7–16 hermaphroditic florets. Phylogenetic studies have shown that *Pseudognaphalium* is a member of the HAP clade (Smitsen et al. 2011; Nie et al. 2013; Galbany-Casals et al. 2014), along with *Achyrocline* (Less.) DC., *Helichrysum* Mill., and *Anaphalis* DC.; *Gnaphaliothamnus* and *Chionolaena* are members of the FLAG clade, which is only distantly related (Smitsen et al. 2011).

*Pseudognaphalium subsericeum* (S.F. Blake) Anderb. (= *Gnaphalium subsericeum* S.F. Blake, 1927), a Costa Rican endemic, was also mentioned as potentially related to *Gnaphaliothamnus salicifolius* by Blake (p. 62). An examination of conspecific material from Costa Rica (F1692005, F1692006) shows *P. subsericeum* more simi-

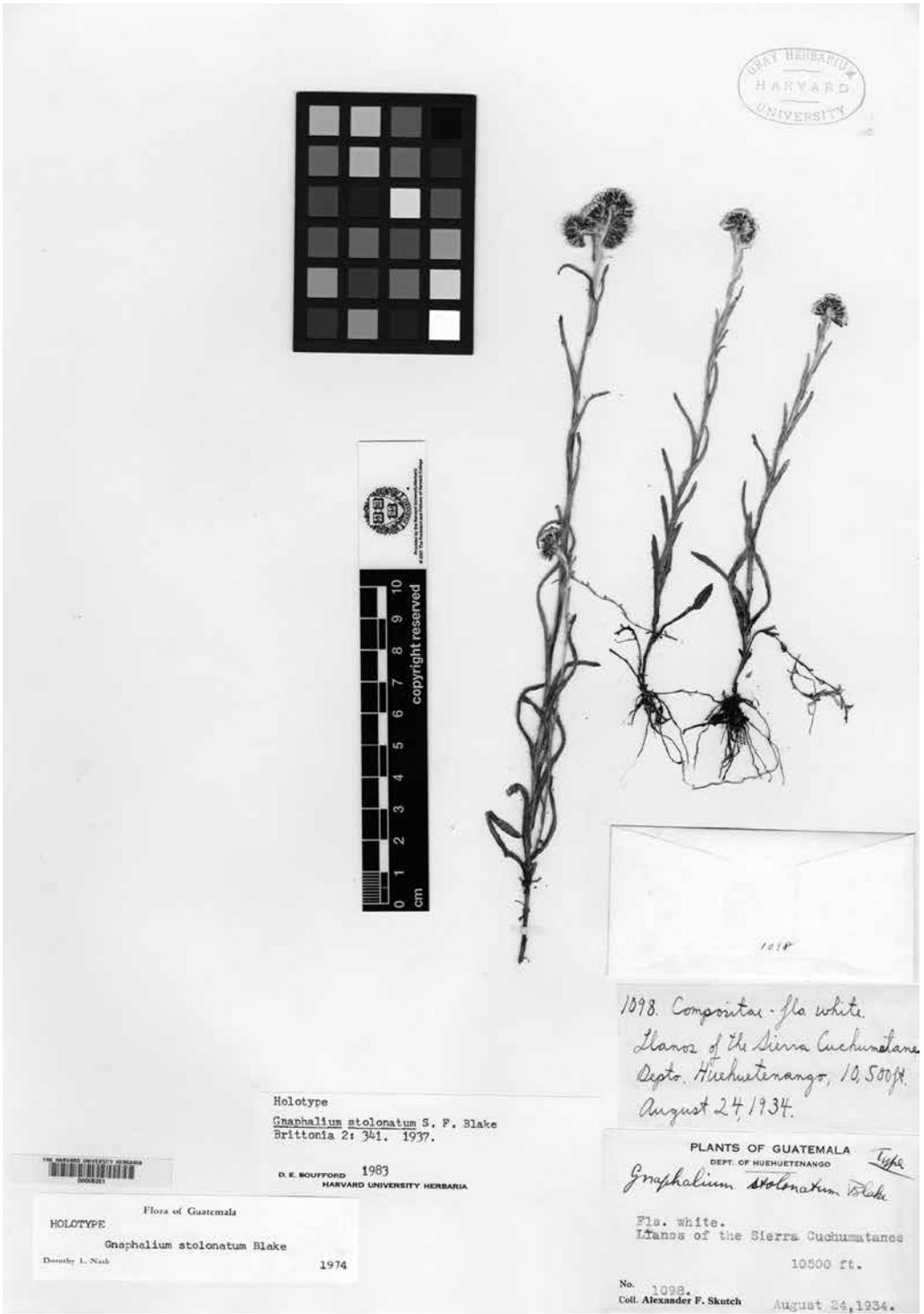


Fig. 4. *Pseudognaphalium stolonatum*. Photograph of holotype collection of *Gnaphalium stolonatum* S.F.Blake, A.F. Skutch 1098 (GH00008351).



Fig. 5. *Pseudognaphalium paramorum*. Photograph of holotype collection of *Gnaphalium paramorum* S.F. Blake, A. Jahn 883 (US1186590, img00129548).

lar to *P. stolonatum* or *P. antennarioides* (DC.) Anderb., the latter an Andean species that has similar overall morphology and cypselar trichomes (Fig. 2D). All these species have capitula in dense cymes or glomerules and phyllaries with showy, white apices.

Additional specimens examined: **GUATEMALA. Huehuetenango:** vicinity of Chemal, summit of Sierra de los Cuchumatanes, 3700–3750 m, 8 Aug 1942, J. A. Steyermark 50253 (F1148157), 50273 (F1148180), 50275 (F1148179).

***Pseudognaphalium paramorum*** (S.F. Blake) M.O. Dillon, comb. nov. (**Fig. 5**). BASIONYM: *Gnaphalium paramorum* S.F. Blake, J. Wash. Acad. Sci. 21:328. 1931. TYPE: VENEZUELA. Estado Mérida: Páramo Quirorá, 2900 m, 24 Feb 1922, A. Jahn 883 (HOLOTYPE: US1186590).

*Gamochaeta paramora* (S.F. Blake) Anderb., Opera Bot. 104:157. 1991.

Blake (1931) commented that *Pseudognaphalium paramorum* had the appearance of *Gnaphalium antennarioides* DC. (= *P. antennarioides* (DC.) Anderb.), and he related it to that taxon, which is a rosulate, stoloniferous herb distributed from Colombia to Bolivia.

Anderberg (1991) transferred *Gnaphalium paramorum* to *Gamochaeta* Wedd.; an examination of the type collection shows it to only superficially resemble *Gamochaeta*. It has a basal rosette of subspathulate leaves and unbranched, ascending stems. The terminal capitulescences are not spicate; they are densely glomerulate corymbs. The type collection has capitular and floral morphology consistent with *Pseudognaphalium*; the cypselas are papillose and lack the 2-celled, sessile trichomes diagnostic for *Gamochaeta*.

#### ACKNOWLEDGMENTS

We thank the curators and staff of the herbaria at F, GH, MO, NY, TEX, and US for permitting access to their material. Especially, we wish to acknowledge Ms. Emily Wood, Collections Manager at the Gray Herbarium, who expedited loan of type material from that institution. We thank John Strother for many constructive suggestions in the review process. Andrés Moreira-Muñoz and Miguel Álvarez provided plant material for phylogenetic studies. Digital images were obtained via the Internet in Figure 4 from GH and Figure 5 from US. We thank Field Museum's Christine Niezgodá, Anna Balla, Daniel Le, and Allie Stone for handling various aspects of loans and digitizing collections.

#### REFERENCES

- ANDERBERG, A. 1991. Taxonomy and phylogeny of the tribe Gnaphalieae (Asteraceae). Opera Bot. 104:1–195.
- ANDERBERG, A. & S.E. FREIRE. 1989. Transfer of two species from *Anaphalis* DC. to *Chionolaena* DC. (Asteraceae, Gnaphalieae). Notes Roy. Bot. Gard. Edinburgh 46(1):37–41.
- BLAKE, S.F. 1927. New Asteraceae from Costa Rica. J. Wash. Acad. Sci. 17(3):59–65.
- BLAKE, S.F. 1931. Nine new American Asteraceae. J. Wash. Acad. Sci. 21(14):325–336.
- BLAKE, S.F. 1937. New Asteraceae from Guatemala and Costa Rica Collected by A.F. Skutch. Brittonia 2(4):329–361.
- DILLON, M.O. 2003. New combinations in *Luciliocline* with notes on South American Gnaphalieae (Asteraceae). Araldoa 10(1):45–60.
- DILLON, M.O. & A. SAGÁSTEGUI-A. 1991. Sinopsis de los géneros de Gnaphaliinae (Asteraceae-Inuleae) de Sudamerica. Araldoa 1(2):5–91.
- DILLON, M.O. & A. SAGÁSTEGUI A. 1990. *Oligandra* Less. Revisited and the need for a new genus, *Pseudoligandra* (Asteraceae: Inuleae). Taxon 39:125–128.
- FREIRE, S.E. 1993. A revision of *Chionolaena* (Compositae, Gnaphalieae). Ann. Missouri Bot. Gard. 80(2):397–438.
- FREIRE, S.E., M.A. CHEMISQUY, A.A. ANDERBERG, S.G. BECK, R.I. MENESES, B. LOEUILLE, & E. URTUBEY. 2015. The *Lucilia* group (Asteraceae, Gnaphalieae): phylogenetic and taxonomic considerations based on molecular and morphological evidence. Pl. Syst. Evol. 301:1227–1248. doi: 10.1007/s00606-014-1147-0.
- GALBANY-CASALS, M., M. UNWIN, N. GARCIA-JACAS, R.D. SMISSEN, A. SUSANNA, & R.J. 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(3):608–624.
- IUCN SPECIES SURVIVAL COMMISSION. 2001. IUCN Red List Categories and Criteria: Version 3.1. IUCN, Gland, Switzerland and Cambridge, United Kingdom, 1–30.

- HESS, R. 1938. Vergleichende Untersuchungen über die Zwillingshaare der Compositen. Bot. Jahrb. Syst. 68:435-496.
- LOEUILLE, B., L. BEBLE, & J.N. NAKAJIMA. 2011. Four new species of *Chionolaena* (Asteraceae: Gnaphalieae) from southeastern Brazil. Kew Bull. 66(2):263–272.
- NESOM, G.L. 1990a. Taxonomy of *Gnaphaliothamnus* (Asteraceae: Inuleae). Phytologia 68(5):366–381.
- NESOM, G.L. 1990b. An additional species of *Gnaphaliothamnus* (Asteraceae: Inuleae) and further evidence for the integrity of the genus. Phytologia 68(6):1–3.
- NESOM, G.L. 1994. Comments on *Gnaphaliothamnus* (Asteraceae: Inuleae). Phytologia 76:185–191.
- NESOM, G.L. 2001. New combinations in *Chionolaena* (Asteraceae: Gnaphalieae). Sida 19(4):849–852.
- NIE, Z.-L., V. FUNK, H. SUN, T. DENG, Y. MENG, & J. WEN. 2013. Molecular phylogeny of *Anaphalis* (Asteraceae, Gnaphalieae) with biogeographic implications in the Northern Hemisphere. J. Plant Res. 126(1):17–32.
- 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.
- ROBINSON, H. 2015. Notes on the genus *Chionolaena* in Colombia with a new species *Chionolaena barclayae* (Asteraceae, Gnaphalieae). PhytoKeys 46:67–71, doi: 10.3897/phytokeys.46.8976
- RONQUIST, F. & J.P. HUELSENBECK. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19:1572–1574.
- SMISSEN, R.D., M. GALBANY-CASALS, & I. BREITWIESER. 2011. Ancient allopolyploidy in the everlasting daisies (Asteraceae: Gnaphalieae): Complex relationships among extant clades. Taxon 60(3):649–662.