

**TAXONOMIC SUMMARY OF *GNAPHALIOTHAMNUS* AND *MEXERION*
(ASTERACEAE: GNAPHALIEAE)**

GUY L. NESOM

Research Associate

Academy of Natural Sciences of Drexel University

Philadelphia, Pennsylvania 19103

guynesom@sbcglobal.net

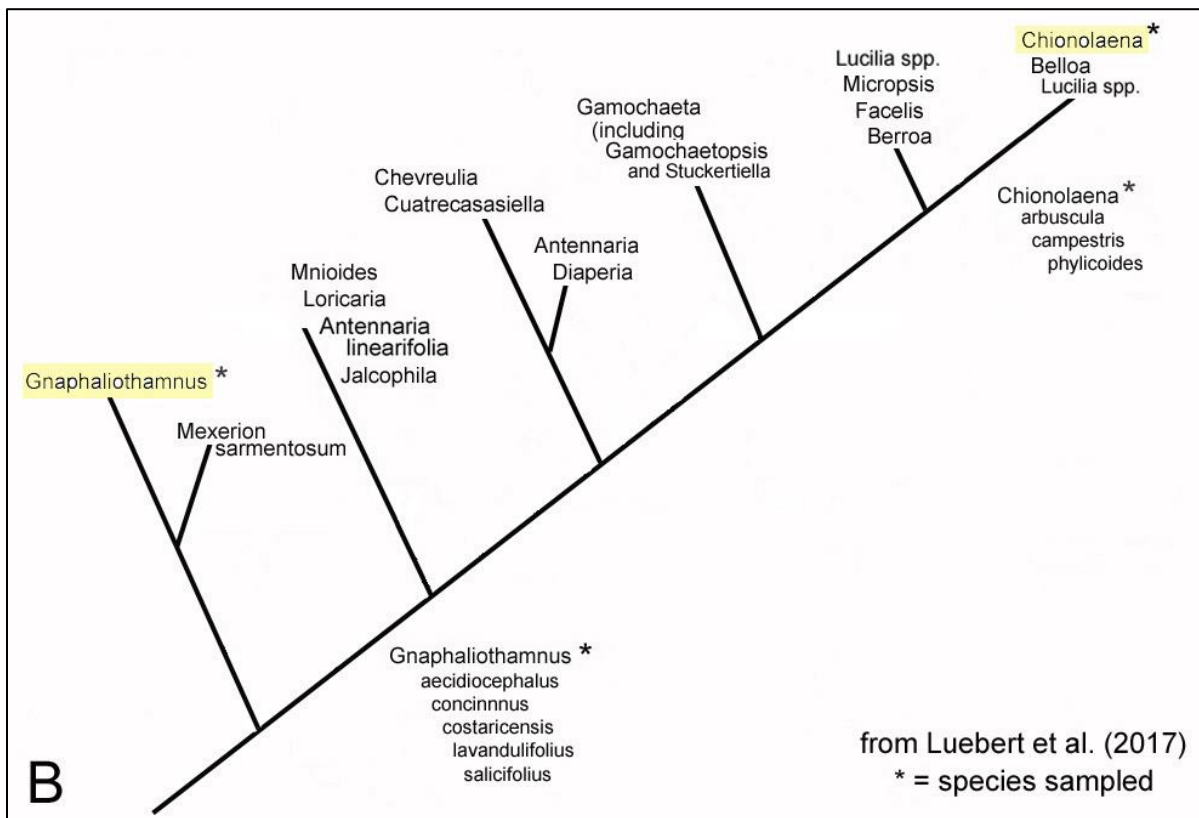
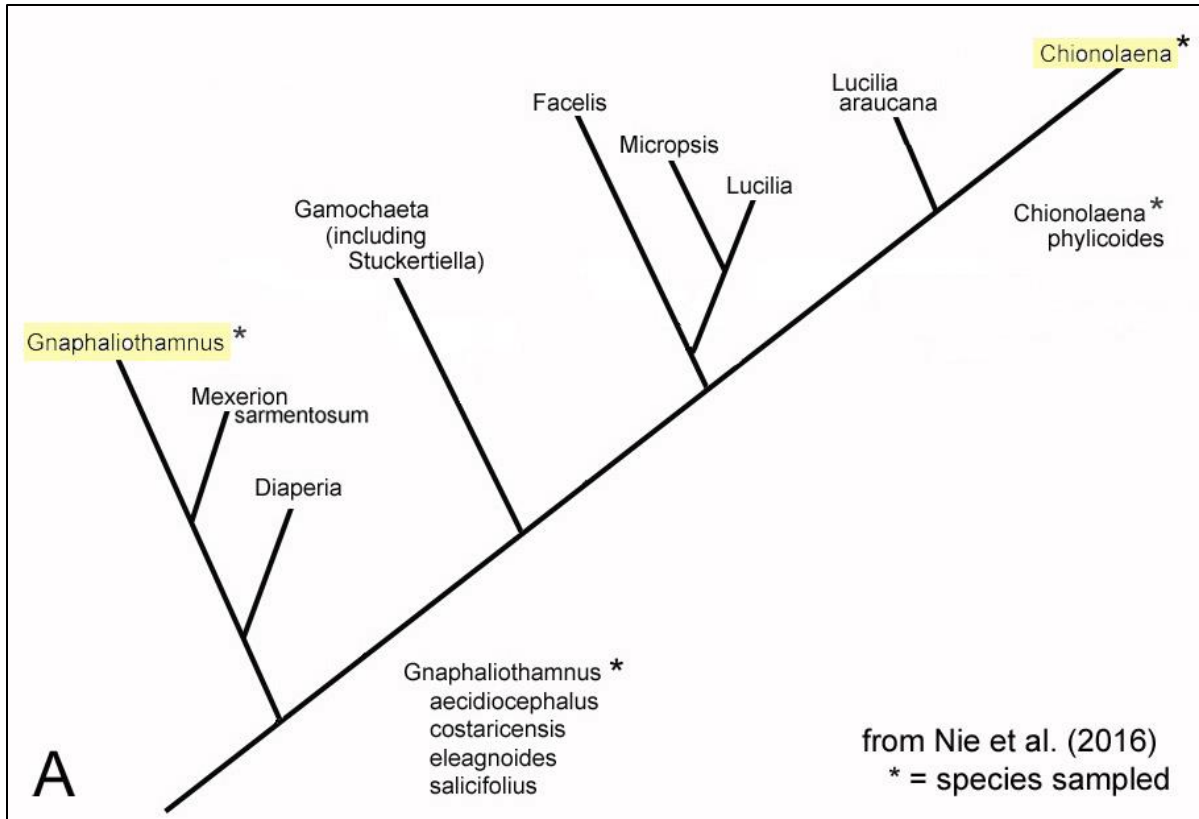
ABSTRACT

Molecular phylogenies (summarized here diagrammatically) show a sister relationship between *Gnaphaliothamnus* and *Mexerion* and show *Gnaphaliothamnus* and the South American (Brazilian) *Chionolaena* in different clades, indicating that their similarities are convergent. *Gnaphaliothamnus* in the concept here comprises 17 species (Mexico, Central America, and Colombia in South America), *Mexerion* 3 species (Mexico and Guatemala), and *Chionolaena* 12 species (Brazil, one with disjunct populations in Venezuela). A taxonomic summary is presented for *Gnaphaliothamnus* and *Mexerion*. ***Gnaphaliothamnus monanthus* Nesom, sp. nov.**, from the Sierra Cuchumatanes in Guatemala and ***Gnaphaliothamnus baru* Nesom, sp. nov.**, from Volcán Barú in Panama are described, and *Chionolaena mexicana* Freire is brought into *Gnaphaliothamnus* as ***Gnaphaliothamnus mexicanus* (Freire) Nesom, comb. nov.** Three species of *Chionolaena* from the Sierra de Santa Marta in northeastern Colombia are transferred to *Gnaphaliothamnus* — ***Gnaphaliothamnus barclayae* (H. Rob.) Nesom, comb. nov.**, ***Gnaphaliothamnus chrysocoma* (Wedd.) Nesom, comb. nov.**, and ***Gnaphaliothamnus colombianus* (Blake) Nesom, comb. nov.** — they are geographically distinct from *Chionolaena* sensu stricto but coherent with *Gnaphaliothamnus* and are hypothesized here to be closely related to *G. lavandulifolius* and *G. costaricensis*. *Mexerion* acquires a third species through the transfer of *Chionolaena* (*Gnaphalium*) *stolonata* (Blake) Pruski, as ***Mexerion stolonatum* (Blake) Nesom, comb. nov.**, a species endemic to the Sierra Cuchumatanes of Guatemala. A detailed distribution map and illustrations of herbarium collections are provided for each species, in situ photos from iNaturalista observations are provided for some.

Studies in *Gnaphaliothamnus* Kirpichn. (Nesom 1990b, 1990c) included 10 species of Mexico and Central America. Freire's taxonomic revision of *Chionolaena* DC. (1993) incorporated all but one of the *Gnaphaliothamnus* species (and added one, *C. mexicana* Freire), but retained *Gnaphaliothamnus salicifolius* as comprising a monotypic genus sister to *Chionolaena* — this concept following Anderberg and Freire (1989) and Anderberg (1991).

I presented evidence (Nesom 1990c, 1994) indicating that *Gnaphaliothamnus salicifolius* could not be separated from the other Mexican species of the genus. But in view of the seemingly subtle differences indicating that the concept of *Chionolaena* should be broadened, I transferred the remaining Mexican species of *Gnaphaliothamnus* to *Chionolaena* (Nesom 2001), noting that (pp. 849-850) "distinctive features of vegetative glandularity and features of achenial vestiture of the Mexican and Central American species ... indicate that they probably constitute a phyletically coherent northern segment of the genus, rather than being cladistically interspersed among the South American species, as postulated by Freire (1993)."

Loeuille et al. (2011) have added four new species of *Chionolaena* sensu stricto from southeastern Brazil, and Robinson (2015) added *C. barclayae* from the Sierra Santa Marta in Colombia. In his treatment of Asteraceae for Flora Mesoamericana, Pruski (2018) has used the broader concept of *Chionolaena* but acknowledged the position of *C. salicifolia* within it.



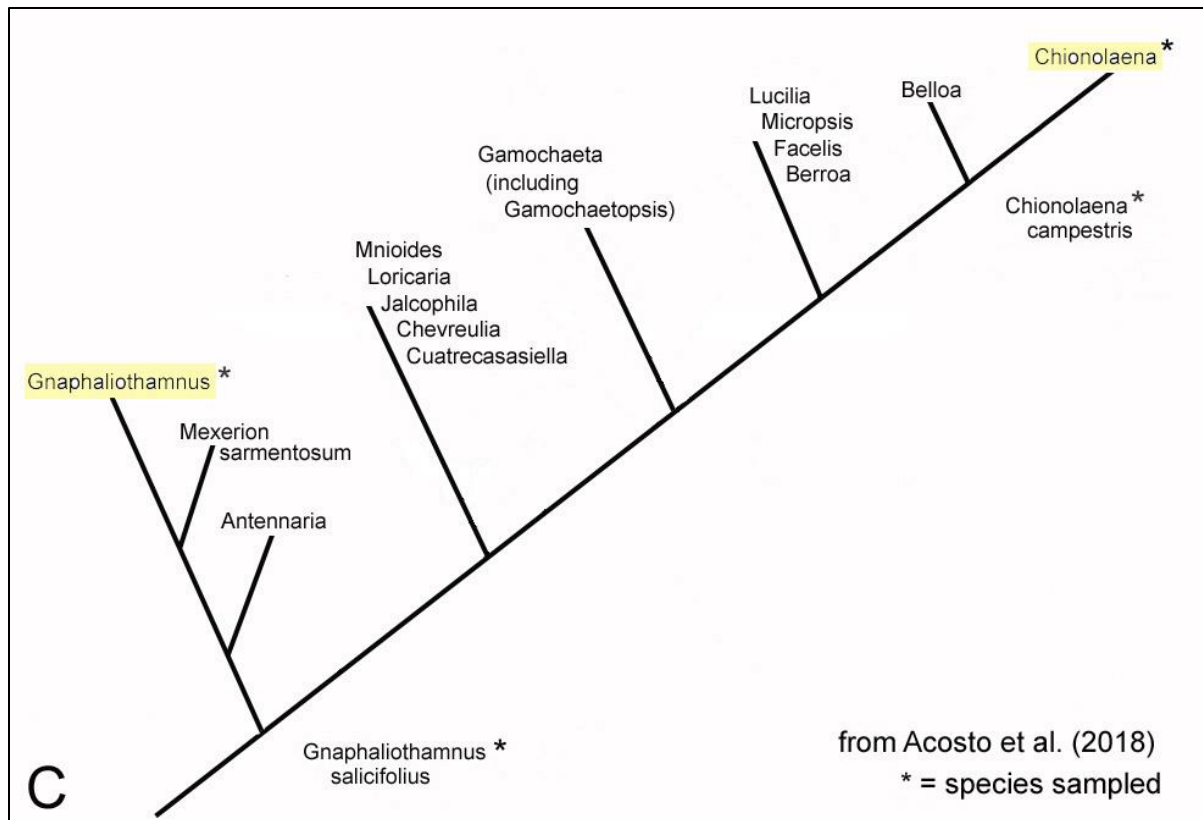


Figure 1. Phylogenetic positions of *Gnaphaliothamnus* and *Chionolaena* based on molecular data. **A.** From Nie et al. (2016) — branch from maximum likelihood tree of 835-taxa dataset of Gnaphalieae, using nrDNA ETS/ITS data. **B.** From Luebert et al. (2017) — branch from Bayesian analysis of a combined ITS + ETS matrix. **C.** From Acosto et al. (2018) — branch from maximum credibility tree, from nrDNA (ITS and 3' ETS regions). The molecular phylogeny of Smissen et al. (2020) is similar to these.

A morphological-phylogenetic study of achenial trichomes in the *Lucilia* group (Luebert et al. 2017) supports the placement of *Gnaphaliothamnus* and *Chionolaena* in different clades. The "twin hair" trichomes in *Gnaphaliothamnus* are relatively shorter and clavate with myxogenic apical cells; those in *Chionolaena* are relatively longer and thinner (cylindric, giving the achenes a loosely strigose appearance), non-myxogenic, and with attenuate-acute apical cells. These differences were observed earlier by Nesom (1990b, 1994) and Dillon & Sagástegui Alva.(1991).

Similarities between *Gnaphaliothamnus* and *Chionolaena* can now be seen as convergent — phylogenetic analyses based on DNA evidence position the two species groups in separate clades (Dillon & Luebert 2015; Nie et al. 2016; Luebert et al. 2017; Acosta-Maindom & Galbany-Casals 2018; Galbany-Casals et al. 2018; Smissen et al. 2020). Examples of these cladistic topologies are shown in Figure 1.

None of the *Chionolaena* species from the Sierra de Santa Marta in Colombia have been included in molecular studies, so a generic distinction might be sought in achenial vestiture. The Santa Marta species, however, have glabrous achenes, as does *Gnaphaliothamnus costaricensis*, which molecular data confirm as *Gnaphaliothamnus*. No species of Brazilian *Chionolaena* has glabrous achenes. Given the close geographic association of the Colombian species to *Gnaphaliothamnus*, their glabrous achenes, and their similarity in phyllary morphology to a group of Mexican/Central American *Gnaphaliothamnus* species (comments below), the immediate ancestry of the Colombian species appears to be with *Gnaphaliothamnus* — the formal nomenclatural transfers are made below.

Two species groups can be seen within *Gnaphaliothamnus*, based mostly on phyllary morphology — (a, the salicifolius group, mostly northern) phyllaries with an oblong, bright white, abruptly delimited apical extension, and (b, the lavandulifolius group, mostly southern) phyllaries ovate-triangular, the apex not sharply distinct from the body and often gray-white. See contrasts (e.g.) in Figs. 1 and 10-11 vs. Figs. 2-4 and 6-7.

- (a) *G. barclayae*, *chrysocoma*, *columbianus*, *costaricensis*, *cryptocephalus*, *lavandulifolius*, *macdonaldii*, *monanthus*, and *sartorii*. *Gnaphaliothamnus barclayae*, *G. chrysocoma*, *G. columbianus*, and *G. costaricensis* have glabrous achenes.
- (b) *G. aecidiocephalus*, *baru*, *concinnus*, *durangensis*, *eleagnoides*, *mexicanus*, *nesomii*, and *salicifolius*

If this difference is confirmed, the evolutionary prediction is not contradicted by phylogenetic topologies indicated in preliminary molecular studies (Fig. 2).

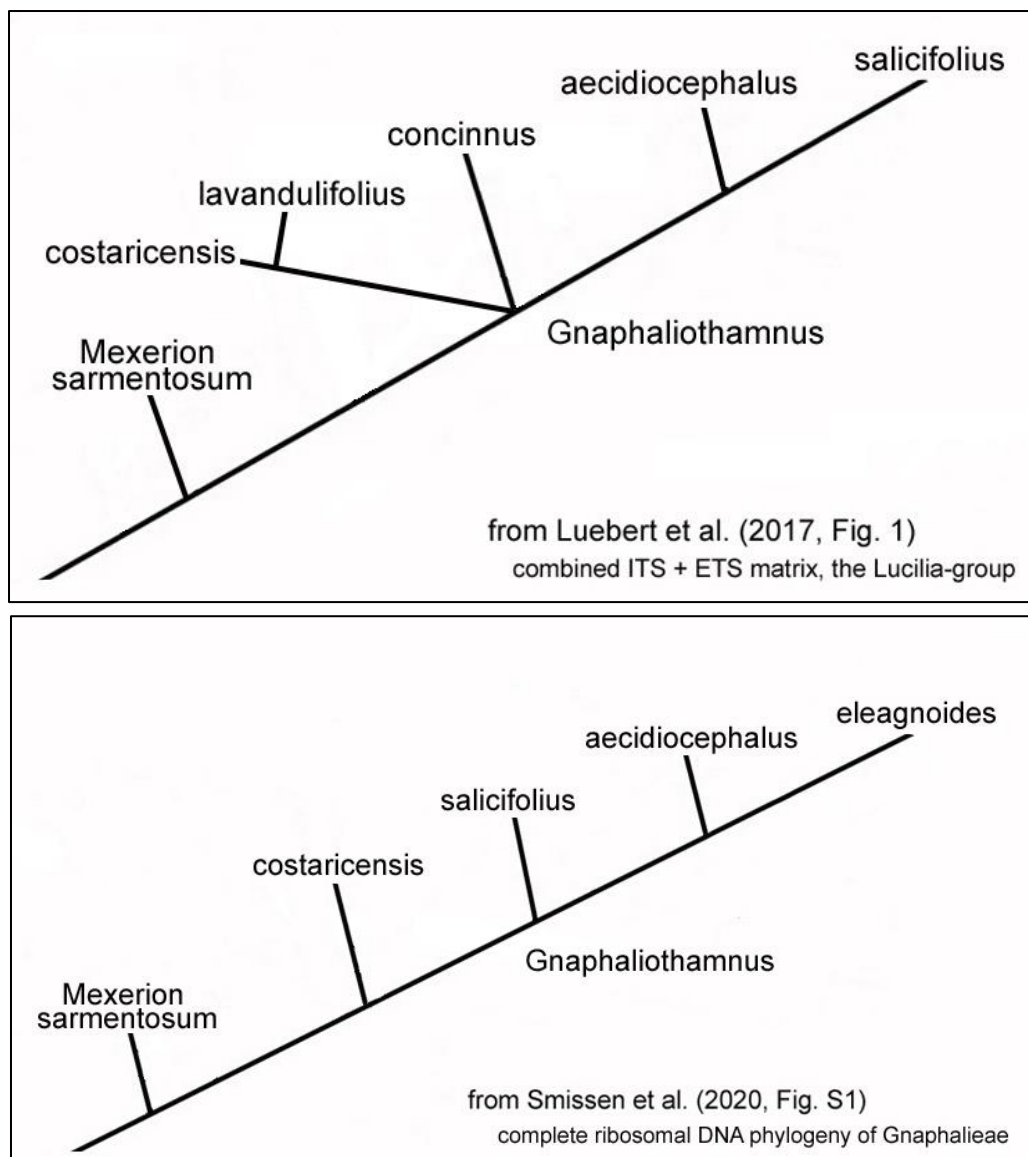


Figure 2. Phylogeny of *Gnaphaliothamnus* species, based on molecular data. **Top:** Luebert et al. (2017). **Bottom:** Smissen et al. (2020). *Mexerion sarmentosum* is positioned as sister to *Gnaphaliothamnus* in both analyses.

GNAPHALIOTHAMNUS Kirpichn., Trudy Bot. Inst. Akad. Nauk S.S.S.R., Ser. 1, Fl. Sist. Vyssh. Rast. 9: 33. 1950. **TYPE SPECIES:** *Gnaphaliothamnus* (*Gnaphalium*) *rhodanthus* (Schultz-Bip.) Kirpichn. = *Gnaphaliothamnus salicifolius*

Gnaphalium subg. *Rhodognaphalium* Schultz-Bip. in Seem., Bot. Voy. Herald, 310. 1856. **TYPE SPECIES:** *Gnaphalium rhodanthum* Schultz-Bip. = *Gnaphaliothamnus salicifolius*

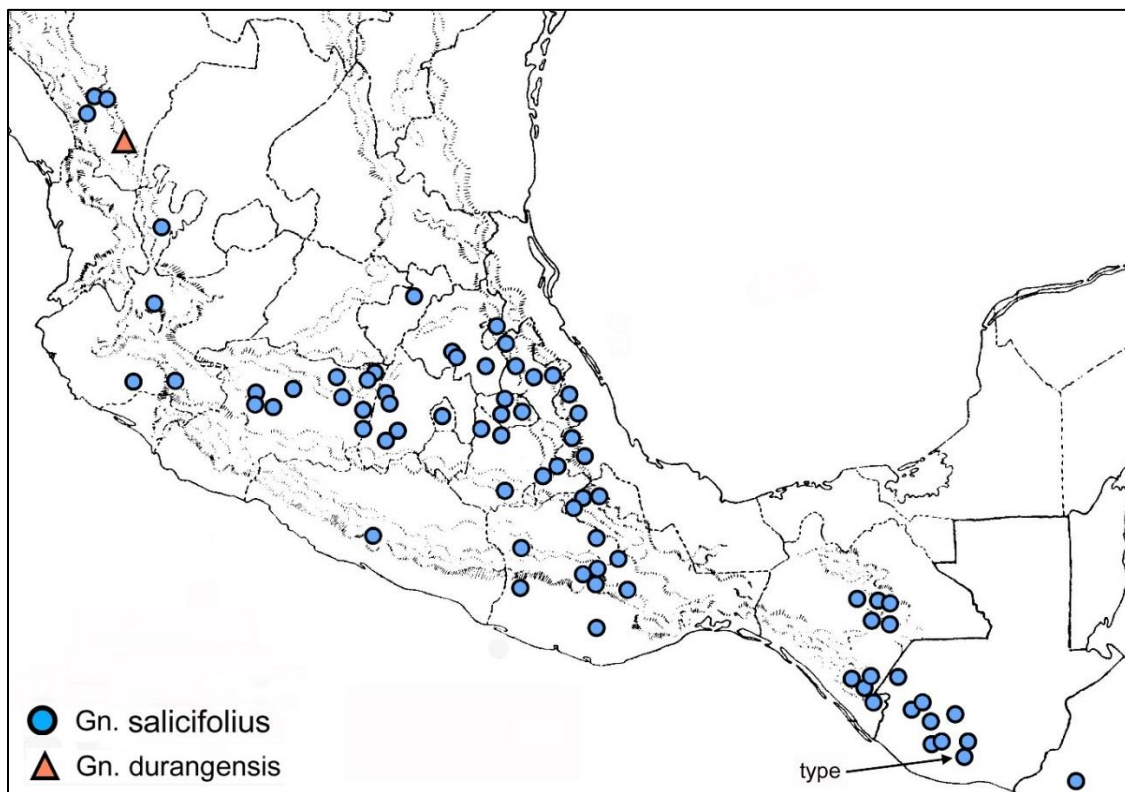
Gnaphalium sect. *Rhodognaphalium* [as "*Eurhodognaphalium*"] Schultz-Bip. in Seem., Bot. Voy. Herald, 310. 1856. **TYPE SPECIES:** *Gnaphalium rhodanthum* Schultz-Bip. = *Gnaphaliothamnus salicifolius*

Gnaphalium sect. *Metalsiopsis* Schultz-Bip. in Seem., Bot. Voy. Herald, 310. 1856. **TYPE SPECIES:** *Gnaphalium seemannii* Schultz-Bip. = *Gnaphaliothamnus salicifolius*

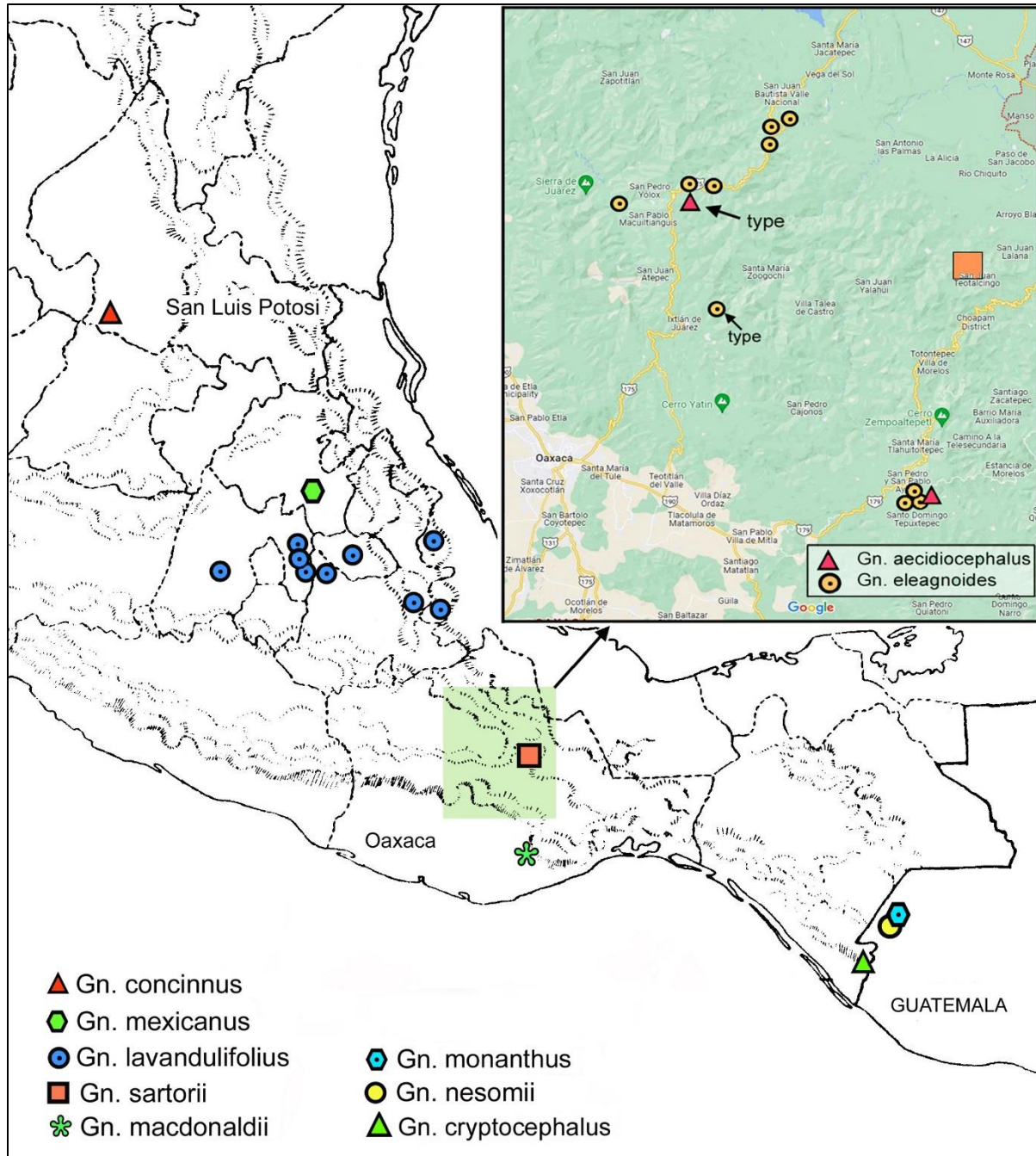
Parachionolaena Dillon & Sagást., Arneloa 1: 42. 1992. **TYPE SPECIES:** *Parachionolaena columbiana* (Blake) Dillon & Sagást. = *Gnaphaliothamnus columbianus*

Pseudoligandra Dillon & Sagást., Taxon 39: 127. 1990. **TYPE SPECIES:** *Pseudoligandra chrysocoma* (Wedd.) Dillon & Sagást. = *Gnaphaliothamnus chrysocoma*

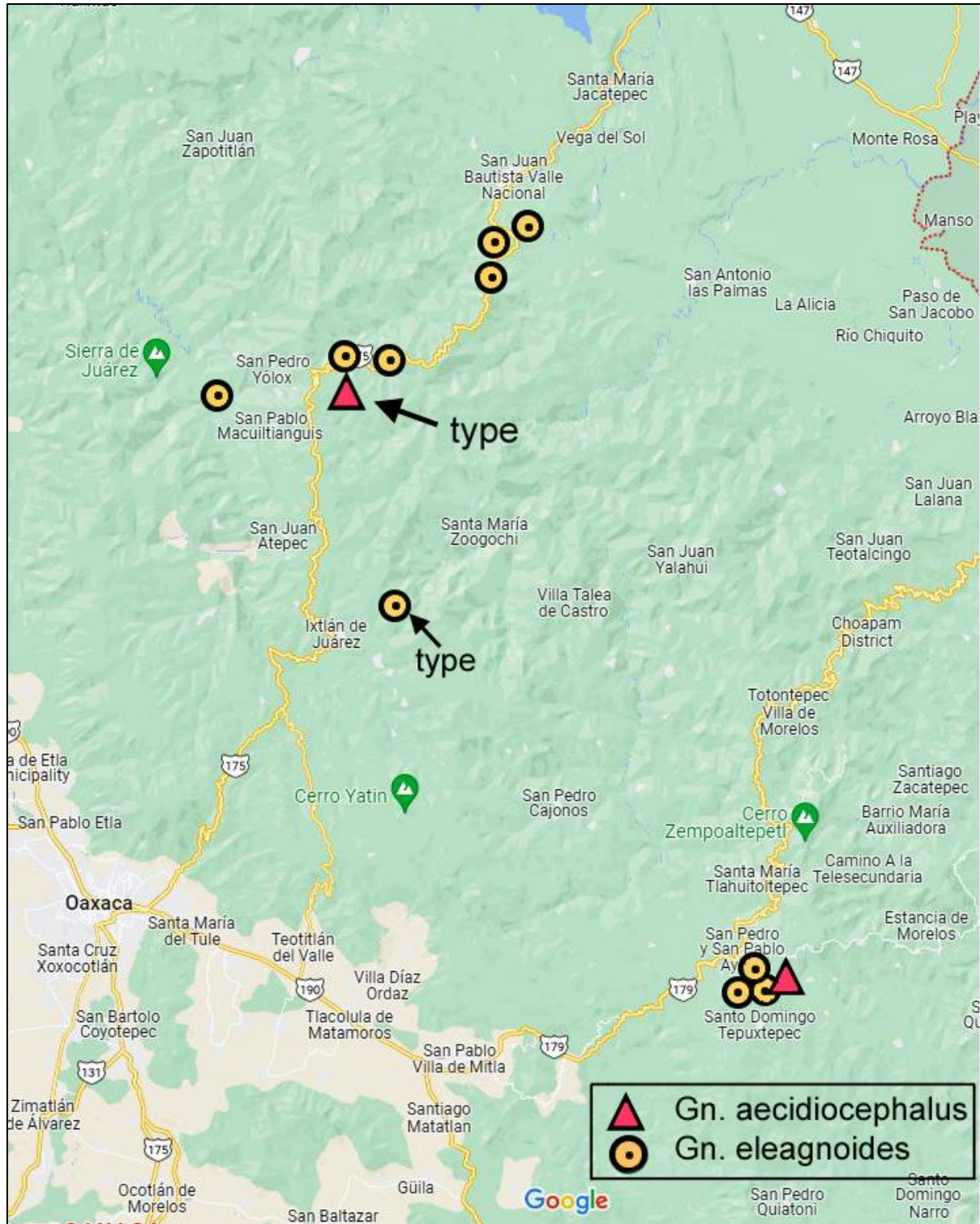
Perennial subshrubs or herbs 10–30 cm tall. **Leaves** linear to oblong or elliptic, not clasping, strongly to weakly bicolor, glandular or eglandular adaxially. **Heads** sessile to subsessile or short-pedicellate in clusters at or above the level of the leaves, rarely solitary. **Phyllaries** with white-opaque apices (except in *G. cryptocephalus*), stereome undivided. **Pistillate florets** (5–)46–70(–85 in *G. baru*). **Disc florets** 3–19, functionally staminate. **Heads** sometimes dioecious (*G. aecidiocephalus*) to polygamodioecious (*G. concinnus*). **Achenes** 1–2 mm long, epidermis smooth (not papillate), glabrous or sparsely invested with myxogenic twin-hairs; pappus bristles with weakly to strongly developed clavate tips (disc florets), weakly adherent-connate to completely separate at the base. **Base chromosome number**, $x=14$.



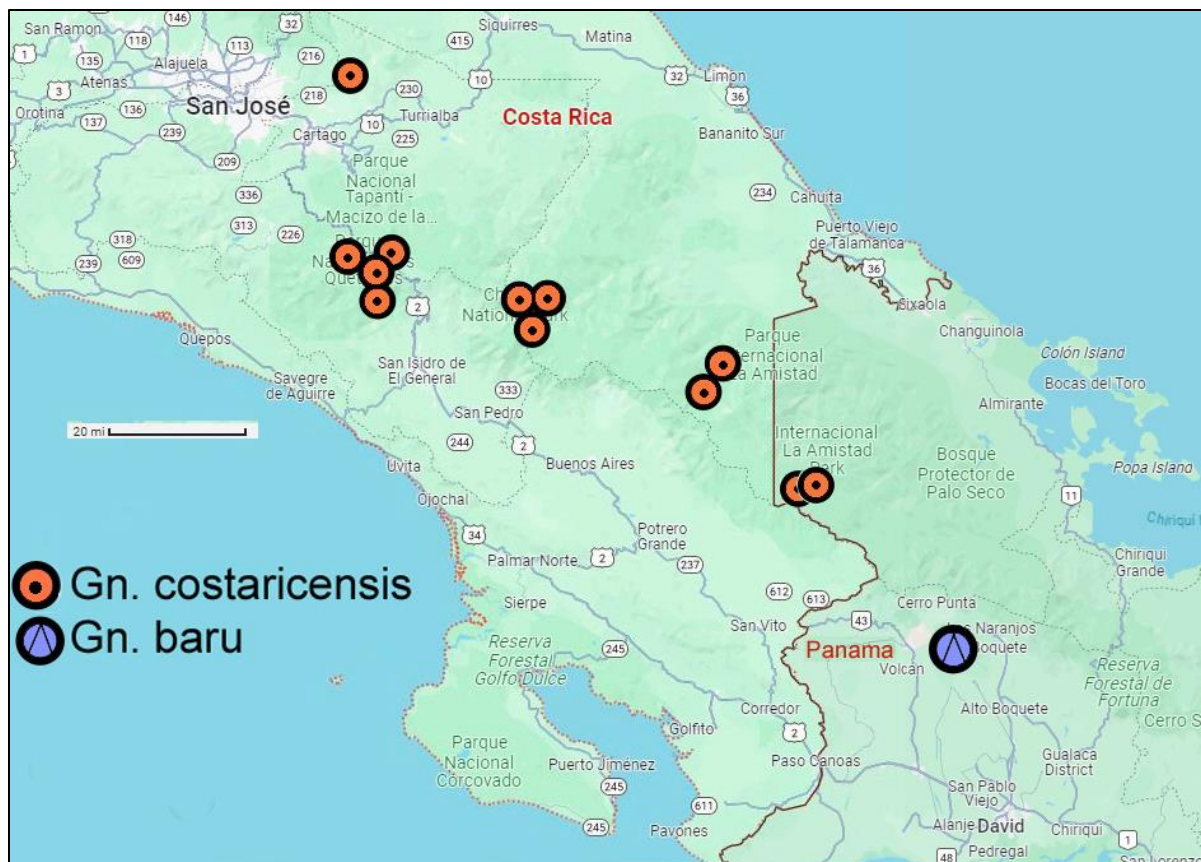
Map 1. Distribution of *Gnaphaliothamnus salicifolius* and *G. durangensis*. The southernmost locality for *G. salicifolius* is in Honduras, the record cited in the text.



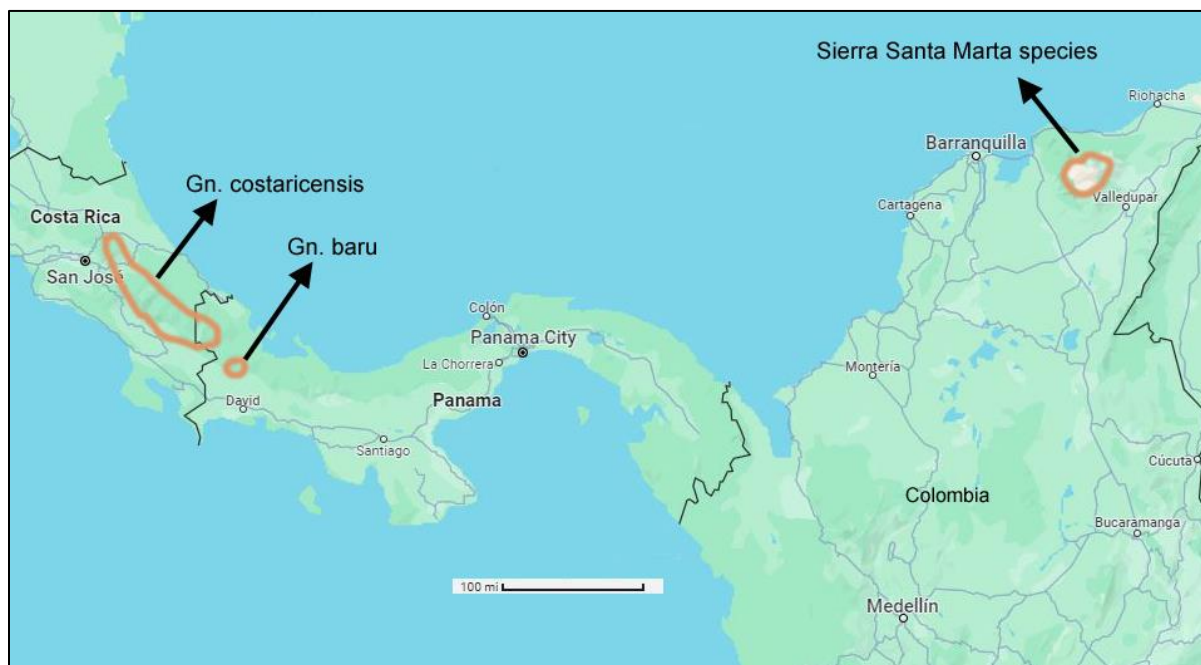
Map 2. Distribution of *Gnaphaliothamnus concinnus*, *G. mexicanus*, *G. lavandulifolius*, *G. sartorii*, *G. macdonaldii*, *G. nesomii*, *G. monanthus*, and *G. cryptocephalus*. The inset for *G. aecidiocephalus* and *G. eleagnoides* is enlarged in Map 3.



Map 3. Distribution of *Gnaphaliothamnus acidioccephalus* and *G. eleagnoides*, central Oaxaca.



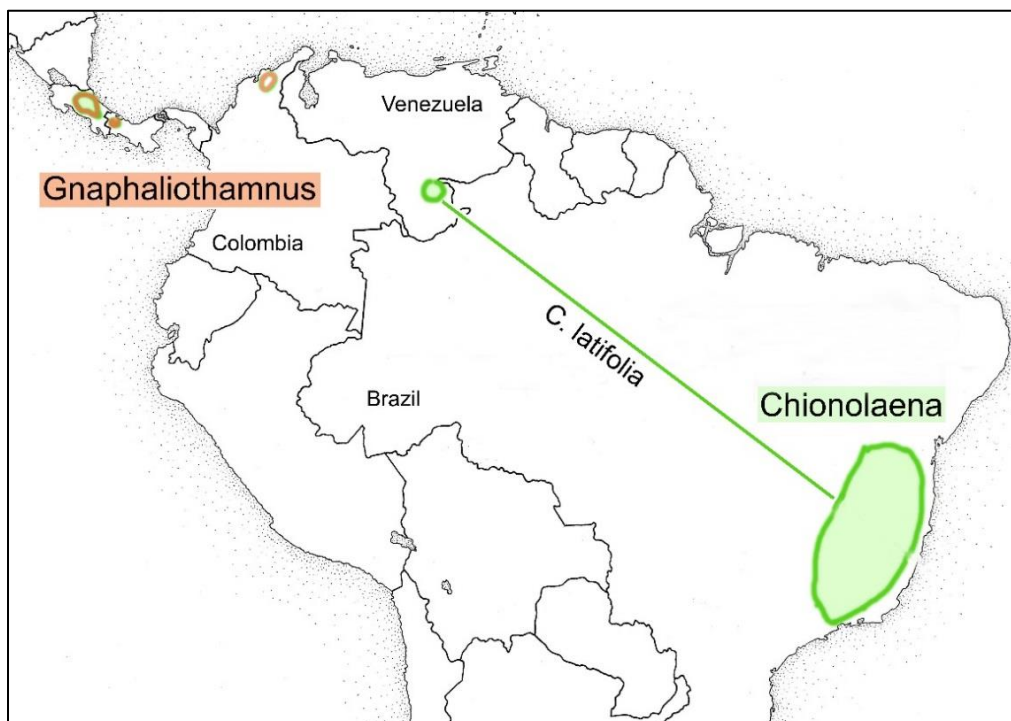
Map 4. Distribution of *Gnaphaliothamnus costaricensis* and *G. baru*.



Map 5. Distribution of *Gnaphaliothamnus costaricensis*, *G. baru*, and the species of the Sierra de Santa Marta — *G. barclayae*, *G. chrysocoma*, *G. columbianus*.



Map 6. Colombia (northern South America), showing location of the Sierra de Santa Marta.



Map 7. Distribution of the southernmost species of *Gnaphaliothamnus* and those of *Chionolaena*. All 12 species of *Chionolaena* sensu stricto are restricted to southeastern Brazil, except *C. latifolia*, which population systems disjunct between southeastern Brazil and the area of Cerro Marahuaca, Venezuela.



Figure 1. *Gnaphaliothamnus aecidiocephalus*. Oaxaca, Mpio. Santiago Comaltepec, Sierra Juarez along Hwy 175, 14 March 2020, iNaturalist photo by Michael Sundue.

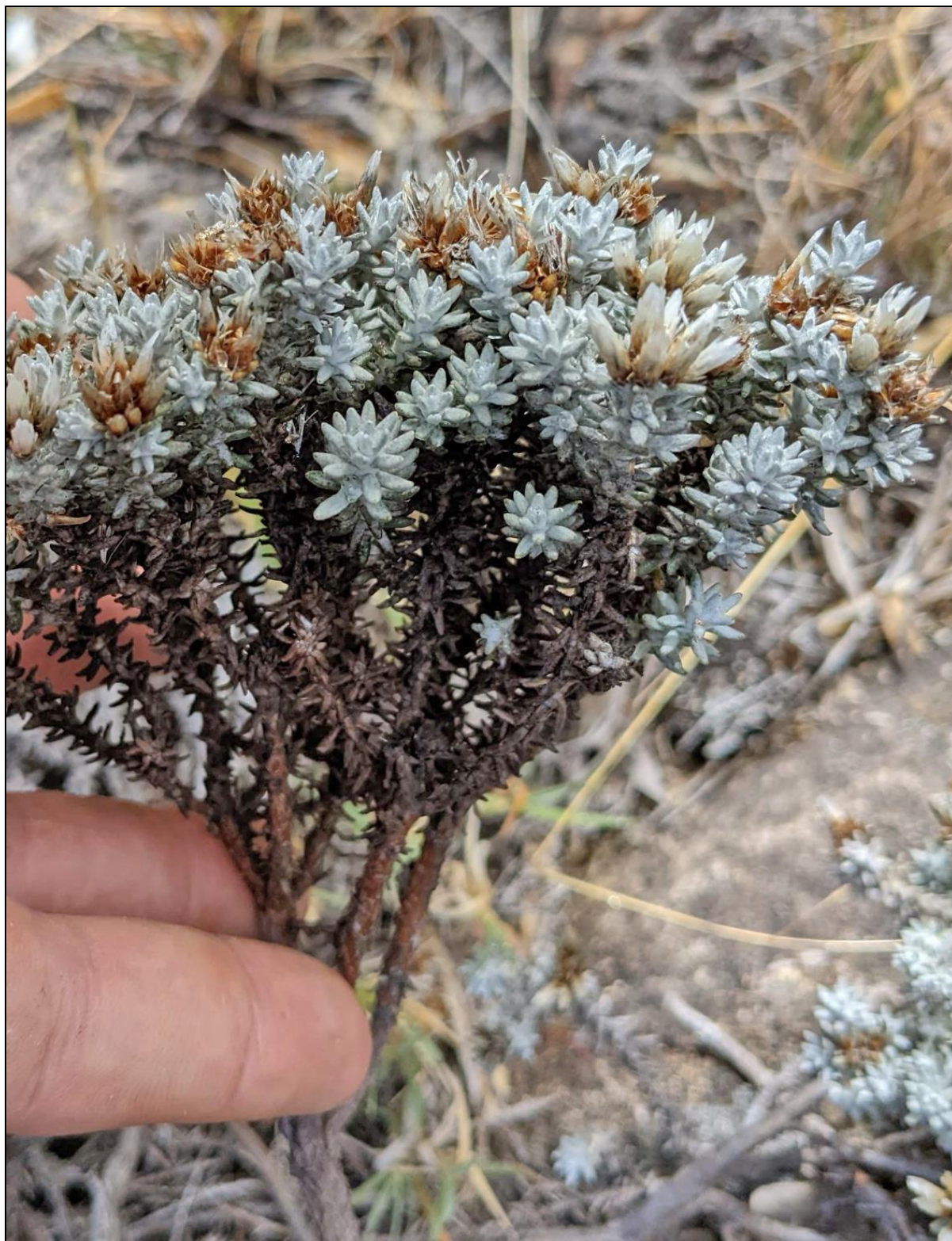


Figure 2. *Gnaphaliothamnus costaricensis*. Costa Rica, Parque Nacional Chirripó, 12 January 2022, iNaturalist photo by Chloe and Trevor Van Loon.



Figure 3. *Gnaphaliothamnus costaricensis*. Costa Rica, Parque Nacional Chirripó, 12 January 2022, iNaturalist photo by Chloe and Trevor Van Loon.



Figure 4. *Gnaphaliothamnus costaricensis*. Costa Rica, Parque Nacional Chirripó, 12 January 2022, iNaturalist photo by Chloe and Trevor Van Loon.



Figure 5. *Gnaphaliothamnus lavandulifolius*. Edo. México, Nevado de Toluca, 20 September 2022, iNaturalist photo by "Lemex" (Sergio).



Figure 6. *Gnaphaliothamnus lavandulifolius*. Edo. México, Nevado de Toluca, 20 September 2022, iNaturalist photo by "Lemex" (Sergio).



Figure 7. *Gnaphaliothamnus lavandulifolius*. Edo. México, Nevado de Toluca, 28 July 2013, iNaturalist photo by "annemirdl" (Anne).



Figure 8. *Gnaphaliothamnus mexicanus*. Hidalgo, El Chico National Park, 15 January 2023, iNaturalist photo by "henicorhina" [Oscar Johnson].



Figure 9. *Gnaphaliothamnus mexicanus*. Hidalgo, El Chico National Park, 15 January 2023, iNaturalist photo by "henicorhina" [Oscar Johnson].



Figure 10. *Gnaphaliothamnus salicifolius*. Hidalgo, Sierra de las Navajas (part of Sierra de Pachuca), 15 January 2023, iNaturalist photo by "henicorhina" [Oscar Johnson].



Figure 11. *Gnaphaliothamnus salicifolius*. Hidalgo, Sierra de las Navajas (part of Sierra de Pachuca), 15 January 2023, iNaturalist photo by "henicorhina" [Oscar Johnson].

1. **GNAPHALIOTHAMNUS AECIDIOCEPHALUS** (Grierson) Nesom, *Phytologia* 68: 373. 1990. *Anaphalis aecidiocephala* Grierson, *Notes Roy. Bot. Gard. Edinburgh* 31: 389. 1972. *Gnaphalium aecidiocephalum* (Grierson) L.O. Williams, *Phytologia* 25: 459. 1973. *Chionolaena aecidiocephala* (Grierson) Anderberg & Freire, *Notes Roy. Bot. Gard. Edinburgh* 46: 37. 1989. **TYPE: MEXICO. Oaxaca.** Ixtlán, Comaltepec, Cerro de Humo Chico, in grass in sun, 3050 m, 2 Mar 1968, *T.B. MacDougall 4129* (holotype: E; isotypes: F, MEXU, S).

Oaxaca, in the Cerro del Humo Chico of the Sierra Juárez and on Cerro Pelón. Subalpine pine woodland and heath; 2850-3050 meters. February-April. Figures 1-2.

Gnaphaliothamnus aecidiocephalus is distinguished by its low habit, small, crowded, deflexed-imbriate, eglandular leaves, red phyllaries with long, white tips, and dioecious sexual condition.

Additional, representative collections. **Oaxaca.** Ixtlán, Mpio. Comaltepec, Cerro de Humo Chico, 3240 m, 8 Feb 1966, *MacDougall s.n.* (MEXU); 40 mi S of Valle Nacional, Hwy 175, above road on rocky hill with *Pinus*, *Oxylobus*, and various grasses, common ascending perennial to 30 cm, 22 Mar 1978, *Poole et al. 1286* (MEXU); Cerro Pelón, ca. 48 km N de Ixtlán por la carretera a Valle Nacional, matorral esclerófilo y bosque de *Pinus rudis*, 2900 m, 2 Feb 1992, *Zamudio R. 8384* (MEXU).

2. **GNAPHALIOTHAMNUS BARCLAYAE** (H. Rob.) Nesom, **comb. nov.** *Chionolaena barclayae* H. Rob., *PhytoKeys* 46: 69. 2015. **TYPE: COLOMBIA. Dpto. Magdalena.** Sierra Nevada de Santa Marta, alrededores de cabeceras de Río Ancho, Páramo de Macotama, high outcrops of bedrock, above and W of second lake, above valley of Río Ancho, Sta. 15, 4900-5000 m, 17 Feb 1959, *H. Barclay 7072* (holotype: US). Figure 3.

Subshrubs to 20 cm tall with short, closely appressed and densely overlapping, gray-concolor leaves, 1-3 heads sessile or subsessile at the branch tips, and glabrous achenes. Pistillate florets ca. 20+, bisexual florets 3-6. Known only from the type collection.

3. **GNAPHALIOTHAMNUS BARU** Nesom, **sp. nov.** **TYPE: PANAMA. Prov. Chiriquí.** Camino de acceso al Parque Nacional Volcán Barú (vertiente oriental), 2950 m, 25 Jun 1991, *M. Vega 183* (holotype: US). Figures 4-6.

Similar to *Gnaphaliothamnus salicifolius* in its congested, linear, bicolor, eglandular leaves and heads above the level of the leaves, and oblong, white phyllary apices, but distinct in its narrower leaves (1.5-2 mm vs. 1.5-3(-5) mm wide), epedunculate heads, shorter involucre (4 mm vs. 6-7 mm), more numerous florets (pistillate ca. 85 vs. [22-]34-55, bisexual ca. 17 vs 3-4[-7], bisexual corollas 2 mm long vs. 3.5-4.5 mm).

Perennial subshrubs. **Stems** ca. 25 cm tall, persistently tomentose with white, matted hairs, eglandular. **Leaves** at congested nodes, linear, mostly 3-6 cm long, 1.5-2 mm wide, margins flat or barely revolute, base not ampliate or clasping, slightly decurrent (1 mm), apex acute, strongly bicolor, adaxial surface sparsely tomentose but quickly glabrescent and then glabrous, eglandular, abaxially persistently matted-tomentose with white hairs. **Heads** epedunculate, compactly congested in a terminal cluster of ca. 25-30, well above the level of the leaves; phyllaries in 3-4 series, inner 4 mm long, stereome brown, apex narrowly oblong, white, without red coloration. **Pistillate florets** ca. 85. **Bisexual florets** ca. 17, corollas 2 mm long. **Achenes** sparsely hairy with short trichomes, mature size not seen; pappus bristles not apically thickened.

Known only from the type collection.

4. **GNAPHALIOTHAMNUS CHRYSOCOMA** (Wedd.) Nesom, **comb. nov.** *Oligandra chrysocoma* Wedd., Chlor. Andina 1: 158. 1855. *Pseudoligandra chrysocoma* (Wedd.) Dillon & Sagást., Taxon 39: 125. 1990. **TYPE: COLOMBIA.** Prov. de Rio Hacha, Sierra Nevada, 3800-4300 m, Mar 1852, *L.J. Schlim 809* (holotype: P; isotypes: BR, G, K).

Subshrubs to 40 cm high. **Leaves** linear, 4–6 mm long, ascending-erect, appressed to stem, and densely overlapping (nodes not visible), glabrous adaxially, white-matted-tomentose abaxially. **Heads** sessile in dense, terminal clusters barely above the level of the leaves. **Pistillate florets** 4–8. **Bisexual florets** 3–6. **Achenes** glabrous. Known by numerous collections from the Sierra de Santa Marta. Figures 7-9.

5. **GNAPHALIOTHAMNUS COLUMBIANUS** (Blake) Nesom, **comb. nov.** *Chionolaena columbiana* Blake, J. Wash. Acad. Sci. 25: 312. 1935. *Parachionolaena columbiana* (Blake) Dillon & Sagást., Arnaldoa 1: 44. 1992. **TYPE: COLOMBIA. Dpto. Magdalena.** Sierra Nevada de Santa Marta, ca. 30 mi inland from Dibulla, paramos, ca. 4390 m, Jul 1932, *W. Seifriz 494* (holotype: US).

To consider the combination *Parachionolaena columbiana* (Blake) Dillon & Sagást. invalid (as by IPNI, "nom. inval., without exact basionym page contrary to Art. 41.5 ICN (2012)") seems overly technical, as the protologue reference to the original publication and basionym is unambiguous. Dillon and Sagástegui cited "J. Wash. 25: 311–325. 1935."

Subshrubs to 30 cm high. **Heads** in dense clusters on sparsely leafy stems above the portions with densely overlapping leaves. **Leaves** linear-oblong to linear-obovate, 1.3–4.5 mm long, densely tomentose, concolor. **Pistillate florets** 7–9. **Bisexual florets** 6–8. **Achenes** glabrous. Known by numerous collections from the Sierra de Santa Marta. Figures 10-11.

6. **GNAPHALIOTHAMNUS CONCINNUS** (A. Gray) Nesom, Phytologia 68: 374. 1990. *Gnaphalium concinnum* A. Gray, Proc. Amer. Acad. Arts 15: 34. 1879. *Anaphalis concinna* (A. Gray) Grierson, Notes Roy. Bot. Gard. Edinburgh 31: 392. 1972. *Chionolaena concinna* (A. Gray) Anderberg & Freire, Notes Roy. Bot. Gard. Edinburgh 46: 40. 1989. **TYPE: MEXICO. San Luis Potosí.** "In the highest mountains SE of San Luis," 6000-8000 ft, Sep 1878, *C.C. Parry & E. Palmer 423* (holotype: GH; isotypes: BM, E, F, K, PH, VT, YU). Figures 12-13. Anderberg & Freire (1989) and Freire (1993) regarded the GH sheet as the lectotype — it is annotated in Gray's handwriting as "*Gnaphalium* (*Rhodognaphalium*) *concinnum* n. sp."

As interpreted from McVaugh (1956), Palmer made the collection (Parry of "Parry & Palmer" having already returned to the USA) in the Sierra San Miguelito immediately south of Cd. San Luis Potosí, with highest elevation at ca. 8800 feet. J.W. Schaffer had made the first collection of the species there two years earlier. Those two historical collections are the only ones I have seen of this distinctive species. The Sierra San Miguelito was designated in 2021 as a national protected natural area.

Additional collection. San Luis Potosí. Du montibus frigid San Miguelito, Sep 1876, *Schaffner 222* (CM, F, GH-mounted with the Parry & Palmer holotype, MEXU-2 sheets, NY, US-Fig. 14).

Gnaphaliothamnus concinnus is recognized by its densely tomentose vestiture (stems and leaves), weakly bicolor, eglandular, obovate to elliptic-obovate, deflexed leaves, prominently pedicellate heads, persistently tomentose phyllaries, pistillate florets 20–27, bisexual florets 11–27, and relatively long, longitudinally twisted achenial hairs.

7. **GNAPHALIOTHAMNUS COSTARICENSIS** Nesom, *Phytologia* 68: 374. 1990. *Chionolaena costaricensis* (Nesom) Nesom, *Sida* 19: 850. 2001. **TYPE: COSTA RICA. Prov. San Jose.** Cerro Asunción, común en peña rocosa, 1 Sep 1987, *L.J. Pareda A. & J.F. Ciccio 4180* (holotype: TEX; isotype: WIS).

Freire (1993), followed by Pruski (2018), treated these plants within *Chionolaena lavandulifolia*, but in addition to their distant disjunction from the plants of central Mexico, they differ in their shorter and stiffer leaves, smaller and mostly solitary heads with fewer pistillate florets, the pattern of coloration in the phyllaries (stereome and apex), and their glabrous achenes with dimorphic pappus bristles. **Figures 15-17.**

Additional collections. COSTA RICA. Cordillera de Talamanca, Prov. Cartago/San Jose border, paramo vegetation off of the Interamerican Hwy about midway between Cerro Asuncion and Cerro Zacatales, 10 Mar 1981, *Almeda 4839* (US); summit of Volcan Irazú, Apr 1880, *Biolley 90* (GH); Cerro de la Muerte, Talamanca range, 19 Feb 1957, *Carlson 3531* (GH); páramo on Cerro de las Vueltas, along the Pan American hwy ca. 90 km S of Cartago, 10 Nov 1960, *Cronquist & Jiménez M. 8852* (GH, TEX); direct line from Hotel La Georgina to Cerro Frío of the Cerro Buenavista complex (Cerro de la Muerte) area with television and radio towers, on highest peak, rocky glass slope, 20 Sep 1983, *Davidse 25035* (US); Cordillera de Talamanca, peak of Cerro Kámuk, Páramo, on rocks on cliffs, 25 Mar 1984, *Davidse 26003* (TEX, US); Cordillera de Talamanca, Cerro de La Muerte, Pan-American highway 5 km above Millsville (ca. 8 km above Nivel), shrub-paramo, crevice in rocks, 3400-3500 m, 25 Jul 1949, *Holm & Iltis 573* (M, US); Cordillera de Talamanca, Cerro de La Muerte region, near summit of Cerro Sakira, 3415 m, 8 Jan 1985, *Horn 38* (UC, WIS); cúspide del Cerro Asunción, carretera Panamericana Sur, 25 Feb 1965, *Jimenez M. 2967* (F, US); Chirripó Grande, 3450 m, 29 Apr 1932, *Kupper 1301a* (M), 27 Apr 1932, *Kupper 1301* (M), 28 Apr 1932, *Kupper 1148* (M); Cantón Dota, Cerro de la Muerte, la cima del paramo, 24 Jun 2007, *Moran 81454* (US); Cerro de Buena Vista, Volcano Irazú, no date, *Niederlein 3430* (US); in summo monte Irazu, Jan 1847, *Oersted 10570* (F, GH-2 sheets, MO, UC, US); rochers de la region superieure du Cerro de Buena Vista, 19 Jan 1891, *Pittier 3430* (GH); Cerro Buenavista (Cerro de la Muerte), along unpaved road, ca. 0.5 km below summit antennas, páramo with large boulders, *Chusquea* abundant, 9 Sep 2004, *Pruski 3836* (US); rochers de la reg. super. du Cerro de Buena Vista, 19 Jan 1891, *Tonduz 3430* (US); KM 88 S of San José on InterAmerican Hwy, barren hills along Cuesta del Muerte, 8 Aug 1981, *Turner 15038* (TEX); Cerro de Chirriposillo (Cuercil) within ca. 200 m of main summit, 3400 m, 2 Mar 1964, *Weston 1551* (UC); Pico Sureste, S to SW of Cerro Chirripó, rain paramó, 9 Dec 1966, *Weston 3615* (US); Buenavista massif, rocky ground on lower slope of Cerro Frio, 3400 m, 14-16 Mar 1969, *Weston 5877* (UC, US); below Sabana Chirripó, Chirripó massif, 3150 m, 24 Feb 1976, *Weston 10122* (UC). **PANAMA. Prov. Chiriquí.** Bocas del Toro, ridges to E of Cerro Fábrega, 09° 06' 20" N, 82° 52' 26" W, bamboo dominated subpáramo, 3300 m, shrublet on rocks, 16 Mar 2006, *Knapp & Monro 10045* (MO); Bocas del Toro, Cerro Fábrega, ca. 1 km SE of peak, transition zone between oak-dominated forest and subparamo grass-dominated vegetation with many shrubs and small trees to 6 ft, many large patches of bamboo, 3300 m, shrublet on rock, rare, 12 Mar 2003, *Monro et al. 4113* (MO).

8. **GNAPHALIOTHAMNUS CRYPTOCEPHALUS** Nesom, *Phytologia* 68: 375. 1990. *Chionolaena cryptocephala* (Nesom) Nesom, *Sida* 19: 850. 2001. **TYPE: MEXICO. Chiapas.** Mpio. Unión Juárez, near the summit of Volcán Tacaná, small meadow with scattered dwarfed *Pinus*, 3800 m, 3 Mar 1972, *D.E. Breedlove 24347* (holotype: TEX; isotype: MEXU). Figure 18.

Gnaphaliothamnus cryptocephalus is similar to *G. lavandulifolius*, *G. macdonaldii*, and *G. costaricensis* in its short, narrow, adaxially glandular leaves. It resembles *G. lavandulifolius* in its nearly monomorphic pappus bristles but is distinct from all in its shorter phyllaries without white-oblong tips, fewer functionally staminate florets with shorter corollas, and fewer pappus bristles. Known only from Volcán Tacaná. **Figures 18-19.**

Additional collection. Chiapas. Mpio. Unión Juárez: SE side of the summit of Volcán Tacaná, flat meadows and steep slopes with *Pinus*, *Juniperus*, and *Buddleia*, 3600 m, 10 Nov 1972, *Breedlove* 29375 (MEXU); en el crater del Volcán Tacaná, 4000-4100 m, paramo de altura con *Pinus*, 9 May 1987, *Martínez S.* 20864 (MEXU).

- 9. GNAPHALIOTHAMNUS DURANGENSIS** Nesom, *Phytologia* 69: 1. 1990. *Chionolaena durangensis* (Nesom) Nesom, *Sida* 19: 850. 2001. **TYPE: MEXICO. Durango.** Mpio. Durango, 65-75 km SW of Cd. Durango on road to La Flor, high ridge with meadows and forests of *Pinus*, *Quercus*, and *Pseudotsuga*, 2620 m, 17 Sep 1979, *D.E. Breedlove* 44285 (holotype: MEXU; isotype: CAS-Figs. 21-22).

Gnaphaliothamnus durangensis is distinct in its strongly bicolor, elliptic-obovate leaves with eglandular adaxial surfaces, relatively few heads barely above the level of the leaves, ovate phyllaries, the outer apically sometimes pinkish and not indurate-opaque or narrowed into an appendage-like extension, and pappus bristles with only slightly dimorphic apices. Known only from the type collection.

- 10. GNAPHALIOTHAMNUS ELEAGNOIDES** (Klatt) Nesom, *Phytologia* 68: 376. 1990. *Chionolaena eleagnoides* Klatt, *Leopoldina* 23: 88. 1887. *Gnaphalium hypochionaeum* Schultz-Bip. ex Klatt, *Leopoldina* 23: 88. 1887 [nom. nudum, as a synonym of *Chionolaena eleagnoides*]. *Gnaphalium eleagnoides* (Klatt) S.F. Blake, *Contr. U.S. Natl. Herb.* 23: 1511. 1926. **TYPE: MEXICO. Oaxaca.** [Mpio. Ixtlán de Juárez]: Pelado [Cerro Pelado], Aug 1841, *F.M Liebmann* 316 (holotype: C, Fig. 22; isotypes: GH ex herb. Klatt-drawing of C plant and fragment, US-photo of C plant and fragment).

Recognized by its obovate to oblanceolate, strongly bicolor leaves with eglandular adaxial surfaces, heads in compact corymbs above the level of the leaves, pistillate florets 16–20, bisexual florets 7–18, and strongly dimorphic, basally persistent pappus bristles.

Oaxaca, mostly on Cerro Pelón and Sierra Juárez. Oak forest, with scattered pines, secondary woods, matorral of Ericaceae; 2850-3000 m. November-March (-July) or probably all year. Figures 23-26.

Collections have been made primarily in two areas (Map 3): (a) around Cerro Pelón and (b) in the Sierra de Juárez. Liebmann's type collection was made at Cerro Pelado, essentially between (a) and (b). Leaf shape varies from broadly to narrowly obovate to oblanceolate but the range of variability is similar in each area.

(a) Cerro Pelón: *Gallardo H.* 1252, 1263, and 1788 (MEXU); *Rzedowski* 28858 (TEX); *Villasenor* 1240 (MEXU).

(b) Sierra de Juárez: *Cronquist* 9645 (MEXU, TEX, US); *Gallardo H.* 1788 (MEXU); *Holmes* 4536 (TEX); *Martínez Calderon* 941 (MEXU); *Trigos* 652 (MEXU); *Turner* 80-A-40 (TEX); *Yahara* 2349 (MEXU).

MacDougall made collections of typical *Gnaphaliothamnus eleagnoides* on Cerro de Humo Chico (3240 m, 8 Feb 1966, *Dougall s.n.*-US; ca. 10,000 ft, 27 Jan 1967, *Dougall* 87-US). He also made mixed collections (27 Jan 1963, *Dougall s.n.*-MEXU-2 sheets; 8 Feb 1966, *Dougall s.n.*-US) that included branches of aff. *G. eleagnoides* and branches of what appear to be *G. aecidiocephalus* with influence of *G. eleagnoides* (Fig. 27). Those of *G. eleagnoides* have heads with 12–13 staminate florets and 11–13 pistillate florets. Those of *G. >aecidiocephalus* have leaves of intermediate size and descending like that species and heads with 22–28 staminate florets and 0–3 pistillate florets. The type collection of *G. aecidiocephalus* was made on Cerro Humo Chico, and it has been collected in typical morphology at other localities in the Sierra de Juárez as well with *G. eleagnoides* on Cerro Pelón. More detailed comments on these putative hybrids are in Nesom (1990c).

11. **GNAPHALIOTHAMNUS LAVANDULIFOLIUS** (Kunth) Nesom, *Phytologia* 68: 377. 1990. *Helichrysum lavandulifolium* Kunth [as *Elychrysum lavandulaefolium*], *Nov. Gen. & Sp.* 4[folio]: 68. 1818. *Gnaphalium lavandulaceum* DC., *Prodr.* 6: 227. 1837 [nom. nov., not *Gnaphalium lavandulifolium* Willd. 1803 = *Helichrysum lavandulifolium* (Willd.) D. Don. 1826 = *Helichrysum graveolens* (M. Bieb.) Sweet]. *Chionolaena lavandulaceum* (DC.) Hemsley [nom. illegit.], *Prodr. Biol. Centr. Amer., Bot.* 2: 134. 1881. *Chionolaena lavandulifolia* (Kunth) Benth. & Hook. f. ex B.D. Jackson, *Index Kew.* 1: 516. 1893. *Gnaphalium lavandulifolium* (Kunth) S.F. Blake, *Contr. Gray Herb.* n.s. 52: 21. 1917 [nom. illegit., not *Gnaphalium lavandulifolium* Willd. 1803]. **TYPE: MEXICO. [Veracruz].** "Crescit in frigidis Andium Mexicanorum in nobilissimo monte Nauhcampatepetle juxta urbem Perote," alt. 1720 hex, Mar 1804, A. *Humboldt s.n.* (holotype: P; probable isotypes: GH-fragment, HAL-ex herb. Willdenow).

Veracruz, Puebla, Tlaxcala, and Edo. México, on volcanic peaks of Perote, Orizaba, Malinche, Ixtaccihuatl, Popocatepetl, Tláloc, and Nevado de Toluca. Cliffs or slopes of bare rock and talus, gravelly or sandy soil among boulders, rock outcrops in alpine meadows, sometimes with scattered junipers or above timberline; 4000-4300 meters. (May-) June-October. Figures 28-30.

Gnaphaliothamnus lavandulifolius is recognized by its low habit (1–2(–3) cm tall), short (7–12 mm long), narrowly oblong, weakly bicolor leaves stipitate-glandular beneath the tomentum, heads in sessile, terminal clusters of 2–5, lanceolate-triangular phyllaries, pistillate florets 21–24, bisexual florets 9–19, and monomorphic pappus bristles. See comments for *Gnaphaliothamnus sartorii*.

12. **GNAPHALIOTHAMNUS MACDONALDII** Nesom, *Phytologia* 68: 378. 1990. *Chionolaena macdonaldii* (Nesom) Nesom, *Sida* 19: 850. 2001. **TYPE: MEXICO. Oaxaca.** Cerro Quiexobra and vicinity, 35 km ESE of Miahuatlán, 5 km NE of Santo Domingo Ozolotepec, 16° 10' N, 96° 15' W, timberline vegetation in open glades along ridges and in mountain "saddles," dominated below by pine forest, 3650-3800 m, rare, on the driest and most exposed rock outcrops, 10 Dec 1989, A. *McDonald 2943* (holotype: TEX; isotypes: F, MEXU, NY, US). Figures 31-34.

Gnaphaliothamnus macdonaldii is similar to the wider-ranging *G. lavandulifolius* and the narrowly endemic *G. costaricensis* and also *G. cryptocephalus* in its short leaves tomentose-glabrescent above with an understory of stipitate-glandular hairs. It is distinct from *G. lavandulifolius* in its lanceolate-triangular phyllaries glabrous or usually with numerous, minute, appressed, viscid, elongate hairs (vs. sparsely to moderately villous-tomentose), pistillate and functionally staminate florets both 12–18 per head, relatively long achenes (1.8–2 mm), and dimorphic pappus bristles. Known only from the type collection.

13. **GNAPHALIOTHAMNUS MEXICANUS** (Freire) Nesom, **comb. nov.** *Chionolaena mexicana* Freire, *Ann. Missouri Bot. Garden* 80: 427. 1993. **TYPE: MEXICO. Hidalgo.** Sierra de Pachuca, ledges, 10,000 ft, 20 Feb 1899, *C.G. Pringle 7700* (holotype: K; isotypes: GH, US). Figures 35-36.

Earlier (Nesom 1994), I placed *Chionolaena mexicana* Freire in synonymy with *Gnaphaliothamnus concinnus*, but Freire's assessment was correct. It is a distinctive species apparently endemic to the Sierra de Pachuca (all populations probably within Parque Nacional El Chico) at 2900-3050 meters elevation. It is distinct in its weakly bicolor (grayish, persistently tomentose on both surfaces, more densely and whiter abaxially), narrowly oblong to narrowly oblong-oblong leaves and heads in sessile and terminal corymbs on the distal branches and hardly above the level of the leaves, pistillate florets 14-15, and disc (functionally staminate) florets ca. 11. Figures 35-38.

Additional collections. **Hidalgo.** Mpio. Mineral del Chico. Sierra de Pachuca. Cerro de las Ventanas, fir forest, 2900-3000 m, 16 May 1981, *Gentry et al.* 32162 (MEXU); Cerro de las Ventanas, 6 km N de Pachuca, bosque de *Abies religiosa*, con manchones de matorral de *Juniperus*, 3000 m, 31 Dec 1963, *Rzedowski* 18220 (MEXU); Cerro de las Ventanas, bosque de *Abies* y claros adyacentes, 2900 m, 16 May 1981, *Rzedowski* 37269 (MEXU).

Typical *Gnaphaliothamnus salicifolius* also occurs in the area of Cd. Pachuca, but at lower elevations than *G. mexicanus*: Vicinity of Mineral del Monte, along Hwy 105 between Pachuca and Tampico, 8 mi E of Pachuca, 3.8 mi W of Guerrero, 5.7 mi. SW of Omitlan, 27 Feb 1987, *Croat* 65792 (MEXU); Mpio. Mineral del Chico, extremo occidental de las Sierra de Pachuca, 2860 m, 2 Feb 2006, *Rodríguez C.* 4 (MEXU). Also see iNaturalist photos above (Figs. 8 and 9—*G. mexicanus*, and Figs. 10 and 11—*G. salicifolius*) from the Sierra de Pachuca.

14. GNAPHALIOTHAMNUS MONANTHUS Nesom, **sp. nov.** **TYPE: GUATEMALA.** [Dept. Huehuetenango.] Sierra de los Cuchumatanes, La Torre, *Juniperus* forest, 3700 m, 18 Jun 1992, *G. Islebe* and *R. Hübner* 1575 (holotype: US). Figures 39-40.

Similar to *Gnaphaliothamnus lavandulifolius* in its low habit, short, linear-oblong, concolor leaves, and ovate to lanceolate-triangular phyllaries; distinct in its large, solitary, sessile heads barely above the level of the leaves.

Perennial subshrubs, probably forming clonal mats from thin, woody rhizome-like caudex branches with persistent, old leaf bases. **Stems** 4–6 cm long, not visible among the leaves, densely and persistently gray-tomentose, eglandular. **Leaves** linear-oblong, congested (internodes not evident), not clasping or decurrent, 5–7 mm long, 1–1.5 mm wide, margins revolute, apex acute, densely gray-woolly-tomentose, concolor, eglandular. **Heads** evidently solitary, sessile, terminal and imbedded in the distalmost leaves. **Phyllaries** in 5–6 series, ovate to ovate-lanceolate, apex acute, longest 7 mm, stereome brown, gradually lightening to a whitish distal zone. **Florets** not counted. **Achenes** not seen.

Because of the paucity of material, after confirming that it is a species of *Gnaphaliothamnus*, I have not opened the single mature head on the type sheet. The overall habit, solitary heads, and phyllary morphology, however, indicate this collection as representative of an undescribed species with similarities to *G. lavandulifolius*. The other Sierra Cuchumatanes endemic, *G. nesomii*, is more similar to *G. salicifolius*.

15. GNAPHALIOTHAMNUS NESOMII Dillon & Luebert, *J. Bot. Res. Inst. Texas* 9: 64. 2015. **TYPE: GUATEMALA.** **Dept. Huehuetenango.** Sierra Cuchumatanes, common on moist bank along road to San Juan Ixcoy, 12-23 Jun 1966, *A. Molina R. et al.* 16441 (holotype: F; isotypes: NY, US). Figure 41.

Distinct in its low habit (5–15 cm tall), bicolor, narrowly oblanceolate (1–4 cm long) leaves, small heads (involucre 5–7 mm long), heads in corymbs well above the leaves, phyllaries with a white-oblong apex, pistillate florets 20–32, functionally staminate florets 13–15, and strongly dimorphic pappus bristles. With its phyllary morphology and corymbose-clustered heads, this species probably is closely related to *Gnaphaliothamnus salicifolius*. Endemic to the Sierra Cuchumatanes of southwestern Guatemala.

16. GNAPHALIOTHAMNUS SALICIFOLIUS (Bertol.) Nesom, *Phytologia* 68: 378. 1990. *Helichrysum salicifolium* Bertol. in Alessandrini, *Nuovi Ann. Sci. Nat.* 3: 139. 1840. *Gnaphalium salicifolium* (Bertol.) Schultz-Bip., *Bot. Zeit.* 3: 172. 1845. *Chionolaena salicifolia* (Bertol.) Nesom, *Sida* 19: 850. 2001. **TYPE: GUATEMALA.** [Protologue: "Vulcan d'acqua," no other collection data]. **[Dept. Sacatepéquez/Escuintla].** Volcán de Agua, *J. Velasquez s.n.* (holotype: BOLO, fide Baldini et al (2019); isotype: US-fragment from Herbarium Bertololini

[BOLO] obtained in 1925 by S.F. Blake). Modern collections of *G. salicifolius* have been made from the Volcán de Agua.

Gnaphalium seemannii Schultz-Bip. in Seem., Bot. Voy. Herald 7-8, 309. 1856. *Chionolaena seemannii* (Schultz-Bip.) Freire, Ann. Missouri Bot. Gard. 80: 432. 1993. **TYPE: MEXICO. [Durango].** Sierra Madre, NW Mexico, *B. Seemann 1994* (holotype: K). Figure 42.

Seemann traveled from Mazatlán to Cd. Durango in late November and early December 1849, essentially along the route now followed by Highway 40 (Seeman 1853). I have seen three other collections of *Gnaphaliothamnus salicifolius* from Durango, each from along this route: 34.2 mi W of El Salto on road to Mazatlán (Hwy 40), 2 mi W of Buenos Aires at overlook and bridge called Puerto Buenos Aires, 14 Mar 1984, *Ayers & Scott 339* (TEX); 2 km W de Neveros, brecha a la Ventana, bosque de pino-encino, 2540 m, 10 Mar 1984, *Tenorio L. 8204* (MEXU, **Fig. 0**); 60 mi W of El Salto, 9.8 mi W of village of La Fragüita, 18 Mar 1982, *Turner 15076* (TEX)

Gnaphalium rhodanthum Schultz-Bip. in Seemann, Bot. Voy. Herald, 310. 1856. *Gnaphaliothamnus rhodanthus* (Schultz-Bip.) Kirpichn., Trudy Bot. Inst. Akad. Nauk SSSR, Ser. 1, Fl. Sist. Vyss. Rast. 9: 33. 1950. **LECTOTYPE** (designated here): **MEXICO. Chiapas.** Jitotole, in pinetis, 6900 ft, Mar 1840, *J.J. Linden 437* (K-K000222204; isolectotype: BR-531 875).

Schultz cited two collections — the Linden specimen is chosen as the lectotype because it is the only one that I have been able to see (via images, JSTOR Plants). The other — **Mexico. Hidalgo.** Prope el Sumate [Peña del Zumate, vicinity of El Chico and Real del Monte], 11,000 ft, *C.A. Ehrenberg 332* (B?). Freire (in 1989, by annotation) regarded *Pringle 6115* from Oaxaca in 1894 as the type of *Gnaphalium rhodanthum*.

Chionolaena corymbosa Hemsley, Diagn. Pl. Nov. 2: 32. 1879. **TYPE: MEXICO. [Durango].** Sierra Madre, NW Mexico, *B. Seemann 1994* (holotype: K). Homotypic with *Gnaphaliothamnus seemannii*.

Gnaphaliothamnus salicifolius is recognized by its long, mostly linear, eglandular, bicolor leaves, heads in corymbs above the leaves, large number of pistillate florets (pistillate (22–)34–55, bisexual 3–4(–7)), and basally caducous, slightly dimorphic pappus bristles. Figures 42–48.

Durango, Jalisco, Michoacán, Guerrero, Edo. México, Morelos, Hidalgo, Veracruz, Puebla, Oaxaca, and Chiapas, Guatemala, Honduras. Steep rocky slopes, ledges, ridges, openings in oak, pine, or fir woods, evergreen cloud forests in Chiapas and Guatemala; (2150–) 2500–3500 (–4100) meters. Mostly October–March.

Gnaphaliothamnus salicifolius is the most widespread and ecologically variable species in the genus — it commonly occurs at high elevations but also in a lower range of elevations than most of the other species. Similarities in vestiture and inflorescence to *G. eleagnoides* suggest a close relationship.

- | | |
|--|--------------------------------------|
| 1. Leaves linear, 2–8 cm long, 1–3(–5) mm wide; pistillate florets (22–)34–55, bisexual florets 3–4(–7); pappus bristles slightly dimorphic, basally caducous | Gnaphaliothamnus salicifolius |
| 1. Leaves obovate to oblanceolate, 1.5–4 cm long, 4–8 mm wide; pistillate florets 16–20, bisexual florets 7–18; pappus bristles strongly dimorphic, basally persistent | Gnaphaliothamnus eleagnoides |

Plants of the apparently disjunct population system around Cerro Teotepec in Guerrero are not outside the morphological range of those from within the main range of *Gnaphaliothamnus salicifolius*. **Guerrero.** Dpto. Galeana, Teotepec, pine forest, 3300 m, 25 Dec 1937, *Hinton 11120* (LL, US); Mpio de Tlacotepec, vertiente SW del Cerro Teotepec, ladera granítica con vegetación de bosque abieto de *Pinus* y *Abies* con abundantes gramíneas, 29 Jan 1965, *Rzedowski & McVaugh 225* (MEXU, TEX); 132.4 km SW of Mex 95 junction, on the way from 33 km N point of Chilpancingo to Atoyac, 17° 27' 41" N, 100° 08' 42" W [area of Cerro Teotepec], open place at bottom of cliff, 3065 m, 4 Dec 2003, *Yahara et al. 2946* (MEXU).

The record for Honduras: Dpto. Lampira, Parque Nacional de Celaque, camino entre la montaña El Mojon y San Manuel Colohete, 14° 32' N, 88° 41' W, bosque [asdfsas] de coníferas y latifoliados, 3600 m, 15 Nov 1991, *House 1127* (MO).

Robinson (2015) identified two collections from the Sierra de Santa Marta in Columbia as *Gnaphaliothamnus salicifolius* — **Dpto. Magdalena**. Sierra Nevada de Santa Marta, on trail above San Pedro de la Sierra, paramo, 3900 m, 29 Dec 1974, *Robins & Kirby 618A* (OXF), *Robins 618B* (OXF, US-fragment). I have not been able to see the specimens, but they surely (99%) represent an undescribed species, joining the 3 others already known from there. Robinson noted that "The specimens differ from Mexican and Central American material examined of the species only in having glabrous achenes" but it seems likely that the phyllary morphology will prove to be closer to that of *G. costaricensis*, *G. monanthus*, and the three known species from the Sierra de Santa Marta.

17. GNAPHALIOTHAMNUS SARTORII (Klatt) Nesom, *Phytologia* 68: 379. 1990. *Chionolaena sartorii* Klatt, *Leopoldina* 23: 89. 1887. *Gnaphalium sartorii* (Klatt) Espinosa-Garcia, *Bol. Soc. Bot. Mexico* 45: 21. 1984. **TYPE: MEXICO. [Oaxaca].** [Cerro] Zempoaltepec [as "Sempoaltepec"], Jun 1942, *F.M. Liebman 308* (possible holotype: C-Figs. 49-50; isotype: GH ex herb. Klatt-drawing of C plants and fragment).

The protologue has this — "2. *Chionolaena Sartorii* F.W. Klatt. (*Gnaphalium Sartorii* Schultz-Bip.)" — with Klatt perhaps crediting Schultz with the description but giving authorship to himself. Similarly, in the same article, Klatt also described *Chionolaena eleagnoides* and parenthetically gave the otherwise unpublished "*Gnaphalium hypochionaeum* Schultz-Bip." as an apparent synonym.

Known only from the type collection, which is the only collection of *Gnaphaliothamnus* I have seen from Cerro Zempoaltepec. Recognized by its small stature, narrow, eglandular leaves (Klatt's description), narrow, subequal phyllaries, and (Klatt's count) 15 pistillate florets and 6 bisexual.

The collection of *Gnaphaliothamnus sartorii* alluded to by the epithet is a collection by *C.H.W. Sartorius* from 10,000 feet in Veracruz (*Sartorius s.n.*, P 1816305) — it is *G. lavandulifolius*. The two taxa are a good match in overall aspect, but heads of *G. lavandulifolius* have 21–24 pistillate florets, 9–19 bisexual florets. The heads of the type collection of *Chionolaena sartorii* are old and fragmenting (Klatt's floret counts from a head missing florets?) and the glandularity of *G. lavandulifolius* is often hidden beneath the tomentum — the Oaxacan plants might prove to be conspecific with *G. lavandulifolius*. The geographic disjunction, however, is consistent with the apparent evolutionary differentiation.

Mexerion -- summary and update

Mexerion (Nesom 1990a) includes two species endemic to Mexico and a third, added here, from the Sierra Cuchumatanes of Guatemala.

Anderberg and Freire (1991) placed *Mexerion sarmentosum* as a synonym of the Argentinian-Andean species *Luciliocline santanica* (Cabrera) Anderb. & Freire. Then, based on molecular data, Freire et al. (2015) placed the genus *Luciliocline* as a synonym of *Mniodes* and further studies have confirmed that taxonomy. *Mexerion sarmentosum*, however, is distinct from *Luciliocline santanica* (e.g., Smissen et al. 2020), and *Mexerion* has been recognized as a genus of two species by Luebert et al. (2017). As noted above, *Mexerion* is the evolutionary sister of *Gnaphaliothamnus*.

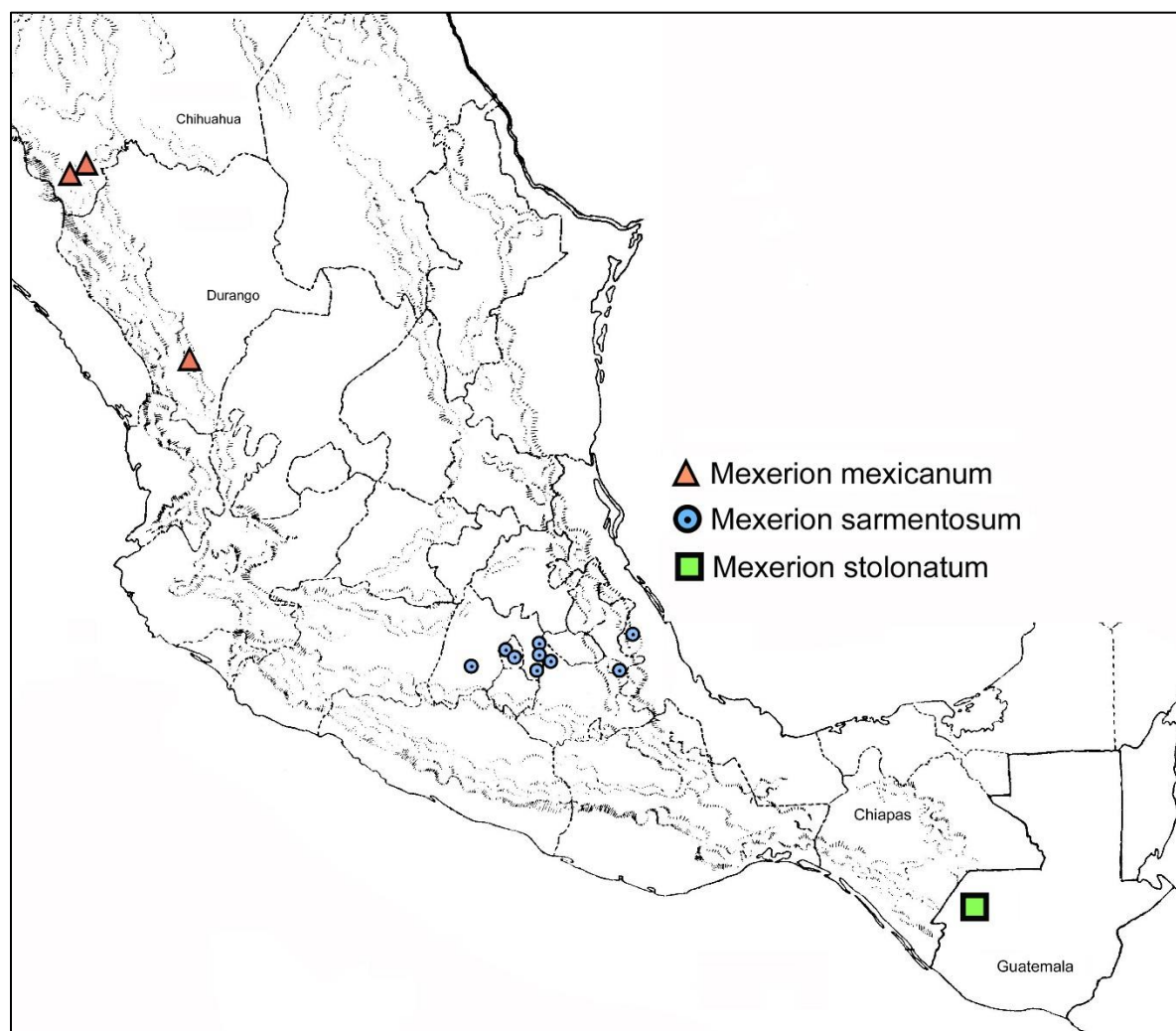
MEXERION Nesom, *Phytologia* 68: 252. 1990. **TYPE SPECIES:** *Mexerion* (*Gnaphalium*) *sarmentosum* (Klatt) Nesom

Perennial herbs, producing slender, leafy stolons from the base. **Stems** erect and unbranched below the heads. **Leaves** weakly bicolor, greenish glabrescent adaxially, minutely stipitate-glandular beneath the tomentum, linear, sessile, not clasping, margins flat or narrowly revolute, basal rosette

persistent but withering. **Phyllaries** mostly oblong-lanceolate, scarious, stramineous but with lateral bands of pigmentation, margins narrow, brown-hyaline, stereome light greenish, basomedial, elliptic to ovate or lanceolate, not divided or fenestrate. **Pistillate florets** 30–150 **Disc florets** 5–8 or 10–25, functionally staminate. **Achenes** (fertile) ca. 1 mm long, with duplex, myxogenic trichomes; pappus bristles not apically expanded, connate basally and deciduous as a ring. Figures 51–55. Three species, each widely disjunct from the others (Map 8).

Key to *Mexerion* species

1. Leaves 1–4 cm long, 3–7 mm wide; pistillate florets 100–150; Transvolcanic Mountains of south-central Mexico (Veracruz, Puebla, Edo. Mexico, Mexico D.F.) ***Mexerion sarmentosum***
1. Leaves 3–7 cm long, 1–3 mm wide; pistillate florets 30–85.
 2. Stems 20–35 cm tall; inner phyllaries 12–14 mm long, apex without a white extension; disc (functionally staminate) florets 5–6; pistillate florets 40–50; Sierra Madre Occidental in southern Chihuahua and Durango ***Mexerion mexicanum***
 2. Stems 10–25 cm tall; inner phyllaries 4.5–5.5 mm long, apex usually with a whitish extension; disc florets (functionally staminate) ca. 11; pistillate florets ca. 85; Sierra de Cuchumatanes in southwestern Guatemala ***Mexerion stolonatum***



Map 8. Distribution of *Mexerion* species. See Nesom (1990a) for collection records of *M. sarmentosum*. All collections of *M. mexicanum* are cited below. *Mexerion stolonatum* is known only from the type.

1. **MEXERION SARMENTOSUM** (Klatt) Nesom, *Phytologia* 68: 252. 1990. *Gnaphalium sarmentosum* Klatt, *Jahrb. Hamb. Wiss. Anst.* 126. 1892. **TYPE: MEXICO. Edo. México.** [Mpio. Zinacantepec], about the timberline of Nevado de Toluca, 6 Sep 1896, *C.G. Pringle 4249* (probable holotype: GH; isotypes: F-2 sheets, GOET, JE, K, MEXU-2 sheets, MO, MSC, PH, PUL, S, VT).
2. **MEXERION MEXICANUM** Nesom, *Phytologia* 68: 250. 1990. **TYPE: MEXICO. Chihuahua.** [Mpio. Guadalupe y Calvo], Sierra Mohinora, ca. 3 mi S of La Rocha, on grassy pine slope, near and about waterfall (tributary of Rio del Soldado), 7000 ft, 18 Oct 1959, *D.S. Correll & H.S. Gentry 23225* (holotype: LL).
- Additional collections. Chihuahua.** [Mpio. Guadalupe y Calvo], Sierra Chinatu, San Juan, rocky open pine slope, 8900 ft, 8 Oct 1959, *Correll & Gentry 22924* (LL). **Durango.** Mpio. Pueblo Nuevo, KM 115, carretera Durango a Mazatlan, 23° 44' 50" N, 105° 27' 00" W, bosque aciculifolio, 2700 m, Oct 1999, *J.L. Martínez 676* (MEXU).
3. **MEXERION STOLONATUM** (Blake) Nesom, **comb. nov.** *Gnaphalium stolonatum* S.F. Blake, *Brittonia* 2: 341. 1937. *Pseudognaphalium stolonatum* (Blake) Dillon, *J. Bot. Res. Inst. Texas* 9: 69. 2015. *Chionolaena stolonata* (Blake) Pruski, *Phytoneuron* 2012-1: 4. 2012. **TYPE: GUATEMALA. Dept. Huehuetenango.** Llanos of the Sierra Cuchumatanes, along trail between Huehuetenango and Soloma, 3200 m, 24 Aug 1934, *A.F. Skutch 1098* (holotype: GH; isotype: LL).

Pruski (2012) placed this species in *Chionolaena* sensu lato and compared it to Mexican species recognized here as *Gnaphaliothamnus*. The stoloniferous, herbaceous habit, however, and characteristic morphology and coloration of the phyllaries and basally connate pappus bristles place it in *Mexerion*. Pruski's concept of the species (including his illustration of *Molina R. 16441*, from the Sierra Cuchumatanes) encompassed plants of what was subsequently described as *Gnaphaliothamnus nesomii* Dillon (Dillon & Luebert 2015). Earlier (Nesom 1990b), I described the central (staminate) florets of *Gnaphalium stolonatum* as fertile, but Pruski (2012) noted that they perhaps are infertile, which is a better fit with the constellation of *Mexerion* features.

ACKNOWLEDGEMENTS

Types cited have been seen first-hand or as images via JSTOR Plants. Thanks to the staff at TEX,LL and at US for help and hospitality during recent visits there and to John Pruski at MO for help with locating collections there.

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Illustrations are alphabetical by species, as follow.



Figure 1. *Gnaphaliothamnus aecidiocephalus*. Oaxaca, Sierra de Juárez, MacDougall s.n. (US).



Figure 2. *Gnaphaliothamnus aecidiocephalus*. Oaxaca, Sierra de Juárez, Poole 1286 (US).



Figure 3. *Gnaphaliothamnus barclayae*. Colombia, Sierra de Santa Marta, *Barclay 7072*, holotype (US).

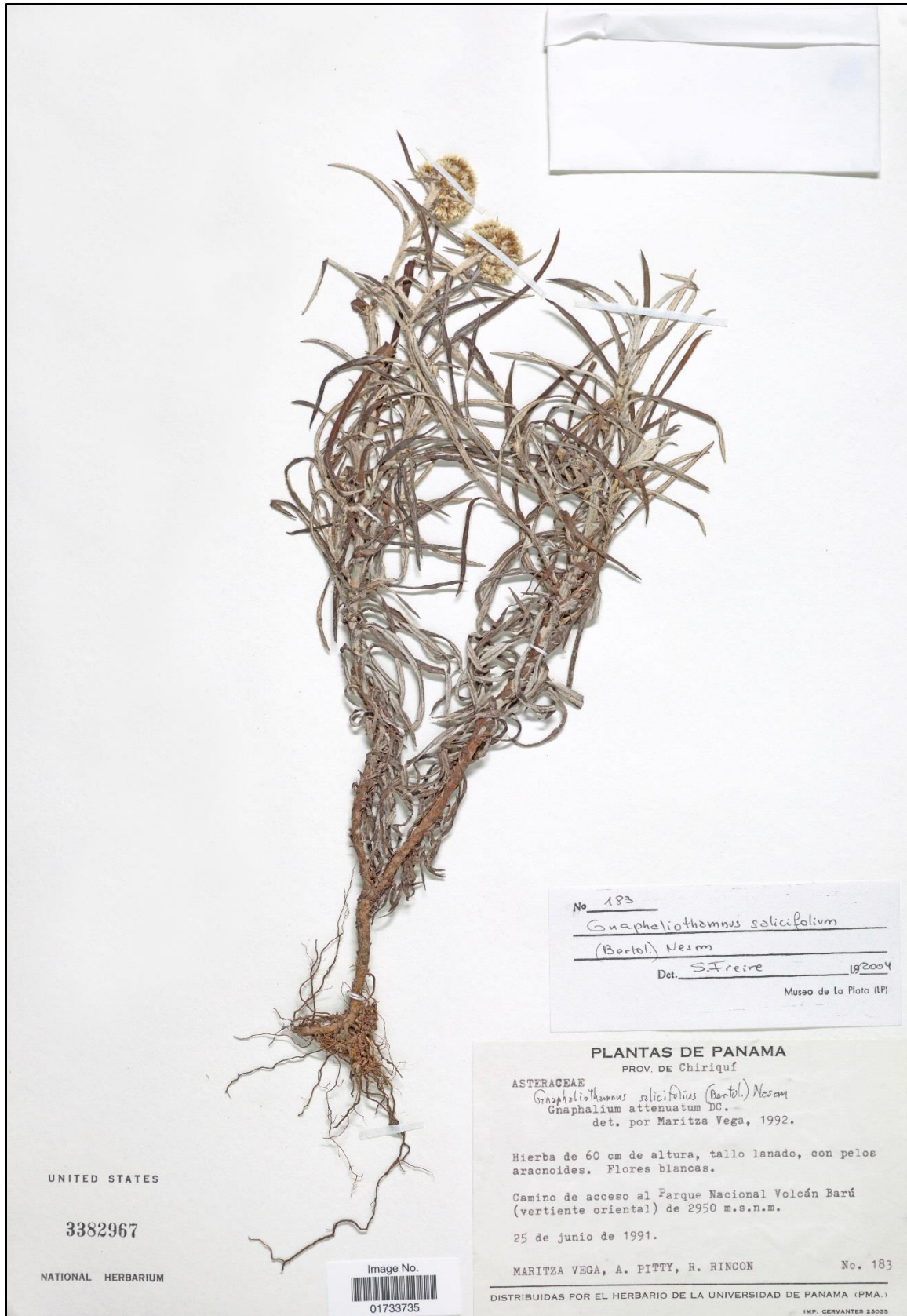


Figure 4. *Gnaphaliothamnus baru*. Panama, Volcán Barú, Vega 183, holotype (US).



Figure 5. *Gnaphaliothamnus baru*. Detail from holotype (US).



Figure 6. *Gnaphaliothamnus baru*. Detail from holotype (US).



Figure 7. *Gnaphaliothamnus chrysocoma*. Colombia, Sierra de Santa Marta, Rangel C. 998 (US).



Figure 8. *Gnaphaliothamnus chrysocoma*. Colombia, Sierra de Santa Marta, Kirkbride & Forero 1801 (US).



Figure 9. *Gnaphaliothamnus chrysocoma*. Colombia, detail from *Rangel C. 998* (US).



Figure 10. *Gnaphaliothamnus columbianus*. Colombia, Sierra de Perijá, Cuatrecasas 25115 (US).



Figure 11. *Gnaphaliothamnus columbianus*. Colombia, Sierra de Santa Marta, Cuatrecasas 24661 (US).



Figure 12. *Gnaphaliothamnus concinnus*. San Luis Potosí, Parry & Palmer 423 (GH, holotype).



Figure 13. *Gnaphaliothamnus concinnus*. Detail from Figure 12.



Figure 14. *Gnaphaliothamnus concinnus*. San Luis Potosí, Schaffner 222 (US).



Figure 15. *Gnaphaliothamnus costaricensis*. Costa Rica, Weston 3615 (US).



Figure 16. *Gnaphaliothamnus costaricensis*. Costa Rica, Pruski 3863 (US).



Figure 17. *Gnaphaliothamnus costaricensis*. Panama, Monro et al. 4113 (MO).



Figure 18. *Gnaphaliothamnus cryptocephalus*. Chiapas, Volcán Tacaná, Breedlove 24347 (MEXU).



Figure 19. *Gnaphaliothamnus cryptocephalus*. Guatemala, Volcán Tacaná, Beaman 3229 (US).

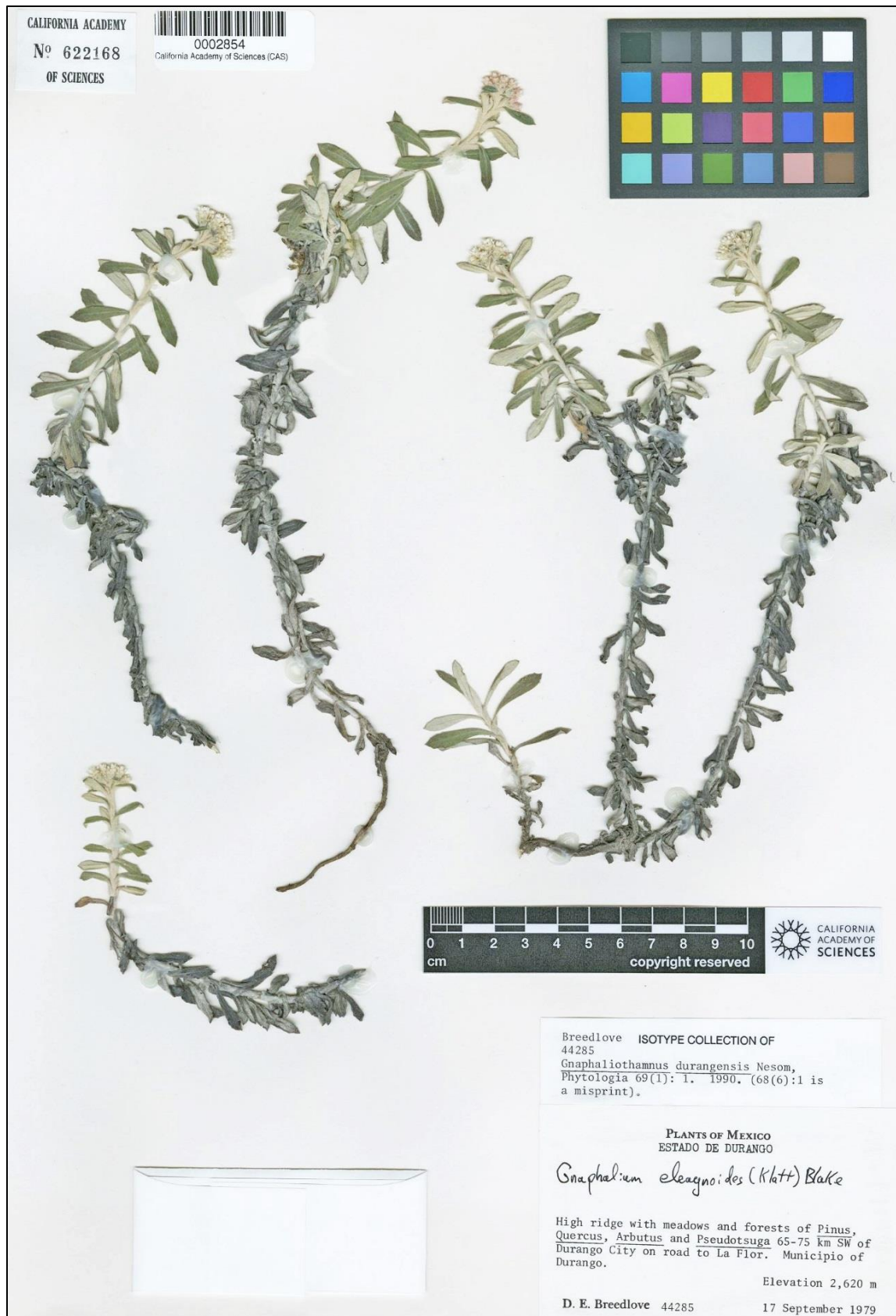


Figure 20. *Gnaphaliothamnus durangensis*. Durango, Breedlove 44285 (CAS, isotype).



Figure 21. *Gnaphaliothamnus durangensis*. Detail from Figure 20.



Figure 22. *Gnaphaliothamnus eleagnoides*. Oaxaca (Cerro Pelado), Liebmann 316 (C, holotype).



Figure 23. *Gnaphaliothamnus eleagnoides*. Oaxaca, Gallardo H. 1252 (MEXU).



Figure 24. *Gnaphaliothamnus eleagnoides*. Oaxaca, Gallardo H. 1263 (MEXU).



Figure 25. *Gnaphaliothamnus eleagnoides*. Oaxaca, Villaseñor 1240 (MEXU).



Figure 26. *Gnaphaliothamnus eleagnoides*. Oaxaca, Martínez C. 941 (MEXU). Unusually narrow-leaved variant.



Figure 27. *Gnaphaliothamnus eleagnoides/acedidiocephalus*, putative ntroggressants. Oaxaca, Cerro de Humo Chico, 27 Jan 1963, MacDougall s.n. (MEXU).

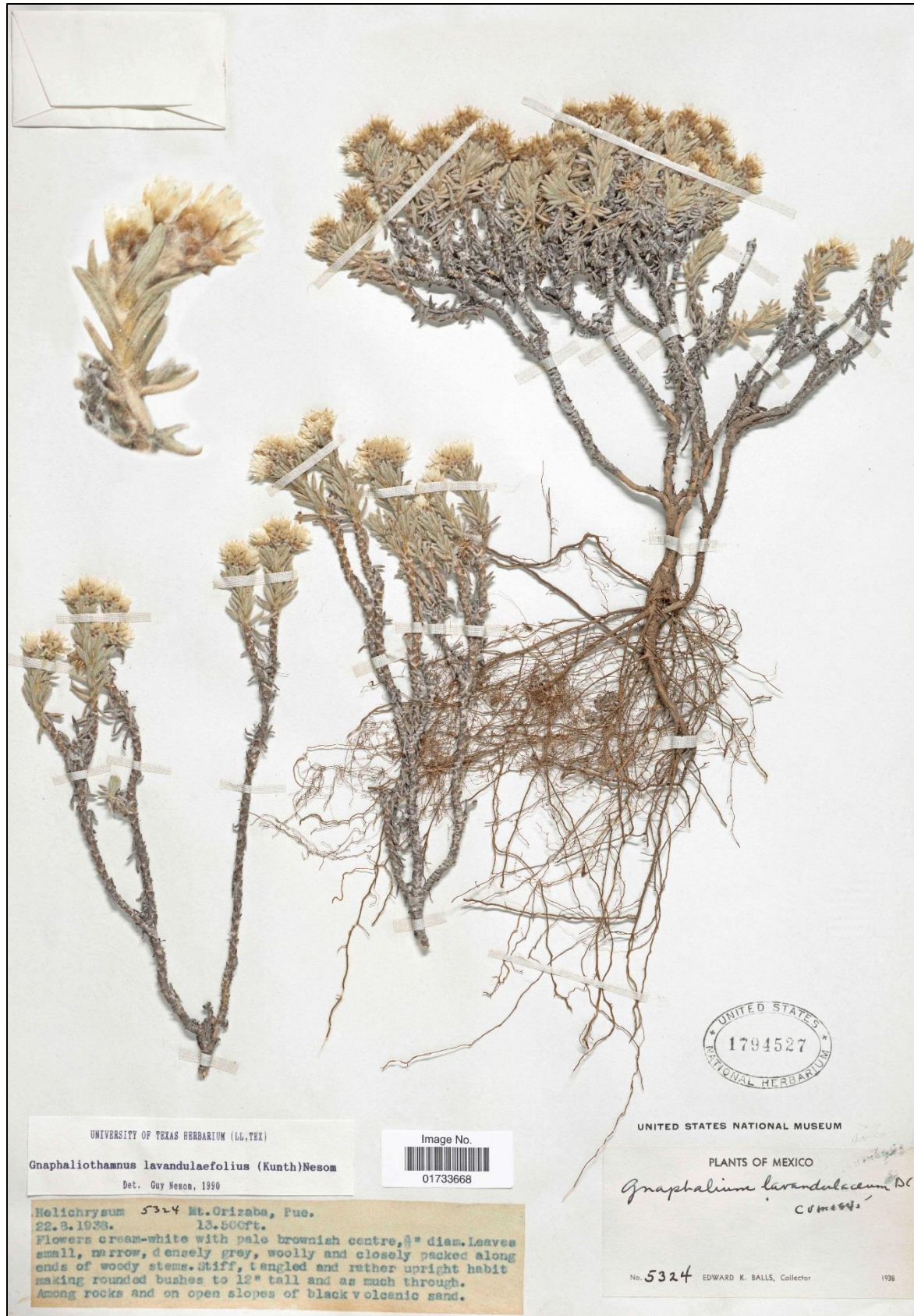


Figure 28. *Gnaphaliothamnus lavandulifolius*. Puebla (Orizaba), Balls 5324 (US).



Figure 29. *Gnaphaliothamnus lavandulifolius*. Veracruz (Perote), Poole 2390 (OBI).



Figure 30. *Gnaphaliothamnus lavandulifolius*. Edo. Mexico (Nevado de Toluca), Hernández X. X-10188 (US).

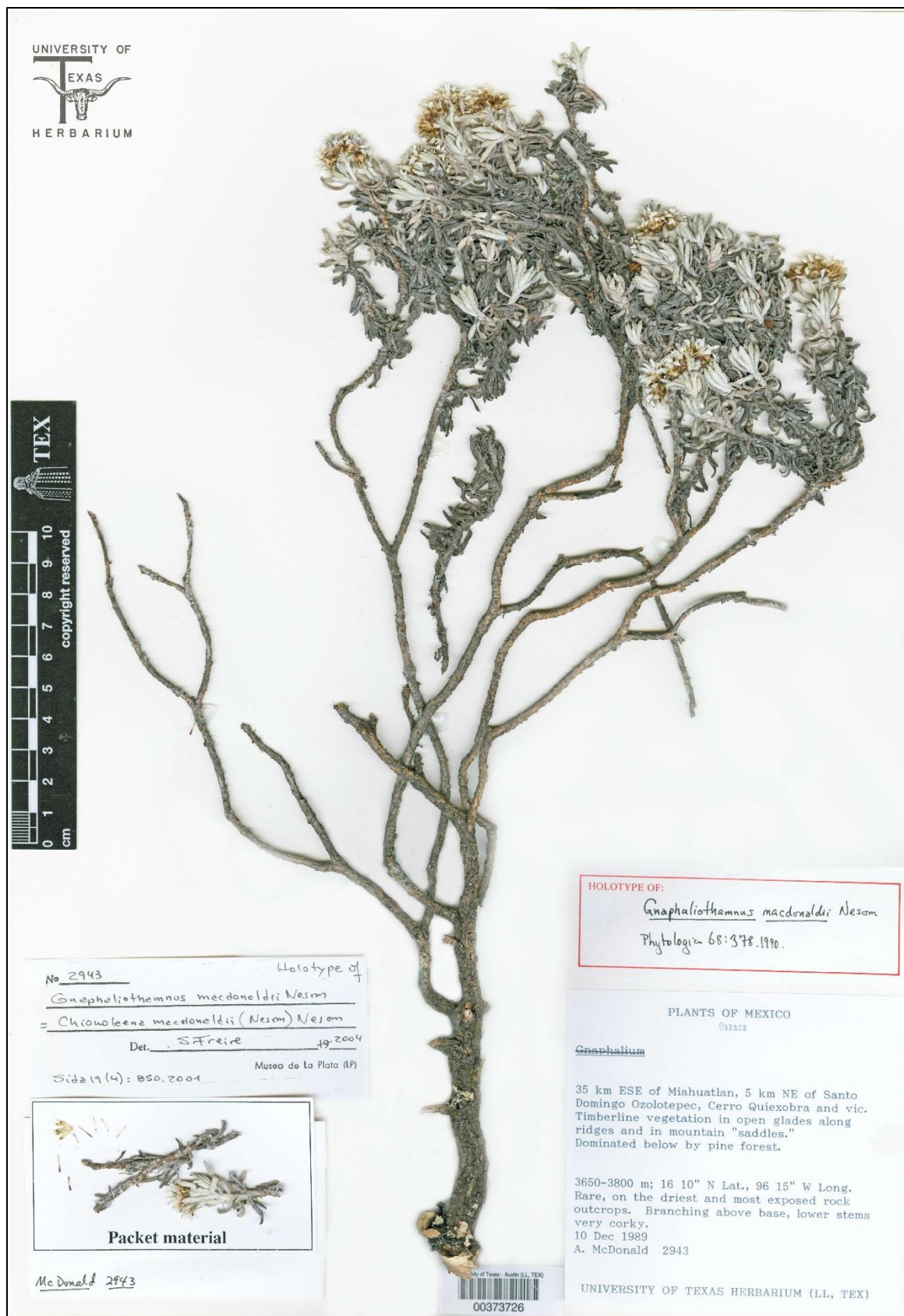


Figure 31. *Gnaphaliothamnus macdonaldii*. Oaxaca, McDonald 2943, holotype (TEX).



Figure 32. *Gnaphaliothamnus macdonaldii*. Oaxaca, McDonald 2943, isotype (GH).



Figure 33. *Gnaphaliothamnus macdonaldii*. Oaxaca, McDonald 2943, detail from GH isotype.



Figure 34. *Gnaphaliothamnus macdonaldii*. Oaxaca, McDonald 2943, detail from NY isotype.



Figure 35. *Gnaphaliothamnus mexicanus*. Hidalgo, Pringle 7700 (GH). Isotype.



Figure 36. *Gnaphaliothamnus mexicanus*. Hidalgo, Pringle 7700 (US). Isotype.



Figure 37. *Gnaphaliothamnus mexicanus*. Hidalgo, Rzedowski 37269 (MEXU).



Figure 38. *Gnaphaliothamnus mexicanus*. Hidalgo, Gentry 32162 (MEXU).



Figure 39. *Gnaphaliothamnus monanthus*. Guatemala, Islebe & Hübner 1575, holotype (US).



Figure 40. *Gnaphaliothamnus monanthus*. Guatemala, *Islebe & Hübner 1575*, detail from holotype, Figure 39.



Figure 41. *Gnaphaliothamnus nesomii*. Molina R. 16441 (US, isotype).



Figure 42. *Gnaphaliothamnus salicifolius*. Holotype of *Gnaphalium seemannii* Schultz-Bip. (K).



Figure 43. *Gnaphaliothamnus salicifolius*. Durango, Tenorio L. 8204 (MEXU).



Figure 44. *Gnaphaliothamnus salicifolius*. Hidalgo, Hernandez M. 5425 (US).



Figure 45. *Gnaphaliothamnus* [aff.] *salicifolius*. Edo. México, Álvarez 14747 (MEXU). Leaves unusually broad, inflorescence only slightly raised, and phyllaries apparently without white tips. From the Reserva de la Biósfera Mariposa Monarca.



Figure 46. *Gnaphaliothamnus salicifolius*. Guerrero, Teotepac, Hinton 11120 (US). See comments in text.



Figure 47. *Gnaphaliothamnus salicifolius*. Oaxaca, García M. 2014 (US).



Figure 48. *Gnaphaliothamnus salicifolius*. Guatemala, Williams 22834 (US).



Figure 49. *Gnaphaliothamnus sartorii*. Liebmann 308, possible holotype (C).



Figure 50. *Gnaphaliothamnus sartorii*. Detail from Figure 49.



Figure 51. *Mexerion sarmentosum*. Pringle 4249 1098 (PH, isotype).



Figure 52. *Mexerion mexicanum*. Correll & Gentry 23225 1098 (LL, holotype).



Figure 53. *Mexerion stolonatum*. Skutch 1098 (GH, holotype).



Figure 54. *Mexerion stolonatum*. *Skutch 1098* (GH, detail from holotype).



Figure 55. *Mexerion stolonatum*. Skutch 1098 (GH, detail from holotype).