

TAXONOMY OF *GNAPHALIOTHAMNUS* (ASTERACEAE: INULEAE)

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ABSTRACT

Nine species of *Gnaphalium* sect. *Rhodognaphalium* are segregated as the genus *Gnaphaliothamnus* Kirpichn. Three new species are proposed: *G. cryptocephalus* Nesom, *G. costaricensis* Nesom and *G. macdonaldii*; the remainder are *G. aecidiocephalus* (Grierson) Nesom, *comb. nov.*, *G. concinnus* (A. Gray) Nesom, *comb. nov.*, *G. eleagnoides* (Klatt) Nesom, *comb. nov.*, *G. lavandulaefolius* (Kunth) Nesom, *comb. nov.*, *G. salicifolius* (Bertol.) Nesom *comb. nov.* and *G. sartorii* (Klatt) Nesom, *comb. nov.* *Gnaphaliothamnus* is characterized by its strongly woody habit, revolute leaves, phyllaries with spreading, white tips, reddish corollas, central hermaphroditic flowers with sterile ovaries, apically swollen pappus bristles and narrowly lanceolate style branches, and ellipsoid to obovoid achenes 1.2-2.0 mm long with minute, myxogenic (in some), slightly elongated, twin hairs. Two of the species are partly to wholly dioecious. The genus is restricted to México and Central America and appears to be most closely similar to other woody genera of South America with "pseudohermaphroditic" central flowers, particularly *Chionolaena* (sensu stricto), to which some of the species have been referred.

KEY WORDS: *Gnaphaliothamnus*, *Gnaphalium*, *Chionolaena*, Asteraceae, Inuleae, México.

In a taxonomic investigation of Mexican *Gnaphalium* L., it quickly became apparent that a group of species was strongly set apart from the rest. These species are characterized by a strongly woody habit, revolute leaves, phyllaries with white opaque, spreading tips, mostly heterogamous heads, reddish corollas, ellipsoid to obovoid achenes 1.2-2.0 mm long with minute, slightly elongated, duplex hairs, and central hermaphroditic flowers with sterile ovaries, apically swollen pappus bristles and narrowly lanceolate style branches with collecting hairs along their whole length. They appear to be confined primarily to peaks of the highest mountains of southcentral México to Costa Rica in Central America. Two of them have been placed in the Old World *Anaphalis*

DC. (Grierson 1972) and five have been formally regarded as species of the otherwise South American genus *Chionolaena* DC. (see Anderberg & Freire 1989). The group was named by Schultz-Bipontinus in 1856 as *Gnaphalium* sect. *Rhodognaphalium* (typified by *G. salicifolium*). Klatt (1887) later recognized the close relationship between the two Mexican species he named as *Chionolaena* and yet two other Mexican species, *Gnaphalium concinnum* and *G. salicifolium*. Finally, *G. salicifolium* also serves as the type of a more recently described genus (Kirpichnikov & Kuprianova 1950) that was considered monotypic at its inception: *Gnaphaliothamnus*.

Grierson (1972) considered two of the Mexican species treated here to be species of *Anaphalis*. That genus is also characterized by revolute leaves, white opaque phyllaries and dimorphic pappus bristles. According to Grierson, it comprises species that range from dioecious to polygamodioecious to others with only heterogamous heads and with no approach to dioecy. The two Mexican species are partly to wholly dioecious. In one of them (*A. aecidiocephala*), heads of staminate plants produce only hermaphroditic flowers with fertile anthers but sterile ovaries, while pistillate plants have heads with pistillate flowers and with completely sterile "hermaphroditic" flowers. The second Mexican species treated by Grierson (*A. concinna*) is polygamodioecious. In his decision regarding the generic placement of these species, Grierson emphasized their sexual condition. He eliminated *Gnaphaliothamnus* (apparently as he understood it to be monotypic) as a member of *Anaphalis*, because it was not dioecious.

The species of *Anaphalis*, in contrast to the Mexican ones treated here, have phyllaries with divided stereomes and their corollas are yellowish to cream in color with glandular apices. Although at least one species of the genus [*A. margaritacea* (L.) Benth. & Hook. f.] is naturalized in the New World, *Anaphalis* appears to be essentially confined in its native range to the Old World. One poorly understood species, *A. chilensis* Reiche, has been recognized as native to South America (Cabrera 1961). Anderberg & Freire (1989) excluded *A. aecidiocephala* from the genus, and I agree with this. While the evidence is suggestive of a relationship between *Anaphalis* and the species of México and Central America treated here, they do not appear to be congeneric and the development of polygamodioecy and dioecy apparently has occurred independently in each.

In view of its strikingly different morphology, it is clear that the relationship of *Gnaphaliothamnus* lies outside of the other traditionally regarded "gnaphalioid" species from México or Central America. *Gnaphalium stolonatum* S.F. Blake, an endemic of Guatemala, produces white tipped bracts and clavate bristle tips and may become woody, but it has fertile central flowers and yellow corollas, and it is more closely related to, if not a member of, *Gnaphalium* sensu stricto rather than of *Gnaphaliothamnus*. The closest relatives of *Gnaphaliothamnus* appear to be among the taxa of South America.

In their overview of the tribe, Merxmüller, *et al.* (1977) listed *Gnaphaliothamnus* as monotypic with the observation that the genus needed to be reconsidered in an overall investigation of *Gnaphalium*. They suggested (p. 594) that a relationship may exist between *Gnaphaliothamnus* and "the central-sterile, subdioecious or dioecious genera *Chionolaena*, *Luciliopsis* [Wedd.], *Mnioides* [(A. Gray) Benth. & Hook.] and *Oligandra* [Less.]." Their listing of *Chionolaena* noted that some of its species were from México.

Anderberg (1989) placed *Chionolaena* in the "Anaxeton clade" apart from the "Lucilia-Oligandra clade," but in his analysis both of these groups are part of a broader lineage characterized by "shrubs or small trees" and "female florets violet to whitish." *Gnaphaliothamnus* also may belong in the "Anaxeton clade" on the basis of character distributions outlined in Anderberg's study, although the occurrence of myxogenic achenial trichomes would be anomalous. Indeed, in an even more recent paper (Anderberg & Freire 1989), *Gnaphaliothamnus* has been considered the sister group of *Chionolaena*.

Anderberg & Freire (1989) distinguished *Gnaphaliothamnus* from *Chionolaena* by its "basally free instead of fused pappus bristles, lacking clavate apical pappus cells" and by an unspecified difference in branching pattern. They transferred the Mexican "*Anaphalis*" *aecidiocephala* to *Chionolaena* on the basis of its "dichotomous branching, deflexed leaves, clavate apical pappus cells etc." and also included *A. concinna* because they saw a close relationship between it and *A. aecidiocephala*. Further, they recognized as *Chionolaena* two of the other four Mexican species named in that genus, although they did not specify which ones. In their view, *Gnaphaliothamnus* remains as a monotypic genus.

In contrast to the view of Anderberg & Freire (1989), I find it difficult to support the recognition of two separate genera among these woody, "central sterile" Mexican and Central American species. Among these taxa, the pappus bristles have strongly to weakly developed clavate tips and the bristle bases vary from weakly adherent by a few cells to completely separate. The degree of basal fusion of bristles of "*Chionolaena*" *aecidiocephala* is exaggerated in the line drawing provided by Anderberg & Freire. The bristles of *Gnaphaliothamnus salicifolius* sometimes are weakly connate and they show a weak but definite development of apical clavate thickening. Further, *C. eleagnoides* Klatt from Oaxaca, México, which has strongly clavate bristles partially connate at the base, is clearly the species most closely related to *G. salicifolius*. The strict dioecism found in "*C.*" *aecidiocephala* is atypical of *Gnaphaliothamnus* and apparently *Chionolaena* as well, but the similarity of that species to the polygamodioecious "*C.*" *concinna* supports the hypothesis that the sexual extreme developed autochthonously in México. Further, although these two species have somewhat more noticeably deflexed leaves than the others of México/Central America, at least the lower leaves in all the species tend to be deflexed and the Brazilian *C. arbuscula* DC. has spreading, only slightly

deflexed leaves, nearly identical in orientation to those of *G. salicifolius*.

Variability similar to that within *Gnaphaliothamnus* also can be seen within other genera of Gnaphaliinae. For example, variation in the degree of basal fusion of pappus bristles occurs in *Gnaphalium* sensu stricto (Hilliard & Burt 1981) and *Omalotheca* (Nesom 1990), and pappus bristles with clavate tips are variably present among species of *Anaphalis* (Grierson 1971). In my opinion, the Mexican/Central American species form a single lineage. Their complete merger, however, with *Chionolaena* cannot be justified because the two groups differ in significant features not discussed by Anderberg & Freire.

Outside of the Mexican species that have been placed in *Chionolaena*, that genus is restricted to southern Brazil in South America. Two species of the Colombian Andes apparently are referred to *Chionolaena* by Anderberg & Freire (1989), *Oligandra chrysocoma* Wedd. and *Chionolaena colombiana* S.F. Blake. Each of these, however, is considered to be a member of a different genus by Dillon & Sagastegui (in press; submitted). Each has glabrous achenes and other features divergent from species of Brazilian *Chionolaena* as well as those from México and Central America. The two latter groups may be more similar between themselves than either is to the Colombian species.

Baker (1882), as did Anderberg & Freire (1989), recognized two sections within *Chionolaena*: sect. *Chionolaena* and sect. *Leucopholis*. Anderberg (1989) himself, however, recently implied that *Leucopholis* is a separate genus and it also has been regarded as separate by Cabrera (1961) and Merxmuller, *et al.* (1977). Baker's division of the genus appears to have been artificial, based only on the number of flowers per head (15-60 per head in sect. *Chionolaena* vs. 8-10 in sect. *Leucopholis*). A more natural division probably will distinguish *Chionolaena* sensu stricto with solitary heads and central flowers with sterile ovaries, from *Leucopholis*, with heads in glomerate to corymboid clusters and the central flowers fully hermaphroditic. In this view, *Chionolaena* sensu stricto apparently would include only three species: *C. arbuscula* DC. (the type), *C. lychnophoroides* Schultz-Bip. and *C. jeffreyi* H. Robinson (see Robinson 1984).

*Gnaphaliothamnus* will not fit in either *Chionolaena* sensu stricto or *Leucopholis*, because it produces numerous heads at the tip of each stem, each head with 12 or more flowers and the central flowers have sterile ovaries. It differs further in features of its leaves and achenes. Except for "*C.*" *aecidiocephala*, which has broadly obovate leaves, the leaf margins of all of the species of México and Central America are fused slightly below the apex and produce a distinctive, teretish, indurated mucro 1-3 mm long. Such is not seen in the Brazilian species.

The achenial trichomes of all the Mexican/Central American species except one are relatively uniform in morphology. They are sparsely represented and about 0.05 mm long. Each is composed of 3 or rarely 4 cells, the basal one short and at least partially sclerified, the two terminal ones longer, thin walled

and joined terminally to form a rounded tip. I have observed these trichomes in two species. *Gnaphaliothamnus salicifolius* and *G. lavandulaefolius*, to open at the tip and release mucilage. The achenial trichomes of "*Chionolaena*" *aecidiocephala* are identical in morphology to these. In "*C.*" *concinna*, however, the hairs are longer (up to 0.3 mm), thinner and the terminal cells have acute, slightly divergent tips and each trichome is longitudinally twisted once or twice. Such a peculiarity makes it improbable that this species has been ancestral to any of the other Mexican/Central American ones, although it certainly must be included in the same lineage as them. In contrast to all of the Mexican/Central American achenial trichomes, those of Brazilian *Chionolaena* and *Leucopholis* are mostly 0.4-0.5 mm long and form a "densely strigose" vestiture.

In conclusion, the relationship between *Chionolaena*, *Leucopholis* and *Gnaphaliothamnus* is not clear, but the Mexican/Central American species appear to represent a monophyletic lineage that can be distinguished from both of the Brazilian groups. *Gnaphaliothamnus* is most closely similar to *Chionolaena* sensu stricto but separated from it by its polycephalous stems, apically mucronate leaves, and sparsely and minutely pubescent achenes. The geographic situation, as well, supports separation of *Gnaphaliothamnus* from the Brazilian taxa. In my opinion, the most reasonable taxonomic solution lies in the recognition of *Gnaphaliothamnus* as a separate genus endemic to México and Central America and the restriction of *Chionolaena* to South America.

*Gnaphaliothamnus* Kirpichn., Trudy Bot. Inst. Akad. Nauk SSSR, Ser. 1, Fl. Sist. Vyss. Rast. 9:33. 1950. Type species: *Gnaphaliothamnus* (*Gnaphalium*) *rhodanthus* (Schultz-Bip.) Kirpichn. ( $\equiv$  *Gnaphaliothamnus salicifolius*). *Gnaphalium* subg. *Rhodognaphalium* Schultz-Bip. in Seem., Bot. Voy. Herald 310. 1856. Type species: *Gnaphalium rhodanthum* Schultz-Bip. ( $\equiv$  *Gnaphaliothamnus salicifolius*). *Gnaphalium* sect. *Rhodognaphalium* [as "*Eurhodognaphalium*"] Schultz-Bip. in Seem., Bot. Voy. Herald 310. 1856. Type species: *Gnaphalium rhodanthum* ( $\equiv$  *Gnaphaliothamnus salicifolius*). *Gnaphalium* sect. *Metalasiopsis* Schultz-Bip. in Seem., Bot. Voy. Herald 310. 1856. Type species: *Gnaphalium seemanii* Schultz-Bip. ( $\equiv$  *Gnaphaliothamnus salicifolius*).

Perennial subshrubs 1-3 dm tall, woody at least at the base, from woody roots or often with elongated, slender, caudexlike rhizomes. Stems and leaves densely woolly-tomentose, sometimes with an understory of stipitate glandular hairs as well. Leaves linear to narrowly oblong or elliptic, with revolute, entire margins and indurated mucronulate tips, sometimes slightly decurrent but not clasping, crowded on the stems, ascending or spreading, the lower commonly withering persistent. Heads sessile to subsessile in compact, terminal glomerules of 2-5 or less commonly in corymbs of up to 40 heads; phyllaries usually easily caducous, the apices elongated, spreading and distinctly

white opaque in contrast to the brown-green or stramineous lower portions. 1 species without prominently white tipped bracts: receptacles naked, shallowly to deeply alveolate. Total minimum number of flowers per head 12-31; pistillate flowers 5-46(-70), the corollas tubular, narrowing upwards from the base, eligulate, purplish-red on the upper half, with minute, appressed, elongate, viscid hairs at the apex; central flowers 3-19, hermaphroditic but the ovaries sterile, the corollas tubular, purplish-red on the upper portions. 2.8-5.0 mm long, eglandular but with minute, appressed, elongate, viscid hairs at the apex; anthers tailed; style branches narrowly lanceolate, with collecting hairs from tips to point of divergence of the branches. Achenes obovoid to ellipsoid, slightly flattened, 1.2-2.0 mm long, the epidermis smooth, sparsely invested with minute, slightly elongated, 3-4 celled, twin hairs (Zwillingshaare) with rounded apices, more elongated with sharp apices in 1 species, clearly myxogenic in 2 species, achenes glabrous in 1 species; carpodium minute but well differentiated; pappus bristles scabrous, basally eciliate, separate or very slightly connate at the very base, persistent, or in 2 species basally caducous, usually dimorphic, with the apex of those of the hermaphroditic flowers with cells swollen clavellate at their apices, those of the pistillate flowers thin and sharp pointed, the bristles monomorphic or nearly so in 2 species. Base chromosome  $x=14$  pairs.

### KEY TO THE SPECIES

1. Inner phyllaries without prominent, white tips ..... *G. cryptocephalus*
- 1' Inner phyllaries with prominent, white, spreading tips ..... (2)
  2. Upper leaf surfaces tomentose to glabrate, eglandular ..... (5)
  - 2' Upper leaf surfaces with stipitate glandular hairs beneath the eglandular tomentum ..... (3)
3. Pistillate flowers 5-10; achenes glabrous; pappus bristles strongly dimorphic, basally caducous ..... *G. costaricensis*
- 3' Pistillate flowers 12-24; achenes pubescent; pappus bristles monomorphic to weakly or strongly dimorphic, basally persistent ..... (4)
  4. Pistillate flowers 12-18, usually about equal the number of hermaphroditic; pappus bristles strongly dimorphic ..... *G. macdonaldii*
  - 4' Pistillate flowers 21-24, usually about twice as many as the hermaphroditic; pappus bristles monomorphic to very weakly dimorphic ..... *G. lavandulaefolius*
5. Leaves 7-8 mm long; phyllaries subequal in length ..... *G. sartorii*

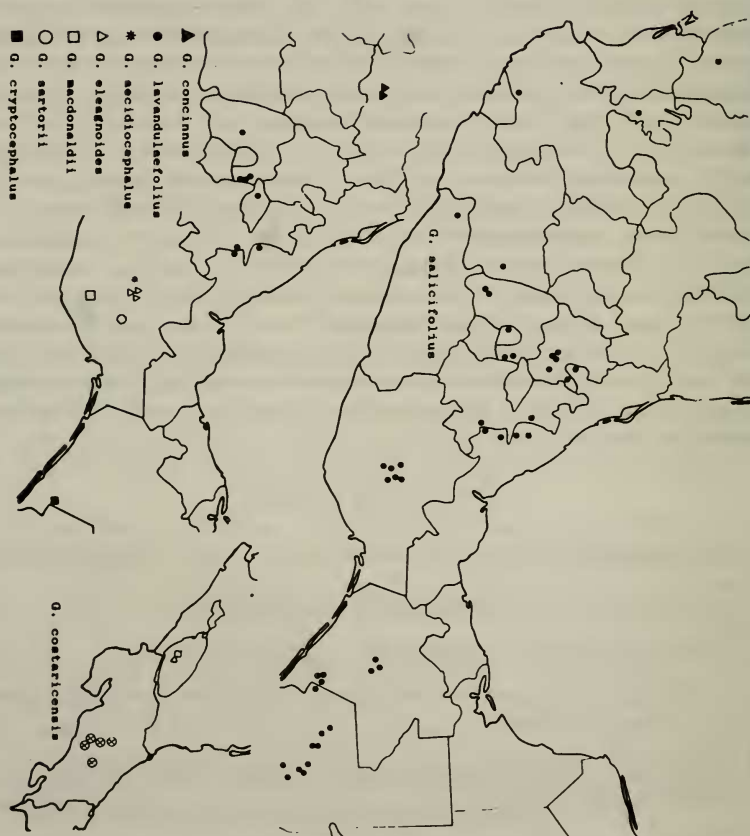


Figure 1. Geographic distribution of the species of *Gnaphaliothamnus*.

- 5' Leaves longer than 15 mm; phyllaries strongly graduated in length ... (6)
6. Leaves weakly bicolored: heads few in tight clusters at tips of leafy stems ..... (8)
- 6' Leaves strongly bicolored: heads numerous in corymbs above the leaves ..... (7)
7. Leaves linear to narrowly oblanceolate: pistillate flowers (22-)34-55, the hermaphroditic 3-4(-7); pappus bristles weakly dimorphic, basally caducous ..... *G. salicifolius*
- 7' Leaves elliptic to elliptic-oblanceolate: pistillate flowers 16-20, the hermaphroditic 7-18; pappus bristles strongly dimorphic, basally persistent ..... *G. eleagnoides*
8. Plants dioecious; leaves 3-5 mm long; phyllaries with a red midregion ..... *G. aecidiocephalus*
- 8' Plants polygamodioecious: leaves 1-2 cm long; phyllaries without a red midregion ..... *G. concinnus*
1. ***Gnaphaliothamnus aecidiocephalus*** (Grierson) Nesom, *comb. nov.*  
 BASIONYM: *Anaphalis aecidiocephala* Grierson, Notes Roy. Bot. Gard. Edinburgh 31:389. 1972. TYPE: MÉXICO. Oaxaca: Cerro del Humo Chico, Comaltepec. Ixtlan. 3050 m, 2 Mar 1968, *T. MacDougall 4128* (E-photo! in Notes Roy. Bot. Gard. Edinburgh 31:pl. 8. 1972). *Gnaphalium aecidiocephalum* (Grierson) L.O. Wms., Phytologia 25:459. 1973. *Chionolaena aecidiocephala* Anderb. & Freire, Notes Roy. Bot. Gard. Edinburgh 46:40. 1989.

Subshrubs. the stems white matted tomentose, woody, 10-16 cm tall, erect, crowded caespitose, forming dense mounds. Leaves elliptic-obovate to obovate, not mucronate, 2.5-4.5 mm long, 2.0-2.5 mm wide, deflexed and slightly falcate, densely crowded and imbricate, densely and closely grayish villous-puberulent above and beneath, when glabrescent, revealing the eglandular, shiny surface. Heads campanulate, 3-5 mm wide, sessile in terminal clusters of 2-3; phyllaries 29-34, lightly woolly on the lower half, red-purple in the midportion, with spreading, white tips. Pistillate heads: pistillate flowers 12-25, fertile, the corollas 3.0-3.2 mm long; hermaphroditic flowers 5-9, ovaries and stamens sterile, the corollas 3.2-3.4 mm long. Staminate heads: hermaphroditic flowers 30-35, the ovaries sterile, pistillate flowers absent. Achenes sparsely pubescent, ca. 1 mm long; pappus bristles 17-27(-32), separate, persistent, strongly dimorphic. Chromosome number,  $n=14$  pairs (Grierson 1972).

Oaxaca, in the Cerro del Humo and Sierra Juárez; subalpine pine woodland and heath; 2850-3050 m; flowering February-April.



*MacDougall 4129*, collected at the same locality on the same day as the type (4128, not "412S," apparently a transcriptional error on the holotype sheet, *vide* annotation by L.O. Williams), has been distributed as the type of an unpublished name by Williams. *Gnaphaliothamnus aecidiocephalus* is distinguished by its small habit, small, deflexed-imbricated leaves, red phyllaries with long, spreading, white tips and dioecious sexual condition.

2. *Gnaphaliothamnus concinnus* (A. Gray) Nesom. *comb. nov.* BASSIONOMY: *Gnaphalium concinnum* A. Gray, Proc. Amer. Acad. Arts 15:34. 1879. TYPE: MÉXICO. San Luis Potosí: in the highest mountains southeast of San Luis, Sep 1876, *Parry & Palmer 423* (HOLOTYPE: GH!: Isotypes: F!,PH!). *Anaphalis concinna* (A. Gray) Grierson, Notes Roy. Bot. Gard. Edinburgh 31:392. 1972. *Chionolaena concinna* Anderb. & Freire, Notes Roy. Bot. Gard. Edinburgh 46:40. 1989. Anderberg & Freire (1989, by annotation) have regarded the GH specimen as the lectotype.

Subshrubs 15-30 cm tall, densely woolly tomentose. Leaves elliptic-obovate to obovate with a terminal mucro, 1-2 cm long, 4-7 mm wide, sharply reduced in size near the heads, mostly strongly deflexed, crowded but not obscuring the stem, densely tawny villous-tomentose beneath, darker and glabrescent above, with eglandular surfaces. Heads campanulate, 3.5-5.0 mm wide, short pedicellate (2-4 mm long) in a compact cluster of 4-9; phyllaries 26-27, densely and persistently woolly. Pistillate flowers 20-27, the corollas 3.0-3.5 mm long. Hermaphroditic flowers 11-27, the corollas 3.2-3.8 mm long. Achenes sparsely pubescent with elongated hairs once or twice longitudinally twisted, mature morphology not observed; pappus bristles dimorphic, separate or slightly connate basally and separating in groups, persistent.

The specimens cited by Espinosa (1985) as *Gnaphaliothamnus concinnus* from Hidalgo and México apparently are *G. salicifolius*. I have seen only two collections of *G. concinnus*: the type and another apparently from near the type locality (*Schaffner 222* - CM,F,GH).

This species is distinctive in its tawny, obovate, deflexed leaves, prominently pedicellate heads and persistently woolly phyllaries. The leaves are larger but their shape is similar to those of *Gnaphaliothamnus aecidiocephalus*. Grierson (1972) noted that in some heads the hermaphroditic flowers are completely sterile and surmised that the species is polygamodioecious and thus related to *G. aecidiocephalus* on the basis of its sexual condition. I have seen no specimens of *G. concinnus* that produce heads strictly of hermaphroditic flowers. The sexual condition of *G. concinnus* appears to be an intermediate step in the direction of the more strict dioecy attained by *G. aecidiocephalus*.

3. *Gnaphaliothamnus costaricensis* Nesom. *spec. nov.* TYPE: COSTA RICA. Prov. San José: Cerro Asunción, common on rocky peak, 1 Sep

1987, *L.J. Pareda A. & J. F. Ciccio 4180* (HOLOTYPE: TEX!: Isotype: WIS!).

*Elychrysum lavandulaefolio* Kunth similis sed capitulis multo minoribus phyllariis et floribus paucioribus. phyllariis ordinatione pigmenti diversa, acheniis glabris, et setis pappo dimorphis differt.

Subshrubs 3-4 dm tall. Leaves ascending or commonly spreading at right angles to the stem, narrowly elliptic-oblongate, 5-8 mm long, 1.0-1.5 mm wide, with a prominent, indurated apiculum protruding from the tomentum, sparsely glandular beneath the tomentum. Heads campanulate-cylindric. 2.0-2.5 mm wide; phyllaries 24-28, lightly woolly at the base, the inner 5.0-6.5 mm long, with white tips 2-3 mm long. Pistillate flowers 5-10, 2.8-3.5 mm long. Hermaphroditic flowers 7-13, 2.8-4.0 mm long. Achenes glabrous, obovoid to cylindric, 1.2-1.6 mm long, flattened; pappus bristles 23-25, separate, very easily basally caducous, dimorphic. Costa Rica, rocky, barren hills or cliffs, páramo; 3000-3550 m; flowering August-February(-March).

Additional collections examined: COSTA RICA, summit of Volcán Irazú, April 1880, *Biolley 90* (F); 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); Prov. Limón, Cordillera de Talamanca, peak of Cerro Kamuk, páramo, 25 Mar 1984, *Davidse, et al. 26003* (TEX); Cordillera de Talamanca, "Cerro de la Muerte" region, near summit of Cerro Sakira, 8 Jan 1985, *Horn 38* (WIS); cuspide del Cerro Asunción, carretera Panamericana Sur, 25 Feb 1965, *Jiménez M. 2967* (F); Irazú, *Orsted 278* (GH); in summo monte Irazú, Jan 1847, *Orsted 10570* (F,GH-2 sheets); Cerro de Buena Vista, 14 Jan 1891, *Pittier 3430* (GH); Km 88 S of San José on Interamerican Hwy, barren hills along Cuesta del Muerte, 8 Aug 1981, *Turner 15038* (TEX).

These plants have been previously identified as *Gnaphalium lavandulaeum* DC., but that species ( $\equiv$  *Gnaphaliothamnus lavandulaefolius*) is now known to be endemic to southcentral México. The Costa Rican plants differ in their much smaller heads with fewer phyllaries and pistillate flowers, the pattern of coloration in the phyllaries, and their glabrous achenes with dimorphic pappus bristles. The leaves are stiffer and usually project strongly at right angles to the stems.

4. *Gnaphaliothamnus cryptocephalus* Nesom, *spec. nov.* TYPE: MÉXICO, Chiapas: Mpio. Unión Juárez, small meadow with scattered dwarfed *Pinus* near the summit of Volcán Tacana, 3800 m, 3 Mar 1972, *D.E. Breedlove 24347* (HOLOTYPE: TEX!).

*Elychrysum lavandulaefolio* Kunth similis sed foliis apiculatis, phyllariis brevioribus sine extensione apicali albida prominenti,

floribus hermaphroditicis paucioribus corollis brevioribus. et setis pappo paucioribus differt.

Perennials with long, sinuous, apparently decumbent, slender but woody, mostly glabrous branches. Leaves clustered near the branch tips, linear to narrowly oblong, 8-13 mm long, 1-2 mm wide, densely white tomentose beneath, glabrescent above, minutely glandular beneath the pubescence, with a glabrous apiculum. Heads sessile, in terminal glomerules of 3-8; phyllaries ca. 17, narrowly ovate-triangular, yellowish-green with brown hyaline apices, densely woolly on the lower half, strongly graduated in 4-5 series, the inner 4-5 mm long, with an erect, whitish apical portion no more than 1 mm long. Pistillate flowers 18-20. Hermaphroditic flowers 4-5, the corollas 2.2-2.4 mm long. Achenes sparsely pubescent, mature size not observed; pappus bristles 12-14, separate, apparently basally caducous, monomorphic, those of the hermaphroditic flowers barely or not at all apically thickened. Known only from the type collection.

*Gnaphaliothamnus cryptocephalus* is similar to *G. lavandulaefolius*, *G. macdonaldii* and *G. costaricensis* in its short, narrow leaves with glandular upper surfaces. Among these three, it resembles the first in its nearly monomorphic pappus bristles. It differs from them all in its shorter phyllaries without long and prominent, white tips, fewer hermaphroditic flowers with much shorter corollas, and fewer pappus bristles. Numerous collections of *G. salicifolius* also have been made from the area of Volcán Tacana.

5. *Gnaphaliothamnus eleagnoides* (Klatt) Nesom, *comb. nov.* BASIO-NYM: *Chionolaena eleagnoides* Klatt, Leopoldina 23:88. 1887. TYPE: MÉXICO. Oaxaca: Pelado. *Liebmann 316* (GH ex herb. Klatt, drawing and fragment!). *Gnaphalium eleagnoides* (Klatt) S.F. Blake, *Contr. U.S. Natl. Herb.* 23:1511. 1926.

*Gnaphalium hypochionaeum* Schultz-Bip. *ex Klatt, nom. nud.*, Leopoldina 23:88. 1887.

Leaves elliptic to elliptic-oblong, 15-42 mm long, 4-8 mm wide, glandular, strongly bicolored with the upper surface glabrous and green, the margins revolute but sometimes only very narrowly so, the apex with a dark, indurated, terete apiculum. Heads distinctly pedicellate, in dense, corymboid cluster of 15-40, held mostly above the leaves; phyllaries glabrous to glabrate, 31-38. Pistillate flowers 16-19, the corollas 2.0-2.2 mm long. Hermaphroditic flowers 7-18, the corollas 2.9-3.0 mm long. Achenes ellipsoid, 1.2-1.4 mm long, sparsely pubescent; pappus bristles 21-29, slightly united basally, not caducous, strongly dimorphic. Central Oaxaca; open oak or pine woods, sometimes on steep, gravelly slopes; 2700-2900 m; flowering October-May.

This species is similar to and almost certainly most closely related to *Gnaphaliothamnus salicifolius* in its eglandular, glabrate, upper leaf surfaces and densely corymboid capitulescences above the leaves. *Gnaphaliothamnus eleagnoides* is clearly distinguished by its shorter, broader leaves, shorter corollas, greater number of hermaphroditic flowers and fewer pistillate flowers, and much thicker tipped, noncaducous pappus bristles. In the same area of Oaxaca where *G. eleagnoides* occurs, numerous collections of *G. salicifolius* have been made. I have seen no intermediates between the two taxa.

In the original description, Klatt counted 5 hermaphroditic flowers per heads on the type specimen, but an annotation by S.F. Blake on the GH sheet notes that there were 18.

6. *Gnaphaliothamnus lavandulaefolius* (Kunth) Nesom, *comb. nov.* BAsIONYM: *Elychrysum lavandulaefolium* Kunth, *Nov. Gen. & Sp.* 4 [folio]:68. 1818; 4 [quarto]:86. 1820. TYPE: MEXICO. Veracruz: "in frigidis Andium Mexicanorum in nobilissimo monte Nauhcampatepetle juxta urbem Perote. alt. 1720 hex. Floret Martio," *Humboldt & Bonpland s.n.* (HOLOTYPE: P fiche!. F photo and fragment!. GH fragment!). *Gnaphalium lavandulaefolium* (Kunth) S.F. Blake, *Contr. Gray Herb.* 52:21. 1917; not *Gnaphalium lavandulaefolium* Willd., 1804 (≡ *Helichrysum lavandulaefolium* [Willd.] D. Don).

*Gnaphalium lavandulaceum* DC., *nom. nov.*, *Prodr.* 6:227. 1837. *Chionolaena lavandulaceum* (DC.) Benth. & Hook. *ex Hemsley, Biol. Centr.-Amer.* 2:134. 1881.

Erect subshrubs from woody bases, 1-2(-3) cm tall. Stems and leaves densely tawny-white woolly-tomentose; stipitate glandular beneath, but this completely obscured by the tomentum. Leaves narrowly oblong, 7-12 mm long, 1.5-2.5 mm wide, the apex blunt, not apiculate. Heads sessile to subsessile in terminal glomerules of 2-5; phyllaries 34-56, strongly graduated in 6-7 series, the inner 8-10 mm long, ovate-lanceolate, the outer broadly obovate, all sparsely to moderately villous-tomentose below the apical portion. Pistillate flowers 21-24. Hermaphroditic flowers 9-19, the corollas 4-5 mm long. Achenes obovoid, 1.5-1.6 mm long, sparsely pubescent; pappus bristles 25-27, monomorphic or nearly so.

Veracruz, Puebla, Tlaxcala, Morelos, México, on the volcanic peaks of Perote, Orizaba, Malinche, Ixtaccihuatl, Popocatepetl, Tlaloc 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, at or above timberline; 4000-4300 m; (May-)June-October.

The plants from Perote and Orizaba are slightly differentiated from the rest of the species. The leaves have an indurated, thick, terete apiculum prominently protruding 0.2-0.5 mm from the tomentum (vs. leaf apex with a shorter

apiculum not protruding from the tomentum), a looser vestiture with the underlying stipitate glandular hairs visible (vs. a close tomentum completely obscuring the glandular understory) and hermaphroditic flowers ranging only 9-10 in number (vs. 10-23). There is some intergradation, however, and compared to differences between other species in the genus, these do not appear significant enough to warrant formal taxonomic recognition.

7. *Gnaphaliothamnus macdonaldii* Nesom, *spec. nov.* TYPE: MÉXICO.

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!).

*Gnaphaliothamnus lavandulaefolio* (Kunth) Nesom similis sed phyllariis glabris et floribus pistillatis et hermaphroditicis 12-18, in numero circa equalibus in capitulo unico. acheniis longioribus, et setis pappo dimorphis differt.

Subshrubs 1-2(-3) dm tall. Leaves equally pubescent above and beneath, with an understory of short, stipitate glandular hairs, but this obscured by the tomentum. Leaves narrowly elliptic-ob lanceolate, 10-12 mm long, 1.5-2.0 mm wide, the apex with an indurated apiculum prominently protruding through the tomentum. Heads campanulate-hemispheric, 6-7 mm wide; phyllaries 27-41, not at all woolly, glabrous or usually with numerous, minute, appressed, viscid, elongate hairs, in 5-7 strongly graduated series, the outer ovate, the inner lanceolate, 7-8 mm long, the apices strongly spreading to slightly reflexed; receptacles shallowly alveolate. Pistillate flowers 12-18, the corollas 4.0-4.5 mm long. Hermaphroditic flowers 12-18, equal within 1-2 to the number of pistillate flowers, the corollas 4.2-4.5 mm long. Achenes ellipsoid, 1.8-2.0 mm long, sparsely pubescent; pappus bristles 19-27, dimorphic.

Known only from the type collection.

*Gnaphaliothamnus macdonaldii* is similar to *G. lavandulaefolius*, *G. costariensis* and *G. cryptocephalus* in its short leaves tomentose-glabrescent above with an understory of stipitate glandular hairs. Other distinctive features are its phyllaries pubescent with viscid, appressed hairs, pistillate and hermaphroditic flowers in nearly equal numbers (both ranging 12-18 per head), relatively long achenes, and dimorphic pappus bristles.

8. *Gnaphaliothamnus salicifolius* (Bertol.) Nesom, *comb. nov.* BASIONYM: *Helichrysum salicifolium* Bertol., Nov. Comm. Acad. Sci. Bonon. 4:433. 1840. TYPE: Guatemala. "Vulcan d'acqua" (US fragment, *fide* Blake 1926). *Gnaphalium salicifolium* (Bertol.) Schultz-Bip., Bot. Zeit. 3:172. 1845.

*Gnaphalium seemannii* Schultz-Bip. in Seem., *Bot. Voy. Herald* 309. 1856. TYPE: MÉXICO. [Durango?]: Sierra Madre. *Seemann 1994* (K).

*Gnaphalium rhodanthum* Schultz-Bip. in Seem., *Bot. Voy. Herald* 310. 1856. SYNTYPES (not seen): MÉXICO. Chiapas: Jitotole, pine forests, 6900 ft. Feb 1840. *Linden 437*; Hidalgo: near El Sumate, 11,000 ft. *Ehrenberg 332*. As synonym *vide* McVaugh (1984).

*Chionolaena corymbosa* Hemsl., *Diagn. Pl. Nov.* 32. 1879. TYPE: MÉXICO. [Durango?]: Sierra Madre, *Seemann 1994* (K).

Subshrubs 1-10 dm tall. Leaves linear to narrowly oblanceolate. 2-8 cm long, 1-3(-5) mm wide, the narrower with prominently revolute margins, e-glandular, strongly bicolored with the upper surfaces greenish and glabrescent. Heads numerous, in dense, corymboid clusters above the leaves; phyllaries 24-37, lightly woolly basally, in 4-7 strongly graduated series, the inner 6-7 mm long, white or pinkish apically. Pistillate flowers (22-)34-55. Hermaphroditic flowers 3-4(-7), the corollas (3.6-)4.0-4.5 mm long. Achenes ellipsoid, 1.0-1.3 mm long, sparsely pubescent; pappus bristles 15-22, slightly dimorphic, basally caducous, slightly connate basally and often released in groups.

Durango, Jalisco, Michoacán, Guerrero, México, Morelos, Hidalgo, Veracruz, Puebla, Oaxaca and Chiapas, Guatemala: steep, rocky slopes, ledges, ridges, openings in oak, pine or fir woods, evergreen cloud forests in Chiapas and Guatemala; (2150-)2500-3500(-4100) m; mostly flowering October-March.

*Gnaphaliothamnus salicifolius* is recognized by its linear, eglandular, bicolored leaves, heads in dense corymbs above the leaves, large number of pistillate flowers and basally caducous, slightly dimorphic pappus bristles. The leaf shape is highly variable in this species, which also is the most widespread and ecologically variable species of the genus. It commonly occurs at high elevations but also in a lower range of elevations than most of the other species.

This species apparently grows in close proximity to several others of the genus without forming hybrids. One sheet from Volcán Ixtaccihuatl ("Rocks above timberline," *Purpus 1529* [GH]) bears plants of *Gnaphaliothamnus salicifolius* and *G. lavandulaefolius*. The leaves of the former are atypically small and pubescent, but it seems to be completely distinct in its diagnostic characters. See additional comments following *G. eleagnoides* and *G. cryptocephalus*.

9. *Gnaphaliothamnus sartorii* (Klatt) Nesom, *comb. nov.* BASIONYM: *Chionolaena sartorii* Klatt, *Leopoldina* 23:89. 1887. TYPE: MÉXICO. [Oaxaca]: "Sempoaltepec" *Liebmann 308* (HOLOTYPE: GH *ex herb.* Klatt drawing and fragment!). *Gnaphalium sartorii* Schultz-Bip. *ex Klatt, nom. nud.* *Leopoldina* 23:89. 1887. *Gnaphalium sartorii* (Klatt) F.J. Espinosa, *Bol. Soc. Bot. Mex.* 45:21. 1983.

Stems apparently less than 10 cm tall, densely tomentose. Leaves crowded, ascending above, deflexed below, narrowly oblong, 7-8 mm long, 1 mm wide, tomentose-glabrescent above, eglandular, the margins revolute. Heads few, pedicellate, in loose clusters slightly above the leaves; phyllaries 20-25, in ca. 3-5 subequal series, all lanceolate, the inner 5-6 mm long, with white, spreading-ascending tips 1-2 mm long. Pistillate flowers 15. Hermaphroditic flowers 6. Achenes not seen.

Known to me only from the type drawing and fragments (small stem portion with leaves and three heads-phyllaries only, no flowers). The small size of the receptacles with few bundle scars roughly confirms Klatt's count of few flowers (21 total, 6 hermaphroditic, 15 pistillate). The combination of its small stature, narrow, eglandular leaves, few flowers and narrow, subequal phyllaries eliminates *Gnaphaliothamnus sartorii* from consideration as any other known species of the genus. It is maintained here as a valid species despite the fragmentary information regarding its morphology. At least one of the specimens cited by Espinosa (1985) as *G. sartorii* is a plant of *G. salicifolius* (Lyonnet 791, from Edo, México).

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