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REPARTITION OF *MAIRIA* (ASTERACEAE: ASTEREAEE)

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ABSTRACT

The genus *Mairia* Nees, as recently treated or discussed, includes three disparate elements, each essentially restricted to South Africa. The typical element of the genus comprises three species and is here hypothesized to be a member of the subtribe Hinterhuberinae. One of the remaining species is treated within the genus *Gymnostephium* as ***G. papposum*** Nesom, *nom. nov.* (= *Mairia corymbosa* Bolus, not *G. corymbosum* [Turcz.] Harvey). The other ten species, including both blue/white-rayed and yellow-rayed taxa, are treated as *Zyrphelis* Cass. (including *Homochroma* DC.). In addition to the nomenclature already available for *Zyrphelis*, four new combinations are proposed: ***Z. angolensis***, ***Z. decumbens***, ***Z. montana***, and ***Z. perezoides***. *Zyrphelis* is closely related to *Gymnostephium* and *Polyarrhena*, as well as to *Felicia* and other genera primarily centered in South Africa, but it is distantly related to the Hinterhuberinae. Taxonomic summaries are presented for *Mairia*, *Zyrphelis*, and *Gymnostephium*.

KEY WORDS: *Mairia*, *Zyrphelis*, *Gymnostephium*, *Polyarrhena*, Hinterhuberinae, Astereae, Asteraceae

The genus *Mairia* Nees has been recognized by Grau (1971, 1973) as a member of the group of primarily South African genera closely related to *Felicia* Cass. Zhang & Bremer (1993) did not comment on the definition of *Mairia* but accepted Grau's phylogenetic disposition of the genus, positioning it within the group of related genera, including *Felicia*, that they referred to as the "Amellus [L.] group." While it is apparent that most of the species currently treated as *Mairia* are part of the *Amellus* group, Harvey (1865, p. 64) noted that the genus comprises "plants associated by an artificial character, the feathery pappus," and followed earlier botanists, including Lessing and DeCandolle, in recognizing infrageneric groups. Grau (1971, 1973, 1977) also

observed that *Mairia* is artificial and composed of subgroups united by the production of plumose pappus bristles on the ray and disc achenes. Grau's opinion (1971) that these subgroups should be separated was unequivocal in a "flow-chart" (p. 278) showing the disposition of a small set of generic level taxa. In that chart he indicated that *Mairia* should be divided into two groups: *Mairia* and *Zyrphelis* Cass. These evidently correspond to "*Mairia* group I" and "*Mairia* group II" of his Figure 3 (1971, p. 277). The present study confirms the polyphyletic nature of *Mairia*.

Nees (1832) originally recognized two species within *Mairia* (*M. crenata* and *M. perezoides*, see taxonomic summary below). DeCandolle (1836) recognized the segregate *Homochroma* DC. but consolidated a number of other species into *Mairia*. *Homochroma* was subsequently incorporated into *Mairia* by Harvey (1865). Kuntze (1891) recognized that Cassini's name *Zyrphelis* predates *Mairia*, and, apparently assuming that all of the species involved represent a single natural group, he made a number of nomenclatural transfers from the latter to the former. The two taxa, however, are heterotypic and their names apply to two of the species groups within *Mairia* that are here hypothesized to be of different phyletic affinity.

Mairia is here reduced to a genus of three species; other species heretofore treated as *Mairia* are distributed between *Zyrphelis* and *Gymnostephium*, which appear to be closely related between themselves but not to *Mairia* sensu stricto. Following is a synoptic account of the three species groups among those taxa generally recognized as *Mairia* (sensu lato), with an indication of their disposition proposed in the present study. A taxonomic summary of the species of each genus is presented at the end of the paper.

1. Herbs with a vestiture of flexuous, thin-based hairs; stems monocephalous, scapose; leaves thick, broadly obovate (10-35 mm wide), in a basal rosette; heads 15-25 mm wide; phyllaries completely herbaceous, flat; ray flowers with broad (3-5 mm), weakly coiling ligules, commonly with staminodia; disc flowers with fertile ovaries; achenes narrowly oblong to oblong-oblancoelate, (2-3-)4-6-nerved, flattened but plump, the surface tan at maturity, glandular and often densely strigose-sericeous, the achenial "twin-hairs" with terminal cells highly uneven in length and strongly divergent; pappus persistent, of 1-2 series of plumose bristles, or with inner series of bristles and an outer series of long scales.
 *Mairia*
1. Subshrubs or basally lignescent herbs with vestiture of stout, thick-based, usually spreading hairs, sometimes also lightly tomentose; stems prominently branching with numerous heads, less commonly monocephalous; leaves linear, almost all cauline or less commonly mostly basally disposed; heads 3-12(-18) mm wide; phyllaries with broad, scarious margins,

strongly concave; ray flowers with narrow (1.0-2.5 mm), tightly coiling ligules, without staminodia; disc flowers with sterile ovaries (fertile in *Zyrphelis perezoides* [Less.] Nesom); achenes oblong-obovate, 2-nerved, strongly flattened, the surface black at maturity and minutely "pebbled", eglandular, sparsely to densely invested with "twin-hairs" with terminal cells even in length and connate to the apex or nearly so, the twin-hairs either (a) filiform or (b) very short and obovate, appearing white-papillate, or the twin-hairs absent; pappus of basally caducous bristles in a single series. (2)

2. Fertile achenes moderately to densely strigose-sericeous with filiform hairs; rays white to blue, or yellow; pappus of ray achenes similar to that of disc (sterile) achenes, of plumose bristles. *Zyrphelis*
2. Fertile achenes moderately to densely invested with short, white papillae, or glabrous to glabrate; rays white to blue; pappus of ray achenes lacking or of only 1-2 plumose or short-serrate bristles (with numerous bristles in one species), disc (sterile) achenes with more bristles. *Gymnostephium*

The position of *Zyrphelis* and *Gymnostephium*

A diagram of relationships among genera of the *Amellus* group by Grau (1973, p. 251) indicates "*Mairia pro parte*" (certainly referring to *Zyrphelis*) most closely resembles the genus *Gymnostephium*, although the diagram implies that *Mairia* p.p. and *Gymnostephium* are each perhaps derived independently from species of *Felicia*. Indeed, *Gymnostephium* is similar to typical *Zyrphelis* in features of habit and vestiture as well as leaf, floral, and achenial morphology. The two genera are notably similar in the consistent ovarian sterility of their disc flowers (except for *Z. perezoides*), their minutely pebbled achene surfaces, and their production of plumose pappus bristles; both are genera mostly restricted to South Africa.

The features common to *Zyrphelis* and *Gymnostephium* that are divergent from *Mairia* are congruent with morphology characteristic of the *Amellus* group. Especially notable among these features are the caducous pappus elements, usually a single series of bristles (of scales and bristles in *Amellus*, *Chrysocoma* L., and *Engleria* O. Hoffm., but the bristles still basally caducous); some species of *Felicia*, however, have persistent bristles. Disc flowers with abortive ovaries occur in all species of *Gymnostephium* Less., all but one of *Zyrphelis*, and some species of *Felicia*, *Polyarrhena* Cass., and *Nolletia* Cass. Achenes in the *Amellus* group are mostly obovate and flat with two, thickened, lateral ribs; they are eglandular, except in *Nolletia*, where achene surfaces are "pocked" and glandular-appearing.

Gymnostephium is distinctive in its reduced pappus, the bristles varying from barbellate to slightly or prominently plumose: the disc achenes (sterile) usually have 2-3 bristles, while the ray achenes are either epappose or produce 1-2 bristles. In *Zyrphelis*, the pappus of both ray and disc achenes is represented by a single series of 8-12 bristles.

One species of *Felicia*, which represents the monotypic genus *Charieis* Cass. (*C. heterophylla* Cass. = *F. heterophylla* [Cass.] Grau), also has plumose pappus bristles, although the plumose lateral extensions are produced mostly on the upper half of the bristles, compared to the entire length of the bristles in *Zyrphelis* and *Gymnostephium*. The ray achenes of *Charieis* are epappose and also are commonly sterile. *Charieis* has been transferred into a subgroup of *Felicia* (Grau 1973) where it appears to fit in chromosome number and other aspects of morphology. Outside of the African species, plumose pappus bristles occur in *Monoptilon* Torr. & Gray of the western United States and, to a reduced degree, in few species of *Vittadinia* A. Rich. of the Australasian region. *Monoptilon* is similar in many respects to the *Amellus* group and apparently closely related to it (Nesom in prep.); *Vittadinia* is not closely related to either the *Amellus* group or to *Mairia* sensu stricto and its putative relatives, as hypothesized here.

The faces of mature achenes of *Gymnostephium* and *Zyrphelis* become minutely pebbled, an easily visible feature with 10-20 \times magnification. Grau (1971) described these distinctive epidermal cells of *Mairia* achenes as "plaster-like." The most reliable distinction between *Zyrphelis* and *Gymnostephium* is in the nature of their achenial vestiture. The achenes of *Zyrphelis* are strigose-sericeous with long, filiform twin-hairs; achenes of *Gymnostephium* (for the most part) are densely white-papillate with short twin-hairs with a rounded-clavate apex. Achenes of *G. gracile* Less., *G. fruticosum* DC., and *G. leve* Bolus commonly are glabrous, but those of *G. leve* sometimes produce very short hairs with minutely divergent apices. Another aspect of achenial variation among *Gymnostephium* species is discussed below in connection with *Polyarrhena*.

The nature of achenial vestiture in *Gymnostephium* is more conservative than features of the pappus (number of bristles on ray and disc, degree of "plumosity"). Based on its achenial vestiture, *Mairia corymbosa* Harvey is transferred in the present paper to *Gymnostephium*, as the achenes of *M. corymbosa* are identical to those of most species of *Gymnostephium* (including the typical ones) in their densely white-papillate faces. Harvey (1865, p. 66) noted that *M. corymbosa* is "Almost identical in aspect and foliage with *Gymnostephium corymbosum* [Harvey], but with a very different involucre and copious feathery pappus." The latter species has hispidulous peduncles and phyllaries (vs. glabrous or glabrate in *M. corymbosa*) and pappus bristles with lateral (plumose) extensions much shorter than *M. corymbosa*. There is variability, however, in pappus "plumosity" among other species of *Gymnos-*

tephium, and there is variation in vegetative vestiture among species of both *Gymnostephium* and *Zyrphelis*. The epithet ("papposa") for the newly transferred species refers to the relatively greater number (within *Gymnostephium*) of pappus bristles on each achene.

The ray flowers of all species of *Gymnostephium* produce white to bluish ligules. Within *Zyrphelis*, the yellow-rayed *Z. ecklonis* (DC.) Kuntze, *Z. lasiocarpa* (DC.) Kuntze, and *Z. angolensis* (Chiov.) Nesom are distinct from the otherwise blue- or white-rayed species. *Zyrphelis ecklonis* was originally described as the monotypic genus *Homochroma* DC., but Harvey (1865) noted that there is essentially nothing except ray color to separate this species from its closest relatives (within *Zyrphelis*), and this synonymy has been followed in recent accounts of South African genera.

Resemblance of *Zyrphelis* and *Gymnostephium* to *Polyarrhena*

Zyrphelis and *Gymnostephium* are similar to the genus *Polyarrhena* (Grau 1970) in habit, vestiture (all have a tendency to produce stipitate-glandularity), leaf morphology, and particularly their tendency to produce disc flowers with sterile ovaries. These three genera appear to constitute a natural group apart from *Felicia*. *Polyarrhena* differs from *Zyrphelis* and *Gymnostephium* in its ligules with a purple, abaxial midstripe (vs. without a midstripe), mature achenes of tan color (vs. black) with smooth, glabrous surfaces (vs. minutely pebbled and strigose-sericeous, papillate, or glabrous) and with a conspicuous, apical collar of light-colored tissue, apparently an outgrowth of the top of the achene wall (vs. without a collar), and serrate pappus bristles (vs. bristles plumose to serrate).

The resemblance between *Polyarrhena* and *Gymnostephium* is emphasized by the observation of what appears to be an incipiently but distinctly formed apical collar on both ray and disc achenes of *G. leve* (e.g., *Esterhuysen 39167* - MO!). The plants of this collection produce glabrous, smooth-faced achenes, and while the apical outgrowth is not as thick as the collar found on achenes of typical *Polyarrhena*, they appear to be homologous. The resemblance is so strong, in fact, that *G. leve* may be better placed within *Polyarrhena*.

A hypothesis of close relationship between *Polyarrhena* and *Zyrphelis* is strengthened by the observation of naturally occurring hybrids between *P. reflexa* (L.) Cass. subsp. *reflexa* and *Z. taxifolia* (L.) Nees on the Cape Peninsula of South Africa. According to label notes on *Esterhuysen 31098* (MO!, distributed from BOL), "A number of plants of this hybrid were present at this locality."

The position of *Mairia* sensu stricto

Grau (1973) was not specific regarding the composition or placement of the portion of *Mairia* not immediately related to *Felicia* and *Gymnostephium* (i.e., the species of *Zyrphelis*). *Mairia* sensu stricto, however, is a remarkably distinct genus that appears to be a member of the Hinterhuberinae (sensu Nesom 1993a, 1993b), showing particular similarities in its tomentose vestiture, broad, coriaceous leaves, multiseriate and persistent pappus, and glandular, multi-ribbed achenes. As such it becomes only the fifth genus of this large subtribe known from the Africa-Madagascar region, joining the African *Pteronia* L. and the Madagascan *Rochonia* DC., *Madagaster* Nesom, and *Apodocephala* J. Baker (the position of *Apodocephala* is discussed in detail in a separate paper, Nesom in prep.). Among these genera, *Mairia* most resembles *Madagaster* and *Rochonia* in leaf and achene morphology and *Madagaster* in ligule color. *Mairia* may be a herbaceous derivative of woody ancestors (i.e., *Madagaster* and *Rochonia* and most other members of the subtribe), as is also the case for several South American genera (e.g., *Laestadia* Kunth, *Oritrophium* [Kunth] Cuatr.). Even if *Mairia* sensu stricto should prove to be more closely related to genera among the *Amellus* group or some other, the argument still remains for the closer relation of *Zyrphelis* and *Gymnostephium*, leaving *Mairia* separate.

The group of species referred to by Grau (1971) as the "herbaceous Diplopappi" or in his "flow chart" of genera (1971, p. 278) as "*Aster harveyanus* O. Kuntze and related species" were treated by Lippert (1971, 1973) within the genus *Aster* L. Grau's observation (1971, p. 279) that "there is still lacking a valid generic name for the herbaceous 'Diplopappi'" implies that he would place these in some other genus, but as detailed in a separate discussion (Nesom in prep.), I have not been able to find justification for separating these from true *Aster*. In their flat achenes with glandular surfaces and persistent, biseriate pappus, these African plants resemble *Mairia* sensu stricto, but their similarity to *Aster* seems more immediate.

Taxonomic summaries

Mairia Nees, *Gen. & Sp. Aster*. 247. 1832. LECTOTYPE (designated here):
Mairia crenata (Thunb.) Nees.

Nees included two species in his original circumscription of the genus. *Mairia crenata* is the best known and longest established of these and is here formally designated as the lectotype, following the implicit suggestion by Pfeiffer (*Nom. Bot.* 2[1]:207. 1874.). The spelling of the genus has sometimes been modified to *Mairea* (e.g., Harvey 1865), as the name commemorates M. Maire, an early collector in South Africa, but the original spelling by Nees is justifiably regarded as correct.

Aster subg. *Pteropappus* Less., *Synops. Gen. Comp.* 166. 1832. *Mairia* sect. *Pteropappus* (Less.) DC., *Prodr.* 5:217. 1836. LECTOTYPE (designated here): *Aster crenatus* (Thunb.) Less. (= *Mairia crenata* [Thunb.] Nees).

Lessing included two species (as *Aster*) in his original description of subg. *Pteropappus*: *Mairia crenata* and *Zyrphelis perezioides*. The decision here to lectotypify it as *Mairia* rather than *Zyrphelis* is somewhat arbitrary.

1. *Mairia coriacea* Bolus, Hook. Ic. Pl., ser. 4, 26:tt. 2541. 1899.
2. *Mairia crenata* (Thunb.) Nees, *Gen. & Sp. Aster.* 248. 1832. BASIONYM: *Arnica crenata* Thunb., *Prodr. Fl. Capens.* 2:154. 1800. *Aster crenatus* (Thunb.) Less., *Synops. Gen. Comp.* 166. 1832. *Gerbera crenata* (Thunb.) Ker-Gawl., *Bot. Reg.* 10:t. 855. 1825. *Zyrphelis crenata* (Thunb.) Kuntze, *Rev. Gen. Pl.* 1:374. 1891.
3. *Mairia hirsuta* DC., *Prodr.* 5:217. 1836. *Zyrphelis hirsuta* (DC.) Kuntze, *Rev. Gen. Pl.* 1:374. 1891.

Zyrphelis Cass., *Ann. Sci. Nat. (Paris)* 17:420. 1829. *Elphegea* subg. *Zyrphelis* (Cass.) Less., *Synops. Gen. Comp.* 183. 1832. *Mairia* sect. *Zyrphelis* (Cass.) DC., *Prodr.* 5:218. 1836. TYPE: *Zyrphelis amoena* Cass. (= *Zyrphelis tazifolia* [L.] Nees).

Homochroma DC., *Prodr.* 5:324. 1836. *Mairia* sect. *Homochroma* (DC.) Harvey in Harvey & Sonder, *Fl. Capens.* 3:64. 1865. TYPE: *Homochroma ecklonis* DC. (= *Zyrphelis ecklonis* [DC.] Kuntze).

1. *Zyrphelis angolensis* (Chiov.) Nesom, *comb. nov.* BASIONYM: *Homochroma angolensis* Chiov., *Boll. Soc. Bot. Ital.* 43. 1924.
2. *Zyrphelis burchellii* (DC.) Kuntze, *Rev. Gen. Pl.* 1:374. 1891. BASIONYM: *Mairia burchellii* DC., *Prodr.* 5:218. 1836.
3. *Zyrphelis decumbens* (Schlechter) Nesom, *comb. nov.* BASIONYM: *Mairia decumbens* Schlechter, *Bot. Jahrb. Syst.* 27:199. 1900.
4. *Zyrphelis ecklonis* (DC.) Kuntze, *Rev. Gen. Pl.* 1:374. 1891. BASIONYM: *Homochroma ecklonis* DC., *Prodr.* 5:324. 1836. *Mairia ecklonis* (DC.) Sonder in Harvey & Sonder, *Fl. Capens.* 3:66. 1865.

5. *Zyrphelis foliosa* (Harvey) Kuntze, *Rev. Gen. Pl.* 1:374. 1891. BASIONYM: *Mairia foliosa* Harvey in Harvey & Sonder, *Fl. Capens.* 3:66. 1865.
6. *Zyrphelis lasiocarpa* (DC.) Kuntze, *Rev. Gen. Pl.* 1:374. 1891. BASIONYM: *Mairia lasiocarpa* DC., *Prodr.* 5:218. 1836. *Felicia lasiocarpa* (DC.) Compton, *Trans. Roy. Soc. S. Africa* 19:312. 1931.
7. *Zyrphelis microcephala* (Less.) Nees, *Gen. & Sp. Aster.* 252. 1832. *Mairia microcephala* (Less.) DC., *Prodr.* 5:218. 1836. BASIONYM: *Elphegea microcephala* Less., *Synops. Gen. Comp.* 184. 1832.

Aster nanus E. Mey. ex DC. [*in syn.*], *Prodr.* 5:218. 1836.

The treatments by Nees and Lessing both appeared in 1832, but it is apparent that Nees had seen Lessing's manuscript and credited him with the original authorship of this name. The same is true for *Zyrphelis perezoides* (below).

8. ***Zyrphelis montana*** (Schlechter) Nesom, *comb. nov.* BASIONYM: *Mairia montana* Schlechter, *Bot. Jahrb. Syst.* 27:199. 1900.
9. ***Zyrphelis perezoides*** (Less.) Nesom, *comb. nov.* *Mairia perezoides* (Less.) Nees, *Gen. & Sp. Aster.* 249. 1832. BASIONYM: *Aster perezoides* Less., *Synops. gen. Comp.* 167. 1832.
10. *Zyrphelis tazifolia* (L.) Nees, *Gen. & Sp. Aster.* 250. 1832. BASIONYM: *Aster tazifolius* L., *Pl. Rar. Afr.* 22. 1761. *Mairia tazifolia* (L.) DC., *Prodr.* 5:218. 1836.

Leyssera ciliata Thunb., *Prodr. Fl. Capens.* 2:160. 1800. *Elphegea ciliata* (Thunb.) Less., *Linnaea* 6:126. 1831.

Zyrphelis amoena Cass., *Ann. Sci. Nat. (Paris)* 17:421. 1829.

Mairia pinifolia Sch.-Bip. ex Walp., *Repert. Bot.* 2:955. 1843.

Mairia lasiocarpa Drege ex Harvey & Sonder [*in syn.*], *Fl. Capens.* 3:65. 1865.

Gymnostephium Less., *Syn. Gen. Comp.* 185. 1832. LECTOTYPE (designated here): *Gymnostephium hirsutum* Less.

DeCandolle included two species in his original circumscription of this genus: *Gymnostephium gracile* and *G. hirsutum* Less. As noted above, *G. gracile* has a distinctive resemblance to the related genus *Polyarrhena*, and to avoid a potential problem (should they prove to be congeneric), *Gymnostephium* is here lectotypified with *G. hirsutum*. The latter species has black achenes with white-papillate surfaces and is similar in other features to the majority of other species included in *Gymnostephium*.

Heteractis DC., *Prodr.* 6:468. 1838. TYPE: *Heteractis falcata* DC. (= *Gymnostephium ciliare* (DC.) Harvey in Harvey & Sonder).

1. *Gymnostephium angustifolium* Harvey in Harvey & Sonder, *Fl. Capens.* 3:67. 1865.
2. *Gymnostephium ciliare* (DC.) Harvey in Harvey & Sonder, *Fl. Capens.* 3:68. 1865. BASIONYM: *Felicia ciliaris* DC., *Prodr.* 5:221. 1836.
Heteractis falcata DC., *Prodr.* 6:469. 1838. *Osteospermum falcatum* E. Mey. ex DC. [*in syn.*], *Prodr.* 6:469. 1838.
3. *Gymnostephium corymbosum* (Turcz.) Harvey in Harvey & Sonder, *Fl. Capens.* 3:67. 1865. BASIONYM: *Agathaea corymbosum* Turcz., *Bull. Soc. Imp. Naturalistes Moscou* 24:60. 1851.
4. *Gymnostephium fruticosum* DC., *Prodr.* 5:300. 1836.
5. *Gymnostephium gracile* Less., *Syn. Gen. Comp.* 186. 1832.
6. *Gymnostephium hirsutum* Less., *Syn. Gen. Comp.* 185. 1832.
7. *Gymnostephium leve* Bolus, *Trans. S. African Philos. Soc.* 16:138. 1907.
8. ***Gymnostephium papposum*** Nesom, *nom. nov.* Based on: *Mairia corymbosa* Harvey in Harvey & Sonder, *Fl. Capens.* 3:66. 1865; not *Gymnostephium corymbosum* (Turcz.) Harvey. *Zyrphelis corymbosa* (Harvey) Kuntze, *Rev. Gen. Pl.* 1:374. 1891.

Taxa excluded from *Mairia*, *Zyrphelis*, and *Gymnostephium* or of uncertain position:

Mairia felicoides Hutch. & Corb., Kew Bull. 10:329. 1920. = *Felicia ovata* (DC.) Compton (Grau 1973).

Mairia pustulata Phillips, Ann. S. African Mus. 9:342. 1917.

This species was described as having obovate leaves in a basal rosette, monocephalous stems, bisexual disc flowers, and a plumose pappus. I have not seen specimens of *Mairia pustulata* but it seems likely that these plants may belong in *Felicia* sect. *Dracontium* Grau (sensu Grau 1973).

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**ERIGERON PATTERSONII (ASTERACEAE: ASTEREAEE), A NEW SPECIES
FROM NUEVO LEON, MEXICO**

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ABSTRACT

A recent collection of *Erigeron* from a gypseous area of central Nuevo León, México, is described as *E. pattersonii* sp. nov. It is a narrow endemic closely similar to two other species also restricted to north-eastern México, *E. chiangii* and *E. scoparioides*. These three species are formally placed in *Erigeron* sect. *Lamprocaules* sect. nov.

KEY WORDS: *Erigeron*, Asteraceae, Astereae, gypsum, México

Recent collections from gypsum deposits in central Nuevo León, México, have brought to light a distinctive population of *Erigeron* that is described here as a new species.

Erigeron pattersonii Nesom, sp. nov. TYPE: MEXICO. Nuevo León, Mpio. Rayones, Sierra Madre Oriental, gypseous slope just E of road leading from Rayones to Galeana, 7.3 mi from jct on S side of Rayones toward Galeana, 24°55'45" N, 100°05'45" W; Tamaulipan scrub - lechuguilla - opuntia - barrel cactus association, 1500 m, 9 April 1994, T.F. Patterson 7479a (HOLOTYPE: MEXU; Isotypes: ANSM, GH, NY, TEX).

Erigeronti scoparioidi Nesom similis caulibus ac foliis paginis nitidis, foliis basalibus carentibus, foliis caulinis lineari-filiformibus stricte ascendenti-erectis apice falcatis-apiculato, gemmis erectis, et capitulis parvis sed differt basi lignea non-rhizomata, caulibus ac foliis paene glabris, capitulis minoribus, phyllariis zona centrali crassi-resinacea, corollis disci induratis, acheniis minoribus, et pappo redactoribus.

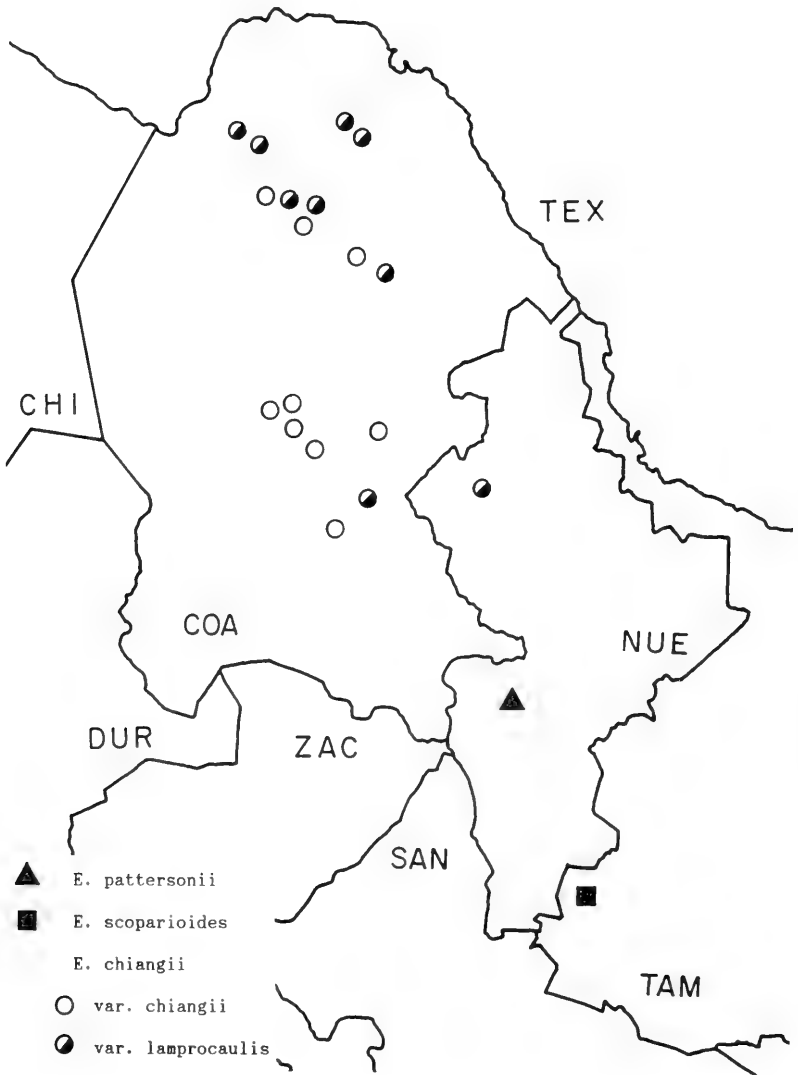
Herbaceous perennials, leaves and stems with a shiny texture, eglandular and otherwise completely glabrous or with only a few Type A trichomes (Nesom 1976) at the base of the involucre and on the lower leaves. Stems strictly erect, wiry, 0.8-1.0 mm wide, ca. 10-20 densely arising from a woody base, 25-35 cm tall, simple or with 1-2 branches in the upper 1/4-1/3. Basal leaves absent, the lower cauline sometimes narrowly oblanceolate, up to 3 cm long, the widest part of the blade 2-5 mm wide; middle and upper cauline leaves linear-filiform, sessile, strictly ascending-erect, 10-20 mm long, 0.5-1.0 mm wide, with a falcate-apiculate apex. Heads 4-6 mm wide, on peduncles 1-3 cm long; buds erect; phyllaries lanceolate, in 3-4 series graduated in length, the inner 2.5-3.0 mm long, the outer ca. 1/2-1/3 as long, midvein not evident but the distal 2/3 with a narrowly oblanceolate, greenish-yellow, thickened and raised zone with prominently quadrate cells, with very narrow, whitish-scarious marginal zones. Pistillate flowers fertile, 28-38 in a single series, the corollas 3.5-4.5 mm long, including the tube ca. 1 mm long, the ligules 0.4-0.6 mm wide, white or pinkish tinged, without a midstripe, not coiling or reflexing. Disc corollas narrowly tubular, 1.5-2.0 mm long, the tube green, 0.3-0.4 mm long, abruptly but slightly expanded into an indurate portion, the lobes triangular-deltate, erect; style branches 0.3 mm long, with shallowly triangular collecting appendages. Achenes obovate-oblong, 0.8-0.9 mm long, sparsely strigose, 2-nerved; pappus of 11-15 fragile, barbellate bristles, with an extremely short outer series of minute scales or setae.

Known only from the type collection.

The new species is named for its collector, Tom Patterson, currently a graduate student in systematic botany at the University of Texas. Tom has a long-standing and continuing interest in the botany of northern México and has made substantial contributions to our knowledge of that flora through his studies, publications, and numerous collections.

Plants of *Erigeron pattersonii* are briefly characterized as follows: perennials with numerous, wiry-thin stems arising from a woody, non-rhizomatous base, the stems usually few-branched near the apex; stems and leaves with shiny surfaces, eglandular and almost completely glabrous; basal leaves absent, the cauline linear, strictly ascending-erect, with a falcate-apiculate apex, the lower cauline sometimes oblanceolate and spreading; buds erect; heads particularly small, producing short, non-coiling ligules; and phyllaries glabrous, strongly graduated in length, with a thick-resinous central area.

A form of *Erigeron modestus* A. Gray also occurs in the same area of gypsum (*Patterson 7473b*). These plants differ from *E. pattersonii* in strigose stems, leaves, and phyllaries, persistent basal leaves with a long, distinct petiole and oblanceolate blade, nodding buds, phyllaries with a narrow, orange-resinous midvein, and more than 100 ray flowers per head, the ligules 5-6 mm long, with a purple, abaxial midstripe. *Erigeron modestus* is related to a much larger group of species (sect. *Olygotrichium* Nutt., including, for exam-



Map 1. Distribution of the taxa of *Erigeron* sect. *Lamprocaules*.

ple, *E. divergens* Torr. & Gray, *E. flagellaris* A. Gray, *E. calcicola* Greenm., *E. pubescens* Kunth) common in northern México (Nesom 1989b).

Erigeron pattersonii is most similar to two other species restricted to northeastern México (Map 1): *E. chiangii* Nesom and *E. scoparioides* Nesom (Nesom 1979, 1989a, 1992b). All three produce glabrous to glabrate stems and leaves (commonly glandular in *E. chiangii*) with shiny surfaces, linear leaves, erect buds, small heads with strongly and evenly graduated phyllaries and few, non-coiling ligules. The falcate-apiculate leaf apices of *E. pattersonii* and *E. scoparioides* are remarkably similar.

In contrast, *Erigeron chiangii* and *E. scoparioides* have a rhizomatous root system without a central axis (vs. woody, non-rhizomatous base in *E. pattersonii*) and both occur in areas of limestone (vs. gypsum); heads are 6-12 mm wide in *E. chiangii*, 6-7 mm wide in *E. scoparioides* (vs. 4-6 mm); disc corollas are 2.6-4.0 mm high (vs. 1.5-2.0 mm); achenes are 1.3-1.8 mm long in *E. chiangii*, ca. 1 mm long in *E. scoparioides* (vs. 0.8-0.9 mm); and the pappus is of 16-22 bristles (vs. 11-15 bristles). *Erigeron chiangii* (var. *chiangii*) produces basal leaves that are sometimes persistent and it is similar to *E. pattersonii* in its tendency to produce somewhat oblanceolate lower cauline leaves, but *E. chiangii* has glandular involucre and the stems are glandular at least near the heads. *Erigeron scoparioides* lacks differentiated basal leaves, the stems are sparsely strigose, and the stems and involucre are eglandular.

Earlier, I suggested that this group of species with shiny, wiry stems and linear-filiform cauline leaves might be closely related to sect. *Linearifolii* (G. Don) Nesom (Nesom 1979, 1992a) or to sect. *Karvinskia* Nesom (Nesom 1989a), as all of these taxa are similar in their numerous stems from the base, lack of strongly differentiated basal leaves, erect buds, and sparsely pubescent stems and leaves. *Erigeron* sect. *Linearifolii* is essentially restricted to California and immediately adjacent areas, and these Californian taxa do not produce wiry stems or linear-filiform cauline leaves similar to those of the "shiny-stemmed species group." The center of diversity of sect. *Karvinskia* is primarily in Central America (Nesom in prep.), where they occur in considerably moister and warmer habitats, the surface texture of the stems and leaves of these plants is not at all indurate-shiny, they typically produce relatively large, oblanceolate leaves with toothed margins, and their phyllaries are subequal.

The three shiny-stemmed species of northeastern México are morphologically coherent but the nature of their relationship to other species within the genus is not clear. They are here formally recognized as a separate section.

Erigeron sect. **Lamprocaules** Nesom, sect. nov. Type species: *Erigeron scoparioides* Nesom; also including *Erigeron chiangu* Nesom and *E. pattersonii* Nesom.

Caules ac folia glabra paginis nitidis; caules tenues; folia caulina lineari-filiformi longitudine paene aequa, basali plerumque carenti; gemmae erectae; capitula parva (4-6 mm lata) phyllariis valde aequaliterque graduatis et ligulis non-circinnatis.

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I thank Billie Turner and Mark Mayfield for their review of the manuscript.

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**COMMENTS ON *MICROGYNELLA*, *SOMMERFELTIA*, AND
ASTEROPSIS (ASTERACEAE: ASTEREAEE)**

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ABSTRACT

Microgynella, *Sommerfeltia*, and *Asteropsis* are accepted as distinct, monotypic genera, and a taxonomic summary is presented for each. All three are limited in distribution to southeastern Brazil, Uruguay, Paraguay, and northeastern Argentina. They are closely related among themselves and to several other South American genera: *Podocoma*, *Rhabdanthus*, *Inulopsis*, *Laennecia*, and *Blakiella*.

KEY WORDS: *Microgynella*, *Sommerfeltia*, *Asteropsis*, Astereae, Asteraceae

Three Astereae species of southeastern South America each represent a monotypic genus. Nomenclatural summaries and comments on their delimitation and relationships are presented here in clarification of their taxonomic status.

The status of *Microgynella* and *Sommerfeltia*

Grau (1975) provided the new generic name *Microgynella* Grau for a South American species originally treated as the monotypic genus *Microgyne* Less. (Lessing 1832) and later transferred by Grisebach (1879) to the genus *Vittadinia* A. Rich. Grau correctly observed that *Vittadinia* is an Australasian endemic; he noted that *Microgynella* should be placed nearest *Hysterionica* Willd. and *Sommerfeltia* Less., but he did not discuss the nature or implication of their relationship to *Microgynella*.

Hysterionica sensu lato comprises two distinct species groups (Nesom 1993) that are now divided into two separate genera, the "jasionoides group" (= *Hysterionica* sensu stricto) and the "pinifolia group" (= *Neja* D. Don) (Nesom

1994). Plants of *Neja*, which are perhaps those referred to by Grau (1975) as *Hysterionica*, are perennial with basally disposed, linear leaves and solitary heads on long scapes or bracteate stems. Both *Hysterionica* and *Neja*, however, differ from *Microgynella* in their uniseriate pistillate flowers, eglandular achenes that are fertile in both ray and disc flowers, prominent orange-resinous ducts accompanying the veins of phyllaries and achenes, and style branches (disc flowers) with deltate collecting appendages. *Microgynella* cannot be regarded as a particularly close relative of either *Hysterionica* or *Neja*.

The resemblance of *Microgynella* to *Sommerfeltia* was early recognized by Hooker & Arnott (1836), who placed the former (as *Microgyne*) as a synonym of the latter. They are similar in the following features: herbaceous-perennial habit, the roots and lower stems lignescent; leaves densely arranged along the stems, glandular, stiff, pinnately lobed or dissected with linear divisions; ray flowers with white, short ligules; style branches with linear-lanceolate collecting appendages (clearly in *Microgynella*, apparently in *Sommerfeltia*, where the stigmatic lines are absent); and erostrate achenes with glandular faces. Both genera are restricted to southeastern Brazil and adjacent areas of Uruguay and Argentina.

In the key to genera of Astereae in the province of Buenos Aires, *Sommerfeltia* was distinguished by Cabrera (1963, p. 10) from *Microgynella* (the latter identified as "*Vittadinia*") and other genera by the following: "Arbustivos enanos, con hojas pinatisectas espiniformes (*Sommerfeltia*)." The putative difference in habit between *Sommerfeltia* and *Microgynella* is slight (both have a suffrutescent tendency), and the leaves of both are rigid and narrowly divided. The differences between the two genera, however, are more numerous and more significant than in Cabrera's comparison, as outlined in the following summary:

Microgynella:

Stems, leaves, and phyllaries with sessile or slightly sunken, resinous glands, sparsely hispid and with arachnoid vestiture; stems monocephalous; leaves linear, apically trifurcate with a pair of linear lobes, but the uppermost and lower leaves commonly entire; disc flowers fertile; achenes densely sericeous on the faces and margins, also densely glandular, broadly oblanceolate-obconic and apically truncate, the margins more or less parallel at the apex, with a broad pappus insertion; and pappus bristles reddish-brown.

Sommerfeltia:

Stems, leaves, and phyllaries stipitate-glandular, without arachnoid vestiture; stems monocephalous or less commonly distally branched and bearing several heads in a loosely paniculate-corymbose capitulescence; leaves pinnately dissected with linear lobes;

disc flowers with sterile ovaries; achenes densely sericeous at the base or on the margins, the faces glandular but sparsely hairy, obovate and apically rounded, the margins apically confluent, with a narrow pappus insertion; and pappus bristles whitish.

Sommerfeltia cabreræ Chebat., a recently described species from northern Uruguay (Chebataroff 1981), cannot be accepted within *Sommerfeltia*. It differs from typical *Sommerfeltia* particularly in its entire leaves, completely fertile disc flowers, and differently shaped achenes with glandular, evenly strigose-sericeous faces. As observed by Chebataroff, it closely resembles *Hysterionica filiformis* (Spreng.) Cabrera (= *Neja filiformis* [Spreng.] Nees), but he rejected the species from *Hysterionica* sensu lato because of its lack of a short, outer series of pappus scales. Pappus variability among other species of *Neja* (Nesom 1994), however, includes such as found in *S. cabreræ*, but the correct generic placement of the latter is still under consideration (Nesom in prep.).

The status of *Asteropsis*

Asteropsis Less. comprises the single species *A. macrocephala* Less., which is restricted to southern Brazil and adjacent Uruguay. The species was regarded as a member of *Podocoma* Cass. by Bentham (1873), apparently because of its rostrate achenes, but it was accepted as an independent genus by Baker (1882) and Hoffmann (1890). Grau (1977) also regarded it as a synonym of *Podocoma*, a position apparently followed in the recent phylogenetic analysis and classification by Zhang & Bremer (1993). If treated within *Podocoma*, this species would have to be set apart from all of the others, differing in its combination of stems simple or 1-2 branched near the apex, densely arachnoid vestiture, entire, linear, non-clasping, densely arranged leaves, and large (20-35 mm in diameter), mostly solitary heads, linear-lanceolate phyllaries in 4-5 slightly graduated series, multiseriate ray flowers with long ligules (apparently white), disc flowers with sterile ovaries, and large (4-5 mm long), broadly obovate achenes with strongly thickened marginal ribs, a distinctively short-beaked apex, and sericeous, eglandular faces and margins. The features of *Asteropsis* place it among a group of South American genera that includes *Podocoma* (Nesom & Zanowiak 1994) as well as *Microgynella*, *Sommerfeltia*, *Inulopsis* Hoffm., *Rhabdanthus* Nesom, *Laennecia* Cass., and *Blakiella* Cuatr. Among these, however, *Asteropsis* is justifiably treated as an independent genus resembling *Microgynella* and *Sommerfeltia* in its densely crowded, linear leaves.

Taxonomic summaries

- I. *Microgynella* Grau (*nom. nov.*), Mitt. Bot. Staats. München 12:185. 1975.
Microgyne Less. [*nom. illeg.*], *Syn. Gen. Comp.* 190. 1832. (not Cass. 1827). TYPE: *Microgyne trifurcata* Less.
- Microgynella trifurcata* (Less.) Grau, Mitt. Bot. Staats. München 12:185. 1975. BASIONYM: *Microgyne trifurcata* Less., *Syn. Gen. Comp.* 190. 1832. *Erigeron trifurcatus* (Less.) Gill. & Don ex Hook. & Arn., *Comp. Bot. Mag.* 2:49. 1836. *Vittadinia trifurcata* (Less.) Benth. & Hook. ex Griseb., *Symb. Fl. Argent.* 24:178. 1879.
- Erigeron tridactylus* DC., *Prodr.* 5:290. 1836.
- II. *Sommerfeltia* Less., *Syn. Gen. Comp.* 189. 1832. TYPE: *Sommerfeltia spinulosa* (Spreng.) Less.
- Sommerfeltia spinulosa* (Spreng.) Less., *Syn. Gen. Comp.* 190. 1832. BASIONYM: *Conyza spinulosa* Spreng., *Syst. Veget.* 3:510. 1826.
- III. *Asteropsis* Less., *Syn. Gen. Comp.* 188. 1832. TYPE: *Asteropsis macrocephala* Less.
- Asteropsis macrocephala* Less., *Syn. Gen. Comp.* 188. 1832. *Podocoma macrocephala* (Less.) Herter, *Fl. Uruguay Pl. Vasc.* [Estud. Bot. Reg. Urug.] 123. 1931.
- Podopappus tomentosus* Hook. & Arn., *Comp. Bot. Mag.* 2:51. 1836.
- Neja macrocephala* DC., *Prodr.* 5:325. 1836. This name is heterotypic with that of *Asteropsis macrocephala* Less.
- Neja* sect. *Phylloneja* DC., *Prodr.* 5:325. 1836. Type (and only species): *Neja macrocephala* DC. (= *Asteropsis macrocephala* Less.).

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TAXONOMIC OVERVIEW OF *PODOCOMA* (ASTEREAE: ASTERACEAE),
WITH THE INCORPORATION OF TWO SPECIES FROM *CONYZA*

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ABSTRACT

Two South American species formerly treated as *Conyza* are here transferred to the genus *Podocoma*: ***P. notobellidiastrum*** (Griseb.) Nesom, *comb. nov.* and ***P. rivularis*** (Gardner) Nesom, *comb. nov.* Except for their achenes with only a short neck instead of a filiform beak and their reduced number of pappus series, these two species closely resemble other species of *Podocoma*, here regarded as a genus of approximately nine species occurring primarily in southern Brazil, eastern Bolivia, Paraguay, Uruguay, and northern Argentina. *Podopappus* Hook. & Arn. is lectotypified as a synonym of *Podocoma*. The monotypic genera *Asteropsis* (= *Podocoma macrocephala*) and *Blakiella* (= *Podocoma bartsiiifolia*) are distinct from *Podocoma*; the Australian genus *Iziochlamys* also includes species that formerly have been treated as *Podocoma*.

KEY WORDS: *Podocoma*, *Conyza*, Astereae, Asteraceae

In independent investigations of relationships among genera of the tribe Astereae, we have observed that two South American species treated as *Conyza* L. are misplaced in that genus: *C. notobellidiastrum* Griseb. and *C. rivularis* Gardner. In their habit and general appearance, particularly their tendency for basally disposed leaves, clasping cauline leaves, and fibrous roots from a short rhizome, as well as more technical characters (below), these two species fit comfortably within the South American genus *Podocoma* Cass. Their relationship to *Podocoma* has not been recognized previously because their achenes

have only a short, incipiently formed neck and pappus of one series of bristles with a short outer series of setae (Figures 1: C and D); in contrast, achenes of typical *Podocoma* are characterized by a narrow, distinct beak (the apex often only attenuate in *P. bellidifolia* Baker) and pappus of bristles in 2(-3) series of even length (Figures 1: A and B).

Apart from the difference in achene and pappus morphology, the separation of *Podocoma* and *Conyza* (with regard to the species under consideration) is more difficult, but the two genera represent separate phylads, and no other species of these two genera have been ambiguously intermixed in their taxonomy. The following comparison emphasizes their essential contrasting features.

PODOCOMA: phyllaries 1-veined without orange resin ducts accompanying the veins; disc corolla tube ca. $2/3$ the total length of the corolla, opening into a non-indurate throat; collecting appendages of the disc style branches lanceolate; achene apex attenuate or constricted into a neck or beak (Figures 1: A,B,C, and D); pappus mostly in 2-3 series of equal length.

CONYZA: phyllaries 3-veined with orange resin ducts accompanying the veins; disc corolla tube ca. $1/3$ - $1/4$ the total corolla length, opening into a slightly to strongly indurate throat; collecting appendages of the disc style branches deltate; achene apex truncate, erostrate (Figures 1: E,F, and G); pappus mostly in a single series, usually without any outer series.

In the features noted above, *Conyza notobellidiastrum* and *C. rivularis* belong with *Podocoma*, even though they appear to represent a specialized element within that genus. The vestiture of these two species is relatively reduced, compared to other *Podocoma*; their achene length is at the small extreme for species of *Podocoma* but larger than those of *Conyza*; and their reduced pappus provides somewhat ambiguous evidence with respect to generic placement, but reduction of pappus occurs commonly within many genera of the tribe and family, and the pappus of *Conyza* usually is uniseriate, without an outer series.

We have maintained *Conyza notobellidiastrum* and *C. rivularis* as distinct species but the difference between them is small, apparently attributable entirely to differences in leaf shape and disposition. Intermediates can be found among the specimens we have examined (ca. 90 altogether, at MO, TEX, and US) and it is possible that only a single species is present. Field observations of populational variation in these plants will be critical in clarifying their systematic status.

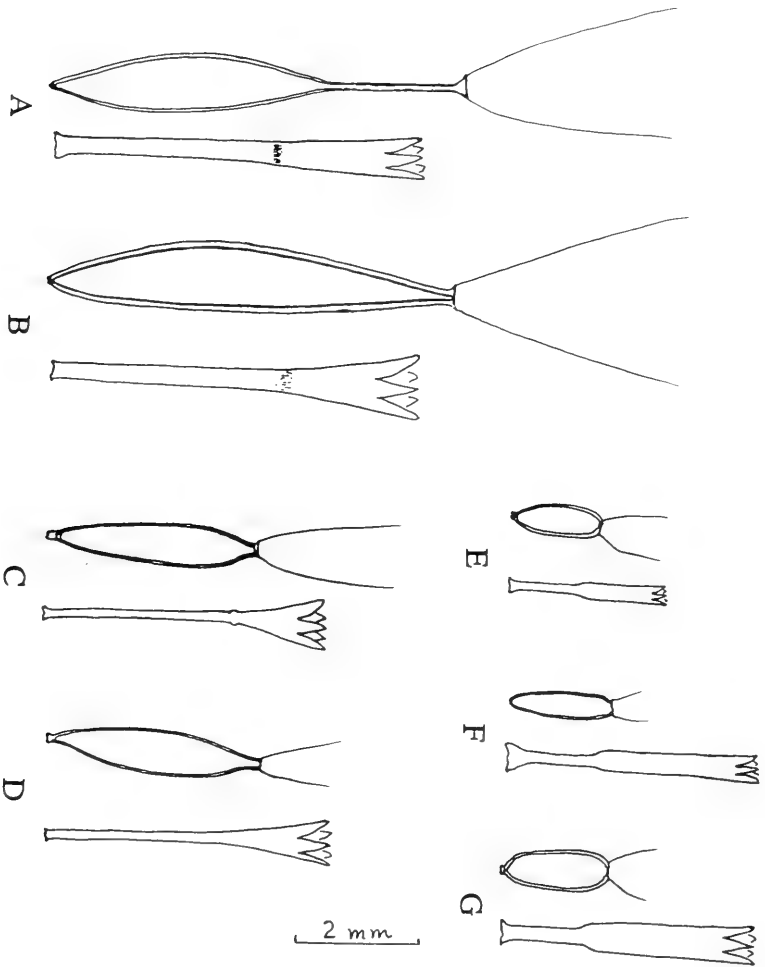


Figure 1. Achenial and pappus morphology of *Podocoma* and *Conyza*: A. *P. hieracifolia* (Poir.) Cass.; B. *P. bellidifolia*; C. *P. notobellidiastrum*; D. *P. rivularis*; E. *C. canadensis* (L.) Cronq.; F. *C. primulifolia* (Lam.) Cuatr. & Lourteig; and G. *C. trihecatactis* (S.F. Blake) Cuatr. The number and series of pappus bristles and their length is not indicated.

In a phylogenetic analysis of New World representatives of the subtribe Baccharidinae and other, putatively related, peripheral genera using restriction site variation in chloroplast DNA (Zanowiak 1991 and in prep.), *Conyza notobellidiastrum* is distantly separated from a strongly monophyletic group that consists of *Erigeron tenuis* Torr. & Gray, *E. strigosus* Muhl. ex Willd., and *Conyza bonariensis* (L.) Cronq. Instead, *C. notobellidiastrum* lies (in Zanowiak's analysis) within the Baccharidinae, between *Baccharis* L. and a monophyletic group consisting of *Archibaccharis* Heer. and *Heterothalamus* Less. On a morphological basis (Nesom in prep.), however, there is no apparent justification for regarding *C. notobellidiastrum* as especially closely related to *Baccharis* and its relatives, but at least the molecular evidence indicates that the phyletic position of this species is disjoined from that of *Conyza*.

The incorporation of *Conyza notobellidiastrum* and *C. rivularis* into *Podocoma* makes the practical identification of *Podocoma* as a genus slightly more difficult, but, as hypothesized here, an extraneous element is removed from *Conyza* and *Podocoma* becomes monophyletic. Following is a taxonomic summary of *Podocoma* expanded by the two species, with preliminary indications of synonymy. We also have constructed a preliminary and highly provisional key to species in an attempt to identify the primary nodes of variation, but the genus is in need of a revisionary study.

Podocoma Cass., Bull. Sci. Soc. Philom. Paris 1817:137. 1817. TYPE:
Podocoma hieracifolia (Poir.) Cass.

Podopappus Hook. & Arn., Companion Bot. Mag. 2:50. 1836. LECTOTYPE (designated here): *Podopappus hirsutus* Hook. & Arn. (= *Podocoma hirsuta* [Hook. & Arn.] Baker).

Perennial herbs, usually coarsely pubescent, eglandular, rhizomatous with fibrous roots. Basal leaves often persistent, the cauline clasping, continuing unreduced upwards or sharply reduced in size above the base. Heads solitary or more commonly in a loose, corymbiform capitulescence; phyllaries in 3-5 strongly graduated series, stiffly indurate, narrowly lanceolate or oblong-lanceolate, greenish in the midportion, the midvein without accompanying orange resin ducts. Pistillate flowers in ca. 2-5 series, corollas white or purplish (yellow in *Podocoma bellidifolia* and *P. blanchetiana* Baker), with short (2-3 mm long), coiling ligules 0.5-0.8 mm wide or the ligules 1-2 mm long, filiform, and mostly erect. Disc flowers relatively few, hermaphroditic, fertile, the corollas with a long tube opening into a narrowly funnelliform limb ca. 1/3 the corolla length, sometimes orange-veined, with deltate lobes; style branches with deltate to triangular collecting appendages. Achenes sparsely strigose, eglandular, strongly flattened with 2 marginal ribs, apically attenuate into a long, nearly filiform beak or short neck or sometimes with only a broad

gradually attenuate apex, (3-)4-6 mm long, including the neck; pappus of capillary bristles in 2(-3) series of even length, or 1 series of bristles with a short, outer series of setae in *P. notobellidiastrum* and *P. rivularis*. Chromosome number, $n=9$: reported for *P. notobellidiastrum* (Coleman 1968; Hunziker *et al.* 1989) and *P. hirsuta* (Coleman 1968).

PROVISIONAL KEY TO SPECIES AND TAXONOMIC SUMMARY

1. Achenes mostly 5-6 mm long, apically attenuate-tapered to a slender or broad neck or beak (Figures 1A, 1B); pappus 2-3 seriate; leaves minutely scabrous to harshly hirsute or hirsute-pilose. (3)
1. Achenes mostly ca. 3 mm long, with short, barely distinct neck (Figures 1C, 1D); pappus 1-seriate, sometimes with scant outer series; leaves glabrate to sparsely hispid-pilose, not rough-hairy or scabrous. (2)
 2. Basal leaves spatulate, 6-18 cm long, blades 2.5-6.5 cm wide, with a broadly winged petiole. *P. notobellidiastrum*
 2. Basal leaves oblanceolate, 4-8(-15) cm long, blades 8-18(-20) mm wide, gradually tapering at the base, without a distinct, winged petiole. *P. rivularis*
3. Leaves persistent at the base, the cauline sharply and strongly reduced upward. (6)
3. Leaves more or less evenly distributed along the stems, the basal not persistent, little or gradually reduced upward, the margins strongly serrate, often coarsely toothed. (4)
 4. Leaves linear to linear-lanceolate or linear-oblanceolate, 3-8 mm wide, slightly subclasping at base but not auriculate. *P. asperrima*
 4. Leaves oblanceolate to elliptic or oblong-lanceolate, 10-50 mm wide, distinctly auriculate-clasping at the base. (5)
5. Culine leaves 3-5 cm long, 10-20 mm wide. *P. hirsuta*
5. Culine leaves 6-11 cm long, 25-50 mm wide. *P. regnellii*
 6. Leaves almost completely basal, broadly oblanceolate to nearly rotund, entire or barely crenate; stems and leaves scabrous with very short hairs. *Podocoma* sp. nov. (see below)
 6. Leaves basal and lower cauline, mostly oblanceolate, shallowly to deeply serrate; stems and leaves hirsute or hirsute-pilose. (7)

7. Rays white; achenes with a filiform neck. *P. hieracifolia*
7. Rays yellow; achenes with a distinctly delimited, filiform neck or else not distinctly rostrate. (8)
8. Leaves shallowly crenulate or merely apiculate; heads 1-2(-3), on peduncles 5-11 cm long; achenes with a broad, tapering apex or sometimes slightly rostrate. *P. bellidifolia*
8. Leaves sharply serrate; heads usually 2-10, on peduncles 1-7 cm long; achenes with a long, filiform neck. *P. blanchetiana*
1. *Podocoma asperrima* Dusen ex Malme, Svensk Vet.-Akad. Handl., ser. 3, 12(2):63. 1933.
- ?*Podocoma spegazzinii* Cabrera, Notas Prelim. Mus. La Plata 1:327. 1931.
2. *Podocoma bellidifolia* Baker in Mart., *Fl. Bras.* 6(3):16. 1882.
- Leucopsis podocomoides* Baker in Mart., *Fl. Bras.* 6(3):6. 1882.
- ?*Podocoma foliosa* Malme, Svensk Vet.-Akad. Handl., ser. 3, 12(2):64. 1933.
3. *Podocoma blanchetiana* Baker in Mart., *Fl. Bras.* 6(3):15. 1882. *Haplopappus blanchetianus* Sch.-Bip. ex Baker (*pro syn.*) in Mart., *Fl. Bras.* 6(3):15. 1882.
4. *Podocoma hieracifolia* (Poir.) Cass., *Dict. Sci. Nat.* 42:60. 1826. BASIONYM: *Erigeron hieracifolius* Poir. in Lam., *Encycl. Method.* 8:491. 1808.
- Podocoma primulifolia* Cass., *Dict. Sci. Nat.* 42:61. 1826. *Erigeron primulifolia* Juss. [*in sched.*] ex Cass., *Dict. Sci. Nat.* 42:61. 1826.
- Podopappus pubescens* Hook. & Arn., *Companion Bot. Mag.* 2:50. 1836.
- Podocoma erigerifolia* Steud., *Nom. Bot.* (ed. 2) 1:584. 1840. (*pro syn. sphalm.* = *P. primulifolia* Cass.).
5. *Podocoma hirsuta* (Hook. & Arn.) Baker in Mart., *Fl. Bras.* 6(3):15. 1882. BASIONYM: *Podopappus hirsutus* Hook. & Arn., *Companion Bot. Mag.* 2:50. 1836.

6. *Podocoma notobellidiastrum* (Griseb.) Nesom, *comb. nov.* BASIONYM: *Conyza notobellidiastrum* Griseb., *Symbol. Fl. Argent.* 24:177. 1879. *Baccharidastrum notobellidiastrum* (Griseb.) Herter, *Rev. Sudamer. Bot.* 6:104. 1939. TYPE: PARAGUAY. Forets vierges pres de l'Aroyo Guazu, a l'est de la Cordillere de Villa-Rica, 21 Sep 1874, Balansa 804 (HOLOTYPE: GOET?; Isotype: G-Delessert, photo-MO!, photo-US!).
- Erigeron paucifolius* Less. [*pro syn.*] *ex Baker in Mart., Fl. Bras.* 6(3):34. 1882.
7. *Podocoma regnellii* Baker *in Mart., Fl. Bras.* 6(3):16. 1882.
8. *Podocoma rivularis* (Gardner) Nesom, *comb. nov.* BASIONYM: *Conyza rivularis* Gardner *in Hook., London J. Bot.* 4:124. 1845. *Baccharidastrum rivulare* (Griseb.) Herter, *Rev. Sudamer. Bot.* 6:104. 1939. *Erigeron gardneri* Cabrera (*nom. nov.*), *Not. Mus. La Plata, Bot.* 2:177. 1937; not *Erigeron rivularis* Sw. (1797) or Spreng. *ex DC.* (1836). TYPE: BRAZIL. Gardner 520 (HOLOTYPE: BM; Isotype: B, photo-MO!, photo-US!).
9. *Podocoma sp. nov.?* ARGENTINA. Prov. Corrientes: Estancia Santa Teresa, "grasslands on rich 'black earth,' seems rare," 4 Jul 1962, T.M. Petersen 1765 (US).

EXCLUDED SPECIES:

1. *Podocoma bartsiiifolia* S.F. Blake, *Contr. U.S. Natl. Herb.* 20:534. 1924. = *Blakiella bartsiiifolia* (S.F. Blake) Cuatr., *Webbia* 24:41. 1969.
- Moritzia* Sch.-Bip. *ex Benth. in Benth. & Hook., Gen. Pl.* 2:279. 1873; non *Moritzia* DC. *ex Meissn.* (1840).
- Blakiella* Cuatr. is a monotypic endemic of the paramos of Colombia and Venezuela (Cuatrecasas 1969). Schultz-Bipontinus's epithet "glandulosa" for this species (*in sched.*, as *Moritzia*) apparently was never published.
2. *Podocoma macrocephala* (Less.) Herter, *Fl. Uruguay Pl. Vasc.* [Estud. Bot. Reg. Urug.] 123. 1931. = *Asteropsis macrocephala* Less., *Syn. Gen. Comp.* 188. 1832.

Asteropsis Less. is a monotypic genus endemic to Brazil and adjacent Uruguay (detailed comments, Nesom 1994a).

3. *Podocoma reineckii* Hochreut. in Briq. & Hochreut., Ann. Conserv. Jard. Bot. Genève 3:171. 1899. TYPE: BRAZIL. [Rio Grande do Sul]: "Pentes ensoleillees et pierreuses de la route de Tristeza," 15 Nov 1897, E.-M. Reineck 119 (HOLOTYPE: G?; Isotype: P, photo-GH!, photo-MO!). = *Stenachaenium campestre* Baker, J. Bot. 16:79. 1878.

3. *Podocoma* in Australia = *Ixiochlamys* F. Muell. & Sonder ex Sonder.

Ixiochlamys is an Australian genus of four species (Grau 1975; Dunlop 1980).

4. *Inulopsis* O. Hoffm.

Grau (1977) noted that this South American genus should be considered a synonym of *Podocoma*, but no nomenclatural transfers have ever been made to formally unite the two taxa. *Inulopsis* is most recently treated as a genus of four species (Nesom 1994b).

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INULOPSIS SYNOPSIS (ASTERACEAE: ASTEREAEE)

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ABSTRACT

The South American genus *Inulopsis* O. Hoffm. is treated here as comprising four species: *I. scaposa* (DC.) O. Hoffm. (the type), *I. stenophylla* Dusen, I. (*Aster*) ***camporum*** (Gardner) Nesom, *comb. nov.*, and ***I. phoenix*** Nesom, *sp. nov.* The genus, which occurs in Brazil, south-eastern Bolivia, eastern Paraguay, Uruguay, and northern Argentina, is hypothesized to be most closely related to the *Podocoma* group of South America, including *Podocoma*, *Asteropsis*, *Sommerfeltia*, *Microgynella*, *Laennecia*, and *Blakiella*. A key, descriptions, and distribution maps are provided for the species of *Inulopsis*.

KEY WORDS: *Inulopsis*, *Aster*, *Podocoma*, Asteraceae, Astereae

Inulopsis was described by Hoffmann in 1890, based on the single species *I. (Haplopappus) scaposa* (DC.) O. Hoffm. This species was suggested by Bentham (1873) to lie within *Hysterionica* Willd.; Baker (1882) included it within the genus *Leucopsis* (DC.) Baker, which is now largely absorbed by *Noticastrum* DC. (Zardini 1965). A second species of *Inulopsis* was added by Dusen (1910). Without any other comment, Grau (1977) noted that *Inulopsis* should be treated as a synonym of *Podocoma*, but no taxonomic proposals have ever been made to formalize such a view. Grau's suggestion apparently was followed by Zhang & Bremer (1993), who did not include *Inulopsis* in their recent taxonomic summary and phylogenetic analysis of the Astereae. In the present treatment, however, *Inulopsis* is considered to be a distinct genus of east-central South America comprising four species. One of these is previously undescribed and one is transferred to *Inulopsis* from the genus *Aster* L.

Inulopsis (DC.) O. Hoffm. in Engler & Prantl, *Naturl. Pflanzenfam.* 4(5):149. 1890. *Haplopappus* sect. *Inulopsis* DC., *Prodr.* 5:349. 1836. Lectotype species (Hoffmann 1890): *Inulopsis scaposa* (DC.) O. Hoffm.

Herbaceous perennials from a ligneous rhizome and fibrous system of thickened roots; leaves and stems glabrate to densely hirsute-villous with Type A trichomes (designation of trichome types follows Nesom 1976), also with resinous, sessile glands in *Inulopsis camporum*, with Type C trichomes, Type B trichomes minute and inconspicuous but often abundant. Leaves all basal or basal and cauline on the lowermost portions of the stem, obovate to linear, toothed to nearly entire, with 1-2 pairs of parallel veins beginning at or near the base. Heads solitary on scapose stems, hemispheric to turbinate; phyllaries lanceolate to lanceolate-oblong, more or less evenly herbaceous, flat (not keeled or concave), 1-nerved (rarely with a lateral pair), in 3-4 subequal series, the outer 1/2-3/4 as long as the inner; receptacles flat, epaleate, sometimes barely alveolate. Disc flowers numerous, functionally staminate, with narrowly funnelform, orange-veined corollas 3-6 mm long, the limb ca. 1/2-5/8 the length of the corolla, without an abrupt widening from the tube to the limb, the 5 lobes deltate and essentially erect, hairy or glabrate; anthers with ovate-lanceolate, eglandular, white apical appendages; style branches connate, without stigmatic lines or clearly demarcated collecting appendages, spreading hairy. Ray flowers uniseriate, ligules white to creamy, sometimes drying yellowish, extending well past the involucre, often coiling at maturity, the tube densely pilose with long, duplex (Type C) trichomes. Achenes eglandular, densely strigose-sericeous to sparsely strigose with white trichomes (Zwillingshaare), 2-4 mm long, oblanceolate to elliptic-oblanceolate, strongly flattened with 2 thick, whitish, lateral ribs, sometimes with an extra rib on each face, apically rounded and the pappus inserted on a barely formed neck; carpopodium 0.1-0.2 mm wide, a ring of white, sclerified cells, 4-6 cells high; pappus of (1-)2-3 series of apically attenuate bristles of equal length, sometimes with a short outer series of setae. Base chromosome number, $x=9$.

DeCandolle (1836) included two species in his *Haplopappus* sect. *Inulopsis*: *H. stoloniferus* DC. and *H. scaposus* DC. He clearly associated *H. stoloniferus* most closely with sect. *Inulopsis*, as it does have a superficial resemblance to *Inula* L. and has been treated within that genus. Hoffmann (1890), however, retained *H. stoloniferus* within *Haplopappus* and segregated *H. scaposus* as the monotypic genus *Inulopsis*, elevated from sectional rank. Greene (1895) observed the disparity of *H. stoloniferus* with *Haplopappus* and made it the type and sole species of his new genus *Osbertia* E. Greene, a member of the primarily North American "goldenaster group" (Nesom 1991) and only distantly related to *Inulopsis*.

KEY TO THE SPECIES OF *INULOPSIS*

1. Heads produced before appearance of basal leaves; leaves and stems glabrate or densely hirsute-villous; phyllaries thin-herbaceous and green-

ish, with greenish-yellow, non-resinous nerves; disc corollas 5-6 mm long; achenes densely sericeous. (3)

1. Heads produced after or concurrently with appearance of basal leaves; leaves and stems glabrate to very sparsely hirsute-villous; phyllaries thickened and orangish, the veins accompanied by dark orange resin canals; disc corollas 3-5 mm long; achenes sparsely strigose. (2)
 2. Leaves obovate, 3-7 cm long, 10-24 mm wide. *I. scaposa*
 2. Leaves linear, 4-10 cm long, 1.5-2.0 mm wide. *I. stenophylla*
3. Stems, leaves, and phyllaries prominently hirsute-villous; outer phyllaries 1.0-1.8 mm wide; disc corolla lobes hairy. *I. camporum*
3. Stems, leaves, and phyllaries glabrous or glabrate; outer phyllaries 1.5-2.5 mm wide; disc corolla lobes glabrate. *I. phoenix*

1. *Inulopsis scaposa* (DC.) O. Hoffm. in Engler & Prantl, *Naturl. Pflanzenfam.* 4(5):149. 1890. *Haplopappus scaposa* DC., *Prodr.* 5:350. 1836. *Hysterionica scaposa* (DC.) Benth. ex Baker [in syn.] in Mart., *Fl. Bras.* 6(3):6. 1882; not in Benth. & Hook., *Gen. Pl.* 2:253. 1873. *Leucopsis scaposa* (DC.) Baker in Mart., *Fl. Bras.* 6(3):6. 1882. LECTOTYPE (here designated): DeCandolle cited two collections, both from Brazil: "prov. Minarum Generalium ad Serro-Frio, [1833], (Vauthier! pl. exs. n. 315)"; "prov. Sancti-Pauli (h. Mus. imp. Bras. n. 436!)." The Vauthier specimen also was among those cited by Baker (1882); it is in the G-DC herbarium (fiche!) and is here designated as the lectotype.

Aster longipes Gardner in Hook., *London J. Bot.* 7:98. 1848. TYPE: BRAZIL. Minas Gerais: "dry campos near the foot of the Serra de Piedade," Sep 1840, *G. Gardner* (BM).

Erigeron nudiscapus Sch.-Bip., *Linnaea* 22:571. 1849. *Nomen nudum*, based on a *Regnell* collection ("l. 252") but without description.

Leaves basal, oblanceolate to obovate, weakly 3-nerved, 3-7 cm long, 10-24 mm wide, thick, the surfaces glabrous to loosely and sparsely to moderately pilose, eglandular, margins mucronulate to widely serrate, sparsely to moderately ciliate near the base; scapes 10-27 cm long, glabrous, with a number of scattered, minute, linear bracts; heads 8-13 mm wide (pressed); phyllaries narrowly lanceolate to linear-lanceolate, in 3-4 series graduated in length, the longest 5-7 mm long, flat, with a single, dark orange vein; ray flowers 25-40; disc corollas 3-5 mm long, the lobes glandular; achenes obovate, sometimes

with an additional rib on one or both faces, 2.0-2.5 mm long, sparsely strigose; pappus of (1-)2 series of even-length bristles, with a few short setae in an outer series; chromosome number, $n=9$ (Coleman 1968). Map 1.

2. *Inulopsis stenophylla* Dusen, Arkiv. Bot. 9(15):22, pl. 7. 1910. TYPE: BRAZIL. Parana: in rocky country between Capao Grande und Villa Velha, 5 Mar 1904, *P. Dusen 3989* (Isotypes: M photo-MO!, MO!).

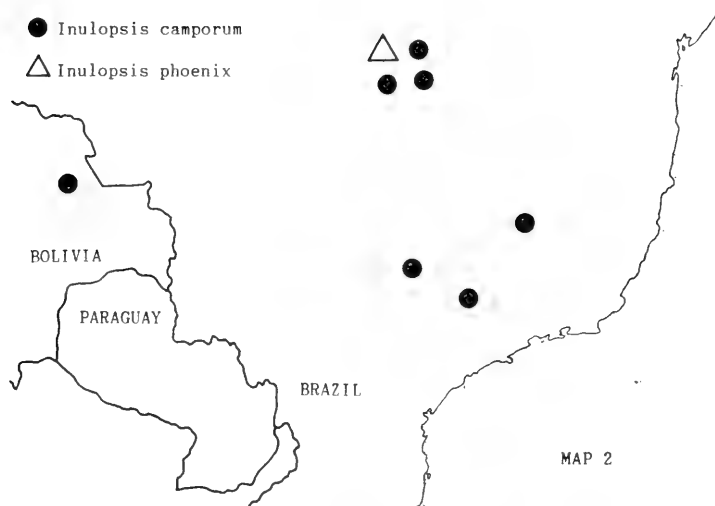
Similar to *Inulopsis scaposa* but different in the following features: leaves basal, linear, apparently 1-nerved, 4-10 cm long, 1.5-2.0 mm wide, subcoriaceous, glabrous or the margins sparsely ciliate near the base, eglandular, margins entire to widely denticulate; scapes 15-22 cm long; ray flowers 16-28; achenes broadly oblanceolate. Map 1.

I have studied one additional specimen besides the type: BRAZIL. Parana: Fortaleza, in campo rupestris, 26 Feb 1910, *Dusen 9556* (GH).

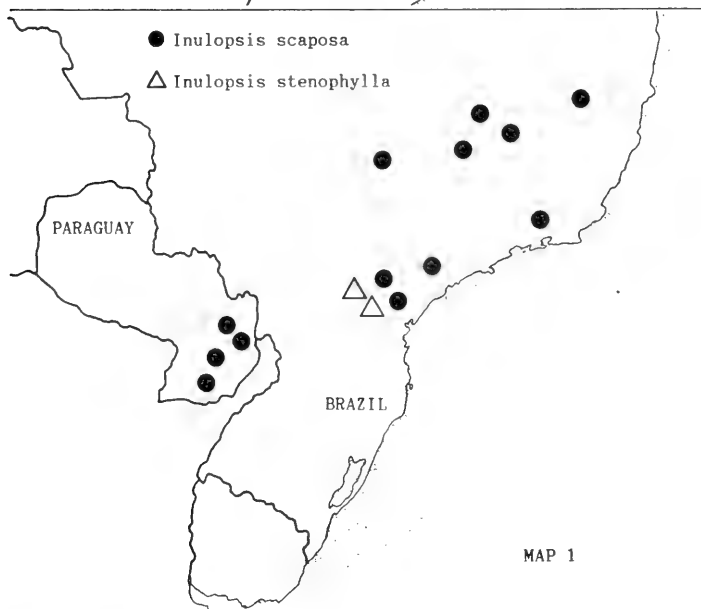
3. *Inulopsis phoenix* Nesom, *sp. nov.* TYPE: BRAZIL. Distrito Federal: area of Cristo Redentor, recently burned cerrado (4 Sep 1990), 18 Sep 1990, *M.L.M. Azevedo & D. Alvarenga 939* (HOLOTYPE: US!).

Inulopsi camporo (Gardner) Nesom similis sed caulibus foliis phyllariisque glabratis trichomatibus glandularibus ac eglandularibus carentibus (praeter caules superos minute pubescentes), phyllariis exterioribus 1.5-2.5 mm latis, et lobis corollarum disci glabratis differt.

Leaves produced after flowering, basally disposed, clusters of basal leaves apparently produced on rhizome tips later in the season (as in *Archer 4093* and *Hatschbach 37239*); stems 9-25 cm tall, with numerous, thin ribs, sometimes branched at the very base early in the season, short lateral branches arising later; stems, leaves, and phyllaries glabrate. Cauline leaves (at flowering) few, the larger somewhat clustered toward the base, subclasping, oblanceolate, 5-50 mm long, up to 25 mm wide, entire or with 2-6 pairs of shallow teeth or mucros on the distal margins, the lowermost scale-like and not enlarging, the upper bracteate, linear-lanceolate. Heads turbinate-hemispheric, 14 mm wide (pressed); inner phyllaries ca. 8 mm long, lanceolate to narrowly oblong-lanceolate, apically acute, midvein narrow, slightly or not at all orange, not raised, occasionally also with a pair of lateral veins. Ray flowers ca. 20, the corollas 10 mm long, the tube 3-4 mm long, densely hairy with long, biseriate trichomes, the ligules 1-2 mm wide and 3-5 veined. Disc corollas 5-6 mm long, the lobes glabrate; style branches linear, 1.5-2.0 mm long. Fertile achenes elliptic-obovate, 4 mm long, 1.2 mm wide, sometimes with an additional rib



MAP 2



MAP 1

Map 1 (below). Distribution of *Inulopsis camporum* and *I. phoenix*.
 Map 2 (above). Distribution of *Inulopsis scaposa* and *I. stenophylla*.

on one or both faces, densely sericeous; pappus of 2-3 series of numerous bristles 6-8 mm long; sterile achenes sericeous, linear, elongating to 5-6 mm but not producing an embryo. Known only from the type collection. Map 2.

These plants are similar to *Inulopsis camporum* and occur within its geographic range. While the strongly reduced vestiture of *I. phoenix* may reflect only a small genetic divergence from *I. camporum*, the difference in appearance is striking. Further, the upper stems of *I. phoenix* produce a large number of minute, appressed, uniseriate hairs (Type B trichomes), in contrast to *I. camporum*, but the achenes are densely sericeous like those of *I. camporum*. The epithet refers to the character of the plants in arising from ashes to live another period.

4. ***Inulopsis camporum*** (Gardner) Nesom, *comb. nov.* **BASIONYM:** *Aster camporum* Gardner in Hook., London J. Bot. 7:79. 1848. *Erigeron camporum* (Gardner) Sch.-Bip. *ex Benth.* (*in syn.*) in Benth. & Hook., *Gen. Pl.* 2:273. 1873. **TYPE:** BRAZIL. Estado Goias: "open campos near Nossa Senhora d'Abadia," Serra Geral, May 1840, G. Gardner 4237 (BM).

Similar to *Inulopsis phoenix* but with the following features: stems, leaves, and phyllaries moderately to densely hirsute-villous with vitreous-whitish, flattened, uniseriate, multicellular trichomes mostly 0.5-1.3 mm long, also with much smaller (Type B) trichomes, leaves and phyllaries with sessile glands producing translucent, orange-resinous heads; heads (9-)12-18 mm wide (pressed); outer phyllaries 1.0-1.8 mm wide; ray flowers 18-35, the corollas 9-12 mm long; disc corolla lobes prominently invested with biseriate glandular hairs and uniseriate eglandular hairs; fertile achenes obovate to elliptic-obovate, 4.0-5.5 mm long, 1.2-1.5 mm wide. Map 2.

After the original description of *Aster camporum*, the species was maintained in *Aster* by Bentham (1873), whose identification was adopted by Baker (1882). In his infrageneric classification of *Aster*, however, Bentham placed *A. camporum* in a position equivalent to other groups at sectional rank, but he did not provide the species with a formally designated name in that category, only noting that its placement within *Aster* was uncertain and that it perhaps should be referred to some other genus. The notation by Schultz-Bipontinus (apparently "*in sched.*") that *A. camporum* should be considered a species of *Erigeron* L. was formally recorded by Bentham, who listed it in synonymy (see above) with Schultz's nomenclatural combination in *Erigeron*. Bentham observed that *A. camporum* resembles the South American *A. vahlii* Hook. & Arn., here considered to be a member of the *Oxytripolium* group of New World *Aster* (in contrast to a previous evaluation of mine, Nesom 1992; detailed comments to follow, Nesom in prep.). Since these 19th century treatments, the

systematic position of *A. camporum* apparently has not been formally evaluated.

Neither "*Aster*" *camporum* nor any of the other species of *Inulopsis* can be accepted in any group currently treated as either *Aster* or *Erigeron*. *Erigeron* has short-tubed disc corollas, fertile disc ovaries, oblong achenes, and 1-seriate pappus bristles; most New World species currently treated as *Aster* have a capitulescence of numerous heads, fertile disc ovaries and subterete, multinerved achenes, and a uniseriate pappus. The Andean genus *Oritrophium* (Kunth) Cuatr., where *Aster vahlii* has sometimes been placed, resembles *Inulopsis* in its scapose and monocephalous stems, basal rosette of leaves, functionally staminate disc flowers, and tendency for flat, 2-nerved achenes, but the similarity is convergent as *Oritrophium* is a member of the Hinterhuberinae and is only distantly related to the *Podocoma* group (Nesom in prep.).

DEFINITION OF *INULOPSIS*

Inulopsis is essentially characterized by the following morphological combination: plants rhizomatous with a fibrous system of thickened roots; leaves weakly 3-nerved, mostly basal, produced after or concurrently with flowering; stems scapose or subscapose, monocephalous; disc flowers functionally staminate, the style branches without stigmatic lines and connate to the apex; ray flowers in a single series, with conspicuous, creamy-white ligules extending well past the involucre; fertile achenes oblong-obovate, flat, with a pair of thickened, whitish, lateral nerves, apically rounded to a narrow pappus insertion, and the faces eglandular but variably invested with Zwillingshaare; and pappus of 2-3 series of apically attenuate bristles of equal length, sometimes with a short outer series. The sessile glands and eglandular tomentum of *I. camporum*, which are absent on the other species, are helpful in assessing the nature of the infratribal relationship of *Inulopsis*. The species of *Inulopsis* are divided into two groups, as noted above in the key, but the coherence of most characters of these species provides evidence of monophyly.

Distinctive habitual features of *Inulopsis* (rhizomatous, with thick storage roots, and rapid production of flowering heads) apparently are directly correlated with the habitat of these plants. They have most commonly been collected in recently burned savannas with a marked wet/dry cycle. The collection data on the type specimen of *I. phoenix* indicates that the flowering stems and mature heads were produced within 14 days after a burn in the area.

RELATIONSHIPS OF *INULOPSIS*

Inulopsis apparently is most closely related to taxa of the primarily South American "Podocoma group" (Nesom in prep.): *Podocoma* Cass., *Asteropsis* Less., *Sommerfeltia* Less., *Microgynella* Grau, *Laennecia* Cass., and *Blakiella* Cuatr. (Nesom 1990a, 1990b, 1994a, 1994b; Nesom & Laferrière 1990; Nesom & Zanowiak 1994). The first three of these genera are similar to *Inulopsis* in geographic distribution, while *Laennecia* and *Blakiella* are primarily Andean. Within the Astereae, Australian genera among those referred to by Zhang & Bremer (1993) as the "Vittadinia [A. Rich.] group" are similar in significant respects to the *Podocoma* group (Nesom in press). For the most part, the genera in both of these continental groups appear to be well-differentiated, although the nature of the inter-relationships among them is difficult to assess. *Inulopsis*, also, is morphologically isolated among these genera.

The *Podocoma* group is characterized (with exceptions) by the following features in which *Inulopsis* is similar: resinous glandularity at least on the leaves (*Podocoma* is eglandular); 1-nerved phyllaries; functionally staminate disc flowers with sterile ovaries (disc ovaries fertile in *Laennecia*, *Microgynella*, and *Podocoma*); fertile achenes flat, obovate to broadly oblanceolate, the faces glandular (eglandular in *Asteropsis* and *Podocoma*), rounded at the apex to a relatively narrow pappus insertion, with at least a tendency to form a neck or beak (erostrate in *Laennecia*, *Microgynella*, and *Sommerfeltia*); and pappus of 2-3 series of equal-length bristles, sometimes with a short, outer series. In large part, however, the other genera of the *Podocoma* group differ from *Inulopsis* in their numerous ray flowers in multiple series, often with short ligules (compared to relatively few ray flowers in a single series, with prominent ligules), although the ligules of *Asteropsis* are long and conspicuous. Except for *Laennecia* and *Inulopsis*, the disc corollas of the *Podocoma* group are funnellform with a linear tube longer than the spreading limb; the tube is distinctly shorter in *Laennecia* but about equal or slightly shorter than the limb in *Inulopsis*. The basis for Grau's association of *Inulopsis* with *Podocoma* was unstated, but *Podocoma* (Nesom & Zanowiak 1994) is divergent from *Inulopsis* particularly in its leafy, branching stems, often with several heads, clasping cauline leaves, fertile disc ovaries, and rostrate achenes.

Inulopsis bears some resemblance to another group of austro-brasilien genera, the "Leptostelma group," comprising *Leptostelma* D. Don, *Apopyros* Nesom, *Neja* D. Don, and *Hysterionica* Willd. (Nesom 1994c, 1994d, in press). These occur in similar habitats and are similar in their eglandular, erostrate achenes, but in other aspects of achenial and phyllary morphology, the *Leptostelma* group appears to be most closely related to *Erigeron* and *Conyza* (Nesom in prep.).

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**PERIPLEURA (ASTERACEAE: ASTEREA): A NEW, AUSTRALIAN GENUS
SEGREGATED FROM VITTADINIA**

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ABSTRACT

The nine species of *Vittadinia* subg. *Peripleura* (sensu Burbidge 1982) are completely distinct from the 20 species of subg. *Vittadinia*. Further, in their achenes with multinervate faces, the species of subg. *Vittadinia* are more similar to those of the Australian *Camptacra* and the New Guinean/Hawaiian *Tetramolopium* than they are to the species of subg. *Peripleura*, which have only a single pair of achenial nerves. Two-nerved achenes are found in other closely related Australian genera as well as related genera from South America. The distinctive tendency to produce multinervate achenial faces apparently is a specialization restricted to subg. *Vittadinia*, *Camptacra*, and *Tetramolopium*; and in the interpretation here, these three taxa are interrelated and occupy a phyletically advanced position relative to the species of subg. *Peripleura*. Accordingly, the latter are here segregated as the new genus **Peripleura** (Burbidge) Nesom, *stat. nov.*, with accompanying new combinations for species and varieties.

KEY WORDS: *Peripleura*, *Vittadinia*, Asteraceae, Astereae, Australia

In a taxonomic revision of the Australasian genus *Vittadinia* A. Rich., Burbidge (1982) recognized 29 species divided into two groups: subg. *Vittadinia* (20 species) and subg. *Peripleura* Burbidge (nine species). She also moved two species of Australian *Vittadinia* into the new genus *Camptacra* Burbidge, endemic to north-central and northeastern Australia (also see recent nomenclatural modification in *Camptacra* by Lander 1987a). The monotypic genus *Eurybiopsis* DC. (*Vittadinia* [*Eurybiopsis*] *macrorhiza* [DC.] A. Gray) was reinstated by Burbidge, but it has more recently been absorbed into *Minuria*

DC. (Lander & Barry 1980b; Lander 1987b). The present paper provides perspective on the taxonomy proposed by Burbidge regarding *Camptacra* and the two subgenera of *Vittadinia*.

The genera under discussion belong within a larger Australasian and South Pacific grouping that includes *Tetramolopium* Nees, a genus divided between New Guinea and the Hawaiian and Cook Islands and hypothesized by Lowrey (1986, p. 204) to be most closely related to *Camptacra* and *Vittadinia*, based on their common possession of "subulate style appendages, prominent barbellate pappus bristles, and several similar achene features." Additional genera of this group are *Iziochlamys* Sond. and *Dichromochlamys* Dunlop (Dunlop 1980a, 1980b), *Minuria* DC., and the closely related *Kippistia* F. Muell. (Lander & Barry 1980a, 1980b), and *Iotasperma* Nesom (Nesom 1994).

Except for the disposition of *Eurybiopsis* as a synonym of *Minuria* and the exclusion of *Isoetopsis* Turcz., this group of essentially Australasian genera is the same as that delimited by Zhang & Bremer (1993) as the "*Vittadinia* group." The integrity of this group is accepted in a classification of the Asteraceae (Nesom in prep.), but at that broader level the *Vittadinia* group is hypothesized to further include the South American genera *Asteropsis* Less., *Blakiella* Cuatr., *Laennecia* Cass., *Microgynella* Grau, *Podocoma* Cass., and *Sommerfeltia* Less. (the "*Podocoma* group"). Morphologically, plants of the Australian *Vittadinia* group are characterized by the following: perennial (rarely annual) herbs or small shrubs with solitary heads on leafy (sometimes long-pedunculate) stems, the leaves and stems commonly glandular; (eglandular in *Minuria*, *Dimorphocoma*, and *Elachanthus*); disc flowers bisexual (with sterile ovaries in *Minuria*, a portion of *Tetramolopium*, *Dimorphocoma*, *Elachanthus*, and two species of *Iziochlamys*), the corollas with short lobes and narrow tube longer than the limb; pistillate flowers numerous and in several series (1-seriate in *Dimorphocoma* and *Elachanthus*), with short, narrow, white to bluish ligules (yellow in *Kippistia*); achenes commonly with glandular surfaces (eglandular in *Minuria*), flat and 2-nerved (the faces multinervate in *Tetramolopium*, *Camptacra*, and *Vittadinia* subg. *Vittadinia*), with a tendency to produce a beak (*Iziochlamys*) or neck (*Dichromochlamys*, *Vittadinia* subg. *Vittadinia*, somewhat less distinctly in *Minuria* and *Vittadinia* subg. *Peripleura*; pappus (1-) 2-3 series of basally persistent bristles (tardily caducous in *Vittadinia* subg. *Peripleura*); all chromosome counts have reported a number of $n=9$.

Burbidge distinguished *Camptacra* and the two subgenera of *Vittadinia* by contrasts in the following key (modified and extended from her original):

1. Achenes narrowly elliptic to elliptic-oblong, dark or purplish when mature, each face with 3 pairs of slender, slightly raised nerves, the pair of marginal nerves not thicker than those of the facial nerves; pappus 1-2-seriate. *Camptacra*
1. Achenes mostly obovate to oblanceolate or cuneate, rarely uniformly pur-

plish though sometimes coloured on exposed parts, the faces with or without raised nervation, with a distinct pair of marginal nerves (except *V. pterochaeta* (Benth.) Black and *V. pustulata* Burbidge); pappus 1-3-seriate. (2)

2. Achenes with the seed in the upper portion, with a prominently narrowed, basal extension below the seed, with a dense basal tuft of appressed-ascending hairs, truncate at the apex to a broad pappus insertion (apex slightly narrowed and neck-like in *V. cervicularis* Burbidge, *V. megacephala* (Benth.) Black), the marginal nerves more or less at right angles to the apex; achenial faces with 3-5(-6) pairs of relatively slender, raised nerves, marginal nerves, conspicuously thickened, much broader than the facial nerves (marginal nerves not visible in *V. pterochaeta*; facial nerves usually not visible in *V. pterochaeta*, *V. pustulata*, and four others (see below); pappus 2-3-seriate, the bristles mostly equal the achene length or slightly longer, neither caducous nor basally coherent.
 *Vittadinia* subg. *Vittadinia*

2. Achenes completely filled by the seed, lacking a narrowed, basal extension, without a basal tuft of hairs, abruptly rounded at the apex to the narrow insertion of the pappus, the marginal nerves usually apically confluent; achenial facial nerves absent, marginal nerves weakly or strongly thickened; pappus 1(-2)-seriate, the bristles mostly 1.5-2.5 times longer than the achene, often tardily caducous in groups minutely coherent at their bases.
 *Vittadinia* subg. *Peripleura*

The two subgenera of *Vittadinia*

The species of subg. *Peripleura* form a morphologically coherent group of closely similar species, most of them recently segregated from a broadly conceived *Vittadinia scabra* DC. by Burbidge (1982). The one other species already recognized at the beginning of Burbidge's study, *V. hispidula* F. Muell. ex A. Gray, was treated by Bentham (1866) as a synonym of *V. scabra*. There are no species of *Vittadinia* that could be interpreted as intermediate between subg. *Vittadinia* and subg. *Peripleura*. *Iotasperma* is the only Australian taxon besides subg. *Peripleura* with obovate, apically rounded achenes; among the South American genera closely related to the *Vittadinia* group, *Sommerfeltia* and *Laennecia* are particularly similar in achene morphology to subg. *Peripleura*.

The species of subg. *Vittadinia* constitute a presumably monophyletic group, based on the distinctively shaped achenes (with a sterile "foot" and truncate

apex) with a dense basal tuft of hairs and 2-3 seriate pappus that are characteristic of all species. Fourteen of these species produce achenes with consistent and conspicuous facial nervation (see Burbidge 1982, plates 3-9). Achenes of the remaining six species have mostly smooth faces (but see caveats below). Burbidge observed that the "species whose cypselas lack facial ribbing were probably derived from ribbed types. This view is based on characters visible in transverse section but it is consistent with the fact that ribbed-cypselas types have the widest geographical distribution" (1982, p. 5). Burbidge did not add any details regarding this observation, but it has been corroborated in the present study by dissecting achenes, removing the embryo, and studying the fruit walls mounted in Hoyer's solution.

The achenial morphology of subg. *Vittadinia* more closely resembles that of other Australasian genera than subg. *Peripleura*. Within the *Vittadinia* group, and including its close relatives in South America, achenes are strictly 2-nerved except in subg. *Vittadinia*, *Camptacra*, and *Tetramolopium*, where they have a number of slightly raised facial nerves in addition to the marginal pair. In these three taxa, however, only the marginal pair of nerves is vascularized; the facial nerves are essentially unvascularized fiber bundles, although a single element or group of tracheids may appear unpredictably and rarely in the fiber bundles, either near the achene base above the divergence of the lateral vascular bundles or toward the middle of the achene.

As noted by Burbidge (1982), the facial nerves in subg. *Vittadinia* arise at the achene base but commonly may not reach the apex; at least one of the *Vittadinia* species noted by Burbidge to lack facial ribbing, *V. megacephala*, sometimes may have such ribs externally visible in lower third of mature achenes. The same occurs in achenes of some *Tetramolopium* species, where facial nerves sometimes extend only a short distance above their basal origin. *Vittadinia pterochaeta* produces nearly terete achenes that are usually without any visible superficial ribbing (including even the lateral nerves), but numerous ribs are sometimes visible, particularly in immature achenes; the ribs are obscured by the heavily fibrous nature of the mature achene wall but their position can be seen more clearly in dissected and cleared material. In *V. pustulata*, the longitudinal ribbing is anastomosing rather than parallel, and the distinctive pustules that characterize the achene surfaces of this species are formed in the resulting interstitial spaces. In *Tetramolopium*, the facial nerves may be variable in number within species, populations, and even single heads, although "each taxon has a predominant number and configuration of nerves" (Lowrey 1986, p. 212).

Among genera outside of the *Vittadinia* group but potentially closely related to it (e.g., within the *Brachycome* Cass. group, the *Grangea* Adans. group, and the *Conyza* L. group; Nesom in prep.), achenes are flat and 2-nerved, or if more nerves are present, most or all tend to be vascularized. The same is true for the genera of the South American *Podocoma* group, which is

closely related to the *Vittadinia* group. Achenes with numerous, essentially unvascularized facial nerves are an evolutionary specialization within the *Vittadinia* group, where they are characteristic of *Vittadinia* subg. *Vittadinia* but not of subg. *Peripleura*.

Camptacra

The species of *Camptacra* differ from those of subg. *Vittadinia* in their achenes without a basal extension or dense basal tuft of hairs. *Camptacra* differs from both subg. *Peripleura* and subg. *Vittadinia* in its achenes with relatively thin marginal nerves that are no thicker than the facial nerves (vs. marginal nerves strongly thickened in most of subg. *Peripleura* and some, but not all, species of subg. *Vittadinia*), embryos with a rounded base (vs. pointed base), and aspects of its disc corolla morphology. In *Camptacra*, the tube of the disc corollas is narrowly funnelliform with the staminal filaments attached at or below the middle, with little or no swelling to indicate the position of attachment (vs. corolla tube narrowly cylindrical with the staminal filaments attached near the middle or in the upper third, the position indicated by a slight swelling). *Camptacra* (as well as subg. *Peripleura*) differs from subg. *Vittadinia* in their reduced number of ray flowers and reduction in the number of pappus series.

Tetramolopium

Tetramolopium has received detailed taxonomic treatment, those of New Guinea by Koster (1966) and van Royen (1981), those of Hawaii in monographic detail by Lowrey (1986). The species are predominately woody shrubs of relatively high elevations, and they are geographically separated in New Guinea and smaller Pacific Islands from the main part of the *Vittadinia* group. Lowrey divided the genus into three sections: sect. *Tetramolopium* and sect. *Sandwicense* Lowrey are restricted to the Hawaiian Islands, except for *T. sylvae* Lowrey (sect. *Tetramolopium*), which also has been reported from the Cook Islands; sect. *Alpinum* Lowrey includes all of the New Guinean species and the Hawaiian *T. humile* (A. Gray) Hillebr.

Successful artificial hybridizations by Lowrey in all combinations among Hawaiian taxa of all three sections of *Tetramolopium* showed that genetic barriers are essentially lacking among these species (the New Guinean taxa have not been included in crossing experiments). There also are high genetic identities among the Hawaiian species, based on allozyme studies (Lowrey & Crawford 1985). In spite of this, there is considerable diversity within *Tetramolopium* in morphology and reproductive characteristics.

In *Tetramolopium* sect. *Alpinum*, the fertile achenes of New Guinean species usually produce a pair of mid-facial nerves, but the achenes of *T. humile* lack facial nerves or have a single pair present only near the achene base. Achenes in the rest of the genus have several nerves on each face in addition to the marginal nerves. The disc flowers in sect. *Tetramolopium* and New Guinean sect. *Alpinum* have consistently sterile ovaries; Koster (1966) noted that among the 21 New Guinean species treated by her, only *T. bicolor* Koster has fertile disc achenes, supplying a caveat that the apparent fertility might not be constant. *Tetramolopium humile*, however, has fertile ovaries, as do the species of sect. *Sandwicense*. The pappus in *Tetramolopium* is either 1- or 2-seriate.

The species of sect. *Sandwicense* stand apart from the others of the genus in their combination of bisexual, fully fertile disc flowers, heads in a corymboid-paniculate capitulescence (vs. solitary heads in other species of the genus), and shorter, relatively flat phyllaries with broad margins. If the genus is indeed monophyletic, and if the Hawaiian species are derived from New Guinean ones, as seems reasonable, one must make the unlikely but necessary hypothesis (as did Lowrey) that the species with a corymboid capitulescence and fertile disc ovaries have been derived from those with solitary heads and sterile ovaries.

Lowrey did not formulate a phyletic hypothesis for the species of *Tetramolopium*, nor did he include New Guinean species in his comparative genetic studies, but in view of the peculiar internal complexity of the genus, a phylogenetic investigation would be interesting, especially in a broader systematic context. Besides the species of sect. *Sandwicense*, there are no others in any genus of the *Vittadinia* group with a corymboid capitulescence, but there are such within *Olearia* Moench and related Australasian genera of subtribe *Hinterhuberinae* (Nesom 1993), which have other suggestive resemblances to these species of *Tetramolopium*.

Other Australasian genera of the *Vittadinia* group

Iziochlamys, *Dichromochlamys*, and *Iotasperma* produce necked or beaked achenes; the first two have markedly elaborated involucre. In *Minuria* and *Kippistia*, the disc flowers have consistently sterile ovaries and the pappus is 2-seriate, with the outer series much shorter than the inner. *Iotasperma* is specialized in its annual duration, reduced habit, and small, short-necked achenes with an essentially 1-seriate pappus. *Dimorphocoma* and *Elachanthus* both comprise eglandular, annual, few-headed herbs with a paucibracteate involucre, 1-seriate pistillate flowers, sterile disc ovaries, and scaly pappus. Among the taxa of the *Vittadinia* group in the Australasian region, *Camptacra* and the two subgenera of *Vittadinia* appear to be relatively unspecialized in most respects.

The foregoing discussion is summarized in the following observations: (1) the species of *Vittadinia* subg. *Peripleura* represent a morphologically distinct lineage not intergrading with subg. *Vittadinia*; (2) the degree of morphological separation between subg. *Peripleura* and subg. *Vittadinia* is roughly equivalent to that between *Camptacra* and subg. *Vittadinia*; and (3) the distinctively specialized, multinervate achenial faces produced by *Camptacra*, *Tetramolopium*, and subg. *Vittadinia* suggest that subg. *Peripleura* occupies a primitive evolutionary position relative to all three. If *Camptacra* is segregated as a genus, which appears to be justifiable, then subg. *Peripleura* should also be treated at generic rank. Burbidge observed that the nature of the relationship between the two subgenera of *Vittadinia* is obscure and noted (p. 17) that "If a narrow circumscription was adopted for genera of *Astereae* in Australia, [subg. *Peripleura*] could be regarded as distinct." In the view here, subg. *Peripleura* is no more narrowly circumscribed as a distinct genus than its close relatives, and the proposal is made below for its formal taxonomic elevation. The following key to the Australasian genera of the *Vittadinia* group provides additional perspective on the distinctions among these genera.

Peripleura (Burbidge) Nesom, *gen. et stat. nov.* BASIONYM: *Vittadinia* subg. *Peripleura* Burbidge, *Brunonia* 5:17. 1982. Type species: *Peripleura hispidula* (F. Muell. ex A. Gray) Nesom.

1. ***Peripleura arida*** (Burbidge) Nesom, *comb. nov.* BASIONYM: *Vittadinia arida* Burbidge, *Brunonia* 5:24. 1982.
2. ***Peripleura bicolor*** (Burbidge) Nesom, *comb. nov.* BASIONYM: *Vittadinia bicolor* Burbidge, *Brunonia* 5:25. 1982.
3. ***Peripleura diffusa*** (Burbidge) Nesom, *comb. nov.* BASIONYM: *Vittadinia diffusa* Burbidge, *Brunonia* 5:20. 1982.
4. ***Peripleura hispidula*** (F. Muell. ex A. Gray) Nesom, *comb. nov.* BASIONYM: *Vittadinia hispidula* F. Muell. ex A. Gray, *Proc. Amer. Acad. Arts* 5:118. 1862.
 - a. *Peripleura hispidula* (F. Muell. ex A. Gray) Nesom var. *hispidula*.
 - b. ***Peripleura hispidula*** (F. Muell. ex A. Gray) Nesom var. ***setosa*** (Burbidge) Nesom, *comb. nov.* BASIONYM: *Vittadinia hispidula* F. Muell. ex A. Gray var. *setosa* Burbidge, *Brunonia* 5:23. 1982.
5. ***Peripleura obovata*** (Burbidge) Nesom, *comb. nov.* BASIONYM: *Vittadinia obovata* Burbidge, *Brunonia* 5:25. 1982.
6. ***Peripleura scabra*** (DC.) Nesom, *comb. nov.* BASIONYM: *Vittadinia scabra* DC., *Prodr.* 5:281. 1836.

7. *Peripleura sericea* (Burbidge) Nesom, *comb. nov.* BASIONYM: *Vittadinia sericea* Burbidge, *Brunonia* 5:26. 1982.
8. *Peripleura spechtii* (Burbidge) Nesom, *comb. nov.* BASIONYM: *Vittadinia spechtii* Burbidge, *Brunonia* 5:19. 1982.
 - a. *Peripleura spechtii* (Burbidge) Nesom var. *kimberleyensis* (Burbidge) Nesom, *comb. nov.* BASIONYM: *Vittadinia spechtii* Burbidge var. *kimberleyensis* Burbidge, *Brunonia* 5:20. 1982.
 - b. *Peripleura spechtii* (Burbidge) Nesom var. *spechtii*.
9. *Peripleura virgata* (Burbidge) Nesom, *comb. nov.* BASIONYM: *Vittadinia virgata* Burbidge, *Brunonia* 5:21. 1982.

KEY TO THE AUSTRALASIAN GENERA OF THE *VITTADINIA*
GROUP (excluding Hawaiian *Tetramolopium*)

1. Achenes apically rounded or truncate, without a neck or beak. (5)
1. Achenes with a short neck or long beak. (2)
 2. Achenes with a long, filiform beak; receptacles flat or nearly so; involucre reflexed after fruiting. *Ixiochlamys*
 2. Achenes with a short neck. (3)
3. Achenes with a prominently narrowed, basal extension below the seed, the basal extension densely tufted with stiff, appressed hairs.
..... *Vittadinia* (in part)
3. Achenes without a narrowed, basal extension below the seed, the hairs at the base no denser than on the surface. (4)
 4. Achenes ca. 1 mm long, with a short, narrow neck; pappus bristles 1-seriate; involucre bracts never incurved. *Iotasperma*
 4. Achenes ca. 2 mm long, with a short, broad neck; pappus bristles 2-seriate, the outer distinctly shorter than the inner; involucre bracts incurved after fruiting. *Dichromochlamys*
5. Achenes with only a pair of lateral nerves, these variable in thickness, sometimes obscure or absent. (8)
5. Achenes usually with 2-numerous facial nerves between the pair of lateral nerves (facial nerves absent in six species of *Vittadinia*). (6)

6. Achenes with a prominently narrowed, basal extension below the seed, the basal extension densely tufted with stiff, appressed hairs. *Vittadinia* (in part)
6. Achenes narrowly oblong to obovate to oblanceolate, without a narrowed, basal extension below the seed, the hairs at achene base no denser than on the achene surface. (7)
7. Disc flowers with fertile ovaries; achenes usually with 3 pairs of facial nerves; herbs from a woody rootstock. *Camptacra*
7. Disc flowers with sterile ovaries; fertile achenes with one pair of facial nerves, rarely none; woody-based shrubs or shrublets. *Tetramolopium*
8. Achenes with a prominently narrowed, basal extension below the seed, the basal extension densely tufted with stiff, appressed hairs. *Vittadinia* (in part)
8. Achenes without a narrowed, basal extension below the seed, the hairs at achene base no denser than on the achene surface. (9)
9. Disc flowers with sterile achenes; pappus of ray and disc achenes different. (10)
9. Disc flowers with fertile achenes; pappus of ray and disc achenes similar. (12)
10. Disc flowers with 5 lobes; pappus of ray achenes of equal-length bristles, pappus of disc achenes of unequal bristles or of bristles and scales. *Minuria*
10. Disc flowers with 3-4 lobes; pappus of ray achenes of scales or scales and bristles, pappus of disc (sterile) achenes of bristles. (11)
11. Leaves linear; ray achenes with pappus of scales. *Elachanthus*
11. Leaves oblanceolate; ray achenes with pappus of scales and bristles. *Dimorphocoma*
12. Ray flowers with yellow corollas, the ovaries often sterile; disc flowers 4-merous; achenes apically truncate, with a corresponding broad pappus insertion. *Kippistia*
12. Ray flowers with white to bluish corollas, the ovaries fertile; disc flowers 5-merous; achenes apically rounded to a narrow pappus insertion. *Peripleura*

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PYTINICARPA (ASTERACEAE: ASTEREAEE), A NEW GENUS FROM NEW CALEDONIA

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ABSTRACT

Two New Caledonian species of white-rayed daisies with solitary heads on scapose stems and leaves in a basal rosette are here separated as the new genus *Pytinicarpa*, with the new combinations *P. neocaledonica* and *P. sarasinii*. They have previously been treated as *Brachycome*, but they differ from that genus particularly in their parallel-veined leaves, disc flowers with sterile ovaries, and narrowly oblong, 6-8-nerved achenes with a short neck. *Pytinicarpa* is hypothesized to be most closely related to *Lagenifera* and related genera but differs from them in its parallel-veined leaves, sharply conical receptacle, 1-seriate pistillate flowers with long ligules, and 6-8 nerved achenes with a short, eglandular neck.

KEY WORDS: *Pytinicarpa*, *Brachycome*, *Lagenifera*, Asteraceae, Astereae, New Caledonia

In a survey of Astereae species, it has become apparent that two species of New Caledonia are taxonomically misplaced: *Brachycome neocaledonica* Guill. and *Brachycome sarasinii* Daniker. Davis did not include extra-Australian species in her monograph (1948) of *Brachycome* Cass.; the taxonomic status of these two species apparently has not been considered since Guillamin's treatment of the New Caledonian Asteraceae (1948). Their phyletic affinity is somewhat equivocal, but they appear to be as close or closer to *Lagenifera* Cass. as to *Brachycome*, as discussed below. They are not accommodated in either of these genera or in any of their relatives, and the two New Caledonian species are formally recognized here as a new genus.

Pytinicarpa Nesom, *gen. nov.* Type species: *Pytinicarpa* (*Brachycome*) *neocaledonica* (Guill.) Nesom.

Herbae perennes eglandulosae foliis rosulatis et capitulis solitariis in caulibus scaposis; folia angusta 3-nervata; phyllaria oblonga vel oblongi-obovata tenuia glabra; receptaculis acute conicis; flosculi disci velut staminati fungentes, ovariis sterilibus ac corollis brevibus; flosculi radii 1-seriati fertiles ligulis circinnatis; achenia glabra epapposa eglandulosa complanata anguste oblonga basi attenuata et brevicircularia ad apicem, plerumque 6-8 nervata. Differt a *Brachycome* Cass. foliis parallelinerviis, ovariis disci sterilibus, et acheniis nervis 6-8 longitudinalibus. Differt a *Lagenifera* Cass. foliis parallelinerviis, receptaculis acute conicis, flosculis radii 1-seriatis ligulis longis, et acheniis 6-8 nervatis.

Perennial, eglandular herbs, with leaves in a basal rosette and solitary heads on scapose stems with a few scattered, filiform bracts, the stems glabrous, 1-ca. 6 from the base, arising from a short, fibrous-rooted rhizome. Leaves narrowly oblanceolate to linear, with 3 parallel veins, the lateral pair sometimes obscure, sparsely villous with thin-based, minutely filiform, usually much-twisted, white hairs up to 3 mm long. Heads solitary, campanulate, 6-10 mm wide; phyllaries in 2-4 series of nearly equal length, inner 2.5-5.0 mm long, the outermost series ca. 1/3-1/4 as long, thin with stomates conspicuously visible, glabrous, flat, oblong, broadly rounded at the apex, with scarious, lacerate to short-ciliate margins and a thin, orange midvein; receptacles sharply conical. Disc flowers functionally staminate, with sterile ovaries; disc corollas 2-4 mm long, orange-veined, the tube 1 mm long, slightly but abruptly expanding into a non-indurated limb, tube sparsely but conspicuously invested with Type C trichomes, the lobes 5, erect, deltate; style branches narrowly triangular with sharply acute apices, 1.0-1.5 mm long, spreading-hairy from tip to base, without stigmatic lines; anther thecae basally truncate, with oblong-rounded apical appendages ca. 1 mm long, filaments adnate to the corolla at the tube-throat junction. Pistillate flowers 1-seriate, fertile, with prominent, white, coiling 4-6-veined ligules, the tube distinctly hairy near the base with Type A trichomes (see Nesom 1976 for trichome terminology). Achenes epappose, flattened, narrowly oblong with a narrowed base and apex and with an eglandular, barely formed neck, usually with 2 marginal nerves and (1-)2(-3) additional nerves on each face, the total number of nerves not greater than 8, the lateral and facial nerves similar in thickness, all nerves vascularized, the faces glabrous, eglandular, tan or becoming distinctly purplish, the surfaces with a minutely "frothy" texture at maturity because of distinctly inflated quadrate cells.

The generic name is derived from "pytine" (Greek, referring to a flask covered with plaited work) and "carpos" (Greek, fruit), alluding to the shape of the achenes and their facial ribbing as well as the putative relationship of *Pytinicarpa* with *Lagenifera* ("lagena," flagon and "fero," to carry, Latin).

KEY TO THE SPECIES

1. Leaves nearly linear, 2-4 mm wide, usually entire, glabrous or nearly so; disc corollas 2.2-2.5 mm long. *P. neocaledonica*
1. Leaves oblanceolate, distinctly broadened in the distal half or third, 5-15 mm wide at the broadest point, usually coarsely toothed; often persistently loosely white-sericeous; disc corollas 3.0-4.0 mm long. *P. sarasinii*

Pytinicarpa neocaledonica (Guill.) Nesom, *comb. nov.* (Figure 1). BASIONYM: *Brachycome neocaledonica* Guill., Bull. Soc. Bot. France 84:61. 1937. SYNTYPES: NEW CALEDONIA: Nehoue, *Pancher 94* and *Deplanche 425*; Gatope, 1861-1867, *Viellard 2823*. I have studied 2 sheets of *Viellard 2823* (AA!,GH!), which include a total of 5 plants.

Leaves 8-18 cm long, mostly linear, very slightly tapered near the base, 2-4 mm wide at the widest point, apex acute, margins usually entire, rarely apically mucronulate, sparsely villous with long, white, loose, thin hairs along the margins and veins, quickly glabrescent; scapes 20-35 cm long; heads 4-6 mm wide; phyllaries in 2-3 series, the inner 2.5-3.0 mm long; ray flowers 15-19, 4-6 mm long including the tube 1 mm long, the ligules ca. 0.5 mm wide; disc corollas 2.2-2.5 mm long, the tube only slightly constricted; achenes ca. 3 mm long.

Pytinicarpa sarasinii (Daniker) Nesom, *comb. nov.* (Figure 2). BASIONYM: *Brachycome sarasinii* Daniker, Mitt. Bot. Mus. Univ. Zürich 142:479. 1933. TYPE: NEW CALEDONIA: am obern Abhang des Mut. Koniambo bei der Mine Boume I, zerstreut im lichten Gebusch an felsigen stellen, 14 Jan 1925, *Daniker 880* (HOLOTYPE: Z).

Leaves 2.5-14.0 cm long, petiolate, oblanceolate, 5-15 mm wide at the widest point, apex acute to obtuse, margins usually with 1-3 pairs of coarse teeth to small mucros on the distal 1/3-1/4, less commonly entire, sparsely villous with long, white, loose, thin hairs along the margins and veins, young leaves often densely white-villous but glabrescent, the hairs more persistent at the leaf base; scapes 14-36 cm long; heads 6-10 mm wide; phyllaries in 3-4 series, the inner 3-5 mm long; ray flowers 26-38, 8-12 mm long including the tube 1 mm long, the ligules 1.5-1.8 mm wide; disc corollas 3.0-4.0 mm long; achenes 2.5-4.0 mm long.

Collections examined: NEW CALEDONIA: top of Mt. Kaala (ca. 15 km SE of Koumac), ca. 1000 m, open soil in rocky, lateritic serpentine area, 9 Dec

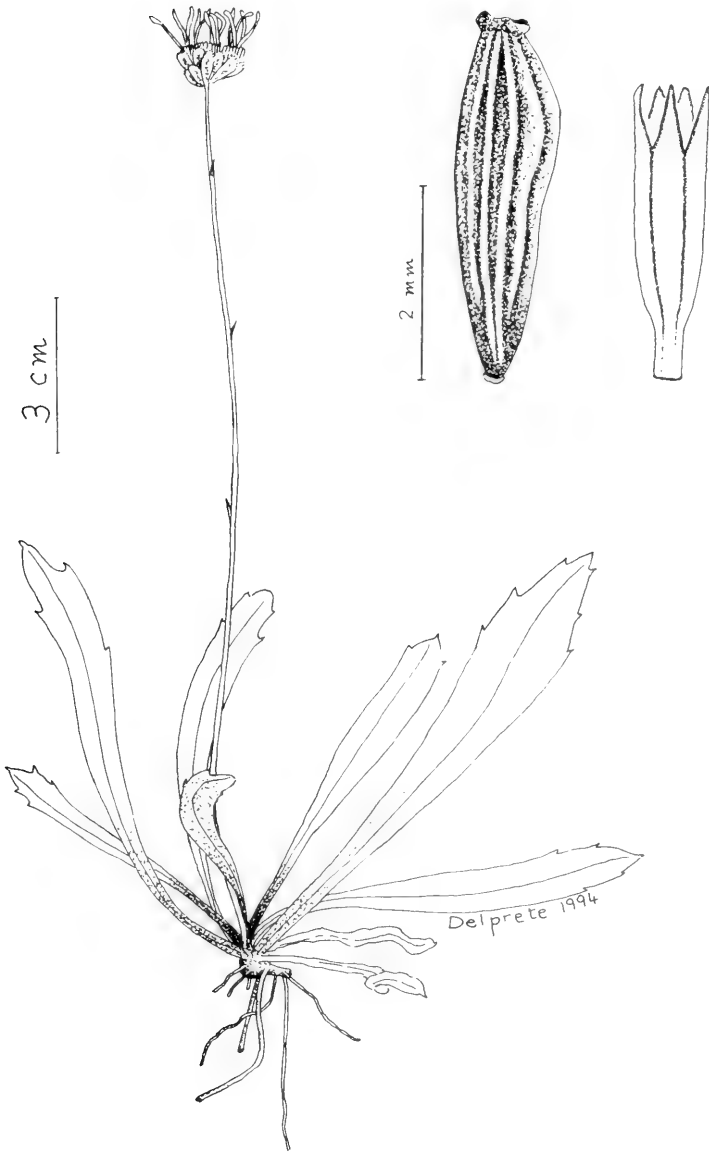


Figure 1. Habit and details of *Pytinicarpa sarasinii*.



Figure 2. Habit of *Pytinicarpa neocaledonica*.

1963, *Green 1817* (AA); Mt. Koniambo, S of Voh, scrub on peridotite, 800 m, 11 Oct 1982. *McPherson 4990* (MO).

Also cited by Daniker (1933): NEW CALEDONIA. Serpentinberg Koniambo bei Voh 400 m, 21 Mar [no year], *Heim 50* (Z); am Koniambo Massiv, ca. 200 m, 14 Jul 1911, *Sarasin 86* (Z). The label data, as well as Daniker's comments (1932-33), note that this species occurs on a serpentine substrate.

Daniker (1933) specifically compared his new species to *Brachycome neo-caledonica* Guill., but the latter name does not appear to have been validly published until 1937. Guillamin (1937) apparently was unaware of Daniker's publication, as *Pytinicarpa sarasinii* apparently is the species identified by Guillamin as *Brachycome scapigera* DC.

There is a remarkable resemblance between the two species of *Pytinicarpa* and many of *Brachycome* (e.g., *B. nivalis* F. Muell., *B. cardiocarpa* F. Muell. ex Benth., *B. scapiformis* DC.) in habit (scapose, rosulate) and phyllary morphology (broad, oblong-obovate, evenly herbaceous, pauciseriate), and most *Brachycome* produce conical receptacles, 1-seriate pistillate flowers, short-tubed disc corollas, and epappose achenes. There are no species of *Brachycome*, however, that produce parallel-veined leaves with shiny-textured surfaces, disc flowers with sterile ovaries, or similarly shaped (relatively long) achenes; further, no achenes of *Brachycome* have longitudinally nerved faces or a short neck. *Brachycome* is primarily an Australian genus with a few species in New Zealand (Allan 1961) and New Guinea (Koster 1966). Two closely related Australasian relatives of *Brachycome* (*Calotis* R. Br. and *Ceratogyne* Turcz.) have functionally staminate disc flowers, but they are generally similar to *Brachycome* in leaf and achene morphology.

Most of these same features (scapose and rosulate habit, few and broad phyllaries, epappose achenes, short-tubed corollas) also are characteristic of *Lagenifera* and genera closely related to it (e.g., *Solenogyne* Cass., *Myriactis* Less., *Keysseria* Lauerb.; see Nesom 1994 and in prep. for general comments), which also occur primarily in the Australasian area. The morphological resemblance and geographic coherence of the taxa of this relatively broad group (*Lagenifera* and its relatives and *Brachycome* and its relatives) suggests that they are related between themselves and that the phyletic affinity of *Pytinicarpa* lies with them. This is not surprising, as the strongest relationship of the New Caledonian flora lies with the Queensland area of Australia (Thorne 1969).

Further, the oblong, short-necked achenes of *Pytinicarpa* are markedly similar to those of *Lagenifera* and related genera, and sterile disc ovaries are common in the *Lagenifera* group. All of these genera, however, produce pinnately veined leaves with dull-textured surfaces, flat to merely low-convex receptacles, flat and 2-nerved achenes, and pistillate flowers in several series. While *Pytinicarpa* cannot be congeneric with any of the *Lagenifera* group, its strongest similarity appears to lie in that direction.

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TAXONOMIC DISPERSAL OF AUSTRALIAN *ERIGERON* (ASTERACEAE:
ASTEREAE)

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ABSTRACT

The native Australian species previously treated as *Erigeron* are more closely related to other genera, necessitating the partition of these species into three new genera. Two of the species are members of the Australasian *Vittadinia* group and are segregated as *Iotasperma* *gen. nov.*, with the nomenclatural combination *I. sessilifolia* (F. Muell.) Nesom and the new name *I. australiensis* Nesom (based on *Erigeron ambiguus* F. Muell., *nom. illeg.*). The remaining species (except one) are closely related to *Lagenifera*: two of these are segregated as *Lagenithrix* *gen. nov.* with the new combinations *L. setosa* (Benth.) Nesom and *L. stellata* (J.D. Hook.) Nesom; *Lagenopappus* *gen. nov.* comprises several species not yet described and three species formally included with the new combinations *L. pappocromus* (Labill.) Nesom, *L. gunnii* (J.D. Hook.) Nesom, and *L. tasmanicus* (J.D. Hook.) Nesom. The phyletic identity of the Australian *Erigeron conyzoides* F. Muell. remains to be determined.

KEY WORDS: *Erigeron*, *Lagenifera*, Astereae, Asteraceae, Australia

In a review of the 7-10 native Australian species treated as *Erigeron* L., it is recognized here that all of them (with the possible exception of one) are closely related to generic groups primarily occurring in Australia but only distantly related to true *Erigeron*. *Erigeron* occurs in the New World and through much of the Old World, but there are no native species of *Erigeron* in the South Pacific or Australasian region (see also Nesom 1994b, in press). *Erigeron karwinskianus* DC. (sometimes identified as *E. mucronatus* DC.), a native of México, occurs widely through Australia as an adventive; a number of species of *Conyza* L. (sometimes identified as *Erigeron*) also are adventive in

Australia. The native Australian species under consideration are here treated among three new genera, described and discussed below in sequence. Species definitions within two of the new genera remain to be worked out in detail.

I. *Iotasperma*, a new genus of the *Vittadinia* group

Two Australian species treated as *Erigeron*, *E. ambiguus* F. Muell. and *E. sessilifolius* F. Muell., are morphologically disparate within *Erigeron*. The Australian plants have glandular leaves and stems, and numerous pistillate flowers in several series, with white, filiform, tightly coiling ligules. Most diagnostically, the achenes are obovate and flattened, with two broad, sclerified marginal ribs, the faces are without secondary nerves, densely strigose (with twin-hairs), and glandular, the glands concentrated near the apex and base but also scattered over the surface (these obscured by the strigose vestiture), and the pappus is formed of basally caducous bristles in a single series. The detailed and oft-reprinted illustration of *E. sessilifolius* by Black (1929) does not show the glandular vestiture.

In their glandular herbage, multiseriate pistillate flowers with filiform ligules, and glandular achenes, these two "*Erigerons*" resemble plants of the group of Australasian genera that includes *Vittadinia* A. Rich., *Camptacra* Burbidge, *Tetramolopium* Nees, *Peripleura* (Burbidge) Nesom, *Minuria* DC., *Kippistia* F. Muell., *Dimorphocoma* F. Muell. & R. Tate, *Elachanthus* F. Muell., *Ixiochlamys* Sond., and *Dichromochlamys* Dunlop. Relationships among these genera (the *Vittadinia* group) are discussed in separate papers (Nesom 1994a and in prep.). These two Australian "*Erigerons*" differ from all taxa within the *Vittadinia* group in their combination of shallowly cupulate heads, funnellform disc corollas, minute, elliptic-obovate, 2-ribbed achenes, and essentially uniseriate pappus. These plants are here formally distinguished as a separate genus, named for the minute achenes probably producing agamospermy initiated embryos (see below).

***Iotasperma* Nesom, gen. nov.** (Figure 1). Type species: *Iotasperma australiensis* Nesom.

Inter *Vittadinia* A. Rich. et genera affinia distinctus capitulis vadose cupulatis, floribus radii seriebus 2-3 ligulis filiformibus circinnatis, floribus discii fertilibus bisexualibusque corollis infundibularibus, acheniis parvis obovatis glandulosi-strigosis costis marginalibus latis sed absque nervis facialibus, et pappo uniseriato setarum caducarum.

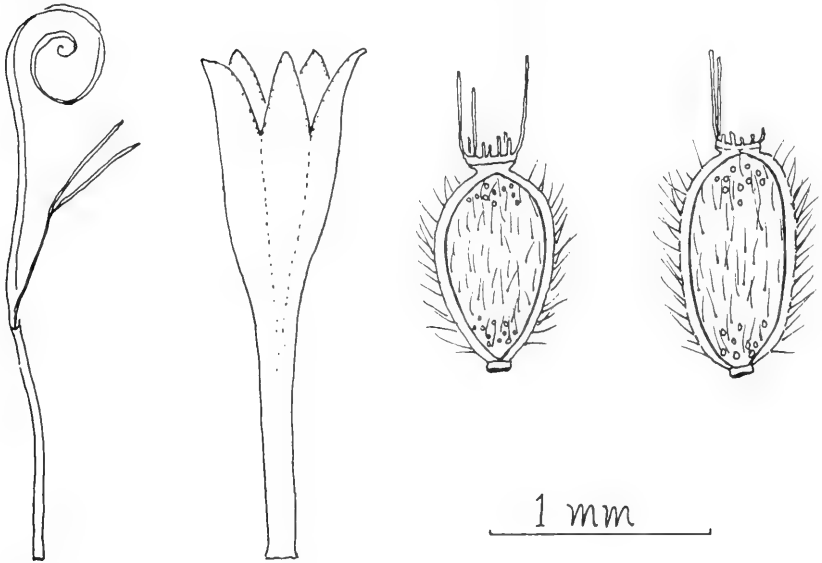


Figure 1. Flowers and achenes of *Iotasperma*: *I. australiensis* (*Maconochie* 2459-US).

Annual herbs from slender taproots, stems erect, 10-35 cm tall, few-branched on the upper half; leaves and stems moderately hispid-pilose and sparsely glandular. Leaves alternate, evenly distributed along the stems, 1-4(-5) cm long, 2-12 mm wide, reduced in size below the heads, oblanceolate-oblong, epetiolate, subclasping, entire or with 1-2 pairs of coarse teeth on the distal half. Heads shallowly cupulate, 8-12 mm wide (pressed), terminal on peduncles 1-3 cm long with reduced leaves, in a loose, corymboid capitulescence; phyllaries in ca. 2 series of equal length, 3-4 mm long, inserted on a broad, veined lamina, flat, narrowly elliptic-lanceolate with broad scarious margins, distinctly 3-veined, moderately stipitate-glandular, green, the inner basally indurate. Disc flowers apparently bisexual, the corollas 2.2-2.5 mm long, the linear tube about half the corolla length, abruptly opening into the obdeltate limb, 5 lobed, without orange venation; staminal filaments inserted at the tube-limb junction; style branches 0.2-0.3 mm long, without lines of stigmatic papillae; anther thecae with lanceolate apical appendages, not basally caudate. Pistillate flowers fertile, numerous in ca. (1-)-2-3 series, with white to purplish, filiform (0.05 mm wide), tightly coiling ligules 1.0-1.5 mm long; style branches without lines of stigmatic papillae. Achenes obovate to broadly elliptic-obovate, 0.9-1.1 mm long, 0.5-0.6 mm wide, rounded at the apex, strongly flattened with a pair of broad, sclerified, glabrous lateral ribs, the faces densely strigose with Zwill-

ingshaare with acute apices, the margins ciliate with similar hairs, minute biseriate glands (Type C trichomes) scattered over the faces but concentrated at the apex and base; carpodium of 4-5 rows of blocky, thick-walled cells; pappus of ray and disc achenes a single series of 6-10(-15) barbellate bristles as long as the disc corollas, these basally caducous but connate at the very base, breaking off and leaving a minute, laciniate-margined corona 0.05 mm high.

1. ***Iotasperma australiensis*** Nesom, *nom. nov.* BASIONYM: *Erigeron ambiguus* F. Muell., Trans. Proc. Philos. Inst. Victoria 3:58. 1859 [non Nuttall 1818; non Sch.-Bip. in Webb. & Berth. 1844.]. TYPE: AUSTRALIA. Queensland: on the Gilbert River, *F. Mueller s.n.* (MEL?).
2. ***Iotasperma sessilifolia*** (F. Muell.) Nesom, *comb. nov.* BASIONYM: *Erigeron sessilifolius* F. Muell., Fragm. Phytogr. Austr. 11:100. 1880. TYPE: none cited by Mueller (MEL?).

According to Jessop (1981, p. 376), *Iotasperma sessilifolia* was originally collected in tropical Northern Territory; it also is "known from 3 or 4 fragments collected in [South Australia] between 1889 and 1927. The differences between this species and the earlier *E. ambiguus* F. Muell. appear slight and require examination." Mueller, however, in the original description of *Erigeron sessilifolius*, provided a diagnosis comparing the two, and Hnatiuk (1990) has listed both species as accepted taxa, showing the distribution of *I. sessilifolia* in Northern Territory and South Australia and that of *I. australiensis* in Northern Territory and Queensland. The presence of *I. australiensis* in the Kimberly Region of West Australia is recorded by Wheeler *et al.* (1992). Cooke (1986) noted that *I. sessilifolia* occurs "on creek edges and waterholes" in South Australia, flowering January to July.

The relationships of *Iotasperma*

The nature of the relationship of *Iotasperma* to other genera of the *Vittadinia* group is obscure, but *Iotasperma* is comparable in various aspects to *Vittadinia*, *Peripleura*, and *Camptacra* and to *Iziochlamys* and *Dichromochlamys*. Both of these generic groups include annuals, and leaves in both groups are morphologically similar to those of *Iotasperma*. In its relatively broad (vs. elongate) heads and funnellform (vs. narrowly tubular) disc corollas, *Iotasperma* is more similar to *Dichromochlamys* and *Iziochlamys*. *Minuria* stands apart from the rest of the *Vittadinia* group, including *Iotasperma*, in its dimorphic pappus (on disc and ray achenes) with both bristles and scales, and consistently

sterile disc ovaries. The small genera *Kippistia*, *Dimorphocoma*, and *Elachanthus* apparently are closely related to *Minuria* and can also be eliminated from consideration as immediate relatives of *Iotasperma*.

In the Astereae, the style branches of disc flowers with fertile ovaries have a pair of marginal, functionally stigmatic lines of small papillae below the non-stigmatic, apical collecting appendages, and the pistillate flowers have style branches with lateral stigmatic lines continuous up to the apex. In *Iotasperma*, although both the ray and disc achenes appear to be completely fertile, stigmatic lines are absent in both types of flowers and the embryos are probably formed agamospermissally. The same lack of stylar differentiation apparently occurs in *Dichromochlamys*.

The achenes of *Iotasperma* are ca. 1 mm long, while those in closely related genera are mostly 2.5 mm long. Apart from their small size, the achenes of *Iotasperma* are similar to those of *Peripleura* in their obovate outline, nerveless faces, and thick, sclerified lateral ribs. Thick lateral ribs are also characteristic of *Vittadinia* but the achenes of *Vittadinia* as well as *Camptacra* are specialized in their multinerved faces; those of *Vittadinia* have a basal extension (below the seed) with a dense, basal tuft of hairs. The achenes of *Ixiochlamys* have a filiform beak and those of *Dichromochlamys* produce a broad neck; there is also a definite tendency for apical constriction of the achenes in *Vittadinia* and *Peripleura* as well as *Minuria*. In rehydrated achenes of *Iotasperma*, a short neck is often evident, but in dried material it is not.

The pappus in genera of the *Vittadinia* group tends to be multiseriate (2-3 series of bristles); one or two of the pappus series may be reduced in length. Reduction in the number of bristles and number of pappus series occurs in *Camptacra* and *Peripleura*, where the pappus tends to be 1-seriate. Among other Australian genera of the *Vittadinia* group, the pappus of two species of *Ixiochlamys* also approaches the highly abbreviated, consistently 1-seriate pappus of *Iotasperma*.

Summary

The Australian species *Erigeron ambiguus* and *E. sessilifolius* are here segregated as the new genus *Iotasperma*. *Iotasperma* is a member of the Australasian *Vittadinia* group, but the nature of the intergeneric relationships within this group is obscure. *Iotasperma* resembles the Australian genera *Vittadinia*, *Camptacra*, and *Peripleura* in some features, but it is more similar to *Ixiochlamys* and *Dichromochlamys* in others.

II. *Lagenithrix*, a new genus related to *Lagenifera*

The treatment of the two Australian species *Erigeron setosus* Benth. and *E. stellatus* (J.D. Hook.) W.M. Curtis as *Erigeron* apparently has emphasized aspects of their rather generalized, *Erigeron*-like appearance, particularly their white rays and pappus of both ray and disc achenes of numerous, persistent, barbellate bristles. On closer examination, however, these species show features that are anomalous within *Erigeron* but that are characteristic of *Lagenifera* and related genera. Their achenes are glabrous or glabrate except for numerous glands near the apex, although the glands usually are not persistent at achene maturity. One of the species has functionally staminate disc flowers (the ovaries sterile) with mostly 4-merous corollas and the other has achenes slightly constricted into a short, thickened neck. Their putative relationship to *Erigeron* is hypothesized to be superficial and they are recognized here as a separate genus.

Lagenithrix Nesom, *gen. nov.* (Figures 2A, 2B). Type species: *Lagenithrix* (*Erigeron*) *setosa* (Benth.) Nesom.

A *Lageniferae* Cass. ac *Myriacti* Less. similis sed habitu nano tagetiformanti, caulibus monocephalis scaposis, floribus disci ovarii sterilibus vel fertilibus, acheniis oblanceolati-oblongis ca. 2 mm longis collo brevi crasso, et pappo 1-2-seriato setarum barbellatarum persistentium dignoscenda.

Herbaceous perennials from short, lignescent, fibrous-rooted stolons, commonly forming low mats, producing clusters of very small leaves at the stolon tips; stems and leaves sparsely to densely hispid-pilose with prominently cross-walled, uniseriate trichomes, glandular or eglandular. Leaves all basal, thick, oblanceolate to spatulate with a rounded apex, entire, with the petiole broadening slightly at the base, 3-nerved from the base, 4-18 mm long, 2-3 mm wide. Heads solitary, hemispheric, 5-12 mm in diameter, sessile or on bracteate scapes; phyllaries in 2-3 series of even length, narrowly oblong-lanceolate, 4-6 mm long, flat, 1-nerved, evenly herbaceous except for very narrow, scarious margins, often purple-tipped, minutely glandular, otherwise glabrous or the outer sparsely pilose; receptacles smooth, barely convex, epaleate. Disc flowers functionally staminate (*Lagenithrix stellata*) or bisexual (*L. setosa*); corollas 3.5-4.5 mm long, funnellform, the linear tube opening into an obtriangular limb 1/2-3/4 the length of the corolla, with 4-5 triangular-ovate lobes; apical appendages of the anthers lanceolate with rounded to acute apices; style branches with deltate collecting appendages (*L. setosa*) or stigmatic lines absent and collecting appendage not differentiated from lower part of style branches (*L.*

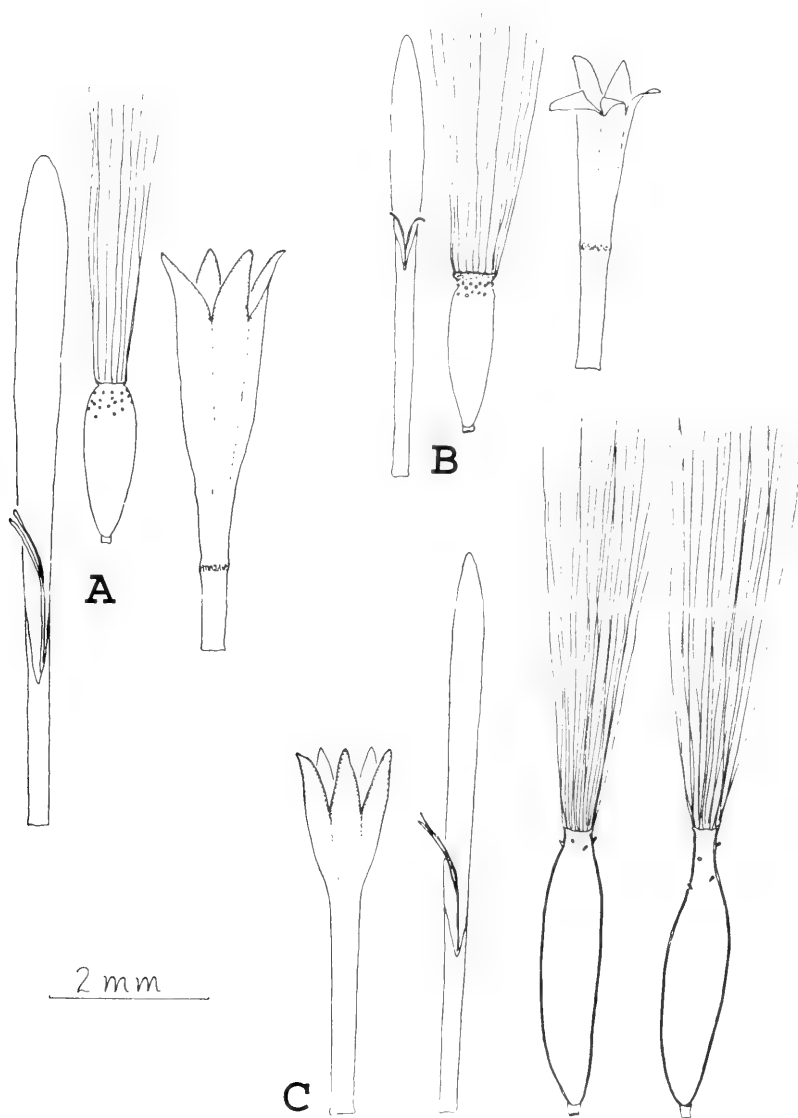


Figure 2. Flowers and achenes of *Lagenithrix* and *Lagenopappus*: A. *Lagenithrix setosa* (Tindale 4056-US); B. *Lagenithrix stellata* (Ratkowsky 185-MO); C. *Lagenopappus gunnii* (Ratkowsky 1088-MO).

stellata). Pistillate flowers ca. 25-36 in 1-2 series, fertile, the corollas 5-8 mm long including the tube, the ligules white, ca. 2-4 mm long, straight, extending slightly past the involucre. Fertile achenes oblanceolate-oblong, 1.8-3.0 mm long, flat with 2, thin, marginal nerves, sometimes with an extra nerve on each face, apically constricted into a short neck with a thickened collar, faces glabrous except for the concentration of viscid, biseriate glands (Type C trichomes) on the upper third or concentrated at the apex, otherwise glabrous or sparsely strigose along the margins. Pappus of ray and disc achenes similar, of 1-2 series of 12-35 apically attenuate, persistent barbellate bristles as long as the disc corollas.

1. **Lagenithrix setosa** (Benth.) Nesom, *comb. nov.* BASIONYM: *Erigeron pappocromus* Labill. var. *setosus* Benth., *Fl. Austral.* 3(5):494. 1867. *Erigeron setosus* (Benth.) M. Gray, *Contr. Herb. Austr.* 6:1. 1974. LECTOTYPE (Gray 1974): AUSTRALIA. [New South Wales]: [Munyang Mountains], in vertice montis Kosciusko, locis glareosis, 6000-6500 ft, Jan 1855, *Dr. F. Mueller s.n.* (MEL).

Leaves spatulate, 4-8(-15) mm long, the blade 2-3 mm wide, sparsely to densely, loosely hirsute-villous on faces and margins with prominently cross-walled, uniseriate (Type A) trichomes, sparsely hairy with minute uniseriate (Type B) trichomes, and minutely glandular with biseriate (Type C) trichomes. Heads (flowering) ca. 5-8 mm in diameter, at first nearly sessile but the scape often elongating up to 7 cm at maturity. Disc corollas with the tube opening into an obtriangular limb about half the length of the corolla, with 5 triangular-ovate lobes; style branches 0.6-0.8 mm long, with distinct stigmatic lines and deltate collecting appendages 0.2 mm long. Pistillate flowers ca. 25-35, the corollas 4-6 mm long including the tube, the ligules ca. 2-3 mm long. Achenes 2-nerved, glabrous except for the concentration of viscid, biseriate glands at the thickened apex. Pappus of 12-15 bristles.

According to Gray (1974, p. 1), "This dwarf species is quite distinctive, and easily recognized by the entire leaves \pm 0.7-1.5 cm long, coarsely hispid with bristly septate hairs, arranged in small rosettes about 1.5-3.5 cm in diameter. The capitula are at first subsessile or on very short scapes as mentioned by Bentham [1867], but the scapes elongate to 7 cm or more in the fruiting stage." The species appears to be endemic to the alpine area of the Kosciusko area along the border of New South Wales and Victoria, where it occurs "mainly in the *Plantago-Neopazia* short alpine herbfield." Gray (1974) cited a number of collections of this species; the collection I have examined (*Tindale 4056-US*) was collected "near a creek, marginal to short alpine herbfield" on 19 Jan 1975; the plants were intermixed with lichens and mosses.

2. ***Lagenithrix stellata*** (J.D. Hook.) Nesom, *comb. nov.* BASIONYM: *Haplopappus stellatus* J.D. Hook., London J. Bot. 6:112. 1847. *Erigeron tasmanicus* (J.D. Hook.) J.D. Hook. var. *stellatus* (J.D. Hook.) J.D. Hook., *Fl. Tasman.* 3(1):183, t. 46A. 1856. *Erigeron pappocromus* Labill. var. *stellatus* (J.D. Hook.) Benth., *Fl. Austral.* 3(5):494. 1867. *Erigeron stellatus* (J.D. Hook.) W.M. Curtis, *Student's Fl. Tasman.* 2:312, 463. 1963. TYPE: AUSTRALIA. "mountains," *Gunn 279* (K).

Leaves oblanceolate or narrowly spatulate, 8-18 mm long, 2-3 mm wide, the faces glabrous and eglandular, the margins spreading-ciliate with prominently cross-walled, uniseriate trichomes. Heads (flowering) 10-12 mm in diameter, sessile or on bracteate scapes up to 3 cm long. Disc corollas with the tube opening into an obtriangular limb about 3/4 the length of the corolla, with 4-5 triangular-ovate lobes; style branches ca. 1 mm long, evenly long-papillate from base to tip, without stigmatic lines. Pistillate flowers ca. 28-36, the corollas 6-8 mm long, ligules ca. 3-5 mm long. Fertile achenes 2-nerved or commonly with an extra nerve on each face, the faces with viscid, sessile, biseriate glands on the upper third but concentrated at the thickened apex, sparsely strigose along the margins and sometimes on the faces; disc achenes lengthening to full mature size but sterile. Pappus of 30-35 bristles.

Lagenithrix stellata is endemic to Tasmania. The collections I have studied (Ratkowsky 957 and 185, MO) were made at 4300 and 4800 feet elevation on Mt. Field West and Mt. Olympus, respectively. This species differs from *L. setosa* in its larger, more oblanceolate leaves with glabrous faces, larger heads with more pistillate flowers, tendency for 4-lobed disc corollas, functionally staminate disc flowers, and greater number of pappus bristles.

The relationships of *Lagenithrix*

On the basis of their low, herbaceous-stoloniferous habit, leaves all basal and spatulate to obovate or oblanceolate, solitary heads on short scapes, multiseriate pistillate flowers with short, white ligules, their tendency to produce functionally staminate disc flowers with 4-merous corollas, and their flat, 2-nerved, oblong achenes with glandular but otherwise essentially glabrous faces, these two species of "*Erigeron*" are placed in the immediate phyletic vicinity of *Lagenifera* Cass. and its close relatives. The Australasian genera *Keysseria* Lauerb., *Myriactis* Less., *Piora* Koster, and *Solenogyne* Cass., as well as several others, are closely related to *Lagenifera*, as observed by many systematists (e.g., Bentham 1973; Cabrera 1966; Koster 1966; Drury 1974; Adams 1979; Zhang & Bremer 1993); a broader commentary on this whole group follows in a separate paper (Nesom in prep.), and another related genus from New Caledonia is newly described in the present volume (Nesom 1994c). *Lagenithrix*

setosus and *L. stellatus* differ from all of these genera in their production of a persistent pappus, otherwise they surely would have been earlier recognized as close relatives of *Lagenifera*. Species of the *Lagenifera* group are epappose except for these two pappose "lagenoids" and those of the genus *Lagenopappus* (described below), and the presence of a pappus in these species must be interpreted as a primitive feature of retention. Although there is a recurrent evolutionary tendency in the Astereae for the loss of pappus bristles, they occur in all other generic groups potentially related to *Lagenifera* (Nesom in prep.).

Among the epappose members of the *Lagenifera* group, plants of *Solenogyne*, *Lagenifera*, and *Myriactis* tend to be low, stoloniferous herbs. Of these, *Lagenifera* and *Solenogyne* occur in Australia and produce scapose, unbranched stems with solitary heads (vs. leafy stems with a few-headed capitulescence in *Myriactis*, which is primarily southeast Asian and Malesian). The achenes of *Lagenopappus* resemble those of *Solenogyne* in their lack of a filiform neck or beak and lack of persistent apical glands; the achenes of *Lagenithrix* are smaller and somewhat differently shaped but they have a persistently glandular, thickened apical area that apparently is homologous with the beak of *Lagenifera*. Thus, despite the similarity between the two groups of "pappose lagenoids," particularly in their prominently ligulate pistillate corollas and pappose achenes, their relationships may lie in different directions rather than most closely with each other, although the interpretation of relationships among these genera is complex. In any case, the two species of *Lagenithrix* are distinct from all others within the *Lagenifera* group.

Summary

The Australian species identified as *Erigeron setosus* (New South Wales) and *E. stellatus* (Tasmania) resemble *Lagenifera* and *Myriactis* in their stoloniferous habit, obovate to spatulate basal leaves, tendency to produce 4-merous disc corollas and sterile disc ovaries, and in their short white ligules and fertile achenes that are glabrous except for the concentration of viscid glands on the short, thickened neck. These two species appear to be most similar to *Lagenifera*, from which they differ in their dwarf, mat-forming habit, smaller, erostrate achenes, and pappus of persistent bristles, and they are here set apart as the new genus *Lagenithrix*.

III. *Lagenopappus*, a new genus of the *Lagenifera* group

The traditional generic placement of *Erigeron pappocromus* Labill. and closely related taxa, like that of *E. setosus* and *E. stellatus* (above), has emphasized the occurrence of pappose achenes. With the observation of achenial

glands and other features that are more similar to Australian genera than to true *Erigeron*, it has become apparent that these few species should be placed in a separate genus.

Lagenopappus Nesom, *gen. nov.* (Figure 2C).

Lageniferae Cass. similis sed differt floribus discii ovariiis fertilibus, acheniis rostrum filiformem vel collum carentibus, glandibus acheniorum celeriter deciduis, et pappo setis numerosis persistentibusque.

Type species: *Lagenopappus (Erigeron) pappocromus* (Labill.) Nesom.

Pappochroma Rafin., *Fl. Tellur.* 2:48. 1836. Type species: *Pappochroma uniflora* Rafin. [*nom. nov. illeg.*] (= *Erigeron pappocromus* Labill. = *Lagenopappus pappocromus* [Labill.] Nesom). "*Pappochroma*" as a generic name was tautonymic at its inception and is illegitimate.

Herbaceous perennials from short, fibrous-rooted stolons, producing clusters of ascending leaves at the stolon tips, commonly forming colonies; stems and leaves sparsely to densely pubescent to hispid-pilose with uniseriate trichomes, stipitate-glandular or eglandular. Leaves all basal, obovate to spatulate, 1-4(-7) cm long, 4-15 mm wide, entire or mucronulate to crenate on the distal third, reticulate-nerved but only the central vein conspicuous. Heads solitary, short-cylindric, 8-12 mm (pressed) in diameter, on bracteate scapes 4-15 cm tall; phyllaries in ca. 3 series of nearly equal length, narrowly oblong-lanceolate with an acuminate apex, 1-nerved, flat or slightly keeled with a raised midvein, evenly herbaceous, tips and distal margins often purple or the outer completely purple; receptacles smooth, barely convex, epaleate. Disc flowers bisexual, fertile, few in number relative to the pistillate flowers; corollas 3.5-4.5 mm long, funnelform, the linear tube abruptly but only slightly opening into a tubular limb 1/2-5/8 the length of the corolla, with 5 triangular lobes; apical appendages of the anthers lanceolate with rounded to acute apices; style branches 0.8-1.0 mm long, with triangular-lanceolate collecting appendages occupying ca. 1/2-1/3 of the style branch length, the stigmatic lines poorly defined in *Lagenopappus gunnii* (J.D. Hook.) Nesom. Pistillate flowers ca. 60-120 in 3-4 series, fertile, the corollas 5-7 mm long including the tube, the ligules white, ca. (3-)6-12 mm long, 0.1-0.4 mm wide, straight, extending slightly past the involucre. Achenes 3-7 mm long, flat with 2, thin, marginal nerves, narrowly oblong to oblong-ob lanceolate, commonly with a short and broad but distinctive neck, the formation of the neck apparently

variable even within a single head, the faces yellowish-tan or sometimes purple, glandular near the apex with viscid, sessile, biseriate glands but these quickly deciduous and usually not evident on the mature achenes, otherwise glabrous. Pappus of ray and disc achenes 1(-2) series of 35-50 apically attenuate, persistent, barbellate bristles of even length, as long as the disc corollas.

1. **Lagenopappus pappocromus** (Labill.) Nesom, *comb. nov.* BASIONYM: *Erigeron pappocromus* Labill., *Nov. Holland. Pl. Specimen* 2:47, t. 193. 1806. *Erigeron phlogotrichus* Sprengel, *Syst. Veget.* (ed. 16) 3:520. 1826 [*nom. nov. illeg.*]. *Haplopappus pappocromus* (Labill.) J.D. Hook., *London J. Bot.* 6:111. 1847. *Erigeron pappocromus* Labill. var. *billardierei* Benth. [*nom. nov.*], *Fl. Austral.* 3(5):494. 1867. TYPE: AUSTRALIA. "in capite Van-Diemen" [Tasmania, Recherche Bay], *Labillardiere s.n.* (LINN). Upon Bentham's decision to recognize varieties within *Erigeron pappocromus*, he used variety *billardierei* (*nom. nov.*) to refer to the typical element of the species (which should have been simply var. *pappocromus*).
2. **Lagenopappus gunnii** (J.D. Hook.) Nesom, *comb. nov.* BASIONYM: *Haplopappus gunnii* J.D. Hook., *London J. Bot.* 6:111. 1847. *Erigeron gunnii* (J.D. Hook.) F. Muell. *ex J.D. Hook.*, *Fl. Tasman.* 1:183, t. 46B. 1856. *Erigeron pappocromus* Labill. var. *gunnii* (J.D. Hook.) Benth., *Fl. Austral.* 3(5):494. 1867. TYPE: AUSTRALIA. Tasmania: Mt. Wellington, *Gunn 1151* (K).

Haplopappus bellidioides J.D. Hook., *London J. Bot.* 6:112. 1847. BASIONYM: *Erigeron gunnii* (J.D. Hook.) F. Muell. *ex J.D. Hook.* var. *bellidioides* J.D. Hook., *Fl. Tasman.* 1:183. 1856. TYPE: AUSTRALIA. Tasmania: Middlesex plains, *Gunn 692* (K).
3. **Lagenopappus tasmanicus** (J.D. Hook.) Nesom, *comb. nov.* BASIONYM: *Haplopappus tasmanicus* J.D. Hook., *London J. Bot.* 6:110. 1847. *Erigeron tasmanicus* (J.D. Hook.) J.D. Hook., *Fl. Tasman.* 1:183, t. 46A. 1856. *Erigeron pappocromus* Labill. var. *oblongatus* Benth., [*nom. et stat. nov.*], *Fl. Austral.* 3(5):494. 1867. TYPE: AUSTRALIA. Tasmania: Mt. Wellington, *Gunn 1150* (K). It is not clear that Bentham's proposed substitution of *E. pappocromus* var. *oblongatus* for *E. tasmanicus* can be taken as legitimate.

Curtis (1963, p. 312) noted that the Tasmanian taxa of the *Erigeron pappocromus* complex "seem to be connected by intermediates" and she treated them as varieties of a single species. Among the relatively few Tasmanian

specimens I have studied, however, the taxa appear to be distinct. Without the direction of a much-needed revision of this complex (see below), three of the taxa are tentatively treated here at specific rank. *Lagenopappus gunnii* has obovate, epetiolate or short-petiolate leaves with crenate-serrate margins and stipitate-glandular vestiture. *Lagenopappus pappocromus* and *L. tasmanicus*, in contrast, are characterized by spatulate, long-petiolate leaves; leaves of the latter are short-pubescent, while those of the former are smaller and glabrous.

Costin *et al.* (1979, p. 364) noted that "The taxonomy of this polymorphic species [= *Erigeron pappocromus*] has not been fully worked out . . ." and there apparently are several taxa yet undescribed. Jacobs & Pickard (1981) listed the occurrence of *Erigeron* "sp. A" and "sp. B" (both "aff. pappocromus") and Porteners (1992) identified two species from New South Wales as simply "species A" and "species B." Modifications will certainly be made in the taxonomy of *Lagenopappus*, perhaps even in that proposed here.

The relationships of *Lagenopappus*

Apparently the only botanist to question the generic placement of *Erigeron pappocromus* has been Given (1973, p. 793), who noted that it is linked to *Celmisia* Cass. and closely related genera by "several attributes." He did not specify the nature of the putative similarity, and his provisional suggestion regarding the relationships of *E. pappocromus* is not supported here.

Lagenopappus is similar to *Lagenifera* and *Myriactis* in its monocephalous, scapose stems arising from a basal rosette of leaves, its flat, herbaceous, often purpling phyllaries, multiseriate pistillate flowers, and apically glandular but otherwise glabrous achenes with a distinct tendency to form a short neck. Analogous variation in leaf shape (obovate to spatulate) occurs in the two genera, and some plants of *Lagenopappus* are closely similar in habit and overall appearance to species of *Lagenifera* (compare, for example, *Lagenopappus gunnii* with *Lagenifera huegelii* Benth. and *L. stipitata* [Labill.] Druce). *Lagenopappus*, however, differs from both *Lagenifera* and *Myriactis* in its oblong achenes with quickly deciduous glands (vs. persistent glands), pappus of persistent bristles (vs. epappose), short-cylindric heads (vs. hemispheric), and ligules that remain straight or nearly so (vs. tightly coiling). The achenial glands, which are significant in the interpretation of the relationships of *Lagenopappus*, can be found by carefully opening relatively young capitula, but they also can be seen on mature achenes, although there they tend to be fragile and easily caducous.

Within the domain of relationship of the pappose species here placed in *Lagenopappus* and *Lagenithrix*, it might appear that only a single genus is represented. There are a number of significant differences between the two groups of species, however, and it is not clear that they are even most closely

related to each other, their similarities apparently plesiomorphic in nature. Further, the differences are nearly coordinate with those among the closely related (and interrelated) epappose genera *Lagenifera*, *Myriactis*, *Keysseria*, *Piora*, and *Sclenogyne*. A study of this whole group may be required to establish the generic boundaries more definitively. As treated here, *Lagenopappus* and *Lagenithrix* are separated by the following contrasts:

1. Rosettes strongly and persistently interconnected, forming low mats; heads hemispheric, sessile or on scapes up to 7 cm long; leaves 4-18 mm long, 2-3 mm wide, basally 3-nervate; achenes 1.8-3.0 mm long, oblanceolate-oblong with a thickened, persistently sessile-glandular, apical collar; disc flowers with fertile or sterile ovaries; pistillate flowers ca. 25-36 in 1-2 series, the corollas with white ligules 2-4 mm long. *Lagenithrix*
1. Rosettes often occurring in clumps of several individuals, but not forming low mats; heads short-cylindric, on scapes 4-15 cm long; leaves 10-40(-70) mm long, 4-15 mm wide, basally 1-nervate; achenes 3-7 mm long, narrowly oblong to oblong-oblanceolate, commonly with a short, broad, and unthickened but distinctive neck, with quickly deciduous short-stipitate glands on the apical portions; disc flowers with fertile ovaries; pistillate flowers ca. 60-120 in 3-4 series, the corollas with white to pink or purplish ligules (3-)6-12 mm long. *Lagenopappus*

Summary

Three species of the complex identified as *Erigeron pappocromus* sensu lato are here segregated as the new genus *Lagenopappus*. *Lagenopappus* appears to be most closely related to *Lagenifera*, *Myriactis*, and *Solenogyne* but is distinctive in its combination of solitary heads on scapose stems, completely fertile disc flowers with 5-lobed corollas, pappose achenes with only a broad, barely formed neck, and caducous achenial glands.

IV. Australian taxa of ambiguous identity or excluded from *Erigeron*

1. *Erigeron conyzoides* F. Muell., Trans. & Proc. Philos. Soc. Victoria 1:105. 1855. TYPE: AUSTRALIA. [New South Wales]: on the sources of the Murray and Snowy Rivers, 4000-5000 ft, F. Mueller (MEL, see comments below by Willis 1972).

In his account of the flora of Victoria, Willis (1972, p. 681) noted that "The only presumptive Victorian specimen of *E. conyzoides* extant in Melbourne Herbarium is labelled 'Snowy River (towards the mouth)' and was collected by Mueller in Feb.-Mar. 1854. Since this species is otherwise exclusively montane to subalpine (4-5000 ft.) in N.S.W., it would appear that some erroneous transposition of field labels had occurred, and the species is deliberately omitted from this handbook." More recent treatments, however, have recorded the presence of this species in both New South Wales and Victoria.

The numerous heads in a corymbose-paniculate capitulescence and numerous pistillate flowers in several series (the outer with filiform ligules, the inner tubular with reduced ligules) suggested to Bentham (1867) that *Erigeron conyzoides* should be placed near *Conyza bonariensis* (L.) Cronq. I have not seen specimens of *E. conyzoides*, but (as described and pictured in literature) the large heads (10-20 mm in diameter, with phyllaries 4-8 mm long) with ligules 6-8 mm long and large achenes (ca. 2.5 mm long) would be unusual in *Conyza*. Numerous species of *Conyza* occur as adventives in Australia, but no one since Bentham has suggested that *E. conyzoides* be placed with those species. The habit (perennials 4-8 dm tall) and capitulescence of *E. conyzoides* would be similarly unusual in *Erigeron*.

Excluded from *Erigeron*:

2. *Erigeron candollei* F. Muell. = *Minuria denticulata* (DC.) Benth.
3. *Erigeron decurrens* DC. = *Streptoglossa decurrens* (DC.) Dunlop.
4. *Erigeron minurioides* Benth. = *Felicia tenella* (L.) DC. (see Willis 1972).
5. *Erigeron brachycomoides* (F. Muell.) Boerl. = *Camptacra brachycomoides* (F. Muell.) Burbidge.
6. *Erigeron liatroides* Turcz. = *Streptoglossa liatroides* (Turcz.) Dunlop.
7. *Erigeron trilobus* Sonder = *Vittadinia australis* A. Rich.
8. *Erigeron vittadinia* F. Muell., *Fragm. Phytogr. Austr.* 5:87. 1865. TYPE: "Australia, e plagis Australiae orientalis Tropicae, etc." as cited in Chapman (1991). Apparently a "nomen nudum," published as a passing reference to a herbarium name.
9. *Conyza* (*Erigeron*) *canadensis* (L.) Cronq. and *Conyza* (*Erigeron*) *bonariensis* (L.) Cronq. (including *Erigeron crispus* Pourret -see Black 1929, and various other synonyms) are now treated within the genus *Conyza* (e.g., Everett 1992) among the numerous adventive species of that genus that occur in Australia.

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**PACIFIGERON (ASTERACEAE: ASTEREA), A NEW GENUS FROM THE
POLYNESIAN ISLAND OF RAPA**

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ABSTRACT

The species originally described as *Erigeron rapensis* F. Brown from the southeastern Polynesian island of Rapa is here separated as a new monotypic genus, **Pacifigeron**, with the new combination **Pacifigeron rapensis**. It is placed in the subtribe Hinterhuberinae of the Astereae, where it is most similar to genera of the Australasian *Celmisia* group.

KEY WORDS: *Pacifigeron*, Hinterhuberinae, Astereae, Asteraceae, Rapa

A species of shrubby daisies originally described as *Erigeron rapensis* F. Brown (Brown 1935) from the southeastern Polynesian island of Rapa (French Oceania) has proved to be distantly related to *Erigeron* L. and more similar to genera of the Australasian "*Celmisia* group" (as detailed below).

Pacifigeron Nesom, *gen. nov.* (Figure 1). Type species: *Pacifigeron (Erigeron) rapensis* (F. Brown) Nesom.

Fruticuli usque ad 1 m alti; folia ad apices caulium conferta, late obovata vel spatulata integra coriacea ad maturitatem glabra, venatio ad basim parallela; capitula sessilia 2-5 in fasciculis terminalibus; phyllaria valde 3-nervata; flosculi pistillati 1(-2)-seriati ligulis brevis albis; corollae radii ac disci antrorse pilosae; ovaria flosculorum disci sterilia; achenia fertilia fusiformia subteretia (parum compressa) sparsim strigosa eglandulosa nervis 9-11 vascularibus; pappus setarum 30-45 barbellatarum 1-seriatarum imprimis compositus serie breva exteriori setarum. Ex affinitate *Celmisiae*

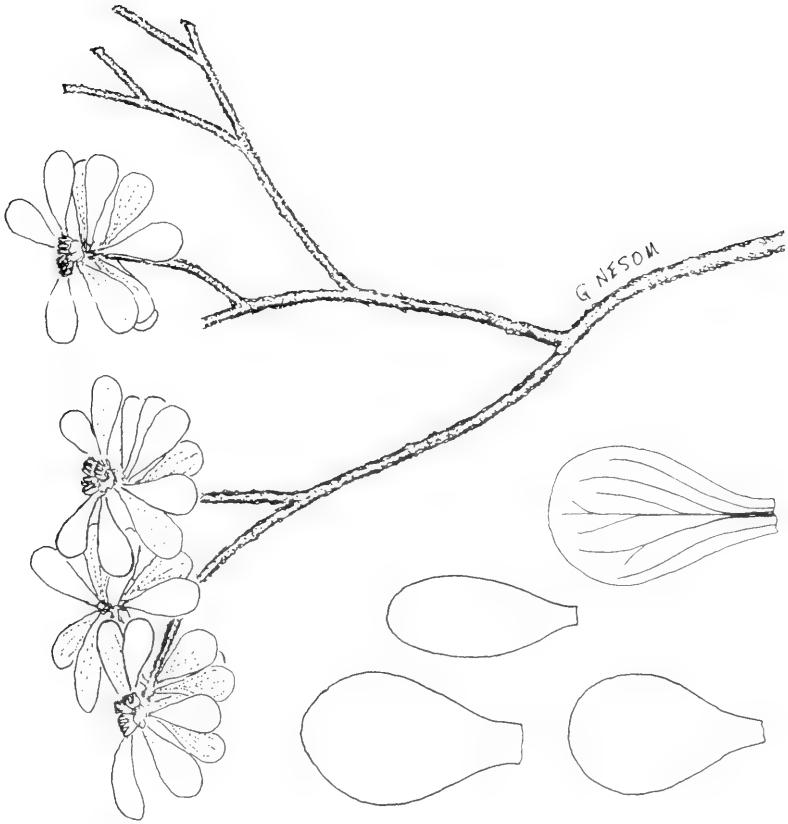


Figure 1. *Pacifigeron rapensis*. Habit and leaf variation, showing pattern of venation.

Cass. et generum affinium sed capitulis parvis subsessilibus in fasciculis terminalibus, antheris extensionem basalem carentibus, ovariis sterilibus flosculorum disci, et corollis disci ac radii antrorse pilosis differt.

"Round-topped shrubs" 0.2-1.0 m tall, lower stems 5-8 mm thick, branching mainly in the upper third. Leaves alternate, apically clustered, the youngest thinly and loosely arachnoid-tomentose with uniseriate, multicellular, thin-walled, unbranched hairs (Type B trichomes; see Nesom 1976; Given 1969), quickly glabrescent, completely glabrous at maturity, broadly obovate to obovate-spatulate with entire, non-revolute margins, 20-45 mm long, 12-27 mm wide, tapering to a broad petiolar region ca. $1/5-1/6$ as long as the blade, not clasping, coriaceous, the veins prominently raised, the midvein usually accompanied near the base by 2 lateral pairs of parallel veins, these spreading and becoming more diffuse distally in the blade and finally somewhat obscurely anastomose; petiole base with a dense and persistent tuft of long, white-villous hairs arising from the axil. Heads 5-7 mm wide (pressed), campanulate, subsessile or on pedicels ca. 1-2 mm long, in terminal clusters of ca. 2-5, imbedded in dense, white tomentum; involucre bracts ca. 18-24 in 2-3(-4) series, flat, triangular to broadly lanceolate, apically acute, somewhat yellowish with 3(-5) parallel, orange veins, finely arachnoid-pubescent, glabrescent, strongly graduated in length, the inner 4-5 mm long, the outer ca. half as long; receptacles nearly flat to slightly concave, epaleate, roughened but not alveolate or foveolate. Pistillate flowers ca. 18-26 in 1(-2) series, fertile, the corollas orange-veined, 2.8-4.0 mm long, tube 1.8-2.5 mm long, the ligules 1-2 mm long, apically 3-dentate, spreading, white or creamy, the upper tube antrorsely pilose-villous with long (0.5-1.0 mm), uniseriate multicellular hairs (Type A trichomes) on the abaxial side. Disc flowers functionally staminate, the ovaries sterile; corollas funnelform, orange-veined, 2.0-3.0 mm long, broadened above the tube but not abruptly so, the tube $1/2-2/5$ the corolla length, the 5 lobes broadly lanceolate, the limb densely antrorsely pilose with uniseriate, thick-walled, multicellular hairs (Type A trichomes) 1.0-1.5 mm long arising mostly from the lower limb and extending above the corolla; style branches 0.4-0.6 mm long, hairy from base to tip, stigmatic lines absent; anthers basally attenuate, the base not tailed or caudate, apical appendage rounded. Mature achenes fusiform, slightly compressed, 2-3 mm long, 0.8-1.0 mm wide, the surface dark brown, with 9-11 raised, vascularized, longitudinal, more or less equally spaced nerves, these distinctively orange-resinous in immature achenes but not obviously so at maturity, sparsely invested with scattered, short Zwillingshaare, eglandular; carpodium a depressed cylinder of 3-4 rows of sclerified cells. Pappus similar in ray and disc, of 30-45 barbellate bristles about as long as the corollas, with a short, outer series of setae 0.3-0.8 mm long.

Pacifigeron rapensis (F. Brown) Nesom, *comb. nov.* BASIONYM: *Erigeron rapensis* F. Brown, Bernice P. Bishop Museum Bull. 130:338. 1935.
TYPE: [French Oceania,] Rapa, [27°35' S, 144°17' W], 400 m, 1921, *E.H. Quayle no. X* (HOLOTYPE: BISH; Isotype: BISH!).

Additional collections examined: French Oceania. Rapa: Kaimaru, S ridge of Mt. Perahu, 500 m, edge of thicket on steep, mossy ridge, 13 July 1934, *St. John & Maireau 15516* (GH,MO-sterile); Taratika, E side of Mt. Perahu, 500 m, wind-swept precipitous ridge, 15 Jul 1934, *St. John & Maireau 15562* (GH).

Lander (1989) provided a summary (with associated references to literature) of the flora and history of botanical study of Rapa. The island lies about 4900 kilometers from New Zealand and more than 7000 kilometers from the closest point in South America.

Operanthus Sherff (Asteraceae: Heliantheae: Coreopsidinae) is endemic to Rapa and the Marquesas Islands (northern French Oceania), but *Pacifigeron* is the second recently described monotypic genus of Asteraceae strictly endemic to the small island of Rapa. *Olearia rapa* F. Brown (Brown 1935) has become the sole constituent of the genus *Apostates* Lander, which was tentatively suggested by Lander (1989) to be a member of the tribe Astereae, although he noted that he could find no potentially close relatives for it there. I agree (Nesom 1993 and in prep.) that *Apostates* would be isolated if placed in the Astereae and have suggested (equally tentatively) that it may instead be closer to the Inuleae sensu lato. In any case, *Apostates* is dissimilar in many ways to *Pacifigeron* and the two cannot be considered more than remotely related, even if *Apostates* could be securely demonstrated to be a member of the Astereae.

Pacifigeron is briefly characterized as follows: shrubs up to 1 m tall; leaves alternate, clustered at the stem tips, broadly obovate to spatulate, entire, coriaceous, initially thinly tomentose on the abaxial surface but quickly glabrescent except in the leaf axils, the venation parallel from the base; heads small, in terminal, subsessile clusters of 2-5; phyllaries strongly 3-veined; pistillate flowers 1(2-)-seriate with short, white ligules; disc corollas antrorsely villous with long uniseriate trichomes; disc flowers functionally staminate, the ovaries sterile; fertile achenes fusiform, subterete (slightly compressed), with 9-11 raised, vascularized nerves, very sparsely short-strigose, eglandular; and pappus of 30-45 barbellate bristles in 1 series, with a short, outer series of setae or bristles.

Pacifigeron cannot be considered to be a close relative of *Erigeron*. The latter has narrowly tubular disc corollas, with a short, abruptly differentiated tube, usually somewhat indurate at the tube-throat junction; disc flowers consistently bisexual and fertile; leaves not coriaceous; Type A, B, and C trichomes all usually present on individuals; and achenes oblong, flat, and 2-nerved (except for one North American group). The greatest diversity of *Erigeron* lies in North America (Nesom 1989), but distinctive elements of the genus, as well as its probable closest relatives, occur in South America (Nesom in press). The

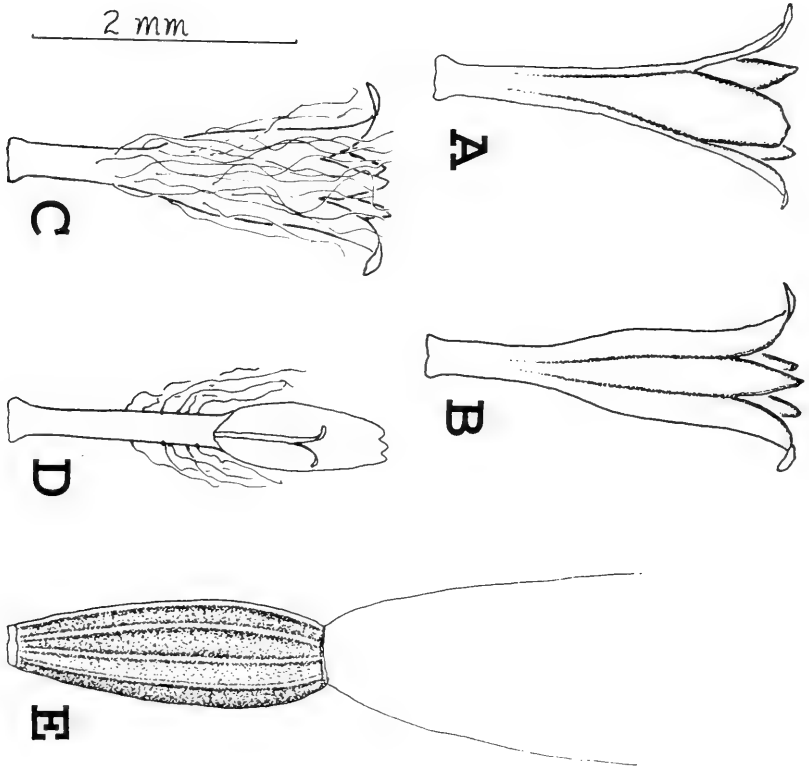


Figure 2. Corollas and achene of *Pacifigeron rapensis*. A and B. Disc corollas, vestiture not shown. C. Disc corolla with characteristic vestiture. D. Ray corolla. E. Fertile achene, full pappus not shown.

genus does not occur natively in the South Pacific or the Australasian region (Nesom 1994).

Pacifigeron is placed here in the subtribe Hinterhuberinae Cuatr., based on its shrubby habit, tomentose vestiture of thin hairs, with persistent tufts of villous hair in the leaf axils, large and coriaceous leaves, and achenes with numerous, vascularized veins. This subtribe has a pan-temperate distribution in the Southern Hemisphere, with representatives in Madagascar, South Africa, South America, and Australasia (Nesom 1993 and in prep.). Within the Hinterhuberinae, *Pacifigeron* is most similar to taxa of the *Celmisia* group: (*Celmisia* Cass., *Pleurophyllum* Hook., *Damnamenia* Given, *Pachystegia* Cheeseman, and some species of *Olearia* Moench, see below). These species are primarily distributed in New Zealand but some occur in Australia and small islands south of New Zealand. They are characterized by a combination of subterete, multinerved, and eglandular achenes and parallel-veined leaves tomentose with simple hairs (branching hairs occur among Australian taxa of *Olearia*), as well as a mix of other characters that occur less regularly among the species: reduced ligules in *Pleurophyllum*; markedly short Zwillings-haare on achenes of the *Olearia chathamica* Kirk group (see below); and a subshrubby habit, with leaves produced in terminal clusters, in sect. *Lignosae* of *Celmisia*.

Primarily, however, plants of the *Celmisia* group are herbaceous with leaves in a basal rosette, and they consistently produce large heads (mostly [1-]2-4[-5] cm wide) that are solitary and long-pedunculate, or racemose in *Pleurophyllum*. *Pacifigeron* differs from all taxa of the *Celmisia* group in its combination of small, subsessile heads in terminal clusters, anthers without any form of basal extension, sterile disc ovaries, and densely antrorsely pilose disc and ray corollas.

Drury (1968) and Given (1973) both have suggested that two species of New Zealand *Olearia* (*O. colensoi* J.D. Hook. and *O. lyalii* J.D. Hook.) with large heads in a raceme are congeneric with *Pleurophyllum*, where a similar capitulescence occurs. The evolutionary origin of the characteristic monocephalous condition of *Celmisia* probably was from similar, racemose, ancestral stock through suppression of the lateral floral buds, as implied by Given (1973), who noted that some species of *Celmisia* occasionally produce heads below the terminal one in the axils of scape bracts. One other group of *Olearia* species (including *O. chathamica*, *O. oporina* [Forst.] J.D. Hook., and several others) also has been noted by both Drury and Given to be of generic-level status and closely related to *Celmisia*. These species complete what is referred to here as "the *Celmisia* group." It also seems likely that some, but not all, of the Australian species of *Olearia* may belong here. Given (1973) provisionally included *Erigeron pappocroma* Labill. as a member of the *Celmisia* group, but an alternative, widely divergent position for this species has been proposed by Nesom (1994). Reports of high levels of polyploidy (mostly 12-ploid,

based on $x=9$) in the species of the *Celmisia* group support a hypothesis that they are closely interrelated (see summary in Nesom 1992), and in the present interpretation, *Pacifigeron* is predicted to have a similar level of ploidy.

The species of the South American genus *Diplostephium* Kunth (Hinterhuberinae, but not part of the *Celmisia* group) are similar to *Pacifigeron* in a number of features: shrubby habit, coriaceous leaves, heads sometimes terminal and sessile, disc ovaries sterile, ligules often reduced, and corollas densely invested with Type A trichomes in some species (e.g., *D. crassifolium* Cuatr.). In *Diplostephium*, however, the achenes are flattened, usually with glandular surfaces and usually with only 3-5 nerves, the disc corollas have a longer tube and more deeply cut limb, and the leaves are consistently pinnately veined. The direction of closest relationship of *Pacifigeron* appears to lie toward the Australasian region rather than South America.

ACKNOWLEDGMENTS

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SEPARATION OF *NEJA* (ASTERACEAE: ASTEREA) FROM
HYSTERIONICA

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ABSTRACT

The six species of *Neja* D. Don are segregated from *Hysterionica* Willd. as a distinct genus, with the hypothesis that they are as close or more closely related to *Leptostelma* and *Apopyros* than to *Hysterionica*. *Neja* is distinct from *Hysterionica* in its branching, lignescent caudices, filiform, basally disposed leaves, solitary heads on nearly scapose stems, and fusiform-cylindric achenes with 7-10 raised, longitudinal, orange-resinous nerves. All four of these genera occur primarily in southeastern Brazil and adjacent Uruguay, Paraguay, and Argentina, although one of the *Neja* species is endemic to western Cuba. Four new combinations are required in *Neja*: *N. dianthifolia*, *N. marginata*, *N. pinifolia*, and *N. pulvinata*. The taxonomy of *Hysterionica* sensu stricto, which comprises seven species, is also summarized.

KEY WORDS: *Neja*, *Hysterionica*, Astereae, Asteraceae

In an earlier paper (Nesom 1993), I noted that the genus *Hysterionica* Willd. comprises two groups of species, the "jasionoides group" (the typical element) and the "pinifolia group." With a clearer understanding of the limits and variability of genera closely related to *Hysterionica*, it now appears that the distinction between these two infrageneric groups is more significant than previously supposed, and the "pinifolia group" is segregated (or re-segregated) as the genus *Neja* D. Don. The following contrasts separate *Neja* from *Hysterionica*:

1. Plants perennial, with branching caudices; leaves filiform to linear-oblongate, primarily basally disposed; heads solitary on long scapes or merely bracteate stems; achenes fusiform-cylindric with 7-10 prominently raised, orange-resinous nerves. *Neja*

1. Plants annual or perennial, taprooted with a simple caudex, the stems sometimes branched at the very base; leaves obovate, the basal sometimes persistent but the cauline also prominent and little reduced upwards; heads solitary or in loose clusters on leafy stems with long to relatively short peduncles; achenes flattened with 2 lateral nerves.
 *Hysterionica*

The difference in habit and leaf morphology between the two genera is immediately distinctive, and there is no species that might be interpreted as intermediate. It also is remarkable that the terete, multinerved achenes of *Neja* apparently have not been described or emphasized in earlier literature, but this morphology is clearly observed from mounted achenes (on slides) with the embryo removed as well as from mature achenes without any preparation. The numerous, raised, orange-resinous nerves are easily observed because the strigose vestiture is primarily restricted to the areas between the nerves, giving the achenes a longitudinally striped appearance, the orange nerves alternating with strigose lines. Achenes of *Hysterionica sensu stricto* are consistently flat and only 2-nerved; achenes of *H. montevidensis* Baker rarely may produce an extra nerve on each of the faces (e.g., *Krapovickas 14949-TEX*).

Neja has been united with *Hysterionica* because of an overall resemblance reflective of a close degree of relationship (see characteristics and comments below), especially their tendency to produce yellow rays, and their production of an outer pappus series that tends to be prominently scaly. In *Neja*, however, the outer pappus varies from short seta-like bristles to broad scales, or it may not be differentiated from the inner series. In *N. marginata* (Griseb.) Nesom, the pappus consists of 2-3 series of ca. 50-60 bristles of somewhat variable length, although there also may be a few long setae in the outermost series; in *N. pulvinata* (Cabrera) Nesom, the outer pappus is a series of slightly flattened bristles about 1/5 as long as the inner series; in *N. pinifolia* (Poir.) Nesom, the outer series consists of broad, lanceolate to obovate scales, with an inner series of ca. 10-15 bristles. In *Hysterionica*, the pappus is usually of bristles and scales, but in *H. aberrans* (Cabrera) Cabrera, the pappus consists of only a corona of connate scales, the inner series apparently completely absent.

Rays are yellow in the two most commonly collected species of *Neja*, *N. filiformis* (Spreng.) Nees and *N. pinifolia*, as well as *N. nidorelloides* DC.; the other four species have white rays. Rays within *Hysterionica* are predominantly yellow, but *H. montevidensis* has white rays (and probably also *H. glaucifolia* [O. Kuntze] Solbrig). *Neja* and *Hysterionica* have been associated with *Chrysopsis* (Nutt.) Ell. because of their tendency to produce yellow rays (e.g., DeCandolle 1836; Bentham 1873), but the similarity is convergent (Nesom 1991).

Hysterionica is among the closest relatives of *Neja*, but other genera equally close are *Leptostelma* D. Don (Nesom in press) and *Apopyros* Nesom (Nesom

1994a). *Erigeron* L. and *Conyza* L. are also closely associated with this group. Comments on other aspects of the interrelationships of these genera are given in the related papers (especially see Nesom in press). The plants of these genera are characterized by the following features: leaves often thick or rigid; phyllaries flat, more or less evenly herbaceous, and commonly 3-nerved, the nerves usually conspicuously orange-resinous; rays 1-3-(or more) seriate, the ligules variably (between species) yellow or white, but tending to dry yellowish even if white when fresh; disc corollas with a short tube; disc style branches short, with deltate collecting appendages; achenes eglandular, erostrate, flat and 2-nerved (terete and multinerved in *Apopyros* and *Neja*); and pappus 1-3-seriate, the outer series of bristles similar to the inner or variably usually reduced and modified. All have an "austro-brasilien" geographic distribution, occurring primarily in southeastern Brazil and adjacent Argentina, Uruguay, Paraguay, and the southeastern tip of Bolivia, although one of the *Neja* species (*N. marginata*) is endemic to western Cuba (Nesom 1993).

Apart from their similarity in the tendency to produce a prominently scaly outer pappus, there is no reason that *Neja* and *Hysterionica* should be considered as most closely related to each other. Within this group of austro-brasilien genera, *Apopyros* is the only other genus besides *Neja* with subterete, multinerved achenes, and *Leptostelma* and *Erigeron* tend to produce a distinctly multiseriate pappus. *Neja* is considered here to occupy a phyletic position coordinate with the other genera of the *Leptostelma* group and is provided with the according taxonomy. Plants with linear leaves and a habit more or less similar to that of *Neja* occur in the austro-brasilien *Inulopsis* O. Hoffm., but the latter apparently is more closely related to *Podocoma* Cass. and its relatives (Nesom 1994b).

In the following taxonomic summary of *Neja*, accepted taxa and synonyms are applied to what appear to be the major "nodes" of variation, with reliance in large part on the interpretations by Cabrera (1946). *Neja*, however, as well as *Hysterionica* sensu stricto, is in need of detailed revisionary study, especially since the studies by Cabrera and Espinar have both expressly avoided dealing with Brazilian taxa and names.

Neja D. Don in Sweet, *Hort. Brit.* (ed. 2) 299. 1830 [*et* Brit. Flow. Gard., ser. 2(1):78. 1831]. Type species: *Neja gracilis* D. Don. (= *Neja filiformis* [Spreng.] Nees).

Neja sect. *Podoneja* DC., *Prodr.* 5:325. 1836. Type species: *Neja gracilis* D. Don (= *Neja filiformis* [Spreng.] Nees).

Neja sect. *Monogyria* DC., *Prodr.* 5:325. 1836. Lectotype species (designated here): *Neja linearifolia* DC. (= *Neja pinifolia* [Poir.] Nesom).

1. ***Neja dianthifolia*** (Griseb.) Nesom, *comb. nov.* BASIONYM: *Erigeron dianthifolius* Griseb., *Symb. Fl. Argent.* 174. 1879. *Hysterionica dianthifolia* (Griseb.) Cabrera, *Notas Mus. La Plata* 11 (Bot. 53):352. 1946.
2. ***Neja filiformis*** (Spreng.) Nees, *Del. Sem. Hort. Vratisl.* 1839 (*et* *Linnaea* 14 [Litt.-Ber.]:168. 1840.). BASIONYM: *Erigeron filiformis* Spreng., *Syst. Veget.* (ed. 16) 3:520. 1826. *Polyactidium sprengelii* DC. [*nom. nov. illeg.*], *Prodr.* 7:274. 1838. *Hysterionica filiformis* (Spreng.) Cabrera, *Notas Mus. La Plata* 11 (Bot. 53):355. 1946.

Neja gracilis D. Don in Sweet, *Hort. Brit.* (ed. 2) 299. 1830 [*et* *Brit. Flow. Gard.*, ser. 2(1):78. 1831.].

A combination in *Hysterionica* for this species, and for *Neja pinifolia* (below), has been attributed to Bentham (*in* Benth. & Hook., *Gen. Pl.* 2:253. 1873.), but in the interpretation here, the formal combination was not made by Bentham.

Diplopappus graminifolius Less., *Syn. Gen. Comp.* 165. 1832.

Diplopappus stenophyllus Hook. & Arn., *Comp. Bot. Mag.* 2:48. 1836.

Neja tenuifolia DC., *Prodr.* 5:326. 1836.

Neja ciliaris DC., *Prodr.* 5:326. 1836.

Hysterionica setuligera Gandoger, *Bull. Soc. Bot. France* 60:23. 1873.

3. ***Neja marginata*** (Griseb.) Nesom, *comb. nov.* BASIONYM: *Haplopappus marginatus* Griseb., *Catalog. Pl. Cubens.* 149. 1866. *Hysterionica marginata* (Griseb.) Gomez Maza, *Anal. Soc. Española Hist. Nat. Madrid* 19:272. 1890.
4. ***Neja nidorelloides*** DC., *Prodr.* 5:325. 1836.
5. ***Neja pinifolia*** (Poir.) Nesom, *comb. nov.* BASIONYM: *Erigeron pinifolius* Poir. in Lam., *Encycl. Method.* 8:40. 1808. *Hysterionica pinifolia* (Poir.) Baker in Mart., *Fl. Brasil.* 6(3):12. 1882.

Erigeron montevidensis Spreng., *Syst. Veget.* (ed. 16) 3:519. 1826.
Neja montevidensis (Spreng.) Sch.-Bip. in Seem., *Bot. Voy. Herald* [8]:302. 1856.

The combination by Schultz-Bipontinus was invalid, as he noted that the species should be regarded as a synonym of *Neja gracilis* DC. (= *N. filiformis* [Spreng.] Nees).

Erigeron resinosus Spreng., *Syst. Veget.* (ed. 16) 3:520. 1826. *Polyactidium sprengelii* Schlecht. [*nom. nov. illeg.*], *Linnaea* 10:475. 1835.
Neja sprengelii (Schlecht.) Sch.-Bip. in Seem., *Bot. Voy. Herald* 8:302. 1856.

Erigeron dubius Spreng., *Syst. Veget.* (ed. 16) 3:520. 1826.

Considered by Schlechtendahl (*Linnaea* 10:475. 1835.) and Baker (in Martius, *Fl. Brasil.* 6(3):13. 1882.) to be conspecific with *Erigeron resinosus* Spreng.

Neja linearifolia DC., *Prodr.* 5:325. 1836. *Hysterionica linearifolia* (DC.) Baker in Mart., *Fl. Brasil.* 6(3):13. 1882.

Neja subvillosa DC., *Prodr.* 5:325. 1836. Not *Hysterionica subvillosa* Griseb. 1874 (= *Hysterionica bakeri* Hicken, see Cabrera 1946).

Diplopappus pinifolius Hook. & Arn., *Comp. Bot. Mag.* 2:48. 1836; not Less. *ex Nees* [*in syn.*], *Linnaea* 14 (Litt.-Ber.):169. 1840.

Neja falcata Nees, *Del. Sem. Hort. Vratisl.* 1839 (*et Linnaea* 14 [Litt.-Ber.]:168. 1840.).

6. *Neja pulvinata* (Cabrera) Nesom, *comb. nov.* BASIONYM: *Hysterionica pulvinata* Cabrera, *Notas Mus. La Plata* 11 (Bot. 53):353. 1946. *Hysterionica dianthifolia* (Griseb.) Cabrera var. *pulvinata* (Cabrera) Espinar, *Darwiniana* 22:540. 1980.

Hysterionica pulvinata was noted by Cabrera in its original description as differing from *H. dianthifolia* in its smaller leaves but Espinar added observations of differences in vestiture, these nearly analogous to the differences that separate *Neja filiformis* and *N. pinifolia*. Apparently in view of the otherwise close resemblance of *N. dianthifolia* and *N. pulvinata*, however, he preferred to recognize them as varieties within a single species. The only possible intermediate that he noted was a plant referred to *H. dianthifolia* but of a smaller stature more typical of *H. pulvinata*. Few specimens of these taxa have yet been critically examined by anyone, and Cabrera's original estimation of their status is accepted here until their taxonomy can be re-evaluated in more detail.

Species excluded from *Neja*:

Neja macrocephala DC., *Prodr.* 5:325. 1836. = *Neja* sect. *Phylloneja* DC., *Prodr.* 5:325. 1836. (Monotypic, *Neja macrocephala* DC. the type) = *Asteropsis macrocephala* Less. (see Nesom 1994c).

Hysterionica Willd., Ges. Naturfr. Freunde Berlin Mag. 1:140. 1807. Type species: *Hysterionica jasionoides* Willd.

For other synonyms within *Hysterionica* sensu stricto, see Baker (1882), Cabrera (1946), and Espinar (1980).

1. *Hysterionica aberrans* (Cabrera) Cabrera, Notas Mus. La Plata, Bot. 11:357. 1946. BASIONYM: *Hysterionica bakeri* Hicken var. *aberrans* Cabrera, Notas Prelim. Mus. La Plata 1:325, fig. 2. 1931.
 - a. *Hysterionica aberrans* (Cabrera) Cabrera var. *aberrans*.
 - b. *Hysterionica aberrans* (Cabrera) Cabrera var. *hunzikeri* Espinar, Darwiniana 22:543. 1980.
2. *Hysterionica bakeri* Hicken, Darwiniana 1:149. 1924.
3. *Hysterionica cabreræ* Espinar, Darwiniana 22:545. 1980.
4. *Hysterionica glaucifolia* (O. Kuntze) Solbrig, Bol. Soc. Arg. Bot. 6(1):29. 1955. BASIONYM: *Erigeron glaucifolius* O. Kuntze, Rev. Gen. Pl. 3(2):145. 1898.
5. *Hysterionica jasionoides* Willd., Ges. Naturfr. Freunde Berlin Mag. 1:140. 1807.
6. *Hysterionica montevidensis* Baker in Mart., Fl. Bras. 6(3):13. 1882. Not *Erigeron montevidensis* Spreng. (= *Neja pinifolia* [Poir.] Nesom, see comments by Cabrera 1946).

Hysterionica villosa (Hook. & Arn.) Cabrera [*comb. illeg.*], Notas Mus. La Plata 11 (Bot. 53):350. 1946. *Diplopappus villosus* Hook. & Arn. [*nom. illeg.*], Comp. Bot. Mag. 2:48. 1836. Not *Diplopappus villosus* Cass. 1819 (= *Aster*) or W.J. Hook. 1834 (= *Chrysopsis*).

7. *Hysterionica pulchella* Cabrera, Notas Prelim. Mus. La Plata 1:323. 1931.

The species of *Hysterionica* sensu stricto are divided into two groups. *Hysterionica montevidensis* and *H. glaucifolia* have uniseriate ray flowers with white, relative broad ligules; the other species have multiseriate ray flowers with yellow, filiform ligules.

A base chromosome number of $x=9$ has been reported for two species of *Hysterionica* (*H. jasionoides* and *H. montevidensis*, the latter as *H. villosa*; Solbrig *et al.* 1964; Bernadello 1986). A count of $n=18$ for *H. bakeri* was obtained by B.L. Turner (as annotated on the specimen, Sanderson 370-TEX!

from Tucumán, Argentina) but it was not published because of a possible "error in bud collection." Turner *et al.* (1979) reported counts of $n=15$ and $n=20$ for *H. jasionoides* from Argentina (vouchers TEX!), but I believe these counts of $x=5$ for *Hysterionica* are likely to have been from buds of some other genus. Hundreds of reported chromosome numbers from genera closely related to *Hysterionica*, including *Erigeron*, *Leptostelma*, and *Conyza*, are all based on $x=9$.

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**APOPYROS (ASTERACEAE: ASTEREAEE), A NEW GENUS FROM
SOUTHERN BRAZIL, ARGENTINA, AND PARAGUAY**

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ABSTRACT

Two species of southern Brazil and adjacent Paraguay and Argentina, formerly identified as *Aster* and *Conyza*, are here treated as **Apopyros** Nesom, *gen. nov.*, with the new combinations **Apopyros warmingii** (Baker) Nesom and **Apopyros corymbosus** (Hook. & Arn.) Nesom. *Apopyros* is hypothesized to be most closely related to species of three other genera with a similar austro-brasilien geographic distribution in east-central South America: *Leptostelma*, *Neja*, and *Hysterionica*. In their parallel-veined leaves with shiny-indurate surfaces, multinerved, nearly terete achenes, and tendency to produce stiffly pilose-hirsute vestiture, *Neja* and *Apopyros* are distinctive among their close relatives.

KEY WORDS: *Apopyros*, *Aster*, Asteraceae, Astereae, South America

Aster warmingii Baker and *Diplopappus corymbosus* Hook. & Arn. (= *Aster tuberosus* Less. = *Aster setosus* Baker = *Conyza blanchetii* Baker, see below) are perennial herbs endemic to south-central Brazil, where at least the first species has often been encountered in periodically burned cerrados. *Aster warmingii* was described after Bentham's systematic overview of the tribe (1873), and neither species was specifically included in Hoffmann's subsequent review of the tribe (1890). Nor, apparently, has either been subject to any other critical taxonomic evaluation since their first recognition. Clearly, they do not belong with any group of *Aster*, even in the broadest sense of that genus (Nesom in prep.). In the interpretation here, *Aster warmingii* and *D. corymbosus* are recognized as a separate genus closely related to three other genera that occur in the same region of east-central South America: *Leptostelma* D. Don (Nesom in press), *Neja* D. Don (Nesom 1994), and *Hysterionica* Willd.

Apopyros Nesom, *gen. nov.* Type species: *Apopyros (Aster) warmingii* (Baker) Nesom.

Caulibus strictis rhizomate ligneo vel tubere exorientibus, foliis caulinis stricte erectis 3(5)-nervatis, valde redactis squamoideisque prope basim caulis, capitulis discoideis, phyllariis uninervatis, floribus pistillatis marginibus corollis inter corollas typicas radii ac disci intermediis, acheniis plerumque 5-nervatis paene cylindricis ad apicem truncatis, et pappo setarum numerosarum serie brevi exteriore carenti dignoscenda.

Herbaceous perennials, eglandular, stiffly pilose-hirsute with Type A trichomes (designation of trichome types follows Nesom 1976) to nearly glabrous, strigillose with Type B trichomes in *Apopyros warmingii*; stems strictly erect, arising from a thick, woody rhizome or tuber. Leaves all cauline, stiffly erect, shiny-indurate in texture, glabrous to stiffly hirsute-pilose, epetiolate, entire, 3(-5)-nerved, those near the stem base reduced and scale-like. Heads disciform, solitary or in a paniculate-corymboid capitulescence; receptacles smooth or alveolate, epaleate; phyllaries with a single, thickened and raised, orange-resinous vein, the cells of the central area minutely but distinctly quadrate. Pistillate flowers fertile, peripheral, the corollas essentially tubular, orange-veined, eligulate but with 3-4 triangular teeth, approaching the disc corollas in morphology but the style branch morphology typical of the pistillate flowers, with lateral stigmatic lines from base to apex. Disc flowers bisexual, fertile, orange-nerved, the veins continuous through the throat, narrowly tubular, 5-lobed, slightly expanded at the throat into the limb, not indurate, abruptly expanded at the very base into a wide, indurate disc; style branches short, with mostly deltate collecting appendages; anthers with white apical appendages 0.6-0.8 mm long, filaments inserted ca. 1 mm above the base of the corolla at the tube-throat junction. Achenes mostly with 5 vascularized nerves, these orange-resinous when young but becoming lighter colored at maturity, nearly cylindric, 1.8-4.0 mm long, oblong in side view, the faces tan, moderate strigose with duplex hairs (Zwillingshaare), eglandular, apically truncate (without shoulders, the nerves parallel); carpodium 2-3 cells high; pappus of (1-)2 series of numerous, apically attenuate bristles of even length, with or without an additional, short, outer series of setae. Chromosome number not reported.

The name of the genus refers to the distinctive habit of the plants, especially *Apopyros warmingii*, in sending up leafy, flowering stems after a fire, sometimes as quickly as one month after the burn.

KEY TO THE SPECIES

1. Heads 7-9 mm wide, numerous in a corymboid panicle; midstem leaves not clasping, 3-6 cm long, 2-8 mm wide; disc flowers 3.5-4.5 mm long; achenes 1.8-2.2 mm long; pappus usually with a short, outer series of setae or setose bristles. *A. corymbosus*
1. Heads 10-14 mm wide, solitary or few; midstem leaves subclasping, 4-7 cm long, 10-15 mm wide; disc flowers 4.5-5.8 mm long; achenes 3-4 mm long; pappus without a short, outer series. *A. warmingii*
1. **Apopyros corymbosus** (Hook. & Arn.) Nesom, *comb. nov.* BASIONYM: *Diplopappus corymbosus* Hook. & Arn., *Compan. Bot. Mag.* 2:48. 1836. TYPE: BRAZIL. Rio Grande do Sul: *Tweedie s.n.* (K?).

Aster tuberosus Less. [*in sched.*] *ex Baker in Martius, Fl. Bras.* 6(3):22. 1882. SYNTYPES (as cited by Baker): BRAZIL. Prov. Rio Grande do Sul: *Tweedie s.n.* (K?); Brasilia australi, sine loci designatione, *Sello 2450* (B). A Sello specimen (B photo-GH!, photo-MO!) is annotated by Lessing as "*Aster tuberosus* n. sp." and may represent type material; the number "14888" is written on the photographic scale ruler but there is no other number on the specimen itself.

Aster setosus Baker *in Martius, Fl. Bras.* 6(3):22. 1882. *Conyza setosa* (Baker) Malme, *Arkiv. Bot.* 24A(6):50. 1931. TYPE: BRAZIL. Brasilia australi, sine loci designatione, *Sello 907* (?).

Conyza blanchetii Baker *in Martius, Fl. Bras.* 6(3):36. 1882. TYPE: BRAZIL. Bahia: in campis ad Igreja Velha, *Blanchet 3316* (HOLOTYPE: BM photo-GH!; Isotypes: B photo-GH!, GH!, MO, P photo-GH!, US!). *Erigeron blanchetii* Sch.-Bip. [*in sched.*] *ex Baker [pro syn.] in Martius, Fl. Bras.* 6(3):36. 1882. Homotypic with *Conyza blanchetii*, the P specimen annotated by Schultz as "*Erigeron blanchetii*."

Perennial herbs from a thick, ligneous, sometimes tuberous rhizome; stems 5-7 dm tall, single from the base, sparsely pilose-hirsute with stiffly spreading Type A trichomes, eglandular. Leaves all cauline, the lowermost scale-like, more or less densely arranged on the stem above the base, shiny-indurate in texture, strictly ascending, linear-lanceolate to narrowly elliptic, 3-6 cm long, 2-8 mm wide at midstem, sessile, not clasping, with entire, stiffly spreading-ciliate margins, the lamina glabrous or stiffly hirsute-pilose, 3-veined from the base, the midvein raised, the lateral veins becoming diffuse in the distal portion of the leaf, upper leaves strongly reduced in size and density toward

and within the capitulescence. Capitulescence a loose but distinct, terminal corymboid panicle of 15-75 heads, the initial heads overtopped by those on lateral branches. Heads 7-9 mm wide (pressed), phyllaries narrowly elliptic oblanceolate, in 3-4 graduated series, the inner 4-5 mm long, outermost 1/3-1/4 as long as the inner, with thick, broad orange-resinous midvein extending to the very apex, margins narrowly thin-hyaline; receptacles slightly convex, distinctly alveolate. Pistillate flowers numerous, the tube 3.0-3.5 mm long. Disc flowers 3.5-4.5 mm long, the tube ca. 1 mm long and distinctly broadened at the very base, slightly but abruptly opening into the limb, the lobes deltate to shallowly triangular; style branches 0.5 mm long, the collecting appendages very shallowly triangular to shallowly deltate; achenes 1.8-2.2 mm long, 5-nerved; pappus of (1-)2 series of 28-38 bristles and shorter, outer series of few setae, the bristles sometimes reddish-brown on the distal 2/3.

Additional specimens examined: ARGENTINA. Prov. Corrientes: Dep. Empedrado, Estancia "Las Tres Marias," 24 Apr 1956, *Pedersen 3901* (GH); Dep. Concepción, Rincón de Luna, Estancia Borvil, 26 Feb 1957, *Pedersen 4478* (GH); Dep. Santo Tomás, Estancia "Garruchos," 12 Feb 1960, *Pedersen 5421* (GH).

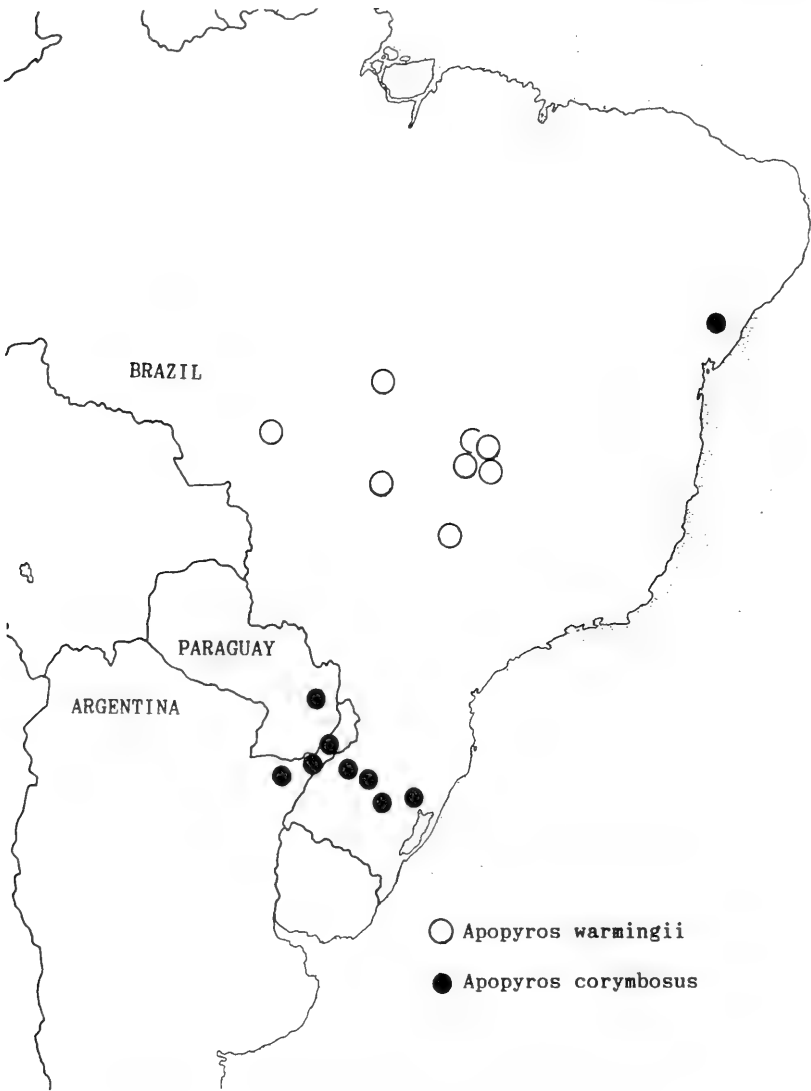
PARAGUAY. Caaguazu: [no date or other data], *Hassler 9222* (GH).

Apopyros corymbosus has been collected in south-central Brazil (Rio Grande do Sul) and adjacent Argentina and Paraguay. The type collections of *Conyza blanchetii* is from the state of Bahia, considerably north of the other localities noted here, but there is no significant difference between these plants and those from more southern localities. The specimens I have studied of *A. corymbosus* were collected in flower from February to May. Several Brazilian distribution records (Map 1) have been added from citations of *Conyza setosa* by Malme (1931, 1933).

Baker (1882) distinguished *Aster tuberosus* from *A. setosus* on the basis of hairiness of the latter, but the vestiture in this species is variable in density. It is not clear why Baker included these two species within *Aster* apart from *Conyza blanchetii*, because his key to genera distinguishes *Aster* from *Conyza* by "Ligulae latae" (*Aster*) vs. "Capitula semper discoidea" (*Conyza*).

2. **Apopyros warmingii** (Baker) Nesom, *comb. nov.* BASIONYM: *Aster warmingii* Baker in Martius, *Fl. Bras.* 6(3):23. 1882. LECTOTYPE (designated here): BRAZIL. Prov. Minas Gerais: in campis ad Lagoa Santa, 25 Oct 1864, *E. Warming 550* (C, photo-GH!, photo-MO!, photo-US!).

Two sheets of this at C are both clearly annotated as "*Aster warmingii* Baker sp. nov." and the identity of the plants on both sheets is unequivocal. Both have the same printed label but one



Map 1. Distribution of *Apopyros corymbosus* and *A. warmingii*.

(*Warming s.n.*) has a date of 9 Nov 1863 handwritten on the printed label; the other (*Warming 550*) has a date of 25 Oct 1864 written on an accompanying slip of paper.

Plants from a thick, lignescent rhizome, the latter sometimes thickening up to 4 cm wide and cormoid or broadly tuberous; leaves, stems, and phyllaries with stomates distinctly visible, appearing glabrous or glabrate but under close inspection the leaves minutely and inconspicuously strigillose with Type B trichomes. Stems mostly several (rarely 1 or up to 30) from the base, 2-6 dm tall, strictly erect, unbranched or with a few branches above midstem, with numerous narrow ribs. Leaves thick, elliptic to narrowly lanceolate, epetiolate, subclasping, 4-7 cm long, 10-15 mm wide, largest at midstem, gradually diminished upward, bracteate immediately beneath the heads, also reduced in size downward with the lowermost nearly scale-like, margins with a sharply delimited, narrow, thickened-hyaline rim, antrorsely ciliate with Type A trichomes 0.2-0.5 mm long, the leaf surfaces sometimes sparsely strigose with similar trichomes. Heads 10-14 mm wide (pressed), 1-4 per main stem on peduncles 1.5-8.0 cm long; phyllaries linear-lanceolate, in 3-4 series, the inner 6-8 mm long, outermost 1/3-5/6 as long as the inner, with an orange-resinous, fleshy-thickened and raised midrib, green lateral areas from near base to apex, and sharply delimited, hyaline, shallowly lacerate-erose margins. Pistillate flowers few. Disc flowers 4.5-5.8 mm long, abruptly expanded into a wide, indurate disc at the very base; style branches 1.0-1.2 mm long, with deltate collecting appendages 0.1-0.2 mm long. Achenes nearly terete or plump-angular in cross-section, with (4-)5(-6) yellowish nerves, 3-4 mm long, 0.6-1.0 mm wide; pappus of (1-)2 series of ca. 30-40 whitish bristles, without a short, outer series.

Apopyros warmingii is endemic to south-central Brazil, where it has most commonly been collected in areas of recently burned cerrado at elevations of ca. 300-1000 meters. It flowers at least from August through February.

Specimens examined: BRAZIL. Distrito Federal: Brasilia, area do Cristo Redentor, 15°57'07" S 47°53'37" W, area queimada recentemente, brejo seco periodicamente, 19 Oct 1988, *Azevedo 181* (US); Brasilia, Campus da Universidade de Brasilia, cerrado, 3 Feb 1968, *Belem 3922* (US); Brasilia, Taguatinga, confluencia correjos Cana do Reino & Vicente Pires, 25 Aug 1981, *Heringer et al. 7356* (US); ca. 10 km E of Brasilia, gallery forest and adjacent burned cerrado, Corrego Jeriva, 975 m, 15 Sep 1965, *Irwin et al. 8329* (US); cerrado adjacencias do Corrego Rajadinha, Bacia do rio São Bartolomeu, local queimado ha cerca de 30 dias, 5 Oct 1983, *Pereira 815* (US). Goias: Serra do Caiapo, 17°12' S, 51°47' W, ca. 30 km N of Jatai on road to Caiaponia, 800-1000 m, 24 Oct 1964, *Irwin et al. 7310* (US) and *7283* (MO,US). Matto Grosso: ca. 70 km N of Xavantina, 14°40' S 52°20' W, burned-over cerrado, 300-400 m, 10 Oct 1964, *Irwin & Soderstrom 6721* (US); Rio Arinos, braco, 26 Sep 1943, *Baldwin 3069* (US). Minas Gerais: Mpio. de Prata, 27 km S of Prata

on Hwy BR-14, Triangulo Mineiro region, open xeromorphic scrub-savanna, 29 Sep 1967, Goodland 4010 (MO).

DEFINITION AND RELATIONSHIPS OF *APOPYROS*

Plants of *Apopyros* are briefly characterized as follows: stems strictly erect, arising from a thick, woody rhizome or tuber; leaves all cauline, stiffly erect-ascending, shiny-indurate in texture, 3(-5)-nerved, those near the stem base reduced and sometimes scale-like; heads disciform, the pistillate flowers 1-seriate, peripheral, tubular with 3-4 apical teeth, eligulate; phyllaries with a single, distally broadened, thickened and raised, orange-resinous vein; achenes mostly 5-nerved, oblong and nearly terete; and pappus of (1-)2 series of numerous bristles of even length, with or without an additional, short, outer series of setae or setose bristles.

Apopyros corymbosus resembles *Conyza* in its numerous, small heads with reduced pistillate corollas, and it is easy to understand why this species has been referred to *Conyza*. Malme's transfer of *Aster setosa* to *Conyza* was explicitly based on his recognition of its similarity to *C. blanchetii*. *Conyza* differs from *Apopyros*, however, in its net-veined leaves, the surface texture not shiny-indurate; phyllaries most commonly 3-nerved; pistillate flowers in several series, with a short ligule or if eligulate, the apex of the tube usually truncate or fimbriate, not distinctly toothed; achenes flattened and 2-nerved; and pappus usually 1-seriate, without a short, outer series.

Presumably, these species were allied with *Aster* because of a convergent resemblance (Nesom in prep.) to species of *Aster* subg. *Oxytripolium* that occur in the same geographic area (e.g., *Aster squamatus* [Spreng.] Hieron., *A. regnellii* Baker). The phyllaries of these species, however, lack orange venation, the leaf texture and vestiture are different, the pistillate flowers are ligulate, and the pappus is uniseriate.

Apopyros is a member of the "*Leptostelma* group" (as noted in other studies: Nesom 1994, in press, and in prep.), which also includes *Leptostelma*, *Hysterionica*, and *Neja*. The plants of these genera are characterized by the following features: leaves often thick or rigid; phyllaries flat, more or less evenly herbaceous, and commonly 3-nerved, the nerves usually conspicuously orange-resinous; rays mostly 2-3-seriate, the ligules variably (between species) yellow or white, but often tending to dry yellowish even if white when fresh; disc corollas with a short tube; disc flowers bisexual and fully fertile, the style branches short, with deltate collecting appendages; achenes eglandular, erostate, flat and 2-nerved (or terete and multinerved in *Apopyros* and *Neja*); and pappus 1-3-seriate, the outer series of bristles similar to the inner or variably usually reduced and modified. All have an "austro-brasilien" geographic distribution, occurring primarily in southeastern Brazil and adjacent Argentina, Uruguay, Paraguay, and Bolivia.

Several specimens of *Apopyros warmingii* have been annotated by Dr. Harold Robinson as "a rayless form of *Erigeron tweediei*" (= *Leptostelma tweediei* [Hook. & Arn.] Nesom). If it were necessary to fit *Apopyros* into a previously established genus, *Leptostelma* is reasonably considered, as plants of the latter tend to be relatively similar in habit, disc corolla and style branch morphology and in their similar habitats in the same geographic region. On the other hand, the nearly cylindrical, multinerved achenes of *Apopyros* would be anomalous within *Leptostelma*, derived with difficulty (at least conceptually) from the flattened, oblong-obovate, and 2-nerved ones of *Leptostelma*. Further, *Leptostelma* produces fibrous-rooted rhizomes, net-veined leaves, 3-veined phyllaries, ligulate pistillate flowers, and foveolate receptacles. If positioned as a member of *Leptostelma*, the two species of *Apopyros* would occupy an isolated position coordinate with the rest of the genus.

Apopyros and *Neja* are similar (and perhaps most closely related to each other) in their terete to subterete, multinerved achenes, parallel-veined leaves with shiny-indurate surfaces, and stiffly pilose-hirsute vestiture. *Neja* differs in its branching, lignescent caudices, filiform, basally disposed leaves, solitary heads on nearly scapose stems, conspicuously ligulate pistillate flowers, and fusiform-cylindrical achenes with 7-10 raised, longitudinal nerves that are thick, raised, and orange-resinous at maturity.

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COMMENTS ON *GNAPHALIOTHAMNUS* (ASTERACEAE: INULEAE)

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ABSTRACT

Gnaphaliothamnus is maintained here as a genus of ten species endemic to México and Central America, in contrast to the view of Anderberg (1991) and Freire (1993), who have included most of *Gnaphaliothamnus* within an expanded *Chionolaena* ranging from southern Brazil to northern South America, Central America, and México. Anderberg and Freire restrict *Gnaphaliothamnus* to a single species, which occurs in México and Guatemala, but *Chionolaena seemannii* (Sch.-Bip.) Freire is a synonym of *G. salicifolius*, the generitype of *Gnaphaliothamnus*. A recently described Mexican species, *C. mexicana* Freire, is here regarded as a synonym of *G. concinnus*.

KEY WORDS: *Gnaphaliothamnus*, *Chionolaena*, Gnaphalieae, Inuleae, Asteraceae

In her recently published amalgamation of the genus *Chionolaena* DC., Freire (1993) united species of *Chionolaena*, *Leucopholis* Gardner, *Pseudoligandra* Dillon & Sagást. (Dillon & Sagástegui 1990a), and *Parachionolaena* Dillon & Sagást. (Dillon & Sagástegui 1990b), from South America (southeastern Brazil, Venezuela, and Colombia) with most of the group of Mexican and Central American species earlier treated as *Gnaphaliothamnus* Kirpichn. (Nesom 1990a, 1990b). Freire retained *Gnaphaliothamnus*, however, recognizing it as a monotypic genus (*G. salicifolius* [Bertol.] Nesom, the single species) and as the sister group of *Chionolaena* sensu lato. This restriction of *Gnaphaliothamnus* was first suggested by Anderberg & Freire (1989) and maintained by Anderberg (1991). Freire hypothesized that the Mexican and Central American species are the primitive elements of this whole group (the broadened *Chionolaena* and the monotypic *Gnaphaliothamnus*). Neither my studies (including new species and new combinations within *Gnaphaliothamnus*) nor the second paper published by Dillon & Sagástegui (1990b) have been discussed by Freire or Anderberg.

Freire characterized *Gnaphaliothamnus* (vs. *Chionolaena*) as distinct in its "free pappus bristles" (vs. basally connate) "with linear apical cells" (vs. apical cells of the bristles swollen and the bristles apically clavate). This distinction, however, is not consistent, because the pappus bristles of *G. salicifolius* are often slightly connate at the base, distinctly basally caducous, and released in groups; and while the bristles of *G. salicifolius* are mostly apically attenuate, there is a definite tendency for the apical cells to be swollen and the bristle apex clavate. Further, there is significant interspecific variation within *Gnaphaliothamnus* in these two characters that makes them unreliable as indicators of generic boundaries. Pappus bristles are consistently separate and basally caducous in two species of *Gnaphaliothamnus*: *G. cryptocephalus* Nesom and *G. costaricensis* Nesom; and bristle apices are consistently attenuate at the apex, rather than clavate, in two species: *G. cryptocephalus* and *G. lavandulifolius* (Kunth) Nesom.

An even more interesting indication that a monotypic *Gnaphaliothamnus* cannot be separated from similar Mexican species is the observation that the taxon included by Freire in *Chionolaena* as *C. seemannii* (Sch.-Bip.) Freire is a synonym of *Gnaphaliothamnus salicifolius*, the generitype of *Gnaphaliothamnus*. Freire mapped *C. seemannii* (in her study, this species known only from the type) along the border of the states of Michoacán and Guanajuato, México, based on Seemann's collection "1994" from the "Sierra Madre, NW Mexico." Seemann's route in northwest México, however, began in Mazatlán (Sinaloa), crossed over the Sierra Madre to Ciudad Durango (through southern Durango), ventured south into northeastern Nayarit, and then was retraced back to Ciudad Durango and Mazatlán (Turner 1992). Only two species of *Gnaphaliothamnus* are known from this general area, *G. durangensis* Nesom (rare) and *G. salicifolius* (relatively common). The latter species is easily recognized by its narrow, eglandular, bicolored leaves with essentially glabrous upper surfaces, pedicellate heads in corymbs above the leaves, and large number of pistillate flowers (relative to the central flowers), these features clearly described and illustrated by Freire in *C. seemannii*.

The species most similar and apparently most closely related to *Gnaphaliothamnus salicifolius* is *G. eleagnoides* (Klatt) Nesom. Both species have eglandular, glabrate upper leaf surfaces and a densely corymboid capitulescence of pedicellate heads produced above the leaves. *Gnaphaliothamnus eleagnoides* has somewhat broader leaves, heads with relatively fewer pistillate flowers, and pappus bristles that are distinctly apically clavate, basally persistent, and slightly connate. Possible relationships among the remainder of the species of *Gnaphaliothamnus* are difficult to perceive, but *G. sartorii* (Klatt) Nesom and *G. concinnus* (A. Gray) Nesom also have distinctly short-pedicellate heads and persistently tomentose but eglandular upper leaf surfaces, and these four species may be closely interrelated. The other six species have sessile or nearly sessile heads and glandular leaves (see comments below).

Definition of *Gnaphaliothamnus* vs. *Chionolaena*

Gnaphaliothamnus salicifolius can be absorbed into Freire's broadly conceived *Chionolaena* with no significant phenetic alteration of the latter, but by doing so, the question of the closest relationships of *Chionolaena* sensu Freire and the problem of its internal systematic structure are brought into a different focus. In order to construct a hypothesis of cladistic relationships among the elements of *Chionolaena* in the broadest sense, an outgroup must be sought among other genera. Following Merxmüller *et al.* (1977), Freire noted that *Chionolaena* sensu Freire belongs with the *Lucilia* group, including *Gnaphaliothamnus* sensu stricto and the South American genera *Lucilia* Cass., *Belloa* Remy, *Chevreulia* Cass., *Facelis* Cass., *Cuatrecasasiella* H. Rob., *Mniodes* (A. Gray) Benth., and *Raouliopsis* S.F. Blake.

In Freire's cladistic analysis, however, only *Gnaphaliothamnus* (monotypic) served as the outgroup to her expanded concept of *Chionolaena*, although the same single species of *Gnaphaliothamnus* was included by another name within her circumscription of *Chionolaena*. Using a mix of unweighted characters that appear to vary widely in their potential phyletic significance, Freire's analysis of *Chionolaena* unites some Mexican species with Brazilian ones on the basis of inner involucre bract shape and one Mexican species with the two Colombian ones on the basis of glabrous achene surfaces. There is a perfect correlation, however, between achene pubescence (Freire's character 10) and geography: "villous" achenes occur in the Brazilian taxa and "shortly pubescent" or "glabrous" achenes are found only in the Mexican, Central American, and Colombian taxa.

As I noted earlier (Nesom 1990a), *Gnaphaliothamnus* is distinct from *Chionolaena* in its short achenial hairs with blunt-rounded apices (vs. longer hairs with attenuate-acute apices); such hairs on *G. salicifolius* and *G. lavandulifolius* also were observed to be myxogenic. The achenial hairs of *Gnaphaliothamnus* (sensu Nesom) are relatively homogeneous in morphology and similar to those of the genotype. Anderberg (1991) also characterized the achenial hairs of *G. salicifolius* (= *Gnaphaliothamnus*) as short, clavate, and myxogenic but, apparently following Freire, he provided a general description of the achenial hairs of *Chionolaena* sensu lato (including most of *Gnaphaliothamnus*) as "elongate."

Anderberg's cladistic analysis placed *Gnaphaliothamnus* and *Chionolaena* as sister genera within his "*Anaphalis* group" (of subtribe Cassiniinae Anderberg), a clade that includes *Anaphalis* DC., *Antennaria* Gaertn., *Ewartia* Beauverd, *Anaxeton* Gaertn., *Petalacte* D. Don, and others. The genera of the *Anaphalis* group are spread over South and Central America, South Africa, Asia, North America, Australia, and New Zealand. The remainder of the Cassiniinae, which occupy a coordinate or basal position with respect to the *Anaphalis* group, are restricted to the Australasian area, primarily in Aus-

tralia. Among all these genera, the achenial hairs of *Gnaphaliothamnus* are scored as similar in morphology (character "66. Cypselas hair type") to those of *Antennaria*, *Anaphalis*, and *Ewartia* but not to those of Brazilian *Chionolaena* and *Leucopholis*, although this is not shown on Anderberg's cladograms either as a difference between *Gnaphaliothamnus* and *Chionolaena* or a synapomorphy between *Gnaphaliothamnus* and genera of the *Anaphalis* group. Among the Cassiniinae, the achenial hairs of only *Gnaphaliothamnus*, *Antennaria*, and several Australian genera are known to be myxogenic (Anderberg 1991).

In addition to differences in achenial hairs, Anderberg scored *Chionolaena* and *Gnaphaliothamnus* as different in features of achenial and pappus morphology and sexuality of the central flowers. The degree of basal fusion of pappus bristles (character 79) has already been noted above as variable within *Gnaphaliothamnus*. Anderberg scored the apical cells of pappus bristles (character 80) in *Gnaphaliothamnus* as acute (vs. clavate), but they are characterized as "subclavate" in his description of *Gnaphaliothamnus* as a genus. He scored (incorrectly) the disc flowers of *Gnaphaliothamnus* as fully fertile (character 49), as opposed to sterile in *Chionolaena*. In the morphology of the disc floret achenes (character 58), the achenes of *Gnaphaliothamnus* are scored as "small, oblong" (= the "*Helichrysum* type," a specialization shared with *Antennaria*, *Anaphalis*, and *Ewartia*), while those of *Chionolaena* and all the rest of the Cassiniinae are "ellipsoid or turbinate" (Anderberg 1991). Freire did not make any distinction between achenes, and her illustrations apparently include a mix of mature and immature achenes. Dillon & Sagástegui (1990b) observed that the collecting appendages of the disc flower style branches of *Chionolaena* sensu stricto are lanceolate-acute, in contrast to the rounded or truncate appendages in the other generic-level taxa included by Freire within *Chionolaena*; this difference was not noted by Freire or by Anderberg.

As noted earlier (Nesom 1991) and in the discussion above, the species of *Gnaphaliothamnus* can be divided into two groups on the basis of leaf glandularity. The adaxial leaf surfaces of six species are densely and conspicuously glandular (beneath the dense layer of eglandular tomentum). The glands are "Type C trichomes" (see Nesom 1976; Karis 1993), which also form the characteristic glandularity in much of the Asteroideae. In *Gnaphaliothamnus* they are relatively long, biseriate hairs with thin walls and with a 2-celled head, the distal cells often crumpled and distorted. In the Cassiniinae, such glandularity occurs only in the group of Australian genera that includes *Cassinia* R. Br., *Izodia* R. Br., and *Ozothamnus* R. Br. (Bremer 1991, character 8), and in *Gnaphaliothamnus*. The presence of this glandularity in *Gnaphaliothamnus* was not noted by Freire (1993) nor was it scored by Anderberg (1991).

In summary, the evidence is unconvincing for treating the ten Mexican species of *Gnaphaliothamnus* as congeneric with the essentially Brazilian *Chionolaena* and *Leucopholis*, although it is likely that they are all correctly placed by Anderberg in the subtribe Cassiniinae. With respect to *Gnaphaliothamnus*,

the analyses of both Anderberg and Freire are internally inconsistent as well as contradictory between themselves. Although the hypothesis of a more broadly monophyletic *Chionolaena* cannot be rejected outright, there is evidence to suggest that *Gnaphaliothamnus* (sensu Nesom) may be more closely related to other genera than to *Chionolaena*. *Gnaphaliothamnus* is justifiably maintained as distinct at least until a more thorough study can be provided in a broader context.

Distribution of *Gnaphaliothamnus eleagnoides*

Gnaphaliothamnus eleagnoides (Klatt) Nesom, *Phytologia* 68:376. 1990. BASIONYM: *Chionolaena eleagnoides* Klatt, *Leopoldina* 23:88. 1887. TYPE: MEXICO. [Hidalgo]: "Pelado," Aug 1841, *F. Liebman* 316 (HOLOTYPE: C; fragment and drawing by Klatt-GH!).

In an earlier study (Nesom 1990a), I noted that the type of *Gnaphaliothamnus eleagnoides* was collected in Oaxaca, assuming that the collection was made from the same area as more numerous, recent collections of that species from southeast of Cd. Oaxaca. As correctly observed by Freire (1993), however, the type locality ("Pelado") is in the state of Hidalgo. Compared to the plants from Oaxaca, those from Hidalgo produce slightly broader leaves with a more persistent vestiture on the upper leaf surfaces, but they are similar in other features. Recognition of *G. eleagnoides* in Hidalgo considerably enlarges the distribution of this species.

Comments on *Gnaphaliothamnus concinnus*

Freire (1993) described a new species within *Chionolaena* based on a collection from México by Pringle (originally identified and distributed as *Gnaphalium lavandulaceum* DC.).

Chionolaena mexicana Freire, *Ann. Missouri Bot. Gard.* 80:427. 1993. TYPE: MEXICO. Hidalgo: Sierra de Pachuca, 10,000 ft, 20 Feb 1899, *Pringle* 7700 (HOLOTYPE: K; Isotype: VT!).

I did not examine plants of this collection in my earlier study of the group, but I have now examined a duplicate (VT), which appears to be conspecific with *Gnaphaliothamnus* (*Gnaphalium*) *concinnus* (A. Gray) Nesom. Further, these plants clearly are the same species as identified by Espinosa (1985) as *Gnaphalium concinnum* A. Gray, which I incorrectly referred to as "apparently" *Gnaphaliothamnus salicifolius* (Nesom 1990a). Espinosa cites two other

collections of *G. concinnus* from Hidalgo (north of Pachuca) and one from Edo. México (east of Amecameca).

Freire acknowledged the close relationship between *Chionolaena mexicana* and *C. concinna* (A. Gray) Freire, distinguishing them as follows in her key (1993, p. 408) to the species of *Chionolaena*:

- “16a. Dichotomously branched, rigid shrub; capitulescence terminal at maturity; leaves slightly attenuate at the base. *C. mexicana*
 16b. Subdichotomously branched subshrub; capitulescence lateral at maturity; leaves subpetiolate. *C. concinna*”

The difference between “dichotomous” and “subdichotomous” branching appears to be variable and subjective; and plants from both areas are erect, otherwise habitally similar, and approximately the same height, even as measured by Freire, so it is not clear why she characterized one as a “shrub” but the other as a “subshrub.” The “lateral” capitulescence of *Chionolaena concinna* may reflect in part the manner in which the plant was originally pressed, with a slight bend near the base of the capitulescence, but the pedicels of the outer heads of *Pringle 7700* tend to be loose with the heads nodding outward (as illustrated by Freire), as is also the case in *C. concinna* sensu stricto. The difference in leaf base is a matter of small degree and application of a similar criterion to other species of *Gnaphaliothamnus* (e.g., *G. salicifolius* and *G. eleagnoides*) would necessitate their taxonomic fragmentation.

I noted earlier (1990a) that the achenial trichomes of *Gnaphaliothamnus concinnus* are narrower than in other species and twisted (this observed from *Schaffner 222-CM*), a feature not observed among the other species. Achenes from other plants of *G. concinnus* in San Luis Potosí, however, appear to have trichomes more similar to those from Hidalgo. The similarity in trichomes of these plants between the two areas also was observed by Freire. More detailed studies of *G. concinnus* may show that some differentiation has occurred among its three general localities (San Luis Potosí, Hidalgo, and Edo. México), the achenes needing particular attention, but there seems to be no clear justification at present for recognizing more than a single species.

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