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A RE-EVALUATION OF THE GENUS AMBROSIA (COMPOSITAE) [1]

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IN SPITE OF THE FOCUS in recent years on the ragweeds and their relatives as sources of allergenic pollen, they are poorly understood biologically and taxonomically. Systematic controversy has centered particularly about the question of the possible congeneric nature of the so-called "true ragweeds," *Ambrosia* spp., and "false ragweeds," *Franseria* spp. Linnaeus (1753) established the genus *Ambrosia* for modern use with the description of four species, *Ambrosia trifida*, *A. elatior*, *A. artemisiifolia* and *A. maritima*, all of which were based upon earlier descriptions. Cavanilles (1793) established the closely allied genus, *Franseria*, with the description of the single species *F. ambrosioides*. The similarity of the two genera was recognized by Cavanilles, as is shown by the specific epithet (*ambrosioides*) he chose for his species and by a statement in the description that he considered the new genus to be intermediate between the ragweeds (*Ambrosia*)

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and the cockleburs (*Xanthium*), "*genus mediam inter Ambrosiam et Xanthiam*" (p. 78). Since the time of Linnaeus and Cavanilles, as we have continued to explore and catalog the floras of the New World, the close affinity of these genera has become ever more apparent, and numerous instances of confusing intermediacy have been remarked between them. This is exemplified by a statement made by T. S. Brandegee, in 1889, in his description of *Franseria acuminata*: "This is *another* of the forms which *too closely* connects the genus with *Ambrosia*" (p. 171, italics mine). Recently Shinners (1949) reviewed the genus *Franseria* for central Texas, and stated, "This genus cannot be distinguished from *Ambrosia* except by mature fruit, and the difference . . . warrants the recognition of a subgenus at most" (p. 173). The work on ragweed biology undertaken at Michigan during the past several years (Gebben, Payne and Wagner, 1963; Payne, 1962a, 1962b, 1963; Payne, Raven and Kyhos, 1964) has convinced me that Shinners is correct and has provided further evidence to support the hypothesis that *Ambrosia* and *Franseria* are, indeed, congeneric. It is the purpose of this paper to present the evidence and to make the necessary nomenclatural changes.

The species of "ambrosioid" and "franserioid" ragweeds are wind pollinated composites with highly specialized inflorescences (Payne, 1963). The floral heads are unisexual, and both staminate and pistillate heads are normally borne on the same plant. The involucral appendages (phyllaries) of the pistillate heads are fused about the enclosed pistillate florets or floret to form a hard, indehiscent conceptacle. The tips of the appendages are more or less evident as spiny processes which project from the surface of the involucre body at maturity. The number and arrangement of these spines provides the single criterion by means of which *Ambrosia* and *Franseria* have been distinguished. In *Franseria*, *sensu stricto,* the plants produce fruiting involucres that characteristically bear numerous spines scattered more or less uniformly over the surface, whereas fruiting involucres of *Ambrosia, sensu stricto*, are characterized as bearing few spines arranged in a single whorl below the involucral beak. This difference is superficial, however, when the variation of all of the species in these complexes is considered. The spines of the pistillate involucres of species such as *Ambrosia artemisiifolia, A. trifida,* and *A. psilostachya* are arranged, in many instances, not in a single whorl, but in two, three, or more, few-spined whorls compacted near the apex of the fruiting involucre body. Intermediate involucral forms are encountered among specimens of a wide variety of franserioid species; fruiting involucres representative for both genera are commonly found among members of the *Franseria confertiflora, F. acanthicarpa,* and *F. canescens* complexes, and species such as *F. bryantii* and *F. linearis* can be placed almost equally well in either genus. Numerous "intergeneric" synonyms are found in the literature which reflect this morphologic interdigitation, and the ambiguity and lack of constancy of the character state used to distinguish *Ambrosia* from *Franseria* constitutes, in itself, as noted by Shinners (op. cit.), a compelling argument for combination of the two.

Furthermore, I have produced an "intergeneric hybrid" in the greenhouse between the two very distinct species *Ambrosia artemisiifolia* (seed parent, $n = 18$) and *Franseria acanthicarpa* (pollen parent, $n = 18$). Morphological features of the parental species and of the hybrid F_1 are illustrated in TEXT-FIG. 1. Consideration of the hybrid series thus initiated lends additional support for combination. Chromosome pairing in the hybrid was observed to be very good; many configurations consisted of 18 bivalents at diakinesis, while others showed only one or two pairs of univalents (TEXT-FIG. 1D). Pollen viability, as estimated by staining in acetocarmine, was approximately 30 per cent. Seeds, formed in abundance, were 40 per cent germinable and produced a vigorous F_2. At the time of writing, the series had been carried through the F_3 generation (pollen viability of individual specimens, 57 to 94.5 per cent; mean viability for 19 specimens, 81.5 per cent; seed viability for two selected seed lots, 63.3 per cent and 96 per cent), and F_4 progeny were growing in the greenhouse. While the occurrence of intergeneric hybridization is not, in itself, of great taxonomic significance, the high degree of chromosomal compatibility and genome homology demonstrated by this hybrid series does not support separation of the parental species in different genera.

Still further support for the union of *Ambrosia* and *Franseria* may be derived from a consideration of the evolutionary relationships of the species or species groups involved. Since the ragweeds, *sensu lato,* comprise a large and morphologically diverse group, numerous characteristics may be analyzed to indicate relative species advancement and relationships. Progressions from primitive to advanced character states which have been worked out within the group include the following:

HABIT

1. From shrubs to perennial herbs and annuals.

LEAVES

1. From petiolate to sessile.
2. From alternate to opposite.
3. From pinnately lobed to palmately lobed or unlobed.
4. From heavily pubescent and somewhat coriaceous to less pubescent and membranaceous.

STAMINATE CAPITULA

1. From stalked to sessile.
2. From capitulous stalks which bear more than one head to one-headed stalks.
3. From centric attachment of the stalk to the involucre to eccentric attachment.
4. From well defined involucral lobes (phyllary tips), separated by deep sinuses, to involucral lobes which are poorly defined or lacking.
5. From large heads with many florets to small heads with few florets.

PISTILLATE CAPITULA

1. From several florets to a single floret per capitulum.
2. From many and scattered (imbricated) spines to few and localized spines.

TEXT-FIG. 1. *Ambrosia artemisiifolia* × *"Franseria" acanthicarpa*. Representative leaves (subscript 1), staminate involucres (subscript 2) and fruiting involucres (subscript 3) for: A, *F. acanthicarpa*, pollen parent, $n = 18$; B, *A. artemisiifolia*, seed parent, $n = 18$; C, the hybrid (superscript numerals denote nodes from which leaves were removed). D, Meiotic chromosome figures drawn from hybrid material (voucher: *Payne ANS-3346*, MICH): D_1 through D_3, configurations demonstrating perfect pairing (18 bivalents); D_4, configuration showing 4 univalents; D_5, configuration showing 2 univalents. The line to the upper right is equivalent to 10 cm. for leaf silhouettes and 10 mm. for involucre drawings.

3. From flat and strongly emergent (phyllary like) spines to terete spines. Secondary modification has given rise to hooked and vestigial spines.

Although the details of evolutionary pathways must still be worked out in many instances, the character progressions cited above, together with simple, nonprogressional similarities, can be used to assess relative advancement and to indicate infrageneric groupings and relationships. In general, species of *Ambrosia, sensu stricto,* appear to be more advanced than, and to have been derived from, species or species groups of *Franseria, sensu stricto.*

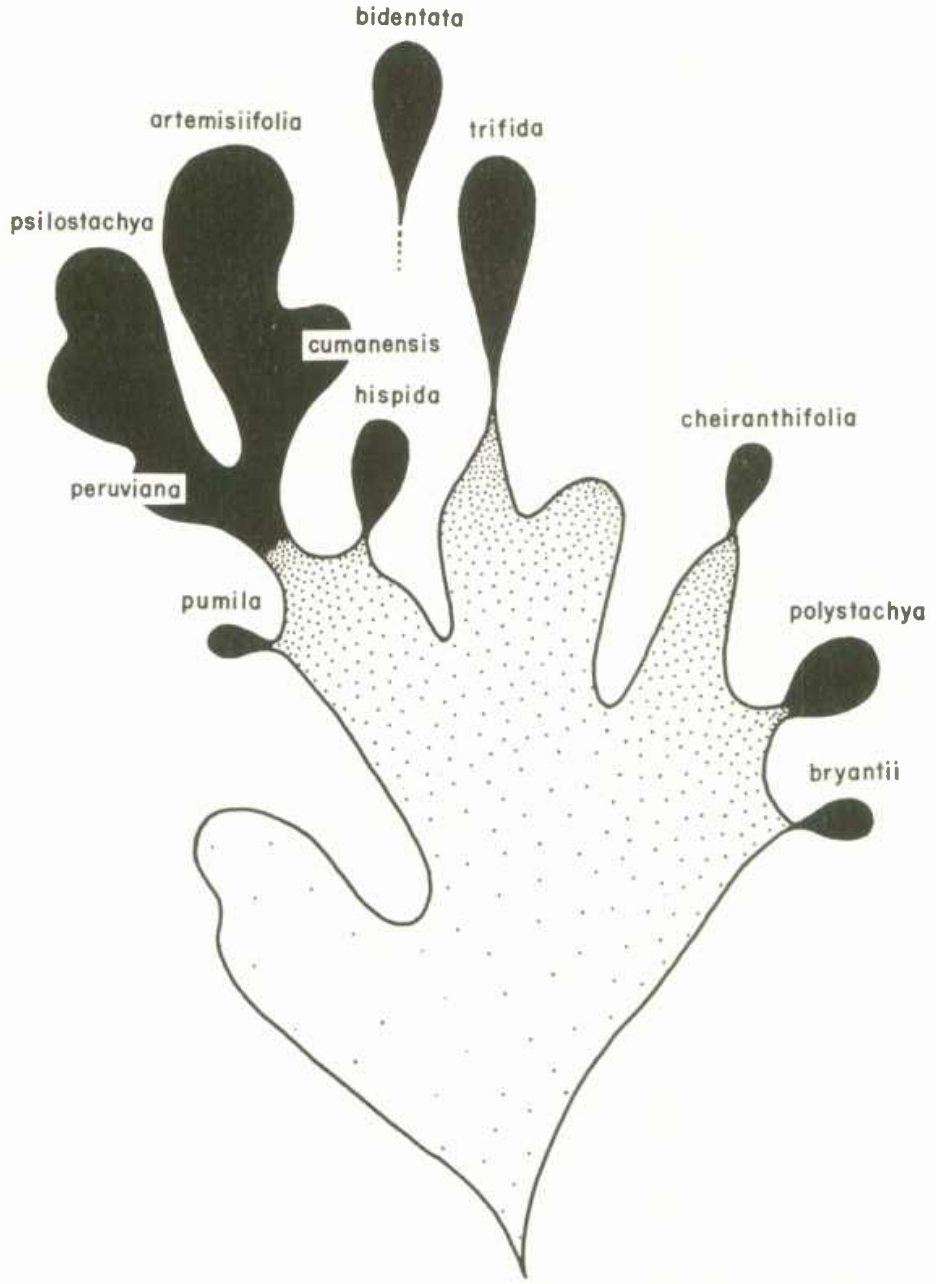
Rydberg (1922) recognizes 15 subgeneric groups among the species of *Ambrosia* and *Franseria*; however, his distinctions are often somewhat slight, serving better to distinguish small parcels of related species than to point out significant groups of evolutionarily related organisms. For the present purposes, therefore, I shall recognize three major subgeneric complexes, two of which include both franserioid and ambrosioid members, and a fourth containing only *Ambrosia bidentata.* These may be characterized as follows:

1. A central or core group, comprised of the majority of the species and characterized by usually quite pubescent (especially on the lower surface), pinnately to tripinnately lobed leaves. The group is, in itself, highly complex, with evolutionary lines apparently leading from the least specialized, shrubby, franserioid species, such as *Franseria dumosa* and *F. eriocentra,* along several derivative pathways to ambrosioid species as follows: To *Ambrosia trifida* along a line characterized by species with striated staminate involucres and nonhooked spines; the closest relatives of *A. trifida* probably include *F. chamissonis* and *F. acanthicarpa.* To *A. cheiranthifolia* through herbaceous species with less lobed, "bicolored" leaves, such as *F. linearis.* To *A. bryantii* via a shrubby line with much divided, irregularly lobed leaves, including such species as *F. camphorata* and *F. magdalenae,* predominant in Baja California, Mexico. To the South American species, A. *polystachya,* through the remarkably similar *F. artemisioides* Willd.

2. A small, derivative group, found in the desert regions of the southwestern United States and western Mexico, made up of shrubby species which are characterized by unlobed (or nearly so) leaves, a heavily glandular indument, and fruiting involucres which closely resemble those of *Xanthium,* the cockleburs. This subgroup includes *Franseria ambrosioides, F. ilicifolia, F. chenopodiifolia* and *F. deltoidea.* This complex displays no obvious, direct affinities with any of the ambrosioid species, although it is connected to franserioid members of group 1, above, and may be closely related to the *Xanthium strumarium* (*sensu lato*) complex.

3. A highly specialized, derivative group of perennial herbs and annuals which are characterized by membranaceous, regularly pinnately to tetrapinnately lobed leaves and small staminate and pistillate involucres, the former without striations and the latter usually one-flowered and with reduced spines. This complex includes *Franseria canescens* and *F. conferti-*

flora, which appear to be related to ambrosioid species as follows: *F. canescens* is probably closely related to the very similar *A. pumila,* the latter being smaller in stature and with reduced fruit spines. *Ambrosia hispida,* a species of the Caribbean strand, closely resembles *A. conferti-*



TEXT-FIG. 2. Schematic representation of the polyphyletic nature of *Ambrosia, sensu stricto.* The stippled body represents the franserioid assemblage; black lobes represent ambrosioid species or species groups, as indicated, which have been derived from it.

flora, having more hispid leaves, reduced fruit spines and a slightly different habit. The large and highly integrated ambrosioid complex which includes *A. artemisiifolia, A. cumanensis, A. peruviana* and *A. psilostachya,* is probably connected to *A. confertiflora* along a different line from that which leads to *A. hispida*, through intermediate species such as *A. velutina* and *A. tenuifolia* Spreng.

4. A fourth group containing the single species *A. bidentata,* the relationships of which are obscure, can be recognized. This is one of the most highly specialized of the ragweeds, with sessile, unlobed (but basally toothed) leaves, medium-sized, one-flowered pistillate involucres with few spines, and sessile staminate involucres with extreme prolongation of the distal lobe. It hybridizes easily with *A. trifida* and shares with it the annual habit, relatively large fruiting involucres and the condition of aneuploidy, but displays none of the morphological peculiarities characteristic of *A. trifida.* On the latter basis, it would appear to be more closely related to group 3, above, but its progenitor cannot be distinguished at present.

The relationships suggested in the foregoing paragraphs are summarized diagrammatically in TEXT-FIG. 2, in which the franserioid complex is represented as a stippled, lobed mass and the derivative, ambrosioid complexes are shown as black, peripheral lobes. This arrangement is supported by the distributional pattern obtained by designating three artificial groups containing the apparently most primitive species, the intermediate species, and the most advanced species. The first group is located in the desert Southwest, the second in less arid regions surrounding it, and the third extends to the northern and eastern periphery of the *Ambrosia-Franseria* range, providing a classic picture of the diversification and outward spread from a center of origin of ever more advanced members of a genus. It is evident that, if the suggested evolutionary lines are even approximately correct, *Ambrosia,* in the strict sense, is a highly polyphyletic group, its divisions involving as ancestral forms different members of *Franseria,* a situation which is unacceptable by present generic standards.

In view of the above arguments in support of combining *Ambrosia* and *Franseria,* including the poorly defined and undependable criteria for separating them, an apparently higher degree of genome and chromosome homology than is ordinarily found between distinct genera, and the polyphyletic nature of *Ambrosia, sensu stricto,* they are combined below, and the necessary nomenclatural changes are made in the following pages. The treatment of the species and the synonymy presented do not constitute a monograph of the genus as newly defined but are intended only to clarify the nomenclature of the "franserioid" members listed.

Ambrosia Linnaeus, Sp. Pl. 2: 987. 1753; Gen. Pl. ed. 5. 425. 1754, non *Ambrosia* sensu Hort. ex Bedevian, Ill. Polyglot. Dict. 170. 1936 (Chenopodiaceae). Type species: *A. maritima* L. Sp. Pl. 2: 988. 1753.

Gaertneria Medicus, Phil. Bot. 1: 45. 1789, non *Gaertnera* Schreb. 1789 (Mal-

phigiaceae), nec *Gaertneria* Neck. 1790 (Gentianaceae), nec *Gaertnera* Retz. 1791 (Campanulaceae), nec *Gaertnera* Lam. 1791 (Loganiaceae). Type species: *Ambrosia fruticosa* Medic. Hist. Comment. Acad. Elect., Theodoro-Palatinae 3: 244. 1775, nomen illeg., *Ambrosia arborescens* Mill. 1768.

Franseria Cavanilles, Ic. Descr. Pl. 2: 78. 1793, nomen cons., Int. Code Bot. Nomencl., Reg. Veg. 23: 318. 1961. Type species: *F. ambrosioides* Cav. *Ibid.* NOTE: This name is erroneously equated in the Code (loc. cit.) with *Ambrosia arborescens* Mill. (1768), an error which may be based on the fact that *A. arborescens* Mill. is synonymous with *Franseria artemisioides* Willd. (1805) and there is, as a result, confusion between the epithets "artemisioides" and "ambrosioides."

Hemiambrosia Delpino, Studi Lign. Anem. Comp. Artem. 16. 1871. Type species: *H. heterocephala* Delp. *Ibid.*, nomen illeg., *Ambrosia pumila* (Nutt.) Gray 1882.

Hemixanthidium Delpino, *Ibid.* 17. Type species: *H. paradoxum* Delp. *Ibid.*, nomen illeg., *Ambrosia acanthicarpa* Hook. 1834.

Xanthidium Delpino, *Ibid.* 17. Type species: *X. tenuifolium* Delp. *Ibid.*, nomen illeg., *Ambrosia confertiflora* DC. 1836.

Acanthambrosia Rydberg, N. Am. Fl. 33: 22. 1922. Type species: *A. bryantii* (Curran) Rydb., nomen illeg., *Franseria bryantii* Curran, 1888.

The genus *Ambrosia*, in the new sense, may be characterized briefly as follows: Shrubs or subshrubs to perennial herbs spreading by means of stem and (or) root proliferations, or strictly annual herbs. Entire plant glandular, aromatic with resinous odor, glandular trichomes (colleters) biseriate, sessile or long-stalked. Leaves diverse (often with considerable intraspecific variation), pinnately lobed or dissected, palmately lobed or unlobed, petiolate or sessile. Anemophilous; staminate and pistillate florets in distinct heads normally borne on the same plant. Staminate heads stalked to subsessile or sessile, borne in usually aphyllous, spicate or racemose clusters at the tips of stems and branches, the phyllaries laterally connate and forming a broadly funnel-shaped to cupulate or saucer-shaped involucre with the phyllary tips more or less prominent as marginal lobes; receptacle paleaceous, pales various; many to several flowered. Staminate florets modified: calyx or pappus lacking; corolla hyaline, campanulate, 5-lobed (rarely 4-lobed), only comissural veins present; stamens 5, alternating with corolla lobes, filaments sometimes connivent, anthers without "tails," weakly connivent, sometimes separating during pollen discharge, terminal appendages deltoid to long-attenuate; pistil reduced (pistillodium), ovary lacking, style short, truncate (stigmatic lobes lacking) with terminal, circular "brush" of hairs (penicillate). Pollen subglobose, echinate, the spines short, 3-pored (rarely 2–6-pored) with bladder-like air chambers developed within the exine between the pores. Pistillate heads borne in sessile or stalked clusters in axils of leaves subtending staminate racemes or spikes; bases of phyllaries fused to form a hard, vase shaped conceptacle; phyllary tips forming more or less spiny processes, straight or uncinate, flattened or terete, strongly emergent or vestigial, rarely lacking, variously arranged or scattered over surface of

fruiting involucre; without pales; florets few (6–7) to one, if more than one, interior of fruiting involucre compartmentalized, each floret in a separate chamber. Pistillate florets reduced: perianth lacking; androecium lacking; mature ovary obovate, base somewhat oblique, abruptly rounded to base of short style; stigmatic lobes elongate, linear, spreading, inner stigmatic surface minutely papillose, exserted through spine-like beaks at apex of involucre, several-flowered involucres usually with distinct beak for each stigma but occasionally with a communal beak.

Basic chromosome number, $x = 18$, the majority of species diploid but outbreeding populations of tetraploids, hexaploids, and octoploids known, in some instances within what are here considered single species; two aneuploid derivatives known, *A. bidentata* ($n = 17$), *A. trifida* ($n = 12$).

Predominantly New World, mostly North American, including species of arid and semi-arid habitats and weedy species of ruderal sites.

Virtually all species exhibit extreme morphological variability. In numerous instances variants which appear to be within the natural limits of variation for given species have received separate names. Measurements cited in the species descriptions which follow are usually given as maxima found in non-teratological specimens from populations growing under favorable conditions.

1. **Ambrosia acanthicarpa** Hook. Fl. Bor. Am. 1: 309. 1834. Type: Banks of the Saskatchewan and Red River; *Douglas* (probably in K but not seen). NOTE: Although I have not seen the type, Douglas' description leaves no doubt of its identity. Among other characters Douglas refers to the bipinnatifid leaves and the "singularly spinescent fruits," the fruit spines being long, rigid and subulate. No other species from the northwestern United States displays this combination of characteristics.

Franseria montana Nutt. Trans. Am. Phil. Soc. ser. 2. **7**: 345. 1840. Type: In Rocky Mountains, near the Colorado of the West, *Nuttall* (possibly in BM [not seen] or PH!; isotype, GH!).

Franseria hookeriana Nutt. *Ibid.* Type: Based upon *Ambrosia acanthicarpa* Hook.

Hemixanthidium paradoxum Delp. Studi Lign. Anem. Comp. Artem. 17, 1871. Type: Based upon *Franseria montana* Nutt.

Gaertnera hookeriana (Nutt.) Kuntze, Rev. Gen. Pl. **1**: 339. 1891.

Franseria acanthicarpa (Hook.) Cov. Contr. U.S. Nat. Herb. **4**: 129. 1893.

Gaertnera acanthicarpa (Hook.) Britt. Mem. Torrey Club **5**: 332. 1894.

Franseria californica Gandoger, Bull. Soc. Bot. Fr. **65**: 54. 1918, non *Ambrosia californica* Rydb. 1922. Type: California, ad San Bernardino, *Parish*, October, 1893 (US!).

Franseria palmeri Rydb. N. Am. Fl. **33**: 25. 1922. Type: California, San Diego, *Dr. E. Palmer*, 1875 (US!).

Erect, annual herb, to 15 dm. high, becoming much branched. Leaves opposite below, alternate above, petiolate, petioles to 6 cm. long, laminar tissue narrowly decurrent to base. Lamina extremely variable, broadly

deltoid to narrowly lanceolate; to ca. 8 cm. long and 6 cm. broad, pinnately to tripinnately lobed, lobes from narrowly linear to subovate and abruptly acute; both surfaces green, sparsely tomentulose to strigose or hispid-scabrous. Inflorescence racemose-spicate. Staminate involucres stalked, stalks to 15 mm. long, usually shorter, 3–12 mm. broad, 3–9-lobed, lobes shallow to well-defined with sinuses separating lobes reaching halfway or more to point of stalk attachment, upper surface of three distal lobes usually marked with heavy, black striations along midveins. Fruiting involucres in sessile clusters below staminate racemes, to 10 mm. long and 14 mm. wide, 1-flowered; spines to 30, flattened, linear to lanceolate, sharply pointed, to 8 mm. long, scattered, occasionally vestigial or lacking. Haploid chromosome number, $n = 18$.

Flowering: June to December.

Range: Prairie and semi-arid regions of the western United States, from the Dakotas, Nebraska and Kansas, west to New Mexico, Arizona, California, Washington and Oregon. Adventive in eastern Minnesota.

Notes: As here circumscribed, this is one of the most heteromorphic of the ragweeds. Most segregates have been delimited on the basis of leaf and fruit spine differences which do not appear at present to be sufficiently correlated to permit recognition of distinct taxa within the complex.

2. **Ambrosia acuminata** (Brandeg.) Payne, comb. nov. PLATE I

Franseria acuminata Brandeg. Proc. Calif. Acad. ser. 2. 2: 171. 1889. Type: Mexico, Lower California, Purísima [Purissima]. *T. S. Brandegee*, February 11, 1889 (UC, no. 88798; NY, photograph!; isotype, US! no. 47364).

Erect shrub, probably over 3 dm. high. Leaves alternate, petiolate, petiole to 18 mm., laminar tissue narrowly decurrent to base, usually with one or more pairs of small lobes below the main laminar region. Lamina lanceolate to ovate-deltoid in outline; to 8 cm. long, pinnately lobed, somewhat irregular, rachis of the lamina broad above first sinus, terminal lobe large, attenuated and comprising major portion of blade. Staminate involucre stalked, stalks to 5 mm. long, lowermost stalks sometimes bearing more than one head, involucre to 3 mm. broad, cupulate; marginal lobes 3–7, shallow. Fruiting involucre to 6 mm. long and 3 mm. broad, 2-flowered; spines few (ca. 4–8), less than 1 mm. long, uncinate, appressed, scattered. Chromosome number unknown.

Flowering: February.

Range: Baja California, Mexico, known only from the type specimen.

3. **Ambrosia ambrosioides** (Cav.) Payne, comb. nov. PLATE I

Franseria ambrosioides Cav. Ic. Descr. Pl. 2: 79. 1793. Type: Not seen, probably at MA. The description of this species is based upon material cultivated at the Royal Bot. Gard., Madrid, and represented by Plate 200, Cav., loc. cit. This plate is very well done and, in view of the unusual morphology of this species, leaves no question as to the identity of the taxon.

Xanthidium ambrosioides (Cav.) Delp. Studi Lign. Anem. Comp. Artem. 18. 1871.

Gaertnera ambrosiodes (Cav.) Kuntze, Rev. Gen. Pl. 1: 339. 1891.

Erect shrub, to 25 dm. high. Leaves alternate, petiolate, petiole to 8 cm. long, usually without obvious decurrent tissue from the lamina. Lamina lanceolate-attenuate (rarely to ovate) 2–18 cm. long or longer, 1–6 cm. wide, unlobed or with marginal teeth developed as weak lobes, both surfaces bright green, tomentose, glandular, sticky when fresh with a strongly resinous odor. Inflorescence racemose, usually much branched below. Staminate involucres stalked, stalks to 14 mm., the lower often bearing more than one head; involucre to 8 mm. broad, lobes 7–12, teeth prominent, sinuses extending 1/3–1/2 way to point of stalk attachment, midveins of lobes darkened upon drying, occasionally marked with obscure striations on upper surface. Fruiting involucre to 15 mm. long and 12 mm. broad, florets 3–5; spines numerous, usually more than 30, scattered thickly over surface of involucre, slender, uncinate, 2–4 mm. long; mature involucres closely resembling those of *Xanthium,* the cocklebur. Haploid chromosome number, $n = 18$.

Flowering: February to May.

Range: Sonoran Desert region, common through southern Arizona, extending into San Diego County, California, and to Sonora and Baja California, Mexico; rare in the Mexican states of Sinaloa and Coahuila.

Notes: The type species of *Franseria*, as mentioned earlier, was erroneously synonymized with *A. arborescens* Mill. in the *International Code of Botanical Nomenclature,* Reg. Veg. **23:** 318. 1961, probably through equation with *F. artemisioides* Willd. which is synonymous with *A. arborescens* Mill.

4. **Ambrosia arborescens** Mill. Gard. Dict. ed. 8. 1768, non *Franseria arborescens* Brandeg. 1903. Lectotype: Garden specimen from Philip Miller collections (BM; photograph MICH!, BH, negative no. 5274). PLATE II

Ambrosia fruticosa Medic. Hist. Comment. Acad. Elect., Theodoro-Palatinae 3: 244. 1775, non *Ambrosia fruticosa* DC. 1836, nec *Franseria fruticosa* Phil. 1891. Type: not designated. NOTE: Medicus' Plate 20 provides a very good illustration of this species, which, together with the description, in which the species is equated with *A. arborescens* Mill., leaves no question as to the identity of the taxon.

Xanthium fruticosum L.f. Suppl. Plant. Syst. Veg. 418. 1781. Type: Based upon *A. arborescens* Mill. NOTE: This name change was apparently made because of the somewhat *Xanthium*-like fruiting involucres of the species and the seeming impossibility of including a plant with such fruits in *Ambrosia* as delimited at that time.

Ambrosia frutescens Lam. Encyc. Meth. 1: 128. 1783, *in synon.*

Franseria artemisioides Willd., Linn. Sp. Pl. ed. 4. 4: 378. 1805, non *Ambrosia artemisioides* Meyen & Walp. ex Meyen, 1843. Type: Based upon *Xanthium fruticosum* L.f. and upon *Ambrosia arborescens* Mill. as described by

Lamarck (loc. cit.). NOTE: A tracing of material of this species from the Willdenow collections (B) was made by F. W. Klatt before 1898 and is now in GH!.

Xanthidium artemisioides (Willd.) Delp. Studi Lign. Anem. Comp. Artem. 18. 1871.

Gaertnera artemisiodes (Willd.) Kuntze, Rev. Gen. Pl. 1: 339. 1891.

Franseria conwayi Rusby, Bull. N.Y. Bot. Gard. 8: 130. 1912. Type: Bolivia, Santa Cruz, *R. S. Williams 1464*, Aug. 25, 1902 (NY!).

Erect shrub, to 40 dm. high. Leaves alternate, petiolate, petioles to 10 cm. long, laminar tissue decurrent to base, several small lobes usually formed below main lamina. Lamina ovate-lanceolate to broadly ovate, deltoid or nearly orbicular in outline, to 20 cm. long and 24 cm. wide, bi- or tripinnately lobed, the second or third order lobes intergrading with the laciniate-serrate marginal teeth; upper surface green, puberulous to glabrate, lower surface gray-green, woolly-tomentose. Inflorescence paniculate-racemose, lower staminate stalks often with several heads. Staminate involucre stalked, stalk to 10 mm., often much shorter, involucre to 6 mm. broad, 5–9-lobed, sinuses between lobes often extending more than ½ way to point of stalk attachment; veins on upper surface of lobes darkened, sometimes with black striations near tips. Fruiting involucres in often massive, sessile clusters below the staminate heads, 5–8 mm. long, 4–7 mm. broad, body thick and heavy, often nearly black, (1)2–4-flowered, stigmas discharged through a communal beak or through poorly defined distinct beaks; spines 12–20, scattered over surface, 1–3 mm. long, bases thick, abruptly narrowed to slender, uncinate tips, somewhat appressed. Chromosome number unknown.

Flowering: Throughout year.

Range: Interandean plains of Ecuador, north to north-central Colombia, south through Peru to western Bolivia.

Notes: A variable species in regard to habit, leaf size, and morphology. *Franseria conwayi* appears to be based upon a specimen with aberrant leaves. *Ambrosia arborescens* is apparently a plant well known to the inhabitants of the regions in which it occurs (colloquial name "Altimisa," sometimes erroneously transliterated to "Artemisia"). Notes of W. H. Camp (specimens *E-2498* and *E-5030,* NY) contain the following remarks " 'it is good to sweep out a house which has too many fleas' . . . it seems to be the only thing used to sweep out ovens after heating and before the bread is put inside. It is sold on the Cuenca [Ecuador] market for this purpose . . . Used as a local application in skin infections." This widespread use may explain arrival of the species in Europe early enough to be included in Miller's *Gardeners Dictionary*.

5. **Ambrosia artemisioides** Meyen & Walp. ex Meyen, Nov. Act. Acad. Caes. Leopold. Carol. 19 (suppl. 1, Nat. Cur., Obs. Bot.): 268. 1843, non *Franseria artemisioides* Willd. 1805, nec *Xanthidium artemisioides* (Willd.) Delp. 1871, nec *Gaertnera artemisiodes* (Willd.) Kuntze, 1891. Neotype: Peru, Tacna, Maisin, in glareosis joropi, *Lechler*

1568, in 1854 (NY!; duplicate in GH). NOTE: The Meyen and Walpers material upon which this taxon was based (Peru: in planitie circa Tacoram, alt. 14–17,000 ped.) was presumably destroyed in Berlin during World War II. Their description is, however, diagnostic "Plant shrubby, erect, pilose, branched; all leaves narrowly linearly pinnatifid, lobes obtuse, entire to pinnately incised, scarcely puberulent, . . . rachis . . . barely 1/2 a line wide, roundish . . . ; fruiting involucre spiny, spines uncinate; stem . . . strongly glutinous." The fact that Hohenacker evidently examined their material in Berlin and equated it with the Lechler specimen which is the type for the following synonym, provides a basis for acceptance of Meyen's name for this species and for the selection of Lechler's specimen as the neotype. PLATE I

Franseria meyeniana Sch. Bip. ex Hohenacker, Bonplandia **4**: 54. 1856. Type: *Lechler 1568* (as above) (W, not seen; isotypes GH, NY!).

Franseria fruticosa Phil. Anal. Mus. Nac. Chile, seg. secc. Botanica. 50. 1891, non *Ambrosia fruticosa* Medic. 1775, nec *Xanthium fruticosum* L.f. 1781, nec *Ambrosia fruticosa* DC. 1836. Type: Chile, Tarapaca, *Philippi*, 1888 (B, not seen; photograph, GH!).

Gaertnera meyeniana (Sch. Bip.) Kuntze, Rev. Gen. Pl. **1**: 339. 1891.

Franseria recurva Rusby, Bull. N.Y. Bot. Gard. **8**: 131. 1912. Type: Peru, Arequipa, 7500 ft., *Rusby 2527*, Aug. 8, 1901 (NY!; isotype US! no. 1098696).

Erect shrub, becoming much branched, new growth stem tending to be brown-black, glutinous, somewhat pilose, bark of older stem gray, lacking pubescence. Leaves alternate, petiolate, petioles to 4 cm. long (usually much shorter) laminar tissue decurrent to base. Lamina ovate in outline to 4 cm. long and 3 cm. wide, irregularly bipinnately lobed, lobes linear; both surfaces green, sparingly puberulent to glabrate, minutely glandular. Inflorescence racemose-spicate. Staminate involucre stalked, stalks to 8 mm. long, occasionally more than one head borne on lower stalks, involucre to 5 mm. broad, 7–12-lobed, lobes often marked with black striations along midveins, sinuses separating lobes extending ca. 1/2 way to point of stalk attachment. Fruiting involucres in small axillary clusters below staminate capitula, 4–6 mm. long, 2–3 mm. wide, 1(?)-fruited; spines to 20, scattered, slender, uncinate, to 2.5 mm. long, easily broken from body. Chromosome number unknown.

Flowering: March to August.

Range: Southern Peru (Arequipa province) to northern Chile (Tarapaca province).

Notes: I have seen only six specimens of this species, including the types, and these display considerable leaf variation, tending to merge with what seems to be an undescribed species of the same area with larger, more broadly lobed leaves, larger staminate heads and fruiting involucres of quite different morphology, viz. *F. W. Pennell 13107* (NY), *Mr. & Mrs. F. E. Hinkley 79* (NY). The spines of the fruiting involucre of *A. artemi-*

sioides appear to be easily broken from the body at an abscission zone, a characteristic unknown elsewhere in the genus.

6. **Ambrosia bryantii** (Curran) Payne, Madroño **16**: 234. 1962. *Franseria bryantii* Curran, Proc. Calif. Acad. ser. 2, **1**: 232. 1888. Type: Mexico, Baja California, Magdalena Bay, Santa Margarita Island, *Walter E. Bryant,* in 1888 (CAS, not seen; isotype, UC). NOTE: Although I have not examined the type material of this species, Dr. Elizabeth McClintock (CAS) and Miss Annetta Carter (UC) have kindly verified its nature and location. Both of the specimens cited probably comprise the original holotype and they have been labelled respectively "part of the type" and "part of type" by Mrs. Curran who, at the time *Franseria bryantii* was published, was the editor of the *Proceedings,* and a member of the staff of the California Academy of Sciences. It is assumed that the material was divided and incorporated into the T. S. Brandegee collections at the University of California after Mrs. Curran's marriage to Brandegee. It is, therefore, appropriate to consider the CAS material as the holotype.

Acanthambrosia bryantii (Curran) Rydb. N. Am. Fl. **33**: 22. 1922.

Erect shrub, reaching ca. 8 dm. Leaves alternate, petiolate, petioles to 3 cm. long, laminar tissue decurrent to base, usually forming several small lobes below main laminar region. Lamina ovate in outline, to 8 cm. long and 6 cm. broad, irregularly bi- to tripinnately lobed, lobes linear; both surfaces green, lower becoming lighter, nearly glabrous to sparsely hispidulous. Inflorescence racemose-spicate. Staminate involucres subsessile to stalked, stalks to 2 mm. long; involucre to 7 mm. broad, 8–12-lobed, lobes shallow, not noticeably striate. Body of fruiting involucre to 10 mm. long and 5 mm. broad, 2–7-flowered, the stigmas discharged through a common beak; spines 5–9, chalk-white, 12–40 mm. long, sharp, clustered near apex of involucre body. Haploid chromosome number, $n = 18$.

Flowering: February to April.

Range: Central to southern Baja California, Mexico.

Notes: A species remarkable for the long, thorny spines of the fruiting involucre, and for retention of a percentage of the fruiting involucres to function as armature through several growing seasons. Segregated in the monotypic genus *Acanthambrosia* by Rydberg because of the discharge of the stigmatic lobes of all contained florets through the single beak, a phenomenon also displayed by other species.

7. **Ambrosia camphorata** (Greene) Payne, comb. nov. PLATE III

Franseria hispida Benth. in Hinds, Bot. Voy. Sulphur, 25. 1844, non *Ambrosia hispida* Pursh, 1814. Type: Mexico, Lower California, Magdalena Bay, Barclay (K, not seen; ARIZ! photograph; GH! drawing of type by Smith, July 4, 1919).

Franseria bipinnatifida sensu Gray ex Wats. Proc. Am. Acad. **11**: 115. 1876, non *Franseria bipinnatifida* Nutt. 1840, nec *Ambrosia bipinnatifida* (Nutt.)

Greene, 1894. Mexico, Baja California, Guadalupe Island, *E. Palmer 40*, in 1875 (NY!; PH!).

Franseria camphorata Greene, Bull. Calif. Acad. **4**: 192. 1886. Type: Mexico, Lower California, Guadalupe Island, *E. L. Greene*, April 24, 1885 (CAS, not seen; isotype, NY!).

Franseria camphorata var. *leptophylla* Gray, Proc. Am. Acad. **22**: 309. 1887. Type: Mexico, Lower California, near San Fernando, *C. R. Orcutt 1352*, May 4, 1886 (US!).

Gaertnera hispida (Benth.) Kuntze, Rev. Gen. Pl. **1**: 339. 1891. NOTE: Kuntze credits the original name to "Barcl.," a misconception probably resulting from the fact that the type of *F. hispida* Benth., collected by Barclay, is labelled "*Franseria hispida* sp. n. Barclay."

Franseria leptophylla (Gray) Rydb. N. Am. Fl. **33**: 32. 1922.

Erect shrub, becoming much branched from the base; to 6 dm. tall; glandular throughout, viscid-sticky when fresh, with strongly resinous odor. Leaves alternate, petiolate, petioles to 10 cm. long, usually shorter, laminar tissue decurrent to base, usually with several medium to small pairs of lateral lobes below main laminar region. Lamina deltoid-lanceolate to ovate or lanceolate in outline, to 10 cm. long and broad, irregularly bi- or tripinnately lobed, lobes various; upper surface gray-green to green, minutely glandular, sparingly puberulent to glabrate, lower surface gray-green to white woolly-tomentose. Inflorescence racemose-spicate. Staminate involucres stalked, stalks to 5 mm. long, involucre to 7 mm. broad 7–12-lobed, upper surface of lobes often marked with obscure striations, sinuses separating lobes extending approximately halfway to point of stalk attachment. Fruiting involucres variable, 1–7-flowered, 5–10 mm. long, 3–11 mm. broad; spines 3–15 (rarely none), terete, variously arranged or scattered, strongly emergent to vestigial. Haploid chromosome number, $n = 36$.

Flowering: September to May.

Range: Throughout Baja California, sporadic in western Sonora and southern San Luis Potosi, Mexico.

Notes: An extremely variable species, especially in regard to fruiting involucre morphology; possibly an aggregate or with several intergraded varieties, needing further study.

8. **Ambrosia canescens** Gray, Proc. Am. Acad. **17**: 217. 1882. Type: Mexico, Aguas Calientes, In arvis communis, *Hartweg 121*, in 1839 (K; photograph MICH!, Kew negative number 715, 715 A; isotypes, GH, NY!). PLATE IV

Ambrosia fruticosa var. *canescens* Benth. Pl. Hartweg. 17. 1839, nomen nudum.
Franseria canescens (Gray) Rydb. N. Am. Fl. **33**: 27. 1922.

Erect perennial herb, perennating by means of shoots from roots. Leaves alternate, petiolate, petioles 1–5 cm. long, laminar tissue decurrent to base, often with 1 or more reduced pairs of lobes below main laminar region. Lamina broadly ovate to lanceolate in outline, to 8 cm. long and 6 cm. wide, finely bi-, tri- or tetrapinnately lobed; both surfaces gray-canescent.

Inflorescence racemose-spicate. Staminate involucre stalked, stalks to 3 mm. long, involucre 3–6 mm. in diameter, 5–10-lobed, the sinuses shallow. Fruiting involucres 1-fruited, 3–6 mm. long, 2–5 mm. broad; spines 0–10, strongly emergent (to 2 mm. long) to vestigial, usually flattened, occasionally uncinate, variously scattered or grouped over surface. Haploid chromosome number, $n = 18$.

Flowering: April to October.

Range: East-central Mexico, from San Luis Potosi to Durango, south to Aguascalientes. Also reported from Chihuahua (*C. G. Pringle 1284*, GH, NY) and Arizona (*H. H. Rusby 680*, NY).

Notes: A species of considerable variability, appearing to intergrade somewhat with *A. confertiflora* in the eastern portion of its range.

9. **Ambrosia carduacea** (Greene) Payne, comb. nov. PLATE II

Franseria arborescens Brandeg. Zöe **5**: 162. 1903, non *Ambrosia arborescens* Mill. 1768. Type: Mexico, Baja California, Ascension, *T. S. Brandegee*, April 18, 1889 (UC, no. 88767, not seen; type photograph, NY!). NOTE: Specimens commonly identified with this name.

Franseria carduacea Greene, Leaflets Bot. Obs. Crit. **2**: 156. 1912. Type: Mexico, Lower California, Aquaje de Santana, 35 miles N. of San Ignacio, alt. 3400 ft., *E. W. Nelson & E. A. Goldman 7187*, October 4, 1905 (US! no. 565273; photograph, NY!).

Franseria sanctae-gertrudis Rydb. N. Am. Fl. **33**: 35. 1922. Type: Mexico, Baja California, rocky slopes, Santa Gertrudis, alt. 6–700 ft., *C. A. Purpus 116*, January–March, 1898 (US! no. 383387; photograph, NY!).

Franseria acerifolia M. E. Jones, Contrib. West. Bot. **18**: 78. 1935. Syntypes: Mexico, Lower California, Arroyo Undo Ranch, Loreto, *Marcus E. Jones 27764*, October 26, 1930 (NY!); Cayuca Ranch, Loreto, *M. E. Jones 27765*, October 23, 1930 (US! no. 1589558).

Erect shrub to 30 dm. high or higher. Leaves alternate, petiolate, petioles to 3 cm. long, without obvious decurrent laminar tissue. Lamina ovate-lanceolate to lanceolate in outline, nearly unlobed to pinnately lobed, leaf segments broad, marginal teeth often forming weak secondary lobes; upper surface green, strigose to hispid-scabrous, lower surface lighter, to densely tomentose. Inflorescence racemose-paniculate. Staminate involucre stalked, stalks to 10 mm., the lower often bearing more than one head, involucre to 5 mm. broad, 5–9-lobed, lobes with darkened veins on upper surface but rarely with obvious striations, sinuses separating lobes extending halfway or more to point of stalk attachment. Fruiting involucres 6–10 mm. long, 3–5 mm. wide, 2-flowered; spines 6–12, somewhat flattened, usually uncinate, less than 3 mm. long, scattered over surface of body. Chromosome number unknown.

Flowering: December to March, possibly throughout year.

Range: Central to southern Baja California, Mexico.

Notes: A species with considerable leaf variation, the synonymous taxa being distinguished primarily on this basis. Another complex requiring further study.

10. **Ambrosia chamissonis** (Less.) Greene, Man. Bot. Reg. San Francisco Bay 188. 1894. PLATE V

Franseria chamissonis Less. Linnaea **6**: 507. 1831. Type: California, *Cel. de Chamisso* (probably in LE, not seen). NOTE: Plants so named by Lessing were collected on a Russian expedition ("Expeditione Romanzoffiana") to California in the 1820's. Although I have not seen the types, Lessing's detailed description leaves no question as to the identity of the plants included. Among the plants collected by Chamisso, Lessing recognized two varieties, var. *malvaefolia* and var. *bipinnatisecta*, characterized respectively by unlobed and bipinnately lobed leaves (one specimen was noted to have leaves of *malvaefolia* below and *bipinnatisecta* above). Much of the nomenclatural confusion, indicated by the numerous synonyms which follow, has resulted from attempts to distinguish these and other leaf forms within the complex.

Franseria bipinnatifida Nutt. Trans. Am. Phil. Soc. ser. 2. **7**: 344. 1840. Type: California, *Nuttall*, in 1835 (?) labeled with an unpublished name (PH!). It is possible that this is an isotype and that the holotype is at BM. NOTE: A sheet labeled "*Franseria bipinnatifida* Nutt." from the Nuttall collections in PH bears three specimens. Two of these, *C. G. Pringle*, April 27, 1882, and *E. Palmer 40*, 1875 (see synonymy of *A. camphorata*) were collected after Nuttall's death and could not have figured in his concept. The third is labeled, by Nuttall, with an unpublished name indicating the decumbent habit. However, it may be that this specimen was at hand when Nuttall described *F. bipinnatifida*, as the description states (loc. cit.): "perennial, herbaceous, decumbent and diffusely branched." Nuttall then equated the species with *F. chamissonis β bipinnatisecta* Less., and described the habit (which is unusual in this species) and morphological features in such a way as to leave no doubt that he was, in fact, dealing with the bipinnatisect form of *A. chamissonis* as recognized here, and that he had seen and examined it in the field, along the Pacific Coast of California.

Franseria cuneifolia Nutt. *Ibid.* 345. Type: Oregon (?), Columbia estuary, *Nuttall*, in 1835 (?) (possibly in BM [not seen] or PH!).

Franseria chamissonis var. *cuneifolia* (Nutt.) Torr. & Gray, Fl. N. Am. **2**: 293. 1842.

Franseria lessingii Meyen & Walp. ex Meyen, Nov. Act. Acad. Caes. Leopold. Carol. **19** (suppl. 1, Nat. Cur., Obs. Bot.): 267. 1843. Type: This is a newly proposed name for the bipinnatifid form of *F. chamissonis*, possibly based upon isotypic material for var. *bipinnatisectis* in the herbarium at Berlin, examined by Meyen and Walpers.

Gaertnera chamissonis (Less.) Kuntze, Rev. Gen. Pl. **1**: 339. 1891.

Ambrosia bipinnatifida (Nutt.) Greene, Man. Bot. Reg. San Francisco Bay 187. 1894.

Franseria bipinnatifida var. *dubia* Eastw. Proc. Cal. Acad. ser. 3. **1**: 117. 1898. Type: California, Ventura County, San Nicolas Island, *Mrs. Blanche Trask*, April, 1897 (CAS, not seen). NOTE: Although I have not seen this specimen, the type material has been verified by Dr. Elizabeth McClintock. Material from the same collector and locality serves to typify the following synonym.

Franseria chamissonis var. *viscida* Eastw. *Ibid.* Type: See preceding note.

Gaertneria bipinnatifida dubia (Eastw.) Heller, Muhlenbergia **1**: 6. 1900.

Gaertneria chamissonis viscida (Eastw.) Heller, *ibid.*

Franseria bipinnatifida var. *insularis* Reiche, Anal. Univ. Chile **112**: 131. 1903. Type: Chile, Isla de la Mocha, en la playa del NE, *Karl Reiche*, in 1892. I have not located this type. NOTE: Distinguished from typical *F. bipinnatifida* Nutt., according to Reiche, principally on the basis of pubescence differences. Reiche notes that the plant is "*probablemente introducida*."

Franseria bipinnatifida villosa Eastw. ex Rydb. N. Am. Fl. **33**: 26. 1922, *in synon.*

Franseria villosa (Eastw.) Rydb. *Ibid.* Type: California, Mendocino County, near Mendocino, *H. E. Brown 843*, June, 1898 (NY! isotype, US! no. 343666).

Franseria chamissonis subsp. *typica* Wigg. & Stockw. Madroño **4**: 120. 1937. Type: Based on *F. chamissonis* var. *malvaefolia* Less.

Franseria chamissonis subsp. *bipinnatisecta* Wigg. & Stockw. *Ibid.* Type: Based on *F. chamissonis* var. *bipinnatisecta* Less.

Erect, decumbent or trailing subshrub, becoming very large since stems and leaves trap sand and continue growth by emergent branch tips. Leaves alternate, petiolate, petioles to 8 cm. long, usually shorter, laminar tissue decurrent to base. Lamina broadly ovate to lanceolate in outline, lobing extremely variable, from unlobed to tripinnately lobed; both surfaces gray-green, silky canescent. Inflorescence racemose. Staminate involucres stalked, stalks to 5 mm. long; involucre 3–8 mm. broad, 7–15-lobed, the sinuses shallow, upper surface of lobes often marked with black striations along veins. Fruiting involucres clustered in often heavy masses below staminate racemes, 6–12 mm. long and 3–9 mm. broad; spines 9–20, to 3 mm. long, terete or flattened above, strongly emergent, sharply pointed, scattered over involucre surface. Haploid chromosome number, $n = 18$.

Flowering: Throughout year.

Range: Along Pacific coast of North America from Vancouver Island, British Columbia to Baja California, Mexico. Adventive along South American coast.

Notes: The variability of this species, especially in regard to leaf morphology, has led to considerable taxonomic confusion, as is evident from the synonymy. The basic problem is that two very different leaf forms are found, one unlobed and one pinnately dissected. As Eastwood (op. cit., p. 117) remarked concerning these, "They are most puzzling to the systematist who endeavors to make boundary lines, because they not only appear to run into each other but each is variable even in regard to what are supposed to be its own individual characteristics. Especially this is true as regards foliage, pubescence and size of the heads." Within what must be considered "normal" populations in every locality in which the species exists in abundance, one encounters both extremes as well as all intermediate forms. I have raised self-pollination progeny of the extremes and of intermediates in the greenhouse and it appears that any form is capable of giving rise to any other form. At the same time, however, there may be regional tendencies which need further investigation. Certainly the forces acting to maintain the observed variability, within what must be regarded as a stable and specialized site preference, are very subtle indeed.

11. **Ambrosia chenopodiifolia** (Benth.) Payne, comb. nov. PLATE IV

Franseria chenopodiifolia Benth. in Hinds, Bot. Voy. Sulphur 26. 1844. Type: Mexico, Baja California, Bay of Magdalena, *Barclay* (K, not seen; photograph, GH).

Gaertneria chenopodiifolia Abrams, Bull. N.Y. Bot. Gard. **6**: 461. 1910.

Franseria lancifolia Rydb. N. Am. Fl. **33**: 36. 1922. Type: Mexico, Baja California, Cedros Island, *A. W. Anthony 290*, March–June, 1897, (US! no. 313846; photograph, NY!).

Erect shrub, becoming much branched at base, to 35 dm. high. Leaves alternate, petiolate, petioles to 6 cm. long, laminar tissue decurrent to base. Lamina ovate-lanceolate to broadly ovate in outline, to 10 cm. long and 3-nerved, tending to become trilobed, lobes weak, sinuses shallow, rarely somewhat pinnately lobed; both surfaces glandular and pubescent, upper gray-green, tomentose, lower becoming white-tomentose. Inflorescence racemose-spicate, becoming paniculate. Staminate involucre stalked, stalks to 8 mm. long, occasionally with more than one head borne on lower stalks; involucre to 6 mm. broad, 5–10-lobed, sinuses between lobes shallow and often irregular, lobes occasionally marked with brownish to black striations on upper surface. Fruiting involucres clustered on lower inflorescence branches, to 7 mm. long and broad, 2–3-fruited, the body usually thickly clothed with woolly white tomentum from which spines and beaks emerge; spines 12–25, slender, uncinate, to 3 mm. long, scattered over surface of involucre. Haploid chromosome number, $n = 36$.

Flowering: January to June.

Range: Baja California, Mexico, from Comondu north into San Diego Co., California.

Notes: This species is very similar in aspect, habit, and leaf morphology to *A. deltoidea,* a species with which it undoubtedly has close affinity. Ordinarily the two can be distinguished at least on the basis of the characters of the fruiting involucre. *A. chenopodiifolia* is characterized by woolly tomentose involucre bodies with terete, uncinate spines and *A. deltoidea* is characterized by non-woolly involucres with flattened, straight spines (see PLATE IV). However, intermediate specimens with woolly involucre bodies and straight spines or with uncinate spines and non-woolly bodies are frequent. This complex needs further study.

12. **Ambrosia confertiflora** DC. Prodr. **5**: 526. 1836. Type: Mexico, Matamoros, *Berlandier 2297,* October, 1830 (G, not seen; photograph from Hb. Delessert, series 33702, GH, MICH!). PLATE V

Ambrosia fruticosa DC. *Ibid.* 525, non *Ambrosia fruticosa* Medic. 1775, nec *Xanthium fruticosum* L.f. 1781, nec *Franseria fruticosa* Phil. 1891. Type: Mexico, Tamaulipas, circa Reynosa, *Berlandier 2112*, April, 1830 (G, not seen; photograph from Hb. Delessert, series 33700, GH, MICH!; isotypes, NY!, GH!).

Franseria tenuifolia Harv. & Gray in Gray, Pl. Fendl. in Mem. Am. Acad. ser. 2. **4**: 80. 1849, non *Ambrosia tenuifolia* Spreng. 1826. Type: California,

Poñi Creek, between Bent's Fort and Sante Fé, *Fendler 406* (not seen). NOTE: Although I have been unable to locate this type, the original description applies to *A. confertiflora* as defined here. Also, see discussion for *F. tenuifolia* var. *tripinnatifida* below.

Franseria tenuifolia var. *tripinnatifida* Gray, Pl. Lindheim. 2. *in* Boston Jour. Nat. Hist. **6**: 227. 1850. Type: Texas, Mountain prairies of the Liano [Llano], *Lindheimer 640* (not seen). NOTE: I have been unable to locate this type, but the description fits *A. confertiflora*, and a specimen labeled *F. tenuifolia* var. *tripinnatifida* by Gray (New Mexico, *C. Wright 1210*, 1851. NY!) is *A. confertiflora*. Also, isotypes of *A. fruticosa* DC. (*Berlandier 2112*, GH!, NY!) have been annotated by Gray, leaving little question as to the identity of this taxon.

Xanthidium tenuifolium Delp. Studi. Lign. Anem. Comp. Artem. 17. 1871. Type: Based upon *Franseria tenuifolia* Harv. & Gray.

Gaertnera tenuifolia (Gray) Kuntze. Rev. Gen. Pl. **1**: 339. 1891.

Franseria confertiflora (DC.) Rydb. N. Am. Fl. **33**: 28. 1922.

Franseria caudata Rydb. *Ibid.* 29. Type: New Mexico, Lincoln County, Gray, *Josephine Skehan 108*, September 1, 1898 (NY!; isotypes, NY!, US!).

Franseria hispidissima Rydb. *Ibid.* Type: Mexico, Zacatecas, Real de Pinos, *Leon Diquet* (NY!).

Franseria incana Rydb. *Ibid.* 30. Type: Arizona, Ft. Huachuca, *Dr. T. E. Wilcox*, Sept. 1892 (NY!; isotype, NY!).

Franseria strigulosa Rydb. *Ibid.* 28. Type: California, Los Angeles County, *L. T. Chamberlain*, Sept. (NY!).

Franseria pringlei Rydb. *Ibid.* Type: Mexico, Coahuila, Valley Jimulco, *C. G. Pringle 192*, May 17, 1885 (NY!; isotype, US!).

Ambrosia simulans Shinners, Field Lab. **17**: 173. 1949. Type: A new name assigned to *F. tenuifolia* Harv. & Gray because of existence of earlier homonym, *Ambrosia tenuifolia* Spreng.

Ambrosia caudata (Rydb.) Shinners, *ibid.* 174.

Erect, perennial herb, perennating from base of stem or by means of adventitious shoots from roots, tending to form large clones; to 18 dm. high. Leaves alternate, petiolate, petioles to 15 cm. long; laminar tissue decurrent, usually with one or more pairs of small lobes below the main laminar region. Lamina ovate-lanceolate to lanceolate in outline, pinnately to tetrapinnately lobed, the lobes lanceolate to linear, attenuated or abruptly terminated, blade to 16 cm. long and 15 cm. broad, usually smaller; both surfaces green to somewhat gray-green, glabrous or nearly so to densely strigose, becoming velutinous. Inflorescence racemose-spicate, often much branched. Staminate involucres stalked, stalks to 8 mm. long, involucre to 10 mm. broad, 5–9-lobed (or more), the lobes obscure and poorly defined or well defined with sinuses extending nearly halfway to point of stalk attachment. Fruiting involucres in sessile, frequently massive clusters below staminate racemes, to 5 mm. long and 4 mm. broad, often much smaller, the base tending to be elongate, leaving the spines arranged on the upper 2/3 of the body, 1 (rarely 2)-flowered; spines 0–20, often fewer than 10, short, 1 mm. or less long to 2 mm. long and slender, uncinate. Haploid chromosome numbers, $n = 36, 54$.

Flowering: Throughout year in various portions of range.

Range: Southwestern United States from Texas and Colorado to California, throughout central Mexico from Nuevo Leon and Tamaulipas through Guanajuato and Jalisco to Sinaloa and Sonora. Adventive in Hawaii on the islands of Oahu and Molokai, and in Puerto Rico.

Notes: An extremely variable species, without doubt the most complex and difficult of the ragweeds, possibly an aggregate species as defined here, needing considerable further study before useful subgroups can be recognized.

13. **Ambrosia cordifolia** (Gray) Payne, comb. nov. PLATE VI

Franseria cordifolia Gray, Syn. Fl. N. Am. 1: 445. 1884. Type: Arizona, Sierra Tucson, *C. G. Pringle*, April 26, 1884 (GH!; isotypes, NY!, US!, MICH!).

Gaertnera cordifolia (Gray) Kuntze, Rev. Gen. Pl. 1: 339. 1891.

Franseria malvacea Rydb. N. Am. Fl. 33: 34. 1922. Type: Mexico, Sinaloa, Culiacan, *Dr. Edward Palmer 1770*, October 25 to November 18, 1891 (NY!; isotype, US!).

Erect shrub, becoming much branched at base, to 13 dm. high. Leaves alternate, petiolate, petioles to 4.5 cm. long, laminar tissue very narrowly decurrent, rarely with a few minute lobes below blade. Lamina ovate-cordate to broadly lanceolate in outline, to 13 cm. long and 10 cm. broad, usually smaller, margin dentate-serrate, 3-veined, weakly trilobed becoming obscurely pinnately lobed, base cordate to cuneate; both surfaces green, upper puberulous, lower lighter, tomentose. Inflorescence racemose-spicate, becoming paniculate. Staminate involucre stalked to subsessile, stalks to 4 mm. long; involucre to 7 mm. broad, shallowly 5–10-lobed, lobes without obvious striations. Fruiting involucres clustered on branches below staminate spikes, to 9 mm. long and 6 mm. broad, 2-fruited; spines 6–30, to 3 mm. long, scattered below the usually divergent beaks, sometimes swollen below, slender above, uncinate. Chromosome number unknown.

Flowering: November to May.

Range: Southern Arizona, south and west into San Luis Potosi, Sonora, Sinaloa, and Baja California, Mexico.

14. **Ambrosia deltoidea** (Torr.) Payne, comb. nov. PLATE IV

Franseria deltoidea Torr. Pl. Fremont. in Smithson. Contr. Knowl. 6: 15. 1854. Type: Southern California, on the Gila River, Fremont in 1849 (NY!). (Label includes pencil drawings of floral structures — Torrey's?). Sheet bears two specimens in addition to the type (which is at the extreme left): *Schott V. 855* (central) and *C. C. Parry 549* (extreme right). The latter is a paratype (duplicate of paratype, NY!).

Gaertnera deltodea (Torr.) Kuntze, Rev. Gen. Pl. 1: 339. 1891.

Erect shrub, to 5 dm. high, occasionally higher, usually much branched from base. Leaves alternate, petiolate, petiole to 2 cm. long, occasionally longer, laminar tissue narrowly decurrent to stem. Lamina narrowly lanceolate to deltoid-lanceolate or somewhat rhombic, abruptly expanded

from cuneate (to nearly straight) base, margin serrate or doubly serrate, unlobed or occasionally with few weak lobes; both surfaces gray-green to whitish-tomentose, strongly resinous and sticky. Inflorescence spicate-racemose to paniculate. Staminate involucre stalked to subsessile, stalks to 5 mm. long; involucres to 7 mm. broad, 6–9(–13)-lobed, lobes sometimes weakly defined, sinuses separating lobes usually extending less than halfway to point of stalk attachment, obscurely striated on upper surface or without striations. Fruiting involucres clustered on axis below staminate spike or on lateral branches, involucres to 10 mm. long and 12 mm. broad, 2 (rarely more)-flowered; spines to 18 (occasionally more), often the lowermost in a well defined whorl resembling the phyllaries of less specialized involucres, flattened, very sharply pointed, rarely somewhat uncinate, to 5 mm. long. Haploid chromosome number, $n = 18$.

Flowering: February to July.

Range: Southern Arizona, extending into Sonora and Baja California, Mexico.

Notes: A species similar to, and with intermediate forms resembling, *A. chenopodiifolia* (see notes for *A. chenopodiifolia*).

15. **Ambrosia divaricata** (Brandeg.) Payne, Pap. Mich. Acad. **49**: 44. 1964.

Franseria divaricata Brandeg. Proc. Calif. Acad. ser. 2. **2**: 171. 1889. Type: Mexico, Lower California, San Gregorio, *T. S. Brandegee*, Feb. 6, 1889 (UC, no. 88805, not seen; photograph, NY!; isotype, US!, no. 47803).

Erect, much branched shrub, probably more than 3 dm. high. Leaves alternate, petiolate, petioles to 15 mm. long, laminar tissue decurrent to base, occasionally with one or more pairs of minute lobes below main laminar region. Lamina broadly ovate, to 4 cm. long and 3.5 cm. broad, 3-veined, shallowly 3–7-lobed, the lobes broad; green both surfaces, somewhat lighter to gray-green below, strigose, becoming tomentose. Inflorescence racemose-paniculate, the lower staminate stalks often bearing more than one head. Staminate heads stalked, stalks to 2 cm. long (or longer); involucres to 7 mm. broad, 7–11-lobed, the lobes well defined, upper surfaces sometimes with weak striations. Fruiting involucres clustered on stalks below staminate racemes, to 9 mm. long and broad, 2-flowered; spines to more than 30, scattered, slender, uncinate, to 3 mm. long. Chromosome number unknown.

Flowering: January to April.

Range: Central Baja California, Mexico.

Notes: A species of great similarity to *A. magdalenae*, being distinguished primarily by the differences in leaf morphology.

16. **Ambrosia dumosa** (Gray) Payne, comb. nov. PLATE VI

Franseria dumosa Gray in Torr. & Frem. in Fremont, Rept. Expl. Exped. Rocky Mtns. 316. 1845. Type: California, sandy uplands of the Mohave River, very common in all that region of California, *Fremont 374*, 1844 (NY!).

Franseria albicaulis Torr. Pl. Frem. in Smithson. Contr. Knowl. 6: 16. 1853. Type: California, Fremont's Expedition, *Fremont*, 1849 (NY!).
Franseria dumosa var. *albicaulis* (Torr.) Gray in Torrey, Bot. Mex. Bound. Surv. 87. 1859.
Gaertnera dumosa (Gray) Kuntze, Rev. Gen. Pl. 1: 339. 1891.

Erect, much branched shrub, to 9 dm. high. Leaves alternate, petiolate, petioles to 20 mm. long, usually much shorter, laminar tissue narrowly decurrent to base. Lamina broadly ovate to narrowly elliptic-lanceolate, to 40 mm. long and 30 mm. broad, usually much smaller, pinnately to bi- or tripinnately lobed, lobes linear to distally expanded; both surfaces gray-green, puberulous, becoming white-tomentose on the under surface. Inflorescence racemose-paniculate, all stalks usually bearing distal staminate heads and one or more proximal pistillate heads subtended by small bracts; capitulous stalks to 8 mm. long. Staminate involucre 3–7 mm. broad, 5–9-lobed, sinuses separating lobes extending about halfway to point of stalk attachment, lobes without striations. Fruiting involucres to 9 mm. long and broad, 1- or 2-fruited; spines 12–30, scattered over surface of involucre, flattened, straight. Haploid chromosome number, $n = 18, 36, 54, 63$ (72?).

Flowering: February to July (fruiting specimens have been collected into September).

Range: Arid regions of Utah, Arizona, Nevada and California, south into Sonora and Baja California, Mexico.

Notes: The organization of the inflorescence of this species is unique for *Ambrosia*. Also, it is the only species which spans all ploidal levels known for the genus, from diploid to octoploid. Several variants may be recognized in the field, and the species may be of greater complexity than is indicated here.

17. **Ambrosia eriocentra** (Gray) Payne, comb. nov. PLATE VI

Franseria eriocentra Gray, Proc. Am. Acad. 7: 355. 1868. Type: Arizona, East slope of Providence Mountain, *J. G. Cooper*, May, 1861 (GH!).
Gaertnera eriocentra (Gray) Kuntze, Rev. Gen. Pl. 1: 339. 1891.

Erect, much branched shrub, to 18 dm. high. Leaves alternate, petiolate to subsessile, petioles to 3 mm. long. Lamina elliptical or narrowly lanceolate to deltoid-lanceolate in outline, to 90 mm. long and 30 mm. broad, usually smaller, unlobed to marginally pinnately lobed, the rachis lamina usually comprising largest portion of blade; upper surface green, puberulous to tomentose, main veins frequently whitened by pubescence, under surface becoming white woolly-tomentose; margin usually strongly revolute. Inflorescence spicate, becoming racemose. Staminate involucre subsessile to stalked, stalks to 2 mm. long, lower stalks often with two or more closely approximate heads resembling a single large head; involucres to 7 mm. broad, 5–9-lobed, the sinuses between lobes shallow to more than halfway to point of stalk attachment, without obvious striations on upper surface. Fruiting involucres to 10 mm. long and 11 mm. broad, 1(–2?)-

flowered; spines to 20, usually emerging near equator of fruit body, flat, sharply pointed, more or less covered with long, white, silky hairs. Haploid chromosome number, $n = 18$.

Flowering: April to July.

Range: Southern Arizona, scattered in arid regions of Nevada, Utah, and California.

18. **Ambrosia flexuosa** (Gray) Payne, comb. nov.

Franseria flexuosa Gray, Proc. Am. Acad. ser. 2. **12** (whole series 20): 298. 1885. Type: Mexico, Lower California, *H. C. & C. R. Orcutt 1103*, July 8, 1884 (GH!; type photograph, NY!).

Erect shrub, similar in general aspect to *A. carduacea*. Leaves alternate, petiolate, petioles to 1 cm. long. Lamina narrowly lanceolate to deltoid-lanceolate in outline, to 5 cm. long and 3 cm. broad, cuneate at base, unlobed to weakly pinnately lobed by prolongation of marginal teeth, teeth stiff; both surfaces green, under surface somewhat woolly before maturity, veins prominent on under surface, yellowish. Inflorescence racemose-paniculate. Staminate involucres stalked, stalks to 7 mm. long; involucres to 5 mm. broad, 5–10-lobed, lobes marked on the upper surface with dark striations. Fruiting involucres in clusters on short or long stalks below staminate racemes, to 8 mm. long and 6 mm. broad, 2-flowered; spines to 15 (or more?), terete, uncinate, broadened at base. Chromosome number unknown.

Flowering: July.

Range: Baja California, Mexico, known only from type collection.

Notes: A species of questionable nature because of the limited material. Gray noted that the foliage was somewhat intermediate in character between *A. ambrosioides* and *A. ilicifolia*, but the fruiting involucres are very different from both, more closely resembling those of *A. cordifolia*. The abundance with which fruiting involucres have been matured on this specimen would argue against a hybrid nature.

19. **Ambrosia grayi** (Nels.) Shinners, Field Lab. 17: 174. 1949.

Franseria tomentosa Gray, Pl. Fendl. in Mem. Am. Acad. ser. 2. **4**: 80. 1849, non *A. tomentosa* Nutt. 1818, nec *Gaertneria tomentosa* (Nutt.) Nels. 1909. Type: Kansas (?), high banks of Walnut Creek, between Council Grove and Fort Mann, of the Arkansas River, *Fendler 412* (GH, not seen).

Gaertnera tomentosa (Gray) Kuntze, Rev. Gen. Pl. **1**: 339. 1891.

Gaertneria grayi Nels. Bot. Gaz. **34**: 35. 1902. NOTE: Based upon *Franseria tomentosa* Gray. New name proposed by Nelson because of earlier homonym, *Gaertneria tomentosa* Nels. (= *A. tomentosa* Nutt.).

Franseria grayi (Nels.) Nels. New Man. Bot. Centr. Rocky Mtns. 542. 1909.

Upright, perennial herb, perennating by means of adventitious shoots from the roots, forming large clonal populations. Leaves alternate, petiolate, petioles to 5 cm. long, laminar tissue decurrent to base, with several small lobes below main laminar region. Lamina ovate-deltoid to lanceolate in

outline, to 10 cm. long and 8 cm. wide, irregularly pinnately lobed, major basal lobes and terminal lobe much the largest, large lobes lanceolate-elliptical, serrate, both surfaces (and entire plant) silvery gray-canescent. Inflorescence racemose-spicate. Staminate involucre stalked, stalks to 5 mm., involucres to 5 mm. broad, 5–9-lobed; lobes often somewhat irregular, shallow, upper surface with dark striations along midveins obscured by pubescence. Fruiting involucres in small axillary clusters below staminate spikes, to 7 mm. long and 4 mm. broad, 2-flowered; spines to 15, scattered, narrowed to slender uncinate tips. Haploid chromosome number, $n = 18$.

Flowering: July to October.

Range: Low, moist areas throughout Kansas and Nebraska, sporadically in Oklahoma, Colorado, and Texas.

Notes: A species well known under the name *Franseria tomentosa*; one of the more handsome ragweeds by virtue of the silvery pubescence.

20. **Ambrosia ilicifolia** (Gray) Payne, comb. nov. PLATE VII

Franseria ilicifolia Gray, Proc. Am. Acad. **11**: 77. 1876. Type: California, Southern part of San Diego County, Tantillas Cañon (GH!).
Gaertnera ilicifolia (Gray) Kuntze, Rev. Gen. Pl. **1**: 339. 1891.

Erect or semi-prostrate shrub, to 12 dm. high. Leaves alternate, sessile, clasping the stem. Lamina broadly ovate, to 9 cm. long and 7.5 cm. broad, usually smaller, typically unlobed but with strong, prickly, marginal teeth, the teeth often prolonged into weak lobes; both surfaces gray-green, minutely glandular-punctate, with ciliate hairs on margins and along veins; stiff and coriaceous, veins whitened and prominent on under surface, sticky and with a strongly resinous odor when fresh. Inflorescence racemose. Staminate involucres stalked, stalks to 12 mm.; involucres to 35 mm. broad including the usually prominent attenuate lobes, lobes to 15, without striations. Fruiting involucres in axillary clusters below staminate racemes, nearly globose, to 20 mm. long and broad; spines numerous, to 50 or more, scattered, to 6 mm. long, slender, uncinate. Haploid chromosome number, $n = 18$.

Flowering: February to June.

Range: Desert regions of southern Arizona and California, south into Sonora and Baja California, Mexico.

21. **Ambrosia linearis** (Rydb.) Payne, comb. nov. PLATE VIII

Gaertneria linearis Rydb. Bull. Torrey Club **32**: 133. 1905. Type: Colorado, Calhan, *DeAlton Saunders*, July, 1893 (NY!).
Franseria linearis (Rydb.) Rydb. N. Am. Fl. **33**: 27. 1922.

Erect, perennial, shrubby herb, perennating by means of adventitious shoots from the base of the stem and from roots. Leaves alternate, sessile. Lamina ovate to lanceolate in outline, to 25 mm. long and 15 mm. broad, pinnately or bipinnately lobed, lobes and rachis more or less linear,

margin revolute; upper surface green, strigose, lower surface white woolly-tomentose. Inflorescence racemose-spicate. Staminate involucres occasionally subtended by bracts, subsessile with stalks to ca. 1 mm., involucres to 5 mm. broad, 5–9-lobed, sinuses separating lobes usually extending less than halfway to point of stalk attachment; lobes without obvious striations. Fruiting involucres borne singly or in small clusters in axils of leaves below staminate spike, ca. 3.5 mm. long and 2.5 mm. broad, 1-flowered; spines to 9, arranged more or less in a single whorl near apex of body, terete, uncinate, to ca. 1 mm. long. Chromosome number unknown.

Flowering: July.

Range: Colorado, Lincoln and El Paso Counties, known only from the type and one other specimen (*Ownbey 1325*) collected in 1937.

Notes: A very distinctive species, inexplicably rarely collected.

22. **Ambrosia magdalenae** (Brandeg.) Payne, comb. nov. PLATE VIII

Franseria magdalenae Brandeg. Proc. Calif. Acad. ser. 2. **2**: 170. 1889. Type: Mexico, Lower California, Magdalena Island, *T. S. Brandegee*, Jan. 13, 1889 (UC, no. 88804, not seen; isotype, US! no. 47365).

Franseria intricata Rydb. N. Am. Fl. **33**: 33. 1922. Type: Mexico, Lower California, San Bartolome Bay, *J. N. Rose 16196*, March 13, 1911 (NY!; isotype US!, no. 638267).

Erect, much branched shrub, to 2 dm. high. Leaves alternate, petiolate, petioles to 4 cm. long, laminar tissue narrowly decurrent to base. Lamina ovate to ovate-lanceolate in outline, to 5.5 cm. long and 3.5 cm. broad, irregularly bipinnately lobed, often with one or more pairs of minute lobes below the main laminar region; upper surface green, sparingly tomentose, lower similiar, to white woolly-tomentose. Inflorescence racemose to racemose-paniculate. Staminate involucres stalked, stalks to 10 mm. long, the lowermost occasionally bearing more than one head; involucre to 5 mm. broad, lobes to 12, sometimes with weak striations along midvein, sinuses between lobes usually extending less than halfway to point of stalk attachment. Fruiting involucres in axillary clusters or clustered on branches below staminate raceme, subglobose, to 8 mm. long and 11 mm. broad, 2-flowered; spines to more than 30, scattered, slender, uncinate, to 3 mm. long. Chromosome number unknown.

Flowering: January to April.

Range: Central Baja California, Mexico.

Notes: A species with considerable variability, particularly in leaf morphology and pubescence. Closely resembling *A. divaricata*, a taxon distinguished primarily on the basis of leaf differences.

23. **Ambrosia nivea** (Rob. & Fern.) Payne, comb. nov. PLATE VIII

Franseria nivea Rob. & Fern. Proc. Am. Acad. **30**: 117. 1895. Type: Mexico, Chihuahua, Plains near Casas Grandes, *C. V. Hartman 813*, 10 Oct. 1891, (GH!; isotypes, NY!, US!, no. 306295).

Erect shrub, to 2.5 dm. high. Leaves alternate, petiolate, petioles to 4 cm. long, laminar tissue decurrent to base, often with 1–3 or more pairs of small lobes below main laminar region. Lamina ovate to triangular in outline, to 80 mm. long and 70 mm. wide or larger, irregularly bi- to tripinnately lobed, both surfaces gray-green, silky-canescent. Inflorescence racemose-spicate. Staminate involucre stalked, stalks to 5 mm. long; involucres to 4 mm. broad, lobes to 10, the distal lobes tending to be somewhat more pronounced, sinuses separating lobes shallow, upper surfaces of lobes without striations. Fruiting involucres clustered in axils of leaves subtending staminate racemes, to 7 mm. long and 6 mm. broad, 2–3-flowered; spines to 20, scattered, to 3 mm. long, terete, heavy, straight. Chromosome number unknown.

Flowering: October.

Range: Northwestern Chihuahua (known only from type collection).

Notes: A distinctive, and unquestionably valid species, even though known only from the type collection.

24. **Ambrosia tomentosa** Nutt. Gen. Am. Pl. **2**: 186. 1818., non *Franseria tomentosa* Gray, 1849, nec *Gaertnera tomentosa* (Gray) Kuntze, 1891. Type: In upper Louisiana on the banks of the Missouri, *Nuttall* (probably BM). NOTE: I have been unable to locate this type in Nuttall's herbarium in PH or elsewhere. However, Nuttall's short description leaves no doubt that he was dealing with the taxon described here, viz.: "Perennial; stem low; leaves bipinnatifid, underside white and tomentose; spikes solitary."

Franseria discolor Nutt. Trans. Am. Phil. Soc. ser. 2 **7**: 345. 1840. Type: In the Rocky Mountains, near the Colorado of the West, *Nuttall* (PH!).

Xanthidium discolor (Nutt.) Delp. Studi Lign. Anem. Comp. Artem. 17. 1871.

Franseria exigua Wawra in Beck, It. Princ. S. Cob. **2**: 41. 1888. Type: Nordamerika, In den Prairien, *Wawra I 13.* I have been unable to locate this type. NOTE: Wawra has included a beautiful and detailed illustration with the description (*Taf. 8, Fig. B*, loc. cit.) which leaves no question whatsoever about the identity of this taxon.

Gaertnera discolor (Nutt.) Kuntze, Rev. Gen. Pl. **1**: 339. 1891.

Gaertneria tomentosa (Nutt.) Nels. Bot. Gaz. **34**: 34. 1902.

Franseria tomentosa (Nutt.) Nels. New Man. Bot. Centr. Rocky Mtns. 542. 1909.

Erect or reclining, perennial herb, perennating by means of adventitious shoots from the roots, forming clonal populations. Leaves alternate, petiolate, petioles to 10 cm. long, laminar tissue decurrent to base, usually with several pairs of small lobes below the main laminar area often obscuring the distinction between petiole and lamina. Lamina ovate-lanceolate in outline, to 10 cm. long and 6 cm. broad, irregularly bi- or tripinnately lobed; upper surface dark green, minutely scabrous, lower surface white woolly-tomentose, margins revolute. Inflorescence racemose-spicate. Staminate involucres stalked, stalks to 10 mm.; involucres to 7 mm. broad,

lobes to 12, sinuses separating lobes extending halfway or less to point of stalk attachment; upper surface of lobes with black striations, mostly along the midveins. Fruiting involucres in sessile clusters in axils of leaves subtending staminate racemes, to 6 mm. long and 3.5 mm. broad, 2-flowered; spines 0–10, scattered, ca. 1 mm. long (rarely to 3 mm.), somewhat appressed. Chromosome number unknown.

Flowering: May to August.

Range: Prairie and semi-arid regions of Wyoming, Nebraska, Colorado, New Mexico, and Arizona; sporadic in Idaho, Iowa, and South Dakota.

Notes: Aptly described by Nuttall (as *Franseria discolor*) as "A remarkable and distinct, as well as elegant species," a comment based, no doubt, on the striking appearance of the white under surface of the leaf, rimmed by the dark green, revolute margin.

LITERATURE CITED

BRANDEGEE, T. S. 1889. A collection of plants from Baja California, 1889. Proc. Calif. Acad. Sci. ser. 2. **2**: 117–216.

CAVANILLES, J. 1793. Icones et Descriptiones Plantarum **2**. Matriti.

GEBBEN, A. I., W. W. PAYNE & W. H. WAGNER, JR. 1962. Botanical Phase. *In*: J. M. SHELDON and E. W. HEWSON (*eds.*), Atmospheric pollution by aeroallergens, prog. rept. 5. University of Michigan, Ann Arbor.

LINNAEUS, C. 1753. Species Plantarum, **2**. Holmiae.

PAYNE, W. W. 1962a. The unique morphology of the spines of an armed ragweed, *Ambrosia bryantii* (Compositae). Madroño **16**: 233–236.

———. 1962b. Biosystematic studies of four widespread weedy species of ragweeds (*Ambrosia*: Compositae). Doctoral thesis (unpublished), University of Michigan, Ann Arbor.

———. 1963. The morphology of the inflorescence of ragweeds (*Ambrosia*—*Franseria*: Compositae). Am. Jour. Bot. **50**: 872–880.

PAYNE, W. W., P. H. RAVEN & D. W. KYHOS. 1964. Chromosome numbers in Compositae. IV. Ambroseae. Am. Jour. Bot. **51**: 419–424.

RYDBERG, P. A. 1922. Ambrosiaceae. *In* N. Am. Fl. **33**: 3–44.

SHINNERS, L. H. 1949. Notes on Texas Compositae III. Field Lab. **17**: 170–176.

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EXPLANATION OF PLATES

Except in FIGS. 38 and 60, staminate and pistillate involucres have been illustrated without pubescence.

PLATE I

FIGS. 1–5, *Ambrosia acuminata* (all from *Brandegee*, Feb. 11, 1889, US). 1, Inflorescence, × 0.5; 2, staminate head, × 3.3; 3, pale from staminate head, × 10; 4, fruiting involucre, × 3.3; 5, leaf silhouette, × 0.33.

FIGS. 6–10, *Ambrosia ambrosioides*. 6, Inflorescence, × 0.5; 7, staminate head,

× 3.3 (6 & 7, from *Wiggins 6379*, MICH); 8, pale from staminate head, × 10 (from *Peebles & Loomis 6728*, ARIZ); 9, fruiting involucre, × 3.3 (from *Peebles 15041*, ARIZ); 10, leaf silhouette (photoduplicated from greenhouse specimen, *Payne AJL*).

FIGS. 11–14, *Ambrosia artemisioides* (all from *Williams 2527*, NY). 11, Inflorescence, × 0.5; 12, staminate head, × 3.3; 13, fruiting involucres, × 3.3; 14, leaf silhouettes, × 1.

PLATE II

FIGS. 15–19, *Ambrosia arborescens*. 15, Inflorescence, × 0.5; 16, staminate head, × 3.3; 17, pale from staminate head, × 10 (15, 16 & 17 from *Killip & Smith 17884*, NY); 18, fruiting involucres, × 3.3 (18a from *Killip & Smith 19676*, NY); 18b from *Pennell 2636*, NY); 19, leaf silhouette, × 0.33 (from *Steinbeck 8817*, NY).

FIGS. 20–24, *Ambrosia carduacea*. 20, Inflorescence, × 0.5; 21, staminate head, × 3.3; 22, pale from staminate head, × 10 (20, 21 & 22 from *Shreve 6944*, ARIZ); 23, fruiting involucres, × 3.3 (23a from *Shreve 6944*; 23b from *Gentry 4128*, ARIZ); 24, leaf silhouettes, × 0.33 (24a & b from *Shreve 6944*, ARIZ; 24c from *Rempel 151*, ARIZ).

PLATE III

FIGS. 25–29, *Ambrosia camphorata*. 25, Inflorescence, × 0.5 (from *Payne 4175*, MICH); 26, staminate heads, × 3.3 (26a from *Payne 4175*, MICH; 26b from *M. E. Jones 24058*, MICH); 27, pale from staminate head, × 10 (from *Payne 4175*, MICH); 28, fruiting involucres, × 3.3 (28a from *Payne 4000*, MICH; 28b from *Payne 4175*, MICH; 28c from *Palmer 757*, NY; 28d from *Palmer 881*, NY; 28e from *Wiggins 7935*, MICH; 28f from *Greene*, April 24, 1885, NY; 28g from *M. E. Jones 24647*, NY; 28h from *Broder 618*, MICH); 29, leaf silhouettes, × 0.33 (29a–g photoduplicated from population sample from southern San Luis Potosi, Mexico, *Payne 4007*, MICH; 29h photoduplicated from greenhouse specimen, *Payne BCK*).

PLATE IV

FIGS. 30–34, *Ambrosia canescens*. 30, Inflorescence, × 0.5; 31, staminate heads, × 3.3; 32, pale from staminate head, × 10 (30, 31 & 32 from *Payne 4030*, MICH); 33, fruiting involucres, × 3.3 (from a single specimen, *Payne 4049*, MICH); 34, leaf silhouettes, × 0.33 (photoduplicated from population sample from Jalisco, Mexico, *Payne 4121*, MICH).

FIGS. 35–39. *Ambrosia chenopodiifolia*. 35, Inflorescence, × 0.5 (from *M. E. Jones 3702*, NY); 36, staminate head, × 3.3; 37, pale from staminate head (36 & 37 from *Orcutt*, April 10, 1885, NY); 38, fruiting involucres, × 3.3 (38a from *Orcutt*, May 7, 1886, MICH; 38b from *Palmer 731*, NY); 39, leaf silhouettes, × 0.33 (photoduplicated from greenhouse population, *Payne BDK*).

FIGS. 40–44, *Ambrosia deltoidea*. 40, Inflorescence, × 0.5 (from *Shreve 7506*, ARIZ, and from *Peebles 15038*, ARIZ); 41, staminate head, × 3.3; 42, pale from staminate head, × 10 (41 & 42 from *Benson 10701*, ARIZ); 43, fruiting involucres, × 3.3 (43a from *Peebles 15038*, ARIZ; 43b from *Gillespie 5436*, NY); 44, leaf silhouettes (photoduplicated from greenhouse population, *Payne AJP*).

PLATE V

FIG. 45, *Ambrosia chamissonis*, leaf silhouettes, × 0.33 (from greenhouse

grown population and progeny from Marin County, California; each leaf represents a different specimen).

FIG. 46, *Ambrosia confertiflora*, leaf silhouettes, × 0.33 (from population in southeastern Coahuila, Mexico, *Payne 3767*, MICH; each leaf represents a different specimen).

PLATE VI

FIGS. 47–51, *Ambrosia cordifolia*. 47, Inflorescence, × 0.5; 48, staminate heads, × 3.3; 49, pale from staminate head, × 10 (47, 48 & 49 from *Shreve 10016*, MICH); 50, fruiting involucres, × 3.3 (50a from *Thornber*, May 10, 1913, ARIZ; 50b from *Turkham*, April 19, 1942, ARIZ); 51, leaf silhouettes, × 0.33 (photoduplicated from greenhouse population, *Payne AJH*).

FIGS. 52–56, *Ambrosia dumosa*. 52, Inflorescence, × 0.5 (from *Harrison & Beldon 3577*, ARIZ); 53, capitulous branch with mature staminate and immature pistillate heads, × 3.3; 54, pale from staminate head, × 10 (53 & 54 from greenhouse specimen, *Payne BDG-a*); 55, fruiting involucres, × 3.3; (55a from greenhouse specimen, *Payne BDG-a*; 55b from *Humphrey SCS-767*, ARIZ); 56, leaf silhouettes, × 0.33 (photoduplicated from greenhouse population, *Payne BDG*).

FIGS. 57–61, *Ambrosia eriocentra*. 57, Inflorescence, × 0.5; 58, staminate head, × 3.3; 59, pale from staminate head, × 10 (57, 58 & 59 from *Kearney & Peebles 13161*, NY); 60, fruiting involucre, × 3.3 (from *Wolf 10683*, NY); 61, leaf silhouettes, × 0.33 (photoduplicated from greenhouse specimen, *Payne AJR*).

PLATE VII

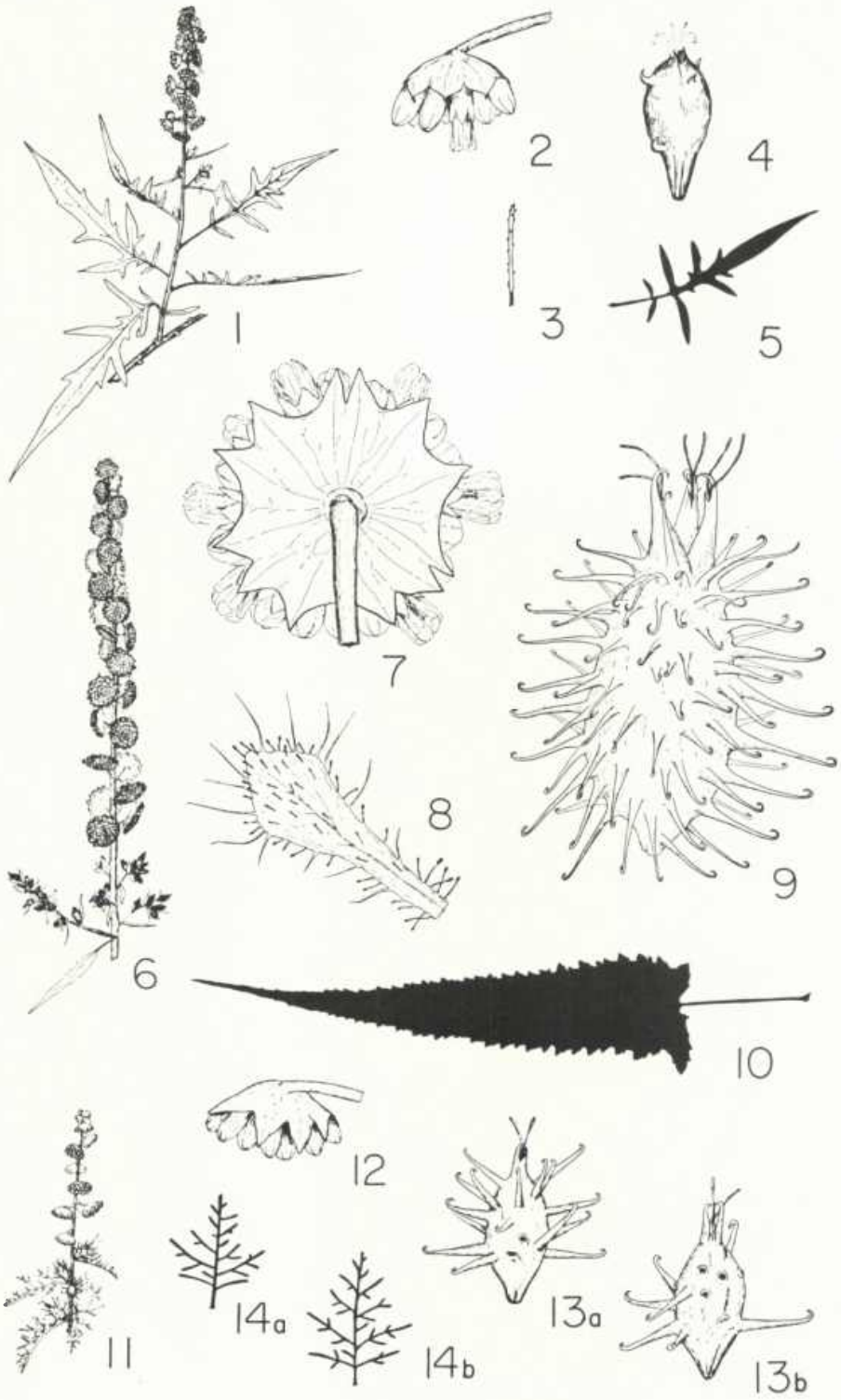
FIGS. 62–67, *Ambrosia ilicifolia*. 62, Inflorescence, × 0.5; 63, staminate head, × 3.3; 64, floret from staminate head, × 10; 65, pale from staminate head, × 10 (62, 63, 64 & 65 from *M. E. Jones*, Feb. 27, 1924, NY); 66, fruiting involucre, × 3.3 (from *Ahles 9087*, ILL); 67, leaf silhouettes, × 0.33 (photoduplicated from greenhouse specimen, *Payne AJO*).

PLATE VIII

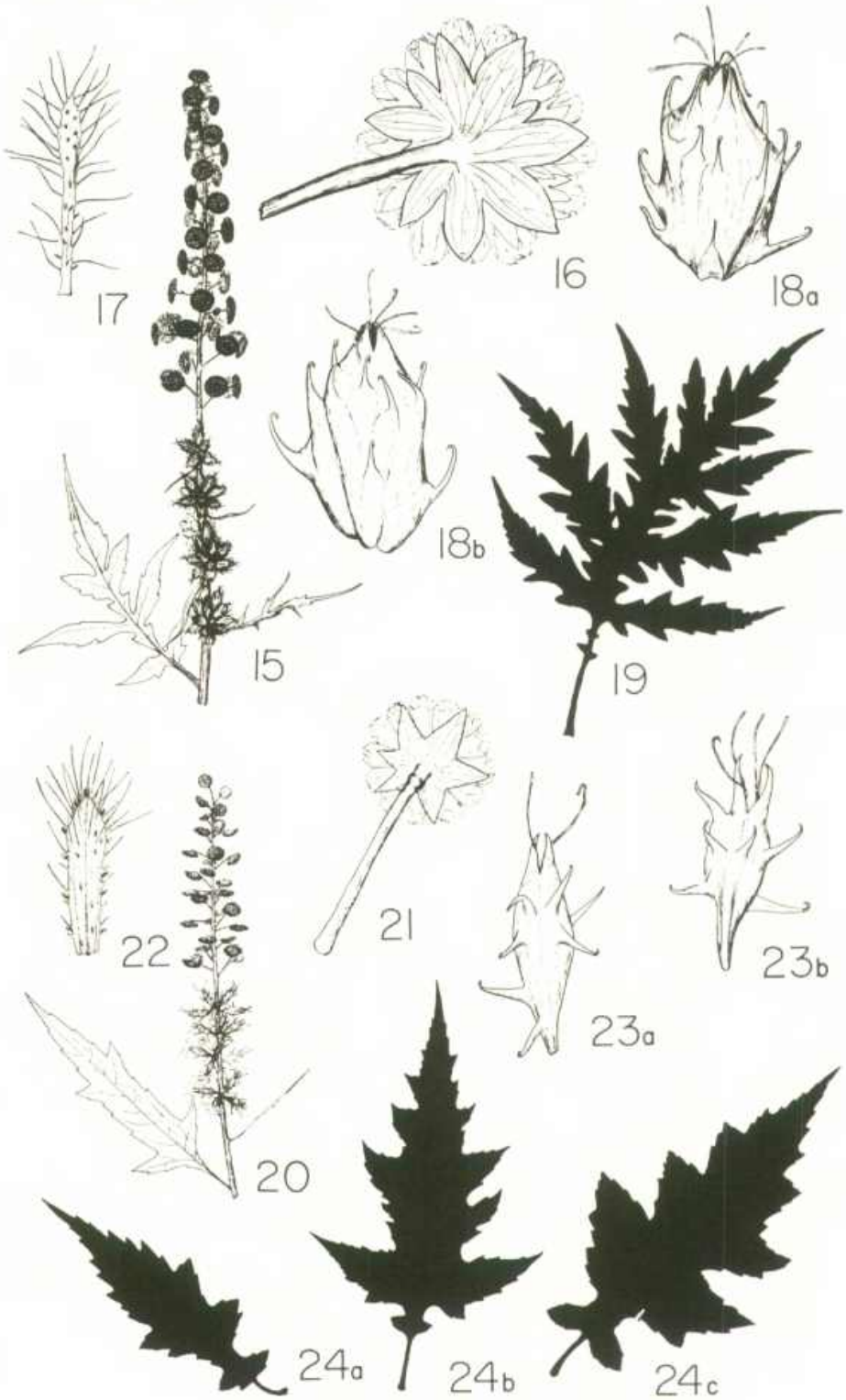
FIGS. 68–72, *Ambrosia linearis*. 68, Inflorescence, × 0.5; 69, staminate heads, × 3.3; 70, pales from staminate head, × 10 (68, 69 & 70 from *Ownbey 1325*, NY); 71, fruiting involucres, × 3.3 (71a from *Saunders*, July, 1893, NY; 71b from *Ownbey 1325*, NY); 72, leaf silhouettes, × 1 (72a & b from *Ownbey 1325*, NY; 72c from *Saunders*, July, 1893, NY).

FIGS. 73–77, *Ambrosia magdalenae* (all from *Brandegee*, Jan. 13, 1889, NY). 73, Inflorescence, × 0.5; 74, staminate head, × 3.3; 75, pale from staminate head, × 10; 76, fruiting involucre, × 3.3; 77, leaf silhouette, × 0.33.

FIGS. 78–82, *Ambrosia nivea* (all from *Hartman 813*, NY). 78, Inflorescence, × 0.5; 79, staminate head, × 3.3; 80, pale from staminate head, × 10; 81, fruiting involucre, × 3.3; 82, leaf silhouette, × 0.33.



PAYNE, THE GENUS AMBROSIA



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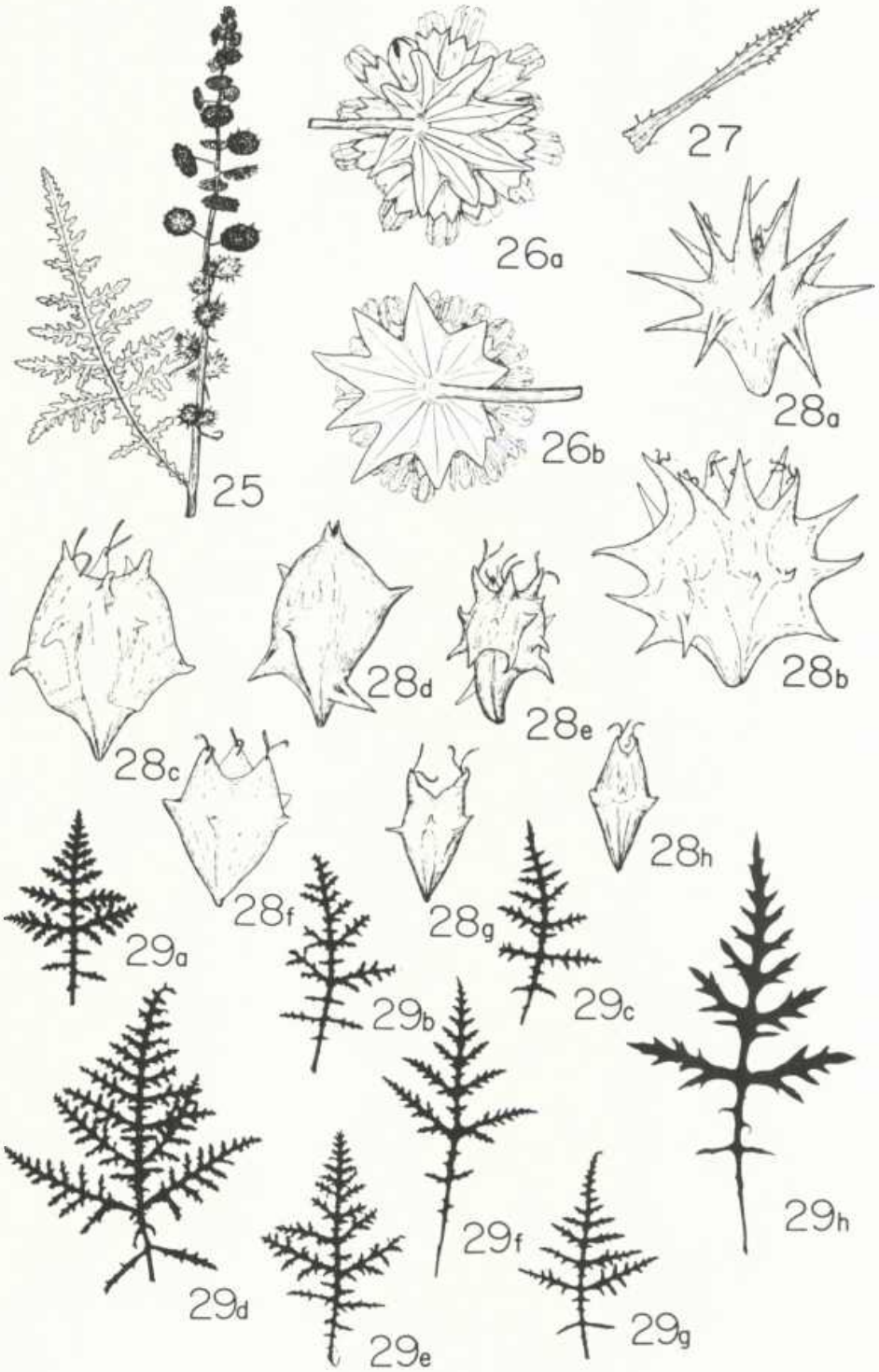

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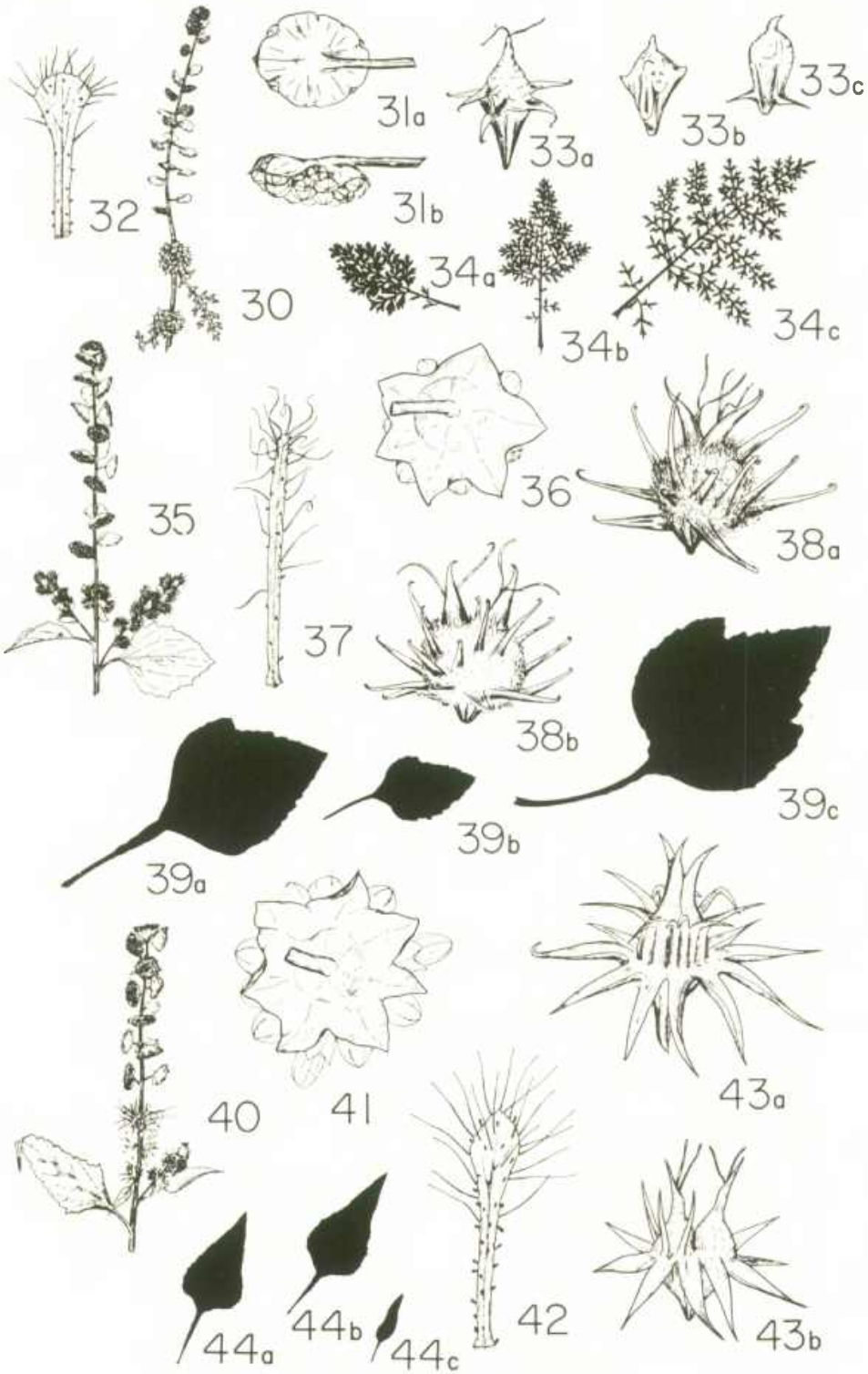

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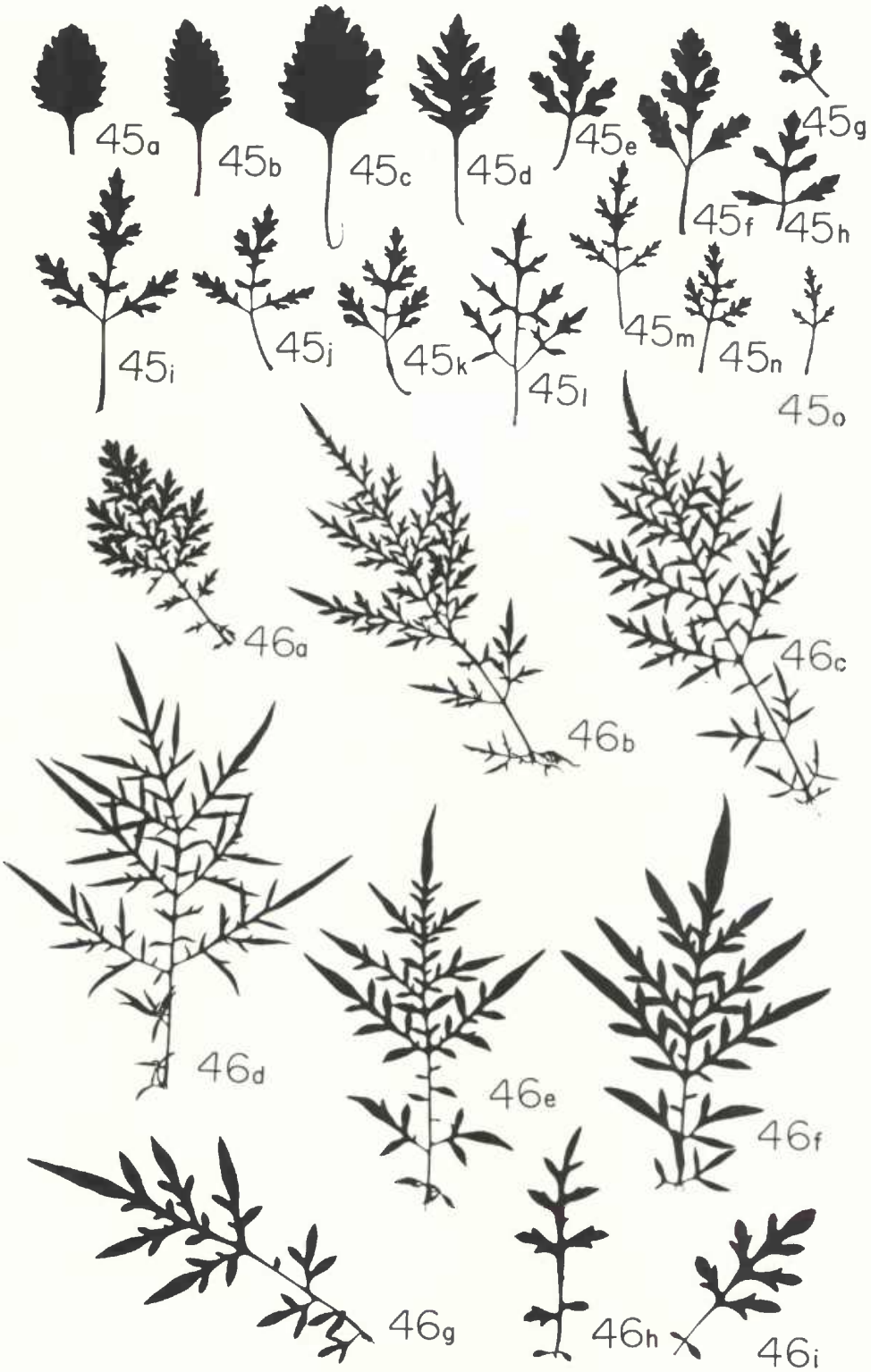

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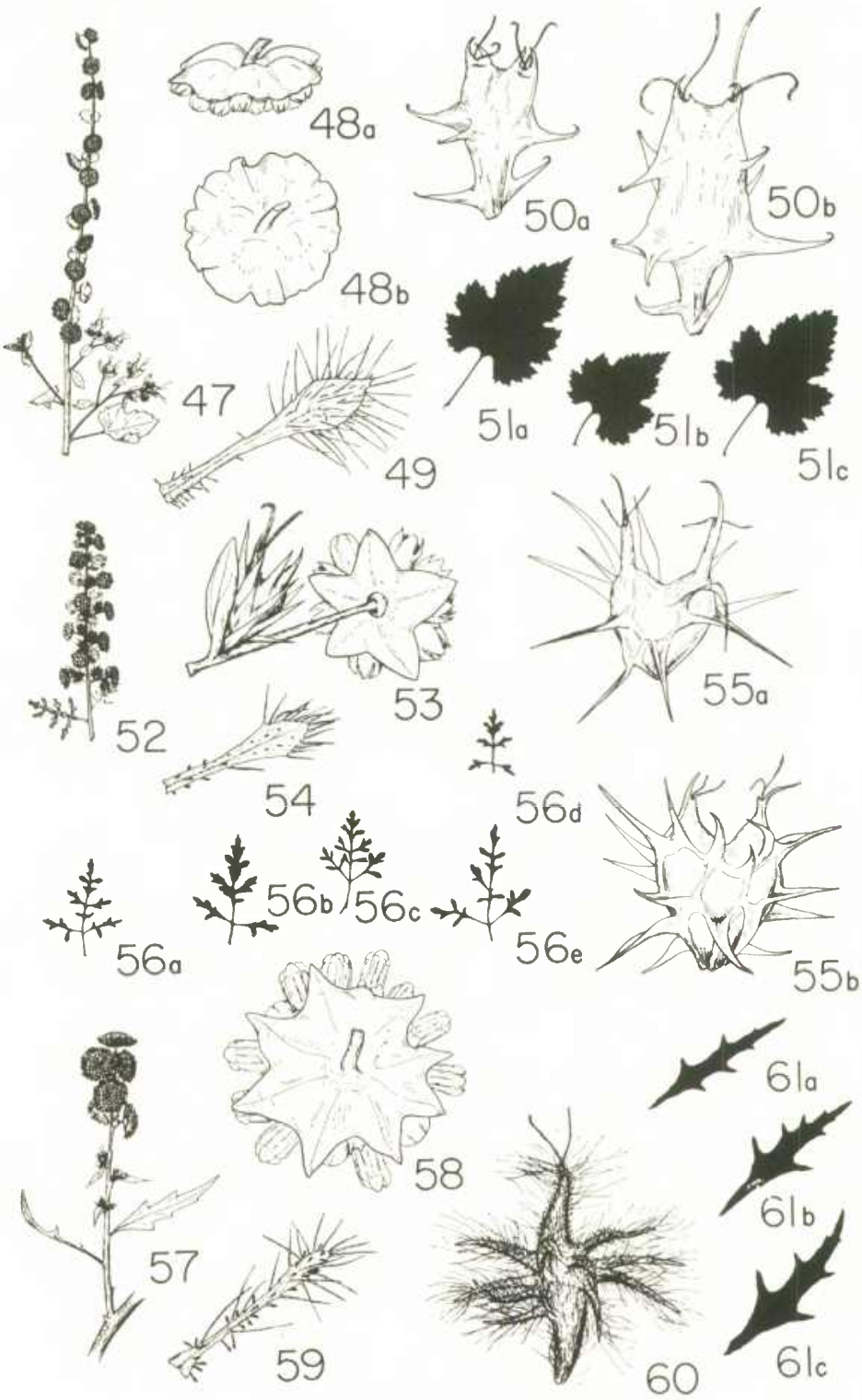

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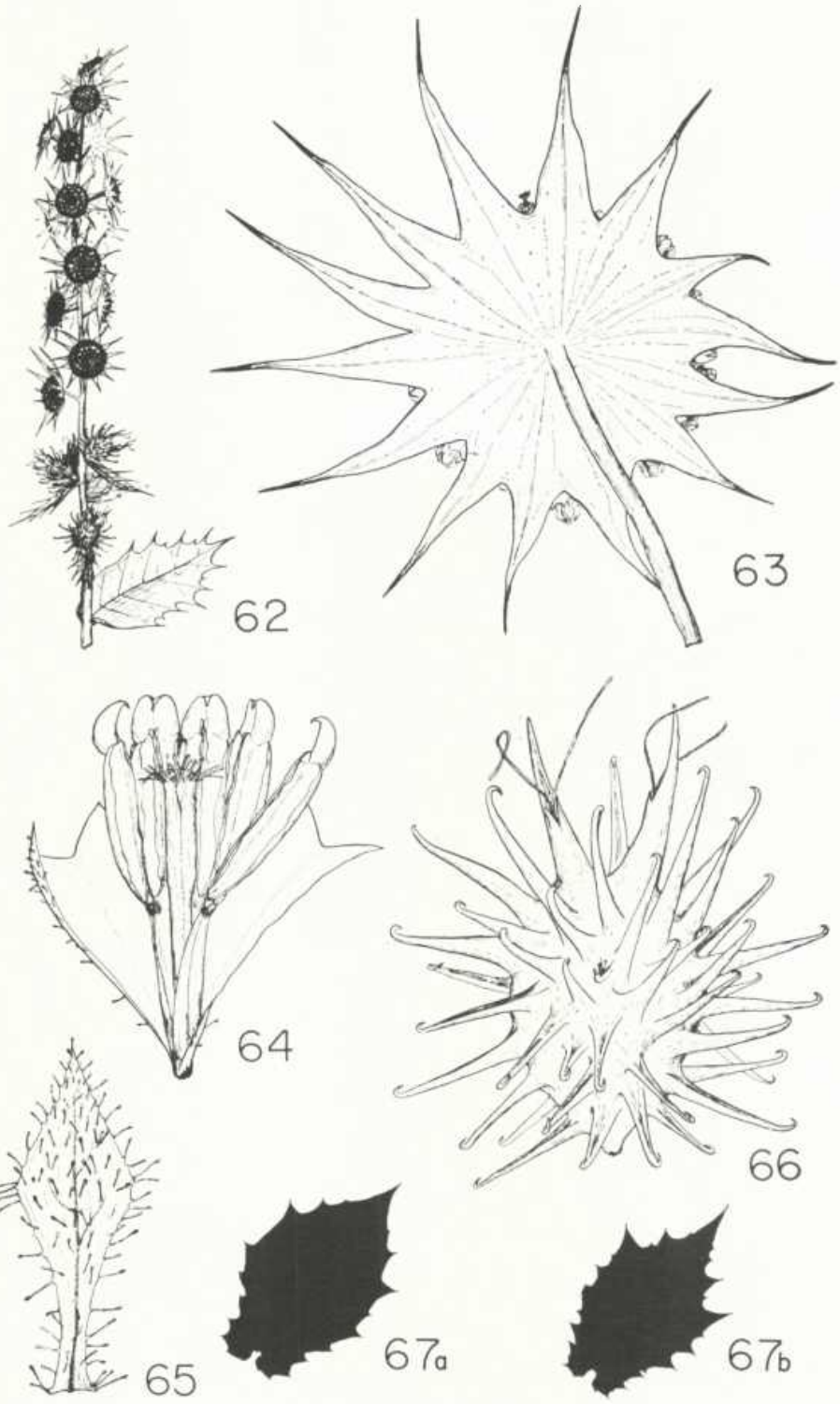

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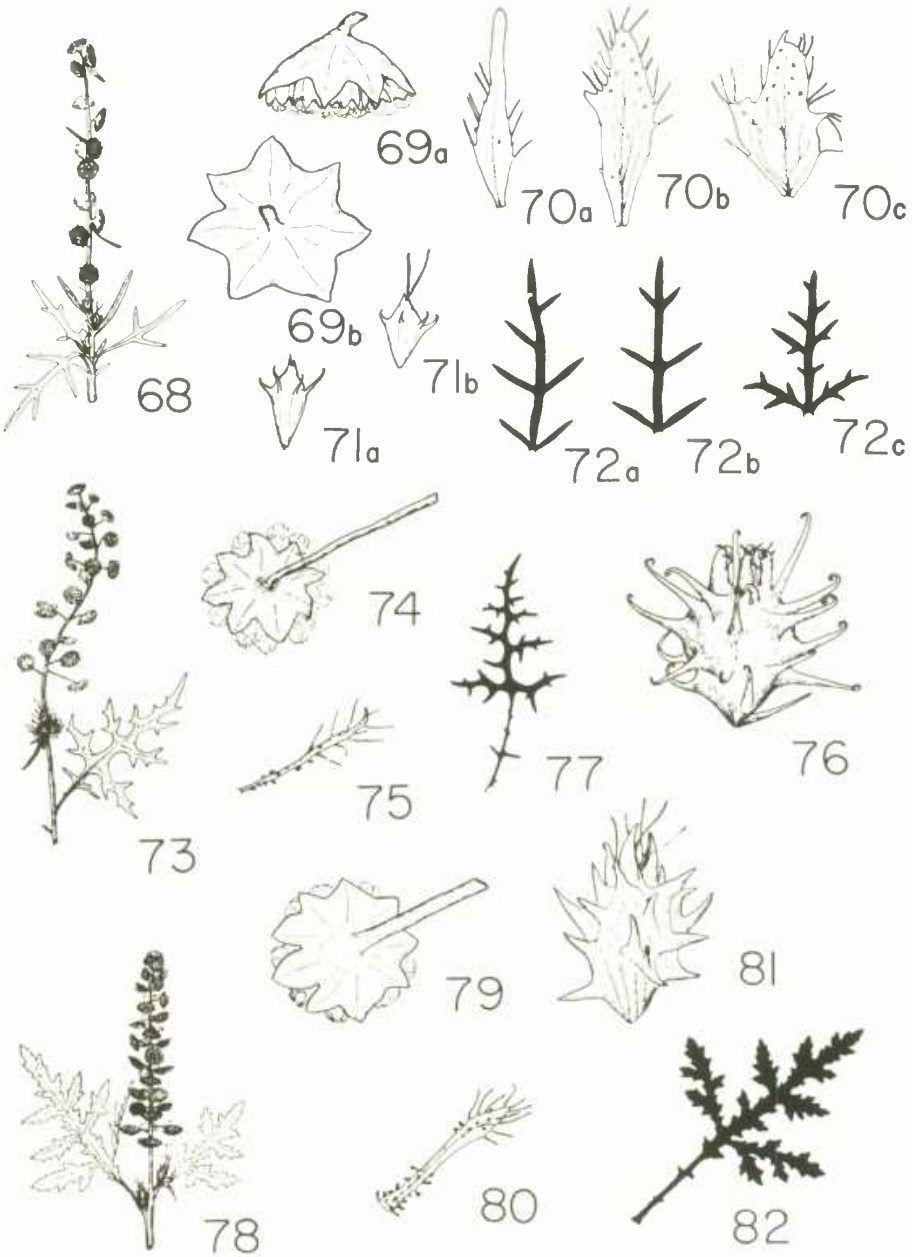

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