

SYNOPTICAL KEYS TO GENERA OF CALIFORNIAN COMPOSITES

JOHN L. STROTHER

University Herbarium, 1001 Valley Life Sciences Building,
University of California, Berkeley, CA 94720-2465

ABSTRACT

Synoptical keys are sometimes preferred to artificial keys. In the synoptical keys provided here, the 207 genera of composites recognized in *The Jepson Manual* represent 2 of the 3 subfamilies and 13 of the 16 tribes used in a classification system differing only slightly from that proposed by Bremer in 1994. Of the 207 genera treated in *The Jepson Manual*, Heliantheae (incl. Helenieae), as circumscribed here, includes 78 (distributed among 17 subtribes) and Astereae and Lactuceae have 33 each. The other ten tribes are represented in *The Jepson Manual* by 1 to 14 genera each.

David Keil (in Hickman 1993) provided excellent, wonderfully workable, well-received artificial keys for identification of genera of composites as treated in *The Jepson Manual* (*JepsMan*). Some plant identifiers readily assimilate characteristics of artificial groupings of taxa and they readily accept artificial keys such as those written by Keil. Other plant identifiers have difficulty assimilating artificial groups but they do readily recognize individual plants as members of certain natural groups, even if they do not recognize the particular species or genus to which an individual plant belongs. Upon finding an artichoke in flower, for example, they may not recognize or "know" the genus to which the plant belongs but they do recognize that it belongs in the tribe with thistles, Cardueae. Some such users of *JepsMan* expressed interest in having synoptical keys to genera organized into natural groups (i.e., into tribes and subtribes). The following notes, diagnoses, and keys were prepared in response to that expressed interest.

Notes. In the classification on which the following treatment is based, 3 subfamilies and 16 tribes are recognized. Representatives of 2 subfamilies and 13 tribes are found among the 207 genera of composites treated in *JepsMan*. Barnadesioideae and its only tribe, Barnadesieae, and two tribes from Cichorioideae (Vernonieae and Liabeae) are not represented in *JepsMan*.

Tribal circumscriptions adopted here match those adopted by Bremer (1994) except that Helenieae and Heliantheae sensu Karis and Ryding (1994a, b) are treated as one tribe, Heliantheae. Tribal and subtribal circumscriptions and classification for Heliantheae used here are sensu H. Robinson (1981). Tribal circumscriptions and classifications for

Gnaphalieae, Inuleae, and Plucheeae are sensu Anderberg (1994a, b, c).

In writing tribal diagnoses, I have tried to balance economy of print with sufficiency of detail and parallel construction. In large measure, the tribal diagnoses are derived from those found in *Manual of the Flowering Plants of California* by W. L. Jepson (1925) and are intended to account only for plants found growing without cultivation within California.

Generic characteristics used in constructing keys have, for the most part, been taken directly from the descriptions in *JepsMan*. So far as practicable, generic characteristics have been verified in specimens in nature and in herbaria, especially in JEPS and in UC, and in accounts (floras, monographs, and revisions) by other authors. Principal publications consulted were Bentham (1873), Bremer (1994), Ferris (1960), Hickman (1993), Jepson (1925), and Robinson (1981). Also, sequence of characteristics in each lead in my keys is usually that commonly used in descriptions. The first trait mentioned in each lead is not necessarily the “best” or “most reliable” or “most easily assessed.”

Terms. Composites share some morphological traits not found in other families of plants, much as do grasses, legumes, orchids, et al. Some of the terms (and spellings) I use in characterizations of composites differ from those used in *JepsMan* and I use some terms in somewhat different senses than they are used in *JepsMan*. The differences are unfortunate. A reviewer suggested that I continue using terms and usages as found in *JepsMan*. I considered and rejected that choice. My usages are briefly reviewed below and are amplified upon where appropriate within the diagnoses and keys.

Inflorescences of composites are called **heads** or capitula. Heads typically comprise multiple florets (small flowers) of one or more kinds borne on a common **receptacle**. The florets are collectively subtended by an **involucre** of bracts (involucral bracts), here called **phyllaries**. Individual florets may be individually subtended by receptacular bracts, here called **paleae** (sing., palea). In *JepsMan*, receptacular paleae are called “chaff scales.” In some other floras, scales of a pappus may be called paleae.

Heads are often characteristically arranged on composites, much as individual flowers are on other kinds of plants. Such arrays of heads are collectively referred to as **capitulescences**. Different forms of capitulescences are referred to by using terms derived from terms for inflorescences: corymbiform, racemiform, spiciform, etc.

In plants with **liguliflorous** heads (e.g., dandelions), all florets in each head are bisexual, fertile, and zygomorphic; all florets in such heads are said to be **ligulate florets**. In **radiate** heads (e.g., daisies), the peripheral florets (**ray florets**), in one or more series, have corollas with zygomorphic limbs and the inner florets (**disc florets**) have acti-

nomorphic corollas. Ray florets may be pistillate (i.e., styliiferous and fertile), styliiferous and sterile, or neuter; disc florets may be bisexual (producing functional pollen and ovules) or functionally staminate (producing functional pollen but without functional ovules). In **discoid** heads (e.g., *ageratum*s), all florets are bisexual and fertile and have actinomorphic corollas. Technically, disc florets are found only in radiate heads. Traditionally (and here), all florets in a discoid head are called disc florets; they correspond morphologically to the true disc florets of radiate heads. In **disciform** heads (e.g., most *everlastings*), the peripheral florets (in one or more series) are pistillate and usually have relatively slender corollas with minute lobes (sometimes the peripheral florets lack corollas); the inner florets may be bisexual or functionally staminate and have actinomorphic corollas. In **radiant** heads (e.g., *cornflowers*), the peripheral florets have much enlarged, actinomorphic to somewhat zygomorphic corollas and may be bisexual, pistillate, or neuter; the inner florets are bisexual and have actinomorphic corollas.

Heads with all florets of one sexual form are called **homogamous** (discoid, liguliflorous, and some radiant heads) and those with florets of two or more sexual forms are called **heterogamous** (radiate, disciform, and most radiant heads).

Despite folklore to the contrary, composites do not always have yellow corollas. Particular corolla colors *are* characteristic of some groups of genera. As used here, **cyanic** includes true blues, mauves, pinks, purples, reds, etc.

In descriptions of corollas of composites, the terms tube, throat, and limb have been variously used. Here, for actinomorphic corollas of bisexual and functionally staminate florets, **tube** refers to the part of the corolla proximal to the insertion of the staminal filaments and **limb** refers to the part that is distal to insertion of the filaments. The limb of the corolla of a disc floret comprises a proximal **throat** and (3–)5 distal **lobes**. As treated here, the distinction between tubes and throats of corollas of disc florets is determined by insertion of filaments, not by external morphology.

The relatively flat, \pm linear, tongue-shaped or strap-shaped, zygomorphic portion of a ligulate corolla is here called a **ligule**. A ligule terminates in 5 teeth or lobes. The similar, relatively flat, zygomorphic portion of a corolla of a ray floret is here called a **lamina**. A lamina terminates in 0–3(–4) teeth or lobes. In *JepsMan*, the term *ligule* is used for corollas of both ray florets and ligulate florets. Bilabiate corollas are characteristic of some members of *Mutisieae* and are seldom found in members of other tribes.

Stamens of composites characteristically are synantherous; the anthers are connate. The individual pollen sacs of each anther may extend below the insertion of the filament (calcarate anthers) or not (ecalcarate anthers). The pollen sacs characteristically bear tails (the

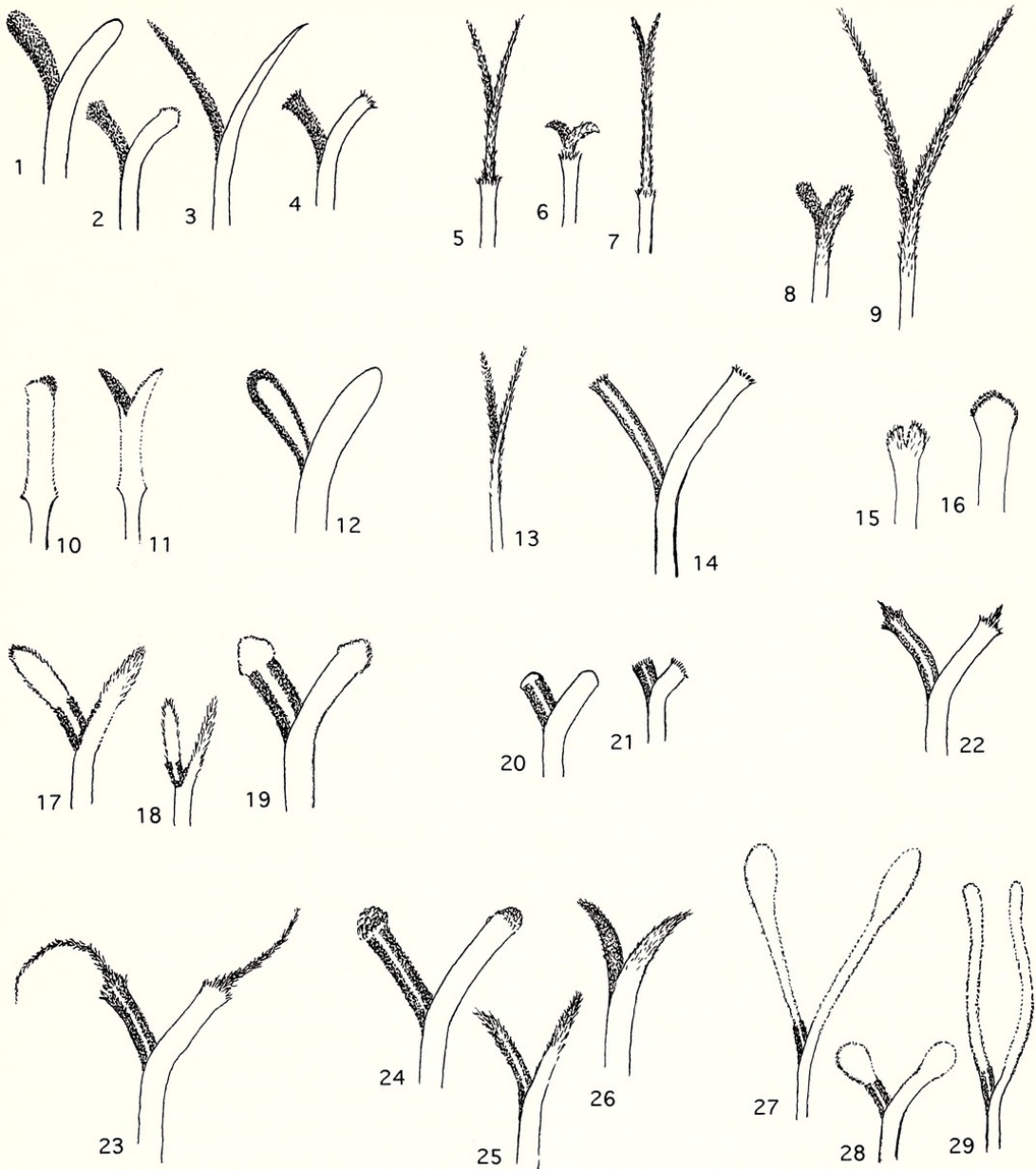
anthers are caudate) in members of the cichorioid tribes (Arctoteae, Cardueae, Lactuceae, Liabeae, Mutisieae, and Vernonieae) and in some asteroid tribes (Inuleae, Plucheeae, Gnaphalieae, and Calenduleae). Anthers of other asteroid composites (Anthemideae, Astereae, Eupatorieae, Heliantheae, and Senecioneae) usually lack tails (the anthers are ecaudate).

Style characteristics such as lengths and shapes of branches, distribution of stigmatic papillae, and shape and vestiture of stylar appendages are uniform across some tribes. Style characteristics are usually determined from bisexual, rarely from functionally staminate, florets (cf. Figs. 1–29).

Fruits of composites have been called “achenes” because they resemble true achenes. Achenes are dry, hard, single-seeded fruits derived from unicarpellate ovaries. Ovaries of composites are bicarpellate. Fruits derived from ovaries of composites are called **cypselae** (sing., cypselae). Shapes and ornamentations of cypselae have been used in distinguishing among genera. In some genera, the cypselae are characteristically \pm lenticular in cross section. Such cypselae are said to be **compressed** or laterally flattened if the longer axis of the cross section is \pm parallel to a radius of the head (e.g., *Helianthus* spp.). Cypselae are said to be **obcompressed** or dorsiventrally flattened if the shorter axis of the cross section is \pm parallel to a radius of the head (e.g., *Coreopsis* spp.).

Distal on the ovary of a composite, just proximal to the corolla, a **pappus** is usually present. Pappus may be homologous with the calyx of other flowers or it may be a novel structure. Pappi show a great range of diversity and are often diagnostic for recognition of genera of composites. The various forms of individual pappus components intergrade. Here, the following arbitrary distinctions are made: Pappus **bristles** and **awns** have \pm circular or polygonal cross sections with the length of the longer diameter of the cross section no more than 3 times that of the shorter diameter. Pappus elements with “flatter” cross sections (i.e., length of longer diameter more than 3 times that of the shorter diameter) are called **scales**, regardless of relative overall length of the pappus element. As used here, “subulate scale” means much the same as “flattened bristle,” as used in *JepsMan* and some other floras. Pliable to stiff bristles with diameters less than ca. 50 μm are called **fine bristles**; pliable to stiff bristles with diameters greater than ca. 50 μm are called **coarse bristles**. Rigid elements with \pm circular or polygonal cross sections greater than 100 μm in diameter are called **awns**. Bristles, awns, and scales may be smooth or, variously, finely to coarsely barbed or plumose. Each scale of a pappus may terminate in one or more bristle-like or awn-like appendages; such scales are said to be **aristate**; the aristae may be smooth, \pm barbellate, or plumose.

Caveat. The following keys are intended for use with Californian specimens of genera of composites as circumscribed in *JepsMan*.



FIGS. 1-29. Style branches from bisexual and functionally staminate florets representative of forms found in some tribes of Compositae. 1-4. Mutisieae. 5-7. Cardueae. 8-9. Lactuceae. 10-11. Arctoteae. 12. Inuleae. 13. Plucheeae. 14. Gnaphalieae, some Heliantheae, Senecioneae. 15-16. Calenduleae. 17-19. Astereae. 20-21. Anthemideae. 22. Senecioneae, some Heliantheae. 23. Heliantheae, some Senecioneae. 24-26. Heliantheae. 27-29. Eupatorieae.

For these keys, I have accepted generic circumscriptions as given. I assume no responsibilities for cavalier users of these keys who may rashly attempt to ply them with other taxonomies or with specimens from elsewhere.

Some couplets here are essentially statements of contrasting probabilities (e.g., corollas yellow in most spp. vs. corollas white in most spp.) rather than statements of contrasting absolutes (e.g., corollas yellow in all spp. vs. corollas white in all spp.). My failure to write

couplets based solely on absolutes may inform users about my ability to write keys. Or, my failure may inform users about circumscriptions of genera, subtribes, and tribes of composites.

KEY TO TRIBES

1. Sap usually milky; heads liguliflorous, florets all bisexual and corollas all zygomorphic, all ligulate (i.e., corolla limbs laminar, \pm linear to flabellate, and 5-lobed or 5-toothed)—styles mostly as in Figs. 8–9. II.C. Lactuceae
- 1' Sap rarely milky; heads not liguliflorous, florets bisexual, unisexual, or neuter and corollas zygomorphic or actinomorphic, none truly ligulate (i.e., corolla limbs in bisexual florets not both laminar and distally 5-lobed or 5-toothed).
 2. Corollas all zygomorphic, all bilabiate—styles mostly as in Figs. 1–4. II.A. Mutisieae p.p.
 - 2' Corollas not all zygomorphic, not all bilabiate, some or all corollas \pm actinomorphic.
 3. Cypselae stalked-glandular—styles of inner, functionally staminate florets undivided. II.A. Mutisieae p.p. (*Adenocaulon*)
 - 3' Cypselae not stalked-glandular.
 4. Actinomorphic corollas deeply cleft, lobes 5, mostly linear, length more than 3 times width in most spp.; anthers calcarate (filament insertion distal to bases of anther sacs) and tailed in most spp.; styles distally dilated or thickened or with a ring of hairs proximal to the branches in many spp., stigmatic surface continuous on adaxial face of each branch (stigmatic papillae not in 2 distinct or contiguous lines).
 5. Florets 1 in each head, the primary heads collected in second-order heads.
 6. Shrubs, mostly 4–7 dm high; leaves usually prickly-dentate, not lobed; cypselae glabrous or glabrate—style branches minute, not figured. II.A. Mutisieae p.p. (*Hecastocleis*)
 - 6' Herbs, thistle-like, mostly 1–2 m high; leaves prickly-margined, pinnately lobed; cypselae villous—styles as in Figs. 5–6. II.B. Cardueae p.p. (*Echinops*)
 - 5' Florets 3–100+ in each head, the heads not collected in second-order heads.
 7. Heads radiate (peripheral florets pistillate or neuter, corollas zygomorphic, the limb of each laminar, 3–4-toothed); pappi none or of ovate scales—styles mostly as in Figs. 10–11. II.F. Arctoteae
 - 7' Heads discoid, disciform, or radiant, not radiate; pappi of bristles (often plumose), setiform scales, or none—styles mostly as in Figs. 5–7. II.B. Cardueae p.p.
 - 4' Actinomorphic corollas not deeply cleft, lobes (3–)5, \pm deltate, length less than 3 times width in most spp. (pistillate florets may lack corollas in some spp.); anthers ecalcarate in most spp., not tailed in most spp. (but see couplet 8); styles not distally thickened nor with a ring of hairs proximal to the branches, stigmatic surfaces in 2 separate lines on each branch in most spp., in 2 contiguous lines in some spp., continuous in very few spp.
 8. Anthers distinctly tailed in most spp. [Among our plants with tailed anthers, some are woolly annuals 1–3(–10) cm high with involucre 1–3 mm high and corollas 0.5–1 mm long. III.C. Gnaphalieae p.p.]

9. Heads radiate (peripheral florets pistillate or neuter, their corollas zygomorphic with laminar, 2–3-toothed limbs).
10. Cypselae usually tuberculate, reticulate-ridged, or winged, rarely smooth, not 5-ribbed; pappi none—styles mostly as in Figs. 15–16. III.D. Calenduleae
- 10' Cypselae \pm 5-ribbed, not ridged, tuberculate, or winged; pappi of bristles or of scales and bristles—styles mostly as in Fig. 12. III.A. Inuleae
- 9' Heads discoid or disciform, all florets with actinomorphic corollas, or corollas wanting.
11. Phyllaries 12–30+ in 3–5+ series, herbaceous, not strongly scarious or broadly scarious-margined—styles mostly as in Fig. 13. III.B. Plucheeae
- 11' Phyllaries none, or 3–10 in 1–2 series, or, if 12–30+ in 3–5+ series, then strongly scarious or broadly scarious-margined—styles mostly as in Fig. 14. III.C. Gnaphalieae
- 8' Anthers not tailed (sagittate in some spp.). [Rarely diminutive woolly annuals with very small heads and corollas.]
12. Heads discoid; corollas white or pinkish to purplish, never yellow; style appendages terete to clavate, 2–3+ times longer than the stigmatic lines in most spp., shorter and \pm flattened in few spp.—see Figs. 27–29. III.I. Eupatorieae
- 12' Heads radiate, discoid, disciform, or radiant; corollas of the disc florets yellow, orange, or brown in most spp., white or cyanic in very few spp.; style appendages less than 2 times as long as stigmatic lines in most spp., longer in very few spp.
13. Phyllaries in 3–5 series and unequal in most spp., margins scarious in most spp.; pappi none or coroniform—styles mostly as in Figs. 20–21; cypselae not papillate. III.F. Anthemideae
- 13' Phyllaries in 1–2 series and \pm equal or in 3–5+ series and unequal, margins not scarious in most spp.; pappi none or variously of scales and/or bristles and/or awns, coroniform in very few spp.
14. Leaves alternate; phyllaries in 1–2 series and subequal in most spp., sometimes coherent, actually free to base or nearly so, involucre proper subtended by a calyculus of bractlets in some spp. (phyllaries in 3+ series and graduated in *Lepidospartum*); receptacles epaleate; cypselae \pm columnar to fusiform or obovoid, not strongly compressed or obcompressed, in most spp.; pappi of 30–100+ fine bristles (never plumose) in most spp. (subulate scales in some *Tetradymia* spp.), pappi none in very few spp.—styles mostly as in Fig. 22, sometimes as in Fig. 14 or 23. III.G. Senecioneae
- 14' Leaves opposite or alternate; phyllaries subequal in 1–2 series or graduated in 3–5+ series, \pm connate in some spp., involucre subtended by a calyculus in few spp. (cf. Heliantheae–Coreopsidinae and Heliantheae–Pectidinae); receptacles pa-

leate or epaleate; cypselae various, often compressed or obcompressed; pappi none or of scales and/or bristles and/or awns.

15. Leaves all alternate in most spp., basal in some spp.; phyllaries graduated in 3–5+ series in most spp., subequal in very few spp., mostly linear to oblanceolate; receptacles epaleate (except *Eastwoodia*, *Rigiopappus*, and some *Baccharis* spp.); laminae of ray corollas becoming coiled like watch springs or butterfly probosci in most spp.; anthers connate; pappi usually of bristles, seldom of scales—style-branch appendages glabrous adaxially, mostly as in Figs. 17–19.

. III.E. Astereae

- 15' Leaves opposite (at least proximally) in most spp., alternate in some spp., basal in some spp.; phyllaries subequal in 1–3 series (then linear to lanceolate) or graduated in 3–5+ series (then lanceolate to ovate or broader); receptacles paleate or epaleate; laminae of ray corollas very rarely coiled; anthers connate or free; pappi usually of scales or awns, seldom of bristles—style-branch appendages usually loosely papillose or hairy adaxially, mostly as in Figs. 23–26, sometimes as in Figs. 14, 21, 22.

. III.H. Heliantheae

I.A. Barnadesieae.

No members of the tribe were treated in *JepsMan*.

II.A. Mutisieae.

Shrubs, herbs. Leaves basal and/or cauline; alternate. Phyllaries in 1–3 series, unequal. Receptacles epaleate—hairy or glabrous. Heads radiate, disciform, or discoid. Corollas zygomorphic (often 2-lipped) or actinomorphic, usually with long lobes, sometimes with short lobes—yellow/orange, cyanic, or white. Anthers calcarate, tailed. Style branches abaxially hispidulous, stigmatic areas continuous, apices acute to rounded or truncate (Figs. 1–4). Cypselae columnar, fusiform, or clavate—often ribbed. Pappi of bristles or coroniform or none.

Key to genera as treated in *JepsMan*

1. Scapiform herbs; leaves mostly in basal rosettes, the blades white-tomentose abaxially; cypselae stalked-glandular. *Adenocaulon*
- 1' Non-scapiform herbs or shrubs; leaves cauline, the blades not white-tomentose abaxially; cypselae not stalked-glandular.
 2. Florets 1 in each head (heads grouped into second-order heads); corollas actinomorphic. *Hecastocleis*
 - 2' Florets 10–20+ in each head; corollas bilabiate.

3. Herbs; corollas pink to white. *Acourtia*
 3' Shrubs; corollas yellow. *Trixis*

II.B. Cardueae.

Herbs, sometimes coarse, to 2+ m tall. Leaves basal and/or cauline; alternate—often pinnately divided, often prickly. Phyllaries in 3–5+ series, unequal—often prickly or spine-tipped. Receptacles epaleate, often hairy or setose. Heads discoid, disciform, or radiant. Corollas mostly actinomorphic with long lobes, rarely weakly zygomorphic—yellow, cyanic, or white. Anthers calcarate, tailed. Styles dilated or with ring of hairs proximal to branches, branches short or linear, stigmatic areas continuous (Figs. 5–7). Cypselae mostly obovoid, often compressed—insertion often lateral. Pappi of bristles or subulate scales, the elements often plumose.

Key to genera treated in *JepsMan*

1. Florets 1 per head, heads grouped into globose, second-order heads. *Echinops*
- 1' Florets 3–250+ per head, heads not in second-order heads.
 2. Leaves not thistle-like, the margins not prickly (phyllaries may have prickly margins).
 3. Carpopodia and insertion scars of cypselae \pm lateral at bases of cypselae.
 4. Heads discoid, disciform, or radiant; peripheral florets often neuter or pistillate and sterile; pappi none or of persistent, nonplumose bristles or scales. *Centaurea*
 - 4' Heads discoid; all florets fertile; pappus bristles not persistent, usually \pm plumose. *Acroptilon*
 3. Carpopodia \pm central at bases of cypselae.
 5. Annuals; heads disciform; peripheral florets sterile. *Crupina*
 - 5' Biennials and perennials; heads discoid; all florets fertile.
 6. Phyllary tips usually attenuate, uncinat; pappus bristles not connate, not plumose. *Arctium*
 - 6' Phyllary tips not attenuate, rarely uncinat; pappus bristles basally connate, distally plumose.
 7. Largest leaves 5–15 cm long; involucre 5–12 mm diam.; florets 10–20 per head. *Saussurea*
 - 7' Largest leaves 60–150+ cm long; involucre 35–100+ mm diam.; florets 100–250+ per head. *Cynara* p.p.
 - 2' Leaves thistle-like, the margins prickly.
 8. Stems notably winged, the wing margins prickly.
 9. Receptacles setose-bristly, not deeply pitted; pappus bristles free. *Carduus*
 - 9' Receptacles deeply pitted, not bristly; pappus bristles basally connate. *Onopordum*
 - 8' Stems rarely winged (sometimes narrowly winged in *Cirsium* spp.).
 10. Leaves variegated with white veins or mottlings; stamen filaments connate. *Silybum*
 - 10' Leaves not variegated; stamen filaments free.
 11. Corollas white or purplish to red; carpopodia and insertion scars \pm at centers of bases of cypselae; pappi of basally connate, plumose bristles.

- 12. Largest leaves 20–50(–110) cm long; involucre 10–50 mm diam.; phyllaries ovate to linear; receptacles not becoming very fleshy. *Cirsium*
- 12' Largest leaves 60–150+ cm long; involucre 35–100+ mm diam.; phyllaries ovate to elliptic; receptacles becoming fleshy. *Cynara* p.p.
- 11' Corollas yellow to orange; carpodia displaced adaxially (toward center of receptacle) at bases of cypselae; pappi none or of free, nonplumose bristles or scales.
- 13. Heads discoid, all florets fertile; receptacles paleate; cypselae \pm 4-angled. *Carthamus*
- 13' Heads disciform, peripheral florets sterile; receptacles setose-bristly; cypselae 20-ribbed. *Cnicus*

II.C. Lactuceae.

Shrubs, herbs—sap milky white. Leaves basal and/or cauline; usually alternate, rarely opposite—often pinnately divided. Phyllaries in 2–5+ series, subequal to unequal—sometimes subtended by calyculi. Receptacles usually epaleate, rarely paleate. Heads liguliflorous. Corollas all ligulate (strap-shaped and 5-toothed)—yellow/orange, cyanic, or white. Anthers calcarate, tailed to sagittate—pollen usually lophate (with geometric patterns of spiny ridges). Style branches abaxially hispidulous, stigmatic areas continuous, apices usually acute (Figs. 8–9). Cypselae columnar, prismatic, fusiform, compressed, or obcompressed—often beaked. Pappi usually of bristles, bristles often plumose; sometimes of scales.

Lactuceae corresponds to Group 7 of *JepsMan* (p. 180–181).

II.D. Vernonieae.

No members of the tribe were treated in *JepsMan*.

II.E. Liabeae.

No members of the tribe were treated in *JepsMan*.

II.F. Arctoteae.

Herbs. Leaves basal and/or cauline; alternate—often pinnately lobed. Phyllaries in 3–5+ series, unequal—often scarious-margined. Receptacles epaleate, sometimes bristly. Heads radiate. Corollas zygomorphic or actinomorphic with short to long lobes—yellow/orange, cyanic, or white. Anthers calcarate, not tailed. Styles dilated distally, branches short, stigmatic areas continuous (Figs. 10–11). Cypselae obovoid, sometimes compressed—often shaggily villous, sometimes winged. Pappi of scales and/or bristles.

Key to genera treated in *JepsMan*

1. Phyllaries basally connate $\frac{1}{3}$ or more their lengths; laminae of ray corollas 5-nerved, 4-lobed or 4-toothed. *Gazania*
- 1' Phyllaries free to base or nearly so; laminae of ray corollas 4-nerved, 3-lobed or 3-toothed.
 2. Corollas of fresh ray florets whitish or purplish; pappi of conspicuous, unobscured scales. *Arctotis*
 - 2' Corollas of fresh ray florets yellow to orange; pappi none or minute or obscured by woolly hairs of cypselae.
 3. Fresh ray corollas uniformly yellow (drying bluish distally); cypselae woolly. *Arctotheca*
 - 3' Fresh ray corollas yellow to orange with purple at base; cypselae glabrous. *Venidium*

III.A. Inuleae.

Herbs. Leaves cauline; alternate. Phyllaries in 3–5+ series, unequal—usually chartaceous. Receptacles usually epaleate. Heads radiate. Corollas zygomorphic or actinomorphic with short lobes—yellow/orange, cyanic, or white. Anthers ecalcarate, tailed. Style branches linear, stigmatic in 2, distally confluent lines, rounded (Fig. 12). Cypselae columnar to prismatic—often ribbed. Pappi of scales and/or bristles.

Pulicaria paludosa Link is the only member of Inuleae s.s. treated in *JepsMan*.

Since *JepsMan* was published, *Dittrichia graveolens* (L.) Greuter [*Inula graveolens* (L.) Desf.] has been recorded as ruderal in \pm wet places near San Francisco Bay in sw Alameda and adjacent Santa Clara counties. The plants are erect, densely glandular (strongly scented) annuals, 2–5+ dm tall, with leaves alternate, leaf blades narrowly lanceolate to oblanceolate, 25–75 mm long, involucre obconic to campanulate, 4–7 mm high, ray corollas yellow, 2–5+ mm long, and pappi of ca. 30 bristles.

III.B. Plucheeae.

Shrubs, coarse herbs. Leaves cauline; alternate. Phyllaries in 3–5+ series, unequal—herbaceous or chartaceous. Receptacles epaleate. Heads disciform. Corollas actinomorphic with short lobes—usually cyanic or white, rarely yellow. Anthers ecalcarate, \pm tailed. Style branches oblong to linear, stigmatic in 2, ill-defined, distally confluent lines, abaxially papillate to hispidulous (Fig. 13). Cypselae \pm columnar to prismatic. Pappi of bristles.

Pluchea is the only genus of Plucheeae treated in *JepsMan*.

III.C. Gnaphalieae.

Mostly herbs—often <5 cm, often woolly. Leaves basal and/or cauline; alternate—entire, often decurrent onto stems. Phyllaries none, or 3–10 in 1–2 series, or 12–30 in 3–5+ series—often scarious-margined.

Receptacles paleate or epaleate. Heads discoid or disciform. Corollas actinomorphic with short lobes—yellow, cyanic, or white. Anthers ecalcarate, tailed. Style branches short to linear, stigmatic in 2, separate lines, obtuse or truncate (Fig. 14). Cypselae mostly obovoid, sometimes compressed. Pappi of free or basally connate bristles, the bristles sometimes plumose.

Key to genera treated in *JepsMan*

1. Plants unisexual or nearly so, the heads either with all or most florets pistillate or with all florets functionally staminate (pistillate heads rarely with 1–4 functionally staminate florets).
 2. Plants often stoloniferous, aerial stems mostly 1–2(–4) dm long; leaves of basal rosettes persisting through anthesis; cauline leaves mostly reduced. *Antennaria*
 - 2' Plants rhizomatous, aerial stems mostly 2–12 dm long; leaves of basal rosettes withering before anthesis; cauline leaves well-developed. *Anaphalis*
- 1' Plants not unisexual, the heads all \pm alike, each with 4–100+ pistillate and 2–20 functionally staminate or bisexual florets.
 3. Annuals or perennials, aerial stems to 120 cm long; phyllaries mostly 20–50+, imbricate in 3–6+ series; receptacles epaleate.
 4. Leaves often sessile, blade lengths mostly 3–5+ times widths; pistillate florets in each head usually far more numerous than bisexual florets. *Gnaphalium*
 - 4' Leaves petiolate, blade lengths 1–1.5 times widths; pistillate florets in each head usually fewer than bisexual florets.
 . . . *Helichrysum petiolare* Hilliard & B. L. Burtt. [Subshrubs, leaf blades rounded-deltate to ovate, 25–40 mm long, 20–35 mm wide, triplinerved, abaxially lanate, adaxially loosely tomentose, heads 40–60+ in crowded, corymbiform clusters, phyllaries chalky white; South African, locally naturalized in Marin County; not in *JepsMan*; noted by J. T. Howell (1970), as *Helichrysum petiolatum* (L.) DC.]
 - 3' Annuals, aerial stems to 20(–55) cm long; phyllaries none or 3–6 in 1(–2) series; receptacles paleate or not.
 5. Leaves mostly cauline and opposite. *Psilocarphus*
 - 5' Leaves mostly basal or alternate.
 6. Paleae \pm plane to concave, persistent. *Hesperervax*
 - 6' Paleae conduplicate, each falling with a cypsel.
 7. Inner florets bisexual, their cypselae pappose. *Filago*
 - 7' Inner florets functionally staminate, their ovaries mostly epappose.
 8. Innermost paleae with hardened, uncinat tips.
 *Ancistrocarphus*
 - 8' Innermost paleae similar to the outer or reduced, not uncinat at tip.
 9. Stems branched mostly from the base; style insertion terminal. *Stylocline*
 - 9' Stems branched distally or not at all; style insertion lateral.
 *Micropus*

III.D. Calenduleae.

Herbs. Leaves cauline; alternate. Phyllaries in 1–2 series, \pm equal—herbaceous. Receptacles epaleate. Heads radiate. Corollas zygomorphic or actinomorphic with short lobes—yellow/orange, cyanic,

or white. Anthers ecalcarate, tailed. Style branches stout to linear, stigmatic in 2, distally confluent lines, apically \pm truncate to deltoid (Figs. 15–16). Cypselae variously straight or coiled—usually ornamented with prickles, ridges, or wings. Pappi none.

Key to genera treated in *JepsMan*

1. Disc florets bisexual, fertile. *Dimorphotheca*
- 1' Disc florets functionally staminate.
 2. Ray corollas yellow to orange; cypselae incurved or coiled, abaxially prickly or warty. *Calendula*
 - 2' Ray corollas purplish or whitish; cypselae straight, smooth or somewhat sculptured with wavy ridges. *Osteospermum*

III.E. *Astereae*.

Shrubs, herbs. Leaves basal and/or cauline; alternate. Phyllaries usually in 3–5+ series, unequal, sometimes in 1–2 series, subequal. Receptacles epaleate, with few exceptions. Heads radiate, discoid, or disciform. Corollas zygomorphic or actinomorphic with short lobes (rarely long)—yellow (rarely orange), cyanic, or white. Anthers ecalcarate, not tailed. Style branches linear, stigmatic in 2, separate lines, adaxial faces of appendages smooth, glabrous (Figs. 17–19). Cypselae mostly obconic to obpyramidal, sometimes compressed. Pappi usually of bristles, sometimes scales or of scales and bristles, rarely none.

Key to genera treated in *JepsMan*

1. Plants unisexual, florets in each head either all pistillate (rarely with rudimentary anthers) or all functionally staminate. *Baccharis*
- 1' Plants not unisexual, not with florets of each head all pistillate or all functionally staminate (rarely some heads with all florets functionally staminate).
 2. Phyllaries equal or subequal in 1–2(–3) series.
 3. Plants scapiform herbs; receptacles conic; pappi none. *Bellis*
 - 3' Plants mostly not scapiform; receptacles mostly flat to convex; pappi usually present in most species.
 4. Pappi wholly or mostly of scales (scales subulate in some spp., see couplets 5 and 6), or an erose crown, or none (then see couplets 5 and 6).
 5. Ray florets 10–20, corollas mostly showy, white or cyanic; pappi coronas or of free or connate, erose to lacinate scales plus (0–)1–12 bristles. *Monoptilon*
 - 5' Ray florets 5–15, corollas inconspicuous, yellow, sometimes tinged with purple; pappi none or of (1–)5 subulate scales. *Rigiopappus*
 - 4' Pappi wholly or mostly of bristles (pappus sometimes none or subulate scales in *Pentachaeta* spp.; see couplet 6).
 6. Annuals; leaves linear, entire; pappi none or of 3–20 bristles or subulate scales. *Pentachaeta*
 - 6' Annuals or perennials; leaves mostly broader, entire, toothed, or pinnatifid; pappi of (5–)20–60+ bristles.
 7. Annuals or perennials; heads radiate or discoid, not dis-

- ciform, corollas of ray florets with \pm conspicuous laminae (1-)3-15+ mm long; disc florets mostly 20-100+ per head. *Erigeron* p.p.
- 7' Annuals; heads mostly disciform (if radiate, the rays inconspicuous, laminae less than 1 mm long); disc florets mostly 5-12(-20) per head. *Conyza*
- 2' Phyllaries unequal, graduated in 3-6+ series.
8. Pappi wholly or mostly of scales (scales subulate to setiform in some spp.; see couplets 9 and 11).
9. Ray florets 12-100 per head, corollas white or cyanic. *Townsendia*
- 9' Ray florets none or 1-60 per head, corollas yellow.
10. Receptacles paleate. *Eastwoodia*
- 10' Receptacles epaleate.
11. Disc florets functionally staminate; cypselae (ray) compressed or flattened with pappi of 5-20 simple or laciniate, free or connate scales (pappus scales of disc ovaries subulate or setiform, often hispidulous, often twisted or contorted). *Amphipappus*
- 11' Disc florets bisexual, fertile; cypselae not compressed or flattened; pappus scales not hispidulous, not twisted or contorted.
12. Leaves mostly serrate to dentate, rarely entire; phyllary tips spreading to recurved or coiled in most spp.; cypselae glabrous; pappus scales usually falling readily. *Grindelia*
- 12' Leaves entire; phyllary tips \pm appressed; cypselae hairy; pappus scales \pm persistent.
13. Involucres \pm cylindric to obconic or turbinate; disc florets 1-13 per head. *Gutierrezia*
- 13' Involucres hemispheric; disc florets 13-80 per head. *Acamptopappus*
- 8' Pappi wholly or mostly of bristles (with shorter, outer scales or setae in some spp.; sometimes wholly of subulate scales in *Lessingia*, see couplet 14).
14. Annuals; heads mostly radiant (all florets bisexual, corollas of 1 or more peripheral florets palmately cleft, zygomorphic; such corollas usually larger than those of more central florets); corollas cyanic in most spp., (yellow in some spp., then often tinged with purple). *Lessingia* p.p.
- 14' Mostly perennials, some annuals; heads disciform, discoid, or radiate, not radiant; disc corollas yellow in most spp., rarely tinged with purple (whitish in some members of *Chrysothamnus*; see couplet 22).
15. Heads discoid (florets all bisexual and fertile; corollas all actinomorphic).
16. Throats of corollas abruptly dilated at base. . . *Isocoma*
- 16' Throats of corollas gradually, if at all, dilated.
17. Cypselae 5-angled, glabrous, 5-10 mm long. *Hazardia* p.p.
- 17' Cypselae flat, compressed, obconic, obpyramidal, or \pm cylindric in most spp., rarely 5-angled, hairy in most spp., 1-4 mm long.
18. Cypselae flat or \pm compressed.

19. Cypselae with 5-7 ribs on each face. . . .
 *Machaeranthera* p.p.
 19' Cypselae not with 5-7 ribs on each face.
 20. Plants mostly rhizomatous, some taprooted; variously glabrous or hairy, surfaces of the hairs smooth.
 *Erigeron* p.p.
 20' Plants taprooted; most plants strigose, surfaces of the hairs knobby or verrucose. *Heterotheca* p.p.
 18' Cypselae not compressed.
 21. Plants herbaceous, aerial stems from rhizomes or caudices. *Aster* p.p.
 21' Plants suffrutescent or shrubby, aerial stems from taproots.
 22. Involucres cylindric or narrowly obpyramidal in most spp.; phyllaries mostly in 4-5 ranks, each phyllary usually keeled or medially gland-thickened, at least distally; florets 2-5(-20) per head. *Chrysothamnus*
 22' Involucres mostly obconic to hemispheric; phyllaries spirally arranged, seldom keeled or gland-thickened; florets (4-) 10-25(-70) per head.
 *Ericameria* p.p.
 15' Heads radiate (peripheral, ray, florets pistillate or neuter, corollas of ray florets with laminae 1.5-30+ mm long).
 **Go to couplet 23**
 23. Corollas of ray florets white or cyanic.
 24. Caespitose herbs or subshrubs; phyllary margins translucent.
 *Chaetopappa*
 24' Habits various, caespitose in very few spp.; phyllary margins not translucent in most spp.
 25. Coarse, rhizomatous, colonial herbs or subshrubs, often thorny; leaves linear and soon falling, or persistent and scale-like. *Chloracantha*
 25' Habits various, not thorny; leaves not soon falling, not scale-like.
 26. Leaves mostly serrate to pinnatifid, the teeth or lobes often bristle-tipped; phyllaries usually whitish to stramineous and \pm chartaceous proximally, green and herbaceous distally (rarely herbaceous throughout).
 27. Mostly herbs; heads mostly in loose, corymbiform clusters; involucres mostly 3-12(-15) mm high; laminae of ray corollas 7-15(-20) mm long. *Machaeranthera* p.p.
 27' Mostly shrubs or subshrubs; heads mostly solitary; involucres mostly 13-19 mm high; laminae of ray corollas (10-)15-30+ mm long. *Xylorhiza*
 26' Leaves entire to serrate, the teeth not bristle-tipped; phyllaries mostly uniformly herbaceous (herbaceous medially and distally and chartaceous only laterally at the base in some spp.).
 28. Phyllaries (all or at least some) each marked with 3 orange veins (at least near base). *Trimorpha*
 28' Phyllaries not marked with 3 orange veins (sometimes 1 orange vein in each phyllary in some spp.).

29. Phyllaries mostly lanceolate to linear, not thickened distally; style branch appendages shorter than stigmatic areas in most spp.; pappi double (with short, outer setae subtending the primary bristles) in many spp. *Erigeron* p.p.
- 29' Phyllaries mostly oblanceolate or broader, often thickened distally; style branch appendages longer than stigmatic areas, or at least longer than wide, in most spp.; pappi simple (without outer setae) in most spp.
30. Stems usually \pm tomentose; ray florets neuter; pappi reddish. *Lessingia* p.p.
- 30' Stems seldom, if ever, tomentose; ray florets pistillate, fertile; pappi seldom reddish. *Aster* p.p.
- 23' Corollas of ray florets yellow in most spp., pale or tinged with purple in some spp.
31. Disc florets all functionally staminate.
32. Annuals; ray florets 5–8 per head; pappi of 2–8 fragile bristles. *Lessingia* p.p.
- 32' Perennials; ray florets 1–3 per head; pappi of 20+ persistent bristles. *Petradoria*
- 31' Disc florets all or mostly bisexual and fertile (the innermost sometimes functionally staminate in *Prionopsis*; see couplet 39).
33. Pappus bristles (disc; ray cypselae often epappose) subtended by scales or setae to 1 mm long. *Heterotheca* p.p.
- 33' Pappus bristles (disc and ray) subequal or intergrading in most spp., the outer seldom shorter than and contrasting with the inner.
34. Habit annual; cypselae fusiform, distally rostrate or beaked. *Tracyina*
- 34' Habit perennial in most spp., annual in some spp.; cypselae not fusiform, not rostrate or beaked.
35. Shrubs with entire leaves. *Ericameria* p.p.
- 35' Herbs or, if shrubby, leaves mostly serrate.
36. Perennials, from rhizomes or caudices.
37. Leaves mostly spatulate to ovate, serrate or entire, not resin-gland-dotted; heads often in second, racemiform clusters; ray florets mostly 3–15(–21) per head. *Solidago*
- 37' Leaves mostly linear, entire, sometimes resin-gland-dotted; heads solitary or in corymbiform clusters; ray florets mostly 15–38 per head.
38. Heads in corymbiform clusters; ray florets 15–25 per head; disc florets 6–15 per head. *Euthamia*
- 38' Heads solitary; ray florets 25–38 per head; disc florets mostly 30–60+ per head. *Erigeron* p.p.
- 36' Perennials (some with branched caudices; see couplet 42), biennials, and annuals from taproots.
39. Annuals, biennials, or short-lived perennials, mostly herbs; leaves serrate to pinnatifid, the teeth or lobes bristle-tipped.
40. Cypselae hairy (ray and disc); pappus bristles \pm free to base, persistent. *Machaeranthera* p.p.
- 40' Cypselae mostly glabrous (those of disc sometimes puberulent); pappus bristles \pm connate at base, falling \pm together, \pm readily. *Prionopsis*

- 39' Perennials, herbs, subshrubs, or shrubs; leaves entire or toothed, the teeth not bristle-tipped in most spp. (if bristle-tipped, see couplet 42).
- 41. Stems \pm prostrate, plants mat-forming; leaves clustered at ends of stems; heads solitary on erect, \pm naked peduncles. *Stenotus*
- 41' Stems decumbent to erect, plants seldom mat-forming; leaves not clustered at ends of stems; heads 1–5+ on leafy stems or bracteate peduncles.
- 42. Shrubs or subshrubs, stems 2–25 dm long; leaves mostly cauline, sometimes with bristle-tipped teeth. *Hazardia* p.p.
- 42' Herbs from woody taproots or branched caudices, stems 5–90 cm long; leaves both basal and cauline or mostly basal, seldom with bristle-tipped teeth.
- 43. Leaves and/or stems loosely tomentose to woolly in most spp., glandular-punctate in some spp., \pm glabrous in some spp., stipitate-glandular (only distally) in some spp.; cypselae obpyramidal, 3–4-angled. *Pyrrocoma*
- 43' Leaves and stems densely stipitate-glandular, \pm viscid throughout or nearly so; cypselae various shapes, not obpyramidal, not 3–4-angled. *Tonestus*

III.F. Anthemideae.

Herbs, rarely subshrubs or shrubs. Leaves mostly cauline, sometimes basal; alternate—often finely dissected, usually strong-scented. Phyllaries in 3–5 series, unequal—scarious-margined. Receptacles paleate or epaleate—sometimes hairy. Heads radiate, discoid, or disciform. Corollas zygomorphic or actinomorphic with short lobes—yellow, cyanic, or white. Anthers ecalcarate, not tailed. Style branches linear, stigmatic in 2, separate lines, usually truncate (Figs. 20–21). Cypselae columnar to prismatic, sometimes compressed—sometimes ribbed or winged. Pappi usually none, sometimes of scales or coroniform—never of bristles.

Key to genera treated in *JepsMan*

- 1. Heads radiate.
 - 2. Receptacles paleate.
 - 3. Capitulescences mostly of 12–50+ heads in close, corymbiform clusters; ray florets 3–8 per head. *Achillea*
 - 3' Capitulescences of 2–10 heads in loose, cymiform clusters or heads solitary; ray florets 10–25 per head.
 - 4. Cypselae 10-ribbed. *Anthemis*
 - 4' Cypselae 2–3-striate or weakly 2–3-ribbed. . . . *Chamaemelum*
 - 2' Receptacles epaleate.
 - 5. Cypselae all 5–10-ribbed, none winged.
 - 6. Laminae of ray corollas 10–40+ mm long. . . . *Leucanthemum*
 - 6' Laminae of ray corollas 5–8 mm long. *Tanacetum* p.p.

- 5' Cypselae of rays 1–4-winged, those of the disc winged or not.
 - 7. Shrubs or subshrubs; ray corollas white in most spp. *Argyranthemum*
 - 7' Annuals; ray corollas yellow to orange in most spp., white with red or purple base in very few spp.
 - 8. Plants \pm glabrous; wings of cypselae not ending in spine-like processes. *Chrysanthemum*
 - 8' Plants viscid; wings of cypselae distally firm and sharp, spine-like. *Heteranthemis*
- 1' Heads discoid or disciform (peripheral, pistillate florets may lack corollas).
 - 9. Heads discoid, all florets bisexual.
 - 10. Receptacles convex, paleate; cypselae 3–5-angled. *Santolina*
 - 10' Receptacles \pm conic, epaleate; cypselae ovoid and smooth or weakly obcompressed and obscurely 5-ribbed on adaxial faces.
 - 11. Shrubs and coarse herbs; capitulescences racemiform or paniculiform; florets 3–30 per head. . . . *Artemisia* p.p. (*Seriphidium*)
 - 11' Annuals; capitulescences of solitary or loosely clustered heads; florets 50–150+ per head. *Chamomilla* (*Matricaria*)
 - 9' Heads disciform, peripheral florets pistillate.
 - 12. Pistillate florets lacking corollas.
 - 13. Heads pedunculate. *Cotula*
 - 13' Heads sessile in leaf axils. *Soliva*
 - 12' Pistillate florets all with corollas.
 - 14. Capitulescences usually tightly corymbiform, sometimes loosely corymbiform; receptacles convex; pappi usually present, coroniform. *Tanacetum* p.p.
 - 14' Capitulescences paniculiform, racemiform, or spiciform, or heads solitary in most spp., corymbiform in very few spp.; receptacles hemispheric to conic; pappi mostly none.
 - 15. Heads mostly 20–200+ per capitulescence; florets 3–25(–60+) per head. *Artemisia* s.s.
 - 15' Heads mostly 1–10 per capitulescence; florets mostly 30–50 per head. *Sphaeromeria*

III.G. Senecioneae.

Shrubs, herbs. Leaves basal and/or cauline; alternate—pinnately divided, toothed, or entire. Phyllaries usually in 1–2 series, subequal (3–5-seriate, unequal in *Lepidospartum*)—sometimes subtended by calyculi. Receptacles epaleate. Heads radiate, discoid, or disciform. Corollas zygomorphic or actinomorphic with short lobes—usually yellow, rarely orange, cyanic, or white. Anthers ecalcarate, not tailed. Style branches linear, stigmatic in 2, separate lines, usually truncate, sometimes appendaged (Figs. 14, 22–23). Cypselae obovoid, columnar, or prismatic. Pappi usually of fine bristles, rarely of subulate scales, the elements never plumose.

Key to genera treated in *JepsMan*

- 1. Receptacles hemispheric to conic; cypselae usually with myxogenic hairs or papillae (exuding mucilage after being wetted).
 - 2. Ray corollas with very short or no tube; disc florets functionally staminate; pappi none. *Blennosperma*

- 2' Ray corollas with distinct tube; disc florets bisexual; pappi of fine bristles.
..... *Crocidium*
- 1' Receptacles flat to convex; cypselae glabrous or variously hairy, not with myxogenic hairs or papillae.
 - 3. Corollas whitish to purplish; anther-bearing florets functionally staminate.
..... *Petasites*
 - 3' Corollas yellow in most spp., white, ochroleucous, or purple in few spp.; anther-bearing florets bisexual.
 - 4. Heads radiate. *Senecio* p.p.
 - 4' Heads discoid or disciform.
 - 5. Heads disciform. *Erechtites*
 - 5' Heads discoid.
 - 6. Herbs (never climbing).
 - 7. Leaves palmately veined and lobed. *Cacaliopsis*
 - 7' Leaves pinnately veined (or 1-nerved).
 - 8. Leaves variously hairy, not both densely white-tomentose abaxially and glabrous-shiny adaxially; involucre often calyculate; phyllaries often black-tipped; style branches truncate-penicillate.
..... *Senecio* p.p.
 - 8' Leaves abaxially densely white-tomentose, adaxially glabrous-shiny; involucre not calyculate; phyllaries not black-tipped; style branches rounded-truncate. ...
..... *Luina*
 - 6' Shrubs or vines.
 - 9. Vines; leaves \pm palmately lobed. *Senecio* p.p.
 - 9' Shrubs; leaves not palmately lobed, mostly spatulate to oblanceolate, or linear to filiform, or scale-like.
 - 10. Capitulescences umbelliform or heads solitary; phyllaries 4–5(–9), subequal in 1–2 series. *Tetradymia*
 - 10' Capitulescences paniculiform; phyllaries 8–23, graduated in 3–5+ series. *Lepidospartum*

III.H. *Heliantheae*.

Shrubs, herbs. Leaves basal and/or cauline; opposite or alternate—blades pinnately divided, toothed, or entire. Phyllaries in 1–2 series and subequal or 3–5+ series and unequal—rarely subtended by calyculi. Receptacles paleate or epaleate. Heads radiate, discoid, disciform, or radiant. Corollas zygomorphic or actinomorphic, usually with short lobes—usually yellow/orange, rarely cyanic or white. Anthers ecalcarate, not tailed. Style branches linear, usually stigmatic in 2, separate lines (sometimes stigmatic areas continuous), adaxial faces of appendages papillate or hairy (Figs. 23–26). Cypselae obovoid, columnar, prismatic, or fusiform, often weakly to strongly compressed or obcompressed, sometimes winged. Pappi usually of scales, sometimes of scales and bristles or wholly of bristles or none—bristles rarely plumose.

Key to subtribes for genera treated in *JepsMan*

- 1. Heads unisexual in most spp.; pistillate florets without corollas in most spp.; anthers free in most spp. (filaments connate in some spp.). *Ambrosiinae*

- 1' Heads not unisexual; pistillate florets bearing corollas in nearly all spp.; anthers connate (filaments not connate).
2. Leaves and/or phyllaries dotted or streaked with pellucid, schizogenous glands containing strong-scented oils. Pectidinae
- 2' Leaves and/or phyllaries rarely streaked or dotted, never with pellucid, schizogenous glands containing strong-scented oils (plants may have sessile or stipitate, surface glands and may be otherwise strong-scented, e.g., from sesquiterpene-lactones; pellucid streaks of some Coreopsidinae do not contain strong-scented oils).
3. Receptacles wholly or partially paleate (i.e., at least one series of paleae between ray florets and disc florets).
 4. Plants with tack-glands or pit-glands on stems, leaves, and/or phyllaries in some species; phyllaries in 1+ series, each phyllary wholly or partially investing the ovary of a subtended floret in most spp.; paleae restricted to a single series at periphery of head in most spp., often connate in a ring (each disc floret subtended by a palea in very few spp.); laminae of ray corollas often flabellate, deeply lobed; pappus elements various, sometimes coarse, plumose or woolly bristles or subulate, plumose or woolly scales. . . Madiinae
 - 4' Plants without tack-glands or pit glands; phyllaries in (1-)2-7+ series, each inner phyllary wholly or partially investing the ovary of a subtended floret in very few spp.; paleae not restricted to periphery of head, all or nearly all disc florets subtended by paleae; laminae of ray corollas seldom flabellate or deeply lobed; pappus elements various, plumose in very few spp.
 5. Phyllaries in 2-3 series, those of the single outer series often shorter than and contrasting sharply with those of the 1-2 inner series (the outer series often termed a calyculus); disc cypselae obcompressed or quadrangular-fusiform. . . . Coreopsidinae
 - 5' Phyllaries in 1-6+ series, the outer \pm similar to or intergrading with the inner; disc cypselae seldom obcompressed or quadrangular-fusiform.
 6. Phyllaries falling with the cypselae in fruit; ray florets (if any) pistillate and fertile.
 7. Anther thecae pale; pappi of \pm plumose, subulate scales or bristles. . . Galinsoginae p.p. (*Galinsoga*)
 - 7' Anther thecae black; pappi none. Milleriinae.
 - 6' Phyllaries persistent in fruit; ray florets (if any) pistillate and fertile, or styliferous and sterile, or neuter.
 8. Receptacles spheric to high-conic or columnar, mostly 8-20+ mm high. Rudbeckiinae
 - 8' Receptacles mostly flat to convex or conic, mostly less than 5 mm high.
 9. Leaves mostly cauline and alternate (none or only the proximal opposite); ray florets neuter, or styliferous and sterile; pappi, if present, of fragile or caducous scales or awns. Helianthinae
 - 9' Leaves mostly basal or opposite, sometimes alternate; ray florets pistillate and fertile in most spp. (if neuter, leaves mostly basal or alternate); pappi present and persistent in most spp.: scales, awns, and/or bristles.
 10. Heads discoid; pappi of 15-30 \pm plumose bristles or subulate scales.
 - Galinsoginae p.p. (*Bebbia*)

- 10' Heads radiate or discoid; pappi none or of 2(–8) non-plumose scales. Ecliptinae
- 3' Receptacles wholly epaleate in most spp., rarely bearing setiform or conic enations (Gaillardinae, *Gaillardia*) or \pm membranous paleae (Chaenactidinae, *Chaenactis carphoclinia*); see also, first lead of couplet 4 (Madiinae).
11. Stems to 5 cm long; phyllaries 2–3; florets 2–3 in each head; pappi of ca. 20 subulate, plumose, basally connate scales. Dimeresiinae
- 11' Stems mostly more than 5 cm long; phyllaries 2–50+; florets 2–100+ in each head; pappi none or of nonplumose bristles and/or scales in most spp.
12. Leaves opposite, oblong to linear or filiform, sessile or nearly so, often somewhat succulent; cypselae cylindric to clavate and 8–15-ribbed.
13. Plants usually erect, seldom rooting at nodes; phyllaries 2–5, subequal, in 1 series. Flaveriinae
- 13' Plants prostrate, rooting at nodes; phyllaries 12–15+, graduated, in 3+ series. Jaumeinae
- 12' Leaves various; cypselae various, not both cylindric to clavate and 8–15-ribbed (cylindric and 5–10-nerved in some *Arnica* spp., in Chaenactidinae).
14. Phyllaries \pm navicular; disc corollas usually 4-lobed; cypselae strongly compressed, callous-margined, often ciliate. Peritylinae
- 14' Phyllaries flat to \pm concave or weakly navicular; disc corollas (4–)5-lobed; cypselae various (strongly compressed and callous-margined or ciliate in very few spp.).
15. Cypselae stoutly obconic to obpyramidal, length seldom more than 2.5(–3.5) times the thickness in most spp.
16. Phyllaries mostly not scarious-margined; disc corollas often with moniliform hairs on tube, throat, and/or lobes; cypselae not both 4-angled and 12–16-ribbed. Gaillardinae
- 16' Phyllaries notably scarious-margined; disc corollas without moniliform hairs; cypselae mostly 4-angled and 12–16-ribbed. . . Hymenopappinae
- 15' Cypselae narrowly obconic or obpyramidal to clavate or columnar, length more than 3.5 times the thickness in most spp. (if shorter, then \pm compressed).
17. Leaves sessile in most spp., obscurely petiolate in few spp., rarely truly petiolate; pappus scales, if any, not medially thickened. Baeriinae
- 17' Leaves clearly petiolate in most spp. (\pm sessile in some spp. of *Arnica*, *Chaenactis*, *Hulsea*); pappus scales, if any, notably medially thickened in most spp. Chaenactidinae

Heliantheae—Ambrosiinae

1. Pistillate and functionally staminate florets together in same head (some spp. with some heads staminate); cypselae not enclosed in perigynia (nut-like or bur-like structures).
2. Cypselae obcompressed or not, without wing-like margins. *Iva*

- 2' Cypselae strongly obcompressed and with toothed or lobed, wing-like margins. *Dicoria*
- 1' Pistillate and functionally staminate florets in separate heads; cypselae enclosed within hardened, often prickly, tuberculate, or winged, perigynia.
 - 3. Phyllaries of staminate heads free to base, receptacles conic. *Xanthium*
 - 3' Phyllaries of staminate heads partially or wholly connate, receptacles flat or convex.
 - 4. Perigynia prickly, tuberculate, or unarmed. *Ambrosia*
 - 4' Perigynia bearing 5–15+ scarious, cuneate to flabellate wings. *Hymenoclea*

Heliantheae—Baeriinae

- 1. Leaves all or mostly opposite. *Lasthenia*
- 1' Leaves mostly alternate (proximal leaves opposite or in rosettes in few spp.).
 - 2. Plants glabrous or granular-glandular, not at all woolly. *Amblyopappus*
 - 2' Plants sparsely to densely woolly on stems and/or leaves and/or phyllaries.
 - 3. Heads disciform (4–7 peripheral florets pistillate, with tubular corollas) or inconspicuously radiate. *Lembertia*
 - 3' Heads conspicuously radiate or truly discoid.
 - 4. Phyllaries becoming reflexed in fruit. *Eatonella*
 - 4' Phyllaries not reflexed in fruit.
 - 5. Ray corollas obscurely bilabiate, with a minute adaxial lobe opposite the lamina. *Monolopia*
 - 5' Ray corollas not bilabiate, or rays none.
 - 6. Annuals or perennials; corollas without rings of hairs at bases of limbs; ray cypselae prismatic, 4–5-angled in most spp. *Eriophyllum*
 - 6' Annuals; corollas each with a ring of hairs at base of limb; ray cypselae \pm obcompressed. *Pseudobahia*

Heliantheae—Chaenactidinae

- 1. Pappi wholly or partially of bristles (pappi none and ray corollas whitish with red veins in *Syntrichopappus lemmonii*; see couplet 3).
- 2. Leaves all or mostly opposite. *Arnica*
- 2' Leaves mostly basal or alternate.
 - 3. Shrubs; leaves linear-filiform. *Peucephyllum*
 - 3' Herbs; leaves not linear-filiform. *Syntrichopappus*
- 1' Pappi none or wholly of scales: all, some, or none of the scales aristate.
 - 4. Leaves all or mostly cauline and all or mostly opposite (some spp. with few distal leaves alternate).
 - 5. Ray corollas persistent, becoming papery; disc florets usually functionally staminate; cypselae obovoid or plumply fusiform, smooth or ca. 20-ribbed. *Whitneya*
 - 5' Ray corollas withering, not becoming papery, or rays wanting; disc florets bisexual, fertile; cypselae obpyramidal, usually 4-angled.
 - 6. Phyllaries 4–9(–12), margins usually purplish or yellowish. *Schkuhria*
 - 6' Phyllaries (5–)8–21+, margins not purplish or yellowish. *Bahia* p.p.
 - 4' Leaves all or mostly basal, or mostly cauline and mostly alternate (some spp. with few proximal leaves opposite).
 - 7. Phyllaries unequal, the outer foliaceous, rotund to broadly ovate, spreading or reflexed. *Venegasia*

- 7' Phyllaries subequal, all linear or lanceolate to spatulate or oblanceolate, appressed.
- 8. Disc corolla lobes lance-linear to linear, length mostly 2 or more times width.
 - 9. Pappus scales 12–18. *Hymenothrix*
 - 9' Pappus scales 4–10. *Palafoxia*
- 8' Disc corolla lobes deltate to lance-deltate or ovate, length mostly less than 2 times width (sometimes more in zygomorphic corollas of some *Chaenactis* spp.; see couplet 11).
- 10. Stems and/or leaves sparsely to densely hairy with white, straight, often conic or fusiform, hairs 0.1–0.8 mm long in most spp., not cobwebby or woolly, some spp. glabrous, some spp. stipitate-glandular, most spp. glandular-punctate or resin-gland-dotted; cypselae obpyramidal, sharply 4–5-angled. *Bahia* p.p.
- 10' Stems and/or leaves thinly cobwebby to densely woolly with crisped, tangled, or matted hairs more than 0.8 mm long, or finely granular-pubescent with bulbous hairs less than 0.2 mm long, or glabrous, some spp. stipitate-glandular or glandular-punctate; cypselae obconic, clavate, or linear, often compressed, obscurely, if at all, 4–5-angled.
 - 11. Ray florets 9–60+. *Hulsea*
 - 11' Ray florets none (corollas of peripheral florets sometimes zygomorphic and larger than the inner ones).
 - 12. Capitulescences loosely corymbiform or heads solitary; disc florets 8–40+. *Chaenactis*
 - 12' Capitulescences tightly corymbiform or glomerulate; disc florets 4–9. *Orochaenactis*

Heliantheae—Coreopsidinae

- 1. Principal phyllaries connate 1/5–7/8 their lengths. *Thelesperma*
- 1' Principal phyllaries free to the base, or nearly so.
- 2. No cypselae strongly 4-angled, all strongly obcompressed, none distally attenuate or beaked.
 - 3. Cypselae orbicular to linear-ovate, usually all within a head \pm winged; pappi not of retrorsely barbed awns. *Coreopsis*
 - 3' Cypselae cuneate or linear to spatulate, few, if any, within a head winged; pappi usually of retrorsely barbed awns. *Bidens* p.p.
- 2' At least innermost cypselae 4-angled, sulcate on the faces, distally attenuate or beaked.
 - 4. Paleae mostly persistent on receptacles; peripheral cypselae mostly much shorter and flatter than the slender, more attenuate inner ones. *Bidens* p.p.
 - 4' Paleae mostly not persistent, commonly falling with the cypselae; cypselae within a head all more-or-less the same shape and intergrading in length. *Cosmos*

Heliantheae—Dimeresiinae

Dimeresia is the only genus in Dimeresiinae.

Heliantheae—Ecliptinae

- 1. Ray corollas sessile, persistent, and becoming papery. *Sanvitalia*
- 1' Ray corollas seldom sessile (i.e., typically the lamina borne on a tube), never persistent and becoming papery, rarely wanting.

2. Receptacular paleae linear-filiform, not conduplicate; corollas of ray and disc florets whitish. *Eclipta*
- 2' Receptacular paleae lanceolate to ovate, conduplicate; corollas of ray and disc florets yellow to orange.
3. Cypselae prismatic, or nearly so, 3–4-angled.
 4. Cauline leaves well-developed; pappi none or 3–4 teeth or scales. *Wyethia*
 - 4' Cauline leaves much reduced; pappi none. *Balsamorhiza*
- 3' Cypselae weakly compressed to strongly flattened, not at all prismatic.
 5. Some or all cypselae winged (i.e., each bordered by a wing of membranous or corky tissue different from that of the body of the cypselae); pappi of 2 persistent subulate or aristate scales or awns without any additional scales. *Verbesina*
 - 5' Cypselae sometimes sharp-edged but none truly winged; pappi various, rarely as above.
 6. Leaves all or mostly basal, scapiform herbs; involucre 20–30+ mm diam. *Enceliopsis*
 - 6' Leaves basal and cauline or mostly cauline, herbs or shrubs; involucre 4–30 mm diam.
 7. Basal leaves persisting; cypselae thin-edged, not white-margined or ciliolate. *Helianthella*
 - 7' Basal leaves ephemeral; cypselae white-margined and ciliolate.
 8. Shrubs. *Encelia*
 - 8' Herbs (annual or perennial). *Geraea*

Heliantheae—Flaveriinae

Flaveria is the only genus of Flaveriinae treated in *JepsMan*.

Heliantheae—Gaillardiiinae

1. Pappi of 35–140 free or basally connate bristles in 1–4 series. *Psathyrotes*
- 1' Pappi none or of 2–12 subulate or broader scales.
 2. Pappus scales 5, ovate to flabellate, deeply and finely lacerate, each seemingly constituted of 8–15+ connate bristles. *Trichoptilium*
 - 2' Pappi none or of 2–12 scales, the scales not flabellate and finely lacerate, variously ovate or spatulate to lanceolate or subulate, entire, erose, or coarsely lacerate, often attenuate or uniaristate.
 3. Phyllaries strongly reflexed in fruit; receptacles mostly globose, with or without setiform enations; disc corollas often brown-purple or marked with brown-purple, with tube much shorter than the abruptly much-dilated, urceolate to campanulate throat, lobes often shaggily hairy with moniliform hairs.
 4. Leaves not linear-filiform or divided into linear-filiform lobes nor with bases decurrent on stems; receptacles usually bearing setiform enations. *Gaillardia*
 - 4' Leaves linear-filiform, or divided into linear-filiform lobes, or broader and not divided (then with bases strongly decurrent on stems); receptacles rarely bearing setiform enations. *Helenium*
 - 3' Phyllaries mostly erect to spreading in fruit; receptacles flat to ovoid, conic, domed, or hemispheric, variously smooth to pitted, without setiform enations; disc corollas uniformly yellow to cream or, sometimes, reddish, with tube much shorter than to about equalling the slightly dilated, funnelform to cylindric throat, lobes not shaggily hairy with moniliform hairs.
 5. Corollas of ray florets withering (rarely none in *Hymenoxys*; see couplet 6), falling early or tardily.

- 6. Outer phyllaries connate 1/5–1/2+ their lengths. *Hymenoxys* (s.s.)
- 6' Outer phyllaries free to the base or nearly so. *Dugaldia*
- 5' Corollas of ray florets persistent (rarely none in *Tetaneuris*; see couplet 8), becoming strongly reflexed and papery.
- 7. Pappi none. *Baileya*
- 7' Pappi of 4–6 scales.
- 8. Plants mostly scapiform with heads borne singly; involucre hemispheric to rotate; ray florets none or 5–21+; disc florets 25–150+. *Hymenoxys* (*Tetaneuris*)
- 8' Plants not scapiform, heads usually in close corymbiform or glomerulate clusters; involucre cylindric to campanulate; ray florets 2–7; disc florets 8–25+. *Psilostrophe*

Heliantheae—Galinsoginae

- 1. Annuals; cypselae of ray florets each shed together with a subtending phyllary and 2 adjacent paleae. *Galinsoga*
- 1' Perennials; cypselae shed separate from the phyllaries and the persistent or tardily falling receptacular paleae. *Bebbia*

Heliantheae—Helianthinae

- 1. Pappi present, caducous. *Helianthus*
- 1' Pappi none, or persistent or falling tardily.
- 2. Leaves mostly 3- or 5-nerved; phyllaries 12–21+ in 2–6+ series, subequal or strongly graduate, the outer ribbed, or keeled, or indurate at base; pappi present or absent. *Viguiera*
- 2' Leaves usually 1-nerved; phyllaries 12–21 in 2–3 series, mostly subequal, uniformly herbaceous; pappi none. *Heliomeris*

Heliantheae—Hymenopappinae

Hymenopappus is the only genus of Hymenopappinae treated in *JepsMan*.

Heliantheae—Jaumeinae

Jaumea is the only genus of Jaumeinae treated in *JepsMan*.

Heliantheae—Madiinae

- 1. Cypselae all \pm cylindric, fusiform, or prismatic, sometimes 8–10-ribbed or -nerved, hairy in most species (if rays none, plants perennial).
- 2. Perennials.
 - 3. Plants mostly scapiform; leaves mostly basal. *Raillardella*
 - 3' Plants not scapiform; leaves mostly cauline. *Raillardopsis*
- 2' Annuals.
 - 4. Corollas yellow to red; pappi of 10, \pm spatulate, nonplumose scales, 5 shorter, alternating with 5 longer. *Achyrachaena*
 - 4' Corollas white (sometimes with reddish nerves); pappi none or of 12–20, subulate, ciliolate to plumose scales.
 - 5. Leaves basal and cauline, the proximal usually toothed; receptacles with paleae in 1(–2) peripheral series; flowering mostly in fall. *Blepharizonia*

- 5' Leaves mostly cauline, entire; receptacles paleate throughout; flowering mostly in late spring. *Blepharipappus*
- 1' Cypselae of ray florets \pm obcompressed, or laterally compressed, or stoutly obovoid, never 8–10-ribbed, usually glabrous (if rays none, plants annual).
6. Involucres closely subtended by 3–6 caducous, phyllary-like bractlets; disc florets 3–6, functionally staminate. *Lagophylla*
- 6' Involucres not closely subtended by caducous bractlets; disc florets 1–60+, usually bisexual and fertile (if functionally staminate, usually more than 6).
7. Leaves and phyllaries bearing open, thick-stalked or sessile pit-glands; each disc floret subtended by a palea, the paleae free. . . . *Holocarpa*
- 7' Leaves and phyllaries gland-bearing or not, none with pit-glands; in most spp. only the peripheral disc florets subtended by paleae, the paleae free or connate in a ring.
8. Receptacular paleae in most spp. connate and persistent; ray, or all, cypselae \pm laterally compressed and \pm arcuate (if \pm obovoid, disc florets 1–2). *Madia*
- 8' Receptacular paleae connate or free, not persistent; ray cypselae \pm obcompressed or none.
9. Ray cypselae each \pm completely invested by a subtending phyllary, the two margins of each phyllary \pm overlapping (or rays none).
10. Perennials; rays 5, corollas inconspicuous, white to purplish; pappi of 1–5 bristles or none; flowering mostly in summer and fall. *Holozonia*
- 10' Annuals; rays none or 3–27, corollas showy, variously yellow, white, or yellow/white; pappi of 2–32 bristles or subulate scales, the scales often plumose or woolly, or pappi none; flowering mostly in spring. *Layia*
- 9' Ray cypselae each only partially invested by a subtending phyllary.
11. Proximal leaves often pinnately lobed or divided; ray florets (3–)5–34+, limbs of the corollas not deeply lobed; disc florets (3–)13–60+. *Hemizonia*
- 11' Proximal leaves entire; ray florets 1–6, limbs of the corollas deeply lobed; disc florets 3–12(–25).
12. Leaves and phyllaries without tack-glands; ray cypselae beaked. *Osmadenia*
- 12' Distal leaves and phyllaries bearing tack-glands; ray cypselae not beaked. *Calycadenia*

Heliantheae—Milleriinae

Guizotia is the only genus of Milleriinae treated in *JepsMan*.

Heliantheae—Pectidinae

1. Leaves opposite, undivided, and proximally bristly-ciliate; ray florets each borne on base of a subtending phyllary; style branches short, knob-like. *Pectis*
- 1' Leaves opposite or mostly alternate, often divided or lobed, bristly-ciliate at base in few spp.; ray florets not borne on bases of subtending phyllaries; style branches linear.
2. Phyllaries free to base or nearly so.
3. Calyculus none; pappi wholly of free, coarse to fine bristles.
. *Porophyllum*
- 3' Calyculus of (0–)1–9 linear to deltate bractlets; pappi wholly or partially of scales (scales may be each constituted of 5–10 basally connate bristles).

- 4. Ray corollas yellow to orange. *Dyssodia*
- 4' Ray corollas white to pink or magenta. *Nicotletia*
- 2' Phyllaries connate at least $\frac{1}{3}$ their lengths (outer margins may be free to base).
- 6. Calyculus none; pappi of 2–5(–10) elements in 1 series, mostly 1–2(–5) shorter, erose or truncate plus 1–2(–5) elongate or uniaristate. . . . *Tagetes*
- 6' Calyculus present; pappi of 8–20 elements in 2 series, variously constituted, not as above.
- 7. Plants mostly less than 2 dm tall; leaves mostly linear-filiform or with linear-filiform lobes; involucre 4–6 mm high, 3–6 mm diam.; phyllaries strongly connate $\frac{2}{3}$ or more of their lengths. *Thymophylla*
- 7' Plants mostly more than 2 dm tall; leaves or lobes linear or broader; involucre 7–18 mm high, 5–12 mm diam.; phyllaries weakly connate $\frac{1}{3}$ – $\frac{2}{3}$ their lengths. *Adenophyllum*

Heliantheae—Peritylinae

- 1. Leaf blades variously lobed or entire, mostly less than 3 cm long; phyllaries 8–16 in 2–3 series, free. *Perityle*
- 1' Leaf blades triangular-hastate to narrowly deltate, not lobed, 3–12 cm long; phyllaries 15–21 in 1(–2) series, wholly or partially connate. *Pericome*

Heliantheae—Rudbeckiinae

Rudbeckia is the only genus of Rudbeckiinae treated in *JepsMan*.

III.I. Eupatorieae.

Shrubs, herbs. Leaves mostly cauline, sometimes basal or basal and cauline; mostly opposite, sometimes alternate. Phyllaries in 2–5+ series, unequal to subequal. Receptacles usually epaleate. Heads discoid. Corollas actinomorphic with short lobes—cyanic or white. Anthers ecalcarate, not tailed. Style branches usually terete to filiform, stigmatic in 2, separate lines—appendages usually 3–6+ times as long as stigmas (Figs. 27–29). Cypselsae usually prismatic and 5-ribbed, sometimes 7–10-ribbed, rarely compressed. Pappi usually of bristles, sometimes bristles and scales, rarely wholly of scales or coroniform or none—bristles rarely plumose.

Key to genera treated in *JepsMan*.

- 1. Phyllaries subequal in 2–3 series, obscurely or not at all striate-nerved.
- 2. Shrubs or coarse perennials; leaves usually petiolate; florets 10–60 per head; pappi of 5–40 bristles. *Ageratina*
- 2' Annuals; leaves sessile; florets 75–125 per head; pappi of 2–6 stout bristles or narrow, aristate scales. *Trichocoronis*
- 1' Phyllaries graduated in 3–5+ series, mostly strongly striate-nerved.
- 3. Cypselsae 10-ribbed; pappi of 10–50+ fine bristles, none basally dilated. *Brickellia*
- 3' Cypselsae 5-ribbed; pappi wholly or partly of aristate to muticous scales or basally dilated bristles.
- 4. Annuals; leaves alternate, sessile, linear; pappi of 3 aristate scales alternating with 3 muticous scales. *Malperia*
- 4' Perennials or shrubs; leaves mostly opposite, petiolate, petioles longer than

the rhombic to pentagonal blades; pappi of 12–24 aristate scales or basally dilated bristles. *Pleurocoronis*

ACKNOWLEDGMENTS

I am grateful to the monographers and floristicians who have painstakingly contributed tiles to the mosaic of our knowledge of composite systematics. For more immediate help with comp characters and/or with key language, I especially thank David Keil and B. Baldwin, M. A. Lane, M. A. Matthews, R. Patterson, T. Rosatti, and A. R. Smith. I am also particularly indebted to participants in Jepson Herbarium Weekend Workshops and to students in taxonomy classes at San Francisco State University.

LITERATURE CITED

- ANDERBERG, A. A. 1994a. Tribe Inuleae. Ch. 14 in K. Bremer, *Asteraceae: Cladistics and classification*. Timber Press, Portland, OR.
- . 1994b. Tribe Plucheeae. Ch. 15 in K. Bremer, *Asteraceae: Cladistics and classification*. Timber Press, Portland, OR.
- . 1994c. Tribe Gnaphalieae. Ch. 16 in K. Bremer, *Asteraceae: Cladistics and classification*. Timber Press, Portland, OR.
- BENTHAM, G. 1873. Notes on the classification, history, and geographical distribution of Compositae. *Journal of the Linnean Society (Botany)* 13:335–577.
- BREMER, K. 1994. *Asteraceae: Cladistics and classification*. Timber Press, Portland, OR.
- FERRIS, R. S. 1960. Compositae. Pp. 98–613 in R. S. Ferris, *Bignoniaceae to Compositae*, vol. IV of L. Abrams and R. S. Ferris, *Illustrated flora of the Pacific states*. Stanford University Press, Stanford, CA.
- HICKMAN, J. C., ed. 1993. *The Jepson manual*. University of California Press, Berkeley.
- HOWELL, J. T. 1970. *Marin flora*, ed. 2, with supplement. University of California Press, Berkeley.
- JEPSON, W. L. 1925. *Manual of the flowering plants of California*. Associated Students Store, Berkeley.
- KARIS, P. O. and O. RYDING. 1994a. Tribe Helenieae. Ch. 21 in K. Bremer, *Asteraceae: Cladistics and classification*. Timber Press, Portland, OR.
- and ———. 1994b. Tribe Heliantheae. Ch. 22 in K. Bremer, *Asteraceae: Cladistics and classification*. Timber Press, Portland, OR.
- ROBINSON, H. 1981. A revision of the tribal and subtribal limits of the Heliantheae (Asteraceae). *Smithsonian Contributions to Botany* 51:i–iv, 1–102.



Strother, John L. 1997. "SYNOPTICAL KEYS TO GENERA OF CALIFORNIAN COMPOSITES." *Madroño; a West American journal of botany* 44, 1-28.

View This Item Online: <https://www.biodiversitylibrary.org/item/185039>

Permalink: <https://www.biodiversitylibrary.org/partpdf/171361>

Holding Institution

Smithsonian Libraries and Archives

Sponsored by

Biodiversity Heritage Library

Copyright & Reuse

Copyright Status: In Copyright. Digitized with the permission of the rights holder

Rights Holder: California Botanical Society

License: <http://creativecommons.org/licenses/by-nc/3.0/>

Rights: <https://www.biodiversitylibrary.org/permissions/>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.