

Classification of Compositae

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INTRODUCTION

The Compositae (Asteraceae) family is nested high in the Angiosperm phylogeny in Asterideae/Asterales. The family contains the largest number of described, accepted, species of any plant family, ca. 24,000, with estimates of the total number reaching 30,000. There are 1600–1700 genera distributed around the globe except for Antarctica. Assuming that there are 250,000–350,000 species of flowering plants, then one out of every eight to twelve species is in Compositae (about 10%). That the family is monophyletic has never been in question. Every early worker in plant classification recognized Compositae as a group at some level (i.e., Tournefort 1700; Berkhey 1760; Vaillant 1719–1723) and in every type of analysis the family is monophyletic (i.e., Small 1919; Bremer 1987; Jansen and Palmer 1987; Hansen 1991; Michaels et al. 1993; Lundberg and Bremer 2003).

The family is characterized by florets arranged on a receptacle in centripetally developing heads and surrounded by bracts, by anthers fused in a ring with the pollen pushed or brushed out by the style, and by the presence of achenes (cypselas) usually with a pappus (Fig. 11.1). Although the family is well-defined, there is a great deal of variation among the members: the habit varies from annual and perennial herbs to shrubs, vines, or trees, although few are true epiphytes; species grow in just about every type of habitat from forests to high elevation grasslands, however, they are less common in tropical wet forests and more common in open areas. Most groups in the family contain some useful and some noxious species as well as common and rare taxa. However,

the general perception of this family as “weedy” is not correct. Certainly there are members that benefit from disturbance, such as a few species of dandelions and thistles, and a few global pests (e.g., *Chromolaena odorata* (L.) R.M. King & H. Rob.), but most species have a restricted distribution and just about every ‘at risk’ habitat in the world contains members of this family that are an important part of the flora.

From the beginning, those who studied this family thought that presence of both ray and disk florets (Fig. 11.1A) represented the basic head pattern. In his classic illustration, Cassini (1816; Chapters 1, 6 and 41) placed Heliantheae at the center, Vernonieae and Eupatorieae at one end, and Mutisieae and Cichorieae (Lactuceae) at the other. The treatment by Bentham (1873a) had 13 tribes (the most frequently used suprageneric rank), which remained more or less the same until the 1980s; although some of the concepts changed, especially in Vernonieae, Liabeae, Senecioneae and Helenieae. Bentham’s work was developed independently from that of Cassini (e.g., 1826), but the 13 tribes of Bentham do correspond to many of the 19–20 tribes of Cassini. Hoffmann’s treatment of Compositae (1890–1894) essentially repeated the classification of Bentham (Turner 1977; Bremer 1994). Bentham (1873b), and more recently Cronquist (1955, 1977) and Turner (1977), all thought that Heliantheae were the most primitive tribe of the family, and accordingly assumed that the ancestor was a perennial herb with opposite leaves and a yellow-flowered, radiate capitulum. In 1977 Cronquist changed his mind and allowed for a woody ancestor, as suggested by Carlquist (1966, 1976). Carlquist (1966) proposed changes to the system of Bentham, but

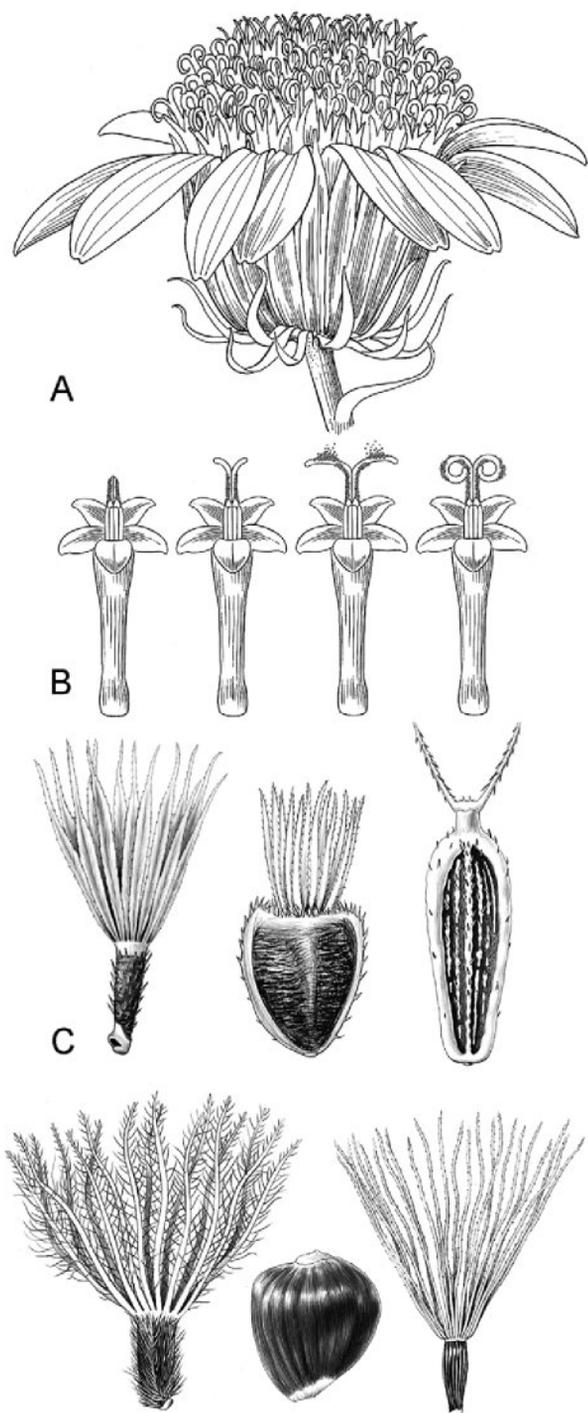


Fig. 11.1. Characters of Compositae. **A** The head with ray florets arranged around the perimeter, disc florets in the center, and an involucre with bracts (phyllaries) surrounding the outermost florets. **B** The pollen is released via the style pushing out through the anthers, which are fused at the margins; sometimes the style branches are recurved and come in contact with the style shaft. **C** Some of the achene (cypsela) and pappus types found in Compositae. [Drawings by Alice Tangerini (US); figure from Funk et al. 2005; achene drawings from Robinson 1981.]

they were not often used and acceptance of the basic 13 tribes continued. In 1975, a meeting on “The Biology and Chemistry of the Compositae” was held in Reading, England (Heywood et al. 1977). The proceedings from that meeting are interesting in that the book used the Bentham system, but several of the chapters made it clear that the data did not fit this classification. A good example is the pollen paper by Skvarla (1977), where he mentions that the pollen structure of Mutisieae is more like closely related families and very different from Heliantheae.

Abandonment of the stand-alone Lactuceae in the subfamily Cichorioideae was inevitable. Poljakov (1967) provided a fair approximation of the modern two groups of tribes with Cichorieae–Arctotideae more basal and Anthemideae–Heliantheae derived. Robinson (1973), Carlquist (1976), Wagenitz (1976), and Jeffrey (1978) all divided Compositae into two groups approximating Asteroideae and non-Asteroideae of recent treatments. Of these authors, only Carlquist and Jeffrey applied the subfamily names Asteroideae and Cichorioideae in their revised sense, and both erred in their placement of Eupatorieae because of its superficial resemblance to Vernonieae.

The biggest change in Composite systematics took place in the late 1980s and early 1990s; it was based on the molecular work by Jansen and Palmer (1987, 1988), Jansen et al. (1991a, b), and Jansen and Kim (1996). They literally turned the Compositae phylogeny upside down, showing that part of Mutisieae was the basal branch of the family and that the tribe Heliantheae s.l. was nested far up in the tree. Furthermore, their work showed that Vernonieae and Eupatorieae, long believed to be closely related, were actually in separate parts of the phylogeny. At the same time, Bremer’s analysis (1987) based mostly on morphological data, for the most part agreed with the molecular findings. However, Bremer’s analysis placed Eupatorieae close to Astereae and not Heliantheae.

Understanding the phylogeny of Compositae has come a long way since the papers of Jansen and Palmer (1987) and Bremer (1987). The advent of new techniques and new markers has greatly increased the amount of sequence data available. Using published trees for the family as a whole, and published and unpublished trees for individual clades, we have constructed a metatree for the family, a tree of trees (Chapter 44). It illustrates the current thinking about the relationships among the major tribes and subfamilies in Compositae. A summary tree shows the position of the major branches (Fig. 11.2). The basal group, which is monophyletic and the sister group to the rest of the family, is the distinctive subfamily Barnadesioideae, which contains less than 1% of the species in Compositae. Also monophyletic is the highly nested subfamily Asteroideae, which contains ca. 65% of the species in the family. Intercalated between the two monophyletic subfamilies are groups that used to be included in the subfamily

Cichorioideae (ca. 35% of the species in the family) and that vary in their morphological and molecular characters. Recently a new higher classification system was proposed for the family (Baldwin et al. 2002; Panero and Funk 2002, 2007, 2008) that recognized new and previously described subfamilies and tribes so that now there are 12 and 43, respectively; two or three are not supported by currently available morphological data and it remains to be seen whether or not these few taxa will be accepted by the Compositae community (see Chapter 12).

Chapter 1 covers the work of many of the scientists who provided early classifications of the family up until 1977 when the Heywood et al. volumes were published. Since that time there have been only two treatments of the whole family, Bremer (1994) and Kadereit and Jeffrey (2007), both of which were based on a mixture of morphological and molecular data. The Bremer book retained the three subfamilies but acknowledged that Cichorioideae were most likely paraphyletic. The Kadereit and Jeffrey treatment included the latest information available at the time. For instance, it broke up Heliantheae into twelve tribes that reflected the current state of knowledge. However, other areas of the family were still in flux (e.g., Mutisieae s.l.) and while some groups such as Pertyeae and Dicomeae were recognized on an informal level, others did not have sufficient data available to make a decision on their placement. Each of these works advanced our knowledge of the family and with this volume we hope to do the same. Our current classification is built on the foundation laid by others from Cassini to Kadereit and Jeffrey.

The treatments in this book are based on our attempt to combine the morphological and molecular data into a meaningful classification.

COMPOSITAE GISEKE (1792)

[ASTERACEAE MARTYNOV (1820)]

Family description (adapted from Jeffrey 2007)

Often annual herbs, also biennial or perennial herbs, subshrubs, shrubs, vines or trees, monocarpic or polycarpic, leptocaul or sometimes pachycaul, usually terrestrial (rarely epiphytic or aquatic), sometimes succulent, usually with one or more of various types of glandular and eglandular hairs, commonly the glandular biseriate and the eglandular uniseriate; tissues usually with schizogenous secretory canals (resin-ducts) and/or with articulated laticifers. Leaves alternate or opposite, rarely whorled, usually simple but often lobed or divided, exstipulate. Unit of inflorescence a capitulum (head), with rare exceptions surrounded by an involucre of one to several series of protective bracts (phyllaries), capitula sometimes solitary at the apices of more or less leafless

stems (scapes) but usually few to many in often corymbiform cymose inflorescences (capitulescences, synflorescence) of various types, sometimes aggregated into often involucre capituliform syncephalia of the second or even third order. Receptacle either naked or hairy and smooth, areolate with polygonal areoles or alveolate with depressions in which the florets are inserted, or paleate with persistent or caducous vascularized scales (paleae, pales, chaff) subtending some or all of the florets, fimbriiferous with non-vascularized fimbriils or scale-like processes surrounding the bases of the florets. Florets (flowers) small, 1–1000 or more per capitulum, sessile or subsessile; calyx a pappus associated with the fruit (see below); corolla gamopetalous, of (3–)5(–6) united petals, more or less regular (actinomorphic) and equally or unequally (3–)5(–6)-lobed or -toothed with the lobes or teeth valvate, or filiform with the lobes reduced or absent or with a minute ray, or variously zygomorphic, bilabiate with a 2-lobed internal (adaxial) lip and a 3-lobed external (abaxial) lip, pseudobilabiate with an unlobed internal (adaxial) lip and a 4-lobed external (abaxial) lip, ligulate with an apically 5-dentate abaxial ligule, or radiate with an abaxial 0–3(–4)-dentate ray, the different types variously arranged within the capitulum, the florets either all alike (homomorphic, isomorphic, capitulum homogamous) and all regular (capitulum discoid), all ligulate (ligulate capitulum) or all bilabiate, or of more than one type (heteromorphic, anisomorphic, capitulum heterogamous) with the inner (disc florets) regular (or rarely bilabiate) and perfect (bisexual, hermaphrodite) or functionally staminate (male) and the outer (ray florets) radiate, often pistillate (female) or sometimes sterile (neuter), in one or more series (capitulum radiate), or the outer filiform pistillate, usually in several series, and the inner regular, perfect or functionally staminate (capitulum disciform), rarely the corolla absent from the pistillate florets, occasionally all the florets pistillate or staminate and the plants dioecious or monoecious, rarely the florets variously otherwise arranged. Stamens with the filaments inserted on the corolla-tube, equal in number to and alternating with the corolla lobes; filaments usually free, rarely connate, the upper part of the filament usually with thick-walled cells, forming a split cylindrical or balusterform anther-collar (or filament-collar); anthers united into a tube surrounding the style, very rarely free, dithecal, introrse, dehiscent by longitudinal slits, usually with an apical appendage, rounded, sagittate, calcarate or tailed at the base; tapetum integumentary; pollen mostly tricolporate, usually echinate (spiny), sometimes echinolophate or lophate (with a pattern of raised ridges) or spinulate (microechinate, spinulose), often caveate; nectary a thickened scale or cup surrounding the style base; style solitary, elongating through the anther-tube and extruding the pollen at its summit, apically divided (except sometimes

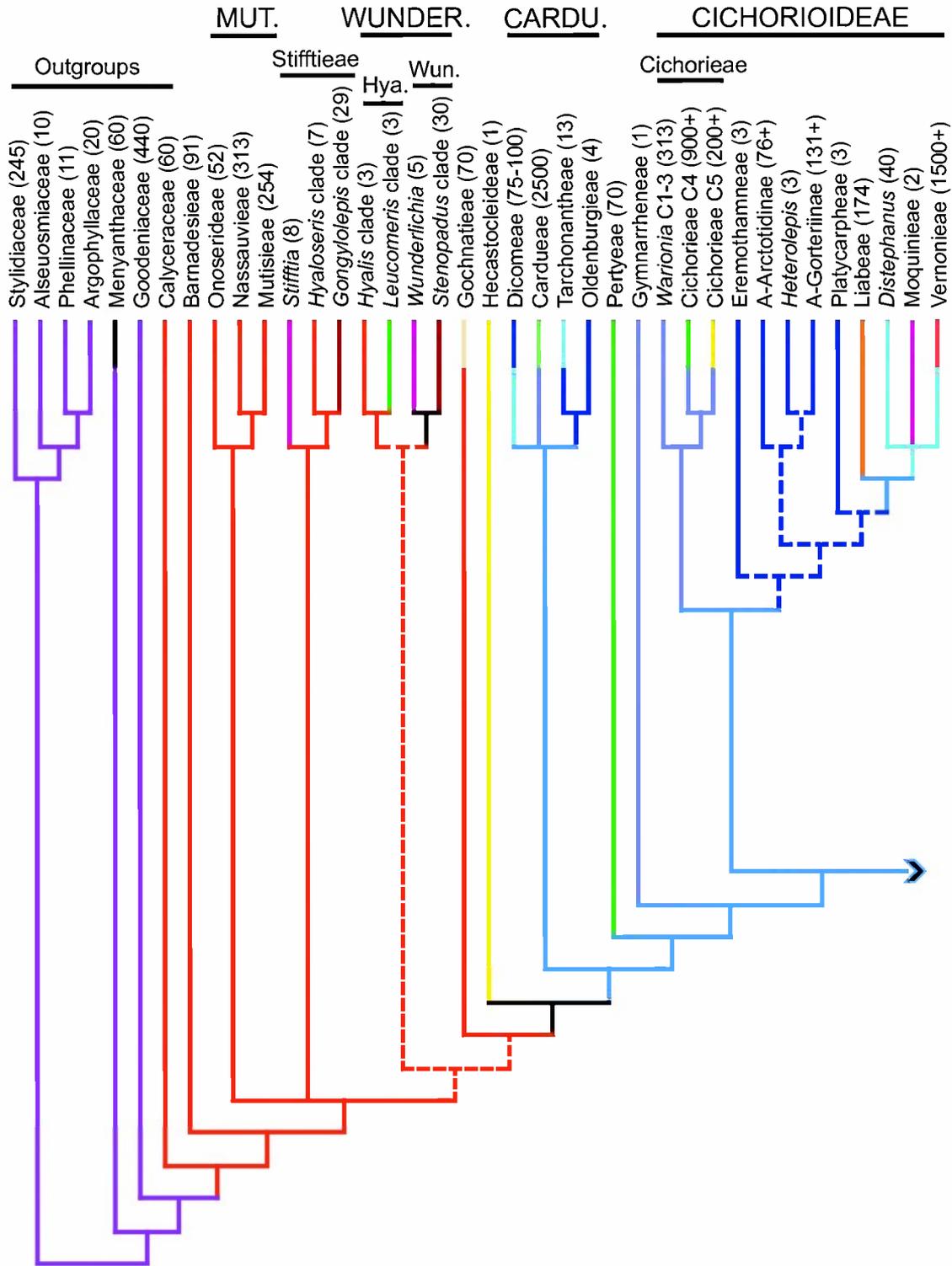
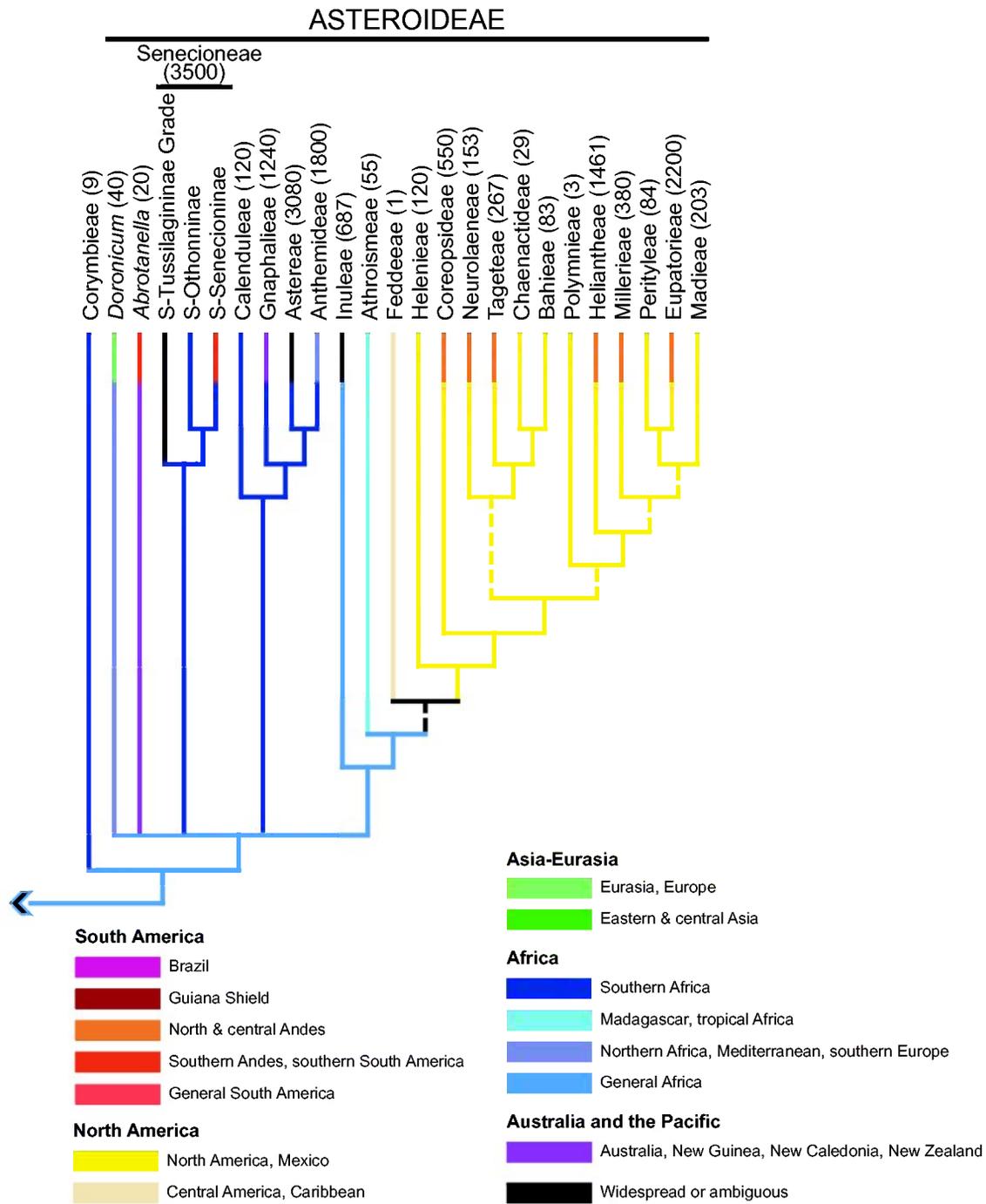


Fig. 11.2. A summary tree based on the metatree (Figs. 44.3–44.7). The tribes or clades have been represented by one to four branches. The branches and internodes were colored according to the distribution of the taxon or the optimization of those distributions. The numbers by the terminal taxa reflect the number of species in that clade. Note that some areas have been combined (e.g., Mexico and North America) and that the red color in Vernonieae represents Tropical America. Subfamilies that have more than one tribe are indicated in capital letters (see classification in this chapter). A = Arctotideae; CARDU. = Carduoideae; Hya. = Hyalideae; MUT. = Mutisioideae; S = Senecioneae; Wun. = Wunderlichieae; WUNDER. = Wunderlichioideae.



in functionally staminate or apomictic florets) into two (rarely three) short to long branches (style arms) with stigmatic areas on their inner (adaxial) surfaces, the apices of the style arms acute to rounded, truncate or with various appendages; stigmas dry, papillose; ovary inferior, of two (rarely three) united carpels, unilocular, with one erect, basal ovule; ovule anatropous, tenuinucellate, unitegmic; fruit, 1-seeded, indehiscent, usually an achene (cypsela), very rarely a drupe, crowned by a pappus formed of (1–)2

to many awns, scales (squamae, squamulae), setae or hairs in one or more series, homomorphic or heteromorphic, or by a more or less coroniform or auriculiform structure, or the pappus caducous or completely absent; abscission scar surrounded by a carpodium, distinguished by the form of its cells and the texture of its surface, of one to many rows of cells, indistinct to prominent, sometimes apparently absent; embryo straight; endosperm scant, forming a thin layer around the embryo.

Current classification

(* = under discussion, see Chapter 12. Recent investigations show that Corymbieae, Gymnarrheneae, Hecastocleideae, Pertyeae, and Wunderlichieae were not validly published in 2002. A republication of these suprageneric names with a Latin diagnosis will be submitted shortly.)

I. Barnadesioideae (D. Don) Bremer & Jansen (1992)

1. Barnadesieae D. Don (1830)

II.* Stiffioideae (D. Don) Panero (2007)

- 2.* Stiffieae D. Don (1830)

III. Mutisioideae (Cass.) Lindl. (1829)

3. Mutisieae Cass. (1819)
4. Onoserideae (Benth.) Panero & V.A. Funk (2007)
5. Nassauvieae Cass. (1819)

IV.* Wunderlichioideae Panero & V.A. Funk (2007)

6. Wunderlichieae Panero & V.A. Funk (2007)
- 7.* Hyalideae Panero (2007)

V. Gochnatioideae (Benth. & Hook.f.) Panero & V.A. Funk (2002)

8. Gochnatieae (Benth. & Hook.f.) Panero & V.A. Funk (2002)

VI. Hecastocleidoideae Panero & V.A. Funk (2002)

9. Hecastocleideae Panero & V.A. Funk (2002)

VII. Carduoideae p.p. Cass. ex Sweet (1826)

10. Dicomeae Panero & V.A. Funk (2002)
11. Oldenburgieae S. Ortiz (2009)
12. Tarchonantheae Kostel. (1833)
13. Cardueae Cass. (1819)

VIII. Pertyoideae Panero & V.A. Funk (2002)

14. Pertyeae Panero & V.A. Funk (2002)
- Catamixis* incertae sedis

IX. Gymnarrhenoideae Panero & V.A. Funk (2002)

15. Gymnarrheneae Panero & V.A. Funk (2002)

X. Cichorioideae (Juss.) Chevall. (1828)

16. Cichorieae Lam. & DC. (1806)
17. Arctotideae Cass. (1819)
18. Eremothamneae H. Rob. & Brettell (1973)
19. Liabeae (Cass. ex Dumort.) Rydb. (1927)
20. Vernonieae Cass. (1819)
21. Platycarphae V.A. Funk & H. Rob. (2009)
22. Moquinieae H. Rob. (1994)

Heterolepis incertae sedis

XI. Corymbioideae Panero & V.A. Funk (2002)

23. Corymbieae Panero & V.A. Funk (2002)

XII. Asteroideae (Cass.) Lindl. (1829)

24. Senecioneae Cass. (1819)
25. Calenduleae Cass. (1819)
26. Gnaphalieae (Cass.) Lecoq. & Juillet (1831)
27. Astereae Cass. (1819)
28. Anthemideae Cass. (1819)
29. Inuleae Cass. (1819)
30. Athroismeae Panero (2002)

“Heliantheae alliance”

31. Feddeae Pruski, P. Herrera, Anderb. & Franc.-Ort. (2008)
32. Helenieae Lindl. (1829)
33. Coreopsidae Lindl. (1829)
34. Neurolaeneae Rydb. (1927)
35. Tageteae Cass. (1819)
36. Chaenactideae B.G. Baldwin (2002)
37. Bahieae B.G. Baldwin (2002)
38. Polymnieae (H. Rob.) Panero (2002)
39. Heliantheae Cass. (1819)
40. Millerieae Lindl. (1929)
41. Madieae Jeps. (1901)
42. Perityleae B.G. Baldwin (2002)
43. Eupatorieae Cass. (1819)

As an aid to understanding the system of classification, short descriptions of tribes with diagnostic features and geographic distribution are provided below. Characters follow a uniform order; + denotes small tribes with only one or two genera. The tribes are broken into two large groups, the Non-Asteroideae (a grade) and the subfamily Asteroideae (a clade). Within the subfamily Asteroideae there is the well recognized clade, the Heliantheae Alliance. The primary providers of the information for most of the tribes are listed; those without attribution are by V.A. Funk. An online key to the tribes can be found on www.compositae.org.

Group 1: ‘Non-Asteroideae’ grade

Tribes *not* contained in the subfamily Asteroideae usually have: stigmatic surface solid on inner surface of style branch; pollen bearing part of anther extending well below the insertion of the filament (spurred; calcarate) and with tails (caudate); pollen psilate, lophate or echinate (Liabeae, some Lactuceae, some Cardueae); disc corollas in many forms but lobes usually longer than wide (deeply lobed); 3-lobed “true ray corollas” are found only in Liabeae and some Arctotideae; leaves alternate except for most Liabeae. Base chromosome number $x = 9$ or 10.

1. Barnadesieae. — (information provided by Estrella Urtubey): Trees, shrubs, subshrubs, perennial or annual herbs without latex; leaves alternate, opposite, fasciculate or whorled; heads discoid or radiate or ligulate, 1-numerous; involucre from cylindrical to widely campanulate, bracts in several series, chartaceous; receptacle usually pilose, occasionally paleous or glabrous; florets usually hermaphroditic, white, yellow, orange, pink, purple to violet; corollas tubular, split, doubly split, ligulate, sub-bilabiate (4 + 1), rarely bilabiate (3 + 2), often villous; anther apical appendage rounded to obtuse or acute, emarginated to bilobed, thecae with or without spurs (calcarate or ecalcarate) and with or without tails (caudate or ecaudate); pollen with or without depressions,

spinulate, microechinate, scabrate-microspinulate, granulate, smooth or rarely lophate; styles vary from thick to slender, shortly bilobed or bifid, apex rounded, papillose rarely pilose, style branches rarely recurving; achenes densely villous, with “barnadesioid trichomes”; pappus in a single whorl, plumose, barbellate, setaceous or rarely absent.

Diagnostic features: axillary spines frequently present; absence of short, stalked, capitate glands (sesquiterpenes lacking); filaments free or rarely fused; absence of twin hairs on achenes, instead they have “barnadesioid trichomes”; and involucre bracts often spine-tipped.

Distribution: southern South America, the Andes, and Brazil.

2. *Stifftieae*

***Stifftia*.** — Trees, shrubs or vines, without latex; leaves alternate; heads discoid, 1–40 florets; involucre corymbose to paniculate, bracts multiseriate, subimbricate, margins not hyaline; receptacle epaleate, plane; florets isomorphic, bisexual, corollas whitish, actinomorphic, tubular-funnelform, deeply 5-lobed, the lobes completely coiled or only near the apex; anther apical appendages acuminate, thecae with spurs (calcarate) with long, smooth to sometimes papillose tails (caudate); pollen prolate, minutely spinulose; styles thick, glabrous, shallowly divided, apex rounded to shortly acute, branches dorsally smooth to slightly rugulose at the apex, never reflexed; achenes glabrous to weakly puberulent; pappus of scabrid bristles, capillary to somewhat paleaceous, the innermost slightly apically broadened and longer.

Diagnostic features: heads discoid; pappus showy, whitish, yellowish or reddish with ca. 100 capillary bristles in 4–5 series; florets actinomorphic, white with corolla lobes rolled; and styles glabrous, shallowly divided, apex rounded to shortly acute.

Distribution: five species are endemic to Brazil and one is endemic to French Guiana.

***Hyaloseris* clade.** — Shrubs or small trees without latex; leaves alternate to opposite, clustered in brachyblasts; heads discoid or ligulate, small to large; involucre cylindrical to funnelform, bracts imbricate, multiseriate, inner longer than outer, without hyaline margins, in 4–6 series; receptacle epaleate, surface unknown; florets isomorphic or with transitional corollas in the same head, bisexual, corollas yellow, white, purplish, ligulate corollas with shallowly 5-dentate limb, occasionally some segments partially connate, sub-bilabiate (4 + 1 corolla lips), rarely bilabiate; anther apical appendages acute, thecae with spurs (calcarate) and with long laciniate, papillose tails (caudate); pollen psilate, subprolate; styles slender, bifid, branches dorsally papillose, remainder of style glabrous, recurving when mature; achenes obovate, angled in cross-section, glabrous to pubescent; pappus of scabrid, capillary bristles.

Diagnostic features: two genera of woody plants of south-central South America with leaves clustered in brachyblasts; heads ligulate.

Distribution: Bolivia and Argentina.

***Gongylolepis* clade.** — Trees or shrubs, rarely subshrubs, without latex; leaves alternate; heads discoid and one-flowered, or radiate, or homogamous and bilabiate, or homogamous and isomorphic (ligulate or bilabiate) or heteromorphic (ligulate and bilabiate), 1–150 florets; involucre cylindrical or hemispherical or campanulate, bracts imbricate but sometimes subequal; receptacle naked or hirsutulous, may be smooth or pitted or foveolate or clavate; florets perfect, corollas zygomorphic or bilabiate (some actinomorphic in *Quelchia*), red or reddish, pale yellow, or white with apices lilac, magenta, or red, outer lip 3-lobed, inner lip 2-cleft (rarely 3-cleft) and coiled or flexuous; anther acute or acuminate at apex, thecae bases calcarate and tailed (caudate), the tails long and free or connate with adjacent anthers; pollen prolate to spheroidal-subprolate, microechinate, echinate, or almost psilate; styles bifid, white, red or purple, branches dorsally smooth, erect, ascending, or recurved; achenes prismatic or cylindrical or cylindrical-turbinate, glabrous to densely pubescent; pappus of setae, multiseriate or few-seriate.

Diagnostic features: woody plants with zygomorphic or bilabiate corollas; 2-cleft inner lip that is often much coiled and so is shorter than outer lip; and styles bifid and dorsally smooth.

Distribution: predominantly on the Guiana Shield with one monotypic genus in the Dominican Republic.

3. *Mutisieae*. — (information provided by G. Sancho): Herbs usually perennial, often scapose and stout, or less commonly trailing shrubs or subshrubs, without latex; leaves alternate; heads radiate (less commonly disciform or discoid), small to large (6 to ca. 200); involucre usually campanulate, bracts imbricate, margins not hyaline; receptacle naked, alveolate; floret corollas white, yellow, cream, pink, purple, blue, orange, or red; marginal corolla when present, strap-shaped with three teeth, bilabiate, sub-bilabiate, or rarely tubular; disc corollas bilabiate or tubular, shallowly lobed, the lobes equal or unequal in length; anther apical appendage not constricted or demarcated from the thecae (rarely demarcated), acute, thecae rarely with spurs (calcarate) but with tails (caudate); pollen usually prolate, exine almost psilate; style slender, shallowly bilobed to bifid with two long branches, rounded at the apex, usually dorsally papillose only above the style bifurcation point, papillae rounded, never acute; achene oblong to sub-obovate, truncate, attenuate to rostrate at the apex, glabrous to pubescent, often glandular, sometimes dimorphic with the marginal achenes conspicuously larger than the central ones; pappus of one to more series of bristles, scabrid to plumose, usually capillary, or absent.

Diagnostic features: corollas often brightly colored; marginal corollas usually bilabiate; disc corollas bilabiate or tubular, shallowly lobed, lobes equal to unequal; anther apical appendage not constricted or demarcated; anthers ecalcarate and caudate; and style shallowly bilobed to bifid, rounded at the apex, usually dorsally papillose only above the style bifurcation point, papillae rounded, never acute.

Distribution: predominately southern South America with outliers in Africa and Asia.

4. Onoserideae. — (information provided by L. Katinas): Annual or perennial herbs, shrubs, sometimes dioecious, without latex; leaves alternate; heads radiate, medium to large; involucre campanulate to hemispheric, bracts imbricate; receptacle naked, alveolate; corollas red, orange, purple, pink, white, or bicolor white-purple; ray corolla bilabiate with a 3-toothed outer lobe and a 1–2-toothed inner lobe, rarely absent; disc corollas with five lobes, the lobes short to long, equal or unequal in length; anther apical appendage acute or truncate, thecae with spurs (calcarate) and tails (caudate); pollen psilate; styles thick, apex rounded, glabrous, rarely papillose on abaxial surface of style arms; achenes elliptical to turbinate; pappus of 2–4-seriate bristles.

Diagnostic features: involucral bracts imbricate; corollas often brightly colored; ray corolla bilabiate (rarely absent); disc corollas tubular with five lobes equal or unequal in length; anther apical appendage acute or truncate, thecae calcarate and caudate; styles thick, apex rounded, glabrous, rarely papillose; achenes elliptical to turbinate, glabrous or pubescent; and pappus of 2–4-seriate bristles.

Distribution: southern South America but also in the Andes.

5. Nassauvieae. — (information provided by L. Katinas): Herbs, subshrubs, shrubs or vines without latex; leaves alternate sometimes rosulate; heads discoid or radiate, small to medium size; involucre cylindrical to campanulate, bracts imbricate; receptacle naked or paleate, alveolate; corollas white, yellow, red, blue, orange, purple, violet; ray corolla bilabiate with a 3-toothed outer lip and 1–2-toothed inner lip, outer lip short or long; disc corolla bilabiate (rarely with five lobes of equal size); anther apical appendage acute, thecae with spurs (calcarate) and tails (caudate); pollen psilate, spheroidal and suboblate; styles thick, apex truncate, rarely rounded, arms with an apical crown of sweeping hairs; achenes elliptical to turbinate, glabrous or pubescent; pappus of capillary, paleaceous, scabrose, or plumose bristles, one to more than one series, or absent.

Diagnostic features: all corollas bilabiate; style apex truncate, the only pubescence is on the arms, which have a unique apical crown of sweeping hairs; pollen exine distinctly bilayered, with the ectosexine and the endosexine clearly columellate.

Distribution: mostly southern South America.

6. Wunderlichieae. — Trees, shrubs, or subshrubs without latex; leaves alternate; heads discoid, 5–100 florets; involucre cylindrical to hemispherical, bracts imbricate or less commonly subimbricate; receptacle epaleate to strongly paleate; disc florets perfect, corollas cream-colored to yellow to magenta with five lobes of equal size, deeply cut; anther apical appendages acute to acuminate, spurs (calcarate), base tailed, tails free to connate with tails of adjacent stamens; pollen prolate or subprolate, psilate, spinulose, or echinate with short spines; styles smooth or slightly asperulous at apex, dorsally papillose or dorsally rugulose to papillose much below the bifurcation point; achenes prismatic and glabrous to pilose; pappus of multiseriate bristles or setae.

Diagnostic features: woody; leaves clustered near stem apex, actinomorphic corollas; styles smooth or slightly asperulous at apex, dorsally papillose or dorsally rugulose to papillose much below the bifurcation point.

Distribution: Guiana Shield and Brazil.

7. Hyalideae. — (information provided by G. Sancho): Small trees, shrubs, or subshrubs without latex; leaves alternate; heads homogamous or heterogamous, radiate or discoid, small to relatively large (5 to ca. 75 florets); involucre cylindrical to campanulate or turbinate, bracts imbricate to sub-imbricate, inner bracts longer than outer, usually in 3–10 series, green with darker or lighter margins but not hyaline, sometimes scabrous (*Leucomeris*); receptacle naked, flat or alveolate; florets dimorphic or isomorphic, bisexual, corollas whitish, pink, or purple, rarely yellow; marginal florets, when present, bisexual or female, sometimes with staminodes (*Ianthopappus*), corollas bilabiate with lobes coiled; central florets one (*Hyalis*) to ca. sixty, bisexual, corollas tubular, deeply 5-lobed, the lobes equal in length and coiled; anther apical appendage apiculate, acute to acute-apiculate, thecae sagittate (spurs; calcarate) with long lacinate or papillose tails (caudate); pollen sub-prolate to prolate, elliptic, exine psilate (to nearly psilate); styles thick to slender, shallowly divided (1.5 mm), glabrous, apex rounded or subrounded, usually with an extension of the stigmatic surface (*Ianthopappus*), style branches never recurving; achenes fusiform, cylindrical, ribbed, villose; pappus of 2- or 3-seriate, scabrid to smooth (occasionally plumose at the apex) capillary bristles, outer ones shorter.

Diagnostic features: marginal corollas usually present, bilabiate; central corollas tubular, deeply lobed; anther apical appendages apiculate; styles glabrous; and pappus of 2- or 3-seriate, scabrid or occasionally plumose at the apex capillary bristles with a reduced number of outer shorter bristles.

Distribution: South America and Asia.

8. Gochnatieae. — (information provided by G. Sancho): Trees, shrubs, subshrubs, or perennial herbs without latex; leaves alternate sometimes rosulate; heads

solitary (or 2–3) or several, homogamous or heterogamous, radiate or discoid (occasionally disciform), small to large (ca. 5–300 florets); involucre oblong to campanulate or turbinate, bracts imbricate in 3–10 series, margins not hyaline; receptacle naked, alveolate; corollas white to orange (seldom pink, lilac, or purple); marginal florets, when present, bisexual or female, usually with staminodes, bilabiate or sub-bilabiate (rarely sub-zygomorphic); central florets bisexual; disc corollas tubular, deeply lobed, the lobes equal in length; anther apical appendages apiculate, thecae with tails (caudate); pollen spheroidal to prolate or elliptic, exine almost psilate; styles slender, usually shallowly divided, glabrous, apex rounded to subrounded, usually with an extension of the stigmatic surface; achenes obovate, villose; pappus of uniseriate or 2- or 3-seriate, scabrid or occasionally plumose (at the apex) capillary bristles or less commonly some of them relatively flat.

Diagnostic features: marginal corollas, when present, bilabiate; disc corollas tubular, deeply lobed; anther apical appendages apiculate; and styles glabrous.

Distribution: America, from southern United States to Argentina and the Caribbean (especially Cuba).

9. +Hecastocleideae. — Small to medium shrub without latex; leaves alternate; heads discoid, small (1 floret); involucre cylindrical to fusiform, bracts imbricate without hyaline margins; receptacle naked; corollas white to reddish to greenish white; disc corollas with five lobes of equal size, deeply divided; anther apical appendages lanceolate not elongate, thecae bases with spurs (calcarate) and slightly fimbriate tails (caudate); pollen psilate and oblong; styles slender and glabrous, branches short (0.1–0.5 mm), apices rounded, not recurving at maturity; achene terete, obscurely 4–5-nerved, glabrescent; pappus of six unequal, lanceolate or multi-toothed scales sometimes fused to form lacerate crowns.

Diagnostic features: stiff holly-like leaves; tricolpate pollen; heads that are single-flowered and re-aggregated on a secondary receptacle, each group of 1–5 heads being subtended by a relatively large spiny whitish or greenish bract.

Distribution: restricted to high elevation areas (1500–2000 m) in southern Nevada and adjacent California including Death Valley.

10. Dicomeae. — (information provided by S. Ortiz): Perennial herbs, shrubs or small trees without latex; leaves alternate; heads discoid or radiate, variable in size; involucre hemispherical to obconic, bracts imbricate often with hyaline margins; receptacle epaleate (rarely paleate), alveolate; corollas white, yellow, cream to pink or mauve; ray corollas bilabiate (inner lips coiled or not) or true rays with three teeth; disc corollas with five lobes of equal size, deeply divided; anther apical appendage acute to acuminate, thecae with spurs (calcarate), rarely without

them (calcarate), and tails (caudate); pollen sub-oblato to prolate, micro-echinate or echinate; styles thick, deeply or shallowly divided, with a subacute to rounded apex and apical or subapical acute sweeping hairs, sometimes recurving at maturity; achenes often obconic but also narrowly oblong to broadly cylindrical with twin hairs; pappus of scabrid to plumose bristles or scales, pluriseriate, isomorphic or dimorphic.

The core group of genera (*Dicoma*, *Pasaccardoa*, *Macleodium*, and *Cloiselia*) of this tribe is characterized by: pungent phyllaries without resin ducts (or ducts reduced); presence of star-shaped calcium oxalate crystals in the corollas, anther filaments and styles; anther tails long tapering; pollen slightly echinate; style branches straight and adjacent; and achenes broadly obconic to cylindrical with twin hairs and without a carpodium. The remaining three genera (*Pleiotaxis*, *Erythrocephalum* and *Gladiopappus*) are rather different from this core group of Dicomeae and their inclusion in this tribe is provisional. *Pleiotaxis* and *Erythrocephalum* can be distinguished by the presence of phyllaries not pungent with resin ducts, calcium oxalate crystals not star-shaped, anther tails with subacute to subrounded apex, style branches separate and often curved, achenes ellipsoid and with carpodium, whereas *Gladiopappus* is characterized by phyllaries with rounded apex, unisexual florets among the bisexual disc florets, marginal florets of the capitula being truly bilabiate with coiled adaxial lobes, and achenes broadly obconic without twin hairs.

Distribution: tropical and southern Africa, including Madagascar and two species range outward to the Arabian Peninsula, India, and Pakistan.

11. +Oldenburgieae. — (information provided by S. Ortiz): Dwarf cushion-forming shrubs to small trees without latex; leaves alternate, mainly coriaceous; heads radiate, large (up to 1000 florets); involucre campanulate to urceolate, bracts imbricate often without hyaline margins; receptacle epaleate, alveolate; corollas white, cream or pinkish-brown; ray corollas bilabiate with the inner lip coiled lobes; disc corollas often actinomorphic (rarely slightly zygomorphic), deeply 5-lobed; anthers apical appendage acuminate, thecae with spurs (calcarate) and tails (caudate); pollen sub-oblato to prolate, echinate; style rather thick with very short branches, rounded at the apex, smooth to papillose, rarely with apical acute sweeping hairs; achenes narrowly ellipsoid to linear; pappus of scabrid to plumose bristles, pluriseriate.

Diagnostic features: woody plants with coriaceous leaves; large heads; bilabiate corollas; and short rounded style branches.

Distribution: South Africa.

12. +Tarchonantheae. — (information provided by S. Ortiz): Dioecious trees or shrubs, without latex; leaves alternate; heads discoid, small (ca. 30, rarely up to 90

florets), unisexual, rarely with a few bisexual florets; involucre campanulate to obconic, bracts imbricate, often without hyaline margins; receptacle epaleate, alveolate; corollas yellowish or whitish; male florets with deeply 5-lobed actinomorphic, tubular corollas; anther apical appendage deltate, thecae with spurs (calcarate) and tails (caudate); style characters reduced; pollen oblate-spheroidal to sub-prolate, micro-echinate; female florets with 3–5-lobed actinomorphic, tubular to filiform corollas; anthers reduced or absent; style with short, often recurved, flattened branches, acute to obtuse at the apex, without sweeping hairs; achenes mainly cylindrical to ellipsoid, flattened or not; pappus of numerous barbellate bristles in 1–2 rows or lacking.

Diagnostic features: dioecious trees or shrubs often aromatic with small discoid capitula of ca. 30 florets and heads that are arranged in generally dense racemes or panicles.

Distribution: tropical Africa (mainly in the eastern part), Madagascar, and southern Africa, and one species also present in the Arabian Peninsula.

13. Cardueae. — (information provided by A. Susanna): Perennial or monocarpic herbs, often subshrubs (less often shrubs or annual herbs, very rarely large shrubs or even treelets), laticiferous ducts present in roots; leaves alternate frequently forming a rosette; heads discoid (very rarely peripheral florets with 5-lobed ligules), usually many-flowered (rarely one-flowered); involucre campanulate, bracts in many rows, often spiny (less frequently unarmed); receptacle scaly or more often setose, rarely naked, alveolate; florets all fertile or the peripherals sterile, corollas purple, pink or yellow, seldom blue, usually tubular, usually actinomorphic, straight or s-shaped, deeply divided in five lobes of equal size; anther apical appendages extending into a rigid, lignified, lanceolate appendage, thecae bases sagittate (calcarate) and tailed (caudate) often with long divisions; pollen psilate, verrucate, scabrate or echinate, oblate, spherical or more prolate; styles slender; apices rounded, at maturity style branches not recurving, shaft with some short hairs above the point where the style branches and below with a papillose-pilose thickening (functionally a pollen brush); achenes usually with hardened pericarp, blackish by presence of phytomelans; pappus of scales or bristles.

Diagnostic features: involucre bracts usually in five rows and spiny-tipped; leaves often spiny; style cylindrical with a thickened articulation below the branches bearing a short collar of stiff hairs; anthers often with lacinate basal appendages, anther filaments usually papillose; and stamens often strongly thigmotropic, making up an elaborate mechanism of pollen presentation.

Distribution: widespread in Eurasia, especially diverse in the Mediterranean region where they constitute an important characteristic of the vegetation; some species are cosmopolitan weeds.

14. Pertyeae. — Perennial herbs, subshrubs or shrubs, without latex; leaves alternate, often rosulate, clustered at the median part of the stem or on secondary short shoots; heads discoid, one to ca. 13–(16) florets; involucre cylindrical to obconic, commonly multiseriate (5–15 rows) to rarely uniseriate of few involucre bracts, usually imbricate with hyaline margins sometimes ciliolate; receptacle epaleaceous usually glabrous, rarely pilose, alveolate or not; florets usually bisexual and fertile (rarely functionally female/male or cleistogamous), corollas white or pink, 5-lobed but zygomorphic with one split deeper than the others, sometimes pseudo-bilabiate or pseudo-ligulate; anther apical appendages truncate or rounded to apiculate, more seldom emarginated, thecae with spurs (calcarate) and with tails long and smooth to pilose (caudate); pollen spheroidal or subprolate, exine microechinate, scabrous, or echinate; styles slender, branches bilobed to shortly branched, variously truncate, rounded or acute at the apex, dorsally pilose to shortly pilose, sometimes swelling slightly on upper part of style with branches recurved; achenes oblong to obovate, (9- or) 10-veined, glabrous or pilose; pappus bristles 1–3-seriate (sometimes absent in functionally male or chasmogamous florets), margins scabrid or plumose.

Diagnostic features: small discoid heads of white, pink, rose or purple florets; corollas irregularly deeply 5-lobed and therefore zygomorphic by having one sinus deeper than the others, appearing pseudo-bilabiate or pseudo-ligulate; and styles thick, branches bilobed to shortly branched, dorsally pilose to shortly pilose.

Distribution: southeast Asia.

+Catamixis incertae sedis. — Shrubs without latex; leaves alternate; heads ligulate, small (6 florets); involucre turbinate, bracts scarcely imbricate, gradate, without hyaline margins; receptacle naked, more or less alveolate; corollas whitish to pale yellow, ligulate with five lobes, sinuses varying in depth; anther apical anther appendages narrow-triangular, acute to somewhat rounded, thecae with spurs (calcarate) and tails (caudate), lacinate; pollen spinulose with widely dispersed spinules (<1 µm in height); styles slender, glabrous, branches relatively short (0.25 mm), apices slightly rounded, dorsally short papillose, at maturity style branches not recurving; achenes densely long-setuliferous/sericeous, apices acute; pappus setae uniseriate, long-barbellate, white.

Diagnostic features: small ligulate heads; distinctive leaves that are obovate, serrate with large teeth, pinnately veined and easily disarticulating; small pollen (30 µm); and phyllary apices, long-acute, often purplish.

Distribution: northern India and adjacent Nepal.

15. +Gymnarrheneae. — Amphicarpic annuals with no reports of latex; leaves alternate forming rosettes; subterranean heads homogamous, female, cleistogamous; florets enclosed in small involucre bracts, corolla vestigial;

pappus absent, vestigial, or of short, somewhat scale-like bristles; aerial heads congested in the center of the leaf rosette, heterogamous, disciform, functionally staminate florets in small groups, loosely connected on very short pedicels, interspersed among the small pistillate florets; corollas small, whitish; anther apical appendage absent, thecae without spurs (ecalcarate) and with tails (caudate); pollen echinate and non-lophate, the spines unevenly-distributed; female florets solitary, each enclosed in a prominent, stiff, white and green bract; corolla filiform; style arms long with rounded apex, glabrous, at maturity style branches not recurving; achenes of three types, those of pistillate florets numerous, tiny, ovoid, ciliate, villous, with long twin hairs; pappus of three types, that of female florets of long-lanceolate, ciliate, acuminate scales.

Diagnostic features: ephemeral, dwarf desert annual, amphicarpic; both chasmogamous aerial heads and cleistogamous subterranean ones and two different types of achenes; corollas 3–4-lobed; 3–4 anthers; and aerial heads clustered together and with functional male and female florets.

Distribution: deserts in northern Africa and the Middle East.

16. Cichorieae. — (information provided by N. Kilian): Annual to perennial herbs (more rarely subshrubs, shrubs, rosette shrubs and rosette treelets) with latex; leaves alternate frequently forming a rosette; heads ligulate (except for *Gundelia* and *Warionia*), homogamous, with one to over 600 florets but mostly with a few dozen; involucre cylindrical, mostly differentiated into a few imbricate outer series of bracts and a longer inner series (rarely uniseriate), bracts with or without hyaline margin; receptacle areolate or alveolate, naked (rarely with scales or bristles); corolla predominantly of some shade of yellow or blue, with 5-toothed ligule, perfect; anther apical appendage elongate, smooth, filaments smooth, thecae calcarate and caudate; pollen echinolophate or echinate; style slender, usually with long, slender branches, sweeping hairs on the shaft and branches; achenes cylindrical, or fusiform to slenderly obconic, mostly ribbed, sometimes compressed or flattened, apically truncate, attenuate or beaked, often somehow sculptured, mostly glabrous, sometimes papillose or hairy, rarely villose, frequently heteromorphic; pappus of scales or scabrid to barbellate or plumose bristles, sometimes absent.

Diagnostic features: almost exclusive presence of homogamous capitula with 5-dentate, ligulate flowers; and exclusive presence of lactiferous canals in both the subterranean and aerial parts.

Distribution: nearly global with centers of diversity in the Mediterranean area and north temperate climates.

17. Arctotideae

Arctotidinae. — (information provided by P.O. Karis): Shrubs, shrublets, and herbs without latex; leaves

alternate; heads radiate; involucre campanulate, cylindrical or urceolate, bracts imbricate, outer with foliaceous tips, inner with scarious tips; receptacle mostly naked, smooth or shallowly honeycombed; ray florets often brightly colored, usually female, corollas 3-lobed; disc corollas shallowly 5-lobed; anther apical appendage short, rounded, soft, wrinkled, thecae with spurs (calcarate) and no tails (ecaudate), endothecium radial, collar usually inconspicuous; pollen echinate, oblate-spheroidal; styles with a thickened apical portion, sweeping hairs small patent, broadly subulate, much longer in a ring below the bifurcation; achenes flattened, ribbed, sometimes winged; pappus of uni- or biseriata scales.

Diagnostic features: radial anther endothecium, inconspicuous anther collar; apically thickened styles, small, patent and broadly subulate sweeping hairs; and pappus scale cells very long and with abaxially reinforced walls.

Distribution: mainly southern Africa.

Gorteriinae. — (information provided by P.O. Karis): Shrubs, shrublets or herbs with latex; leaves usually alternate, with spines or longitudinally striate hairs; heads generally radiate; involucre campanulate, cylindrical, urceolate or obconic, bracts connate, herbaceous; receptacle deeply alveolate with projections along alveole margins; ray florets sterile, corollas usually 4-lobed; disc corollas with sclerified lobe margins; apical anther appendage firm, rather short, thecae with spurs (calcarate) and with (caudate) or without tails (ecaudate), endothecium without lateral wall thickenings or some polarized; pollen echinate, sublophate or lophate generally oblate-spheroidal; styles with clavate or subulate-ensiform sweeping hairs, longer in a ring below the bifurcation; achenes somewhat flattened, usually ribbed; pappus usually of uni- or biseriata scales.

Diagnostic features: latex; connate involucre bracts; deeply alveolate receptacles; 4-lobed, sterile ray florets; and disc corolla lobes with sclerified margins.

Distribution: southern Africa.

18. +Eremothamneae. — (information provided by H. Robinson): Erect branching shrubs without latex; leaves alternate; heads radiate or discoid, small (5 florets in *Hoplophyllum*) or medium (12–20 rays and 25–30 disk florets in *Eremothamnus*); involucre cylindrical to campanulate, bracts multiseriate, gradate, distally papyraceous and usually with apical spine; receptacle naked, surface unknown; corollas yellow; ray corollas when present, strap-shaped with three short teeth; disc corollas with five linear lobes of equal size; anther apical appendage oblong, apiculate or broadly elongate, thecae with spurs (calcarate) and tails (caudate); pollen spinulose with larger spines in intercolpi and smaller crowded spines around poles; styles slender, elongated, branches narrow, upper portion of style shaft and outer surfaces of branches covered with elongate sweeping hairs formed by two or

three cells separated by longitudinal walls, at maturity style branches not recurved; achenes densely sericeous; pappus of many stout scabrid-barbellate capillary bristles in 2–3 series, somewhat gradate in length.

Diagnostic features: slender style branches bearing relatively long sweeping hairs divided longitudinally into two or three cells; pollen spinulose with larger spines in intercolpi and smaller crowded spines around poles; and involucre bracts multiseriate, gradate, distally papyraceous and usually with apical spine.

Distribution: western South Africa and southern Namibia.

19. Liabeae. — (information provided by M. Dillon): Annual or perennial herbs, shrubs, or small trees usually with latex; leaves usually opposite; heads radiate (3 to ca. 320 florets); involucre campanulate, bracts graduate, without hyaline margins; receptacle alveolate, without chaff; corollas yellow (rarely red, purple, or white); ray corolla present, strap-shaped with three lobes; disc corollas with five lobes of equal size, longer than wide; anther apical appendage acute, thecae with spurs (calcarate) and tails (caudate) fringed or digitate; pollen echinate, spherical; styles slender, apex attenuate, sweeping hairs on upper style shaft and backs of branches, at maturity style branches recurving; achenes oblong or columnar; pappus of numerous long inner capillary bristles and short outer series of squamellae, sometimes with scales or plumose bristles or absent.

Diagnostic features: leaves usually opposite; latex present in most taxa; corollas usually yellow; and pollen echinate.

Distribution: tropical America with the vast majority in Peru and Ecuador.

20. Vernonieae. — (information provided by H. Robinson): Perennial herbs (few annuals), shrubs, vines or small trees, latex mostly lacking; leaves mostly alternate; heads one to many, homogamous; involucre with bracts subequal to gradate, inner persistent or deciduous, without hyaline margins; receptacles rarely paleate, with or without hairs; corollas mostly blue to reddish or purple, actinomorphic (rarely zygomorphic), 5-lobed (rarely with lobes grouped as four outer and one inner), lobes elongate; anther apical appendage oblong-ovate, thecae usually spurred, often tailed; pollen spherical, mostly 35–70 μm in diameter in medium, not caveate, usually sublophate or lophate, often with perforated tectum partially or totally missing; style branches spreading tangentially, slender and tapering, with long sweeping hairs on outer surface extending onto upper part of style shaft; achenes usually prismatic with 5–10 ribs, sometimes obcompressed, rarely winged; pappus usually capillary, often with short outer series, sometimes coroniform or lacking.

Diagnostic features: alternate leaves with pinnate venation, often with T-shaped or stellate hairs; heads with-

out rays; corollas mostly blue to reddish or purple; slender tapering style branches, long sweeping hairs on outside extending onto upper style shaft; achenes usually with twin hairs, rarely with phytomelanin in walls, usually with raphids; pollen sublophate or lophate; and anther endothelial cells with thickenings on upper and lower ends; rich in sesquiterpene lactones, one group with 5-alkyl-coumarins.

Distribution: tropical and southern Africa, south-east Asia to Australia and the Pacific, and the Western Hemisphere.

21. +Platycarpheae. — Acaulescent perennial herbs without latex; leaves arranged around edge of secondary head; heads discoid, one- to many-flowered; involucre subglobose to cylindrical, bracts somewhat imbricate without hyaline margins; receptacle naked, alveolate; corollas purple, mauve, lilac, or pink, occasionally whitish, with five lobes of equal size; anther apical appendage acute not elongate, thecae subequally sagittate (calcarate) and without tails (sometimes with very short tails) (ecaudate or caudate); pollen echinate, spines regularly and irregularly arranged; styles slender, in *Platycarpella* apex slightly rounded and styles with a few distal hairs, otherwise glabrous, in *Platycarpha* apex slightly tapered, branches terete, with hairs nearly to tip, at maturity style branches arched but not recurved; achenes 3- or 5-sided, dark, oblong, with faint ribs, rugose or smooth, glabrous; pappus of persistent white scales.

Diagnostic features: complicated secondary head structures; leaves that are elongate and prostrate; stolons that emanate from the crown at the base of the secondary head; secondary head and leaves lying more or less flat on the ground; anthers purple; styles lavender; and pollen echinate with spines in a regular arrangement or in irregularly arranged ridges surrounding the colpi in a unique bowtie pattern.

Distribution: three species in southern Africa.

22. +Moquinieae. — (information provided by H. Robinson): Shrubs without latex; leaves alternate; heads with one or five florets, homogamous or with anthers aborted in functionally female florets; involucre cylindrical, bracts green-brown with short hairs and small hyaline margins; corollas lavender to purplish, actinomorphic, 5-lobed, lobes elongate; anthers apical appendages oblong-ovate, thecae spurred (calcarate) and short tailed (caudate); pollen spherical, echinate, non-lophate, non-caveate, with baculae not aligned with spines; styles slender below, swollen and scabrous above near branches, branches short, scabrous outside, with continuous stigmatic surface inside, branches in multiflowered heads spreading tangentially; achenes prismatic, 10–17-ribbed, with numerous twin hairs, idioblasts and raphids obscure, without phytomelanin; pappus capillary in ca. two series, outer somewhat shorter.

Diagnostic features: hairs simple; homogamous or gynodioecious florets; anthers spurred; styles swollen distally with short scabrae, continuous stigmatic surface inside; achenes without phytomelanin; pollen echinate, non-lophate, non-caveate, with non-aligned baculae; leaf blades elliptical to obovate, with pinnate veins; endothelial cells with thickenings at upper and lower ends.

Distribution: restricted to Brazil.

+*Heterolepis incertae sedis*. — Shrubs or subshrubs without latex; leaves alternate; heads, radiate, up to 6 cm in diameter; involucre broadly campanulate with 2–3 rows of bracts somewhat connate at base, apically scarious and lacinate; receptacles shallowly alveolate; corollas yellow; ray corollas female, strap-shaped with three teeth and four veins but also staminoides and a filiform lobe ventrally in the sinus of the tube; disc corollas with five lobes of equal size, deeply divided; anther apical appendages soft and oblong, thecae with short spurs (calcarate) and barely branched tails (caudate); pollen spherical, echinate with spines evenly and deeply separated; styles slender, style branches short, shaft slightly thickened below the style branches, sweeping hairs on backs of style branches acute, somewhat longer hairs in a ring below the bifurcation, apex slightly rounded with short hairs, style branches not recurving; small achenes covered with dense white twin hairs; pappus biseriate, of 1–10 yellow-brown, stout, sublanceolate, bristle-like scales of varying length.

Diagnostic features: ray florets that generally have staminoides and a filiform lobe ventrally in the sinus of the tube; pappus of bristle-like scales which form a pom-pom-like shape in older heads; small achenes covered with dense white twin hairs; and partially connate involucral bracts.

Distribution: three species endemic to South Africa, mostly in the Cape Floristic Region.

23. +*Corymbieae*. — (information provided by B. Nordenstam): Scapose perennial herbs without latex; leaves alternate mainly rosulate; heads discoid, single-flowered; involucre cylindrical, few-calyculate, two bracts, enclosing the floret, without hyaline margins; receptacle naked, flat; corollas pink to purplish or white with five oblong to linear lobes of equal size; anther apical appendage reduced, thecae blackish, shortly sagittate (calcarate) and without tails (eacaudate); pollen echinate, caveate, non-lophate; styles slender, apex tapering gradually to a slightly rounded point, short hairs on the back side of linear style branches and upper part of shaft, at maturity style branches recurving; achene oblong, terete or subcompressed, densely pubescent; pappus of basally connate short scales and/or discrete fine bristles.

Diagnostic features: tufted parallel-veined leaves from a silky-hairy rhizome; involucre of two bracts; single-flowered capitula; and elongated, densely hirsute ovary.

Distribution: the area occupied by the genus coincides with the Cape Floristic Region in South Africa.

Group 2: *Asteroideae* clade

Tribes contained in the subfamily *Asteroideae* usually have: stigmatic surface in two lines on inner surface of style branch; anthers without spurs (ecalcarate); pollen echinate with spines regularly or somewhat irregularly spaced; disc florets usually actinomorphic and corolla lobes are as long as wide (shallowly lobed); when a ray/disc arrangement occurs the ray corollas are 3-toothed 'true rays'; leaves alternate except for members of *Heliantheae* s.str. and closely related tribes, which have opposite leaves (some alternate). Base chromosome number $x = 9$ or 10 , or $x = 19$ (*Heliantheae* Alliance).

24. *Senecioneae*. — (information provided by B. Nordenstam): Herbs, shrubs, lianas, epiphytes or trees, without latex; leaves alternate sometimes rosulate (rarely opposite); heads radiate, disciform or discoid, of various sizes; involucre calyculate or ecalyculate, bracts uniseriate and subequal or sometimes in two or more series; receptacle naked or fimbriate, denticulate or hairy; ray florets female, fertile (rarely sterile), corolla yellow or orange, white, pink, purple, red or blue; disc florets perfect or functionally male, corolla tubular or with a campanulate 4- or 5-lobed limb; anthers four or five, apical appendage flat, thecae basally obtuse to sagittate or caudate, endothelial tissue radial (*Othonninae* and *Senecioninae*) or polarized (*Tussilagininae*), filament collar baluster-form (*Othonninae* and *Senecioninae*) or cylindrical and straight (*Tussilagininae*); pollen echinate, caveate, exine with columellae solid (rarely with internal foramina); style bifurcate or simple, sweeping hairs in apical tuft or distributed abaxially on style branches, branches apically truncate or obtuse to conical, sometimes with tuft, pencil, or appendage; achenes terete or flattened, sometimes ribbed, winged or angled; pappus of barbellate bristles, rarely a single scale, sometimes absent, white or straw-colored, red or purple.

Diagnostic features: uniseriate involucre (although not universal); di-ester type pyrrolizidine alkaloids and the eremophilane types of sesquiterpene lactones; polyacetylenes lacking; raphids not in walls of achenes, but in ovules; in *Senecio* and many other genera of *Senecioninae* the stigmatic surface is divided into two parallel bands, but most members of *Tussilagininae* have a continuous stigmatic surface.

Distribution: worldwide with the most marked center of diversity in South Africa, also with centers in Central America, the Andes (Peru to Colombia), and Southeast Asia.

25. *Calenduleae*. — (information provided by B. Nordenstam): herbs, shrubs, or small trees without latex; leaves alternate or opposite; heads radiate, various sizes; involucre campanulate or cup-shaped, bracts 1–3-seriate, sometimes with hyaline margins; receptacle naked, glabrous; ray corollas female fertile or sterile or neuter,

yellow to orange or white, pink, purple or blue; disc corollas hermaphrodite, perfect or functionally male, 5-lobed, yellow to orange or reddish, sometimes purplish-black-tipped; anther apical appendage flat triangular-ovate, endothelial tissue polarized, thecae without spurs (ecalcarate) but with tails (caudate); pollen spinulose, exine without baculae; styles fertile or sterile, entire or bilobed, with sweeping hairs in a subapical collar or rarely extending down the style branches; achenes homo- or heteromorphic, terete or flattened, sometimes curved, rostrate, winged or fenestrate, exocarp sometimes fleshy and colored; pappus absent.

Diagnostic features: lack of pappus; sterile styles in many taxa; widespread heterocarpy; and unusual fruit structures such as fenestrate cavities and a fleshy exocarp.

Distribution: mainly Africa with a distinct center in South Africa; only *Calendula* extending outside Africa into Macaronesia, South and Central Europe, and Anatolia eastwards to Iran.

26. Gnaphalieae. — (information provided by J. Ward): Herbs, subshrubs, or shrubs, without latex; leaves alternate, entire; heads disciform or discoid (rarely radiate), size varies; involucre bracts imbricate in several rows, generally with a papery upper part (lamina) and a thickened, cartilaginous basal part (stereome); receptacle generally flat to convex, sometimes conical or peg-like, generally epaleate, rarely paleate, squamose or fimbriate; female outer florets generally filiform or often absent; central florets generally perfect, sometimes functionally male; anther thecae without spurs, with tails and with endothelial tissue almost always polarized; pollen with a two-layered ectexine comprising an outer columellate layer and an irregularly interlaced basal layer (“gnaphalioid” type); style branches with hairs apically or sometimes apically and dorsally (rarely dorsally only); achenes generally small and oblong to obovoid; pappus generally of plumose or barbellate to scabrid capillary bristles (occasionally of bristles and scales, only scales, or absent).

Diagnostic features: involucre bracts with a papery, often brightly colored lamina and a cartilaginous basal part (stereome); “gnaphalioid” pollen, with a 2-layered ectexine comprising an outer columellate layer and an irregularly interlaced basal layer; stems generally with fibers in phloem and without resin canals; leaves entire; anthers tailed; and achenes small.

Distribution: centers of diversity in southern Africa, Australia, New Zealand, and South America.

27. Astereae. — (information provided by L. Brouillet): Annual or perennial herbs, subshrubs, shrubs, rarely trees or vines, usually without latex; leaves alternate (rarely opposite); heads radiate, disciform, or discoid, usually small to medium-sized (rarely large); involucre cylindrical to campanulate (hemispheric), not calyculate,

bracts in (2–)3–5(–9) rows, usually imbricate, sometimes nearly equal, without well-developed hyaline margin; receptacle usually naked, nearly always flat or convex; ray corollas white, yellow, or pink to blue or purple, usually strap-shaped (rarely bilabiate), usually female; disc corollas yellow to white, with five or four (rarely three) equal lobes, filiform to funnelliform or with abruptly ampliate limb, bisexual or functionally male; anther apical appendages flat, lanceolate to deltate, rarely lacking, thecae rarely with basal tail; pollen spherical, tricolporate and echinate; style slender, style branch with acute appendage, scabrous or plumose on outer surface, stigmatic lines running up to base of lanceolate to triangular tip, sweeping hairs on entire outer surface of appendage, style branches pronate; achenes compressed and 2-nerved or angular to terete and multi-nerved (rarely obcompressed); pappus usually of 1–4 series of barbellate or rarely plumose bristles, persistent or caducous, sometimes with outer scales or awns, or lacking.

Diagnostic features: receptacle usually naked; bracts in 3–5 rows and usually imbricate; and style branches pronate, with acute appendage, scabrous or plumose on outer surface, stigmatic lines running up to base of lanceolate to triangular tip.

Distribution: worldwide with major centers of diversity in Africa, North America, and Australia.

28. Anthemideae. — (information provided by C. Oberprieler): Herbs, subshrubs or shrubs without latex; leaves usually alternate; heads various; involucre often hemispheric, bracts in 2–7 rows, imbricate and almost always with scarious margins and apex; receptacles flat, hemispherical or conical, glabrous or hairy, paleate or epaleate; ray corollas white and/or yellow (rarely blue-violet, pinkish or reddish), limbs with three lobes; outer disc florets (if present in disciform capitula) yellow, in one to several rows, corolla with 0–5 lobes; central disc corolla yellow or rarely whitish or reddish, actinomorphic with 3–6 apical lobes; anther apex usually ovate or triangular, generally rounded, thecae usually ecalcarate and ecaudate (rarely shortly tailed); pollen echinate (rarely rugose or smooth) and spherical; style slender, apex truncate with parallel stigmatic surfaces, style hairs rather short and apically rounded; achenes various; pappus never capillary.

Diagnostic features: leaves generally variously dissected, rarely entire with characteristic aromatic smell; involucre bracts with hyaline margin; no tails on anthers; tubular florets hermaphrodite or functionally male, tubular or funnel-shaped; upper part of the filament with cells with thickened walls, forming a split cylindrical or balusterform anther collar (filament collar); and achenes without a carbonized layer, often with glandular hairs, mucilage cells and resin sacs/ducts.

Distribution: mainly in southern Africa, central Asia, and the Mediterranean region.

29. Inuleae. — (information provided by A. Anderberg): Shrubs or herbs without latex; leaves alternate; heads, radiate, disciform or discoid, small to large (> 100 flowers); involucre cylindrical, campanulate or cup-shaped, bracts imbricate without hyaline margins, generally in several rows; receptacle naked or paleate; corollas yellow, pink, violet or white; ray corolla when present, strap-shaped with three lobes; outer florets often filiform, tubular; disc corollas with five lobes of equal size, lobes mostly shorter than wide; anther apical appendage acute, thecae normally without spurs (ecalcarate) but generally with distinct tails (caudate); pollen spinulose, caveate with one baculate layer; styles slender or thick, apex rounded to acute, with short acute or obtuse sweeping hairs above or extending below where the style divides, style branches recurving at maturity; achenes generally homomorphic, elliptic, prismatic or quadrangular, often with glandular hairs and/or non-myxogenic twin hairs, walls without phytomelanin; pappus of capillary bristles, of bristles and scales, of scales only, of awns, or absent.

Diagnostic features for Inulinae: heads usually radiate and yellow-flowered; achenes with elongated crystal in each epidermal cell; and acute sweeping hairs on style branches.

Distribution: mainly Mediterranean, Saharo-Sindian, but also in East Africa.

Diagnostic features for Plucheinae: heads often purple-flowered, disciform with filiform; tubular florets; achenes without large epidermal crystal; and style frequently with obtuse sweeping hairs extending below style bifurcation.

Distribution: warm climate areas worldwide.

30. Athroismeae. — (information provided by A. Anderberg): Shrubs or herbs without latex; leaves alternate; heads disciform, discoid or radiate, small to medium with up to 45 florets (except for *Anisopappus* which can have 100's of florets); involucre cup-shaped to cylindrical, often much reduced, bracts imbricate without hyaline margins, in few rows; receptacle naked or paleate; corollas white or yellow; ray corolla when present, strap-shaped with three teeth; outer florets often filiform, tubular; disc corollas with five lobes of equal size; anther apical appendage acute, thecae generally without spurs (ecalcarate) but often with distinct tails (caudate); pollen spinulose, caveate with one baculate layer, or with irregularly interlaced inner layer; styles slender or thick, apex slightly rounded with short obtuse sweeping hairs above where the style divides, at maturity style branches recurving; achenes without large elongated crystals; pappus of scales, awns or missing.

Diagnostic features: heads sometimes in pseudocephalia, some achenes have phytomelanin; and anthers with tails.

Distribution: mainly Africa and Australia.

Heliantheae Alliance

Information for all tribes of the Heliantheae Alliance was provided by B. Baldwin unless indicated otherwise.

Diagnostic features: involucral bracts usually 1–3-seriate; anther thecae often blackened, without spurs (ecalcarate) or tails (ecaudate); styles usually with sweeping hairs above where the style divides, at least as terminal tuft, at maturity style branches recurving, style appendages usually shorter than stigmatic portion (except in Eupatorieae); most taxa with phytomelanin layer in the achene; and base chromosome number $x = 19$.

Distribution: Western Hemisphere.

31. +Feddeae. — (information provided by B. Baldwin and A. Anderberg): Vine without latex; leaves alternate; heads discoid, large but few-flowered (9–12 florets); involucre cylindrical, multiseriate, bracts without hyaline margins but with median resiniferous duct; receptacle naked; corolla white with five lobes of equal size; anther apical appendage acute, thecae without spurs (ecalcarate) and with long tails (caudate); pollen spherical, spinulose, caveate, baculate with ramified basal layer, without internal foramina; styles slender, branches elongate, apex blunt, hairs inconspicuous, at maturity style branches slightly reflexed; achenes subcylindrical, glabrous, walls without large elongated epidermis crystal and without phytomelanin; pappus of uniseriate tawny capillary bristles.

Diagnostic features: white hermaphroditic florets; leathery entire leaves; multiseriate involucre; and bracts with resiniferous duct.

Distribution: confined to Cuba.

32. Helenieae. — Annual to perennial herbs (rarely shrubs) without latex; leaves alternate (rarely opposite); heads radiate or discoid, mostly medium-sized to large, sometimes small; involucre cylindrical to hemispheric, bracts in two or more series, sometimes reflexed, margins (at least of outer) usually not hyaline or scabrous; receptacle usually naked (sometimes with palea-like receptacular outgrowths, rarely truly paleate) and sometimes alveolate; ray florets, if present, pistillate or sterile, corollas yellow or white to red or purple, strap-shaped with three lobes, sterile; disc corollas yellow or red to purple, tubular, with five lobes of equal size, lobes usually not longer than wide; anther apical appendage ovate to round, thecae not blackened, without spurs (ecalcarate) and with or without short sterile tails (caudate or ecaudate); pollen echinate and spherical; styles slender, branches usually truncate, with terminal tuft of hairs otherwise glabrous or papillose; achenes more or less clavate, glabrous to densely hairy, walls lack phytomelanin and usually include few, large crystals; pappus of scales or bristles (rarely absent).

Diagnostic features: combination of alternate leaves; usually epaleate receptacles; markedly lobed ray corollas;

truncate style branches; non-carbonized achenes (with large crystals in achene-wall cells); and scaly pappus.

Distribution: New World (mainly southwestern North America).

33. Coreopsidaeae. — (information provided by D. Crawford and M. Tadesse): Herbs or shrubs without latex; leaves opposite or alternate; heads radiate or discoid, 2–15 cm wide; involucre cylindrical to hemispheric, bracts usually in two or more continuous series, outermost green, linear to lanceolate, striations dark green or brownish-black, inner with brownish-orange striations and scarious margins, usually ovate; receptacle with brownish-orange striated paleae, flat to conical; corollas mostly yellow or white; ray florets neuter or pistillate and then either sterile or fertile; disc corollas with (4–)5 lobes of equal size; anthers brown to black, apical appendage ovate, thecae without spurs (ecalcarate) and short-tailed (caudate); pollen radially symmetrical, isopolar, spherical, echinate and tricolporate; style undivided or shortly cleft to bifurcate, branches conic with short papillae on the outer surface, recurved at maturity, apex penicellate or truncate with fringes of papillae; achenes flat to quadrangular, rarely narrowed toward the apex and beaked; pappus of 2–15 smooth, antrorsely or retrorsely barbed bristles or short awns, rarely absent.

Diagnostic features: outer phyllaries differentiated from inner in color and shape, inner phyllaries with orange-brown striations (resin ducts); paleae with brownish-orange striations; and achenes flat obcompressed to quadrangular.

Distribution: centered in North and South America

34. Neurolaeneae. — Annual or perennial herbs or shrubs (rarely trees) without latex; leaves alternate or opposite (rarely whorled); heads radiate or discoid, small to medium-sized; involucre cylindrical to hemispheric, bracts 1–8-seriate without hyaline or scabrous margins; receptacle usually paleate; ray florets, if present, pistillate, corollas highly reduced or well-developed, yellow to white, tubular or strap-shaped, usually 3-lobed; disc corollas yellow, tubular, usually with five lobes of equal size not longer than wide; anther apical appendage ovate to deltate, thecae usually blackened, without spurs (ecalcarate) and without tails (ecaudate); pollen echinate and spherical; styles slender, apices more or less acute with terminal tuft of hairs, remainder of style glabrous or papillose, at maturity style branches recurving; achenes usually not flattened, walls with phytomelanin layer; pappus absent or of scales, awns, or bristles, sometimes coroniform.

Diagnostic features: stems fistulose and rooting at nodes or not; paleae tightly enfolding achenes in aquatic or marsh-dwelling taxa; receptacle usually paleate; anthers usually blackened; achenes blackened.

Distribution: mainly Neotropics (few species in Palearctica).

35. Tageteae. — Annual or perennial herbs or shrubs (rarely trees) without latex; leaves alternate or opposite; heads usually radiate (rarely discoid), size varies; involucre cylindrical to hemispheric, bracts in 1–5 series; receptacle usually naked, smooth or pitted; ray florets pistillate, corollas yellow to red or white, strap-shaped with 2–3 lobes; disc corollas yellow with 5(–6) lobes of usually equal size or 1–2 lobes larger than others; anther apical appendages usually sclerified, thecae not blackened, without spurs (ecalcarate) and without tails (ecaudate); pollen echinate and spherical; styles slender, apices of style branches truncate or deltate to acuminate, usually variously papillose, recurving at maturity; achene walls striate or ribbed, with phytomelanin layer; pappus of scales and/or bristles (rarely absent).

Diagnostic features: epaleate receptacles, most with glandular pockets (dark spots); characteristic smell (monoterpenes); and if glands lacking, then achenes usually strongly 9–15-ribbed.

Distribution: warm temperate to tropical New World (1 sp. of *Flaveria* in Australia), mostly southwestern North America.

36. Chaenactideae. — Annual or perennial herbs (rarely subshrubs) without latex; leaves usually alternate; heads discoid, small to medium-sized; involucre cylindrical to more or less broadly campanulate, bracts 1–2-seriate without hyaline margins; receptacle naked (rarely partially paleate), smooth; corollas of peripheral florets sometimes zygomorphic, corollas white to reddish or yellow with five lobes of equal or unequal size (peripheral lobes sometimes enlarged); anther apical appendage more or less round to ovate, thecae not blackened, without spurs (ecalcarate) and without tails (ecaudate); pollen echinate and spherical; styles slender, apices usually acute with short hairs, glabrous or hairy below style bifurcation, at maturity style branches recurving; achene walls striate, with phytomelanin layer; pappus of setose to obovate scales without thickened bases or midribs and sometimes fused at base into deciduous unit.

Diagnostic features: combination of alternate, often lobed, leaves; discoid heads; epaleate receptacles; pale or reddish (not blackened) anthers; more or less terete (not flattened), striate achenes; and unribbed and unthickened pappus scales, sometimes deciduous as a unit.

Distribution: western and southwestern North America, mainly California.

37. Bahieae. — Annual to perennial herbs (rarely shrubs) without latex; leaves alternate or opposite; heads radiate or discoid, mostly small to medium-sized, sometimes large; involucre cylindrical to obconic or hemispheric, bracts imbricate, with or without hyaline margins in 1–4 series; receptacles usually naked; ray florets, if present, pistillate, corollas usually yellow to orange or white, sometimes pink to purplish, strap-shaped with usually

2–3 lobes; disc corollas yellow or white, sometimes pink to purplish, with 4–5 lobes of equal or unequal size; anther apical anther appendage usually ovate, thecae without spurs (ecalcarate) and without tails (eacaudate); pollen echinate and spherical; styles slender, apices deltate to acuminate with short hairs, style below bifurcation usually glabrous, at maturity style branches recurving; achene walls usually striate, with phytomelanin layer; pappus of scales with thickened base or midrib (if scales not thickened, then disk corollas 4-lobed) or of brownish-to-reddish, often fasciculate or hooked bristles.

Diagnostic features: combination of epaleate heads; pale or reddish (not blackened) anthers; blackened, striate, usually unflattened achenes; and pappus usually of basally thickened or costate scales or of fascicled or hooked bristles.

Distribution: mainly southwestern North America (also temperate and montane South America, tropical Africa, and South Pacific).

38. +Polymnieae. — Perennial herbs without latex; leaves opposite; heads radiate, small to medium-sized; involucre campanulate to hemispheric, bracts imbricate without hyaline margins in 2–3 series; receptacle paleate; ray corollas white, limbs 3-lobed, middle lobe longer and wider than lateral lobes; disk florets yellow, tubular with five equal lobes, functionally staminate; anther apical appendages deltate, anther thecae pale, without spurs (ecalcarate) or tails (eacaudate); pollen echinate and spherical; styles slender, branches tapering with short hairs, remainder of style glabrous, at maturity style branches not recurving; achenes dorsiventrally compressed, achene walls smooth, with phytomelanin layer; pappus absent or coroniform.

Diagnostic features: combination of opposite leaves; paleate receptacles; functionally staminate disc florets; pale anthers; and uncompressed smooth achenes.

Distribution: eastern North America.

39. Heliantheae. — Annual or perennial herbs, shrubs, trees, or vines without latex; leaves alternate or opposite; heads radiate or discoid (rarely disciform), size varies; involucre cylindrical to hemispheric, bracts in 1–7 series, often foliaceous; receptacle paleate (rarely naked) with paleae enfolding achenes and usually persistent; ray florets if present pistillate or sterile, corollas usually yellowish, sometimes white (rarely orange to reddish), strap-shaped with usually three lobes; disc corollas yellow with five lobes of usually equal (rarely unequal) size; anther apical appendage usually ovate, thecae usually blackened, usually without spurs (ecalcarate), often sagittate (rarely with short tails = caudate); pollen echinate and spherical; styles slender, branches with separate or fused stigmatic lines, apices often terminated by tuft of hairs, the style glabrous below the bifurcation, at maturity style branches recurving; achenes compressed (rarely obcompressed), achene

walls smooth or striate, with phytomelanin layer; pappus of awns or scales, sometimes coroniform (rarely absent).

Diagnostic features: combination of paleate receptacles, with paleae enfolding ovaries; usually blackened anthers; style apices terminated by tuft of papillae; achenes blackened, flattened; and pappus usually of awns or scales.

Distribution: mainly warm temperate and tropical New World.

40. Millerieae. — Annual or perennial herbs, shrubs, or trees without latex; leaves usually opposite; heads radiate (rarely discoid), size varies; involucre obconic to hemispheric, bracts in 1–5 series; receptacle paleate; ray florets pistillate (rarely sterile), ray corolla usually yellow or white, strap-shaped with three lobes or limb sometimes absent, sterile; disk florets bisexual or functionally staminate, corollas yellow with (4–)5 lobes of equal or sometimes unequal size; anther apical appendage usually lanceolate to ovate, thecae usually blackened, sometimes pale (green in *Guardiola*), without spurs (ecalcarate) and tails (eacaudate); pollen echinate and spherical; styles slender, apices of branches often acute to penicillate, with short hairs, remainder of style glabrous, at maturity style branches erect or recurving; achenes usually more or less terete, achene walls usually striate, with phytomelanin layer; pappus absent or of scales or bristles.

Diagnostic features: combination of usually opposite, often glandular leaves; scarious paleae; usually blackened anther thecae; more or less terete, usually striate, blackened achenes; and radially-arrayed (or absent) pappus scales or bristles.

Distribution: mainly Mexico and northern Andes (also Old World tropics, especially Africa).

41. Madieae. — Annual or perennial herbs or shrubs, trees, or vines, without latex; leaves alternate, opposite, or whorled; heads radiate or discoid (rarely disciform), mostly small to medium-sized, sometimes large; involucre cylindrical or globose, bracts usually subequal in 1–2 series (rarely gradate in 3–4+ series), without hyaline margins; receptacle naked or paleate (paleae often restricted to periphery of receptacle), sometimes clasping ray ovaries, smooth; ray florets pistillate, corollas usually yellow or white, strap-shaped with usually three lobes; disk florets bisexual or functionally staminate, corollas yellow with five lobes of equal size; anther apical appendage rounded or usually more or less ovate to deltate, anther thecae pale or purplish, without spurs (ecalcarate) or tails (eacaudate); pollen echinate and spherical; styles slender, deeply divided or sometimes undivided, branches truncate to subulate with short hairs, remainder of style glabrous (except in *Blepharipappus*); achenes compressed, obcompressed, or terete, achene walls often striate, with phytomelanin layer; pappus of scales or bristles, sometimes absent.

Diagnostic features: combination of often glandular foliage; usually subequal phyllaries (often with one

phyllary per ray ovary and with phyllary at least partially clasping ray ovary); epaleate or often partially paleate receptacle (with paleae limited to periphery of receptacle, between ray and disc florets); often deeply 3-lobed ray corollas; often dark purple (not blackened) anther thecae; often flattened ray achenes; and often striate, blackened disc achenes.

Distribution: mainly western North America (especially California).

42. Perityleae. — Annual or perennial herbs or shrubs of rocky sites, without latex; leaves usually opposite; heads radiate or discoid, small to medium-sized; involucre cylindrical to hemispheric, bracts subequal in 1–2 series, usually navicular, without hyaline margins; receptacles usually naked, smooth; ray florets pistillate, corollas yellow or white, often 3-lobed; disc corollas yellow with 4–5 lobes of equal size; anther apical appendage usually ovate, thecae pale, without spurs (ecalcate) or tails (ecaudate); pollen echinate and spherical; styles slender, deeply divided, apices of branches tapered to rounded with short hairs, style glabrous below the bifurcation, at maturity style branches recurving; achene walls smooth, with phytomelanin layer; pappus of (usually two) bristles and crown of scales or absent.

Unique or diagnostic features include: rupicolous herbs and shrubs; glandular foliage; subequal, usually navicular phyllaries; epaleate receptacles; usually 4-lobed disc corollas; pale, ecaudate anthers; smooth, blackened achenes; and pappus (if present) usually of (1–)2 bristles and rudimentary scales. Distribution: mainly deserts of southwestern North America (also Andes and Desventuradas Islands of South America).

43. Eupatorieae. — (information provided by H. Robinson): Annual or perennial herbs to subshrubs, scrambling shrubs or small trees, without latex; leaves opposite or alternate; heads discoid, varying in size; involucre campanulate to cylindrical, bracts persistent to totally deciduous; receptacle often conical, with or without hairs, rarely with simple paleae; florets one to many in a head, corollas white to reddish, blue or lavender, actinomorphic (rarely peripheral florets with outer one or three lobes enlarged, 4- or 5-lobed); anthers often with glands, with apical appendages hollow, reduced or lacking, thecae not spurred or tailed; style branches spreading radially (not in some *Praxelinae*), apical appendages not recurving, greatly enlarged, filiform, flattened or fusiform, often colored as in corolla, usually nearly smooth; achenes 4–10-ribbed with phytomelanin in walls, without raphids, usually with twin hairs; pappus usually uniseriate, of plumose bristles, scales or lacking; pollen spherical, echinate, mostly 18–25 µm in diam. (in medium), caveate.

Diagnostic features: all members of the tribe (with a few exceptions) have mono-ester type pyrrolizidine alkaloids secreted by nectaries; also with pentayne acetylenes, some monoterpenes and sesquiterpene lactones, an ent-kaurine diterpene glycoside, kolavane derivatives, chromenes, benzofurans; raphids in the achenes are completely lacking. Other diagnostic features: mostly opposite leaves; hairs simple; heads discoid; corollas actinomorphic and whitish to reddish or lavender (never yellow); anther appendages hollow or poorly developed; and style branches with enlarged “club shaped” appendages that are often the color of the corolla. Distribution: Western Hemisphere with a few pantropical genera.

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Note added in proof

A recent paper has shown that two separate base pair deletions link *Catamixis* with the Pertyoideae. Panero, J. 2008. Shared molecular signatures support the inclusion of *Catamixis* in subfamily Pertyoideae. *Phytologia* 90: 418–424.