

Toward a phylogenetic subfamilial classification for the Compositae (Asteraceae)

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Abstract.—Molecular studies of the flowering plant family Compositae (Asteraceae) based on comparative DNA sequence data of chloroplast genes provide new insights into the evolution and radiation of the family. The results support the creation of new groups to maintain a classification that reflects evolutionary history. We are proposing the following new names: subfamilies Corymbioideae, Gochnatioideae, Gymnanthoideae, Hecastocleideae, and Pertyoideae; tribes Athroismeae, Corymbieae, Dicomeae, Gochnatieae, Gymnantheae, Hecastocleideae, Polymnieae; subtribe Rojasianthinae. The totals now stand at 11 subfamilies and 35 tribes. Only one tribe, the Mutisieae, is non-monophyletic having two branches. Most of the new groups are derived from taxa included in tribe Mutisieae, long suspected to be a paraphyletic group. Molecular studies that support these changes are discussed elsewhere but a summary of their results is presented.

Molecular phylogenetic studies of the family Compositae (Asteraceae) have been instrumental in providing important insight into the evolution and radiation of the family. Assessments of phylogenetic relationships in the family using molecular data began with restriction fragment length polymorphisms of the chloroplast genome. These studies identified a 22 kb inversion present in all members of the Compositae except the Mutisieae subtribe Barnadesieae (Jansen & Palmer 1987), which had a chloroplast organization similar to the rest of land plants. This result was used to elevate the Barnadesieae to subfamily status (Bremer & Jansen 1992), & the traditional two subfamily system consisting of Cichorioideae and Asteroideae was expanded to include the Barnadesioideae. Kim & Jansen (1995) published what can arguably be viewed as one of the most important papers using DNA sequence data aimed at elucidating the phylogeny of the Compositae. In this paper they identified the major clades

of the Compositae using sequence data of the chloroplast gene *ndhF* and provide additional evidence for the parphyly of subfamily Cichorioideae. Their data provided some support for the recognition of three main groups within subfamily Cichorioideae s.l. splitting sequentially from above the Barnadesioideae: 1) Mutisieae, followed by 2) Cardueae, and finally, 3) the tribes Cichorieae, Liabeae, Vernonieae, and Aratoteae forming a monophyletic group sister to Asteroideae. The latter group plus Asteroideae was recognized by Bremer (1994, 1996) as the vernonioid group. Since the publication of the molecular phylogeny of the Compositae by Kim & Jansen (1995) only the study by Bayer & Starr (1998) has provided a competing hypothesis of tribal relationship based on noncoding regions of the chloroplast genome, but this study did not provide good support for any new patterns of relationship. Most studies using the *ndhF* data matrix to date have concentrated on elucidating the placement of a particular

taxon in the tree of life of daisies (Karis et al. 2001).

The goal of our study was to use several molecular markers to produce a phylogeny that would clarify the phylogenetic relationships of members of the tribe Mutisieae s.l., and the circumscription of the subfamily Cichorioideae in general. Our data matrix includes the genes and markers *ndhF*, *trnL-trnK*, *matK*, *ndhD*, *rbcL*, *rpoB*, *rpoC1* exon1, *23S-trnI*, and *ndhI* for an approximate total data matrix of 13,380 bp. Combining these chloroplast markers has produced a solid phylogeny of the Compositae. Included here is a strict consensus tree of the relationships of Compositae based on our studies for the Cichorioideae (Panero & Funk, in prep.) and those of Panero et al. (in prep.) for tribe Heliantheae and relatives (Fig. 1). This phylogeny includes a majority of genera of the classical Mutisieae and representatives of most other tribes of Compositae as well as genera deemed, based on their morphology, to be of difficult placement (see Bremer 1994). The resulting phylogeny has clarified substantially the relationships of the Compositae and resulted in the need to publish new names to maintain a formal taxonomic nomenclature for monophyletic clades. All groups are now monophyletic and reflect the evolutionary history of the family except for two branches near the base of the tree that constitute a paraphyletic Mutisieae. It is most likely that additional data will provide enough support to recognize the "Stiffia group" as a new subfamily and tribe, however the data are missing several of the genera that should fall into the "Stiffia group" clade and final resolution of the problem will have to wait until those genera have been collected and analyzed. The two nonotypic subfamilies proposed, Corymbioideae and Gymnarrhenoideae, contain genera whose placement has long been problematic. Their isolated placement on the cladogram combined with their unusual morphology supports their being named at the subfamily (and tribal) level. One might argue that

eventually they might be part of the Asteroideae and Cichorioideae respectively, but given the amount of data that support this cladogram and the fact that the isolated position of these genera has long been recognized, it is doubtful. Details of the analyses and a discussion of the resulting clade will be published elsewhere (Funk & Panero, in prep.; Panero et al., in prep.); we publish these names here so that they are available for use those papers.

The changes to the classification of the family proposed herein have been carefully reviewed by the authors with the understanding that these changes represent the largest overhaul to the classification of the Compositae since Bentham (1873). Our confidence in proposing these changes is based on two things, first, an analysis of one of the largest data matrices for any group of flowering plants produced to date—a combination of multiple genetic markers and a broad sampling of taxa—and second, an analysis of these data by conservative methods (i.e., maximum parsimony) without the coding of indels or character weighting of any type. Bootstrap support for nearly all of the clades being recognized as new taxa is 100%. Our experience with this large data matrix shows that additions of new data partitions only solidifies the phylogenetic signal and branch support. It is clear that past a certain threshold, unique to each dataset and determined by the number of characters and taxa sampled, the phylogenetic signal stabilizes. It is our view that the addition of new data partitions in the future will only solidify the branch support reported here.

Subfamilies

Corymbioideae Panero & V. A. Funk, subfam. nov., Corymbieae Panero & V. A. Funk, trib. nov.

Type: *Corymbium* L., Coroll. Gen. 14 (1737).

Monotypic (7 species).

Plantae in foliis sessilibus et in laminis

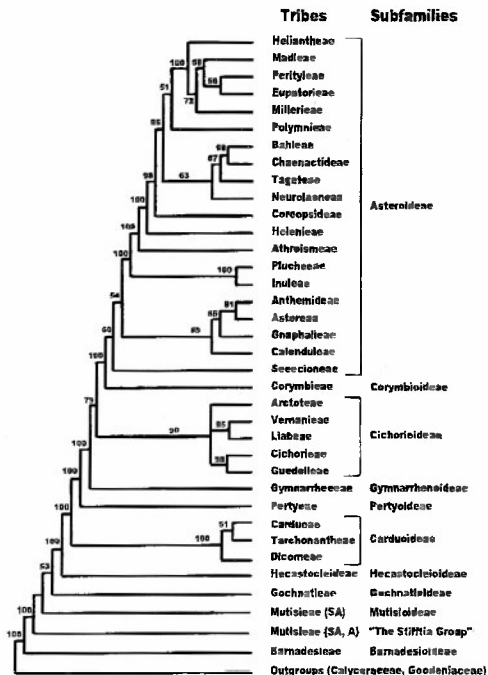


Fig. 1. Strict consensus tree of 12 most parsimonious trees for 122 representative Compositae taxa based on chloroplast DNA sequence data. Bootstrap values indicated above nodes, SA = South America, A = Asia. Tree is simplified to show only tribe and subfamily placement and arrangement.

conduplicatis. Capitula uniflora; bracteis involucri biseriatis, dimorphis; bracteis interioribus 2, involutis; limbis corollarum salverformibus.

Scapose, perennial herbs, tufted and forming rosettes. Leaves alternate, sessile, sometimes conduplicate, blades lanceolate to linear, leaf bases attenuate, leaf apices acuminate, terete, involute or flat in cross section, margins entire, venation parallel, leaf surfaces glabrous to villose or hirsute, sometimes with glandular trichomes. Inflorescence of open to congested corymbiform cymes at the end of scapes that are as tall or taller than the rosette leaves. Heads with one floret, involucre narrowly cylindrical, conspicuously gradated, phyllaries in two series, chartaceous-coriaceous to herbaceous, green with purple tips or suffused with purple when young, outer series of 2-3 phyllaries, apex acute to acuminate or rounded, glabrous or pubescent inner series of 2 phyllaries, these approximately 2 to 5 times longer than those of outer series, oval to oblong in outline, involute, enclosing floret, bifid or trifid, glabrous or pubescent; receptacle flat. Florets actinomorphic and bisexual, salverform, corolla mauve, pink, or white, lobes longer than tube with a tuft of papillae on the distal end, apiculate at apex with a raised, triangular arch of sclerified cells immediately below the lobe apex rendering the tip of the apex apiculate; anthers 5, thecae black, ecaudate, shallowly calcarate, anther connective of long, fusiform, conspicuously sclerified cells, endothecium dimorphic, proximal or inner rows composed of quadratic cells with bipolar thickenings and single bridges, these cells separated from distal or outer endothelial cells by a single cell row of tightly sclerified isodiametric cells, distal endothelial cell rows composed of cells approximately twice as large as those of the inner endothecium with bipolar thickenings and single bridges, anther appendage lacking and reduced to a series of elongated cells arising from the anther connective; styles dissected, color as in corollas, style branches linear,

obtuse or acute, with short sweeping hairs on abaxial side, sweeping hairs restricted to style and scarcely present below bifurcation point on the style shaft. Achenes linear to elliptic, hirsute or villous, silvery white, pappus of short, crown-like scales variously fused or divided into lobes and bristles. Chromosome number: $2N = 16$ (Weitz 1989).

The phylogenetic position of the South African genus *Corymbium* has been historically controversial (Bentham 1873) and in the latest revision of the family at the generic level, the genus is placed in subfamily Cichorioideae unassigned to a tribe (Bremer 1994). *Corymbium* is unusual in the Compositae because of its single-flowered heads, heads with two innermost involucre bracts enclosing the flower, the broad, patent lobes of the corolla, and the narrowly lanceolate leaves with parallel venation. Our studies reveal that the genus occupies a position next to the base of the subfamily Asteroideae. These results together with the distinctive morphology of *Corymbium* warrant its inclusion in a new subfamily *Corymbioideae*.

Gymnarrhenoideae Panero & V. A. Funk, subfam. nov., Gymnarrheneae Panero & V. A. Funk, trib. nov.

Type: *Gymnarrhena* Desf., Memoires du Museum d'histoire naturelle, Paris. 4:1. t. 1. 1818.

Monotypic (1 species).

Herbae perennes rosetiformes. Synflorescentiae simplices vel complexae; capitulis subterraneis et aeriis; acheniis dimorphis.

Perennial amphicarpic herbs. Leaves simple, forming dense rosettes, sessile, smooth, narrowly lanceolate to narrowly ovate, apex narrowly acute to attenuate, margins denticulate, base truncate, surfaces smooth and glabrous. Inflorescences subterranean or congested in the center of the leafy rosette. Subterranean heads homogamous and female, corolla vestigial enclosed

in involucrel bracts. Achenes of subterranean heads laterally flattened, blackish, sparsely hairy; pappus absent or of short bristles that are flattened at the base approaching scale-like, but bristle-like at the apex with rounded apices. Aerial heads bearing florets of two types: male florets in small groups that are loosely connected on very short peduncles and interspersed among single female florets each of which is strongly enclosed in a stiff white and green bract, with a few rows of chartaceous phyllaries. Florets with whitish corollas, male florets greatly reduced in size with 3-4 lobes and anthers, anther apex abbreviated, filament not elongated into an apical appendage, thecae with base short rounded, ecalcarate, ecaudate; female florets filiform, style branches long with rounded apices. Achenes obovate, ciliate, with elongate twin hairs, cell walls appear to be thin; pappus of long, acuminate, laciniate bristles with acute apices; ovaries of male florets with a vestigial pappus or lacking. Chromosome number: $2N = 20$.

A monotypic genus extending from North Africa to the Middle East.

Amphicarp (the ability to produce aerial as well as subterranean fruits) is uncommon in flowering plants being found in only ca. 50 species worldwide (Lev-Yadum 2000). Data are available that show that a high preponderance (eight) of those taxa are found in Israel (Lev-Yadum 2000).

This taxon has repeatedly been described as having male central florets and peripheral female florets, but the male florets are not always grouped in the center of the head. In fact some groups of male florets are found at the outer edge of the receptacle. It seems more likely that the aerial heads are actually groups of heads, some of which are few-flowered male heads and others are single-flowered female heads. Thus the monoecious plants bear heads of both sexes grouped in a common synflorescence. The fruits of the two types of heads of *Gymnarrhena* have different developmental patterns: the larger subterra-

nean fruits develop first and the aerial fruits are produced later and only in wet years. The aerial fruits are wind dispersed whereas the subterranean fruits germinate underground and appear to be more drought tolerant. It is possible that amphicarp in *Gymnarrhena* and other plants is an adaptive mechanism developed in response to inconsistent and/or low water-availability (Koller & Roth 1964).

Gymnarrhena is an unusual member of the Compositae and its history reflects its unique morphology. Bentham (1873), Hoffmann (1894), and Cronquist (1955) placed this genus in the Inuleae s.l. and Bentham's alternate choice was the Astereae. Skvarla et al. (1977) pointed out that the pollen did not support either of the above placements as the genus has Anthemoid pollen and they suggested a possible placement in the Anthemideae. Bremer (1994) listed the genus as belonging to the Cichorioideae s.l. but as "unassigned to tribe" along with several other problem genera. In our cladograms *Gymnarrhena* is consistently located by itself below the Cichorioideae s.s. and above the Pertyoideae ("Asian Mutisieae") clade.

Gochnatioideae (Benth. & Hook. f.) Panero & V. A. Funk, subfam. stat. nov., Gochnatieae (Benth. & Hook. f.) Panero & V. A. Funk, trib. stat. nov. Basionym: Gochnatinae Benth. & Hook. f., Gen. Pl. 168, 216. 7-9 Apr 1873.

Type *Gochnatia* Kunth in HBK, Nov. Gen. et Sp. 4:19, t. 309. 1820.

Includes: *Cnicothamnus* Griseb. (2 species), *Cyclolepis* Gill ex D. Don (1 species), *Gochnatia* Kunth in HBK (ca. 60 species), *Richterago* Kuntze (including *Actinoseris* (Endl.) Cabrera, 17 species), and possibly *Chucoa* Cabrera (1 species).

A Mutisieae in stylis glabris apice rotundatis, in appendices antherarum apiculatis et in bracteis involucri multiseriatis differt.

Many perennial herbs but also shrubs and trees or rarely dioecious subshrubs or gynodioecious shrubs or monoecious rosulate

herbs; branches rarely spiny. Leaves simple, alternate, coriaceous or smooth, lanceolate, oblanceolate, elliptic, ovate, obovate, spatulate to narrowly linear; apex acute, obtuse, mucronulate to acuminate, and spinose; margins entire, spinose-dentate, dentate to denticulate; base attenuate, truncate, or rounded; surfaces tomentose, glandular punctuate, glabrescent or glabrous; subsessile to petiolate, petiole base expanded laterally, sometimes pubescent; veins pinnate or parallel. Inflorescence solitary and terminal or few in number to numerous in racemes or cymes. Heads pedunculate or rarely sessile; peduncle bracteate; cylindrical or campanulate; receptacle epaleate, rarely paleate, flat to shallowly convex; discoid and homogamous or radiate and heterogamous; phyllaries in 4-15 series, imbricate, outer ones ovate-lanceolate to lanceolate, inner ones subequal to longer than the outer ones, linear-lanceolate to lanceolate, acute, acuminate, lanate, sericeous or glabrescent. Florets few-many (5-300); corolla tubes glabrous, pubescent, and/or glandular. Marginal bilabiate florets (when present) pistillate, (3+1, 3+2, 4+1), 10-60, white to pinkish with or without rose-colored veins; staminodia 4-5, free, hyaline (in gynodioecious plants flowers of male plants are hermaphroditic and female plants have flowers without anthers). Disc florets hermaphroditic or functionally male, actinomorphic with 5 deeply divided lobes, yellow, white, rose, or orange-yellow; anther-appendages acuminate to apiculate, anther-tails glabrous or pubescent; style slender, shortly bilobed, glabrous, apex rounded or obtuse. Achenes cylindrical, inconspicuously ribbed, villose, sericeous, sometimes glandular; pappus uniseriate or biseriate, bristles 25-50, simple (rarely branched), basally free or connate into a fleshy ring; setae serrulate, straw-colored. Chromosome numbers: *Cyclolepis* $2N = 54$, *Cnicothamnus* $2N = 44$, and *Gochnania* $2N = 46$.

This clade is located above the Mutisieae s.s. clade and below *Hecastocleis* and the *Carduoideae* clade. Its members are con-

fined to the Americas. The clade has consistently appeared in all versions of the analysis. The genera in this subfamily are characterized by glabrous styles and anthers with apiculate appendages. The genus *Chucoa* referred by Cabrera (1955, 1977) to the Mutisieae subtribe Gochnatiinae may belong in this group, however, we were unable to obtain recently collected material for analysis and the genus differs from other genera of the Gochnatioideae by having pubescent style branches. Final placement of this genus will have to await further study.

Hecastocleioideae Panero & Funk, subfam. nov. *Hecastocleideae* Panero & V. A. Funk, trib. nov.

Type: *Hecastocleis* A. Gray, Proc. Amer. Acad. Arts 17:220, 1882.

Monotypic (1 species)

Ad Mutisieas similes sed in synflorescentiis biordinatis in capitulis solitariis in bracteis spiniferis et in corollas profunde lobatis differt.

Stoloniferous shrubs with deep roots, growing on vertical cliffs in the cracks of rocks or in very well-drained, sandy soil. young stems bright green turning white-brown with age, glabrous, old stems ash gray to brown, trichomes simple, white, restricted to leaf internodes of rapidly growing shoots. Leaves alternate, sessile, blades narrowly ovate to broadly acicular, leaf bases attenuate, leaf apices ending in a lignified mucro or spine; margins entire with 2-3 spines on each side of the leaf, spines mostly confined to basal half; central vein lignified with age and turning into a soft spine as leaf blade falls off at senescence; venation triplinerved with the two secondary veins parallel to the main vein, unarmed leaves produced from short lateral branches if growing conditions are favorable, leaf abaxial and adaxial surfaces concolorous and essentially glabrous. Inflorescence of multiple single-flowered capitula aggregated into compound heads, each aggregation of 1-5 heads associated with a scariosus to co-

riaceous oval to ovate bract with 3-9 spines on each side, the terminal inflorescence with 4-10 capitula surrounded by 4-5 bracts. Heads with 1 floret, involucre of 20-30 phyllaries in 4-5 series, phyllaries narrowly ovate, prominently apiculate, herbaceous to scarious, green, densely strigose to lanose on mid area to basal attachment; receptacle flat. Zygomorphic or liguliform florets absent, actinomorphic florets perfect, corollas purple-white changing to white with age, deeply lobed, lobes narrowly triangular and as long as tube, patent at anthesis, tube obtrullate in outline, druses present, veins 5, parallel to each other along the tube and splitting below the sinus of the lobe, the fiber bundle splitting unequally just above the sinus level, producing two strong veins and a thin vein that dissipates in the space between the two main veins and the corolla lobe edge, the two main veins diverge from each other and reach the apex of the lobe where they dissipate into the surrounding tissue, the adaxial corolla lobe strongly sclerified, sclerified cell proliferation coincides with splitting of primary veins, the sclerified cells appear in the middle lower middle portion of the lobe and radiate to the edges to cover approximately $\frac{1}{3}$ of the lobe surface, additional layers of sclerified cells repeat the same overall distribution pattern as the lower layers but approximately halfway the length of the lobe. Anthers 5, calcarate and caudate, purplish to pale pink, anther collar with isodiametric, thickly and evenly sclerified cells, these changing abruptly to narrowly fusiform cells with strongly sclerified walls, the anther collar uneven in composition with numerous sclerified cells abaxially and a band of one to few cells on its adaxial side, anther tails approximately $\frac{1}{3}$ the total length of the anther thecae with endothecium tissue extending approximately $\frac{1}{3}$ to $\frac{1}{2}$ the length of the tail, the distalmost end of the tail twisted in some anthers, the strongly sclerified tissue of the connective gradually expands ending in a strongly sclerified anther appendage, those cells proximal to the

connective unevenly thickened and therefore producing a "radial" thickening pattern under light microscopy conditions, this pattern gradually changing to polar thickened cells with those cells ending the endothecium having minimal thickened areas, pollen tricolpate, smooth. Style glabrous with no sweeping hairs, dissected into two, rounded style branches, each style branch ending with a laminar cell proliferation. Achenes oval, black, essentially glabrous, pappus of a crown of scales, minutely lacerate. Chromosome number: $2N = 16$ (Powell et al. 1974).

Hecastocleis was described by Asa Gray (1882) and in the protologue of the species he remarked on the distinctiveness of the genus and of its affinities to the Asian genus *Ainsliaea*. This commentary is probably based on the similarity in corolla morphology between the Pertyoideae and *Hecastocleis* in which corollas are deeply dissected and the lobes are spreading. Our molecular studies reveal that *Hecastocleis* represents an isolated lineage, possibly the survivor of an old radiation of the family into the North American continent.

Pertyoideae Panero & V. A. Funk, subfam. nov., Pertyeae Panero & V. A. Funk, trib. nov.

Type: *Pertya* Schultz-Bip., *Bonplandia*, 10: 109, t. 10. 1862

Includes: *Ainsliaea* DC. (50 species), *Diaspananthus* Miq. (1 species, sometimes placed in synonymy with *Ainsliaea*), *Macroclinidium* Maxim. (3 species), *Myrriopsis* Bunge (1 species), and *Pertya* Schultz-Bip. (15 species).

Ad Mutisaeas similes sed in capitulis minoribus solitariis vel paucis in corollis non bilabiatis; lobis 5 profunde dissectis variabiliter connatis distinctae.

Many perennial herbs but also some shrubs or vines and one (*Myrriopsis*) gynodioecious shrub; glabrous to densely pubescent. Leaves simple, scattered and alternate, or congested and rosulate at midpoint or

basal, sessile to petiolate, lanceolate, oblanceolate, elliptic, ovate, obovate, spatulate to narrowly-linear or cordate; apex acute, rounded, acuminate, or mucronulate; margins entire, pubescent, dentate to denticulate; base attenuate or rounded; surfaces from densely tomentose, to glabrous; petiole sometimes narrowly winged; blades mostly with 3 or 5 veins but a few pinnate. Inflorescence solitary or heads few in number in spike-like or racemiform to thyriform cymes. Heads discoid or disciform and homogamous, pedunculate or sessile; peduncle bracteate sometimes minutely so; involucre cylindrical or campanulate, phyllaries in 3-8 series, imbricate, outer ones ovate-lanceolate to lanceolate, inner ones linear-lanceolate to lanceolate, apex acute or acuminate, minutely pubescent or more rarely glabrous. Florets one to few, perfect, corollas actinomorphic with 5 equal sized, deeply divided lobes fused unequally (sometimes in the same head) with some fulfilling the criteria for bilabiate but always with 10 veins (most common patterns 3+2, 3+1+1), sometimes secund; white, white suffused with pink, purple, or red, anthers calcarate, caudate, anther appendages small, acuminate to acute, anther-tails usually pilose and sometimes very long; style slender, shortly bilobed, dorsally with short hairs or papillae, apex slightly rounded to acute. Achenes cylindrical, ribbed, glabrous to densely villose; pappus of scabrid bristles or in *Pertya*, plumose bristles. Chromosome numbers: *Ainsliaea* 2N = 24, 26, 30; *Pertya* 2N = 24, 26, 28.

All the members of this clade are found in Asia, from Afghanistan through India to China, Taiwan, Japan, and SE Asia. The only two wholly Asian genera of the Mutisieae not in this clade are *Leucomeris* D. Don and *Nouelia* Pranch., which form a clade only known from southwestern China and adjacent regions. This China clade is found near the base of the tree in the Mutisieae s.s. (Fig. 1). The *Pertya* clade is well supported and is located above the Cardueae plus "African Mutisieae" clade (Car-

duoideae). This is the only group of Mutisieae s.l. taxa that is located above the Carduoideae on the tree and its placement shows the diversity and variability of the taxa previously contained in the Mutisieae s.l.

The most interesting feature of this group is the deeply but unequally divided actinomorphic corolla. Some corollas appear to be actinomorphic, some bilabiate and some are intermediate between the two. All corollas of this group have five equal sized lobes with 10 veins. The variation occurs in the fusion of these lobes and it happens at all levels. Even in the same head where some corollas have a 3+2 division and others have a regular corolla while still others have 3+1+1 or even 3+1. In some species of *Ainsliaea* the corollas have nearly evenly divided lobes with all of the lobes skewed to one side or secund which gives a startling appearance to the heads.

Tribes

Dicomeae Panero & V. A. Funk, trib. nov.
Type: *Dicoma* Cass., Bull. Soc. Philom. 12. 1817.

Includes: *Dicoma* Cass. (ca. 40 species), *Erythrocephalum* Benth. (13 species), *Gladiopappus* Humbert (1 species), *Macleodium* (Cass.) DC., *Cloiselia* S. Moore. (2 species), *Pasaccardoa* Kuntze (4 species), *Pleiotaxis* Steetz (26 species).

Ad Mutisieae similes sed in ramis stylo-
rum base caespitose pilosis et in cellulis superficialibus corollarum typis senecioidis differt.

Perennial herbs, shrubs or small trees, young stems glabrous or pubescent, trichomes multicellular. Leaves alternate, pedunculate or sessile, blades linear to broadly ovate, glabrescent to densely pubescent on abaxial surface, margins entire to serrate, leaf bases various, leaf apices sometimes terminating in a spine or mucro. Inflorescence terminal, solitary, or open thyriform cymes. Heads homogamous or heterogamous, involucre campanulate to

hemispherical or obconic with innermost row of phyllaries producing a strong constriction at the end of the involucre, phyllaries in multiple series, herbaceous to scarious sometimes innermost phyllaries herbaceous with scarious margins, sometimes with a prominent midrib, patent or spreading, receptacle epaleate, rarely paleate. Florets actinomorphic or sometimes peripheral florets zygomorphic and usually termed bilabiate with 3 of the lobes greatly expanded and appearing liguliform, corollas, white, yellow, cream or various shades of pink, mauve or lilac, tube narrow variously glabrous to pubescent, lobes conspicuous and longer than tube, either erect or spreading; anthers 5, caudate and calcarate, tails with or without antrorse ramifications, appendage apiculate to acute or slightly acuminate, pollen smooth or echinate; styles with two or four veins, style branches straight or curved, with sweeping hairs restricted to bifurcation point and above, lowermost trichomes slightly to conspicuously longer than those at the distal end of style branches. Achenes ellipsoid to obovoid or obconic, glabrescent to densely pubescent, pubescence on ribs or in the space between them, carpodium absent or rarely present, achene wall smooth to ribbed, pappus present or absent, isomorphic or dimorphic, sometimes in several rows, persistent or caducous. Chromosome numbers; *Dicoma* 2N = 22; *Pleiotaxis* 2N = 20.

This tribe contains most genera centered around *Dicoma* and found in Africa. These genera were previously classified in Mutisieae subtribe Gochnatinae. The major exception is the genus *Gerbera* L. and allies that remain in Mutisioideae. Our molecular studies support the exclusion of this *Dicoma* clade from the Mutisieae as proposed by Hansen (1991) and their inclusion in subfamily Carduoideae. Hansen (1991) stressed corolla cell morphology and collective patterns derived from these cells as his strongest evidence to support the exclusion of the African Mutisieae from South American Mutisieae. These genera show a

rugose, corolla epidermis pattern as opposed to the crested outer walls typical of Mutisieae. However, the occurrence of a particular corolla cell morphology is not an unequivocal indicator of phyletic relationship within the family—see for instance genera such as *Ainsliaea* and *Pertya*, included by Hansen in Mutisieae but here referred to the Pertyoideae.

The genus *Oldenburgia* Less. is not included in tribe Dicomeae as it appears from present data to be sister to the *Tarchonanthus-Brachylaena* clade (Tarchonanthae) and collectively the three genera are sister to the Cardueae. Ortiz (2000) considered *Oldenburgia* a basal lineage of the tribe and used this taxon along with *Gochnatia* as outgroups in his phylogenetic analyses of *Dicoma* and related genera. Bond (1987) considered *Oldenburgia* not to be closely related to any other members of tribe Dicomeae and believed its sister taxon to be found among American members of tribe Mutisieae subtribe Gochnatinae. Additional data are needed to ascertain the phylogenetic position of *Oldenburgia*.

The Dicomeae is recognized because its members are morphologically distinct from their sister clade the *Oldenburgia-Tarchonanthae-Cardueae* and there are no morphological characters that unify these taxa. Also, the sister relationship of the Tarchonanthae and *Oldenburgia* with the Cardueae is weak and additional data may show that the Tarchonanthae and *Oldenburgia* are sister to the Dicomeae and not the Cardueae.

Athroismae Panero, trib. nov.

Type: *Athroisma*, DC., Guill. Arch. Bot. 2: 516. 1833.

Includes: *Athroisma* DC. (12 species), *Blepharispermum* Wight ex DC. (15 species), *Leucoblepharis* Arnott (1 species).

Capitula discoidea vel disciformia paleata, floribus peripheralibus 0–2 femineis in corollis tubiformibus; thecis antherarum

base breiter caudatis, parietibus acheniorum phytomelaniniferous.

Perennial herbs, shrubs or small trees, young branches glabrous to pubescent, old stems gray to brown. Leaves alternate or fasciculate in brachyclasts, petiolate or sessile, petioles sometimes with a basal spine; blades linear, lanceolate to ovate, obovate, bases attenuate, apices acuminate to retuse, cuneate or truncate, margins entire, dentate or serrate, venation triplinerved or with a single vein, abaxial surface with sessile glandular trichomes. Inflorescence a congested glomerule-like cyme solitary or arranged in open, thyriform cymas. Heads disciform, heterogamous, involucre narrowly campanulate, narrowly conical, phyllaries 0-2, involute, narrowly elliptical, ovate to oval, apiculate, shallowly to strongly keeled, apical end entire, trilobed or variously lobed, or ciliate, hyaline, scarious, abaxial surface glabrous, pubescent and/or glandular; receptacle paleate; pales normally narrower and longer than phyllaries or in the case of *Athroisma* wider than the phyllaries, commonly with a round apex, rarely apiculate. Florets all actinomorphic, female florets present or absent, 2 to several, corollas tubular, hermaphrodite florets 2-25, in *Blepharispermum* functionally staminate and only 2-4 present, corolla campanulate, white, greenish-white, purple, tube white or greenish, glabrous or pubescent mostly with twin hair glands, lobes (4-) 5; anthers 5, ecalcarate, caudate, thecae white, to pale purple, endothecium with polarized thickenings, appendage a continuation of the connective and shallowly constricted above thecae level sometimes with apical gland; styles divided or filiform, filiform styles associated with functionally staminate flowers, stigmatic area in divided styles is divided into two rows which are confluent at style branch apex, sweeping hairs present at style apex or slightly below rarely present below the style branch bifurcation. Achenes black, radially flattened, ovate to oval, elliptic to suborbicular in outline, lateral ridges ciliate, trichomes fused at base, twin tri-

chomes with apical diverging cells straight or recurved, ovaries of functionally staminate flowers in *Blepharispermum* obconical, brown, pappus of fertile flower achenes either a crown of twin trichomes sometimes with recurved apices or of deeply lacerated fused squamellae. Chromosome numbers: *Athroisma* $2N = 20$ (Eriksson 1993); *Blepharispermum* $2N = 20$ (Eriksson 1992).

The Athroismeae contains the genera *Athroisma* DC., *Blepharispermum* Wight ex DC., and *Leucoblepharis* Arnott centered in eastern tropical Africa. These genera were considered to be members of the Inuleae until they were placed in the Heliantheae (Eriksson 1991). Eriksson allied the genera of his *Blepharispermum* group to members of subtribe Ecliptinae, more specifically to the genera *Salmea* DC. and *Acmella* Rich. ex Pers. (Eriksson 1992). This choice of a sister group in America is a logical one given that these genera share a series of superficially similar characteristics with the *Blepharispermum* group such as a combination of carbonized achenes, T-shaped twin hairs on the achenes, the suborbicular to broadly elliptical shape of the achenes, and the white corollas. The genera *Salmea* and allies such as *Acmella* and *Spilanthes* Jacq. differ from the *Blepharispermum* group in having laterally compressed achenes, heads with numerous hermaphroditic disc flowers with peripheral ray flowers instead of pistillate, tubular flowers peripheral to the heads in the *Blepharispermum* group, anthers with round and not sagittate appendages, and anthers without tails. It is indeed this last characteristic that excludes the *Blepharispermum* group from tribe Heliantheae, as there are no taxa in Heliantheae with such anther tails.

Results from molecular studies of Heliantheae sensu lato and related genera (Pannero et al. in prep) show that the *Blepharispermum* group (represented by *Blepharispermum* and *Athroisma* in our studies) is basal to the Heliantheae sensu lato. This result supports the recognition of this group as a new tribe in the Compositae. Molecular

studies of members of tribe Inuleae (Eldenas et al. 1999) have revealed that the genus *Anisopappus* Hook. & Arn. is a basal element in the tribe and possibly another member of tribe Athroismeae. Further molecular studies will be necessary to elucidate the relationships of *Anisopappus* to members of the Athroismeae as circumscribed here.

Polymniaceae (H. Rob.) Panero, trih. stat. nov., Basionym: Polymniaceae H. Rob. *Phytologia* 41:43, 1978.

Type: *Polymnia* L., *Diss. Chen.* 22. 1751; *Amoen. Acad.* 3:15. 1756.

Monotypic, 3 species

Perennial herbs or annuals, stems sparsely to densely pubescent with a strigose to softly hispid pubescence, internodes terete to shallowly angular, yellowish green to green with scattered purple spots, trichomes white to slightly brown, some trichomes up to 2.5 mm long, glandular trichomes with terminal brown cells, the base formed from two rows of trichome cells. Leaves opposite, petiolate, blades mostly ovate to suborbicular in outline, bases attenuate to truncate, round, apices acuminate, margins entire to shallowly lobed or deeply dissected, venation pectinate, abaxial surface densely covered with sessile glandular trichomes, tapered trichomes scattered along major veins, adaxial surface with a few sessile glandular trichomes and scattered, multicellular trichomes with raised multicellular bases. Inflorescence an open, paniculiform cyme. Heads radiate, involucre campanulate to hemispherical, subequal, phyllaries in two series, outer series herbaceous, inner series stramineous, chartaceous, with several resin ducts, resin dark yellow; phyllaries sparsely to densely pubescent on abaxial surface with both tapered and glandular trichomes; receptacle slightly convex, paleaceous; outermost pales broadly ovate to oval with irregularly lacerate distal ends, this grading into filiform pales in the center of the head, distal end sparsely pubescent

on abaxial surface with long tapered trichomes reminiscent of those on tube of ray corolla, glandular trichomes either sessile or stipitate, pales with several resin tubes, resin yellowish. Ray florets 3–8, pistillate and fertile, corolla white, tube densely pubescent, limb deeply trilobed with central lobe longer than flanking ones, adaxial surface along margins with a few multicellular trichomes with tapered, terminal cells, abaxial surface with scattered glandular and multicellular trichomes. Disc corollas 10–85+, functionally staminate, 5-lobed, corolla white to yellowish white or yellow, tube narrowly cylindrical, approximately half as long as throat, glabrous, throat broadly campanulate, lobes with a few, broadly based trichomes on abaxial surface; anthers 5, ecaudate and ecalcarate, anther thecae pale brown or tan, endothecium cells bipolar with 2–4 bridges, connective and anther collar thickenings radial, anther appendage conspicuously deltate with glandular trichomes on abaxial surface; pollen 25–27 micrometers in diameter. Style of ray flowers divided into two separate branches each with prominent stigmatic lines, sweeping hairs reduced to small papillate protuberances on distal portion of abaxial surface of the tapering stigmas, stigmas of disc flowers deltate and fused with no stigmatic surfaces with prominent sweeping hairs on abaxial surface of distal half. Achenes suborbicular in outline and asymmetric in cross section, the abaxial half round and larger than the flattened adaxial half compressed in its development by adjoining pale walls, with a ridge on each lateral edge and two additional ridges on the adaxial surface that can be variously distinct or fused, brown to black with a minutely coroniform pappus probably derived from the basal cells of the corolla tube, with no striation on the achene wall. Chromosome numbers: $N = 15$ II with 1 fragment (Smith et al. 1992, Freeman and Brooks 1988); other numbers include $N = 16$, $33+1$ and $2N = 60$, >50 .

The genus *Polymnia* was revised by Wells (1965) to include 19 species from

North and South America with yellow and white ray corollas. Robinson (1981) provided a list of characters including the pale colored anther thecae, the lack of a differentiated involucre, and a distinctive set of trichomes on the corolla lobes to justify the transfer of most species of *Polymnia* into the genus *Smallanthus* Mackenzie. The three species presently recognized in *Polymnia* are endemic to wet, riverbanks in mesic, hardwood deciduous forests of the eastern United States and Canada.

Molecular phylogenetic studies of members of Heliantheae s.l. (Panero et al., unpublished data) support Robinson's concept of the genus *Polymnia* and clarify its phylogenetic position. The genus *Polymnia* is a single lineage, basal to the tribes Heliantheae, Perityleae, Madieae, Eupatorieae, and Millerieae. As suggested by Robinson (1981) *Polymnia* is not related to members of subtribe Melampodiinae. There two reasons for elevating the Polymniinae to tribal status: 1) the phylogenetic position of the genus in the molecular study of the tribe Heliantheae (Panero et al. in prep.), and 2) the decision by Baldwin et al. (2002) to split the traditional Helenieae. This decision reflects the desire of most workers to maintain the Eupatorieae as a tribe, and not a subtribe of a very large tribe Heliantheae.

Subtribes

Rojasianthinae Panero, subtrib. nov.

Type: *Rojasianthe* Standley & Steyermark,
Publ. Field Mus. Nat. Hist. Bot. Ser. 22:
311. 1940.

Monotypic (1 species)

Ad subtribustet Montanoinas similae sed in paleis margine spiniferis, in corollis disci bicoloratis, et in setis pappi pluribus caduceis differt.

Shrubs or small trees, young stems terete, purplish green to brown, densely villous on leaf internodes and growing shoots, trichomes multicellular, tapered with a few sessile glandular trichomes interspersed, old stems and trunk smooth, coppery-brown in

color. Leaves opposite, petiolate, blades palmate, suborbicular in outline with 2-7 lobes on each side of the leaf, base shallowly hastate, apex acuminate, margins broadly serrate to crenate, each lobe ending with a prominent mucro, venation triplinerved, abaxial surface paler green than adaxial surface, sessile glandular trichomes moderately distributed across blade interspersed with a few tapered multicellular trichomes especially along veins, adaxial surface bright green, sparsely pubescent with scattered, thickened multicellular trichomes, with prominent bases. Inflorescences terminal, open cymes of 3-18 heads. Heads radiate, nodding, involucre hemispherical, gradate, imbricate, glabrous, phyllaries suborbicular to round, green rimmed with purple, in 3 series, receptacle paleaceous, slightly convex; pales conduplicate, keeled, margins lacerated with 5-6 sclerified awns on each side, without a terminal awn but rather the distalmost awns on each side of the pale joined and diverging from the pale apex, glabrous, pales growing with age, spreading and turning the fruiting head into a spiny ball. Ray florets 9-15, neutral, corolla white suffused with purple or pink on abaxial side, densely pubescent on abaxial surface with a few scattered glandular trichomes, essentially glabrous on adaxial surface. Disc florets 200+, perfect, lobes deeply dissected and spreading, distal section of corolla black, basal half white, tube densely pubescent, trichomes multicellular, tapered, blackish-green, throat sparsely to moderately pubescent, pubescence decreasing toward distal end and lobes, lobes 5, black, essentially glabrous; anthers 5, ecaudate and ecalcarate, black, filament densely pubescent on its distal end immediately below anther collar, trichomes multicellular, terminal cell shallowly rounded, black, those on basalmost area of filament hyaline, apical appendage deltate, black; style white, style branches white rimmed with black on outer edge, densely pubescent abaxially towards distal third of length and then abruptly glabrous on distalmost tip, black. Achenes ob-

ovate, purple-raspberry in color, turning brownish when mature, sparsely pubescent to glabrous when mature, pappus of multiple caducous awns, awns golden yellow. Chromosome number: $2N = 38$ (Strother 1983).

The monotypic genus *Rojasianthe* is endemic to the mountainous regions of Mesoamerica on the border between Mexico and Guatemala. The range of the species is more extensive in Guatemala. In Mexico it is found in open cloud forests or natural clearings in the forest especially along waterways. To the casual observer with some experience with tropical American sunflowers *Rojasianthe* is reminiscent of a species of *Montanoa* Cerv., especially *M. liebmanni* S. F. Blake. It shares with this genus the same chromosome number, opposite phyllotaxy, accrescent pales, blackish disc corollas (e.g., *Montanoa pteropoda* S. F. Blake), and neutral ray flowers with white corollas. It is however, the accrescent pales that are probably the most interesting morphological feature shared by these two genera. No other American sunflower has this characteristic. *Rojasianthe*, like *Montanoa*, produces conspicuous fruiting balls that, as in some species of *Montanoa*, are very spiny to the touch once the pales become lignified and dry up.

Results from molecular studies of the Heliantheae and relatives (Panero et al., in prep.) reveal that *Montanoa* and *Rojasianthe* constitute the basal lineages of the two different clades of Heliantheae sensu stricto. *Montanoa* is sister to the species of subtribe Ecliptinae as emended by Panero et al. (1999). *Rojasianthe* is basal to a clade containing members of the Verbesiniinae, Rudbeckiinae, Zaluzaniinae, Zinninae, Helianthinae, Engelmanniinae, and Ambrosiinae. *Montanoa*, with its 25 species, and the monotypic *Rojasianthe* are each sister to a radiation in the American continents of a total of approximately 1500 species of sunflowers with mostly yellow corollas.

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