

**NEW COMBINATIONS AND INFRAFAMILIAL TAXA IN THE
ASTERACEAE**

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ABSTRACT

Molecular studies of Asteraceae support the recognition of tribe **Doronicaceae** of subfamily Asteroideae, subtribes **Anisopappinae**, **Athroismaeae**, and **Centipediniae** of tribe Athroismaeae, **Chromolepidinae**, **Dugesiinae**, **Enceliinae**, and **Spilanthinae** of tribe Heliantheae, and **Dyscritothamninae** and **Jaegeriinae** of tribe Millerieae. The combinations *Euphrosyne acerosa*, *Euphrosyne dealbata*, and *Euphrosyne nevadensis* are also proposed.

KEY WORDS: Athroismaeae, Asteraceae, Asteroideae, Classification, *Euphrosyne*, Heliantheae, Millerieae.

Comparative studies of DNA sequence data for several coding regions of the chloroplast DNA of the Asteraceae have revealed several lineages that require names to maintain a classification that reflects monophyletic groups. These studies expand on the results of Panero and Funk (2002) and are aimed at elucidating the major lineages of the Asteraceae recognized at the tribal level.

Doronicaceae Panero, **tribus nov.** –Type: *Doronicum* L.

A Asteroideae ceteris, differt caracteribus conjuncte: habitu herbaceo; foliis alterniis, petiolatis, laminiis integris; capitulis ligulatis; phyllariis 2-3 seriatis; receptaculis epaleatis; flosculis radorum pistillatis; flosculis discorum bisexualibus, corollis actinomorphis, lobis 5; antheris ecaudatis; ramis stylorum truncatis; cypselae teretibus 10-angularibus; pappi radorum presentibus vel absentibus, pappi

discorum presentibus, pappi 1-3 seriatis, setis papporum albis vel albo-flavis.

Perennial rhizomatous herbs. Leaves alternate, petiolate, sometimes clasping, blades ovate, elliptic or obovate. Capitulescences terminal, solitary or open paniculiform cymes. Capitula radiate. Involucre hemispherical, phyllaries in 2-3 series, herbaceous to somewhat chartaceous. Ray florets fertile, bifid or trifid, corollas yellow. Disc florets bisexual, fertile, corollas yellow, essentially glabrous or sparsely to moderately pubescent at base. Cypselas cylindrical to obovate with 10 ribs, brown to greenish or blackish, essentially glabrous to pubescent, pappose, sometimes absent on ray florets, pappus of capillary bristles arranged in 1-3 series, white to yellowish. Base chromosome number, $x = 30$.

Monotypic, *Doronicum* contains 26 species found mostly in Asia, Europe and northern Africa (Alvarez-Fernández, 2003)

The genus *Doronicum*, because of its distinctive chemistry and multiseriate involucre, has traditionally been allied to *Arnica* L. and relatives of the Madieae (Nordenstam 1977). Nordenstam (1994) believed *Doronicum* to be one of the most plesiomorphic members of the Senecioneae and consider the genus as an outgroup in his cladistic studies of the Calenduleae. Comparative DNA studies support the distinctive nature of *Doronicum* as an independent lineage of the Asteroideae with affinities to the Calenduleae clade. For this reason, I propose the recognition of tribe Doroniceae.

New subtribes of the Athroismeae

Athroisminae Panero, **subtrib. nov.** -Type: *Athroisma* DC.

A Athroismeae ceteris, differt characteribus conjuncte: habitu herbaceo; foliis alternis vel fasciculatis, capitulis discoformis; phyllariis absentibus vel 1-seriatis, receptaculis paleatis; flosculorum peripherialium pistillatis, corollis cylindraceutis, flosculi discorum

bisexualibus vel fungenter staminatis, lobis (4-) 5; antheris caudatis, brevioribus; cypselae compressis, pappi vel squamis.

Perennial herbs, shrubs or small trees. Leaves alternate or fasciculate in brachyblasts, petiolate or sessile, petioles sometimes with a basal spine; blades linear, lanceolate to ovate, obovate, venation triplinerved or with a single vein. Capitulescence a congested glomerule-like solitary cyme or arranged in open to compact, paniculiform cymes. Capitula disciform or discoid, homogamous or heterogamous, involucre narrowly campanulate, phyllaries 0-2. Receptacle paleate. Florets all actinomorphic, female florets present or absent, 2 to several, corollas tubular, bisexual florets 2-25, corollas campanulate, white, greenish-white, purple or yellow-white, lobes (4-) 5; anthers (4-) 5, ecalcarate, caudate, thecae white to pale purple, appendages sometimes with apical gland; styles divided or filiform and undivided, filiform styles associated with functionally staminate florets, stigmatic area divided and confluent at style branch apices, sweeping hairs present at style apex, or slightly below, rarely present below the style branch bifurcation. Cypselae tangentially flattened, ovate to oval, obovate to obcordate, elliptic to suborbicular in outline, lateral ridges ciliate, black, pappus of fertile floret cypselas either a crown of twin trichomes, sometimes with recurved apices or of deeply lacerated and fused squamellae, sometimes with two stronger awns at lateral ridge of cypselae, pappus of functionally staminate floret ovaries with a variously lacerated crown or of a few, free, lacerated scales. Base chromosome number, $x = 10$

The subtribe contains three genera including *Athroisma* (12 spp.), *Blepharispermum* Wight ex DC. (15 spp.) and *Leucoblepharis* Arn. (1 sp.) with most species in eastern Africa, and a few species in western Africa, India, Madagascar, southeast Asia, and Indonesia.

Centipedinae Panero, **subtrib nov.** -Type: *Centipeda* Lour.

A Athroismeae ceteris, differt characteribus conjuncte: habitu herbaceo; foliis alternis, capitulis discoiformis vel radiatis; phyllariis 1-2 seriatis, receptaculis epaleatis; flosculorum peripherialium

pistillatis, corollis zygomorphis, cylindraceis, ligulis brevioribus, lobis 2-3 vel absentibus; flosculi discorum bisexualibus, corollis actinomorphis, lobis 4; antheris caudatis, brevioribus; ramis stylorum subtruncatis, brevioribus; cypselae subteretibus, pappi absentibus.

Annual or perennial herbs. Leaves alternate, sessile, blades obovate, variously toothed, rarely entire. Capitulescence sessile to shortly pedunculate, axillary, rarely terminal, solitary. Capitula disciform or radiate. Involucre campanulate to hemispherical, phyllaries in 1-2 series, subequal, herbaceous. Receptacles shallowly convex, epaleate. Peripheral/radiate florets in several series, pistillate, fertile, sometimes lobes extremely reduced and corolla seemingly tubular, corollas creamy white, green, light yellow or purplish. Disc florets bisexual, fertile, corollas tetramerous, creamy white, green, light yellow or purplish, essentially glabrous with a few glandular trichomes, lobes of corollas not vascularized; stamens 4, anthers hyaline, tailed, ecalcarate, appendages wanting or if present, minute, oval; styles with two vascular strands, style branches with divided stigmatic surfaces, concave, urceolate in outline, apices acute, papillose. Cypselas subterete, deeply ridged, glabrescent on basal end, cells of distal end with raised apical tips, eventually tips elongating and forming biseriate trichomes, trichomes increasing in density at apical end forming a shallow cup around corolla tube, trichome cells shallowly ridged; pappus absent.

Monotypic, *Centipeda* contains five species found in Australia, southeast Asia, Africa and southern South America.

The genus *Centipeda* has been placed in several tribes including Anthemideae and Astereae but Bremer (1994), in his excellent account of the family, considered the genus difficult to place but maintained it in Asteroideae, unassigned to a tribe. Nesom (1994) believed the genus to be a member of the Astereae. Comparative studies of the ITS region of the nuclear ribosomal DNA by Wagstaff and Breitwieser (2002) found strong support for the exclusion of the genus from the Astereae. Their studies revealed *Centipeda* to be an isolated lineage sister to

Athroismeae and the Heliantheae alliance. More recent studies (Panero et al., in prep.) support the inclusion of *Centipeda* in the Athroismeae.

Anisopappinae Panero, **subtrib nov.** -Type: *Anisopappus* Hook. & Arn.

A Athroismeae ceteris, differt characteribus conjuncte: habitu herbaceo; foliis alterniis; capitulis radiates plerumque discoideis; phyllariis 1-2 seriatis; receptaculis paleatis plerumque epaleatis; flosculi radiorum pistillatis; flosculi discorum bisexualibus, corollas actinomorhis plerumque zygomorphis, lobis 5; antheris caudatis, brevioribus; cypselae subteretibus, pappi absentibus vel multi squamis.

Annual or perennial herbs. Leaves alternate, petiolate to sessile, blades linear to ovate sometimes subcordate, simple to pinnatifid, triplinerved, sometimes pinnate. Capitulescences terminal, solitary, open paniculiform cymes, rarely subumbelliform cymes. Capitula radiate, rarely discoid. Involucre campanulate to mostly hemispherical. Receptacles convex, rarely shallowly conical, paleate, rarely epaleate. Ray florets pistillate, sometimes with staminodes, fertile, corollas yellow. Disc florets bisexual, fertile, corollas 5-lobed, golden-yellow; stamens 5, anthers yellowish to brown, shallowly calcarate or ecalcarate, tailed, appendages ovate; style branches with divided stigmatic surfaces, with obtuse papillae. Cypselae subterete, edges wanting, epidermis without crystals, pappus of small scales or absent.

Monotypic, *Anisopappus* contains 40 species found mostly in Africa and Madagascar, with one ruderal species extending into southeast Asia and China.

New subtribes of the Heliantheae

Chromolepidinae Panero, **subtribus nov.**-Type: *Chromolepis* Benth.

A Heliantheae ceteris, differt characteribus conjuncte: habitu herbaceo, palustris

foliis alterniis, petiolatis, laminis integris vel lobatis/runcinatis; capitulis ligulatis; phyllariis 2-3 seriatis, dimorphis; receptaculis paleatis; flosculis radiorum pistillatis; flosculis discorum bisexualibus, corollis actinomorpha, lobis 5; antheris ecaudatis; ramis styliorum sublinearis, deltatis; cypselae radiorum compressis; cypselae discorum quadratis; pappi radiorum absentibus, pappi discorum coroniformibus, breviorum.

Rosette-like, perennial, semiaquatic herbs. Leaves alternate, petiolate, semi-succulent, ovate to narrowly lanceolate, entire or pinnatifid. Capitulescences axillary, solitary. Capitula radiate. Involucre campanulate, phyllaries dimorphic in 2-3 series, subequal, membranaceous with black markings. Receptacles convex, paleate. Ray florets pistillate, fertile, corollas white. Disc florets bisexual, fertile, corollas pentamerous, yellow; stamens 5, anthers yellow-hyaline sometimes with dark connectives, appendages papillose; styles with two vascular strands, style branch with divided stigmatic surfaces, apices broadly acute to shallowly deltate. Ray cypselas tangentially flattened, triquetrous to weakly quadrate in cross section, glabrous. Disc cypselas obpyramidal, quadrate, sparsely pubescent, conspicuously smaller than ray cypselas, pappus a crown of minute awns and squamellae, absent in ray cypselas.

Monotypic, *Chromolepis* contains one species found in vernal pools in mid elevation grasslands of central and western Mexico.

The Chromolepidinae occupy a derived position within the Heliantheae, sister to Dugesiinae and collectively sister to Zaluzaniinae (Panero et al. 2001). Robinson (1981) placed *Chromolepis* in the Zaluzaniinae because of its fertile ray florets and shallowly quadrart cypselas. The genus is unusual among Mexican sunflowers because of its aquatic, rosette-like habit, and conspicuous blackish colorations on phyllaries and abaxial side of ray corollas. The heterochromatic capitula and dimorphic involucre of *Chromolepis* are characteristics not seen elsewhere in Zaluzaniinae.

Dugesiiinae Panero, **subtribus nov.** -Type: *Dugesia* A. Gray

A Heliantheae ceteris, differt characteribus conjuncte: habitu herbaceo; foliis alterniis, petiolatis, laminis runcinatis, lobatis; capitulis ligulatis; phyllariis 2-3 seriatis; receptaculis paleatis; flosculis radiorum pistillatis; flosculis discorum fungenter staminatis, corollis actinomorphis, lobis 5; antheris ecaudatis; ramis stylorum sublinearis; cypselae compressis; pappi radiorum absentibus, plerumque coroniformibus breviorum.

Prostrate, stoloniferous perennial herbs. Leaves alternate, petiolate, blades obovate to oval in outline, runcinate to pinnatifid. Capitulescences axillary, solitary, or small paniculiform cymes. Capitula radiate. Involucres hemispherical, phyllaries in 2-3 series, subequal, outermost foliaceous. Receptacles flat to slightly convex, paleate. Ray florets pistillate, in two series, fertile, corollas lemon to golden-yellow with greenish to black veins on abaxial side, corolla apices deeply 2- rarely 3-lobed. Disc florets functionally staminate, corollas pentamerous, yellow; stamens 5, anthers black, appendages oval to trullate with a visible constriction between appendage and thecae, shallowly carinate; style branches of disc florets narrowly tapered and papillose, style branches or ray floret spreading with broad, divided stigmatic surfaces. Ray cypselas tangentially flattened, biconvex, essentially glabrous with a few trichomes on the neck, margins with shallowly lacerate wings, pappus absent or of a minute crown.

Monotypic, *Dugesia* contains one species found in disturbed, gravelly or sandy soils, in the dry highlands of eastern-central Mexico.

The Dugesiiinae are sister to *Parthenium* with which they share strongly bifid ray corollas, tangentially flattened ray cypselas, and functionally staminate disc florets. More extensive sampling of the Heliantheae in the future may reveal subtribe Ambrosiinae to be paraphyletic and that *Parthenium* L. and *Parthenice* A. Gray should be included in the Dugesiiinae.

Enceliinae Panero, **subtribus nov.**-Type: *Encelia* Adans.

A Heliantheae ceteris, differt caracteribus conjuncte: habitu herbaceo vel fruticoso, foliis alterniis, petiolatis, laminis integris plerumque lobatis/dissectis; capitulis ligulatis plerumque discoideis; phyllariis 2-5 seriatis; receptaculis paleatis, paleae deciduis; flosculis radiorum plerumque pistillatis; flosculis discorum bisexualibus, corollis actinomorphis, lobis 5; antheris ecaudatis; ramis stylosum sublinearis; cypselae compressis; pappi absentibus vel 1-2 squamis.

Annual or perennial herbs, shrubs, rarely trees. Leaves alternate, rarely opposite, petiolate, rarely sessile, sometimes with resinous exudates, blades linear to ovate or trullate, sometimes lacinate, pinnately veined or triplinerved, rarely pentanerved. Capitulescences terminal, solitary and scapose, or in paniculiform or corymbiform cymes. Capitula radiate or discoid. Involucres turbinate, campanulate or hemispherical, phyllaries in 2-5 series, subequal, rarely graduated, herbaceous, rarely chartaceous sometimes with resinous exudates. Receptacles flat to convex, pales deciduous. Ray florets neuter or rarely pistillate and sterile, corollas golden-yellow sometimes with biseriate trichomes on tube, rarely on limb. Disc florets bisexual, fertile, corollas 5-lobed, golden-yellow or purple, mostly without fibers embedding the vascular strands, lobes sometimes with thickened cells or with glandular or multicellular trichomes on abaxial surfaces of the lobes; stamens 5, anthers yellow, brown or black, appendages ovate to linear, sometimes with glandular trichomes, endothecium cells fusiform, rarely quadrate with 1-3 polar bridges; style branches with fused stigmatic surfaces, some species with two stigmatic surfaces that fuse slightly above style bifurcation point, densely papillose below, apices acute to broadly acute. Cypselae radially flattened, rarely thickened or terete, obovate to oblong, densely sericeous, rarely glabrous, sometimes with conspicuous wings or corky edges on sides and neck, pappus of two slender awns (rarely absent) with or without squamellae in between them, rarely of awns fused to a crown surrounding the neck.

The subtribe contains five genera including *Encelia* (15 spp.), *Enceliopsis* (A. Gray) A. Nelson (4 spp.), *Flourensia* A. DC. (33 spp.), *Geraea* Torr. & A. Gray (2 spp.), *Helianthella* Torr. & A. Gray (8 spp.) found mostly in western North and South America.

The Enceliinae are an isolated lineage of the Heliantheae nestled between the Engelmanniinae and the clade containing the Ambrosiinae, Chromolepidinae, Dugesiinae, Helianthinae, Spilanthinae, Zaluzaniinae, and Zinniinae (Panero et al. 2001). The subtribe shares with subtribe Helianthinae sterile ray florets. In addition, the strongly flattened and sericeous cypselas, along with the caducous pales of the Enceliinae are only seen elsewhere in the Heliantheae in a few members of the Helianthinae (e.g., *Syncretocarpus* S. F. Blake, and some species of *Viguiera* Kunth).

Spilanthinae Panero, **subtribus nov.**-Type: *Spilanthes* Jacq.

A Heliantheae ceteris, differt caracteribus conjuncte: habitu herbaceo vel fruticoso; foliis oppositiis, petiolatis plerumque sessilibus, laminis integris plerumque lobatis; capitulis ligulatis plerumque discoideis; phyllariis 1-5 seriatis; receptaculis paleatis plerumque epaleatis, conoideis; flosculis radiorum pistillatis; flosculis bisexualibus, corollis actinomorpha, lobis 5 plerumque 4; antheris ecaudatis; ramis styliorum sublinearis; cypselae compressis; pappi presentibus, 1-3 squamis.

Erect or decumbent annual or perennial herbs, sometimes rooting at the nodes, rarely scandent shrubs. Leaves opposite, petiolate or subsessile, blades linear to ovate, sometimes reniform, entire, triplinerved. Capitulescences axillary or terminal, solitary, simple to congested cymes, peduncles sometimes fistulose. Capitula discoid or radiate. Involucre campanulate to hemispherical, phyllaries in 1-5 series, subequal, rarely dimorphic, mostly herbaceous, sometimes bases indurate and coriaceous. Receptacles convex to conical, especially with age, mostly paleate, rarely epaleate, pales chartaceous, rarely coriaceous. Ray florets pistillate, fertile, corollas purplish, yellow-orange or white. Disc florets, bisexual, fertile, corollas pentamerous,

rarely tetramerous, purplish, white, or yellow; stamens 5, rarely 4, anthers brown or black, appendages ovate or deltate with or without glands; style branches with fused stigmatic surfaces, apices acute and papillose, without appendages. Ray cypselae tangentially flattened, triquetrous, obovoid, sparsely to densely ciliate, trichomes with recurved tips with age. Disc cypselae radially flattened, sometimes peripheral ones triquetrous, terete, sometimes quadrate and narrowly rhombic, rarely square in outline, mostly shallowly winged or sometimes conspicuously winged, corky, ciliate, glabrous to sparsely pubescent, pappus of a minute crown, a single awn fused to a broad ring around the neck of the cypselae, or more commonly of 2-3 slender awns as a continuation of the wings, sometimes with squamellae in between.

The subtribe contains five genera including *Acmella* Rich. ex Pers. (30 spp.), *Oxycarpha* S. F. Blake (1 sp.), *Salmea* DC. (10 spp.), *Spilanthes* (6 spp.), and *Tetranthus* Sw. (2-4 spp.). Most species of the subtribe are found in the New World tropics, but a few species of *Acmella* and *Spilanthes* are endemic to the tropical and subtropical regions of the Old World.

The Spilanthinae are sister to the Zinniinae (Panero et al 2001) and share with them opposite leaves, the tendency for solitary, long-pedunculate capitulescences, and conical receptacles. The Spilanthinae differ from the Zinniinae in lacking marcescent ray corollas.

New subtribes of tribe Millerieae

Dyscritothamninae Panero, subtribus nov. -

Type: *Dyscritothamnus* B. L. Rob.

A Millerieae ceteris, differt characteribus conjuncte: habitu herbaceo vel fruticoso foliis oppositiis plerumque alterniis, petiolatis vel sessilibus, laminiis integris plerumque lobatis/dissectis; capitulis ligulatis plerumque discoideis; phyllariis 1-4-seriatis; receptaculis paleatis plerumque epaleatis; flosculis radiorum pistillatis; flosculis discorum bisexualibus, corollis actinomorpha, lobis 5; antheris

ecaudatis; ramis styliorum sublinearis; cypselae subteretibus; pappi presentibus, setis papporum plumosis.

Annual or perennial herbs or shrubs. Leaves mostly opposite, sometimes alternate, petiolate or sessile, sometimes clasping or perfoliate, blades linear to broadly ovate, sometimes trilobed to deeply lobed, rarely deltate or acicular, triplinerved, rarely uninerved. Capitulescences terminal, solitary and scapose or open paniculiform cymes, rarely congested cymes. Capitula radiate, rarely discoid. Involucre cylindrical, campanulate or hemispherical, phyllaries in 1-4 series, subequal, sometimes graduated and dimorphic with inner series chartaceous and much longer than the outer herbaceous series, sometimes reduced to only 4 fleshy, herbaceous phyllaries enclosing florets in a pyramid-like, valvate bud. Receptacles convex to conical, paleate, rarely epaleate, pales sometimes chartaceous, hyaline. Ray florets fertile, corollas golden-yellow, white, pink or magenta. Disc florets bisexual, fertile, corollas 5-lobed, golden-yellow, green, white, pink or purplish; stamens 5, anthers yellow or brown, appendages ovate; style branches with divided stigmatic surfaces. Cypselae mostly terete to shallowly radially flattened or quadrate, glabrous to densely sericeous, pappus of multiple bristles or scales, rarely a very reduced crown.

The subtribe contains five genera including *Bebbia* Greene (2 spp.), *Cymophora* B. L. Rob. (5 spp.), *Dyscritothamnus* (2 spp.), *Tetragonotheca* L. (4 spp.), and *Tridax* L. (30 spp.). Most species are distributed in montane, tropical North America with a few species in the north and central Andes of South America.

The Dyscritothamninae are sister to the Melampodiinae (Panero et al. 2001). The monophyly of the Dyscritothamninae and their subtribal relationships are well supported.

Jaegeriinae Panero, **subtribus nov.**-Type: *Jaegeria* Kunth

A Millerieae ceteris, differt characteribus conjuncte: habitu herbaceo, terrestri, palustri vel aquatico; foliis oppositis, petiolatis

vel sessilis, laminis integris; capitulis ligulatis; phyllariis 1- seriatis; receptaculis paleatis; flosculis radiorum pistillatis; flosculis discorum bisexualibus, corollis actinomorphis, lobis 5; antheris ecaudatis; ramis stylorum sublinearis; cypselae teretibus; pappi absentibus plerumque coroniformibus breviorum.

Annual or perennial herbs, rooting at the nodes. Leaves opposite, sessile to petiolate, blades linear to ovate. Capitulescences axillary or terminal, solitary or of open paniculiform cymes. Capitula radiate. Involucres campanulate to hemispherical, phyllaries in 1 series, subequal, herbaceous with hyaline, ciliate wings wrapping around the ray cypselae, caducous and shed along with cypselae as a unit (perigynia). Receptacles strongly convex to conical, paleate. Ray florets pistillate, fertile, corollas white, white-pink, white-purple, yellow, marcescent, tube short or absent. Disc florets bisexual, fertile, corollas yellow or yellow-green, sometimes whitish gray, lobes 5 rarely 4, tube abruptly narrowed into the throat; stamens 5, anthers yellow, appendages ovate; style branches recurved, apices round to obtuse. Cypselae terete to obscurely angled, clavate, bases tapered, glabrous, shiny black, ray cypselas slightly larger than disc cypselas otherwise equivalent; pappus absent or a minute crown. Base chromosome number, $x = 9$.

Monotypic, *Jaegeria* contains nine species found in the New World tropics with most species concentrated in the highlands of Mexico.

The Jaegeriinae are sister to the clade containing Milleriinae, Desmanthodiinae, Espeletiinae, and Galinsoginae (Panero et al. 2001).

New Combinations in subtribe Ambrosiinae.

Studies of Heliantheae subtribe Ambrosiinae by Miao et al. (1995) support the expansion of the genus *Euphrosyne* DC. to include five species. This new concept of *Euphrosyne* requires the creation of the following combinations:

Euphrosyne acerosa (Nutt.) Panero, **comb. nov.** *Oxytenia acerosa* Nutt., J. Acad. Phil. N. S. 1:172. 1847.

Euphrosyne dealbata (A. Gray) Panero, **comb. nov.** *Iva dealbata* A. Gray, Pl. Wright. 1:104. 1852.

Euphrosyne nevadensis (M. E. Jones) Panero, **comb. nov.** *Iva nevadensis* M. E. Jones, Amer. Natur. 17: 973. 1883.

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