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CLASSIFICATION OF SUBTRIBE CONYZINAE (ASTERACEAE: ASTEREAE)

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Abstract: Subtribe Conyzinae includes *Erigeron*, New World *Conyza*, the North American genus *Aphanostephus*, and a small group of South American species segregated as the genera *Apopyros*, *Darwiniothamnus*, *Hysterionica*, *Leptostelma*, and *Neja*. *Erigeron* is the only genus with species native to regions outside of the New World. About 500 species are included in the subtribe. All North American, Central American, and South American species of *Erigeron* are included in the present treatment and assigned to one of the 35 sections recognized here. Ten new sections of *Erigeron* are recognized: sect. **Disparipili**, sect. **Filifolii**, sect. **Gyrifolium**, sect. **Lonchophylli**, sect. **Meridionales**, sect **Microcephalum**, sect. **Quercifolium**, sect. **Radicati**, sect. **Rhizonexus**, and sect. **Terranea**. *Conyza* is at least biphyletic; each of the groups is represented in the treatment but not all of the South American species are included. Molecular data have made it clear that traditional, North American species of *Erigeron* form the basal and terminal clades in the evolutionary topology of the subtribe, thus *Conyza*, *Aphanostephus*, and the other segregate genera have arisen from within the branches of *Erigeron*. *Erigeron*, as currently treated and tentatively maintained here, is paraphyletic. Broad taxonomic alternatives that include only monophyletic taxa are: (1) to treat the whole subtribe as *Erigeron* or, (2) to recognize *Aphanostephus* or *Aphanostephus*, *Conyza*, and the other South American segregates and at least an additional 5 to 10 new generic-level segregates from species groups traditionally treated as North American *Erigeron*.

Keywords: Compositae, *Conyza*, *Erigeron*.

Subtribe Conyzinae includes *Erigeron* L., New World *Conyza* Less., the North American genus *Aphanostephus* DC., and several small groups of South American species sometimes segregated as the genera *Apopyros* G.L. Nesom, *Darwiniothamnus* Harling, *Hysterionica* Willd., *Leptostelma* D. Don., and *Neja* D. Don (Nesom, 1994d; Nesom and Robinson, 2006). A molecular-phylogenetic study of *Erigeron* and relatives (Noyes, 2000a) essentially confirmed this view of the subtribal composition, with a few caveats. One Mexican species originally described as *Erigeron* (Sundberg and Nesom, 1990) is excluded and now segregated as the monotypic genus *Batopilasia* G.L. Nesom & R.D. Noyes (Nesom and Noyes, 2000); another Mexican species originally described as *Erigeron* now is recognized as the genus *Chloracantha* G.L. Nesom et al. (Nesom et al. 1991). Native African species of *Conyza* belong in a different subtribe, as suggested by Nesom (1990a) and confirmed by Noyes and Rieseberg (1999). The genus *Laennecia* Cass. is segregated from *Conyza* (Zardini, 1981; Nesom, 1990f, 1990g, 1992d, 2001; Nesom & Laferriere, 1990). The evolutionary origin of *Aphanostephus* now appears unequivocal—it arose from within the evolutionary matrix of *Erigeron*, as indicated by the ITS data (Fig. 1) of Noyes (2000a), confirming earlier research results based on data from chloroplast DNA (Morgan, 1990). Morphology had suggested that *Aphanostephus* was related to a different subtribe (Nesom, 1994d). Native species of Australia previously identified as *Erigeron* have been transferred to *Pappochroma* Raf. (Nesom, 1994e, 1994f). *Erigeron rapensis* F. Brown, a shrub from the Polynesian island of Rapa, now constitutes the monotypic genus *Pacifigeron* Nesom (Nesom, 1994g).

In contrast to an hypothesis that the Conyzinae arose from ancestors in the

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Southern Hemisphere (Nesom, 1994d), Noyes and Rieseberg (1999) found that the evolutionary origin of the subtribe was from within a North American clade. South American Conyzinae are derived from North American ancestors.

In its current definition, the Conyzinae comprises about 500 species, about 400 of these generally identified as *Erigeron*. *Erigeron* is the only genus of Conyzinae with species native to regions outside of the New World. An earlier summary (Nesom, 1989c) presented an outline of classification of the New World species of *Erigeron*, recognizing 17 sections. In the last decade, however, new species and new sections have been described in the genus and new ideas regarding infrageneric classification have come to light (citations below). In order to provide a coherent framework for further studies in the systematics and evolution of the Conyzinae, a taxonomic update of the subtribe, including all of the North American and Caribbean species, is presented here. Boundaries of some groups of South American *Erigeron* and *Conyza* are being clarified, but a complete account of these species is not yet possible. The South American taxa generally identified as *Conyza* are represented in the present overview by relatively few species. The classification of the Eurasian species of *Erigeron* has not yet been studied in detail, but many of them belong with sect. *Trimorpha* (Cass.) DC. and sect. *Erigeron* (see references by Huber and associates), some apparently with sect. *Fruticosus* G. Don

Taxonomic treatments with keys to species of New World *Erigeron* are available: North America north of Mexico (Nesom, 2006); Mexico (Nesom, in ms.); Central America (Nesom & Pruski, in ms.); and South America (Solbrig, 1962).

Overview of Subtribal Taxonomy

Molecular data indicate that *Erigeron* and *Conyza* as currently treated are not monophyletic (Noyes, 2000a, his cladogram reproduced here as Fig. 1). Subtribe Conyzinae has species of *Erigeron* at the base and apex of the phylogenetic topology, with the primarily Brazilian clade including *Leptostelma*, *Apopyros*, *Neja*, and *Hysterionica* having originated in a sister relationship with *Erigeron* species. *Conyza* appears to be polyphyletic, at least biphyletic, and there is little understanding of the patterns of variation among the South American species (excluding sect. *Caenotus*). Morphological boundaries between *Erigeron* and *Conyza* are not clear and critical species of both have not been included in the molecular analyses. The distinctive and long-recognized genus *Aphanostephus* apparently has arisen in a sister relationship to an internal clade of *Erigeron*. Classification at the generic rank within the Conyzinae remains tentative.

If Noyes's cladogram is accepted as a reasonable phylogenetic hypothesis for the Conyzinae, at least in broad strokes and acknowledging that it is tentative, three broad taxonomic alternatives for the recognition of genera within the subtribe are possible.

1. Adopt a strictly clade-based taxonomy, treating cladistically coordinate groups at coordinate ranks, recognizing *Aphanostephus*, *Apopyros*, *Conyza* sensu stricto, *Darwiniothamnus*, *Hysterionica*, *Leptostelma*, and *Neja*, as well as *Erigeron* sensu stricto (to include *Trimorpha* Cass. and perhaps *Leptilon* Raf., the horse-weed conyzas) and at least eight other generic-level segregates comprising various species groups traditionally treated within *Erigeron*. Simply the acceptance of *Aphanostephus* within this conceptual framework would necessitate recognition of at least five new generic-level segregates, even if *Conyza* and the Brazilian segregates all were maintained within *Erigeron* sensu stricto—and all five of these segregates would come from within North American and Central American *Erigeron* as currently recognized.

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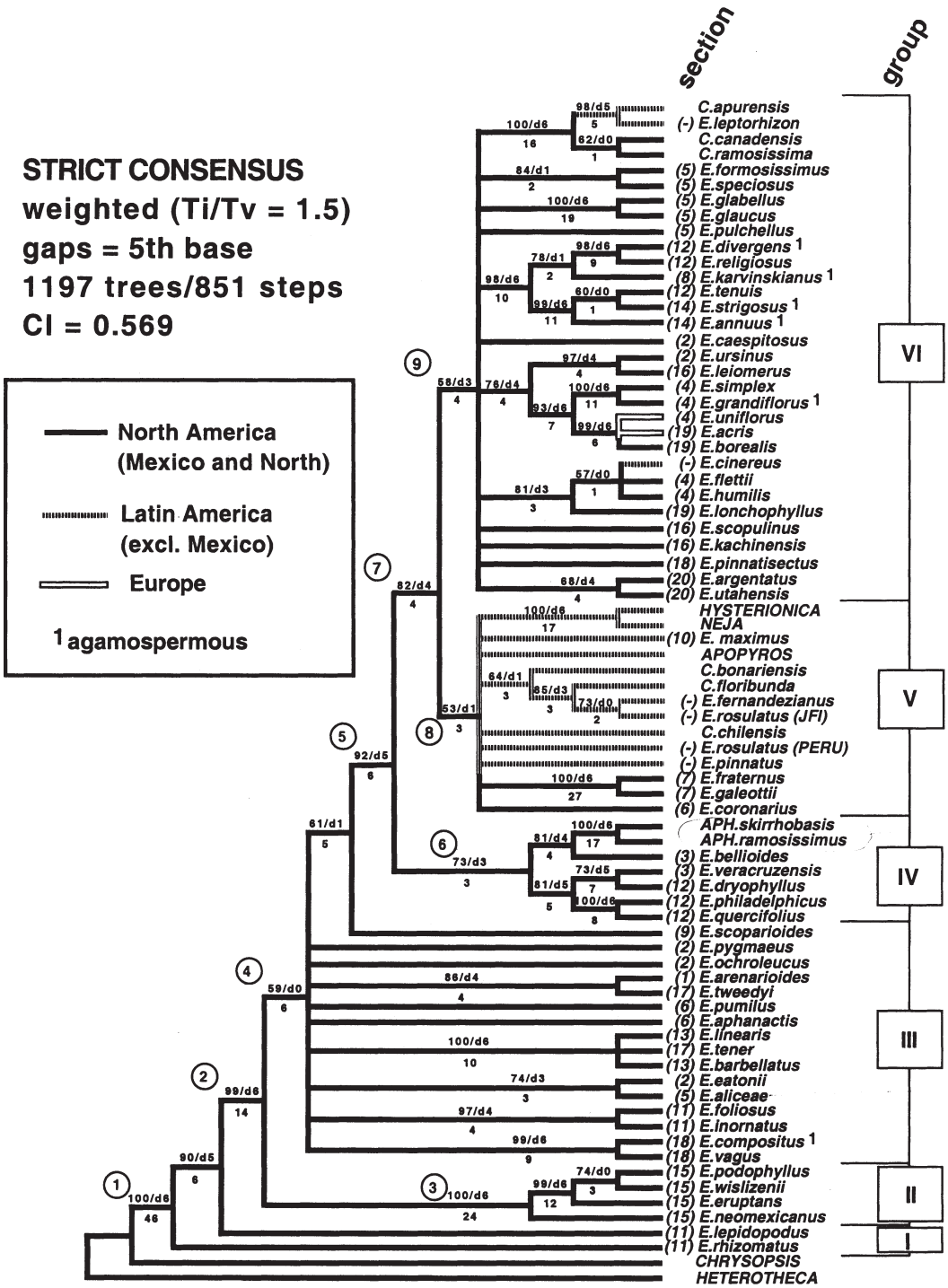


FIG. 1. Strict consensus tree for parsimony analysis of ITS nucleotide sequence data for Conyzinae. Reproduced with permission from Noyes (2000a). Numbers above the branches are bootstrap and decay indices. Branch lengths from one abrbitrarily delected tree are given below branches. Circled numbers identify topologically important nodes. ''Section'' refers to sections of *Erigeron* according to Nesom 1989c, 1990a, 1994d. Groups I–VI are groups of taxa, subjectively selected, sharing relationship as determined by the cladogram. E= *Erigeron*, C= *Conyza*.

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2. Enlarge *Erigeron* to include all species of Conyzinae, which would imply the submergence of all previously recognized segregate genera, including *Aphanostephus*. This alternative, in effect, is the opposite extreme of the first alternative.
3. Maintain monophyletic and morphologically well-defined groups currently recognized as genera at generic rank (*Aphanostephus*, *Apopyros*, *Darwiniothamnus*, *Hysterionica*, *Leptostelma*, and *Neja*) —keeping most of the remaining species within *Erigeron*, which then would be explicitly recognized as a non-monophyletic (paraphyletic) genus. The taxonomic rank for treatment of *Conyza* sensu stricto and other well-defined groups, including *Leptilon* (= *Erigeron* sect. *Caenotus* Nutt.), needs to be considered in detail.

Regarding the broader taxonomic approach, whether or not to recognize paraphyletic taxa with formal rank, the Conyzinae provides an archetypal example. Many botanists have signed a lengthy statement noting that they support formal recognition of paraphyletic taxa (Nordal and Stedje and 148 signatories, 2005), and the Conyzinae comprises a large group of species where it may be useful to sustain contrasting philosophical positions.

Definitions of genera within the Conyzinae clearly need to be adjusted and refined. The present overview represents a first step toward that end.

Taxonomic Overview

Astereae subtribe Conyzinae Horan., Char. Ess. Fam. 93. 1847. Type genus, *Conyza* L. Subtribe Erigeroneae Gren. & Godr., Fl. France 2: 83, 92. 1850. Type genus, *Erigeron* L.

Genera included:
Aphanostephus DC.
Apopyros G.L. Nesom
Conyza Less.
Darwiniothamnus Harling
Erigeron L.
Hysterionica Willd.
Leptostelma D. Don
Neja D. Don

Erigeron L., Sp. Pl. 2: 863. 1753 [nom. conserv. prop.]. (see Heath, 1994)

Type: *Erigeron uniflorus* L. (M.L. Green, Prop. Brit. Bot. 181. 1929; W. Huber, Taxon 41: 563. 1992 – Herb. Linn., No. 994.23, typ. conserv. prop.) (also see comments in Nesom, 1989c).

Infrageneric groups were recognized for most of the New World species by Nesom (1989c), and others have subsequently been added (Nesom and Noyes, 1999; Nesom, 1990c, 1994a). The analysis of Noyes (2000a) and recent work on the species-level taxonomy of *Erigeron* for the FNA treatment (Nesom, 2006) have indicated that some of the groups of *Erigeron* earlier recognized by Nesom are not monophyletic. This reflects the misplacement of individual species, but in larger part it results from recognition of a number of over-broadly defined groups. For example, informally treated subgroups of sect. *Asteroidea* do not cohere as a single phyletic element, sect. *Olygotrichium* and sect. *Fruticosus* include evolutionarily disparate subgroups of species, and sect. *Geniculactis* (sensu Nesom, 1990c) comprises two separate groups. More strictly defined groups convey a better understanding of the evolutionary patterns and distribution of diversity within the genus. Eventual refinement of the phylogenetic arrangement of these groups may suggest or require additional categories and the composition and rank of some groups may be altered, depending on philosophical point-of-view and development of further data useful for systematic interpretation.

Erigeron as treated here includes about 400 species. 304 are New World species (enumerated below); Old World species are estimated to be around 80–100 (most numerous in eastern Asia and Russia). Figures 2–7 illustrate various aspects of habit and floral diversity in the genus.

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FIG. 2. *Erigeron speciosus* (sect. *Fruticosus*). Photo by Mrs. W.D. Bransford, 1986, from the Image Gallery of the Lady Bird Johnson Wildflower Center.

1. Sect. *Arenarioides* (Rydb.) Nesom, Phytologia 67: 70. 1989. *Erigeron* [unranked sp. group] *Arenarioides* Rydb., Fl. Rocky Mts. 897. 1918, in clave. TYPE: *Erigeron arenarioides* (D.C. Eaton ex A. Gray) A. Gray ex Rydb.

Taprooted, perennial; caudex branching, retaining old leaf bases; glabrous; stems branched; leaves filiform or linear to linear-oblanceolate, not clasping; heads erect in bud; rays white, often with an abaxial midstripe, not coiling or reflexing; achenes 1.5–2.2 mm long, 2-nerved; pappus of 10–16 bristles.



FIG. 3. *Erigeron clokeyi* (sect. *Stenactis*). Ray corollas are reflexing, heads nodding in bud. Photo by Christopher L. Christie, 2003, from CalPhotos database.

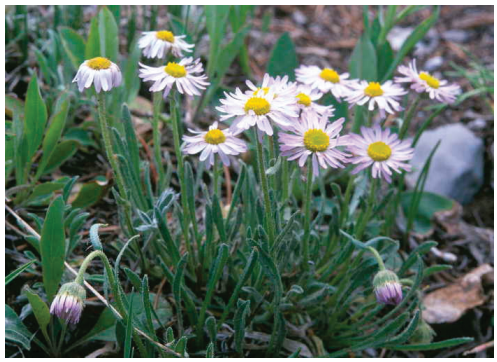


FIG. 4. *Erigeron vetensis* (sect. *Stenactis*). Ray corollas are reflexing, heads nodding in bud. Photo by Robert Sivinsky, 2004, from CalPhotos database, used with Sivinsky's permission.

E. arenarioides (D.C. Eaton ex A. Gray) A. Gray ex Rydb.

E. salmonensis Brunsfeld & Nesom

Erigeron salmonensis was recently described (Brunsfeld and Nesom, 1989); the two species of sect. *Arenarioides* were regarded as closely related but isolated within the genus. Molecular data (Noyes, 2000a) indicate that *E. tweedyi* Canby (sect. *Spathifolium*) is closely related to *E. arenarioides* – with this molecular pointer, morphological similarities between sect. *Spathifolium* and sect. *Arenarioides* are apparent, but sect. *Spathifolium*, as represented by *E. tener*, is placed by the molecular data most closely related to sect. *Osteocaulis*.



FIG. 5. *Erigeron chrysopsidis* (sect. *Disparipili*). Heads are nodding in bud. Yellow-rayed species have evolved among white- and blue-rayed ones in sects. *Disparipili*, *Erigeron*, and *Osteocaulis*. Photo by Christopher L. Christie, 2004, from CalPhotos database.

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FIG. 6. *Erigeron bloomeri* (sect. *Osteocaulis*). Ray florets are completely absent. Photo by Steve Matson, 2006, from CalPhotos database.

2. Sect *Asterigeron* Rydb., Fl. Rocky Mts. 891. 1918. TYPE: *Erigeron watsonii Erigeron* sect. *Spathifolium* Nesom, Phytologia 67: 84. 1989. TYPE: *Erigeron tener* (A. Gray) A. Gray

Perennial, taprooted; caudex simple or more commonly a multicipital crown or with elongating branches, forming mats (*E. acomanus*, *E. tener*) connected by systems of lignescent rhizomes and caudex branches; vestiture short-strigillose to villous, hirsute, or glabrous, hairs white (*E. tener*, *E. acomanus*, *E. tweedyi*, and *E. wilkenii* have similar vestiture; *E. cronquistii*, *E. evermannii*, *E. subglaber* glabrous to glabrate); stems branching (simple in *E. acomanus*, *E. wilkenii*); leaves spatulate to oblanceolate, entire, with expanded and indurate petiole bases, often folding, not clasping; heads 1 or 1–3, nodding in bud (*E. acomanus*, *E. tweedyi*), behavior unknown in others; phyllaries with a broad green midband, minutely glandular; rays white to pink, not coiling (or coiling in *E. garrettii*?) or reflexing; achenes 1.5–3.2 mm long (1–1.2 in *E. cavernensis*, 3.2–3.5 mm in *E. evermanii*), 2-nerved; pappus of 10–35 bristles.



FIG. 7. *Erigeron filifolius* (sect. *Filifolii*). Close-up of head. Photo by Steve Matson, 2006, from CalPhotos database.

Group A. U.S.A.; leaves thin, long-petioled, vestiture relatively sparse.

E. cavernensis S.L. Welsh & N.D. Atwood
E. cronquistii Maguire
E. evermannii Rydb.
E. uncialis Blake (incl. *E. conjugans* Blake)
E. watsonii (A. Gray) Cronquist

Group B. U.S.A.; leaves thick, short-petioled; vestiture closely white-strigillose.

E. acomanus Spellenb. & P. Knight
E. tener (A. Gray) A. Gray
E. tweedyi Canby
E. wilkenii O'Kane (O'Kane 1990)

Group C. U.S.A.; leaves thick, short-petioled; glabrous to glabrate; caudex multicipital.

E. garrettii Rydb.
E. subglaber Cronquist

Group D. Mexico.

E. cuatrocienegensis G.L. Nesom
E. gypsoverus G.L. Nesom
E. unguiphyllus G.L. Nesom

Molecular data (Noyes, 2000a) indicate that *E. tweedyi* is closely related to *E. arenarioides* (sect. *Arenarioides*), but the

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closer morphological associates of *E. tweedyi* instead seem to be in sect. *Spathifolium*. Noyes's data also suggest that sect. *Spathifolium* (as represented by *E. tener*) may be closely related to sect. *Osteocaulis*. The vestiture in sect. *Spathifolium* is similar to that of sects. *Wyomingia*, *Arenarioides*, and *Osteocaulis*, but the species in the latter sections produce conspicuously coiling rays. There also are suggestive similarities between sect. *Spathifolium* and sect. *Asterigeron*.

Erigeron subglaber has leaves oblanceolate to broadly oblanceolate or subspatulate and differs from the other U.S.A. species, which usually have distinctly spatulate leaves. This species apparently exists only as a single population system on the Elk Mountain Ridge of the Sangre de Cristo Mountains in San Miguel Co., New Mexico (ESE of Cowles, ca. 10,000–11,500 ft elevation). If not a member of sect. *Spathifolium*, it apparently is isolated geographically as well as morphologically from other possible close relatives (except one) within the genus. The identification of the original collection was *E. leiomerus* (sect. *Asterigeron*), to which it is similar but which has nodding buds and reflexing rays; the assessment of these behaviors in *E. subglaber* is based on somewhat ambiguous observations of herbarium specimens and online photographs. *Erigeron garrettii* appears to be very similar to *E. subglaber*, and they are placed here as closely related despite their considerable separation in geography.

The species of Group B are gypsophilic endemics of northeastern Mexico (Coahuila, Nuevo León, and San Luis Potosí, respectively), tentatively placed in sect. *Spathifolium* emphasizing their short-strigillose vestiture and ray behavior. They are geographically disjunct from the more typical members of the section; the closest species of the section sensu stricto is *E. acomanus* from northwestern New Mexico. None of the other species of northeastern Mexico show features that suggest that they might have been the immediate forebearers of *E. cuatrocienegensis* and *E. gypsoverus*.

3. Sect. *Asteroidea* Nutt., Trans. Amer. Philos. Soc. ser. 2, 7: 308. 1841. LECTOTYPE): *Erigeron decumbens* Nutt. (Nesom, 1989c)

Erigeron [unranked sp. group] *Decumbentes* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *Erigeron decumbens* Nutt.

Erigeron [unranked sp. group] *Asperuginei* Rydb., Fl. Rocky Mts. 897. 1918, in clave. TYPE: *Erigeron asperugineus* (D.C. Eaton) A. Gray

Perennial, taprooted; caudex branches generally slender (rhizome-like in *E. decumbens*); sparsely to densely strigillose or strigose to hirsute or hirtellous, stems and involucres often minutely glandular; stems simple or branched, basally ascending to decumbent; leaves linear to oblanceolate or subspatulate, entire, usually with indistinct petiole region, usually 3-nerved, cauline gradually reduced, not clasping; heads 1–7+, commonly more than 1, erect in bud; rays white to blue, not coiling or only weakly so; achenes 1.2–3.5(–4.5) mm long, 2-nerved; pappus of (6–)12–30 bristles.

- *E. asperugineus* (D.C. Eaton) A. Gray
- *E. canaani* S.L. Welsh (incl. *E. higginsii* S.L. Welsh)
- *E. corymbosus* Nutt.
- *E. decumbens* Nutt.
- *E. eatonii* A. Gray (incl. *E. sonnei* Greene, *E. nevadincola* Blake)
- *E. jonesii* Cronquist (incl. *E. wahwahensis* S.L. Welsh, see Cronquist 1994)
- *E. lassenianus* Greene (incl. *E. flexuosus* Cronquist)
- *E. maniopotamicus* G.L. Nesom & T. Nelson
- *E. robustior* (Cronquist) G.L. Nesom

Sect. *Asteroidea* previously was interpreted to include a broader array of species and species groups (Nesom, 1989c), but it is here limited to the strict sense (the "*Erigeron decumbens* group" of Nesom, 1989), following indications of molecular data (Noyes, 2000a). Studies of this group of species have recently been published (Strother and Ferlatte 1988; Nesom, 1992b, 1992c, 2004); *E. maniopotamicus* is newly described (Nesom and Nelson, 2004).

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Molecular evidence (Noyes, 2000a) suggests that *Erigeron aliceae* is most closely related to species of sect. *Asteroidea* but it is closer in morphology to sect. *Fruticosus*, especially in its fibrous-rooted rhizomes, clasping leaves, villous involucres, coiling rays, and relatively large, 2(–4)-nerved achenes.

Erigeron asperugineus has a set of features common to sect. *Asteroidea*: slender-taprooted with a simple or branched caudex, stems decumbent-ascending, leaves mostly basal, spatulate, and 1-nerved or weakly 3-nerved, heads 1(–2), phyllaries often purple, sparsely to moderately hirsutulous, densely minutely glandular, rays blue, not coiling or reflexing, achenes 2.5–3.1 mm, and pappus bristles 20–30. The hirtellous vestiture is more like sect. *Pseuderigeron*; the often strongly petiolate-spatulate leaves are suggestive of Group A of sect. *Asterigeron*. The range of *E. asperugineus* in Idaho, Montana, Nevada, and Utah is more similar to species of section *Radicati*.

4. Sect. *Cincinnactis* Nesom, Phytologia 67: 73. 1989. TYPE: *Erigeron longipes* DC.

Fibrous-rooted, rhizomatous (taprooted in *E. oaxacanus*), perennial (annual in *E. narcissus*); caudex simple or divided into slender, rhizomelike branches; vestiture; stems simple, rarely branched; leaves ovate-lanceolate, ovate-lanceolate, clasping or subclasping; heads erect (?) in bud; rays (80–)120–350, mostly filiform, white, tightly coiling at maturity; achenes ca 0.6–1 mm long, 2-nerved; pappus of 12–23 bristles (absent or reduced in number in *E. narcissus*).

E. longipes DC.
E. narcissus G.L. Nesom
E. oaxacanus Greenm.
E. procumbens (Houston ex Mill.) G.L. Nesom (syn = *E. myriactis* Small)
E. stanfordii I.M. Johnst. ex Nesom
E. tephropodus G.L. Nesom

Erigeron stanfordii is placed here because of its tightly coiling rays (see images of isotypes at MO, NY), although the laminae are distinctly wider and fewer (45–76) and the achenes longer (2 mm long) than in the other species of *Cincinnactis*. Molecular data (Andrus et al., sin prep.), in contrast, suggest that *E. stanfordii* is phyletically basal-most or near it in the whole genus, far separated from the species of sect. *Cincinnactis*.

Erigeron basilobatus and *E. veracruzensis*, placed in sect. *Cincinnactis* in 1989, are transferred here to sect. *Quercifolium*, as suggested by the molecular data of Noyes (2000a). The group of Caribbean species with tightly coiling rays, including *E. bellioides* and *E. cuneifolius* and placed by Nesom (1989) within sect. *Cincinnactis*, is here treated as sect. *Microcephalum*. *Erigeron exilis* has been transferred to sect. *Lamprocaules* G.L. Nesom & R.D. Noyes (Nesom and Noyes, 1999). *Erigeron crenatus* and *E. socorrensis* are transferred to sect. *Caenotis*.

5. Sect. **Disparipili** Nesom, sect. nov.

Vestimento caulino trichomatibus patentibus in longitudine valde inequali, capitulis in alabastro erectis, et radiis cincinatis distinctus. TYPE: *Erigeron disparipilus* Cronquist

Taprooted, perennial; caudex simple; cauline vestiture with spreading hairs of markedly unequal length (*E. chrysopsidis*, *E. disparipilis*, *E. poliospermus*); stems simple or branched; leaves narrowly oblanceolate and 1-nerved, entire, not clasping, mostly basal, or cauline well-developed; leaf margins/petioles coarsely ciliate; heads erect in bud or on arching peduncles; rays present (absent in *E. chrysopsidis* var. *austiniae*), white (yellow in *E. chrysopsidis*, *E. piperianus*), coiling; achenes 1.6–1.8 mm (*E. piperianus*) to 2.1–3 mm to 3.5–4.5 mm (*E. latus*) long, 2-nerved; pappus of 14–30 bristles.

E. chrysopsidis A. Gray
E. davisii (Cronquist) G.L. Nesom
E. disparipilus Cronquist
E. latus (A. Nelson & J.F. Macbr.) Cronquist
E. nanus Nutt.
E. piperianus Cronquist
E. poliospermus A. Gray

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Cronquist (1994) hypothesized that *Erigeron nanus* (and *E. rydbergii* Cronquist) are closely related to *E. untermannii* S.L. Welsh but the latter is placed here in sect. *Wyomingia*. The distinction of *E. davisii* and its relationship to this group were noted by Nesom (2004).

6. Sect. *Erigeridium* Torr. & A. Gray, Fl. N. Amer. 2(1): 176. 1841. TYPE: *Erigeron vernus* (L.) Torr. & A. Gray

Fragmosa Raf., Fl. Tellur. 2: 50. 1836. LECTOTYPE (Nesom 1989c): *Erigeron nudicaulis* Michx. (= *Erigeron vernus* (L.) Torr. & A. Gray)

Erigeron [unranked sp. group] *Verni* Small, Man. Southeastern Fl. 1395. 1933, in clave. TYPE: *Erigeron vernus* (L.) Torr. & A. Gray

Fibrous-rooted, perennial, sometimes rhizomatous or stoloniferous; caudex simple; glabrous to sparsely strigose or hispid; stems simple or branched; leaves obovate to spatulate, often thick, entire or shallowly toothed, not clasping; heads erect in bud; rays white, not coiling or reflexing; achenes 1.2–1.6 mm, 4-nerved; pappus of 16–30 bristles.

E. hintoniorum G.L. Nesom
E. morelensis Greenm.
E. palmeri A. Gray
E. vernus (L.) Torr. & A. Gray
E. wellsii G.L. Nesom

This group of species was earlier included within the primarily western U.S.A. sect. *Fruticosus* (Nesom, 1989c) as the "*E. palmeri* group." The apparent morphological coherence of these five species, however, and the geographic range divided between the eastern USA and the eastern sierra of Mexico, also characteristic of other groups in various genera, indicate that sectional status is appropriate for the *E. palmeri* group. Species of sect. *Erigeridium* have not yet been included in molecular studies.

7. Sect. *Erigeron*

Erigeron sect. *Uniflori* G. Don in Loudon, Hort. Brit. 343. 1830. TYPE: *Erigeron uniflorus* L.

Aster sect. *Pauciflori* G. Don in Loudon, Hort. Brit. 346. 1830. LECTOTYPE: *Aster pulchellus* Willd. (= *Erigeron venustus* Botsch.) (Sundberg and Jones, 1987)

Erigeron [unranked sp. group] *Uniflori* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *Erigeron uniflorus* L.

Erigeron sect. *Monocephali* Vierh., Beih. Bot. Centralbl. 19: 492. 1906. LECTOTYPE (Nesom 1989c): *Erigeron uniflorus* L.

Erigeron sect. *Siphonoglossa* Botsch., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk SSSR 16: 393. 1954. TYPE: *Erigeron uniflorus*

Erigeron sect. *Platyglossa* Botsch., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk SSSR 16: 388. 1954. TYPE: *Erigeron venustus* Botsch.

Perennial; fibrous-rooted, usually from a short, suberect rhizome; caudex simple or with short, thick branches; strigose to hirsute or villous; stems simple; leaves mostly basal oblanceolate to obovate or spatulate, entire, not clasping; heads 1, erect in bud; rays white or blue (yellow in *E. aureus*), coiling (not coiling in *E. uniflorus*); achenes 1.6–2.8 mm long, 2-nerved; pappus of (7–)10–30 bristles (accrescent in *E. uniflorus*).

North America

E. algidus Jeps. (incl. *E. petiolaris* Greene, see Nesom, 1992b, 1992c)
E. aureus Greene
E. alpiniformis Cronquist
E. X *arthurii* Boivin
E. denalii A. Nelson
E. eriocephalus J. Vahl
E. flettii G.N. Jones
E. grandiflorus Hooker (incl. *E. simplex* Greene)
E. hultenii Spongberg (status uncertain; Nesom and Murray 2004)
E. humilis Graham
E. hyperboreus Greene (incl. *E. alaskanus* Cronquist)
E. melanocephalus A. Nelson
E. muirii A. Gray
E. porsildii Nesom & D. Murray

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South America (The *E. andicola* DC. complex, see Solbrig, 1962)
Erigeron andicola DC.
Erigeron ciliaris Phil.
Erigeron cinereus Hook. & Arn.
Erigeron incertus (d'Urville) Skottsb.
Erigeron lanceolatus Wedd.
Erigeron leptopetalus Phil.
Erigeron myosotis Pers.
Erigeron patagonicus Phil.
Erigeron pratensis Phil.
Eurasia (China and Russia not represented)
E. anisophyllus Rech. f.
E. caucasicus Steven
E. cedretorum Rech. f.
E. cilicicus Boiss. ex Vierh.
E. daenensis Vierh.
E. eriocalyx (Ledeb.) Vierh.
E. hyrcanicus Bornm. & Vierh.
E. komarovii Botsch.
E. koraginensis (Komarov) Botsch.
E. miyabeanus Tatew. & Kitam.
E. multiradiatus (DC.) C.B. Clarke
E. petroiketes Rech. f.
E. plesiogeron Rech. f.
E. pseuderiocephalus M. Popov
E. silenifolius (Turcz.) Botsch.
E. thunbergii A. Gray
E. uniflorus L.
E. zederbaueri Vierh.

Molecular data (Noyes, 2000a) indicate that the species of sect. *Trimorpha* (at least the European species *Erigeron acris* and *E. borealis*) are more closely related to *E. uniflorus* and to *E. grandiflorus* (incl. *E. simplex*) than they are to a group of American species including *E. flettii*, *E. humilis*, *E. cinereus*, and *E. lonchophyllus*. In fact, sect. *Trimorpha* and sect. *Erigeron* sensu stricto appear to be more closely related to sect. *Rhizonexus* than to the latter group of sect. *Erigeron*. The implication of this is that sect. *Erigeron* (as outlined above) is biphyletic. The amphi-Atlantic *E. humilis*, however, is hypothesized to have arisen as an allotetraploid offspring of a cross between *E. uniflorus* and a species similar to *E. melanocephalus* and *E. hyperboreus* (Engelskjön, 1967; Spongberg, 1971). In the Noyes analysis, the Andean taxa of South America are represented by *E. cinereus*.

Among the North American taxa, *Erigeron uniflorus* alone has accrescent pappus bristles, a feature shared with the species of sect. *Trimorpha*.

8. Sect. **Filifolii** (Rydb.) Nesom, comb. et stat. nov. *Erigeron* [unranked sp. group] *Filifolii* Rydb., Fl. Rocky Mts. 897. 1918, in clave. TYPE: *Erigeron filifolius* Nutt.

Perennial, taprooted; caudices multicipital, often with relatively short and thin, stemlike, lignescent branches; sparsely to densely strigose with loosely appressed to ascending, fine hairs, densely white-strigose at least proximally; leaves linear to filiform, basal (not in a rosette) and cauline (gradually or little reduced distally); heads 1–5(–10+) from distal branches, in loosely corymbiform arrays, erect in bud; rays weakly coiling; achenes 1.4–1.8(–2) mm long, 2-nerved.

Erigeron filifolius Nutt.

Erigeron filifolius has features in common with sect. *Wyomingia* (but is geographically displaced and ecologically incongruent and lacks the multinerved achenes of the multi-headed species) and sect. *Osteocaulis* (but lacks the characteristic indurate-sheathing leaf bases) and some features in common with Group A of sect. *Asteroidea*. It is without obvious near-sister species and placed here in a monotypic section, with speculation that its closest relatives are geographically close, perhaps those of sect. *Osteocaulis*.

9. Sect. *Fruticosus* G. Don in Loudon, Hort. Brit. 343. 1830. TYPE: *Erigeron glaucus* Ker-Gawler

Woodvillea DC., Prodr. 5: 318. 1836. TYPE: *Erigeron glaucus* Ker-Gawler

Erigeron sect. *Phoenactis* Nutt., Trans. Amer. Philos. Soc. ser. 2, 7: 310. 1841. LECTOTYPE (Nesom, 1989c): *Erigeron speciosus* (Lindl.) DC.

Erigeron [unranked sp. group] *Elatiores* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *Erigeron elatior* (A. Gray) Greene

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Erigeron [unranked sp. group] *Salsuginosi* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *Erigeron salsuginosus* (Rich.) A. Gray (= *E. peregrinus* subsp. *callianthemus* (Greene) Cronq. = *E. glacialis* Nutt.)

Erigeron [unranked sp. group] *Macranthi* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *Erigeron macranthus* Nutt. (= *E. speciosus*)

Erigeron [unranked sp. group] *Glabelli* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *Erigeron glabellus* Nutt.

Erigeron [unranked sp. group] *Asperi* Rydb., Fl. Rocky Mts. 897. 1918, in clave. TYPE: *Erigeron asper* Nutt. (= *E. glabellus*)

Erigeron sect. *Peregrinus* Nesom, Syst. Bot. 7: 463. 1982. TYPE: *Erigeron peregrinus* (Pursh.) Greene

Perennial, fibrous-rooted, rhizomatous, sometimes with stolons; caudex branched; glabrate to strigose, hirsute, or villous; stems usually branched; leaves oblanceolate to spatulate, entire or toothed cauline nearly even-sized upward, clasping to subclasping; heads 1 (*E. howellii*) or 1–15(–22) in a loosely corymbiform arrangement, nodding in bud (apparently erect in *E. aliceae*, *E. glaucus*, *E. glacialis*); rays white to blue or pink, weakly coiling or not at all; achenes 1.1–3 mm long; pappus of 14–32 bristles.

Group A. Basal leaves persistent; achenes 2-nerved (*E. arizonicus*, *E. cervinus*, *E. formosissimus*, *E. glabellus*, *E. yukonensis*) or mostly 2(–4)-nerved (*E. aliceae*, *E. eximius*, *E. glaucus*, *E. potosinus*) or (4–)5(–7)-nerved (*E. glacialis*, *E. howellii*, *E. peregrinus*); buds apparently erect (*E. aliceae*, *E. cervinus*, *E. glacialis*, *E. glaucus*), or nodding? (*E. formosissimus*).

- *E. aliceae* Howell
- *E. arizonicus* A. Gray
- *E. cervinus* Greene (incl. *E. delicatus* Cronquist)
- *E. eximius* Greene
- *E. formosissimus* Greene
- *E. glabellus* Nutt.
- *E. glacialis* Nutt. (syn = *E. peregrinus* var. *callianthemus* (Greene) Cronquist)
- *E. glaucus* Ker-Gawler
- *E. howellii* A. Gray
- *E. peregrinus* (Pursh) Greene
- *E. potosinus* Standl.
- *E. thunbergii* A. Gray complex (Asia)
- *E. yukonensis* Rydb. (syn = *E. glabellus* var. *yukonensis* (Rydb.) Hultén)

Group B. Basal leaves persistent; achenes 2-nerved or 2(–4)-nerved; buds nodding (*E. coulteri*, *E. rybius*), behavior unknown in others.

- *E. coulteri* Porter
- *E. rybius* G.L. Nesom
- *E. hessii* G.L. Nesom
- *E. kuschei* Eastw.

Group C. Basal leaves scalelike or not strongly differentiated; achenes 2-nerved or 2(–4)-nerved; buds nodding.

- *E. elatior* (A. Gray) Greene
- *E. speciosus* (Lindl.) DC.
- *E. subtrinervis* Rydb.
- *E. uintahensis* Cronquist
- *E. vreelandii* Greene (incl. *E. platyphyllus* Greene)

Erigeron yukonensis is rhizomatous and fibrous-rooted, although the caudices or rhizomes sometimes resemble taproots. Hultén (1968) considered it to be closely related to *E. glabellus*.

Molecular evidence (Noyes, 2000a) indicates that *Erigeron aliceae* is most closely related to species of sect. *Asteroidea*, but it is closer in morphology to sect. *Fruticosus*, especially in its fibrous-rooted and rhizomatous habit, clasping leaves often relatively large and even-sized up the stem, villous involucres, non-coiling rays, and relatively large (2–2.8 mm long), 2(–4)-nerved achenes.

Erigeron arizonicus is rhizomatous and fibrous-rooted but the caudices or rhizomes are relatively thick and sometimes resemble a taproot; basal leaves are usually persistent, spatulate, obovate to ovate, or elliptic, and cauline leaves are subclasping, but they often are 3-nerved and have shallowly serrate margins, features unusual in Group A of sect. *Fruticosus*.

Erigeron cervinus is relatively isolated, as early observed by Cronquist (1947, p. 217), who noted that "Aside from *E. cervinus*, [*E. delicatus*] has no very close relatives known

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to me.'' For *E. cervinus* he noted that it is ''probably derived from *E. peregrinus*, but the connection is now remote.''

10. Sect. *Geniculactis* Nesom, Phytologia 69: 250. 1990. TYPE: *Erigeron coronarius* Greene

Taprooted, annual or short-perennial; caudex simple; hirsute to hispid; stems branched; leaves linear to linear-oblong, -lanceolate, or -oblanceolate, not clasping, entire to toothed, rarely lobed; heads erect in bud; disc corollas often prominently inflated above the short tube; rays 40-200, white, reflexing or (in *Erigeron sceptrifer*) downward curving-reflexing, barely longer than the involucre in *E. zacatensis*; achenes 0.5–1 mm long, 2-nerved (orange); pappus of 2–17 bristles or (in *E. reinana*) absent. *E. reinana* has relatively few, loosely coiling rays and uninflated disc corollas.

E. arisolius G.L. Nesom
E. coronarius Greene
E. janivultus G.L. Nesom
E. reinana G.L. Nesom
E. sceptrifer G.L. Nesom
E. zacatensis G.L. Nesom

The species of sect. *Geniculactis* are restricted to Mexico, except for two that also occur in southern Arizona – *E. arisolius* and *E. sceptrifer*. *Erigeron reinana* was recently added to the group (Nesom, 1998). The *E. pumilus* group was tentatively included in the original circumscription of sect. *Geniculactis* (Nesom, 1990c) but is here treated separately as sect. *Stenactis* Cass.

Erigeron reinana is recognized by its taprooted habit, coarse vestiture, narrow, entire leaves, numerous heads on short peduncles, erect buds, loosely coiling rays, and much reduced, essentially bristle-less pappus. It differs from *E. coronarius* and the other species of sect. *Geniculactis* in its fewer, loosely coiling rays and uninflated disc corollas; it might be placed with less technical/diagnostic anomaly in sect. *Imbarba*, but the vestiture, leaf morphology, and capitulescence of *E. reinana* are more similar to sect. *Geniculactis*.

11. Sect. *Geronpternix* Nesom & Noyes, Sida 18: 1163. 1999. TYPE: *Erigeron rhizomatus* Cronquist

Perennial, rhizomatous, with thick fibrous roots, rhizomes or rhizomelike caudex branches creeping-ascending; slender, scale-leaved, without well-defined central axes; strigose to strigose-hirsutulous; stems simple or 1–3 branched; leaves cauline, mostly linear at midstem, entire, not clasping; heads 1(–3), nodding or erect in bud; rays with abaxial lilac midstripe, not coiling or reflexing; achenes 3.5–4.5 mm long, 2–4-nerved (*E. lepidopodus*) or 5–6-nerved (*E. rhizomatus*); pappus of 25–50 bristles.

E. lepidopodus (B.L. Rob. & Fernald) G.L. Nesom

E. rhizomatus Cronquist

These two species, previously hypothesized to be sister species (Nesom, 1989c), were tentatively treated as members of the *E. foliosus* group (sect. *Pycnophyllum*) in the Nesom (1989c) overview of *Erigeron* but were shown by Noyes (2000a) to be the phyletically basalmost species of the Conyzinae. As noted by Noyes (2000a, p. 106), these two species are characterized by a ''4-bp insertion that is shared with outgroup taxa *Chrysopsis* and *Heterotheca* and with all other Astereae, but that is absent in all other Conyzinae.''

12. Sect. **Gyrifolium** Nesom, sect. nov.

Radice palari crassa, foliis basalibus persistentibus spatulati-obovatis, capitulis in alabastro erectis(?), et radiis leniter cincinatis vel noncincinatis distinctus. TYPE: *Erigeron oreganus* A. Gray

Perennial, taprooted (stout); caudex branches short, thick; hirsute to villous, stipitate-glandular or minutely glandular; stems simple or branched; basal leaves persistent, spatulate-obovate, 1(-3)-nerved, toothed, cauline leaves little reduced upward (clasping to subclasping in *E. cascadensis*, *E. leibergii*); heads usually 1 but sometimes 2–4 more developed from lower axils, erect? in bud; phyllaries relatively broad, erect, and even-length; rays white, coiling but sometimes

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weakly or not at all; disc corollas with long (1.2–1.5 mm) tubes; achenes 1.2–2.2 mm long, 2-nerved; pappus of 12–20 bristles.

E. cascadensis A.A. Heller
E. leibergii Piper
E. oreganus A. Gray

The species of sect. *Gyrifolium* are rare and grow on ledges and cliffs in western Washington, Oregon, and British Columbia. They were previously placed within sect. *Fruticosus*, emphasizing the relatively well-developed and subclasping cauline leaves, but the taproot and other features (caudex, leaves, ray corollas, and phyllaries) suggest that the two groups are not so closely related. The name ('gyrifolium') alludes to a resemblance of a spinning top to the whorl of basal leaves atop a thick taproot.

13. Sect. *Imbarba* Nesom, Phytologia 67: 78. 1989. TYPE: *Erigeron galeottii* (A. Gray ex Hemsl.) Greene

Perennial (annual in *E. strigulosus*), rhizomatous (sometimes taprooted in *E. strigulosus*), sometimes with basal offsets or producing stolons or runners; caudex simple or branched; glabrous to sparsely strigose, hirsute, or pilose; stems simple or few-branched; leaves spatulate to oblanceolate, entire or toothed, cauline clasping to subclasping or not clasping; heads erect in bud; rays white, weakly coiling; achenes 1–3 mm long, 2-nerved; pappus a fimbriolate or scaley crown, bristles absent or occasionally a few, short, vestigial bristles present, or pappus in *E. macdonaldii* of 5–7 short, persistent bristles 1/2–2/3 as long as the disc corollas.

E. astranthioides De Jong & G.L. Nesom
E. forreri (Greene) Greene
E. fraternus Greene
E. galeottii (A. Gray ex Hemsl.) Greene
E. guatemalensis (Blake) G.L. Nesom
E. macdonaldii G.L. Nesom
E. mimus (Blake) G.L. Nesom
E. quiexobrensis G.L. Nesom
E. strigulosus Greene

Two new species have been added to sect. *Imbarba* after the Nesom (1989c) overview: *E. macdonaldii* (Nesom, 1990d) and *E. quiexobrensis* (Nesom, 1990e). All species of the section are restricted to Mexico and Central America. Sect. *Imbarba* and sect. *Geniculactis* are the closest relatives of most South American Conyzinae, according to the molecular data of Noyes (2000a).

14. Sect. *Karvinskia* Nesom, Phytologia 67: 79. 1989. TYPE: *Erigeron karvinskianus* DC.

Perennial (annual in *E. barbarensis*), taprooted (*E. barbarensis*, *E. karvinskianus*, *E. irazuensis*, *E. pacayensis*?) or rhizomatous (*E. aquarius*, *E. fluens*, *E. heteromorphus*); caudex simple; strigose to hirsute; stems branched; leaves spatulate to oblanceolate or linear, entire or toothed, not clasping; heads erect in bud; rays white, becoming lavender at maturity, slightly coiling or not at all; achenes 1–1.9 mm long, 2-nerved; pappus of 10–27 bristles.

E. aquarius Standl. & Steyerm.
E. barbarensis Nesom & T.R. Van Devender
E. fluens G.L. Nesom
E. heteromorphus B.L. Rob.
E. irazuensis Greenm.
E. karvinskianus DC.
E. pacayensis Greenm.

Two new species have recently been added to sect. *Karvinskia* (Nesom 1998; Nesom and Van Devender, 2007). The native range of these species is restricted to Mexico and Central America; *Erigeron karvinkianus* has become a worldwide weed in tropical and subtropical latitudes. *Erigeron pacayensis* appears to be sometimes taprooted, sometimes rhizomatous.

15. Sect. *Lamprocaules* Nesom, Phytologia 76: 99. 1994. TYPE: *Erigeron pattersonii* G.L. Nesom

Perennial, fibrous-rooted, slender-rhizomatous (taprooted in *E. tuerckheimii*); caudex divided into short or slender, rhizomelike branches; glabrous to sparsely strigose; stems simple or branched, glabrate, shiny; leaves coriaceous, basal (apparently produced only in *E. chiangii*) spatulate to oblanceolate, entire to shallowly few-toothed, cauline filiform to

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linear to narrowly elliptic, not clasping; heads erect in bud; rays white, weakly coiling or not at all; achenes 0.8–1.8 mm long, 2-nerved; pappus of 11–22 bristles.

E. chiangii G.L. Nesom
E. exilis A. Gray
E. pattersonii G.L. Nesom
E. scoparioides G.L. Nesom
E. tuerckheimii Urb. (incl. *E. ocoensis* Urb. & Eckman?)

Erigeron exilis was recently transferred to sect. *Lamprocaules* from sect. *Cincinnactis* (Nesom and Noyes, 1999).

Erigeron tuerckheimii is endemic to the Caribbean island of Hispaniola. The plants are small shrubs up 20 cm tall, from a woody taproot producing thick branches with persistent old leaves. The leaves are linear to nearly filiform, with a hard, shiny texture, purple at the base, and are very densely arranged on the stems. The heads are solitary on naked or few-bracteate peduncles. Rays are white, apparently neither coiling nor reflexing. There is no other Caribbean species similar to it (except the possibly conspecific *E. ocoensis*), and it is placed here with this group of Mexican species on the basis of their similarity in leaf morphology. *Erigeron tuerckheimii* is comparable in habit to species of *Neja*, but the achenes are flat and 2-nerved, in contrast to those of *Neja*, which are terete and multi-nerved.

16. Sect. *Linearifolii* (G. Don) Nesom, Phytologia 67: 79. 1989.

Aster sect. *Linearifolii* G. Don in Loudon, Hort. Brit. 346. 1830. LECTOTYPE: *Erigeron hyssopifolius* Michx. (Sundberg and Jones, 1987)

Perennial, rhizomatous, fibrous-rooted; caudices sometimes branched; strigose to strigose-villous; stems branched; basal and proximal cauline leaves much reduced or present as scales, cauline blades linear to linear-oblong or oblong-lanceolate, not clasping; heads erect in bud; rays white, not coiling or reflexing; achenes 1.3–1.6 mm long, 5–6-nerved; pappus of 25–35 bristles.

E. hyssopifolius Michx.

This species of northern North America has been regarded as closely similar to the primarily Californian *Erigeron foliosus* group, treated here as sect. *Pycnophyllum* Cronquist (Cronquist, 1947; Nesom, 1989c, 1992a), but *E. hyssopifolius* was regarded as more isolated and formally segregated as a monotypic section by Nesom and Noyes (1999).

17. Sect. **Lonchophylli** Nesom, sect. nov.

Habitu fibrosi-radicato non-rhizomato, caudice simplici, capitulis plerumque 3–12 plerumque in dispositione laxe racemiformi in alabastro erectis, radiis filiformibus non-reflexis noncincinatis involucro parum longioribus distinctus. TYPE: *Erigeron lonchophyllus* Hook.

Biennial or short-lived perennial (sometimes appearing annual), fibrous-rooted, not rhizomatous; caudex simple; sparsely to densely hirsute, eglandular; stems branched; basal leaves oblanceolate to spatulate, entire, cauline mostly linear, not clasping; heads 1 or 3–12 usually in a loosely racemiform arrangement, erect in bud; rays white to pink, filiform, slightly longer than the involucre, not reflexing or coiling; achenes 1.3–1.8 mm, 2-nerved; pappus of 20–30 nonaccrescent bristles.

E. lonchophyllus Hook.

Erigeron lonchophyllus is similar to species of sect. *Trimorpha* in its fibrous-rooted habit, narrow involucres in a racemiform arrangment, filiform suberect rays, and it was earlier included in sect. *Trimorpha* (Nesom 1989c). It lacks, however, the inner zone of eligulate pistillate florets characteristic of sect. *Trimorpha*, and molecular data (Noyes, 2000a) indicate that it is more closely related to a group of American species including *E. flettii*, *E. humilis*, and *E. cinereus*, placed here in sect. *Erigeron*.

18. Sect. **Meridionales** G.L Nesom & N. Andrus, sect. nov.

Habitu rhizomato fibrosi-radicato, capitulis solitariis in pedunculis scaposis vel plerumque in dispositione laxe corymbi-

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formi in alabastro erectis distinctus. TYPE: *Erigeron fasciculatus* Colla

Perennial herbs or subshrubs, rhizomatous, fibrous-rooted; caudex simple or multicipital; glabrous to strigose or villous; stems branched; leaves oblanceolate to lanceolate, entire to toothed or lobed, not clasping; heads 1 on scapose peduncles (*Erigeron othonnifolius*, *E. turricola*) or mostly in loosely corymbiform arrays, erect in bud; rays white to purple, not coiling or reflexing; achenes 1–4 mm long (0.5–1.0 mm in *D. alternifolius*), 2(–3)-nerved; pappus of [not counted] bristles.

Darwiniothamnus alternifolius Lawesson & Adsersen
Erigeron campanensis Valdeb., Lowrey, & Stuessy
Erigeron chionophilus Wedd.
Erigeron ecuadoriensis Hieron.
Erigeron fasciculatus Colla
Erigeron incaicus Solbrig
Erigeron luxurians (Skottsb.) Solbrig
Erigeron othonnifolius Hook. & Arn.
Erigeron paramensis Aristeg. & Cuatrec.
Erigeron raphaelis Cuatrec.
Erigeron rosulatus Wedd.
status unknown:
Erigeron adscendens Turcz. (Ecuador)
Erigeron apiculatus Benth. (Ecuador)
Erigeron (*Aster*) *gilliesii* (Hook. & Arn.) Cabrera (Patagonia)
Erigeron pauper Benoist (Ecuador)

Molecular evidence (Andrus et al., in prep.) suggests that sect. *Meridionales* may not be monophyletic. *Erigeron ecuadoriensis* is indicated by molecular data (Andrus et al., submitted) to be more closely related to *E. maximus* (*Leptostelma*) than others of sect. *Meridionales*. The group of Juan Fernandez hexaploids segregated here as sect. *Terranea* probably are derived from sect. *Meridionales*.

19. Sect **Microcephalum** G.L. Nesom, sect. nov.

Habitu fibrosi-radicato non-rhizomato, caudice simplici, caulibus simplicibus, foliis basalibus in rosette, capitulis in alabastro erectis, radiis filiformibus arcte cincinatis distinctus. TYPE: *Erigeron cuneifolius* DC.

Annual to perennial, fibrous-rooted, not rhizomatous, stoloniferous in some; caudex simple; glabrous to sparsely strigose; stems simple, less commonly branched, filiform, bracteate; basal leaves in a rosette, spatulate with orbicular to obovate or cuneiform blades (oblanceolate-elliptic in *E. purpuripes*), 1-nerved, entire to shallowly crenate or serrate on the distal half, lobed to pinnatifid in some, cauline bracteate, subclasping or not clasping; heads 1(–few), tiny (involucres 2–6 mm long, 2–7(–8) mm wide), erect in bud; rays 24–54, 40–80(–100), white, filiform, tightly coiling; disc corollas 10–17, fewer than the ray; achenes 0.8–1.4 mm long, rectangular, 2-nerved (orange-resinous); pappus of 17–28 bristles.

E. bellidiastroides Griseb. (Cuba)
E. bellioides DC. (Puerto Rico, Cuba, or Hispaniola)
syn= *E. semiovalis* Urb. (Cuba)
E. capillipes Ekman & Urb. (Cuba)
E. cuneifolius DC. (Puerto Rico)
E. hyoseroides Griseb. (Cuba)
E. libanensis Urb. (Cuba)
E. ocoensis Urb. & Ekman (Hispaniola)
E. paucilobus Urb. (Cuba)
E. purpuripes Britton & P. Wilson (Cuba)
E. taylori Britton & P. Wilson (Cuba)
E. thrincioides Griseb. (Cuba)
E. vegaensis Urb. (Hispaniola)

These species were not fully accounted for in Nesom's (1989c) overview of *Erigeron*, except for the observation that the group, as characterized by *E. cuneifolius* and *E. bellioides*, probably belonged with sect. *Cincinnactis*. *Erigeron bellioides* shows as the sister taxon to *Aphanostephus* in the molecular analysis by Noyes (2000a). *Erigeron cuneifolius* has become a pantropical weed. The group is in need of revisionary study.

20. Sect. *Olygotrichium* Nutt., Trans. Amer. Philos. Soc. ser. 2, 7: 311. 1841. TYPE: *Erigeron divergens* Torr. & A. Gray

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Heterochaeta DC., Prodr. 5: 282. 1836 (non Besser 1827). LECTOTYPE: *Erigeron pubescens* Knuth (Nesom, 1989c)

Erigeron [unranked sp. group] *Bellidiastra* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *Erigeron bellidiastrum* Nutt.

Erigeron [unranked sp. group] *Divergentes* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *Erigeron divergens* Torr. & A. Gray

Erigeron [unranked sp. group] *Flagellares* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *Erigeron flagellaris* A. Gray

Annual to biennial or perennial; taprooted or fibrous-rooted, not rhizomatous, sometimes producing runners or stoloniform branches; caudex usually simple; villous to hirsute to strigose or glabrate; stems simple or branched; leaves oblanceolate to obovate or spatulate, entire to toothed or lobed, not clasping (slightly subclasping in *E. calcicola*); heads nodding in bud; ray white to pink, often with an abaxial lilac midstripe, not coiling or reflexing; achenes (0.5–)0.7–1.6(–1.8) mm long, 2-nerved; pappus of 6–18(–19) bristles (16–25 in *E. fundus*, 23–30 in *E. mihianus*; bristles absent in *E. onofrensis*, *E. versicolor*).

Group A.

E. bellidiastrum Nutt.
E. bigelovii A. Gray
E. calcicola Greenm.
E. calvus Coville
E. divergens Torr. & A. Gray
E. flagellaris A. Gray
E. fundus G.L. Nesom
E. lemmonii A. Gray
E. metrius Blake
E. mihianus Blake
E. modestus A. Gray
E. multiceps Greene
E. onofrensis G.L. Nesom
E. pinkavii B.L. Turner
E. pubescens Kunth
E. religiosus Cronquist
E. sionis Cronquist (incl. *E. proselyticus* G.L. Nesom)
E. tracyi (syn = *E. colomexicanus* A. Nelson)
E. versicolor (Greenm.) Nesom (syn = *E. gilensis* Wooton & Standl.; syn = *E. mimegletes* Shinners)
E. vicinus G.L. Nesom

Group B.

E. lobatus A. Nelson
E. piscaticus G.L. Nesom
E. velutipes Hook. & Arn.

The three species of Group B (all taprooted annuals) are closely interrelated, apparently part of sect. *Olygotrichium*. They are characterized by a densely stipitate-glandular and sparsely hispid-pilose vestiture with straight, spreading hairs 0.6–1.5 (–2) mm long. Their distinctions, with description of a new species, were discussed by Nesom (1989d). The report of *E. velutipes* in Arizona (Nesom and Baker, 1991) notes variability in habit, suggesting that a taxonomic review of this group would be useful.

Erigeron bigelovii should be investigated for possible affinities elsewhere, possibly with sect. *Lamprocaules* G.L. Nesom & R.D. Noyes. The short-hispid vestiture, wiry, brittle, highly branched stems, and involucral morphology are unusual in sect. *Olygotrichium*. *Erigeron mihianus* also is somewhat anomalous in sect. *Olygotrichium*, especially in its geography (Mt. Zempoaltepetl, Oaxaca) and high number of pappus bristles; on the other hand it produces leafy stolons and nonclasping, pinnatifid leaves.

21. Sect. *Osteocaulis* G.L. Nesom, Phytologia 67: 82. 1989. TYPE: *Erigeron linearis* (Hook.) Piper

Erigeron [unranked sp. group] *Lutei* Rydb., Fl. Rocky Mts. 897. 1918, in clave. TYPE: *Erigeron luteus* A. Nelson (= *E. linearis*)

Taprooted, perennial; caudex branched; stem vestiture of short, white, closely appressed hairs; stems simple or less commonly branched; leaves linear, entire, not clasping, leaf and stem bases white-indurate; heads erect (*E. linearis*) or nodding (*E. bloomeri*, *E. elegantulus*) in bud; rays coiling, yellow in *E. linearis*, absent in *E. bloomeri*; achenes (1.8–)3–4 mm long, 2-nerved; pappus of 10–50 bristles.

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E. barbellatus Greene
E. bloomeri A. Gray
E. elegantulus Greene
E. linearis (Hook.) Piper

Molecular data (Noyes, 2000a) suggest that sect. *Osteocaulis*, sect. *Spathifolium*, and sect. *Arenarioides* may be closely interrelated. Species of sect. *Arenarioides* have white and highly sclerified leaf bases similar to those of sect. *Osteocaulis*. All have similar vestiture, as also does sect. *Wyomingia*.

22. Sect. *Pauciflori* G. Don in Loudon, Hort. Brit. 343. 1830. LECTOTYPE (Nesom 1989c): *Erigeron bellidifolius* Willd. (= *Erigeron pulchellus* Michx.)

Musteron Raf., Fl. Tellur. 2: 50. 1836. TYPE: "*Erigeron bellidifolium*" Raf. (probably = *E. bellidifolius* Willd. = *E. puchellus* Michx.)

Erigeron [unranked sp. group] *Pulchelli* Small, Man. Southeastern Fl. 1395. 1933, in clave. TYPE: *Erigeron pulchellus* Michx.

Perennial, rhizomatous, fibrous-rooted, primary rhizomes relatively slender, producing slender, herbaceous, scale-leaved, stoloniform rhizomes; caudex simple; villous; stems branched; leaves oblanceolate, toothed, clasping; heads nodding in bud; rays white, coiling tardily at tips; achenes 1.3–1.8 mm long, 2(–4)-nerved; pappus of (22–)28–36 bristles.

E. pulchellus Michx.

Erigeron pulchellus was earlier placed within sect. *Fruticosus* (see commentary in Nesom, 1989c) and the molecular analysis by Noyes shows it in an unresolved position close to species of that section. In view of its distinctive morphology and isolated geography, however, it seems reasonable to recognize the monotypic sect. *Pauciflori*, especially since it is not clear that sect. *Fruticosus*, as delimited here, is monophyletic.

23. Sect. *Phalacroloma* (Cass.) Torr. & A. Gray, Fl. N. Amer. 2(1): 175. 1841. *Phalacroloma* Cass., Dict. Sci. Nat. 39: 404. 1826. TYPE: *Erigeron strigosus* Muhlenb. ex Willd.

Diplemium Raf., Fl. Tellur. 2: 50. 1836. LECTOTYPE (Nesom, 1989c): *Erigeron strigosus* Muhlenb. ex Willd.

Erigeron [unranked sp. group] *Ramosi* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *Erigeron ramosus* (Walter) B.S.P. (= *E. strigosus* Muhlenb. ex Willd)

Erigeron [unranked sp. group] *Annui* Small, Man. Southeastern Fl. 1395. 1933, in clave. TYPE: *E. annuus* (L.) Pers.

Annual to biennial or short-lived perennial, fibrous-rooted, rhizomatous in some forms of *E. strigosus*; caudex simple; strigose to sparsely hirsute; stems branched; leaves oblanceolate, toothed, not clasping; heads loosely paniculiform or corymbiform, nodding in bud; rays white, not coiling or reflexing; achenes (0.5–)0.8–1.2 mm long, 2(–4)-nerved; pappus (disc florets) of 8–15 bristles, bristles absent (in *E. annuus* and *E. strigosus*) on ray florets.

E. annuus (L.) Pers.
E. strigosus Muhlenb. ex Willd.
E. tenuis Torr. & A. Gray

Sect. *Phalacroloma* has been restricted to two species that have pappose disc achenes but that lack the series of bristles on the ray achenes—*Erigeron strigosus* and *E. annuus* (Cronquist, 1947; Nesom, 1989c). Molecular data (Noyes, 2000a) place *E. tenuis* and *E. strigosus* as sister species, with *E. annuus* sister to this pair. Occasional plants are encountered that suggest hybridization occurs between *E. tenuis* and *E. strigosus*.

The reproductive biology and evolution of *Erigeron strigosus* and *E. annuus* are undergoing detailed study (Noyes and Rieseberg, 2000; Noyes, 2000b; Noyes, 2005; Noyes and Allison, 2005; Noyes, 2006a, 2006b; Noyes et al. 2007). Formal variants have recently been described at varietal rank within *E. strigosus* (Allison and Stevens, 2001; Noyes et al., 2006).

24. Sect. *Polyactis* (Less.) G.L. Nesom, Phytologia 66: 416. 1989. *Polyactis* Less., Syn. gen. Comp. 188. 1832. TYPE: *Erigeron delphinifolius* Willd.

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Stenactis Cass., Dict. Sci. Nat. 37: 485. 1825 (non *Erigeron* sect. *Stenactis* Torr. & A. Gray). TYPE: *Erigeron delphinifolius* Willd.

Polyactidium DC., Prodr. 5: 281. 1836. TYPE: *Erigeron delphinifolius* Willd.

Achaetogeron A. Gray, Mem. Amer. Acad. Arts, n. ser. 4 (Pl. Fendl.): 72. 1849. TYPE: *Erigeron wislizeni* (A. Gray) Greene

Perennial and fibrous-rooted or taprooted and annual; caudex simple or rarely branched, rhizomatous in some species; hirsute to strigose; stems branched, less commonly simple; leaves mostly oblanceolate to oblong, toothed or lobed to pinnatifid, less commonly entire, clasping or not clasping; heads usually in loosely corymbiform to paniculiform arrays, solitary in a few species, arching-nodding in bud; rays white to blue, filiform, reflexing; achenes 1–1.3 mm long, 2–4-nerved; pappus bristles 8–12 (to 17 in *E. podophyllus*), basally caducous, absent or greatly reduced in some species.

E. annuactis G.L. Nesom
E. basaseachensis G.L. Nesom
E. caulinifolius G.L. Nesom
E. circulis G.L. Nesom
E. coroniglandifer G.L. Nesom
E. dactyloides (Greenm.) G.L. Nesom
E. delphinifolius Willd.
E. eruptens G.L. Nesom
E. griseus (Greenm.) G.L. Nesom
E. inoptatus A. Gray
E. jenkinsii G.L. Nesom
E. mayoensis G.L. Nesom
E. nacoriensis G.L. Nesom
E. neomexicanus A. Gray
E. oreophilus Greenm.
E. podophyllus G.L. Nesom
E. polycephalus (Larsen) G.L. Nesom
E. rhizomactis G.L. Nesom
E. seemannii (Schultz-Bip.) Greene
E. subacaulis (McVaugh) G.L. Nesom
E. wislizeni (A. Gray) Greene

Two species have been described since the published revision of this section (Nesom, 1989a): *E. jenkinsii* (Nesom, 1993a) and *E. mayoensis* (Nesom, 1993b).

25. Sect. *Pseuderigeron* Torr. & A. Gray, Fl. N. Amer. 2(1): 177. 1841. LECTOTYPE: *Erigeron caespitosus* Nutt. (Nesom, 1989c)

Erigeron [unranked sp. group] *Caespitosi* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *Erigeron caespitosus* Nutt.

Perennial, taprooted; caudex branches relatively thick and short, retaining old leaf bases; stems simple, erect to decumbent-ascending; stems and leaves eglandular, involucres glandular or eglandular; leaves basal (persistent) and cauline, narrowly oblanceolate to spatulate (1–)3-nerved, cauline gradually reduced, not clasping; heads 1–4, erect? in bud; rays white to blue, coiling, often weakly; achenes 1.5–2.2 mm long, 2-nerved; pappus of 12–25 bristles.

E. abajoensis Cronquist
E. caespitosus Nutt.
E. goodrichii S.L. Welsh

Erigeron abajoensis is a segregate of *E. caespitosus*, separated from the latter only by its strigose (versus hirsute) stems and leaves and greater tendency for 1-nerved leaves.

26. Sect. *Pycnophyllum* Cronquist, Brittonia 6: 141. 1947. TYPE: *Erigeron foliosus* Nutt.

Perennial, taprooted; short caudexlike branches or relatively slender, rhizomelike caudex branches producing numerous, basally ascending stems, sometimes with slender, lignescent offsets; hirsute to strigose, puberulous, or glabrous; stems few-branched, rarely simple; leaves filiform to linear-oblanceolate, entire, not clasping; heads 1 or 2–5(–10) in loosely corymbiform arrays, erect in bud; rays white to blue, weakly coiling, sometime only at the tips, sometimes apparently not coiling, absent in some species; achenes 1.8–3 mm long, 2–4 (–5)-nerved; pappus of 17–45(–61 in *E. reductus*) bristles.

E. aequifolius Hall
E. angustatus Greene
E. biolettii Greene
E. blochmaniae Greene
E. breweri A. Gray
E. elmeri (Greene) Greene

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E. foliosus Nutt.
E. inornatus A. Gray
E. klamathensis (G.L. Nesom) G.L. Nesom
E. mariposanus Congdon
E. miser A. Gray
E. oxyphyllus Greene
E. petrophilus Greene
E. reductus (Cronquist) G.L. Nesom
E. sanctarum S. Watson
E. serpentinus G.L. Nesom
E. supplex A. Gray

This group (as sect. *Linearifolii*) was revised by Nesom (1992a), bringing a number of changes in circumscriptions of taxa; one new species, *E. serpentinus*, was added. *Erigeron klamathensis* was raised in rank (Nesom, 2004). *Erigeron hyssopifolius* was excluded by Nesom and Noyes (1999) to constitute the monotypic sect. *Linearifolii*. *Erigeron supplex* and *E. sanctarum* are placed here in sect. *Pycnophyllum* for the first time, although Cronquist (1947) earlier noted the resemblance of *E. supplex* to this group of species and to a putative close relationship between *E. supplex* and *E. sanctarum*. Sect. *Pycnophyllum* is centered in California, extending northward to Washington and southward into Baja California; *E. oxyphyllus* is the southeasternmost species, occuring in Sonora and Arizona.

27. Sect. **Quercifolium** G.L. Nesom, sect. nov.

Duratione annuo vel breviviventi, caudice simplici, foliis serratis vel lobatis amplexicaulibus vel subamplexicaulibus, vestimento caulino deflexo, et radii non-cincinatis distinctus. TYPE: *Erigeron quercifolius* Lam.

Erigeron [unranked sp. group] *Philadelphici* Rydb., Fl. Colorado 359. 1906, in clave (non Small 1933). TYPE: *Erigeron philadelphicus* L.

Annual or short-lived perennial, fibrous-rooted, taprooted in *E. geiseri*, *E. tenellus*, *E. turnerorum*, stoloniferous in *E. basilobatus*, *E. cieloensis*, *E. domingensis*, *E. polycladus*, *E. psilocaulis*, rhizomatous in *E. dryophyllus*, *E. veracruzensis*; caudex simple; strigose-pilose to hirsute, often deflexed on the proximal portions of stem; stems branched; leaves oblanceolate, to elliptic, entire or crenately toothed to pinnately lobed, cauline clasping to subclasping or not; heads 1 or 2–35(–50) in diffuse arrays from distal branches, nodding or arching-nodding in bud; rays not coiling or reflexing, white to blue; achenes 0.6–1.8 mm long, 2-nerved; pappus of 8–32 bristles.

North American
E. basilobatus Blake (ne Mexico)
E. cieloensis G.L. Nesom (ne Mexico)
E. dryophyllus A. Gray (ne Mexico)
E. geiseri Shinners (central Texas and s Oklahoma)
E. heleniae G.L. Nesom (ne Mexico)
E. philadelphicus L. (e USA)
E. quercifolius Lam. (e USA)
E. tenellus DC. (ne Mexico, s Texas)
E. turnerorum G.L. Nesom (ne Mexico)
E. veracruzensis G.L. Nesom (ne Mexico)

Caribbean
E. caeruleus Urb. (Hispaniola)
E. darrellianus Hemsl. (Bermuda)
E. dissectus Urb. (Hispaniola)
E. domingensis Urb. (Hispaniola)
E. fuertesii Urb. (Hispaniola)
E. jamaicensis L. (Jamaica)
syn= *E. earlei* Britton & P. Wilson (Cuba)
syn= *E. polycladus* Urb. (Martinique)
syn= *E. rivularis* Sw. (Jamaica, Hispaniola)
E. pinetorum Urb. (Hispaniola) (= *E. buchii* Urban?)
E. polycladus Urb. (Martinique)
E. psilocaulis Urb. (Hispaniola)

Some species of this group (*Erigeron quercifolius*, *E. philadelphicus*, *E. caeruleus*, *E. dryophyllus*, *E. turnerorum*, and *E. tenellus*) were placed by Nesom (1989c) within sect. *Olygotrichium*, while another related group (including *E. darrellianus*, *E. jamaicensis*, and others) was noted as probably belonging in the same section. A new species was described (Nesom, 1989e)—*E. cieloensis*, putatively the sister species of *E. basilobatus*,

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which is transferred here from sect. *Cincinnactis* (sensu Nesom, 1989c). *Erigeron heleniae* is recently described (Nesom, 2007). Molecular data of Noyes (2000a) indicate that sect. *Quercifolium* is phyletically coordinate with the clade that includes *Aphanostephus* and *Erigeron* sect. *Microcephalum*.

Sect. *Quercifolium*, as delimited here, is the only section of *Erigeron* with a distribution divided between the Caribbean, Mexico, and the United States. The Caribbean species (type localities in parenthesis) are closely similar to *E. quercifolius*: *E. caeruleus*, *E. dissectus*, *E. fuertesii* (perhaps conspecific with *E. caeruleus*), and *E. jamaicensis*. *Erigeron darrellianus* apparently is the only Northern Hemisphere species of the genus to have developed a distinctly shrubby habit. *Erigeron domingensis* is remarkably similar in habit to *E. flagellaris* (of sect. *Olygotrichium*, with herbaceous stolons, tendency for a single head on the erect stems), but *E. domingensis* has more herbaceous phyllaries, white to blue or purple rays without an abaxial midstripe, and up to 3 capitula per stem, probably derived from its relatives with a corymbiform capitulescence.

Erigeron tenuis, previously regarded as closely related to *E. geiseri* (Nesom, 1987, 1989e), is placed in the present treatment with sect. *Phalacroloma*. *Erigeron pinetorum* Urb. was previously placed as a close relative of the species related to *E. quercifolius* but is now known to be conspecific with *Conyza primulifolia* (Lam.) Cuatrec. & Lourteig (= *Conyza chilensis* Spreng.).

28. Sect. **Radicati** (Rydb.) Nesom, comb. et stat. nov.

Erigeron [unranked sp. group] *Radicati* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *Erigeron radicatus* Hook.

Erigeron [unranked sp. group] *Laetevirentes* Rydb., Fl. Rocky Mts. 897. 1918, in clave. TYPE: *Erigeron laetevirens* Rydb. (= *E. ochroleucus*)

Perennial, taprooted; caudex multicipital or with short, thick branches; hirsutulous to villosulous, hairs with purplish cross walls (except in *E. rydbergii*); stems simple, less commonly branched; leaves oblanceolate to spatulate, entire, not clasping, abaxial faces glabrous or glabrate, adaxial faces strigose to villous (both faces hairy in *E. parryi*); heads 1(–3), behavior in bud not known, phyllaries minutely glandular; rays coiling (not coiling in *E. parryi*); achenes 1.8–2.8 mm, 2-nerved; pappus of 12–20 bristles (caducous in *E. parryi*, *E. radicatus*).

E. lackschewitzii G.L. Nesom & Weber
E. ochroleucus Nutt. (incl. *E. scribneri* Canby ex Rydb.)
E. parryi Canby & Rose
E. radicatus Hook. (incl. *E. huberi* S.L. Welsh & N.D. Atwood)
E. rydbergii Cronquist

Erigeron parryi differs from the other species in its apparently non-coiling rays and leaves equally strigose to hirsute-strigose on both faces; like most of the others, however, it produces hairs with purplish cross walls and the pappus bristles are basally caducous, as also in *E. radicatus* (Nesom, 2004). This group was placed in sect. *Asteroidea* in 1989 as the "*E. radicatus* group."

29. Sect. **Rhizonexus** G.L. Nesom, sect. nov.

Distinctus habitu fibrosi-radicato rhizomato, caudex systemata diffusa ramorum tenuium rhizomiformium formans. TYPE: *Erigeron ursinus* D. Eaton

Perennial, rhizomatous, fibrous-rooted, forming diffuse systems of slender, rhizome-like caudex branches; glabrous or sparsely strigose; stems simple or few-branched; leaves narrowly oblanceolate to oblong, entire, not clasping; heads 1(–3), erect in bud; rays blue to pink or purple, not reflexing or coiling or sometimes coiling slightly at the tips; achenes 1.5–2 mm long, 2-nerved; pappus of 10–21 bristles.

E. gracilis Rydb.
E. ursinus D. Eaton

The morphological similarity of *Erigeron gracilis* and *E. ursinus* and their apparent morphological isolation as a group were noted by Cronquist (1947) and by Nesom

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(1989c), where they were treated as the "*E. ursinus* group" of sect. *Asteroidea*. *Erigeron leiomerus* (treated here within sect. *Asterigeron*) was placed by molecular data (Noyes, 2000a) in a sister relationship to *E. ursinus*, but *E. gracilis* was not included in the molecular sampling.

30. Sect. *Scopulincola* Nesom, Phytologia 67: 84. 1989. TYPE: *Erigeron scopulinus* G.L. Nesom & Roth

Perennial, taprooted; caudex branches long, slender, rhizomelike; glabrous or nearly so; stems simple or branched; leaves oblanceolate to obovate or spatulate, entire or pinnatisect in some, folding along the midvein, not clasping; heads 1–4, nodding in bud, phyllaries graduate and densely glandular but otherwise glabrous to sparsely strigose, often purplish; rays white, reflexing (absent in *E. mancus*); achenes 1.2–2.3 mm long, 2-nerved; pappus of 11–30 bristles.

Group A. Leaves spatulate, entire; Arizona, New Mexico, Colorado, Utah, Nevada, Montana, Wyoming.

E. kachinensis S.L. Welsh & Moore
E. leiomerus A. Gray
E. nauseosus (M.E. Jones) A. Nelson
E. scopulinus Nesom & Roth

Group B. Leaves mostly toothed to pinnatifid; Arizona.

E. anchana G.L. Nesom
E. heliographis G.L. Nesom
E. pringlei A. Gray
E. saxatilis G.L. Nesom

Group C. Leaves pinnatisect; high elevation in New Mexico, Colorado, Utah, Wyoming.

E. mancus Rydb.
E. pinnatisectus (A. Gray) A. Nelson

Sect. *Scopulincola* (especially Group A) is distinguished from sect. *Asterigeron* primarily on the basis of the reflexing ray behavior. The toothed to pinnatifid leaves of Groups B and C are a further distinction. A recent study of the *Erigeron. pringlei* group (Nesom, 1990b) resulted in the description of three additional species related to *E. pringlei*, all separated here as Group B.

The Noyes analysis (2000a) suggests that *E. pinnatisectus* is closely related to sect. *Scopulincola*, where its pinnatifid leaves are similar to those of *E. pringlei*, rather than to the 3-parted ones of sect. *Tridactylia*. *Erigeron mancus*, closely similar to *E. pinnatisectus*, is also transferred here from sect. *Tridactylia*. Both species also have folding leaves and reflexing rays like others of sect. *Scopulincola*.

31. Sect. *Stenactis* Torr. & A. Gray, Fl. N. Amer. 2(1): 172. 1841. LECTOTYPE (Nesom 1989c): *Erigeron pumilus* Nutt.

Erigeron [unranked sp. group] *Pumili* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *Erigeron pumilus* Nutt.

Perennial, taprooted; caudex branches not thickened, leaf bases not marcescent; petiole bases ciliate; heads commonly more than 1 per stem, nodding in bud; leaves linear-oblanceolate to narrowly oblanceolate or oblanceolate-spatulate, 1-nerved, cauline well-developed (except var. *condensatus*); rays reflexing (laminae reduced in *E. aphanactis*, *E. calvus*, *E. concinnus*; ray florets 0 in *E. ovinus*); disc corolla throat white-indurate and inflated (not inflated in *E. pygmaeus*); achenes 1.2–2 mm long (2.3–2.8 mm in *E. pygmaeus*); pappus bristles 7–27.

E. aphanactis (A. Gray) Greene
E. calvus Coville
E. clokeyi Cronquist
E. concinnus (Hook. & Arn.) Torr. & A. Gray
E. engelmannii A. Nelson
E. maguirei Cronquist
E. pumilus Nutt. (incl. *E. zothecinus* S.L. Welsh)
E. pygmaeus (A. Gray) Greene
E. vetensis Rydb.

This group was placed by Nesom (1989c) as the "*Erigeron pumilus* group" of sect. *Asteroidea*. It was later treated with other species with sharply reflexing rays as an informal subgroup within sect. *Geniculactis* (Nesom, 1990c). Molecular data, in contrast, indicate that the *E. pumilus* group is phylogenetically removed from sect. *Geniculactis* sensu stricto, and the distinctive

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morphology of the group suggests that it be separately and formally recognized. The species occur at low to mid-level elevations in the western U.S.A. *Erigeron pygmaeus* grows at higher elevations and is anomalous in several morphological features.

The narrow Utah endemic *Erigeron maguirei* fits within sect. *Stenactis* in features of habit as well as ray and bud behavior. Among the other species, it is most similar in its subspatulate leaves to the rare *E. calvus* from the Inyo Mountains of California.

The placement here of *Erigeron ovinus* emphasizes the tendency for reduction or loss of rays prevalent in the section. Bud behavior is not known, and the 3-nerved leaves and deflexed-hirsute cauline vestiture suggest that it may instead be related to *E. caespitosus* (sect. *Asteroidea*, Group B) (Blake first described *E. ovinus* as *E. caespitosus* var. *anactis*). It also is similar in some respects to *E. nauseosus* (sect. *Scopulincola*, Group A). *Erigeron ovinus* is endemic to the Sheep and Groom ranges and Mount Irish in Clark and Lincoln cos., Nevada

32. Sect. **Terranea** (Colla) Nesom, comb. et stat. nov.

Terranea Colla, Mem. Accad. Sci. Torino 38 (Pl. Rar. Chil., Fasc. 4): 11, t. 23. 1835 [reprints 1834]. TYPE: *Terranea fernandeziana* Colla

Perennial herbs to subshrubs or (*Erigeron fernandezianus*) woody shrubs or small trees, rhizomatous; caudex simple; glabrous to strigose; stems branched; leaves oblanceolate, to lanceolate, entire to toothed or pinnatifid, not clasping; heads 1 or in a loosely corymbiform array, erect in bud; rays, white, not coiling or reflexing; achenes 1–2 mm long, 2-nerved; pappus of [not counted] bristles. All species are hexaploid, $2n = 54$ (Valdebenito et al. 1992).

E. ingae Skottsb.
E. luteoviridis Skottsb.
E. fernandezianus (Colla) Solbrig
E. rupicola Phil.
E. "stuessyi" (ined.)
E. turricola Skottsb.

Sect. *Terranea* comprises a group of six apparently closely related species endemic to the Juan Fernandez Islands of Chile and are hypothesized (based on an analysis of morphological, chromosomal, and flavonoid data) to have radiated from a single introduction to the island more distant from the mainland (Isla Masafuera; Valdebenito et al., 1992). The epithet "stuessyi" was applied to one of the species in the publication by Valdebenito et al. (1992), but the name has never been validated.

Among South American mainland species included in a survey for possible ancestors, the Valdebenito et al. (1992) study placed *Erigeron leptorhizon* DC. ($2n = 18$) (see *Conyza* group A = *Erigeron* sect. *Caenotus*) as the species most similar to the *E. fernandezianus* group, but the molecular analysis of Noyes (2000a) instead places *E. fernandezianus* as closely related to the other group of species commonly placed in *Conyza* (see *Conyza* group B), distantly related to *E. leptorhizon*. As noted by Valdebenito et al. (1992, p. 477), "Continental species with a chromosome number of $n = 27$ would be more probable as an ancestral taxon." Plants of the mainland species *E. ecuadoriensis* and *E. lanceolatus* (see sect. *Meridionales*) are known to be hexaploid, and it seems likely that the Juan Fernandez endemics are derived from sect. *Meridionales*.

The Noyes (2000a) molecular analysis included two samples of *Erigeron rosulatus*: the mainland sample is closely related to other mainland species (here in sect. *Meridionales*), while the sample from the Juan Fernandez Islands clusters with the species of sect. *Terranea*.

33. Sect. *Tridactylia* Nutt., Trans. Amer. Philos. Soc. ser. 2, 7: 310. 1841. TYPE: *Erigeron compositus* Pursh.

Erigeron series *Multifidi* Rydb. ex J.F. Macbr. & Payson, Contr. Gray Herb. 49: 73. 1917. *Erigeron* [unranked sp. group] *Multifidi* Rydb., Fl. Colorado 359. 1906, in clave. LECTOTYPE: *Erigeron compositus* Pursh. (Nesom, 1989c)

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Erigeron [unranked sp. group] *Compositi* Rydb., Fl. Rocky Mts. 896. 1918, in clave. TYPE: *Erigeron compositus* Pursh.

Taprooted, perennial; caudex divided into slender, rhizomelike branches (variable in *Erigeron compositus*); glabrous to strigose or hispid; stems simple (few-branched in *E. basalticus* and *E. allocotus*); leaves oblanceolate to spatulate 3-lobed or 3-toothed near the apex, not clasping; heads erect in bud; rays white, weakly coiling or not at all (sometimes distinctly in *E. compositus*); achenes 1.5–2.7 mm long (3.5–4 mm in *E. lanatus*), 2-nerved; pappus of 10–20 bristles (25–35 in *E. lanatus*).

E. allocotus Blake
E. basalticus Hoover
E. compositus Pursh
E. denalii A. Nelson (incl. *E. mexiae* K. Becker)
E. flabellifolius Rydb.
E. lanatus Hook.
E. pallens Cronquist
E. purpuratus Greene
E. salishii Douglas & Packer
E. trifidus Hook.
E. vagus Payson

Recent studies have explored the nature of variation in sexual and agamospermic populations of *E. compositus* (Noyes and Soltis, 1996; Noyes et al., 1995). *Erigeron pinnatisectus* was shown by Noyes (2000a) to be distantly related to sect. *Tridactylia*; *E. pinnatisectus* and its close relative *E. mancus*, both of which have pinnately dissected leaves (vs 3-lobed or 3-toothed), are here transferred to sect. *Scopulincola*.

A possible relationship of *Erigeron lanatus* to sect. *Erigeron* needs to be investigated; the leaves are entire or weakly 3-toothed at the apex, and the species was speculated to be involved as a parent in the hybrid origin of *E. trifidus* (Packer, 1983). The origin of *E. trifidus* through hybridization between *E. lanatus* and *E. compositus* was confirmed by Burke (2005), although as currently recognized, *E. trifidus* probably is polyphyletic. An ambiguous, slender taprootlike structure sometimes is observed in *E. lanatus* at the base of the caudex, but this may be a rhizome; the diffuse system of relatively long, slender, rhizomelike, branches is similar to morphology in sect. *Tridactylia*.

34. Sect. *Trimorpha* (Cass.) DC., Prodr. 5: 290. 1836. *Trimorpha* Cass., Bull. Sci. Soc. Philom. Paris 1817: 137. 1817. *Erigeron* subg. *Trimorpha* (Cass.) Popov, Acta Inst. Bot. Acad. Sci. URSS, Ser. 1, Fasc. 7: 10. 1948. TYPE: *Erigeron acris* L.

Trimorpha sect. *Brachyglossae* Vierh., Beih. Bot. Centralbl. 19: 423. 1906. *Erigeron* subsect. *Brachyglossae* (Vierh.) Pawlowski, Fragm. Florist. Geobot. 16: 256. 1970. LECTOTYPE (Nesom, 1989b): *Erigeron acris* L.

Trimorpha sect. *Macroglossae* Vierh., Beih. Bot. Centralbl. 19: 424. 1906. LECTOTYPE (Nesom, 1989b): *Erigeron alpinus* L.

Tessenia P. Bubani, Fl. Pyrenaea 2: 264. 1899. LECTOTYPE: *Erigeron alpinus* L. (Nesom, 1989b)

Erigeron [unranked sp. group] *Acres* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *Erigeron acris* L.

Fibrous-rooted, perennial, biennial, or annual; caudex usually simple; stems usually branched; leaves mostly entire, not clasping; heads erect in bud, in a corymbiform to broadly racemiform cluster; inner involucral bracts long-attenuate to caudate; ray (pistillate) florets in 2 zones, those of the outer zone with erect, filiform, white to pink or purplish lamina, not coiling or reflexing, those of inner zone without lamina; achenes 2–2.4 mm long, 2-nerved; pappus bristles 12–35, accrescent (elongating in fruit to ca. 2 times involucres).

E. acris L. * (incl. *E. kamtschaticus* DC., *E. angulosus* Gaudichaud*, *E. droebachiensis* O.F. Müll.*, *E. elongatus* Ledeb., and *E. politus* Fries*)
E. alpinus L.*
E. atticus Villars*
E. baicalensis Botsch.
E. borealis (Vierh.) Simmons*
E. canariensis O. Sida
E. caucasicus Steven*

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E. cyanactis Rech. f.
E. elatus Hook.
E. epiroticus (Vierh.) Halácsy*
E. glabratus Hoppe & Hornsch. ex Bluff & Fingerh.*
E. granatensis Lippert
E. hispanicus (Vierh.) Maire
E. lalehzaricus (Rech.) O. Sida
E. leptocladus Rech. f.
E. macrophyllus Herbich
E. mesatlanticus Maire
E. nannogeron Rech. f.
E. neglectus Kerner*
E. nivalis Nutt. (= *E. debilis* (A. Gray) Rydb.; *E. scotteri* Boivin)
E. orientalis Boiss.
E. podolicus Besser
E. pseudoelongatus Botsch.
E. semibarbatus DC.
E. serotinus Weihe
E. uralensis Less.
E. venustus Botsch.*

(*asterisks denote Eurasiatic species studied by Huber and Nilsson, 1995)

Nesom (1989b) hypothesized that sect. *Trimorpha* (as the genus *Trimorpha*) is separate from *Erigeron*, more closely related to *Conyza*, and provided nomenclatural transfers for North American taxa. Studies by Walter Huber and colleagues and by Noyes (2000a), however, have made it clear that species of sect. *Trimorpha* are closely related to those of sect. *Erigeron* and that both sections are relatively recently derived within the genus (Huber, 1993; Huber and Leuchtmann, 1992; Huber and Nilsson, 1995; Huber and Zhang, 1991; Oberhänsli and Huber, 1993; Utelli et al., 1995).

The North American species are *Erigeron acris* (circumboreal), *E. elatus*, and *E. nivalis*. The Eurasiatic species are diploids with identical karyotypes and their high genetic identities suggest very recent evolutionary differentiation. Some of these are among nine species listed by Sida (1988) as "Species excludendae"—he gave no comment about the reason for their exclusion or their suggested disposition: *E. alpinus*, *E. atticus*, *E. borealis*, *E. epiroticus*, *E. gaudinii* Brügger, *E. hungaricus* (Vierh.) Pawl., *E. neglectus*, *E. orientalis* Boiss., and *E. rhodopaeus* (Vierh.) Hayek.

Sida (1988) formally divided sect. *Trimorpha* into three series, based primarily on form of the capitulescence and vestiture: ser. *Trimorpha* O. Sida, ser. *Politae* O. Sida, and ser. *Macrophyllae* O. Sida.

As suggested by Nesom (1994c) and as discussed in detail and experimentally confirmed by Huber and Nilsson (1995) and Noyes (2000a), autogamous breeding systems apparently have arisen independently in a number of Astereaean groups, including *Trimorpha* and *Conyza*. In these, the pistillate florets of a head are greatly increased in number (often outnumbering the bisexual florets), in several series, the inner sometimes reduced to filiform eligulate florets, and the outer with reduced lamina.

35. Sect. *Wyomingia* (A. Nelson) Cronquist, Brittonia 6: 140. 1947.

Wyomingia A. Nelson, Bull. Torrey Bot. Club 26: 249. 1899. TYPE: *Erigeron pulcherrimus* A.A. Heller

Erigeron [unranked sp. group] *Cani* Rydb., Fl. Colorado 359. 1906, in clave. TYPE: *Erigeron canus* A. Gray

Erigeron [unranked sp. group] *Tetrapleuri* Rydb., Fl. Rocky Mts. 897. 1918, in clave. TYPE: *Erigeron tetrapleuris* (A. Gray) Heller (= *E. utahensis*)

Taprooted; perennial; caudex simple or with short, thick branches; vestiture strigillose of short, closely appressed hairs; stems simple or branched; leaves linear to narrowly oblanceolate, not clasping; heads erect in bud (nodding? in *Erigeron compactus*); rays white to blue, coiling (reflexing in *E. canus*, *E parishii*); achenes (1.5–)2–3.4 mm long, 2-nerved, (2–)4(–6)-nerved, or 6–8-nerved, (8–)10–14-nerved (*E. canus*), strigose to strigose-sericeous or with velutinous-ciliate margins and glabrous faces; pappus of 15–50 bristles (9–10 in *E. katiae*).

Group A. Stems branched; cauline leaves prominent; heads numerous, erect in bud; rays coiling; achenes (2–)4(–6)-nerved, sparsely strigose.

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E. sparsifolius Eastw.

E. utahensis A. Gray

Group B. Stems simple, heads 1; leaves mostly basal and linear, cauline reduced; heads 1; achenes 2-nerved, faces glabrous, margins pilose-sericeous.

E. compactus Blake

E. consimilis Cronquist

E. sivinskii G.L. Nesom

Group C. Stems simple or branched, heads 1–4; leaves basal and cauline; achenes 2-nerved, villous-hirsute; pappus of 9–10 (*E. katiae*) or 15–25 (*E. nematophyllus*) bristles.

E. katiae N.D. Atwood and S.L. Welsh (2007)

E. nematophyllus Rydb.

Group D. Stems simple; leaves mostly basal and linear, cauline reduced; heads 1; achenes 2-nerved (*Erigeron untermannii*) or 4–8-nerved, faces strigose-sericeous.

E. argentatus A. Gray

E. pulcherrimus A.A. Heller (incl. *E. bistiensis* G.L. Nesom & Hevron)

E. untermannii S.L. Welsh (incl. *E. carringtonae* S.L. Welsh)

Group E. Stems simple or branched; leaves linear, mostly basal (*Erigeron canus*) or basal and cauline (*E. parishii*); heads 1–4 (*E. canus*) or 1–5(–10) (*E. parishii*), nodding in bud; rays reflexing (also slightly coiling at tips in *E. parishii*); achenes (8–)10–14-nerved, terete, glabrous (*E. canus*) or 4-nerved, angled, sparsely strigose to pilose (*E. parishii*).

E. canus A. Gray

E. parishii A. Gray

Sect. *Wyomingia*, as outlined here, is a heterogeneous group united by strigillose vestiture, linear leaves, and coiling rays (except in Group E). Achenes tend to be multi-nerved in Groups A and E and densely hairy in Groups B, C, and D. The leaves of *Erigeron untermannii* are often spatulate and glabrous to glabrate abaxially, features more similar to *E. radicatus* and its close relatives; rays of *E. untermannii* apparently tend to both coil and reflex. The two species of Group E are unique in their combination of nodding heads and reflexing rays. Problems in discerning relationships among the subgroups also were pointed out in the original description of *E. sivinskii* (Nesom, 1991).

Studies by Tonne (1999) indicate that *Erigeron bistiensis* is a synonym of *E. pulcherrimus* and support the hypothesis (Nesom and Hevron, 1995) that *E. untermannii* and *E. carringtonae* are conspecific. Neel and Ellstrand (2001) studied patterns of allozyme diversity in *E. parishii*, which is threatened by mining. Distinctions between *E. utahensis* and *E. sparsifolius* were noted by Nesom (2004).

APHANOSTEPHUS DC., Prodr. 5: 310. 1836. TYPE: *Aphanostephus ramosissimus* DC.

Keerlia DC., Prodr. 5: 309. 1836. LECTOTYPE (designated here): *Keerlia ramosa* DC. = *Aphanostephus ramosissimus* var. *ramosus* (DC.) B.L. Turner & Birdsong

Leucopsidium Charpentier ex DC., Prodr. 6: 43. 1838. TYPE: *Leucopsidium arkansanum* DC. = *Aphanostephus skirrhobasis* (DC.) Trel.

Aphanostephus subg. *Euaphanostephus* Blake, Contr. Gray Herb. 53: 24. 1918. TYPE: *A. ramosissimus* DC.

Aphanostephus subg. *Pappophanus* Blake, Contr. Gray Herb. 53: 24. 1918. TYPE: *A. skirrhobasis* var. *hallii* (A. Gray) Blake

Aphanostephus sect. *Pappophanus* (Blake) Shinners, Wrightia 1: 101. 1946.

Aphanostephus sect. *Pappopecus* Shinners, Wrightia 1: 108. 1946. LECTOTYPE: *A. ramosissimus* DC. (designated here)

Annual or perennial, taprooted; caudex simple, stems branched; leaves oblanceolate, slightly clasping or not clasping; heads nodding in bud; rays with abaxial midstripe, not coiling or reflexing; achenes thick-ribbed, columnar, 4-angled, often bearing duplex trichomes with a coiled or recurved apex; pappus a low, fimbriate- or ciliate-rimmed corona (in *A. skirrhobasis* var. *kidderi* (Blake) B.L. Turner, the pappus members may appear as relatively slender, barbellate bristles with expanded bases). The genus is distinguished by its combination of

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ovate-lanceolate, thin-margined phyllaries, conical receptacles, achene morphology, pappus, and base chromosome number of $x = 5$.

A. pilosus Buckley

A. ramosissimus DC. (incl. *A. arizonicus* A. Gray, *A. humilis* (Benth.) A. Gray, *A. jaliscensis* Shinners, *A. pachyrrhizus* Shinners, *A. potosinus* Shinners, and *A. ramosus* (DC.) A. Gray)

A. riddellii Torr. & A. Gray

A. skirrhobasis (DC.) Trel. (incl. *A. kidderi* Blake)

Aphanostephus includes four species (including eight varietal taxa) restricted to the south-central USA and the northern half of Mexico, as recognized by Turner (1984). Turner's phylogenetic reconstruction of the genus, based on morphology, was largely corroborated by Elisens et al. (1992).

Compared to *Aphanostephus*, other species of Conyzinae are conservative in involucral morphology (phyllaries linear-lanceolate, without wide, thin-scarious margins), achene morphology and vestiture (thin-walled, flat, mostly 2-nerved but subterete and multinerved in a few taxa, the duplex hairs never glochidiate), pappus (of barbellate bristles or reduced), and base chromosome number (x = 9) (see Nesom, 2000a). The genus was hypothesized to be closely related to *Townsendia*, *Astranthium*, and a group of Southern Hemisphere genera (subtribe Brachyscominae) on the basis of morphological features (Nesom, 1994d). In contrast, molecular data (cf. Morgan, 1990; Noyes, 2000a; Noyes and Rieseberg, 1999) indicate that *Aphanostephus* has arisen from within the Conyzinae, apparently closely related to sect. *Microcephalum* and sect. *Cincinnactis*.

APOPYROS Nesom, Phytologia 76: 177. 1994. TYPE: *Apopyros warmingii* (Baker) G.L. Nesom

Perennial, from a thick, ligneous, sometimes tuberous rhizome; caudex simple; glabrate to sparsely pilose-hirsute; stems simple or branched; leaves all cauline, the proximal scalelike, linear-lanceolate to elliptic above, with 3 parallel nerves, entire, not clasping; heads 1–4 or 15–75 in a thyrsoid-cormbiform arrangement, erect in bud; rays absent (peripheral florets pistillate, fertile, tubular with 3–4 apical teeth); achenes 1.8–4 mm long, subcylindric, with (4–)5(–6) orange-resinous nerves; pappus of 28–40 bristles.

A. corymbosus (Hook. & Arn.) Nesom

A. warmingii (Baker) Nesom

Apopyros includes two species mostly in Brazil but reaching Paraguay and northeastern Argentina. Nesom (1994c) observed that *Apopyros* is similar to *Neja* in its parallel-veined leaves with shiny-indurate surfaces, multinerved and nearly terete achenes, and tendency to produce stiffly pilose-hirsute vestiture, but Noyes (2000a) found that *Apopyros* is more closely related to *Leptostelma*.

CONYZA [group A]

Erigeron sect. *Caenotus* Nutt., Gen. Plant. 2: 148. 1818. *Conyza* sect. *Caenotus* (Nutt.) Cronquist ex Cuatrec., Webbia 24: 211. 1969. TYPE: *Erigeron canadensis* L.

Conyzella Fabr., Enum. (ed. 1) 86. 1759. TYPE: *Erigeron canadensis* L.

Leptilon Raf., Amer. Monthly Mag. 268. 1818. TYPE: *Erigeron divaricatus* Michx.

Erigeron sect. *Multiflori* G. Don in Loudon, Hort. Brit. 343. 1830. LECTOTYPE (Nesom 1989c): *Erigeron canadensis* L.

Suffrutescent perennial (*Erigeron crenatus*, *E. socorrensis*) or annual; taprooted; caudex simple; hirsute to nearly glabrous; stems branched; leaves linear to lanceolate or oblanceolate, entire or toothed, not clasping; heads erect in bud, in a columnar to pyramidal or loosely corymbiform arrangement; rays white, filiform, lamina slightly longer than the involucre, not coiling (apparently coiling in *E. socorrensis*) or reflexing; achenes 0.8–1.5 mm long, 2-nerved; pappus of 11–20 bristles.

Erigeron canadensis L. (= *Conyza canadensis* (L.) Cronquist)

Erigeron crenatus Eastw.

Erigeron divaricatus Michx. (= *Conyza ramosissima* Cronquist)

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Erigeron leptorhizon DC. (= *E. gaudi chaudii* DC.)
Erigeron socorrensis I.M. Johnston
Erigeron subalpinus Urb.

Variation in *Erigeron crenatus* and *E. socorrensis*, from Isla Socorro of the Revillagigedo Islands, Mexico, was studied by Nesom (1990h). *Erigeron subalpinus* is endemic to Cuba and was described as very similar to *Erigeron canadensis*.

CONYZA [group B]

Conyza Less., Syn. Gen. Comp. 203. 1832. *Erigeron* sect. *Conyza* (Less.) Baill., Hist. Pl. 8: 143. 1882. TYPE: *Conyza chilensis* (Spreng.) d. Don ex D. Don = *Conyza primulifolia* Lourteig & Cuatrec.

Astradelphus E.J. Remy [nom. nov.], Ann. Sci. Nat. Bot. ser. 3, 12: 185. 1849. *Gusmania* E.J. Remy in C. Gay, Hist. Chile Bot. [Fl. Chilena] 4: 12. 1849 (non *Guzmania* Ruiz & Pavon 1802). TYPE: *Astradelphus chilensis* (Spreng.) E.J. Remy = *Gusmania chilensis* (Spreng.) E.J. Remy = *Conyza chilensis* Spreng. = *Conyza primulifolia* (Lam.) Cuatrec. & Lourteig = *Erigeron chilensis* (Sprengel) D. Don ex G. Don in Loudon = *Erigeron remyanus* Wedd.

Annual to perennial; taprooted; caudex simple; hirsute to strigose, often strongly glandular; stems simple or branched; leaves lanceolate to oblanceolate or spatulate, entire to toothed or lobed, clasping or not clasping; heads erect in bud; rays white, lamina absent to slightly longer than the involucre; achenes 0.8–2 mm long, 2-nerved; pappus of ca. 10–25 bristles.

Conyza arabidifolia E.J. Remy
Erigeron bonariensis L. (= *Conyza bonariensis* (L.) Cronquist)
Conyza burkartii Zardini
Erigeron chilensis (Spreng.) D. Don ex G. Don in Loudon (= *Conyza primulifolia* (Lam.) Lourteig & Cuatrec. = *Conyza chilensis* Spreng.)
Conyza deserticola Phil.
Erigeron floribundus (Kunth) Schultz-Bip. (= *Conyza floribunda* Kunth)
Erigeron laevigatus Rich. (= *Conyza laevigata* (Rich.) Pruski = *Conyza apurensis* Kunth)
Conyza microcephala Hemsl.
Erigeron pazensis Schultz-Bip. ex Rusby
Erigeron pinnatus Turcz. 1851 (non L. 1753) (= *Conyza cardaminifolia* Kunth; *E. cardaminifolia* (Kunth) Wedd.; *E. turczaninowii* Wedd.)
Erigeron spiciformis Griseb. (= *Conyza spiciformis* (Griseb.) Zardini)
Erigeron spiculosus Hook. & Arn. (= *Conyza spiculosa* (Hook. & Arn.) Zardini)
Erigeron stenophyllus Hook. & Arn. (= *Conyza gayana* Phil.)
Erigeron sumatrensis Retz. (if distinct from *E. floribundus*; = *Conyza sumatrensis* (Retz.) E. Walker)
Erigeron trihecatactis Blake (= *Conyza trihecatactis* (Blake) Cuatrec.)
Erigeron tunariensis Kuntze (= *Conyza tunariensis* (Kuntze) Zardini)
Erigeron uliginosa Benth. (= *Conyza uliginosa* (Benth.) Cuatrec.)
Erigeron variifolius Blake (= *Conyza coronopifolia* Kunth)

Erigeron pazensis usually is not included among these species, but the habit and general aspect suggest that it belongs here. Solbrig (1962, p. 37) noted that it is "A species morphologically similar to *Conyza*, it is undoubtedly an *Erigeron* due to the preponderance of tubular over ligulate flowers, and the ligules, which are clearly longer than the tubes."

An accurate estimate of the number of South American species generally treated as *Conyza* has not been developed, but there probably are between 60 and 100 (e.g., see Zardini, 1976). Relatively few of the species are included here.

Cronquist (1943), Cuatrecasas (1969), Zardini (1976), Nesom (1990a), and Thébaud and Abbott (1995) have provided suggestions toward a distinction between *Conyza* and *Erigeron*. Group B of *Conyza* is heterogeneous and likely will prove to be non-monophyletic.

DARWINIOTHAMNUS Harling, Acta Horti Berg. 20: 108. 1962. TYPE: *Darwiniothamnus tenuifolius* (Hook. f.) Harling

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Perennial shrubs, fibrous-rooted; caudex simple or branched; glabrous to strigose; leaves linear to oblanceolate, entire to mucronate, in condensed terminal whorls; stems branching; heads in a condensed-corymbiform capitulescence mostly within the leaves; rays white, strongly coiling; achenes dimorphic, ray 2(–4)-nerved, disc 3–5(–6)-nerved.

D. tenuifolius (Hook. f.) Harling (= *Erigeron tenuifolius* Hook. f.)

D. lancifolius (Hook. f.) Harling (= *Erigeron lancifolius* Hook. f.)

Darwiniothamnus, an endemic of the Galápagos Islands, has been treated at generic rank by various authors (e.g., Harling, 1962; Cronquist, 1971; Lawesson and Adsersen, 1987). Infraspecific taxa have been described in each of the two species.

Darwiniothamnus alternifolius, the most recently described species (Lawesson and Adsersen, 1987), does not have significant features of the two species upon which the generic concept was based: the plants lack the shrubby ''rosette'' habit, the leaves are not in condensed terminal whorls, the heads are not in a condensed-corymbiform capitulescence mostly within the leaves, and the achenes are not dimorphic. Further, the ray floret lamina do not coil and molecular evidence indicates that its closest relationships are elsewhere (Andrus et al., in press); it belongs among the species of *Erigeron* sect. *Meridionales*, where it is listed here.

Nesom (1989c) suggested that *Darwiniothamnus* is related to the primarily Mexican group *Erigeron* sect. *Cincinnactis*. Recent molecular evidence (Noyes, 2000a; Andrus et al., in press.) shows that the two *Darwiniothamnus* species are most closely related to sect. *Cincinnactis* and the Caribbean sect. *Microcephalum*.

HYSTERIONICA Willd., Ges. Naturfr. Freunde Berlin Mag. 1: 140. 1807. TYPE: *Hysterionica jasionioides* Willd.

Annual or perennial herbs to subshrubs, taprooted; caudex simple; glandular and otherwise glabrous to hirsute or hispid; stems sometimes branched at the base; leaves mostly oblanceolate, entire to pinnatisect, not clasping; heads 1-several, erect in bud; rays yellow or white, not coiling or reflexing; achenes 1–2 mm long, 2-nerved; pappus of scabrid bristles.

H. aberrans (Cabrera) Cabrera

H. bakeri Hicken

H. cabrerae Espinar

H. glaucifolia (O. Kuntze) Solbrig

H. jasionioides Willd.

H. montevidensis Baker

H. nebularis Deble, Oliveira & Marchiori

H. pinnatiloba Matzenb. & Sobral

H. pinnatisecta Matzenb. & Sobral

H. pulchella Cabrera

Overviews of *Hysterionica* have been provided by Cabrera (1946), Ariza Espinar (1980), and Nesom (1993c, 1994b). Three species from Brazil have recently been added (Matzenbacher and Sobral, 1996; Deble et al., 2004).

LEPTOSTELMA D. Don in Sweet, Brit. Fl. Gard. ser. 2. 38. 1830. TYPE: *Erigeron maximus*

Erigeron sect. *Leptostelma* (D. Don) Benth. & Hook., Gen. Pl. 2: 280. 1873.

Perennial herbs, rhizomatous and fibrous-rooted; caudex simple; glabrous to puberulent or hispid; stems branched; leaves ovate to oblanceolate, net-veined, entire or toothed, clasping; heads erect in bud; rays yellow to white, not coiling or reflexing; achenes 2(–3)-nerved, glabrous; pappus of 30–40 bristles.

Erigeron camposportoi Cabrera

Erigeron catharinensis Cabrera

Leptostelma maximum D. Don (= *Erigeron maximus* (D. Don) DC.)

Erigeron meyeri Cabrera

Erigeron tucumanensis Cabrera

Leptostelma tweediei (Hook. & Arn.) Hind & G.L. Nesom (= *Erigeron tweediei* Hook. & Arn.; *Erigeron seneciiformis* Blake)

The remaining combinations to *Leptostelma* are being made by Aristônio Teles in connection with his synopsis of the tribe Astereae in Brazil.

NEJA D. Don in Sweet, Hort. Brit. (ed. 2) 299. 1830. TYPE: *Neja gracilis* D. Don = *Neja filiformis* (Spreng.) Ness

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Neja sect. *Podoneja* DC., Prodr. 5: 325. 1836. TYPE: *Neja gracilis* = *Neja filiformis* (Spreng.) Ness

Neja sect. *Monogyria* DC., Prodr. 5: 325. 1836. LECTOTYPE (Nesom, 1993b): *Neja linearifolia* DC. = *Neja pinifolia* (Poir.) G.L. Nesom

Perennial herbs; taprooted; caudex branched; glabrous to glabrate to sparsely pilose; stems usually branched; leaves mostly basal, filiform to lnear-oblanceolate, entire, not clasping; heads solitary, long-pedunculate or on sparsely bracteolate stems, erect in bud; rays yellow or white, not coiling; achenes fusiform-cylindric, with 7–10 raised, thick, orange-resinous nerves; pappus of scabrid bristles.

N. dianthifolia (Griseb.) Nesom
N. filiformis (Spreng.) Nees
N. marginata (Griseb.) Nesom
N. nidorelloides DC.
N. pinifolia (Poir.) Nesom
N. pulvinata (Cabrera) Nesom

Nesom (1994b, 1994c) suggested that *Neja* might be most closely related to *Apopyros* but molecular data (Noyes, 2000a) indicate that it is probably the sister group to *Hysterionica*, the genus from which it has been segregated. The six species of *Neja* occur in southeastern Brazil and adjacent Uruguay, Paraguay, and Argentina, except for the Cuban endemic *N. marginata* (Nesom, 1993c, 1994b, 2000).

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