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Abstract  The classification of the family Compositae (Asteraceae) has been much improved in the last decades by the application of molecular methods culminating in the recompilation published in 2009, Systematics, evolution, and biogeography of Compositae. Additional evidence of relationships has come from the use of high-throughput sequencing methods. Our late colleague Vicki Ann Funk (1947–2019) was a pioneer in this line of research. Together with her team, she contributed to the achievement of a mature classification of the family, which she left outlined. In this paper, we contribute this classification including all of the recent advances at the subtribal level and review in depth all contributions to Compositae classification made since the 2009 compilation.

Keywords  Asteraceae; Dicomoideae; family classification; next-generation-sequencing; Tarchonanthoideae

INTRODUCTION

The impact of the work of Vicki Ann Funk on the systematics of the Compositae is enormous. She galvanized synantherologists around the world and, under her remarkable leadership and her enviable talent to bring out the best in people, unified our efforts in a collective work that still remains an indispensable resource ten years later. The publication of the book Systematics, evolution, and biogeography of Compositae (Funk & al., 2009) marked a turning point in the study of the family by collecting and updating in a single work the major advances in our understanding of Compositae evolution that had been made since the arrival of molecular methods. An important outcome from this work was identifying the taxa that warranted the greatest future efforts and represented potential goals for synantherology.
By 2010, a new set of molecular tools had emerged, the most potent that systematic botanists have known to date, phyllogenomics, based on the novel methods collectively named next-generation sequencing (NGS). A target enrichment procedure applicable to the whole Compositae was soon designed (Mandel & al., 2014). Vicki Funk understood the power of NGS, and it was not long before that a pioneer study was carried out with the help of Jennifer Mandel, one of the promoters of these new approaches. A first preliminary phylogeny was produced, which demonstrated the applicability of these methods throughout the whole phylogenetic spectrum of the Compositae (Mandel & al., 2015); a preliminary phyllogenomic study of the family followed (Mandel & al., 2017), and a phylogeny of the backbone of the family without ambiguities was finally obtained (Mandel & al., 2019).

As a result of this effort by Funk, Mandel, and their team, we have now reached a phylogenetic classification of Compositae that, at least at the subfamily and tribal levels, can be considered robust (Mandel & al., 2019). Regarding subtribal classification, the information that backs the classification presented here is dispersed among studies of the various tribes that preceded or followed publication of the family review (Funk & al., 2009). Gathering all the advances in classification of the family in a single compilation is our personal tribute to the memory of Vicki Ann Funk.

**MATERIALS AND METHODS**

This classification was left outlined by Vicki Funk. We have added the currently accepted subtribes based on Funk & al. (2009), and we have included the revised authorship, place and date of publication of all subfamilies, tribes, and subtribes, using as starting point Reveal’s (1997) huge nomenclatural contribution. All of the names and protologues have been revised. Subtribal classification changes that have occurred since 2009 have been noted. The notes by Funk are conserved [as commentaries between brackets]. The tribes that will require nomenclatural changes, new descriptions, or more detailed studies are grey-shadowed.

**CLASSIFICATION OF COMPOSITAE**


III. *Stifftioideae* Panero in Phytologia 89: 356. 2007 [or put all into *Mutisioideae*]
6. *Stifftieae* *Hyalooseris* Clade [*Hyalooseris + Dinoseris*]
7. *Stifftieae* *Gongylolepis* Clade [zygomorphic tepui genera]

IV. *Mutisioideae* Lindl. in Loudon, Encycl. Pl.: 1074. 1829

12. *Cyclolepis*? [weakly linked to Wunderlichieae in Mandel & al., 2019 but weakly linked to Gochnatieae in analyses using some chloroplast data by Funk] [*Cyclolepis* Gillies ex D.Don, incertae sedis]
VI. **Wunderlichioideae** Panero & V.A.Funk in *Phytologia* 89: 357. 2007
13. Wunderlichieae Panero & V.A.Funk in *Phytologia* 91: 570. 2009 [*Wunderlichia* + *Stenopadus* Clade (actinomorphic tepui genera)]


IX. **Tarchonanthoideae** S.Ortiz [*Oldenburgieae and Tarchonantheae firmly linked into the same clade; new family, see below*]

X. **Dicomoideae** S.Ortiz [*possibly Dicomoideae*] (new family, see below)
   Dicominae S.Ortiz in *Taxon* 62: 532. 2013
   Pleiotaxinae S.Ortiz in *Taxon* 62: 534. 2013

XI. **Carduoideae** Sweet, *Hort. Brit.*: 213. 1826
   Carduinae Dumort., *Fl. Belg.*: 73. 1827
   Carlininae Dumort., *Fl. Belg.*: 72. 1827
   Centaureinae Dumort., *Fl. Belg.*: 72. 1827
   Xerantheminae Cass. ex Dumort., *Anal. Fam. Pl.*: 32. 1829


XIII. **Vernonioideae** Lindl. in Loudon, *Encycl. Pl.*: 1074. 1829
   Arctotidinae Cass. ex Dumort., *Anal. Fam. Pl.*: 32. 1829

   **Heterolepis** Cass., incertae sedis

Paranepheliinae H.Rob. in Smithsonian Contr. Bot. 54: 44. 1983


   Elephantopinae Less. in Linnaea 5: 135. 1830
   Lychnophorinae Bentham. in Bentham & Hooker f., Gen. Pl. 2: 165. 1873
   Rolandrinae Cass. ex Dumort., Anal. Fam. Pl.: 313. 1829
   Trichospirinae Less. in Linnaea 6: 690. 1831
   Vernoniiinae Cass. ex Dumort., Anal. Fam. Pl.: 313. 1829

   Catananchinae K.Bremer in Novon 3: 329. 1993
   Crepiderinae Cass. ex Dumort., Fl. Belg.: 60. 1827
   Hieraciinae Cass. ex Dumort., Fl. Belg.: 62. 1827
   Hyoseridinae Less., Syn. Gen. Compos.: 127. 1832
   Hypochaeridinae Less., Syn. Gen. Compos.: 130. 1832
   Lactucinae Cass. ex Dumort., Fl. Belg.: 59. 1827
   Malacothricinae K.Bremer in Novon 3: 329. 1993
   Microseridinae Stebbins in Madroño 12: 71. 1953
   Scolyminae Less., Syn. Gen. Compos.: 126. 1832
   Scorzonerae Cass. ex Dumort., Fl. Belg.: 63. 1827
   Sonchinae K.Bremer in Novon 3: 329. 1993
   Stephanomeriinae Stebbins in Madroño 12: 71. 1953

XVI. Asteroideae Lindl. in Loudon, Encycl. Pl.: 1074. 1829
   Othoniinae Less. in Linnaea 6: 93. 1831
   Senecioninae Dumort., Fl. Belg.: 65. 1827
   Tussilagininae Dumort., Fl. Belg.: 64. 1827
32b. Doroniceae Panero in Phytologia 87: 1. 2005
   Anthemidinae Dumort., Fl. Belg.: 69. 1827
   Artemisiinae Less. in Linnaea 5: 163. 1830
   Cotulinae Kitt., Taschenb. Fl. Deutschl., ed. 3: 684. 1853
   Glebionidinae Oberpr. & Vogt in Willdenowia 37: 106. 2007
   Leucanthemopsisinae Oberpr. & Vogt in Willdenowia 37: 104. 2007
   Matricariinae Willk. in Willkomm & Lange, Prodr. Fl. Hispan. 2: 92. 1865
   Osmotopsisinae Oberpr. & Himmelr. in Willdenowia 37: 94. 2007
   Pentziaeinae Oberpr. & Himmelr. in Willdenowia 37: 99. 2007
   Phymasperminae Oberpr. & Himmelr. in Willdenowia 37: 99. 2007
   Santolininae Willk. in Willkomm & Lange, Prodr. Fl. Hispan. 2: 76. 1865
   Asterinae Dumort., Fl. Belg.: 66. 1827
   Baccharidinae Less. in Linnaea 5: 145. 1830
   Bellidinae Willk. in Willkomm & Lange, Prodr. Fl. Hispan. 2: 30. 1865
   Brachyscominae G.L.Nesom in Phytologia 76: 203. 1994
   Chrysopsidinae G.L.Nesom in Phytologia 76: 203. 1994
   Conyzae Horan., Char. Ess. Fam.: 93. 1847
   Grangeinae Benth. in Bentham & Hooker., Gen. Pl. 2: 176. 1873
   Hinterhuberininae Cuatrec. in Webbia 24: 5. 1969
   Homochrominae Benth. in Bentham & Hooker, Gen. Pl. 2: 177. 1873
   Lagenophorinae G.L.Nesom in Phytologia 76: 207. 1994
   Machaeranthinae G.L.Nesom in Phytologia 76: 208. 1994
   Podocominae G.L.Nesom in Phytologia 76: 209. 1994
   Solidagininae O.Hoffm. in Engler & Prantl, Nat. Pflanzenfam. 4(5): 145. 1890
   Symphytirochicae G.L.Nesom in Phytologia 76: 211. 1994
   Gnaphaliinae Dumort., Anal. Fam. Pl.: 31. 1829
   Relhaninae Less. in Linnaea 6: 232. 1831
   Inulinae Dumort., Fl. Belg.: 67. 1827
   Anisopappinae Panero in Phytologia 87: 5. 2005
Athroisminae Panero in Phytologia 87: 2. 2005
Centipedinae Panero in Phytologia 87: 3. 2005
Lowryantheinae Pruski & Anderb. in Taxon 66: 417. 2017
Anisochaeta DC., incertae sedis

“Heliantheae alliance”

39. Helenieae Lindl. in Loudon, Encycl. Pl.: 1074. 1829
   Gaillardiae Less. in Linnaea 6: 516. 1831
   Marshalliae H.Rob. in Phytologia 41: 42. 1978
   Tetraneuridinae Rydb. in Britton & al., N. Amer. Fl. 34(2): 100. 1915
40. Millerieae Lindl. in Loudon, Encycl. Pl.: 1074. 1829
   Desmanthodiinae H.Rob. in Phytologia 41: 40. 1978
   Dyscritothamminae Panero in Phytologia 87: 10. 2005
   Espeletiinae Cuatrec. in Phytologia 35: 48. 1976
   Galinsoginae Benth. in Bentham & Hooker, Gen. Pl. 2: 198. 1873
   Jaegeriinae Panero in Phytologia 87: 11. 2005
   Melampodiinae Less. in Linnaea 5: 149. 1830
   Milleriinae Benth. in Bentham & Hooker, Gen. Pl. 2: 166. 1873
   Clappiinae H.Rob. in Phytologia 41: 39. 1978
   Coulterellinae H.Rob. in Phytologia 41: 40. 1978
   Jaumeinae Benth. in Bentham & Hooker, Gen. Pl. 2: 168. 1873
   Pectidinae Less., Syn. Gen. Compos.: 152. 1832
   Tagetinae Dumort., Anal. Fam. Pl.: 31. 1829
   Varillinae B.L.Turner & A.M.Powell ex H.Rob. in Phytologia 41: 44. 1978
42. Madieae Jeps., Fl. W. Calif.: 527. 1901
   Baeriinae Benth. in Bentham & Hooker, Gen. Pl. 2: 200. 1873
   Madiinae Benth. in Bentham & Hooker, Gen. Pl. 2: 198. 1873
   Lycapsinae H.Rob. in Phytologia 46: 120. 1980
   Peritylinae Rydb. in Britton & al., N. Amer. Fl. 34 (4): 289. 1914
   Adenostemmatinae B.L.Rob. in Proc. Amer. Acad. Arts 49: 435. 1913
   Alominae Less., Syn. Gen. Compos.: 154. 1832
   Ayapaninae R.M.King & H.Rob. in Phytologia 46: 446. 1980
   Critoniinae R.M.King & H.Rob. in Phytologia 46: 447. 1980
   Disynaphiinae R.M.King & H.Rob. in Phytologia 39: 133. 1978
DISCUSSION AND CONCLUSIONS

Changes in subtribal classification in the outline here presented are minor if compared to the subtribes suggested in Funk & al. (2009). There are, however, some higher-level taxonomic changes that have not yet been formally proposed. One example pertains to subtribe Distephaninae (Vernonieae), which should be recognized as an independent tribe (V.A. Funk & H. Robinson, in prep.). Another example is the need to recognize subfamilies Tarchonanthoideae and Dicomioideae resulting from the break-up of subfamily Carduoideae (Mandel & al., 2019); they are described below.

This new classification recognizes 16 subfamilies instead of 12, and 50 tribes instead of 43 (compared to Funk & al.,...
If tribe Doroniceae is finally accepted as independent from Senecioneae, the number of tribes would be 51. Many of the changes in classification are not yet formally proposed. More molecular study and new morphological work focused on these potential new tribes are needed to support their formal recognition. We hope that the publication of this proposal containing the suggestions made by our late friend Vicki Funk in her unpublished manuscript will spur new studies in the family, and the few doubts that still remain on the position of some tribes will be soon resolved.

Regarding the Mandel & al. (2019) demonstration of the grade rather than clade situation represented by recent concepts of Cichorioideae, we should note that morphological justification for this finding is extremely limited. Only the lack of long, liguliform, 5-toothed corollas throughout the capitula in the excluded tribes is consistent. The excluded tribes often have true disc florets, true ray florets, or even long-lobed, zygomorphic, bisexual florets (Stokesia L’Hér. and Elephantopsis L.). Latex is not restricted to Cichorieae, occurring in many taxa of Liabeae and some of Vernonieae. Lophate pollen occurs in many taxa of Cichorieae, Vernonieae, and Arctoteae. Corolla color varies from blue to lavender in most taxa of Vernonieae, yellow in most taxa of Liabeae and Distephanus, and yellow to partly red in many taxa of Arctotidaceae. Any formal subdivision of the recent concepts of Cichorioideae into several tribes at this time would require much more extensive justification.

Finally, there is an unresolved question on the subtribal classification of Cichorieae. If Microseridinae are recognized in a narrow sense to the exclusion of taxa traditionally placed in Malacothricinae and Stephanomeriinae (which are included in this list as accepted subtribes), then other subtribes also need to be recognized for a phylogenetically natural classification (Lee & Baldwin, 2004). Otherwise, Microseridinae must be recognized in a broad sense, including Malacothricinae and Stephanomeriinae, to achieve a monophyletic subtribal classification.

**NEW INFRAFAMILIAL TAXA**

**Tarchonanthoideae** S.Ortiz, subfam. nov. – Type: *Tarchonanthus* L., Sp. Pl.: 842. 1753

Perennial herbs and shrubs with conspicuously coriaceous leaves and bisexual, large capitula, as well as dioecious shrubs and trees with herbaceous to subcoriaceous leaves and small capitula, distinguished from other early-diverging subfamilies of Compositae by having short style branches with rounded apices, and acute sweeping trichomes from the apex to near the bifurcation, or lacking trichomes completely; cypselae with carpododium, and testa collapsed or with the lateral and basal walls of the testa epidermis strengthened.

Includes the genera *Brachylaena* R.Br., *Oldenburgia* Less. and *Tarchonanthus* L.


Annual or perennial herbs, shrubs, and small trees distinguished from other early-diverging subfamilies of Compositae by having pluriseriate involucres composed by mostly coriaceous and pungent phyllaries; epidermal cuticle of the corolla cells mostly longitudinally striate; pollen echinate; stylar sweeping trichomes acute, usually arranged in an apical or subapical tuft, never reaching below the shaft bifurcationpoint; cypselae mostly broadly turbinate-cylindrical, lacking carpododium.


**AUTHOR CONTRIBUTIONS**

AS and JRM designed and outlined the paper based on a draft by V.A. Funk. SO described the new subfamilies Dicomoideae and Tarchonanthoideae. JMB prepared the schematic classification in Fig. 1. BGB, RJB, JMB, NGJ, SCK, HR, and TFS reviewed the systematic layout and contributed to the discussion. — AS, https://orcid.org/0000-0003-4717-9063; BGB, https://orcid.org/0000-0002-0028-2242; RJB, https://orcid.org/0000-0002-7827-5886; JMB, https://orcid.org/0000-0003-0377-3853; NGJ, https://orcid.org/0000-0003-1893-5122; SCK, https://orcid.org/0000-0003-1581-6478; JRM, https://orcid.org/0000-0003-3539-2991; SO, https://orcid.org/0000-0003-2160-3161; TFS,
LITERATURE CITED


FIGURE CAPTIONS

Fig. 1. An unrooted representation of the current Compositae classification. Circle size is indicative of species diversity. Gray background on names indicates taxa that will require nomenclatural changes, new descriptions, or more detailed studies. Dotted lines indicate uncertainty in the phylogenetic position. Species numbers taken from Funk & al. (2009) and Anderberg & al. (2007). Species number for Cichorieae does not include microspecies or apomictic species.

Fig. 2. Vicki Funk in early 2018 conducting fieldwork in the Cotopaxi volcano (Ecuadorian Andes). Photograph by Mauricio Bonifacino.