[Article Category: SYSTEMATICS AND PHYLOGENY]

[Running Header:] Susanna & al. • **Compositae classification**

Article history: Received: 31 Jan 2020 | returned for (first) revision: 4 Mar 2020 | (last) revision received: 9 Mar 2020 | accepted: 19 Mar 2020
Associate Editor: Dirk C. Albach |

The classification of the Compositae: A tribute to Vicki Ann Funk (1947–2019)

Alfonso Susanna,[1] Bruce G. Baldwin,[2] Randall J. Bayer,[3] José Mauricio Bonifacino,[4] Núria Garcia-Jacas,[1] Sterling C. Keeley,[5] Jennifer R. Mandel,[3] Santiago Ortiz,[6] Harold Robinson[7] & Tod F. Stuessy[8,9]

1 *Botanic Institute of Barcelona (IBB, CSIC-Ajuntament de Barcelona), Pg. del Migdia s.n., 08038 Barcelona, Spain*
2 *Jepson Herbarium and Department of Integrative Biology, University of California, Berkeley, California 94720, U.S.A.*
3 *Department of Biological Sciences, Center for Biodiversity, University of Memphis, Memphis, Tennessee 38152, U.S.A.*
4 *Laboratorio de Botánica, Facultad de Agronomía, Av. Garzón 780, Montevideo, CP 12900, Uruguay*
5 *Department of Botany, University of Hawaii, Honolulu, Hawaii 96822, U.S.A.*
6 *Laboratorio de Botánica, Facultade de Farmacia, Universidade de Santiago, 15782 Santiago de Compostela, Galicia, Spain*
7 *Department of Botany, MRC 166, NMNH box 37013, Smithsonian Institution, Washington, D.C. 20012-7013, U.S.A.*
8 *Herbarium, Museum of Biological Diversity, The Ohio State University, 1315 Kinnear Road, Columbus, Ohio 43212, U.S.A.*
9 *Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14, 1030 Vienna, Austria*
Address for correspondence: *Alfonso Susanna, asusanna@ibb.csic.es*

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, phylogenomics, 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 phylogenomic 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

I. Barnadesioideae Bremer & Jansen in Ann. Missouri Bot. Gard. 79: 415. 1992
1. Barnadesieae D.Don in Trans. Linn. Soc. London 16: 273. 1833

II. Famatinanthoideae S.E.Freire, Ariza & Panero in Molec. Phylogen. Evol. 80: 49. 2014
2. Famatinantheae S.E.Freire, Ariza & Panero in Molec. Phylogen. Evol. 80: 50. 2014

III. Stifftioideae Panero in Phytologia 89: 356. 2007 [or put all into **Mutisioideae**]
3. Hyalideae Panero in Phytologia 89: 358. 2007 p.p. [*Ianthopappus* + *Hyalis*]
4. Hyalideae Panero p.p. *Leucomeris* Clade [*Nouelia* + *Leucomeris*]
5. Stifftieae D.Don in Trans. Linn. Soc. London 16: 291. 1833 *Stifftia* Clade [*Stifftia*]
6. Stifftieae *Hyaloseris* Clade [*Hyaloseris* + *Dinoseris*]
7. Stifftieae *Gongylolepis* Clade [zygomorphic tepui genera]

IV. Mutisioideae Lindl. in Loudon, Encycl. Pl.: 1074. 1829
8. Onoserideae Panero & V.A.Funk in Phytologia 89: 359. 2007
9. Nassauvieae Cass. in J. Phys. Chim. Hist. Nat. Arts 88: 198. 1819
10. Mutisieae Cass. in J. Phys. Chim. Hist. Nat. Arts 88: 199. 1819

V. Gochnatioideae Panero & V.A.Funk in Proc. Biol. Soc. Wash. 115: 764. 2002
11. Gochnatieae Panero & V.A.Funk in Proc. Biol. Soc. Wash. 115: 764. 2002 [includes *Cnicothamnus*]
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)]

VII. Hecastocleidoideae Panero & V.A.Funk in Proc. Biol. Soc. Wash. 115: 765. 2002
14. Hecastocleideae Panero & V.A.Funk in Phytologia 91: 569. 2009

VIII. Pertyoideae Panero & V.A.Funk in Proc. Biol. Soc. Wash. 115: 766. 2002
15. Pertyeae Panero & V.A.Funk in Phytologia 91: 569. 2009 [incl. *Catamixis*]

IX. Tarchonanthoideae S.Ortiz [Oldenburgieae and Tarchonantheae firmly linked into the same clade; new family, see below]
16. Oldenburgieae S.Ortiz in Compositae Newslett. 47: 2. 2009
17. Tarchonantheae Kostel., All. Med.-Pharm. Fl. 2: 668. 1833

X. Dicomoideae S.Ortiz [possibly Dicomoideae] (new family, see below)
18. Dicomeae Panero & V.A.Funk in Proc. Biol. Soc. Wash. 115: 767. 2002 (Ortiz & al., 2013)
    Dicominae S.Ortiz in Taxon 62: 532. 2013
    Pleiotaxinae S.Ortiz in Taxon 62: 534. 2013

XI. Carduoideae Sweet, Hort. Brit.: 213. 1826
19. Cardueae Cass. in J. Phys. Chim. Hist. Nat. Arts 88: 155. 1819 (Herrando-Moraira & al., 2019)
    Arctiinae N.Garcia & Susanna in Molec. Phylogen. Evol. 137: 329. 2019
    Berardiinae N.Garcia & Susanna in Molec. Phylogen. Evol. 137: 327. 2019
    Cardopatiinae Less., Syn. Gen. Compos.: 14. 1832.
    Carduinae Dumort., Fl. Belg.: 73. 1827
    Carlininae Dumort., Fl. Belg.: 72. 1827
    Centaureinae Dumort., Fl. Belg.: 72. 1827
    Dipterocominae N.Garcia & Susanna in Molec. Phylogen. Evol. 137: 326. 2019
    Echinopsinae Cass. ex Dumort., Anal. Fam. Pl.: 32. 1829.
    Onopordinae N.Garcia & Susanna in Molec. Phylogen. Evol. 137: 328. 2019
    Saussureinae N.Garcia & Susanna in Molec. Phylogen. Evol. 137: 329. 2019
    Staehelininae N.Garcia & Susanna in Molec. Phylogen. Evol. 137: 327. 2019
    Xerantheminae Cass. ex Dumort., Anal. Fam. Pl.: 32. 1829

XII. Gymnarrhenoideae Panero & V.A.Funk in Proc. Biol. Soc. Wash. 115: 763. 2002
20. Gymnarrheneae Panero & V.A.Funk in Phytologia 91: 569. 2009

XIII. **Vernonioideae** Lindl. in Loudon, Encycl. Pl.: 1074. 1829
21. Eremothamneae H.Rob. & Brettell in Phytologia 26: 164. 1973
22. Platycarpheae V.A.Funk & H.Rob. in Compositae Newslett. 47: 25. 2009
23. Arctotideae Cass. in J. Phys. Chim. Hist. Nat. Arts 88: 159. 1819
    Arctotidinae Dumort., Anal. Fam. Pl.: 32. 1829
    Heterolepis Cass., incertae sedis
24. Arctotideae-G subtribe [possible new tribe Gorterieae] (described as Gorterieae Lindl. in Loudon, Encycl. Pl.: 1073(. 1829]
    Gorteriinae Benth. in Bentham & Hooker, Gen. Pl. 2: 167. 1873
25. Liabeae Rydb. in Britton & al., N. Amer. Fl. 34(4): 289. 1927
    Liabinae Cass. ex Dumort., Anal. Fam. Pl.: 31. 1829
    Munnoziinae H.Rob. in Smithsonian Contr. Bot. 54: 49. 1983

Paranepheliinae H.Rob. in Smithsonian Contr. Bot. 54: 44. 1983
Sinclairiinae H.Rob. in Funk, Susanna, Stuessy & Bayer, Syst. Evol. Biogeogr. Compositae: 473. 2009
26. Distephanus Clade [Distephaninae S.C.Keeley & H.Rob. in Funk, Susanna, Stuessy & Bayer, Syst. Evol. Biogeogr. Compositae: 448. 2009] (new tribe Distephaneae; cf. V.A.Funk & H.Robinson, in prep.)
27. Moquinieae H.Rob. in Taxon 43: 39. 1994
28. Vernonieae Cass. in J. Phys. Chim. Hist. Nat. Arts 88: 203. 1819
Centrapalinae H.Rob. in Proc. Biol. Soc. Wash. 112: 223. 1999
Centratherinae H.Rob., R.M.King & F.Bohlmann in Phytologia 46: 425. 1980
Chrestinae H.Rob. in Smithsonian Contr. Bot. 89: 11. 1999
Dipterocypselinae S.C.Keeley & H.Rob. in Funk, Susanna, Stuessy & Bayer, Syst. Evol. Biogeogr. Compositae: 448. 2009
Elephantopinae Less. in Linnaea 5: 135. 1830
Erlangeinae H.Rob. in Proc. Biol. Soc. Wash. 112: 222. 1999
Gymnantheminae H.Rob. in Proc. Biol. Soc. Wash. 112: 224. 1999
Hesperomanniinae S.C.Keeley & H.Rob. in Funk, Susanna, Stuessy & Bayer, Syst. Evol. Biogeogr. Compositae: 450. 2009
Leiboldiinae H.Rob. in Smithsonian Contr. Bot. 89: 8. 1999
Lepidaploinae S.C.Keeley & H.Rob. in Funk, Susanna, Stuessy & Bayer, Syst. Evol. Biogeogr. Compositae: 450. 2009
Linziinae S.C.Keeley & H.Rob. in Funk, Susanna, Stuessy & Bayer, Syst. Evol. Biogeogr. Compositae: 451. 2009
Lychnophorinae Benth. in Bentham & Hooker f., Gen. Pl. 2: 165. 1873
Mesanthophorinae S.C.Keeley & H.Rob. in Funk, Susanna, Stuessy & Bayer, Syst. Evol. Biogeogr. Compositae: 451. 2009
Pacourininae H.Rob. in Proc. Biol. Soc. Wash. 112: 218. 1999
Piptocarphinae H.Rob., R.M.King & F.Bohlmann in Phytologia 46: 426. 1980
Rolandrinae Cass. ex Dumort., Anal. Fam. Pl.: 313. 1829
Sipolisiinae H.Rob. in Smithsonian Contr. Bot. 89: 13. 1999
Stokesiinae H.Rob. in Proc. Biol. Soc. Wash. 112: 216. 1999
Trichospirinae Less. in Linnaea 6: 690. 1831
Vernoniinae Cass. ex Dumort., Anal. Fam. Pl.: 313. 1829

XIV. Cichorioideae Chevall., Fl. Gen. Env. Paris 2: 531. 1828
29. Cichorieae Lam. & DC., Syn. Pl. Fl. Gall.: 255. 1806
Catananchinae K.Bremer in Novon 3: 329. 1993
Cichoriinae Cass. ex Dumort., Anal. Fam. Pl.: 30. 1829
Crepidinae 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
Scorzonerinae Cass. ex Dumort., Fl. Belg.: 63. 1827
Sonchinae K.Bremer in Novon 3: 329. 1993
Stephanomeriinae Stebbins in Madroño 12: 71. 1953
Warioniinae Gemeinholzer & N.Kilian in Funk, Susanna, Stuessy & Bayer, Syst. Evol. Biogeogr. Compositae: 380. 2009.

XV. Corymbioideae Panero & V.A.Funk in Proc. Biol. Soc. Wash. 115: 761. 2002
30. Corymbieae Panero & V.A.Funk in Phytologia 91: 568. 2009

XVI. Asteroideae Lindl. in Loudon, Encycl. Pl.: 1074. 1829

31. Calenduleae Cass. in J. Phys. Chim. Hist. Nat. Arts 88: 161. 1819

32a. Senecioneae Cass. in J. Phys. Chim. Hist. Nat. Arts 88: 195. 1819

Abrotanellinae H.Rob., G.D.Carr, R.M.King & A.M.Powell in Ann. Missouri Bot. Gard. 84: 896. 1998

Othoniinae Less. in Linnaea 6: 93. 1831

Senecioniinae Dumort., Fl. Belg.: 65. 1827

Tussilagininae Dumort., Fl. Belg.: 64. 1827

32b. Doroniceae Panero in Phytologia 87: 1. 2005

33. Anthemideae Cass. in J. Phys. Chim. Hist. Nat. Arts 88: 192. 1819

Anthemidinae Dumort., Fl. Belg.: 69. 1827

Artemisiinae Less. in Linnaea 5: 163. 1830

Athanasiinae Lindl. ex Pfeiff., Nomencl. Bot. 1(1): 323. 1873

Cotulinae Kitt., Taschenb. Fl. Deutschl., ed. 3: 684. 1853

Glebionidinae Oberpr. & Vogt in Willdenowia 37: 106. 2007

Handeliinae Bremer & Humphries in Bull. Nat. Hist. Mus. London, Bot. 23: 108. 1993

Leucantheminae Bremer & Humphries in Bull. Nat. Hist. Mus. London, Bot. 23: 136. 1993

Leucanthemopsidinae Oberpr. & Vogt in Willdenowia 37: 104. 2007

Matricariinae Willk. in Willkomm & Lange, Prodr. Fl. Hispan. 2: 92. 1865

Osmitopsidinae Oberpr. & Himmelr. in Willdenowia 37: 94. 2007

Pentziinae 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

Ursininae Bremer & Humphries in Bull. Nat. Hist. Mus. London. Bot. 23: 91. 1993

34. Astereae Cass. in J. Phys. Chim. Hist. Nat. Arts 88: 195. 1819

Asterinae Dumort., Fl. Belg.: 66. 1827

Astranthiinae G.L.Nesom in Sida 19: 265. 2000

Baccharidinae Less. in Linnaea 5: 145. 1830

Bellidinae Willk. in Willkomm & Lange, Prodr. Fl. Hispan. 2: 30. 1865

Boltoniinae G.L.Nesom in Sida 19: 266. 2000

Brachyscominae G.L.Nesom in Phytologia 76: 203. 1994

Chaetopappinae G.L.Nesom in Sida 19: 264. 2000

Chrysopsidinae G.L.Nesom in Phytologia 76: 203. 1994

Conyzinae Horan., Char. Ess. Fam.: 93. 1847

Grangeinae Benth. in Bentham & Hooker., Gen. Pl. 2: 176. 1873

Hinterhuberinae 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

Machaerantherinae G.L.Nesom in Phytologia 76: 208. 1994

Pentachaetinae G.L.Nesom in Sida 19: 264. 2000

Podocominae G.L.Nesom in Phytologia 76: 209. 1994

Solidagininae O.Hoffm. in Engler & Prantl, Nat. Pflanzenfam. 4(5): 145. 1890

Symphiotrichinae G.L.Nesom in Phytologia 76: 211. 1994

35. Gnaphalieae Lecoq & Juill., Dict. Rais. Term. Bot.: 296. 1831 (Smissen & al., in press)

Gnaphaliinae Dumort., Anal. Fam. Pl.: 31. 1829

Relhaniinae Less. in Linnaea 6: 232. 1831

36. Inuleae Cass. in J. Phys. Chim. Hist. Nat. Arts 88: 193. 1819 (Nylinder & Anderberg, 2015)

Inulinae Dumort., Fl. Belg.: 67. 1827

Plucheinae Cass. ex Dumort., Anal. Fam. Pl.: 31. 1829

37. Athroismeae Panero in Proc. Biol. Soc. Wash. 115: 768. 2002

Anisopappinae Panero in Phytologia 87: 5. 2005

Athroismeae Panero in Phytologia 87: 2. 2005
Centipedinae Panero in Phytologia 87: 3. 2005
Lowryanthinae Pruski & Anderb. in Taxon 66: 417. 2017
Symphyllocarpinae Smoljan. in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 20: 288. 1960
Anisochaeta DC., incertae sedis

"Heliantheae alliance"

38. Feddeeae Pruski, P.Herrera, Anderb. & Franc.-Ort. in Syst. Bot. 33: 199. 2008 [in or out of HA?]
39. Helenieae Lindl. in Loudon, Encycl. Pl.: 1074. 1829
    Gaillardiinae Less. in Linnaea 6: 516. 1831
    Marshalliinae H.Rob. in Phytologia 41: 42. 1978
    Psathyrotinae B.G.Baldwin in Syst. Bot. 25: 535. 2000
    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
    Dyscritothamninae Panero in Phytologia 87: 10. 2005
    Espeletiinae Cuatrec. in Phytologia 35: 48. 1976
    Galinsoginae Benth. in Bentham & Hooker, Gen. Pl. 2: 198. 1873
    Guardiolinae H.Rob. in Phytologia 41: 41. 1978
    Jaegeriinae Panero in Phytologia 87: 11. 2005
    Melampodiinae Less. in Linnaea 5: 149. 1830
    Milleriinae Benth. in Bentham & Hooker, Gen. Pl. 2: 166. 1873
41. Tageteae Cass. in J. Phys. Chim. Hist. Nat. Arts 88: 162. 1819
    Clappiinae H.Rob. in Phytologia 41: 39. 1978
    Coulterellinae H.Rob. in Phytologia 41: 40. 1978
    Flaveriinae Less., Syn. Gen. Compos.: 235. 1832
    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
    Arnicinae B.G.Baldwin in Syst. Bot. 27: 193. 2002
    Baeriinae Benth. in Bentham & Hooker, Gen. Pl. 2: 200. 1873
    Hulseinae B.G.Baldwin in Syst. Bot. 27: 194. 2002
    Madiinae Benth. in Bentham & Hooker, Gen. Pl. 2: 198. 1873
    Venegasiinae B.G.Baldwin in Syst. Bot. 27: 194. 2002
43. Chaenactideae B.G.Baldwin in Syst. Bot. 27: 192. 2002
44. Bahieae B.G.Baldwin in Syst. Bot. 27: 192. 2002
45. Perityleae B.G.Baldwin in Syst. Bot. 27: 192. 2002
    Galeaninae Panero & B.G.Baldwin in Kubitzki, Fam. Gen. Vasc. Pl. 8: 508. 2007
    Lycapsinae H.Rob. in Phytologia 46: 120. 1980
    Peritylinae Rydb. in Britton & al., N. Amer. Fl. 34 (4): 289. 1914
46. Eupatorieae Cass. in J. Phys. Chim. Hist. Nat. Arts 88: 202. 1819
    Adenostemmatinae B.L.Rob. in Proc. Amer. Acad. Arts 49: 435. 1913
    Ageratinae Less., Syn. Gen. Compos.: 155. 1832
    Alomiinae 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
    Eupatoriinae Dumort., Anal. Fam. Pl: 31. 1829

Fleischmanniinae R.M.King & H.Rob. in Phytologia 46: 447. 1980
Gyptidinae R.M.King & H.Rob. in Phytologia 46: 446. 1980
Hebecliniinae R.M.King & H.Rob. in Phytologia 46: 448. 1980
Hofmeisteriinae R.M.King & H.Rob. in Phytologia 46: 449. 1980
Liatrinae R.M.King & H.Rob. in Phytologia 46: 447. 1980
Mikaniinae R.M.King & H.Rob. in Phytologia 46: 448. 1980
Neomirandeinae R.M.King & H.Rob. in Phytologia 46: 448. 1980
Oaxacaniinae R.M.King & H.Rob. in Phytologia 46: 449. 1980
Oxylobinae R.M.King & H.Rob. in Phytologia 46: 449. 1980
Piqueriinae Benth. in Bentham & Hooker, Gen. Pl. 2: 172. 1873
Praxelinae R.M.King & H.Rob. in Phytologia 46: 448. 1980
Trichocoroninae R.M.King & H.Rob. in Phytologia 46: 446. 1980
Trichogoniinae V.L.Rivera, S.C.Ferreira & Panero in Phytotaxa 260: 298. 2016

47. Neurolaeneae Rydb. in Britton & al., N. Amer. Fl. 34(4): 303. 1927
Enydrinae H.Rob. in Phytologia 41: 398. 1979
Heptanthinae H.Rob. in Phytologia 41: 41. 1978
Neurolaeninae Stuessy, B.L.Turner & A.M.Powell in Heywood, Harborne & Turner, Biol. Chem. Compositae: 645. 1977

48. Coreopsideae Lindl. in Loudon, Encycl. Pl.: 1074. 1829.
Coreopsidinae Cass. ex Dumort., Anal. Fam. Pl.: 31. 1829
Chrysanthellinae Ryding & K.Bremer in Syst. Bot. 17: 650. 1992
Pinillosiinae H.Rob. in Phytologia 41: 42. 1978

49. Polymnieae Panero in Proc. Biol. Soc. Wash. 115: 770. 2002

50. Heliantheae Cass. in J. Phys. Chim. Hist. Nat. Arts 88: 189. 1819
Ambrosiinae Less. in Linnaea 5: 151. 1830
Chromolepidinae Panero in Phytologia 87: 5. 2005
Clibadiinae H.Rob. in Phytologia 41: 39. 1978
Dugesiinae Panero in Phytologia 87: 7. 2005
Ecliptinae Less. in Linnaea 6: 153. 183
Enceliinae Panero in Phytologia 87: 8. 2005
Engelmanniinae Stuessy in Heywood, Harborne & Turner, Biol. Chem. Compositae: 645. 1977
Gaillardiinae Nutt., Gen. N. Amer. Pl. 2: 177. 1818 [“Galardieae”]
Helianthinae Dumort., Fl. Belg.: 71. 1827
Montanoinae H.Rob. in Phytologia 41: 40. 1978
Rojasianthinae Panero in Proc. Biol. Soc. Wash. 115: 771. 2002
Rudbeckiinae H.Rob. in Phytologia 41: 43. 1978
Spilanthinae Panero in Phytologia 87: 9. 2005
Verbesiniinae Benth. in Bentham & Hooker, Gen. Pl. 2: 193. 1873
Zaluzaniinae H.Rob. in Phytologia 41: 44. 1978
Zinniinae Benth. in Bentham & Hooker, Gen. Pl. 2: 193. 1873

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 Dicomoideae 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.,

2009). 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 yellow in Cichorieae, while it is 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 Arctotideae. 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 carpopodium, 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.

Dicomoideae S.Ortiz, **subfam. nov.** – Type: *Dicoma* Cass. in Bull. Sci. Soc. Philom. Paris 1817: 12. 1817

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 carpopodium.

Includes the genera *Cloiselia* S.Moore, *Dicoma* Cass., *Dicomopsis* S.Ortiz, *Erythrocephalum* Benth., *Gladiopappus* Humbert, *Macledium* Cass., *Pasaccardoa* Kuntze, and *Pleiotaxis* Steetz.

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,

https://orcid.org/0000-0002-0124-2453

LITERATURE CITED

Anderberg, A.A, Baldwin, B.G., Bayer, R.J., Breitwieser, I., Jeffrey, C., Dillon, M.O., Eldenäs, P., Funk, V.A., Garcia-Jacas, N., Hind, D.J.N., Karis, P.O., Lack, H.W., Nesom, G., Nordenstam, B., Oberprieler, C., Panero, J.L., Puttock, C., Robinson, H., Stuessy, T.F., Susanna, A., Urtubey, E., Vogt, R., Ward, J. & Watson, L.E. 2007. Compositae. Pp. 61–588 in: Kadereit, J.W. & Jeffrey, C. (eds.), *The families and genera of vascular plants*, vol. xx. Berlin, Heidelberg: Springer.

Funk, V.A., Susanna, A., Stuessy, T.F. & Bayer, R.J. 2009. *Systematics, evolution, and biogeography of Compositae*. Vienna: IAPT.

Herrando-Moraira, S., Calleja, J.A., Galbany-Casals, M., Garcia-Jacas, N., Liu, J.-Q., López-Alvarado, J., López-Pujol, J., Mandel, J.R., Massó, S. & Montes-Moreno, N. 2019. Nuclear and plastid DNA phylogeny of tribe Cardueae (Compositae) with Hyb-Seq data: A new subtribal classification and a temporal diversification framework. *Molec. Phylogen. Evol.* 137: 313–332. https://doi.org/10.1016/j.ympev.2019.05.001

Lee, J. & Baldwin, B.G. 2004. Subtribes of principally North American genera of Cichorieae (Compositae). *Novon* 14(3): 309–313. https://www.jstor.org/stable/3393289

Mandel, J.R., Dikow, R.B., Funk, V.A., Masalia, R.R., Staton, S.E., Kozik, A., Michelmore, R.W., Rieseberg, L.H. & Burke, J.M. 2014. A target enrichment method for gathering phylogenetic information from hundreds of loci: An example from the Compositae. *Applic. Pl. Sci.* 2: 1300085. https://doi.org/10.3732/apps.1300085

Mandel, J.R., Dikow, R.B. & Funk,V.A. 2015. Using phylogenomics to resolve mega-families: An example from Compositae. *J. Syst. Evol.* 53: 391–402. https://doi.org/10.1111/jse.12167

Mandel, J.R., Barker, M., Bayer, R.J., Dikow, R., Gao, T.-G., Jones, K., Keeley, S., Kilian, N., Ma, H., Siniscalchi, C., Susanna, A., Watson, L., Thapa, R. & Funk, V.A. 2017. The Compositae Tree of Life in the age of phylogenomics. *J. Syst. Evol.* 55: 405–403. https://doi.org/10.1111/jse.12265

Mandel, J.R., Dikow, R.B., Siniscalchi, C.M., Thapa, R., Watson, L.E. & Funk, V.A. 2019. A fully resolved backbone phylogeny reveals numerous dispersals and explosive diversifications throughout the history of Asteraceae. *Proc. Natl. Acad. Sci. U.S.A.* 116: 14083–14088. https://doi.org/10.1073/pnas.1903871116

Nylinder, S. & Anderberg, A.A. 2015. Phylogeny of the Inuleae (Asteraceae) with special emphasis on the Inuleae–Plucheinae. *Taxon* 64: 110–130. https://doi.org/10.12705/641.22

Ortiz, S., Carbajal, R., Serrano, M., Rodríguez-Oubiña, J. & Iglesias, I. 2013. Phylogeny of the African Mutisieae s.l. (Asteraceae) based on *ndhF* and *trnL-F* sequences (cpDNA). *Taxon* 62: 525–536. https://doi.org/10.12705/623.11

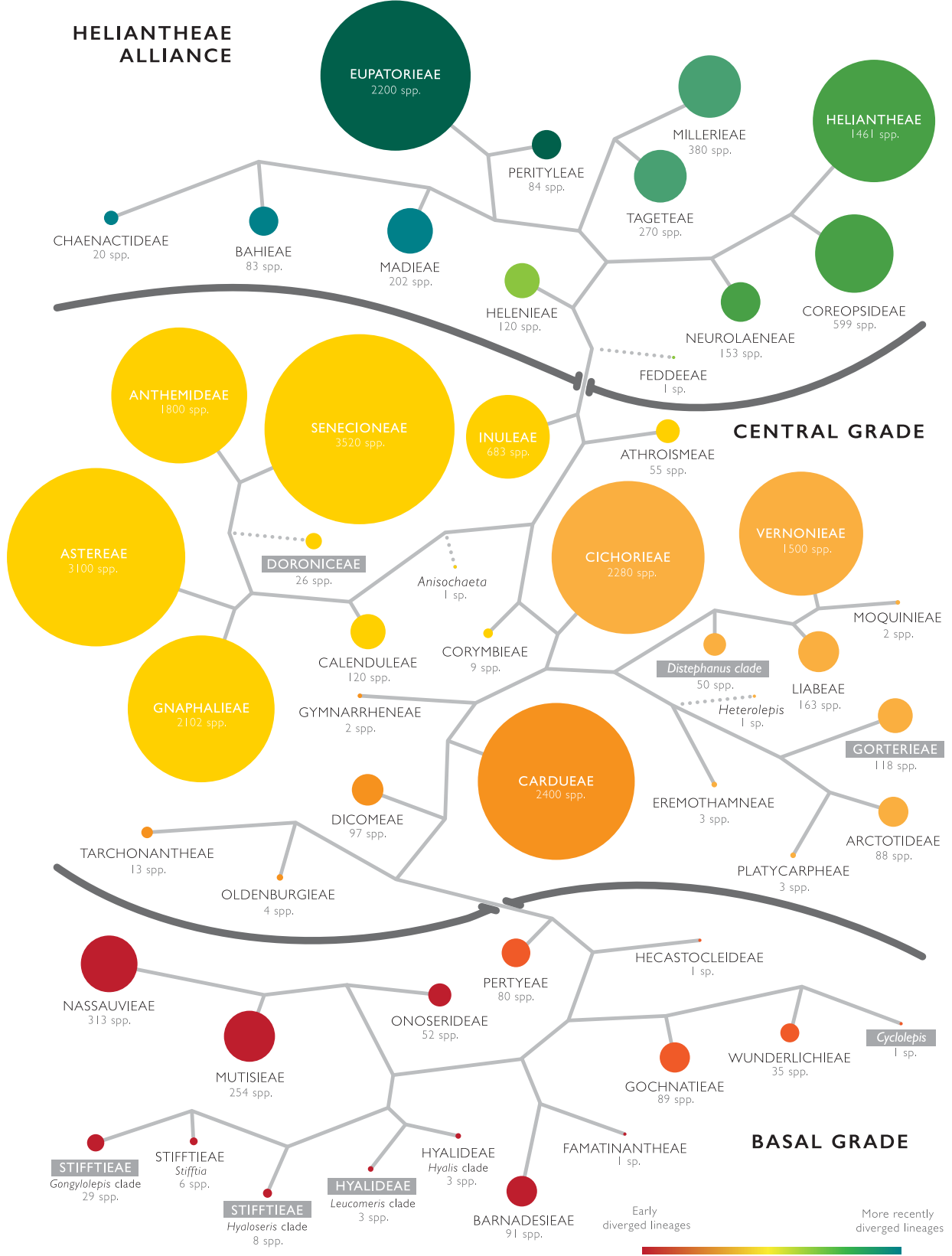
Reveal, J.L. 1997. Early suprageneric names in Asteraceae. *Compositae Newslett.* 30: 29–45.

Smissen, R., Bayer, R.J., Bergh, N.G., Breitwieser, I., Freire, S.E., Galbany-Casals, M., Schmidt-Lebuhn, A.N. & Ward, J.M. In press. A revised subtribal classification of Gnaphalieae (Asteraceae). *Taxon*.

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.


HELIANTHEAE ALLIANCE
EUPATORIEAE
2200 spp.
PERITYLEAE
84 spp.
MILLERIEAE
380 spp.
HELIANTHEAE
1461 spp.
TAGETEAE
270 spp.
CHAENACTIDEAE
20 spp.
BAHIEAE
83 spp.
MADIEAE
202 spp.
HELENIEAE
120 spp.
NEUROLAENEAE
153 spp.
COREOPSIDEAE
599 spp.
FEDDEEAE
1 sp.
ANTHEMIDEAE
1800 spp.
SENECIONEAE
3520 spp.
INULEAE
683 spp.
ATHROISMEAE
55 spp.
CENTRAL GRADE
ASTEREAE
3100 spp.
DORONICEAE
26 spp.
Anisochaeta
1 sp.
CICHORIEAE
2280 spp.
VERNONIEAE
1500 spp.
MOQUINIEAE
2 spp.
CALENDULEAE
120 spp.
CORYMBIEAE
9 spp.
Distephanus clade
50 spp.
LIABEAE
163 spp.
GNAPHALIEAE
2102 spp.
GYMNARRHENEAE
2 spp.
Heterolepis
1 sp.
GORTERIEAE
118 spp.
CARDUEAE
2400 spp.
EREMOTHAMNEAE
3 spp.
DICOMEAE
97 spp.
ARCTOTIDEAE
88 spp.
TARCHONANTHEAE
13 spp.
PLATYCARPHEAE
3 spp.
OLDENBURGIEAE
4 spp.
HECASTOCLEIDEAE
1 sp.
PERTYEAE
80 spp.
NASSAUVIEAE
313 spp.
ONOSERIDEAE
52 spp.
MUTISIEAE
254 spp.
WUNDERLICHIEAE
35 spp.
Cyclolepis
1 sp.
GOCHNATIEAE
89 spp.
BASAL GRADE
STIFFTIEAE
Gongylolepis clade
29 spp.
STIFFTIEAE
Stifftia
6 spp.
HYALIDEAE
Hyalis clade
3 spp.
FAMATINANTHEAE
1 sp.
STIFFTIEAE
Hyaloseris clade
8 spp.
HYALIDEAE
Leucomeris clade
3 spp.
BARNADESIEAE
91 spp.
Early diverged lineages
More recently diverged lineages