

REVISED SUBTRIBAL CLASSIFICATION OF ASTEREAЕ (ASTERACEAE)

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ABSTRACT

In the classification proposed here, tribe Astereae includes 252 genera, arranged in 36 subtribes. Twenty (20) new subtribes are described: **Afroasterinae**, **Celmisiinae**, **Chamaegerinae**, **Chiliotrichinae**, **Denekiinae**, **Doellingeriinae**, **Egletinae**, **Eschenbachiinae**, **Formaniinae**, **Geissolepinae**, **Gutierrezinae**, **Ionactinae**, **Iranoasterinae**, **Oclemeninae**, **Oritrophiinae**, **Madagasterinae**, **Mairiinae**, **Nannoglottidinae**, **Printziinae**, and **Pteroniinae**. Six new combinations at specific rank are made: **Eschenbachia gouanii** (L.) Nesom, **comb. nov.**, **Eschenbachia subscaposa** (O. Hoffm.) Nesom, **comb. nov.**, **Eschenbachia tigrens** (Oliv. & Hiern.) Nesom, **comb. nov.**, and **Eschenbachia ulmifolia** (Burm. f.) Nesom, **comb. nov.**; **Psiadia ageratoides** (DC.) Nesom, **comb. nov.** and **Psiadia humilis** (Humbert) Nesom, **comb. nov.**

Earlier subtribal arrangements for Astereae (Zhang & Bremer 1993; Bremer 1994; Nesom 1994a; Nesom & Robinson 2007) were based mostly on morphology, predating a surge of molecular-taxonomic studies that show that the earlier classifications were often far from the mark. Many groups were polyphyletic and relatively smaller natural groups often were misplaced or proved to be more phyletically isolated than thought. Geographic proximity, in particular, has proved to be a more effective indicator of evolutionary relationship than recognized previously.

As part of the development of an updated account of Astereae genera (CWG 2020; Nesom 2020a), a subtribal arrangement is useful in conceptualizing patterns of evolutionary relationships and facilitating reference to groups of genera and species. The taxonomy presented here draws from molecular studies and hopefully aids in summarizing those studies as well as providing as a hypothetical taxonomic framework. Generic boundaries in many species groups remain to be clearly delimited and new genera remain to be described. Polyphyletic or otherwise non-monophyletic subgroups are indicated in the classification.

The concept of subtribe used here is subjective. Distinctive and evolutionarily isolated genera, especially those in primitive positions, are treated as monotypic subtribes. Some groups of genera are morphologically coherent and are given subtribal rank. On the other hand, some subtribes recognized here comprise morphologically diverse groups that would not have been seen as monophyletic except for the molecular data — subtribes segregated from these might justifiably be recognized.

Major lineages or groups of Astereae are indicated on Figure 1:

Basal grade, including isolated genera, the South American-Oceania group of Chiliotrichinae/Celmisiinae/Oritrophiinae, the mainly African Homochrominae/Pteroniinae and Eschenbachiinae, and the group of woody genera from Madagascar (Madagasterinae).

Bellis lineage, including the Eurasian Bellidinae and Chamaegerinae and the primarily African Grangeinae.

Aster lineage, including the Asian Asterinae and major Australian-Oceania groups (Lagenophorinae, and Brachyscominae — the relative positions of these four groups are unresolved, even though they are specified (speculatively) in Fig. 1). Figure 2 summarizes hypothetical relationships among the genera and groups of Asterinae.

Baccharis lineage, including the mostly South American Baccharidinae, Podocominae, and Hinterhuberinae, merged here into a single subtribe, Baccharidinae. Sister to the North American lineage. Figure 3 summarizes hypothetical relationships among genera and groups of Baccharidinae.

North American lineage, including the diverse array of subtribes that radiated mostly in Mexico and the USA, with some groups spreading into South America.

Table 1 gives an alphabetical list of the Astereae subtribes with the linear sequence number for each. Table 2 lists all genera of Astereae accepted here, with the subtribal assignment for each.

Construction of the phylogenetic diagrams

The phylogenetic diagrams (Figs. 1–3) might be thought of as intuitively constructed consensus trees, summarizing published phylogenetic analyses based on DNA sequence data. They are working hypotheses. The diagram position of some taxa is speculative, reflecting a subjective choice from among ambiguous placements in molecular phylogenies. Species included in molecular analyses are indicated in the classification within square brackets. Species and genera not included in molecular analyses are placed on the basis of morphology and geography.

Published molecular analyses of Astereae vary widely in the genera and species included, and phylogenetic patterns indicated among various cladograms are often obscure. The series of cladograms published by Brouillet et al. (2009) is the most complete in providing an overview of the whole tribe, but many additional studies have been published subsequently and these additional insights have been considered.

Subtribes in the linear classification are numbered consecutively and mostly arranged alphabetically within major geographic regions — North America/Central America, South America, Oceania, Eurasia, and Africa/Madagascar/SE Asia. The linear arrangement is not intended to show relationships among subtribes. In Figures 1 and 2, the number for each subtribe matches that in the consecutive numbering of the linear arrangement.

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LITERATURE CITED

- Anderberg, A.A. et al. 2007. Compositae. Pp. 61–636, in J.W. Kadereit and C. Jeffrey (eds.). Families and Genera of Vascular Plants, Vol. VIII. Flowering Plants, Eudicots, Asterales. Springer.
- Bayer, R.J. and E.W. Cross. 2002. A reassessment of tribal affinities of the enigmatic genera *Printzia* and *Isoetopsis* (Asteraceae), based on three chloroplast sequences. Austral. J. Bot. 50: 677–686.
- Bean, A.R. 2020. A taxonomic revision of *Camptacra* N.T. Burb. (Asteraceae: Astereae). Austrobaileya 10: 564–575.
- Beck, J.B. et al. 2004. Is subtribe Solidagininae (Asteraceae) monophyletic? Taxon 53: 691–698.
- Beuzenberg, E.J. and J.B. Hair. 1984. Contributions to a chromosome atlas of the New Zealand flora—27 Compositae. New Zealand J. Bot. 22: 353–356.
- Bello, A.O., J.S. Boatwright, M. Van der Bank, and A.R. Magee. 2020. Four new species of *Pteronia* (Astereae, Asteraceae) from South Africa. Phytotaxa 430: 25–32.
- Bonifacino, J. 2008. Reinstatement of *Ocyroe* (Compositae: Astereae). Brittonia 60: 205–212.
- Bonifacino, J. 2009. Taxonomic revision of the *Chilotrichum* group sensu stricto (Compositae: Astereae). Smithson. Contr. Bot. 92: 1–118.
- Bonifacino, J. and G. Sancho. 2004. *Guynesomia* (Asteraceae, Astereae), a new genus from central Chile. Taxon 53: 673–678.

- Bonifacino, J. and V. Funk. 2012. Phylogenetics of the *Chiliotrichum* group (Compositae: Astereae): The story of the fascinating radiation in the paleate Astereae genera from southern South America. *Taxon* 61: 180–196.
- Bremer, K. 1994. *Asteraceae. Cladistics & Classification*. Timber Press, Portland, Oregon.
- Brouillet, L., T.K. Lowrey, L. Urbatsch, V. Karaman-Castro, G. Sancho, S.J. Wagstaff, and J.C. Semple. 2009. Astereae. Pp. 589–629, in V.A. Funk et al. (eds.). *Systematics, Evolution, and Biogeography of Compositae*. International Association for Plant Taxonomy, Vienna.
- Callmänder, M.W. and P.B. Phillipson. 2011. The genus *Vernoniopsis* Humbert (Asteraceae) in Madagascar. *Candollea* 66: 409–412.
- Chen, Y and L. Brouillet. 2011. *Eschenbachia*. Pp. 555–558, in *Flora of China*, Vol. 20-21. Science Press (Beijing) and Missouri Botanical Garden Press (St. Louis).
- Compositae Working Group (CWG). 2020. Global Compositae Database. <<https://www.compositae.org/index.php>> Accessed June 2020.
- Cross, E.W., C.J. Quinn, and S.J. Wagstaff. 2002. Molecular evidence for the polyphyly of *Olearia* (Astereae: Asteraceae). *Pl. Syst. Evol.* 235: 99–120.
- Cuatrecasas, J. 1986. Un género nuevo de Astereae, Compositae, de Colombia. *Anales Jard. Bot. Madrid* 42: 415-426.
- Denda, T., K. Watanabe, K. Kosuge, T. Yahara, and M. Ito. 1999. Molecular phylogeny of *Brachycome* (Asteraceae). *Pl. Syst. Evol.* 217: 299–311.
- Eastwood, A., M. Gibby, and Q.C.B. Cronk. 2004. Evolution of St. Helena arborescent Astereae (Asteraceae): Relationships of the genera *Commidendrum* and *Melanodendron*. *Bot. J. Linn. Soc.* 144: 69–83.
- Farhani, A., S. Kazempour-Osaloo, H. Zare-Maivan, and V. Mozaffarian. 2018. Evolutionary history of the tribe Astereae in the Flora Iranica area: Systematic implications. *Phytotaxa* 379: 95–117.
- Fayed, A. 1979. Revision der Grangeinae (Asteraceae-Astereae). *Mitt. Bot. Staats. Munchen* 15: 425–576.
- Field, B.L., A. Houben, J.N. Timmis, and C.R. Leach. 2006. Internal transcribed spacer sequence analyses indicate cytoevolutionary patterns within *Brachycome* Cass. (Asteraceae). *Pl. Syst. Evol.* 259: 39–51.
- Fiz-Palacios, O., V. Valcárcel, and P. Vargas. 2002. Phylogenetic position of Mediterranean Astereae and character evolution of daisies (*Bellis*, Asteraceae) inferred from nrDNA ITS sequences. *Molec. Phylogen. Evol.* 25: 157–171.
- Fu, Z.X., G.-J. Zhang, Y.-Z. Shao, Y.-Y. Liu, X.-C. Yang, T.-G. Gao, and X. Tian. 2019. Rediscovery of *Aster polius* (Astereae: Asteraceae), a rare and endemic species from China, after one century. *Phytotaxa* 423: 247–258.
- Heads, M. 1998. Biodiversity in the New Zealand divaricating tree daisies: *Olearia* sect. nov. (Compositae). *Bot. J. Linn. Soc.* 127: 239–285.
- Heenan, P.B., P.J. de Lange, G.J. Houlston, A. Barnaud, and B.G. Murray. 2008. *Olearia telmatica* (Asteraceae; Astereae), a new tree species endemic to the Chatham Islands. *New Zeal. J. Bot.* 46: 567–583.
- Heiden, G., A. Antonelli, and J.R. Pirani. 2019. A novel phylogenetic infrageneric classification of *Baccharis* (Asteraceae: Astereae), a highly diversified American genus. *Taxon* 68: 1048–1081.
- Herman, P.P.J. and U. Zinnecker-Wiegand. 2016. A taxonomic revision of the genus *Mairia* (Asteraceae, Astereae) in South Africa. *South African J. Bot.* 105: 45–60.
- Humbert, H. 1960. *Composées*. *Fl. Madagascar Comores* 189. Tome I. Muséum National d'Histoire Naturelle, Paris.
- Jafari, F., S.K. Osaloo, and V. Mozffarian. 2015. Molecular phylogeny of the tribe Astereae (Asteraceae) in SW Asia based on nrDNA ITS and cpDNA *psbA-trnH* sequences. *Willdenowia* 45: 77–92.
- Karaman-Castro, V. and L.E. Urbatsch. 2009. Phylogeny of *Hinterhubera* and related genera (Hinterhuberinae: Astereae) based on the nrDNA ITS and ETS sequences. *Syst. Bot.* 34: 805–817.
- Karanović, D., J. Luković, L. Zorić, G. Anačkov, and P. Boža. 2015. Taxonomic status of *Aster*, *Galatella* and *Tripolium* (Asteraceae) in view of anatomical and micro-morphological evidence. *Nordic J. Bot.* 33: 484-497.

- Klingenberg, L. 2007. Monographie der südamerikanischen Gattungen *Haplopappus* Cass. und *Notopappus* L. Klingenberg (Asteraceae-Astereae). *Bibl. Bot.* 157: 1–331.
- Kolberg, H. and M. Van Slageren. 2014. A synopsis of the genus *Pteronia* (Compositae: Astereae) in Namibia including the resurrection of *Pteronia quadrifaria*. *Kew Bull.* 69: 1–44.
- Korolyuk, E.A. 1997. Structure of seed surfaces of the subtribe Asterinae (Asteraceae) from Siberia. *Bot. Zh.* 82: 29–34 (in Russian).
- Korolyuk, E.A. 1999. The subtribe Asterinae O. Hoffm. (Asteraceae Dumort.) in Siberia (taxonomy, khorology). *Disser.*: 03.00.05 (in Russian).
- Korolyuk, E., A. Makunin, and T. Matveeva. 2015. Relationships and generic delimitation of Eurasian genera of the subtribe Asterinae (Astereae, Asteraceae) using molecular phylogeny of ITS. *Turk. J. Bot.* 39: 808–824.
- Koster, J. Th. 1952. Notes on Malay Compositae III. *Blumea* 7: 288–291.
- Lander, N.S. 2013. *Pilbara*, a new genus of Asteraceae (tribe Astereae) from Western Australia. *Nuytsia* 23: 117–123.
- Lane, M.A., D.R. Morgan, Y. Suh, B.B. Simpson, and R.K. Jansen. 1996. Relationships of North American genera of Astereae, based on chloroplast DNA restriction site data. Pp. 49–77, *in* D.J.N. Hind and H.J. Beentje (eds.). *Compositae: Systematics. Vol. 1, Proc. Interntl. Compositae Conf., Kew, 1994.*
- Li, W.-P., F.-S. Yang, T. Jivkova, and G.-S. Yin. 2012. Phylogenetic relationships and generic delimitation of Eurasian *Aster* (Asteraceae: Astereae) inferred from ITS, ETS and *trnL-F* sequence data. *Ann. Bot.* 109: 1341–1357.
- Li, W.-P., F.-M. Qian, X.-L. Yang, and S.-M. Chen. 2014. Systematic position of *Cyathocline* Cass. (Asteraceae): Evidences from molecular, cytological and morphological data. *Pl. Syst. Evol.* 300: 595–606.
- Li, Z., G.-S. Yin, M. Tang, and W.-P. Li. 2017. *Aster oliganthus* (Asteraceae, Astereae), a new species from western Sichuan, China, based on morphological and molecular data. *Phytotaxa* 326: 54–62.
- Lippert, W. 1973. Revision der Gattung *Aster* in Afrika. *Mitt. Bot. Munchen* 11: 153–258.
- Liu, J.Q., T.-G. Gao, Z.-D. Chen, and A.-M. Lu. 2002. Molecular phylogeny and biogeography of the Qinghai-Tibet Plateau endemic *Nannoglottis* (Asteraceae). *Molec. Phylog. Evol.* 23: 307–25.
- Lowrey T.K. 1995. Phylogeny, adaptive radiation, and biogeography of Hawaiian *Tetramolopium* (Asteraceae, Astereae). Pp. 195–220, *in* W.L. Wagner and V.A. Funk (eds.). *Hawaiian Biogeography.* Smithsonian Inst. Press, Washington, D.C.
- Lowrey, T.K., C.J. Quinn, R.K. Taylor, R. Chan, R.T. Kimball, and J.C. De Nardi. 2001. Molecular and morphological reassessment of relationships within the *Vittadinia* group of Astereae (Asteraceae). *Amer. J. Bot.* 88: 1279–1289.
- Messina, A., N.G. Walsh, S.E. Hoebee, and P.T. Green. 2014. A revision of *Olearia* section *Asterotriche* (Asteraceae: Asterae). *Austral. Syst. Bot.* 27: 199–240.
- Morgan, D.R. and B.B. Simpson. 1992. A systematic study of *Machaeranthera* (Asteraceae) and related groups using restriction site analysis of chloroplast DNA. *Syst. Bot.* 17: 511–531.
- Mozaffarian, V. 1996. Studies on the flora of Iran, new species, new combinations and new records. *Iran. J. Bot.* 7: 127–142.
- Nakamura, K., T. Denda, G. Kokubugata, P.I. Forster, G. Wilson, C.-I. Peng, and M. Yokota. 2012. Molecular phylogeography reveals an amphitropical distribution and local diversification of *Solenogyne* (Asteraceae) in the Ryukyu Archipelago of Japan and Australia. *Biol. J. Linn. Soc.* 105: 197–217.
- Nesom, G.L. 1991a. A phylogenetic hypothesis for the goldenasters (Asteraceae: Astereae). *Phytologia* 71: 136–151.
- Nesom, G.L. 1991b. Morphological definition of the *Gutierrezia* group (Asteraceae: Astereae). *Phytologia* 71: 252–262.
- Nesom, G.L. 1993. *Madagaster* (Asteraceae: Astereae), a new genus of subtribe Hinterhuberinae. *Phytologia* 75: 94–99.
- Nesom, G.L. 1994a. Subtribal classification of the Astereae (Asteraceae). *Phytologia* 76: 193–274.

- Nesom, G.L. 1994b. Review of the taxonomy of *Aster* sensu lato (Asteraceae: Astereae), emphasizing the New World species. *Phytologia* 77: 141–297.
- Nesom, G.L. 2018a. *Bathysanthus sinforosa* (Asteraceae, Astereae), a new genus and species from southern Chihuahua. *Phytoneuron* 2018-37: 1–9.
- Nesom, G.L. 2018b. Notes on *Stenotus* and *Nestotus* (Asteraceae: Astereae). *Phytoneuron* 2018-44: 1–19.
- Nesom, G.L. 2018c. *Aquilula* (Asteraceae: Astereae), a new genus for *Ericameria riskindii*. *Phytoneuron* 2018-24: 1–11.
- Nesom, G.L. 2020a. *Toiyabea* (Asteraceae: Astereae) enlarged to include four species. *Phytoneuron* 2020-10: 1–26.
- Nesom, G.L. 2020b. Taxonomic decisions at generic rank in tribe Astereae (Asteraceae) for the Global Compositae Database. *Phytoneuron* 2020-24: 1–6.
- Nesom, G.L. 2020c. *Helodeaster*, a new genus for Hawaiian *Keysseria* (Asteraceae: Astereae). *Phytoneuron* 2020-54: 1–6.
- Nesom, G.L. 2020d. *Kitamuraia*, a new monotypic genus for *Aster glehnii* (Asteraceae: Astereae). *Phytoneuron* 2020-55: 1–11.
- Nesom, G.L. 2020e. The genus *Aster* (Asteraceae) in the strictest sense. *Phytoneuron* 2020-56: 1–22.
- Nesom, G.L. 2020f. *Yonglingia*, *Chaochienchangia*, and *Sinobouffordia* (Asteraceae: Astereae), new genera segregated from *Aster* in China. *Phytoneuron* 2020-57: 1–25.
- Nesom, G.L. 2020g. *Metamyriactis* (Asteraceae, Astereae), a new genus of southeast Asian asters. *Phytoneuron* 2020-58: 1–35.
- Nesom, G.L. 2020h. *Chlamydites* (Asteraceae: Astereae) revived. *Phytoneuron* 2020-59: 1–14.
- Nesom, G.L. 2020i. *Cordiofontis* (Asteraceae: Astereae), a new genus of Himalayan species segregated from *Aster*. *Phytoneuron* 2020-60: 1–20.
- Nesom, G.L. 2020j. *Cardiagyris* (Asteraceae: Astereae), a new genus for the *Doellingeria*-like species of Asia. *Phytoneuron* 2020-61: 1–26.
- Nesom, G.L. 2020k. Lectotypification of *Heterochaeta* DC. (Asteraceae). *Phytoneuron* 2020-62: 1.
- Nesom, G.L. 2020l. *Tibetiodes* Nesom, gen. nov. (Asteraceae: Astereae), including 27 species of Himalayan *Aster*. *Phytoneuron* 2020-63: 1–30.
- Nesom, G.L. 2020m. New genera from Asian *Aster* (Asteraceae: Astereae). *Phytoneuron* 2020-64: 1–44.
- Nesom, G.L. 2020n. New genera from Australian *Olearia* (Asteraceae: Astereae). *Phytoneuron* 2020-65: 1–94.
- Nesom, G.L., Y. Suh, D.R. Morgan, and B.B. Simpson. 1990. *Xylothamia* (Asteraceae: Astereae), a new genus related to *Euthamia*. *Sida* 14: 101–116.
- Nesom, G.L. and H.E. Robinson. 2007. Astereae. Pp. 284–342, in J.W. Kadereit and C. Jeffrey (eds.). *The Families and Genera of Vascular Plants*, Vol.8. Springer, Berlin.
- Noyes, R.D. 2000. Biogeographical and evolutionary insights on *Erigeron* and allies (Asteraceae) from ITS sequence data. *Pl. Syst. Evol.* 220: 93–114.
- Noyes, R.D. and L.H. Rieseberg. 1999. ITS sequence data support a single origin for North American Astereae (Asteraceae) and reflect deep geographic divisions in *Aster* s.l. *Amer. J. Bot.* 86: 398–412.
- Pruski, J.F. 2011. Studies of Neotropical Compositae–III. *Dichrocephala integrifolia* (Astereae: Grangeinae) in Guatemala, an exotic genus and species new to the Americas. *Phytoneuron* 2011-65: 1–9.
- Pruski, J.F. 2017. Compositae of Central America–IX. *Talamancaster* (Astereae), a new grangeoid genus from Guatemala, Costa Rica, Panama, and Venezuela. *Phytoneuron* 2017-61: 1–35.
- Roberts, R.P. 2002. Phylogeny of *Ericameria*, *Chrysothamnus* and related genera (Asteraceae: Astereae) based on nuclear ribosomal DNA sequence data. Ph.D. diss., Louisiana State Univ., Baton Rouge.
- Roberts, R.P. and L.E. Urbatsch. 2003. Molecular phylogeny of *Ericameria* (Asteraceae, Astereae) based on nuclear ribosomal 3' ETS and ITS sequence data. *Taxon* 52: 209–228.
- Roberts, R.P. and L.E. Urbatsch. 2004. Molecular phylogeny of *Chrysothamnus* (Asteraceae, Astereae) based on nuclear ribosomal 3' ETS and ITS sequence data. *Syst. Bot.* 29: 199–215.

- Roberts, R.P., L.E. Urbatsch, and K.M. Neubig. 2005. *Nestotus* and *Toiyabea*, two new genera of Asteraceae: Astereae from the western United States and Canada. *Sida* 21: 1647–1655.
- Saldivia, P., L. Faúndez, A. Marticorena, and J.L. Panero. 2014. *Kieslingia chilensis* (Asteraceae: Astereae), a new genus and species from northern Chile. *Phytotaxa* 177: 280–290.
- Saldivia, P., O.M. Vargas, D.A. Orlovich, and J.M. Lord. 2019. Nomenclatural priority of the genus *Linochilus* over *Piofontia* (Asteraceae: Astereae). *Phytotaxa* 424: 158–166.
- Saldivia, P., K.R. Wood, D.A. Orlovich, and J.M. Lord. 2020. *Pacifigeron indivisus* (Asteraceae: Astereae), a new species endemic to Rapa, Austral Islands, and a new delimitation of the *Celmisia* group. *Phytotaxa* 442: 239–266.
- Sancho, G. 2012. *Exostigma*, a new genus of Astereae (Compositae) from southern South America. *Syst. Bot.* 37: 516–524.
- Sancho, G. and V. Karaman-Castro. 2008. A phylogenetic study in American Podocominae (Asteraceae: Astereae) based on morphological and molecular data. *Syst. Bot.* 33: 762–775.
- Sancho, G., D.J.N. Hind, and J.F. Pruski. 2010. Systematics of *Podocoma* (Asteraceae: Astereae): A generic reassessment. *Bot. J. Linn. Soc.* 163: 486–513.
- Sancho, G., P.J. de Lange, M. Donato, J. Barkla, and S.J. Wagstaff. 2015. Late Cenozoic diversification of the austral genus *Lagenophora* (Astereae, Asteraceae). *Bot. J. Linn. Soc.* 177: 78–95.
- Scott, A.J. 1991. Notes on Compositae-Astereae for the 'Flore des Mascareignes.' *Kew Bull.* 46: 339–353.
- Shin, H., S.-H. Oh, Y. Lim, C.-W. Hyun, S.-H. Cho, Y.-I. Kim, and Y.-D. Kim. 2014. Molecular evidence for hybrid origin of *Aster chusanensis*, an endemic species of Ulleungdo, Korea. *J. Plant Biol.* 57: 174–185.
- Short, P.S. 2014a. A taxonomic review of *Brachyscome* Cass. s. lat. (Asteraceae: Astereae), including descriptions of a new genus, *Roebuckia*, new species and new infraspecific taxa. *J. Adelaide Bot. Gard.* 28: 1–219.
- Short, P.S. 2014b. Three new genera of Australian Astereae (Asteraceae). *Muelleria* 20: 53–66.
- Strijk, J.S., R.D. Noyes, D. Strasberg, C. Cruaud, F. Gavory, M.W. Chase, R.J. Abbott, and C. Thébaud. 2013. In and out of Madagascar: Dispersal to peripheral islands, insular speciation and diversification of Indian Ocean daisy trees (*Psiadia*, Asteraceae). *PLoS One* 8(8).
- Suh, Y. 1989. Phylogenetic studies of North American Astereae (Asteraceae) based on chloroplast DNA. Ph.D. dissertation, Univ. of Texas, Austin.
- Suh, Y. and B.B. Simpson. 1990. Phylogenetic analysis of chloroplast DNA in North American *Gutierrezia* and related genera (Asteraceae: Astereae). *Syst. Bot.* 15: 660–670.
- Swenson, U. and K. Bremer. 1994. The genus *Lagenocypselia* (Asteraceae, Astereae) in New Guinea. *Austral. J. Bot.* 7: 265–273.
- Turner, B.L. 1970. Chromosome numbers in the Compositae. XII. Australian species. *Amer. J. Bot.* 57: 382–389.
- Urbatsch, L.E., R.P. Roberts, and V. Karaman. 2003. Phylogenetic evaluation of *Xylothamia*, *Gundlachia*, and related genera (Asteraceae, Astereae) based on ETS and ITS nrDNA sequence data. *Amer. J. Bot.* 90: 634–649.
- Vargas, O.M. 2018. Reinstatement of the genus *Piofontia*: A phylogenomic-based study reveals the biphyletic nature of *Diplostephium* (Asteraceae: Astereae). *Syst. Bot.* 43: 485–496.
- Vargas, O.M., E.M. Ortiz, and B.B. Simpson. 2017. Conflicting phylogenomic signals reveal a pattern of reticulate evolution in a recent high-Andean diversification (Asteraceae: Astereae: *Diplostephium*). *New Phytol.* 214: 1736–1750.
- Wagstaff, S.J., I. Breitwieser, and M. Ito. 2011. Evolution and biogeography of *Pleurophyllum* (Astereae, Asteraceae), a small genus of megaherbs endemic to the sub-Antarctic islands. *Amer. J. Bot.* 98: 62–75.
- Wang, J. and A.R. Bean. 2019. A taxonomic revision of *Lagenophora* Cass. (Asteraceae) in Australia. *Austrobaileya* 10: 405–442.
- Wang, J. and A.R. Bean. 2020. A taxonomic revision of *Lagenophora* Cass. (Asteraceae) in New Guinea. *Austrobaileya* 10: 576–582.

Watanabe, K., K. Kosuge, R. Shimamura, N. Konishi, and K. Taniguchi. 2006. Molecular systematics of Australian *Calotis* (Asteraceae: Astereae). *Australian Syst. Bot.* 19: 155–168.

Zhang, X.-P. and K. Bremer. 1993. A cladistic analysis of the tribe Astereae (Asteraceae) with notes on their evolution and subtribal classification. *Pl. Syst. Evol.* 184: 259–283.

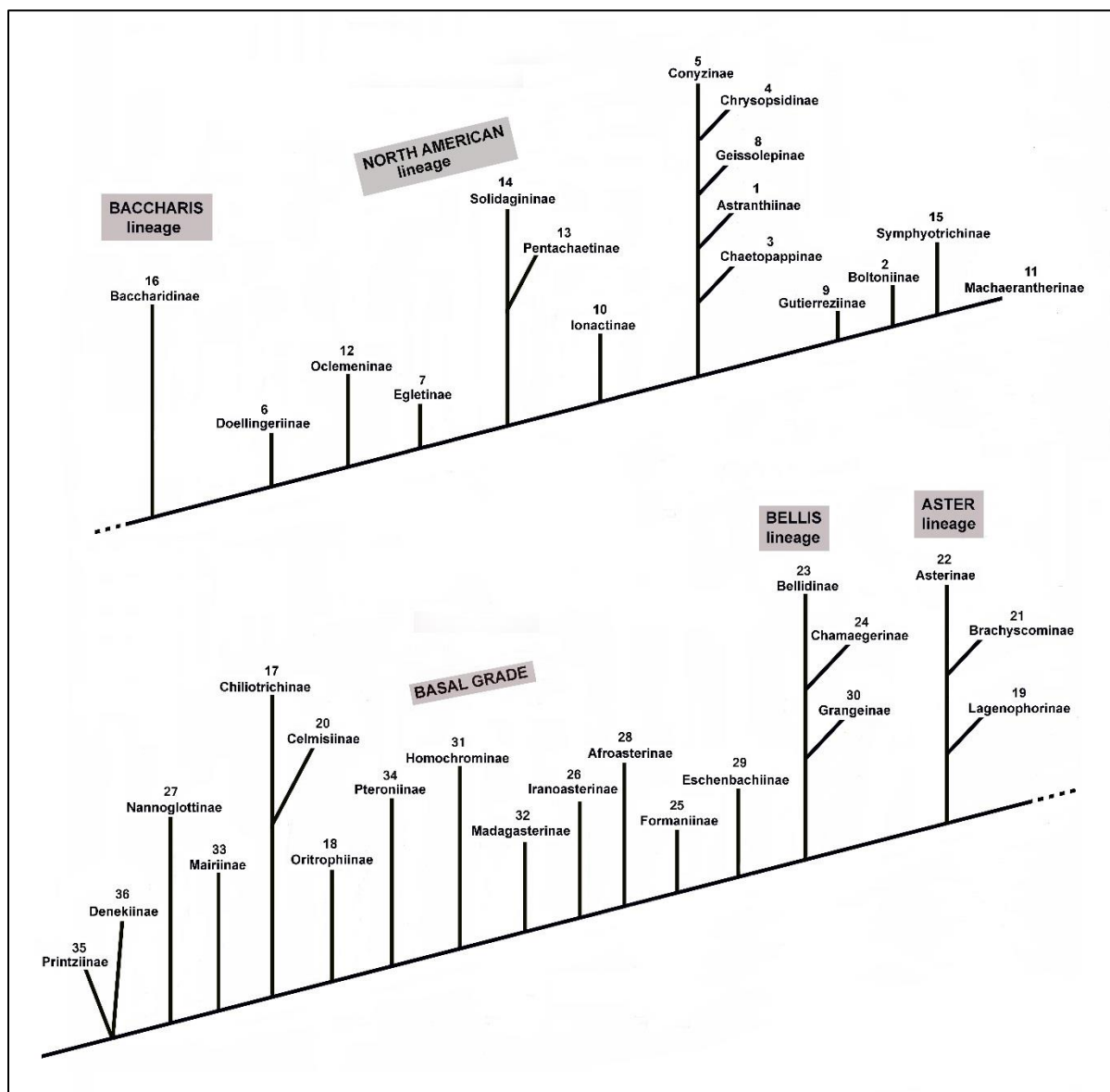


Figure 1. Hypothetical subtribal phylogeny of Astereae. See "Construction of the phylogenetic diagrams" in the introduction. Most, if not all, published trees have been studied as the basis for this intuitively constructed diagram. It is an approximation and hopefully will serve at least as a guide for further analyses.

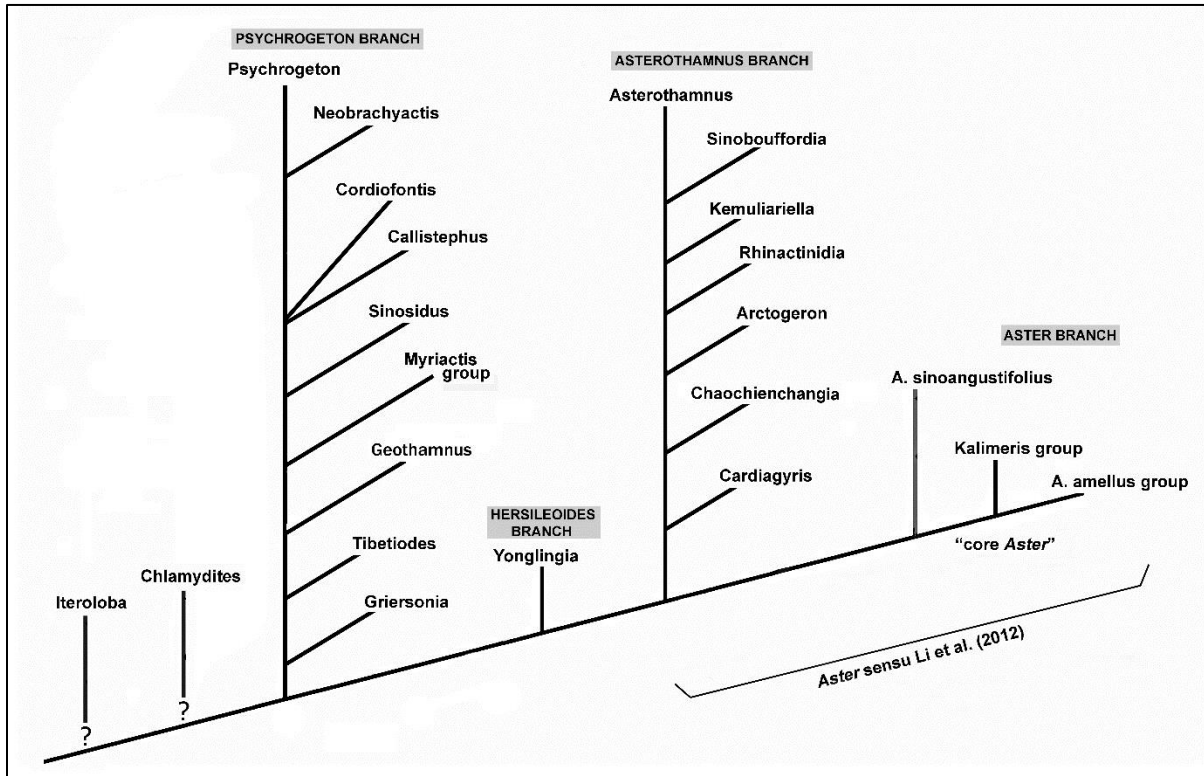


Figure 2. Hypothetical phylogeny of genera and groups of genera of subtribe Asterinae. The Kalimeris group includes *Sheareria*, *Kalimeris*, *Heteropappus*, *Aster* sect. *Ageratoides*, and a clade sister to sect. *Ageratoides*. The Aster amellus group includes *Aster* sensu stricto, *Miyamayomena*, *Rhynchospermum*, *Turczaninovia*, and a diverse group of unplaced species. *Aster sinoangustifolius* is sister to the rest of "core Aster." Li et al. (2012) considered the *Asterothamnus* branch as part of *Aster* sensu stricto.

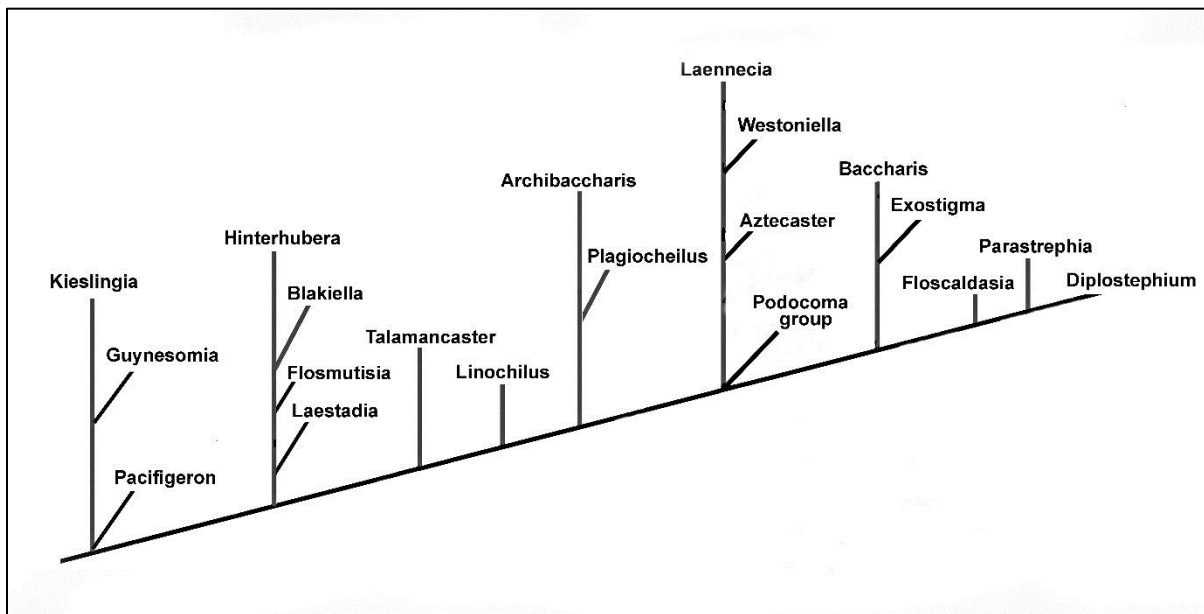


Figure 3. Hypothetical phylogeny of genera and groups of genera of subtribe Baccharidinae. The Podocoma group includes *Podocoma*, *Asteropsis*, *Inulopsis*, *Microgyne*, and *Sommerfeltia*. Genera previously treated within Hinterhuberinae and Podocominae are included within the Baccharidinae.

Table 1. Subtribes of Astereae. Numbers refer to sequence in the linear classification.

Afroasterinae	28	Geissolepineae	8
Astranthiinae	1	Grangeinae	30
Asterinae	22	Gutierrezinae	9
Baccharidinae	16	Homochrominae	31
Bellidinae	23	Ionactinae	10
Boltoniinae	2	Iraoasterinae	26
Brachyscominae	21	Lagenophorinae	19
Celmisiinae	20	Machaerantharinae	11
Chamaegerinae	24	Madagasterinae	32
Chiliotrichinae	17	Mairiinae	33
Chaetopappinae	3	Nannoglottidinae	27
Chrysopsidinae	4	Oclemeninae	12
Conyzinae	5	Oritrophiinae	18
Denekiinae	36	Pentachaetinae	13
Doellingeriinae	6	Printziinae	35
Egletinae	7	Pteroniinae	34
Eschenbachiinae	29	Solidagininae	14
Formaniinae	25	Symphyotrichinae	15

Table 2. Genera of Astereae.

Acamptopappus (A. Gray) A. Gray	Solidagininae	Boltonia L'Hér.	Boltoniinae
Achnophora F. Muell.	Brachyscominae	Brachyscome Cass.	Brachyscominae
Afroaster Manning & Goldblatt	Afroasterinae	Bradburia Torr. & Gray	Chrysopsidinae
Akeassia Lebrun & Stork	Grangeinae	Brintonia Greene	Solidagininae
Almutaster Löve & Löve	Symphyotrichinae	Cabreraea Bonif.	Chiliotrichinae
Amellus L.	Homochrominae	Callistephus Cass.	Asterinae
Ampelaster Nesom	Symphyotrichinae	Calotis R. Br.	Brachyscominae
Amphiachyris (DC.) Nutt.	Guttieriziinae	Camptacra Burb.	Brachyscominae
Amphipappus Torr. & Gray ex Gray	Solidagininae	Canadanthus Nesom	Symphyotrichinae
Aphanostephus DC.	Conyzinae	Cardiagyris Nesom	Asterinae
Apodocephala J. Baker	Madagasterinae	Celmisia Cass.	Celmisiinae
Apopyros Nesom	Conyzinae	Ceratogyne Turcz.	Brachyscominae
Aquilula Nesom	Gutierrezinae	Ceruana Forssk.	Grangeinae
Archibaccharis Heering	Baccharidinae	Chaetopappa DC.	Chaetopappinae
Arctogeron DC.	Asterinae	Chamaegeron Schrenk	Chamaegerinae
Aster L.	Asterinae	Chaochienchangia Nesom	Asterinae
Asteropsis Less.	Baccharidinae	Chiliophyllum Phil.	Chiliotrichinae
Asterothamnus Novopokr.	Asterinae	Chiliotrichiopsis Cabrera	Chiliotrichinae
Astranthium Nutt.	Astranthiinae	Chiliotrichum Cass.	Chiliotrichinae
Aylacophora Cabrera	Chiliotrichinae	Chlamydites J.R. Drummond	Asterinae
Aztecaster Nesom	Baccharidinae	Chloracantha Nesom et al.	Boltoniinae
Baccharis L.	Baccharidinae	Chondropyxis D.A. Cooke	Brachyscominae
Bathysanthus Nesom	Solidagininae	Chrysocoma L.	Homochrominae
Batopilasia Nesom & Noyes	Boltoniinae	Chrysoma Nutt.	Solidagininae
Bellidiastrum Scop.	Bellidinae	Chrysopsis (Nutt.) Ell.	Chrysopsidinae
Bellis L.	Bellidinae	Chrysothamnus Nutt.	Solidagininae
Bellium L.	Bellidinae	Colobanthera Humbert	Grangeinae
Benitoa Keck	Machaerantharinae	Columbiadoria Nesom	Solidagininae
Bigelowia DC.	Gutierrezinae	Commidendrum Burch. ex DC.	Homochrominae
Blakiella Cuatrec.	Baccharidinae	Cordiofontis Nesom	Asterinae

- Nardophyllum (Hook. & Arn.) Hook. & Arn.
 Chiliotrichinae
 Neja D. Don Conyzinae Conyzinae
 Neobrachyactis Brouillet Asterinae
 Neolaria Nesom Brachyscominae
 Nestotus Roberts et al. Solidagininae
 Nidorella Cass. Grangeinae
 Nolletia Cass. Homochrominae
 Noticastrum DC. Chrysopsidinae
 Notopappus Klingeb. Machaerantherinae
 Novaguinea D.J.N. Hind Lagenophorinae
 Novenia S.E. Freire Oritrophiinae
 Oclemena Greene Oclemeninae
 Ocyroe Phil. Chiliotrichinae
 Olearia Moench Brachyscominae
 Oligoneuron Small Solidagininae
 Oonopsis (Nutt.) Greene Machaerantherinae
 Oreochrysum Rydb. Solidagininae
 Oreostemma Greene Machaerantherinae
 Oritrophium (Kunth) Cuatrec. Oritrophiinae
 Osbertia Greene Chrysopsidinae
 Pachystegia Cheeseman Celmisiinae
 Pacifigeron Nesom Baccharidinae
 Pappochroma Raf. Brachyscominae
 Parastrephia Nutt. Baccharidinae
 Pentachaeta Nutt. Pentachaetinae
 Peripleura (Burb.) Nesom Brachyscominae
 Petradoria Greene Solidagininae
 Phaseolaria Nesom Brachyscominae
 Pilbara Lander Brachyscominae
 Piora J. Kost. Lagenophorinae
 Pityopsis Nutt. Chrysopsidinae
 Plagiocheilus Arn. ex DC. Baccharidinae
 Pleurophyllum Hook. f. Celmisiinae
 Podocoma Cass. Baccharidinae
 Poecilolepis Grau Homochrominae
 Polyarrhena Cass. Homochrominae
 Printzia Cass. Printziinae
 Psiadia Jacq. ex Willd. Grangeinae
 Psilactis A. Gray Symphyotrichinae
 Psychogeton Boiss. Asterinae
 Pteronia L. Pteroniinae
 Pyrrocoma Hook. Machaerantherinae
 Pytinicarpa Nesom Lagenophorinae
 Rayjacksonia Hartm. & Lane Machaerantherinae
 Remya Hillebr. ex Benth. & Hook. f.
 Brachyscominae
 Rhamphogyne S. Moore Grangeinae
 Rhinactinidia Novopokr. Asterinae
 Rhynchospermum Reinw. ex Reinw. Asterinae
 Rigiopappus A. Gray Pentachaetinae
 Rochonia DC. Madagasterinae
 Roodebergia B. Nord. Homochrominae
 Sanrobertia Nesom Symphyotrichinae
 Sericocarpus Nees Solidagininae
 Sheareria S. Moore Asterinae
 Sinobouffordia Nesom Asterinae
 Sinosidus Nesom Asterinae
 Solenogyne Cass. Lagenophorinae
 Solidago L. Solidagininae
 Sommerfeltia Less. Baccharidinae
 Stenotus Nutt. Solidagininae
 Stephanodoria Greene Machaerantherinae
 Symphyotrichum Nees Symphyotrichinae
 Talamancaster Pruski Baccharidinae
 Tetramolopium Nees Brachyscominae
 Thespis DC. Eschenbachiinae
 Thurovia Rose Gutierrezinae
 Tibetiodes Nesom Asterinae
 Toiyabea Roberts et al. Solidagininae
 Tomentaurum Nesom Chrysopsidinae
 Tonestus A. Nels. Solidagininae
 Townsendia Hook. Astranthiinae
 Tracyina S.F. Blake Pentachaetinae
 Triniteurybia Brouillet et al. Machaerantherinae
 Tripolium Nees Bellidinae
 Turczaninovia DC. Asterinae
 Vernoniopsis Humbert Madagasterinae
 Vittadinia A. Rich. Brachyscominae
 Walsholaria Nesom Brachyscominae
 Welwitschiella Engler Grangeinae
 Westoniella Cuatrec. Baccharidinae
 Wollemiaster Nesom Brachyscominae
 Xanthisma DC. Machaerantherinae
 Xanthocephalum Willd. Machaerantherinae
 Xylorhiza Nutt. Machaerantherinae
 Xylothamia Nesom et al. Gutierrezinae
 Yonglingia Nesom Asterinae
 Zyrphelis Cass. Homochrominae

SUBTRIBAL CLASSIFICATION OF ASTEREAE

The Astereae includes ca. 3100 species, distributed primarily in temperate regions. The group is characterized by ecaudate, non-calcarate anther bases (a few primitive genera have caudate bases) and disc floret styles with separated, marginal stigmatic lines and deltate to triangular or lanceolate style appendages glabrous adaxially, with sweeping hairs abaxially.

NORTH AMERICA /CENTRAL AMERICA

1. ASTRANTHIINAE Nesom, Sida 19: 265. 2000.

Astranthium Nutt. [*Astranthium integrifolium*]

Dichaetophora A. Gray [*Dichaetophora campestris*] Monotypic.

Townsendia Hook. [*Townsendia florifer*]

2. BOLTONIINAE Nesom, Sida 19: 266. 2000.

Batopilasia Nesom & Noyes [*Batopilasia byei*] Monotypic.

Boltonia L'Hér. [*Boltonia asteroides*, *B. diffusa*]

Chloracantha Nesom [*Chloracantha spinosa*]

3. CHAETOPAPPINAE Nesom, Sida 19: 264. 2000.

Chaetopappa DC. [*Chaetopappa bellioides*, *C. effusa*, *C. ericoides*]

Monoptilon Torr. & Gray [*Monoptilon bellioides*]

4. CHRYSOPSIDINAE Nesom, Phytologia 76: 203. 1994.

Bradburia Torr. & Gray [*Bradburia hirtella*, *B. pilosa*]

Chrysopsis (Nutt.) Elliott [*Chrysopsis delaneyi*, *C. dressei*, *C. godfreyi*, *C. gossypina*, *C.*

highlandsensis, *C. lanuginosa*, *C. linearifolia*, *C. mariana*, *C. scabrella*, *C. subulata*]

Croptilon Raf. [*Croptilon divaricatam*, *C. rigidifolium*]

Heterotheca Cass. [*Heterotheca camporum*, *H. horrida*, *H. jonesii*, *H. oregona*, *H. shevockii*, *H.*

subaxillaris, *H. rutteri*, *H. villosa*, *H. viscida*, *H. zionensis*]

Noticastrum DC. [*Noticastrum marginatum*]

Osbertia Greene [*Osbertia stolonifera*] See Morgan and Simpson (1992).

Pityopsis Nutt. [*Pityopsis aspera*, *P. falcata*, *P. flexuosa*, *P. graminifolia*, *P. pinifolia*]

Tomentaurum Nesom Monotypic, not included in molecular sampling.

See Nesom (1991a) for a cladistic analysis of Chrysopsidinae based on morphological characters.

5. CONYZINAE Horan., Char. Ess. Fam., 93. 1847.

Aphanostephus DC. [*Aphanostephus ramosissimus*, *A. skirrhobasis*]

Apopyros Nesom [*Apopyros warmingii*]

Erigeron L. (including *Conyza* L. *sensu stricto*) [many species; see Noyes 2000]

Hysterionica Willd. [*Hysterionica jasionoides*]

Leptostelma D. Don [*Leptostelma maxima*]

Neja D. Don [*Neja filiformis*]

In a strict application of monophyly, all species of Conyzinae would be identified as *Erigeron* (Noyes 2000). Species identified as *Conyza* have arisen evolutionarily from within *Erigeron* at least twice. *Apopyros*, *Hysterionica*, *Leptostelma*, and *Neja* are distinctive monophyletic groups of "austro-brasilien" South America most closely related to *Conyza* (*Erigeron*) *bonariensis*, *Conyza* (*Erigeron*) *primulifolia*, and probably most of the South American conyzas, to South American *Erigeron* species, and to several groups of Mexican *Erigeron*. *Aphanostephus*, a genus of the southwestern USA and Mexico, was not suspected of close relationship to *Erigeron* until molecular analysis showed it so. See further commentary in Nesom (2020b).

6. DOELLINGERIINAE Nesom, subtr. nov. TYPE: *Doellingeria* Nees

Perennial herbs (fibrous-rooted in *Doellingeria*, rhizomatous in *Eucephalus*) with scale-like basal and lower cauline leaves; leaves eglandular; capitulescence corymbiform to paniculiform; phyllaries strongly graduate in length, rounded (*Doellingeria*) or keeled (*Eucephalus*); rays absent or relatively few (2–20), white to violet; achenes eglandular, broadly columnar with 5–9 resinous veins (*Doellingeria*) or strongly flattened and 2-nerved (*Eucephalus*); pappus bristles in 2–4 subequal series, apices clavate.

Doellingeria Nees [genus of 3 species, eastern USA; all included by Allen et al.]

Eucephalus Nutt. [genus of 10 species, western USA; all included by Allen et al.]

All 13 species of this group have been united as *Doellingeria* (Allen et al. 2019), based on molecular analyses showing *Doellingeria* and *Eucephalus elegans* as a sister group to the rest of *Eucephalus* (ITS/ETS sequences) or as considerably more distantly related to the rest of *Eucephalus* (chloroplast sequences). The nuclear sequences suggest that the *Doellingeria* species arose as a derived lineage from within *Eucephalus*, while (as noted by Allen et al.) the plastid sequences suggest a more complex evolutionary history in the origin of *Doellingeria* and *Eucephalus*, involving species of the group identified here as Baccharidinae. Their taxonomic option was based on the nuclear sequences.

Doellingeria and *Eucephalus*, in any case, are widely separated in geography and discontinuously distinct in morphology and there is nothing in *E. elegans* to suggest that it is closest to *Doellingeria*. The gain in considering the two groups congeneric seems outweighed by evolutionary information conveyed by maintaining them as separate.

7. EGLETINAE Nesom, subtr. nov. TYPE: *Egletes* Cass.

Taprooted, annual herbs, glandular-resinous; leaves pinnatifid to bipinnatifid to lobed or toothed; receptacles conical; disc flowers bisexual, corollas 3–5-lobed; ray flowers multiseriate (usually 2–4 series) with white, filiform ligules; achenes compressed, 2-nerved, faces usually glandular; pappus absent, the achene apex extended into a whitish, cartilaginous crown or cup, this sometimes broad and flaring.

Egletes Cass. [*Egletes liebmannii*]

Egletes comprises about 6 species from South America though Central America and Mexico into the southern USA. It was earlier placed (Nesom 1994a) in the mostly African Grangeinae, with which its features seem closely aligned, but molecular data indicate that *Egletes* arose from within the North American clade and similarities to Grangeinae apparently are convergent. Fayed (1979) included *Egletes* in his revision of Grangeinae but concluded that it did not belong there.

8. GEISSOLEPINAE Nesom, subtr. nov. TYPE: *Geissolepis* B.L. Rob.

Perennial, stoloniferous herbs with prostrate stems; leaves succulent, linear-oblongate; receptacles steeply conic, paleate; ray flowers 8–12, ligules white; disc flowers bisexual, fertile; achenes 3–4-angled, with ca. 8 orange-resinous ribs, faces with glochidiate (anchor-shaped) duplex hairs; pappus of 6–8 narrow pales with uncinat-ciliate margins.

Geissolepis B.L. Rob. [*Geissolepis suaedifolia*]

Geissolepis, a monotypic Mexican endemic, was earlier regarded (Nesom 1994a) as closely related to *Astranthium* and *Townsendia*, with which it shares a conical receptacle, reduced pappus, and glochidiate achenial hairs, but molecular data indicate that it is a basal element in the North American clade, its evolutionary affinity ambiguous.

9. GUTIERREZIINAE Nesom, subtr. nov. TYPE: *Gutierrezia* Lag.

Shrubs, subshrubs, or annual or perennial herbs; leaves punctate-glandular, mostly sessile, 1-nerved or with 3–5 parallel veins; disc flowers 2–30(–50) in *Gundlachia*, anther filaments inserted at the junction of the corolla tube and limb (vs. well below the tube apex); ray flowers yellow, rarely white; achenes subterete, (2–)4–10 nerved, sparsely to densely strigose, eglandular; pappus or bristles or scales or absent.

Amphiachyris (DC.) Nutt. [*Amphiachyris dracunculoides*]
Aquilula Nesom [*Aquilula riskindii*] Monotypic.
Bigelowia DC. [*Bigelowia nudata*, *B. nuttallii*]
Euthamia (Nutt.) Cass. [*Euthamia graminifolia*, *E. leptcephala*, *E. occidentalis*, *E. tenuifolia*]
Gundlachia A. Gray [*Gundlachia corymbosa*]
Gutierrezia Lag. [*Gutierrezia sarothrae*, *G. texana*]
Gymnosperma Less. [*Gymnosperma glutinosa*] Monotypic.
Medranoa Urbatsch & Roberts (incl. *Chihuahuana*, *Neonesomia*, and *Xylovirgata*) [*Medranoa johnstonii*, *M. palmeri*, *M. parrasana*, *M. pseudobaccharis*]
Thurovia Rose [*Thurovia triflora*] Monotypic.
Xylothamia Nesom, Suh, Morgan, & Simpson [*Xylothamia diffusa*, *X. triantha*, *X. truncata*]

These genera were previously placed (Nesom 1994a) in the Solidagininae although their unity as a natural group was earlier recognized (Suh 1989; Suh & Simpson 1990; Nesom et al. 1990; Nesom 1991b). See Nesom (2018c) for a taxonomic summary of *Aquilula*, *Gundlachia*, *Medranoa*, and *Xylothamia*.

10. IONACTINAE Nesom, **subtr. nov.** TYPE: *Ionactis linariifolia* Greene

Perennial herbs from thick taproots and woody caudex, rarely rhizomatous; leaves cauline, stiff, narrow, 1-nerved; heads 1 or few in loose corymbs; phyllaries strongly keeled, without herbaceous tips; ray flowers 8–21, ligules violet to bluish or white, coiling; disc flowers bisexual, fertile (one species functionally staminate); achenes narrowly obovate, compressed, in rays (2–)3-nerved, in disc florets 2(–4)-nerved, strigose to sericeous (1 species glandular); pappus bristles 1–2-seriate, apically acute, outer series of short bristles or scales.

Ionactis Greene [*Ionactis caelestis*, *I. elegans*, *I. linariifolia*, *I. stenomeres*]

The position of *Ionactis* is largely unresolved in molecular phylogenies. One species is widespread in the eastern USA (*I. linariifolia*, the type); the other 4 are from the western USA.

11. MACHAERANTHERINAE Nesom, Phytologia 76: 208. 1994.

*Basal grade

Eurybia (Cass.) Gray [*Eurybia avita*, *E. chlorolepis*, *E. divaricata*, *E. eryngiifolia*, *E. furcata*, *E. gracilis*, *E. integrifolia*, *E. paludosa*, *E. radulina*, *E. sibirica*]
Herrickia Woot. & Standl. [*Herrickia glaucescens*, *H. horrida*, *H. kingii*, *H. wasatchensis*]
Oreostemma Greene [*Oreostemma alpigenum*, *O. elatum*]
Triniteurybia Brouillet, Urbatsch, & Roberts [*Triniteurybia aberrans*] Monotypic.

These four genera form a grade basal to the "core" *Machaerantharinae* (Brouillet et al. 2009).

*Machaeranthera group

Dieteria Nutt. [*Dieteria bigelovii*, *D. canescens*]
Leucosyris Greene (= *Arida* (Hartm.) Morgan & Hartm.) [*Leucosyris blepharophylla*, *L. parviflora*, *L. riparia*, *L. turneri*]
Machaeranthera Nees [*Machaeranthera tanacetifolia*]
Oonopsis (Nutt.) Greene [*Oonopsis engelmannii*, *O. wardii*]
Xanthisma DC. [*Xanthisma blephariphyllum*, *X. coloradoense*, *X. crutchfieldii*, *X. gracile*, *X. gymnocephalum*, *X. spinulosum*, *X. stenolobum*, *X. rhizomatum*, *X. texanum*, *X. viscidum*]
Xylorhiza Nutt. [*Xylorhiza tortifolia*, *X. wrightii*]

*Haplopappus group

Haplopappus Cass. [*Haplopappus foliosus*, *H. glutinosus*, *H. macrocephalus*, *H. marginalis*, *H. paucidentatus*]
Grindelia Willd. [*Grindelia ciliata*, *G. lanceolata*, *G. nana*]

Notopappus Klingenb.

Genus of 5 species (Andean Chile and Argentina) segregated from *Grindelia* and *Haplopappus* (Klingenberg 2007).

Hazardia Greene [*Hazardia cana*, *H. detonsa*, *H. squarrosa*, *H. whitneyi*]

*Xanthocephalum group

Isocoma Nutt. [*Isocoma acradenia*, *I. menziesii*, *I. rusbyi*, *I. tenuisecta*, *I. veneta*, *I. wrightii*]

Rayjacksonia Hartm. & Lane [*Rayjacksonia phyllocephala*]

Xanthocephalum Willd. [*Xanthocephalum gymnospermoides*]

Stephanodoria Greene [*Stephanodoria tomentella*] Monotypic.

Pyrocoma Hook. [*Pyrocoma clementis*, *P. crocea*, *P. lanceolata*]

*Lessingia group

Corethrogyne DC. [*Corethrogyne filaginifolia*] Monotypic.

Benitoa Keck [*Benitoa occidentalis*] Monotypic.

Lessingia Cham. [*Lessingia arachnoidea*, *L. germanorum*, *L. glandulifera*, *L. hololeuca*, *L. leptoclada*, *L. micradenia*, *L. nana*, *L. nemaclada*, *L. pectinata*, *L. ramulosa*, *L. tenuis*, *L. virgata*]

12. OCLEMENINAE Nesom, **subtr. nov.** TYPE: *Oclemena* Greene

Perennial herbs with scale-like basal and lower cauline leaves; leaves gland-dotted; capitulescence loosely corymbiform, buds and young heads on arching-nodding peduncles; phyllaries graduate in length, linear-lanceolate, evenly herbaceous, slightly keeled; achenes densely glandular, fusiform to narrowly obovate or oblong, 4–8-nerved; pappus bristles in 2–3 subequal series, the outer series sometimes short, apices acute.

Oclemena Greene [*Oclemena acuminata*, *O. nemoralis*, *O. reticulata*]

Molecular data (e.g., Brouillet et al. 2009) indicate that *Oclemena* is without close relatives in the North American clade and in a relatively basal but phylogenetically unresolved position. One of the three species has been formally treated within *Doellingeria*, which also produces a corymboid capitulescence and scale-like basal and lower cauline leaves, but it did not belong there.

13. PENTACHAETINAE Nesom, Sida 19: 264. 2000.*Pentachaeta group

Pentachaeta Nutt. [*Pentachaeta aurea*, *P. exilis*]

Rigiopappus A. Gray [*Rigiopappus leptocladus*] Monotypic.

Tracyina S.F. Blake [*Tracyina rostrata*] Monotypic.

*Ericameria group

Ericameria Nutt. [many species; see Roberts & Urbatsch 2003]

Morphological differences between the *Pentachaeta* group (mostly annual herbs) and the *Ericameria* group (shrubs) are striking and each might reasonably be treated at subtribal rank. Molecular data indicate that they have a sister relationship and together are distant from other genera.

14. SOLIDAGININAE O. Hoffm. in Engler & Prantl, Nat. Pflanzenf. 4(5): 145. 1890.*Unresolved genera (ambiguous placement in molecular phylogenies)

Eastwoodia Brandeg. [*Eastwoodia elegans*] Monotypic.

Columbiadoria Nesom [*Columbiadoria hallii*] Monotypic.

*Sericocarpus group

Sericocarpus Nees [*Sericocarpus asteroides*, *S. linifolia*, *S. oregonensis*, *S. tortifolius*]

***Cuniculotinus group**

Cuniculotinus Urbatsch, Roberts, & Neubig [*Cuniculotinus gramineus*] Monotypic.

***Chrysothamnus group**

Acamptopappus (A. Gray) A. Gray [*Acamptopappus shockleyi*, *A. sphaerocephala*]

Amphipappus Torr. & Gray ex A. Gray [*Amphipappus fremontii*] Monotypic, 2 varieties.

Chrysothamnus Nutt. [*Chrysothamnus depressus*, *C. eremobius*, *C. greenii*, *C. humilis*, *C. molestus*, *C. stylosus*, *C. vaseyi*, *C. viscidiflorus*]

***Solidago group**

Bathysanthus Nesom Monotypic, southern Chihuahua (Nesom 2018a). No molecular sample.

Brintonia Greene [*Brintonia discoidea*]

Oligoneuron Small [*Oligoneuron nitidum*, *O. rigidum*]

Solidago L. [*Solidago bicolor*, *S. canadensis*, *S. fistulosa*, *S. patula*, *S. petiolaris*, *S. sempervirens*, *S. shortii*]

Chrysoma Nutt. [*Chrysoma pauciflosculosa*] Monotypic.

***Stenotus group**

Nestotus Roberts, Urbatsch, & Neubig Genus of 3 species (Nesom 2018b). *Nestotus lanuginosus*, *N. macleanii*, *N. stenophyllus*).

Oreochrysum Rydb. [*Oreochrysum parryi*] Monotypic.

Tonestus A. Nels. Genus of 2 species. [*Tonestus lyallii*, *T. pygmaeus*].

Lorandersonia Urbatsch, Roberts, & Neubig [*Lorandersonia baileyi*, *L. linifolia*, *L. microcephala*, *L. pulchella*, *L. salicina*] The genus also includes a sixth species, *Lorandersonia spathulata*.

Stenotus Nutt. Genus of 3 species (Nesom 2018b). [*Stenotus acaulis*, *S. armerioides*, *S. pulvinatus*].

Toiyabea Roberts, Urbatsch, & Neubig Four species of California and Nevada. *Toiyabea alpina*, *T. eximia*, *T. granitica*, *T. peirsonii*. See Nesom (2020a) for taxonomy that contradicts molecular data.

Petradoria Greene [*Petradoria pumila*] Monotypic.

15. SYMPHYOTRICHINAE Nesom, *Phytologia* 76: 211. 1994.

Sanrobertia Nesom [*Sanrobertia gypsophila*] Monotypic.

Canadanthus Nesom [*Canadanthus modestus*] Monotypic.

Ampelaster Nesom [*Ampelaster carolinianus*] Monotypic.

Almutaster Löve & Löve [*Almutaster pauciflorus*] Monotypic.

Psilactis A. Gray [*Psilactis asteroides*, *P. boltoniae*, *P. brevilingulata*, *P. odysseus*, *P. tenuis*]

Symphotrichum Nees [many species, incl. *Symphotrichum chapmanii*, *S. ciliatum*, *S. cordifolium*, *S. dumosum*, *S. ericoides*, *S. moranense*, *S. sericeum*, *S. subulatum*, *S. turbinellum*]

SOUTH AMERICA**16. BACCHARIDINAE** Less., *Linnaea* 5: 145. 1830.***Baccharis group**

Baccharis L. (syns = *Baccharidastrum*, *Baccharidiopsis*, *Heterothalamulopsis*, *Heterothalamus*, *Heterothalamulopsis*, *Lanugothamnus*, *Molina*, *Neomolina*, *Pingraea*, *Pseudobaccharis*, *Psila*, *Sergilus*, *Stephananthus*, *Tursenia*; see Heiden et al. 2019)

The phylogenetic position of *Baccharis* is ambiguous but most indications (e.g., Vargas et al. 2017) are that it arose from among species previously treated as *Hinterhuberinae*, with *Aztecaster*, *Archibaccharis*, *Parastrephia*, and species of *Diplostephium* sensu lato among its closest woody relatives.

Exostigma Sancho [*Exostigma notobellidiastrum*]

The position of *Exostigma* is not resolved; several molecular analyses place it as most closely related to *Baccharis*, with which it seems to have little in common morphologically.

*Hinterhubera group (Hinterhuberinae Cuatr., Webbia 24: 5. 1969)

Blakiella Cuatr. [*Blakiella bartsiiifolia*] Monotypic.

Flosmutisia Cuatr. Monotypic. Not included in molecular sampling.

Flosmutisia paramicola is distinctive in its rosulate habit, solitary heads, multiseriate rays, subbilibiate ray corollas, and functionally male disc flowers. Cuatrecasas (1986) noted that its probable closest relatives are *Hinterhubera*, *Blakiella*, and *Westoniella*.

Hinterhubera Sch.-Bip. ex Wedd. [*Hinterhubera adenopetala*, *H. columbica*, *H. ericoides*, *H. imbricata*, *H. lanuginosa*, *H. laseguei*]

Laestadia Kunth ex Less. [*Laestadia costaricensis*, *L. muscicola*, *L. pinifolia*]

*Linochilus group

Linochilus Benth. (segregated from *Diplostephium*) [many species sampled; see Vargas 2018 and Saldivia et al. 2019]

*Laennecia group

Laennecia Cass. [*Laennecia schiedeana*, *L. sophiiifolia*]

Talamancaster Pruski (segregated from *Lagenophora*; Pruski 2017) [*Talamancaster cuchumatana*, *T. panamensis*]

Westoniella Cuatr. [*Westoniella chirripoensis*, *W. eriocephala*, *W. kohkemperi*, *W. triunguifolia*]

*Aztecaster group

Aztecaster Nesom [*Aztecaster matudae*, *A. pyramidatus*]

*Archibaccharis group

Archibaccharis Heering [*Archibaccharis androgyna*, *A. asperifolia*, *A. schiedeana*]

Plagiocheilus Arn. ex DC. [*Plagiocheilus bogotensis*, *P. soliviformis*]

*Diplostephium group

Diplostephium Kunth sensu stricto [incl. *Dysaster* H. Rob. & Funk = *Diplostephium serratifolium*; many species sampled; see Vargas 2018]

Floscaldasia Cuatr. [*Floscaldasia hypsophila*]

Parastrephia Nutt. [*Parastrephia lepidophylla*, *P. lucida*, *P. phyllicaeformis*, *P. quadrangularis*, *P. teretiusscula*]

*Pacifigeron group

Guynesomia Bonif. [*Guynesomia scoparia*] Monotypic.

Kieslingia Faúndez, Saldivia, & Martic. [*Kieslingia chilensis*] Monotypic.

Pacifigeron Nesom [*Pacifigeron indivisus*, *P. rapensis*]

Genus of 2 species from the island of Rapa in French Polynesia; see Saldivia et al. (2020).

*Podocoma group (Podocominae Nesom, Phytologia 76: 209. 1994)

Podocoma itself is perhaps separate from the others.

Asteropsis Less. [*Asteropsis megapotamica*] Monotypic.

Inulopsis (DC.) O. Hoffm. [*Inulopsis scaposa*]

Microgyne Less. [*Microgyne marchesiana*, *M. trifurcata*]

Podocoma Cass. [*Podocoma asperrima*, *P. hieracifolia*, *P. hirsuta*]

Sommerfeltia Less. [*Sommerfeltia cabrerae*, *S. spinulosa*]

17. CHILIOTRICHINAE Bonifacino, **subtr. nov.** TYPE: *Chiliotrichum* Phil.

Contributed by Mauricio Bonifacino

Shrubs (usually densely branched) or small scandent trees; leaves coriaceous, usually reduced and ericoid (except in *Llerasia*) and usually densely tomentose abaxially; receptacles paleate or partially paleate (rarely epaleate; i.e., *Llerasia*, *Ocyroe*); ploidy level 2x or 4x. Mostly Andean South America. See analysis by Bonifacino and Funk (2012).

Aylacophora Cabrera [*Aylacophora deserticola*] Monotypic.*Cabreraea* Bonif. [*Cabreraea andina*] Monotypic.*Chiliophyllum* Phil. [*Chiliophyllum densifolium*]*Chiliotrichiopsis* Cabrera [*Chiliotrichiopsis keidelii*, *C. ledifolia*, *C. peruviana*]*Chiliotrichum* Cass. [*Chiliotrichum diffusum*, *C. fuegianum*]*Haroldia* Bonif. [*Haroldia mendocina*] Monotypic.*Katinasia* Bonif. [*Katinasia cabreræ*] Monotypic.*Lepidophyllum* Cass. [*Lepidophyllum cupressiforme*]*Llerasia* Triana [*Llerasia lindenii*, *L. lucidula*, *L. ledifolia*, *L. rufescens*, *L. soratensis*]*Nardophyllum* (Hook. & Arn.) Hook. & Arn. (incl. *Palaepappus* Cabr.) [*Nardophyllum bryoides*, *N. lanatum*, *N. chiliotrichioides*, *N. genistoides*, *N. patagonicum*]*Ocyroe* Phil. [*Ocyroe armata*] Monotypic.**18. ORITROPHIINAE** Nesom, **subtr. nov.** TYPE: *Oritrophium* (Kunth) Cuatr.

Related to Chiliotrichinae but distinct in its combination of herbaceous habit, narrow, 1-veined or parallel-veined leaves in basal rosettes, leaf axils with tufts of hairs, epaleate receptacles, disc flowers with sterile ovaries, blunt anther thecae bases, and multinerved achenes with persistent pappus bristles; ploidy level 2x or 4x.

Novenia Freire [*Novenia acaulis*]*Oritrophium* (Kunth) Cuatr. [*Oritrophium hieracioides*, *O. peruvianum*]**OCEANIA****19. LAGENOPHORINAE** Nesom [as "Lageniferinae"], *Phytologia* 76: 207. 1994.

Keysseria Lauterb. (type = *Keysseria papuana* = *Keysseria radicans*). Including 9 species, all of alpine habitats in New Guinea (Koster 1966) and including considerable diversity in habit. Hawaiian species previously treated as *Keysseria* are separated as *Helodeaster* (see Asterinae-Psychrogeton branch, the Myriactis group; Nesom 2020c).

Lagenocypsela Swenson & Bremer A single species, *Lagenocypsela (Rhamphogyne) papuana*.*Lagenophora* Cass. (type = *Lagenophora stipitata*) [*Lagenophora barkeri*, *L. cuneata*, *L. gracilis*, *L. hariotii*, *L. hirsuta*, *L. huegelii*, *L. lanata*, *L. montana*, *L. nudicaulis*, *L. petiolata*, *L. pinnatifida*, *L. pumila*, *L. stipitata*, *L. strangulata*]

Lagenophora gracilis and *L. huegelii* (Australia) and *L. lanata* (s and se Asia, Malaysia, New Guinea, Australia) are more closely related to *Solenogyne* than to the rest of *Lagenophora* (Nakamura et al. 2012; Sancho et al. 2015). Species of Australia and New Guinea are treated by Wang and Bean (2019, 2020).

Novaguinea D.J.N. Hind*Piora* Koster A single species, *Piora ericoides*.*Pytinicarpa* Nesom

Solenogyne Cass. (type = *Solenogyne bellioides*) [*Solenogyne gunnii*, *S. dominii*, *S. bellioides*, *S. mikadoi*] Also [*Lagenophora gracilis*, *L. lanata*, and *L. huegelii*], which apparently form part of *Solenogyne* rather than *Lagenophora*; see *Lagenophora*.

20. CELMISIINAE Saldivia, **subtr. nov.** TYPE: *Celmisia* Cass., Dict. Sci. Nat., ed. 2. 37: 259. 1825, nom. cons., non *Celmisia* Cass., Bull. Sci. Soc. Philom. Paris 1817: 32. 1817, nom. rej. (\equiv *Capelio* B. Nord.). Contributed by Patricio Saldivia.

Small trees (rarely up to 18 m), erect or plagiotropic shrubs, subshrubs, or perennial herbs with large leaves; phyllotaxis alternate (2/5) or opposite, abaxial surface of the leaves covered by dense white to ferruginous tomentum in most of the species (hairs long aseptate, T- or Y-shaped, or lepidote); shoots indeterminate with typically lateral flowering or plants with long shoots determinate by abortion rather than by floral development and short shoots (brachyblasts) bearing capitula and leaves; capitula radiate, or rarely disciform or discoid; capitulescences fasciculate, paniculate, corymbose or capitula solitary; ray flowers pistillate, occasionally with staminodes; disc flowers bisexual or functionally staminate (only in some *Olearia* pro parte species from New Guinea); anthers caudate and with a conspicuous apical appendage; receptacles epaleate, alveolate; achenes fusiform-cylindrical (mostly), obconic or gibbous, 4–13 ribbed, often covered with twin trichomes; ploidy level mainly 12x (but also 10x, 24x, 32x, 36x, and 48x; see Beuzenberg & Hair 1984). Ca. 159 species endemic to Australasia.

Celmisia Cass. [*Celmisia argentea*, *C. armstrongii*, *C. asteliifolia*, *C. bellidioides*, *C. glandulosa*, *C. holosericea*, *C. laricifolia*, *C. lateralis*, *C. longifolia*, *C. mackaui*, *C. tomentella*]

Ca. 60 species from mainland New Zealand (North, South, and Stewart islands), 6 species endemic to southeast mainland Australia, and 2 Tasmanian species. Biphyletic in Saldivia et al. (2020).

Damnamenia Given [*Damnamenia vernicosa*]

Monotypic, endemic to the sub-Antarctic Campbell and Auckland Islands of New Zealand.

Olearia Moench in part (84 species in total)

- a. Macrocephalous *Olearia* species (6 species, New Zealand) [*Olearia angustifolia*, *O. chathamica*, *O. colensoi*, *O. lyallii*, *O. operina*, *O. semidentata*]
- b. Sect. *Divaricaster* (13 species, New Zealand) [*Olearia fimbriata*, *O. solandri*, *O. traversiorum*, *O. virgata*] See Heads (1998) and Heenan et al. (2008).
- c. New Zealand species with lepidote trichomes (8 species) [*Olearia albida*, *O. nummularia*, *O. paniculata*]
- d. New Guinea species (19 species) [*O. rufa*, *O. velutina*]
- e. Species with T- or Y-shaped trichomes and no divaricate architecture (except for the type species *Olearia tomentosa*), 14 species from New Zealand [*Olearia allomii*, *O. arborescens*, *O. cheesemaniae*, *O. fragrantissima*, *O. furfuracea*, *O. rani*], 23 species from mainland Australia and Tasmania [*Olearia argophylla*, *O. chrysophylla*, *O. covenyi*, *O. ledifolia*, *O. megalophylla*, *O. myrsinoides*, *O. oppositifolia*, *O. pannosa*, *O. rosmarinifolia*], 1 species from Lord Howe Island [*Olearia mooneyi*].

Olearia species from Celmisiinae (formerly the *Celmisia* group) cannot be retained in *Olearia* since the type species, *O. tomentosa* from mainland Australia, belongs to a different lineage, Brachyscominae (see below and Saldivia et al. 2020). Molecular and morphological data (Cross et al. 2002; Wagstaff et al. 2011; Saldivia et al. 2020; Saldivia et al., unpublished data) indicate that the *Olearia* species from Celmisiinae need to be placed in two or more new genera.

Pachystegia Cheeseman [*Pachystegia insignis*, *P. rufa*] 3 species.

Pleurophyllum Hook. f. [*Pleurophyllum criniferum*, *P. hookeri*, *P. speciosum*]

3 species endemic to the sub-Antarctic New Zealand (Campbell, Auckland, and Antipodes) and Australian (Macquarie) islands.

21. BRACHYSCOMINAE Nesom, Phytologia 76: 203. 1994.

Annual to perennial herbs, subshrubs, and shrubs. Morphologically heterogeneous, suggested to be monophyletic by molecular analyses although many taxa have not been included in molecular

sampling. Almost all of the species are from Australia — the geography also supports a hypothesis of monophyly.

*Brachyscome group

Brachyscome Cass. (incl. *Allittia* P.S. Short, *Brachystephium* Less., *Paquerina* Cass., *Pembertonia* P.S. Short, *Roebuckia* P.S. Short, *Steiroglossa* DC.)

Chromosome numbers, $2n = 4, 6, 8, 10, 12, 14, 16, 18, 22, 24, 26, 27, 28, 30, 36$.

For comments on the spelling of *Brachyscome* (vs. *Brachycome*), see Short (2014, pp. 27-28).

Ceratogyne Turcz.

Ceratogyne obionoides has not been included in molecular analyses but it previously has been placed in Astereae (Zhang & Bremer 1993; Nesom 1994a; Nesom & Robinson 2007). It is characterized by tiny heads with phyllaries in a single series, functionally staminate disc flowers, ray flowers with reduced ligules, and highly modified achenes (margins thickened and involute with glochidiate Zwillingshaare, arm-like, apically spreading wings, without pappus). Among Australian Astereae, its chromosome number of $2n = 12$ (Turner 1970) occurs elsewhere only in *Brachyscome*, where it apparently has been independently derived several times (Field et al. 2006). "Given the diversity and parallel variability that exists within *Brachyscome* [e.g., Short 2014], it would not be surprising if *Ceratogyne* eventually proved to be a specialized derivative within some group of [*Brachyscome*]" (Nesom 1994a, p. 217). Features of *Ceratogyne* achene morphology approach those of species recently segregated as the genus *Roebuckia*, but the chromosome number of those species is consistently $n = 9$.

*Calotis group (both genera, $x=8$; Brachyscominae otherwise $x=9$ except for *Brachyscome* and *Ceratogyne*)

Calotis R. Br. [*Calotis anthemoides*, *C. cuneata*, *C. cymbacantha*, *C. dentex*, *C. erinacea*, *C. hispidula*, *C. inermis*, *C. lappulacea*, *C. latiuscula*, *C. multicaulis*, *C. plumulifera*, *C. porphyroglossa*, *C. scabiosifolia*, *C. scapigera*, *C. squamigera*, *C. xanthosioidea*]

Erodiophyllum F. Muell. [*Erodiophyllum elderi*]

*Vittadinia group

Peripleura (Burbidge) Nesom (except for *P. diffusa*)

Tetramolopium Nees (except for *T. vagans*)

Vittadinia A. Rich.

These genera together comprise a single clade but each apparently is polyphyletic (e.g., Lowrey et al. 2001). Current taxonomy does not accord with evolutionary patterns as reflected in molecular analyses.

*Elachanthus group

Chondropyxis D.A. Cooke [*Chondropyxis halophila*]

Elachanthus F. Muell. [*Elachanthus pusillus*]

Isoetopsis Turcz. [*Isoetopsis graminifolia*]

Kippistia F. Muell. [*Kippistia suaedifolia*]

Minuria DC. in part (type = *Minuria leptophylla*) [*Minuria cunninghamia*]

Minuria apparently is polyphyletic or else shows evidence of ancient gene flow; see below for *M. integerrima* and *M. macrorhiza*.

*unresolved

Achnophora F. Muell. [*Achnophora tatei*]

Camptacra Burbidge [*Camptacra barbata*, *C. gracilis*, and *C. robusta* (the latter identified in Cross et al. 2002 as *Olearia arguta*; see Bean 2020, Nesom 2020n)]

Dichromochlamys Dunlop [*Dichromochlamys dentata*]

Dimorphocoma Muell. & Tate

Hullsia P.S. Short

Perennial herbs from a taproot, stems erect, distally branched; leaves cauline and evenly spaced, narrowly lanceolate, 3-nerved, glaucous and succulent, glabrous, eglandular; involucre 8–12 mm wide, phyllaries in 2–3 series of subequal length; disc florets functionally staminate, corollas 5-lobed; ray corollas with prominent, coiling ligules; achenes 2.7–3.1 mm long, flattened, 2-nerved, glabrous, carpododium annular; pappus absent. *Hullsia argillicola*, northern Australia. Short (2004b) considered possible relatives in Brachyscominae and Lagenophorinae but found *Hullsia* isolated; its placement here seems more likely than in Lagenophorinae.

Iotasperma Nesom

Ixioclamys Sond. [*Ixioclamys cuneifolia*, *I. filicifolia*]

Minuria DC. in part [*Minuria macrorhiza*, related to *Peripleura diffusa*; *M. integerrima*, suggest by molecular data as related to *Walsholaria*].

Pappochroma Raf. [*Pappochroma nitidum*]

Pilbara Lander

Monotypic genus endemic to the Pilbara region of Western Australia. Highly branched shrubs up to 60 cm tall, with exfoliating, fissured, and fibrous bark; leaves tightly clustered distally, petiolate, coarsely and irregularly serrate, stipitate-glandular; heads few, discoid; phyllaries herbaceous; receptacles strongly convex, paleate; disc corollas white, tube filiform, abruptly opening into the limb; anther bases obtuse; achenes ellipsoid, 3.3–4.6 mm long, 5-ribbed; pappus 1-seriate, of barbellate bristles half as long as the corollas.

Lander (2013) compared *Pilbara* to *Erodiophyllum* but the two seem to have little in common except for paleate receptacles. It seems likely that *Pilbara* is more evolutionarily isolated than tentatively placed here.

Remya Hillebr. ex Benth. & Hook. f. [*Remya kauiensis*, *R. mauiensis*]

Three species in Hawaii. The only genus of Brachysominae without Australian species.

**Olearia* Moench sensu stricto ("clade A" of Cross et al. 2002)

After segregation of *Olearia* species of subtr. Celmisiinae (all of which eventually will be transferred to other genera — but see comments below on *Olearia tomentosa*), and after recognition of recently segregated genera (Nesom 2020n), the genus comprises three groups essentially restricted to Tasmania and the Australian mainland. Sect. *Asterotriche* is monophyletic, while the taxonomic status of various subgroups of sect. *Eriotriche* (Nesom 2020n) remains to be resolved. It seems likely that "clade A" sect. *Eriotriche* (as a whole or in parts) and sect. *Asterotriche* will be recognized at generic rank apart from *Olearia*. The placement of *Olearia tomentosa* (the type of the genus, with "T-shaped" hairs, sect. *Dicerotriche*) as distantly related to other Australian species with similar hairs (but all unequivocally placed in Celmisiinae although apparently not forming a monophyletic group) is surprising — morphological evidence supporting a hypothesis of evolutionary parallelism in *O. tomentosa* is discussed by Saldivia et al. (2020) and Messina et al. (2014). Circumscription of *Olearia* in the strictest sense and its evolutionary position are unsettled but it seems possible that the genus *Olearia* eventually may be recognized as monotypic, sister to the Australian sect. *Asterotriche* species.

sect. *Olearia* (formerly sect. *Dicerotriche*) [*O. tomentosa*]

sect. *Asterotriche* [*O. asterotricha*, *O. astroloba*, *O. brevipedunculata*, *O. canescens*, *O. frostii*, *O. gravis*, *O. heterocarpa*, *O. hygrophila*, *O. lasiophylla*, *O. lirata*, *O. montana*, *O. nernstii*, *O. phlogopappa*, *O. quercifolia*, *O. rugosa*, *O. stellulata*, *O. stenophylla*, *O. viscidula*]

sect. *Eriotriche* [*O. algida*, *O. ballii*, *O. floribunda*, *O. microphylla*, *O. passerinoides*, *O. pimeleoides*, *O. ramosissima*, *O. ramulosa*, *O. teretifolia*] See Nesom (2020n) for subgroups of sect. *Eriotriche*.

*unresolved — *Olearia segregates* (Nesom 2020n)

Landerolaria Nesom [*Landerolaria stuartii*] 10 species.

Neolaria Nesom [*Neolaria ferresii*] 3 species.

Phaseolaria Nesom [*Phaseolaria elliptica*] 3 species.

- Walsholaria* Nesom [*Walsholaria calcarea*, *W. muelleri*] 4 species.
Muellerolaria Nesom [*Muellerolaria rudis*, *M. picridifolia*] 2 species.
Eoglandula Nesom [*Eoglandulosa glandulosa*] 2 species.
Linealia Nesom [*Linealia floctoniae*] Monotypic.
Vicinia Nesom [*Vicinia ciliata*] 2 species.
Wollemiaster Nesom [*Wollemiaster cordatus*] Monotypic.
Ephedrides Nesom *Ephedrides trifurcata*, not included in molecular sampling. Monotypic.

EURASIA

22. ASTERINAE (Cass.) Dumort., Fl. Belg. Prodr. 66. 1827.

A. ASTERINAE-PSYCHROGETON branch

*Psychrogeton group

Neobrachyactis Brouillet (*Neobrachyactis roylei*-the type) [*Neobrachyactis obovatus*, *N. roylei*] [*Psychrogeton pseudoerigeron*]

In contrast to the other species of *Neobrachyactis*, *N. anomala* (DC.) Brouillet is perennial and does not have accrescent pappus bristles — features that are more like *Psychrogeton*. The taxonomy and evolutionary position of *Neobrachyactis* remain to be clarified.

Psychrogeton Boiss. (excluding *Psychrogeton obovatus*, which was transferred to *Neobrachyactis* by Farhani et al. 2018) [*Psychrogeton aellenii*, *P. alexeenkoi*, *P. amorphoglossus*, *P. aucheri*, *P. cabulicus*, *P. chionophilus*, *P. nigromontanus*]

*Callistephus group

Callistephus Cass. [*Callistephus chinensis*]

Cordiofontis Nesom [*Cordiofontis* (Aster, Kalimeris) *longipetiolata*]

Cordiofontis longipetiolata (as *Kalimeris*) is included in the analyses of Li et al. (2012) and Farhani et al. (2018), based on the same sample; the voucher was collected in Sichuan, deposited at HNNU. *Cordiofontis* includes 4 other Himalayan species (Nesom 2020i).

*Albescentes group

Sinosidus Nesom [*Sinosidus* (Aster) *albescens*, *S. argyropholis*, *S. fulgidulus*, *S. lavanduliifolius*, *S. polius*]

Sinosidus includes 7 species (Nesom 2020m).

*Myriactis group

Helodeaster Nesom [*Helodeaster helenae*, *H. maviensis*]

Segregated from *Keysseria* (Nesom 2020c), including 3 species from Hawaii.

Myriactis Less. (type = *Myriactis nepalensis*) [*Myriactis humilis*, *M. nepalensis*, *M. wallichii*, *M. wightii*]

Metamyriactis Nesom [*Metamyriactis* (Aster) *pandurata*, *Aster auriculatus*, *M. pycnophylla*]

Metamyriactis includes 5 species (Nesom 2020g; *Aster auriculatus* is a synonym of *M. pandurata*).

*Batangensis group

Geothamnus Nesom [*Geothamnus* (Aster) *batangensis*] (Nesom 2020m).

*Asteroides group

Tibetiodes Nesom [*Tibetiodes* (Aster) *asteroides*, *T. brachytricha*, *T. diplostephioides*, *T. flaccida*, *T. salwinensis*, *T. setchuanensis*, *T. yunnanensis*]

Tibetiodes includes 27 species (Nesom 2020l).

***Fuscescens group**

Griersonia Nesom [*Griersonia* (Aster) *fuscescens*, *G. senecionoides*]

Griersonia comprises 3 species, including one previously treated at varietal rank within *Aster fuscescens* (Nesom 2020m).

***Unresolved placement**

Chlamyditis J.R. Drummond (syn = *Wardaster* J. Small; *W. lanuginosus* = *Aster neolanuginosus* Brouillet et al.) No molecular sample: *Chlamyditis prainii* (Nesom 2020h). Monotypic.

Iteroloba Nesom No molecular sample: *Iteroloba* (Aster) *bipinnatisecta* (Nesom 2020m) Monotypic.

B. ASTERINAE-HERSILEOIDES branch

Yonglingia Nesom [*Yonglingia* (Aster) *hersileoides*; *Y. nitida*]

The 2 species of *Yonglingia* (Nesom 2020f) together appear in molecular analyses as basal (sister) to the Aster/Asterothamnus branches of Asterinae.

C. ASTERINAE-ASTEROTHAMNUS branch***Asterothamnus group**

Arctogeron DC. [*Arctogeron gramineus*]

Asterothamnus Novopokr. [*Asterothamnus centraliasiatricus*, *Asterothamnus fruticosus*]

Kemulariella Tamamsch. Placed here by morphology and geography.

Rhinactinidia Novopokr. (syn = *Krylovia* Schischk.) [*Rhinactinidia eremophila*, *R. limoniifolia* (= *Aster lingii*)]

The analysis of Li et al. (2012) places *Aster eremophilus* and *A. limoniifolius* (of *Rhinactinidia*) in close relationship to *A. amellus*. Koryluk et al. (2015), using the Li et al. samples, place them similarly — using new samples, however, their analysis places *Rhinactinidia* as closely related to *Asterothamnus*, a hypothesis adopted here, favored by morphology, geography, and ecology (see Korolyuk (1997, 1999; fide Korolyuk et al. 2015) for morphological support for monophyly of *Arctogeron*, *Asterothamnus*, *Kemulariella*, and *Rhinactinidia*).

Sinobouffordia Nesom [*Sinobouffordia* (Aster) *poliothamnus*, *S. sikuensis*] (Nesom 2020f).

Chaochienchangia Nesom [*Changchaochienia* (Aster) *falcifolia*] (Nesom 2020f).

***Cardiagyris group**

Cardiagyris Nesom (the *Aster scaber* group) [*Cardiagyris dimorphophylla* = *Aster dimorphophyllus*; *C. komonoensis*, *C. japonica* (as *Aster miquelianus*), *C. rugulosa*, *C. scabra*; *C. dolichophylla*, *C. huangpingensis*]

Molecular data place *Cardiagyris* (9 species) as sister to the *Asterothamnus* group. (Nesom 2020j).

D. ASTERINAE-ASTER branch***Sinoangustifolius group**

Aster sinoangustifolius Brouillet et al. (replacement name for *Aster angustifolius* C.C. Chang). [*Aster sinoangustifolius*]

This species is sister to the *Aster amellus*/*Kalimeris* combined group. It has been placed in *Kalimeris* and *Miyamayomena* and seems morphologically closest to the latter.

***Amellus group**

Aster L. sensu stricto [*Aster amellus*; *Aster alpinus*] See Nesom (2020e).

Aster, unplaced species [*A. maackii*; *A. procerus*; *A. pseudosimplex*; *A. sampsonii*; *A. taiwanensis*; *A. taliangshanensis*; *A. tataricus*; *A. tenuicaulis*; *A. tianmenshanensis*; *A. tonglingensis*; *A. viscidulus*] [*Aster baccharoides*; *A. jishouensis*; *A. turbinatus*]

Rhynchospermum Reinw. [*Aster verticillatus*]

Miyamayomena Kitam. sensu stricto [*Aster piccolii*, *A. pseudosimplex*, *A. simplex* (China), *A. savatieri* (Japan-Korea). *Miyamayomena koraiensis* (= *Aster koraiensis*) clusters with the Kalimeris group. The position of *A. savatieri* (the type) is ambiguous.

Turczaninovia DC. [*Turczaninovia fastigiata* = *Aster fastigiatus*]

***Kalimeris group**

Kalimeris (Cass.) Cass. [*Aster incisus*, *A. indicus*, *A. integrifolius*, *A. pekinensis*, *A. pinnatifidus*, *A. yomena*]

Heteropappus Less. [*Aster altaicus*, *A. asagrayi*, *A. crenatifolius*, *A. hispidus*, *A. kantoensis*]

Aster sect. *Ageratoides* (Kitam.) Nesom sensu stricto [*Aster ageratoides* var. *lasiocladus*, *A. oliganthus*, *A. saxicola*]

Aster, sect. *Ageratoides* clade [*A. leiophyllus*, *A. myendorffii*, *A. oharai*, *A. pseudoglehnii*, *A. semiamplexicaulis*, *A. shusanensis*, *A. spathulifolius*]

Aster, sect. *Ageratoides* clade [*A. fanjingshanicus*]

Aster, sect. *Ageratoides* clade [*A. brevicaulis*, *A. dianchuanensis*, *A. handelii*, *A. homochlamydeus*, *A. tongolensis*]

Aster, sect. *Ageratoides* clade [*A. heterolepis*, *A. smithianus*]

Aster, sect. *Ageratoides* clade [*A. dolichopodus*, *A. mangshanensis*, *A. oreophilus*]

Aster, sect. *Ageratoides* clade [*A. souliei*]

Aster, sect. *Ageratoides* clade [*A. vestitus*]

Miyamayomena Kitam. in part [*M. koraiensis* = *Aster koraiensis*, placed in the Kalimeris clade fide Shin et al. 2014 and Jafari et al. 2015], apparently closely related to *A. spathulifolius*.

Sheareria S. Moore [*Sheareria nana*]

23. BELLIDINAE Willk. in Willk. & Lange, Prodr. Fl. Hispan. 2: 30. 1870.

***Bellis group**

Bellis L.

Bellium L.

Bellidiastrum Scop.

See analyses in Fiz-Palacios et al. (2002), including many species of Bellidinae.

***Galatella group**

Galatella (Cass.) Cass. [*Galatella altaica*, *G. angustissima*, *G. biflora*, *G. dahurica*, *G. divaricata*, *G. dracunculoides*, *G. hauptii*, *G. litvinovii*, *G. scoparia*, *G. tatarica*, *G. villosa*]

Crinitina Soják [*Crinitina linosyris*]

Tripolium Nees [*Tripolium vulgare* = *Tripolium pannonicum*]

Relationships among species of the *Galatella* group are unresolved, but analyses of Farhani et al. (2018) and others suggest that *Tripolium* and *Galatella* are reasonably treated as distinct, with *Crinitina* included in the latter.

***Kitamura group**

Kitamura Nesom [*Kitamura glehnii* = *Aster glehnii*]

Monotypic genus, endemic to Japan, Sakhalin, and the Kuriles (Nesom 2020d).

Relationships among the three Bellidinae groups are unresolved by molecular data but the subtribe as summarized here is indicated to be monophyletic (Brouillet et al. 2009). Morphological similarities exist

between *Kitamuraia* and the Galatella group (Nesom 2020d) but as a pair they are distant from the Bellis group.

24. CHAMAEGERINAE Nesom, **subtr. nov.** TYPE: *Chamaegeron* Schrenk

Annual or biennial herbs, taprooted, stipitate-glandular; heads relatively small (except *L. gossypinum*), in loose panicles; ray flowers 1–2-seriate, ligules white to blue, pink, or violet, coiling; disc flowers bisexual, fertile; achenes glabrous to sericeous-villous, eglandular; pappus bristles 1-seriate, connate in basal ring and basally caducous as a unit.

Chamaegeron Schrenk [*Chamaegeron asterellus*, *C. bungei*, *C. keredjensis*, *C. oligocephalus*]

Lachnophyllum Bunge [*Lachnophyllum gossypinum*, *L. noaeum*]

The two species of *Lachnophyllum* are highly distinct from each other in morphology — *L. noaeum* is similar to *Chamaegeron* in its short vestiture and relatively small heads in a loose panicle, while *L. gossypinum* (the type) is cobwebby-sericeous and produces fewer and larger heads with longer and broader rays. The nrDNA ITS data of Jafari et al. (2015) placed *L. gossypinum* with *Chamaegeron*. In the analyses of Farhani et al. (2018), nuclear DNA (ITS+ETS) data place both *Lachnophyllum* species with *Chamaegeron*, while plastid DNA *trnL-F* data place *L. noaeum* with *Chamaegeron* but *L. gossypinum* within the Callistephinae, suggesting that its genome has been influenced by ancient hybridization/ introgression events.

25. FORMANIINAE Nesom, **subtr. nov.** TYPE: *Formania* W. Smith & J. Small

Sprawling shrubs, stems 30–100 cm long; leaves alternate, thickened, margins shallowly lobed to coarsely and irregularly serrate with spinulose teeth, surfaces minutely stipitate glandular in pits and viscid. heads terminal in loose corymbs; involucre cylindrical; phyllaries in 4 strongly graduate series, scarious, stipitate-glandular and resinous, with a green apical patch; receptacles fimbriate, epaleate; ray flowers ca. 10, ligules 2.5–3 mm long, pale yellow; disc flowers ca. 8, bisexual, corolla lobes 5, triangular; anther bases sagittate with a short, acute auricle at base, apical appendages long acute; style branch tips lanceolate; achenes obovoid, 3-ribbed, strigose and sparsely stipitate glandular; pappus of 5–6 linear, acute-tipped pales and a shorter series of bristles. Dry rocky slopes and rock faces; western Sichuan and northwest Yunnan.

[*Formania mekongensis*]

The molecular analysis of Fu et al. (2016) places *Formania* in a clade with *Dichrocephala benthamii* and *Aster flaccidus* (Asterinae). Their sampling, however, was sparse and *Callistephus chinensis* (Asterinae) does not cluster with the *Formania* group. The position of *Formania* within the Astereae is secure but other inferences are not justified on the basis of the Fu et al. analysis. The phylogenetic positioning (Fig. 1) of *Formania* is speculative.

Formania resembles some species of Grangeinae in its tendency for glandular, lobed leaves and glandular achenes but it is distinct from all in its combination of a shrubby habit, campanulate involucre with scarious phyllaries in 4–5 graduate series, broad, yellow rays, bisexual disc flowers, tailed anther bases, and pappose achenes. It has little in common with the *Psiadia* group of Grangeinae.

Brouillet et al. (2009) reckoned that tailed anther bases are primitive in Astereae. As noted here, they occur in *Printzia* and *Denekia*, Chiliotrichinae and Celmisiinae, Mairiinae, and Madagasterinae — their presence in *Formania* suggests that it also is a primitive element in the tribe.

26. IRANOASTERINAE Nesom, **subtr. nov.** TYPE: *Iranoaster* Kaz.-Osalo

Perennial herbs from a thick, woody taproot; stems 5–20 cm tall, mostly unbranched except near the base; leaves all cauline, evenly spaced up to the heads, sessile to short-petiolate, 1–1.5 cm long, lowermost cauline scale-like; heads solitary, involucre ca. 15 mm wide, phyllaries in 3–5 strongly graduate series; ray flowers 10–16, ligules purple to whitish-pink, coiling; achenes ca. 2.5 mm long, linear to obovate, sericeous; pappus bristles 1-seriate, apically attenuate.

Iranoaster Kaz.-Osaloo, Farhani, & Mozaff.

Including a single species, *Iranoaster* (*Aster*) *bachtiaricus*, from the Zagros Mountains of Iran. A line drawing is part of the species protologue (Mozaffarian 1996; image of type collection not available; holotype, TARI). This species apparently is basal to a large part of the Astereae (Farhani et al. 2018).

27. NANNOGLOTTIDINAE Nesom, **subtr. nov.** **TYPE:** *Nannoglottis* Maxim.

Subshrubs (*N. ravidata*) or perennial herbs, stipitate-glandular; basal leaves large, petiolate, margins evenly sharp-dentate, cauline leaves reduced, sessile, decurrent to clasping; heads relatively large, solitary (*N. ravidata*) or loosely corymboid; flowers trimorphic — rays pistillate, yellow; inner pistillate in several series, eradiate; disc flowers functionally staminate, lobes deeply cut, reflexing-coiling, anther thecae without tails; fertile achenes subterete, 8–10-ribbed, eglandular; pappus of barbellate bristles in 1 series.

Nannoglottis Maxim. [8 species sampled; see analysis by Liu et al. 2002]

Nannoglottis includes 9 species endemic to the Tibetan Plateau of central Asia. *Nannoglottis ravidata*, a subshrub of alpine habitas, comprises the sister clade to the others, which are perennial herbs of the coniferous forest (Liu et al. 2002). Liu et al. suggested that, because the Astereae apparently originated in the Southern Hemisphere, the best explanation for origin of *Nannoglottis* is "a long dispersal using Southeast Asia as a stepping-stone."

AFRICA/ MADAGASCAR/ SE ASIA**28. AFROASTERINAE** Nesom, **subtr. nov.** **TYPE:** *Afroaster* Manning & Goldblatt

Perennial herbs from tuberous roots; basalmost leaves scale-like, cauline mostly on proximal 1/3–2/3 of stem, narrow and elongate, parallel-veined, hispid to glabrous, eglandular; heads 1–10(–15) on ebracteate or few-bracteate peduncles; involucre campanulate, phyllaries in 3–4 graduate to subequal series; ray flowers sometimes with staminodes, ligules white to blue or lilac, with a darker, abaxial midstripe, coiling; disc flowers bisexual, fertile; achenes narrowly elliptic to obovate, flat, mostly 2-nerved, often glandular or glandular and strigose-hirsute; pappus of 2 series of barbellate bristles, inner elongate, outer short.

Afroaster Manning & Goldblatt [*Afroaster comptonii*, *A. harveyanus*, *A. perfoliatus*]

Afroaster includes 18 species from Tanzania to South Africa (Eswatini, Lesotho, Malawi, Mozambique, South Africa, Transvaal, Zambia); revised by Lippert (1973) as *Aster*.

29. ESCHENBACHIINAE Nesom, **subtr. nov.** **TYPE:** *Eschenbachia* Moench

Annuals to perennial herbs or shrubs, taprooted or rhizomatous; leaves entire to serrate or pinnatifid, glandular or eglandular; heads discoid, in compact or loose clusters; outer florets pistillate, fertile, eligulate; disc florets fertile or with sterile ovaries; achenes 0.4–1.2 mm long, compressed, 2-nerved; pappus 1-seriate, bristles often accrescent, basally connate (typical) or free. Morphologically heterogeneous, indicated to be monophyletic by molecular analyses, badly needing taxonomic study.

Eschenbachia Moench (type = *Eschenbachia aegyptiaca* (L.) Brouillet = *Conyza aegyptica*)

[*Eschenbachia* (*Conyza*) *aegyptica*, *E. (C.) bliinii*, *E. (C.) japonica*, *E. (C.) muliensis*, *E. (C.) gouanii*, *E. (C.) subscaposa*, *E. (C.) tigrensis*, *E. (C.) ulmifolia*]

Combinations above in *Eschenbachia* (species in molecular analyses) have been made by Brouillet (in Chen & Brouillet 2011) and Koster (1952) and are completed here:

Eschenbachia gouanii (L.) Nesom, **comb. nov.** *Erigeron gouanii* L., Mant. Pl. 469. 1771. *Conyza gouanii* (L.) Willd., Sp. Pl. 3: 1928. 1803.

Eschenbachia subscaposa (O. Hoffm.) Nesom, **comb. nov.** *Conyza subscaposa* O. Hoffm., Bot. Jahrb. Syst. 20: 225. 1894.

Eschenbachia tigrensis (Oliv. & Hiern.) Nesom, **comb. nov.** *Conyza tigrensis* Oliv. & Hiern., Fl. Trop. Afr. 3: 316. 1877.

Eschenbachia ulmifolia (Burm. f.) Nesom, **comb. nov.** *Baccharis ulmifolia* Burm. f., Fl. Indica 26. 1768. *Conyza ulmifolia* (Burm. f.) Kuntze, Revis. Gen. Pl. 3(3): 142. 1898.

Conyza L. in part (molecular analyses suggest that each of these three groups might be segregated at generic rank)

[*Conyza limosa*, *C. pinnata*]

[*Conyza attenuata*]

[*Conyza neocandolleana*]

Psiadia Jacq. ex Willd in part (see *Psiadia* sensu stricto in Grangeinae)

[*Psiadia amygdalina*, *P. anchusifolia*, *P. argentea*, *P. aspera*, *P. boivinii*, *P. callocephala*, *P. insignis*, *P. montana*, *P. laurifolia*, *P. reticulata*, *P. rivalsii*, *P. salaziana*, *P. sericea*]

Thespis DC. (lectotype = *Thespis divaricata*) [*Thespis divaricata*]

30. GRANGEINAE Benth. in Benth. & Hook., Gen. Pl. 2: 178. 1873.

Akeassia Lebrun & Stork

Ceruana Forssk.

Colobanthera Humbert

A single species from Madagascar; distinct among African Grangeinae in its functionally staminate disc flowers and broadly fusiform achenes, perhaps evolutionarily isolated and not part of this group.

Conyza Less. in part [*Conyza incisa*, *C. stricta*]

Dacryotrichia Wild

Dichrocephala L'Hér. ex DC. (*D. integrifolia*, the type) [*Dichrocephala benthamii*, *D. integrifolia*]

These two species are allied with *Grangea* in most analyses, but Farhani et al. 2018 place them with *Myriactis* and *Metamyriactis* based on ETS/ITS data, with *Grangea* based on based on plastid DNA. Fayed (1979) treated *Dichrocephala* among the genera of Grangeinae. The two species in the molecular sampling are similar to *Myriactis* in their Indian/southeast Asian geography (vs. African); the other two species of the genus (*D. chrysanthemifolia* and *D. alpina*) are primarily African in distribution, as with the rest of the subtribe. See Pruski (2011) for a summary of the genus.

Grangea Adans. [*Grangea maderaspatana*]

Grangeopsis Humbert

Grauanthus Fayed

Gyrodoma Wild

Heteromma Benth.

Mtonia Beentje

Nidorella Cass. [*Nidorella polycephala*, *N. resedifolia*]

Rhamphogyne S. Moore

A single species, *Rhamphogyne rhynchocarpa* S. Moore, endemic to Rodrigues.

*Psiadia group

Heteroplexis C.C. Chang

Species of *Heteroplexis* have not been included in molecular sampling but they are erect to climbing herbaceous perennials with small, few-flowered heads in terminal clusters, punctate-glandular leaves, ray corollas foreshortened or absent, and small achenes (ca. 1 mm long) — features similar to *Microglossa* and *Psiadia*. All five species are endemic to Guangxi, China, distinct in geography from the Southern Hemisphere-centered *Microglossa* and *Psiadia*.

Microglossa DC. (type = *M. volubilis*) [*Microglossa pyrifolia*] Molecular data suggest that the following should be included within *Microglossa*:

Conyza Less. in part [*Conyza pyrhopappa*, *C. scabrida*]

Psiadia in part [*Psiadia pascalii*]

Psiadia Jacq. ex Willd. sensu stricto (type = *Psiadia glutinosa*) [*Psiadia alticola*, *P. angustifolia*, *P. arguta*, *P. coarctata*, *P. coronopus*, *P. dentata*, *P. dimorpha*, *P. glutinosa*, *P. godotiana*, *P. leucophylla*, *P. melastomatoides*, *P. nigrescens*, *P. punctulata*, *P. serrata*, *P. viscosa*]

Psiadia sensu stricto also includes the following:

[*Sarcanthemum coronopus* = *Psiadia coronopus* (Lam.) Balf. f.]

[*Conyza ageratoides*]

[*Psiadiella humilis*]

The analysis of Strijk et al. (2013) indicates that *Conyza ageratoides* and *Psiadiella humilis* arose from within *Psiadia*.

Psiadia ageratoides (DC.) Nesom, **comb. nov.** *Conyza ageratoides* DC., Prodr. 5: 385. 1836.

Other species of *Conyza* in Madagascar (at least those in Fig. L, p. 255, of Humbert 1960), probably also belong in *Psiadia*.

Psiadia humilis (Humbert) Nesom, **comb. nov.** *Psiadiella humilis* Humbert, Mém. Soc. Linn.

Normandie 25: 39 (f. 1–10). 1923.

Welwitschiella Engler [*Welwitschiella nereifolia*]

Cyathocline Cass. (3 species, tropical Asia) was included within subtr. Grangeinae by Nesom and Robinson (2007) but evidence now shows that it is a member of tribe Inuleae (Li et al. 2014).

31. HOMOCHROMINAE Benth. in Benth. & Hook., Gen. Pl. 2: 174. 1873. (syn = Feliciinae Nesom)

*Amellus group

Amellus L. [*Amellus microglossus*, *A. strigosus*, *A. tridactylus*]

Chrysocoma L. [*Chrysocoma ciliata*]

Engleria O. Hoffm.

Felicia Cass. (type = *F. tenella*) *Felicia* is polyphyletic; see summary in Brouillet et al. 2009)

Sect. Felicia [*Felicia uliginosa*, *F. clavipilosa*] (these cluster with *Nolletia*)

Sect. Neodetrus [*Felicia aethiopica*, *F. minima*, *F. namaquana*] (separate clade, sister to *Amellus*/

Polyarrhena/*Zyrphelis*/*Felicia*)

Sect. Anhebecarpaea [*Felicia echinata*] (with *Polyarrhena* and *Zyrphelis*)

Sect. Lignofelicia [*Felicia filifolia*, *F. fruticosa*, *F. linifolia*] (with *Polyarrhena* and *Zyrphelis*)

Gymnostephium Less.

Heteromma Benth.

Jeffreya Wild

Nolletia Cass. [*Nolletia chrysocomoides*]

Poecilopsis Grau [*Poecilopsis ficoidea*]

Polyarrhena Cass. [*Polyarrhena reflexa*]

Roodebergia B. Nord.

Zyrphelis Cass. (syn = *Homochroma* DC.) [*Zyrphelis decumbens*, *Z. microcephala*]

*Commidendron group

Commidendron Burch. ex DC. [*Commidendron rugosum*, *C. rotundifolium*, *C. robustum*, *C. spurium*]

Melanodendron DC. [*Melanodendron integrifolium*]

These two genera of trees, both endemic to island of Saint Helena, are evolutionary sisters — their ancestor apparently is a shrubby, *Felicia*-like species from the African mainland (Noyes & Rieseberg 1999; Eastwood et al. 2004).

32. MADAGASTERINAE Nesom, **subtr. nov.** TYPE: *Madagaster* Nesom

Subshrubs, shrubs, or small trees; leaves coriaceous, glabrous or abaxially tomentose, eglandular, venation camptodromous to brochidodromous; inflorescence terminal and 1-headed to corymboid; involucre cylindrical (*Vernoniopsis*) or campanulate (*Madagaster*, *Rochonia*); receptacles epaleate; rays white to blue (*Madagaster*) yellow (*Rochonia*), or absent (*Vernoniopsis*); disc flowers bisexual, corolla lobes

triangular to linear-lanceolate; anther thecae bases caudate; achenes oblong-cylindric to fusiform, subterete, 4–10-nerved, eglandular; pappus of barbellate bristles. *Apodocephala* differs in its punctate-glandular leaves, paleate receptacles, deeply cut disc corolla lobes, and lack of pappus. Madagascar endemics.

Morphological similarities and geography support the hypothesis that *Apodocephala* (8 species; Humbert 1960), *Madagaster* (5 species; Nesom 1993), *Rochonia* (4 species; Humbert 1960), and *Vernoniopsis* (2 species; Callmender & Phillipson 2011) constitute a monophyletic group. *Madagaster* and *Rochonia* have radiate heads and campanulate involucre, while *Apodocephala* and *Vernoniopsis* are eradiate with cylindrical involucre, but all species are trees or shrubs with coriaceous densely tomentose leaves (abaxially) and caudate anther thecae.

Madagaster Nesom [*Madagaster madagascariensis*, *M. mandrarensis*]

Rochonia DC.

Vernoniopsis Humbert

Apodocephala J. Baker

Shrubs or small trees; leaves coriaceous, abaxially tomentose, punctate-glandular, venation camptodromous to brochidodromous; inflorescence densely corymboid; involucre cylindrical to campanulate; receptacles paleate; ray flowers absent; disc flowers few, corolla lobes narrowly lanceolate, cut to very base of limb; style branches strongly recurving-resupinate, collecting appendages ovate-deltate to linear-lanceolate, ca. 1/3–1/5 the length of the branches, branches internally papillate; anther thecae dark purplish, bases caudate, apical appendages white; achenes prismatic, 2–4-nerved, stipitate-glandular distally; pappus absent. 8 species, Madagascar.

Apodocephala was rejected as a member of Astereae by Nesom (1994a) and later unclaimed by any tribe, not included in a recent conspectus of the family (Kadereit & Jeffrey 2007). Humbert (1960), however, placed it as Astereae and given its overall similarity to the other Magasterinae genera, especially *Vernoniopsis*, probability is high that he was correct.

33. MAIRIINAE Nesom, **subtr. nov.** TYPE: *Mairia* Nees

Perennial herbs from woody rhizomes with succulent roots; stems scapose; leaves coriaceous to succulent or subsucculent, in a basal rosette, glandular or eglandular; heads 1 or less commonly 2–8, involucre mostly campanulate, 15–35 mm wide; phyllaries in 3–4(–6) weakly graduate series; receptacles epaleate; ray flowers with staminodes, ligules 3–5 mm wide, weakly coiling, white or pink to violet, staminodes nearly always present; disc flowers bisexual, thecae bases short-caudate, style branches with deltoid to triangular apical appendages; achenes narrowly fusiform to cylindrical, (2–)4–7 nerved, punctate-glandular, sometimes strigose-sericeous; pappus 2-seriate, inner series of plumose bristles basally smooth or barbellate and coherent in a ring, outer series of long scales or reduced barbellate or plumose bristles.

Mairia Nees [*Mairia hirsuta*]

Mairia comprises 6 species (Herman & Zinnecker-Wiegand 2016), all endemic to coastal or near-coastal localities along the southern tip of South Africa.

34. PTERONIINAE Nesom, **subtr. nov.** TYPE: *Pteronia* L.

Evergreen shrubs, punctate-glandular or eglandular; leaves mostly opposite but sometimes alternate, linear to oblanceolate or ovate-oblong, often fleshy; heads discoid (ray flowers absent) on short peduncles, solitary or usually in corymbs; involucre campanulate to cylindrical, phyllaries graduate and densely imbricate; receptacles epaleate; disc corollas usually yellow, sometimes white; style branches with deltate to triangular collecting appendages; anther thecae mostly obtuse at base; achenes often contracted at apex, villous to glabrous, glandular or eglandular; pappus bristles 2-seriate, barbellate, often basally connate or scale-like and broadened.

Pteronia L. [*Pteronia camphorata*, *P. uncinata*, *P. glomerata*, *P. incana*]

The genus comprises about 80 species (Bello et al. 2020) of southern Africa (Angola, Botswana, Lesotho, Namibia, South Africa, Swaziland, Zambia, Zimbabwe). The greatest concentration occurs in the Cape Floristic Region and the Succulent Karoo of South Africa and Namibia. Kolberg and Van Slageren (2014) recognized 24 species in Namibia.

35. PRINTZIINAE Nesom, **subtr. nov.** TYPE: *Printzia* Cass.

Shrubs; leaves coriaceous, tomentose abaxially; heads solitary on short peduncles; involucre cylindrical; phyllaries 4–6-seriate, subequal; receptacle flat, epaleate; ray flowers 1-seriate, ligulate, purple or blue to white or yellowish, often coiled, rarely filiform, staminodes sometimes present; disc flowers bisexual, corollas yellow; anther thecae with long tails; style appendages lanceolate; achenes ellipsoid, mostly terete, multinerved, strigose, glandular; pappus of barbellate to subplumose bristles in 1–2 series.

Printzia Cass. [*Printzia polifolia*]

Six species, South Africa and LeSotho.

Printzia and *Denekia* are sister taxa in the analysis of Brouillet et al. (2009), at the very base of the Astereae. They are disparate in morphology (Figs. 4–12, below) — *Printzia* is generalized in morphology while *Denekia* is specialized. Species of both genera have tomentose abaxial leaf surfaces, tailed anthers, and subplumose to plumose pappus bristles, but otherwise their close common ancestry is hard to imagine.

Similarity in aspect of *Printzia* to *Rochonia*, *Madagaster* (Madagascar), *Diplostephium* (South America), and *Olearia* (Australia, New Zealand) suggests that features of these species are primitive for the tribe. As noted by Bayer and Cross (2002), in the protologue Cassini observed close similarities to *Olearia* and *Chilotrimum* but *Printzia* differs from these in pollen type and style branch morphology

36. DENEKIINAE Nesom, **subtr. nov.** TYPE: *Denekia* Thunb.

Perennial herbs; leaves herbaceous, tomentose abaxially; heads in dense terminal clusters of few-20; involucre cupulate-campanulate; phyllaries 1(–2)-seriate; receptacle flat, epaleate; ray flowers with short 2-lobed ligules, blue or white, without staminodes; disc flowers with sterile ovaries, corollas blue or white; anther thecae with short tails; style appendages truncate; achenes ellipsoid, sparsely pilose, eglandular; pappus a single series of apically plumose bristles.

Denekia Thunb. [*Denekia capensis*]

One species, southern Africa (Angola, Botswana, Lesotho, Malawi, Mozambique, Namibia, South Africa, Swaziland, Tanzania, and Zimbabwe).



Figure 4. *Printzia pyrifolia*. South Africa. Photo by Cameron McMaster.



Figure 5. *Printzia pyrifolia*. Sitamani near Boston, South Africa. Photo by Peter R Warren, iNaturalist.



Figure 6. *Printzia pyrifolia*. Sitamani near Boston, South Africa. Photo by Peter R Warren, iNaturalist.



Figure 7. *Printzia pyrifolia*. Sitamani, South Africa. Photo by Christeen Grant (Life Wonderings of a Nature Lover.com site).



Peter R Warren. Public Domain.

Figure 8. *Printzia auriculata*. Above the Mahai River, South Africa. Photo by Peter R. Warren, iSpot.



Figure 9. *Printzia aromatica* (above and below). Greyton Nature Reserve, South Africa. Photo by Klaus Wehrin, iNaturalist.



Figure 10. *Denekia capensis*. Connemara Lake, Zimbabwe. Photo by M. Harvey-Hyde (Flora of Caprivi).



Figure 11. *Denekia capensis*. Spitskop Nature Reserve, South Africa. Photo by "JMK" on Wikipedia.

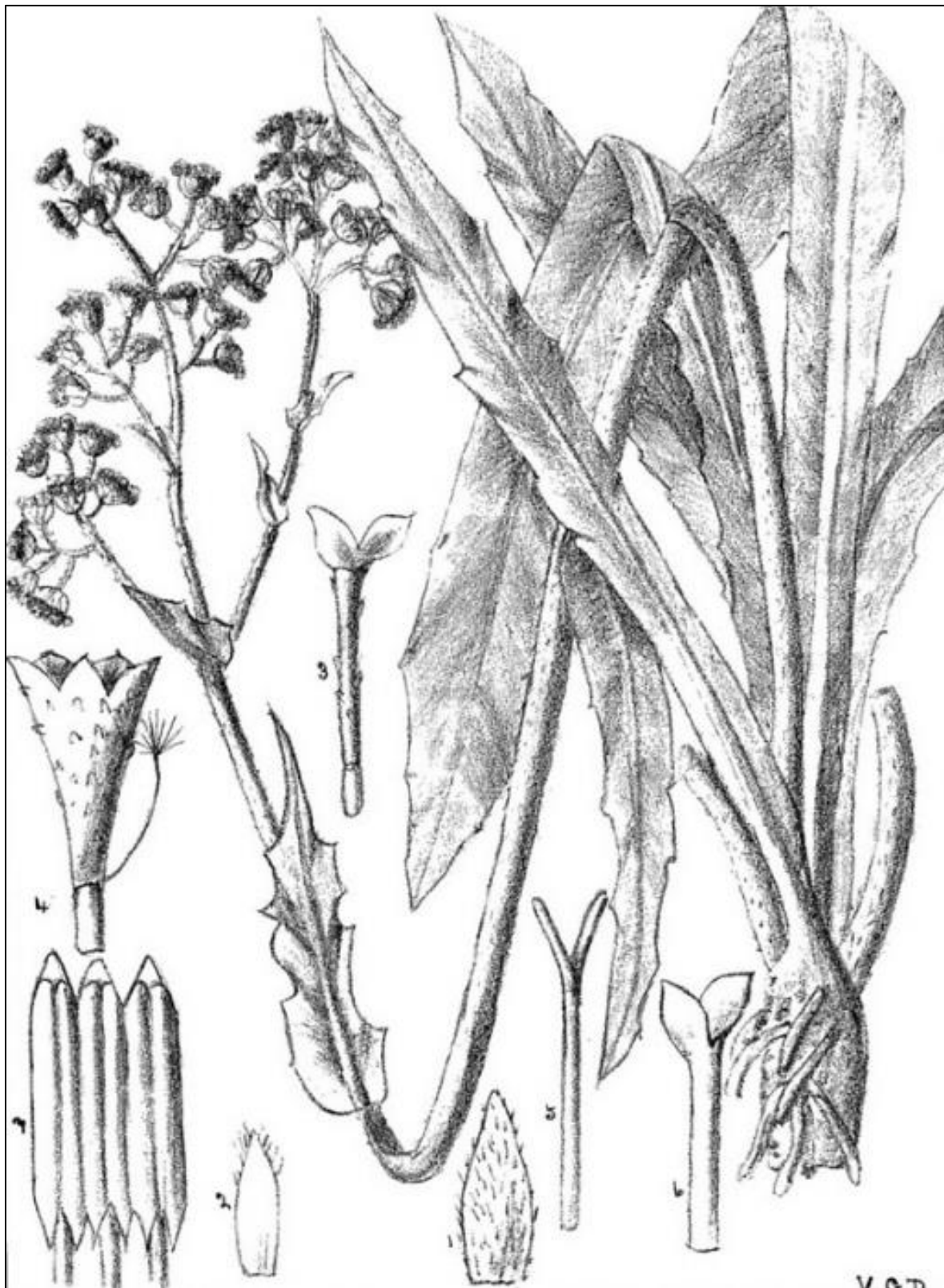


Figure 12. *Denekia capensis*. From J.M. Wood and M.S. Evans. 1898. Natal Plants: Descriptions and Figures of Natal Indigenous Plants. Natal Government and Durban Botanic Society.