REVISED SUBTRIBAL CLASSIFICATION OF ASTERAEA (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, Celmiiniinae, Chamaegerinae, Chilitrachelinae, Denekinae, Doellingeriinae, Egentinae, Eschenbachiinae, Formaniinae, Geissolepinae, Gutierreziiinae, Ionacontinae, Iranoasterinae, Olemeninae, Oritrophiinae, Madagasterinae, Mairiinae, Nannoglottidinae, Printziinae, and Pteroniinae. Six new combinations at specific rank are made: Eschenbachia gouanii (L.) Nesom, comb. nov., Eschenbachia subscaposa (O. Hofm.) Nesom, comb. nov., Eschenbachia tigrensis (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 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 Chilitrachelinae/Celmiiniinae/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.

ACKNOWLEDGEMENTS

Many thanks to Patricio Saldívia for suggestions and comments and for contribution of Celmisiniae and to Mauricio Bonifacino for contribution of Chiliotrichinae, general comments, and the stimulus toward starting this summary.

LITERATURE CITED


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.

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Table 2. Genera of Astereae.

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Nesom: Revised subtribal classification of Astereae

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Crinanthina Soják Bellidinae
Cripitotrichia Wild Grangeinae
Dacryotrichia Wild Grangeinae
Dennannenia Given Celmisinae
Dentekia Thunb. Denekiiinae
Dichactophora A. Gray Astrapthinae
Dichrocephala L'Hér. ex DC. Grangeinae
Dichromochlamys Dunlop Brachyscominae
Dieteria Nutt. Machaerantherinae
Dimorphocoma Muell. & Tate Brachyscominae
Diplostephiun Kunth Baccharidinae
Doellingeria Nees Doellingeriinae
Eastwoodia Brandeg. Solidagininae
Elegtes Cass. Elegtiinae
Elachanthis F. Muell. Brachyscominae
Engleria O. Hoffm. Homochrominae
Eoglandula Nesom Brachyscominae
Ephedrides Nesom Brachyscominae
Ericsamria Nutt. Pentachaetinae
Erigera Nut. Conyzinae
Erodiphyllum F. Muell. Brachyscominae
Eschenbacia Moench. Eschenbachiinae
Eucalphalus Nutt. Doellingeriinae
Eurybia (Cass.) Gray Machaerantherinae
Euthamia (Nutt.) Cass. Gutierreziinae
Exostigma Sancho Baccharidinae
Felicia Cass. Homochrominae
Floscaldasia Cuatrec. Baccharidinae
Flosmutisia Cuatrec. Baccharidinae
Formania W. Smith & J. Small Formaniiinae
Galatella (Cass.) Cass. Bellidinae
Geissolepis B.L. Rob. Geissolepidinae
Geothamus Nesom Asterinae
Grangea Adans. Grangeinae
Grangeopsis Humbert Grangeinae
Grauanthus Fayed Grangeinae
Griersonia Nesom Asterinae
Grindelia Willd. Machaerantherinae
Gündelachia A. Gray Gutierreziinae
Gutierrezia Lag. Gutierreziinae
Guynesomia Bonif. & Sancho Baccharidinae
Gymnosperma Less. Gutierreziinae
Gymnogynum Less. Homochrominae
Gyrodema Wild Grangeinae
Haplopappus Cass. Machaerantherinae
Haroldia Bonif. Chliotrichinae
Hazardia Greene Machaerantherinae
Heleodeaster Nesom Asterinae
Herrickia Woot. & Standl. Machaerantherinae
Heteromma Bentham Homochrominae
Heteropappus Less. Asterinae
Heteroplexis C.C. Chang Grangeinae
Heterotheca Cass. Chryspisidinae
Hinterhuberia Sch.Bip. ex Wedd. Baccharidinae
Hullsia P.S. Short Brachyscominae
Hysteronica Willd. Conyzinae
Inulopsis (DC.) O. Hoffm. Baccharidinae
Ionactis Greene Chaetopappinae
Iotasperma Nesom Brachyscominae
Iranoaster Kaz.-Osaloo et al. Iranoasterinae
Isocoma Nutt. Machaerantherinae
Isotopsis Turcz. Brachyscominae
Iteroloba Nesom Asterinae
Ixiochlamys Muell. & Sond. Brachyscominae
Jeffreya Wild Homochrominae
Kalimeris (Cass.) Cass. Asterinae
Katinasia Bonif. Chliotrichinae
Kemularia Tamamsch. Asterinae
Keysseria Lauterb. Lagenophorinae
Kieslingia Faundez et al. Chliotrichinae
Kippistia F. Muell. Brachyscominae
Kitamura Nesom Bellidinae
Lachnophyllum Bunge Chamaegereinae
Laennecia Cass. Baccharidinae
Laestadia Kunth ex Less. Baccharidinae
Lagenocypsela Swenson & Bremer
Lagenophorinae
Lagenophora Cass. Lagenophorinae
Landerolaria Nesom Brachyscominae
Lepidophyllum Cass. Chliotrichinae
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Leucosyris Greene Machaerantherinae
Linealia Nesom Brachyscominae
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Llerasia Triana Chliotrichinae
Lorandersonia Urbatsch et al. Solidagininae
Machaeranthera Nes Machaerantherinae
Madagaster Nesom Madagasterinae
Mairia Nes Mairiinae
Medranoa Urbatsch & Roberts Gutierreziinae
Melanodendron DC. Homochrominae
Metamyriactis Nesom Asterinae
Microglossa DC. Grangeinae
Microgyna Less. Baccharidinae
Minuria DC. Brachyscominae
Miyamayomena Kitam. Asterinae
Monoptilon Torr. & Gray Chaetopappinae
Mtonia Beentje Grangeinae
Muellerolaria Nesom Brachyscominae
Myriactis Less. Asterinae
Nannoglottis Maxim. Nannoglottidinae


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 Klingemb. Machaerantherinae

Novaguineia 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

Orastemma Greene Machaerantherinae

Orichropium (Kunth) Cuatrec. Oritrophiinae

Osbertia Greene Chrysopsidinae

Pachystegia Cheeseman Celmisiinae

Pacificgeron Nesom Baccharidinae

Pappochroma Raf. Brachyscominae

Parastraphia Nutt. Baccharidinae

Pentachaela 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

Poeclilepis Grau Homochrominae

Polyarthra Cass. Homochrominae

Printzia Cass. Printziinae

Psadia Jacq. ex Willd. Grangeinae

Psilactis A. Gray Symphyotrichinae

Psychogeton Boiss. Asterinae

Pteronia L. Pteroninae

Pyrocoma Hook. Machaerantherinae

Pytinacarpa Nesom Lagenophorinae

Rayjacksonia Hartm. & Lane Machaerantherinae

Remya Hillebr. ex Benth. & Hook. f. Brachyscominae

Rhamphogyne S. Moore Grangeinae

Rhinaclinidia Novopokr. Asterinae

Rhynechospermum 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

Sinonisidus 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

Thespsis DC. Eschenbachinae

Thurovia Rose Gutierrezinae

Tibetiodes Nesom Asterinae

Toiyabea Roberts et al. Solidagininae

Tomentaurum Nesom Chrysopsidinae

Tonestus A. Nels. Solidagininae

Townsendia Hook. Astrancthinae

Tracyina S.F. Blake Pentachaetinae

Trinitureybia Brouillet et al. Machaerantherinae

Tripolium Nees Bellidinae

Turczaninovia DC. Asterinae

Vernoniopsis Humbert Madagasterinae

Vittadinia A. Rich. Brachyscominae

Walshhalaria Nesom Brachyscominae

Welwitschiella Engler Grangeinae

Westoniella Cuatrec. Baccharidinae

Wollemiaster Nesom Brachyscominae

Xanthocephalum Wildl. Machaerantherinae

Xylorhiza Nutt. Machaerantherinae

Xylothamia Nesom et al. Gutierrezinae

Yonglingia Nesom Asterinae

Zyrphelis Cass. Homochrominae
SUBTRIBAL CLASSIFICATION OF ASTEREEAE

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

Astranthium Nutt. [Astranthium integrifolium]
Townsendia Hook. [Townsendia florifer]

Boltonia L'Hér. [Boltonia asteroides, B. diffusa]
Chloracantha Nesom [Chloracantha spinosa]

Chaetopappa DC. [Chaetopappa bellioides, C. effusa, C. ericoides]
Monoptilon Torr. & Gray [Monoptilon bellioides]

Bradburia Torr. & Gray [Bradburia hirtella, B. pilosa]
Croptilon Raf. [Croptilon divaricatam, C. rigidifolium]
Noticastrum DC. [Noticastrum marginatum]
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 "austrobrasilien" 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 corymbose 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 uncinate-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 *Gundellachia*), anther filaments inserted at the junction of the corolla tube and limb (vs. well below the tube apex); ray flowers yellow, rarely white; achenes suberete, (2–)4–10 nerved, sparsely to densely strigose, eglandular; pappus or bristles or scales or absent.
Amphiachyris (DC.) Nutt. [Amphiachyris dracunculoides]
Bigelowia DC. [Bigelowia nudata, B. nuttallii]
Euthamia (Nutt.) Cass. [Euthamia graminifolia, E. leptocephala, E. occidentalis, E. tenuifolia]
Gundlachia A. Gray [Gundlachia corymbosa]
Gutierrezia Lag. [Gutierrezia sarothrae, G. texana]
Medranoa Urbatsch & Roberts (incl. Chihuahua, Neonesmia, and Xylothamia) [Medranoa johnstonii, M. palmeri, M. parrasana, M. pseudobaccharis]
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 corymb; phyllaries strongly keeled, without herbaceous tips; ray
flowers 8–21, ligules violet to bluish or white, coiling; disc flowers bisexual, fertile (one species functionally
stamine); 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. stemoreres]

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.


*Basal grade

Eurybia (Cass.) Gray [Eurybia avita, E. chlorolepis, E. divaricata, E. eryngifolia, E. furcata, E.
gracilis, E. integriflora, E. paludosa, E. radulina, E. sibirica]
Herrickia Woot. & Standl. [Herrickia glaucescens, H. horrida, H. kingii, H. wasatchensis]
Oreostemma Greene [Oreostemma alpigenum, O. elatum]

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

*Machaerantha group

Dieteria Nutt. [Dieteria bigelovii, D. canescens]
Leucosyris Greene (= Arida (Hartm.) Morgan & Hartm.) [Leucosyris blepharophylla, L. parviflora,
L. riparia, L. turneri]
Machaerantha Nees [Machaerantha tanacetifolia]
Oonopsis (Nutt.) Greene [Oonopsis engelmannii, O. wardii]
Xanthisma DC. [Xanthisma blepharophyllum, X. coloradoense, X. cruchfieldii, X. gracile, X.
gynnocephalum, 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 Klingcnb.
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* Wild. [*Xanthocephalum gymnospermoides*]

*Stephanodoria* Greene [*Stephanodoria tomentella*] Monotypic.

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

*Lessingia* group

*Corethrogyne* DC. [*Corethrogyne filaginifolia*] Monotypic.

*Benitoa* Keck [*Benitoa occidentalis*] Monotypic.


12. **Oclemeniae** 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.


*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.


*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

*Chrysothamnus group
Acamptopappus (A. Gray) A. Gray  [Acamptopappus shockleyi, A. sphaerocephala]
Chrysothamnus Nutt.  [Chrysothamnus depressus, C. eremobius, C. greenei, 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
Tonsetus A. Nels.  Genus of 2 species.  [Tonsetus lyallii, T. pygmaeus].
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.

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

South America

*Baccharis group
Baccharis L.  (syns = Baccharisstrum, 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 Aztecastor, Archibaccharis, Parastrephia, and species of Diplostephiurn sensu lato among its closest woody relatives.
Exostigma Sancho  [Exostigma notobelliadstrum]
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 bartsiifolia*] Monotypic.
*Flosmutisia* Cuatr. Monotypic. Not included in molecular sampling.

*Flosmutisia* *paramicola* is distinctive in its rosulate habit, solitary heads, multiseriate rays, subbiliabiate 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. lasguei*]

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

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

*Laennecia group*
*Laennecia* Cass. [*Laennecia schiedeana, L. sophiifolia*]
*Talamancaster* Pruski (segregated from *Lagenophora*; Pruski 2017) [*Talamancaster cuchumatanica, 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. phylicaeformis, P. quadrangularis, P. teretiuscula*]

*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).

Cabreraea Bonif. [Cabreraea andina] Monotypic.
Chiliophyllum Phil. [Chiliophyllum densifolium]
Chiliotrichiopsis Cabrera [Chiliotrichiopsis keidilii, C. ledifolia, C. peruviana]
Chiliotrichum Cass. [Chiliotrichum diffusum, C. fuegoanum]
Lepidophyllum Cass. [Lepidophyllum cupressiforme]
Llerasia Triana [Llerasia lindenii, L. lucidula, L. ledifolia, L. rufescens, L. soratensis]

18. ORITROPHINAE 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. LAGENOPHORAINEsom [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-Psychogeton branch; Nesom 2020c).
Lagenocypsela Swenson & Bremer A single species, Lagenocypsela (Rhamphogyne) papuana.
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.
Pythinicarpa Nesom
Solenogyne Cass. (type = Solenogyne belliioides) [Solenogyne gunnii, S. dominii, S. belliioides, S. mikadot] Also [Lagenophora gracilis, L. lanata, and L. huegelii], which apparently form part of Solenogyne rather than Lagenophora; see Lagenophora.

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 ferrugineous tomentum in most of the species (hairs long aspetate, 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 epiulate, 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 Australasian.


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]


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. cheesemani, 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.


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*


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 cauleine and evenly spaced, narrowly lanceolate, 3-nerved, glaucous and succulent, glabrous, eglandular; involucres 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

Ixiochlamys Sond. [Ixiochlamys cuneifolia, I. filicifolia]

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

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. muiensis]

Three species in Hawaii. The only genus of Brachyscominae 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. Asterotriches is monophyletic, while the taxonomic status of various subgroups of sect. Eriotriches (Nesom 2020n) remains to be resolved. It seems likely that "clade A" sect. Eriotriches (as a whole or in parts) and sect. Asterotriches will be recognized at generic rank apart from Olearia. The placement of Olearia tomentosa (the type of the genus, with "T-shaped" hairs, sect. Dicerotriches) 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. Asterotriches species.

sect. Olearia (formerly sect. Dicerotriches) [O. tomentosa]


*unresolved — Olearia segregates (Nesom 2020n)

Landerolaria Nesom [Landerolaria stuartii] 10 species.

Neolaria Nesom [Neolaria ferresii] 3 species.

Phaseolaria Nesom [Phaseolaria elliptica] 3 species.
Muellerolaria Nesom [Muellerolaria rudis, M. picridifolia] 2 species.
Eoglandula Nesom [Eoglandulosa glandulosa] 2 species.
Vicinia Nesom [Vicinia ciliata] 2 species.
Ephedrides Nesom  Ephedrides trifurcata, not included in molecular sampling.  Monotypic.

EURASIA


A. ASTERINAE-PHYCROGETON branch

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

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

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

*Callistephus group
Callistephus Cass. [Callistephus chinensis]
Cordiofontis Nesom [Cordiofontis (Aster, Kalimeris) longipetiola]

Cordiofontis longipetiola (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 Keyssera (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

*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
Chlamydites J.R. Drummond  (syn = Wardaster J. Small; W. lanuginosus = Aster neolanuginosus
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 centraliasiaticus, 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).
Chaochienchangia Nesom  [Chaochienchangia (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, 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
Heteropappus Less. [Aster altaicus, A. asagrayi, A. crenatifolius, A. hispidus, A. kantoiensis]
Aster sect. Ageroides (Kitam.) Nesom sensu stricto [Aster ageroides var. lasiocladus, A. oliganthus, A. saxicola]
Aster, sect. Ageroides clade [A. fanjingshanicus]
Aster, sect. Ageroides clade [A. brevicaulis, A. dianchuanensis, A. handelii, A. homochlamydeus, A. tongolensis]
Aster, sect. Ageroides clade [A. heterolepis, A. smithianus]
Aster, sect. Ageroides clade [A. dolichopodus, A. mangshanensis, A. oreophilus]
Aster, sect. Ageroides clade [A. soulier]
Aster, sect. Ageroides 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]

*Bellis group
Bellis L.
Bellium L.
Bellidiastrum Scop.

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

*Galatella group
Crinitina Sojak [Crinitina linosyris]
Tripolium Nees [Tripolium linosyris = 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 glehnnii = Aster glehnnii]

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 Kitamura 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. keredensis, C. oligocephalus*

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

The two species of *Lachnophyllum* are highly distinct from each other in morphology — *L. noaeanum* 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. noaeanum* with *Chamaegeron* but *L. gossypinum* within the Callistephinae, suggesting that its genome has been influenced by ancient hybridization/ introgression events.

25. **FORMANINAE** 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; involucres cylindric; phyllaries in 4 strongly graduate series, scarious, stipitate-glandular and resinous, with a green apical patch; receptacles fimbrillate, 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*, Chliotrichinaceae and Celmisiaceae, 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.-Osaloo

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, involucres 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) bacthiaricus, 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. ravida) or perennial herbs, stipitate-glandular; basal leaves large, petiolate, margins evenly sharp-dentate, cauline leaves reduced, sessile, decurrent to claspings; heads relatively large, solitary (N. ravida) or loosely corymbose; 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 ravida, 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; involucres 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, Tanzania, Transvaal, Zambia); revised by Lippert (1973) as Aster.

29. ESCHENBACHINAE 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, elongate; 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.


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


*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. boivinii*, *P. callocephala*, *P. insignis*, *P. montana*, *P. laurifolia*, *P. reticulata*, *P. rivalsii*, *P. salaziana*, *P. sericea*]

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


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 pyrrhopappa*, *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:

[Sarcanthenum 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.


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. Neodetris [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]

Poeciliopsis Grau [Poeciliopsis ficoidea]

Polyarrhena Cass. [Polyarrhena reflexa]

Koodebergia 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 corymboide; involucres cylindrical (Vernoniopsis) or campânulate (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; Callmander & Phillipson 2011) constitute a monophyletic group. *Madagaster* and *Rochonia* have radiate heads and campanulate involucres, while *Apodocephala* and *Vernoniopsis* are eradiate with cylindric involucres, 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 campodromous to brochidodromous; inflorescence densely corymboid; involucres cylindric 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 sub succulent, in a basal rosette, glandular or eglandular; heads 1 or less commonly 2–8, involucres 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 cylindric, (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 corymb; involucres campanulate to cylindric, 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]*


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

Shrubs; leaves coriaceous, tomentose abaxially; heads solitary on short peduncles; involucres cylindric; 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 *Chiliotrichum* 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; involucres 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).
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 Wehrlin, 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.