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Taxonomic novelties in the *Asteraceae–Inuleae* with the description of a new genus, *Galgera* separate from *Laggera*

Arne A. Anderberg¹ & Annika Bengtson¹

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Abstract: Phylogenetic analyses of DNA sequences from the plastid gene *ndhF* from a large number of species of the *Asteraceae* tribe *Inuleae* reveal the need for some taxonomic and nomenclatural changes. The genera *Laggera*, *Pentanema* and *Pluchea* as presently understood are all polyphyletic. It is concluded that the old name *Vicoa* should be used for three species of *Pentanema*, and a new species of the genus is described. Two species of *Cyathocline* (previously recognized as a genus in the tribe *Astereae*) are confirmed to be close to *Blumea* of the *Inuleae–Inulinae* and are included here in the latter genus, requiring a new combination. The new genus *Galgera*, sister to *Antiphonia*, is described for a former *Laggera* species.

Keywords: *Asteraceae*, *Blumea*, *Compositae*, *Cyathocline*, *Inuleae*, *Laggera*, *ndhF*, new genus, *Pentanema*, phylogenetic analysis, taxonomy, *Vicoa*

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Introduction

The *Asteraceae* tribe *Inuleae* has been subject of study over a number of years, resulting in a fairly good understanding of generic interrelationships therein. Morphological investigations of floral microcharacters and analyses of DNA sequence data have played important roles in achieving the present picture. In molecular analyses (Pornpongrueng & al. 2007; Englund & al. 2009; Nylinder & Anderberg 2015; Nylinder & al. 2016; Gutiérrez-Larruscain & al. 2018), new information on generic relationships within the tribe emerged. One of the major clades of the *Inuleae–Plucheinae* in Nylinder & Anderberg (2015) may be referred to as the “Plucheoid” clade, a diverse group comprising a number of intermingled genera. The apparent paraphyly of the large and morphologically diverse genus *Pluchea* Cass. is a matter that would need future consideration, particularly with respect to *Tessaria* Ruiz & Pav. (a name that has priority over *Pluchea*). Apart from the *Pluchea* problem, taxonomic problems relating to the genera *Laggera* Sch. Bip. ex Benth. & Hook. f. and *Pentanema* Cass. have also emerged. Molecular analyses have shown both *Laggera* and *Pentanema* to be polyphyletic (Nylinder & Anderberg 2015; Gutiérrez-Larruscain & al. 2018), and the taxonomic problems are discussed here. *Cyathocline*

Cass. was transferred from *Astereae* to *Inuleae* by Li & al. (2013), but the study included only one species and the position of *Cyathocline* is tested here. Based on the results of the present study, and those of previous phylogenetic analyses of the *Asteraceae–Inuleae*, one new genus is described for a former member of *Laggera*, the systematic position of *Cyathocline* is accepted as closely related to *Blumea* DC., and one new species of the genus *Vicoa* Cass. is described.

Material and methods

Taxon sampling

A total of 166 taxa, representing both *Inuleae* subtribes and selected based on earlier studies (Englund & al. 2009; Nylinder & Anderberg 2015; Gutiérrez-Larruscain & al. 2018), were included in the present study. The plastid *ndhF* region was selected and analysed to address the taxonomic problems relating to *Laggera* and *Pentanema*, as well as to test the systematic position of *Cyathocline*. Four new *ndhF* sequences were generated for this study; the remaining sequences were obtained from GenBank, most of them from the study by Nylinder & Anderberg (2015).

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Table 1. Primers used to amplify the *ndhF* region. Primers marked with an X are internal primers that were designed and used for the amplification of *ndhF* for *Cyathocline lutea*.

Primer	Sequence (5'–3')	Direction	Reference
RJ1	AGGTAAGATCCGGTGAATCGGAAAC	F	Kim & Jansen (1995)
ndhF-225R_Cya	TCCAAGACCATACATATTGATAGACAGAAC	R	X
ndhF-160F_Cya	TTCGTCGTATGTGGGCTTTTCAGAGC	F	X
ndhF-452R_Cya	GTAAC TAATCGCAACATGGAAGTACTG	R	X
ndhF-386F_Cya	ATAGTGATAATTATATGTCTCATGATCACG	F	X
ndhF-644R_Cya	TCAAGTTATTGAATATTTGGAATAAATCACG	R	X
ndhF-628F_Cya	TTAGGCATTTTAGGATTTTATTGGGTAACG	F	X
ndhF-893R_Cya	CCCTATCAAAGATATAAAATTCATTATGTG	R	X
ndhF-861F_Cya	GTAGCAGCGGGAATTTTCTTG TAGC	F	X
ndhF16	GTAAACCTCCCATAAGCACCATATTCTGAC	R	Källersjö & al. (2000)
ndhF-1130F_Cya	GATCGTGATCCGTTATTCACTCAATGG	F	X
ndhF-1366R_Cya	CCTTCAAAGTAAGTAAATAGATCCGACAC	R	X
ndhF1260	TCTTAATGATAGTTGGTTGTATTACC	F	Eldenäs & al. (1999)
ndhF1750R-Ast2	AATTAATATAAGTATTGGGAATAACATCG	R	Nylinder & al. (2013)
ndhF-1617F_Cya	AAACATGATCCAACCCTTTCTTTCTATTCC	F	X
ndhF-1864R_Cya	AAATATTCCGAAAGAGGCTATACTACTG	R	X
ndhF-1822F_Cya	CATAAAAATTCAAACAATTCAATAGATTGG	F	X
ndhF10B	CCTACTCCATTTGGAATTCCATC	R	Källersjö & al. (2000)
ndhF1950F-Ast1	GGTTACATAGATGCCTTTTATGGAACATT	F	Nylinder & al. (2013)
ndhF5	GTCTCAATTGGGTTATATGATG	F	Olmstead & Sweere (1994)
RJ14	ACCAAGTTCAATGTTAGCGAGATTAGTC	R	Kim & Jansen (1995)
ndhF431F	GATACAAATTTATATTTTTTTGGG	F	Eldenäs & al. (1999)
ndhF520R	CAAATGCTTTTGTACAAGCATTTGCCGC	R	Anderberg & Swenson (2003)
ndhF1650F-Ast1	TATGATCCAACCCTTTMTTMTATTCC	F	Nylinder & al. (2013)

DNA extraction, amplification and sequencing

DNA was extracted from herbarium material of *Cyathocline lutea* J. S. Law ex Wight, *C. purpurea* (Buch.-Ham. ex D. Don) Kuntze, *Pentanema (Vicoa) indicum* (L.) Y. Ling and one undescribed taxon using a DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) according to the manufacturer's protocol. The plastid *ndhF* region was amplified using Hot Start Mix RTG beads (GE Healthcare, Little Chalfont, U.K.) following the standard protocol of the manufacturer, using the primers listed in Table 1 and following the thermal profile described in Bengtson & Anderberg (2018). Amplified products were purified using one portion of Exonuclease I (20 u/μl) and four portions Shrimp Alkaline Phosphatase (rSAP, 1U/μl; New England Biolabs). Purified PCR products were sequenced by MacroGen Europe (Amsterdam, the Netherlands; <https://www.macrogen-europe.com/>).

Sequences were assembled and edited using the Staden package (Staden 1996) and manually aligned using BioEdit (v.7.2.5; Hall 1999). New sequences have been submitted

to GenBank; accession numbers and voucher information are listed in Appendix 1. The *ndhF* sequence alignment is provided in Appendix 2 (see Supplemental content online).

Phylogenetic analyses

A dataset consisting of 166 accessions was assembled and analysed. Bayesian inference analyses were performed using MrBayes (v.3.2.2; Ronquist & al. 2012), using the online XSEDE platform of the CIPRES Science Gateway (Miller & al. 2010). The nucleotide substitution model was set to GTR+I+G, selected as best fit under the Akaike information criterion (AIC) as implemented in jModelTest (v.2.1.10 v20160303; Guindon & Gascuel 2003; Darriba & al. 2012). Analyses consisted of two independent runs with eight chains each, with the temperature parameter set to 0.1. The Markov chain Monte Carlo (MCMC) was run for 50 million generations, with a sampling frequency of 5000. Convergence of Markov chains was assessed in Tracer (v.1.7.1; Ram-

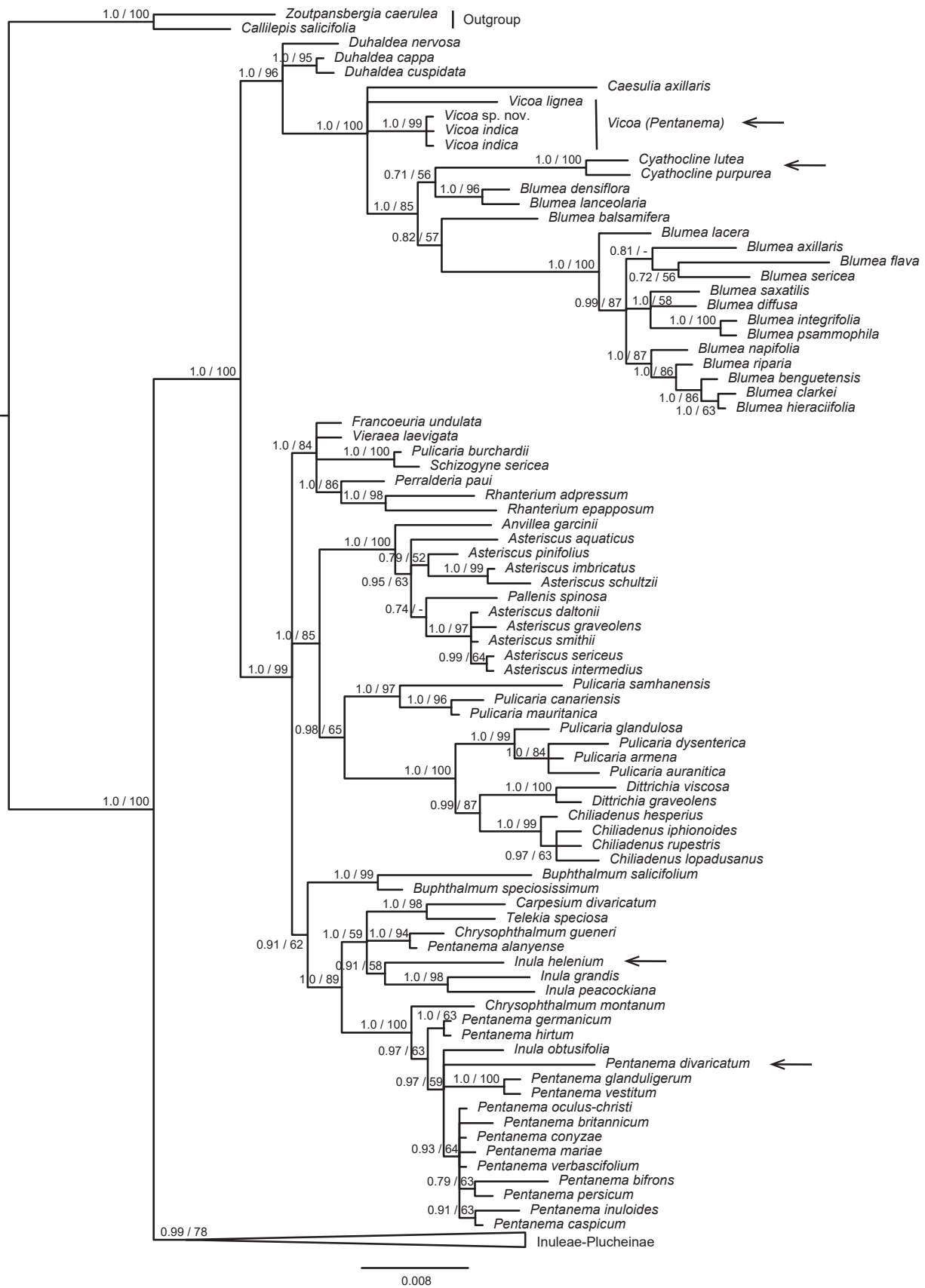


Fig. 1. Phylogeny of *Inuleae* (continued in Fig. 2). *Inuleae*–*Inulinae*. Showing position of *Vicoa* next to *Blumea*, distant from *Pentanema*, as well as systematic position of *Cyathocline* within *Blumea*. Arrows also mark the types of *Pentanema* (*P. divaricatum*) and *Inula* (*I. helenium*). Numbers at nodes indicate posterior probability (PP) and bootstrap support (BS) values; bootstrap support values <50 are indicated by a dash. Scale bar shows number of nucleotide substitutions per site.



Fig. 2. Phylogeny of Inuleae (continued from Fig. 1). Inuleae–Plucheinae. An arrow marks the position of *Galgera decurrens* (*Laggera decurrens*) as sister group of *Antiphiona* in a lineage distant from that comprising the remaining species of *Laggera* (the type, *L. pterodonta* [= *L. crispata*], also indicated by an arrow). Numbers at nodes indicate posterior probability (PP) and bootstrap support (BS) values; bootstrap support values <50 are indicated by a dash. Scale bar shows number of nucleotide substitutions per site.

baut & al. 2018), as well as by checking average standard deviation values of split frequencies. The first 25% of the trees were excluded as a burn-in phase.

Maximum parsimony analyses were conducted using PAUP (v. 4.0a169; Swofford 2002). The most parsimonious trees were searched for using a heuristic search strategy, with 10 000 random addition replicates, TBR branch-swapping and saving only a single most-parsimonious tree per replicate. Bootstrap support (BS) was estimated using 10 000 replicates, each with 10 random addition replicates, saving only the most parsimonious tree per replicate.

Callilepis salicifolia Oliv. and *Zoutpansbergia caerulea* Hutch. were selected as outgroup taxa for the analyses. All analyses were run twice, using the settings described above.

Results

The *ndhF* dataset consisted of 2257 aligned characters, 351 of which were parsimony informative. The parsimony analysis yielded 1341 most parsimonious trees, 1242 steps long (consistency index, CI = 0.55; retention index, RI = 0.89, excluding uninformative characters). Bayesian and parsimony analyses produced trees with similar topologies, with only minor differences in little-supported nodes. A fifty-percent majority-rule consensus tree from a Bayesian analysis, due to its size shown in two parts, corresponding to the different subtribes, is presented in Fig. 1 and 2.

Analyses resolved the two species of *Cyathocline* as monophyletic (posterior probability, PP = 1.0, bootstrap support, BS = 100) and placed them within the *Blumea* clade of the *Inuleae–Inulinae* (PP = 1.0, BS = 85; Fig. 1). *Vicoa* was resolved as distant from *Pentanema* (Fig. 1), with the undescribed species placed together with *V. indica* (L.) DC. (PP = 1.0, BS = 99). Analyses resolved *Laggera* as polyphyletic, with *L. decurrens* (Vahl.) Hepper & J. R. I. Wood placed as sister to *Antiphiona* Merxm. (PP = 1.0, BS = 99; Fig. 2).

Discussion

The results of the current study agree with those of earlier studies (Englund & al. 2009; Li & al. 2013; Nylander & Anderberg 2015; Gutierrez-Larruscain & al. 2018). The molecular phylogenetic analysis of the *Inuleae* was designed to address the taxonomic issues of *Cyathocline*, *Pentanema/Vicoa* and *Laggera* and the results and their implications are discussed in detail below.

Cyathocline

Li & al. (2013) showed that *Cyathocline purpurea* (*Asteraceae–Astereae*) is not a member of the tribe

and subtribe *Astereae–Grangeinae* (Fayed 1979) but instead a member of *Blumea* of the tribe *Inuleae*. *Cyathocline* differs from all other taxa of this clade by having distinctly dissected leaves. Li & al. used *trnL-F* and ITS sequences but included only this one species of the genus. The authors consequently moved *C. purpurea* to *Blumea* under the name *B. purpurea* (Buch.-Ham. ex D. Don) W. P. Li, which unfortunately is a homonym antedated by *B. purpurea* DC. from 1836. We have here tested the position of *Cyathocline* in *Blumea* by analysing *ndhF* sequence data, and also by including a second species (*C. lutea*) in the analysis. Our results corroborate the conclusion of Li & al. (2013), because both *C. purpurea* and *C. lutea* were placed in the *Blumea* clade of the *Inuleae–Inulinae* (Fig. 1). There are two further recognized species of *Cyathocline* (not seen by us), viz. *C. manilaliana* C. P. Raju & R. R. V. Raju from India, which is said to resemble *C. purpurea*, and *C. birmanica* Gand. from Myanmar, said to resemble *C. lyrata* Cass. (now a synonym of *C. purpurea*). Most likely, both these species belong to the same clade as *C. purpurea* and *C. lutea* found here. The new combination *Blumea lutea* (J. S. Law ex Wight) K. C. Mohan has already been published for *C. lutea*, but because Li's combination *B. purpurea* is illegitimate (as a later homonym), a new name is required. Among the many synonyms of *C. purpurea*, many have epithets that have already been used for *Blumea* species. Therefore, it seems that "*Tanacetum gratum* Wall." and *C. stricta* DC. are the oldest available names that could be used. Both were published by Candolle, but "*T. gratum*" not validly so because it was merely cited as a synonym under *C. lyrata*. Therefore, we find that the oldest available basionym for the new combination in *Blumea* would be *C. stricta*.

***Blumea stricta* (DC.) Anderb. & Bengtson, comb. nov.**
 ≡ *Cyathocline stricta* DC., Prodr. 5: 374. 1836. – Lectotype (designated by Fayed 1979: 514): "342. *Tanacetum viscosum* Wall. in herb. F. *Artemisia stricta* herb. Heyne" (G-DC G00452565); isolectotype: Herb. Heyne in Herb. Wallich, Kew no. 3232.F (K-W K001118872).

= *Tanacetum purpureum* Buch.-Ham. ex D. Don, Prodr. Fl. Nepal.: 181. 1825 ≡ *Cyathocline purpurea* (Buch.-Ham. ex D. Don) Kuntze, Revis. Gen. Pl. 1: 333. 1891
 ≡ *Blumea purpurea* (Buch.-Ham. ex D. Don) W. P. Li in Pl. Syst. Evol. 300: 603. 2013, nom. illeg. [non *Blumea purpurea* DC., Prodr. 5: 443. 1836]. – Type: according to the protologue, the species was collected by Hamilton in Nepal, but no specimens could be traced.

= *Cyathocline lyrata* Cass. in Ann. Sci. Nat. (Paris) 17: 420. 1829 [non *Blumea lyrata* (Kunth) V. M. Badillo in Bol. Soc. Venez. Ci. Nat. 10: 257. 1946]. – Type: according to the protologue, only a few capitula were collected by Reynaud from Pégu (Bago, Myanmar), but no specimens could be traced.

- “*Tanacetum viscosum* Wall.” Wallich, Numer. List: no. 3232. 1831, nom. inval., nom. nud.
- “*Tanacetum gratum* Wall.” Candolle, Prodr. 5: 374. 1836, nom. inval., pro syn.

Pentanema/Vicoa

Ling (1965) synonymized *Vicoa* with *Pentanema* (*Inuleae–Inulinae*), and until recently the genus was considered to be comprised of predominantly low, woody dwarf shrubs with small capitula and few capillary pappus bristles, although the two species *P. divaricatum* Cass. and *P. vestitum* (Wall. ex DC.) Y. Ling differ by being herbaceous. The distinction between *Pentanema* and *Vicoa* has been unclear, and the opinion has varied regarding what name to use for plants with inuloid habit and few pappus bristles. Russian authors, viz. B. A. Fedtschenko and O. A. Fedtschenko (Consp. Fl. Turkestanicae 4: 174. 1911), S. G. Gorschkova (Fl. URSS 25: 479. 1959), R. V. Kamelin (Fl. Sist. Vyssh. Rast. 1: 177. 1933), G. K. Kinzikaëva (Fl. Tadzhikskoi SSR 9: 528, 312. 1988), I. M. Krascheninnikov (Fl. Sist. Vyssh. Rast. 1: 177. 1933), M. M. Nabiev (Opred. Rast. Sred. Azii 10: 462. 1993) and S. A. Nevski (Fl. Sist. Vyssh. Rast. 4: 280. 1937) have described several species from C Asia either as *Vicoa* or as *Pentanema*, and in some cases transferred species from one genus to the other. The analyses by Pornpongrungrueng & al. (2007), Englund & al. (2009) and Nylander & Anderberg (2015) showed that *P. indicum* (former genus *Vicoa*) and *P. ligneum* Mesfin belong to a lineage more closely related to *Blumea* and *Duhaldea* DC. than to the type of *Pentanema* (*P. divaricatum*), hence meriting recognition of *Vicoa* as a genus separate from *Pentanema*. Englund & al. (2009) also showed that *Inula* L. was paraphyletic, with most species belonging to another clade than *I. helenium* L. (the type of *Inula*). This led Gutiérrez-Larruscain & al. (2018) to transfer a large number species from *Inula* to *Pentanema*, and they also reinstated the genus *Vicoa*. Most C Asian species named *Vicoa* belong to the group today known as *Pentanema* and not to the same clade as the type of *Vicoa* (*V. auriculata* Cass. = *V. indica* [= *P. indicum*]).

Vicoa now counts the following species: (1) *V. indica* (L.) DC. (= *Inula indica* L. = *Pentanema indicum* (L.) Y. Ling = [among others] *Inulaster kotschyi* Sch. Bip., *V. auriculata* Cass. and *V. leptoclada* (Webb) Dandy = *Inula leptoclada* Webb); (2) *V. cernua* Dalzell (= *P. cernuum* (Dalzell) Y. Ling = *V. gokhalei* Gosavi & al.); (3) *V. lignea* (Mesfin) D. Gut. Larr. & al. (= *P. ligneum* Mesfin); (4) *V. sahyadrica* Nandikar & Sardesai.

Our analyses support the separation of *Vicoa* from *Pentanema* (Fig. 1), and we have also found a yet undescribed species from China belonging to the *Vicoa* clade (*V. anisopappoides* Anderb. & Bengtson, described below). In our study, *V. anisopappoides* and *V. indica*

group together (Fig. 1). The morphologically similar species *V. cernua* is most likely a close relative of *V. indica*, as is the recently described *V. sahyadrica* from India (Nandikar & Sardesai 2021). *Vicoa* is placed here in an unresolved clade together with the *Blumea* clade, the monotypic genus *Caesulia* Roxb., and the Somalian *V. lignea* (Fig. 1). In Pornpongrungrueng & al. (2007), analyses of ITS and plastid data placed *P. cernuum*, *P. indicum* and *P. ligneum* together in a clade sister to *Caesulia* and the *Blumea* clade. *Vicoa indica* has a distribution in tropical and subtropical regions from W Africa to China. *Vicoa cernua* is found in similar conditions from Pakistan to SE Asia, *V. sahyadrica* is endemic to India and *V. lignea* is endemic to Somalia. The new species *V. anisopappoides* is known only from Yunnan in China.

Vicoa anisopappoides Anderb. & Bengtson, **sp. nov.** – Fig. 3–5.

Holotype: China, Yunnan, nearby Yisa city, Yisa, Honghe county, dry and hot grassy slope, 900 m, 9 Mar 2007, PH & al. 6033 (S S07-16156).

Description — Perennial herb. *Leaves* alternate, narrowly elliptic, xeromorphic, somewhat bullate, with revolute margin, dark green and scabrid on upper surface, white tomentose on lower surface. *Capitula* in loose terminal corymbs, heterogamous. *Involucral bracts* in c. 3 rows, narrowly triangular, glandular hairy. *Receptacle* epaleate. *Outer florets* female, radiate; corolla yellow; ray lamina 3-dentate; *achene* hairy, epappose. *Disc florets* hermaphroditic, tubular; corolla yellow; *style* with acute sweeping-hairs not reaching furcation; *anthers* tailed, with rounded apical appendage and endothelial tissue with radial wall thickenings; *achene* ellipsoid, with elongated twin hairs; *pappus* with c. 10 barbellate capillary bristles.

Remarks — *Vicoa anisopappoides* differs from other species of *Vicoa* in having heterogamous radiate capitula with epappose ray achenes, together with narrowly elliptic, xeromorphic, bullate, scabrid, revolute leaves white tomentose underneath. At first glance, the new species may show some resemblance to *Anisopappus chinensis* Hook. & Arn. but is easily distinguished by its epaleate receptacles and disc floret achenes with long capillary pappus bristles.

Laggera

Laggera Sch. Bip. ex Benth. & Hook. f., Gen. Pl. 2: 290. 1873. – **Type (designated here):** *Laggera pterodonta* (DC.) Sch. Bip. ex Oliv. in Trans. Linn. Soc. London 29: 94. 1873 = *Blumea pterodonta* DC. in Wight, Contr. Bot. India: 16. 1834. – **Lectotype (designated here):** Peninsula Ind. orientalis, Wight 1437 (K K000974744).

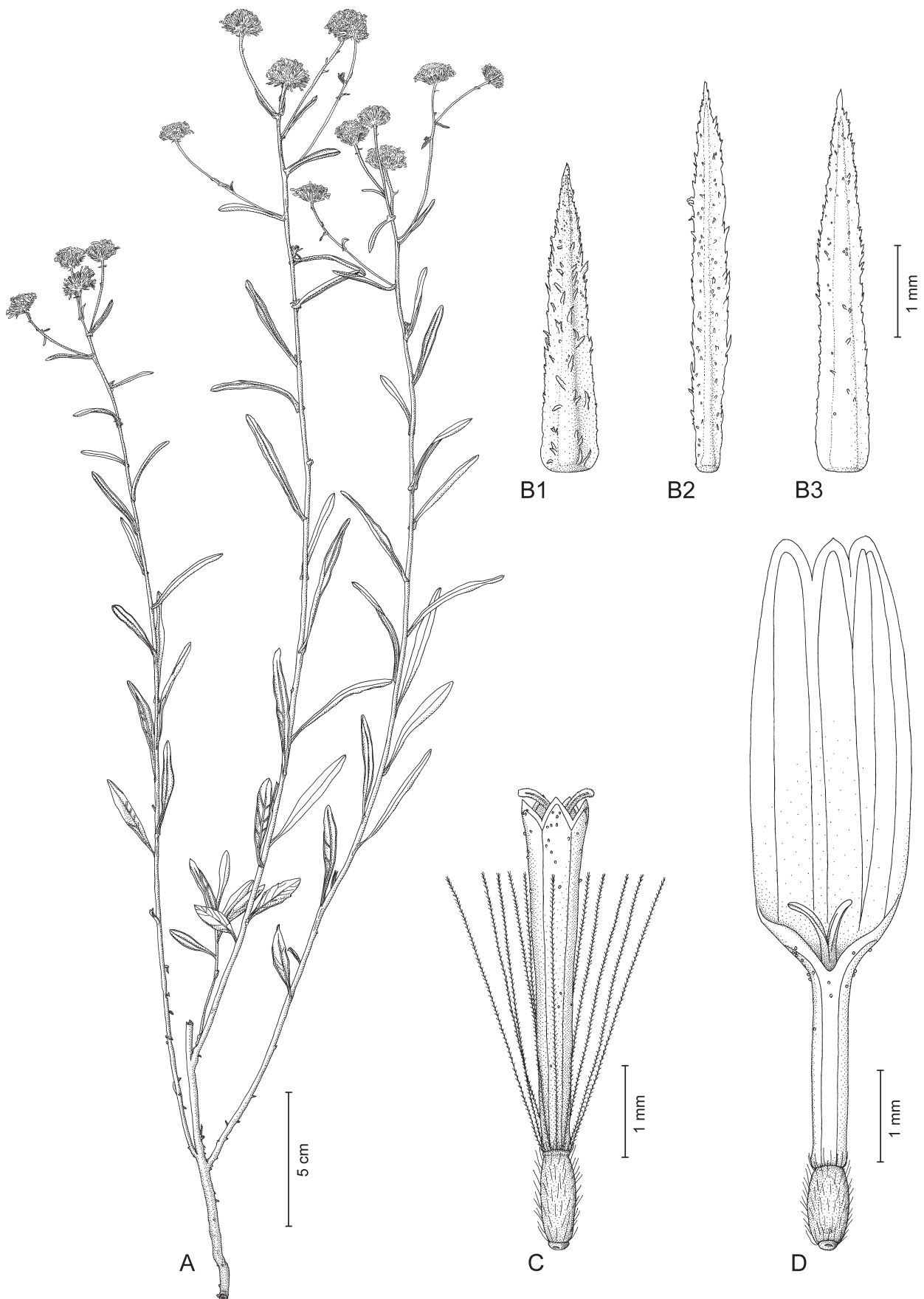


Fig. 3. *Vicoa anisopappoides* – A: habit of plant; B1–B3: involucre bracts; C: disc floret; D: ray floret. – A–D: from the holotype, PH & al. 6033 (S S07-16156), drawn by Jennifer Kearey.



Fig. 4. *Vicoa anisopappoides* – A: capitulum and revolute leaves; B: synflorescence with three capitula; C: xeromorphic leaves with bullate, scabrid upper surface, revolute margins and white tomentose lower surface. – A–C: from the holotype, *PH & al.* 6033 (S S07-16156), photographs by Jennifer Kearey.

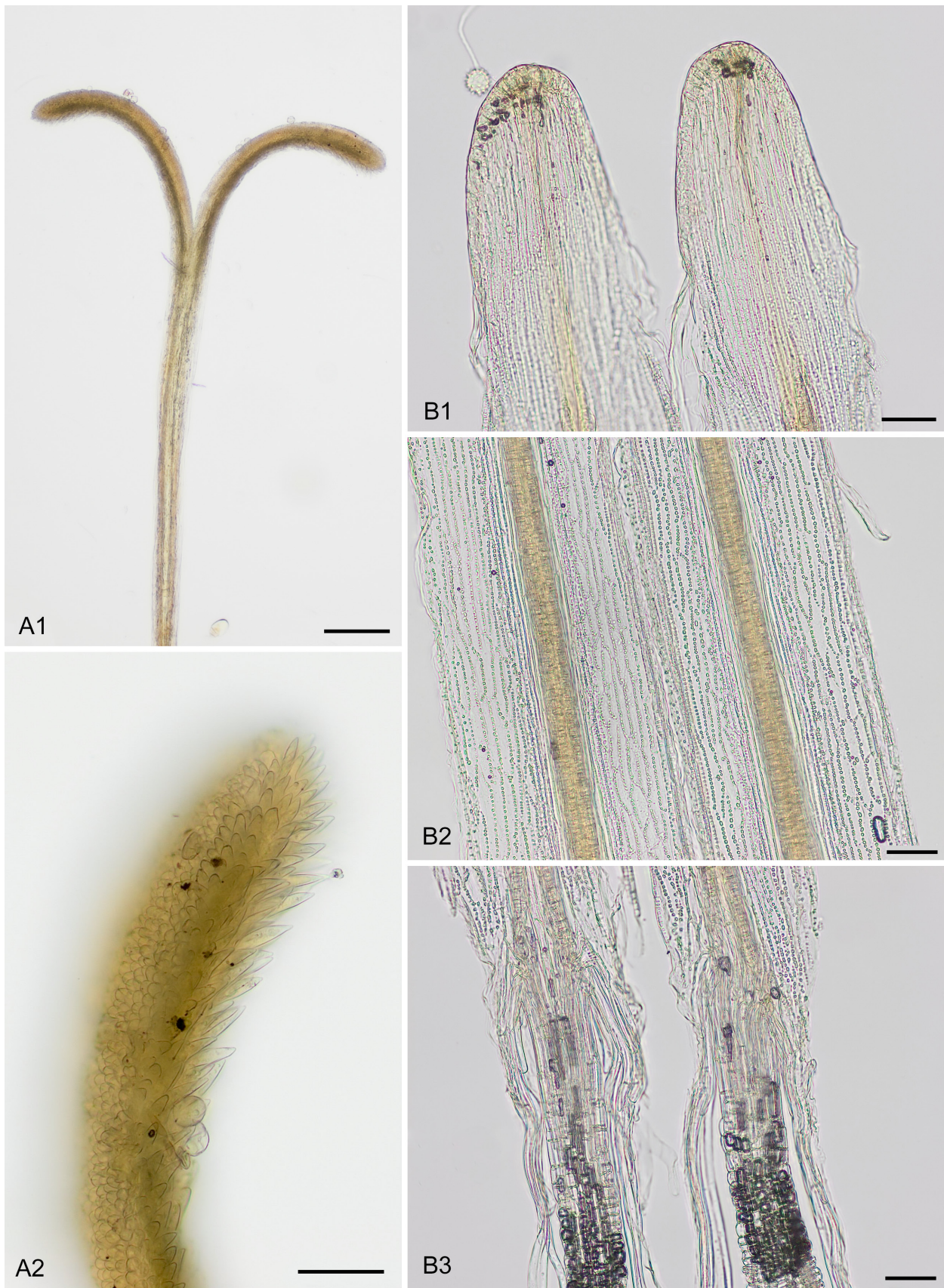


Fig. 5. *Viccoia anisopappoides*, floral microcharacters – A: style; A1: style branches with sweeping-hairs confined to distal portion of branches; A2: style branch showing acute sweeping-hairs; B: anthers; B1: rounded anther apex; B2: endothecial tissue with radial wall-thickenings; B3: well-developed anther tails. – Scale bars: A1 = 200 μm ; A2, B1–3 = 50 μm . – A, B: from the holotype, *PH & al.* 6033 (S S07-16156), photographs by Lars Hedenäs.



Fig. 6. *Galgera decurrens* – Namibia, Caprivi Strip, Bukalo, 31 Jan 2018. – Photograph by Bart Würsten.

This genus is a member of the *Inuleae–Plucheinae* related to, e.g., *Nicolasia* S. Moore and *Doellia* Sch. Bip. ex Walp. in the large “Pluchoid” clade mentioned above (Nylinder & Anderberg 2015; Fig. 2). *Laggera* species (Anderberg 1991) have winged stems or at least long decurrent leaf bases, florets with purple or pink corollas, and styles with obtuse sweeping-hairs extending below the bifurcation. Nylinder & Anderberg (2015) found that *Laggera* was polyphyletic as presently circumscribed because one of its species, viz. *L. decurrens*, belongs in a different clade within the subtribe. Apart from its distant relationships to other species of *Laggera*, *L. decurrens* also differs from them in morphology by having capitula with yellow corollas, tailed anthers with polarized endothelial tissue wall thickenings, and styles with acute sweeping-hairs ending above the bifurcation. It is here found as sister to *Antiphiona* close to the *Geigeria–Ondetia* and *Calostephane–Pegolettia* clades (Fig. 2). In Nylinder & Anderberg (2015) the *Geigeria–Ondetia* pair is sister to *Antiphiona–Laggera decurrens*. Like *Antiphiona*, these were formerly members of the *Inuleae–Inulinae*. They have florets with yellow corollas (purple with yellow tips in *Antiphiona*), styles with acute sweeping-hairs ending above the bifurcation (below in *Geigeria* Griess.) and polarized endothelial tissue. In these respects, they correspond well with the character

states in *L. decurrens*. The reason *L. decurrens* has been placed with *Laggera* may have been its decurrent leaves and filiform female marginal florets, but neither of these character states is unique to *Laggera*; they occur here and there in the *Inuleae*. Filiform female florets are found in, e.g., *Blumea* and winged stems in, e.g., *Calostephane* Benth., *Geigeria* and *Ondetia* Benth. Given the present results, we conclude that *L. decurrens* cannot remain in *Laggera*, but also that it would be an odd addition to the small and morphologically homogeneous *Antiphiona* with its homogamous capitula, florets with purple corollas and non-decurrent, pinnatifid or bipinnatifid leaves. Therefore, we describe it here as a new genus.

***Galgera* Anderb. & Bengtson, gen. nov.**

Type: *Galgera decurrens* (Vahl) Anderb. & Bengtson.

Description — Branched, aromatic annual to perennial herb, sometimes more than 1 m tall. *Stems* and leaves grey, densely silky tomentose. *Leaves* alternate, narrowly elliptic, 1–5 cm long, 2–7 mm wide, base long decurrent on stem (therefore stem often winged, wings entire, to 3 mm wide), margin entire, apex acute to obtuse. *Capitula* heterogamous, solitary or in terminal corymbs, cylindric, often somewhat wider at base, 5–8 mm long. *Involucral bracts* narrow, in several rows. *Receptacle* epaleate. *Florets* with yellow (sometimes whitish) corollas; outer florets female, numerous, with filiform corolla, achenes similar to those of disc florets; disc florets hermaphroditic, fewer than outer florets, with narrowly campanulate corolla. *Anthers* tailed; endothelial tissue polarized. *Style* with acute sweeping-hairs not reaching bifurcation. *Achenes* narrowly cylindric, c. 1 mm long, with elongate twin-hairs; epidermis without elongate oxalate crystals; *pappus* of 3–5 mm long barbellate capillary bristles.

Remarks — The new genus differs from the type of *Laggera* (*L. pterodonta* = *L. crispata* (Vahl) Hepper & J. R. I Wood) and all other species of that genus by having florets with yellow corollas, tailed anthers, polarized endothelial tissue and acute stylar sweeping-hairs ending above the bifurcation. In studies of the *Inuleae*, differences in floral microcharacters have often been neglected but in retrospect demonstrated to be useful taxonomic markers, all the more in the light of DNA analyses. Examples are the separation of *Doellia* and *Pluchea incisa* Elmer from *Blumea* (Anderberg 1995, 2012). *Antiphiona*, the sister group of *Galgera*, has wingless stems, pinnatifid or bipinnatifid leaves without decurrent bases, and homogamous capitula with florets with purple corollas. In comparison, *Galgera* is characterized by entire leaves with decurrent bases, often long and forming stem wings, and heterogamous capitula with florets with yellow corollas and filiform female outer florets. The generic name is an anagram of *Laggera*.

Galgera decurrens (Vahl) Anderb. & Bengtson, **comb. nov.** [Fig. 6] ≡ *Erigeron decurrens* Vahl, Symb. Bot. 1: 72. 1790 ≡ *Conyza arabica* Willd., Sp. Pl. 3: 1949. 1803 [non *Conyza decurrens* L., Sp. Pl., ed. 2, 2: 1206. 1763] ≡ *Laggera arabica* (Willd.) Deflers, Voyage Yemen: 149. 1889 ≡ *Laggera decurrens* (Vahl) Hepper & J. R. I. Wood in Kew Bull. 38: 84. 1983 ≡ *Blumea decurrens* (Vahl) Merxm. in Mitt. Bot. Staatssamml. München 20: 5. 1984. – Holotype: Arabia, *Forsskål* (C).
= *Blumea gariepina* DC., Prodr. 5: 448. 1836. – Holotype: Garip, bei Verleptpram, am Ufer des Flusses, *J. F. Drège* 2722 (G-DC G00456270; isotypes: in many herbaria, e.g. P P032406, P P032407, P P032408, S S07-9874, S S07-9875).
– “*Laggera gariepina*” Randeria in *Blumea* 10: 298. 1960, nom. inval.

Author contributions

AAA designed the study. AB assembled the dataset and analysed the data. AAA wrote the manuscript with contributions from AB.

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Appendix 1

Voucher information and GenBank accession numbers for sequences used in the phylogenetic study. An asterisk (*) indicates sequences generated for this study.

Adelostigma senegalensis Benth., *Jaeger* 8125, LN607597; *Allopterigeron filifolius* (F. Muell.) Dunlop, *Short & Dunlop* 4758, LN607726; *Antiphiona fragrans* (Merxm.) Merxm., *Nordenstam & Lundgren* 909, LN607598; *Antiphiona pinnatisecta* (S. Moore) Merxm., *Nordenstam & Lundgren* 678, LN607767; *Anvillea garcinii* (Burm. f.) DC., *Anderberg* 576, LN607715; *Asteriscus aquaticus* (L.) Less., *Santos-Guerra & Francisco-Ortega s.n.*, AF372670; *Asteriscus daltonii* Walp., *Bot. Gard. Bonn Index Seminum* 1995 022-11-94-10, G97036, AF372662; *Asteriscus graveolens* (Forssk.) Less., *Bot. Gard. Tel Aviv Univ. Index Seminum* 1995 s.n., AF372665; *Asteriscus imbricatus* DC., *Santos-Guerra s.n.*, AF372668; *Asteriscus intermedius* (DC.) Pit. & Proust, *Francisco-Ortega & Jansen s.n.*, AF372664; *Asteriscus pinifolius* Maire & Wilczek, *Podlech* 49163, LN607773; *Asteriscus schultzei* (Bolte) Pit. & Proust, *Santos-Guerra & Francisco-Ortega* 1996, AF372669; *Asteriscus sericeus* DC., *ex Hort. Bot. Orotava s.n.*, AF372663; *Asteriscus smithii* Walp., *Bot. Gard. Bonn Index Seminum* 1995 022-12-94-10, AF372661; *Blumea adamsii* J.-P. Lebrun & Stork, *Raynal* 12396, LN607600; *Blumea axillaris* (Lam.) DC., *Leonard* 4312, FM208906; *Blumea balsamifera* (L.) DC., *Peng & Chen* 10780, LN607601; *Blumea benguetensis* (Elmer) Matf., *Ray Ong s.n.*, LN607660; *Blumea clarkei* Hook. f., *Pornpongrungrueng* 385, FM208908; *Blumea densiflora* DC., *Pornpongrungrueng* 390, FM208909; *Blumea diffusa* R. Br. ex Benth., *Cowie & Dunlop* 8426, FM208910; *Blumea flava* DC., *Thor* 1614, LN607607; *Blumea hieracifolia* (D. Don) DC., *Pornpongrungrueng* 418, FM208911; *Blumea integrifolia* DC., *Telford* 6307, LN607602; *Blumea lacera* (Burm. f.) DC., *Thulin* 11430, LN607603; *Blumea lanceolaria* (Roxb.) Druce, *Pornpongrungrueng* 387, FM208912; *Blumea napifolia* DC., *Pornpongrungrueng* 372, FM208913; *Blumea obliqua* (L.) Druce, *Fagerlind & Klackenberg* 513, LN607599; *Blumea psammophila* Dunlop, *Wightman & Dunlop* 1287, LN607604; *Blumea riparia* DC., *Peng & al.* 15102, LN607605; *Blumea saxatilis* Zoll. & Moritz, *Cowie* 6734, LN607606; *Blumea sericea* (Thomson) Anderb. & A. K. Pandey, *Sardesai* 2547, LN607743; *Bupthalmum salicifolium* L., *Anderberg* 7292, LN607788; *Bupthalmum speciosissimum* L., *Fior s.n.*, LN607608; *Caesulia axillaris* Roxb., *Pandey* 3021, LN607609; *Callilepis salicifolia* Oliv., *Bayer SAF-01009*, LN607610; *Ca-*

- lostephane angolensis* (O. Hoffm.) Anderb., *Robinson* 6557, LN607661; *Calostephane divaricata* Benth., *Kers* 67, LN607611; *Calostephane marlothiana* O. Hoffm., *Merxmüller & Giess* 28120, LN607717; *Carpesium divaricatum* Siebold & Zucc., *Chung & Anderberg* 1422, LN607612; *Chiliadenus hesperius* (Maire & Wilczek) Brullo, *Rechinger 0-783*, LN607613; *Chiliadenus iphionoides* (Boiss. & C. I. Blanche) Brullo, *Danin s.n.*, LN607614; *Chiliadenus lopadusanus* Brullo, *Anderberg L07-01*, LN607615; *Chiliadenus rupestris* (Pomel) Brullo, *Mateo & Silvestre SS 19/8/95*, LN607616; *Chrysophthalmum gueneri* Aytac & Anderb., *Duman* 7072, LN607618; *Chrysophthalmum montanum* (DC.) Boiss., *Rechinger 11679*, LN607791; *Coleocoma centaurea* F. Muell., *Albrecht 10563*, LN607619; *Cratystylis conocephala* (F. Muell.) S. Moore, *Nordenstam & Anderberg* 604, LN607718; *Cratystylis microphylla* (F. Muell. & Tate) S. Moore, *Nordenstam & Anderberg* 613, LN607751; *Cyathocline lutea* Law ex Wight, *Stocks s.n.*, OP407670*; *Cyathocline purpurea* (Buch.-Ham. ex D. Don) Kuntze (i.e. *Blumea stricta* (DC.) Anderb. & Bengtson), *Björnsäter s.n.*, OP380578*; *Cylindrocline commersonii* Cass., *Nordenstam* 9192, LN607733; *Cylindrocline lorencei* A. J. Scott, *Friedman* 2711, LN607789; *Delamerea procumbens* S. Moore, *Le Houerou s.n.*, LN607620; *Dittrichia graveolens* (L.) Greuter, *Deschatres s.n.*, LN607621; *Dittrichia viscosa* (L.) Greuter, *Trift & al.* 22, LN607622; *Doellia bovei* (DC.) Anderb., *Kilian & Hein NK4724*, LN607772; *Doellia cafra* (DC.) Anderb., *Koekemoer* 2693, LN607721; *Duhaldea cappa* (Buch.-Ham. ex D. Don) Pruski & Anderb., *Luo* 0253, LN607713; *Duhaldea cuspidata* (Wall. ex DC.) Anderb., *Koelz* 1530, FM208928; *Duhaldea nervosa* (Wall. ex Hook. f.) Anderb., *Larsen & al.* 44933, FM208930; *Epaltes australis* Less., *Anderberg & Anderberg* 7938, LN607796; *Epaltes cunninghamii* (Hook.) Benth., *Nordenstam & Anderberg* 972, LN607714; *Epaltes divaricata* (L.) Cass., *Bremer & al.* 43, LN607799; *Epaltes gariepina* Steetz, *Wanntorp & Wannorp* 769, LN607750; *Francoeuria undulata* (L.) Lack, *Karis* 734, LN607623; *Geigeria brachycephala* Muschl., *Merxmüller & Giess* 32008, LN607628; *Geigeria chenopodiifolia* Mattf., *Krausel* 848, LN607631; *Inula grandis* Schrenk ex Fisch. & C. A. Mey., *Anders* 6663, LN607650; *Inula helenium* L., *Lindström* 93023, FM208945; *Inula obtusifolia* A. Kern., *Grey-Wilson & Hewer* 1348, LN607654; *Inula peacockiana* (Aitch. & Hemsl.) Korovin, *Rechinger* 4956, LN607656; *Iphionopsis oblanceolata* N. Kilian, *Thulin & al.* 10659, LN607782; *Iphionopsis rotundifolia* (Oliv. & Hiern) Anderb., *Thulin & Warfa* 5914, LN607657; *Karelinia caspia* (Pall.) Less., *Nikulina s.n.*, LN607658; *Laggera brevipes* Oliv. & Hiern, *LaCroix* 3960, LN607659; *Laggera crispata* (Vahl) Hepper & J. R. I. Wood, *Friis & al.* 1448, LN607780; *Laggera decurrens* (Vahl) Hepper & J. R. I. Wood (i.e. *Galgera decurrens* (Vahl) Anderb. & Bengtson), *Kilian & al.* NK 4562, LN607745; *Monarrhenus pinifolius* Cass., *Cadet* 1840, LN607742; *Monarrhenus salicifolius* Cass., *Swenson & Ulfsson* 821, LN607662; *Neojeffreya decurrens* (L.) Cabrera, *Emanuelsson* 491, LN607746; *Nicolasia coronata* Wild, *Bidgood & al.* 4080, LN607792; *Nicolasia costata* (Klatt) Thell., *Smith* 3733, LN607735; *Nicolasia felicioides* (Hiern.) S. Moore, *Robinson* 5682, LN607764; *Nicolasia heterophylla* S. Moore, *Volk* 1249, LN607747; *Nicolasia nitens* (O. Hoffm.) Leins, *Eriksson & al.* 531, LN607748; *Nicolasia pedunculata* S. Moore, *Fanshawe* 5769, LN607737; *Nicolasia stenoptera* (O. Hoffm.) Merxm., *Volk* 1403, LN607749; *Ondetia linearis* Benth., *Emanuelsson* 1021, LN607723; *Pallenis spinosa* (L.) Cass., *Karis* 951, LN607663; *Pechuel-loeschea leubnitziae* O. Hoffm., *Bremer* 455, LN607716; *Pegolettia gariepina* Anderb., *Nordenstam & Lundgren* 349, LN607727; *Pegolettia pinnatilobata* (Klatt) O. Hoffm., *Kers* 163, LN607730; *Pegolettia plumosa* M. D. Hend., *Nordenstam* 2172, LN607724; *Pegolettia retrofracta* (Thunb.) Kies, *Nordenstam* 1755, LN607664; *Pentanema alanyense* H. Duman & Anderb., *Duman* 5504, LN607719; *Pentanema bifrons* (L.) D. Gut. Larr. & al., *Barbezat s.n.*, LN607645; *Pentanema britannicum* (L.) D. Gut. Larr. & al., *Svensson AS02100*, LN607646; *Pentanema caspicum* (F. K. Blum ex Ledeb.) G. V. Boiko, *Sukhorunov s.n.*, LN607647; *Pentanema conyzae* (Griess.) D. Gut. Larr. & al., *Anderberg B01-24*, LN607648; *Pentanema divaricatum* Cass., *Rechinger* 19401, FM208978; *Pentanema germanicum* (L.) D. Gut. Larr. & al., *Segelberg* 30661/22, LN607649; *Pentanema glanduligerum* (Krasch.) Gorschk., *Rechinger* 18595, LN607720; *Pentanema hirtum* (L.) D. Gut. Larr. & al., *Greuter* 12665, LN607651; *Pentanema inuloides* (Fisch. & C. A. Mey.) D. Gut. Larr. & al., *Tsvelev* 194, LN607725; *Pentanema mariae* (Bordz.) D. Gut. Larr. & al., *Sorger & Buchner* 82 122, LN607652; *Pentanema oculus-cristi* (L.) D. Gut. Larr. & al., *Korobeynikova s.n.*, FM208954; *Pentanema persicum* (DC.) D. Gut. Larr. & al., *Akhani* 11698, LN607706; *Pentanema verbascifolium* (Willd.) D. Gut. Larr. & al., *Rechinger* 20377, LN607653; *Pentanema vestitum* (Wall. ex DC.) Y. Ling, *Axt s.n.*, LN607665; *Perralderia pauu* Font Quer, *Molero & al.* JMM 3216/1, LN607666; *Pluchea dodoneifolia* (Hook. & Arn.) H. Rob. & Cuatrec., *Novara* 5539, LN607669; *Pluchea dunlopii* Hunger, *Hunger & Kilian* 3948, LN607752; *Pluchea ferdinandi-muelleri* Domin, *Hunger & Kilian* 3828, LN607800; *Pluchea indica* (L.) Less., *Kilian & al.* NK4601, LN607728; *Pluchea kelleri* (Thell.) Thulin, *Thulin & Mohammed* 6953, LN607732; *Pluchea littoralis* Thulin, *Thulin & al.* 10634, LN607783; *Pluchea nogalensis* Chiov., *Thulin & Warfa* 6150, LN607794; *Pluchea obovata* Balf. f., *Thulin & Gifri* 8831, LN607671; *Pluchea polygonata* (DC.) Gagnep., *Hansen & Smitinand* 12728, LN607784; *Pluchea rubelliflora* (F. Muell.) B. L. Rob., *Albrecht* 10962, LN607674; *Pluchea sagittalis* (Lam.) Cabrera, *Chung & Anderberg* 1171, LN607676; *Pluchea sericea* Coville, *Davis & Lightowl-*

- ers 66328, LN607756; *Pluchea yucatanensis* G. L. Nesom, *Jones & Jones 12656*, LN607731; *Porphyrostemma chevalieri* (O. Hoffm.) Hutch. & Dalziel, *Jorgensen & al. 670*, LN607798; *Porphyrostemma grantii* Benth. ex Oliv., *Eriksson & al. 581*, LN607778; *Pseudoconyza viscosa* (Mill.) D'Arcy, *Kilian & al. NK 4607*, LN607758; *Pterocaulon pycnostachyum* (Michx.) Elliott, *Tehler & al. 162*, LN607769; *Pterocaulon redolens* (Willd.) Fern.-Vill., *Baumann-Bodenheim 6164*, LN607682; *Pterocaulon serrulatum* (Montrouz.) Guillaumin, *Nordenstam & Anderberg 302*, LN607683; *Pulicaria armena* Boiss. & Kotschy, *Sorger 84-82-6*, LN607684; *Pulicaria aurantica* Mouterde, *Rechinger 13062*, LN607685; *Pulicaria burchardii* Hutch., *Gomiz s.n.*, LN607686; *Pulicaria canariensis* Bolle, *Bremer & Bremer s.n.*, LN607687; *Pulicaria dysenterica* (L.) Bernh., *Anderberg B01-23*, LN607688; *Pulicaria glandulosa* Caball., *Gomiz s.n.*, LN607689; *Pulicaria mauritanica* Bratt., *Blanche & al. 9359*, LN607690; *Pulicaria samhanensis* N. Kilian & P. Hein, *Hein & Kilian 5591*, LN607691; *Rhanterium adpressum* Coss. & Durieu, *Anderberg 454*, LN607770; *Rhanterium epapposum* Oliv., *Nilsson & al. 16436*, LN607692; *Rhodogeron coronopifolium* Griseb., *Matos & Torres 2/22/01*, AY226799; *Sachsia polycephala* Griseb., *Gutierrez & Nilsson 6*, LN607693; *Schizogyne sericea* (L. f.) DC., *Wikstrom & al. 93*, LN607694; *Sphaeranthus africanus* L., *Fagerlind 4514*, LN607695; *Sphaeranthus angolensis* O. Hoffm., *Emanuelsson 532*, LN607779; *Sphaeranthus bullatus* Mattf., *Eriksson & al. 522*, LN607759; *Sphaeranthus flexuosus* O. Hoffm., *Wall s.n.*, LN607696; *Sphaeranthus indicus* L., *Bremer & al. 44*, LN607734; *Sphaeranthus kirkii* Oliv. & Hiern., *Eriksson 601*, LN607768; *Stenachaenium campestre* Baker, *Pedersen 3014*, LN607702; *Stenachaenium megapotamicum* (Spreng.) Baker, *Malme 672 B*, LN607729; *Streptoglossa cylindriceps* (J. M. Black) Dunlop, *Nordenstam & Anderberg 376*, LN607762; *Streptoglossa decurrens* (DC.) Dunlop, *Nordenstam & Anderberg 301*, LN607766; *Streptoglossa odora* (F. Muell.) Dunlop, *Short 4269*, LN607763; *Telekia speciosa* (Schreb.) Baumg., *Thoran 4100*, LN607703; *Tessaria absinthioides* (Hook. & Arn.) DC., *Subieta 293*, LN607667; *Tessaria fastigiata* (Griseb.) Cabrera, *Beck & Lieberman 9613*, LN607670; *Tessaria integrifolia* Ruiz & Pav., *Daly & al. 6392*, LN607793; *Thespidium basiflorum* (F. Muell.) F. Muell. ex Benth., *Cowie & Dunlop 3923*, LN607704; *Triplocephalum holstii* O. Hoffm., *Mwasumbi & al. LBM 10861*, LN607705; *Vicoa indica* (L.) DC., *Egushi 2181*, FM208980; *Vicoa indica* (L.) DC., *Friis & al. 9213*, OP380580*; *Vicoa lignea* (Mesfin) D. Gut. Larr. & al., *Thulin & al. 10591*, FM208981; *Vicoa* sp. nov. (i.e. *V. anisopappoides* Anderb. & Bengtson), *PH & al. 6033*, OP380579*; *Vieraea laevigata* Webb. & Berthel., *Englund 05-002*, LN607707; *Zoutpansbergia caerulea* Hutch., *Koekoemoer 2259*, LN607708.

Supplemental content online

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Appendix 2. DNA *ndhF* sequence alignment in nexus format.

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