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

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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 *Antiphiona*, 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 (Pornpongrungrueng & 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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Primer	Sequence (5'-3')	Direction	Reference
RJ1	AGGTAAGATCCGGTGAATCGGAAAC	F	Kim & Jansen (1995)
ndhF-225R_Cya	TCCAAGACCATACATATTGATAGACAGAAC	R	Х
ndhF-160F_Cya	TTCGTCGTATGTGGGGCTTTTCAGAGC	F	Х
ndhF-452R_Cya	GTAACTAATCGCAACATGGAAGTACTG	R	Х
ndhF-386F_Cya	ATAGTGATAATTATATGTCTCATGATCACG	F	Х
ndhF-644R_Cya	TCAAGTTATTGAATATTTGGAATAAATCACG	R	Х
ndhF-628F_Cya	TTAGGCATTTTAGGATTTTATTGGGTAACG	F	Х
ndhF-893R_Cya	CCCTATCAAAGATATAAAATTCATTATGTG	R	Х
ndhF-861F_Cya	GTAGCAGCGGGAATTTTTCTTGTAGC	F	Х
ndhF16	GTTAAACCTCCCATAAGCACCATATTCTGAC	R	Källersjö & al. (2000)
ndhF-1130F_Cya	GATCGTGATCCGTTATTCACTCAATGG	F	Х
ndhF-1366R_Cya	CCTTCAAAAGTAAGTAAATAGATCCGACAC	R	Х
ndhF1260	TCTTAATGATAGTTGGTTGTATTCACC	F	Eldenäs & al. (1999)
ndhF1750R-Ast2	AATTAATATAAGTATTGGGAATAACATCG	R	Nylinder & al. (2013)
ndhF-1617F_Cya	AAACATGATCCAACCCTTTCTTTCTATTCC	F	Х
ndhF-1864R_Cya	AAATATTCCGAAAGAGGCTATACTSACTG	R	Х
ndhF-1822F_Cya	CATAAAAATTCAAACAATTCAATAGATTGG	F	Х
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	GATACAAATTTATATTTTTTGGG	F	Eldenäs & al. (1999)
ndhF520R	CAAATGCTTTTTGACAAGCATTTGCCGC	R	Anderberg & Swenson (2003)
ndhF1650F-Ast1	TATGATCCAACCCTTTMTTTMTATTCC	F	Nylinder & al. (2013)

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*.

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 Chalfront, 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 *Pen-tanema*, 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.

0.008



Fig. 2. Phylogeny of *Inuleae* (continued from Fig. 1). *Inuleae–Plucheinae*. An arrow marks the position of *Galgera decurrens* (*Lag-gera 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; Nylinder & 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 Nylinder & 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 $[\equiv P. indicum]).$

Vicoa now counts the following species: (1) *V. indica* (L.) DC. (\equiv *Inula indica* L. \equiv *Pentanema indicum* (L.) Y. Ling = [among others] *Inulaster kotschyi* Sch. Bip., *V. auriculata* Cass. and *V. leptoclada* (Webb) Dandy \equiv *Inula leptoclada* Webb); (2) *V. cernua* Dalzell (\equiv *P. cernuum* (Dalzell) Y. Ling = *V. gokhalei* Gosavi & al.); (3) *V. lignea* (Mesfin) D. Gut. Larr. & al. (\equiv *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 endothecial 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: involucral 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. *Vicoa 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 μ m; A2, B1–3 = 50 μ m. – 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 "Plucheoid" 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 endothecial 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 endothecial 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; endothecial 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 endothecial 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 schultzii (Bolle) Pit. & Proust, Santos-Guerra x 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) Mattf., 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 hieraciifolia (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. & Moritzi, Cowie 6734, LN607606; Blumea sericea (Thomson) Anderb. & A. K. Pandey, Sardesai 2547, LN607743; Buphthalmum salicifolium L., Anderberg 7292, LN607788; Buphthalmum speciosissimum L., Fior s.n., LN607608; Caesulia axillaris Roxb., Pandey 3021, LN607609; Callilepis salicifolia Oliv., Bayer SAF-01009, LN607610; Calostephane 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 Aytaç & 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 & Wanntorp 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 paui 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 auranitica 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., Koekemoer 2259, LN607708.

Supplemental content online

See https://doi.org/10.3372/wi.52.52306

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

Willdenowia

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