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New subtribal and generic limits in the tribe *Athroismeae* (*Asteraceae*) and further disintegration of the subtribe *Madagasterinae* of the tribe *Astereae*

Annika Bengtson[1] **& Sylvain G. Razafimandimbison**[1]

Abstract: The *Astereae* subtribe *Madagasterinae* (*Asteraceae*) sensu Nesom encompassing four Malagasy genera (*Apodocephala*, *Madagaster*, *Rochonia* and *Vernoniopsis*) is polyphyletic, as *Apodocephala* is a member of the Malagasy subtribe *Lowryanthinae* of the tribe *Athroismeae*. While *Madagaster* was shown to belong to *Astereae*, the phylogenetic positions of *Rochonia* and *Vernoniopsis* (now *Jalantzia*) in this tribe remained to be tested with molecular data. *Lowryanthinae* presently contains *Apodocephala* with nine species and the monospecific *Lowryanthus*. The monophyly of *Apodocephala* remained to be assessed using a comprehensive sampling. The aims were to: (1) assess the phylogenetic placements of *Rochonia* and *Jalantzia* (*Vernoniopsis*) and test the monophyly of *Jalantzia*; (2) assess phylogenetic relationships within *Lowryanthinae*; and (3) re-assess the subtribal and generic limits within the tribe *Athroismeae*. New phylogenetic analyses based on plastid sequence data confirmed the position of *Rochonia* in *Astereae*. *Jalantzia* (*Vernoniopsis*) was resolved as sister to the subtribe *Lowryanthinae* and therefore transferred to *Athroismeae*. A new subtribe, *Jalantziinae*, is described to accommodate *Jalantzia*. *Apodocephala* is paraphyletic with respect to *Lowryanthus*, which is formally merged with *Apodocephala.* A description of the emended subtribe *Madagasterinae* containing *Madagaster* and *Rochonia* is presented.

Keywords: *Apodocephala*, *Asteraceae*, *Astereae*, *Athroismeae*, *Compositae*, *Jalantzia*, *Jalantziinae*, *Lowryanthinae*, *Lowryanthus*, Madagascar, *Madagaster*, *Madagasterinae*, molecular phylogeny, *Rochonia*, *Vernoniopsis*

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Introduction

Madagascar is known for its biodiversity and high level of endemism. The daisy family, *Asteraceae*, with c. 555 species on Madagascar, 86.9 % of which are endemic, is one of the most species-rich flowering plant families (Madagascar Catalogue 2022). The species represent 103 different genera, but only 20 of these are endemic to Madagascar. Five of the endemic genera are formally grouped in two subtribes: the *Athroismeae* subtribe *Lowryanthinae* (Bengtson & al. 2017, 2021) and the *Astereae* subtribe *Madagasterinae* (Nesom 2020).

Athroismeae, as defined by Bengtson & al. (2017), is a small, morphologically diverse tribe, whose circumscription has gradually changed over the years (Panero & Funk 2002; Wagstaff & Breitwieser 2002; Panero 2005; Anderberg 2009; Pruski 2014; Bengtson & al. 2017, 2021). Bengtson & al. (2017) presented the first molecular phylogenetic study of the tribe, which resulted in an amended circumscription. The tribe currently consists of ten genera classified in four morphologically diverse subtribes (*Anisopappinae*, *Athroisminae*, *Lowryanthinae* and *Symphyllocarpinae*; Bengtson & al. 2017, 2021). *Lowryanthinae* consist of two genera: *Lowryanthus* Pruski and *Apodocephala* Baker. *Lowryanthus* was described by Pruski (2014), who postulated it to be closely related to the *Blepharispermum* group (= subtribe *Athroisminae*). Bengtson & al. (2017) later confirmed its position in the tribe *Athroismeae*, where it was resolved as sister to subtribe *Athroisminae*. *Lowryanthus* was, however, placed in its own subtribe, *Lowryanthinae*, mainly due to differences in synflorescences and capitula. *Lowryanthus* is a monospecific genus endemic to Madagascar and consists of shrubs or small trees with red synflorescences with coral-red discoid capitula and florets with reddish to pink corollas (Fig. 1B). A recent phylogenetic study by Bengtson & al. (2021) revealed the Malagasy endemic genus *Apodocephala* to be sister to *Lowryanthus* and therefore another member of subtribe *Lowryanthinae*. This study, however, included only two of the nine described *Apodocephala* species. The *Apodocephala* species most morphologically resembling *Lowryanthus* were not included

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Fig. 1. A: *Apodocephala pauciflora*; B: *Lowryanthus rubens*; C: *Jalantzia* (*Vernoniopsis*) *caudata*; D: *Rochonia cinerarioides*; E: *Madagaster* sp. – Photographs by S. E. Rakotoarisoa (A; CC BY-NC © 2023), M. Thulin (B; CC BY-NC-SA © 2023), S. Razafimandimbison (C, E) and M. Arnerup (D).

and, therefore, the phylogenetic relationships within subtribe *Lowryanthinae* remained unclear.

Apodocephala was earlier placed in the tribe *Astereae*, where it has, based on morphology, been associated with the Malagasy genera *Vernoniopsis* Humbert, *Rochonia* DC. and *Madagaster* G. L. Nesom (Humbert 1960; Bremer 1994; Nesom 2020; Fig. 1A, C, D, E), later classified in Nesom's (2020) subtribe *Madagasterinae*. *Apodocephala* was, however, omitted from *Astereae* by Nesom & Robinson (2007) in their account of the tribe. Subtribe *Madagasterinae* are characterized by their arborescent habit, coriaceous and abaxially tomentose leaves and their caudate anthers. Bengtson & al. (2021) have shown *Madagasterinae* to be non-monophyletic, because *Apodocephala* belongs to the tribe *Athroismeae*. *Apodocephala* consists of nine species of shrubs or trees with discoid capitula and florets with white or whitish corollas (Fig. 1A). Molecular phylogenetic studies have confirmed the position of *Madagaster* within *Astereae* (Brouillet & al. 2009), but the phylogenetic placement of the Malagasy *Rochonia* and *Vernoniopsis* within *Astereae* and their relationships to *Apodocephala* remain untested by molecular analysis. *Rochonia* encompasses four species and has campanulate, radiate capitula with yellow ray florets (Fig. 1D). This genus is morphologically more similar to *Madagaster. Vernoniopsis*, however, resembles *Apodocephala* in having discoid 1- to few-flowered capitula with cylindric involucres and florets with whitish corollas. *Vernoniopsis* was originally described as monospecific with two subspecies differing in leaf and cypsela sizes (Humbert 1955), *V. caudata* (Drake) Humbert subsp. *caudata* and subsp. *lokohensis* Humbert. The latter subspecies was later raised to species level (Callmander & Phillipson 2011). The monophyly of *Vernoniopsis* has never been tested.

The aims of the study were to: (1) assess the phylogenetic placements of *Rochonia* and *Vernoniopsis* and test the monophyly of *Vernoniopsis* as defined by Callmander & Phillipson; (2) assess phylogenetic relationships within the subtribe *Lowryanthinae*; and (3) to re-assess the subtribal and generic limits within the tribe *Athroismeae*.

Material and methods

Taxon sampling

Herbarium specimens from MO, P and S (herbarium codes according to Thiers 2023+), as well as newly collected specimens from Madagascar were included in the study. Thirteen specimens of *Apodocephala*, representing all but one species (no specimens of *A. coursii* Humbert suitable for DNA-extraction could be located), both species of *Vernoniopsis*, and *Rochonia cinerarioides* DC. were included in the molecular study. The systematic positions of *Vernoniopsis* and *Rochonia* were analysed in a large dataset, including 139 taxa and representing a wide coverage of *Asteraceae* tribes. Molecular phylogenetic analyses of the *Athroismeae*, with a focus on the subtribe *Lowryanthinae* were then conducted, including 60 taxa and representatives of all known genera of the tribe. Four different loci were sequenced for the study, two from the nuclear genome (ETS, ITS) and two from the plastid genome (*ndhF*, *trnL-trnF*). A complete list of sampled taxa and voucher information is given in Appendix 1.

DNA extraction, amplification and sequencing

DNA was extracted from herbarium material or, if available, from silica-gel dried leaves, using a DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) according to the manufacturer's instructions. The DNA regions of interest were amplified using Hot Start Mix RTG beads (GE Healthcare, Little Chalfont, United Kingdom) following the manufacturer's standard protocol. The nuclear ribosomal (nr) DNA external transcribed spacer (ETS) was amplified using primers Ast-1 (Markos & Baldwin 2001) and 18S-ETS (Baldwin & Markos 1998), and the nrDNA internal transcribed spacer (ITS, including ITS1, ITS2 and the 5.8S gene) was amplified using primers 5.8SRPEny (Nylinder & al. 2013), 5.8F-chrys (Howis & al. 2009), 18SF and 26SR (Rydin & al. 2004). The plastid DNA *ndhF* gene was amplified using primers RJ1, RJ14 (Kim & Jansen 1995), ndhF16 (Källersjö & al. 2000), ndhF5 (Olmstead & Sweere 1994), 1750R-Ast2, 1650F-Ast (Nylinder & al. 2013), ndhF431F (Eldenäs & al. 1999) and ndhF520R-Ast (Anderberg & Swenson 2003), and the plastid *trnL-trnF* region (including the *trnL* intron and *trnL-trnF* intergenic spacer) with the “c”, “d”, “e” and “f” primers of Taberlet & al. (1991). All regions were amplified following the thermal profile described in Bengtson & Anderberg (2018). Amplified products were purified using one portion of Exonuclease I (20u/µl) and four portions of FastAP Thermosensitive Alkaline Phosphatase (1u/µl) (Thermo Scientific; Vilnius, Lithuania). Purified PCR-products were sequenced by Macrogen Europe (Amsterdam, Netherlands, https://www.macrogen-europe.com/). Resulting sequences were assembled and carefully checked and edited using the Staden package (Staden 1996). New sequences have been submitted to GenBank, and accession numbers are cited in the voucher list (Appendix 1).

Phylogenetic analyses

Sequences were aligned using MUSCLE v.3.8.425 (Edgar 2004) as implemented in AliView v.1.24 (Larsson 2014) and manually edited using BioEdit v.7.2.5 (Hall 1999). Two different datasets were compiled and analysed (Supplementary appendices S1, S2); we initially performed analyses of an *ndhF* matrix, including 139 accessions and a representing wide coverage of the *Asteraceae* tribes, in order to determine the tribal positions of *Vernoniopsis* and *Rochonia* within the family. A second dataset with a focus on the tribe *Athroismeae* consisting of ETS, ITS, *ndhF* and *trnL-trnF* sequence data from 60 accessions was then analysed. *Boopis anthemoides* Juss. (*Calyceraceae*) was used as outgroup in analyses of the *Asteraceae ndhF* matrix and *Callilepis salicifolia* Oliv. in analyses of the combined *Athroismeae* dataset, following Bengtson & al. (2017). All the analyses were conducted with Bayesian and parsimony methods. Prior to analyses of the combined dataset each region was analysed separately to check for incongruences by simply comparing the topologies.

Bayesian inference analyses were conducted using MrBayes v.3.2.2 (Ronquist & al. 2012) using the online XSEDE platform in the CIPRES Science Gateway (Miller & al. 2010). Nucleotide substitution models were set to GTR+I+G for the *Asteraceae ndhF* dataset, and to GTR+G for ETS and GTR+I+G for ITS and the plastid markers (*ndhF*, *trnL-trnF*) for the combined dataset, selected as best fit for the data using the Akaike information criterion (AIC) as implemented in jModeltest v. 2.1.10 (Guindon & Gascuel 2003; Darriba & al. 2012). Analyses consisted of two independent runs, with eight chains each. The Markov Chain Monte Carlo (MCMC) was run for 75 million generations with a sampling frequency of 7500 for the *ndhF* matrix, and for 50 million generations with a sampling frequency of 5000 for the combined dataset. Convergence of Markov chains was examined using Tracer v.1.7.1 (Rambaut & al. 2018) as well as by checking the average standard deviation values of split frequencies. The first 25 % of the trees were excluded as a burn-in phase. Consensus trees were visualized using FigTree v.1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/). Maximum parsimony analyses were conducted using PAUP v.4.0a (Swofford 2002), using the settings described in Bengtson & al. (2021). All analyses were run multiple times using the settings described above.

Results

The *Asteraceae ndhF* dataset consisted of 2292 aligned characters, 559 of which were parsimony informative, and the combined *Athroismeae* dataset of 4436 aligned characters, 773 of which were parsimony informative.

The parsimony analysis of the *ndhF* dataset yielded 6840 most parsimonious trees, 2912 steps long (consistency index, CI = 0.38; retention index, RI = 0.68, excluding uninformative characters), and the parsimony analysis of the *Athroismeae* dataset yielded two most parsimonious trees, 2717 steps long (CI = 0.51, RI = 0.83). Analyses of separate regions resulted in less resolved trees. One incongruence was detected in Bayesian analyses of the ITS region where *Anisochaeta* DC. was resolved as sister to *Vernoniopsis* (posterior probability, PP = 0.93, not shown).

Bayesian and parsimony analyses produced trees with similar overall topologies. A majority-rule consensus tree from a Bayesian analysis of the *ndhF* dataset, including representatives from the entire *Asteraceae*, is shown in Fig. 2. The analyses resolved *Rochonia cinerarioides* as part of a clade consisting of members of the tribe *Astereae* (posterior probability, PP = 1.0, bootstrap support, BS = 100, Fig. 2). The *Vernoniopsis* specimens were resolved as monophyletic (PP = 1.0, BS = 100) and placed as sister to the *Lowryanthinae* subtribe (PP = 0.99, BS = 59, Fig. 2) within a poorly supported tribe *Athroismeae* (PP = 0.85, BS < 50, Fig. 2). A majority-rule consensus tree from a Bayesian analysis of the *Athroismeae* dataset, consisting of both nuclear (ETS, ITS) and plastid (*ndhF*, *trnL-trnF*) data is presented in Fig. 3. The analysis confirmed the position of *Vernoniopsis* within *Athroismeae* (PP = 1.0, BS = 87) where it was resolved as sister to the subtribe *Lowryanthinae* (PP = 0.97, BS < 50, Fig. 3). The subtribe *Lowryanthinae*, consisting of *Apodocephala* and *Lowryanthus*, was resolved as monophyletic with high support (PP = 1.0, BS = 100). The analysis resolved *L. rubens* within *Apodocephala*, in a poorly supported clade together with *A. radula* Humbert and *A. minor* Scott Elliot (PP = 0.75, BS = 61, Fig. 3). The remaining *Apodocephala* species were resolved in a well-supported clade (PP = 1.0, BS = 100, Fig. 3). *Apodocephala urschiana* Humbert, *A. angustifolia* Humbert, *A. begueana* Humbert, *A. pauciflora* Baker var. *pauciflora* and one undetermined *Apodocephala* formed a well-supported subclade (PP = 1.0, BS = 85), and *A. multiflora* Humbert, *A. oliganthoides* Humbert and *A. pauciflora* var. *cacuminum* Humbert formed another highly supported subclade (PP = 0.98, BS = 75, Fig. 3).

Discussion

Phylogenetic positions of *Vernoniopsis* and *Rochonia*

Nesom (2020) placed the Malagasy genera *Apodocephala*, *Vernoniopsis*, *Rochonia* and *Madagaster* in his new subtribe, *Madagasterinae* of the tribe *Astereae*, based on their arborescent habit with coriaceous abaxially tomentose leaves, caudate anther thecae and isolated geographic distribution. *Madagaster* has been confirmed to be a member of the tribe *Astereae* (Brouillet & al. 2009); however, *Apodocephala* was recently shown to belong to the tribe *Athroismeae* and transferred there (Bengtson & al. 2021), implying the non-monophyly of *Madagasterinae* as defined by Nesom (2020). The monophyly of *Madagasterinae* is further rejected by our analyses, because *Vernoniopsis* was resolved sister to the *Apodocephala-Lowryanthus* clade (Fig. 2, 3). *Vernoniopsis* is therefore another addition to the *Athroismeae* (Fig. 2, 3).

The phylogenetic position of *Rochonia* (here represented by *R. cinerarioides*) within *Astereae* is strongly supported (Fig. 2), consistent with Nesom (2020). *Rochonia* consists of four species of shrubs or subshrubs with radiate capitula bearing ray florets with yellow corollas (Fig. 1D). The genus resembles *Madagaster* in morphology, and Humbert (1932) even described the taxa currently placed under *Madagaster* and *Rochonia* (then *Aster* L.) as mainly differing in the colour of the ray floret corollas (*Madagaster* have ray florets with white to bluish corollas). Nesom (1993) described the genus *Madagaster* for the white-rayed species, considered to be a lineage separate from, but close to, *Rochonia*. We agree that *Madagaster* and *Rochonia* are likely to be closely related based on their morphological similarities; however, whether they are sisters remains to be seen. In summary, only two out of the four genera of Nesom's (2020) subtribe *Madagasterinae*, *Madagaster* and *Rochonia*, remain.

Monophyly of *Vernoniopsis* (now *Jalantzia*)

Our analyses strongly support the monophyly of *Vernoniopsis* (here represented by its two species, *V. caudata* (Drake) Humbert and *V. lokohensis* (Humbert) Callm. & Phillipson; Callmander & Phillipson 2011) and its phylogenetic position in the tribe *Athroismeae* as delimited by Bengtson & al. (2021), where it is resolved as sister to the *Apodocephala-Lowryanthus* clade (Fig. 2, 3). This finding is inconsistent with Bremer (1994) and Nesom (2020), who classified the genus in the tribe *Astereae*. Members of *Vernoniopsis* are shrubs or small trees with coriaceous leaves and discoid homogamous capitula containing 1–4 florets with white corollas (Fig. 1C; Humbert 1960; Callmander & Phillipson 2011). *Vernoniopsis caudata*, the generitype, was originally described by Drake (1899) as *Vernonia caudata* Drake because of its *Vernonia*-like habit and inflorescences, inconsistent with our results. Humbert (1955) totally rejected this taxonomic decision and described his new genus *Vernoniopsis* to accommodate *Vernonia caudata* in the tribe *Astereae* based on differences in the stigmatic surfaces of the style branches. The name *Vernoniopsis* was recently noted to be an illegitimate later homonym of *Vernoniopsis* Dusén and has therefore been replaced by *Jalantzia* D. J. N. Hind (Hind & Langhorne 2024). The recognition of *Vernoniopsis* (now *Jalantzia*) at generic level is consistent with our findings. *Jalantzia* (*Vernoniopsis*) has been suggested to be closely related to the Malagasy genus *Apodocephala* based on their discoid capitula with white corollas and the presence of shortly caudate anthers (Humbert 1960; Bremer 1994; Nesom 2020). The molecular phylogenetic analyses here con-

Fig. 2. Bayesian fifty-percent majority-rule consensus tree from an analysis of the *Asteraceae ndhF* dataset, showing position of *Rochonia* within *Astereae* and *Jalantzia* (*Vernoniopsis*) within *Athroismeae*. Numbers above branches indicate posterior probability (PP) and bootstrap values (BS), bootstrap values <50 are indicated by a dash. Scale bar shows number of substitutions per site.

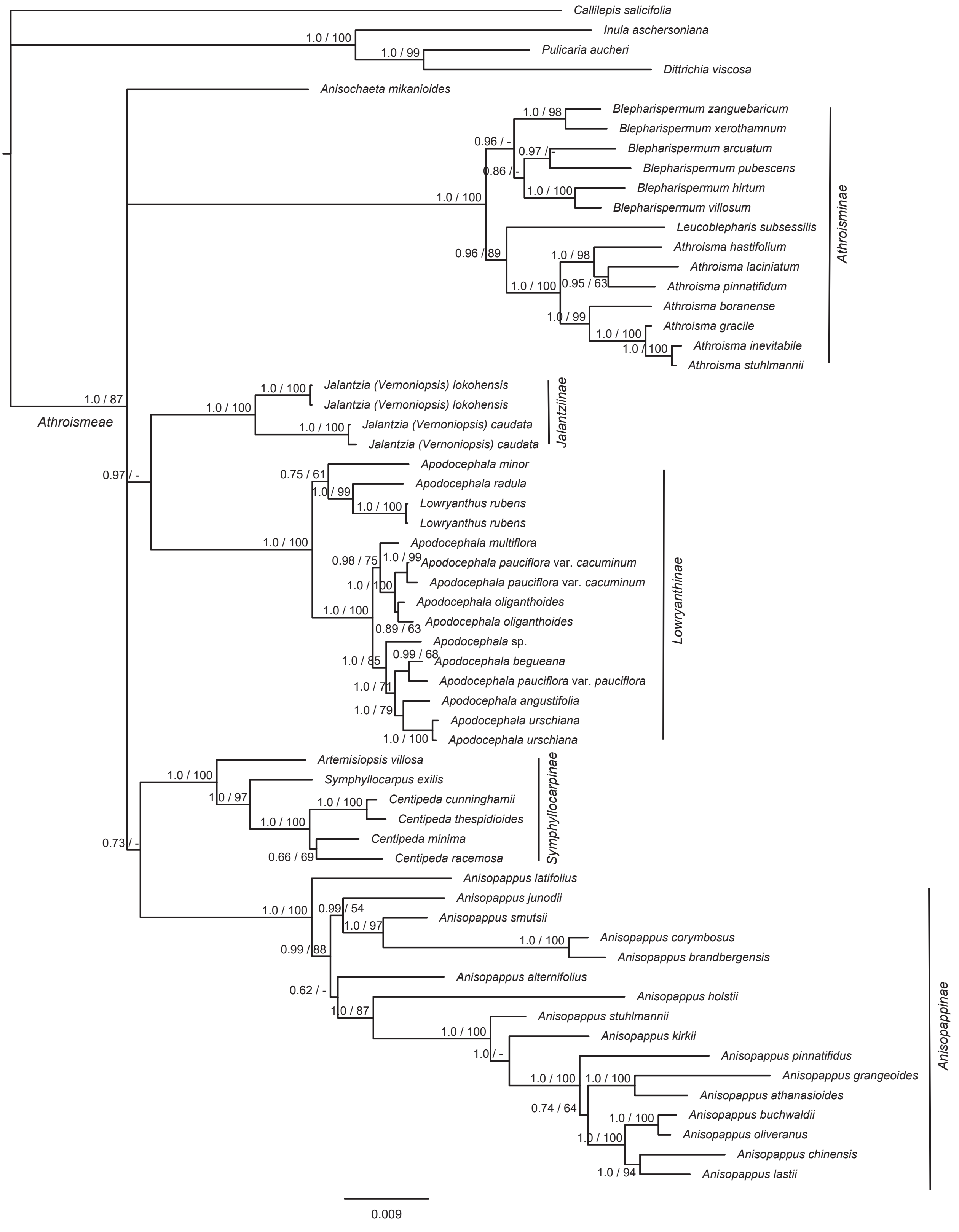

Fig. 3. Bayesian fifty-percent majority-rule consensus tree from an analysis of the combined *Athroismeae* dataset (including ETS, ITS, *ndhF* and *trnL-trnF*). Numbers above branches indicate posterior probability (PP) and bootstrap values (BS), bootstrap values <50 are indicated by a dash. Scale bar shows number of substitutions per site.

firm the close relationship of *Apodocephala* and *Jalantzia* (Fig. 2, 3). *Jalantzia* differs from *Apodocephala* in having epaleate receptacles and a pappus of scabrid bristles, whereas *Apodocephala* has paleate receptacles and lacks a true pappus. Therefore, we maintain the current generic status of *Jalantzia*.

Table 1. Distinguishing characters between *Apodocephala pauciflora* var. *pauciflora* and *A. pauciflora* var. *cacuminum*.

Feature	***A. pauciflora*** var. ***pauciflora***	***A. pauciflora*** var. ***cacuminum***
Leaf shape	lanceolate	obovate-lanceolate
Leaf size	10–20 × 4–8 cm	4–10 × 2–3 cm
Cypsela shape	flattened	subprismatic
Distribution	northeastern to central Madagascar	northeastern Madagascar
Habitat	rainforest	ericoid vegetation
Flowering time	August–December	March

Further, our analyses support the recognition of *Vernoniopsis caudata* subsp. *lokohensis* Humbert at species level (Callmander & Phillipson 2011). *Jalantzia* (*Vernoniopsis*) *caudata* (Drake) D. J. N. Hind and *J. lokohensis* (Humbert) D. J. N. Hind do not grow sympatrically. The former commonly grows along the littoral forests of the eastern coast of Madagascar, while the latter is restricted to the highland rainforests of the Marojejy massif in northeastern Madagascar between 1300 and 2000 m in elevation. In other words, *Jalantzia* (*Vernoniopsis*) contains two geographically distinct lineages, the northeastern group (*J. lokohensis*) and the eastern-southeastern group (*J. caudata*). A similar pattern has recently been reported by Razafimandimbison & al. (2022) in the Malagasy *Schismatoclada farahimpensis* Homolle (*Rubiaceae*), which was resolved in two geographically and morphologically distinct lineages: northern and southern groups, that could be recognized at subspecies level (Razafimandimbison, unpublished data).

Phylogenetic relationships within *Apodocephala*

Apodocephala currently consists of nine species of trees or shrubs with discoid paleate capitula in terminal corymbiform-paniculate inflorescences, all endemic to Madagascar: *A. angustifolia*, *A. begueana*, *A. coursii*, *A. minor*, *A. multiflora*, *A. oliganthoides*, *A. pauciflora*, *A. radula* and *A. urschiana*. Our analyses demonstrate that *Apodocephala* is paraphyletic with respect to the monospecific Malagasy genus *Lowryanthus* (here represented by two individuals of *L. rubens*). This is inconsistent with Bengtson & al. (2021), who resolved *Lowryanthus* as sister to two species of *Apodocephala* (Fig. 3). *Apodocephala* is resolved into two major clades: one containing *A. minor*, *A. radula* and *L. rubens* and the other formed by *A. angustifolia*, *A. begueana*, *A. multiflora*, *A. oliganthoides*, *A. pauciflora* and *A. urschiana*. *Apodocephala* and *Lowryanthus* mainly differ in the colour of the peduncles, capitula and florets (Fig. 1A, B). The latter has a striking appearance with bright red inflorescences and florets, whereas *Apodocephala* has florets with white or whitish corollas. Aside from that, *L. rubens* resembles *Apodocephala*, both consist of shrubs or trees with discoid mainly few-flowered paleate capitula in terminal corymbiform-paniculate inflorescences and have cypselas that lack a true pappus. Bengtson & al. (2021) noted additional similarities in the cypselas of *Lowryanthus* and *Apodocephala* (Fig. 4). *Lowryanthus* has geniculate-rostrate cypselas with a tightly curved rostrum (Pruski 2014), a character also found in several species of *Apodocephala*. The flattened rostrate cypselas of *A. coursii* and *A. radula* (see Humbert 1962: 86) especially resemble those of *L. rubens*, but *A. minor* and *A. urschiana* also have cypselas with a narrowed curved rostrum (Fig. 4; Humbert 1960, 1962). The character therefore occurs in both clades (Fig. 3, 4).

The two major clades of *Apodocephala* are geographically separated. *Apodocephala minor* and *A. radula* are both found in close geographical proximity of the known localities of *Lowryanthus rubens* in southeastern Madagascar. However, the three species do not grow sympatrically and occupy different habitats. *Lowryanthus rubens* is found in low-elevation humid evergreen forests from 100–300 m in elevation, whereas *A. radula* is found in siliceous rocky habitats at higher elevations and *A. minor* grows in rocky habitats at low elevations (Humbert 1960; Pruski 2014). The remaining sampled *Apodocephala* species form a well-supported clade (Fig. 3) and have a much wider geographic distribution along eastern Madagascar, ranging from Ivohibe in the southeast to Daraina in northern Madagascar. It can be concluded that geographic proximity is sometimes a better predictor of evolutionary history than morphology; a similar pattern has recently been reported from the Malagasy endemic *Rubiaceae* genera *Payera* Baill. and *Schismatoclada* Baker (Razafimandimbison & al. 2022). Despite the geographical separation of the two clades, we argue that *Lowryanthus* should be formally merged in *Apodocephala* (which has the priority over the former), because there is no morphological difference between the two clades that would justify dividing *Apodocephala* in two.

Humbert (1955) divided *Apodocephala pauciflora* into two varieties, *A. pauciflora* var. *pauciflora* and *A. pauciflora* var. *cacuminum*, differing in leaf size and shape (see Table 1) as well as in shape of involucral bracts and capitulum size, where *A. pauciflora* var. *cacuminum* appears to have somewhat larger capitula. Morphological comparisons also show differences in the shape of the cypselas, which are shorter and more subprismatic in var. *cacuminum* (Fig. 4G, H). The two varieties differ in distribution and habitat. *Apodocephala pauciflora* var. *pauciflora* grows in rainforests at 800–1900 m in elevation and has a wider distribution ranging from Marojejy in the northeast to Fianarantsoa in central Madagascar. In contrast, *A. pauciflora* var. *cacuminum* is restricted to the Marojejy massif in the northeast, where it is found in ericoid vegetation in rocky places from 1300 to over 2000 m in elevation (Humbert 1955, 1960). Further, *A. pauciflora*

Fig. 4. Cypselas – A, B: *Lowryanthus rubens*, *Razafimandimbison & al. 1531* (S); C, D: *Apodocephala radula*, *Humbert 20708* (S); E: *A. minor*, *Sabouraeu* (P); F: *A. urschiana*, *McPherson & van den Werff 16551* (MO); G: *A. pauciflora* var. *pauciflora*, *Turk & Randriamanatena 203* (MO); H: *A. pauciflora* var. *cacuminum*, *Razafimandimbison & Razafindrahaja 2951* (S); I: *A. oliganthoides*, *Razafimandimbison & Razafindrahaja 2975* (S); J: *A. multiflora*, *Ranarivelo & Ravelnarivo 771* (MO); K: *A. begueana*, *Service Forestier de Madagascar 13551-SF* (P); L: *A. angustifolia*, *Rakotomalala & Narison 124* (MO). – All scale bars = 1 mm.

var. *pauciflora* and var. *cacuminum* also appear to differ in flowering time (Table 1). Analyses place the two varieties in different clades, a specimen of *A. pauciflora* var. *pauciflora* is placed sister to *A. begueana*, in a clade also consisting of *A. urschiana* and *A. angustifolia*, whereas two specimens of *A. pauciflora* var. *cacuminum* form a monophyletic group sister to *A. oliganthoides* in a clade comprising also *A. multiflora* (Fig. 3). *Apodocephala pauciflora* var. *cacuminum* resembles *A. oliganthoides* in having oblanceolate leaves and capitula with rounded involucral bracts. Our results support that *A. pauciflora* var. *pauciflora* and var. *cacuminum* should be considered separate species.

Apodocephala coursii could not be included in the molecular study, but morphological comparison shows similarities to *A. radula* and *A. rubens*, and it is likely to be closely related to those species. *Apodocephala coursii*, *A. radula* and *A. rubens* all have similar flattened cypselas with a curved rostrum, and *A. coursii* and *A. rubens* also have cypselas with long marginal and apical trichomes (Humbert 1960, 1962; Pruski 2014). *Apodocephala coursii*, *A. radula* and *A. rubens* all have distributions in southeastern Madagascar. *Apodocephala coursii* is only known from the Atsimo-Atsinanana region in eastern Madagascar where it grows in rainforest vegetation (Humbert 1962).

Based on the evidence presented above, two new combinations are made: *Apodocephala rubens* (Pruski) Bengtson & Razafim. and *A. cacuminum* (Humbert) Bengtson & Razafim. (see below).

Implications on the subtribal classification of the tribe *Athroismeae*

Athroismeae sensu Bengtson & al. (2021) is currently divided into four morphologically distinct subtribes: *Anisopappinae*, *Athroisminae*, *Lowryanthinae* and *Symphyllocarpinae*; in addition to this, the tribe also contains the unplaced monospecific *Anisochaeta* (Bengtson & al. 2017). The subtribe *Lowryanthinae* is endemic to Madagascar and now encompasses the broadly defined *Apodocephala* (including *Lowryanthus*). The subtribe has earlier been placed as sister to subtribe *Athroisminae* (Bengtson & al. 2017, 2021). Similar obcompressed carbonized asymmetrically rostrate cypselas, and cypselas with long marginal and apical twin hairs, occur in members of both subtribes (Humbert 1960; Eriksson 1990, 1992, 1995; Pruski 2014), and this is also what first led Pruski (2014) to place *Lowryanthus* in *Athroismeae*. These characters are, however, not found in *Jalantzia* (*Vernoniopsis*). Phylogenetic analyses place *Jalantzia* here as sister to subtribe *Lowryanthinae* as defined by Bengtson & al. (2021), and the morphological similarities to *Apodocephala* support the position of *Jalantzia* as close to *Lowryanthinae*. *Jalantzia*, however, differs from the members of *Lowryanthinae* in having epaleate receptacles and a true pappus of scabrid bristles, and we have therefore chosen not to include this Malagasy genus in subtribe *Lowryanthinae* but instead to describe a new subtribe, *Jalantziinae*, to accommodate *Jalantzia*.

Taxonomic treatment

Athroismeae

Apodocephala rubens (Pruski) Bengtson & Razafim., **comb. nov.** ≡ *Lowryanthus rubens* Pruski in Phytoneuron 2014(51): 1. 2014. – Holotype: Madagascar, Toliara, Anosy Région, Bemangidy Forest, *Lowry P. P. II, Rabenantoandro J., Randriatafika F., Lowry E., Ramisy E. & Mara B. 6648.* (MO [barcode 2383282 / accession no. 6012800 image!]; isotypes: NY [barcode 02361522 image!], P [barcode P00722630 image!], S [herbarium no. S08-78]!, TAN, US [barcode 01268912 image!]).

Apodocephala cacuminum (Humbert) Bengtson & Razafim., **comb. & stat. nov.** ≡ *Apodocephala pauciflora* var. *cacuminum* Humbert in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 6: 158. 1955. – **Lectotype (designated here):** Madagascar, sommet oriental du Massif de Marojejy, 1949, *Humbert & Cours 23762* (P [barcode P00435128 image!]; isolectotype: P [barcode P00435129 image!]).

Note — The type specimen in P indicated in the protologue is actually a gathering consisting of two duplicate specimens, with no indication in the protologue, or on the specimens, as to which is the holotype and which is the isotype. A holotype cannot consist of two specimens (Art. 8.1). As a result, a lectotypification is needed.

Jalantziinae Bengtson & Razafim., **subtrib. nov.**
Type: *Jalantzia* D. J. N. Hind in Curtis's Bot. Mag. 40: 410. 2024 (≡ *Vernoniopsis* Humbert in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 6: 154. 1955, nom. illeg. [non *Vernoniopsis* Dusén in Beih. Bot. Centralbl., Abt. 2, 38: 284. 1921]).

Description — Shrubs or trees, 1–8 m tall. *Leaves* oblanceolate, coriaceous, pinnately veined, margin entire. *Inflorescence* terminal, corymbiform. *Capitula* discoid, epaleate; florets 1–4; corollas white to whitish. *Cypselas* oblong, ribbed, glabrous. *Pappus* of scabrid bristles.

Genus — *Jalantzia* D. J. N. Hind.

Astereae

Madagasterinae G. L. Nesom in Phytoneuron 2020(53): 28. 2020, emend. Bengtson & Razafim. – Type: *Madagaster* G. L. Nesom.

Description — Subshrubs, shrubs or small trees. *Leaves* coriaceous, glabrous or abaxially tomentose, eglandular, venation camptodromous to brochidodromous. *Inflorescences* terminal and 1-headed to corymboid. *Involucres* campanulate; receptacles epaleate; ray limbs white to blue or yellow; disc florets bisexual, corolla lobes triangular to linear-lanceolate; anther thecae bases caudate. *Cypselas* oblong-cylindric to fusiform, subterete, 4–10-veined, eglandular. *Pappus* of barbellate bristles.

Genera — *Madagaster* G. L. Nesom, *Rochonia* DC.

Conclusions

The Malagasy *Rochonia* is confirmed to be a member of the tribe *Astereae*, whereas *Vernoniopsis* (now *Jalantzia*) is resolved as sister to the *Apodocephala*-*Lowryanthus* clade and therefore another addition to the growing tribe *Athroismeae*. The non-monophyly of the *Astereae* subtribe *Madagasterinae* is further supported. This group now only contains the Malagasy genera *Madagaster* and *Rochonia*, and a description of the emended subtribe *Madagasterinae* is presented. Phylogenetic analyses demonstrate the paraphyly of *Apodocephala* with respect to the Malagasy monospecific *Lowryanthus*, and a broad delimitation of *Apodocephala* (including *Lowryanthus*) was adopted to render this genus monophyletic. The newly re-circumscribed *Apodocephala* was resolved in two geographically segregated clades. The *Athroismeae* now consist of ten genera that are currently classified in five morphologically different subtribes (although *Anisochaeta* is still unplaced). Much remains unclear regarding how the different subtribes and the *Athroismeae* as a whole have evolved. Also, the backbone of the tribe is still largely unresolved. It is not unlikely that more additions to the tribe are in the Malagasy flora.

Author contributions

AB and SGR designed the study. AB did the laboratory work, analysed the data and wrote the first draft of the manuscript. Both authors revised the manuscript.

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References

Anderberg A. A. 2009: *Athroismeae*. – Pp. 681–688 in: Funk V. A., Susanna A., Stuessy T. F. & Bayer R. J. (ed.) Systematics, evolution and biogeography of *Compositae*. – Vienna: IAPT.

Anderberg A. A. & Swenson U. 2003: Evolutionary lineages in *Sapotaceae* (*Ericales*): a cladistics analysis based on *ndhF* sequence data. – Int. J. Pl. Sci. **164:** 763–773. https://doi.org/10.1086/376818

Baldwin B. G. & Markos S. 1998: Phylogenetic utility of the external transcribed spacer (ETS) of 18S–26S rDNA: congruence of ETS and ITS trees of *Calycadenia* (*Compositae*). – Molec. Phylogen. Evol. **10:** 449–463. https://doi.org/10.1006/mpev.1998.0545

Bengtson A. & Anderberg A. A. 2018. Species diversification in the Mediterranean genus *Chiliadenus* (*Inuleae–Asteraceae*). – Pl. Syst. Evol. **304:** 853–860. https://doi.org/10.1007/s00606-018-1515-2

Bengtson A., Anderberg A. A. & Razafimandimbison S. G. 2021: The Malagasy enigmatic genus *Apodocephala* (*Asteraceae*), a new member of the tribe *Athroismeae*. – Willdenowia **51:** 221–230. https://doi.org/10.3372/wi.51.51205

Bengtson A., Englund M., Pruski J. F. & Anderberg A. A. 2017: Phylogeny of the *Athroismeae* (*Asteraceae*), with a new circumscription of the tribe. – Taxon **66:** 408–420. https://doi.org/10.12705/662.8

Bremer K. 1994: Tribe *Astereae*. – Pp. 377–434 in: *Asteraceae*: cladistics and classification. – Portland: Timber Press Inc.

Brouillet L., Lowrey T. K., Urbatsch L., Karaman-Castro V., Sancho G., Wagstaff S. & Semple J. C. 2009: *Astereae*. – Pp. 589–629 in: Funk V. A., Susanna A., Stuessy T. F. & Bayer R. J. (ed.), Systematics, evolution and biogeography of *Compositae*. – Vienna: IAPT.

Callmander M. W & Phillipson P. B. 2011: The genus *Vernoniopsis* Humbert (*Asteraceae*) in Madagascar. – Candollea **66:** 409–412. https://doi.org/10.15553/c2011v662a21

Darriba D., Taboada G. L., Doallo R. & Posada D. 2012: jModelTest 2: more models, new heuristics and parallel computing. – Nature, Meth. **9:** 772. https://doi.org/10.1038/nmeth.2109

Drake del Castillo E. 1899: Sur deux genres de Madagascar de la famille des Composées: *Cullumiopsis* (nov. gen.) et *Centauropsis* Boj. – Bull. Mus. Hist. Nat., Paris **5:** 100–104.

Edgar R. C. 2004: MUSCLE: multiple sequence alignment with high accuracy and high throughput. – Nucl.

Acids Res. **32:** 1792–1797. https://doi.org/10.1093/nar/gkh340

Eldenäs P., Källersjö M. & Anderberg A. A. 1999: Phylogenetic placement and circumscription of tribes *Inuleae* s.str. and *Plucheeae* (*Asteraceae*): evidence from sequences of chloroplast gene *ndhF*. – Molec. Phylogen. Evol. **13:** 50–58. https://doi.org/10.1006/mpev.1999.0635

Eriksson T. 1990: Reinstatement of the genus *Leucoblepharis* Arnott (*Asteraceae–Heliantheae*). – Bot. Jahrb. Syst. **112:** 167–191.

Eriksson T. 1992: The genus *Blepharispermum* (*Asteraceae*, *Heliantheae*). – Pl. Syst. Evol. **182:** 149–227. https://doi.org/10.1007/BF00939188

Eriksson T. 1995: The genus *Athroisma* (*Asteraceae*, *Heliantheae*). – Bot. J. Linn. Soc. **119:** 101–184. https://doi.org/10.1111/j.1095-8339.1995.tb00733.x

Guindon S. & Gascuel O. 2003: A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. – Syst. Biol. **52:** 696–704. https://doi.org/10.1080/10635150390235520

Hall T. A. 1999: BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. – Nucl. Acids Symp. Ser. **41:** 95–98.

Hind D. J. N. & Langhorne J. 2024: 1076. *Vernonia missurica* Raf.: *Compositae*. – Curtis's Bot. Mag. **40:** 397–415. https://doi.org/10.1111/curt.12531

Howis S., Barker N. P. & Mucina L. 2009: Globally grown, but poorly known: species limits and biogeography of *Gazania* Gaertn. (*Asteraceae*) inferred from chloroplast and nuclear DNA sequence data. – Taxon **58:** 871–882. https://doi.org/10.1002/tax.583015

Humbert H. 1932: Sur deux Astereés nouvelles de Madagascar en voie d'extinction. – Bull. Mus. Natl. Hist. Nat., sér. 2, **4:** 1013–1019.

Humbert H. 1955: Composeés. – Pp. 145–198 in: Une merveille de la nature à Madagascar. Première exploration botanique du Massif du Marojejy et de ses satellites. – Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. **6:** 1–210, pl. 1–25.

Humbert H. 1960: Flore de Madagascar et de Comores (plantes vasculaires). 189^{e} famille Composées. Tome **I.** – Paris: Firmin-Didot & C^{ie}.

Humbert H. 1962: *Apodocephala Coursii* H. Humb. sp. nov. – Pp. 85–87 in: Composées nouvelles de Madagascar. – Adansonia **2:** 85–91. https://www.biodiversitylibrary.org/page/59816916

Källersjö M., Bergqvist G. & Anderberg A. A. 2000: Generic realignment in primuloid families of the *Ericales* s.l.: a phylogenetic analysis based on DNA sequences from three chloroplast genes and morphology. – Amer. J. Bot. **87:** 1325–1341. https://doi.org/10.2307/2656725

Kim K.-J. & Jansen R. K. 1995: *ndhF* sequence evolution and the major clades in the sunflower family. – Proc. Natl. Acad. Sci. U.S.A. **92:** 10379–10383. https://doi.org/10.1073/pnas.92.22.10379

Larsson A. 2014: AliView: a fast and lightweight alignment viewer and editor for large datasets. – Bioinformatics **30:** 3276–3278. https://doi.org/10.1093/bioinformatics/btu531

Madagascar Catalogue 2022: Catalogue of the plants of Madagascar. Missouri Botanical Garden, St. Louis, U.S.A. & Antananarivo, Madagascar. – Published at https://www.tropicos.org/Project/Madagascar [accessed Oct 2022].

Markos S. & Baldwin B. G. 2001: Higher-level relationships and major lineages of *Lessingia* (*Compositae*, *Astereae*) based on nuclear rDNA internal and external transcribed spacer (ITS and ETS) sequences. – Syst. Bot. **26:** 168–183.

Miller M. A., Pfeiffer W. & Schwartz T. 2010: Creating the CIPRES Science Gateway for inference of large phylogenetic trees. – Pp. 1–8 in: Proceedings of the Gateway Computing Environments Workshop (GCE), 14 November 2010. – New Orleans: Institute of Electrical and Electronics Engineers (IEEE). https://doi.org/10.1109/GCE.2010.5676129

Nesom G. L. 1993: *Madagaster* (*Asteraceae*: *Astereae*), a new genus of subtribe *Hinterhuberinae*. – Phytologia **75:** 94–99.

Nesom G. L. 2020: Revised subtribal classification of *Astereae* (*Asteraceae*). – Phytoneuron **2020**(53). https://www.phytoneuron.net/2020-publications/

Nesom G. & Robinson H. 2007: *Astereae*. – Pp. 284–342 in: Kadereit J. W. & Jeffrey C. (ed.), The families and genera of vascular plants **8.** Flowering plants. Eudicots. *Asterales*. – Berlin, Heidelberg: Springer. https://doi.org/10.1007/978-3-540-31051-8

Nylinder S., Cronholm B., de Lange P. J., Walsh N. & Anderberg A. A. 2013: Species tree phylogeny and character evolution in the genus *Centipeda* (*Asteraceae*): evidence from DNA sequences from coding and non-coding loci from the plastid and nuclear genomes. – Molec. Phylogen. Evol. **68:** 239–250. https://doi.org/10.1016/j.ympev.2013.03.020

Olmstead R. G. & Sweere J. A. 1994: Combining data in phylogenetic systematics: an empirical approach using three molecular data sets in the *Solanaceae*. – Syst. Biol. **43:** 467–481. https://doi.org/10.1093/sysbio/43.4.467

Panero J. L. 2005: New combinations and infrafamilial taxa in the *Asteraceae*. – Phytologia **87:** 1–14.

Panero J. L. & Funk V. A. 2002: Toward a phylogenetic subfamilial classification for the *Compositae* (*Asteraceae*). – Proc. Biol. Soc. Washington **115:** 909–922.

Pruski J. F. 2014: *Lowryanthus rubens* (*Compositae*: *Athroismeae*), a new genus and species from southeastern Madagascar. – Phytoneuron **2014**(51). https://www.phytoneuron.net/2014-publications/

Rambaut A., Drummond A. J., Xie D., Baele G. & Suchard M. A. 2018: Posterior summarization in Bayesian phylogenetics using Tracer 1.7. – Syst. Biol. **57:** 901–904. https://doi.org/10.1093/sysbio/syy032

Razafimandimbison S. G., Wikström N., Khodabandeh A. & Rydin C. 2022: Phylogeny of the Madagascar-centred tribe *Danaideae* (*Rubiaceae*) as a precursor to taxonomic revision: insights into its generic and species limits, affinities and distribution. – Ann. Bot. **130:** 849–867. https://doi.org/10.1093/aob/mcac121

Ronquist F., Teslenko M., Van der Mark P., Ayres D. L., Darling A., Höhna S., Larget B., Liu L., Suchard M. A. & Huelsenbeck J. P. 2012: MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. – Syst. Biol. **6:** 539–542. https://doi.org/10.1093/sysbio/sys029

Rydin C., Raunsgaard Pedersen K. & Friis E. M. 2004: On the evolutionary history of *Ephedra*: cretaceous fossils and extant molecules. – Proc. Natl. Acad. Sci. U.S.A. **101:** 16571–16576. https://doi.org/10.1073/pnas.0407588101

Staden R. 1996: The Staden sequence analysis package. – Molec. Biotechnol. **5:** 233–241. https://doi.org/10.1007/BF02900361

Swofford D. L. 2002: PAUP*: Phylogenetic analysis using parsimony (*and other methods), version 4. – Sunderland, Massachusetts: Sinauer.

Taberlet P., Gielly L., Pautou G. & Bouvet J. 1991: Universal primers for amplification of three non-coding regions of chloroplast DNA. – Pl. Molec. Biol. **17:** 1105–1109. https://doi.org/10.1007/BF00037152

Thiers B. M. 2023+ [continuously updated]: Index herbariorum: a global directory of public herbaria and associated staff. – Published at https://sweetgum.nybg.org/science/ih/

Turland N. J., Wiersema J. H., Barrie F. R., Greuter W., Hawksworth D. L., Herendeen P. S., Knapp S., Kusber W.-H., Li D.-Z., Marhold K., May T. W., McNeill J., Monro A. M., Prado J., Price M. J., Smith GF. (ed.) 2018: International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. – Regnum Veg. **159.** – Glashütten: Koeltz Botanical Books. https://doi.org/10.12705/Code.2018

Wagstaff S. J. & Breitwieser I. 2002: Phylogenetic relationships of New Zealand *Asteraceae* inferred from ITS sequences. – Pl. Syst. Evol. **231:** 203–224. https://doi.org/10.1007/s006060200020

Appendix 1

Voucher information and GenBank accession numbers for sequences used in the phylogenetic study. Taxon, voucher (including country of origin, collector and herbarium), and GenBank accession numbers for ETS, ITS, *ndhF* and *trnL–trnF*. Additional *Asteraceae ndhF* sequences with GenBank accession numbers. A dash (–) indicates missing data. An asterisk (*) indicates sequences generated for this study.

Athroismeae **dataset:** ***Anisochaeta mikanioides*** DC., South Africa, *Brand, Abbott & Bosch 478* (S), KY209964, KY210088, KY210128, KY210047; ***Anisopappus alternifolius*** (Less.) Bengtson & Anderb., Madagascar, *Anderberg & al. 249* (S), KY209939, KY210065, KY210105, KY210023; ***Anisopappus athanasioides*** Paiva & S. Ortiz, Angola, *da Silva 2070* (S), KY209943, KY210068, KY210108, KY210026; ***Anisopappus brandbergensis*** (P. P. J. Herman) Bengtson & al., Namibia, *Nordenstam 2548* (S), KY209971, KY210095, KY210135, KY210054; ***Anisopappus buchwaldii*** (O. Hoffm.) Wild, Tanzania, *Hedrén & al. 565* (S), HE862088, HE861963, HE862290, HE974615; ***Anisopappus chinensis*** Hook. & Arn., Nigeria, *Hepper 2894* (S), KY209931, KY210057, KY210098, KY210015; ***Anisopappus corymbosus*** Wild, Angola, *Kers* 3622 (S), KY209968, KY210092, KY210132, KY210051; ***Anisopappus grangeoides*** (Vatke & Höpfner ex Klatt) Merxm., Angola, *Fritsche 88* (S), KY209932, KY210058, KY210099, KY210016; ***Anisopappus holstii*** (O. Hoffm.) Wild, Tanzania, *Greenway & Polhill 11667* (S), KY209933, KY210059, KY210100, KY210017; ***Anisopappus kirkii*** (Oliv.) Brenan, Zimbabwe, *Goldsmith 103/68* (S), KY209934, KY210060, KY210101, KY210018; ***Anisopappus lastii*** (O. Hoffm.) Wild, Tanzania, *Tanner 409* (S), KY209936, KY210062, KY210102, KY210020; ***Anisopappus latifolius*** (S. Moore) B. L. Burtt, South Africa, *Codd 8304* (PRE), KY209935, KY210061, AF063068, KY210019; ***Anisopappus oliveranus*** Wild, Tanzania, *Eriksson & al. 564* (S), HE862089, HE861964, HE862291, HE974616; ***Anisopappus pinnatifidus*** (Klatt) O. Hoffm. ex Hutch., Namibia, *Nordenstam 2273* (S), KY209938, KY210064, KY210104, KY210022; ***Anisopappus smutsii*** Hutch., South Africa, *Sidey 3278* (S), KY209940, U84768, AF063070, KY210024; ***Anisopappus stuhlmannii*** (O. Hoffm.) Bengtson & al., Tanzania, *Thulin & Mhoro 1023b* (UPS), KY209972, KY210096, KY210136, KY210055; ***Apodocephala angustifolia*** Humbert, Madagascar, *Rakotomalala & al. 217* (MO MO04882274), OQ410980*, OQ429281*, OQ427102*, OQ410993*; ***Apodocephala begueana*** Humbert, Madagascar, *Service Forestier de Madagascar 13551-SF* (P P03997213), –, OQ429289*, –, OQ411001*; ***Apodocephala minor*** Scott Elliott, Madagascar, *Sabouraeu* (P P00605013), –, OQ429288*, –, OQ411000*; ***Apodocephala multiflora*** Humbert, Madagascar, *Miller & Randrianasolo 4657* (MO MO3762392), OQ410978*, OQ429279*, –, OQ410991*; ***Apodocephala oliganthoides*** Humbert, Madagascar, *Razafimandimbison & al. 2975* (S S20-19252), MZ352988, MZ352991, MZ352997, MZ352994; ***Apodocephala oliganthoides***, Madagascar, *Ravelonarivo & al. 2710* (MO MO6335251), OQ410983*, OQ429284*, OQ427105*, OQ410996*; ***Apodocephala pauciflora*** var. ***cacuminum*** Humbert, Madagascar, *Razafimandimbison & al. 2951* (S S20-19242), MZ352987, MZ352990, MZ352996, MZ352993; ***Apodocephala pauciflora*** var. ***cacuminum***, Madagascar, *Rakotovao & al. 2861* (MO

MO6180688), OQ410988*, OQ429291*, OQ427109*, OQ411003*; ***Apodocephala pauciflora*** Baker var. ***pauciflora***, Madagascar, *Turk & Randriamanatena 203* (MO MO5814955), OQ410987*, OQ429290*, OQ427108*, OQ411002*; ***Apodocephala radula*** Humbert, Madagascar, *Humbert 20708* (S S-G-549), OQ410976*, OQ429277*, OQ427098*, OQ410989*; ***Apodocephala* sp.**, Madagascar, *Randrianaivo & al. 532* (MO MO5333410), OQ429280*, OQ429280*, OQ427101*, OQ410992*; ***Apodocephala urschiana*** Humbert, Madagascar, *Randrianasolo & Solo 10* (MO MO5814962), OQ410981*, OQ429282*, OQ427103*, OQ410994*; ***Apodocephala urschiana***, Madagascar, *van den Werff & al. 13754* (MO MO5814948), OQ410982*, OQ429283*, OQ427104*, OQ410995*; ***Artemisiopsis villosa*** (O. Hoffm.) Schweick., Namibia, *Volk 1076* (S), KY209966, KY210090, KY210130, KY210049; ***Athroisma boranense*** Cufod., Ethiopia, *Eriksson 751* (S), KY209944, KY210069, KY210109, KY210027; ***Athroisma gracile*** (Oliv.) Mattf., Kenya, *Eriksson & al. 612* (S), KY209945, KY210070, KY210110, KY210028; ***Athroisma hastifolium*** Mattf., Tanzania, *Eriksson & al. 535* (S), KY209946, AF229258, KY210111, KY210029; ***Athroisma inevitabile*** T. Erikss., Uganda, *Chandler 866* (S), KY209947, KY210071, KY210112, KY210030; ***Athroisma laciniatum*** DC., India, *Helfer 189* (S), KY209948, KY210072, KY210113, KY210031; ***Athroisma pinnatifidum*** T. Erikss., Madagascar, *Eriksson & al. T954* (S), KY209949, KY210073, KY210114, KY210032; ***Athroisma stuhlmannii*** O. Hoffm., Tanzania, *Eriksson & al. 539* (S), KY209950, KY210074, KY210115, KY210033; ***Blepharispermum arcuatum*** T. Erikss., Tanzania, *Eriksson & al. 561* (S), KY209953, KY210077, KY210118, KY210036; ***Blepharispermum hirtum*** Oliv., Oman, *Kilian & Hein NK 5375* (S), KY209954, KY210078, KY210119, KY210037; ***Blepharispermum pubescens*** S. Moore, Uganda, *Taylor 1682* (S), KY209956, KY210080, KY210121, –; ***Blepharispermum villosum*** O. Hoffm., Ethiopia, *Anderberg 1729* (S), KY209959, KY210082, KY210123, KY210042; ***Blepharispermum xerothamnum*** Mattf., Tanzania, *Greenway & Polhill 11709* (S), KY209958, –, –, KY210041; ***Blepharispermum zanguebaricum*** Oliv. & Hiern, Tanzania, *Eriksson & al. 571* (S), KY209957, KY210081, KY210122, KY210040; ***Callilepis salicifolia*** Oliv., South Africa, *Bayer & al. SAF-01009* (S), LN606837, LN607423, AY780851.2, LN607070; ***Centipeda cunninghamii*** (DC.) A. Braun & Asch., New Zealand, *de Lange s.n.* (S), KY209960, KY210083, KY210124, KY210043; ***Centipeda minima*** (L.) A. Braun & Asch., Japan, *Anderberg & Lundin 58* (S), HE862168, KY210084, HE862354, HE974693; ***Centipeda racemosa*** (Hook.) F. Muell., Australia, *Walsh 4976* (MEL), HE862197, HE862069, HE862379, HE974722; ***Centipeda thespidioides*** F. Muell., Australia, *Weber 2981* (S), KY209961, KY210085, KY210125, KY210044; ***Dittrichia viscosa*** (L.) Greuter, Greece, *Trift & al. 22* (S), –, EF210966, LN607622, EF211061; ***Inula aschersoniana*** Janka, Greece, *Rechinger 45149* (S), –, FM995373, FM208933, FM997845; ***Leucoblepharis subsessilis*** Arn., India, *Yadav 2342* (S), KY209951, KY210075, KY210116, KY210034; ***Lowryanthus rubens*** Pruski, Madagascar, *Antilahimena & al.4801* (S S08-80), KY209962, KY210086, KY210126, KY210045; ***Lowryanthus rubens***, Madagascar, *Razakamalala & al. 2369* (S S08-79), KY209963, KY210087, KY210127, KY210046; ***Pulicaria aucheri*** Jaub. & Spach, Iran, *Sojak 4947* (S), –, FM995393, FM208991, FM997867; ***Rochonia cinerarioides*** DC., Madagascar, *Razafimandimbison 2858* (S S20-19232), –, –, OQ427099*, –; ***Symphyllocarpus exilis*** Maxim., Russia, *Antonova s.n.* (S), KY209967, KY210091, KY210131, KY210050; ***Vernoniopsis caudata*** (Drake) Humbert, Madagascar, *Ratovoson 1918* (MO MO6590064), OQ410985*, OQ429286*, OQ427107*, OQ410998*; ***Vernoniopsis caudata***, Madagascar, *Razafimandimbison, Razafindrahaja, Atahaly & Swenson 1448* (MO MO6840514), OQ410986*, OQ429287*, OQ427106*, OQ410999*; ***Vernoniopsis lokohensis*** (Humbert) Callm. & Phillipson, Madagascar, *Razafimandimbison & Razafindrahaja 2969* (S S20-19251), OQ410977*, OQ429278*, OQ427100*, OQ410990*; ***Vernoniopsis lokohensis***, Madagascar, *Miller & Lowry 4132* (MO MO04870174), OQ410984*, OQ429285*, –, OQ410997*.

Additional *ndhF* sequences: ***Achillea millefolium*** L. (*Anthemideae*), L39442; ***Acourtia microcephala*** DC. (*Nassauvieae*), L39407, L39408; ***Adenocaulon himalaicum*** Edgew. (*Mutisieae*), L39466; ***Ainsliaea acerifolia*** Sch. Bip. (*Pertyeae*), L39410; ***Ambrosia trifida*** L. (*Heliantheae*), L39382; ***Anastraphia parvifolia*** Britton (*Gochnatieae*), L39397; ***Anisothrix integra*** (Compton) Anderb. (*Gnaphalieae*), L39437; ***Antennaria howellii*** Greene (*Gnaphalieae*), L39436; ***Arctotis stoechadifolia*** P. J. Bergius (*Arctotideae*), L39425; ***Atractylodes japonica*** Koidz. ex Kitam. (*Cardueae*), L39413; ***Baccharis neglecta*** Britton (*Astereae*), L39448; ***Bahia absinthifolia*** Benth. (*Bahieae*), L39464; ***Barnadesia caryophylla*** S. F. Blake (*Barnadesieae*), L39394; ***Bellis perennis*** L. (*Astereae*), L39446; ***Blennosperma nanum*** (Hook.) S. F. Blake (*Senecioneae*), L39433; ***Boopis anthemoide***s Juss. (*Calyceraceae*), L39384; ***Calendula officinalis*** L. (*Calenduleae*), L39439; ***Carlina vulgaris*** L. (*Cardueae*), L39412; ***Carthamus tinctorius*** L. (*Cardueae*), L39417; ***Centaurea americana*** Nutt. (*Cardueae*), L39416; ***Chromolaena* sp.** (*Eupatorieae*), L39375; ***Chrysanthemum morifolium*** Ramat. (*Anthemideae*), L39443; ***Chuquiraga jussieui*** J. F. Gmel. (*Barnadesieae*), L39393; ***Cichorium intybu***s L. (*Lactuceae*), L39390; ***Cirsium arvense*** (L.) Scop. (*Cardueae*), L39419; ***Cirsium texanum*** Buckley (*Cardueae*), L39418; ***Conyza* sp.** (*Astereae*), L39451; ***Coreopsis tinctoria*** Nutt. (*Coreopsideae*), L39461; ***Cosmos bipinnatus*** Cav. (*Coreopsideae*), L39462; ***Coulterella capitata*** Vasey & Rose (*Tageteae*), L39380;

Dahlia coccinea Cav. (*Coreopsideae*), L39460; ***Dasyphyllum argenteum*** Kunth (*Barnadesieae*), L39392; ***Delairea odorata*** Lem. (*Senecioneae*), L39435; ***Dimorphotheca pluvialis*** (L.) Moench (*Calenduleae*), L39438; ***Dipterocome pusilla*** Fisch. & C. A. Mey. (*Cardueae*), FJ813488; ***Doniophyton anomalum*** (D. Don) Kurtz (*Barnadesieae*), L39396; ***Echinops exaltatus*** Schrad. (*Cardueae*), L39411; ***Eremothamnus marlothianus*** O. Hoffm. (*Arctotideae*), L39424; ***Eupatorium atrorubens*** (Lem.) N. E. Br. (*Eupatorieae*), L39376; ***Feddea cubensis*** Urb. (*Feddeeae*), EF089566; ***Felicia bergeriana*** (Spreng.) O. Hoffm. (*Astereae*), L39445; ***Fitchia*** **sp.** (*Coreopsideae*), L39459; ***Flaveria ramosissima*** Klatt (*Tageteae*), L39465; ***Gazania splendens*** Lem. (*Arctotideae*), L39423; ***Geigeria acaulis*** O. Hoffm. (*Inuleae*), LN607711; ***Geraea canescens*** Torr. & A. Gray (*Heliantheae*), L39381; ***Gerbera jamesonii*** Adlam (*Mutisieae*), L39403; ***Gerbera piloselloides*** (L.) Cass. (*Mutisieae*), L39404; ***Gutenbergia polytrichomata*** Wech. (*Vernonieae*), L39429; ***Gymnanthemum capense*** (A. Spreng.) J. C. Manning & Swelank. (*Vernonieae*), L39427; ***Haplocarpha scaposa*** Harv. (*Arctotideae*), L39426; ***Helianthus annuus*** L. (*Heliantheae*), L39383; ***Inula germanica*** L. (*Inuleae*), LN607649; ***Jasonia tuberosa*** (L.) DC. (*Inuleae*), AY780844; ***Jaumea carnosa*** (Less.) A. Gray (*Tageteae*), L39378; ***Lactuca sativa*** L. (*Lactuceae*), L39389; ***Leibnitzia anandria*** (L.) Turcz. (*Mutisieae*), L39402; ***Lopholaena coriifolia*** (Sond.) E. Phillips & C. A. Sm. (*Senecioneae*), L39434; ***Lychnophora tomentosa*** (Mart. ex DC.) Sch. Bip. (*Vernonieae*), L39428; ***Madia elegans*** D. Don ex Lindl. (*Madieae*), L39374; ***Marshallia caespitosa*** Nutt. ex DC. (*Helenieae*), L39458; ***Munnozia gigantea*** (Rusby) Rusby (*Liabeae*), L39420; ***Mutisia acuminata*** Ruiz & Pav. (*Mutisieae*), L39400; ***Nassauvia gaudichaudii*** (Cass.) Cass. (*Nassauvieae*), L39405; ***Onoseris hyssopifolia*** Kunth (*Onoserideae*), L39398; ***Oritrophium peruvianum*** (Lam.) Cuatrec. (*Astereae*), L39450; ***Osteospermum muricatum*** E. Mey. ex DC. (*Calenduleae*), L39440; ***Palafoxia arida*** B. L. Turner & M. I. Morris (*Bahieae*), L39463; ***Piptocarpha axillaris*** (Less.) Baker (*Vernonieae*), L39431; ***Pluchea obovata*** Balf. f. (*Inuleae*), LN607671; ***Psilostrophe gnaphalodes*** DC. (*Helenieae*), L39457; ***Pyrrocoma*** **sp.** (*Astereae*), L39447; ***Rosenia humilis*** (Less.) K. Bremer (*Gnaphalieae*), AF063080; ***Santolina chamaecyparissus*** L. (*Anthemideae*), L39444; ***Saussurea eriophylla*** Nakai (*Cardueae*), L39414; ***Schlechtendalia luzulifolia*** Less (*Barnadesieae*), L39395; ***Sinclairia glabra*** (Hemsl.) Rydb. (*Liabeae*), L39421; ***Sinclairia pringlei*** (B. L. Rob. & Greenm.) H. Rob. & Brettell (*Liabeae*), L39422; ***Stifftia chrysantha*** J. C. Mikan (*Stifftieae*), L39399; ***Stokesia laevis*** (Hill) Greene (*Vernonieae*), L39430; ***Symphyotrichum cordifolium*** (L.) G. L. Nesom (*Astereae*), L39449; ***Syneilesis palmata*** (Thunb.) Maxim. (*Senecioneae*), L39432; ***Synurus deltoides*** (Aiton) Nakai (*Cardueae*), L39415; ***Tagetes erecta*** L. (*Tageteae*), L39466; ***Tarchonanthus camphoratus*** L. (*Tarchonantheae*), L39409; ***Thymophylla pentachaeta*** (DC.) Small (*Tageteae*), L39467; ***Tragopogon porrifolius*** L. (*Lactuceae*), L39391; ***Trixis californica*** Kellogg (*Nassauvieae*), L39406; ***Ursinia nana*** DC. (*Anthemideae*), L39441; ***Venegasia carpesioides*** DC. (*Madieae*), L39379; ***Verbesina robinsonii*** (Klatt) Fernald ex B. L. Rob & Greenm. (*Heliantheae*), L39377.

Supplemental content online

See https://doi.org/10.3372/wi.54.54107

Supplementary appendix S1. DNA ndhF sequence alignment in nexus format.

Supplementary appendix S2. DNA sequence alignment in nexus format for the combined dataset.

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