The Malagasy enigmatic genus Apodocephala (Asteraceae), a new member of the tribe Athroismeae

Authors: Bengtson, Annika, Anderberg, Arne A., and Razafimandimbison, Sylvain G.

Source: Willdenowia, 51(2) : 221-230

Published By: Botanic Garden and Botanical Museum Berlin (BGBM)

URL: https://doi.org/10.3372/wi.51.51205

Willdenowia

Annals of the Botanic Garden and Botanical Museum Berlin

ANNIKA BENGTSON[1*], ARNE A. ANDERBERG[1] & SYLVAIN G. RAZAFIMANDIMBISON[1]

The Malagasy enigmatic genus *Apodocephala* (*Asteraceae*), a new member of the tribe *Athroismeae*

Abstract: *Apodocephala* is a small genus of nine species of shrubs and trees endemic to Madagascar and currently classified in the tribe *Astereae* (*Asteraceae*). However, its present tribal position has been questioned, as it lacks some of the salient morphological features of that tribe. This study includes for the first time DNA sequences from *Apodocephala* (two species including the type of the generic name) to test its phylogenetic position. Phylogenetic analyses based on sequence data from nuclear ribosomal (ETS and ITS) and plastid (*ndhF* and *trnL–trnF*) DNA regions, using Bayesian inference and maximum parsimony methods, strongly reject the placement of *Apodocephala* in the *Astereae*. Our results, instead, support its position as sister to the Malagasy monospecific genus *Lowryanthus* within the tribe *Athroismeae*. Morphological comparison of these sister genera reveal similarities in cypsela morphology, and the inclusion of *Apodocephala* in the subtribe *Lowryanthinae* is proposed here. The tribe *Athroismeae* is now represented by ten genera (*Anisochaeta*, *Anisopappus*, *Apodocephala*, *Artemisiopsis*, *Athroisma*, *Blepharispermum*, *Centipeda*, *Leucoblepharis*, *Lowryanthus* and *Symphyllocarpus*), six of which occur in Madagascar. The Malagasy *Athroismeae* occur in all Malagasy terrestrial ecosystems (rainforests, deciduous dry forests, thicket spiny forests and savannas) and are likely the result of multiple independent colonization events mostly from mainland Africa.

Key words: *Apodocephala*, *Asteraceae*, *Athroismeae*, *Compositae*, *Lowryanthinae*, Madagascar, molecular phylogenetics

Article history: Received 19 April 2021; peer-review completed 3 June 2021; received in revised form 10 June 2021; accepted for publication 16 June 2021.

Citation: 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. doi: https://doi.org/10.3372/wi.51.51205

Introduction

Madagascar is known for its high biodiversity with a flora showing extraordinary levels of species diversity and endemism; around 82% of the vascular plant species are endemic (Callmander & al. 2011). The daisy family (*Asteraceae*) is one of the most species-rich families in Madagascar, with no fewer than 540 species, of which about 88% are endemic. One representative of the Malagasy *Asteraceae* is *Apodocephala* Baker, a small genus of nine species of shrubs or trees characterized by its coriaceous leaves drying brown (S. Razafimandimbison, pers. obs.), discoid capitula and florets with white or whitish corollas (Fig. 1A, B) (Humbert 1955, 1960, 1962). Members of the genus are mainly found in rainforests and rocky habitats at high altitudes (Humbert 1955, 1960, 1962).

Apodocephala is currently placed in the tribe *Astereae*, where it has been associated with *Vernoniopsis* Humbert, another genus of small trees with discoid capitula and white florets, but also with *Madagaster* G. L. Nesom and *Rochonia* DC., all endemic to Madagascar (Humbert 1960; Bremer 1994; Nesom 2020). The *Astereae* are one of the largest tribes of the family and typically consist of annual or perennial herbs (rarely shrubs) with heterogamous capitula, containing numerous radiate or filiform marginal florets, and with distributions ranging from the Arctic to the tropics. *Astereae* members are characterized by having ecaudate and ecalcarate anther bases, disc floret styles with two distinct, non-confluent marginal stigmatic lines and often deltate to triangular or lanceolate style appendages that are adaxially glabrous and with sweeping hairs abaxially (Bremer 1994; Brouillet & al.

---

[1] Department of Botany, Swedish Museum of Natural History, P. O. Box 50007, SE-104 05 Stockholm, Sweden: *e-mail: annika.bengtson@nrm.se (author for correspondence).

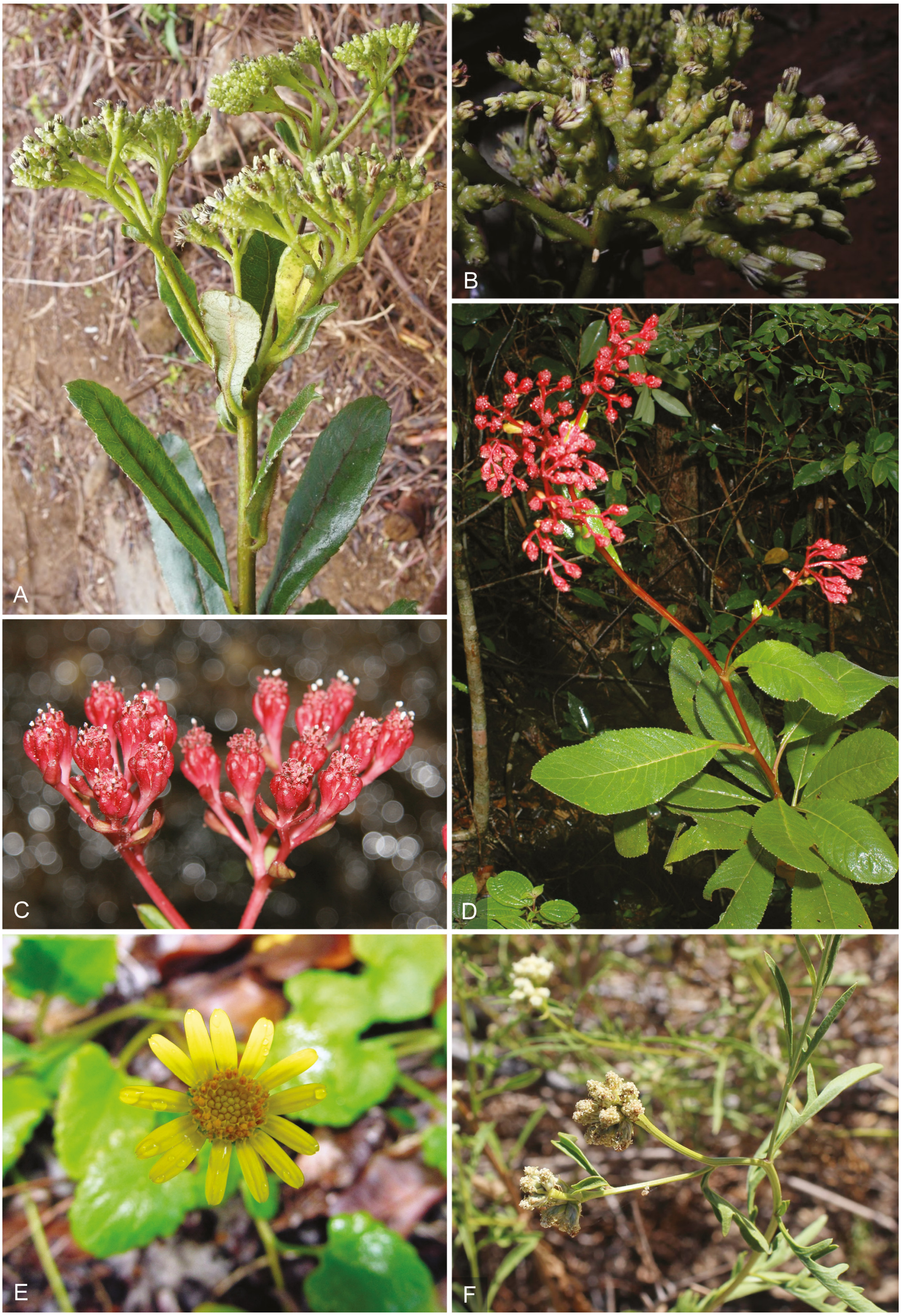

Fig. 1. Representatives of the Malagasy endemic *Athroismeae* – A, B: *Apodocephala* sp.; C, D: *Lowryanthus rubens*; E: *Anisopappus longipes* (Cass.) Wild; F: *Athroisma proteiforme* (Humbert) Mattf. – Photographs by P. Antilahimena (A, B; MBG-Madagascar, CC-BY-NC-ND © 2021), K. Kainulainen (C), P. P. Lowry II (D; MBG, CC-BY-NC-ND © 2021), F. Ratovoson (E; MBG-Madagascar, CC-BY-NC-ND © 2021) and L. Ramon (F; CC-BY-NC-ND © 2021).

2009). *Apodocephala* is, however, noted to have shortly caudate anthers (Humbert 1960; Bremer 1994) and also differs from the more typical *Astereae* genera by being shrubs or trees and in the lack of filiform or radiate marginal female florets. The current placement of *Apodocephala* in the tribe *Astereae* has not previously been tested by analysis of molecular data.

Two of the nine species of *Apodocephala*, *A. oliganthoides* Humbert and *A. pauciflora* Baker (the type of the generic name), were collected in 2020 by one of the authors (SGR) in north-eastern Madagascar. Leaf samples of these species preserved in silica gel (Chase & Hills 1991) were available for the first time for DNA sequencing and analysis. The aim of this study is to test the phylogenetic position and tribal affiliation of the genus *Apodocephala* within *Asteraceae*. The taxonomic and biogeographic implications of our findings are discussed.

Material and methods

Taxon sampling

Three specimens of *Apodocephala*, one specimen of *A. oliganthoides* and two specimens of *A. pauciflora* were included in the study. The systematic position of *Apodocephala* was analysed in a family-wide dataset based on 130 taxa that represented a wide coverage of *Asteraceae* tribes. This broad analysis (Fig. 2) clearly indicated a position of the genus in the tribe *Athroismeae*. The three *Apodocephala* specimens were subsequently analysed together with representatives of all known genera of *Athroismeae* (Bengtson & al. 2017). A complete list of taxa included in the molecular study is given in Appendix 1.

DNA extraction, amplification and sequencing

DNA was extracted 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 Chalfront, U.K.) following the standard protocol of the manufacturer. The nuclear ribosomal (nr) DNA internal transcribed spacer (ITS, including ITS1, ITS2 and the 5.8S gene) was amplified using primers 18SF and 26SR (Rydin & al. 2004), and the nrDNA external transcribed spacer (ETS) using primers Ast–1 (Markos & Baldwin 2001) and 18S–ETS (Baldwin & Markos 1998). Two plastid DNA regions were amplified with the following primers: the *trnL–trnF* region (including the *trnL* intron and *trnL–trnF* intergenic spacer) with the "c", "d", "e" and "f" primers of Taberlet & al. (1991), and the *ndhF* gene with the 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). All regions were amplified according to 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, Ipswich, Massachusetts, U.S.A.). 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). The newly generated sequences have been submitted to GenBank; accession numbers and voucher details are listed in 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.7.0.5.3 (Hall 1999). Alignments are available as supplementary Appendices 2 and 3. Two different datasets were compiled and analysed. We initially performed analyses of a *ndhF* matrix with 130 taxa, representing a wide coverage of the *Asteraceae* tribes, in order to determine the tribal position of *Apodocephala* within the *Asteraceae*. *Boopis anthemoides* Juss. (*Calyceraceae*) was used as outgroup, following Bengtson & al. (2017). The results of the *ndhF* analyses allowed us to narrow down the sampling to a focus on the tribe *Athroismeae*. A second dataset of ETS, ITS, *ndhF* and *trnL–trnF* sequence data from 45 taxa of the *Athroismeae* was analysed. *Callilepis salicifolia* Oliv. was used as outgroup to root trees. All the analyses were conducted with the Bayesian and parsimony methods. Prior to analyses of the combined dataset, each region was analysed separately to check for incongruence by simply comparing topologies.

Bayesian inference analyses were conducted using MrBayes v.3.2.7a (Ronquist & al. 2012) using the online XSEDE platform on the CIPRES Science Gateway (Miller & al. 2010). For the larger *ndhF* dataset, nucleotide substitution models were set to GTR+I+G; for the combined dataset they were set to GTR+G for ETS and to GTR+I+G for ITS and the plastid markers (*ndhF* and *trnL–trnF*), chosen using the Akaike information criterion (AIC) as implemented in jModeltest v.2.1.10v20160303 (Guindon & Gascuel 2003; Darriba & al. 2012). Analyses consisted of two independent runs, with eight chains each and the temperature parameter set to 0.1. The Markov Chain Monte Carlo (MCMC) was run for 75 million generations for the larger *ndhF* dataset, with a sampling frequency of 7500, and for 30 million generations, with a sampling frequency of 3000, for the combined dataset. Convergence of Markov chains was examined using Tracer v.1.7.1 (Rambaut & 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

Fig. 2. Bayesian fifty-percent majority-rule consensus tree from an analysis of the *Asteraceae ndhF* dataset. Numbers above branches indicate posterior probability (PP) and bootstrap support (BS) values, bootstrap support values < 50 are indicated by a dash.

strategy, with 10,000 random addition replicates, TBR branch-swapping and saving only the most parsimonious tree each replicate. Bootstrap support (BS) was estimated using 10,000 replicates, each with 10 random addition replicates and saving only a single most parsimonious tree each replicate. All analyses were run multiple times.

Results

The *ndhF* dataset consisted of 2298 aligned characters, 556 of which were parsimony informative, and the combined *Athroismeae* dataset of 4470 characters, 720 of which were parsimony informative. The parsimony analysis of the *ndhF* dataset yielded 6113 most parsimonious trees, 2882 steps long (consistency index, CI = 0.38; retention index, RI = 0.67, excluding uninformative characters), and the parsimony analysis of the *Athroismeae* dataset yielded six most parsimonious trees, 2417 steps long (CI = 0.54, RI = 0.81). Analyses of separate regions produced partly unresolved trees (results not shown), but showed no signs of incongruence. Bayesian and parsimony analyses of the two datasets produced trees with similar topologies, differing only in little-supported nodes. Parsimony analyses resulted in somewhat less-resolved trees.

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 analysis resolved the two sampled *Apodocephala* species as monophyletic and with strong support as sister to the Malagasy *Lowryanthus rubens* Pruski (posterior probability, PP = 1.0, bootstrap support, BS = 99, Fig. 2), and placed them in a poorly supported tribe *Athroismeae* (PP = 0.85, BS = -). A majority-rule consensus tree from a Bayesian analysis of the combined dataset, consisting of both nuclear (ETS, ITS) and plastid (*ndhF*, *trnL–trnF*) data, and with a focus on the tribe *Athroismeae*, is shown in Fig. 3. The analysis confirmed the position of *Apodocephala* within *Athroismeae* (PP = 1.0, BS = 95, Fig. 3), and the sister-group relationship between *Apodocephala* and *Lowryanthus* (PP = 1.0, BS = 100, Fig. 3). The *Apodocephala–Lowryanthus* clade was resolved as sister to the subtribe *Athroisminae* (PP = 1.0, BS = -, Fig. 3).

Discussion

Our results strongly support the phylogenetic placement of *Apodocephala* in the tribe *Athroismeae* as sister to *Lowryanthus*, and therefore we reject its current position in the tribe *Astereae* (Grau 1977; Bremer 1994; Nesom 2020) (Fig. 2). *Apodocephala* and the Malagasy genus *Vernoniopsis* (*Astereae*) have been suggested to have a close affinity on the basis of their discoid capitula with white florets and presence of shortly caudate anthers (Bremer 1994; Nesom 2020). On the other hand, *Vernoniopsis* is distinct by having a pappus of scabrid bristles and epaleate receptacles, whereas *Apodocephala* lacks a true pappus and has paleate receptacles (Humbert 1960). Nesom (2020) placed *Apodocephala* and *Vernoniopsis* in his *Astereae* subtribe *Madagasterinae* together with *Madagaster* and *Rochonia*, all of which are endemic to Madagascar. *Madagaster* and *Rochonia* differ from *Apodocephala* and *Vernoniopsis* in having radiate heads and campanulate involucres, and from *Apodocephala* in having epaleate receptacles and a pappus of barbellate bristles (Humbert 1960; Nesom 2020). Molecular phylogenetic studies place *Madagaster* within *Astereae* (Brouillet & al. 2009). *Rochonia* and *Vernoniopsis* have yet to be included in a molecular phylogenetic analysis, meaning that their phylogenetic positions within the *Asteraceae* remain untested. Given the present results, it is possible that these two genera are also misplaced in the *Astereae*.

The tribe *Athroismeae* was originally described by Panero & Funk (2002) to accommodate the genera *Athroisma* DC., *Blepharispermum* Wight ex DC. and *Leucoblepharis* Arn., previously members of the *Inuleae*, but had since then been classified in a broadly delimited tribe *Heliantheae*, as the *Athroisma* group (Kim & Jansen 1995). Over the years, the limits of the tribe have greatly changed, as more genera have been found to belong there (Wagstaff & Breitwieser 2002; Panero 2005; Anderberg 2009; Pruski 2014; Bentley & al. 2015; Bengtson & al. 2017). Bengtson & al. (2017) presented the first molecular phylogenetic study of the tribe, which resulted in an amended circumscription. Three monospecific genera (*Anisochaeta* DC., *Artemisiopsis* S. Moore and *Symphyllocarpus* Maxim.), all earlier placed in other tribes, were also shown to belong in the *Athroismeae*. This broadly delimited *Athroismeae* are a morphologically diverse lineage of nine genera, which are classified in four subtribes (*Athroisminae*, *Anisopappinae*, *Lowryanthinae* and *Symphyllocarpinae*). The tribe is difficult to characterize morphologically and there seem to be no obvious apomorphic morphological characters that unite its members. Bengtson & al. (2017) noted that, considering the history of the tribe, it would not be unlikely that new additions to the tribe would be discovered as more of the odd genera of the family *Asteraceae* were sequenced.

Our analyses resolve the two sampled species of *Apodocephala*, *A. oliganthoides* and *A. pauciflora*, as a monophyletic group, which is sister to the Malagasy *Lowryanthus rubens* (Fig. 3). The *Apodocephala–Lowryanthus* clade is in turn sister to the subtribe *Athroisminae* (Fig. 3). *Lowryanthus* is a monospecific genus described by Pruski (2014) and consists of shrubs or small trees with bright red, corymbiform-paniculiform synflorescences bearing coral red, discoid capitula with reddish to pink florets and red involucres (Fig. 1C, D). The genus has carbonized, obcompressed, geniculate-rostrate cypselas, which led Pruski (2014) to correctly postulate its close affinities with the *Blepharispermum* group (= subtribe *Athroisminae*) of the tribe *Athro-*

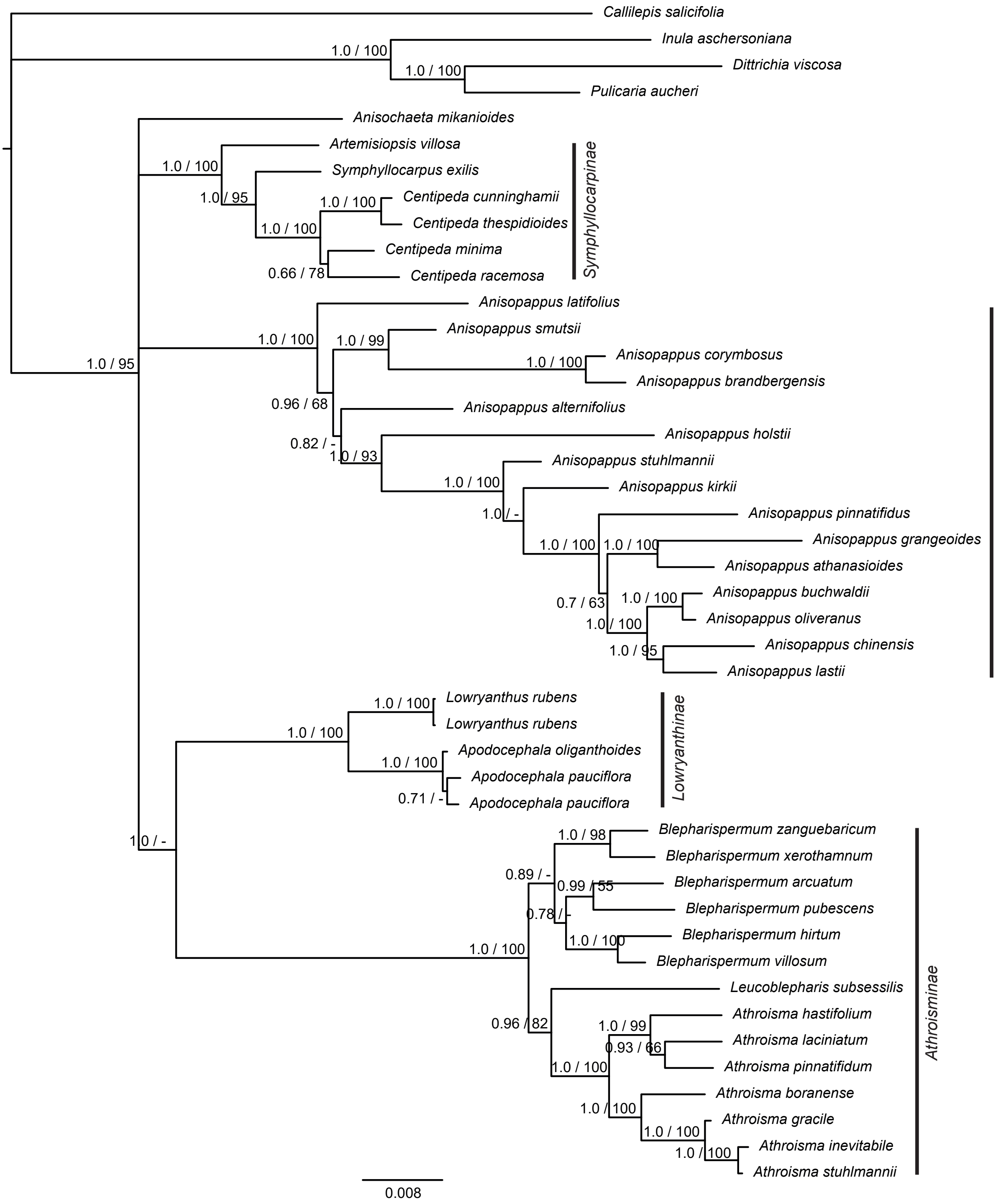

Fig. 3. Bayesian fifty-percent majority-rule consensus tree from an analysis of the combined *Athroismeae* dataset (ETS, ITS, *ndhF* and *trnL–trnF*). The different subtribes are marked in the figure. Numbers above branches indicate posterior probability (PP) and bootstrap support (BS) values, bootstrap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

ismeae. Eriksson (1990, 1992) described the *Blepharispermum* group to have cypselas with a neck, which in some species is abaxially curved; similar features are also found in *Lowryanthus*. The molecular phylogenetic study of *Athroismeae* by Bengtson & al. (2017) confirmed the placement of *Lowryanthus* in the *Athroismeae*, and showed that the genus is sister to the subtribe *Athroisminae*. *Lowryanthus*, however, differs from the members of *Athroisminae* in having free, solitary capitula rather than capitula assembled in secondary heads, and was therefore placed in its own subtribe, *Lowryanthinae* (Bengtson & al. 2017).

The sister-group relationship of *Apodocephala* and *Lowryanthus* is supported by both genera having discoid capitula with bisexual florets arranged in corymbiform-paniculiform synflorescences, paleate receptacles and cypselas lacking a true pappus (Humbert 1960; Pruski 2014). Morphological studies of cypsela characters reveal further similarities. *Lowryanthus* has geniculate-rostrate cypselas with a tightly curved rostrum. This character is also found in *Apodocephala*, where several species have cypselas elongated to a closely curved, s-shaped neck (Humbert 1960, 1962). *Apodocephala coursii* Humbert and *A. radula* Humbert in particular have cypselas resembling those of *Lowryanthus*. *Apodocephala oliganthoides* and *A. pauciflora*, the two species included in the molecular phylogenetic analyses, do not share this character, and it has evidently been lost. Further, both *Lowryanthus* and members of the *Athroisminae* have cypselas with long marginal and apical hairs (Eriksson 1990, 1992, 1995; Pruski 2014), which are also found in *A. coursii* (Humbert 1962). The morphological similarities in cypselas support the position of *Apodocephala* as sister to *Lowryanthus* and as part of the *Lowryanthinae* subtribe of the *Athroismeae*. The different *Apodocephala* species, however, show much variation in capitula and cypsela characters, and it is worth noting that the species included in the molecular study are not the ones most resembling *Lowryanthus*.

Apodocephala and *Lowryanthus* differ greatly in general appearance, in the colour of the peduncles, capitula and florets, and in the shape of the capitula and involucral bracts (Fig. 1). They also have distinct geographic ranges, meaning that they do not grow sympatrically. *Apodocephala* and *Lowryanthus* are not the only examples of morphologically distinct sister genera. Another example from Madagascar is *Landiopsis* Capuron ex Bosser and *Bremeria* Razafim. & Alejandro in *Rubiaceae*, which have been shown to be sister genera by molecular studies but share no known synapomorphies (Alejandro & al. 2005). The former genus is monospecific and is restricted to the dry deciduous forests in northern Madagascar. In contrast, the latter genus is commonly found throughout the lowland and montane rainforests. The Central African genus *Colletoecema* E. M. A. Petit and its sister genus, the Seychellan *Seychellea* Razafim. & al. (*Rubiaceae*), constitute another example, however both genera are restricted to lowland rainforests (Razafimandimbison & al. 2020).

Biogeographic remarks

Madagascar is a biodiversity hotspot, with remarkable levels of diversity and endemism. Biogeographical studies show that the majority of the lineages ancestral to the Malagasy endemics have African origins. Numerous endemic clades result from dispersals from the African mainland, followed by subsequent diversification (Yoder & Nowak 2006). The Malagasy *Athroismeae* also seem to fit this biogeographical pattern, although a biogeographical analysis would be needed to confirm this. The tribe *Athroismeae* has a mainly African distribution, but with several species in the Arabian Peninsula, Asia, and even Australia and New Zealand (*Centipeda* Lour.). All four subtribes of the *Athroismeae* have representatives in Madagascar, and six out of the ten genera in *Athroismeae* (*Anisopappus* Hook. & Arn., *Apodocephala*, *Athroisma*, *Blepharispermum*, *Centipeda* and *Lowryanthus*) occur in Madagascar. Comparisons of the phylogeny and distributions show that the Malagasy *Athroismeae* result from multiple independent colonization events, mostly from the African mainland (Bengtson & al. 2017, 2021). Two genera (*Apodocephala* and *Lowryanthus*), and about 12 species (three *Athroisma* and about nine *Anisopappus*; the Malagasy *Anisopappus* under revision, Bengtson & al. in prep.) are endemic to Madagascar and two additional species (*Blepharispermum arcuatum* T. Erikss. and *Centipeda minima* (L.) A. Braun & Asch.) are present on the island but are not endemic there.

Anisopappus (Fig. 1E) is represented by nine species in Madagascar, and shown by Bengtson & al. (2021) to be the result of two separate colonization events from mainland Africa followed by subsequent diversification. *Athroisma* (Fig. 1F) contains three species endemic to Madagascar (Eriksson 1995), although only one of the species is included in this study and in Bengtson & al. (2017); whether these three species result from a single dispersal event or not remains to be seen. The analyses place the Malagasy *Athroisma pinnatifidum* T. Erikss. within an African clade and as sister to a specimen of *Athroisma laciniatum* DC. from India. The sister-group relationship indicates that they could be the result of a single dispersal event from Africa to Madagascar followed by secondary dispersal to India or vice versa (a single dispersal event to India from Africa followed by a second dispersal to Madagascar from India). The subtribe *Lowryanthinae*, consisting of *Lowryanthus* and *Apodocephala*, is endemic and appears to result from a single colonization event, followed by subsequent diversification in Madagascar.

Lowryanthus and most *Apodocephala* are restricted to rainforest habitats. In contrast, *Athroisma* seems to be confined to dry forest or scrub habitats in western and southern Madagascar (Eriksson 1995), while *Anisopappus* mainly thrives in open habitats (e.g. woodland savannas or forest gaps) or rocky habitats (Humbert 1960). *Lowryanthus rubens* is known only from the Bemangidy forest in the northern part of the Tsitongambarika protected area in southeastern Madagascar, where it is found in low-elevation humid evergreen forests between 100 and 300 m elevation (Pruski 2014). In contrast, *Apodocephala* has a wider distribution ranging from the southeast, the central plateau, the north and northeast of Madagascar and mostly occurs in higher elevations from 700 m to 1500–2000 m, where the species are found in montane rainforests. The only exception is *Apodocepha-*

la minor Scott Elliot, which occurs at low altitudes in siliceous, rocky habitats in southeastern Madagascar (Humbert 1960). *Apodocephala minor* and *A. radula* are the *Apodocephala* species found in the closest geographical proximity of the known *Lowryanthus* localities; however, the two *Apodocephala* species and *Lowryanthus* differ in habitat and *A. radula* occurs at higher elevations.

It is worth noting that the subtribe *Lowryanthinae* joins the growing list of the Malagasy endemic plant lineages. Beside the six Malagasy endemic plant families (*Aphloiaceae*, *Asteropeaceae*, *Barbeuiaceae*, *Physenaceae*, *Sarcolaenaceae* and *Sphaerosepalaceae*), other examples are: tribe *Coleeae* (*Bignoniaceae*), subfamily *Didiereoideae* (*Didiereaceae*), subfamily *Diegodendroideae* (*Bixaceae*), tribe *Humbertieae* (*Convolvulaceae*) and tribe *Tseboneae* (*Sapotaceae*, Gautier & al. 2013).

Conclusions

Apodocephala is here revealed to be part of the tribe *Athroismeae* rather than *Astereae*, and therefore forms another addition to this tribe. *Lowryanthus* and *Apodocephala* are sisters that constitute the Malagasy endemic subtribe *Lowryanthinae*. A more detailed morphological study including all *Apodocephala* would be rewarding, as it could shed light on the potential morphological synapomorphy of the *Apodocephala–Lowryanthus* clade (in prep.).

Taxonomic treatment

Lowryanthinae Pruski & Anderb. in Taxon 66: 417. 2017, emend. Bengtson, Anderb. & Razafim. – Type: *Lowryanthus* Pruski.

Shrubs or trees, 1–4(–30) m tall. Leaves alternate, petiolate; blade oblanceolate to narrowly obovate, coriaceous, glabrous to hirsute, pinnately veined, margin entire to denticulate. Capitulescence terminal, corymbiform-paniculate. Capitula discoid, paleate; florets (1–)3 or 4(–20); corolla white, whitish or red. Cypselas oblong and subprismatic to obovate and obcompressed, in some species rostrate, brown or black, epappose.

Genera: *Apodocephala* Baker, *Lowryanthus* Pruski.

Acknowledgements

The authors thank the DGF (Direction Générale des Forêts) and MNP (Madagascar National Parks) in Madagascar for issuing collecting and exportation permits (permit no. 005/20/MEDD/SG/DGEF/DGRNE) for SGR in 2020; the Missouri Botanical Garden, Madagascar Program for logistical support; the Parc Botanique et Zoologique de Tsimbazaza and the Missouri Botanical Garden, Madagascar Program (F. Lantoarisoa) for arranging collecting and exportation permits for SGR; Kent Kainulainen, Patrice Antilahimena, Porter P. Lowry II, Fidy Ratovoson and Laurence Ramon for allowing us to use their photos; Norbert Kilian and another anonymous reviewer for valuable comments on the manuscript; and the Royal Swedish Academy of Science and Stiftelsen Harald E. Johanssons fund for financial support to SGR and AB, respectively.

References

Alejandro G. D., Razafimandimbison S. G. & Liede-Schumann S. 2005: Polyphyly of *Mussaenda* inferred from ITS and *trnT-F* data and its implication for generic limits in *Mussaendeae* (*Rubiaceae*). – Amer. J. Bot. **92:** 544–557.

Anderberg A. A. & Swenson U. 2003: Evolutionary lineages in *Sapotaceae* (*Ericales*): a cladistic analysis based on *nhdF* sequence data. – Int. J. Pl. Sci. **164:** 763–773.

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.

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.

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.

Bengtson A. & Anderberg A. A. 2018: Species diversification in the Mediterranean genus *Chiliadenus* (*Inuleae–Asteraceae*). – Pl. Syst. Evol. **304:** 853–860.

Bengtson A., Osborne J. & Anderberg A. A. 2021: Phylogeny of *Anisopappus* with species circumscriptions revisited (*Asteraceae*: *Athroismeae*). – Taxon. **70:** 351–364.

Bentley J., Klaassen E. S. & Bergh N. G. 2015: *Philyrophyllum* (*Asteraceae*) transferred from *Gnaphalieae* to *Athroismeae* based on phylogenetic analysis of nuclear and plastid DNA sequence data. – Taxon **64:** 975–986.

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., Schatz G. E., Andriambololonera S., Rabarimanarivo M., Rakotonirina N., Raharimampionona J., Chatelain C., Gautier L. & Lowry P. P. 2011: The endemic and non-endemic vascular flora of Madagascar updated. – Pl. Ecol. Evol. **144:** 121–125.

Chase M. W. & Hills H. H. 1991: Silica gel: an ideal material for field preservation of leaf samples for DNA studies. – Taxon **40:** 215–220.

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

Edgar R. C. 2004: MUSCLE: multiple sequence alignment with high accuracy and high throughput. – Nucl. Acids Res. **32:** 1792–1797.

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.

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

Eriksson T. 1991: The systematic position of the *Blepharispermum* group (*Asteraceae*, *Heliantheae*). – Taxon **40:** 33–39.

Eriksson T. 1992: The genus *Blepharispermum* (*Asteraceae*, *Heliantheae*). – Pl. Syst. Evol. **182:** 149–227.

Eriksson T. 1995: The genus *Athroisma* (*Asteraceae*, *Heliantheae*). – Bot. J. Linn. Soc. **119:** 101–184.

Gautier L., Naciri Y., Anderberg A. A., Smedmark J. E. E., Randrianaivo R. R. & Swenson U. 2013: A new species, genus and tribe of *Sapotaceae*, endemic to Madagascar. – Taxon **62:** 972–983.

Grau J. 1977: *Astereae* – a systematic review. – Pp. 539–565 in: Heywood V. H., Harborne J. B. & Turner B. L. (ed.), The biology and chemistry of *Compositae* **1.** – London: Academic Press.

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

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.

Humbert H. 1955: Composeés. – Pp. 145–198 in: Une merveille de la nature a Madagascar. Premier Exploration Botanique du Massif du Marojejy et de ses Satellites. – Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. **6.**

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

Humbert H. 1962: *Apodocephala Coursii* H. Humb. in: Composées nouvelles de Madagascar. – Adansonia, n.s., **2:** 85–87.

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.

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.

Larsson A. 2014: AliView: a fast and lightweight alignment viewer and editor for large datasets. – Bioinformatics **30:** 3276–3278.

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 2010). – New Orleans: IEEE.

Nesom G. L. 2020: Revised subtribal classification of *Astereae* (*Asteraceae*). – Phytoneuron **2020-53:** 1–39.

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.

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.

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:** 1–11.

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.

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.

Razafimandimbison S. G., Kainulainen K., Senterre B., Morel C. & Rydin C. 2020: Phylogenetic affinity of an enigmatic *Rubiaceae* from the Seychelles revealing a recent biogeographic link with Central Africa: gen. nov. *Seychellea* and trib. nov. *Seychelleeae*. – Molec. Phylogen. Evol. **143:** 106685.

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.

Shaw J., Lickey E. B., Schilling E. E. & Small R. L. 2007: Comparison of whole chloroplast genome sequences to choose noncoding regions for phylogenetic studies in angiosperms: the tortoise and the hare III. – Amer. J. Bot. **94:** 275–288.

Staden R. 1996: The Staden sequence analysis package. – Molec. Biotechnol. **5:** 233–241.

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.

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

Yoder A. D. & Nowak M. D. 2006: Has vicariance or dispersal been the predominant biogeographic force in Madagascar? Only time will tell. – Annual Rev. Ecol. Evol. Syst. **37:** 405–431.

Supplemental content online

See https://doi.org/10.3372/wi.51.51205

Appendix 1

Voucher information and GenBank accession numbers for sequences used in phylogenetic study.

Appendix 2

DNA *ndhF* sequence alignment in nexus format.

Appendix 3

DNA sequence alignments in nexus format for the combined *Athroismeae* dataset.

Willdenowia

Open-access online edition bioone.org/journals/willdenowia

Online ISSN 1868-6397 · Print ISSN 0511-9618 · 2020 Journal Impact Factor 0.985

Published by the Botanic Garden and Botanical Museum Berlin, Freie Universität Berlin